THE SEASONAL HAULOUT CYCLE OF THE DECLINING SOUTHERN ELEPHANT SEAL, *MIROUNGA LEONINA*, POPULATION AT MARION ISLAND

by

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ABSTRACT

Data recorded from annual tagging and regular tag resightings of southern elephant seals at Marion Island, permitted the investigation of temporal variation in the terrestrial haulout cycle of this species, and estimation of participation levels in the little understood resting haulout phase, that could be related to age, sex, and sexual status. Primigravid females moulted later, and were less inclined to rest, than nulligravid females of the same age, but moulted earlier than mature females, among which the mean moulting dates of respective age-classes were practically the same. It is proposed that earlier implantation among primigravid females, as a function of their returning to sea and regaining condition before parous females, resulted in the earlier mean breeding haulout date of primiparous females. The mean haulout dates of breeding and moulting males were negatively and postively correlated with ascending age, respectively. More than half of the surviving individuals of each immature age- and sex-class were observed to haul out to rest, with participation levels generally consistent from year to year, indicating that the autumn-winter haulout represents more than simple random haulout events. It is suggested that elephant seals are faced with a trade-off between maximising their time spent foraging, and gaining valuable experience at terrestrial functioning, in their immature years.

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>
> Aldo Leopold

CHAPTER 1

INTRODUCTION

1.1 Brief description of the study animal

Southern elephant seals, *Mirounga leonina*, are the largest of the extant Pinnipedia (King 1983, McCann 1985, McCann & Rothery 1988), and are extremely sexually dimorphic, with adult males reaching up to ten times the size of adult females (McCann *et al.* 1989, Le Boeuf & Laws 1994). Breeding males typically weigh from about 1500 to 3000kg (Fedak *et al.* 1994), and weights of up to 3700 kg have been reported (Ling & Bryden 1981), while female weights range between about 350 and 850 kg at the onset of lactation (Fedak *et al.* 1994, Carlini *et al.* 1997). Polygyny is extreme in elephant seals, and harems, social units composed of variable numbers of females, their pups, and a few males of varying social rank (Le Boeuf & Briggs 1977), containing several hundred females have been recorded at Macquarie Island (Carrick *et al.* 1962*a*, Ling & Bryden 1992). The few dominant males monopolise sexual activity (McCann 1981, Wilkinson 1992, Campagna *et al.* 1993, Baldi *et al.* 1996, Wilkinson & van Aarde 1999).

Females have been recorded to give birth for the first time at age three (Laws 1956*a*, Wilkinson 1992), and there is strong circumstantial evidence that females mate for the first time at sea (Laws 1956*a*, Carrick & Ingham 1960, Carrick *et al.* 1962*a*). Embryonic development ceases after fertilisation, as with all pinnipeds (Boyd 1991), and foetal growth is believed to resume after the summer moult, about 16 weeks later (Laws 1956*b*, Carrick *et al.* 1962*a*, Ling & Bryden 1992). Parturition takes place about 32-33 weeks after implantation (Ling & Bryden 1992), and females give birth to a single pup weighing between about 36 and 50 kg (Condy 1980, Laws 1984, McCann *et al.* 1989, Fedak *et al.* 1994, Burton *et al.* 1997, Carlini *et al.* 1997), with birth weight varying between populations (Laws 1984, Burton *et al.* 1997). Males are thought to reach puberty at age four (Laws 1956*a*), but are rarely observed to be attendant in a breeding season before age six or seven (Laws 1956*b*, Jones 1981). Longevities of 20 and 23 years have been recorded for males and females, respectively (McCann 1985, Hindell & Little 1988).

Adult male and female southern elephant seals spend a total of approximately four and two months of the year ashore, respectively, for the temporally separate purposes of breeding and moulting during the austral spring and summer, on remote coastal beaches and oceanic islands (Laws 1956*a*, Carrick *et al.* 1962*a*, Condy 1979, Hindell & Burton 1988, Wilkinson 1992, Laws 1994). Apart from the moulting haulout phase, which is obligatory for all age groups, immature individuals haul out for short periods during autumn and winter, a terrestrial phase for which no specific function has as yet been ascribed (Carrick *et al.* 1962*b*, Condy 1979, Ling & Bryden 1981, Hindell & Burton 1988, Bell *et al.* 1997) and which will hereafter be referred to as the 'resting' haulout. Elephant seals need to be able to endure protracted fasts during their terrestrial phases, as all feeding takes place pelagically (Laws 1956*a*).

When at sea, southern elephant seals are known to range extensively, and dive continuously for long periods at a time, in search of food (Campagna *et al.* 1995, McConnell & Fedak 1996). Post-breeding and post-moulting females from Marion Island have been shown to range up to 1460 km and 3133 km from the island, respectively (Bester & Pansegrouw 1992, Jonker & Bester 1998), while adult males have been shown to stay relatively close to Marion Island (Malherbe 1998). Dives of up to 1444 and 1452 meters have been recorded for adult females and males from Marion Island respectively (Jonker & Bester 1994, Malherbe 1998). The diet of southern elephant seals consists primarily of fish and squid (Laws 1977, McCann 1985, Green & Burton 1993, Slip 1995), the proportions of which are thought to vary with distance from coastlines (Pascal 1985), and differences in diet have been shown to exist between populations (Green & Burton 1993).

1.2 Distribution

Southern elephant seals have a circumpolar distribution in the Southern Ocean (Figure 1; Carrick & Ingham 1962), and their main breeding populations occur on both sides of the Antarctic Polar Front (McCann 1985, Ling & Bryden 1992). The total population is considered to consist of four main stocks, namely: South Georgia and other islands of the Scotia Arc; Patagonia and the Falkland Islands; the Heard-Kerguelen stock, which includes Îles Crozet and the Prince Edward islands; and the Macquarie Island stock (Slip & Burton 1999).

1.3 Status

Southern elephant seals were exploited by man for their high quality oil to such an extent that their numbers were reduced to uneconomic levels (Hindell & Burton 1988). Hunting was ceased early this century, apart from a well organized harvest that was maintained at South Georgia until 1964 (McCann 1980), and by the 1950's most populations appeared to have recovered (Carrick & Ingham 1962). However, declines in population abundance have been reported at several sites, including Îles Crozet (Barrat & Mougin 1978, Guinet *et al.* 1992), Îles Kerguelen (van Aarde 1980, Bester & Lenglart 1982, Pascal 1985), Heard Island (Burton 1986, Slip & Burton 1999), Macquarie Island (Hindell & Burton 1987, Hindell *et al.* 1994), the Campbell Islands (Taylor & Taylor 1989), the non-breeding population at Vestfold Hills,

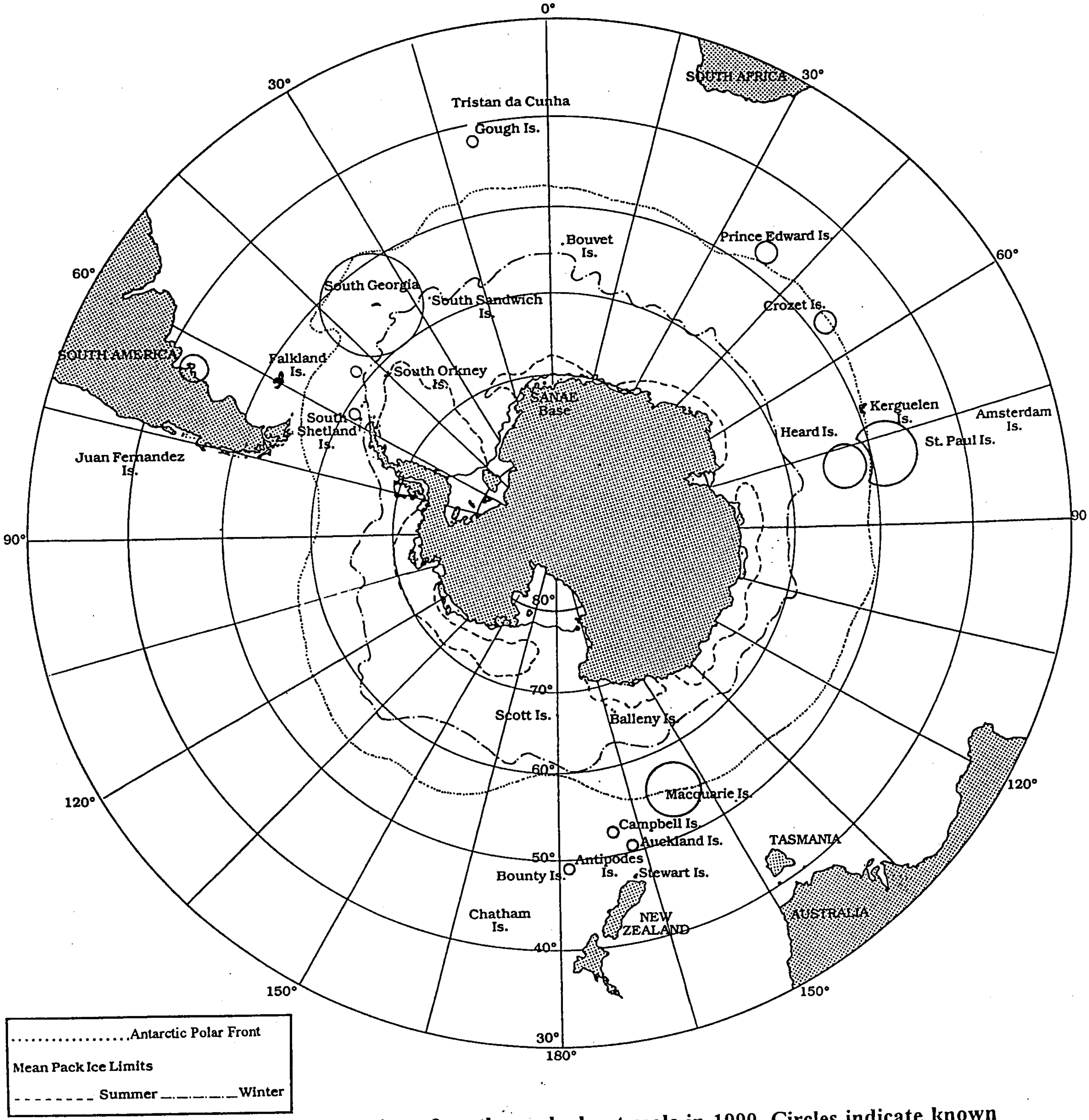

Figure 1. Breeding distribution of southern elephant seals in 1990. Circles indicate known breeding colonies and areas of circles are proportional to the estimated population sizes except for colonies of less than 5000 (Modified from Laws 1994).

Antarctica (Gales & Burton 1989) and Marion Island in the Prince Edward Archipelago (Wilkinson & Bester 1988, Bester & Wilkinson 1994). The rates of decline at most of these sites are reported to have diminished in recent years, namely at Macquarie Island (Slip & Burton 1999), Heard Island (Slip & Burton 1999), Îles Kerguelen (Pascal 1985, Guinet *et al.* 1992 & 1999) and Îles Crozet (Guinet *et al.* 1999). Although the rate of population decline at Marion Island has also decreased during the present decade (Pistorius *et al.* 1999), it has been surpassed in overall propensity in previous decades only by the population declines at Îles Crozet (Guinet *et al.* 1992) and the Campbell Islands (Taylor & Taylor 1989).

The total population size at South Georgia, where 54% of the world population of southern elephant seals breed, has not changed significantly over the past 45 years (Boyd *et al.* 1996), while the population at Península Valdés, Patagonia, has increased (Campagna & Lewis 1992). Generally, therefore, population declines have been a feature of islands in the southern Pacific and southern Indian oceans, while South Atlantic populations, with the possible exception of Gough Island (Bester 1990), are apparently stable or increasing (Boyd *et al.* 1996).

There has been much speculation as to the cause(s) of the decline in southern elephant seal numbers in the southern Indian and southern Pacific oceans (Condy 1979, van Aarde 1980, Skinner & van Aarde 1983, McCann 1985, Pascal 1985, Burton 1986, Hindell & Burton 1987, Guinet *et al.* 1992, Hindell *et al.* 1994, Slip & Burton 1999), but findings have been inconclusive. It is obvious that the causative factor(s) are effective during the pelagic phases of the annual cycle (Laws 1994, Hindell *et al.* 1994), certainly at Marion Island (Wilkinson & Bester 1988, Bester & Wilkinson 1994), as opposed to the days of land-based seal hunting. Nevertheless, it is important to gather information pertaining to the biology of the species during their terrestrial phases, as topics for scrutiny may be highlighted.

1.4 Objectives

The annual haulout cycle of southern elephant seals is characterised by its regularity and its organisation, with different age- and sex-classes hauling out on land at different times (Carrick *et al.* 1962*b*, Condy 1979). Temporal haulout patterns have been described for a number of breeding colonies, including Signy Island in the South Orkney Islands (Laws 1956*a*), Îles Crozet (Barrat & Mougin 1978), Îles Kerguelen (van Aarde 1980), Marion Island (Condy 1979, Skinner & van Aarde 1983), Macquarie Island (Carrick *et al.* 1962*b*, Hindell & Burton 1988) and Heard Island (Slip & Burton 1999). Some accounts have concentrated only on the breeding season, and most have been accomplished by classifying individuals into broad population components based on subjective evaluations of body size and appearance, often using the descriptive method of Laws (1953*a*) or Carrick & Ingham (1962). Carrick *et al.* (1962*b*) made use of known-age animals in describing the timing and duration of events during the terrestrial cycles of the elephant seal populations at Macquarie Island and Heard Island, but did not accurately quantify age- and sex-specific variation in the timing of haulouts.

The only previous description of the terrestrial cycle of southern elephant seals at Marion Island, that encompassed all three haulout phases, was based on counts of animals that were classified into subjectively defined population components (Figure 2, Condy 1979). The existence of sex- and age-specific data recorded from annual tagging and regular tag resightings since 1983 at Marion Island (see Chapter 3.2) permits an objective approach to studying temporal haulout behavior, whereby inconsistency in assigning seals to subjective classificatory categories is avoided. The timing of haulouts by distinct age- and sex-classes can, furthermore, be statistically

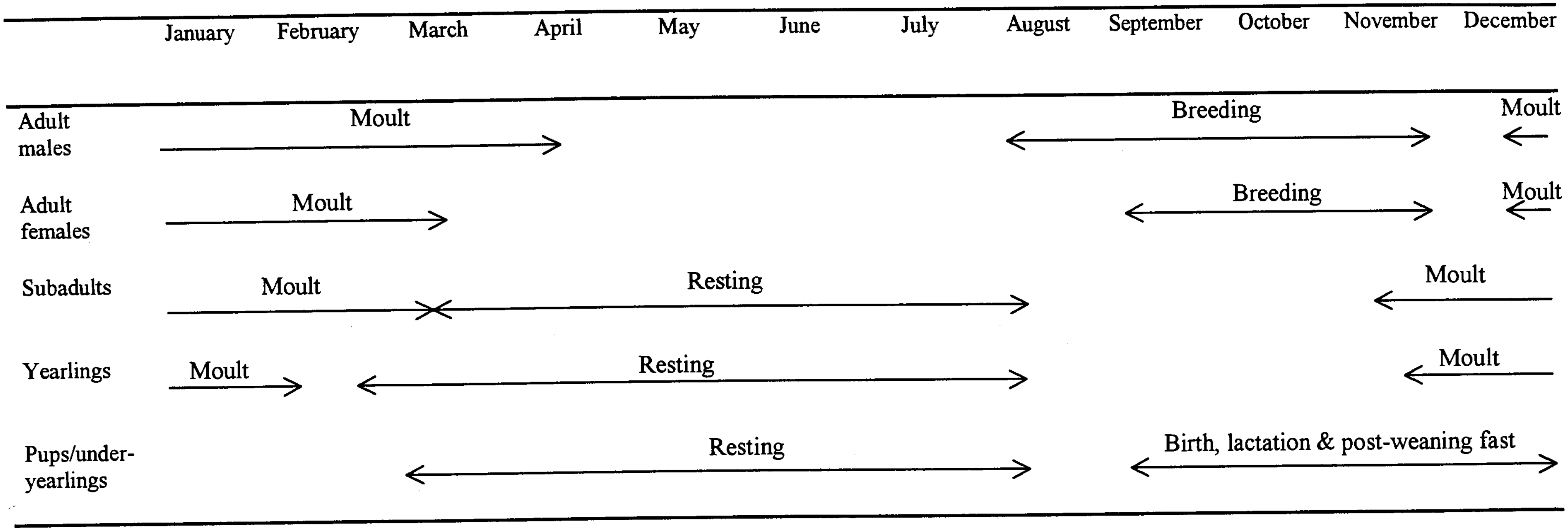

Figure 2. Schematic presentation of the terrestrial haulout cycles of subjectively defined age- and sex-classes of southern elephant seals at Marion Island (adapted from Condy 1979 & Wilkinson 1992).

described and compared, and changes therein related to growth and development can be observed. Moreover, haulout records of known age animals during the autumn-winter period permits the investigation of age- and sex-specific temporal aspects and participation levels in the resting haulout, the terrestrial phase that has been least regarded in previous studies concerning the terrestrial haulout cycle of southern elephant seals.

The objectives of this study are thus:

(a) to describe the temporal breeding, moulting and resting haulout patterns of Marion Island elephant seals age- and sex-specifically,

(b) to expand on possible causal factors effecting age- and/or sex-specific similarities or differences in temporal haulout behavior, and

(c) to investigate the age- and sex-specific level of participation in the resting haulout.

Temporal aspects of the breeding and moulting haulouts are investigated in a single chapter, Chapter 4. Temporal aspects of the resting haulout are investigated separately, in Chapter 5. In concluding (Chapter 6), the findings of Chapters 4 and 5, and the contribution of this study to an increased understanding of the temporal haulout behavior of southern elephant seals, shall be discussed.

CHAPTER 2

STUDY SITE

2.1 Location

Marion Island (46°54'S, 37°45'E) is the southern-most and largest of two islands within the Prince Edward Island group, approximately 2300 km south-east of Cape Town, South Africa. The northerly island, Prince Edward, is some 20 km north of Marion, and the next closest land is Îles Crozet, about 925 km to the west.

2.2 Topography

Marion Island is roughly oval in shape, with an area of about 290km^2, and a circumference of approximately 90 km. The beaches on the west coast of the island, exposed to the prevailing wind direction, are typically irregular and rough by nature. On the more sheltered eastern side of the island, beaches are generally made up of small rounded rocks, stones and pebbles, and have a flat, regular appearance. Many of these beaches occur at the mouths of streams, and elephant seals can gain access to inland moulting sites along the drainage lines. Elephant seals almost exclusively occupy the eastern half of the island during their terrestrial phases (Figure 3).

