

### **CHAPTER THREE:**

## **TEMPORARY MARKING OF UNWEANED SOUTHERN ELEPHANT SEAL PUPS**

*de Bruyn et al. 2008*

### **Abstract**

Like many pinniped species, southern elephant seals are conducive to long-term population studies using mark-recapture techniques. The twenty-four year longitudinal data set at sub-Antarctic Marion Island has already provided much insight into elephant seal population dynamics. However, a limitation of the present dataset is that mother/pup relatedness cannot be examined because pups are only tagged after their tagged mothers have abandoned them. We test the usefulness of two different temporary marking techniques (tagging and “strapping”), and four different marker types over two consecutive breeding seasons for use on pups with attending marked mothers. We show that strapping is an ineffective way to mark unweaned southern elephant seals. By comparison, “Supersmall®” Dalton plastic tags allow quick, effective and easy marking of large numbers of pups with known mothers, without excessive marker loss.

### **Introduction**

The major objective in studies of population dynamics is to detect and analyse differences in life history traits among groups of individuals through temporal and spatial scales (Lebreton et al. 1992). Such differences affect rates of population change through variations in survival and fecundity (Siniff et al. 1977). Longitudinal life history studies (Clobert et al. 1994) require sufficiently large marked/known-age samples of a given population to allow for analysis of age structure and demography (Erickson et al. 1993). At Marion Island, a total of 11830 (average: 473 annually, range: 389 - 700) southern elephant seal pups were double tagged in their hind-flippers immediately after/at weaning from 1983 to 2007. A great deal of research has been aimed at demographic aspects of the southern elephant seal population at Marion Island owing to this longitudinal dataset (1983 – present)(e.g. Bester and Wilkinson 1994; Pistorius et al. 2004; McMahon et al. 2005). However, analyses investigating the mother-pup relationships (e.g. first year survival related to mother age) cannot be undertaken because pups are tagged only after the maternal bond has been severed (weaning) and thus the mothers’ identity becomes anonymous.

In addition, the polygynous breeding system of this species, i.e. the formation of a 'harem' of cows on a beach defended by at least one adult bull (beachmaster), complicates the marking of a large number of pups before weaning, primarily by making access to the pups dangerous. Also, the disturbance caused in reaching any particular pup disrupts the rest of the harem, causing animals to mingle, resulting in further mother-pup pairs not being easily identifiable. To mark all pups with marked mothers (range: 1 - 60 pups/harem on Marion Island) at this early stage requires intrusion into the harem and hence disturbance to the adults. We therefore tested four potential methods for quickly marking large numbers of unweaned pups and report on the most effective of these methods to enable accurate identification of mother-pup pairs.

## Methods

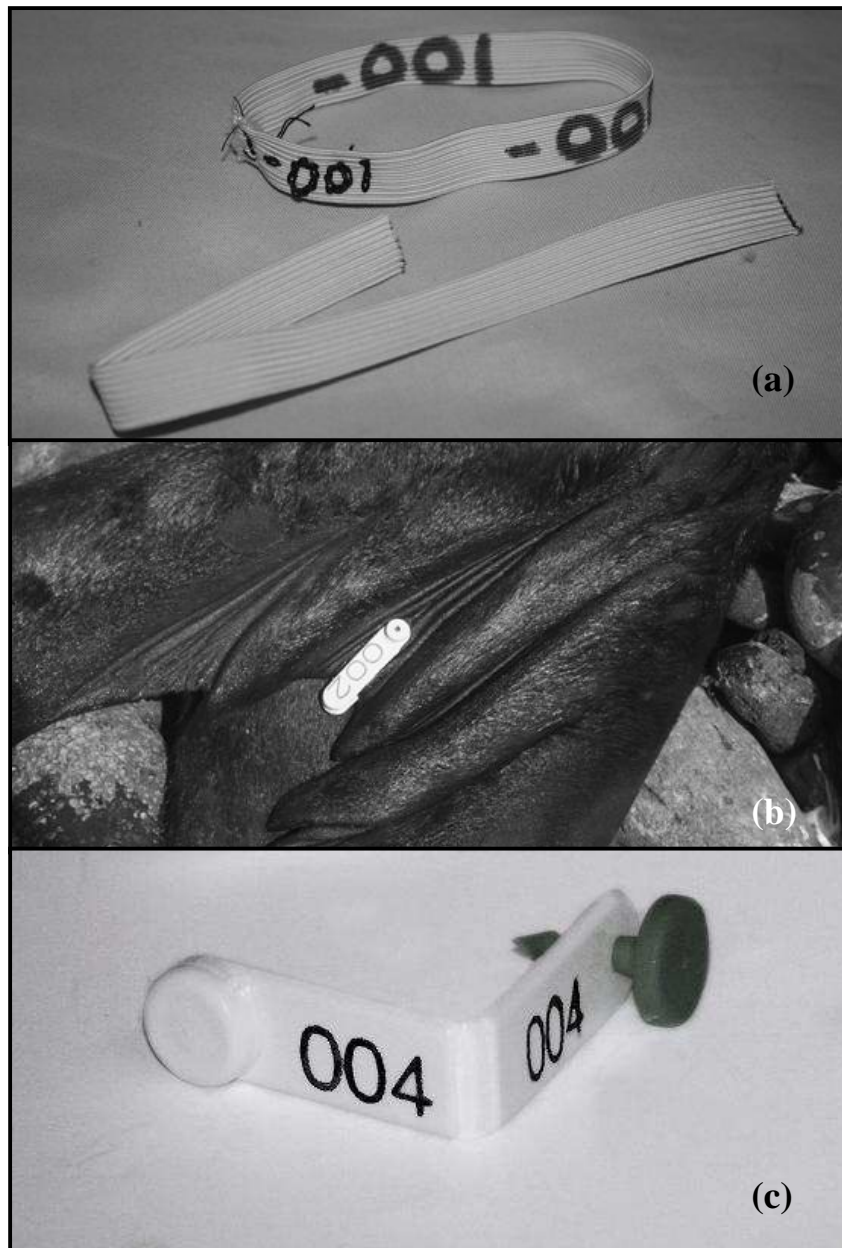
### *Study Area*

Marion Island (46°54'S, 37°45'E) is situated in the Southern Indian Ocean and is approximately 290 km<sup>2</sup> in area. Southern elephant seals use the more easily accessible beaches on the eastern and northern shores of the island, which include approximately 54 km of coastline (Fig. 1.2).

### *Data collection*

During the 2006 southern elephant seal breeding season a total of 120 bands were fashioned by stitching the two ends of a 235 mm (16 mm width) section of ballet elastic (manufacturer's dimension code - BE16) fabric strip together with a 10mm overlap (Fig. 3.1). During the 2007 breeding season a further 99 bands were made, 53 of which were 20 mm wide. Regular garment stitching/sewing Polycote® thread was used to attach the two ends of each band. Double 'zigzag' stitching provided strong binding of the two ends but also allowed eventual (after ~1.5 months) unravelling/breaking (owing to natural wear) to avoid entanglement and possible injury to the seals' 'ankle' if the band was not otherwise removed. The inside and outside of each band was inscribed with a unique number using indelible fabric ink (Staedtler® Lumocolor laundry marker) and the same unique number was embroidered (polyester M782 thread) on the outside of the band (Fig. 3.1). All bands were either white or light pink to improve visibility once attached. Although soiling reduced the sightability of bands, not all bands become soiled thus some advantage

was retained by using light coloured elastic. The two band types (16 mm and 20 mm) were regarded as different marker types.



**Fig. 3.1.** The different marker types used to identify unweaned southern elephant seal pups at Marion Island. (a) Band markers (Note the embroidered and ink numbers with a dash as pretext to ascertain the numbers' correct orientation), (b) Supersmall® tags placed in the inner inter-digital webbing of the hind flipper of an unweaned pup, and (c) Temptags®.

During the 2007 breeding season we also tested two types of temporary livestock ear-tags, Supersmall® tags and Temptags® (Dalton Supplies Ltd., Henley-on-Thames, U.K.) (Fig. 3.1). These tags are designed for short-term temporary use on young animals to minimise injury to delicate/soft tissue at the tag site, and as such

are not made to withstand natural wear and tear for longer than six months ([http://www.dalton.co.za/za/products/pages\\_pr/research/r\\_supers.htm](http://www.dalton.co.za/za/products/pages_pr/research/r_supers.htm)). Forty-seven Supersmall® tags and forty-eight Temptags® were tested, each type was uniquely numbered from 001 to 047 / 048 on the outside of outer and inner tag components, while the inside of both components was inscribed with 'Marion Is', the attachment locality. The shape and size of the tag types were distinct. Supersmall® tags were white only and Temptags® were white with a green fixing pin. Supersmall® tags are inserted with an applicator, while Temptags® are inserted by hand. We did not test the application of a single Jumbotag® to unweaned pups for the following reasons:

- (1) Jumbotags® are more robust (for longer lifespan) with a larger piercing pin that causes greater injury to the soft interdigital webbing of unweaned pups.
- (2) Application of the latter therefore needs to be carefully done to ensure reduced tag-loss resulting from incorrect application (Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009). Double tagging of an unweaned pup while at the side of the mother in a harem is difficult and dangerous, because after application of the first tag, the element of surprise is lost.
- (3) Given the longstanding (1983 – present) and continuing double tagging regime for weaned pups at Marion Island, single tagging of Jumbotags® would require that the identical remaining Jumbotag® of a pair (for tagging the other flipper) would need to be stored and the correct pup located later/after weaning to insert the correct other tag of the pair. Additionally, this procedure would affect the estimation of tag-loss of the Jumbotags®, because each tag would have different application dates (Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009).
- (4) A single uniquely numbered Jumbotag® can be inserted pre-weaning, but if not removed prior to/at the application of the differently numbered pair of Jumbotags® at weaning, can result in later resighting confusion.

Marker bands were attached to either 'ankle' of unweaned pups. A single tag was attached to either of the two parts of inner-interdigital webbing in the right hind flipper of unweaned pups. Only pups with attending known-age (tagged) mothers were marked and only one marker (band or tag) was applied per pup. Attachment of markers was spread among 30 breeding colony beaches along a 50.4 km section of the Marion Island coastline. Mothers had been previously double tagged in each of the hind flippers with colour-coded, uniquely numbered Dal 008 Jumbotags® (Dalton

Supplies Ltd., Henley-on-Thames, U.K.) at weaning. The band/tag number of each unweaned pup was noted in combination with the tag number of the mother. Pup age was estimated from weekly (at least) observations of their mothers following the resighting schedule described in Bester and Wilkinson (1994). All bands, but not tags, were removed after weaning, and all pups were then tagged with colour-coded uniquely numbered Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, U.K.) in the upper, outer interdigital webbing of each hind flipper. We did not remove any of the Supersmall® tags or Temptags®, based on the manufacturer's assurance that the tags are of temporary design and are automatically lost as the animal grows and pressure is exerted on the tag.

#### *Data analysis*

The retention of markers over time since attachment is assessed and the marker types with the highest retention rates over the 3 weeks of suckling were deemed suitable for identifying individual unweaned pups.

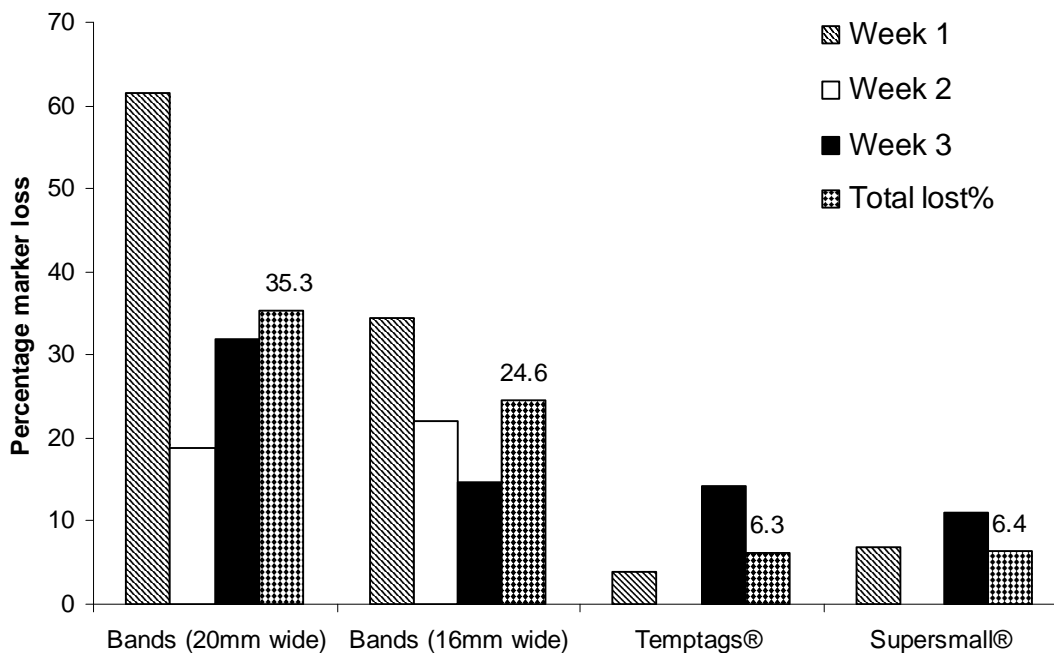
#### **Results**

The numbers of bands attached in 2006 and 2007 are given in Table 3.1. Attachment effort was constant throughout the study period. A violent storm and heavy seas on 27 October 2007 resulted in several pups disappearing prior to weaning. Differentiation between marker loss and pup loss was impossible for those pups where marker retention was not confirmed prior to the storm. It is assumed that the loss of pups was random, regardless of marker type, with negligible effects on the results. Unweaned, marked pups that were subsequently confirmed dead ( $n = 2$ ; 2006 and 2007) were removed from analysis.

Figure 3.2 illustrates the loss rates for the four different markers attached during the three-week pre-weaning period. Marker loss was the greatest for one-week-old pups for both the 20mm (loss = 61.5%) and 16mm (loss = 34.4%) bands (Fig. 3.2). Marker loss of 16mm bands decreased as the pups aged, with only 14.6% loss for three-week-old pups. Marker loss of 20mm bands showed an initial decrease (loss = 18.8% for two-week-old pups), followed by an increase in band loss for three-week-old pups (31.8%) (Fig. 3.2).

**Table 3.1.** Numbers of different marker types attached on unweaned southern elephant seal pups during the 2006 and 2007 breeding seasons at Marion Island.

Identifier type	Attachment Year	Preweaned pup age			Total number attached
		Week 1	Week 2	Week 3	
Bands (16mm wide)	2006	49	40	31	120
Bands (16mm wide)	2007	15	19	17	51
Bands (20mm wide)	2007	13	16	22	51
Temptags®	2007	26	8	14	48
Supersmall®	2007	29	9	9	47



**Fig. 3.2.** Percentage marker loss relative to the number attached in each week on unweaned southern elephant seal pups at Marion Island during the three-week pre-weaning period.

Temptags® ( $n = 48$ ) and Supersmall® ( $n = 47$ ) tags were mainly attached on one-week-old pups (Table 3.1) in 2007. Temptags® were well retained throughout the study, with overall retention at 93.7%. Loss was greatest when attached on three-week-old pups (loss = 14.3%). Supersmall® tags were retained at an overall rate of 93.6%. Loss of Supersmall® tags was also greatest when attached on three-week-old pups (loss = 11.1%).

In total 109 and 150 pups with known mothers were identified during 2006 and 2007 respectively representing 43% (2006) and 60% (2007) of tagged mothers from Marion Island.

Six months after application of Supersmall® tags on pups, only one of seven resighted individuals retained the small tag, while one of 12 resighted animals that had received Temptags® retained its tag.

## Discussion

Marking large numbers of individuals within a population facilitates various studies such as demography, life history, behaviour, dispersal and growth. Individual marking of pinnipeds is relatively easy due to unrestricted access to weaned animals (Bester 1988). Unweaned pups are less accessible for marking due to the gregariousness and aggression of their mothers during the breeding season. Thus identifying relatedness of unweaned pups and their attending mothers is difficult. However, knowledge of relatedness of mothers and pups may shed light on evolutionary systems such as in-breeding, incest avoidance, maternal investment or genetic/hereditary characteristics. Studies requiring a relatively small sample of very young pups with known (tagged) mothers have been achieved by focussing efforts on a single breeding harem/group of animals (e.g. Wilkinson and Bester 1990; Wilkinson 1991; Wilkinson and van Aarde 2001). However, to gain indepth knowledge of the demographic variables driving population behaviour and structure, relatedness information of large numbers of animals are necessary. Various pinniped species have been temporarily marked with a variety of materials including the application of dyes, bleach and paint and techniques such as fur clipping (Erickson et al. 1993). These methods are often unsuitable for use on large samples of grouped animals spread over an extensive area due to logistical difficulties such as the

quantity of material to be transported, requirement for animals to be dry, time constraints and manpower. The current method, in conjunction with an intensive monitoring programme, allows for the expansion of sample sizes and representativeness within the sample.

We show that of the four methods tested here, marking individual unweaned pups with Temptags® and Supersmall® tags provides an easy, reliable method of temporary marking large numbers of southern elephant seal pups with known-age (tagged) mothers. Animals marked with bands showed poor overall pre-weaning marker retention when compared to animals marked with Temptags® and Supersmall® tags. The poor performance of band markers attached early in the pups' life could be due to a variety of factors. The age of the pup may play a role as one-week-old pups showed higher marker loss (compared to older pups) possibly because their hind flippers were slender and soft allowing the band to slip off. The band cannot be reduced in diameter for fear of becoming too tight as the pups grow. Alternatively, the durability of the bands might decrease with time as the band is exposed to the corrosive influences of sea water, ultraviolet radiation and general wear and tear brought about by the activity of the pup in a congested harem located on a coarse sandy/pebbly/boulder strewn substrate. As the pups grow, more pressure is exerted on the fibre, resulting in higher rates of marker loss, especially if the pup has been wearing the marker for some time. Field experience shows that bands take a little longer to fit over the 'ankle' of a pup, compared to tagging the pup. Given that pups are not removed from the harem for marking purposes, and considering the aggressive behaviour of adults in these harems, a fast-as-possible incursion of the harem for marking unweaned pups is important.

Flipper tags are not exposed to the same pressures as bands, thus displaying higher overall retention rates than the bands because the tags are protected within the folds of the flipper. The retention rates of tags decreased when attached on older pups; this could be as a result of the thicker interdigital webbing (causing incomplete piercing of the thin tag pin) and stronger flippers (allowing more powerful / vigorous rubbing of the site of new pain stimulus due to tag application) of older pups. Field experience shows that the ease with which Supersmall® tags are applied makes them even more suitable than Temptags® for future use. The fixing pin of the



Temptags® occasionally created application difficulties, by dropping out /not aligning properly at the last moment.

We suggest the use of Supersmall® tags as a very effective, quick and inexpensive method of temporarily marking unweaned pups of southern elephant seals. If continued over time, this marking method will allow for more intense exploration of relatedness research topics. This method is likely to be suitable for other phocids breeding in groups or where very young animals need to be marked for future studies.

### Literature Cited

- Bester MN (1988) Marking and monitoring studies of the Kerguelen stock of southern elephant seals, *Mirounga leonina*, and their bearing on biological research in the Vestfold hills. *Hydrobiologia* 165:269-277
- Bester MN, Wilkinson IS (1994) Population ecology of southern elephant seals at Marion Island. In: Le Boeuf BJ, Laws RM (eds) *Elephant seals: population ecology, behavior, and physiology*. University of California Press, Berkeley, pp 85-97
- Clobert J, Lebreton J-D, Allaine D, Gaillard JM (1994) The estimation of age-specific breeding probabilities from recapture or resightings in vertebrate populations: II. Longitudinal models. *Biometrics* 50:375-387.
- Erickson AW, Bester MN, Laws RM (1993) Marking techniques. In: Laws RM (ed) *Antarctic seals: research methods and techniques*. University Press, Cambridge, pp 89 - 118
- Lebreton J-D, Burnhan KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67-118
- McMahon CR, Bester MN, Burton HR, Hindell MA, Bradshaw CJA (2005) Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Rev* 35:82-100
- Oosthuizen WC, de Bruyn PJN, Bester MN, Girondot M (2009) Cohort and tag-site specific tag-loss rates in mark-recapture studies: a southern elephant seal cautionary case. *Mar Mamm Sci In press* [Appendix 2]

- Pistorius PA, Bester MN, Kirkman SP, Boveng PL (2000) Evaluation of age- and sex-dependent rates of tag-loss in southern elephant seals. *J Wildl Manage* 64:373-380
- Pistorius PA, Bester MN, Lewis MN, Taylor FE, Campagna C, Kirkman SP (2004) Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal. *J Zool Lond* 263:107-119
- Siniff DB, DeMaster DP, Hofman RJ, Eberhardt LL (1977) An analysis of the dynamics of a Weddell seal population. *Ecol Monogr* 47:319-335
- Wilkinson IS, Bester MN (1990) Duration of post-weaning fast and local dispersion in the southern elephant seal, *Mirounga leonina*, at Marion Island. *J Zool Lond* 222:591-600
- Wilkinson IS (1991) Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. PhD thesis University of Pretoria Pretoria
- Wilkinson IS, Van Aarde RJ (2001) Investment in sons and daughters by southern elephant seals, *Mirounga leonina*, at Marion Island. *Mar Mamm Sci* 17:873-887

**CHAPTER FOUR:**  
**IMPROVED SURVIVORSHIP, AND IMMIGRATION, DRIVE A POPULATION  
STATE CHANGE IN SOUTHERN ELEPHANT SEALS AT MARION ISLAND**

**Abstract**

Vital rates of large mammal populations are believed to be closely linked with both extrinsic and intrinsic drivers. Demographic studies spanning the longevity of large mammals are rare and survivorship schedules gleaned from such studies are particularly useful in elucidating population regulating factors. This study uses a unique life history dataset for southern elephant seals, *Mirounga leonina*, spanning a quarter of a century, encompassing periods of decline and increase in this small population. We use Program MARK to re-evaluate significant earlier findings from the first half of this dataset (Pistorius et al. 1999. *Oecologia*, 121:201-211) and extend it by a further 10 years using matching analytical techniques. Increases in juvenile survival (both sexes) and adult female survival during the period of increase took place. Increased juvenile survival appears to precede such an increase in adult female survival and thus the prior is identified as the initiator of a population state change that is subsequently maintained by stable and high adult female survival. We provide distinction between the point of inflexion in survivorship as 1994, and the point of inflexion in the trend of this population as 1997/8, and believe that lack of this distinction between survival and population size estimates have fueled past debate. Significant overdispersion in our data, particularly violation of homogeneity in recapture model assumptions, may indicate unquantified dispersal by marked Marion Island southern elephant seals. Continued low apparent survival of pubescent male seals may be linked to such emigration. Immigration to this population may suggest a combined effect with increased survivorship in driving the state change in this small population. Holistic, ecosystem-wide research conducted with a multistate modeling approach is required to further illuminate the relative contribution of different extrinsic and intrinsic driving factors in this population.

## Introduction

Population response in large marine vertebrates is purported to be sensitive to environmental regime shifts (Weimerskirch et al. 2003) and manifested in the form of per capita control of vital rates (e.g. fecundity, survival) over relatively short time periods (McMahon et al. 2009). Southern elephant seals, *Mirounga leonina*, are apex predators within the Southern Ocean ecosystem with wide distribution (McMahon et al. 2005a) and extensive foraging areas (Jonker and Bester 1998; Biuw et al. 2007; Tosh et al. 2009), conducive to studies of environmental regime shifts. Recently, research on this species has shifted from identifying the causes for the large population decreases evident for many southern elephant seal populations through the 1950s and 1990s (McMahon et al. 2005a) to a focus on establishing which extrinsic and intrinsic drivers of this decline have changed to allow stabilization or even increase in some of the populations. Vital rates are influenced by a complex interplay of intrinsic and extrinsic factors in the regulation of apex predator populations (e.g. de Little et al. 2007). Differences in population size, however, may obscure the relative contributions of intrinsic or extrinsic regulating factors. For example, while predation may have negligible effects on large prey populations, significant top-down control may drive small populations to a decreasing state (Springer et al. 2003). Consequently, extrinsic drivers (including predation pressure or food availability via environmental fluxes) or intrinsic drivers (population density) may impact on vital rates of large and small populations differently (McMahon et al. 2005b). Life-history parameters that may be influenced by these drivers and are fundamental in determining population numbers include survival, fecundity and dispersal (Caughley 1977; Siniff et al. 1977). Survival is a particularly useful demographic parameter because changes in this parameter are often associated with size and structure changes in a population (Lebreton et al. 1993). Relatively slight perturbations, particularly in survival (Eberhardt and Siniff 1977) and immigration/emigration (Cooper and Stewart 1983) for large mammals, can significantly alter the state of a small population. Although fecundity is obviously a vital parameter in regulating the growth of any sized population, physiological limits to its rate of increase in large mammals particularly, reduces its relative (compared to survival's) ability to regulate a population (Saether 1997; Bester and Wilkinson 1994; Pistorius et al. 2001).

The southern elephant seal population at Marion Island in the south Indian Ocean, is one such small population that has experienced substantial decline since the 1950s (Pistorius et al. 1999a; McMahon et al. 2005a) until a recent change to stabilization (mid- to end 1990s – McMahon et al. 2003; Pistorius et al. 2004) and current increase (McMahon et al. 2009). Long term, intensive population demographic studies (1983 – present) (Bester 1988) have allowed assessment of vital rates and population numbers to elucidate the causes for these population fluctuations. The first detailed study to assess the survivorship of this population identified increased adult female mortality (hypothesized to be ultimately caused by food limitation) as the proximal cause for the observed decline of the population at the time (Pistorius et al. 1999b). Indeed, prior to that study, Wilkinson (1991) and Bester and Wilkinson (1994) noted young adult females as possible drivers of the population decline. Pistorius et al. (2004) provided further evidence that an increase in prime-aged adult female survival caused the recent stabilization in this population, and showed that postbreeding and postmoulting mortality risk varied independently over time, demonstrating the importance of an intra-annual approach in population studies of southern elephant seals (Pistorius et al. 2008a). Conversely, based on comparative studies of decline in a large (Macquarie Island) and small (Marion Island) population of these seals, McMahon et al. (2003, 2005b) argued that juvenile survival was principally involved in the regulation of both these populations. Indeed, in this species, most populations with available life-history data have been shown to be chiefly regulated by juvenile survival (McCann 1985; Hindell 1991; McMahon et al. 2005b). Juvenile survival is often thought to be a key regulating factor in population dynamics in many mammalian populations (Eberhardt and Siniff 1977; Gaillard et al. 1998; Baker and Thompson 2007), while others argue the role that adult survival plays in shaping population dynamics (Gaillard and Yoccoz 2003; Coulson et al. 2005; Toïgo et al. 2007), thus the population demographics of southern elephant seals at Marion Island are not unique in fueling this debate.

