

Life history studies of the southern elephant seal population at Marion Island

by

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Declaration:

I, ...**Petrus Jacobus Nicholas de Bruyn**..... declare that the thesis/dissertation, which I hereby submit for the degree**PhD Zoology**..... at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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There is a pleasure in the pathless woods;
There is a rapture on the lonely shore;
There is society, where none intrudes,
By the deep sea, and music in its roar:
I love not man the less, but Nature more

George Gordon Noel Byron, Lord Byron. (1788–1824)

This work is dedicated to the wild inhabitants of that Jewel of the Southern Ocean, Marion Island, and to all the intruders who have expended much blood, sweat and tears in the glorious quest for knowledge.

Life history studies of the southern elephant seal population at Marion Island

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Holistic studies of mammalian life history factors and their consequences on population demography require an intensive, multifaceted field methodology and effort over long temporal scales. A 25-year longitudinal mark-recapture experiment on southern elephant seals, *Mirounga leonina*, at Subantarctic Marion Island provides such a foundation for demographic analyses and relevant methodology advancement. Two gaps in the methodology related to life history and population demographic research are, the absence of large samples of known mass individuals, and an inability to identify mother-pup relatedness. A novel three-dimensional photogrammetric technique is designed here that allows for mass estimation of large samples of southern elephant seals in the field. An effective temporary marking technique for unweaned pups is implemented that allows for identification of large samples of pups with known mothers prior to the maternal bond being severed at weaning. These known pups can then be marked with more robust tags and relatedness information is preserved long-term. Thus, mass estimates can now be applied as covariates in modelling analyses to address questions of, for example, maternal investment, kinship associated behaviour, and the consequences thereof on survival and reproductive parameters.

The state change in the Marion Island southern elephant seal population from decrease to stabilisation/increase is shown to have resulted from improved survivorship in both juvenile and adult female age classes. Male seals of all ages did not indicate improved survivorship following the period of decline. The inflexion in survivorship is identified as 1994, whence improved survivorship of juvenile seals preceded that of young adult females. This inflexion in survivorship is postulated to have resulted in a population trend inflexion around 1998.

Female southern elephant seals do not show evidence of actuarial senescence, but reproductive senescence is apparent after 12 years of age. A long-term reproductive cost (reduced breeding effort) is associated with early primiparity (age three) as compared with later primiparity (4- 5- or 6-year-old). The mean proportion of 3-year-old breeders has not increased after 1994 as has been hypothesized in previous studies. Contrary to previous assumptions, females do not as a rule breed every year. Annually interrupted breeding efforts are more common than consecutive breeding efforts. No difference in the proportions of interrupted *versus* uninterrupted breeding efforts was identified between periods of population decline and stabilisation/increase. Longevity as predicted by survival estimates exceeds the observed frequencies. This study provides unique longevity and fertility schedules for the species.

The improved survivorship, reproductive senescence and breeding schedules of female southern elephant seals in this population provide groundwork for re-evaluation of previous studies and their conclusions. The addition of relatedness and body condition information will allow for sophisticated multistate modelling of population demography in future studies. However, analytical procedures and techniques employed need to be meticulously designed and thoroughly thought through to avoid mis-interpretation of biological data.

In addition to a multistate single species analytical approach, the importance of an ecosystem approach to species population demographic studies is highlighted through the augmenting of data on relevant potential drivers of population change, such as killer whales, *Orcinus orca*.

Key words: *Mirounga leonina*, Southern Ocean, phocids, photogrammetry, mark-recapture, tagging, survivorship, senescence, longevity, population demography, methodology advancement, experimental design, ecosystem approach research

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- Tosh CA, **de Bruyn PJN**, and MN Bester (2008) Preliminary analysis of the social
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Disclaimer

Each of the research chapters within this thesis was structured with scientific journal publication in mind. I apologise for some overlap and repetition in methods sections.

CHAPTER ONE:

GENERAL INTRODUCTION

Introduction

An adequate study of animal population biology requires an understanding of population dynamics (Lebreton et al. 1993). 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 changes in survival and fecundity (Siniff et al. 1977). The detection of these changes may indicate large-scale shifts in ecosystem processes (Weimerskirch et al. 2003; McMahon and Burton 2005). Long-term monitoring programmes are ideal to trace the fate of numerous animals within the population from birth throughout life (i.e. longitudinal life history studies) (Clobert et al. 1994).

A great deal of research has in recent years been aimed at demographic aspects of the Marion Island southern elephant seal population as a long-term longitudinal dataset is in existence (1983 – present). The focus has in particular been on changes in population sizes (Bester and Wilkinson 1994; Pistorius et al. 1999a), and causal factors contributing to these changes, both proximate and ultimate (Bester and Wilkinson 1994; Pistorius et al. 1999b). The Marion Island elephant seal population has declined by 83% since 1951 (Laws 1994) and by 37.2% between 1986 and 1994 at an annual rate of change of 5.8%, which was linear over the period (Pistorius et al. 1999a). Pistorius et al. (1999b, 2001, 2008) suggested a change in population trend, from decrease to stability, around 1994. Bradshaw et al. (2002) argued that this conclusion was preliminary, based on a limited timeline of data. Subsequently, McMahon et al. (2005a, 2009) argued that the population trend inflexion point was situated around 1998. Pistorius et al. (1999a, 1999b, 2001a, 2001b, 2002, 2004, 2005, 2008a, 2008b) and Pistorius and Bester (2002a, 2002b) tested several hypotheses to understand what could be driving the regulation of the Marion Island elephant seal population, ultimately concluding that adult female survival due to food limitation was the proximate cause of the decline in the population. McMahon et al. (2003, 2005b) contended that juvenile survival was of greater importance in both the decline and recent stabilization (McMahon et al. 2009) of this population. Notwithstanding the significant contribution that these studies have

made to understanding the demographic drivers of southern elephant seal population rates at this locality, their limited temporal data, assumptions of various life-history parameter states, and the contention that has arisen from these studies demand further in-depth exploration of life history parameters for this population.

Southern Elephant Seal Biology

Southern elephant seals (*Mirounga leonina*) belong to the family phocidae (Order: Pinnipedia) and share the genus *Mirounga* with the northern elephant seal (*M. angustirostris*) (Le Boeuf and Laws 1994). These species are extreme capital breeders (Boyd 2000). Southern elephant seals are the largest living pinnipeds (King 1983) and portray strong sexual dimorphism, with adult males (3000 – 4000 kg) weighing up to 10 times more than adult females (400 – 900 kg) (Laws 1953). Breeding and mating is cyclic and females commence with their first mating attempts between the ages of 2 and 6 years while males, although sexually mature at age ~ 4, become socially mature after age 7 (Laws 1953; Condy 1979). The mating system of the species is strongly polygynous, with an often large ‘herd/harem’ of females congregating on a haul-out beach and guarded and mated by adult bulls at ratios (cows:bulls) varying from 9:1 (Wilkinson and van Aarde 1999) to 277:1 (Carrick et al. 1962), depending on the locality. Males do not contribute to the growth or rearing of offspring. Females give birth to a single pup (weighing as much as 40 – 46 kg) about a week after hauling out (Laws 1993) and wean the pup in 3 weeks during which time a substantial transfer of energy takes place (Fedak et al. 1996). The harem master mates with the cow at approximately the time of weaning of her pup, after which she departs to sea (Condy 1979). It is not known whether first mating in life occurs at sea, given the absence of juvenile cows from the breeding harems. Southern elephant seals undergo two, sometimes three, fasting periods during the course of one year in the breeding, moulting and winter haulouts (Condy 1979; Kirkman et al. 2001, 2003, 2004).

Southern Elephant Seal Distribution

Southern elephant seals are distributed in the Southern Ocean region between about 35°S and 70°S (Laws 1994) (Fig. 1.1). They haul-out onto sub-Antarctic islands and some mainland sites on the coasts of Argentina and Antarctic to breed, moult and over-winter (Laws 1994; McMahon et al. 2005a).

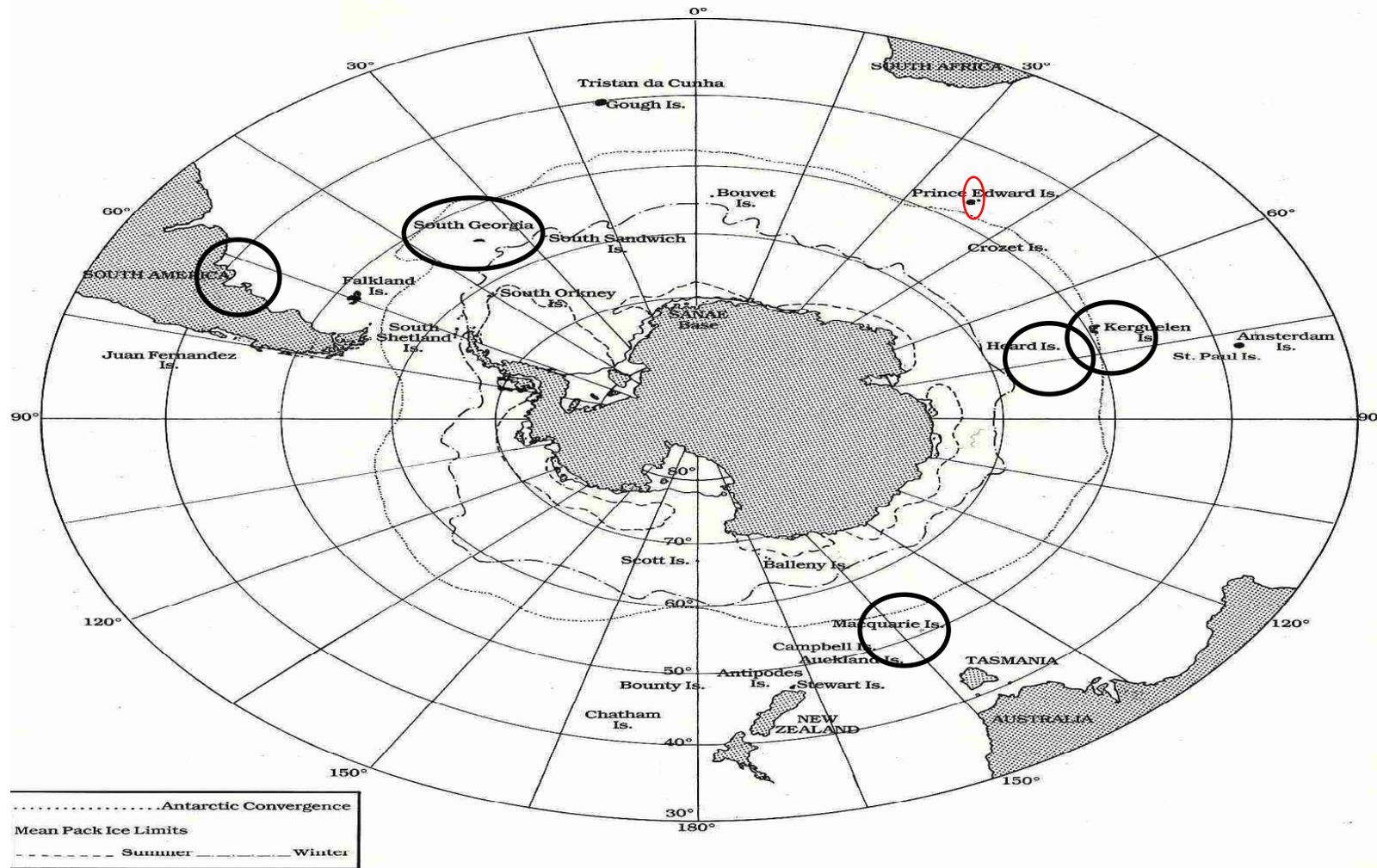


Fig. 1.1. Distribution of the five largest populations of southern elephant seals (large circles indicating relative population sizes). The smallest circle (red) illustrates the position of the small Prince Edward Islands population. Antarctica is displayed in the centre of the map.

The global population of southern elephant seals is divided into four genetically distinct sub-populations or “stocks”, namely the 1) Peninsula Valdés - Argentina, 2) South Georgia, 3) Kerguelen, and 4) Macquarie stocks (Slade et al. 1998; Hoelzel et al. 2001) (Fig. 1.1). The elephant seals on Marion Island form part of the Kerguelen or South Indian Ocean stock.

Present Worldwide Population Status

Ninety-eight percent of the global stock of southern elephant seals, are comprised of the South Georgia population, the Heard and Kerguelen islands populations, Macquarie Island and Peninsula Valdés populations (McMahon et al. 2005a). The remaining 2% of the global population consist of small subpopulations occurring on islands throughout the Subantarctic and adjoining regions (Laws 1994), including the population of interest in this study at Marion Island.

The South Georgia population (the largest globally) has remained stable since 1951. The Kerguelen stock, comprised of six island subpopulations has experienced precipitous declines since the 1950s, although recent evidence suggests most of these populations have stabilized during the 1990s. The Macquarie Island stock has experienced a similarly steep decline, while the only mainland centred population, at Peninsula Valdés is also the only population that has increased for the past few decades (reviewed in McMahon et al. 2005a). The most recent two reviews of the global population status in this species, documented these mainly declining trends pre-1990's (Laws 1994; McMahon et al. 2005a), while the period between these reviews (1994 - 2003) seems to have seen a stabilisation in the global population at around 740 000 southern elephant seals (McMahon et al. 2005a).

Study Area and Marine Surrounds

Subantarctic Marion – and smaller Prince Edward Island, encompasses the Prince Edward Islands (PEIs) archipelago. The islands are situated approximately 22km apart, with Marion Island (46°54'S, 37°45'E) located southeast of its sister island. The islands are emerged, quasi-active volcanic islands in the Southern Ocean, about half way between South Africa and the Antarctic Continent (Fig. 1.1). The islands are governed under the sovereignty of South Africa.

The PEIs are situated within the Polar Frontal Zone (PFZ), in the direct path of the Antarctic Circumpolar Current (ACC), bounded to the north and south by the dynamically changing Subantarctic Front (SAF) and Antarctic Polar Front (APF) respectively (Lutjeharms and Valentine 1984). The islands are situated along the south-west Indian ridge, a series of undersea mountain ranges and fracture zones or canyons that stretches from the mid-Atlantic ridge in the west to the central Indian ridge in the east. These bathymetrical features interact with the ACC to form eddies, which enhance the mesoscale variability in this region of the Southern Ocean (Lutjeharms and Valentine 1988). Pockets of cold water (cyclonic eddies) from south of the APF and warmer waters (anticyclonic eddies) from north of the SAF are responsible for carrying foreign organisms into the ACC (Froneman et al. 1999, Bernard et al. 2007) and for enhancing the primary productivity of the region.

Marion Island is approximately 300km² in area rising to 1240m above sea level (Meiklejohn and Smith 2008), and has a coastline of approximately 90km (Fig. 1.2). The coastline is comprised mostly of volcanic cliff-faces, interspersed with small pebble, boulder or rock-strewn beaches and only two that can be considered sandy, namely Ship's Cove and Goodhope Bay beaches (black beaches). The western half of the island is characterised by mostly vertical cliffs rising directly out of the sea and few rugged beaches, while the eastern half of the island has a gentler transition from sea to land and more accessible beaches. Southern elephant seals occur mainly on the leeward east and north coasts due to the greater availability of haul-out beaches and terraces, although a few sites on the south coast are frequently used (Fig. 1.2) (Condy 1978).