2.3 Climate

Marion Island lies within the "Roaring Forties", and in the proximity of the Antarctic Polar Front (Figure 1), which is the boundary between cold, dense, Antarctic surface waters with relatively low salinity levels, and warmer, less dense sub-Antarctic waters with higher salinity. The outstanding climatic features are strong, predominantly westerly winds, often of gale force

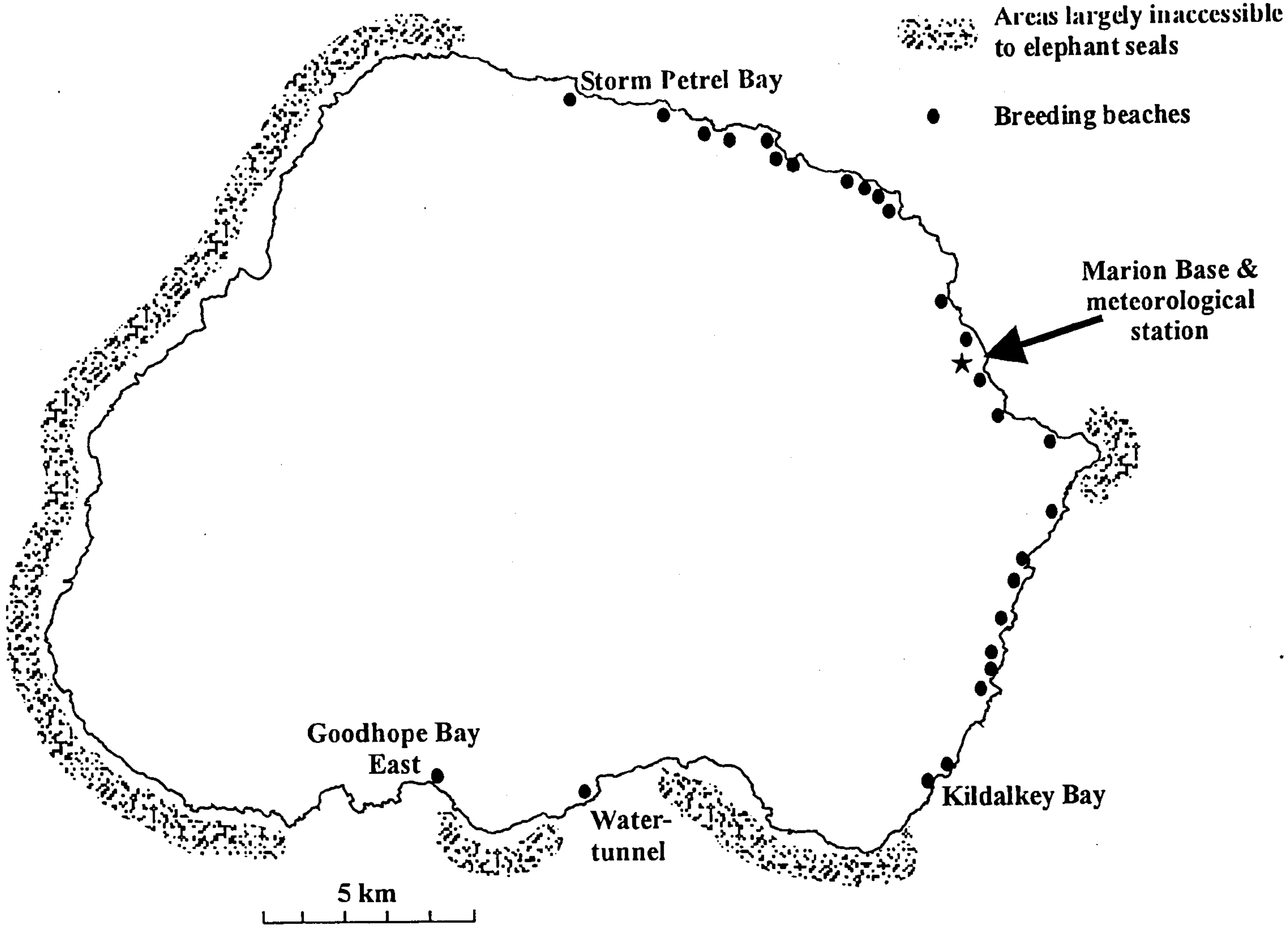

Figure 3. Marion Island, showing the distribution of elephant seal breeding localities and areas largely inaccessible to elephant seals (Adapted from Wilkinson & Bester 1990).

strength; relatively low meaner temperatures of about 5°C, showing little annual or diurnal variation; high relative humidity with little annual or diurnal variation from 80%; abundant precipitation with an annual mean of about 2500mm, in the form of rain, snow, or ice-rain; and a high degree of cloudiness, with only about 20-33% of possible sunshine reaching the surface (Schulze 1971).

CHAPTER 3

METHODS

The methods presented in this chapter are relevant to both Chapter 4 (the breeding and moulting haulout phases) and Chapter 5 (the resting haulout phase). Sections 3.1 to 3.3 and section 3.5 are relevant to both chapters, but section 3.4 only pertains to Chapter 5.

3.1 Data collection and preparation

Since November 1983, weaned pups were double tagged in the webbing of their hind flippers with colour coded, three-digit numbered "Jumbo" rototags (Dalton Supplies Ltd, Henley-on-Thames, UK; Figure 4), and whenever possible, sexed simultaneously. Most beaches on the eastern side of the island, from Storm Petrel Bay to Goodhope Bay East (Figure 3), were censused on foot on a regular basis (every seven days during the breeding season, and every ten days outside of the breeding season) since 1983. Tag resightings were recorded concurrently with all censuses. From 1983-1989, censuses only took place from August of one year to April or May of the following year, and the resting haulout went largely unrecorded, but censuses have been conducted on a year-round basis since 1990.

Tags were resighted with as little disturbance to the animals as possible, with the aid of binoculars, or by sneaking up behind an animal and gently parting its hind flippers (Figure 5). However, it was often necessary to use a blunt-hooked pole in order to part the flippers, especially during the breeding season, at which time the seals were more nervous and aggressive. When resighting a tagged individual, tag colour(s) (indicating the year of application), tag number (indicating sex and identity of individual), location, date, and haulout type (breeding, moulting or

Figure 4. A "Jumbo" rototag in the hind flipper of an adult male southern elephant seal.

Figure 5. Checking the hind flippers of an adult male southern elephant seal for the presence of tags.

resting) were all recorded. Resighting records collected in this way up until April 1998 (the end of the 1997/98 moulting season), were available for this study. All records were captured to DBase 4 files (Ashton Tate), which were validated using SAS procedures (SAS Institute Inc., release 6.09) to pinpoint possible errors in the data records, and correct or eliminate them.

As censuses were not conducted during the winter months in the years prior to 1990, and during this time were often ensued only after the onset of the breeding male, and sometimes the breeding female, haulout period, and/or were discontinued before the termination of the adult male moulting season, the years 1983 to 1989, including the 1989/90 moulting season (the moulting haulout phase is the only terrestrial phase that extends from one calendar year to the next), were excluded from the study. Thus, observations used in the calculation and comparison of age- and sex-specific temporal haulout behavior, included records of resting and breeding animals from 1990 to 1997, and moulting animals from the 1990/91 to the 1997/98 moulting seasons.

Sampling procedures at Marion Island were initiated primarily with the aim of obtaining demographic population parameters such as age- and sex-specific survival and fecundity, and standing age-distribution of the elephant seal population, and are thus not necessarily suited for reliable descriptions of age- and sex-specific temporal haulout behavior. The intervals between censuses are too large to accurately assess the haulout parameters of age- and sex-classes during one season, let alone confidently test for temporal differences in haulout behavior between different age- and sex-classes. Also, the inter-annual variation in census dates (corresponding censuses were not necessarily conducted on the same date every year) preclude reliable between-year comparisons of matching classes. Moreover, the value of within- and between-year descriptions or comparisons of age- and sex-specific classes is often limited by relatively low sample sizes of known-age individuals, especially among the older age classes, that are resighted on Marion Island within a year (see Appendices I-III). It was decided to increase sample sizes, and at the same time enhance the continuity of the data by reducing the effects of inter-annual variability and intervals between observation dates, by pooling all the records of individuals of each age- and sex-class over the study period (1990-1997/98).

Each haulout type was allocated its own unique temporal scale, measured in days from day 0 (a starting date appropriate to each haulout type), to which all relevant observation dates for each year of the study period could be converted, to facilitate comparison. Day 0 is equivalent to 1 August in the case of the breeding haulout, 15 October for the moulting haulout, and 15 January for the resting haulout. Observations of marked individuals ashore, representing distinctive age- and sex-classes, were discretely totalled over the whole study period and converted to the relevant common temporal scales, giving numerical distributions over time. When sample sizes permitted, numerical haulout distributions over time were also derived for each age- and sex-class for each distinct year of the study period, utilising the same temporal scales as used for the pooled data, to compare inter-annual consistency in temporal haulout distributions.

The sexual status of marked animals at any time could be assumed from their individual life histories according to resighting records, subject to certain limitations (see Section 3.5). For the purposes of this study, sexual status among females is determined by whether individuals (a) have yet to be impregnated (nulligravid), or (b) have yet to give birth (nulliparous), (c) are pregnant for the first time (primigravid), (d) have given birth on one occasion (primiparous), or (e) have given birth on more than one occasion (multiparous), after Carrick *et al.* (1962*a*). Among males, sexual status is determined by whether individuals have been attendant during a breeding season (mature) or not (immature). Certain age- and sex-classes that were identified as being heterogenous with regard to the sexual status of their component individuals, were divided into sub-classes to facilitate assessment of the effects of variation in sexual status on temporal haulout behavior. Thus (Table 1), two-year-old females were divided into nulligravid and primigravid sub-classes, three-year-old females were divided into nulliparous and primiparous sub-classes, and four-year-old females were divided into nulliparous, primiparous and multiparous sub-classes. Six- and seven-year-old males were divided into mature and immature sub-classes. Five-year-old males (all immature) were further defined as to whether they were observed to haul out in the subsequent breeding season (at age six) or not. For convenience sake, the former are referred to as pre-breeding males and the latter as laggards, while still aged five. Numerical haulout distributions over time were derived for each sub-class, utilising the same temporal scales as used for the pooled data.

During the 1998 breeding season (August to November), censuses were conducted every two days along the approximately 20 km strip of coastline from the personnel base and meteorological station to Kildalkey Bay (Figure 1), during which tag colour combinations of marked females were observed, specifically for the purpose of describing their age-specific haulout distributions. Observations of individuals of each female age-class were converted to the same temporal scale used for the pooled breeding data, to compare the outcomes of the two approaches.

3.2 Quantifying temporal haulout behavior

Temporal haulout parameters were calculated for the numerical haulout distributions over time of each age- and sex-class, and sub-class, as pooled over the entire study period, using a univariate descriptive statistics procedure (SAS Institute Inc., release 6.09). The temporal haulout distributions of breeding females counted at two-day intervals during 1998, and of each distinct year of the study period for each age- and sex-class, were also described. The temporal haulout parameters describe temporal haulout distributions, in terms of measures of central tendency and variability of age- and sex-classes or sub-classes. It should be noted that while measures of variability (standard deviation and range) may show differences in the durations that classes or sub-classes are ashore, they are not necessarily indications of the length of time that individuals of a class are ashore. The latter requires daily searches for marked individual seals (e.g. Wilkinson 1992, Arnbom *et al.* 1997, Slip & Burton 1999), which was beyond the scope of this study.

As a measure of central tendency, the mode reflects the date on the temporal scale with the greatest frequency of observations, or the date of peak numbers hauled out ashore, a parameter that has been widely employed to describe the timing, and shifts in the timing of haulout phases (particularly that of the breeding female component), within and between elephant seal populations (Carrick *et al.* 1962*b*, Barrat & Mougin 1978, Condy 1979, McCann 1985, Hindell & Burton 1988, Vergani & Stanganelli 1990, Guinet *et al.* 1992, Wilkinson 1992, Campagna *et al.* 1993, Slip & Burton 1999). However, the modal value is disregarded in this study, as it is biased towards dates on which counts were more likely to occur, and cannot represent a date on which no censuses were conducted over the duration of the study period. As the mean reflects the value of each observation in a distribution, and because its precisely defined mathematical value permits other statistical techniques to be based upon it (Fowler & Cohen 1990), it is the principal measure of central tendency in this study, despite the fact that it does not reflect the peak haulout date in a skewed temporal distribution.

Table 1. The separation of age- and sex-classes into sub-classes according to the observed sexual status of individuals.

Sex	Age-class (years)	Sub-class	Allocation of individuals to sub-classes
Female	2	Nulligravid	Not observed to breed at age 3
		Primigravid	Observed to breed at age 3
	3	Nulliparous	Not observed to breed at age 3
		Primiparous	Observed to breed at age 3
	4	Nulliparous	Not observed to breed at age 3 or 4
		Primiparous	Observed to breed for the first time at age 4
		Multiparous	Observed to breed for the second time at age 4
Male	5	Laggards	Not observed to attend breeding at age 6
		Pre-breeding	Observed to attend breeding at age 6
	6	Immature	Not observed to attend breeding at age 6
		Mature	Observed to attend breeding at age 6
	7	Immature	Not observed to attend breeding at age 6 or 7
		Mature	Observed to attend breeding at age 7

3.3 Statistical comparisons of temporal haulout distributions

Normal probability plots of the temporal haulout distributions of each age- and sex-class and sub-class were constructed, and those that did not approximate normality, and had low sample sizes, were omitted from analyses. These included moulting and breeding animals of each gender that were older than nine and ten years, respectively. Statistical comparisons were performed amongst the following age- and sex-classes, and sub-classes: (a) breeding females aged three to ten years, (b) breeding females aged three to ten years, counted at two-day intervals during 1998, (c) breeding males aged six to ten years, (d) moulting females and males aged one to nine years, (e) moulting nulligravid and primigravid two-year-old females, nulliparous and primiparous three-year-old females, and nulliparous, primiparous and multiparous four-year-old females, (f) moulting pre-breeding and laggard five-year-old males, immature and mature six- and seven-year-old males, (g) resting male age-classes from underyearlings (aged 0-12 months) to six-year-olds, (h) resting male and female age-classes from underyearlings to three-year-olds, (i) nulligravid and primigravid two-year-old females, (j) and pre-breeding and laggard five-year-old males. The age-specific temporal haulout parameters of females breeding in 1998, aged three to ten years, were also statistically compared. No between-year comparisons were performed among age- and sex-classes, due to low sample sizes, long intervals between census dates, and inter-annual variation in census dates.

The equality of the variances of temporal haulout distributions to be compared were tested for using Levene's test (BMDP Statistical Software, Inc., Version 7) with confidence limits set at 95 %. When the variances were found to be heterogenous, each observation of the comparative classes or sub-classes was weighted with the inverse of the standard deviation of the specific class before performing analysis of variance (ANOVA). Age- and sex-related differences in temporal haulout behavior, interactions therein, and differences related to sexual status, were tested for by ANOVA using SAS General Linear Models with Bonferonni's Post Test (SAS Institute Inc., release 6.09). Confidence limits were set at 95%. According to cumulative normal probability plots that were constructed against the residuals, *a posteriori*, all the comparative temporal haulout distributions fitted the models.

3.4 Estimating participation levels in the resting haulout

For each year from 1990 to 1995, participation levels of male and female age-classes, from underyearlings to six-year-olds and three-year-olds, respectively, were estimated by calculating the fractions of surviving individuals of each age- and sex-class that were observed to rest, as well as the fraction of surviving individuals that rested on more than one occasion during the same autumn-winter period. Individuals were said to have hauled up for more than one resting haulout bout in a year, interrupted by a pelagic foraging trip, if there was an interval of at least three census periods (representing a minimum of about 40 days) between resightings of an individual. This was done in view of the relative ease of resighting individuals at Marion Island, under which conditions it is difficult to overlook an individual on three consecutive censuses, and the fact that elephant seals observed to rest on more than one occasion in a year at Macquarie Island hauled out at intervals of approximately two or three months (Carrick *et al.* 1962).

Individuals observed to rest during an autumn-winter period but not resighted within the subsequent three years were omitted from analyses to prevent over-estimation of participation levels, while individuals not observed to rest during an autumn-winter period, but resighted within the subsequent three years, were included in analyses. Resightings of individuals later than three years after the relative-autumn winter haulout were disregarded when estimating participation levels, to achieve consistency in estimation of surviving individuals between years. Years subsequent to 1995 were excluded, as they are not followed by three data years.

Chi-square tests with 95% confidence limits were performed to test whether age- and sex-specific participation in the resting haulout was constant between years over the study period. If so, the years 1990 to 1995 were then pooled , and Chi-square tests (95 % confidence limits) were used to test for age-related differences in the level of participation among each sex. Sex-related variation in participation among age-classes, and variation related to differing sexual status between component individuals of age- and sex-classes, were tested for using Fisher's Exact Test with 95% confidence intervals. Differences in participation levels that could be related to age, sex, or sexual status, were expressed by stating the differences in the proportions of animals resting as odds-ratios (ω), where

$$\omega = \frac{q_1/p_1}{q_2/p_2}$$

(from Sokal & Rohlf 1995)

where q_1 and p_1 represent proportions of a class that were and were not observed to rest, or that were observed to rest once and at least twice, respectively, and q_2 and p_2 represent proportions of the comparative class that were and were not observed to rest, or that were observed to rest once and at least twice, respectively.

3.5 Limitations and assumptions

(1) Southern elephant seals at Marion Island are assumed to age a year on 15 October, the peak of the breeding season haulout (Wilkinson 1992). Thus, an individual born in 1990 becomes a one-year-old, or a yearling, on 15 October 1991. For convenience sake, a year was added onto

the age of all tagged breeding animals at the time of their first resighting during any breeding season, even if the animal was observed before 15 October, so that each breeding animal had only one age during a breeding season.

(2) It is assumed that the intensity and efficiency of the search effort between Storm Petrel Bay and Kildalkey Bay (Figure 3), over the duration of the study period, was constant, and that due to the relative ease of observing seals on the numerous small beaches and inland moulting areas, age-related behavioral differences did not affect the likelihood of observing different age- and sex-classes.

(3) Temporal haulout distributions were generated using the sum of observations of individuals of known age and sex per census, and are independent of differences in the numbers of pups initially tagged in each cohort, as well as of age- and sex-related differential rates of survival, tag-loss, dispersion or site-fidelity.

(4) The sample sizes of haulout distributions were constituted by the sum total of observations of marked animals belonging to the relevant class, not by the number of individuals of the class hauled out over that period. Each marked individual present was likely to have been counted on at least two occasions, on different dates, during a single haulout phase, and each individual may thus contribute multiple units to the sample size. It was thus assumed that all individuals present in the study area, participating in a particular haulout phase, had an equal likelihood of being observed during a census, and each single observation was mutually exclusive from any other.

(5) Age-specific classes of the same gender invariably include observations of the same

individuals at different ages. Since this study is concerned with detecting age-related temporal shifts in haulout behavior of the population as a whole, different age groups were treated as being mutually exclusive of one another.

(6) The calculated temporal haulout parameters of the different age- and sex-classes and sub-classes should not be interpreted as precise descriptions of the temporal haulout distributions. Although the effects of the relatively long intervals between observation dates were reduced by grouping years together, the descriptive statistics do not necessarily simulate what may have been achieved by conducting counts at one to two day intervals, which are ideal for the quantification of haulout parameters (e.g. Hindell & Burton 1988, Vergani & Stanganelli 1990, Wilkinson 1992). It is assumed that all age- and sex-classes were equally affected by any lack of continuity in the field methods, and that statistical differences between them are real.