In addition to the controversy surrounding the main drivers of population regulation of elephant seals at Marion Island, the point of inflexion from a declining to a stable/increasing population also remains debated. Stabilization is suggested to be around 1994 (Pistorius et al. 1999a, b, 2001, 2004, 2008b), while others contend that 1998 is a more likely point of inflexion in the population trend (McMahon et al. 2003,

2005b, 2009). The pivotal role that the Pistorius et al. (1999b) study has played as foundation for much of the subsequent work on this topic, and the continued debate surrounding aspects of the demography of this population, prompted the compilation of this paper. We use a 25-year longitudinal dataset (1983-2008) that extends the Pistorius et al. (1999b) study by a further 10 consecutive cohorts and an additional 10 years of intensive recapture histories, to re-evaluate the survival rates of the Marion Island elephant seal population. The analytical approaches in that study (Pistorius et al. 1999b), in particular the treatment of extra-binomial variation in the dataset, are explored by following the exact same analytical procedure, amended to include some omissions. Fortuitously, the dataset is roughly divided between a period of decline and current stabilization/increase (McMahon et al. 2009). This provides a unique opportunity to study a complete generational survivorship schedule of a small population of large mammals in an attempt to clarify two contentious issues, that of sex- and age- specific drivers of regulation and the timing of inflexion in the state of this population. In so doing, we present the only uninterrupted longitudinal survivorship schedule for this species, that surpasses the proven longevity (23 years) of southern elephant seals (Hindell and Little 1988).

## **Materials and Methods**

### *Study site*

Sub-Antarctic Marion Island (46°54'S, 37°45'E) is situated in the Southern Indian Ocean (Fig. 1.1) and is approximately 296 km<sup>2</sup> in area. Southern elephant seals use the more easily accessible beaches particularly on the eastern and northern shores and limited parts of the southern shore, hauling out to rest, breed or moult (Condy 1978) on some 54 beaches along approximately 52 km of coastline (Fig. 1.2).

### *Tagging and resighting of seals*

An intensive tagging program of southern elephant seals commenced in 1983 at Marion Island (Bester 1988). From 1983 to 2002, a total of 9473 (average: 474 annually, range: 389–700) newly weaned pups were double tagged in their hindflippers using Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, U.K.) (see Chapter 3 for details – de Bruyn et al. 2008). From 1983 to 1999, tags were placed in the centre of either of the inner two interdigital webbing sections of the

hindflipper, while from 2000 to 2002 tags were placed in the upper outer-interdigital webbing sections, but always with approximately one-third of the length of the tag extending beyond the edge of the webbing. The sex of each seal, date and location were noted at tagging. The self-piercing tags were uniquely embossed with a three-digit number, and colour-coded to denote the year of application, while the tagging site (Marion Is.) appeared on the inside of each tag component.

All beaches known as elephant seal haul-out sites were checked for tagged seals every seven days during the breeding season (mid-Aug to mid-Nov) and every 10 days during the moulting period (mid-Nov to mid-Apr) from 1983 to 1990. From 1990 the resighting effort every 10 days also extended through the entire non-breeding period (mid-Nov to mid-Aug). The increased difficulty in reading tags in harems as compared with the non-breeding period when seals are more dispersed and less aggressive was countered by increased frequency of resighting effort during the breeding season (every seven days, all years). For each seal that was resighted, the tag number, tag colour combination, number of tags remaining (one or two), location and date of the sighting were noted. Appendix 2 (Oosthuizen et al. 2009) describes the tag-loss rates for this population of seals by age-, sex- and cohort and these were used to correct apparent survival estimates in this study.

### *Analysis*

For analysis, only the last resight of multiple resightings of each individual within any given year was used. If an animal was sighted only once after an absence of four years and then never again, the entry was judged to be erroneous and was removed from analyses. Single sightings of any individuals during the course of a year were carefully inspected alongside previous and subsequent (year) records and the validity of such single resights during a year judged against previous haul-out behaviour (i.e. philopatry to habitual haul-out area, social status of the individual at the time of haul-out etc.). However, the resighting schedule (see above) resulted in comparatively few single resights during a year compared with multiple resights, thereby allowing confidence in correct resighting data. All seals were assumed to age on 15 October, which is the peak adult female haul-out date at Marion Island (Kirkman et al. 2004). Capture-history matrices were constructed using the resighting (recapture) data from the 1983 to 2002 cohorts, up to but not including the

commencement of the 2008 breeding season. This allowed 24 years of resighting history for the 1983 cohort and 5 years for the 2002 cohort, effectively doubling the number of cohorts and resighting history timespan over that of the Pistorius et al. (1999b) study.

These capture-history matrices (depicting absence or presence of individuals per year as 0 or 1 respectively, over time) were condensed to 40 sex-specific input files for the 20 cohorts (mimicking the analytical design used by Pistorius et al. [1999b]). These capture-history matrices were used as input files for the software package MARK (White and Burnham 1999), an application for the analysis of marked individuals, used to obtain maximum-likelihood estimates of survival and resight probability. MARK provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model and under several models that appear as special cases of this model (Lebreton et al. 1992). As it was impossible to distinguish between mortality and permanent emigration, we imply apparent rather than absolute survival. The two fundamental parameters of these models are:

$\Phi_i$  = the apparent survival probability for all animals between the  $i$ th and  $(i + 1)$ th sample ( $i = 1, \dots, k - 1$ ), and

$\rho_i$  = the recapture probability for all animals in the  $i$ th sample ( $i = 2, \dots, k$ ).

The first step in the mark-recapture analyses involves Goodness-of-Fit (GOF) tests for the CJS model, and we used Program RELEASE to validate the model assumptions. Despite some support for no age dependence in apparent survival (hereafter 'survival') of primiparous adult female southern elephant seals from this population (Pistorius et al. 2004), our inclusion of both sex and all age categories in analysis resulted in age-dependence being assumed in this study and as such Test 3.Sm was retained (see Lebreton et al. 1992). In this study time-dependent and age-dependent survival could not be differentiated due to time and age intervals being equivalent, as a result of the exclusive use of single cohorts as separate input matrices for MARK.

Five models were considered for each sex. Firstly, a candidate set of 4 models with varying constraints on survival and resighting probability, exactly replicating those used by Pistorius et al. (1999b) were considered for each sex to establish the survivorship schedule. Based on indications from McMahon et al. (2003) and



Pistorius et al. (2004, 2008a), an additional age-constrained model describing age-dependence in survival up to (and including) earliest age at primiparity (3 yrs), followed by constant survival, was added for females. A fifth model, describing constant survival of males after age six was defined, based on the relative cessation of the secondary growth spurt evident in males between the ages of 4 and 6 (Pistorius et al. 2005) and indications of breeding by some males in this younger age bracket at Marion Island (M.N. Bester unpubl. data). The most parsimonious model out of the set of 4 or 5 models *per sex per cohort* (with and without the addition of the extra models to be comparable with Pistorius et al. [1999b]), was selected using the small sample corrected Akaike Information Criterion ( $AIC_c$ ) (Lebreton et al. 1992; Anderson et al. 1994).  $AIC_c$  weighs the deviance (quality of fit) and the precision (via number of estimable parameters) to select a model that best describes the data (Lebreton et al. 1992). Violation of one or more of the CJS model assumptions, as identified in GOF testing, would require correction for extra-binomial variation using a variance inflation factor ( $\hat{c}$ ) by adjusting  $AIC_c$  estimates ( $QAIC_c$ ) for the CJS and nested models. Despite over-dispersion in their data,  $\hat{c}$  adjustments to  $AIC_c$  estimates were not performed by Pistorius et al. (1999b). Thus, the model sets (with four models *per sex per cohort*) exactly comparable with the Pistorius et al. (1999b) procedure were not adjusted for overdispersion ( $AIC_c$ ), while the model sets (with five models *per sex per cohort*) were adjusted for overdispersion ( $QAIC_c$ ). In so doing, the relative effects of adjustment and non-adjustment of mark-recapture results, corollary to model assumption violations (see also Appendix 1 in de Little et al. 2007), are provided to illustrate potentially erroneous biological interpretation of survivorship data. In accord with Pistorius et al. (1999b), a major aim of this study was to determine which age categories were most closely related with the population state change, and thus estimates from the simplest model (constant survival and capture) were not selected for estimate outputs.

Real parameter estimates for survival and resighting probability from the two permutations of model selection (i.e. four candidate models  $AIC_c$ , and five candidate models  $QAIC_c$ ) were used to create cohort (as opposed to “stationary”) life tables (Caughley 1977), representing the general survival schedule for the Marion Island southern elephant seal population. Life tables have the benefit of representing the survival schedule of a population while reducing the possible effects of short-term

fluctuations in environmental and demographic variables. The product of all survival values ( $\Phi$ ) prior to a given age ( $x$ ) were used to calculate the probability of survival to that age ( $l_x$ ). These  $l_x$  values were used to calculate the probability of dying ( $d_x = l_x - l_{x+1}$ ) and mortality rate ( $q_x = d_x / l_x$ ), while survival rates were taken from the MARK survival estimates ( $p_x = \Phi$ ). These life tables were used to identify if noteworthy differences were observable in survival schedule based on the two permutations of model selection. Parameter outputs from the most parsimonious models for each of the model sets ( $AIC_c$  and  $QAIC_c$ ) were selected to continue with the analysis of survivorship.

Age-specific survival estimates from the 20 cohorts were plotted against each other, to firstly represent interannual differences in survival estimates, secondly to identify years of poor survival and thirdly to compare findings with those of Pistorius et al. (1999b). The continued disputed timing of the point of trend inflexion in this population prompted a survivorship aligned investigation in this study to help clarify this issue. Consequently, age-specific survival estimate means were compared; firstly, between the 1983 – 1993 and 1994 – 2008 periods, and secondly, between the 1983 – 1998 and 1999 – 2008 periods. The median value was included into both periods in cases where means were calculated using uneven numbers of estimates.

## Results

### *Goodness-of-Fit*

Goodness-of-fit test results (program RELEASE) are shown in Table 4.1.

All, except for the 1983 female cohort, showed significant ( $P < 0.001$ ) departures from the assumptions of the global CJS model. The overall data were analysed further with program RELEASE to elucidate the causes for lack of fit (Burnham et al. 1987). Test 2, was identified for each sex and cohort as indicating significant variations in recapture (resighting) rates of seals. In general, Test 2 is sensitive to short-term recapture effects, or non-random temporary emigration. It highlights failure of the homogeneity assumption among animals and between occasions. Violation thereof may indicate that seeing an animal is dependent on if/when it was previously seen.

**Table 4.1.** Goodness-of-fit test results from Program RELEASE, of Cormack-Jolly-Seber (CJS) general models by southern elephant seal cohorts (1983 -2002).

Cohort	Males			Females		
	$\chi^2$	<i>df</i>	<i>P</i>	$\chi^2$	<i>df</i>	<i>P</i>
1983	40.532	14	0.0002	9.894	12	0.6252
1984	30.508	14	0.0065	30.466	15	0.0103
1985	76.938	14	0.0000	105.671	32	0.0000
1986	46.705	11	0.0000	73.787	19	0.0000
1987	87.786	15	0.0000	98.484	23	0.0000
1988	51.194	14	0.0000	59.821	20	0.0000
1989	38.250	13	0.0003	73.542	18	0.0000
1990	79.158	13	0.0000	73.144	15	0.0000
1991	53.797	14	0.0000	118.940	21	0.0000
1992	73.174	15	0.0000	52.213	15	0.0000
1993	96.627	13	0.0000	148.667	25	0.0000
1994	44.229	10	0.0000	128.675	23	0.0000
1995	80.692	13	0.0000	94.819	22	0.0000
1996	32.219	11	0.0007	118.432	21	0.0000
1997	74.124	12	0.0000	44.926	17	0.0002
1998	48.104	11	0.0000	46.309	12	0.0000
1999	45.669	11	0.0000	18.312	9	0.0317
2000	73.605	10	0.0000	92.892	15	0.0000
2001	37.229	8	0.0000	59.076	8	0.0000
2002	48.483	6	0.0000	54.209	7	0.0000

To a far lesser extent and for fewer cohorts, Test 3 indicated heterogeneity in survival rates. Because some heterogeneity in recapture and survival probabilities do not affect survival rate estimates substantially (Carothers 1979; Nichols et al.1982; Barker 1992), we present our survival estimates from MARK, but report both over-dispersion adjusted and non-adjusted model outputs to illustrate the possible differences in results.

#### *Model selection and extra-binomial variation*

Table 4.2 shows the selection of models based on the two selection criteria (see Methods). The constant survival and capture probability model ( $\Phi_c, \rho_c$ ) was most parsimonious for 19 of the male and 16 of the female cohorts, respectively, although the relative support for this model as compared to the next most parsimonious model in females was sometimes modest (see QAIC<sub>c</sub> weights in Table 4.2). Selection of this simplest model is fairly expected as a consequence of the  $\hat{c}$  adjustments, which change the estimated standard errors for each parameter in a model, resulting in QAIC<sub>c</sub> favouring a model with reduced parameters rather than one that describes the

biological variation best (Anderson et al. 1994). We selected the next most parsimonious model for gaining survival estimates in light of our objective for assessing age-specific associations with population state change. In all cases this resulted in parsimonious selection of constant recapture and ‘constant survival after age 3’ model for females, and ‘constant survival after age 6’ model for males, respectively (Table 4.2). When these models were excluded from the candidate list and no overdispersion adjustments made, following Pistorius et al. (1999b), the  $AIC_c$  selected models varied considerably (Table 4.2).

**Table 4.2.** Elimination of non-significant effects from the global CJS model for each sex within each cohort (1983 – 2003) of southern elephant seals at Marion Island. For each model the Quasi-Akaike Information Criterion ( $QAIC_c$ ) and overdispersion adjustments are given for each sex in each cohort ( $\hat{c}$ );  $QAIC_c$  weight, number of estimable parameters ( $NP$ ) and Quasi-Deviance ( $QDEV$ ) are given. Apparent survival probabilities are referred to as  $\Phi$  and recapture probabilities as  $\rho$ . The figures in the model refer to time-dependence up to a particular year of life,  $\Phi_{1-4/7/9}$  survival probability constant after age 3/6/8; t – time dependent; c – constant over time. Models  $\Phi_{1-7}, \rho_c$  (for males), and  $\Phi_{1-4}, \rho_c$  (for females) were not tested in Pistorius *et al.* (1999b).  $QAIC_c$  highlighted in **bold-face** depicts the selected model for real parameter outputs, while # $QAIC_c$  (without  $\hat{c}$  adjustment =  $AIC_c$ ) selected models (for parameter outputs) are comparable with selection criteria in Pistorius *et al.* (1999b).

Cohort	Males					Females				
	Model	$QAIC_c^{(\hat{c})}$	$QAIC_c$ weights	np	QDev	Model	$QAIC_c^{(\hat{c})}$	$QAIC_c$ weights	np	QDev
1983	(1) $\Phi_t, \rho_t$ (CJS)	397.013 <sup>(2.895)</sup>	0.000	25	50.570	(1) $\Phi_t, \rho_t$ (CJS)	1059.702 <sup>(0.825)</sup>	0.000	35	101.272
	(2) $\Phi_t, \rho_c$	375.571	0.000	14	53.050	(2) $\Phi_t, \rho_c$	1046.159	0.001	19	123.304
	(3) $\Phi_c, \rho_c$	354.468	0.995	2	56.808	(3) $\Phi_c, \rho_c$	1038.731	0.029	2	151.328
	(4) $\Phi_{1-7}, \rho_c$	<b>365.311</b>	0.004	8	55.375	(4) $\Phi_{1-4}, \rho_c$	<b>1032.120</b>	0.791	5	138.627
	(5) $\Phi_{1-9}, \rho_c$	# 369.103	0.001	10	55.007	(5) $\Phi_{1-7}, \rho_c$	# 1035.088	0.179	8	135.434
1984	(1) $\Phi_t, \rho_t$ (CJS)	548.470 <sup>(2.179)</sup>	0.000	29	46.659	(1) $\Phi_t, \rho_t$ (CJS)	657.060 <sup>(2.031)</sup>	0.000	35	100.267
	(2) $\Phi_t, \rho_c$	527.619	0.000	16	54.170	(2) $\Phi_t, \rho_c$	636.231	0.000	20	112.161
	(3) $\Phi_c, \rho_c$	506.566	0.985	2	62.130	(3) $\Phi_c, \rho_c$	625.405	0.001	2	138.632
	(4) $\Phi_{1-7}, \rho_c$	<b>515.297</b>	0.013	8	58.614	(4) $\Phi_{1-4}, \rho_c$	<b>610.874</b>	0.953	5	118.027
	(5) $\Phi_{1-9}, \rho_c$	# 518.691	0.002	10	57.863	(5) $\Phi_{1-7}, \rho_c$	# 616.934	0.046	8	117.958
1985	(1) $\Phi_t, \rho_t$ (CJS)	345.355 <sup>(5.496)</sup>	0.000	22	31.040	(1) $\Phi_t, \rho_t$ (CJS)	678.539 <sup>(3.302)</sup>	0.000	37	102.165
	(2) $\Phi_t, \rho_c$	328.312	0.000	13	32.785	(2) $\Phi_t, \rho_c$	653.339	0.000	21	111.149
	(3) $\Phi_c, \rho_c$	309.906	0.990	2	36.800	(3) $\Phi_c, \rho_c$	622.668	0.772	2	119.505
	(4) $\Phi_{1-7}, \rho_c$	<b>319.583</b>	0.008	8	34.320	(4) $\Phi_{1-4}, \rho_c$	<b>625.267</b>	0.210	5	116.052
	(5) $\Phi_{1-9}, \rho_c$	# 322.436	0.002	10	33.082	(5) $\Phi_{1-7}, \rho_c$	# 630.226	0.018	8	114.917
1986	(1) $\Phi_t, \rho_t$ (CJS)	# 339.504 <sup>(4.246)</sup>	0.000	23	30.367	(1) $\Phi_t, \rho_t$ (CJS)	508.145 <sup>(3.884)</sup>	0.000	35	68.864
	(2) $\Phi_t, \rho_c$	326.272	0.000	14	36.237	(2) $\Phi_t, \rho_c$	479.001	0.000	19	73.851
	(3) $\Phi_c, \rho_c$	308.373	0.956	2	42.982	(3) $\Phi_c, \rho_c$	455.569	0.587	2	85.300
	(4) $\Phi_{1-7}, \rho_c$	<b>314.795</b>	0.039	8	37.197	(4) $\Phi_{1-4}, \rho_c$	<b>456.592</b>	0.352	5	80.266
	(5) $\Phi_{1-9}, \rho_c$	318.687	0.006	10	36.970	(5) $\Phi_{1-7}, \rho_c$	# 460.103	0.061	8	77.680
1987	(1) $\Phi_t, \rho_t$ (CJS)	279.995 <sup>(5.852)</sup>	0.000	23	28.349	(1) $\Phi_t, \rho_t$ (CJS)	508.726 <sup>(4.282)</sup>	0.000	34	64.945
	(2) $\Phi_t, \rho_c$	260.050	0.000	13	29.515	(2) $\Phi_t, \rho_c$	485.492	0.000	19	73.556
	(3) $\Phi_c, \rho_c$	242.851	0.979	2	34.834	(3) $\Phi_c, \rho_c$	458.556	0.755	2	81.451
	(4) $\Phi_{1-7}, \rho_c$	<b>250.832</b>	0.018	8	30.622	(4) $\Phi_{1-4}, \rho_c$	<b>461.072</b>	0.215	5	77.915

	(5) $\Phi_{1-9}, \rho_c$	# 254.640	0.003	10	30.318	(5) $\Phi_{1-7}, \rho_c$	# 464.983	0.030	8	75.733
1988	(1) $\Phi_t, \rho_t$ (CJS)	444.014 <sup>(3.657)</sup>	0.000	25	41.012	(1) $\Phi_t, \rho_t$ (CJS)	# 602.738 <sup>(2.991)</sup>	0.000	36	85.642
	(2) $\Phi_t, \rho_c$	423.293	0.000	14	43.536	(2) $\Phi_t, \rho_c$	586.035	0.000	20	103.294
	(3) $\Phi_c, \rho_c$	405.032	0.987	2	49.841	(3) $\Phi_c, \rho_c$	568.449	0.111	2	122.745
	(4) $\Phi_{1-7}, \rho_c$	<b>414.059</b>	0.011	8	46.687	(4) $\Phi_{1-4}, \rho_c$	<b>564.501</b>	0.802	5	112.738
	(5) $\Phi_{1-9}, \rho_c$	# 417.008	0.002	10	45.530	(5) $\Phi_{1-7}, \rho_c$	568.966	0.086	8	111.099
1989	(1) $\Phi_t, \rho_t$ (CJS)	414.435 <sup>(2.942)</sup>	0.000	24	42.132	(1) $\Phi_t, \rho_t$ (CJS)	# 431.956 <sup>(4.086)</sup>	0.000	36	49.547
	(2) $\Phi_t, \rho_c$	396.946	0.004	14	46.094	(2) $\Phi_t, \rho_c$	410.173	0.000	19	64.550
	(3) $\Phi_c, \rho_c$	390.432	0.100	2	64.318	(3) $\Phi_c, \rho_c$	383.968	0.664	2	73.403
	(4) $\Phi_{1-7}, \rho_c$	<b>386.487</b>	0.717	8	48.136	(4) $\Phi_{1-4}, \rho_c$	<b>385.500</b>	0.309	5	68.868
	(5) $\Phi_{1-9}, \rho_c$	# 389.261	0.179	10	46.773	(5) $\Phi_{1-7}, \rho_c$	390.354	0.027	8	67.605
1990	(1) $\Phi_t, \rho_t$ (CJS)	# 232.106 <sup>(6.089)</sup>	0.000	24	23.850	(1) $\Phi_t, \rho_t$ (CJS)	375.064 <sup>(4.876)</sup>	0.000	34	48.890
	(2) $\Phi_t, \rho_c$	216.851	0.000	15	27.873	(2) $\Phi_t, \rho_c$	347.369	0.000	18	55.364
	(3) $\Phi_c, \rho_c$	194.633	0.993	2	32.465	(3) $\Phi_c, \rho_c$	321.161	0.753	2	61.993
	(4) $\Phi_{1-7}, \rho_c$	<b>205.082</b>	0.005	8	30.688	(4) $\Phi_{1-4}, \rho_c$	<b>323.511</b>	0.232	5	58.284
	(5) $\Phi_{1-9}, \rho_c$	207.805	0.001	10	29.281	(5) $\Phi_{1-7}, \rho_c$	# 328.985	0.015	8	57.655
1991	(1) $\Phi_t, \rho_t$ (CJS)	330.892 <sup>(3.843)</sup>	0.000	27	34.244	(1) $\Phi_t, \rho_t$ (CJS)	387.373 <sup>(5.664)</sup>	0.000	31	76.374
	(2) $\Phi_t, \rho_c$	308.973	0.000	15	38.176	(2) $\Phi_t, \rho_c$	361.850	0.000	17	80.407
	(3) $\Phi_c, \rho_c$	288.295	0.981	2	44.312	(3) $\Phi_c, \rho_c$	338.234	0.554	2	87.455
	(4) $\Phi_{1-7}, \rho_c$	<b>296.492</b>	0.016	8	40.281	(4) $\Phi_{1-4}, \rho_c$	<b>338.771</b>	0.424	5	81.940
	(5) $\Phi_{1-9}, \rho_c$	# 300.083	0.003	10	39.741	(5) $\Phi_{1-7}, \rho_c$	# 344.701	0.022	8	81.778
1992	(1) $\Phi_t, \rho_t$ (CJS)	238.512 <sup>(4.878)</sup>	0.000	25	25.687	(1) $\Phi_t, \rho_t$ (CJS)	429.750 <sup>(3.481)</sup>	0.000	29	58.219
	(2) $\Phi_t, \rho_c$	216.874	0.000	14	27.975	(2) $\Phi_t, \rho_c$	408.079	0.000	16	64.256
	(3) $\Phi_c, \rho_c$	200.619	0.918	2	36.583	(3) $\Phi_c, \rho_c$	394.040	0.099	2	78.957
	(4) $\Phi_{1-7}, \rho_c$	<b>205.758</b>	0.070	8	29.447	(4) $\Phi_{1-4}, \rho_c$	<b>389.721</b>	0.857	5	68.572
	(5) $\Phi_{1-9}, \rho_c$	# 209.314	0.012	10	28.841	(5) $\Phi_{1-7}, \rho_c$	# 395.668	0.044	8	68.404
1993	(1) $\Phi_t, \rho_t$ (CJS)	218.023 <sup>(7.433)</sup>	0.000	28	24.316	(1) $\Phi_t, \rho_t$ (CJS)	307.837 <sup>(5.947)</sup>	0.000	27	54.592
	(2) $\Phi_t, \rho_c$	191.986	0.000	15	26.256	(2) $\Phi_t, \rho_c$	283.972	0.000	15	56.156
	(3) $\Phi_c, \rho_c$	170.582	0.978	2	31.637	(3) $\Phi_c, \rho_c$	264.060	0.672	2	62.877
	(4) $\Phi_{1-7}, \rho_c$	<b>178.472</b>	0.019	8	27.307	(4) $\Phi_{1-4}, \rho_c$	<b>265.652</b>	0.303	5	58.404
	(5) $\Phi_{1-9}, \rho_c$	# 182.407	0.003	10	27.116	(5) $\Phi_{1-7}, \rho_c$	# 270.675	0.025	8	57.315
1994	(1) $\Phi_t, \rho_t$ (CJS)	268.159 <sup>(4.423)</sup>	0.000	25	21.082	(1) $\Phi_t, \rho_t$ (CJS)	# 369.434 <sup>(5.595)</sup>	0.000	23	63.622
	(2) $\Phi_t, \rho_c$	246.669	0.000	14	23.445	(2) $\Phi_t, \rho_c$	355.651	0.000	13	71.013
	(3) $\Phi_c, \rho_c$	230.480	0.935	2	32.087	(3) $\Phi_c, \rho_c$	341.375	0.520	2	79.283
	(4) $\Phi_{1-7}, \rho_c$	<b>236.450</b>	0.047	8	25.792	(4) $\Phi_{1-4}, \rho_c$	<b>341.710</b>	0.439	5	73.545