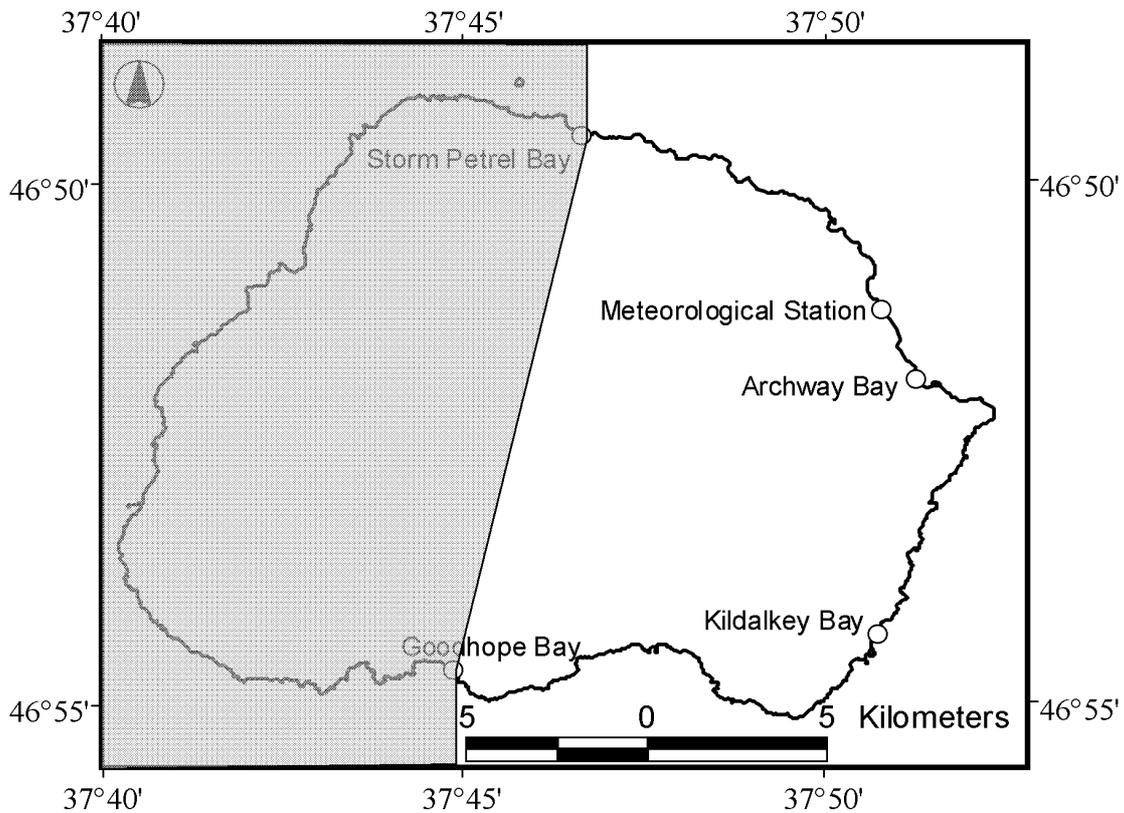


Fig. 1.2. Subantarctic Marion Island (46°54'S, 37°45'E). The unshaded part of the map depicts the coastlines preferred by southern elephant seals for haul-out activities. The unshaded stretch of coastline is traversed regularly on foot for resighting of tagged southern elephant seals. The rugged coastline in the shaded area offers virtually no preferred haul-out beaches to this species.

Large beds of bull kelp, *Durvillaea antarctica*, form an almost continuous ring around the island close inshore (<100m offshore) while further offshore (500 to 1000m offshore) a similar ring of giant kelp, *Macrocystis pyrifera*, surrounds the island. From an elephant seal point of view, these kelp communities are important for two principal reasons. Firstly, they are an important contributor to “wrack beds” composed of storm dislodged kelp fronds that contribute to the temporal accessibility and suitability of certain beaches used by seals. Secondly, these ‘kelp forests’ provide ambushing habitat for killer whales, *Orcinus orca*, (PJNdB personal observation). Killer whales are an important seal predator here (see Appendix 3 - Tosh et al. 2008) close inshore (Fig. 1.3.).



Fig. 1.3. The large kelp beds immediately offshore of Marion Island (left) are depicted. Killer whales, *Orcinus orca*, (foreground) are important predators of southern elephant seals and use these kelp beds for concealment. Prince Edward Island is visible in the top right.

Aims and Objectives of this study

Studies of animal demography are fundamentally anchored in the monitoring and analyses of life history traits of individuals (Lebreton et al. 1992). Yet, such analyses require large numbers of identifiable individuals to be monitored through time, typically in a capture-mark-recapture framework. Large wild mammals are inherently difficult study subjects for individual life history monitoring, because they are often dangerous and difficult to locate, approach or physically handle. The ubiquitous terrestrial phases displayed by pinnipeds (i.e. seals) make them some of the more easily approachable mammalian groups, some species more than others. Southern elephant seals, particularly adult females, show a high degree of site fidelity to their natal island (Bester 1989) making the species ideal for long-term monitoring studies (Bester 1988; Erickson et al. 1993).

During perusal of the population demographic literature at the commencement of this PhD, some methodological limitations were striking. In particular, analyses of life history parameters with body condition (directly related to body mass in southern

elephant seals) as covariate, are rare and usually the samples are small. Additionally, methods of identifying relatedness in southern elephant seal populations, in particular the temporal and spatial variation in condition of mothers and their offspring, suffered from small sample sizes. Such limitations impede progress in holistic demographic research. These impediments may be generally restrictive to life history and demography studies, or they could be species - or site specific. The long-term nature of mark-recapture population demographic studies unfortunately results in extended lag times for novel methodological advancements to become useful. Consequently, I use a long-term and valuable mark-recapture dataset for life-history analyses without the latest methodological field improvements presented here. However, these advancements are intentionally presented prior to the population demographic analyses so as to allow the reader the opportunity to relate the potential of these advances to future demographic analyses.

Consequently, the general purpose of this thesis is twofold:

- (1) To investigate and advance certain field research techniques of direct relevance to studies of population demography in southern elephant seals and potentially for other large vertebrates.
- (2) To investigate/identify life history parameters that are most important for population regulation in the Marion Island population of southern elephant seals, and attempt to clarify existing disputes in this regard.

The specific objectives of this research are to:

- 1.1) Ease the measurement of body mass for large southern elephant seals, specifically to simplify effort to gain large sample sizes and to allow for broad applicability to various field scenarios. I therefore aim to advance the use of photogrammetry for estimating the individual mass of southern elephant seals.
- 1.2) Given an inability to assess the relationship in survival and reproductive parameters between mothers and offspring with the current elephant seal dataset, I aim to investigate field methods that would allow the future identification of large samples of pups with known mothers.
- 1.3) I aim to use the current 25-year longitudinal dataset to determine age- and sex-dependent survivorship in the Marion Island population of southern elephant seals. For comparative purposes I aim to repeat the analytical procedure

presented in the earlier survivorship analyses (Pistorius et al. 1999b) that was based on approximately half of the current dataset. That study provided a catalyst for numerous subsequent published works, some of which incite contention about the fundamental demographic drivers of this population. I aim to clarify some of this contention.

- 1.4) I aim to conduct a study of senescence in these long lived capital breeders, with added emphasis on longevity and fertility in female southern elephant seals at this locality. I aim to address these topics from primarily a population regulation point of view, but also to include life history descriptors that are useful for the evolutionary study of senescence.
- 1.5) I aim to provide a philosophically angled discussion of the use of sophisticated analytical tools in population demographic studies (specifically mark-recapture). I aim to use an example from the elephant seal dataset to illustrate my argument.
- 1.6) Finally, I aim to gain a more holistic perspective of the drivers and descriptors of southern elephant seal population dynamics at Marion Island, through initiation of related fields of study. I aim to initiate work on alternative methods of chemical immobilisation of these seals, to further investigation into tag-loss rates in this population of seals, and lastly to gain a better understanding of the population characteristics of the understudied killer whales (as predators of seals) around Marion Island. (*Appendices*)

Several key questions arise as a consequence of these aims and objectives:

- a) Can photogrammetry be broadly applicable to mass estimation of seals in many field scenarios and with seals resting in any position, contrary to the *status quo* for the method?
- b) What method of photographing seals for ultimate mass estimation can be conducted with minimal manpower and equipment, and is cost-effective?
- c) Is it possible to mark large samples of unweaned southern elephant seal pups within congested harems over time, when these harems consist of aggressive mothers and harem-masters?
- d) What method of marking unweaned pups can be conducted with minimal manpower and equipment, and be cost-effective and relatively safe for the fieldworker?

- e) Has the Marion Island southern elephant seal population stabilised since 1994?
- f) What is the survivorship of the population in relation to age, sex and cohort?
- g) Is juvenile or adult female survival at Marion Island the major contributing factor in population regulation?
- h) Do southern elephant seal females show actuarial senescence, and if so what are the demographic consequences thereof?
- i) Is there evidence for reproductive senescence in southern elephant seal females, and if so what are the demographic consequences thereof?
- j) What are the observed and predicted longevity and fertility schedules of southern elephant seal females for the Marion Island population?
- k) What mark-recapture analyses can (cannot) be performed with program MARK, and what does this mean for science in general?
- l) Can ketamine-hydrochloride be used in combination with reversible drugs (other than xylazine) for the immobilisation of elephant seals? (*Appendices*)
- m) Does tag-site (on the flipper) affect the rates of tag-loss in southern elephant seals? (*Appendices*)
- n) What are the rates of age- and sex-dependent tag-loss for each cohort in this population? (*Appendices*)
- o) Is the social organisation of killer whales at Marion Island comparable to the mammal-eating transient sociality of northern hemisphere killer whales? (*Appendices*)
- p) What are the consequences of killer whale sociality, for the killer whale prey animals? (*Appendices*)

Thesis Structure

The structure of this thesis follows a progression of firstly, field method advancement for population demographic studies, followed by an investigation of life-history parameters that may be regulating this population, and finally an initiation of studies into broader ecological questions of relevance in population demographic studies.

In Chapter Two, I approach the question of the field estimation of body condition (specifically mass) because it is a fundamental parameter that is valuable for covariate analyses in life-history studies. However, for large southern elephant

seals, the estimation of body mass is (at best) possible only with extensive manpower and effort for a small sample of individuals under specific field conditions, or (at worst) impossible if field conditions do not permit access to weigh individuals or if individuals are too large. Photogrammetry has previously been attempted with some success, but limitations persist. I use a large sample of weighed individuals to test a novel three-dimensional photogrammetric body mass estimation approach specifically with broad field applicability in mind.

In Chapter Three, I embark upon a quest to find the simplest, most cost-effective method to individually identify unweaned southern elephant pups. Southern elephant seal pups are simple to mark (with long-term/permanent marks) once they have weaned because they move out of the harem where aggressive adults would impede such marking. However, at that stage the maternal bond has been severed and pups cannot be assigned to respective mothers. A temporary marking technique whereby unweaned pups can be assigned to their known (marked) mothers, to be identifiable upon weaning, is required. Different markers and techniques are evaluated to surmount these field limitations.

Chapters Two and Three, thereby address two major obstacles in population demographic research on southern elephant seals at Marion Island, and should, over time increase the robustness of the mark-recapture work to gain a better understanding of population regulation.

Chapter Four, uses the existing 25-year longitudinal mark-recapture (resight) dataset for this species at Marion Island, to advance on the 15-year survivorship results presented for this same population by Pistorius et al (1999b). A modelling approach using program MARK is employed to gain insight into life-history parameter estimates. The fortuitous temporal setting of the current dataset, encompassing both periods of decline and increase in the population, provides a solid foundation for additional investigation of the contention surrounding the drivers of the population. I therefore attempt to clarify the role that juveniles and adult females play in regulation of this population.

In Chapter Five, I investigate whether female southern elephant seals portray either actuarial or reproductive senescence. I also add relevant investigations and descriptions of longevity and fertility of female seals from this population. The significance of these life-history traits are discussed in relation to their importance for, and possible regulating role in population demography.

Chapters Four and Five therefore provide a detailed investigation into some of the most noticeable gaps in our current knowledge of demography in this population of seals, and attempt to clarify the existing published disputes in this regard.

Chapter Six provides a more philosophical examination of the potential obstacles faced by researchers when using sophisticated analytical software, with a particular emphasis on capture-mark-recapture data and the software program MARK. I use an analysis aimed at identifying potential marker confusion (due to tag colour) in the Marion Island elephant seal population, to illustrate the point.

The Appendices of this thesis investigate various factors of broad relevance to both field methodology and their ecological interactions with elephant seal population demography research. Although I initiated the research pertaining to the appendices and contributed significantly to their current form, much of the analyses and thus lead authorship on Appendices 2 and 3 were contributed by collaborators as shown.

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CHAPTER TWO:

HOW TO WEIGH AN ELEPHANT SEAL WITH ONE FINGER: A SIMPLE THREE-DIMENSIONAL PHOTOGRAMMETRIC APPLICATION

de Bruyn et al. 2009

Abstract

Several studies have developed photogrammetric techniques for indirect mass estimation of seals. Unfortunately, these techniques are often narrowly delineated for specific field scenarios or species. Many require sophisticated, custom-designed equipment or analytical tools, limiting their applicability. We aimed to devise a photogrammetric technique for accurate volume / mass estimation of seals under a variety of field scenarios without manipulation of the animal and with minimal equipment. We use Photomodeler Pro[®] three-dimensional modelling software to estimate the mass of fifty-three weighed southern elephant seals, *Mirounga leonina*. The method is centred on animal volume estimation in relation to the three-dimensional area around it, rather than features of the animal itself, an approach that liberates limitations associated with earlier studies. No morphometric body measures are required for such volume / mass estimation. We offer predictive equations that allow high confidence in mass estimates relative to measured mass (95% confidence interval of mean deviation from measured mass from ± 1.34 % to ± 3.83 % depending on the field scenario). A single photographer with a measuring stick and non-customised digital photographic equipment can use this technique to determine the mass of an elephant seal anywhere in the field with the push of a button.

Introduction

Body size of vertebrates (including related characteristics such as body mass) is a central theme in studies investigating geographical scaling patterns, physiological, behavioural and life history parameters of individuals and populations (Peters 1983). Body mass estimation of terrestrial and marine mammal species are regularly based on scaling procedures of various body measurements (e.g. Bryden 1969; Christiansen 1999) and Trites and Pauly (1998) observed strong linearity when maximum body length of 17 marine mammals species were plotted against mean individual mass. The ubiquitous terrestrial phase of pinniped species and their cumbersome movement on land as compared with truly terrestrial large mammals,

have prompted biologists to use pinnipeds (more so than other mammalian groups) as study subjects to attempt body mass predictions based on morphological features.