(7) It should be noted that respective age- and sex-classes and sub-classes merely reflect the temporal terrestrial activity of their component individuals according to resighting records. While the creation of sub-classes provided a means of diminishing the heterogeneity of parent classes, and significant differences in temporal haulout behavior between sub-classes are assumed to reflect variation in sexual status, sub-classes themselves may not be entirely homogenous with regard to sexual status. For instance, if an individual bred further afield than the study area in any year, any assumption of that individuals sexual status may be incorrect. Although southern elephant seal females exhibit a high degree of philopatry (Hindell & Little 1988), and the majority of the Marion Island population that reach a reproductive age are thought to return for breeding (Bester 1989), this limitation needs to be considered when interpreting the results.

(8) Site fidelity by individuals within an elephant seal population may be affected by age-

and sex-specific differences in foraging areas or migratory behavior (Burton 1985, Wilkinson & Bester 1990, Guinet *et al.* 1992). As an assumption, consistency in age- and sex-specific site fidelity is thus contestable, and age- and sex-specific differences in participation in the resting haulout should be interpreted with this in mind.

CHAPTER 4

THE BREEDING AND MOULTING HAULOUTS

4.1 Introduction

The southern elephant seal breeding season at Marion Island commences in early August, when the first males arrive and position themselves on the beaches, followed by the first pregnant females arriving in early September (Condy 1979). The females give birth approximately six days after hauling out (Condy 1979, Wilkinson 1992). Copulation occurs at about 18 days after parturition (Condy 1979, Wilkinson 1992), and pups are weaned around 19 to 25 days post-partum, after which the females return to sea (Wilkinson 1992). Most females have departed by early November, and sightings of adult males are rare by December (Condy 1979). Yearlings (aged 12-24 months) and subadults of both sexes start their moulting haulout at the end of the breeding season (early November), with a peak in numbers moulting in mid-December, while peaks in the numbers of moulting adult females and adult males occur during mid-January and mid-February, respectively (Condy 1979).

The timing of the breeding season varies between some southern elephant seal populations, but within a population there is consistency between years (Carrick *et al.* 1962*b*, Hindell & Burton 1988, Wilkinson 1992, Guinet *et al.* 1999). Temporal variation in breeding between populations is usually indicated by differences in the date of the peak of the breeding season haulout, as inferred from the numbers of breeding females ashore (Wilkinson 1992). Female numbers peak around mid-October at Marion Island (Condy 1979, Skinner & van Aarde 1983, Wilkinson 1992), and at other breeding colonies in the Indian and Pacific Oceans (Sorenson

1950, Carrick *et al.* 1962*a*, Barrat & Mougin 1978, van Aarde 1980, Hindell & Burton 1988, Guinet *et al.* 1999, Slip & Burton 1999), up to ten days earlier than populations of the Scotia Arc (Laws 1956*b*, McCann 1985, Vergani & Stanganelli 1990), and about two weeks later than the population at Peninsula Valdés (Campagna *et al.* 1993). Differences in day length, food availability and thermal conditions have been proposed as factors affecting the clines in the timing of reproduction between populations (Campagna *et al.* 1993).

The moult of elephant seals has been referred to as a catastrophic process (Laws 1956*a*, Bonner 1994), during which the previous season's hair as well as the superficial layer of skin is shed in patches before the new hair appears (Laws 1956*a*, Carrick *et al.* 1962*b*, Ling 1965). Hair follicle activity is initiated at sea months before the actual moult, which is merely the completion of the process (Ling 1965). The duration of the moulting haulout is about 40 days for adult males and 28 days for adult females (Ling & Bryden 1981), and is obligatory for all age classes except underyearlings, which lose their natal coat in the first few weeks of life (Laws 1956*a*, Ling 1965, Condy 1979, Panagis 1981, Lenglart & Bester 1982). Energy reserves that are built up during the pre-moult pelagic phase are invested in the production of new skin and hair, while the remainder is metabolized to support the animal while fasting (Boyd 1993, Fedak *et al.* 1994).

At Macquarie Island, between-year consistency in the timing of moulting by juveniles has been documented, but inter-annual variation in the moulting peaks of adult males and females, of four and two weeks, respectively, have also been recorded (Carrick *et al.* 1962*b*, Hindell & Burton 1988). Hindell and Burton (1988) acknowledged that while observed differences may simply reflect natural variation in the timing of haulouts, inconsistency between years in assigning seals to age categories may also have contributed to the recorded differences. Most previous studies of the temporal aspects of moulting and breeding behavior have, in fact, been based on counts and/or observations of individuals classified into different, often subjectively defined, population components. These studies have attempted to determine the timing and/or duration of haulouts and/or associated reproductive or physiological stages or processes (e.g. Laws 1956*a*, Carrick *et al.* 1962*a*, 1962*b*, Ling 1965, Barrat & Mougin 1978, Condy 1979, Rothery & McCann 1987, Hindell & Burton 1988, Wilkinson 1992, Campagna *et al.* 1993, Arnbom *et al.* 1997, Slip & Burton 1999), often with the aim of enabling the estimation of, and/or a means of predicting population status (e.g. van Aarde 1980, McCann 1985, Hindell & Burton 1987 & 1988, McCann & Rothery 1988, Campagna & Lewis 1992, Guinet *et al.* 1992, 1999, Boyd *et al.* 1996, Slip & Burton 1999). No study has yet shown quantifiable temporal variation in these two haulout phases at the level of distinctive classes of known age and gender.

This chapter examines the temporal breeding and moulting haulout behavior of Marion Island elephant seals, by:

a) describing the timing of haulouts age- and sex-specifically, and

b) investigating the influence of growth and development on the timing and duration of haulouts, and expanding on possible factors affecting similarities or differences in temporal haulout behavior.

4.2 Results

Age- and sex- specific temporal haulout parameters calculated for each year of the study period are shown in Appendices I (breeding) and II (moulting). Descriptive parameters of the temporal haulout distributions of breeding males (group A) breeding females (group B); breeding females counted at two-day intervals during 1998 (group C); moulting males and females (group

D); sub-classes of moulting five-, six- and seven-year-old males (group E); and sub-classes of moulting two-, three- and four-year-old females (group F), are displayed in Tables 2 to 7, respectively. Measures of central tendency of haulout distributions are presented as actual dates for the sake of clarity, converted from the temporal scale utilised during quantification. Box-and-whisker plots depicting the temporal haulout distributions of groups A to F are presented in Figures 6 to 12, respectively (■ represents the mean haulout day, horizontal lines represent, from below, the 1st quartile, median haulout day and 3rd quartile, respectively, and error bars depict the range of observations about the mean haulout day).

According to Levene's test, the variances in the distribution of observations between the component age- and sex-classes were not homogenous at 95% confidence levels for groups A ($F_{4,1111} = 4.93$, $P < 0.05$), C ($F_{7,1319} = 6.69$, $P < 0.05$), D (sex, $F_{1,15562} = 320.61$; age, $F_{8,15562} = 64.58$; interaction, $F_{8,15562} = 84.02$; $P < 0.05$), E ($F_{5,1125} = 5.92$, $P < 0.05$) and F ($F_{6,3879} = 8.75$, $P < 0.05$). Individual observations were thus weighted with the inverse of the standard deviation of their specific class prior to performing ANOVA. The variances in the distribution of observations between the age- classes of group B were homogenous at 95% confidence levels ($F_{7,4685} = 1.33$, $P > 0.05$).

Significant variation was found among the classes of group A ($F_{4,1111} = 6.89$, $P < 0.05$), with the mean haulout dates of breeding males postponed with descending order of age, and the mean haulout dates of younger males (six- and seven-year-olds) significantly later than those of nine- and ten-year-olds. There was also significant variation among classes of groups B ($F_{7,4685} = 4.29$, $P < 0.05$), where the mean haulout date of breeding three-year-old females was significantly earlier than those of five-, six- and seven-year-old females; and C ($F_{7,1319} = 12.76$, P

Table 2. Temporal breeding haulout parameters based on the total number of observations of marked six- to 10-year-old males resighted over the sampling period 1990-1997. [Means with the same superscripts are not significantly different to each other at 95% confidence levels].

Age-class (years)	*n*	Mean haulout date	S. D. (± days)
6	131	15 October^{a}	19.9
7	351	12 October^{ab}	22.6
8	349	8 October^{bc}	23.0
9	189	5 October^{c}	25.7
10	96	2 October^{c}	25.7

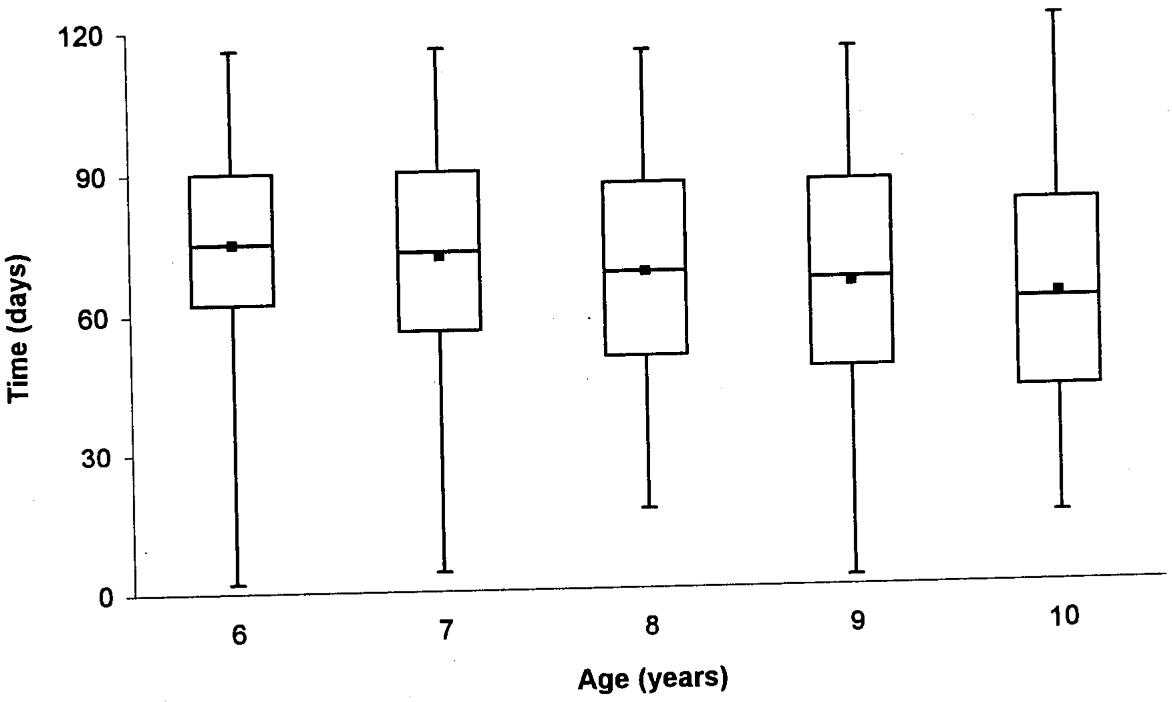

Figure 6. Temporal haulout distributions of breeding males aged six to 10, for the period 1990-1997.

Table 3. Temporal breeding haulout parameters based on the total number of observations of marked three- to 10-year-old females resighted over the sampling period 1990-1997. [Means with the same superscripts are not significantly different to each other at 95% confidence levels].

Age-class (years)	*n*	Mean haulout date	S. D. (± days)
3	597	10 October^{a}	11.2
4	1199	11 October^{ab}	11.6
5	946	13 October^{b}	11.5
6	747	13 October^{b}	11.8
7	558	13 October^{b}	12.2
8	296	12 October^{ab}	11.6
9	231	12 October^{ab}	11.8
10	119	11 October^{ab}	11.9

Figure 7. Temporal haulout distributions of breeding females aged three to 10, for the period 1990-1997.

Table 4. Temporal breeding haulout parameters based on the total number of observations of three- to 10-year- females recorded during counts at two-day intervals during the 1998 breeding season [Means with the same superscript are not significantly different to each other at 95% confidence levels].

Age-class (years)	*n*	Mean haulout date	S. D. (± days)
3	251	8 October^{a}	13.1
4	185	13 October^{bc}	10.8
5	259	12 October^{b}	11.1
6	184	14 October^{cd}	9.9
7	132	16 October^{d}	8.6
8	160	11 October^{ab}	11.8
9	96	18 October^{d}	8.4
10	60	12 October^{b}	13.0

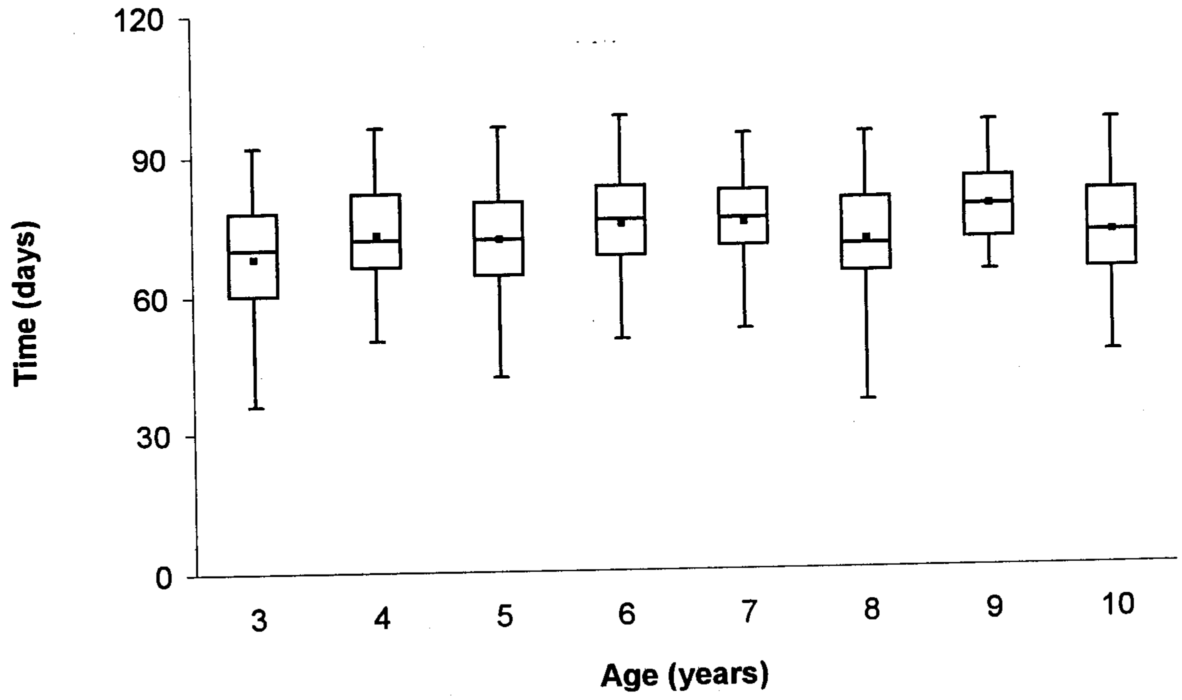

Figure 8. Temporal haulout distributions of breeding females aged three to 10, during 1998.

Table 5. Temporal moulting haulout parameters based on the total number of observations of marked one- to nine-year-old males and females resighted over the sampling period 1990-1997/98. [Means with the same superscript are not significantly different to each other, and means without superscripts are significantly different to all other means, at 95% confidence levels].

Sex	**Age-class (years)**	***n***	**Mean haulout date**	**S. D. (± days)**
Male	1	1526	6 December	14.5
	2	1511	15 December	16.8
	3	1357	19 December	17.6
	4	990	21 December^{a}	18.9
	5	680	25 December	21.9
	6	460	7 January	27.0
	7	258	3 February	35.3
	8	97	19 February^{b}	29.8
	9	48	25 February^{b}	22.5
Female	1	1702	8 December	13.9
	2	1749	20 December^{a}	18.1
	3	1579	4 January	18.8
	4	1153	13 January^{c}	17.5
	5	896	14 January^{c}	16.8
	6	663	13 January^{c}	16.3
	7	463	13 January^{c}	14.5
	8	264	14 January^{c}	13.9
	9	184	12 January^{c}	14.8

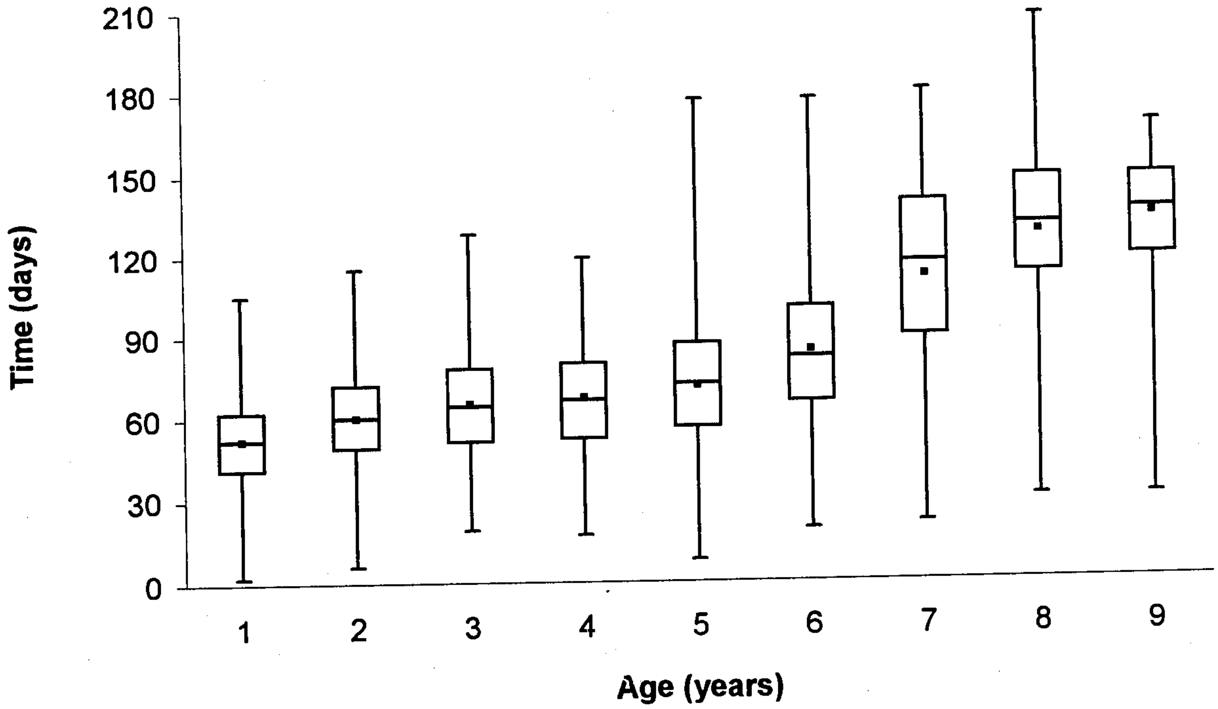

Figure 9. Temporal haulout distributions of moulting males aged one to nine, for the period 1990-1997/98.