	(5) $\Phi_{1-9}, \rho_c$	# 238.410	0.018	10	23.596	(5) $\Phi_{1-7}, \rho_c$	346.486	0.040	8	72.190
1995	(1) $\Phi_t, \rho_t$ (CJS)	203.281 <sup>(6.207)</sup>	0.000	20	25.300	(1) $\Phi_t, \rho_t$ (CJS)	369.434 <sup>(4.310)</sup>	0.000	23	63.622
	(2) $\Phi_t, \rho_c$	187.656	0.001	12	26.717	(2) $\Phi_t, \rho_c$	355.651	0.000	13	71.013
	(3) $\Phi_c, \rho_c$	174.618	0.947	2	34.258	(3) $\Phi_c, \rho_c$	341.375	0.520	2	79.283
	(4) $\Phi_{1-7}, \rho_c$	<b>180.761</b>	0.044	8	28.148	(4) $\Phi_{1-4}, \rho_c$	<b>341.710</b>	0.439	5	73.545
	(5) $\Phi_{1-9}, \rho_c$	# 184.137	0.008	10	27.377	(5) $\Phi_{1-7}, \rho_c$	# 346.486	0.040	8	72.190
1996	(1) $\Phi_t, \rho_t$ (CJS)	307.756 <sup>(2.929)</sup>	0.000	19	29.720	(1) $\Phi_t, \rho_t$ (CJS)	315.971 <sup>(5.640)</sup>	0.000	21	57.674
	(2) $\Phi_t, \rho_c$	# 293.246	0.004	11	32.420	(2) $\Phi_t, \rho_c$	300.391	0.000	12	60.874
	(3) $\Phi_c, \rho_c$	282.303	0.979	2	40.075	(3) $\Phi_c, \rho_c$	283.529	0.900	2	64.388
	(4) $\Phi_{1-7}, \rho_c$	<b>290.722</b>	0.015	8	36.183	(4) $\Phi_{1-4}, \rho_c$	<b>288.091</b>	0.092	5	62.890
	(5) $\Phi_{1-9}, \rho_c$	294.437	0.002	10	35.717	(5) $\Phi_{1-7}, \rho_c$	# 293.072	0.008	8	61.767
1997	(1) $\Phi_t, \rho_t$ (CJS)	208.473 <sup>(6.177)</sup>	0.000	19	22.950	(1) $\Phi_t, \rho_t$ (CJS)	570.628 <sup>(2.643)</sup>	0.000	19	76.661
	(2) $\Phi_t, \rho_c$	193.589	0.000	11	25.003	(2) $\Phi_t, \rho_c$	556.068	0.000	11	78.807
	(3) $\Phi_c, \rho_c$	176.147	0.996	2	26.028	(3) $\Phi_c, \rho_c$	539.008	0.946	2	80.100
	(4) $\Phi_{1-7}, \rho_c$	# <b>187.802</b>	0.003	8	25.440	(4) $\Phi_{1-4}, \rho_c$	<b>544.873</b>	0.050	5	79.899
	(5) $\Phi_{1-9}, \rho_c$	191.515	0.000	10	25.012	(5) $\Phi_{1-7}, \rho_c$	# 550.228	0.003	8	79.137
1998	(1) $\Phi_t, \rho_t$ (CJS)	233.523 <sup>(4.373)</sup>	0.000	17	23.514	(1) $\Phi_t, \rho_t$ (CJS)	# 337.377 <sup>(3.859)</sup>	0.000	17	31.625
	(2) $\Phi_t, \rho_c$	# 219.981	0.001	10	24.920	(2) $\Phi_t, \rho_c$	331.924	0.002	10	40.813
	(3) $\Phi_c, \rho_c$	205.417	0.996	2	26.847	(3) $\Phi_c, \rho_c$	319.684	0.891	2	44.908
	(4) $\Phi_{1-7}, \rho_c$	<b>216.565</b>	0.004	8	25.685	(4) $\Phi_{1-4}, \rho_c$	<b>324.189</b>	0.094	5	43.337
						(5) $\Phi_{1-7}, \rho_c$	328.040	0.014	8	41.053
1999	(1) $\Phi_t, \rho_t$ (CJS)	236.218 <sup>(4.152)</sup>	0.000	15	23.968	(1) $\Phi_t, \rho_t$ (CJS)	# 505.487 <sup>(2.035)</sup>	0.002	15	34.247
	(2) $\Phi_t, \rho_c$	# 225.171	0.002	9	25.642	(2) $\Phi_t, \rho_c$	503.037	0.007	9	44.382
	(3) $\Phi_c, \rho_c$	213.028	0.992	2	27.894	(3) $\Phi_c, \rho_c$	493.449	0.801	2	49.115
	(4) $\Phi_{1-7}, \rho_c$	<b>223.182</b>	0.006	8	25.738	(4) $\Phi_{1-4}, \rho_c$	<b>496.414</b>	0.182	5	45.989
						(5) $\Phi_{1-7}, \rho_c$	502.524	0.009	8	45.939
2000	(1) $\Phi_t, \rho_t$ (CJS)	146.308 <sup>(7.361)</sup>	0.000	13	14.611	(1) $\Phi_t, \rho_t$ (CJS)	# 240.612 <sup>(6.193)</sup>	0.001	13	30.036
	(2) $\Phi_t, \rho_c$	# <b>136.742</b>	0.004	8	15.553	(2) $\Phi_t, \rho_c$	235.172	0.009	8	34.954
	(3) $\Phi_c, \rho_c$	125.713	0.996	2	16.824	(3) $\Phi_c, \rho_c$	225.925	0.907	2	37.918
						(4) $\Phi_{1-4}, \rho_c$	<b>230.693</b>	0.084	5	36.610
2001	(1) $\Phi_t, \rho_t$ (CJS)	200.719 <sup>(4.654)</sup>	0.001	11	18.736	(1) $\Phi_t, \rho_t$ (CJS)	# 173.007 <sup>(7.384)</sup>	0.001	11	13.195
	(2) $\Phi_t, \rho_c$	# <b>193.146</b>	0.058	7	19.506	(2) $\Phi_t, \rho_c$	166.764	0.017	7	15.210
	(3) $\Phi_c, \rho_c$	187.566	0.941	2	24.148	(3) $\Phi_c, \rho_c$	158.897	0.863	2	17.512
						(4) $\Phi_{1-4}, \rho_c$	<b>162.845</b>	0.120	5	15.379
2002	(1) $\Phi_t, \rho_t$ (CJS)	118.555 <sup>(8.080)</sup>	0.002	9	8.505	(1) $\Phi_t, \rho_t$ (CJS)	# 145.933 <sup>(7.744)</sup>	0.002	9	10.653

---

(2) $\Phi_t, \rho_c$	# <b>112.690</b>	0.031	6	8.856	(2) $\Phi_t, \rho_c$	140.620	0.034	6	11.514
(3) $\Phi_c, \rho_c$	105.808	0.967	2	10.133	(3) $\Phi_c, \rho_c$	134.107	0.874	2	13.132
					(4) $\Phi_{1-4}, \rho_c$	<b>138.643</b>	0.090	5	11.581

---



### Cohort life tables

Table 4.3a, b, and 4.4a, b, present the cohort life tables constructed by using the survival estimates gleaned from the two different permutations of model selection. Little discrepancy was evident in juvenile male life history parameters between the different life tables, with juvenile males showing increased mortality rate in their 4<sup>th</sup> and 5<sup>th</sup> years of life throughout. Variation in model selection criteria influenced findings for adult male survival, whence discrepancy arose in the importance of especially 8<sup>th</sup>, 9<sup>th</sup> and 10<sup>th</sup> year increased mortality rates. Notwithstanding these differences, the 20 cohorts of adult males in this population (Tables 4.3a, b) clearly illustrate similar survival schedules to the 10 cohorts studied by Pistorius et al. (1999b). Among females, estimates from both permutations of model selection indicated high 3<sup>rd</sup> year survival, in contrast to Pistorius et al. (1999b), while Table 4.4b indicates equally high 4<sup>th</sup> year survival. Females aged 4, 5 and to a lesser extent those aged 6, showed relatively heightened mortality in all but Table 4.4b but not in Table 4.4a, while females aged 9 to 19 illustrated either consistently very high survival rates (Table 4.4a), or fluctuating (but high) survival rates (Table 4.4b).

**Table 4.3a.** Life table for male southern elephant seals constructed from survival estimates derived from models depicted in **bold-face** in table 4.2. Survival rate ( $p_x$ ) estimates are corrected for tag-loss based on Appendix 2 (Oosthuizen et al. 2009).

Age (x)	Survival ( $l_x$ )	Mortality ( $d_x$ )	Mortality rate ( $q_x$ )	Survival rate ( $p_x$ )
0	1.000	0.424	0.424	0.576
1	0.576	0.136	0.236	0.764
2	0.440	0.125	0.283	0.717
3	0.315	0.098	0.312	0.688
4	0.217	0.067	0.308	0.692
5	0.150	0.049	0.329	0.671
6	0.101	0.038	0.373	0.627
7	0.063	0.022	0.354	0.646
8	0.041	0.014	0.355	0.645
9	0.026	0.009	0.332	0.668
10	0.018	0.006	0.321	0.679
11	0.012	0.004	0.303	0.697
12	0.008	0.002	0.283	0.717
13	0.006	0.002	0.270	0.730
14	0.004			

**Table 4.3b.** Life table for male southern elephant seals constructed from survival estimates derived from  $\hat{\#}$  ( $\hat{c}$  non-adjusted) models in table 4.2, comparable with selection criteria in Pistorius et al. (1999b). Survival rate ( $p_x$ ) estimates are corrected for tag-loss based on Appendix 2 (Oosthuizen et al. 2009).

Age (x)	Survival ( $l_x$ )	Mortality ( $d_x$ )	Mortality rate ( $q_x$ )	Survival rate ( $p_x$ )
0	1.000	0.422	0.422	0.578
1	0.578	0.137	0.237	0.763
2	0.441	0.126	0.285	0.715
3	0.315	0.099	0.313	0.687
4	0.216	0.067	0.309	0.691
5	0.149	0.050	0.336	0.664
6	0.099	0.032	0.319	0.681
7	0.068	0.022	0.328	0.672
8	0.045	0.016	0.350	0.650
9	0.030	0.011	0.365	0.635
10	0.019	0.008	0.421	0.579
11	0.011	0.004	0.326	0.674
12	0.007	0.003	0.360	0.640
13	0.005	0.002	0.470	0.530
14	0.002			

**Table 4.4a.** Life table for female southern elephant seals constructed from survival estimates derived from models depicted in **bold-face** in table 4.2. Survival rate ( $p_x$ ) estimates are corrected for tag-loss based on Appendix 2 (Oosthuizen et al. 2009).

Age (x)	Survival ( $l_x$ )	Mortality ( $d_x$ )	Mortality rate ( $q_x$ )	Survival rate ( $p_x$ )
0	1.000	0.368	0.368	0.632
1	0.632	0.139	0.220	0.780
2	0.494	0.094	0.191	0.809
3	0.399	0.091	0.228	0.772
4	0.308	0.069	0.224	0.776
5	0.239	0.053	0.223	0.777
6	0.186	0.040	0.215	0.785
7	0.146	0.031	0.213	0.787
8	0.115	0.023	0.204	0.796
9	0.091	0.018	0.196	0.804
10	0.073	0.014	0.190	0.810
11	0.059	0.011	0.186	0.814
12	0.048	0.009	0.180	0.820
13	0.040	0.007	0.177	0.823
14	0.033	0.006	0.173	0.827
15	0.027	0.004	0.166	0.834
16	0.023	0.004	0.167	0.833
17	0.019	0.003	0.164	0.836
18	0.016	0.002	0.159	0.841
19	0.013			

**Table 4.4b.** Life table for female southern elephant seals constructed from survival estimates derived from  $\hat{\epsilon}$  (non-adjusted) models in table 4.2, comparable with selection criteria in Pistorius et al. (1999b). Survival rate ( $p_x$ ) estimates are corrected for tag-loss based on Appendix 2 (Oosthuizen et al. 2009).

Age (x)	Survival ( $l_x$ )	Mortality ( $d_x$ )	Mortality rate ( $q_x$ )	Survival rate ( $p_x$ )
0	1.000	0.366	0.366	0.634
1	0.634	0.136	0.214	0.786
2	0.499	0.102	0.204	0.796
3	0.397	0.078	0.196	0.804
4	0.319	0.076	0.239	0.761
5	0.243	0.055	0.225	0.775
6	0.188	0.044	0.232	0.768
7	0.144	0.030	0.209	0.791
8	0.114	0.023	0.204	0.796
9	0.091	0.020	0.220	0.780
10	0.071	0.013	0.189	0.811
11	0.057	0.014	0.246	0.754
12	0.043	0.008	0.179	0.821
13	0.036	0.007	0.188	0.812
14	0.029	0.006	0.213	0.787
15	0.023	0.003	0.141	0.859
16	0.020	0.003	0.142	0.858
17	0.017	0.002	0.133	0.867
18	0.015	0.003	0.214	0.786
19	0.011			

#### *Survivorship trend inflexion and state change*

Estimates gleaned from the selection criteria involving either the  $\hat{\epsilon}$ -adjusted full candidate set of models, or that mimicking Pistorius et al. (1999b), provided evidence for a positive shift in survivorship for young (0 - 3yrs) males, but especially for all age-categories (0 – 9 yrs old) of females, after 1994 (Table 4.5a). Table 4.5b indicates more varied (some positive, and some negative) differences in survival rates for the periods before and after 1999 for both males and females. This finding lends support to the hypothesis that the survivorship point of inflexion rests closer to 1994. However, this inflexion in survival rates around 1994 would have coincided with a population trend inflexion around 1997/1998 if a lag-time from all increased juvenile survival (1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> year age-classes) around 1994 related to increased survival (thus breeding potential) of 4<sup>th</sup>, 5<sup>th</sup> and 6<sup>th</sup> year adult females around 1998.

**Table 4.5a.** Comparison of mean age-specific survival ( $\phi$ ) estimates between two time periods (1983–1993 and 1994–2002) for southern elephant seals at Marion Island, using models depicted in **bold-face** in table 4.2 (†) and those depicted as # (comparable with Pistorius et al. 1999b) in table 4.2 (‡). ‘Survival’ ( $\phi$ ) depicted as probabilities; Standard error (SE) of survival estimates, and ‘ $\phi$  Difference’ as a percentage (%) are shown.

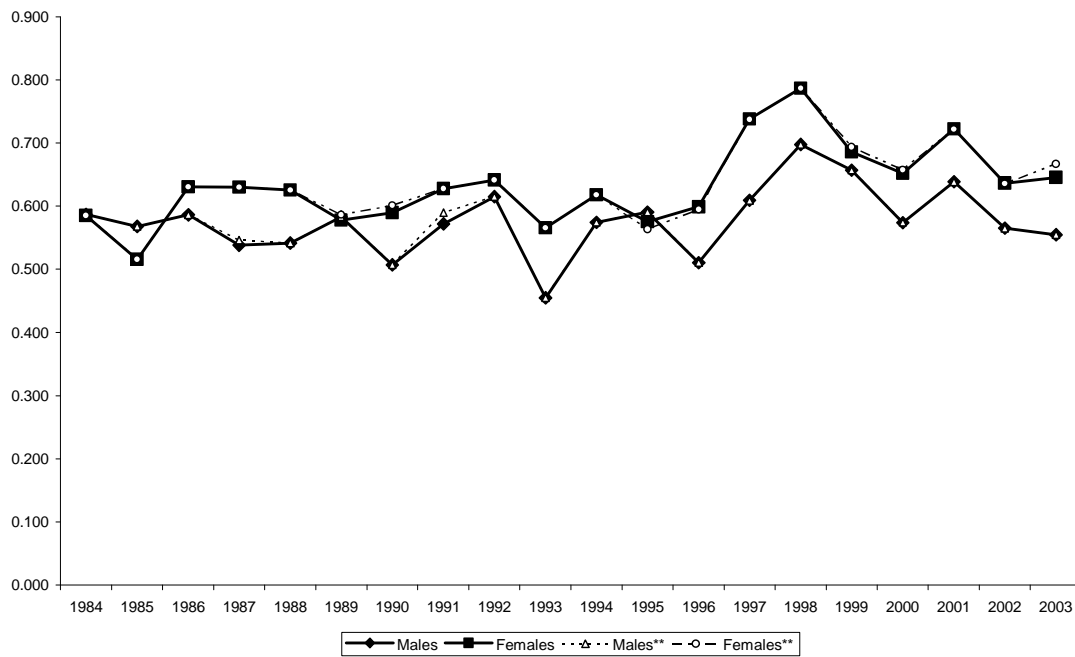
Age	Cohorts	Males (†)			Males (‡)			Females (†)			Females (‡)		
		Survival	SE	$\phi$ Difference	Survival	SE	$\phi$ Difference	Survival	SE	$\phi$ Difference	Survival	SE	$\phi$ Difference
0	1983-1993	0.555	0.071		0.558	0.036		0.599	0.062		0.601	0.034	
	1994-2002	0.597	0.091	4.179	0.597	0.045	3.926	0.666	0.079	6.712	0.668	0.037	6.683
1	1983-1993	0.739	0.094		0.737	0.049		0.771	0.078		0.776	0.045	
	1994-2002	0.787	0.115	4.781	0.787	0.058	4.959	0.803	0.092	3.166	0.812	0.046	3.628
2	1983-1993	0.702	0.115		0.698	0.059		0.774	0.086		0.755	0.051	
	1994-2002	0.733	0.134	3.119	0.733	0.068	3.496	0.836	0.097	6.170	0.824	0.050	6.841
3	1983-1993	0.636	0.131		0.639	0.069		0.750	0.040		0.796	0.057	
	1994-2002	0.722	0.155	8.525	0.716	0.080	7.723	0.788	0.045	3.838	0.818	0.054	2.197
4	1983-1993	0.735	0.166		0.725	0.084		0.758	0.038		0.747	0.065	
	1994-2002	0.666	0.185	-6.869	0.669	0.097	-5.634	0.791	0.045	3.291	0.780	0.061	3.354
5	1983-1993	0.660	0.202		0.650	0.102		0.756	0.038		0.730	0.076	
	1994-2002	0.676	0.218	1.572	0.668	0.114	1.862	0.798	0.043	4.201	0.810	0.071	7.990
6	1983-1993	0.632	0.127		0.661	0.126		0.760	0.036		0.748	0.039	
	1994-2002	0.634	0.152	0.163	0.692	0.130	3.096	0.799	0.044	3.903	0.783	0.054	3.444
7	1983-1993	0.656	0.121		0.708	0.172		0.761	0.035		0.759	0.041	
	1994-2002	0.639	0.150	-1.644	0.712	0.152	0.320	0.798	0.044	3.726	0.797	0.048	3.791
8	1983-1993	0.685	0.114		0.685	0.108		0.770	0.033		0.760	0.044	
	1994-2002	0.650	0.146	-3.549	0.622	0.094	-6.252	0.798	0.043	2.756	0.777	0.053	1.628
9	1983-1993	0.717	0.112		0.636	0.105		0.732	0.031		0.721	0.054	
	1994-2002	0.658	0.138	-5.963	0.666	0.088	2.997	0.800	0.042	6.894	0.808	0.052	8.745

**Table 4.5b.** Comparison of mean age-specific survival ( $\phi$ ) estimates between two time periods (1983–1998 and 1999–2002) for southern elephant seals at Marion Island, using models depicted in **bold-face** in table 4.2 (†) and those depicted as # (comparable with Pistorius et al. 1999b) in table 4.2 (‡). ‘Survival’ ( $\phi$ ) depicted as probabilities; Standard error (SE) of survival estimates, and ‘ $\phi$  Difference’ as a percentage (%) are shown.

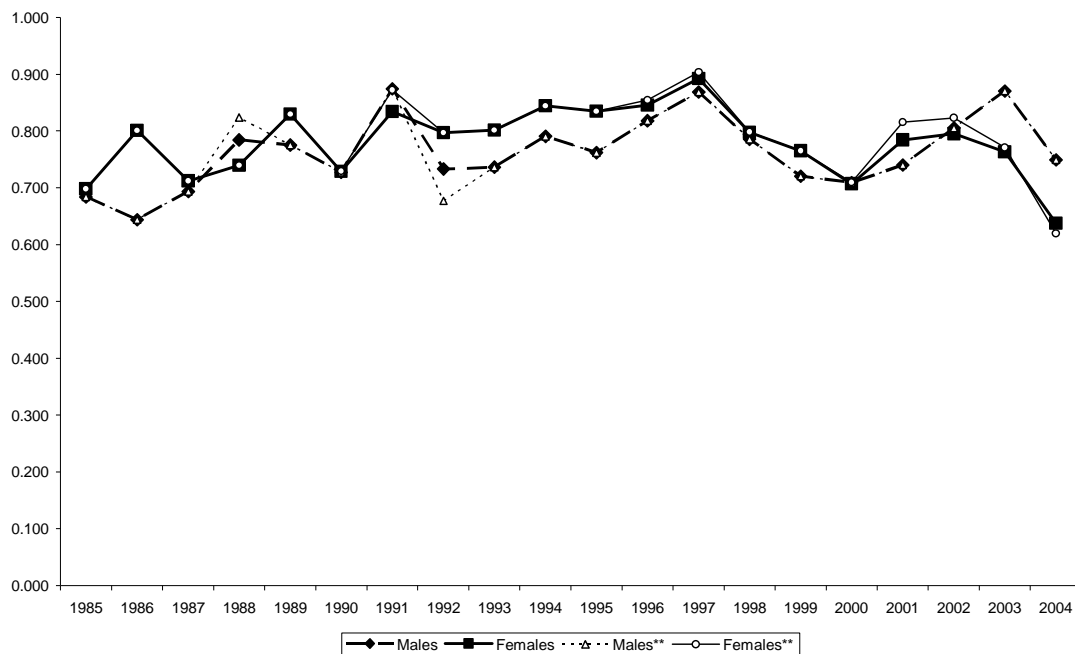
Age	Cohorts	Males (†)			Males (‡)			Females (†)			Females (‡)		
		Survival	SE	$\phi$ Difference	Survival	SE	$\phi$ Difference	Survival	SE	$\phi$ Difference	Survival	SE	$\phi$ Difference
0	1983-1998	0.569	0.076		0.571	0.040		0.620	0.067		0.621	0.034	
	1999-2002	0.598	0.094	2.879	0.598	0.040	2.717	0.669	0.082	4.812	0.675	0.038	5.463
1	1983-1998	0.763	0.100		0.761	0.049		0.797	0.084		0.801	0.045	
	1999-2002	0.769	0.119	0.646	0.769	0.066	0.763	0.763	0.088	-3.395	0.777	0.048	-2.423
2	1983-1998	0.724	0.121		0.722	0.058		0.794	0.093		0.779	0.050	
	1999-2002	0.708	0.138	-1.644	0.708	0.079	-1.410	0.846	0.089	5.138	0.829	0.052	4.934
3	1983-1998	0.694	0.139		0.691	0.068		0.773	0.041		0.812	0.055	
	1999-2002	0.668	0.159	-2.546	0.668	0.093	-2.285	0.772	0.046	-0.143	0.800	0.055	-1.248
4	1983-1998	0.716	0.173		0.714	0.084		0.771	0.041		0.767	0.062	
	1999-2002	0.637	0.190	-7.930	0.637	0.110	-7.724	0.795	0.046	2.329	0.768	0.063	0.053
5	1983-1998	0.698	0.203		0.687	0.101		0.771	0.040		0.764	0.070	
	1999-2002	0.616	0.230	-8.143	0.614	0.128	-7.303	0.810	0.044	3.849	0.821	0.078	5.721
6	1983-1998	0.637	0.129		0.694	0.120		0.774	0.040		0.776	0.044	
	1999-2002	0.627	0.173	-0.979	0.664	0.144	-2.958	0.811	0.045	3.721	0.767	0.061	-0.851
7	1983-1998	0.655	0.129		0.744	0.157		0.769	0.040		0.750	0.051	
	1999-2002	0.624	0.166	-3.135	0.657	0.157	-8.718	0.822	0.044	5.226	0.850	0.038	9.970
8	1983-1998	0.656	0.127		0.538	0.117		0.769	0.040		0.766	0.059	
	1999-2002	0.655	0.160	-0.106	0.765	0.068	22.726	0.826	0.044	5.661	0.784	0.041	1.803
9	1983-1998	0.656	0.130		0.638	0.091		0.781	0.038		0.764	0.075	
	1999-2002	0.671	0.142	1.495	0.693	0.088	5.416	0.811	0.045	3.011	0.844	0.024	7.974

### *Age-specific survival estimates*

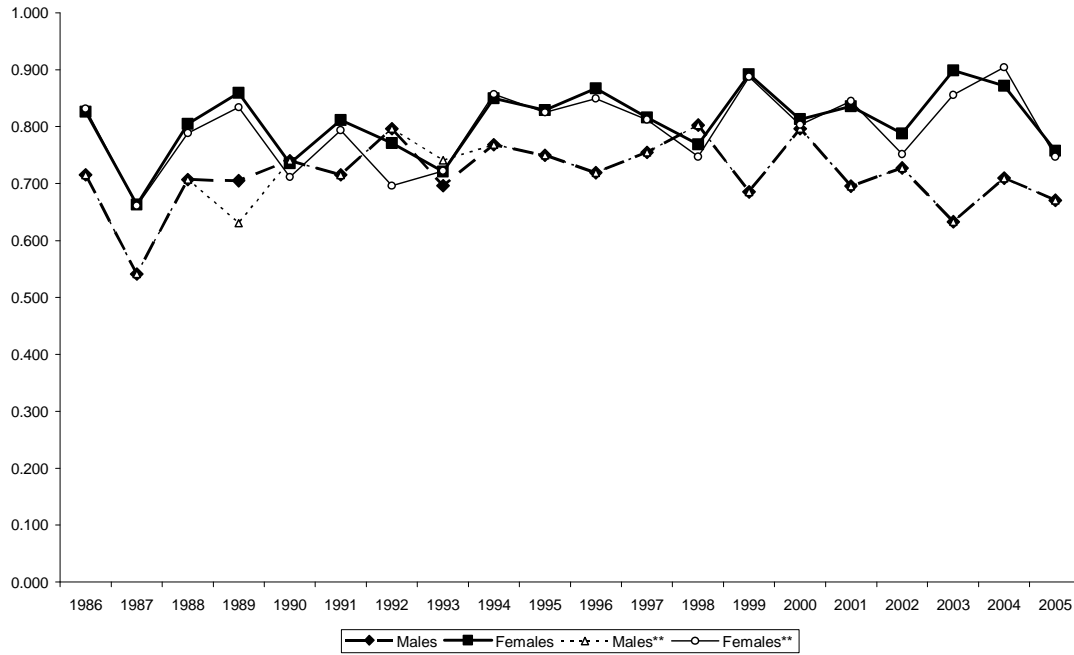
First year survival estimates for both sexes have remained relatively constant and high (~ >50%) for the entire study period (1984-2003), although particularly high survival between 1996 and 1998 for both sexes is evident, following a trough in estimates during 1993 by comparison (Fig. 4.1a). Mean second year survival for both sexes showed a slow increase between 1992 (males = 0.733, females = 0.797) and 1997 (males = 0.869, females = 0.892), followed by a considerable trough through 2001 (both sexes ~ 0.710), recovering slightly before a recent decrease in 2004 (Fig. 4.1b). Third year female survival showed a slight overall increase after 1993, with 1998, 2002 and 2005 identified as higher mortality years, concomitant with the trough in second year survival after 1997 to 2002 (Fig. 4.1c). Lower 4<sup>th</sup>, 5<sup>th</sup> and 6<sup>th</sup> year survival in pubescent males was progressively associated with 2003, 2004 and 2005 (Fig. 4.1d, e, f), while lower 4<sup>th</sup>, 5<sup>th</sup>, 6<sup>th</sup>, 7<sup>th</sup> and 8<sup>th</sup> year female survival was progressively associated with 2003 through to 2007 (Fig. 4.1d, e, f, g, h). Adult male survival increasingly fluctuated, especially if model selection replicating Pistorius et al. (1999b) were used for estimates, while adult female survival remained stable (~ 0.800) through to the 14<sup>th</sup> year of life (Fig. 4.1i, j, k, l, m, n). High mortality in 4<sup>th</sup> year females during 1993, progressed annually to 14<sup>th</sup> year survival in 2005, based on estimates from the selection of 'constant-survival-after-age-3' models (Table 4.2) from the full candidate set of  $\hat{c}$ -adjusted models (Fig. 4.1d, e, f, g, h, i, j, k, l, m, n). The estimates from the models replicating the Pistorius et al. (1999b) criteria offered varied annual descriptors of survival, particularly for adult females (older than 3 yrs), identifying 1993 and 2003 as high mortality years for females in their 4<sup>th</sup> and 5<sup>th</sup> years (Fig. 4.1d, e). Similarly, females in their 6<sup>th</sup>, 7<sup>th</sup>, 8<sup>th</sup> and 9<sup>th</sup> years experienced high mortality during 2006, based on these model outputs (Fig. 4.1 f, g, h, i).