Given the scaling relationships between morphological measures and body size/mass, various photogrammetric techniques (the use of photographs to measure objects) have been used to determine diverse morphological measures of mammals, including shoulder height and back length of African elephants, *Loxodonta africana* (Hall-Martin and Rüther 1979; Schrader et al. 2006), dorsal fin analyses of killer whales, *Orcinus orca* (Keith et al. 2001), and baleen rack shape and size in bowhead whales, *Balaena mysticetus* (Lambertsen et al. 2005). In pinnipeds, Haley et al. (1991) initiated photogrammetric use for body mass estimation in northern elephant seals, *Mirounga angustirostris*, while Bell et al. (1997) applied a combined photogrammetric and morphometric technique of estimating body mass in southern elephant seals. However, the constraints under which current methods of photogrammetry can be used to accurately estimate seal mass are rigid. Animals have to be on a completely flat surface (e.g. hard/packed sandy beach), lying straight in ventral recumbency with no tolerance for movement, and the images captured when the animal has inhaled completely (Haley et al. 1991; Bell et al. 1997). The photographer is required to know the exact distance between the camera and the seal and scaling measure. More recently, Ireland et al. (2006) and Waite et al. (2007) made significant advances using new technology to estimate the masses of Weddell seals, *Leptonychotes weddellii*, and Steller sea lions, *Eumetopias jubatus*, respectively. These methods have increased the accuracy of mass estimation for the particular species but introduced (or maintained) various constraining field procedures, restricting their use in the field. The Ireland et al. (2006) method requires customised photographic equipment that is bulky and impractical in situations where the only method of traversing large distances between study subjects is by walking. Proffitt et al. (2008) successfully improved the photogrammetric mass estimation and confidence of the Ireland et al. (2006) procedure, by *post hoc* body form analysis using elliptical Fourier decomposition. However, the study did not simplify the field photographic component. The Waite et al. (2007) technique required sophisticated targeting on the seal and synchronized images from different angles to allow the three-dimensional modelling of the subjects and required best estimates to remain morphologically correlated. Thus, all these

methods require physical contact with the animal to acquire a morphometric measure or to manipulate posture. Restricted accessibility to haul-out locations, uneven substrates at haul-out sites, adverse weather conditions, and the behaviour of wild seals render all these methods largely unsuitable for extensive and simple field implementation.

We report on a novel three-dimensional photogrammetric field technique for mass estimation of pinnipeds without many of the abovementioned constraints. This technique is based on a volumetric estimation method that requires only one photographer with a digital camera and a calibrated measuring stick in the field. The technique was developed with the logistical challenges of isolated study areas and with varying substrate topography, in mind. Additionally, analyses can be performed with a non-customised commercially available software package.

Methods

Study area

This study was conducted through several seasons between April 2006 and February 2008 at Antarctic-maritime Bouvetøya (BVT) (54°25'S, 03°20'E), Stranger Point on King George Island (KGI) in the South Shetlands (62°14'S, 58°40'W) and Subantarctic Marion Island (MI) (46°54'S, 37°45'E) (Fig. 1.1). Beach topography varied considerably between the three localities and within each site, ranging from flat sandy or pebble strewn to heavily bouldered substrates, sometimes covered in kelp and/or snow and ice, i.e. heterogeneity in beach topography that severely negates the use of existing photogrammetric techniques.

Field techniques

Fifty-three southern elephant seals of both sexes and varying age classes (Table 2.1) were weighed and photographed according to the procedures set out below.

Table 2.1. Number of southern elephant seals, in each age - and sex class, included in this study. The mean body mass and range within each class are shown.

Sex	Age category	Age (years)	No. animals	Mean body mass - kg (range)
Male	Underyearling	<1	2	145 (140-149)
Male	Yearling	1	0	-
Male	Juvenile	2-3	12	314 (212-387)
Male	Subadult	4-5	11	443 (348-569)
Female	Underyearling	<1	0	-
Female	Yearling	1	2	166 (132-200)
Female	Juvenile	2	7	226 (163-269)
Female	Adult	>3	19	431 (295-636)
Total			53	359 (132-636)

Weighing procedure

Animals at MI and KGI were immobilised using an intramuscular dose of ketamine hydrochloride ($2.4\text{-}6.2 \text{ mg kg}^{-1}$ estimated body weight) (Bester 1988; also see Appendix 1), while animals at BVT were immobilised using an intravenous dose of zolazepam:tiletamine (1:1) (Zoletil[®]; $\sim 0.5 \text{ mg kg}^{-1}$) after temporary restraint of the seal using the canvas head-bag technique (McMahon et al. 2000). Animals were then weighed in either a net stretcher or broad strapping suspended from a load cell (different manufacturers depending on the location), attached to a block-and-tackle and suspended from either a steel, aluminium or carbon-fibre tripod. Seal mass ($\pm 0.5 \text{ kg}$) was corrected in all cases for additional mass resulting from nets or strapping. Scales were calibrated with a known mass between weighings. Standard length measurements were taken for each animal while in ventral recumbency (Bonner and Laws 1993).

Photographic procedure

Following weighing, each animal was photographed between eight and ten times from several different angles and heights (Fig. 2.1a and 2.1b). The placement of camera stations (i.e. the approximate angle relative to the animal from which the photograph was taken) was roughly standardised (Fig. 2.1), but exact distances from the seal or measuring stick need not be known. A Canon EOS350D digital SLR

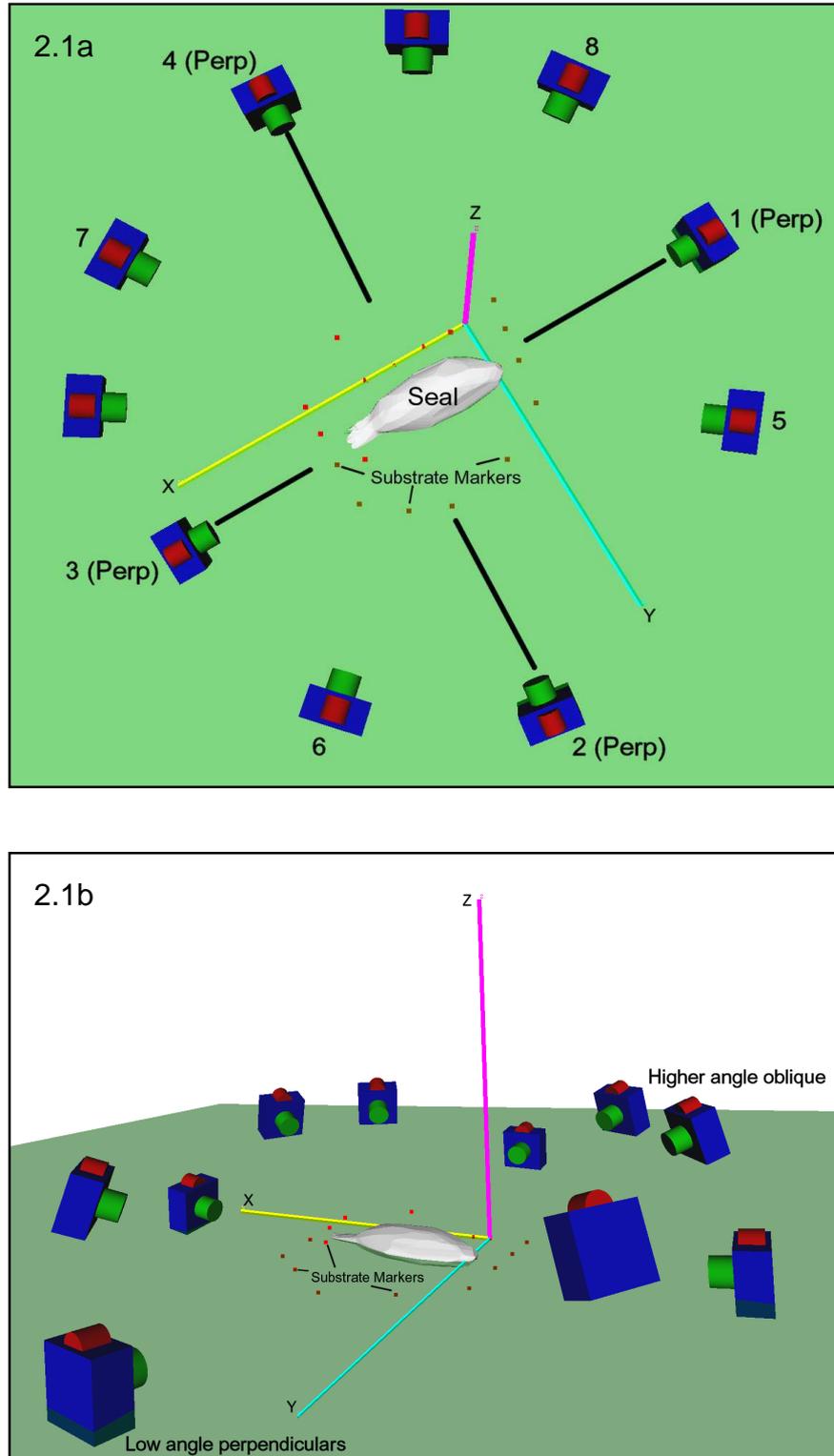


Fig. 2.1. The placement of camera stations (positions from where the photographs are taken) around the object to be modelled (2.1a - top view); and photographs should be taken at varying heights around the object (2.1b - side view). Note the placement of the low angle perpendicular photographs.

camera (high-resolution: 8-megapixels), with 18mm Canon lens was used for photography at MI and BVT, while a Samsung Digimax 201 compact digital camera (medium-resolution: 2-megapixels) at an EXIF focal length of 5.6mm was used at KGI. An independent project was done for each of the 53 seals and either one or the other camera was used per project. A single photographer circling the seal took the photographs. Miscellaneous objects (5 to 15; e.g. tags, tag applicators etc.) were randomly distributed on the substrate immediately around the seal as landscape/substrate markers (in addition to natural markers such as stones). Importantly, these markers remained unmoved during photography. A calibrated measuring stick 150cm in length, was placed somewhere amongst the markers to provide a scaling measure and also remained unmoved. The whole seal, markers and measuring stick were included in each photograph where the camera station allowed. Providing that the measuring stick/ each marker was entirely visible in at least three of the photographs in a project, the seal in the foreground obscuring markers and/or measuring stick behind it was acceptable. Given the objective of providing a photogrammetric method with tolerance for seals resting on a variety of substrates (for applicability in the natural scenario), the substrate on which the animal was resting was categorised as either even (flat) or uneven (rough). Even surfaces had no depressions or protuberances (rocks), and a flat plane with little or no curvature under the seal (e.g. a hard sandy - or finely pebbled beach). Uneven substrates had significant depressions or protuberances under the seal (such as a rocky/boulder beach, undulating moulting wallow or deep kelp bed), which may displace or “swallow” some of its volume. On uneven substrates, the seal can thus be classified as not having a uniform planar surface where its body is in contact with the substrate. The body posture of seals was not manipulated for photographic purposes and subjects were left undisturbed to assume a position of choice after the weighing procedure.

Photogrammetric analyses

Volumetric estimation

Volumetric estimation procedures were performed using the commercially available three-dimensional (3-D) modelling software package, Photomodeler Pro[®] Version 6.2 (EOS Systems Inc., Vancouver, British Columbia). In an independent, stringent evaluation of this software, Deng and Faig (2001) confirmed the high level

of accuracy in the creation of the relevant 3-D space, justifying its use especially for digital close-range (i.e. not remote sensing) photogrammetry. The initial step (prior to fieldwork) is to individually calibrate each camera (and relevant lens combination) using the procedure and test pattern provided by the software. The program requires calibration resulting in known focal length of the lens, the digitizing scale (the charge-coupled device - CCD - format size of a digital camera), the principal point (where the optical axis of the lens intersects the photograph) and parameters that describe distortion characteristics of the lens. Following camera calibration, the photographer need not know the distance from the object and each camera station can be randomly placed at various distances (and heights) around the object. This provides the option for using images from different non-identical cameras in one project provided each camera is calibrated (see Photomodeler Pro[®] help file). Calibration for each camera/lens combination occurs only once before its first use.

We initially attempted to create a 3-D model of each seal based on the technique used by Waite et al. (2007) for Steller sea lions whereby orientation points on the seal are cross-referenced between photographs to create a 3-D space. Our attempts at this method failed because, firstly, natural marks on seals are scarce and/or difficult to identify for cross-referencing between photographs, and secondly, seals (even when immobilised) move when breathing or otherwise, resulting in slight shifts of orientation points between photographs. To surmount this problem, initial 3-D model construction was shifted away from the seal and focussed on the inanimate elements of each photograph, the substrate landmarks. Points identified on substrate markers (natural or inserted) were then cross-referenced between photographs containing those points, to create a 3-D space within which to continue the model construction. On average, 22 (range 16-36) cross-reference points were used per individual project (e.g. Fig. 2.2) to orientate all photographs, although all points were not visible on all photographs in a project. The software requirements for maintaining minimum “residual error (RMS)” of each point (below 5.0; see Photomodeler Pro[®] help file) on each photograph were adhered to (see Graff and Gharib 2008, for details of accuracy in point based 3-D volumetric measurement systems). Once all photographs were successfully orientated based on the cross-referenced substrate points and an acceptable (RMS < 5.0) 3-D space created as a result, the scale measure was marked on this orientated substrate (Fig. 2.2). The object (seal) shape

was subsequently modelled in this 3-D space using the “silhouette” method (Fig. 2.2) of object model construction (see Photomodeler Pro[®] help file). In the case of visual obstruction of a part of the seal, e.g. by rocks in the foreground of the photograph, the imaginary outline was followed. If >30% of the seal was obstructed from view, the photograph was discarded.

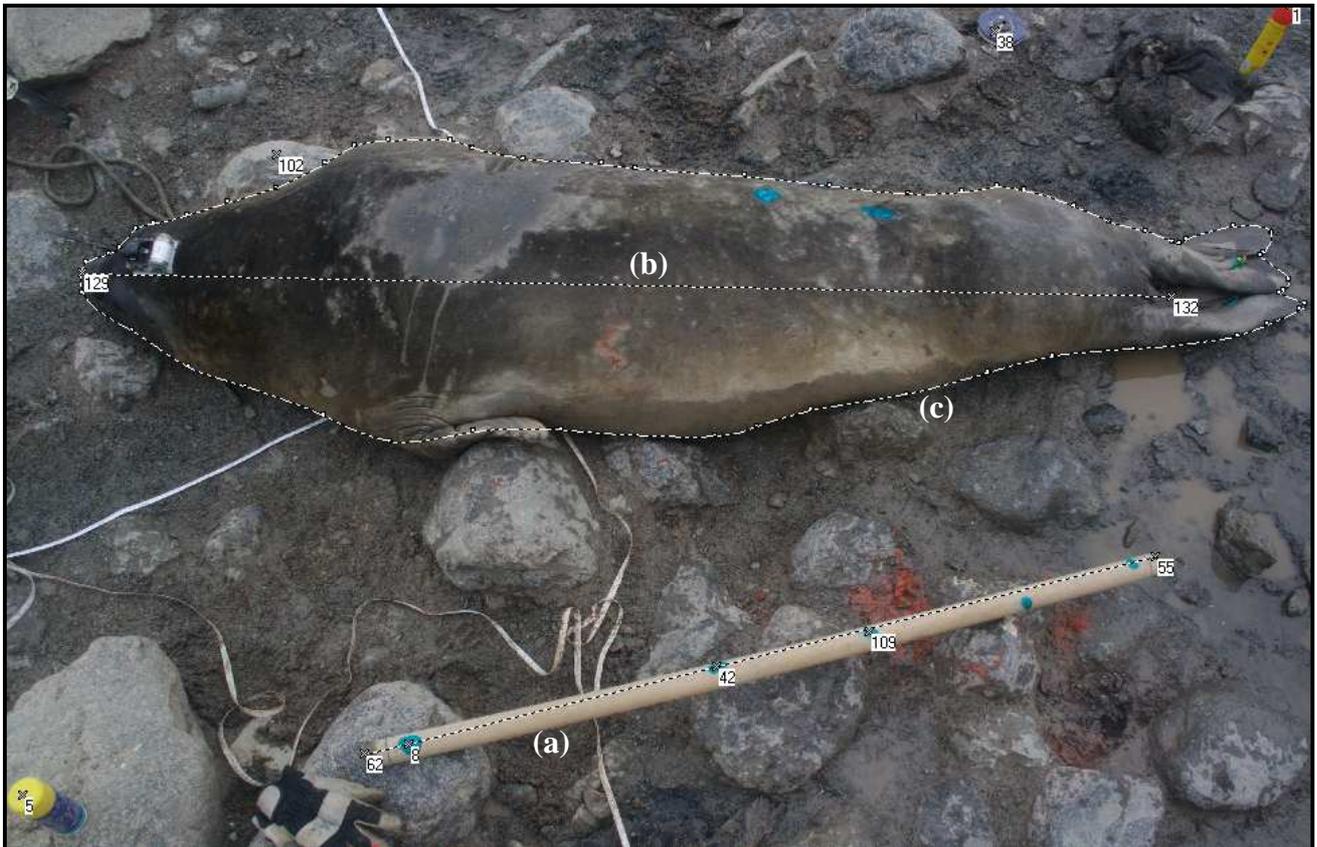


Fig. 2.2. An image of a southern elephant seal depicting the two scaling measures used separately for calculation of volume: (a) measuring stick or (b) standard length. Note the silhouette line (c) traced on the outline of the seal, which has been cross-referenced with similar silhouettes traced around the same animal on other photographs. Substrate markers (randomly numbered) have been used to create a three-dimensional space, by cross-referencing these points with the same points on other photographs.