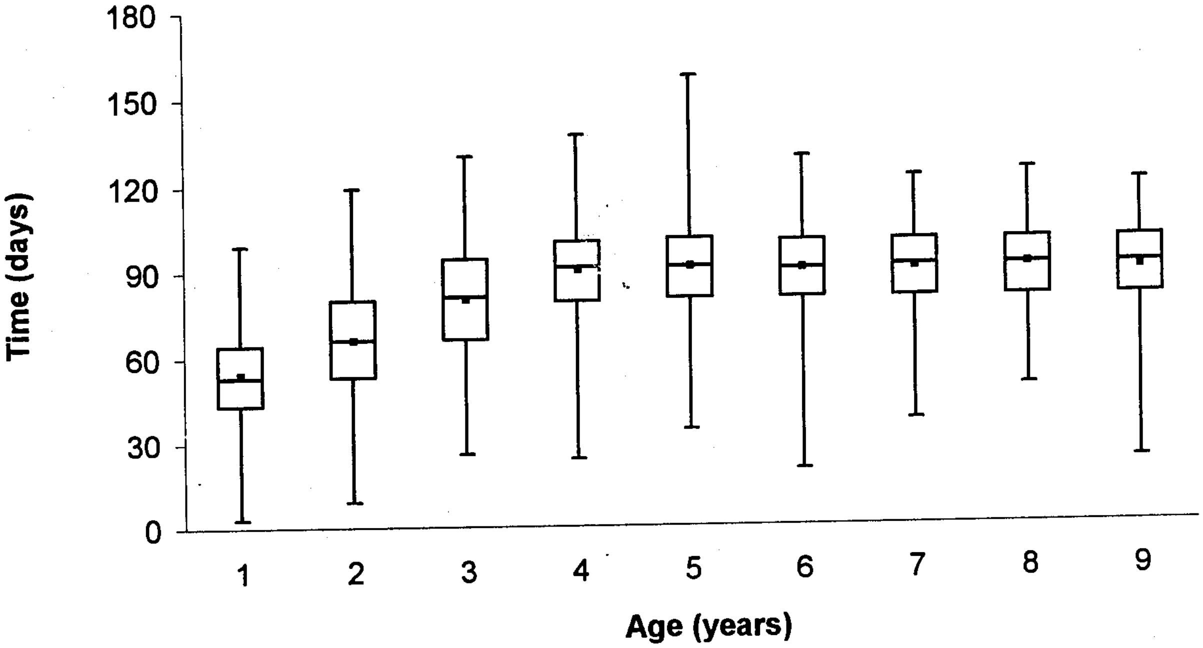

Figure 10. Temporal haulout distributions of moulting females aged one to nine, for the period 1990-1997/98.

Table 6. Temporal moulting haulout parameters based on the total number of observations of marked five-year-old pre-breeding and laggard males, and immature and mature six- and seven-year-old males, resighted over the sampling period 1990-1997/98. [Means with the same superscripts are not significantly different to each other at 95% confidence levels].

Sexual status	**Age Class (years)**	***n***	**Mean haulout date**	**S. D. (± days)**
Immature	5[1]	128	20 December^{a}	22.4
	5[2]	285	29 December^{b}	22.5
	6	335	30 December^{b}	22.3
	7	94	9 January^{c}	30.8
Mature	6	125	27 January^{d}	30.0
	7	164	18 February^{e}	28.2

[1] Pre-breeding males

[2] Laggard males

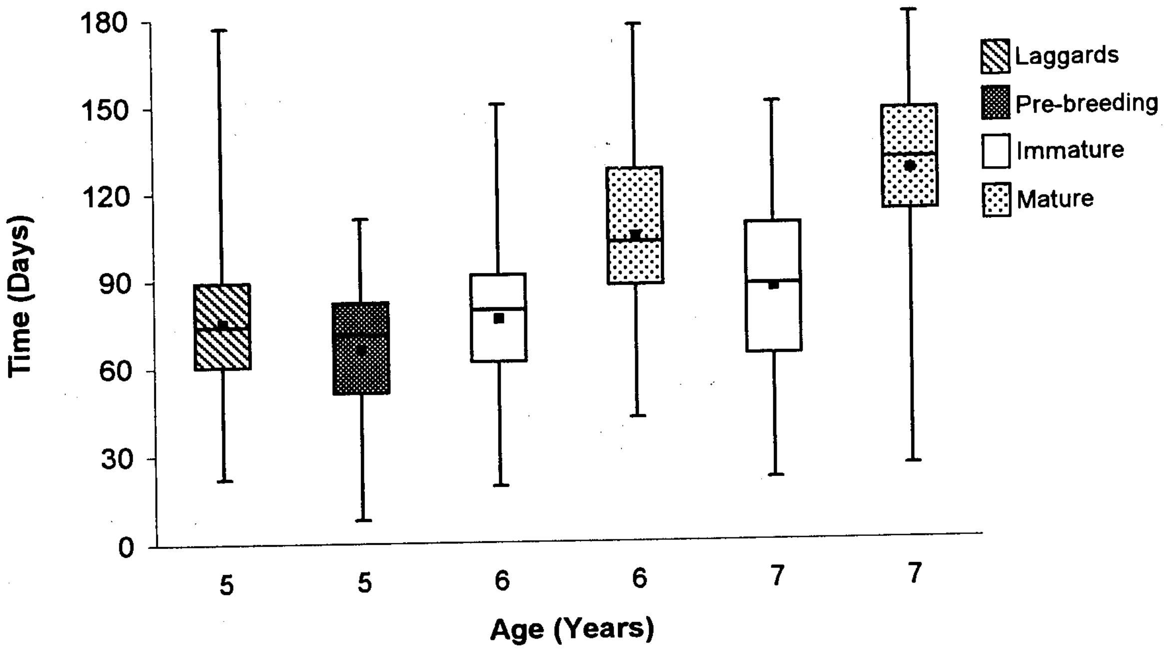

Figure 11. Temporal haulout distributions of moulting males of different sexual status aged five to seven, for the period 1990-1997/98.

Table 7. Temporal moulting haulout parameters based on the total number of observations of marked nulligravid and primigravid two-year-old females and nulliparous, primiparous and multiparous three- and four-year-old females, resighted over the sampling period 1990-1997/98 [Means with the same superscript are not significantly different to each other at 95% confidence levels].

Age-class (years)	*n*	Mean haulout date	S. D. (± days)
2[1]	740	17 December^{a}	18.2
2[2]	474	26 December^{b}	16.4
3[3]	1113	30 December^{c}	18.4
3[4]	466	13 January^{d}	15.6
4[3]	212	1 January^{c}	19.6
4[4]	603	17 January^{a}	14.7
4[5]	278	14 January^{d}	15.4

[1] Nulligravid

[2] Primigravid

[3] Nulliparous

[4] Primiparous

[5] Multiparous

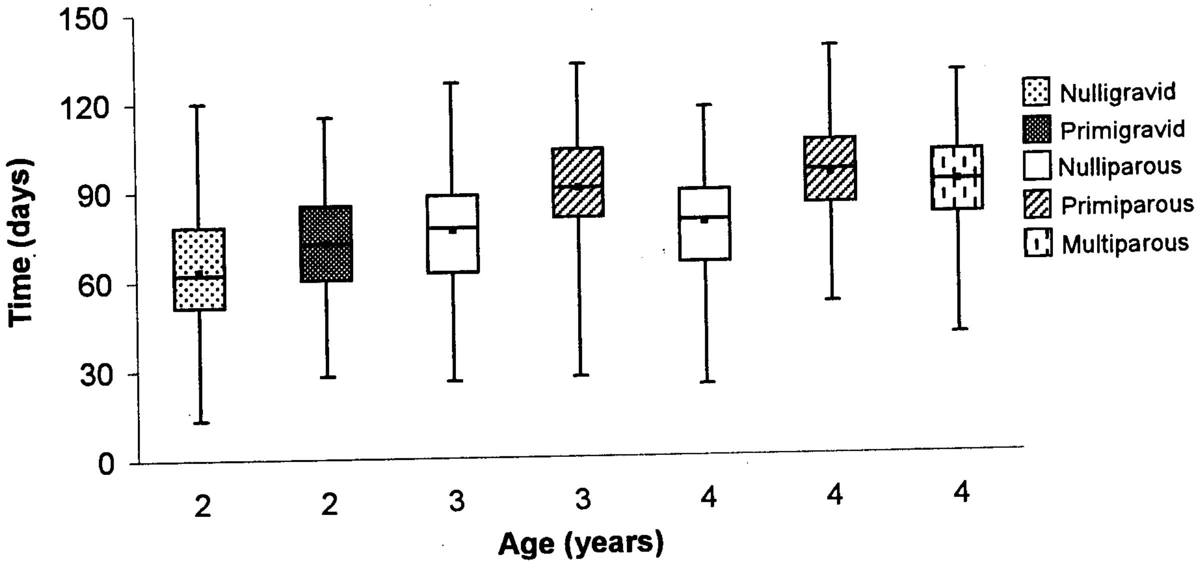

Figure 12. Temporal haulout distributions of moulting females of different sexual status, aged two to four, for the period 1990-1997/98.

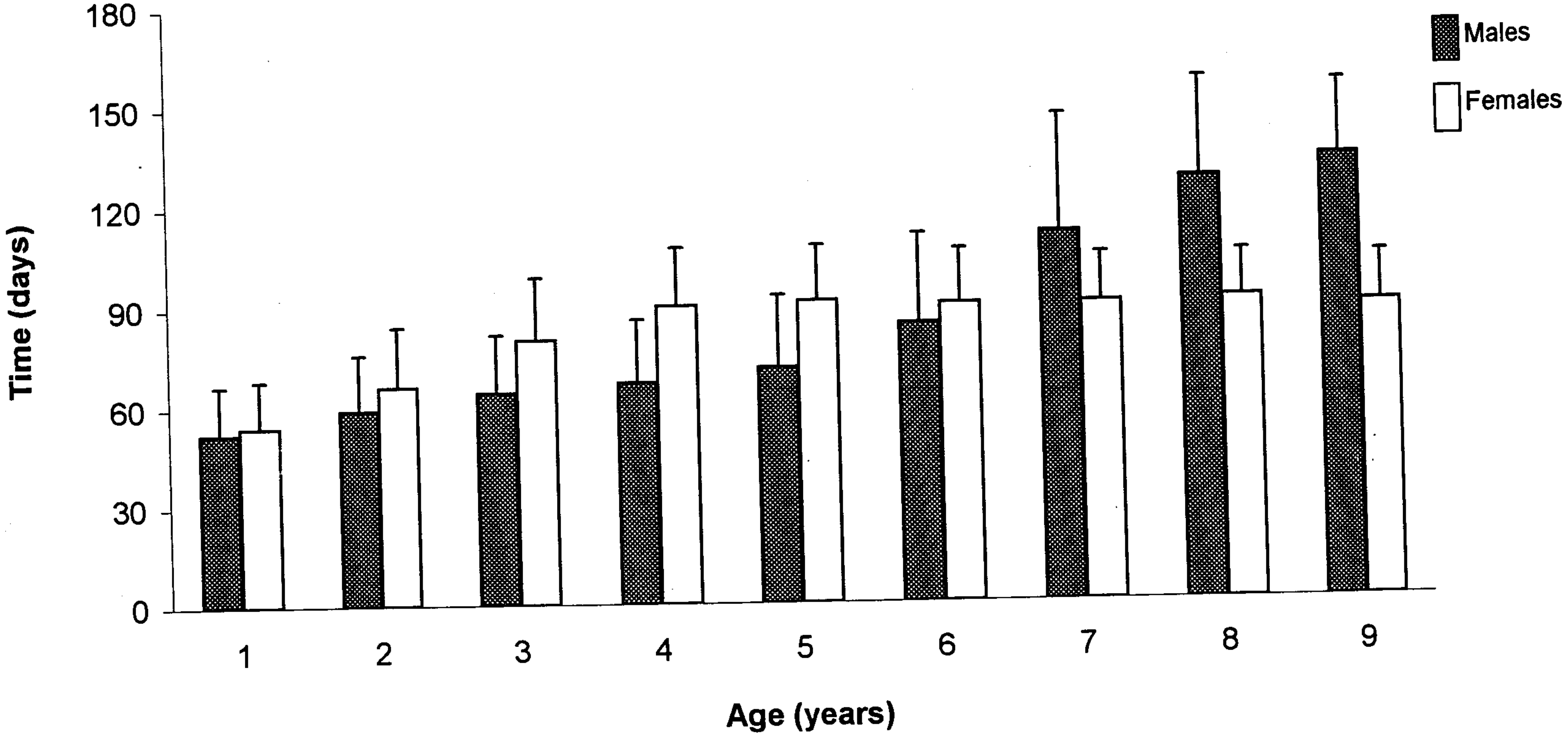

Figure 13. The interactive effect of age and sex on the mean (with standard error bars) moulting dates of males and females aged one to nine, for the period 1990-1997/98.

< 0.05), where the results of B were supported by three-year-old females having an earlier mean breeding haulout date than older age-classes.

Variation in the timing of moulting haulouts of group D resulted from differences in both age and sex, which were interactive (age, $F_{8,15562} = 1129.03$; sex, $F_{1,15562} = 36.09$; interaction, $F_{8,15562} = 206.11$; $P < 0.05$). The mean haulout dates of moulting immature females (aged one to three years) were significantly later than those of males of the same age, but although the mean haulout dates of each male age-class were significantly later with age, at least until age eight, those of female age-classes of breeding age were practically the same as each other (Figure 13). There was also significant variation between the sub-classes in group E ($F_{5,1125} = 127.56$, $P < 0.05$), where the mean moulting haulout date of pre-breeding five-year-old males was significantly earlier than that of laggards of the same age, while age and sexual status both affected the timing of moulting in the older sub-classes, resulting in later mean haulout dates with increasing age and sexual status. Pregnancy was found to delay the timing of moulting among two-year-olds in group F ($F_{6,3879} = 266.88$, $P < 0.05$), while females that had given birth moulted significantly later than those that had not.

4.3 Discussion

Between-year comparison of age- and sex-specific temporal haulout parameters

Taking into consideration the inter-annual variation in census dates and the intervals between censuses, the relative consistency in age- and sex-specific haulout parameters between years, particularly among breeding females, moulting females and moulting yearling and subadult males (up until age five), is an indication of the regularity that has previously been documented as characterising the terrestrial cycle of southern elephant seals at Marion Island (Condy 1979, Wilkinson 1992) and at other sites (Carrick *et al.* 1962*b*, Barrat & Mougin 1978, Hindell & Burton 1988, Guinet *et al.* 1992, 1999). Daily fluctuations in the numbers of subordinate males ashore, as observed by Jones (1981) and Hindell & Burton (1988), probably contribute to the inter-annual temporal variability observed for the breeding male haulout, particularly among the younger age-classes of breeding males (six- and seven-year-olds). Although some seven- and even six-year-old males have been observed to control harems in recent years (S.P. Kirkman pers. obs.), most are still of bachelor status and can return to the sea at any time, their presence on land possibly being affected by ambient weather conditions (Burton 1985), or aggression by other males (S.P. Kirkman pers. obs.). Low sample sizes in some years may also contribute to differences in the observed mean haulout dates between years, within age-classes of breeding males.

Breeding males

Increasing standard deviations of the haulout distributions of breeding males, with age, observed in this study, is indicative of the longer period over which older age-classes are ashore during the breeding season. Larger males can fast for longer periods than smaller males as they have lower metabolic rates (Bartholomew 1970) and more extensive blubber reserves to metabolise (Laws 1977, McCann 1981). Indeed, reproductive success has been positively correlated to size (McCann 1981, Modig 1996) and age (Jones 1981, McCann 1981), with successful males remaining hauled out for the longest period (Carrick *et al.* 1962*a*, Modig 1996) and beachmasters generally only leaving once the last cows have been mated (McCann 1980 & 1982*a*, Campagna *et al.* 1993). The fact that large males usually arrive early at the breeding beaches (Modig 1996), and numbers of bachelor males increase towards the end of the breeding season (Carrick *et al.* 1962*a*, Bester 1980, Laws & Sinha 1993), probably contribute to the reverse order of the mean haulout dates of breeding males at Marion Island, with respect to age.

Moulting males (mature)

The large standard deviations of the moulting haulout distributions of six to eight-year-old males is an indication of the heterogenous nature of these age-classes, which consist of males of breeding and non-breeding status. The dramatic increase in the delay of the male moult that takes affect from ages six to eight is largely a result of increasing proportions of those age groups being attendant during the breeding season, as evidenced by the differences in mean moulting haulout dates between immature and mature six- and seven-year-old males. Temporal separation in the timing of moulting between non-breeding and breeding males is consistent with findings of previous studies on southern elephant seals (Carrick *et al.* 1962*b*, Condy 1979, Hindell & Burton 1988) and other phocids (e.g. Stewart & Yochem 1984, Ashwell-Erickson 1986).

Ashwell-Erickson *et al.* (1986) suggested that age differences in the timing of the moult of male harbour seals, *Phoca vitulina*, and spotted seals, *Phoca largha*, may be due to variations in reproductive status, and Thompson & Rothery (1987) related differences in the timing of the moult of *P. vitulina* to age and reproductive status, and to possible differential changes in the levels of sex hormones. Hair follicle activity is thought to be initiated as early as late July/August among southern elephant seals, with moulting commencing once new hairs have grown to the stage just prior to eruption at the skin's surface (Ling 1965). A mechanism whereby the reproductive (sexual) status of male elephant seals is thought to affect the timing of moulting is through testosterone-induced inhibition of pelage growth (Ling 1965, 1970, 1972). High oestrogen or testosterone levels have been shown to retard hair growth in domestic animals (Muller *et al.* 1983), and testosterone to inhibit antler development among red deer, *Cervus elaphus* (Lincoln *et al.* 1970), and horn growth of mouflon rams, *Ovis musimon* (Lincoln 1998). Age- and dominance-related differences in plasma testosterone levels of breeding males (Bartsh *et al.* 1992, Lincoln 1998), and dominance-related variation in the period of time before testosterone suppression occurs (Bartsh *et al.* 1992), may result in variation in the timing of onset of normal hair follicle activity among adult males. However, plasma testosterone has been shown to peak in September in southern elephant seal males (Griffith 1984*a*), which are reproductively quiescent after November (Griffiths 1984*a*, 1984*b*, 1985), so that while high testosterone levels may retard moulting and permit participation in the breeding season without hair loss, gonad-induced inhibition of hair growth is unlikely to be solely responsible for the protracted delay in the moult of adult male elephant seals.

Reproductive effort, expressed as the percentage of body mass lost over the breeding season, has been correlated with level of dominance and reproductive success among northern elephant seal, *Mirounga angustirostris*, males (Deutsch *et al.* 1990, 1994), and with size and reproductive activity among Weddell seals, *Leptonychotes weddellii* (Bartsh *et al.* 1992) and grey seals, *Halichoerus grypus* (Anderson & Fedak 1985). Dominance is affected by male size among northern elephant seals (Haley *et al.* 1994) and is correlated with size and age among southern elephant seals (Jones 1981, McCann 1981, Modig 1996), while both the rate of mass loss and total mass loss in breeding elephant seal males is much larger and more variable than in lactating females (Fedak *et al.* 1994). Thus, levels of energy expenditure during the breeding season, as a function of activity level and duration of fasting, affect the nutritional status of post-breeding males and most likely ultimately determine the timing of the moult of adult males by influencing the duration of the pre-moult pelagic phase. The mechanism whereby the nutritional status of an animal may influence the timing of the moult haulout is through hormonal inhibition of pelage growth, either through the thyroid system as a feedback mechanism, or through nutritional stress inducing secretion of adrenal hormones, or both (Ling 1965, 1970, 1972). Stewart (1989) showed that increased energy requirements necessitate longer pre-moult pelagic phases among northern elephant seals, where females that reared their pups successfully, thus using a greater amount of their energy reserves than those whose pups died, remained at sea significantly longer than the unsuccessful females.