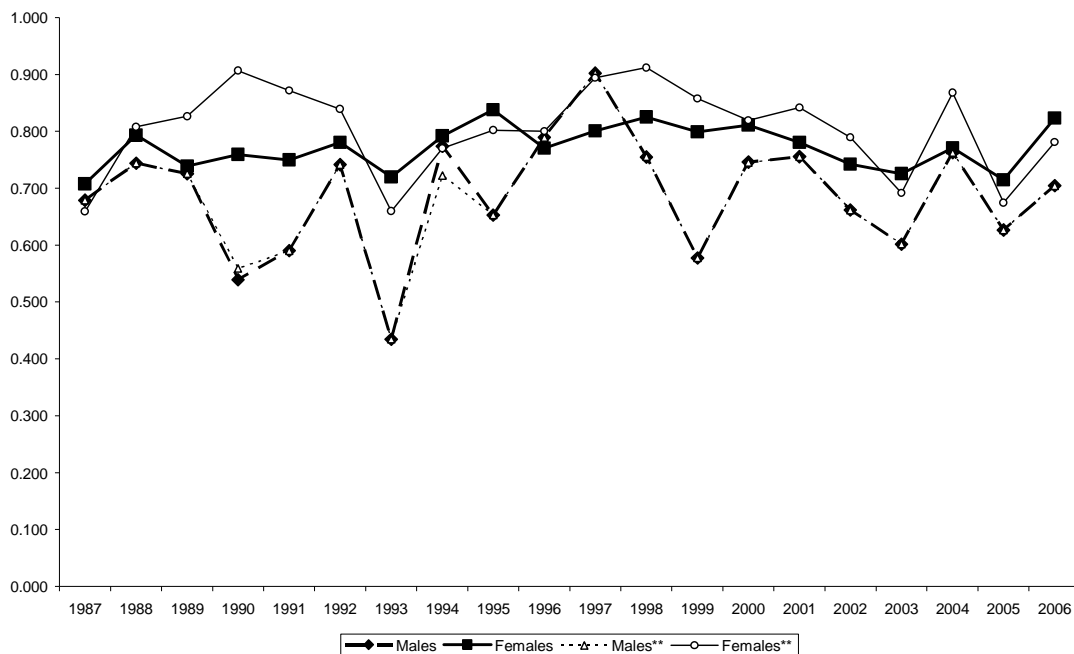
**Fig. 4.1a.** Mean first year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



**Fig. 4.1b.** Mean second year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.

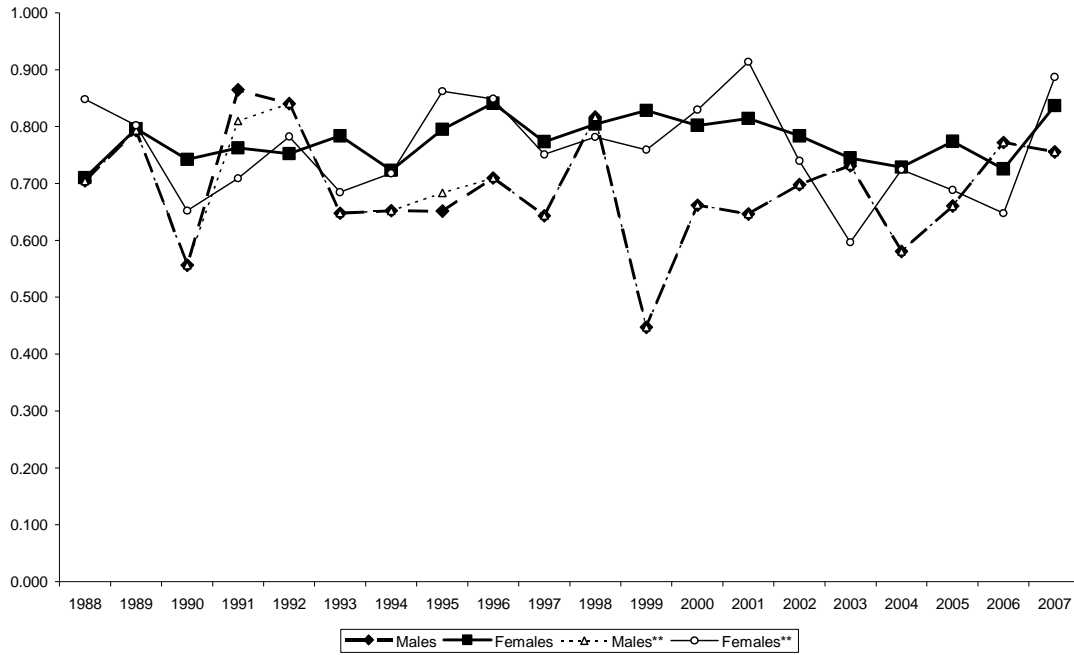


**Fig. 4.1c.** Mean third year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.

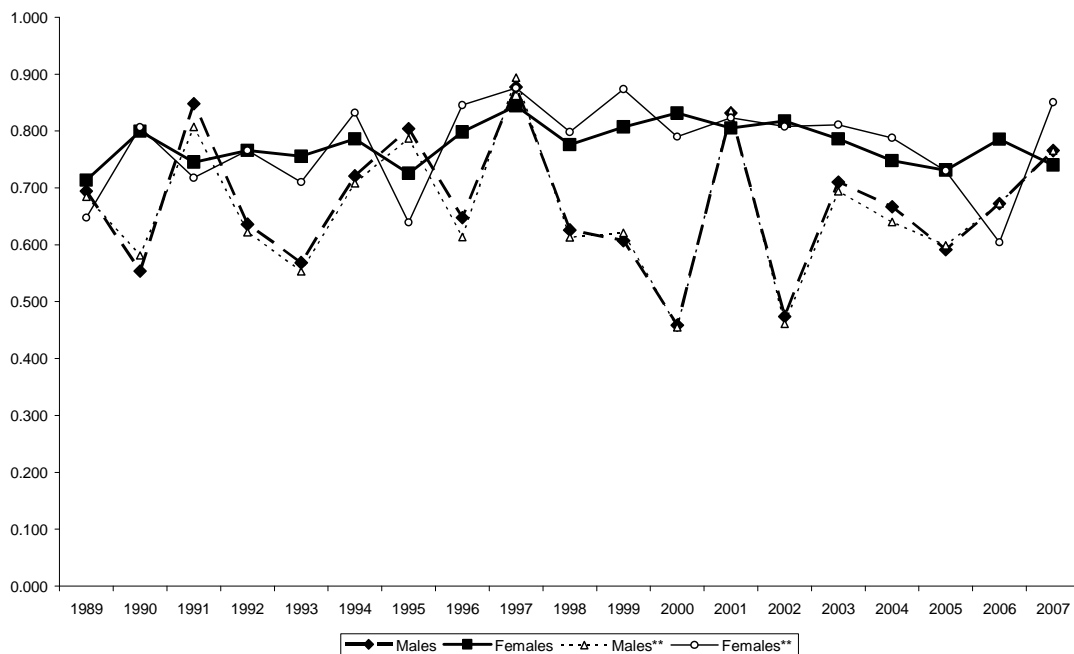


**Fig. 4.1d.** Mean fourth year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.

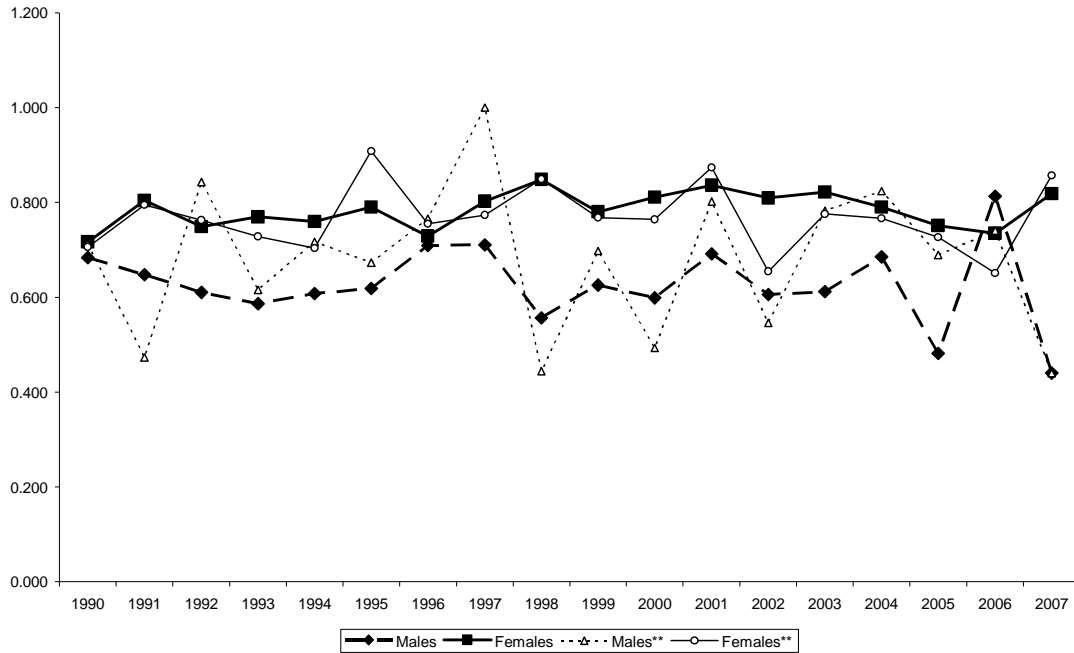




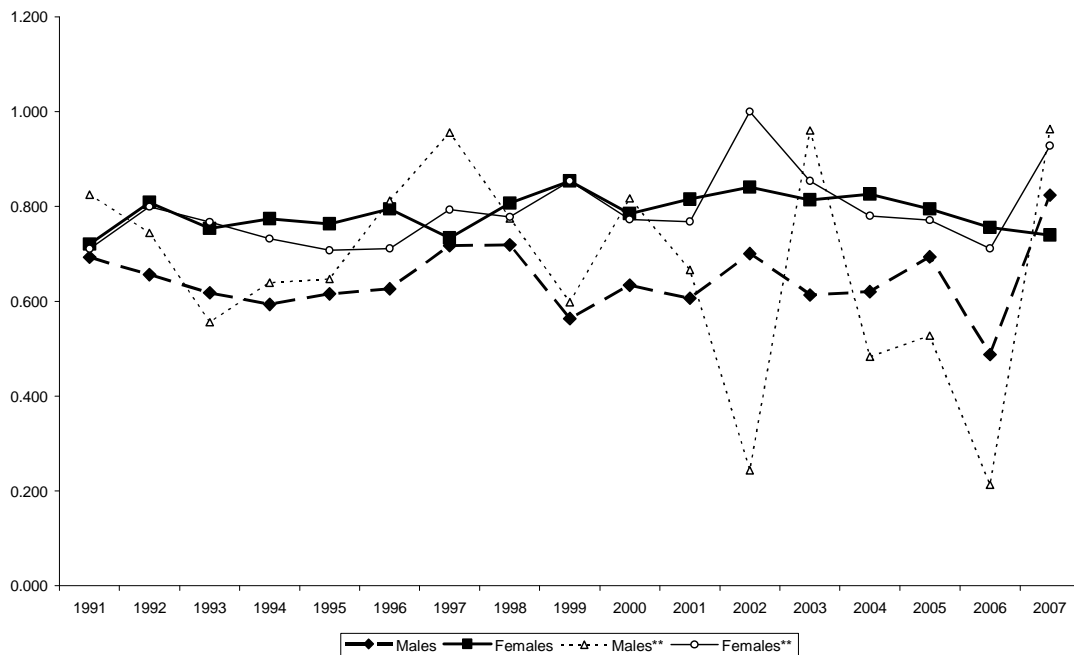
**Fig. 4.1e.** Mean fifth year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



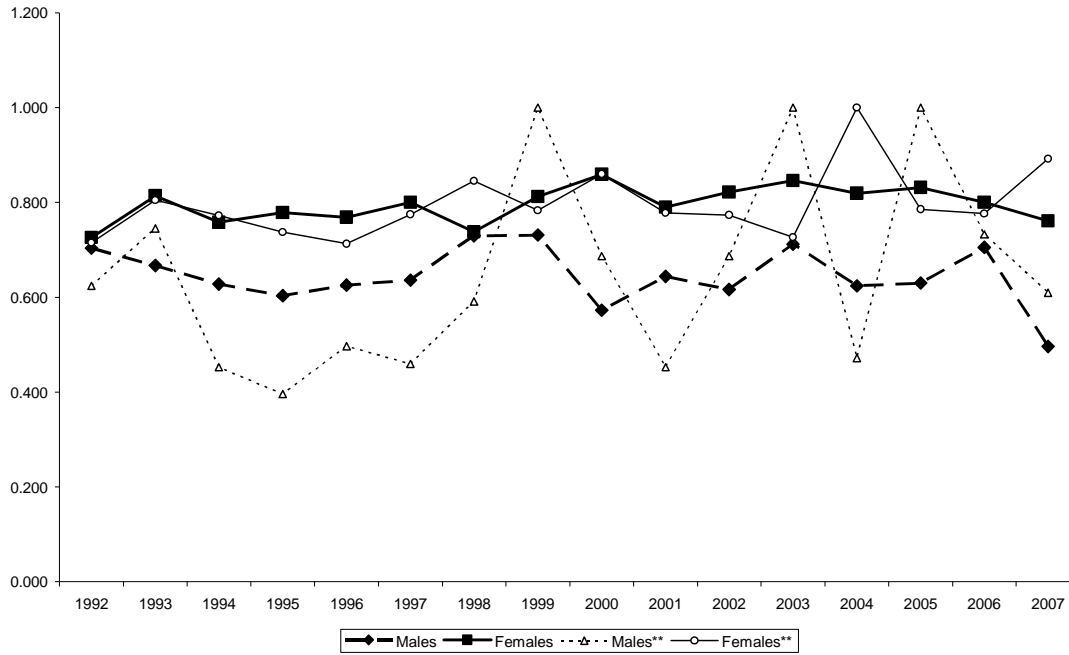
**Fig. 4.1f.** Mean sixth year survival for 19 cohorts (birth year: 1983-2001) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



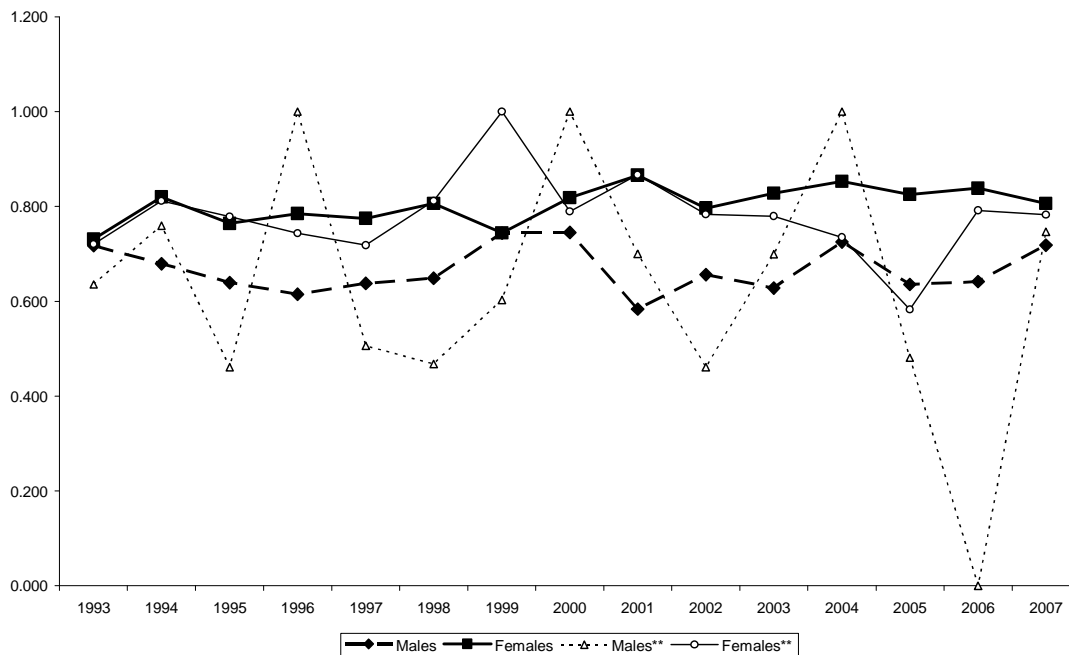
**Fig. 4.1g.** Mean seventh year survival for 18 cohorts (birth year: 1983-2000) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



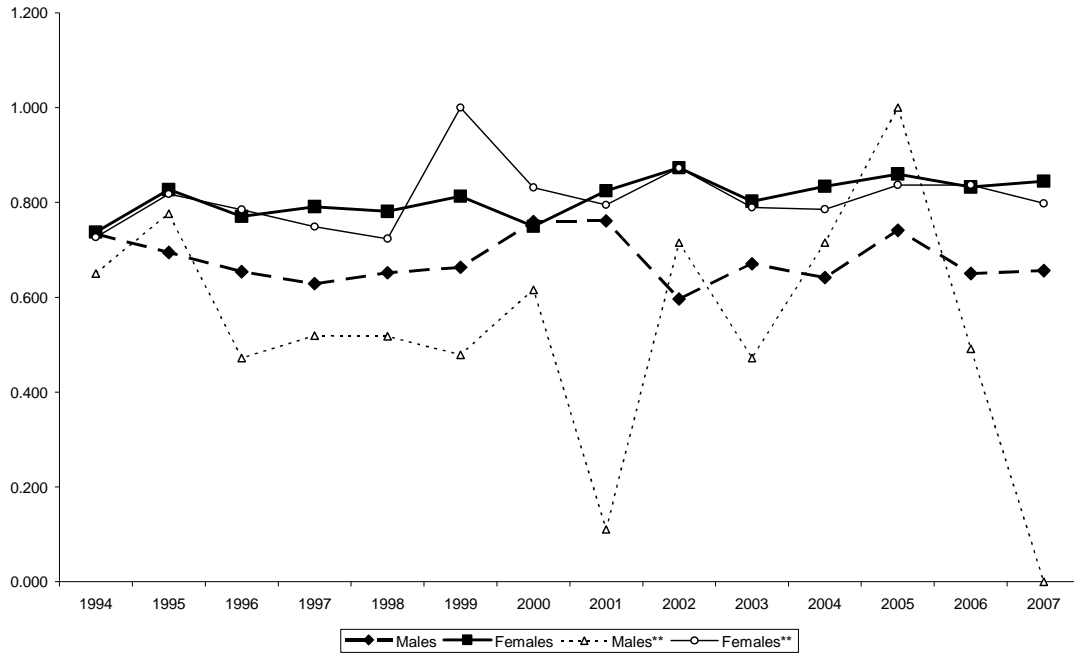
**Fig. 4.1h.** Mean eighth year survival for 17 cohorts (birth year: 1983-1999) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



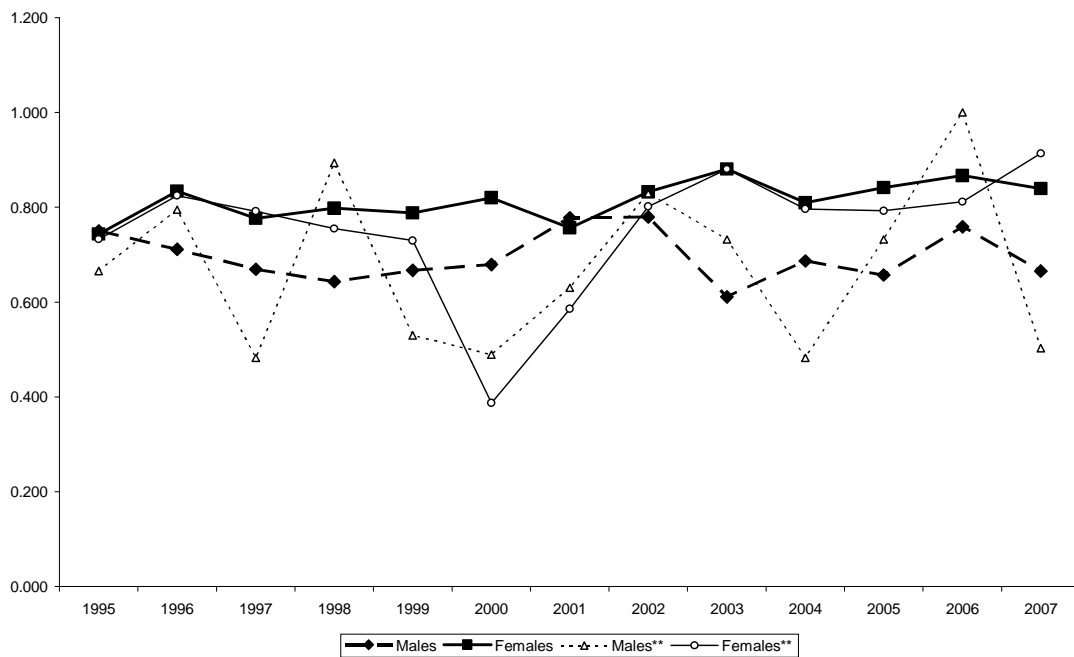
**Fig. 4.1i.** Mean ninth year survival for 16 cohorts (birth year: 1983-1998) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



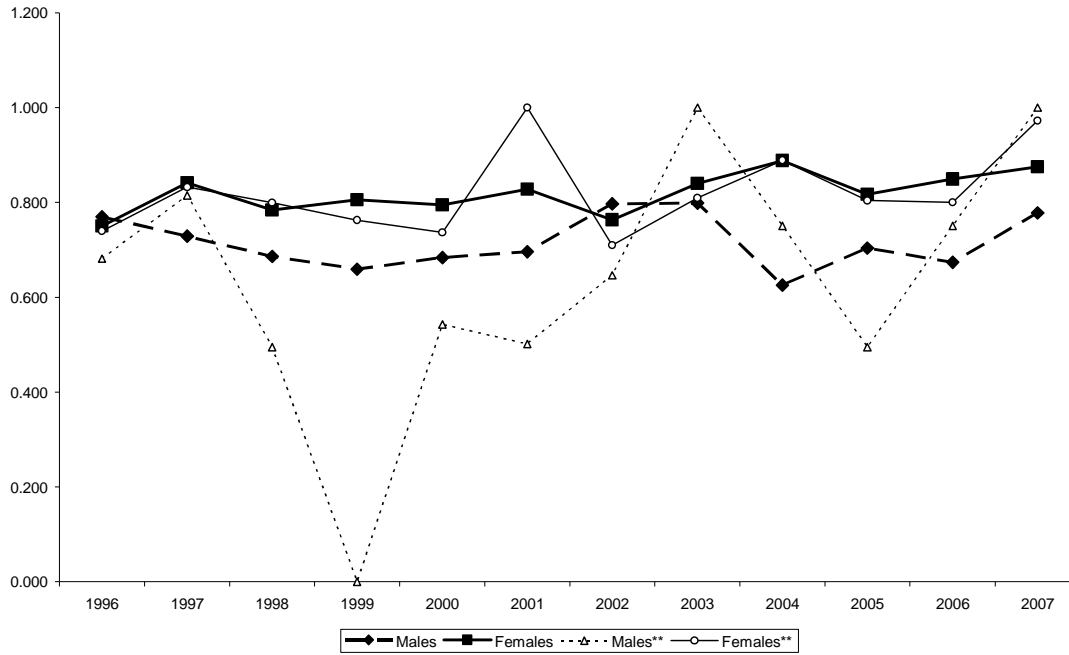
**Fig. 4.1j.** Mean tenth year survival for 15 cohorts (birth year: 1983-1997) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



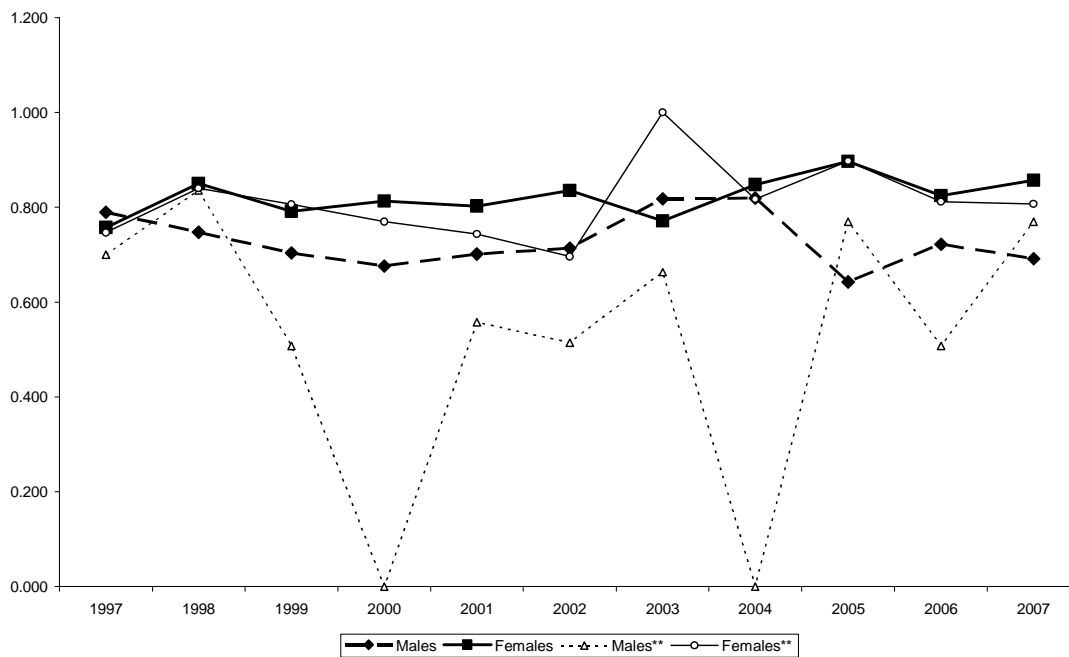
**Fig. 4.1k.** Mean eleventh year survival for 14 cohorts (birth year: 1983-1996) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



**Fig. 4.1l.** Mean twelfth year survival for 13 cohorts (birth year: 1983-1995) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



**Fig. 4.1m.** Mean thirteenth year survival for 12 cohorts (birth year: 1983-1994) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.