Seal silhouettes were sequentially traced for each photograph (one silhouette *per* photograph) and volumetric estimates were obtained after the addition of each silhouette, starting at 3 silhouettes (the minimum needed to create a shape) through to 10 silhouettes, to test if volume estimates reached an asymptote after the addition of a specific number of photographs (camera stations) to the project. The Photomodeler Pro[®] measuring tool was used to assign a scaling measure to the project based on the measuring stick in the photographs. To test if morphometric

measures of the seal should be used as a scaling measure to improve ultimate estimates (see Waite et al. 2007), we marked the standard length of the seal on the photographs, assigned this as the scaling measure for the model, and compared the derived volumetric estimate with that gained from using the measuring stick in the image. Standard-length-scaled and measuring-stick-scaled volume estimates were compared for all 53 projects.

We extended/constricted some silhouettes in a project incorrectly (but realistically) to mimic head, flipper or breathing related movement between photographs and recalculated the volume estimates. Front-flippers were not included in the silhouette outline but hind-flippers were. Front-flippers are easy to exclude by following the bodyline of the seal. Head and hind-flipper movement of up to 45° (angle between two head positions in the same project) in any direction was mimicked, while some full inhalation silhouettes and some complete exhalation silhouettes were modelled in the same project. Totally immobile - and “movement related” volume estimates were compared for 20 projects.

To test Photomodeler Pro®'s specification that projects with overall project RMS < 5.0 are accurate, we re-orientated ten animals three times as separate projects to test whether variation in substrate cross-referencing quality (that may be caused by different users for example) caused variation in ultimate volume estimates.

Mass estimation

The volume estimates of each object gained from Photomodeler Pro® were separately multiplied by two different density values to calculate the mass of each seal. Firstly, the annual haul-out cycle of southern elephant seals (Kirkman et al. 2001, 2003, 2004) and its effect on body composition (blubber vs. lean-mass) was considered. Mean percentage body blubber content for seals of different sexes and ages (Bryden 1972; Slip et al. 1992; Carlini et al. 1999, 2005; Field et al. 2005) were converted into a blubber to lean-mass density ratio based on the densities of blubber (0.95kgm⁻³; Gales and Burton 1987) and lean-mass (1.10 kgm⁻³; Le Boeuf et al. 2000), and this ratio applied to the volumetric estimates to obtain estimated mass. Secondly, a density of 1.01 kgm⁻³, the mean (±0.04 kgm⁻³) total-body density for healthy mammals regardless of total body fat content (Durnin and Womersley 1974;

Wang et al. 1999) was used for mass estimation of all animals. Use of the latter broadly applicable density thus precluded judgement of the body condition of the seals.

Data analysis

The deviation in predicted mass to measured body mass (% under- or overestimate, hereafter called percentage error) was calculated for all projects and was used to evaluate predicted mass estimates. Firstly, we determined the minimum number of photographs that a project should use by comparing volumetric estimates from projects spanning three to ten photographs. The first four photographs (1 to 4) used were always those at perpendicular angles to the subject (Fig. 2.1a), and further photographs from remaining camera stations (Fig. 2.1a) were sequentially added to each project in the same order as was done for other projects. Then we tested for differences in percentage error from projects using a measuring stick or a standard length morpho-measure scale (Fig. 2.2). We also compared the percentage error from different cameras, although we were not able to compare the effect of different cameras on the same subject. Since camera differences were non-significant, and the use of a measuring stick resulted in significantly lower deviation from measured mass (see results), we grouped data from all study sites and used data from measuring-stick-scaled projects only in subsequent analyses. We compared the percentage error for all projects based on a mean density of 1.01 kgm^{-3} and on a blubber-to-lean-mass density ratio as predicted by haul-out type. Using the best volume to mass density conversion factor, we computed the mean effect of missing a single perpendicular photograph, or missing photographs encompassing an entire side view (180°), compared to the full view model by deleting relevant photos from full view projects. We fitted a general linear model to evaluate the effects of animal sex, age class (juvenile, subadult, adult), haul-out type (winter, pre-moult, mid-moult, post-moult), head movement during photographs (present or absent), and substrate (even or uneven) on predicted mass estimates. We constructed a single global main effects model relating one continuous predictor variable to multiple (all) classification predictor variables. We did not test for interactions between explanatory variables, which would have been the first term to eliminate in a model selection process, and were interested in the importance of variables only, not their model estimates. All analyses were performed using STATISTICA 7.0 (StatSoft; Oklahoma,

USA), except the linear model that was fitted in SAS 9.1 (SAS Institute; Cary, NC). Data were tested for normality using the Shapiro-Wilk W test. The deviation in predicted mass to measured mass (percentage error) is presented as mean \pm 95% CI and probability values are considered statistically significant at $p \leq 0.05$. Proportional data were arcsine transformed where relevant.

Results

Our results indicate that confident (percentage error 95% CI from ± 1.34 % to ± 3.83 % depending on the field scenario) mass estimates relative to measured mass can be obtained with the use of this method. A mean of 6 minutes (range: 2 to 10 min) in field effort was required for photography of each of the 53 animals. On average, 50 minutes (range: 20 to 210 min) were required by a user to create a 3-D modelled space and object shape (i.e. one project).

Volumetric estimation

The same project cross-referenced anew (three repeats) never provided identical project RMS values. However, in maintaining RMS < 5.0 for each of the three projects, ultimate volumetric estimates of the seal shape between the three iterations varied only by a third of a percent (range: 0.02% - 0.28%). Mean overall project RMS for individual projects ($n = 53$) was 1.518 pixel units (range: 0.774 - 3.576).

The “totally immobile” and mimicked “movement related” volume estimates tested in 20 projects were identical. If the bulk of the body shifted more than ~ 15 cm in any direction between photographs, the resulting 3-D model was visibly affected, resulting in “tolerance violation” (see Photomodeler Pro[®] help file) and the software rendered the volume calculation unsolvable.

Project volume estimates improved significantly with every additional silhouette (after three) included in the model (dependent t-test, from 3 to 8 photographs $p < 0.001$). An asymptote was reached at eight photographs ($t_{(8-9 \text{ photographs})} = 0.35$, $p = 0.72$; $t_{(8-10 \text{ photographs})} = -1.10$, $p = 0.28$) (Fig. 2.3). Adding additional photographs to an eight-image project (mean project silhouette volume

$0.355 \pm 0.033 \text{ m}^3$) therefore did not significantly improve volume estimates (mean project silhouette volume for ten-image project $0.352 \pm 0.033 \text{ m}^3$).

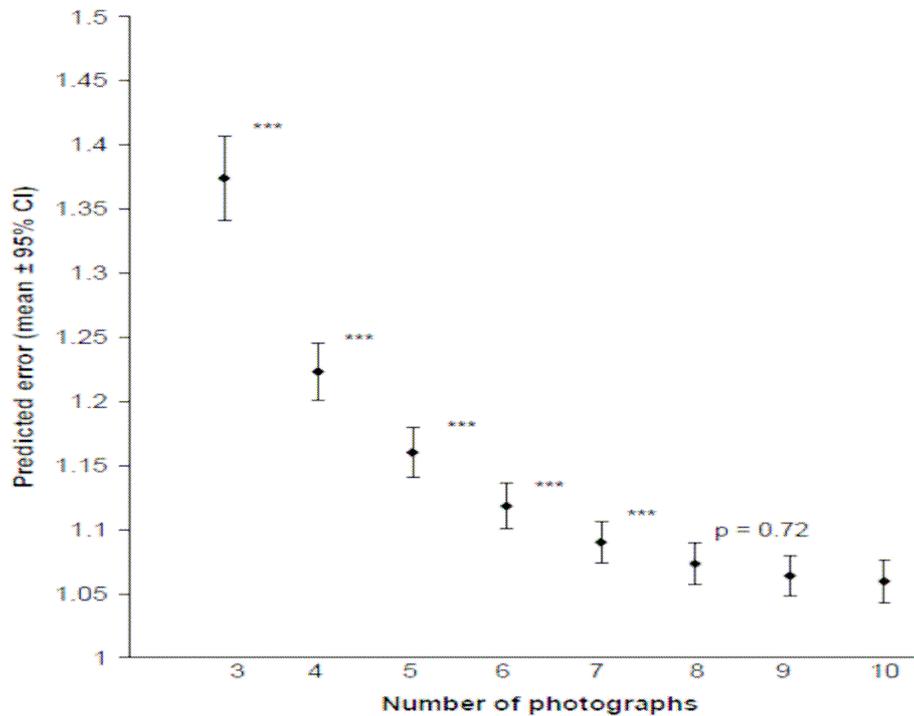


Fig. 2.3. Number of cross-referenced silhouettes (1 silhouette per photograph) required in Photomodeler Pro[®] before an asymptote of volumetric estimation was approached. Volumetric accuracy increased significantly with addition of every silhouette up to 8 photographs in a project. ***Significant decrease in volumetric predicted error ($p < 0.001$).

Mass estimation

Mass estimates of full view projects based on a measuring stick had less variation and were closer to measured mass ($9.71 \pm 1.27\%$) than those based on morphometric standard length measurements ($12.73 \pm 2.30\%$; dependent t-test, $t = -2.78$, $p < 0.01$). The two different cameras used had similar percentage error estimates (Canon $8.60 \pm 2.91\%$ and Samsung $10.10 \pm 1.37\%$, independent t-test, $t_{(104)} = -1.03$, $p = 0.31$). Model accuracy decreased significantly when the ratio density method was used compared to estimates based on a mean density of 1.01 kgm^{-3} (dependent t-test $t_{(52)} = -36.48$ $p < 0.001$). The full view model consistently overestimated measured mass ($6.59 \pm 1.52\%$). Overestimates of predicted mass increased further when a single perpendicular angle or an entire side view were deleted from projects, with the percentage error significantly higher than for the full model (repeated measures ANOVA, $F_{(2,70)} = 203.46$, $p < 0.001$) for both perpendicular ($9.36 \pm 2.09\%$) and missing side view ($20.83 \pm 2.72\%$) models

(Tukey's HSD *post hoc* test for unequal sample sizes; $p < 0.01$). The variables included in the linear model explained little of the remaining variation in photogrammetric mass estimates ($F_{(5, 41)} = 4.69$, $p = 0.018$, $R^2 = 0.36$), with substrate type the only significant determinant (beta = -8.25, $F = 17.78$, $p < 0.001$). Even substrates resulted in an overestimate of predicted mass with narrow confidence intervals ($8.54 \pm 1.34\%$), while uneven substrates provided estimates close to the measured mass ($0.57 \pm 2.69\%$), albeit with greater variance.

Predictive equations

We applied equations to the predicted mass data (based on the mean percentage error) to adjust the mean overestimation of measured mass as estimated by this method (Table 2. 2). All equations are dependent on the use of a measuring stick for volumetric scaling in the project and a mean density volumetric conversion factor of 1.01 kgm^{-3} . R^2 values were derived by plotting measured mass, against predicted mass and corrected mass using the appropriate equations (Fig. 2.4).

Table 2.2. Predictive equations to approximate body mass of southern elephant seals. The full view model depicts a minimum of 8 photographs including all perpendiculars and all sides of the object (Fig. 2.1). R^2 values are the resultant linear regression fit of measured mass to predicted body mass for this dataset.

Model	Equation ^a	N	R^2
<i>Even substrates:</i>			
Full view	$\text{PBM} = \text{ME} - [\text{ME} \times (0.085 \pm 0.013)]$	40	0.98
Missing one perpendicular	$\text{PBM} = \text{ME} - [\text{ME} \times (0.108 \pm 0.019)]$	31	0.97
Missing an entire side view	$\text{PBM} = \text{ME} - [\text{ME} \times (0.244 \pm 0.026)]$	40	0.96
<i>Uneven substrates:</i>			
Full view	$\text{PBM} = \text{ME} - [\text{ME} \times (0.006 \pm 0.027)]$	13	0.98
Missing one perpendicular	$\text{PBM} = \text{ME} - [\text{ME} \times (0.004 \pm 0.038)]$	5	0.97
Missing an entire side view	$\text{PBM} = \text{ME} - [\text{ME} \times (0.099 \pm 0.034)]$	13	0.97

^a PBM - Predicted body mass (kg)

ME - Mass estimate from photogrammetric volume (kg)