Moulting males (immature)

The age-related progressively later moult of immature males found in this study contrasts with the findings of Carrick *et al.* (1962*b*), who found no evidence of any tendency to moult later with age among immature animals (using individual records of marked animals). The timing of moulting among immature males may also be affected by nutritional status and/or androgen levels of males. Puberty is delayed among elephant seals (Boyd 1991), but may be attained some years before sexual maturity (Laws 1956*a*, McCann 1985) as defined in this study. Once puberty has been attained, peak plasma testosterone concentrations increase with each successive breeding season until sexual maturity is reached (Bartsh *et al.* 1992, Lincoln 1998), and testosterone-induced inhibition of pelage growth may affect the time of moulting of pubescent, sexually immature males. However, this on its own does not explain the age-related differences in the timing of moulting of sexually immature, non-pubescent males (one- to three-year-olds).

Absolute energy requirements of animals increase with size, and despite the fact that mass-specific energy requirements decrease with size (Schmidt-Nielsen 1975), and hence with age of growing pinnipeds (Miller & Irving 1975, Doidge & Croxall 1985, Thompson *et al.* 1987), the overall energy expenditure associated with foraging (including heat increments of locomotion and feeding, assimilation efficiency and duration of foraging) by individual male southern elephant seals has been shown to increase with age (Boyd *et al.* 1994). Thus, as males age, they may take longer to fulfil their energy requirements, contributing to the age-related delay in the moult of immature males. The fact that moulting five-year-old males (pre-breeding) that were present during the subsequent breeding season moulted significantly earlier than males of the same age that were not observed in the subsequent breeding season (laggards), is interesting. There is no evidence to suggest that pre-breeding males are more sexually mature than laggards at the time of moulting, but if males which fulfil their nutritional requirements earliest are the first in their age-class to haul out to moult, it would appear that foraging efficiency determines whether or not males negotiate the breeding season in their sixth year. Males that complete their moult soonest have more time at their disposal to fatten up before the subsequent resting and breeding periods.

Breeding females

The early mean breeding haulout of three-year-old females, which are all primiparous, corresponds with the findings of Laws (1956*a*) and McCann (1982*b*), who found primiparous females to be among the first to pup at South Georgia. At Macquarie Island, pup birth weight increased as the breeding season progressed (Carrick *et al.* 1962*a*), possibly due to pup size being correlated with maternal size, and hence age (McCann 1982*b*), which indicates that younger, smaller females may pup earlier in the season there. Wilkinson (1992), however, found the timing of the breeding female haulout at Marion Island to be independent of age, using study animals that were subjectively aged according to facial colouring and neck scarring, while Arnbom *et al.*

(1997) found no relationship between the postpartum mass of mothers and parturition date at South Georgia.

Possible explanations for the earlier mean haulout date of breeding three-year-old females in this study, are: (a) if, as Carrick *et al.* (1962*a*) suggested, females unsuccessful in weaning a pup come into oestrus earlier than other females, and consequently return to sea sooner, on average, than successful females, lower weaning success rates among primiparous females may affect their mean haulout date, (b) females may improve the timing of hauling out with experience (Carrick *et al.* 1962*b*, Boyd 1996), (c) gestation length may vary with maternal age and size (Boyd & McCann 1989, Trites 1991), and (d) implantation may occur earlier among primigravid females. These possibilities are discussed below.

Wilkinson (1992) found that older, larger females weaned a greater proportion of their pups than did younger, smaller females, although the differences were not significant, and Huber (1987) found that the weaning success of primiparous three-year-old northern elephant seal females was significantly lower than that of primiparous four- and five-year-old females. However, pre-weaning mortality at Marion Island is low (4 % for all pups, of tagged and untagged females, during 1990-1996; Pistorius *et al.* 1999), and considering that only 34 % of breeding females observed from 1991 to 1996 had tags (S.P. Kirkman unpubl. data, data for 1990 unavailable), and only tagged individuals are pertinent to this study, the effect of pup mortality on the mean haulout dates of known-age-classes is likely to be negligible. Furthermore, Boyd (1991) found no evidence to indicate that loss of suckling time advances the timing of oestrus in southern elephant seals.

Very early or late pups may not achieve nutritional independence at a favorable time with respect to available marine resources (McCann 1982*b*), but if the timing of hauling out by breeding females improves with age, one would expect the standard deviations of the age-specific haulout distributions to decrease with age, but they do not in this study. Active gestation, the time period between implantation and parturition (Boyd 1991), may be affected by age and/or maternal mass in Antarctic fur seals, *Arctocephalus gazella*, and northern fur seals, *Callorhinus ursinus*, (Boyd & McCann 1989, Trites 1991), but primiparous females of these species have been shown to give birth later, on average, than multiparous females (Trites 1991, Lunn *et al.* 1994), in contrast to elephant seal females in this study.

The breeding component of the southern elephant seal's annual cycle is synchronized ultimately through selection for reproductive success (Carrick *et al.* 1962*b*, Boyd 1991) in the predictable but seasonally changeable subantarctic and Antarctic environments. Reproduction among pinnipeds is characterised by delayed implantation of three months or more after fertilisation, among southern elephant seals (Gibbney 1957, Carrick *et al.* 1962*b*, Boyd 1991, Bonner 1994). Changing day length (photoperiod) is believed to be the most important proximate environmental factor regulating the annual temporal consistency that is characteristic of pinnipeds breeding at high latitudes (Carrick *et al.* 1962*b*, Griffiths & Bryden 1981, Temte 1985, 1994, Boyd 1991, 1996, York & Scheffer 1997), by stimulating the reactivation of the reproductive system and implantation (Boyd 1991, Bester 1995), and synchronizing the timing of parturition (Temte 1985, Boyd 1991, Trites 1991). However, it seems probable that there is some flexibility in the timing of implantation (Boyd 1991). Among grey seals, implantation is associated with an increase in the body condition of the females (Boyd 1984), among northern fur seals, *Callorhinus ursinus*, implantation occurs earlier among older, larger females (York & Scheffer 1997), while timing of parturition is earlier among older, heavier Antarctic fur seals, and northern elephant seals (Reiter *et al.* 1981, Boyd *et al.* 1990, Lunn *et al.* 1994, Boyd 1996), and generally later among

Antarctic fur seals in years with reduced food availability (Boyd 1996). Thus, female condition may play an important secondary role in the timing of implantation.

Moulting females

Among southern elephant seals, implantation is thought to occur after the completion of moulting (Laws 1956*b*, Carrick *et al.* 1962*b*, Ling 1970). Assuming that reactivation of the reproductive system is influenced by the timing of the onset of the post-moult pelagic phase and/or the physical condition of the female, in conjunction with photoperiod, it is likely that implantation would on average occur first among primigravid southern elephant seals, which moult significantly earlier than parous females, and consequently return to sea earlier and regain condition sooner. Thus, earlier implantation among primigravid females could contribute to the slightly earlier mean breeding haulout time of primiparous females.

Moulting among fur seals is a much more gradual, less obtrusive affair than that of elephant seals (King 1983, Bonner 1994), and being on land is not a prerequisite, as evidenced by lactating females that moult and forage concurrently (Bester 1981). Grey seals are also not nearly as wholly terrestrial when moulting as elephant seals (Bonner 1981), in which the moult is hastened by shedding large sheets of cornified epidermis along with hair (Ling 1970). Thus, any age-related temporal differences in the timing of moulting among northern fur seals, Antarctic fur seals and grey seals are less likely to influence the timing of implantation by affecting physical condition at optimum photoperiodicity, than among elephant seals. Among northern elephant seals, the only congeneric of the southern species, older, heavier females give birth earlier in the season (Reiter *et al.* 1981). However, the duration of the moulting seasons of northern elephant seal adult and subadult females are longer than those of the southern species (Le Boeuf & Laws

1994), and there seems to be little temporal separation of moulting between adult and immature females (Riedman 1990, Le Boeuf & Laws 1994), with adult females, on average, hauling out a little before immature females (Odell 1974). This is in contradiction to the southern species at Marion Island, where the mean moulting haulout dates of parous females are approximately 15 and 30 days later than the mean moulting haulout dates of nulliparous and nulligravid females, respectively. Postponement of the moult among parturient females has also been documented for the Hawaiian monk seal, *Monachus schauinslandi* (Johanos *et al.* 1994).

The uniformity of moulting between adult female age-classes found in the present study contrasts with the suggestion of Carrick *et al.* (1962*b*) that adult females moult progressively later each year, and there was no evidence of inter-annual variation in the peak of female haulouts, as found by Carrick *et al.* (1962*b*) and Hindell & Burton (1988). Ling (1965, 1970, 1972) proposed that the apparently inhibitory effects of oestrogen on hair growth, cause a delay in the moult of reproductive females, and Condy (1979) suggested that the synchronisation of events during the breeding female haulout resulted in a relatively uniform decline in the levels of inhibitory oestrogens among females, thus contributing to the equally well synchronised timing of the female moult. Differences in post-lactating female masses do not seem to affect the duration of the pre-moult pelagic phase (Carlini *et al.* 1997). This is probably due to the fact that although absolute mass loss by elephant seal females during lactation has been found to increase with size (McCann *et al.* 1989, Deutsch *et al.* 1994, Fedak *et al.* 1996, Carlini *et al.* 1997) and age (Deutsch *et al.* 1994) of females, the percentage of body mass lost over lactation has been shown to be independent of size (Deutsch *et al.* 1994, Fedak *et al.* 1996) or age (Deutsch *et al.* 1994), implying that the proportion of body mass that needs to be recovered before females can haul out to moult would vary little between females of different ages and sizes.

The staggered moulting sequence of non-pregnant and pregnant nulliparous females contrasts with Gibbney's (1957) and Carrick *et al.*'s (1962*b*) opinion that primigravid females moult at the same time as other immatures. On average, two- and three-year-old females moult later than males of the same age. Two-year-old females, as well as nulliparous three-year-old females, include individuals that have been fertilised for the first time. Virgin females are almost certainly mated at sea, as there is little or no evidence of them being attendant in harems (Laws 1956*a*, 1956*b*, Carrick *et al.* 1962*a*, Wilkinson 1992, S.P. Kirkman pers. obs.). Hair growth in these primigravid females is probably restrained for a period due to an increase in oestrogen levels, causing them to moult later than non-pregnant females of the same age, but as they do not suffer the levels of nutritional stress incurred by fasting and lactation, their mean moulting haulout date is significantly earlier than that of females that reared pups in the preceding breeding season.

The relatively high standard deviations of the moulting haulout distributions of females aged two to six years, and especially three-year-old and four-year-old females, reflect the heterogenous nature of these groups. Two-year-old females include nulligravid and primigravid animals, three-year-olds include these and primiparous females, some four-year-olds are already multiparous, while some five-year-old and six-year-old females are still primiparous. After being separated into sub-classes according to their sexual status, it is interesting that the standard deviations of the moulting haulout distributions of nulligravid and primigravid two-year-old females, as well as nulliparous two-, three- and four-year-old females were still relatively high. The fact that the nulliparous three- and four-year-old groups are still not entirely homogenous with regard to sexual status, as they contain both pregnant and non-pregnant females, may contribute to this, as could the chance that females which gave birth at another location were incorrectly sub-classified regarding their sexual status (see Methods). However, the moulting haulout of immature females (mean = 44.2 days) was found to be much longer than that of mature females (mean = 29.0 days) at Macquarie Island (Ling & Bryden 1981). Thus, it is possible that longer moulting haulouts of immature females also contributed to the large standard deviations of these sub-classes.

Assuming that the duration of the moulting haulouts are similar to those observed at Macquarie Island (Ling & Bryden 1981), immature females in the present study would nevertheless depart for their post-moult pelagic phase earlier, on average than adult females. By applying the average total haulout durations documented for immature and mature females at Macquarie Island (Ling & Bryden 1981) to the estimated peaks of primigravid two-year-old females and adult females aged four and over at Marion Island (this study), primigravid females are found to complete their moulting haulout on average, around January 15, compared to January 28 in adult females. Thus, despite possible longer moulting haulout periods, females pregnant for the first time return to sea earlier, on average, than multigravid females, supporting the case for them gaining condition sooner, and implanting earlier.

While it is widely accepted that among pinnipeds, younger females, and females in poorer condition, conceive, implant or give birth later than older and larger conspecifics (Reiter *et al.* 1981, Bigg 1984, Boyd 1984, 1996, Lunn *et al.* 1994, York & Scheffer 1997), the timing of the events within the annual cycle of female southern elephant seals, particularly the delay in moulting among parturient females relative to primigravid females, appear conducive to implantation occurring earlier among the latter than among more experienced females, resulting in the relatively early mean breeding haulout date of primiparous females, found in this study.

CHAPTER 5

THE RESTING HAULOUT

5.1 Introduction

The resting haulout phase occurs in between the moulting and breeding phases of southern elephant seals, and may last from a few days at a time up to several weeks (Carrick *et al.* 1962*b*). Resting haulout is characteristic of immature southern elephant seals of both sexes, and is virtually replaced by attendance during the breeding season in later years (Carrick *et al.* 1962*b*), although adult males (Hindell & Burton 1988) and females (Laws 1956*b*, Gibbney 1957, Carrick *et al.* 1962*b*) have also been observed to haul out on rare occasions for no obvious reason between the moulting and breeding seasons.

The resting haulouts of elephant seals at Marion Island and Macquarie Island appear to be broadly similar: subadults, yearlings and underyearlings begin hauling out during February and March, and their numbers ashore decline during August when breeding bulls return for the breeding season. Very few immature animals remain by September (Carrick *et al.* 1962*b*, Condy 1979). The situation appears to be different at haulout sites to the south of the Antarctic Polar Front. At Heard Island and the non-breeding colony at the Vestfold Hills (Antarctica), sightings of elephant seals in winter are rare after June (Laws 1956*a*, Carrick *et al.* 1962*b*, Gales & Burton 1988), and although data on the autumn-winter haulout at South Georgia and the South Orkney Islands are limited, they seem to confirm that resting also occurs earlier there than at Macquarie Island or Marion Island (Laws 1956*a*), probably owing to lower air tempertatures and/or the presence of pack ice in winter (Le Boeuf & Laws 1994). The resting haulout is also characteristic of the seasonal cycle of immature northern elephant seals, but is referred to as the "fall" haulout by researchers of this species (Odell 1974, Stewart & Yochem 1984, Le Boeuf & Laws 1994).

Most resting animals at Macquarie Island, Heard Island and the Vestfold Hills have been reported to be in good condition (Carrick *et al.* 1962*b*, Burton 1985, Gales & Burton 1988), and it has been proposed that this terrestrial phase is optional (Carrick *et al.* 1962*b*). However, despite suggestions that have been put forward, no specific function has yet been ascribed to the resting haulout (Carrick *et al.* 1962*b*, Condy 1979, Ling & Bryden 1981, Burton 1985, Hindell & Burton 1988, Bell *et al.* 1997), the terrestrial phase that has been least regarded in previous studies concerning the seasonal haulout cycle of southern elephant seals.

An increased understanding of the effects of age, sex and sexual status on the degree and timing of participation in the resting haulout could provide clues to the function(s) of this haulout phase, but as of yet, no studies have shown quantifiable variation in age- and sex-specific participation and timing in the resting haulout. Thus, the aims of this chapter are to investigate:

(a) the effects of age, sex and sexual status on the timing of the resting haulout, and

(b) the effects of age, sex and sexual status on the level of participation in the resting haulout.

5.2 Results

Age- and sex- specific temporal resting haulout parameters calculated for each year of the study period are shown in Appendix III. There was much less consistency in mean resting haulout dates between years than there was in the timing of moulting by the same age- and sex-classes (see Appendix II), and the large standard deviations of temporal haulout distributions of age- and sex-classes show that the resting haulout is relatively non-synchronised. However, the skewness in the temporal haulout distributions of yearling females, and particularly yearling males (evidenced by large differences in the mean and median haulout dates), was apparent in every year from 1990 to 1997.

The haulout parameters of resting males (from underyearlings to six-year-olds), resting males and females (from underyearlings to three-year-olds), and resting sub-classes of two-year-old females and five-year-old males, are given in Tables 8-11, respectively. Box-and-whisker plots depict the temporal haulout distributions of the resting male and female age-classes (Figure 14), and sub-classes (Figure 15). In the figures, ■ represents the mean haulout day, horizontal lines represent, from the bottom: 1st quartile, median haulout day and 3rd quartile, respectively, and error bars depict the range of observations about the mean haulout day.

According to Levene's test (with 95% confidence limits), the variances in the distribution of observations between (a) the age-classes of resting male underyearlings to six-year-olds ($F_{6,5475} = 146.38$, $P < 0.0001$), (b) age- and sex-classes of resting male and female underyearlings to three-year-olds (age, $F_{3,7721} = 66.74$, $P < 0.0001$; sex, $F_{1,7721} = 61.44$, $P < 0.0001$; interaction, $F_{3,7721} = 29.37$, $P < 0.0001$), and (c) resting nulligravid and primigravid females ($F_{1,268} = 8.75$, $P < 0.05$) were not homogenous, and individual observations were thus weighted with the inverse of the standard deviation of their specific class. The variances in the distribution of observations between resting laggard and pre-breeding five-year-old males were homogenous at 95% confidence limits ($F_{1,194} = 0.87$, $P > 0.05$).

Significant variation was found among resting male underyearlings to six-year-olds ($F_{6,5475} = 30.32$, $P < 0.0001$), where the mean resting haulout date of yearling males was significantly earlier than that of two-year-old males, both of which rested significantly earlier than the other

Table 8. Temporal resting haulout parameters based on the total number of observations of marked underyearling to six-year-old males resighted over the sampling period 1990-1997. [Means with the same superscripts are not significantly different to each other at 95% confidence levels].

Age (years)	*n*	Mean haulout date	S. D. (± days)
<1	1103	1 June^{a}	49.7
1	1659	16 May^{b}	60.9
2	1069	25 May^{c}	47.2
3	780	7 June^{a}	40.7
4	485	7 June^{a}	34.6
5	264	8 June^{a}	30.2
6	122	1 June^{ac}	31.4

Table 9. Temporal resting haulout parameters based on the total number of observations of marked underyearling to three- and six-year-old females and males, respectively, resighted over the sampling period 1990-1997. [Means with the same superscripts are not significantly different to each other at 95% confidence levels].