**Fig. 4.1n.** Mean fourteenth year survival for 11 cohorts (birth year: 1983-1993) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (\*\*) represent those gained from # represented models in table 4.2.

## Discussion

A population is regulated by four fundamental parameters, namely birth, death, immigration and emigration (Caughley 1977). At Marion Island, an increase in birth rates as measured through fecundity estimates had a limited effect in the state shift from decline to increase, despite the early age at primiparity of adult females at this locality (Bester and Wilkinson 1994; Pistorius et al. 2001; McMahon et al. 2003; Pistorius et al. 2004). The assumption for low levels of dispersal (especially emigration) in the southern elephant seal population at Marion Island has as its basis the high philopatry between natal- and later haul-out sites of the species at this locality (Hofmeyr 2000), and the appreciable genetic differences between the major global stocks of southern elephant seals indicating little cross-dispersal (Slade et al. 1998; McMahon et al. 2005a). Firstly, dispersal *across* stocks is not required for an animal to be lost to a mark-recapture study if more than one haul-out locality (island) is available *within* the geographic limits of one 'stock'. Secondly, Hofmeyr (2000) based that philopatric analyses on tagged animals from Marion Island returning to sites on Marion Island, and suggested high fidelity to natal sites. However, these analyses could not identify temporary emigration of tagged seals, even if their fidelity to their natal site was high at each visit to this island. The extra-binomial variation identified in the present dataset, particularly as a consequence of failure in the "recapture" assumption of homogeneity between animals and capture occasions, further suggests that the hitherto quoted "negligible emigration from the study site" in all studies concerned with this dataset, may not be as robust (particularly for temporary emigration) as has been assumed. While the CJS approach is biologically sensible and estimates gleaned from this approach are useful to illustrate changes in vital rates that may well regulate a given population, caution should be exercised not to 'over-interpret' the results. We suggest that a multistate modelling approach, including an 'unobservable' state to explain the suggested Markovian temporary emigration of seals from the study site, be implemented in future to further elucidate the survival schedules of this population (Kendall and Nichols 2002; Schaub et al. 2004).

Field observations suggests that as many as half of the breeding adult females on Marion Island during a breeding season (for example) are untagged (PJNdB, MNB personal observation). Low rates of tag-loss reported for this population cannot

account for this relatively high percentage of untagged cows (see Appendix 2 – Oosthuizen et al. 2009) given that virtually every weaned pup on this island are double-tagged (see Chapter 3 – de Bruyn et al. 2008). This influx of untagged animals into the population, perhaps from nearby (and unstudied) Prince Edward Island (23km distant) and Îles Crozet (1000km distant), requires quantification before changes in vital rates of tagged Marion Island elephant seals can be solely linked to changes in population size, as has been done (Pistorius et al. 1999a, b, 2001, 2004, 2005; McMahon et al. 2003, 2005a, b, 2009). In fact, with the use of population viability analysis, McMahon et al. (2005b) hypothesised that the Marion Island population showed a high probability of extinction within 150yrs, unless a dramatic change in fundamental life history parameters, and/or population supplementation (i.e. immigration) occurred. Indication from vital rates in the McMahon et al. (2005b) study (from cohorts 1993 to 1997) annulled chances for an impending change in population state from decline to increasing; contrary to recent analysis with added years of data (McMahon et al. 2009, this study). We therefore suggest, that the survival estimates gained from the present study are useful in revealing regulatory mechanisms for this population (as shown by Pistorius et al. 1999b), particularly if ‘immigrants (i.e. untagged animals)’ are subject to the same extrinsic and intrinsic drivers, but that immigration may have been additionally critical in the state shift and requires serious analytical attention.

Notwithstanding this source of bias, longitudinal mark-recapture studies of this duration for large mammals (this study) are extremely rare, and if results are adequately represented to acknowledge such bias, remain inimitable in population demographic studies. Our results suggest that violation of the “recapture” assumption was plausible in the Pistorius et al. (1999b) study as it is here, and not correcting for extra-binomial variation, could have resulted in misinterpretation of the available data through erroneous model selection (Pistorius et al. 1999b). De Little et al. (2007) show minimal effects of  $\hat{c}$  adjustments on their selection of models, contrasting with some of our findings, albeit that we used simpler models. However, significant departures between  $\hat{c}$ -adjusted and non-adjusted model selection occurred mostly with older animals in the present study. Thus, perhaps the relative paucity of older cohorts in the Pistorius et al. (1999b) study prevented noteworthy misinterpretation of results (in the absence of  $\hat{c}$  adjustment), but this serves to caution future studies of

the danger of not adjusting for overdispersion particularly in long term datasets (Anderson et al. 1994). While model selection in the Pistorius et al. (1999b) study was accomplished without ‘correction’ for violated model assumptions, comparison with our adjusted models are possible. We identify similarly high first year survival in both sexes over the entire study period, while a clear increase in mean survival during 1<sup>st</sup>, 2<sup>nd</sup> and 3<sup>rd</sup> years of life for both sexes, but particularly for females, after 1994 (with a substantial peak between 1996 and 1999) lend support to the assertion by McMahon et al. (2003, 2005b) that this component is important in regulation of this population. However, without juvenile survival translating into increased adult survival, a change in population state would not occur (McNamara and Houston 1996). Indeed, adult female (4<sup>th</sup> year onwards) survival estimates over the entire study period are considerably higher than those reported for the first 10 cohorts only (Pistorius et al. 1999b). However, we suggest that continuation of the “adult-female vs. juvenile survival” debate may have been fuelled in part by the inconsistency in classification of the three year old (animals in their 4<sup>th</sup> year of life) category as adult females (e.g. Pistorius et al. 1999b) or as part of the juvenile age-group (1- to 3-year-old – e.g. McMahon et al. 2003, 2005b). The reduced survival of three year old females contributed significantly to the respective assertions for and against juvenile or adult survival in these studies. Here we again identify three year old females as significant contributors to the evidenced state change in population survivorship. Additionally, mean estimates of survival for these age classes (4<sup>th</sup> year onwards) prior to- and after 1994 differ markedly, in support of, not only a point of inflexion in the population state around this year, but also support the assertion that adult female survival has increased to allow a population state change (Pistorius et al. 1999b). McMahon et al. (2003) showed an increase in weanling masses at Marion Island over a seven year period (centred around 1992/3) as compared to stability therein at Macquarie Island (both populations declining at the time), indicating either (a) that there has been an increase in resources available to their mothers during the pre-breeding period, or (b) that there has been an increase in the mean age of females at Marion Island, older (larger) females weaning larger pups (McMahon and Bradshaw 2004). They propose the latter to be unlikely, because for this to occur adult survival would have had to increase relative to juvenile survival over two distinct periods (prior to 1992, and after 1993) (McMahon et al. 2003). We show that adult survival increased (prior to 1992: mean =  $0.754 \pm 0.03$ ; after 1993:  $0.806 \pm 0.04$ ; increase =



5.2%) at a similar rate as juvenile survival (mean =  $0.710 \pm 0.10$ ; vs. mean =  $0.761 \pm 0.10$ ; increase = 5.1%) over these two periods respectively, and can only conclude that this has resulted from a per capita increase in food availability for both age classes. The onset of a substantial increase in 2<sup>nd</sup> year female survival during 1991 continuing to 1997, resulted in increased survival of 3- and 4-year-olds after 1993 through to 1997, lending support to the McMahon et al. (2003, 2005b) finding that increased survival in juvenile categories (esp. 2-year-olds) preceded higher survival probabilities in primiparous adult females (aged 3, 4 and 5 years). Mean adult female (4 - 12 years old) survival over the entire study period is higher in this study ( $0.794 \pm 0.02$ ) as compared with Pistorius et al. (1999b) ( $0.761 \pm 0.03$ ), indicating that perhaps their shorter time series (thus fewer records for older animals) limited the full assessment of this portion of the population. Clearly, the survivorship schedule for all Marion Island female southern elephant seals has changed positively since the Pistorius et al. (1999b) study, while male survivorship has remained largely similar, with pubescent males continuing to suffer high mortality rates (Pistorius et al. 2005). The complex interplay of extrinsic and intrinsic factors (de Little et al. 2007) makes it difficult to ascertain which component of the female population was chiefly responsible for the state change in this population, since clearly pubescent and adult males were not responsible. However, these results concur with the hypothesis that increased juvenile (0 – 3yr old) survival (of both sexes) is important in the population recovery, while increased adult female survival has assisted in maintenance of that state.

There has been no recent detectable change in the numbers of killer whales (*Orcinus orca*) frequenting the waters around Marion Island (Keith et al. 2001; Pistorius et al. 2002; Appendix 3 – Tosh et al. 2008), and based on the assumption that their dietary preferences have remained similar over time, there is no indication for a change in top-down pressure on the elephant seal population here. Our findings therefore support the notion that a bottom-up controlling system (Weimerskirch et al. 2003) particularly food availability, has largely been responsible for changes in survivorship in this population (Pistorius et al. 2004; this study). However, the positive effects on population numbers of these changes in survivorship seem to have been augmented with an influx of immigrants. It may be argued that if these immigrants originate from adjacent Prince Edward Island (or if the untagged

component at Marion Island has remained stable over time), the foraging ranges would overlap and extrinsic and intrinsic factors would act on the archipelago's elephant seals as a whole. This would lend greater support to a change in survivorship for the archipelago's elephant seal population, in line with our results from the tagged subsample of this population. The continued high mortality in pubescent males may contest the alleviation of food limitation hypothesis (Pistorius et al. 2005), however, recent evidence suggests differing foraging patterns for this class compared to adult females (M.N. Bester unpublished data). Additionally, we suggest that this class (juvenile and pubescent males) may be more prone to permanent emigration (M.N. Bester unpublished data), which would lower estimates of apparent survival.

A complex suite of factors, both intrinsic and extrinsic are responsible for the regulation of southern elephant seal populations (de Little et al. 2007). We presented evidence for survivorship as a critical driver of population state change, in particular the importance of both juvenile and adult female survival in small population regulation. We emphasise the potential influence of immigration on a small population and the need for far-reaching research questions, related to the whole ecosystem, in studies of population demography. Several facets of this ecosystem that require study for a more holistic idea of elephant seal demographics are highlighted:

- (1) Dispersal within the Kerguelen elephant seal stock needs attention through; a) high resolution genetic surveying (see also Chauke 2008), b) increased effort for longitudinal telemetry deployments concurrent with the mark-recapture programme at Marion Island, c) additional wean weight data, and estimation of foraging success of adults through photogrammetric analyses (see Chapter 2 - de Bruyn et al. 2009a); d) an assessment of the origin of untagged animals on Marion Island and their similarity in survivorship, movement and foraging success, compared with the tagged sample.
- (2) Continued monitoring of the social structure of the resident Marion Island killer whale population following Tosh et al. (2008) to assess impact on elephant seals and energetic requirements based on dietary composition.
- (3) Long-term oceanographic sampling (physical and biological) in prime elephant seal foraging areas.

- (4) Possible interspecific competition with large resident populations of fur seal *Arctocephalus spp.* and penguin populations (e.g. Guinet et al. 1996), especially during the postweaning pelagic period of elephant seals when diving behaviour (<500m – Georges et al. 2000; Biuw et al. 2003) and ranging distance ( $\leq 1000$ km – Bester 1989; Field et al. 2005, de Bruyn et al. 2009b) are likely to be more comparable.
- (5) As a unique demographic study of this duration on southern elephant seals (this study), continuing efforts at Marion Island would greatly benefit from concurrent mark-recapture studies on other islands, such as neighbouring (20km) Prince Edward Island, the proximate (1000km) Îles Crozet and distant Îles Kerguelen (Setsaas et al. 2008) within the same stock, and in particular a resurrection of the Macquarie Island mark-recapture study (McMahon et al. 2006), and mark-recapture intensification at the Valdés Peninsula, Argentina (Lewis et al. 1998; Pistorius et al. 2004). While comparisons with large demographic datasets for other populations of the species (e.g. McCann 1985, Hindell 1991) are useful and have been done (Pistorius et al. 1999b; McMahon et al. 2005b), an ecosystem such as the Southern Ocean subsequent to a regime shift and perhaps now functioning differently (Weimerskirch et al. 2003), may reduce the relevance of temporally inconsistent comparisons.

### Literature Cited

- Anderson DR, Burnham KP, White GC (1994) AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780-1793
- Baker JD, Thompson PM (2007) Temporal and spatial variation in age-specific survival rates of a long-lived mammal, the Hawaiian monk seal. *Proc. R. Soc. B* 274: 407-415
- Barker R (1992) Effect of heterogeneous survival on birdbanding model confidence interval coverage rates. *J Wildl Manage* 56:111–116
- Bester MN (1988) Marking and monitoring studies of the Kerguelen stock of southern elephant seals, *Mirounga leonina*, and their bearing on biological research in the Vestfold hills. *Hydrobiologia* 165:269-277
- Bester MN (1989) Movements of southern elephant seals and Subantarctic fur seals in relation to Marion Island. *Mar Mamm Sci* 5: 257 – 265.

- Bester MN, Wilkinson IS (1994) Population ecology of southern elephant seals at Marion Island. In: Le Boeuf BJ, Laws RM (eds) Elephant seals: population ecology, behavior, and physiology, University of California Press, Berkeley, pp. 85-97
- Biuw M, Boehme L, Guinet C, Hindell M, Costa D, Charrassin JB, Roquet F, Bailleul F, Meredith M, Thorpe S, Tremblay Y, McDonald B, Park YH, Rintoul SR, Bindhoff N, Goebel M, Crocker D, Lovell P, Nicholson J, Monks F, Fedak MA (2007) Variations in behaviour and condition of a southern ocean top predator in relation to in situ oceanographic conditions. Proc Nat Acad Sci USA 104:13705 – 13710
- Biuw M, McConnell B, Bradshaw CJA, Burton H, Fedak M (2003) Blubber and buoyancy: monitoring the body condition of free-ranging seals using simple dive characteristics. J Exp Biol 206:3405-3423
- Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release–recapture. Am Fish Soc Monogr 5:1–437
- Caughley G (1977) Analysis of vertebrate populations. Wiley, London
- Carothers AD (1979) Quantifying unequal catchability and its effect on survival estimates in an actual population. J Anim Ecol 48: 863-869
- Chauke LF (2008) Genetic variation and population structure in southern elephant seals, *Mirounga leonina*, at Marion Island as inferred from microsatellite and mitochondrial DNA. MSc thesis, University of Pretoria, Pretoria [Unpublished]
- Condy PR (1978) The distribution and abundance of southern elephant seals *Mirounga leonina* (Linn.) on the Prince Edward islands. S Afr J Antarct Res 8:42-48
- Cooper CF, Stewart BS (1983) Demography of northern elephant seals, 1911- 1982. Science 219: 969-971
- Coulson T, Gaillard JM, Festa-Bianchet M (2005) Decomposing the variation in population growth into contributions from multiple demographic rates. J Anim Ecol 74:789–801
- de Bruyn PJN, Tosh CA, Oosthuizen WC, Phalanndwa MV, Bester MN (2008) Temporary marking of unweaned southern elephant seal (*Mirounga leonina* L.) pups. S Afr J Wildl Res 38:133-137 [Chapter three]

- de Bruyn PJN, Bester MN, Carlini AR, Oosthuizen WC (2009a) How to weigh an elephant seal with one finger: a simple three-dimensional photogrammetric application. *Aquat Biol* 5:31-39 [Chapter two]
- de Bruyn PJN, Tosh CA, Oosthuizen WC, Bester MN, Arnould JPY (2009b) Bathymetry and frontal system interactions influence seasonal foraging movements of lactating Subantarctic fur seals from Marion Island. *Mar Ecol Prog Ser* *Accepted*
- de Little SC, Bradshaw CJA, McMahon CR, Hindell MA (2007) Complex interplay between intrinsic and extrinsic drivers of long-term survival trends in southern elephant seals. *BMC Ecol* 7:3
- Eberhardt LL, Siniff DB (1977) Population dynamics and marine mammal management policies. *J Fish Res Board Can* 34:183-190
- Field IC, Bradshaw CJA, Burton HR, Sumner MD, Hindell MA (2005) Resource partitioning through oceanic segregation of foraging juvenile southern elephant seals. *Oecologia* 142:127-135
- Gaillard J-M, Festa-Bianchet M, Yoccoz NG (1998) Population dynamics of large herbivores: variable recruitment with constant adult survival. *Trends Ecol Evol* 13:58–63
- Gaillard J-M, Yoccoz NG (2003) Temporal variation in survival of mammals: a case of environmental canalization? *Ecology* 84:3294–3306
- Georges J-Y, Tremblay Y, Guinet C (2000) Seasonal diving behaviour in lactating Subantarctic fur seals on Amsterdam Island. *Polar Biol* 23:59-69
- Guinet C, Cherel Y, Ridoux V, Jouventin P (1996) Consumption of marine resources by seabirds and seals in Crozet and Kerguelen waters: changes in relation to consumer biomass 1962-85. *Antarct Sci* 1:23-30
- Hindell MA (1991) Some life-history parameters of a declining population of southern elephant seals, *Mirounga leonina*. *J Anim Ecol* 60:119–134
- Hindell MA, Little GJ (1988) Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at Macquarie Island. *Mar Mammal Sci* 4:168-171
- Hofmeyr GJG (2000) Dispersal and dispersion of southern elephant seals at Marion Island. MSc. thesis, University of Pretoria: Pretoria.

- Jonker FC, Bester MN (1998) Seasonal movements and foraging areas of adult southern female elephant seals, *Mirounga leonina*, from Marion Island. *Antarct Sci* 10:21-30
- Keith M, Bester MN, Bartlett PA, Baker D (2001) Killer whales (*Orcinus orca*) at Marion Island, Southern Ocean. *Afr Zool* 36:163-175
- Kendall WL, Nichols JD (2002) Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology* 83:3276-3284
- Kirkman SP, Bester MN, Hofmeyr GJG, Jonker FC, Pistorius PA, Owen R, Strydom N (2004) Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Austr J Zool* 52: 379-388
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67-118
- Lebreton J-D, Pradel R, Clobert J (1993) The statistical analysis of survival in animal populations. *Trends Ecol Evol* 8:91-95
- Lewis M, Campagna C, Quintana F, Falabella V (1998) Estado actual y distribucion de la poblacion del elefante marino del sur en la Península Valdés, Argentina. *Masto Neotr* 5:29-40
- McCann TS (1985) Size, status and demography of southern elephant seal (*Mirounga leonina*) populations. In: Ling JK, Bryden MM (eds) *Sea Mammals in South Latitudes: Proceedings of a Symposium of the 52nd ANZAAS Congress*, South Australian Museum, Adelaide, pp. 1–17
- McMahon CR, Bradshaw CJA (2004) Harem choice and breeding experience of female southern elephant seals influence offspring survival. *Behav Ecol Sociobiol* 55:349-362
- McMahon CR, Burton HR, Bester MN (2003) A demographic comparison of two southern elephant seal populations. *J Anim Ecol* 72:61-74
- McMahon CR, Bester MN, Burton HR, Hindell MA, Bradshaw CJA (2005a) Population status, trends and a re-examination of the hypotheses explaining the recent declines of the southern elephant seal *Mirounga leonina*. *Mammal Rev* 35:82-100

- McMahon CR, Bester MN, Hindell MA, Brook BW, Bradshaw CJA (2009) Shifting trends: detecting environmentally mediated regulation in long lived marine vertebrates using time-series data. *Oecologia* 159: 69-82
- McMahon CR, Bradshaw CJA, Hays GC (2006) Branding can be justified in vital conservation research. *Nature* 439:392
- McMahon CR, Hindell MA, Burton HR, Bester MN (2005b) Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge. *Mar Ecol Prog Ser* 288:273-283
- McNamara JM, Houston AI (1996) State-dependent life histories. *Nature* 380:215-221
- Nichols JD, Stokes LS, Hines JE, Conroy MJ (1982) Additional comments of the assumption of homogeneous survival rates in modern bird banding estimation models. *J Wildl Manage* 46:953–962
- Oosthuizen WC, de Bruyn PJN, Bester MN, Girondot M (2009) Cohort and tag-site specific tag-loss rates in mark-recapture studies: a southern elephant seal cautionary case. *Mar Mamm Sci* *In press* [Appendix 2]
- Pistorius PA, Bester MN, Kirkman SP (1999a) Dynamic age-distributions in a declining population of southern elephant seals. *Antarct Sci* 11:445-450
- Pistorius PA, Bester MN, Kirkman SP (1999b) Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex and cohort. *Oecologia* 121:201-211
- Pistorius PA, Bester MN, Kirkman SP, Taylor FE (2001) Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biol* 24:343-348
- Pistorius PA, Taylor FE, Louw C, Hanise B, Bester MN, De Wet C, Du Plooy A, Green N, Klasen S, Podile S, Schoeman J (2002) Distribution, movement, and estimated population size of killer whales at Marion Island, December 2000. *S Afr J Wildl Res* 32:86-92
- Pistorius PA, Bester MN, Lewis MN, Taylor FE, Campagna C, Kirkman SP (2004) Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal. *J Zool Lond* 263:107-119
- Pistorius PA, Bester MN, Hofmeyr GJG, Kirkman SP, Taylor FE (2008a) Seasonal survival and the relative cost of first reproduction in adult female southern elephant seals. *J Mammal* 89:567-574

- Pistorius PA, Taylor FE, Bester MN, Hofmeyr GJG, Kirkman SP (2008b) Evidence for density dependent population regulation in southern elephant seals in the southern Indian Ocean. *Afr Zool* 43:75-80
- Pistorius PA, Bester MN, Taylor FE (2005) Pubescent southern elephant seal males: population changes at Marion Island and the food limitation hypothesis. *S Afr J Wildl Res* 35:215-218
- Saether B (1997) Environmental stochasticity and population dynamics of large herbivores: a search for mechanisms. *Trends Ecol Evol* 12:143-149
- Schaub M, Gimenez O, Schmidt BR, Pradel R (2004) Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology* 85:2107–2113
- Setsaas TH, Bester MN, van Niekerk JH, Roux JP, Hofmeyr GJG (2008) Dispersion during the moult haulout of southern elephant seals at the Courbet Peninsula, Iles Kerguelen. *Polar Biol* 31:249-253
- Siniff DB, DeMaster DP, Hofman RJ, Eberhardt LL (1977) An analysis of the dynamics of a Weddell seal population. *Ecol Monogr* 47:319-335
- Slade RW, Moritz C, Hoelzel AR, Burton HR (1998) Molecular population genetics of the southern elephant seal *Mirounga leonina*. *Genetics* 149:1945–1957
- Springer AM, Estes JA, van Vliet GB, Williams TM, Doak DF, Danner M, Forney KA, Pfister B (2003) Sequential megafaunal collapse in the North Pacific Ocean: An ongoing legacy of industrial whaling? *Proc Nat Acad Sci USA* 100:12223–12228
- Toïgo C, Gaillard J-M, Festa-Bianchet M, Largo E, Michallet J, Maillard D (2007) Sex- and age-specific survival of the highly dimorphic Alpine ibex: evidence for a conservative life-history tactic. *J Anim Ecol* 76:679-686
- Tosh CA, de Bruyn PJN, Bester MN (2008) Preliminary analysis of the social structure of killer whales, *Orcinus orca*, at subantarctic Marion Island. *Mar Mamm Sci* 24:929-940 [Appendix 3]
- Tosh C, Bornemann H, Ramdohr S, Schröder M, Martin T, Carlini A, Plötz, J, Bester MN (2009) Adult male southern elephant seals from King George Island utilize the Weddell Sea. *Antarct Sci* 21:113-121
- Weimerskirch H, Inchausti P, Guinet C, Barbraud C (2003) Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. *Antarctic Sci* 15:249-256



White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Suppl.):120-138

Wilkinson IS (1991) Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. PhD thesis University of Pretoria Pretoria

**CHAPTER FIVE:**  
**FERTILITY, LONGEVITY AND REPRODUCTIVE SENESCENCE IN FEMALE**  
**SOUTHERN ELEPHANT SEALS AT MARION ISLAND**

**Abstract**

Research on ageing is fundamental to the understanding of life-history parameters and their consequences on population demography. Senescence studies in wild animals using longitudinal datasets are relatively rare, and particularly so for marine mammals. We use program MARK to analyse a 25-year longitudinal capture-mark-recapture (CMR) dataset of southern elephant seals to address questions of senescence, fertility and longevity. Evaluation of state-dependent models indicates that actuarial senescence is not evident in the species, but reproductive senescence after the age of 12 is apparent. Costs associated with the age at primiparity are illustrated through reduced reproductive output in later life. Additionally, a hypothesised decrease in the mean age at primiparity between periods of decline and increase in the population is not supported. Frequency of breeding is shown to be interrupted throughout life and unrelated to age, thereby challenging the often-cited assumption that females older than 5 years breed annually. Breeding frequency did not vary between the periods of hypothesised food limitation and abundance. We illustrate that longevity as predicted from CMR survival estimates exceed the observed. We provide unique fertility and longevity schedules for the species, based on >5000 individually identifiable female seals. Senescence is difficult to recognize in wild populations in the face of confounding intrinsic and extrinsic variables. Yet, a multifaceted approach using longitudinal data for many individuals can provide meaningful conclusions in aid of population demographic analyses and studies of the evolutionary ecology of ageing.