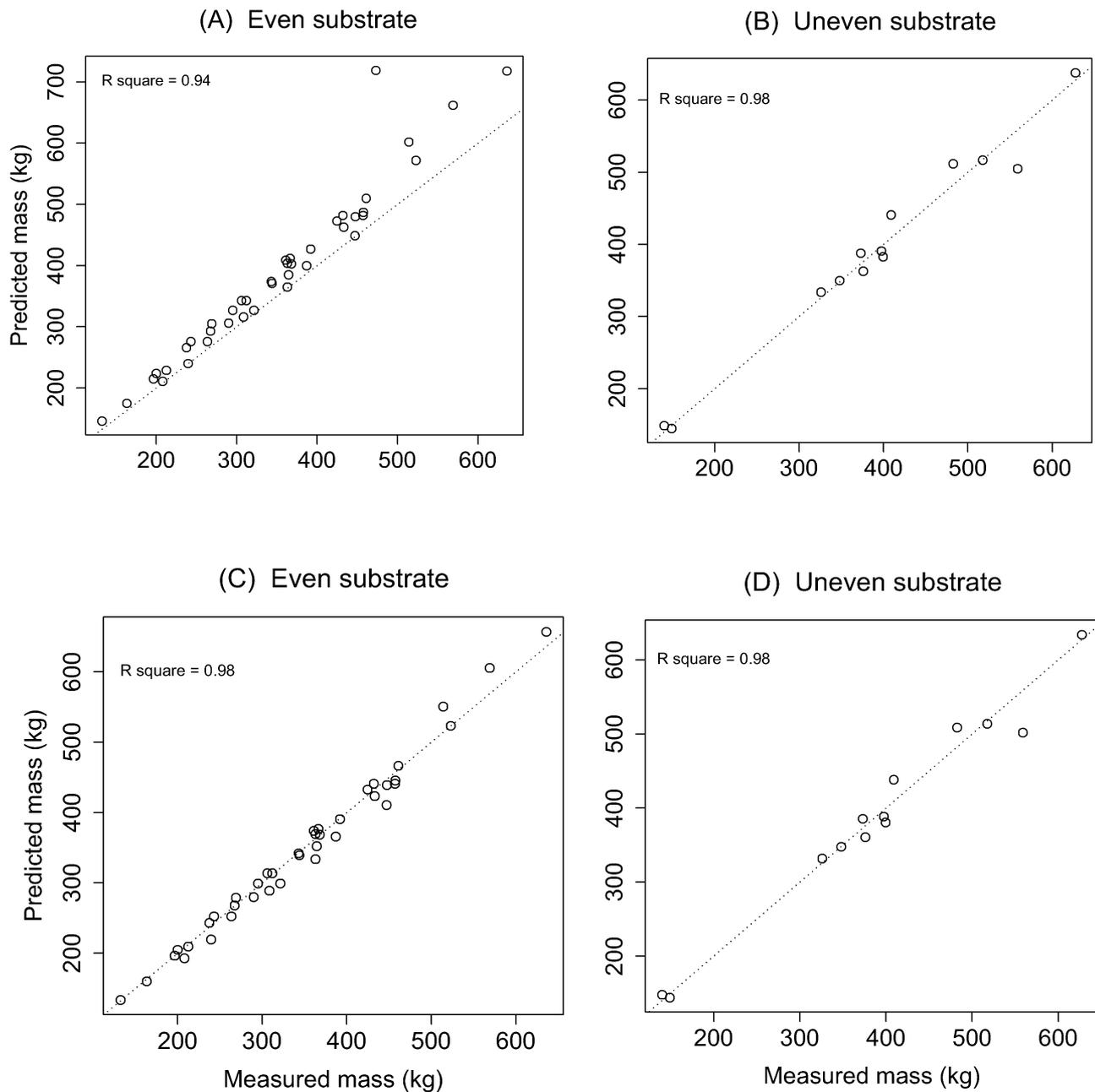


Fig. 2.4. Regression of predicted body mass against measured body mass for southern elephant seals on even and uneven substrates. A and B represent the predicted mass values obtained from full view photogrammetric projects, while C and D are the predicted mass estimates multiplied by the appropriate correction factors given in Table 2.2. The dotted line represents the true regression line (intercept = 0, slope = 1).

Discussion

This photogrammetric mass estimation method centres on the accurate estimation of the volume of an object within a 3-D space orientated by cross-referencing of inanimate points surrounding this object. This approach ensures that

the animate object to be modelled (seals in our case) is not dependent on features of itself, but rather on the more stable substrate to create an accurate 3-D space. This liberates many constraints associated with modelling of an object (Proffitt et al. 2007, 2008), such as absolute immobility of the object, clearly recognisable 'landmarks' or measures on the object (morphometrics), and specific object postures or shapes (Haley et al. 1991; Bell et al. 1997; Ireland et al. 2006; Waite et al. 2007). In so doing, this 3-D modelling procedure addresses our objective for simple photography of seals (without physical contact) on a variety of substrates without the need for sophisticated, bulky or custom designed equipment. Because cross-referenced silhouettes do not depend on accuracy measures of the silhouetted object, but rather on the surrounding substrate markers, slight movement of the object (and thus the marked silhouette), or object complexity, has a limited influence on ultimate project accuracy and the volume estimate. Thus, although an animal needs to be stationary, our results suggest some tolerance for movement (particularly of head or appendages). Additionally, this method diverges from the morphometric-to-body-mass scaling procedures used to date. Firstly, it removes the constraint to immobilize and physically measure study subjects. It can therefore be used on stationary seals without the need to handle seals. Secondly, this method is not restricted to the scaling relationships of a specific species. In light thereof, it seems probable to determine the volume of a large mammal regardless of the species or surroundings, and to calculate the mass of a particular animal based on the narrow total-body density range applicable to mammals (Durnin and Womersley 1974; Wang et al. 1999). However, our results are based only on southern elephant seals, and while the physics and functionality of the software and method suggests its applicability to other mammalian groups, its accuracy therein remain to be confirmed.

The immobility of the study subject when using this method is a by-product of the single photographers' need to circle the animal (for field application), however the software provides the option for the processing of photographs depicting the same object but produced by different calibrated cameras. In projects where seals rested on highly uniform substrates (e.g. snow, sand), the addition of non-natural substrate markers (e.g. unique, coloured marbles) around the seal reduced analysis time considerably (less time required than to search for natural markers). This is superfluous for model construction when adequate natural markers are present.

Three iterations of 3-D space construction for the same project did not produce identical results due to the difficulty (even for the same user) of placing a mark on exactly the same pixel in an image in three exclusive attempts. However, ultimate volumetric estimates of the seal shape between the three iterations (e.g. different users) remained negligible if software stipulations were adhered to (i.e. $RMS < 5.0$). No significant difference between the use of a medium – or high-resolution digital camera was evident in estimates. Consequently, one is not obliged to purchase expensive or sophisticated digital camera equipment to apply this method.

High - and low angle photographs from camera stations around the subject (top views are especially useful, albeit not crucial) are critical for accurate model construction (PJNdB personal observation). This is due to the silhouette method simply calculating the shape and size of an object from the silhouette projection algorithm when the silhouette is referenced on three or more orientated photographs. This effectively means that a missing side view results in an overestimation of the extent of the object on the opposite side of the missing camera stations because there are not sufficiently angled camera stations to allow the software to trim the model. This silhouette projection algorithm is also likely the cause for the difference in mass estimates between animals on even and uneven substrates. Because photographs of the object cannot be captured from a camera station exactly at / or lower than ground level, the 3-D model based on silhouettes result in a convex, rather than planar, lower surface for the object. The volume of an animal resting on an uneven substrate where some of its volume may in reality be “swallowed” by a depression under it would therefore be more correctly modelled as having a convex lower surface. The greater variance around estimates for uneven surfaces result from not every animal on an uneven surface having a completely convex lower surface, (e.g. sometimes it may be partially convex and partially concave due to uneven terrain). An animal resting on an even surface would in reality have a planar lower surface but that would still be modelled as convex, resulting in the consistent overestimates (but with greater confidence) reported here. We provide predictive equations for field scenarios where an incomplete set of photographs are available (missing a side view due to a large boulder preventing camera stations on a specific side for example) for subjects resting on even or uneven substrates, but caution their use for high accuracy mass estimation.

An added advantage of using the substrate point referenced 3-D space method (this study) is that a measuring stick can be photographed on the substrate where the animal was situated, *after* its departure. These photographs are then orientated with those where the subject is present to provide a scale to the project. Alternatively, a unique feature on the substrate can be measured after photographs were taken and included as the scaling measure. The significantly poorer performance of a morphometric measure as compared with an inanimate measure in the project results from the inability to accurately mark standard length on animals in the photographs. This can be due to some points of the animal (such as tail tip) not being visible on photographs, movement of the head resulting in error when the apex of the nose is cross-referenced, or the posture of the animal.

The technique can greatly assist longitudinal studies (see Chapter 3 - de Bruyn et al. 2008) that would traditionally have required reweighing of marked animals (Fedak and Anderson 1987). It reduces limitations for mass estimation under the following requirements: (1) Use a calibrated digital camera, (2) Take at least eight photographs around the stationary animal (Fig. 2.1) and include sufficient substrate in each photograph to facilitate point identification, (3) Include a measuring stick (preferably greater than 1.5m in length for large mammals) in at least three of the eight photographs.

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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 km² 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.

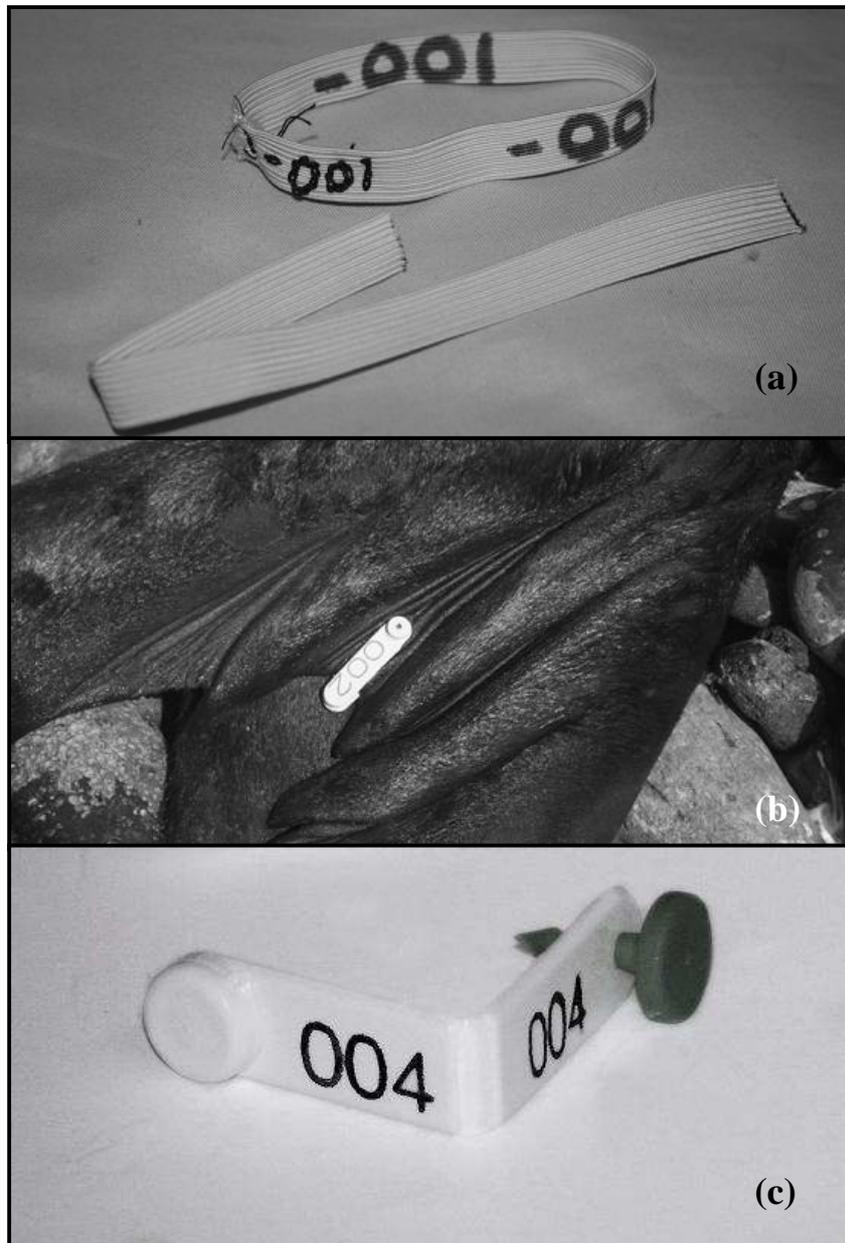


Fig. 3.1. The different marker types used to identify unweaned southern elephant seal pups at Marion Island. (a) Band markers (Note the embroidered and ink numbers with a dash as pretext to ascertain the numbers' correct orientation), (b) Supersmall® tags placed in the inner inter-digital webbing of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

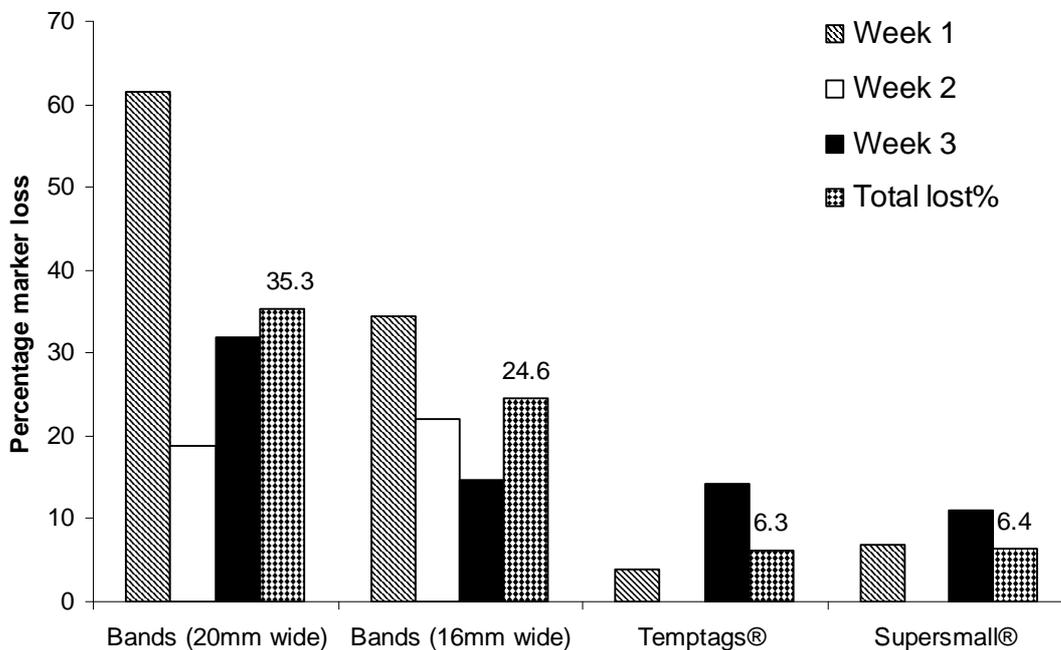


Fig. 3.2. Percentage marker loss relative to the number attached in each week on unweaned southern elephant seal pups at Marion Island during the three-week pre-weaning period.

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.