Sex	Age-class (years)	*n*	Mean haulout date	S. D. (± days)
Male	<1	1103	1 June^{ab}	49.7
	1	1659	16 May^{c}	60.9
	2	1069	25 May^{b}	47.2
	3	780	7 June^{d}	40.7
Female	<1	1120	30 May^{ab}	44.7
	1	1329	30 April^{e}	47.2
	2	598	1 June^{a}	38.9
	3	71	7 June^{abd}	41.2

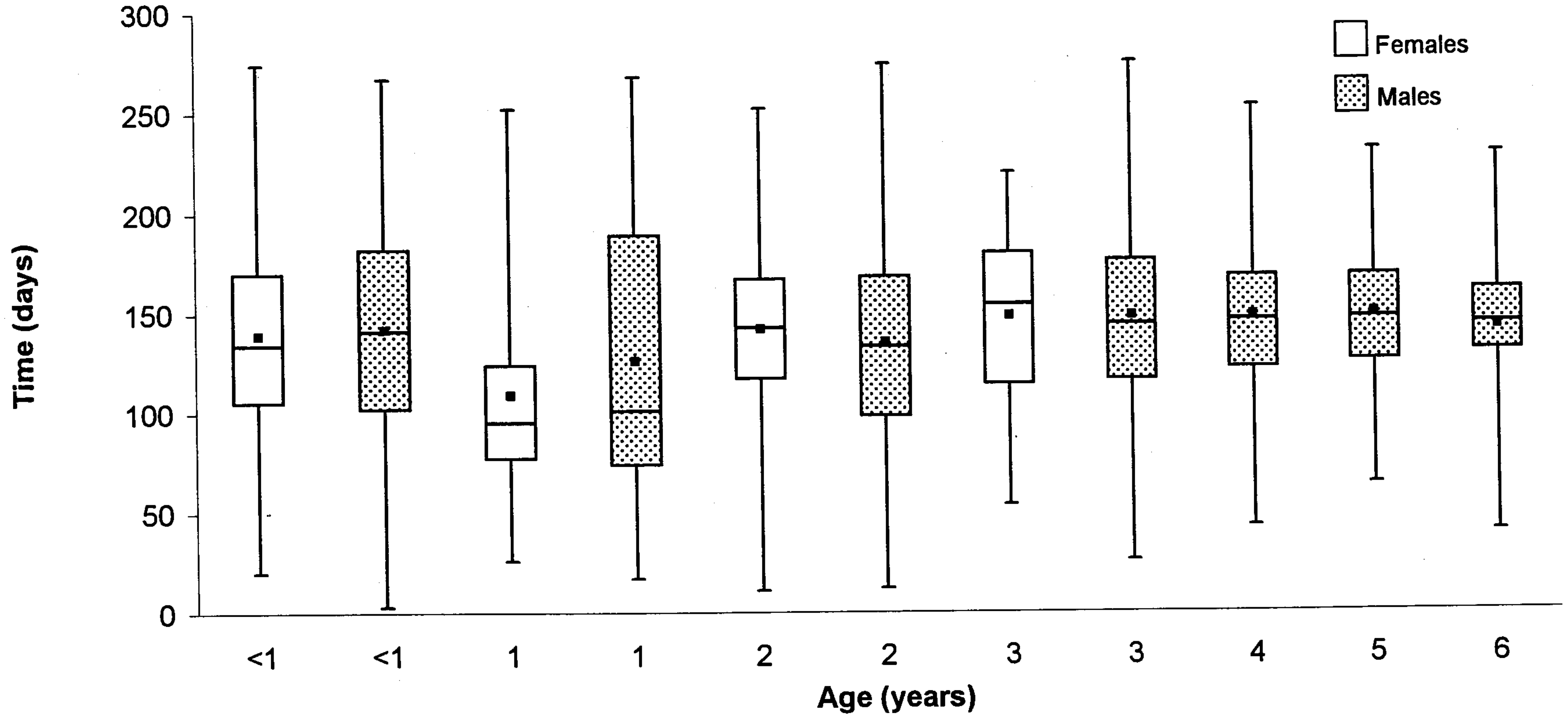

Figure 14. Haulout distributions of resting males and females, from underyearlings to six- and three-year-olds, respectively, for the period 1990-1997.

Table 10. Temporal resting haulout parameters based on the total number of observations of laggard and pre-breeding five-year-old males resighted over the sampling period 1990-1997 [Means with the same superscript are not significantly different to each other at 95% confidence levels].

Sexual status	***n***	**Mean haulout date**	**S. D. (± days)**
Laggard	133	17 June^{a}	27.2
Pre-breeding	63	27 May^{a}	25.9

Table 11. Temporal resting haulout parameters based on the total number of observations of nulligravid and primigravid two-year-old females resighted over the sampling period 1990-1997 [Means with the same superscript are not significantly different to each other at 95% confidence levels].

Sexual status	***n***	**Mean haulout date**	**S. D. (± days)**
Nulligravid	232	3 June^{a}	35.0
Primigravid	38	19 May^{b}	55.6

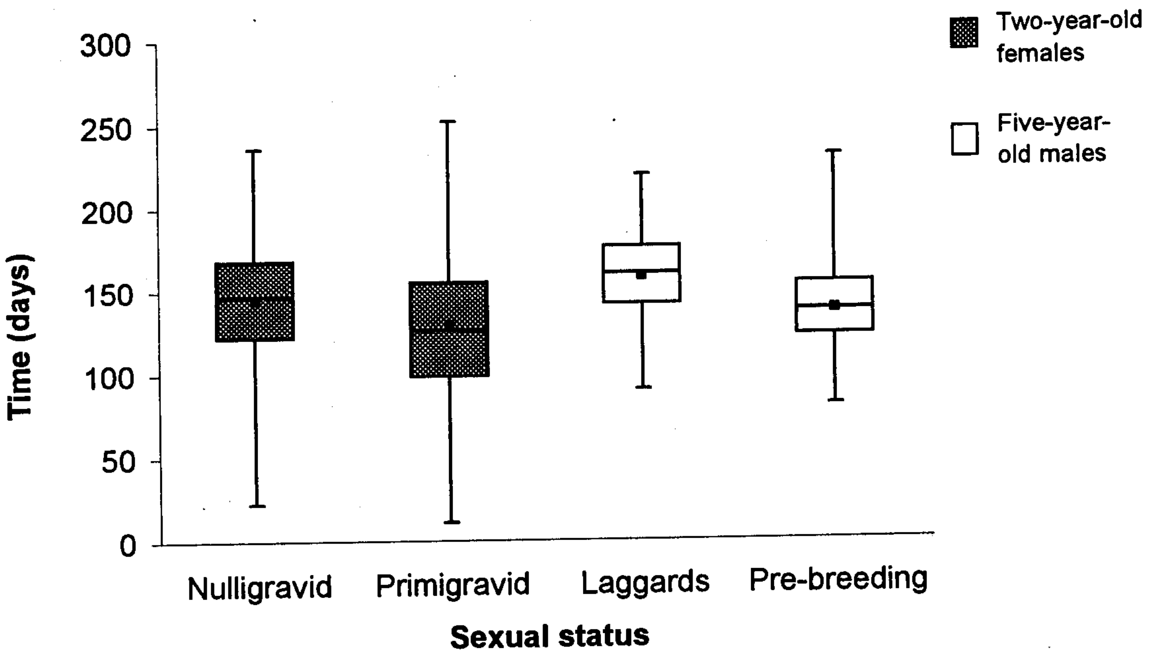

Figure 15. Resting haulout parameters of two-year-old females and five-year-old males, of differing sexual status, for the period 1990-1997.

male age-classes. Variation in the timing of resting by male and female underyearlings to three-year-olds resulted from differences between age-classes, rather than between the genders, although the effects of age and sex were found to be interactive (age, $F_{3,7721} = 125.34$, $P < 0.0001$; sex, $F_{1,7721} = 3.44$, $P > 0.05$; interaction, $F_{3,7721} = 22.79$, $P < 0.0001$; Figure 14). Among the sub-classes of five-year-old males, pre-breeding males rested significantly earlier than laggards ($F_{1,194} = 25.55$, $P < 0.0001$), but participation in the resting haulout between these two sub-classes was equal (Fisher's Exact Test, $P > 0.05$; $\omega = 1.07{:}1$, 95% confidence limits 0.45-2.61). Differences in the timing of moulting between nulligravid and primigravid resting two-year-old females were not significant ($F_{1,268} = 3.65$, $P > 0.05$), but this may have been affected by the low sample size of the latter, as primigravid females were significantly less inclined to rest (Fisher's Exact Test, $P < 0.0001$; $\omega = 4.40{:}1$, 95% confidence limits 2.73-7.88).

Participation in the resting haulout by distinctive age- and sex-classes was generally consistent between years during 1990 to 1995 (Table 12), except among underyearling females (a lower proportion hauled out to rest during 1993 than in other years), underyearling males (lower proportions hauled out on two or more occasions during the autumn-winter seasons of 1990 and 1995 than in the intervening years), and five-year-old males (a smaller fraction rested in 1990 than in the other years). Data from the years 1990-1995 were pooled for each class to investigate the effects of age and sex on participation levels, but results should be interpreted with the inconsistency between years among the above-mentioned age- and sex-classes in mind.

Overall (Figure 16), the proportion of male underyearlings to six-year-olds participating in the resting haulout varied with age ($\chi^2 = 40.03$, df = 6, $P < 0.0001$), as did the proportions that hauled out twice or more times during an autumn-winter period ($\chi^2 = 81.70$, df = 6, $P < 0.0001$).

Table 12. Results of chi-square tests (95% confidence limits and degrees of freedom =5) investigating homogeneity in the age- and sex-specific level of participation in the resting haulout between years, during 1990 to 1995. The first test for each age- and sex-class compared the differences in annual proportions of individuals that were observed to rest. The second test compared the differences in annual proportions of individuals that were observed to rest on at least two occasions. Results showing significant differences in the levels of participation between years are depicted by an asterisk. Negligible numbers of six-year-old males and three-year-old females hauled out to rest on more than one occasion in a season.

Sex	**Age class**	**χ^2 Statistic**		***P*-value**	
		Test 1	**Test 2**	**Test 1**	**Test 2**
Male	<1	7.03	13.00	0.219	0.023*
	1	9.57	6.00	0.089	0.306
	2	6.10	7.08	0.296	0.215
	3	6.29	8.30	0.279	0.141
	4	6.65	3.92	0.248	0.562
	5	11.20	4.36	0.048*	0.500
	6	9.08	-	0.106	-
Female	<1	13.71	3.12	0.018*	0.682
	1	9.57	6.00	0.089	0.306
	2	7.91	6.42	0.162	0.267
	3	10.58	-	0.060	-

Table 13. Sex-related variation in participation levels between age-classes expressed as odds ratios (ω). Significant differences between sexes in the proportions of animals resting, according to Fisher's Exact Tests (95 % confidence limits), are denoted by an asterisk. *N* represents the total number of males and females of each age-class known to be surviving at the time of the haulout.

Age-class (years)	***n***	ω^1	**95 % confidence limits of ω^1**	ω^2	**95 % confidence limits of ω^2**
<1	1396	0.98:1.00	0.80-1.21	1.43:1.00*	1.00-2.03
1	1277	1.49:1.00*	1.16-1.90	2.97:1.00*	2.10-4.19
2	951	3.30:1.00*	2.51-4.30	6.07:1.00*	2.81-13.09
3	700	26.32:1.00*	16.47-42.08	-	-

[1] The proportion of surviving males to surviving females that hauled out to rest on at least one occasion during the year.

[2] The proportion of surviving males to surviving females that hauled out to rest on two or more occasions during the year.

Yearling males were more inclined to haul out on one or more occasions than other male age-classes. Males were less likely to rest more than once a year as they grew older ($\chi^2 = 48.08$, df = 1, $P < 0.0001$), but the proportion of males foregoing the resting haulout altogether did not increase significantly from their first year (underyearlings) up to age six ($\chi^2 = 0.86$, df = 1, $P > 0.05$), despite the fact that six-year-old males were the only male age-class of which less than half of the surviving component individuals rested. Disregarding underyearlings, of which a significantly smaller fraction were observed to rest than yearlings (Fisher's Exact Test, $P < 0.0001$, $\omega = 1.98:1$, 95% confidence limits 1.56-2.53) and six-year-olds, there was a significant decline in the proportions of males participating in the rest from age one to five ($\chi^2 = 12.40$, df = 1, $P < 0.05$).

Age-related differences (Figure 17) were also found in the proportion of female underyearlings to three-year-olds that hauled out to rest ($\chi^2 = 390.10$, df = 3, $P < 0.0001$) and the fraction thereof that rested twice or more times per annum ($\chi^2 = 22.42$, df = 3, $P < 0.0001$), with yearling females more inclined to rest than any other age-class. Generally, the proportion of females resting more than once a year declined with age ($\chi^2 = 17.14$, df = 1, $P < 0.0001$), and females were increasingly inclined to forego the resting haulout altogether as they got older ($\chi^2 = 293.60$, df = 1, $P < 0.0001$), although a significantly greater fraction of yearlings than underyearlings were observed to rest (Fisher's Exact Test, $P < 0.05$; $\omega = 1.32:1$, 95% confidence limits 1.06-1.63).

Participation behavior between underyearlings of each sex was relatively similar, but sex-related variation in participation among age-classes were increasingly apparent with ascending age

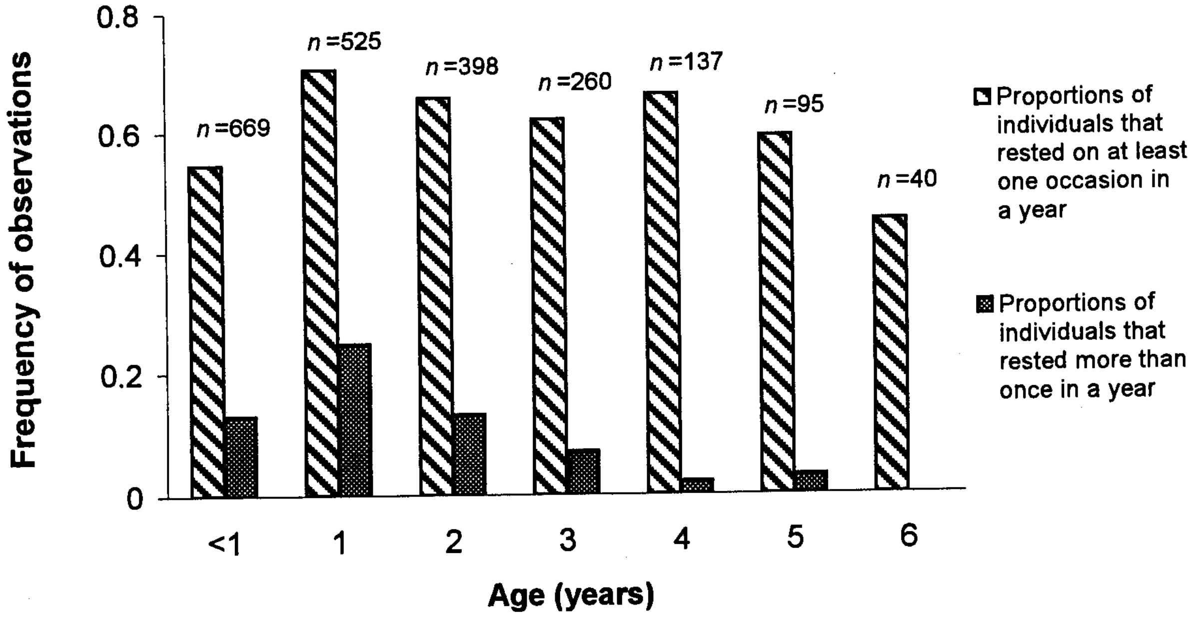

Figure 16. Age-specific participation in the resting haulout by males, from underyearlings to age six, for the period 1990-1995. *N* represents the number of surviving individuals in each age-class

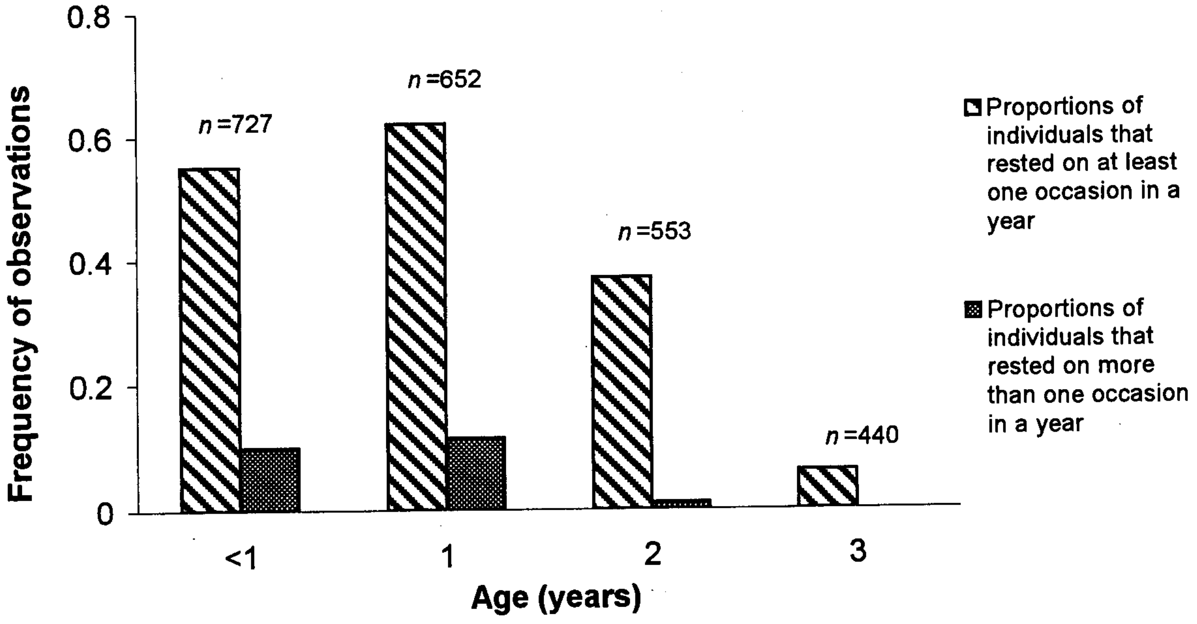

Figure 17. Age-specific participation in the resting haulout by females, from underyearlings to age three, for the period 1990-1995. *N* represents the number of surviving individuals in each age-class

(Table 13), and negligible numbers of three-year-old females were observed to rest two or more times during the year.

5.3 Discussion

The low levels of consistency in the inter-annual timing of resting by immature age- and sex-classes, when compared to the moulting haulouts of these groups, is consistent with the finding of Carrick *et al.* (1962*b*) that the seasonal timing of resting is less co-ordinated than that of the other haulout types. This result may prevent reliable conclusions as to age- and sex-specific differences in resting haulout parameters pooled over the 1990 to 1997 period. However, the earlier mean haulout dates and skewed temporal haulout distributions of yearlings of both gender, relative to other age- and sex-classes, as well as age- and sex-related differences in levels of participation in the resting haulout, are conspicuous, particularly as these findings were mostly consistent from year to year. The skewed temporal haulout distributions of yearlings of both sexes, particularly males, correspond with the findings of Condy (1979), who described a second peak in hauling out by yearlings at Marion Island during autumn-winter. The larger fraction of yearlings hauling out for more than one resting bout in a year, relative to other age-classes of matching gender, contributes to this phenomenon.

Given the tendency of immature southern elephant seals also to haul out at sites other than their birth site (Burton 1985, Bester 1988, 1989, Wilkinson & Bester 1990, Guinet *et al.* 1992, Lewis *et al.* 1996), the fact that over half of the surviving animals of each immature male age-class, from underyearlings to five-year-olds, were observed to rest at Marion Island, seems to attest to the importance of this haulout phase in the life cycle of the species. In the breeding season, dominance and mating success of elephant seal males are affected by size (McCann 1981, Haley *et al.* 1994, Modig 1996), and feeding efficiency naturally influences size, and hence reproductive success. Therefore, the fact that at least over half the pre-breeding five-year-old males at Marion Island do not forego resting prior to hauling out for breeding purposes at age six, indicates that the fitness benefits associated with the autumn-winter haulout of immature elephant seals may outweigh the costs of spatial separation from foraging areas, even at an age associated with increased food requirements and rapid secondary growth in males (Ling & Bryden 1981, Laws 1984). This is also supported by the fact that at least 21 % of primigravid two-year-old females hauled to rest, at a time when they would have a paramount need to conserve energy (Ling & Bryden 1981).