## **Introduction**

Studies of population dynamics are not comprehensive without assessments of senescence and its demographic consequences. Organismal senescence is broadly divided into “actuarial senescence” (increase in the probability of dying with age) and “reproductive senescence” (decrease in reproductive effort with advancing age). Senescent individuals are clearly capable of demanding equivalent resources but without the contribution to population growth that prime age animals may provide. Subtle effects of senescence on population dynamics have not been widely considered, and yet may be of considerable importance (Gaillard et al. 2000). For example, deleterious environmental factors experienced by red deer early in life can result in earlier than usual senescent effects, with negative effects on recruitment and population growth (Nussey et al. 2006, 2007). Additionally, most studies of senescence in the wild have focused on survival (or equivalently mortality) probabilities only. Such focus on actuarial senescence ignores the intertwined role that reproduction plays through trade-offs manifested in maternal and somatic investment (Kirkwood and Holliday 1979; Partridge and Barton 1996; Hadley et al. 2007). Maternal investment strategies in different systems (Clutton-Brock 1991) also enter the fray at this point and may further complicate the identification and description of senescent effects. Questions of maternal investment and frequency of reproductive events are fundamentally related to questions of age-specific probabilities of mortality (e.g. Hadley et al. 2007), and thus a study of senescence should not solely be based on one of these two factors (McNamara and Houston 1996). While some argue that a focus on survival only, is adequate to identify overall senescence in a range of species (Jones et al. 2008), the general consensus is that a clearer picture of overall senescence should be sought through analyses of individual fitness composed of both survival and reproductive facets (Monaghan et al. 2008; Nussey et al. 2008). The measurement of senescence in the wild not only furthers our understanding of the evolutionary ecology of senescence (Monaghan et al. 2008), but also its consequences on the dynamics of populations (e.g. Coulson et al. 2006). However, identifying and measuring senescence in wild populations poses considerable difficulties, due to the need for longitudinal studies encompassing large samples of individuals (Gaillard et al. 1994; Nussey et al. 2008), rather than the simpler and more commonly used cross-sectional age structure or age at death approaches (Promislow 1991). However, even when using longitudinal datasets to

identify senescence, it is important to consider that age-specific changes in the risk of death can appear age-related when they may in fact be environmentally confounded. Longitudinal senescence studies should thus be conducted on more than a single cohort in the wild (Monaghan et al. 2008).

Several cohorts of individually identifiable southern elephant seals (*Mirounga leonina*) have been followed as part of a capture-mark-recapture (CMR) experiment over a 25-year period at subantarctic Marion Island (see Chapter 3 – de Bruyn et al. 2008). This provides an ideal long-term longitudinal dataset for the investigation of senescence. Additionally, the change in population growth in southern elephant seals at this locality over the past decades demands investigation as to the importance that senescence may have had therein. Adult females have been hypothesized as the most important drivers (Pistorius et al. 1999, 2008; Pistorius and Bester 2002a) of the decline and recent stabilization/increase of this population (McMahon et al. 2009). Conversely, McMahon et al. (2003, 2005) contended that juvenile survival is the demographic class responsible for this population trend change, and suggested that there were insufficient data in the Pistorius and Bester (2002a) time series with which to detect a significant change and from which to draw conclusions about the effects that key demographic parameters have on population behaviour. Nevertheless, a recent analysis confirms that in fact both these sectors of the population are important (see Chapter 4), justifying in-depth reproductive and survival analyses of particularly the adult female component for further clarification.

The complex interplay of extrinsic and intrinsic drivers of southern elephant seal population change (de Little et al. 2007) undoubtedly complicates identification of senescence in the species. Distinction between intrinsic and extrinsic mortality risks is central to the theoretical prediction that reduction in mortality factors that are age- and condition independent, should lead to selection for delayed senescence (Williams et al. 2006). Such distinction is of course complicated in natural systems where studies of senescence have become increasingly important relative to laboratory experiments. Additionally, the high rate of mortality associated with wild populations introduces analytical difficulties by dramatic reduction of statistical power where small samples of very old animals are available in a given dataset.

Longitudinal studies exceeding the estimated lifespan of numerous cohorts are thus necessary to allow for sufficient numbers of old individuals.

Monaghan et al. (2008) suggest that rather than to attempt separation of these drivers, a more productive approach may be to consider the extent to which a given factor has components that are senescence dependent and independent. Additionally, reproductive and survival trade-offs predicted by the antagonistic pleiotropy and disposable soma life-history theories (Williams 1957; Kirkwood and Holliday 1979; Partridge and Barton 1996) may be more apparent in populations that are resource limited (Ricklefs and Cadena 2007).

Tests for trade-offs between early reproductive effort and rates of senescence in reproductive performance are particularly rare for wild bird and mammal populations (Nussey et al. 2006). The Marion Island southern elephant seal population has recently recovered from such a resource limited decline (Pistorius et al. 1999; McMahon et al. 2009; see Chapter 4). Thus, as a longitudinal CMR dataset (exceeding the known lifespan of the species), encompassing many cohorts, and studied over periods of proposed resource limitation and limitation alleviation (Ricklefs and Cadena 2007; Monaghan et al 2008; Nussey et al. 2008), the Marion Island southern elephant seal population appears suitable for a study of senescence.

The only previous longitudinal study of senescence in southern elephant seals, by Pistorius and Bester (2002b) used six cohorts (1983 -1988) from the Marion Island dataset with resighting histories spanning 1983 to 2000. No actuarial or reproductive senescence was identified, although the authors acknowledged the weakness in that study of a very small sample of old individuals capable of being senescent. We use CMR analyses to investigate 15 cohorts including those used in the Pistorius and Bester (2002b) study, and resighting data up to 2008, to re-evaluate senescence in this population. We also evaluate the potential implications of age at primiparity on reproductive senescence, given our knowledge that age at primiparity does not prejudice future survival (Pistorius et al. 2004) but that primiparous females (regardless of age) appear more susceptible than older breeders to reproductive costs (Pistorius et al. 2008). In light thereof, we provide additional, unique longevity and fertility information on the species from several generations of identifiable

individuals. This progresses on the only currently known longitudinal description of these aspects in southern elephant seals, of two very old females from Macquarie Island (Hindell and Little 1988). We consider the demographic consequences of senescence, longevity and fertility on the dynamics of this population.

## Materials and Methods

### *Study area and mark-recapture experiment*

An intensive tagging programme of southern elephant seals commenced in 1983 at sub-Antarctic Marion Island (Bester 1988) in the Southern Indian Ocean (46°54'S, 37°45'E) (Fig. 1.1). From 1983 to 2004, a total of 5331 (average: 237 annually, range: 193–350) newly weaned female pups were double tagged in their hindflippers using Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, U.K.). Tags were uniquely embossed with a three-digit number, and colour-coded to denote the year of application (see Chapter 3 – de Bruyn et al. 2008 for details). The more easily accessible beaches, particularly on the eastern and northern shores and limited parts of the southern coast, are preferred by elephant seals for hauling out to rest, breed or moult (Condy 1978; Mulaudzi et al. 2008). Seals haul out among 54 beaches along approximately 52 km of coastline (Fig. 1.2). All elephant seals on all beaches were checked for tags every seven days during the breeding season (mid-Aug to mid-Nov) and every 10 days during the moulting period (mid-Nov to mid-Apr) from 1983 to 1990. From 1990 onwards, the breeding season resighting schedule continued unchanged while the 10-day resighting effort was extended through the entire non-breeding period, including winter (mid-Nov to mid-Aug). The increased difficulty in reading tags in harems as compared with the non-breeding period when seals are more dispersed and less aggressive was countered by increased frequency of resighting effort during the breeding season (every seven days, all years). For each seal that was resighted, the tag number, tag colour combination, number of tags remaining (one or two), location and date of the sighting were noted. Pistorius et al. (2000) and Oosthuizen et al. (2009 – Appendix 2) describes the tag-loss rates for this population of seals and age-, sex- and cohort specific adjustments thereof from the latter study were used to correct apparent survival and recapture estimates in this study. The intensive and repetitive resighting schedule allows confidence that detectability of tagged seals in this mark-resighting experiment approaches 100%. All seals were assumed to age on 15 October, which is the peak adult female haul-out

date at Marion Island (Kirkman et al. 2004), and forthwith 'year' refers to 'seal year' from 15 October in year  $x$ , to 14 October in year  $x+1$ .

### *Longevity schedule*

To address longevity of female seals, the multiple resights (resighting data from 1983 to 2008) of each individual (from cohorts 1983 to 2004) within any given year was limited to include only the last resight in that year. These mark-recapture (resighting) data, used to elucidate the survivorship of female seals within this population (see Chapter 4), was also used to construct predicted longevity schedules for 5331 females. Probabilities of survival ( $l_x$ , Table 4.4a, in Chapter 4) at relevant ages were multiplied by the original sample of tagged individuals, and the result at each age subtracted from the result at the previous age to provide a predicted number of animals dying at a given age. These predicted longevity values were transformed to percentage surviving to a given age and compared by chi-squared analysis with percentages of animals (of the original tagged sample) actually observed to have attained that age.

### *Actuarial senescence*

Capture-history matrices were constructed using the last resight in every year for adult females ( $n = 1352$ ) from cohorts tagged from 1983 to 1997 (15 cohorts; total weanlings tagged = 3369), and including resighting data up to but not including the commencement of the 2008 breeding season. This allowed 24 years of resighting history for the 1983 cohort and 10 years for the 1997 cohort.

Capture-history matrices (depicting absence or presence of individuals per year as 0 or 1 respectively, over time) were condensed to input files for each of the cohorts using age three as the record of "release". Juveniles were excluded due to their poor philopatry to the natal area during their first few years (Hofmeyr 2000). These capture-history matrices were used as input files for the software package MARK (White and Burnham 1999), an application for the analysis of marked individuals used to obtain maximum-likelihood estimates of survival and resight probability. MARK provides parameter estimates under the essential Cormack-Jolly-Seber (CJS) model and under several models that appear as special cases of this model (Lebreton et al. 1992). As it was impossible to distinguish between mortality

and permanent emigration, we imply apparent rather than absolute survival. The two fundamental parameters of these models are:

$\Phi_i$  = the apparent survival probability for all animals between the  $i$ th and  $(i + 1)$ th sample ( $i = 1, \dots, k - 1$ ), and

$\rho_i$  = the recapture probability for all animals in the  $i$ th sample ( $i = 2, \dots, k$ ).

The first step in the mark-recapture analyses involves Goodness-of-Fit (GOF) testing of the fully time-dependent CJS model, and Program RELEASE was used here to validate the model assumptions. As different cohorts were treated separately and age-dependence assumed, Test 3.Sm was retained (see Lebreton et al. 1992). In this study time-dependent and age-dependent survival could not be differentiated due to time and age intervals being equivalent, as a result of the exclusive use of single cohorts as separate input matrices for MARK.

To allow explicit comparison with the only other senescence study for this species, model structuring and testing for separate cohorts replicated the procedure in Pistorius and Bester (2002b). A candidate set of three models was structured for estimating female survival and the presence or absence of actuarial senescence. These included the full time-dependent model, constant capture probability model, and a state dependent (prime age – 4 to 7 years old; and potentially senescent – 8 and older age group) age-constrained survival model. In addition, and not possible previously (Pistorius and Bester 2002b), an age constrained model (constant for ages 4 to 14 and then from 15 years onwards) was structured for cohorts 1983 to 1989 (7 cohorts,  $n = 624$  adult females) to assess if very old females suffered actuarial senescence. The small sample corrected Akaike Information Criterion ( $AIC_c$ ) (Lebreton et al. 1992; Anderson et al. 1994) was used for model selection, with the lowest  $AIC_c$  model being selected for real parameter estimate outputs.  $AIC_c$  weighs the deviance (quality of fit) and the precision (via number of estimable parameters) to select a model that best describes the data (Lebreton et al. 1992). Violation of one or more of the CJS model assumptions, as identified in GOF testing, would require adjustment for extra-binomial variation using a variance inflation factor ( $\hat{c}$ ) to adapt  $AIC_c$  estimates ( $QAIC_c$ ) for the CJS and nested models. Additionally, a likelihood ratio test (LRT) was used to test the null hypothesis that adult female survival varied with time (i.e. age-effect), by comparing a full time dependent model with one that was constrained with constant survival from age 4 onwards.



### *Reproductive senescence*

Encounter history matrices were constructed from the pooled, breeding season only, resight data of the 1983 to 1988, 1983 to 1992, and 1989 to 1992 female cohorts respectively. Multiple sightings within a breeding season (one annually) were reduced to include only the last resighting record for that season. As with actuarial senescence analysis, program MARK was used to obtain maximum likelihood estimates but in this instance the emphasis rested on the recapture probability rather than survival probabilities. Age-specific capture probabilities during the breeding season are a rational index of age-specific breeding probabilities, because virtually every female hauled out during a given breeding season does so to give birth (Wilkinson 1991; Pistorius et al. 2001a). Indeed, the status of every female hauled out during the breeding season is judged as “with-pup” or “without-pup” at each sighting. Consequently, any female’s presence at a breeding beach for the duration of a given season without an attending pup can be ascertained, and such occurrences are excluded from analyses ( $n = 140$  out of a possible ~16 000 breeding seasons cumulatively for all cows over the duration of this study). All remaining breeding season presences by all cows are thus synonymous with actual pupping events. Practically all females are recruited into the adult population by their 7<sup>th</sup> year (Wilkinson 1991; this study) and the encounter history matrices were thus restricted to animals 6 years and older, using age 5 as the “release” occasion. Model structuring exactly imitated the procedures in Pistorius and Bester (2002b) for comparative purposes. However, the additional ten years of recapture data in the present study allowed modelling of very old (>16 years) individuals from 6 cohorts (1983-1988) and an increased sample of 13- to 15-year-olds from 10 cohorts (1983-1992), which was not possible in the Pistorius and Bester (2002b) study. A constrained recapture model, assuming constant recapture probabilities between the ages of 6 to 12, 13 to 15 and 16 to 19 respectively, for the 1983 to 1988 cohorts was compared to full-time dependent and constant capture probability models using AIC<sub>c</sub>. Similarly, a constrained recapture analysis excluding the 16 to 19 year old category was modelled for 10 cohorts (1983 to 1992). Additionally, a distinct set of 4 cohorts (1989-1992) not used in the Pistorius and Bester (2002b) study for these analyses, but old enough now to allow an independent analysis (excluding cohorts used in that study) of reproductive senescence were also similarly analysed here. Based on

fertility results (see below) we also constructed three iterations of constrained capture probability models to compare with full time-dependent and constant survival but age-dependent capture probability models for females from 10 cohorts (1983 – 1992) that were primiparous at different ages (3, 4 and 5yrs) to assess if early primiparity affects later life reproductive effort.

### *Fertility*

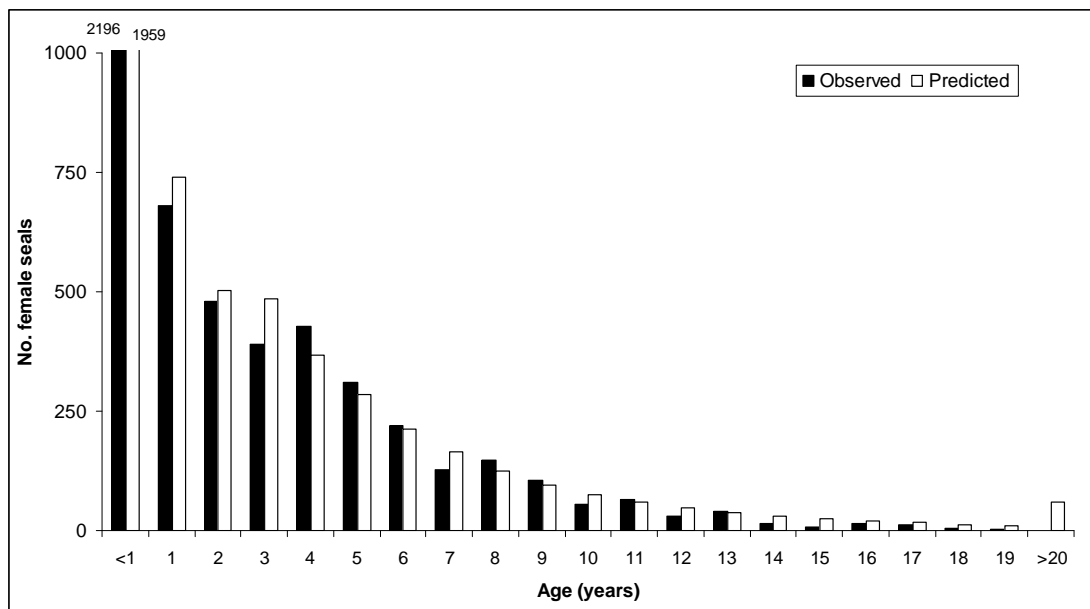
Importantly, we distinguish between fertility (this study) and fecundity as follows. *“The term ‘fertility’ differs from fecundity in that it describes the actual (or current) reproductive performance of a female, and it is a generalization of the terms ‘maternity’, ‘birth rate’ and ‘natality’ which refer to the average number of offspring produced by an individual female of a particular age per unit time”* (McMahon and Bradshaw 2008). Firstly, we assessed fertility of adult female southern elephant seals from 15 pooled cohorts (1983 to 1997) of individuals that had bred at least once ( $n = 1032$ ) and belonged to cohorts that had attained at least 10 years of age. Relative numbers of adult females observed to be primiparous at ages 3, 4, 5 and 6 respectively, were calculated. The relative numbers of females breeding annually before a missed breeding season (with subsequent return), uninterrupted (from primiparity to ‘death’) and non-annual/interrupted (continuously interrupted) breeding schedule, respectively for different primiparous ages was calculated. We tested for a difference in frequency of breeding as related to age at primiparity, between 7 cohorts (1983-1989) born well before 1994 (the hypothesized point of survivorship inflexion, see Chapter 4) and 7 distinct cohorts born after 1994 (1995-2001) to assess if resource limitation reduced breeding frequencies prior to 1994. Secondly, a frequency distribution of the total number of breeding attempts per individual ( $n = 1358$ ) for 20 cohorts (1983-2002), over the period 1983 to 2007 (breeding seasons) was calculated. We used a chi-squared test to distinguish differences in consecutive breeding attempts for all females (regardless of primiparous age) between the periods 1983 to 1994 and 1995 to 2007. A difference between these periods would provide support for the notion that resource limited individuals (as during the hypothesized food limited decline period prior to 1994, Pistorius et al. [1999]) would experience greater lifetime reproductive success by not breeding every year, in so doing conferring greater survival potential for future breeding attempts. Individuals that are not resource limited (after 1994) are hypothesized to experience little

physiologically adverse affects that may lead to lowered survival if adopting an annual breeding strategy. Significantly more frequent breeding efforts by each individual are thus expected for the post-1994 period. Statistica v7.0 (StatSoft Inc. USA) was used for fertility and longevity statistical tests.

## Results

### Longevity

Figure 5.1 illustrates the significant difference ( $\chi^2 = 124.232$ ,  $df = 19$ ,  $p < 0.001$ ) for female seals, between longevity schedules constructed from observed (resight) data only, and that predicted from survival structured, tag-loss corrected estimates as derived from survivorship data (see Chapter 4). More animals were observed in certain prime age years (age 4 to 6, but not 7) and middle age years (age 8, 9 and 11, but not 10) than that predicted from mark-resighting gleaned survival estimates. Longevity in females was predicted to be markedly greater than what has been observed, with 59 females predicted to live beyond 20 years of age, while to date only one animal has been observed to survive to this age (female GW506, double tagged as weanling on 30 October 1988, and observed to return for 12 breeding seasons, including that in October 2008 at 20 years of age).



**Fig. 5.1.** Frequency distribution of longevity for tagged female southern elephant seals at Marion Island (cohorts pooled; 1983 to 2004). ‘Observed’ values correspond to resighted individuals, while ‘Predicted’ longevity values are derived from survival probability data and corrected for tag-loss as presented in Chapter 4.

*Actuarial senescence*

Nine of the 15 cohorts showed significant departures from the global CJS model in program RELEASE GOF testing (Table 5.1). Overdispersion adjustments ( $\hat{c}$ ) were thus required to facilitate accurate model selection (Anderson et al. 1994). Some heterogeneity in capture and survival probabilities as a consequence of departures from the CJS model assumptions, have been shown not to substantially affect survival estimates (Carothers 1979; Nichols et al. 1982; Burnham et al. 1987) and given the relatively low extra-binomial variation observed, we present our estimates as those calculated from program MARK.

**Table 5.1.** Goodness-of-fit test results from Program RELEASE, of Cormack-Jolly-Seber (CJS) general models for adult (age >3) female southern elephant seal cohorts (1983 - 1997) at Marion Island.

Cohort	Females		
	$\chi^2$	df	P
<b>Modelling actuarial senescence</b>			
1983	8.560	8	0.381
1984	10.401	10	0.406
1985	32.939	20	0.034
1986	14.237	9	0.114
1987	19.242	8	0.014
1988	19.693	9	0.020
1989	28.574	10	0.002
1990	38.661	12	<0.001
1991	69.345	21	<0.001
1992	11.133	8	0.194
1993	51.557	15	<0.001
1994	28.607	12	0.005
1995	8.863	13	0.783
1996	40.544	11	<0.001
1997	7.308	11	0.774
<b>Modelling reproductive senescence</b>			
1983-88	28.399	21	0.129
1983-92	32.170	18	0.021
1988-92	34.815	21	0.030
1983-92 <sup>prim3</sup>	35.148	26	0.109
1983-92 <sup>prim4</sup>	27.056	20	0.134
1983-92 <sup>prim5</sup>	20.001	17	0.274

The state dependent age constrained survival model ( $\Phi_{4-7, 8-}, \rho_c$ ) was selected as most parsimonious for all 15 cohorts, time-dependent capture probability was most parsimonious for only the 1995 cohort while all other cohorts illustrated constant capture probability over time (Table 5.2). The likelihood ratio test results confirm that age effects in survival were absent in all cohorts (Table 5.3), supporting our use of

state-dependent age-constrained models to describe survival probabilities (Table 5.4).

**Table 5.2.** Elimination of non-significant effects from the CJS model in modelling survival and capture probability for adult female southern elephant seals within each cohort (1983 – 1997) at Marion Island. For each model the Quasi-Akaike Information Criterion (QAIC<sub>c</sub>) and overdispersion adjustments ( $\hat{c}$ ) are given in each cohort; number of estimable parameters (NP) and Quasi-Deviance (QDEV) are given. Survival probabilities are shown as  $\phi$  and recapture probabilities as  $\rho$ . Numbers in the actuarial senescence model refer to constant survival probability between ages 4 and 7 (prime age), and from 8 to death (old age) -  $\phi_{4-7,8-}$ ; similarly, numbers in reproductive senescence model refer to constant capture probability between relevant ages; t – time dependent; c – constant over time. The most parsimonious model (based on QAIC<sub>c</sub>) is shown in **boldface**.

Cohort	Females Model	QAIC <sub>c</sub> <sup>(c)</sup>	NP	QDev
<b>Modelling actuarial senescence</b>				
1983	(1) $\phi_t, \rho_t$ (CJS)	371.850 <sup>(1.070)</sup>	29	38.552
	(2) $\phi_t, \rho_c$	354.873	16	55.306
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>340.337</b>	4	67.699
1984	(1) $\phi_t, \rho_t$ (CJS)	482.498 <sup>(1.040)</sup>	29	92.203
	(2) $\phi_t, \rho_c$	465.517	17	104.214
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>448.395</b>	4	115.444
1985	(1) $\phi_t, \rho_t$ (CJS)	507.019 <sup>(1.646)</sup>	31	90.629
	(2) $\phi_t, \rho_c$	490.046	18	103.897
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>468.332</b>	4	112.163
1986	(1) $\phi_t, \rho_t$ (CJS)	420.989 <sup>(1.582)</sup>	29	40.558
	(2) $\phi_t, \rho_c$	396.229	16	45.291
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>382.498</b>	4	56.960
1987	(1) $\phi_t, \rho_t$ (CJS)	314.102 <sup>(2.405)</sup>	26	29.626
	(2) $\phi_t, \rho_c$	299.258	15	39.412
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>280.313</b>	4	43.665
1988	(1) $\phi_t, \rho_t$ (CJS)	315.578 <sup>(2.188)</sup>	30	44.844
	(2) $\phi_t, \rho_c$	310.615	17	69.868
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>296.024</b>	4	83.005
1989	(1) $\phi_t, \rho_t$ (CJS)	228.642 <sup>(2.857)</sup>	30	23.809
	(2) $\phi_t, \rho_c$	210.525	16	39.253
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>189.077</b>	4	43.781
1990	(1) $\phi_t, \rho_t$ (CJS)	231.249 <sup>(3.221)</sup>	28	30.320
	(2) $\phi_t, \rho_c$	206.475	15	35.168
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>186.001</b>	4	38.015
1991	(1) $\phi_t, \rho_t$ (CJS)	315.757 <sup>(3.302)</sup>	25	75.200
	(2) $\phi_t, \rho_c$	297.460	14	80.970
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>278.935</b>	4	83.306
1992	(1) $\phi_t, \rho_t$ (CJS)	411.373 <sup>(1.392)</sup>	23	46.500
	(2) $\phi_t, \rho_c$	400.319	13	57.943
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>390.383</b>	4	67.053
1993	(1) $\phi_t, \rho_t$ (CJS)	229.813 <sup>(3.437)</sup>	21	36.206
	(2) $\phi_t, \rho_c$	213.196	12	39.429
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>198.277</b>	4	41.298
1994	(1) $\phi_t, \rho_t$ (CJS)	288.437 <sup>(2.384)</sup>	19	60.539
	(2) $\phi_t, \rho_c$	281.408	11	71.368
	(3) $\phi_{4-7, 8-}, \rho_c$	<b>271.123</b>	4	75.889

1995	(1) $\Phi_t, \rho_t$ (CJS)	572.086 <sup>(1.000)</sup>	17	92.132
	(2) $\Phi_t, \rho_c$	586.708	10	122.243
	(3) $\Phi_{4-7, 8-}, \rho_t$	<b>566.032</b>	12	97.222
1996	(1) $\Phi_t, \rho_t$ (CJS)	208.635 <sup>(3.686)</sup>	15	26.529
	(2) $\Phi_t, \rho_c$	200.432	9	31.101
	(3) $\Phi_{4-7, 8-}, \rho_c$	<b>192.379</b>	4	33.402
1997	(1) $\Phi_t, \rho_t$ (CJS)	583.034 <sup>(1.000)</sup>	13	55.040
	(2) $\Phi_t, \rho_c$	575.049	8	57.801
	(3) $\Phi_{4-7, 8-}, \rho_c$	<b>567.614</b>	4	58.711
<b>Modelling reproductive senescence</b>				
1983-1988	(1) $\Phi_t, \rho_t$ (CJS)	1381.936 <sup>(1.352)</sup>	27	209.705
	(2) $\Phi_c, \rho_t$	1369.406	15	222.431
	(3) $\Phi_c, \rho_{7-12, 13-15, 16-19}$	<b>1363.225</b>	5	236.7513
1983-1992	(1) $\Phi_t, \rho_t$ (CJS)	1872.646 <sup>(1.787)</sup>	19	188.739
	(2) $\Phi_c, \rho_t$	1861.784	11	194.228
	(3) $\Phi_c, \rho_{7-12, 13-15}$	<b>1854.227</b>	4	200.828
1988-1992	(1) $\Phi_t, \rho_t$ (CJS)	1018.216 <sup>(1.658)</sup>	19	166.542
	(2) $\Phi_c, \rho_t$	1008.903	11	174.068
	(3) $\Phi_c, \rho_{7-12, 13-15}$	<b>1000.225</b>	4	<b>179.761</b>
1983-92 <sup>prim3</sup>	(1) $\Phi_t, \rho_t$ (CJS)	1265.878 <sup>(1.352)</sup>	23	247.392
	(2) $\Phi_c, \rho_t$	1255.950	13	258.569
	(3) $\Phi_c, \rho_{4-6, 7-12, 13-15}$	<b>1244.537</b>	4	<b>265.630</b>
1983-92 <sup>prim4</sup>	(1) $\Phi_t, \rho_t$ (CJS)	2054.584 <sup>(1.352)</sup>	21	251.684
	(2) $\Phi_c, \rho_t$	<b>2042.084</b>	12	<b>257.679</b>
	(3) $\Phi_c, \rho_{5-6, 7-12, 13-15}$	2047.578	4	279.390
1983-92 <sup>prim5</sup>	(1) $\Phi_t, \rho_t$ (CJS)	2001.549 <sup>(1.177)</sup>	19	213.975
	(2) $\Phi_c, \rho_t$	<b>1990.825</b>	11	<b>219.734</b>
	(3) $\Phi_c, \rho_{6, 7-12, 13-15}$	1992.331	4	235.455

**Table 5.3.** Testing the null hypothesis that adult female southern elephant seal survival rates were constant over time versus the alternative hypothesis describing adult survival as age-dependent.