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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 km² 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:

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

ρ_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 (Φ) 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		
	χ^2	df	P	χ^2	df	P
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 (Φ_c, ρ_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_c 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_c 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 Φ and recapture probabilities as ρ . 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 Φ_{1-7}, ρ_c (for males), and Φ_{1-4}, ρ_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) Φ_t, ρ_t (CJS)	397.013 ^(2.895)	0.000	25	50.570	(1) Φ_t, ρ_t (CJS)	1059.702 ^(0.825)	0.000	35	101.272
	(2) Φ_t, ρ_c	375.571	0.000	14	53.050	(2) Φ_t, ρ_c	1046.159	0.001	19	123.304
	(3) Φ_c, ρ_c	354.468	0.995	2	56.808	(3) Φ_c, ρ_c	1038.731	0.029	2	151.328
	(4) Φ_{1-7}, ρ_c	365.311	0.004	8	55.375	(4) Φ_{1-4}, ρ_c	1032.120	0.791	5	138.627
	(5) Φ_{1-9}, ρ_c	# 369.103	0.001	10	55.007	(5) Φ_{1-7}, ρ_c	# 1035.088	0.179	8	135.434
1984	(1) Φ_t, ρ_t (CJS)	548.470 ^(2.179)	0.000	29	46.659	(1) Φ_t, ρ_t (CJS)	657.060 ^(2.031)	0.000	35	100.267
	(2) Φ_t, ρ_c	527.619	0.000	16	54.170	(2) Φ_t, ρ_c	636.231	0.000	20	112.161
	(3) Φ_c, ρ_c	506.566	0.985	2	62.130	(3) Φ_c, ρ_c	625.405	0.001	2	138.632
	(4) Φ_{1-7}, ρ_c	515.297	0.013	8	58.614	(4) Φ_{1-4}, ρ_c	610.874	0.953	5	118.027
	(5) Φ_{1-9}, ρ_c	# 518.691	0.002	10	57.863	(5) Φ_{1-7}, ρ_c	# 616.934	0.046	8	117.958
1985	(1) Φ_t, ρ_t (CJS)	345.355 ^(5.496)	0.000	22	31.040	(1) Φ_t, ρ_t (CJS)	678.539 ^(3.302)	0.000	37	102.165
	(2) Φ_t, ρ_c	328.312	0.000	13	32.785	(2) Φ_t, ρ_c	653.339	0.000	21	111.149
	(3) Φ_c, ρ_c	309.906	0.990	2	36.800	(3) Φ_c, ρ_c	622.668	0.772	2	119.505
	(4) Φ_{1-7}, ρ_c	319.583	0.008	8	34.320	(4) Φ_{1-4}, ρ_c	625.267	0.210	5	116.052
	(5) Φ_{1-9}, ρ_c	# 322.436	0.002	10	33.082	(5) Φ_{1-7}, ρ_c	# 630.226	0.018	8	114.917
1986	(1) Φ_t, ρ_t (CJS)	# 339.504 ^(4.246)	0.000	23	30.367	(1) Φ_t, ρ_t (CJS)	508.145 ^(3.884)	0.000	35	68.864
	(2) Φ_t, ρ_c	326.272	0.000	14	36.237	(2) Φ_t, ρ_c	479.001	0.000	19	73.851
	(3) Φ_c, ρ_c	308.373	0.956	2	42.982	(3) Φ_c, ρ_c	455.569	0.587	2	85.300
	(4) Φ_{1-7}, ρ_c	314.795	0.039	8	37.197	(4) Φ_{1-4}, ρ_c	456.592	0.352	5	80.266
	(5) Φ_{1-9}, ρ_c	318.687	0.006	10	36.970	(5) Φ_{1-7}, ρ_c	# 460.103	0.061	8	77.680
1987	(1) Φ_t, ρ_t (CJS)	279.995 ^(5.852)	0.000	23	28.349	(1) Φ_t, ρ_t (CJS)	508.726 ^(4.282)	0.000	34	64.945
	(2) Φ_t, ρ_c	260.050	0.000	13	29.515	(2) Φ_t, ρ_c	485.492	0.000	19	73.556
	(3) Φ_c, ρ_c	242.851	0.979	2	34.834	(3) Φ_c, ρ_c	458.556	0.755	2	81.451
	(4) Φ_{1-7}, ρ_c	250.832	0.018	8	30.622	(4) Φ_{1-4}, ρ_c	461.072	0.215	5	77.915

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

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

(2) Φ_t, ρ_c	# 112.690	0.031	6	8.856	(2) Φ_t, ρ_c	140.620	0.034	6	11.514
(3) Φ_c, ρ_c	105.808	0.967	2	10.133	(3) Φ_c, ρ_c	134.107	0.874	2	13.132
					(4) Φ_{1-4}, ρ_c	138.643	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 4th and 5th years of life throughout. Variation in model selection criteria influenced findings for adult male survival, whence discrepancy arose in the importance of especially 8th, 9th and 10th 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 3rd year survival, in contrast to Pistorius et al. (1999b), while Table 4.4b indicates equally high 4th 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 (1st, 2nd and 3rd year age-classes) around 1994 related to increased survival (thus breeding potential) of 4th, 5th and 6th year adult females around 1998.

Table 4.5a. Comparison of mean age-specific survival (ϕ) 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’ (ϕ) depicted as probabilities; Standard error (SE) of survival estimates, and ‘ ϕ Difference’ as a percentage (%) are shown.

Age	Cohorts	Males (†)			Males (‡)			Females (†)			Females (‡)		
		Survival	SE	ϕ Difference	Survival	SE	ϕ Difference	Survival	SE	ϕ Difference	Survival	SE	ϕ 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 (ϕ) 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’ (ϕ) depicted as probabilities; Standard error (SE) of survival estimates, and ‘ ϕ Difference’ as a percentage (%) are shown.

Age	Cohorts	Males (†)			Males (‡)			Females (†)			Females (‡)		
		Survival	SE	ϕ Difference	Survival	SE	ϕ Difference	Survival	SE	ϕ Difference	Survival	SE	ϕ 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 4th, 5th and 6th year survival in pubescent males was progressively associated with 2003, 2004 and 2005 (Fig. 4.1d, e, f), while lower 4th, 5th, 6th, 7th and 8th 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 14th year of life (Fig. 4.1i, j, k, l, m, n). High mortality in 4th year females during 1993, progressed annually to 14th 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 4th and 5th years (Fig. 4.1d, e). Similarly, females in their 6th, 7th, 8th and 9th years experienced high mortality during 2006, based on these model outputs (Fig. 4.1 f, g, h, i).

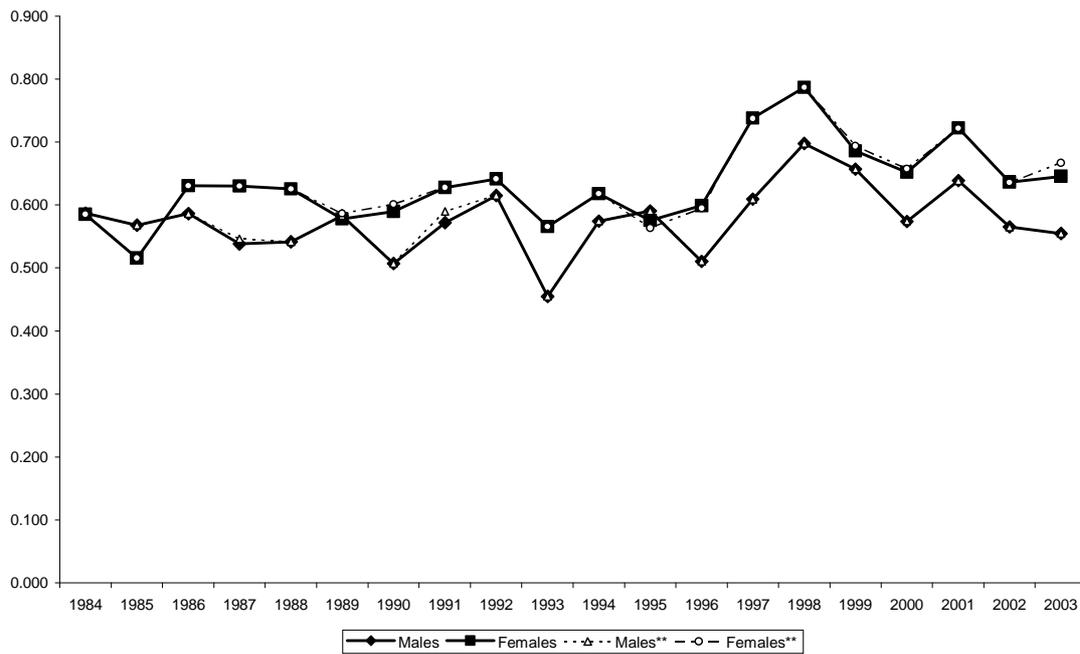


Fig. 4.1a. Mean first year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

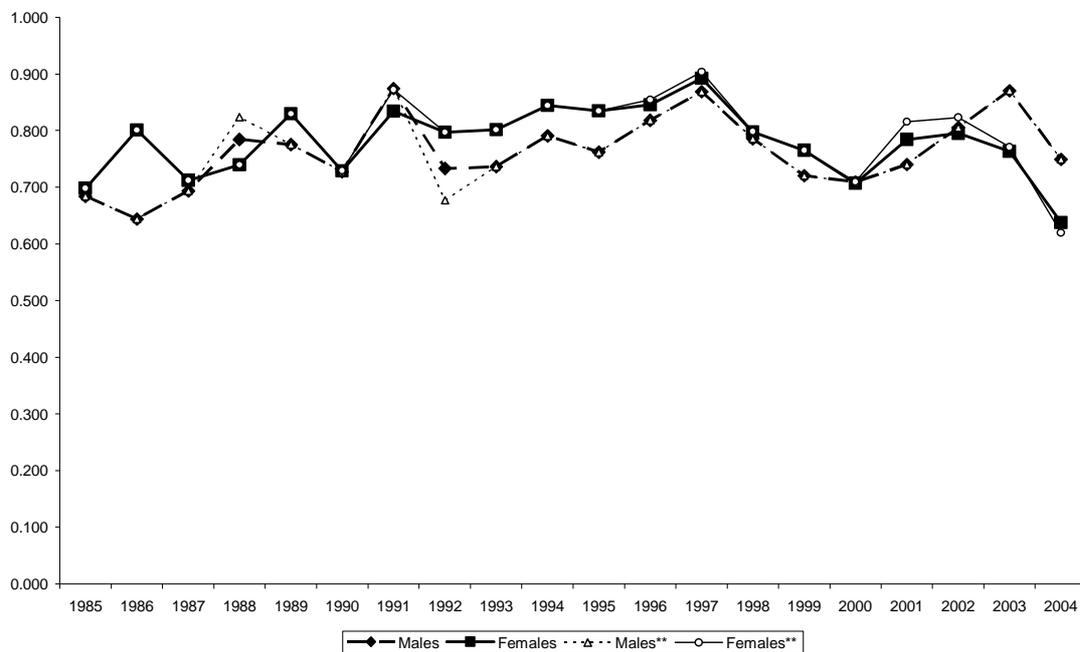


Fig. 4.1b. Mean second year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

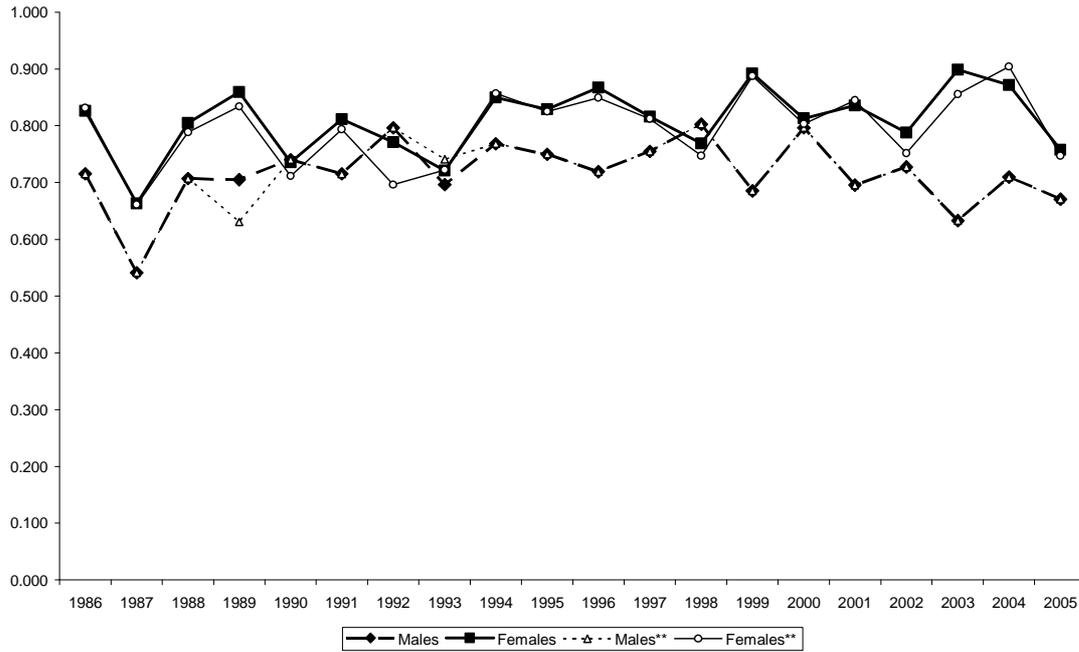


Fig. 4.1c. Mean third year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

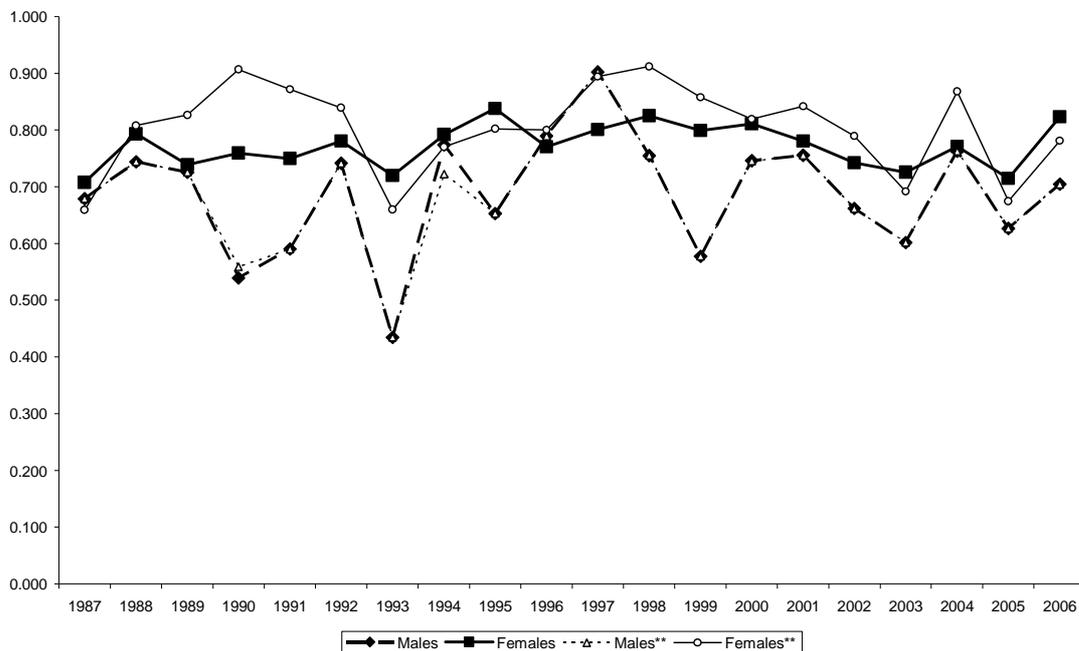


Fig. 4.1d. Mean fourth year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

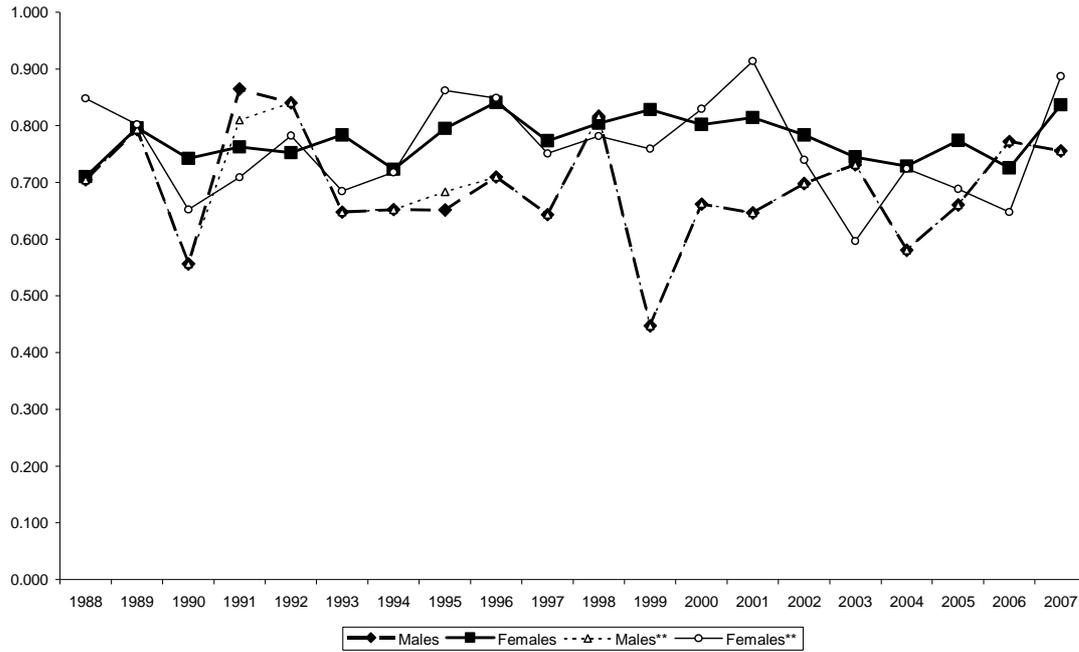


Fig. 4.1e. Mean fifth year survival for 20 cohorts (birth year: 1983-2002) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