Bell *et al.* (1997) suggested that, as the term implies, elephant seals may simply require physical rest at times. However, immature animals, including underyearlings, are known to forage at considerable distances from land (Le Boeuf *et al.* 1993, Slip *et al.* 1997), and it is doubtful whether a need for rest would necessitate movement of hundreds of kilometres to land by one of the most poorly adapted pinnipeds for a terrestrial habitat (see Carrick *et al.* 1962, Ling 1969), only to incur the energetic costs of fasting, terrestrial locomotion and thermoregulation.

With deference to juvenile harbour seals that foraged nocturnally and hauled out on a daily basis, Thompson (1993) postulated that the presence of aquatic predators could favour shore visits whenever seals are not actively foraging. Elephant seals that can afford to forego foraging for periods of time and haul out on land may reduce the number of days of the annual cycle that they are exposed to predation. It follows that if there was a need for a protracted period of physical rest it would be safer to fulfil the requirement out of reach of predators. Southern elephant seals have only one major pelagic predator, the killer whale, *Orcinus orca* (Ling &

Bryden 1981). Predation by killer whales on weaned pups and older animals have been recorded at Marion Island (Condy 1978, Condy *et al.* 1978), Îles Crozet (Guinet 1992, Guinet *et al.* 1992) and Península Valdés (Vergani & Stanganelli 1990). The impact killer whales have on elephant seals during their pelagic existence is uncertain, but as elephant seals, from an early age, dive deeply and continuously for long durations (over 90% of the time at sea is spent underwater), usually making rapid ascents and descents and spending little time (usually less than three minutes) at the surface in between dives (Hindell *et al.* 1991, Jonker & Bester 1994, Le Boeuf 1994, Slip *et al.* 1994, Campagna *et al.* 1995, Slip 1997), it follows that pelagic encounters between killer whales and elephant seals are likely to be opportunistic, and of less consequence than predation at or nearby haulout beaches. During autumn-winter, resting elephant seals are less removed from the water than during either the moulting or breeding phases (with the exception of the subordinate males in the breeding season), and commonly swim between beaches (Carrick *et al.* 1962, Condy *et al.* 1978, Bester & Wilkinson 1990) or swim and mock-fight in rock pools or shallow inshore areas (S.P. Kirkman pers. obs.). Killer whales are commonly sighted at Marion Island during March and April, and although sightings are much less common during the rest of winter than during the summer months (Condy *et al.* 1978), elephant seals expose themselves to encounters by venturing into shallow inshore areas (Guinet 1992), particularly as most killer whale sightings are within 100 m of the coast at Marion Island (Condy *et al.* 1978). Elephant seals thus by no means escape predation risk during their autumn-winter haulout periods, and whether the probability of encountering killer whales is lowered by resting, is debatable.

The essence of Burton's (1985) suggestion that avoidance of intraspecific competition with underyearlings and pregnant females, for the benefit of these groups, may bring about the haulout of subadult males during autumn-winter, is group selection, a concept which has been largely rejected as an evolutionary mechanism (Wiens 1966, Williams 1966). Moreover, underyearlings, the age-class with the highest rate of mortality among both elephant seal species (Laws 1960, Hindell 1991, Le Boeuf *et al.* 1994, Pistorius *et al.* 1999), commonly haul out during autumn-winter (Carrick *et al.* 1962, Hindell & Burton 1988, Wilkinson & Bester 1990, Le Boeuf & Laws 1994, this study). By hauling out themselves, underyearlings do not stand to gain from reduced competition for food resulting from resting by subadult males, particularly as their period of haulout was found to overlap with all other immature age-classes in the present study.

The theory of Carrick *et al.* (1962) that the resting haulout constitutes a training period for the lengthy and demanding terrestrial activities of adults, remains perhaps the most plausible explanation for the occurrence of this terrestrial phase. The extreme levels of sexual dimorphism, polygyny and fasting that characterize the breeding season of elephant seals, involve risks to both males and females, including: (a) fitness-reducing or life-threatening injuries (Deutsch *et al.* 1994), (b) mother and pup separation, due to, amongst other factors, male activity, agonistic encounters between females, and exclusion of lower ranked females and their pups from areas in the harem that are less prone to disruption (Le Boeuf & Laws 1994), and (c) inability to regain condition following the depletion of reserves after fasting and breeding activity (Haley *et al.* 1994). As size and physical condition are important in negotiating these risks, they contribute to reproductive success of both males and females (Laws 1956*a*, McCann 1981, 1982, Wilkinson 1992, Haley *et al.* 1994, Modig 1996). The significance of the earlier resting haulout, and concomitant longer pre-breeding pelagic phase of pre-breeding five-year-old males, may therefore be in maximising energy intake, thus enhancing size, physical condition and energy reserves. Nevertheless, apart from the obvious benefits of enhanced size and condition, individuals that are most competent and confident with a terrestrial existence, in terms of their efficiency at conserving and utilising energy reserves (Carrick *et al.* 1962), their locomotory capability (Carrick *et al.* 1962), and, among males, their adeptness at fighting and mating (Burton 1985), would no doubt have an advantage over less proficient individuals. It is feasible that elephant seals may be faced with a trade-off between maximising their time spent foraging, and gaining valuable experience at terrestrial functioning, in their immature years. Hence (a) the relatively high levels of resting participation among all immature age-classes at Marion Island, including the sub-class of pre-breeding males, (b) the fact that animals apparently not in optimum physical condition haul out during autumn-winter (Condy 1979, Bell *et al.* 1997), and (c) some primigravid females do not forego resting prior to giving birth.

The observation that a smaller fraction of male and female underyearlings hauled out to rest, on one or more occasions, than yearlings of matching gender, corresponds with the finding of Carrick *et al.* (1962) during autumn-winter at Macquarie Island. If resting among underyearlings is characteristic of animals in good condition, their relative scarcity may be due to their poorer feeding efficiency relative to other age-classes (Carrick *et al.* 1962). However, Carrick *et al.* (1962) found underyearlings to be the only age-class that included noticeably sick animals during autumn-winter, and emaciated resting underyearlings are also sighted at Marion Island, albeit only occasionally (S.P. Kirkman pers. obs.). Northern elephant seal underyearlings at Año Nuevo, California, were found to barely maintain their departure mass during their first foraging migration (Thorson & Le Boeuf 1994), despite similar trip durations to underyearlings at Macquarie Island (Le Boeuf *et al.* 1996, Bell *et al.* 1997) where they increase their body mass during the initial trip (Bell *et al.* 1997). The fact that underyearlings that returned to rest at Macquarie Island in autumn were generally lighter and in poorer condition than those that returned in mid- to late winter (Bell *et al.* 1997), indicates that nutritional status does not ultimately determine whether or not underyearlings haul out to rest, but may effect the timing, and possibly the duration, of the haulout.

The smaller fraction of underyearlings, relative to older immature age-classes, that were observed to rest in this study, may rather be explained by the frequent haulout of underyearlings born at Marion Island at other islands, during autumn-winter (Bester 1989, Wilkinson & Bester 1990). During their first pelagic phase, underyearlings of both elephant seal species have to travel large distances and forage without maternal guidance (Le Boeuf *et al.* 1996, Slip 1997), and the first movements may be random (or at least less directional than movements of more experienced animals) until reliable concentrations of food are located (Slip 1997). Many underyearlings may thus haul out at the first suitable haulout site that they encounter during their initial foraging excursion (Wilkinson & Bester 1990), or may forego resting, if no land is encountered. Indeed, while resightings of tagged northern elephant seal underyearlings suggest a similar migratory path to that of older animals of this species, several underyearlings have been sighted at aberrant haulout sites (Le Boeuf *et al.* 1996). Thus, the apparent increased tendency for yearlings of each gender to participate in the resting haulout, compared to underyearlings, may in fact represent an increased level of philopatry by this age-class. Le Boeuf (1994) found that northern elephant seal yearlings, when translocated from their resting site, showed strong homing behavior in returning to that site. Why the mean resting dates of male and female yearlings are so much earlier than those of other age- and sex-classes in this study is unclear, but it is consistent with findings at Macquarie Island (Carrick *et al.* 1962). Carrick *et al.* (1962) also reported that just less than one-fifth of resting immature animals at Macquarie Island hauled out for two separate resting bouts, at intervals of two or three months.

The decline in resting participation evident in female age-classes older than one year can be accounted for by the fact that pregnant females were much less inclined to rest than nulligravid individuals. Attendance during the preceding breeding season by some six-year-old males (this study) would explain why less than half of the surviving animals of this age-class hauled out to rest, as the onset of breeding largely replaces the resting haulout (Carrick *et al.* 1962). However, the tendency for diminishing fractions of males to rest, from age one to five years, although significant, was far less apparent than the reduction in the fractions of individuals of male age-classes that were observed to rest twice or more times in a season. Carrick *et al.* (1962) found the average duration of resting bouts to increase with age at Macquarie Island, and although measurements of haulout durations were beyond the scope of the present study, the apparent decline in the tendency to haul out for more than one resting bout in a year, with age, may be related to a concomitant increase in duration of single haulouts, with age, among immature males.

Considering the inter-annual consistency in participation levels by distinctive age- and sex-classes over the study period, not only in terms of the fractions of individuals that rested in a year, but in the fractions that rested on more than one occasion in a year, and the consistently earlier mean haulout dates of yearlings relative to other age-classes, it is apparent that the autumn-winter haulout constitutes more than simple random haulout events. It is possible that rather than representing an ancestrally retained terrestrial phase, the resting haulout has evolved for the function of furthering the animals' potential to successfully negotiate the energetically expensive and potentially hazardous breeding season.

CHAPTER 6

CONCLUSION

The principal contributions of this study to an understanding of the terrestrial cycle of southern elephant seals, are the quantification of (a) variation in the timing of each of the three haulout phases (breeding, moulting and resting), and (b) of levels of participation in the little understood resting haulout, that could be related to age, sex and sexual status. However, the study was based simply on recorded observations of known age individuals, and one can only postulate as to causes of similarities and differences in participation and timing, by relating the results to reproductive, physiological, behavioral and ecological findings of other studies, involving this and other elephant seal populations, as well as other pertinent species.

It is apparent that the three haulout phases are not exclusive events. The moult of mature males and females are postponed as a result of their reproductive activities, while the earlier mean moulting date of primigravid females relative to parous females, itself probably a product of primigravid females not having had to incur the costs of fasting and lactation in the preceding breeding season, may result in earlier implantation among these females, and concomitantly, a slightly earlier mean haulout date in the following breeding season, relative to multiparous females.

Reproductive activity also affects participation levels in the resting haulout phase: pregnancy, among females, and attendance during the breeding season, among males, significantly reduced the fractions of two- and six-year-old females and males that hauled out to rest, respectively. At least among five-year-old subadult males, there appears to be a relationship between temporal moulting and temporal resting behavior, with males that were attendant during the following breeding season (at age six) moulting and resting significantly earlier than those not observed to haul out for breeding purposes at age six. The significance of this is thought to be in maximising the length of the pelagic phase between the resting and the breeding phases, in order to maximise the intake of food.

Considering the inter-annual consistency in the levels of participation by distinctive age- and sex-classes in the resting haulout, and the consistently earlier haulout of yearlings relative to other age-classes, over the study period, it is apparent that the autumn-winter haulout represents more than simple random haulout events. It is conceivable that elephant seals are faced with a trade-off in their immature years, between maximising their time spent foraging, and gaining valuable experience at terrestrial functioning. Comparisons of survival and reproductive success rates between individuals showing unlike levels of participation in their immature years may elucidate whether resting attaches any fitness benefits to participating individuals, but it cannot be assumed that animals unsighted during an entire autumn-winter period did not haul out elsewhere, especially in view of the reduced levels of philopatry associated with the resting phase, relative to the breeding and moulting haulout phases. The present study would be complemented by research aimed at accurate quantification of age-, sex- and sexual status-related variation in the duration of haulouts by elephant seals. This would entail regular searches (daily or every second day), of accessible beaches and/or moulting areas favoured by elephants seals.

SUMMARY

The dearth of information on age- and sex-specific variation in temporal aspects of the terrestrial haulout cycle of southern elephant seals, prompted this study. The existence of known age data recorded from annual tagging and regular tag resightings of elephant seals at Marion Island, permitted an objective approach to the study of temporal haulout behavior, whereby the timing of haulouts by distinct age- and sex-classes, could be statistically described and compared, and changes therein related to growth and development observed. Furthermore, haulout records of known age animals during the autumn-winter period, permitted the investigation of age-, sex- and sexual status-related variation in levels of participation in the little understood resting haulout.

It was necessary to make a number of assumptions and to recognise certain limitations in the study, because (a) the sampling procedures at Marion Island were initiated primarily for purposes other than describing age- and sex-specific temporal haulout behavior, and (b) when interpreting variation between groups delineated according to their perceived sexual status, based on records of their observed reproductive activity at Marion island, or age-, sex- or sexual status-related variation in resting phase participation levels, based on records of presence or absence of individuals during autumn-winter, cognisance needed to be taken of the likelihood that many individuals tagged at Marion Island hauled out further afield than the study area during their lifetime. Attempts were made to explain causes of variation in timing and participation between classes or sub-classes, by relating the results to physiological, behavioral, reproductive and ecological findings of other studies, involving the Marion Island and/or other elephant seal populations, or other pertinent species.

Sex, age and sexual status were all found to affect the timing of moulting among both

male and female southern elephant seals. The timing of the adult female moult was found to be as uniform, if not more so, than the female breeding haulout. A relatively synchronous decline in oestrogen levels, and inconsiderable variation between adult female age-classes in the proportion of body mass that needs to be recovered during the pre-moult pelagic phase is thought to account for this. Oestrogen levels may be responsible for postponing the mean moulting haulout date of primigravid females relative to that of nulligravid females of the same age, but because primigravid females did not have to replenish the costs of lactation, their mean moulting date was significantly earlier than that of parous females. The fact that primigravid females moulted significantly earlier than parous females, may result in earlier implantation among them, and the observed earlier mean date of their breeding season haulout.

Males that were attendant during the breeding season moulted significantly later than those that were not observed hauled out at this time. Neuro-endocrine inhibition of hair growth may postpone the moult of mature males, thus preventing hair loss during the breeding season, but it is thought that the timing of their moult is ultimately determined by nutritional status, as a function of the age-affected levels of energy expenditure during the breeding season. The mean moulting haulout date of immature males was found to be postponed in a stepwise fashion, with age. The mechanism whereby this occurs is thought to function through growth-related increasing nutritional requirements with age, although testosterone activity may also affect the timing of moulting, at least among pubescent, immature males.

More than half of the surviving individuals of each immature age- and sex-class were observed to haul out to rest, and many individuals that went unsighted during autumn-winter periods were likely to have hauled up at other sites. Attendance during the breeding season by males, and pregnancy among females, resulted in declines in participation in the resting haulout at age six and age two, respectively. Considering the inter-annual consistency in the levels of participation by distinctive age- and sex-classes in the resting haulout, and the consistently earlier haulout of yearlings relative to other age-classes, over the study period, it is apparent that the autumn-winter haulout represents more than simple random haulout events. It is possible that elephant seals are faced with a trade-off in their immature years, between maximising their time spent foraging on the one hand, and gaining valuable experience at terrestrial functioning on the other.

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APPENDIX I

Table 14. Annual temporal breeding haulout parameters of distinctive age-classes for (a) male and (b) female southern elephant seals. The total number of observations of marked animals belonging to respective age- and sex-classes is represented by *n*. Temporal haulout parameters are not presented for classes for which there were less than ten observations in a season.

(a) Males

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
6	1990	13	10 October	29.2	15 October	13 August - 15 November
	1991	10	17 October	30.8	23 October	1 August - 25 November
	1992	18	23 October	20.1	30 October	28 August - 14 November
	1993	20	22 October	16.7	26 October	18 September - 12 November
	1994	26	11October	15.4	7 October	9 September - 11 November
	1995	14	6 October	17.4	4 October	7 September - 7 November
	1996	15	18 October	16.4	18 October	14 September - 18 November
	1997	15	11 October	13.3	10 October	19 September - 7 November
7	1990	10	19 October	19.5	24 October	16 September - 15 November
	1991	11	19 October	29.4	25 October	22 August - 25 November
	1992	36	18 October	17.1	23 October	11 September - 14 November
	1993	59	12 October	22.7	8 October	19 August - 12 November
	1994	80	13 October	23.1	14 October	4 August - 22 November
	1995	73	10 October	25.2	10 October	16 September - 19 November
	1996	26	19 October	15.4	18 October	17 September - 24 November
	1997	56	14 October	19.1	17 October	9 September - 18 November

(Continued)

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
8	1990	-	-	-	-	-
	1991	32	12 October	21.2	15 October	3 September - 13 November
	1992	15	8 October	18.6	9 October	4 September - 9 November
	1993	57	8 October	25.7	8 October	21 August - 24 November
	1994	45	8 October	21.9	8 October	19 August - 22 November
	1995	67	6 October	23.5	6 October	18 August - 20 November
	1996	71	6 October	25.0	8 October	18 August - 24 November
	1997	62	11 October	19.9	11 October	30 August - 18 November
9	1990	-	-	-	-	-
	1991	-	-	-	-	-
	1992	42	2 October	24.1	3 October	20 August - 14 November
	1993	18	11 October	23.4	15 October	5 September - 12 November
	1994	26	18 October	20.8	21 October	16 September - 22 November
	1995	26	4 October	21.9	4 October	27 August - 14 November
	1996	16	22 September	26.5	22 September	2 August - 1 November
	1997	61	4 October	28.7	4 October	8 August - November
10	1990	-	-	-	-	-
	1991	-	-	-	-	-
	1992	-	-	-	-	-
	1993	40	28 September	27.0	28 September	16 August - 12 November
	1994	27	7 October	21.7	6 October	26 August - 12 November
	1995	12	13 October	31.5	13 October	24 August - 30 November
	1996	10	27 September	25.2	25 September	21 September - 6 November
	1997	7	-	-	-	-

(b) Females

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
3	1990	53	12 October	10.8	15 October	16 September - 2 November
	1991	53	10 October	10.4	12 October	20 September - 2 November
	1992	60	11 October	11.8	10 October	18 September - 15 November
	1993	105	6 October	8.7	8 October	17 September - 22 October
	1994	80	11 October	12.2	13 October	16 September - 10 November
	1995	108	12 October	12.5	12 October	15 September - 20 November
	1996	68	13 October	10.9	12 October	13 September - 9 November
	1997	70	10 October	11.0	10 October	9 September - 7 November
4	1990	210	10 October	11.9	12 October	14 September - 15 November
	1991	148	12 October	12.7	13 October	2 September - 2 November
	1992	113	8 October	11.7	10 October	5 September - 31 October
	1993	88	11 October	12.1	8 October	18 September - 12 November
	1994	172	12 October	10.6	13 October	16 September - 10 November
	1995	168	13 October	11.2	12 October	15 September - 7 November
	1996	127	14 October	9.9	11 October	14 September - 8 November
	1997	173	12 October	12.0	11 October	13 September - 13 November
5	1990	97	11 October	11.5	12 October	14 September - 8 November
	1991	122	15 October	12.3	18 October	16 September - 15 November
	1992	60	11 October	11.8	10 October	18 September - 15 November
	1993	108	13 October	12.7	8 October	17 September - 12 November
	1994	97	14 October	10.4	14 October	23 September - 10 November
	1995	108	12 October	12.5	12 October	15 September - 20 November
	1996	126	14 October	9.8	16 October	20 September - 1 November
	1997	127	12 October	10.1	11 October	17 September - 4 November