Cohort	$\hat{c}$	$\chi^2$	df	P
1983	1.070	14.108	13	0.366
1984	1.040	11.419	14	0.653
1985	1.646	8.857	15	0.885
1986	1.582	11.672	13	0.555
1987	2.405	4.256	12	0.978
1988	2.188	13.344	14	0.500
1989	2.857	5.323	13	0.967
1990	3.221	3.514	12	0.991
1991	3.302	2.341	11	0.997
1992	1.392	9.800	10	0.458
1993	3.437	1.880	9	0.993
1994	2.384	4.555	8	0.804
1995	1.000	9.621	7	0.211
1996	3.686	2.991	6	0.810
1997	1.000	1.289	5	0.936

After tag-loss correction (see Appendix 2 – Oosthuizen et al. 2009) there was no evidence for an increase in the probability of dying due to increasing age in southern elephant seal females (Table 5.4). For cohorts 1983-1989 (7 cohorts) where sufficient data was available, model  $\Phi_{4-14, 15-}$ ,  $\rho_c$  was also structured to assess if high middle age survival inflated the likelihood of very old females surviving. This model was most parsimonious for five of these cohorts (results not included in Table 5.2). For two cohorts (1984 & 1987) survival probabilities declined by 30% and 36% respectively, after 14 years of age, while for two other cohorts (1988 & 1989) survival probabilities increased by 25% and 27% respectively after this age, thus it seems unlikely that actuarial senescence is experienced in this population.

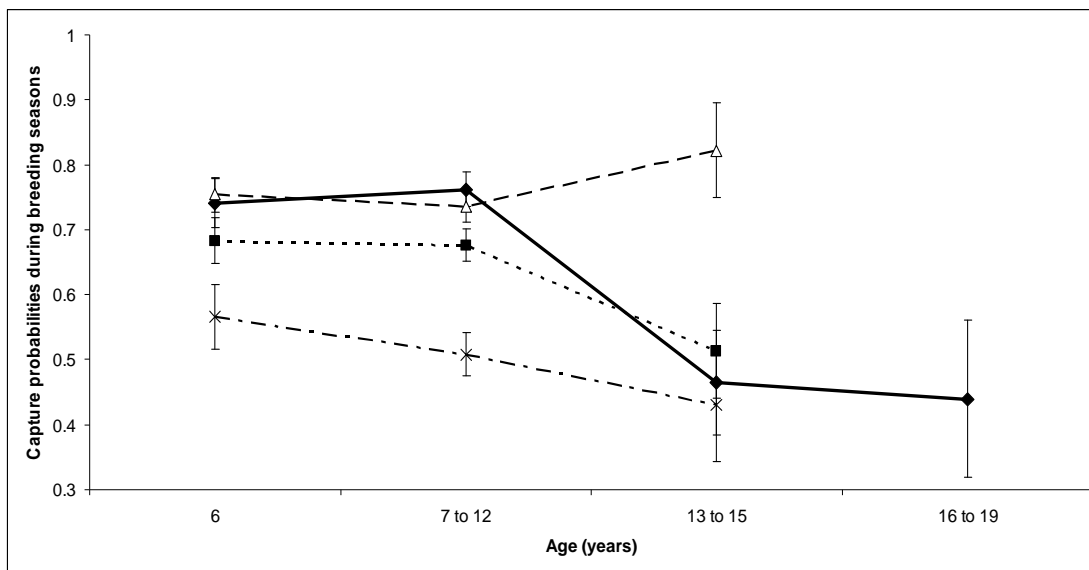
**Table 5.4.** State dependent survival rates (tag-loss corrected) of adult female southern elephant seals from Marion Island to study actuarial senescence.

Cohort	4th-7th years Survival		8th year onwards Survival	
	probability	SE	Probability	SE
1983	0.754	0.043	0.668	0.085
1984	0.785	0.036	0.860	0.044
1985	0.708	0.042	0.812	0.057
1986	0.713	0.039	0.752	0.068
1987	0.710	0.047	0.747	0.087
1988	0.776	0.045	0.783	0.069
1989	0.714	0.064	0.863	0.082
1990	0.812	0.051	0.776	0.084
1991	0.847	0.044	0.894	0.052
1992	0.781	0.037	0.766	0.061
1993	0.773	0.054	0.831	0.084
1994	0.814	0.047	0.879	0.063
1995	0.767	0.032	0.853	0.053
1996	0.820	0.047	0.771	0.103
1997	0.756	0.031	0.858	0.075
<i>Mean</i>	<i>0.769</i>	<i>0.044</i>	<i>0.807</i>	<i>0.071</i>

### *Reproductive senescence*

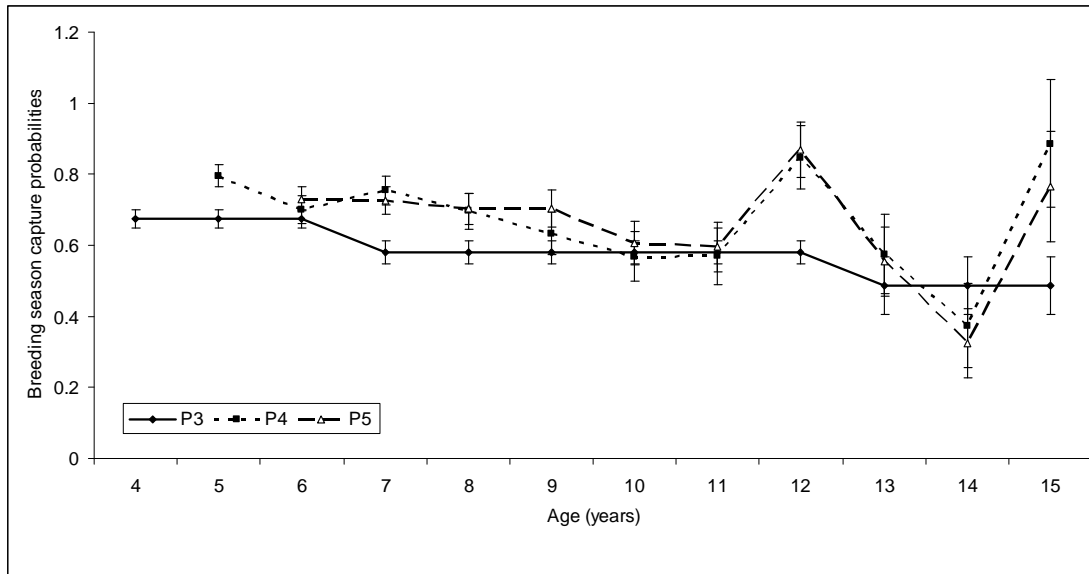
The state-dependent age constrained recapture model was consistently most parsimonious for the three sets of pooled cohorts (Table 5.2) and were used to obtain capture probability estimates. Estimates for six cohorts (1983 to 1988) that had reached at least 19 years of age indicated a considerable reduction in capture probability (used as indices for breeding probability) in the post-prime age (i.e. old age, 13-15 yrs old) and very old (16-19 yrs old) age categories (Fig. 5.2a). Albeit at a

slightly reduced trajectory, the pooled data from 10 cohorts (1983-1992) that had reached at least 15 years of age corroborated these findings. A third pooled group of four cohorts (1989-1992) confirmed the reduction in breeding probability in older age classes (Fig. 5.2a). Females breeding for the first time at age three showed a decline in reproductive potential later in life (Fig. 5.2b). Females primiparous at age 4 and 5 respectively indicated remarkably similar, but fluctuating breeding probabilities in older age classes (Fig. 5.2b).



**Fig. 5.2a.** Capture probabilities (during breeding seasons) of pooled cohorts of female southern elephant seals, as indices of breeding probabilities. The solid line indicates capture probabilities for six cohorts (1983 to 1988) that have reached 19 years of age. The dotted line (square) illustrates capture probabilities for 10 pooled cohorts (1983 to 1992) to have reached at least 15 years of age. The dashed line (X) shows capture probabilities for four cohorts (1989-1992). The dashed line (triangle) shows capture probabilities taken from Pistorius and Bester (2002b), using pooled data from three cohorts (1983-1985) that had reached 15 years of age at that stage. Survival was modelled as constant through time.



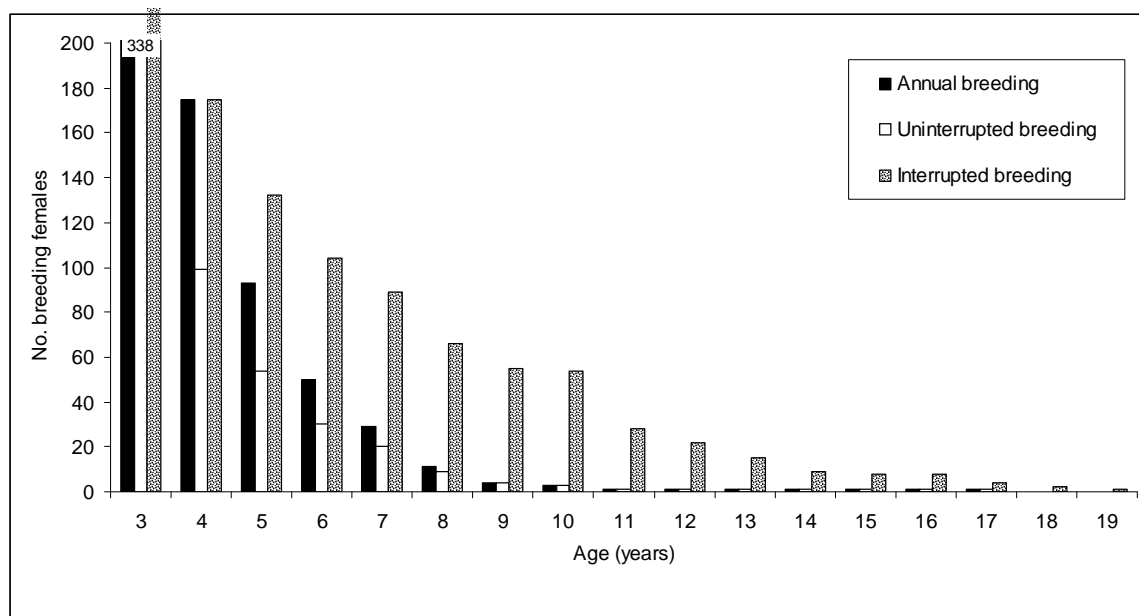


**Fig. 5.2b.** Capture probabilities (during breeding seasons) of pooled cohorts (1983 to 1992) of female southern elephant seals primiparous at different ages (P3 – age 3; P4 – 4 yrs; P5 – 5 yrs) shown as indices of breeding probabilities. Survival was modelled as constant through time.

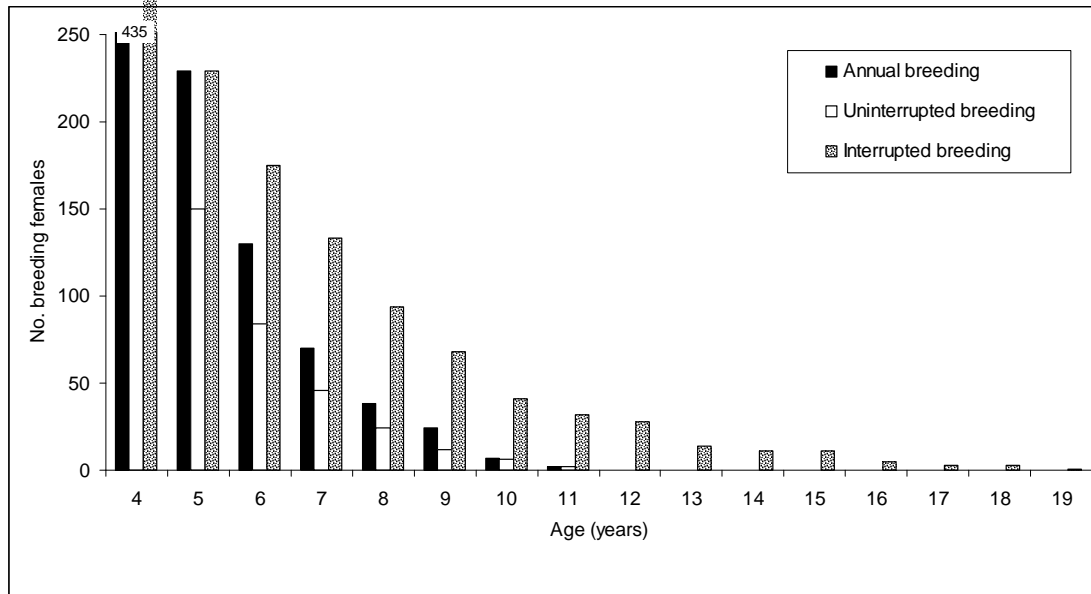
### Fertility

A total of 1032 adult southern elephant seal females (28% of 3723 tagged weanling female seals from 1983 to 1997) were observed to return to the island to breed between 1983 and 2007. The survivorship schedule for this population (see Chapter 4) predicts that from this original sample of 3723 tagged female weanlings (1983 to 1997), a total of 1487, 1148 and 891 should have survived to their 3<sup>rd</sup>, 4<sup>th</sup> and 5<sup>th</sup> years respectively. Given that many of these were consecutive breeders in each subsequent age category, it follows that at least 1000 females from these cohorts were part of the breeding clade of 3 to 5 year olds over this timeframe. This gives a good indication that most females that had survived to breeding age, were in fact observed (n = 1032) returning to breed at this locality. Age at primiparity was not constant for these 15 pooled cohorts (1983 to 1997), with 338 three-year-olds (33% of breeders), 435 four-year-olds (42%), 148 five-year-olds (14%) and 66 six-year-olds (6%) respectively, commencing breeding for the first time at Marion Island. When 7 cohorts of breeding females (1983-1989; n = 439 individuals) from the period of population decline, were compared to 7 distinct cohorts (1995-2001; n = 496 individuals) from the period after 1994 (population stability/increase, see Chapter 4), no significant difference ( $\chi^2 = 1.778$ , df = 3, p = 0.619) in the proportion of 3, 4, 5, and 6 year old primiparous breeders was identified. Figure 5.3a-d illustrate the relative numbers of

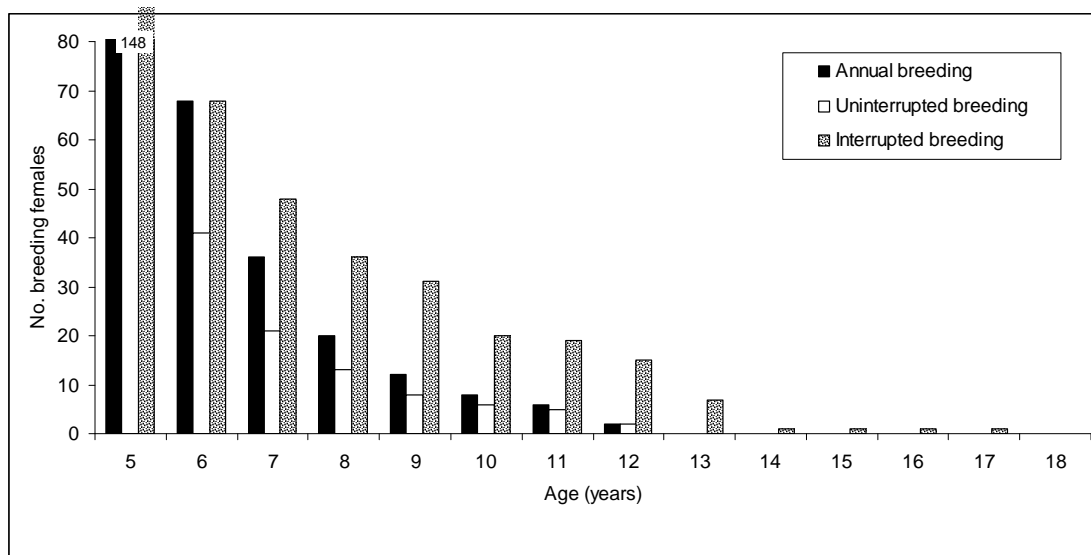
females breeding annually before a missed breeding season (with subsequent return), uninterrupted (from primiparity to ‘death’) and non-annual (continuously interrupted) breeding schedule, respectively for different primiparous ages. No difference ( $\chi^2 = 3.311$ ,  $df = 6$ ,  $p = 0.769$ ) was observed in the percentage of consecutive breeding events (from 3 to 9 consecutive events) per individual between the distinct periods of 1983 to 1993 and the period 1994 to 2007. Overall, females primiparous at age 4 consistently participated in more consecutive breeding attempts than 3-, 5- and 6-year-olds respectively (Fig. 5.4). No consecutive breeding events for any female extended beyond 12 years of age. Figure 5.5 illustrates the frequency distribution of the total observed number of breeding attempts (not necessarily consecutive) per individual female southern elephant seal ( $n = 1358$ ) from 20 pooled cohorts (1983-2002) at Marion Island over the breeding periods from 1983 to 2007. Only one female participated in 15 breeding seasons, and nearly 40% of females participated in only one breeding season (Fig. 5.5). Figure 5.6 shows the simple pup production data over the period 1986 to 2007, to augment discussion on the above breeding results.



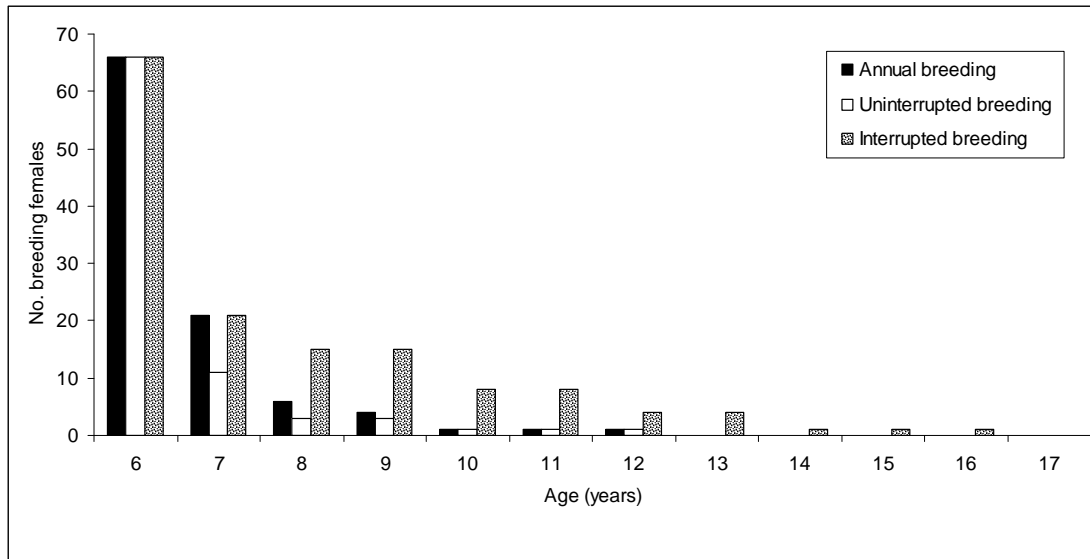
**Fig. 5.3a.** Fertility schedule of adult female southern elephant seals observed to be primiparous at age three. Annual breeding – females that bred in consecutive years before a sabbatical and a subsequent resumption of breeding. Uninterrupted breeding – females that bred annually from primiparity to disappearance from the study (‘death’). Interrupted breeding – random sabbaticals between breeding years.



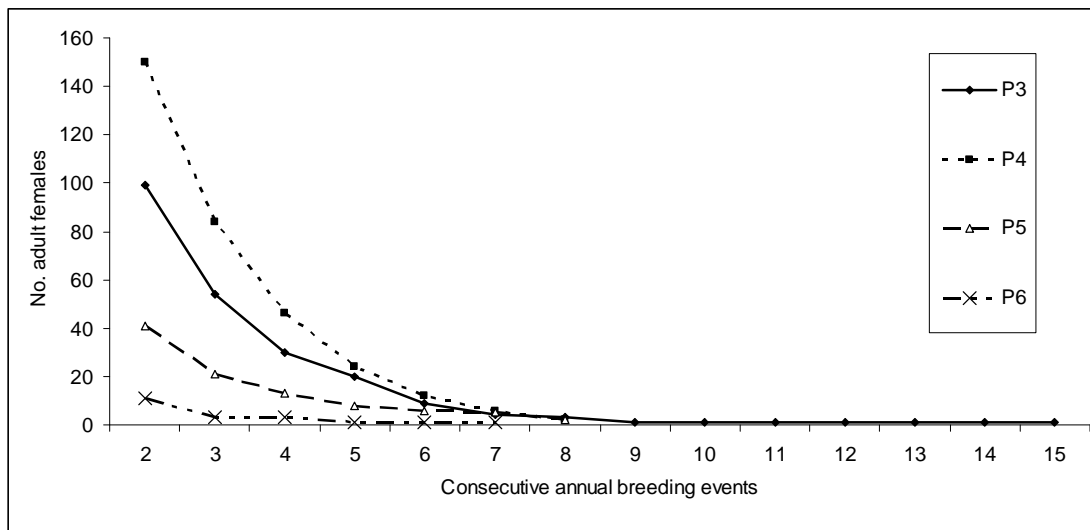
**Fig. 5.3b.** Fertility schedule of adult female southern elephant seals observed to be primiparous at age four.



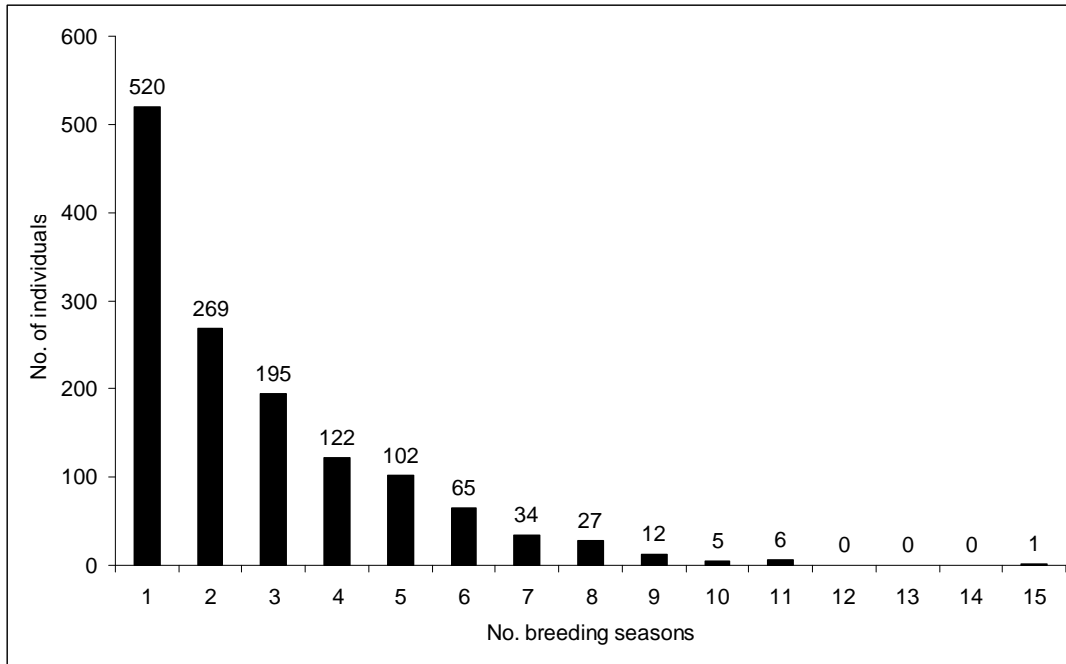
**Fig. 5.3c.** Fertility schedule of adult female southern elephant seals observed to be primiparous at age five.



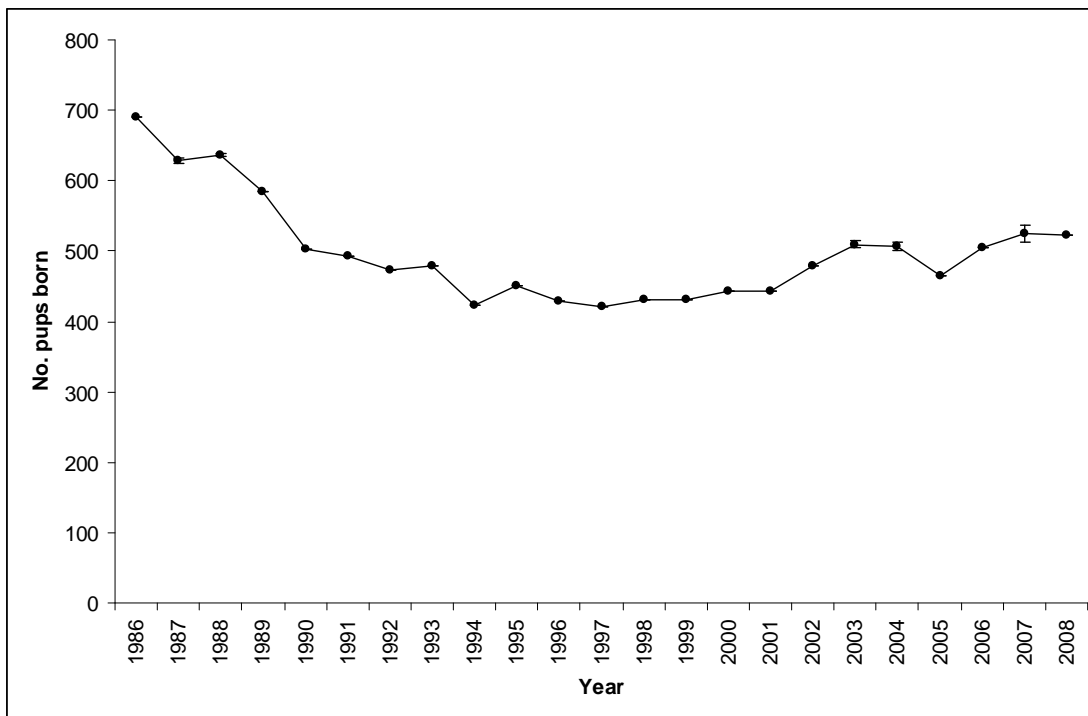
**Fig. 5.3d.** Fertility schedule of adult female southern elephant seals observed to be primiparous at age six.