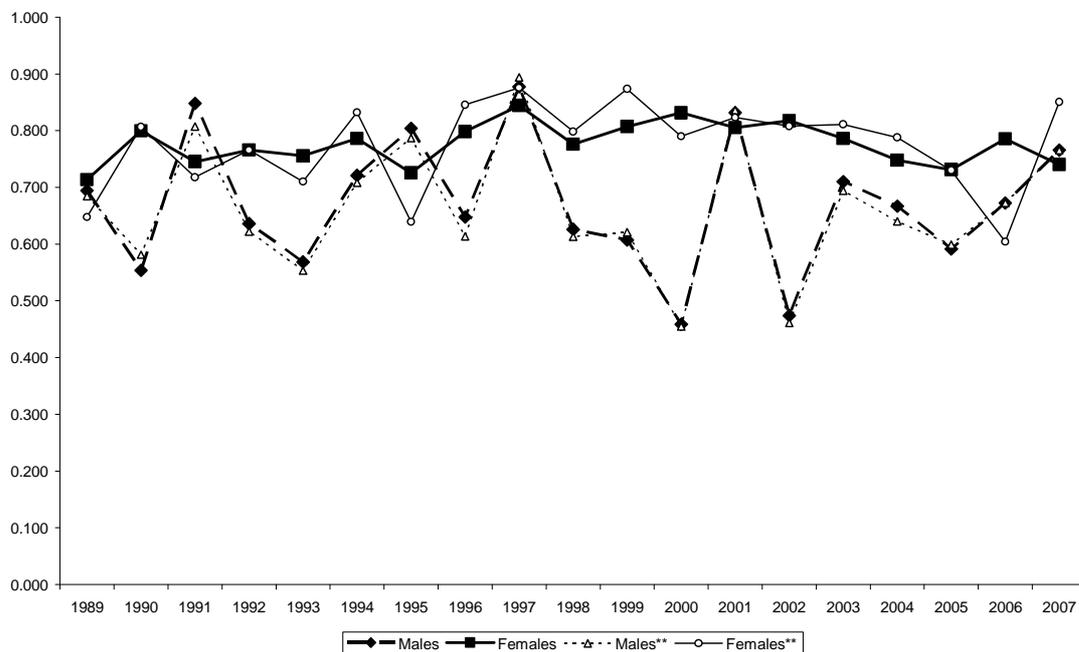


Fig. 4.1f. Mean sixth year survival for 19 cohorts (birth year: 1983-2001) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

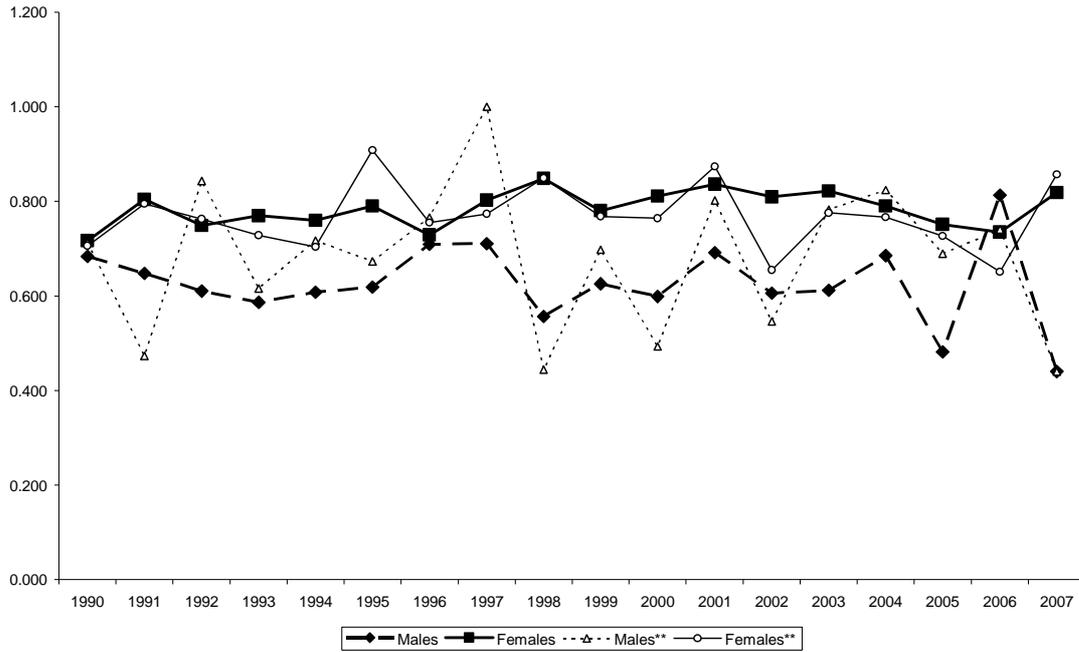


Fig. 4.1g. Mean seventh year survival for 18 cohorts (birth year: 1983-2000) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

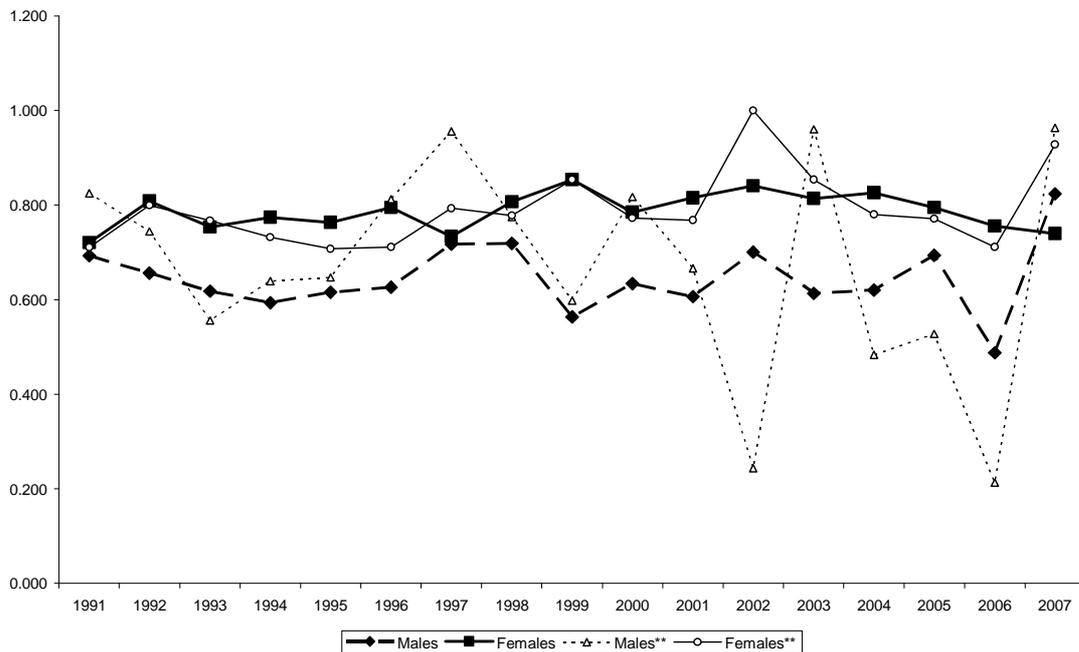


Fig. 4.1h. Mean eighth year survival for 17 cohorts (birth year: 1983-1999) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

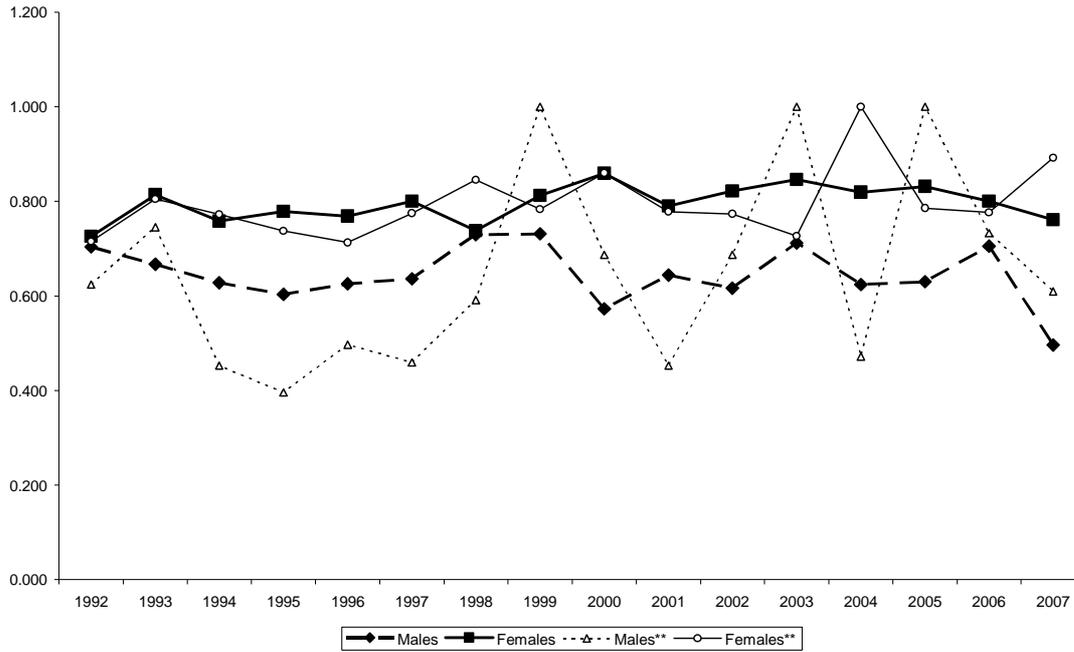


Fig. 4.1i. Mean ninth year survival for 16 cohorts (birth year: 1983-1998) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

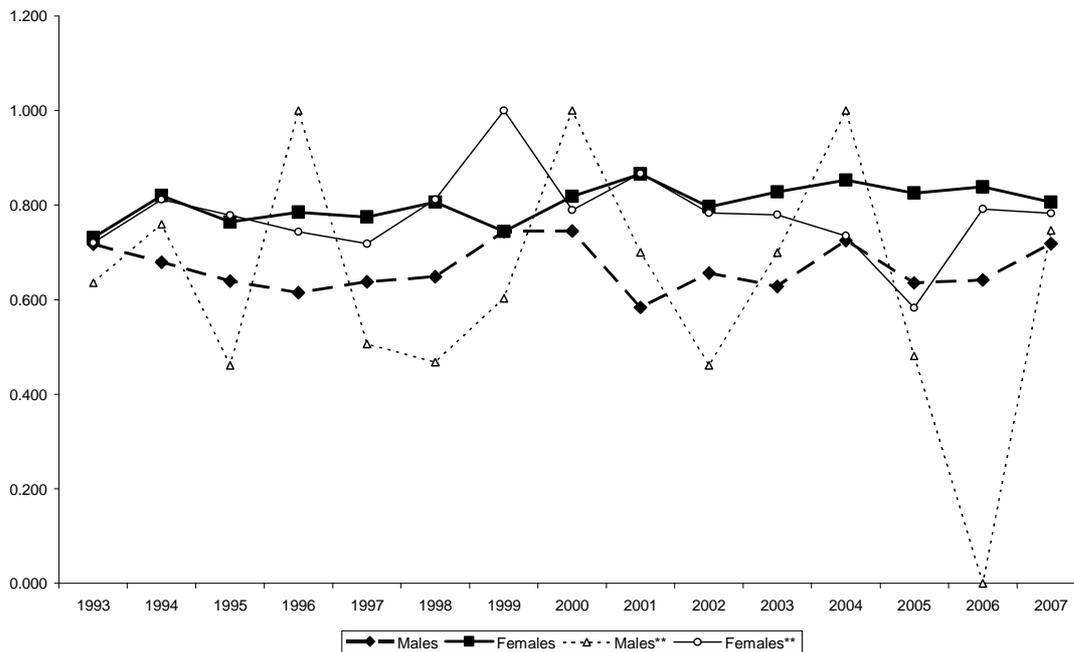


Fig. 4.1j. Mean tenth year survival for 15 cohorts (birth year: 1983-1997) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

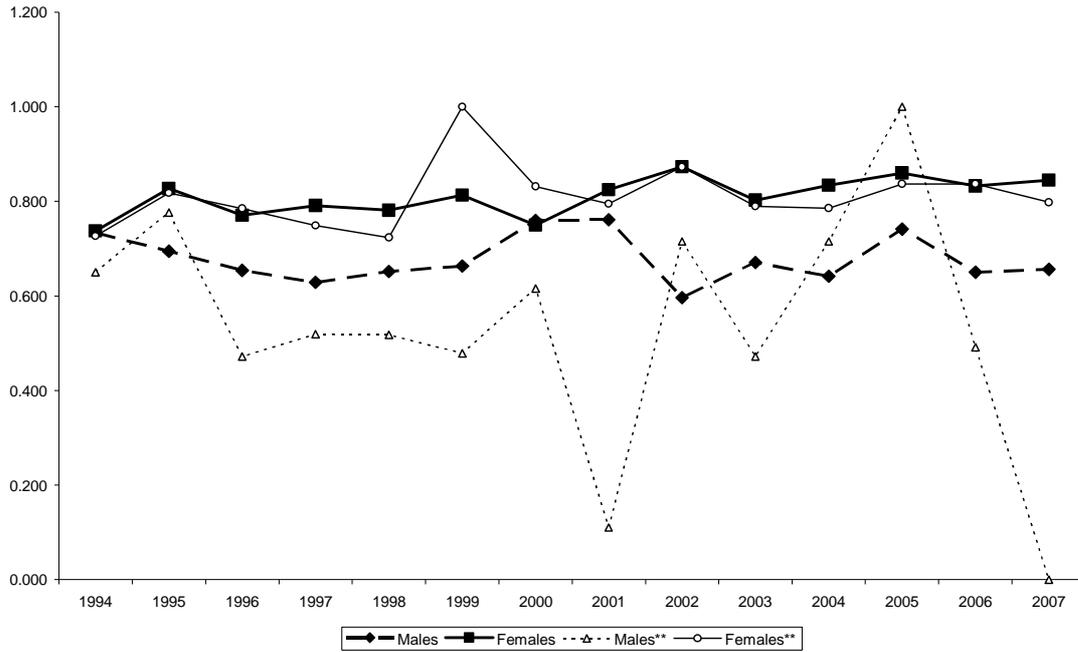


Fig. 4.1k. Mean eleventh year survival for 14 cohorts (birth year: 1983-1996) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