(Continued)

Age-class (years)	**Year**	***n***	**Mean haulout date**	**S.D. (days)**	**Median haulout date**	**Range**
6	1990	80	12 October	13.4	15 October	16 September - 16 November
	1991	72	11 October	12.2	12 October	13 September - 3 November
	1992	100	10 October	12.3	10 October	18 September - 13 November
	1993	88	14 October	12.5	8 October	24 September - 12 November
	1994	113	15 October	11.5	14 October	17 September - 11 November
	1995	62	15 October	10.8	18 October	21 September - 3 November
	1996	96	12 October	10.6	11October	17 September - 6 November
	1997	136	13 October	11.1	11October	13 September - 2 November
7	1990	51	10 October	11.0	12 October	14 September - 2 November
	1991	54	13 October	14.6	13 October	13 September - 15 November
	1992	53	10 October	10.6	10 October	18 September - 30 November
	1993	77	13 October	14.4	8 October	17 September - 12 November
	1994	85	12 October	11.9	13 October	17 September - 12 November
	1995	104	15 October	12.3	13 October	17 September - 10 November
	1996	44	16 October	9.6	18 October	24 September - 8 November
	1997	90	12 October	11.1	11 October	17 September - 4 November
8	1991	-	-	-	-	-
	1991	25	14 October	12.6	18 October	13 September - 2 November
	1992	25	6 October	12.7	4 October	18 September - 8 November
	1993	42	12 October	12.9	8 October	17 September - 12 November
	1994	64	8 October	10.9	7 October	16 September - 29 October
	1995	35	16 October	9.9	17 October	21 September - 2 November
	1996	64	16 October	11.1	17 October	20 September - 6 November
	1997	41	14 October	9.4	11 October	30 September - 2 November

(Continued)

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
9	1990	-	-	-	-	-
	1991	-	-	-	-	-
	1992	18	12 October	9.6	10 October	27 September - 1 November
	1993	34	10 October	14.8	8 October	17 September - 12 November
	1994	44	13 October	11.2	13 October	23 September - 4 November
	1995	51	11 October	11.1	12 October	15 September - 2 November
	1996	29	16 October	9.6	17 October	17 September - 30 October
	1997	55	10 October	12.3	7 October	12 September - 2 November
10	1990	-	-	-	-	-
	1991	-	-	-	-	-
	1992	-	-	-	-	-
	1993	9	-	-	-	-
	1994	37	9 October	12.1	8 October	16 September - 12 November
	1995	31	13 October	10.7	12 October	21 September - 2 November
	1996	24	11 October	14.6	10 October	14 September - 11 November
	1997	18	15 October	9.1	18 October	30 September - 30 October

APPENDIX II

Table 15. Annual temporal moulting haulout parameters of distinctive age-classes for (a) male and (b) female southern elephant seals. The total number of observations of marked animals belonging to respective age- and sex-classes is represented by *n*. Temporal haulout parameters are not presented for those classes for which there were less than ten observations in a season.

(a) Males

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
1	1990	162	6 December	14.5	6 December	1 November - 10 January
	1991	189	6 December	14.1	5 December	1 November - 5 January
	1992	192	7 December	14.1	5 December	13 November - 12 January
	1993	136	4 December	14.5	5 December	1 November - 5 January
	1994	210	6 December	13.9	10 December	4 November - 12 January
	1995	233	7 December	14.4	7 December	2 November - 16 January
	1996	196	6 December	14.8	7 December	30 October - 28 January
	1997	208	4 December	15.4	5 December	17 October - 16 January
2	1990	232	15 December	15.7	17 December	5 November - 7 February
	1991	164	10 December	17.2	16 December	21 October - 14 January
	1992	162	13 December	16.3	13 December	6 November - 4 February
	1993	196	16 December	15.8	14 December	5 November - 23 January
	1994	145	13 December	17.0	11 December	6 November - 31 January
	1995	224	14 December	16.7	14 December	13 November - 5 February
	1996	193	12 December	16.6	12 December	30 October - 28 January
	1997	195	13 December	18.0	13 December	4 November - 30 January

(Continued)

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
3	1990	202	18 December	17.6	17 December	10 November - 8 February
	1991	198	19 December	17.8	17 December	8 November - 25 January
	1992	136	17 December	18.7	15 December	14 November - 1 February
	1993	156	20 December	17.1	14 December	12 November - 4 February
	1994	170	20 December	16.3	19 December	10 November - 23 January
	1995	174	20 December	18.3	20 December	3 November - 5 February
	1996	162	17 December	16.6	17 December	16 November - 31January
	1997	159	18 December	18.6	18 December	4 November - 20 February
4	1990	102	19 December	19.6	17 December	5 November - 11 February
	1991	127	20 December	19.5	16 December	1 November - 2 February
	1992	113	23 December	17.6	22 December	13 November - 3 February
	1993	86	20 December	19.0	20 December	5 November - 23 January
	1994	127	23 December	20.5	20 December	11 November - 8 February
	1995	145	21 December	17.6	22 December	10 November - 25 January
	1996	123	19 December	19.1	18 December	6 November - 31 January
	1997	167	22 December	18.7	24 December	10 November - 4 February
5	1990	87	25 December	18.4	24 December	8 November - 3 February
	1991	77	24 December	21.9	26 December	3 November - 13 February
	1992	79	26 December	19.2	2 January	8 November - 5 February
	1993	110	22 December	19.8	26 December	1 November - 4 February
	1994	60	29 December	30.9	20 December	11 November - 10 April
	1995	115	22 December	20.7	27 December	23 October - 31 January
	1996	70	28 December	24.3	28 December	6 November - 3 March
	1997	82	31 December	20.7	28 December	24 November - 28 February

(Continued)

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
6	1990	25	12 January	25.5	12 January	26 November - 2 March
	1991	68	31 December	23.9	3 January	3 November - 23 February
	1992	60	14 January	31.9	13 January	14 November - 14 March
	1993	68	8 January	28.3	5 January	12 November - 16 March
	1994	76	6 January	25.2	4 January	21 November - 10 April
	1995	51	30 December	26.4	30 December	7 November - 3 March
	1996	52	11 January	23.9	15 January	18 November - 7 March
	1997	60	8 January	27.2	3 January	17 November - 10 March
7	1990	28	23 January	29.3	22 January	26 November - 22 March
	1991	7	-	-	-	-
	1992	45	1 February	38.5	9 February	14 November - 13 April
	1993	31	27 January	39.1	4 February	5 November - 24 March
	1994	37	20 February	33.4	24 February	1 December - 9 April
	1995	54	8 February	34.4	13 February	10 November - 2 April
	1996	32	29 January	35.0	27 January	9 November - 23 March
	1997	24	29 January	26.2	30 January	15 December - 10 March
8	1990	-	-	-	-	-
	1991	12	4 February	26.9	9 February	5 December - 11 March
	1992	5	-	-	-	-
	1993	17	8 March	21.4	5 March	2 February - 17 April
	1994	17	25 February	45.4	12 March	3 December - 31 January
	1995	8	-	-	-	-
	1996	18	20 February	20.5	17 February	6 January - 23 March
	1997	20	9 February	20.0	15 February	23 December - 9 March

(Continued)

Age-class (years)	**Year**	***n***	**Mean haulout date**	**S.D. (days)**	**Median haulout date**	**Range**
9	1990	-	-	-	-	-
	1991	-	-	-	-	-
	1992	15	12 February	29.6	9 February	14 November - 15 March
	1993	6	-	-	-	-
	1994	11	15 March	14.0	20 March	12 December - 8 February
	1995	5	-	-	-	-
	1996	1	-	-	-	-
	1997	10	24 February	10.3	25 February	9 February - 10 March

(b) Females

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
1	1990	184	8 December	14.3	9 December	1 November - 12 January
	1991	234	8 December	14.5	5 December	3 November - 15 January
	1992	215	8 December	13.7	13 December	8 November - 12 January
	1993	184	7 December	13.8	5 December	1 November - 13 January
	1994	228	7 December	13.4	10 December	29 October - 12 January
	1995	211	8 December	14.5	8 December	18 October - 14 January
	1996	205	8 December	13.9	7 December	8 November - 22 January
	1997	241	8 December	13.5	7 December	7 November - 10 January
2	1990	216	17 December	18.2	17 December	28 October - 2 February
	1991	191	19 December	18.6	16December	24 October - 13 February
	1992	232	23 December	17.5	22 December	8 November - 3 February
	1993	232	22 December	17.7	26 December	5 November - 2 February
	1994	225	20 December	18.9	19 December	4 November - 31 January
	1995	274	22 December	18.5	22 December	7 November - 11 February
	1996	179	19 December	18.0	18 December	6 November - 11 February
	1997	200	20 December	16.8	18 December	13 November - 31 January
3	1990	212	1 January	17.9	1 January	26 November - 8 February
	1991	192	3 December	18.7	3 January	15 November - 13 February
	1992	134	2 January	18.3	4 January	14 November - 12 February
	1993	197	6 January	17.5	5 January	24 November - 11 February
	1994	225	5 January	20.3	10 January	11 November - 20 February
	1995	255	8 January	18.8	8 January	10 November - 22 February
	1996	199	4 January	17.0	6 January	18 November - 9 February
	1997	165	30 December	19.7	28 December	18 November - 19 February

(Continued)

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
4	1990	140	15 January	18.9	20 January	8 November - 5 March
	1991	115	15 January	16.5	14 January	25 November - 22 February
	1992	102	13 January	15.5	13 January	3 December - 14 February
	1993	111	11 January	17.6	13 January	12 November - 12 February
	1994	172	15 January	16.5	12 January	22 November - 20 February
	1995	217	12 January	17.4	14 January	13 November - 22 February
	1996	157	11 January	17.7	14 January	9 November - 16 February
	1997	139	9 January	18.3	10 January	13 November - 19 February
5	1990	75	14 January	15.9	12 January	26 November - 11 February
	1991	125	14 January	16.9	14 January	25 November - 13 February
	1992	103	14 January	14.7	13 January	3 December - 14 February
	1993	116	16 January	17.3	14 January	24 November - 22 February
	1994	75	17 January	21.0	21 January	21 November - 21 March
	1995	163	13 January	16.1	14 January	30 November - 22 February
	1996	133	12 January	17.3	15 January	18 November - 23 February
	1997	106	13 January	14.9	10 January	24 November - 10 February
6	1990	60	8 January	20.9	11 January	4 November - 11 February
	1991	51	14 January	13.0	13 January	5 December - 4 February
	1992	81	13 January	14.5	13 January	13 December - 21 February
	1993	87	10 January	16.8	11 January	5 December - 12 February
	1994	94	15 January	17.8	22 January	1 December - 20 February
	1995	66	11 January	19.1	14 January	7 November - 15 February
	1996	97	14 January	13.6	16 January	7 December - 13 February
	1997	127	14 January	14.6	16 January	13 December - 19 February

(Continued)

Age-class (years)	**Year**	***n***	**Mean haulout date**	**S.D. (days)**	**Median haulout date**	**Range**
7	1990	35	15 January	12.3	12 January	20 December - 11 February
	1991	39	15 January	14.0	14 January	16 December - 12 February
	1992	35	8 January	17.6	12 January	23 November - 9 February
	1993	62	13 January	12.4	14 January	14 December - 11 February
	1994	76	14 January	16.3	12 January	21 November - 8 February
	1995	93	13 January	14.1	14 January	30 November - 10 February
	1996	42	15 January	12.2	15 January	22 December - 14 February
	1997	81	12 January	15.4	16 January	29 November - 14 February
8	1990	-	-	-	-	-
	1991	26	11 January	14.4	14 January	5 December - 4 February
	1992	20	12 January	16.7	13 January	14 December - 14 February
	1993	30	14 January	13.5	13 January	26 December - 11 February
	1994	50	11 January	14.6	12 January	3 December - 8 February
	1995	43	14 January	14.5	13 January	11 December - 16 February
	1996	64	15 January	13.3	16 January	12 December - 13 February
	1997	31	16 January	11.2	16 January	27 December - 4 February
9	1990	-	-	-	-	-
	1991	-	-	-	-	-
	1992	16	11 January	11.5	12 January	21 December - 3 February
	1993	33	15 January	14.7	14 January	14 December - 12 February
	1994	27	8 January	15.2	10 January	3 December - 31 January
	1995	44	10 January	18.1	14 January	7 November - 5 February
	1996	24	12 January	11.4	15 January	22 December - 4 February
	1997	40	16 January	13.0	16 January	26 December - 10 February

APPENDIX III

Table 16. Annual temporal resting haulout parameters of distinctive age-classes for (a) male and (b) female southern elephant seals. The total number of observations of marked animals belonging to respective age- and sex-classes is represented by *n*. Temporal haulout parameters are not presented for those classes for which there were less than ten observations in a season.

(a) Males

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
<1	1990	122	27 May	48.8	28 May	5 March - 7 September
	1991	149	27 May	44.7	21 May	13 March - 3 September
	1992	134	23 May	44.5	23 May	14 February - 6 September
	1993	118	2 June	53.5	7 June	13 February - 10 September
	1994	141	12 June	50.8	12 June	23 February - 9 September
	1995	117	7 June	44.8	9 June	23 January - 15 September
	1996	162	3 June	50.8	24 May	16 February - 11 October
	1997	160	30 May	55.2	20 May	13 January - 27 September
1	1990	215	23 May	57.9	10 May	2 February - 21September
	1991	174	14 May	63.4	23 April	5 February - 19 September
	1992	158	7 May	61.5	14 April	27 January - 29 August
	1993	219	8 May	61.8	14 April	4 February - 24 September
	1994	168	25 May	61.9	29 April	5 February - 9 September
	1995	235	17 May	58.8	21 April	30 January - 8 September
	1996	235	19 May	63.2	22 April	21 February - 5 October
	1997	255	11 May	58.1	17 April	10 February - 20 September

(Continued)

Age-class (years)	**Year**	***n***	**Mean haulout date**	**S.D. (days)**	**Median haulout date**	**Range**
2	1990	146	6 June	47.6	8 June	13 February - 16 September
	1991	162	20 May	47.0	20 May	22 January - 7 September
	1992	112	21 May	55.1	19 May	5 February - 5 September
	1993	133	27 May	53.1	23 May	13 February - 27 August
	1994	141	25 May	50.8	1 June	16 March - 9 September
	1995	107	23 May	42.3	11 May	12 March - 17 August
	1996	150	20 May	45.0	6 May	21 February - 11 October
	1997	145	26 May	48.6	20 May	24 February - 29 August
3	1990	103	12 June	38.4	8 June	15 March - 14 September
	1991	100	6 June	44.0	28 May	1 April - 12 October
	1992	104	27 May	40.1	23 May	5 February - 29 August
	1993	96	28 May	36.7	23 May	25 March - 29 August
	1994	109	17 June	42.1	12 June	25 March - 24 September
	1995	81	12 June	36.8	12 June	22 March - 16 September
	1996	61	11 June	50.5	21 June	14 March - 27 August
	1997	126	4 June	35.5	5 June	27 March - 22 August
4	1990	83	16 June	32.9	9 June	5 March - 7 September
	1991	57	1 June	39.9	22 May	22 February - 20 September
	1992	47	7 June	41.1	25 May	14 April - 5 September
	1993	78	4 June	28.2	6 June	23 March - 16 August
	1994	49	4 June	33.9	1 June	25 March - 27 August
	1995	65	4 June	37.7	1 June	21 March - 17 August
	1996	57	5 June	28.8	1 June	5 April - 13 August
	1997	49	13 June	34.9	10 June	27 March - 24 August

(Continued)

Age-class (years)	**Year**	***n***	**Mean haulout date**	**S.D. (days)**	**Median haulout date**	**Range**
5	1990	10	13 June	35.1	18 June	23 April - 4 August
	1991	39	11 June	25.9	6 June	28 April - 25 July
	1992	26	19 June	33.5	13 June	4 May - 29 August
	1993	37	4 June	34.5	6 June	15 March - 12 August
	1994	39	6 June	29.4	3 June	8 April - 5 August
	1995	31	5 June	31.6	31 May	10 April - 31 July
	1996	45	31 May	26.2	1 June	5 April - 16 July
	1997	37	13 June	29.0	10 June	27 March - 24 August
6	1990	14	3 June	18.9	4 June	23 April - 7 June
	1991	4	-	-	-	-
	1992	23	3 June	23.7	2 June	11 March - 10 July
	1993	9	-	-	-	-
	1994	20	11 June	20.9	12 June	10 May - 23 July
	1995	11	26 May	22.5	21 May	12 April - 20 June
	1996	23	30 May	37.8	7 June	14 March - 6 August
	1997	18	13 June	17.3	14 June	15 May - 16 July

(b) Females

Age-class (years)	Year	*n*	Mean haulout date	S.D. (days)	Median haulout date	Range
<1	1990	182	25 May	43.1	25 May	5 March - 14 September
	1991	152	24 May	42.9	21 May	30 January - 23 August
	1992	113	3 June	40.2	31 May	11 March - 11 October
	1993	162	27 May	46.7	12 May	5 March - 24 September
	1994	132	6 June	44.4	3 June	12 February - 17 September
	1995	105	4 June	44.9	1 June	1 March - 4 October
	1996	143	2 June	44.9	27 May	12 March - 25 September
	1997	161	23 May	47.5	19 May	10 February - 10 October
1	1990	160	3 May	47.9	20 April	5 February - 31 August
	1991	166	20 April	42.0	15 April	22 February - 7 September
	1992	156	28 April	47.3	14 April	5 February - 19 September
	1993	141	6 May	53.4	24 April	12 February - 5 September
	1994	151	8 May	48.4	29 April	23 February - 9 September
	1995	177	25 April	45.1	11 April	21 February - 11 September
	1996	183	27 April	42.2	15 April	6 February - 8 September
	1997	195	26 April	49.7	10 April	10 February - 29 August
2	1990	131	1 June	38.2	31 May	5 February - 31 August
	1991	85	23 May	41.7	22 May	21 January - 3 September
	1992	60	8 June	46.5	2 June	11 March - 19 September
	1993	62	12 June	33.5	13 June	23 March - 27 August
	1994	66	7 June	35.5	12 June	23 February - 19 August
	1995	55	23 May	38.5	31 May	21 February - 18 August
	1996	68	26 May	37.9	24 May	5 February - 4 August
	1997	71	1 June	35.5	2 June	1 February - 14 August

(Continued)

Age-class (years)	**Year**	***n***	**Mean haulout date**	**S.D. (days)**	**Median haulout date**	**Range**
3	1990	11	17 May	49.6	10 May	23 March - 13 August
	1991	15	7 June	46.7	23 June	13 March - 14 August
	1992	4	-	-	-	-
	1993	13	17 June	31.7	25 June	24 April - 23 July
	1994	4	-	-	-	-
	1995	8	-	-	-	-
	1996	8	-	-	-	-
	1997	8	-	-	-	-