**Fig. 5.4.** Relative numbers of adult females participating in consecutive annual breeding events dependent on their age at primiparity (ages three - P3, four - P4, five - P5, and six - P6), from a total sample of 1032 individuals from 15 consecutive cohorts (1983 to 1997)



**Fig. 5.5.** Frequency distribution of the total observed number of breeding attempts (not necessarily consecutive) per individual female southern elephant seal ( $n = 1358$ ) from 20 pooled cohorts (1983-2002) at Marion Island over the breeding periods from 1983 to 2007.



**Fig. 5.6.** Number of southern elephant seal pups born at Marion Island (1986 to 2008).

## Discussion

Senescence hypothesis predicts that the oldest individuals within a population will have the lowest reproductive investment, somatic investment (i.e. self investment), and annual survival. Pistorius and Bester (2002b) suggested that southern elephant seal females do not display senescence in either survival or reproduction. Similarly, Hindell and Little (1988) predicted that southern elephant seals are not senescent based on the observations of two very old (>20 years) individuals that remained within a breeding population. To our knowledge only one other phocid species (Hawaiian monk seal, *Monachus schauinslandi*) has recently been reported to show senescence (Baker and Thompson 2007), although senescence has been shown for some otariids (e.g. Bester 1995; Beuplet et al. 2006). We used a significantly larger sample of individually identifiable southern elephant seals than the Pistorius and Bester (2002b) study to reassess senescence in this species. Southern elephant seals do not show signs of actuarial senescence, corroborating earlier findings from Pistorius and Bester (2002b). Similarly to the previous study, average survival for females older than 7 years exceeded that for prime-aged (4-7 yrs old) females by 3.8%, and even some very old (>15 years) individuals showed markedly increased (>20%) survival probabilities compared to their middle aged counterparts. The absence of actuarial senescence in this species and other capital breeding phocids is however not entirely surprising. Drent and Daan (1980) predicted that long-lived species should incur costs to reproduction before they incur costs to their own survival according to the 'prudent parent' hypothesis. Additionally, a fundamental obstacle in studies of senescence in the wild is the surprising lack in understanding of causes of mortality in wild populations (Ricklefs 2008). This shrouds the temporal scale of death in that factors that may contribute to a slow degeneration of the organism (e.g. cellular functioning) or those causing a sudden demise (e.g. predation), cannot always be disentangled. The largely pelagic existence of phocids, including southern elephant seals (Bester 1988, 1989) makes identifying causes of mortality difficult. For example, the deep diving abilities of some marine mammals make them potentially vulnerable to long-term degenerative conditions such as osteonecrosis (e.g. sperm whales, *Physeter macrocephalus*, Moore and Early 2004), while predation (e.g. by killer whales, *Orcinus orca*, see Appendix 3 – Tosh et al. 2008) would obviously result in sudden death. Within a CMR framework the analytical end result remains the same however, and thereby

complicates identification of actuarial senescence based on survival probabilities. Disentangling causes of death will greatly enhance our understanding of the evolution of actuarial senescence. Longevity in females in this seal population is predicted to be greater than the observed, but this could be as a result of the pooled survival estimates from several old and younger cohorts, where the increased survival of the younger cohorts after population stabilization (see Chapter 4) may predict greater longevity for these cohorts, and this remains to be observed in years to come. However, in support of our predicted longevity results, individuals of the species are known to attain maximum ages in excess of 20 years (Hindell and Little 1988).

On the other hand, while old females may persist in the population and return typically during annual moulting events that confirm their survival, our results suggest that most do not return to breed as frequently (as during their prime age years) beyond the age of 12 years. This is remarkably similar to the purported onset of senescence at age 13 reported for Subantarctic fur seals, *Arctocephalus tropicalis* (Bester 1995; Beuplet et al. 2006), but markedly earlier than that at 17 years of age reported for Hawaiian monk seals (Baker and Thompson 2007). Notwithstanding the persistence of a few elephant seal females breeding into old age, senescence theory refers to within-individual changes in reproductive performance with age and not between-individual variation because variation in quality is common in vertebrate populations (Forslund and Part 1995). Longitudinal analyses are better suited to distinguish between these sources of individual variation than cross-sectional analyses (Nussey et al. 2008). The very large longitudinal dataset at Marion Island thus shows clear support for reproductive senescence in this species, in contrast to earlier findings by Pistorius and Bester (2002b) and Pistorius et al. (2004) based on a smaller sample of individuals from the same population. Additionally, our results provide rare evidence for a delayed reproductive cost associated with early primiparity. This lends support to previous findings for northern elephant seals, *Mirounga angustirostris* (Reiter and Le Boeuf 1991), despite subsequent speculation surrounding the analytical procedure for that study (Sydeman and Nur 1994). Reproductive effort in later life associated with early primiparity can be associated with differences in mass gain after early-life breeding attempts (Festa-Bianchet et al. 1995). Body mass is a particularly important determinant of survival and breeding

success in pinnipeds (see Chapter 2 – de Bruyn et al. 2009). Early breeding females subsequently may be sub-optimal contributors to population growth if their early breeding results in lowered mass gain in subsequent seasons. However, to accurately assess the impact of early primiparity on mass gain, future reproductive potential, survival and pup performance, large temporal samples of known mass breeding females (see Chapter 2 – de Bruyn et al. 2009) and their relationships with offspring (see Chapter 3 – de Bruyn et al. 2008) are required.

The contradiction of our findings with Pistorius et al. (2004)'s assertion that age at primiparity does not incur lifetime reproductive cost is likely due to that study being based on a smaller sample of individuals and was temporally limited by resighting effort (only up to 1999) in terms of potential maximum attainable age for several cohorts. Our results supplement the findings of short-term costs to reproduction in capital breeding phocids reported by Hadley et al. (2007) and Pistorius et al. (2008). Pistorius et al. (2008) provided evidence for primiparous southern elephant seal females (regardless of their age at primiparity) suffering higher probabilities of mortality than did old females, following a breeding season. Hadley et al. (2007) illustrate similar immediate costs in subsequent year survival, associated with reproduction in primiparous Weddell seals, *Leptonychotes weddellii*. The mounting evidence for senescence, particularly in reproductive effort in pinnipeds (Reiter and Le Boeuf 1991; Bester 1995; Beauplet et al. 2006; Baker and Thompson 2007; this study), draws attention to potentially significant ecological consequences related to population demography in this important group of marine top-predators.

Annually interrupted breeding effort is more common than uninterrupted breeding effort in southern elephant seal females at Marion Island. Although seemingly counter-advantageous in some systems, interrupted breeding (i.e. breeding less frequently than the species seems capable of) may confer higher lifetime fecundity than regular frequency breeding (annual in southern elephant seals) if the lower frequency breeding strategy confers increased survival (McMahon and Bradshaw 2008), improved parturition condition, and thus increased offspring survival (McMahon et al. 2000). Resource limitation may be causative in such infrequent breeding. However, the hypothesised food limitation prior to 1994 in the



Marion Island population (Pistorius et al. 1999) did not correspond to less frequent breeding attempts by adult females as compared to the period after 1994 (this study). The state shift in the population at Marion Island from decline to increase (McMahon et al. 2009) therefore did not result in a higher frequency of annual breeders, nor did it appear to reduce the mean age at primiparity in the population (i.e. nor the proportion of younger primiparous animals; this study) as suggested by others (Pistorius et al. 1999, 2001a; McMahon et al. 2009). Additionally, different ages at primiparity did not influence the proportion of consecutive *versus* interrupted breeding efforts over time. The proportion of interrupted to uninterrupted breeding schedules remained similar for younger and older seals regardless of their age at primiparity, although reproductive senescence became clearly pronounced after age 12 when virtually no consecutive breeding events occurred.

Pistorius et al. (2001a) made the assumption that, females older than 5 years breed virtually every year, as a basis for calculation of temporal changes in fecundity in adult females. This study shows that this assumption is incorrect for this species, and corroborates Bradshaw et al. (2002)'s suspicion that southern elephant seal females do not as a rule breed every year, regardless of their age. This finding has important consequences in light of conclusions drawn in previous studies where this assumption has been made (Pistorius et al. 2004, 2008; McMahon et al. 2003, 2005, 2009). Thus, while aspects of fertility can be illuminated (this study), studies of fecundity in this population *per se* should be approached with caution. Nevertheless, it seems plausible that while increases in fertility are not evident to have contributed to the stabilisation of this population, an increased number of survivors (see Chapter 4) recruited into the breeding population and breeding at what appears to be an optimum rate for the species (this study) have resulted in a positive feedback augmenting population stabilisation/increase (McMahon et al. 2009). Older more experienced breeders are, however, more successful in weaning their pups (Pistorius et al. 2001b) and these pups better survive their first year (McMahon and Bradshaw 2004). Additionally, in some phocids more experienced mothers are not subject to lowered survival probability following a breeding season, unlike primiparous breeders (Hadley et al. 2007; Pistorius et al. 2008) suggesting a higher likelihood of young mothers not breeding in consecutive years. Despite the unchanged breeding schedules of adult females before and after survivorship inflexion (1994, see Chapter

4), the number of pups born after 1994 have steadily increased (see Fig. 5.6), supporting the assertion that increased survivorship of juveniles and adult females is chiefly responsible for the current positive population trend (McMahon et al. 2009), rather than a dramatic increase in fertility amongst females. Thus, simply more females are available to produce more pups.

Increased reproductive effort by way of greater investment in current offspring as the number of future potential offspring declines over a mother's lifetime, as stipulated by the residual reproductive value (RRV) hypothesis, should be evident in reduced survival or lowered future reproductive success in the mother (Clutton-Brock 1991). Marion Island southern elephant seals provide evidence in support of the RRV hypothesis, because while survival in very old females remains high, a marked decrease in reproductive effort is apparent. The need for increased relative investment in offspring by older mothers in this species as predicted by the RRV thus seems a plausible explanation for the missed annual breeding efforts. However, Cameron et al. (2000) argued that more experienced ("older and wiser") female Kaimanawa horses (*Equus caballus*) did not necessarily invest more in their offspring, but rather targeted their investment more successfully during offspring rearing, as predicted by their targeted reproductive effort (TRE) hypothesis. Such targeted investment effort seems improbable in a species portraying brief postpartum maternal care of offspring as with the three-week weaning period in southern elephant seals (Laws 1953), although this has not been tested. Somatic investment therefore appears to take precedence over investment in offspring in southern elephant seals (RRV hypothesis). This is also in accordance with the 'prudent parent' hypothesis (Drent and Daan 1980).

However, the persistence of some individuals with unimpeded annual breeding efforts, and those with interrupted but regular efforts into old age, suggest that reproductive effort may not be intrinsically (physiologically) constrained, but rather extrinsically controlled (resource availability). Some extra-binomial variation, evident in GOF tests (for the global CJS model) in this dataset, indicates consistent violation of Test 2 (the "recapture test"), providing additional evidence for either, sabbatical years when a female does not breed and does not haul out, or where she breeds elsewhere. Although individual variation in the degree of philopatry is

acknowledged, high philopatry to particular breeding beaches subsequent to an initial return to Marion Island for a breeding season for most females (Hofmeyr 2000) suggests that the latter option is unlikely. Additionally, recent data from two satellite tracked individuals that had pupped in a particular season showed that when unobserved during the subsequent breeding season, they were at sea and not hauled out to breed elsewhere (M.N. Bester unpublished data). This suggests that extrinsic drivers (potentially resource limitation, Pistorius et al. 1999) force a trade-off for potential mothers between somatic or offspring investment prior to and during certain breeding seasons, related to previous breeding attempts. The high frequency of continuously interrupted breeding schedules of adult females in this population may propose such a dynamic trade-off over time for each individual (McNamara and Houston 1996) dependent on their foraging areas and success in foraging (Biuw et al. 2007). Perhaps, the few high quality individuals that do not experience reproductive senescence (primiparous at a later age, this study) and have an interrupted breeding schedule, may achieve increased lifetime fertility and hence fecundity may exceed that for early primiparous individuals that adopt a shorter period of uninterrupted breeding before senescence sets in. Either option is of course likely to be environmentally mediated according to foraging efficiency at sea (Biuw et al. 2007) and behavioural choices on land (McMahon and Bradshaw 2004). This “less-frequent-but-into-old-age” *versus* “more-frequent-for-fewer-years” breeding approach poses a dichotomy with considerable challenges to our understanding of not only the evolution of senescence in capital breeding top marine predators, but also our understanding of population regulating factors in these seal populations. A multistate modelling approach that includes an ‘unobservable’ state (Kendall and Nichols 2002; Schaub et al. 2004) within model structuring may further elucidate the survival and reproductive probabilities in aid of senescence studies (e.g. Beauplet et al. 2006).

A weakness of the present study is the absence of covariates (particularly body mass, e.g. Pomeroy et al. 1999; McMahon et al. 2000) as indices of maternal fitness in model design, and the absence of knowledge of mother-offspring relatedness in the dataset. Such data would allow assessment of the future survival of offspring as related to maternal condition, and of particular interest in senescence studies, the effect of maternal investment/condition/age on her future survival and

reproductive effort (e.g. Cameron et al. 2000). Life-history theory predicts age-dependent fluctuations in resource allocation that may or may not be related to senescence. Therefore, the integration of life-history theory with studies of senescence remains a challenge in wild populations (Nussey et al. 2008). To this end, recent developments to simplify the assessment of body mass of large seals (see Chapter 2 – de Bruyn et al. 2009) and to augment the current mark-resighting database at Marion Island with relatedness information (see Chapter 3 – de Bruyn et al. 2008) should allow future illumination of the above questions. Another weakness was that many cohorts used in this study were born and spent their juvenile and prime age years within the hypothesized population decline, food limitation period (Pistorius et al. 1999). Cohorts born after survivorship inflexion (1994, see Chapter 4) have not aged sufficiently to allow this approach to a study of senescence, and therefore comparative questions of resource 'limited vs. non-limited' during early life and its' effects on ageing (Nussey et al. 2007) remain comparatively unstudied. Nevertheless, this study provides a comprehensive investigation into the fertility and reproductive capabilities of southern elephant seals, with associated descriptors of fundamental population parameters such as frequency of breeding, longevity and costs of early primiparity. These senescence, fertility and longevity data (based on a longitudinal experiment), bring valuable information to the study of senescence and augment continuing demographic studies aimed at understanding the fundamental drivers of southern elephant seal populations. We have additionally illustrated important facets of the life-history of this population that allow for reconsideration of conclusions drawn in earlier population demographic studies.

### **Literature Cited**

- Anderson DR, Burnham KP, White GC (1994) AIC model selection in overdispersed capture-recapture data. *Ecology* 75:1780-1793
- Baker JD, Thompson PM (2007) Temporal and spatial variation in age-specific survival rates of a long-lived mammal, the Hawaiian monk seal. *Proc R Soc B* 274:407-415.
- Beauplet G, Barbraud C, Dabin W, Küssener C, Guinet C. (2006) Age-specific survival and reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos* 112:430–441

- Bester MN (1988) Marking and monitoring studies of the Kerguelen stock of southern elephant seals, *Mirounga leonina*, and their bearing on biological research in the Vestfold hills. *Hydrobiologia* 165:269-277
- Bester MN (1989) Movements of southern elephant seals and subantarctic fur seals in relation to Marion Island. *Mar Mamm Sci* 5:257–265
- Bester MN (1995) Reproduction in the female subantarctic fur seal *Arctocephalus tropicalis*. *Mar Mamm Sci* 11: 362 – 375.
- Biuw M, Boehme L, Guinet C, Hindell M, Costa D, Charrassin JB, Roquet F, Bailleul F, Meredith M, Thorpe S, Tremblay Y, McDonald B, Park YH, Rintoul SR, Bindhoff N, Goebel M, Crocker D, Lovell P, Nicholson J, Monks F, Fedak MA (2007) Variations in behaviour and condition of a southern ocean top predator in relation to in situ oceanographic conditions. *Proc Nat Acad Sci USA* 104:13705–13710
- Bradshaw CJA, McMahon CR, Hindell MA, Pistorius PA, Bester MN (2002) Do southern elephant seals show density dependence in fecundity? *Polar Biol* 25:650–655
- Burnham KP, Anderson DR, White GC, Brownie C, Pollock KH (1987) Design and analysis methods for fish survival experiments based on release–recapture. *Am Fish Soc Monogr* 5:1–437
- Cameron EZ, Linklater WL, Stafford KJ, Minot EO (2000) Aging and improving reproductive success in horses: declining residual reproductive value or just older and wiser? *Behav Ecol Sociobiol* 47:243–249
- Carothers AD (1979) Quantifying unequal catchability and its effect on survival estimates in an actual population. *J Anim Ecol* 48:863-869
- Clutton-Brock TH (1991) The evolution of parental care. Princeton University Press, Princeton, NJ
- Condy PR (1978) The distribution and abundance of southern elephant seals *Mirounga leonina* (Linn.) on the Prince Edward islands. *S Afr J Antarct Res* 8:42-48
- Coulson T, Benton TG, Lundberg P, Dall SRX, Kendall BE, Gaillard JM (2006) Estimating individual contributions to population growth: evolutionary fitness in ecological time. *Proc R Soc B* 273:547–555

- de Bruyn PJN, Tosh CA, Oosthuizen WC, Phalanndwa MV, Bester MN (2008) Temporary marking of unweaned southern elephant seal (*Mirounga leonina* L.) pups. S Afr J Wildl Res 38:133-137 [Chapter 3]
- de Bruyn PJN, Bester MN, Carlini AR, Oosthuizen WC (2009) How to weigh an elephant seal with one finger: a simple three-dimensional photogrammetric application. Aquat Biol 5:31-39 [Chapter 2]
- de Little SC, Bradshaw CJA, McMahon CR, Hindell MA (2007) Complex interplay between intrinsic and extrinsic drivers of long-term survival trends in southern elephant seals. BMC Ecol 7:3
- Drent RH, Daan S (1980) The prudent parent: energetic adjustments in avian breeding. Ardea 68:225–252
- Festa-Bianchet M, Jorgenson JT, Lucherini M, Wishart WD (1995) Life history consequences of variation in age of primiparity in bighorn ewes. Ecology 76:871-881
- Forslund P, Part T (1995) Age and reproduction in birds – hypotheses and tests. Trends Ecol Evol 10:374–378
- Gaillard JM, Allaine D, Pontier D, Yoccoz NG, Promislow DEL (1994) Senescence in natural-populations of mammals – a reanalysis. Evolution 48:509–516
- Gaillard JM, Festa-Bianchet M, Yoccoz NG, Loison A, Toïgo C (2000) Temporal variation in fitness components and population dynamics of large herbivores. Ann Rev Ecol Syst 31:367–393
- Hadley GL, Rotella JJ, Garrott RA (2007) Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. J Anim Ecol 76:448-458
- Hindell MA, Little GJ (1988) Longevity, fertility and philopatry of two female southern elephant seals (*Mirounga leonina*) at Macquarie Island. Mar Mammal Sci 4:168-171
- Hofmeyr GJG (2000) Dispersal and dispersion of southern elephant seals at Marion Island. MSc. thesis, University of Pretoria: Pretoria.
- Jones OR, Gaillard JM, Tuljapurkar S, Alho JS, Armitage KB, Becker PH, Bize P, Brommer J, Charmantier A, Charpentier M, Clutton-Brock T, Dobson FS, Festa-Bianchet M, Gustafsson L, Jensen H, Jones CJ, Lillandt G, McCleery R, Merila J, Neuhaus P, Nicoll MAC, Norris K, Oli MK, Pemberton J, Pietiainen H, Ringsby TH, Roulin A, Saether BE, Setchell JM, Sheldon BC, Thompson PM, Weimerskirch H, Wickings EJ, Coulson T (2008) Senescence rates are

- determined by ranking on the fast-slow life-history continuum. *Ecol Lett* 11:664-673
- Kirkman SP, Bester MN, Hofmeyr GJG, Jonker FC, Pistorius PA, Owen R, Strydom N (2004) Variation in the timing of the breeding haulout of female southern elephant seals at Marion Island. *Austr J Zool* 52: 379-388
- Kendall WL, Nichols JD (2002) Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology* 83:3276-3284.
- Kirkwood TBL, Holliday R (1979) Evolution of aging and longevity. *Proc R Soc B* 205:531–546
- Laws RM (1953) The elephant seal (*Mirounga leonina* Linn.). I. Growth and age. *Falkland Isl Depend Surv Sci Rep* 8:1–62
- Lebreton J-D, Burnham KP, Clobert J, Anderson DR (1992) Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol Monogr* 62:67-118
- McMahon CR, Bradshaw CJA (2008) Fecundity. In: Jørgensen SE, Fath BD (eds) *Population Dynamics*, Vol. 2 of *Encyclopaedia of Ecology*, 5 vols. Elsevier, Oxford, pp. 1535-1543
- McMahon CR, Burton HR, Bester MN (2000) Weaning mass and the future survival of juvenile southern elephant seals, *Mirounga leonina*, at Macquarie Island. *Antarct Sci* 12:149–153
- McMahon CR, Bradshaw CJA (2004) Harem choice and breeding experience of female southern elephant seals influence offspring survival. *Behav Ecol Sociobiol* 55:349-362
- McMahon CR, Burton HR, Bester MN (2003) A demographic comparison of two southern elephant seal populations. *J Anim Ecol* 72:61-74
- McMahon CR, Hindell MA, Burton HR, Bester MN (2005) Comparison of southern elephant seal populations, and observations of a population on a demographic knife-edge. *Mar Ecol Prog Ser* 288:273-283
- McMahon CR, Bester MN, Hindell MA, Brook BW, Bradshaw CJA (2009) Shifting trends: detecting environmentally mediated regulation in long lived marine vertebrates using time-series data. *Oecologia* 159: 69-82
- McNamara JM, Houston AI (1996) State-dependent life histories. *Nature* 380:215-221

- Moore MJ, Early GA (2004) Cumulative sperm whale bone damage and the bends. *Science* 306: 2215
- Monaghan P, Charmantier A, Nussey DH, Ricklefs RE (2008) The evolutionary ecology of senescence. *Funct Ecol* 22:371-378
- Mulaudzi TW, Hofmeyr GJG, Bester MN, Kirkman SP, Pistorius PA, Jonker FC, Makhado AB, Owen JH, Grimbeek RJ (2008) Haulout site selection by southern elephant seals at Marion Island. *Afr Zool* 43:25-33
- Nichols JD, Stokes LS, Hines JE, Conroy MJ (1982) Additional comments of the assumption of homogeneous survival rates in modern bird banding estimation models. *J Wildl Manage* 46:953–962
- Nussey DH, Kruuk LEB, Donald A, Fowlie M, Clutton-Brock TH (2006) The rate of senescence in maternal performance increases with early-life fecundity in red deer. *Ecol Lett* 9:1342–1350
- Nussey DH, Kruuk LEB, Morris A, Clutton-Brock TH (2007) Environmental conditions in early life influence ageing rates in a wild population of red deer. *Current Biol* 17:R1000–R1001
- Nussey DH, Coulson T, Festa-Bianchet M, Gaillard J-M (2008) Measuring senescence in wild animal populations: towards a longitudinal approach. *Funct Ecol* 22:393–406
- Oosthuizen WC, de Bruyn PJN, Bester MN, Girondot M (2009) Cohort and tag-site specific tag-loss rates in mark-recapture studies: a southern elephant seal cautionary case. *Mar Mamm Sci* *Accepted* [Appendix 2]
- Partridge L, Barton NH (1996) On measuring the rate of ageing. *Proc R Soc B* 263:1365–1371
- Pistorius PA, Bester MN (2002a) Juvenile survival and population regulation in southern elephant seals at Marion Island. *Afr Zool* 37:35-41
- Pistorius PA, Bester MN (2002b) A longitudinal study of senescence in a pinniped. *Can J Zool* 80:395–401
- Pistorius PA, Bester MN, Kirkman SP (1999) Survivorship of a declining population of southern elephant seals, *Mirounga leonina*, in relation to age, sex and cohort. *Oecologia* 121:201-211
- Pistorius PA, Bester MN, Kirkman SP, Boveng PL (2000) Evaluation of age- and sex-dependent rates of tag-loss in southern elephant seals. *J Wildl Manage* 64: 373-380.



- Pistorius PA, Bester MN, Kirkman SP, Taylor FE (2001a) Temporal changes in fecundity and age at sexual maturity of southern elephant seals at Marion Island. *Polar Biol* 24:343-348
- Pistorius PA, Bester MN, Kirkman SP, Taylor FE (2001b) Pup mortality in southern elephant seals at Marion Island. *Polar Biol* 24:828–831
- Pistorius PA, Bester MN, Lewis MN, Taylor FE, Campagna C, Kirkman SP (2004) Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal. *J Zool Lond* 263:107-119
- Pistorius PA, Bester MN, Hofmeyr GJG, Kirkman SP, Taylor FE (2008) Seasonal survival and the relative cost of first reproduction in adult female southern elephant seals. *J Mammal* 89:567-574
- Pomeroy PP, Fedak MA, Rothery P, Anderson S (1999) Consequences of maternal size for reproductive expenditure and pupping success of grey seals at North Rona, Scotland. *J Anim Ecol* 68:235–253
- Promislow DEL (1991) Senescence in natural-populations of mammals – a comparative-study. *Evolution* 45:1869–1887
- Reiter J, Le Boeuf BJ (1991) Life history consequences of variation in age at primiparity in northern elephant seals. *Behav Ecol Sociobiol* 28:153-160
- Ricklefs RE (2008) The evolution of senescence from a comparative perspective. *Funct Ecol* 22:379–392
- Ricklefs RE, Cadena CD (2007) Lifespan is unrelated to investment in reproduction in populations of mammals and birds in captivity. *Ecol Lett* 10:867–872
- Schaub M, Gimenez O, Schmidt BR, Pradel R (2004) Estimating survival and temporary emigration in the multistate capture-recapture framework. *Ecology* 85:2107–2113
- Sydeman WJ, Nur N (1994) Life history strategies of female northern elephant seals. In: *Elephant seals: population ecology, behavior, and physiology*, Le Boeuf BJ, Laws RM (eds.). Berkeley: University of California Press.
- Tosh CA, de Bruyn PJN, Bester MN (2008) Preliminary analysis of the social structure of killer whales, *Orcinus orca*, at subantarctic Marion Island. *Mar Mamm Sci* 24:929-940 [Appendix 3]
- White GC, Burnham KP (1999) Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Suppl.):120-138

Wilkinson IS (1991) Factors affecting reproductive success of southern elephant seals, *Mirounga leonina*, at Marion Island. PhD thesis. University of Pretoria, Pretoria.

Williams GC (1957) Pleiotropy, natural selection, and the evolution of senescence. *Evolution* 11:398–411

Williams PD, Day T, Fletcher Q, Rowe L (2006) The shaping of senescence in the wild. *Trends Ecol Evol* 21:458–463