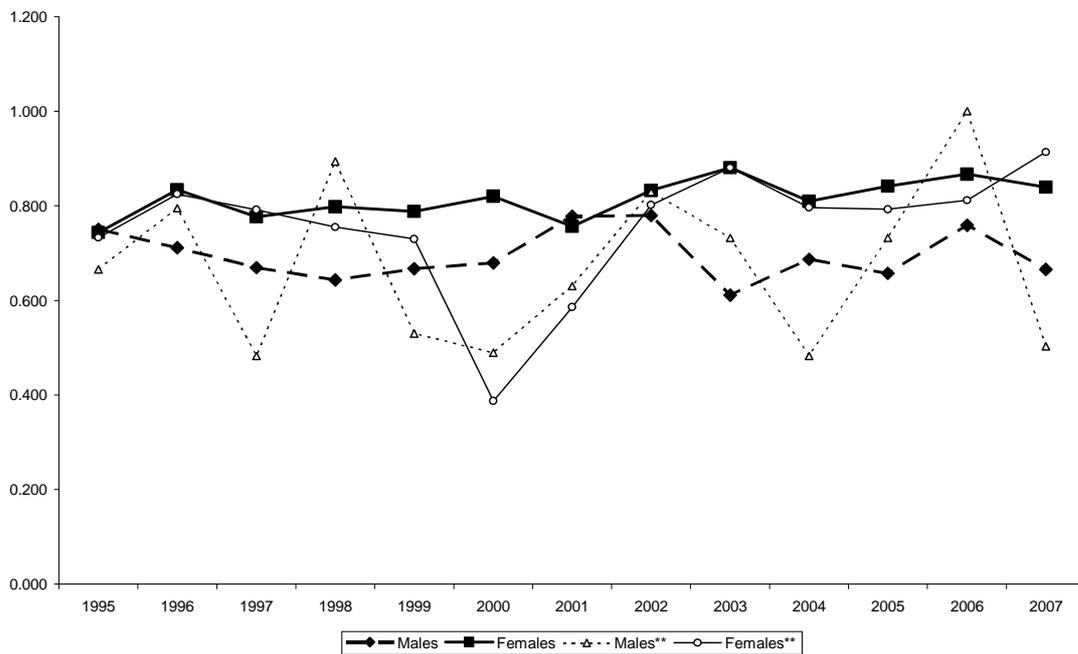


Fig. 4.1l. Mean twelfth year survival for 13 cohorts (birth year: 1983-1995) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

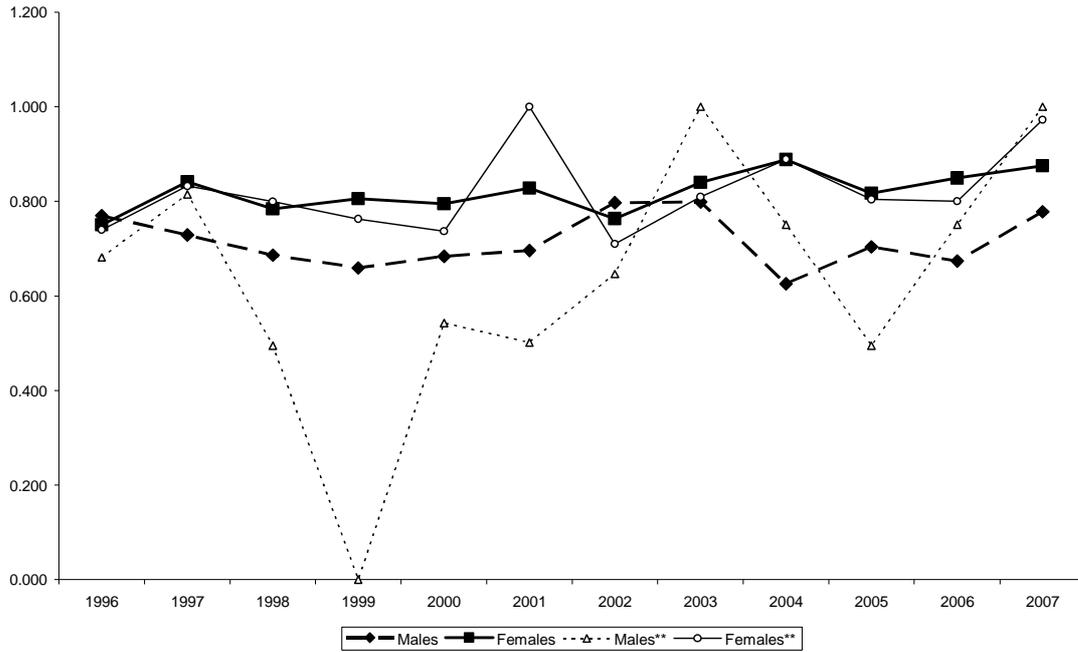


Fig. 4.1m. Mean thirteenth year survival for 12 cohorts (birth year: 1983-1994) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

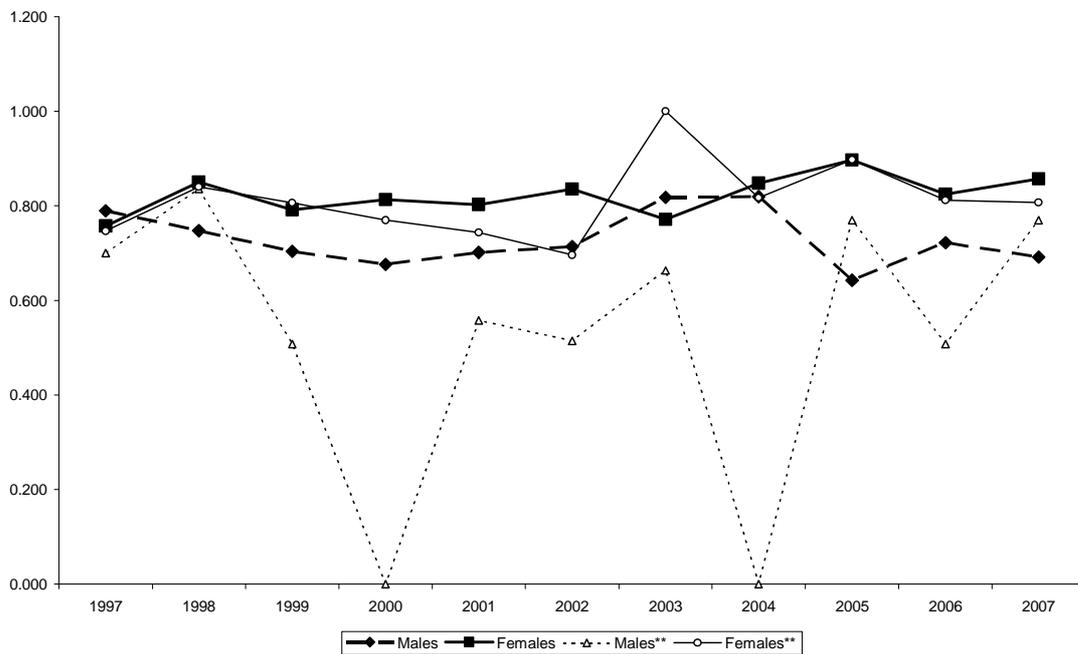


Fig. 4.1n. Mean fourteenth year survival for 11 cohorts (birth year: 1983-1993) of southern elephant seals from Marion Island. Solid lines depict estimates gained from **bold-face** selected models in table 4.2, while dashed lines (**) represent those gained from # represented models in table 4.2.

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 1st, 2nd and 3rd 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 (4th 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 4th 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 (4th 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 ± 0.03 ; after 1993: 0.806 ± 0.04 ; increase =

5.2%) at a similar rate as juvenile survival (mean = 0.710 ± 0.10 ; vs. mean = 0.761 ± 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 2nd 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 ± 0.02) as compared with Pistorius et al. (1999b) (0.761 ± 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 ($\leq 1000\text{km}$ – 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.

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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:

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

ρ_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 7th 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_c. 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).

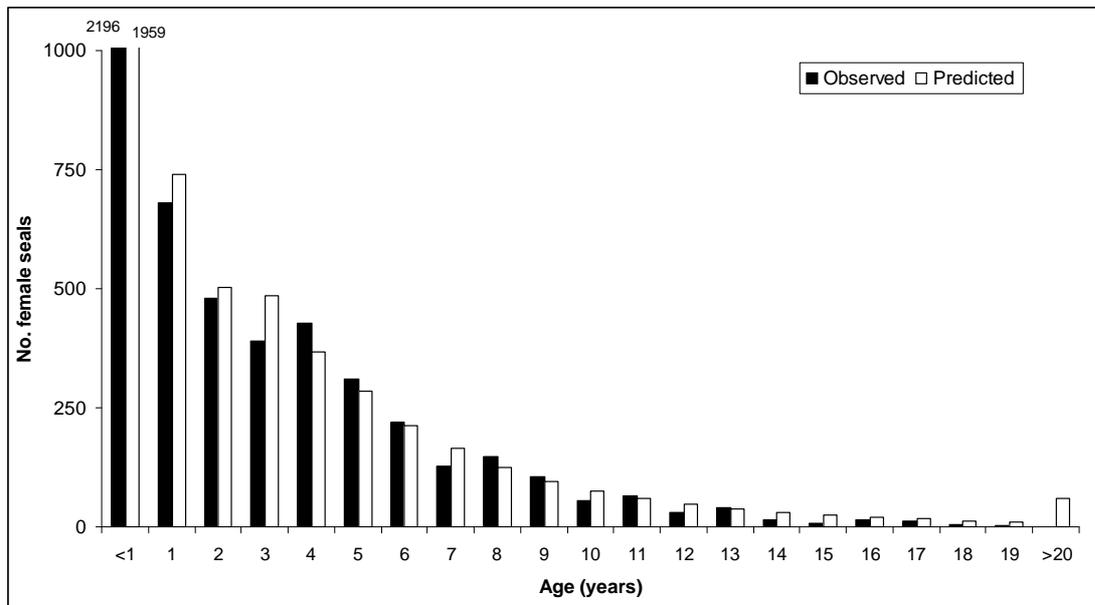


Fig. 5.1. Frequency distribution of longevity for tagged female southern elephant seals at Marion Island (cohorts pooled; 1983 to 2004). 'Observed' values correspond to resighted individuals, while 'Predicted' longevity values are derived from survival probability data and corrected for tag-loss as presented 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		
	χ^2	df	P
Modelling actuarial senescence			
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
Modelling reproductive senescence			
1983-88	28.399	21	0.129
1983-92	32.170	18	0.021
1988-92	34.815	21	0.030
1983-92 ^{prim3}	35.148	26	0.109
1983-92 ^{prim4}	27.056	20	0.134
1983-92 ^{prim5}	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_c) 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 ϕ and recapture probabilities as ρ . 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_c) is shown in **boldface**.

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

1995	(1) Φ_t, ρ_t (CJS)	572.086 ^(1.000)	17	92.132
	(2) Φ_t, ρ_c	586.708	10	122.243
	(3) $\Phi_{4-7, 8-}, \rho_t$	566.032	12	97.222
1996	(1) Φ_t, ρ_t (CJS)	208.635 ^(3.686)	15	26.529
	(2) Φ_t, ρ_c	200.432	9	31.101
	(3) $\Phi_{4-7, 8-}, \rho_c$	192.379	4	33.402
1997	(1) Φ_t, ρ_t (CJS)	583.034 ^(1.000)	13	55.040
	(2) Φ_t, ρ_c	575.049	8	57.801
	(3) $\Phi_{4-7, 8-}, \rho_c$	567.614	4	58.711
Modelling reproductive senescence				
1983-1988	(1) Φ_t, ρ_t (CJS)	1381.936 ^(1.352)	27	209.705
	(2) Φ_c, ρ_t	1369.406	15	222.431
	(3) $\Phi_c, \rho_{7-12, 13-15, 16-19}$	1363.225	5	236.7513
1983-1992	(1) Φ_t, ρ_t (CJS)	1872.646 ^(1.787)	19	188.739
	(2) Φ_c, ρ_t	1861.784	11	194.228
	(3) $\Phi_c, \rho_{7-12, 13-15}$	1854.227	4	200.828
1988-1992	(1) Φ_t, ρ_t (CJS)	1018.216 ^(1.658)	19	166.542
	(2) Φ_c, ρ_t	1008.903	11	174.068
	(3) $\Phi_c, \rho_{7-12, 13-15}$	1000.225	4	179.761
1983-92 ^{prim3}	(1) Φ_t, ρ_t (CJS)	1265.878 ^(1.352)	23	247.392
	(2) Φ_c, ρ_t	1255.950	13	258.569
	(3) $\Phi_c, \rho_{4-6, 7-12, 13-15}$	1244.537	4	265.630
1983-92 ^{prim4}	(1) Φ_t, ρ_t (CJS)	2054.584 ^(1.352)	21	251.684
	(2) Φ_c, ρ_t	2042.084	12	257.679
	(3) $\Phi_c, \rho_{5-6, 7-12, 13-15}$	2047.578	4	279.390
1983-92 ^{prim5}	(1) Φ_t, ρ_t (CJS)	2001.549 ^(1.177)	19	213.975
	(2) Φ_c, ρ_t	1990.825	11	219.734
	(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}	χ^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 $\Phi_{4-14, 15-}$, ρ_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).

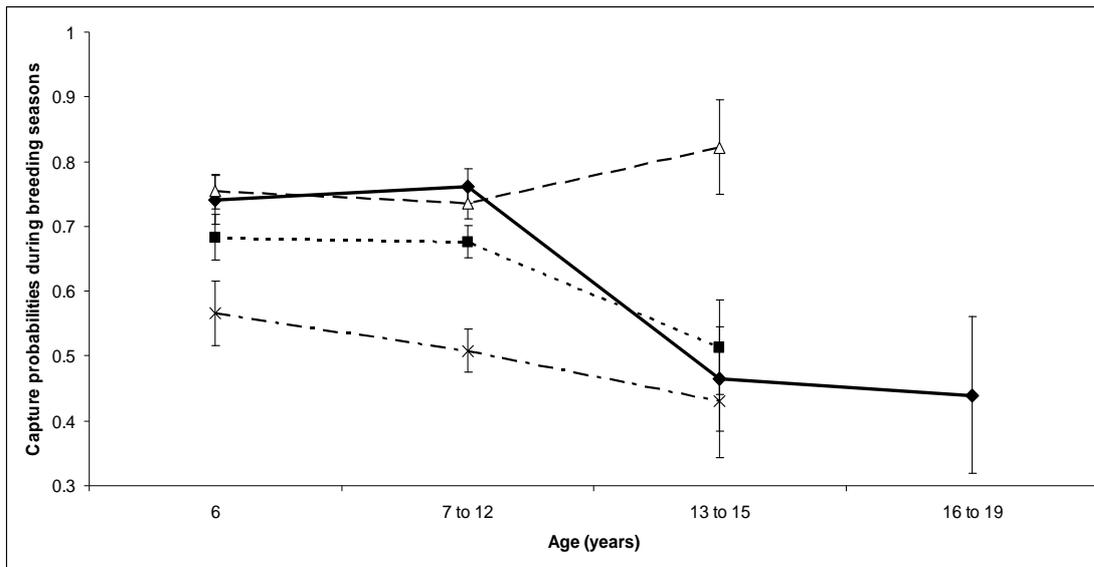


Fig. 5.2a. Capture probabilities (during breeding seasons) of pooled cohorts of female southern elephant seals, as indices of breeding probabilities. The solid line indicates capture probabilities for six cohorts (1983 to 1988) that have reached 19 years of age. The dotted line (square) illustrates capture 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.

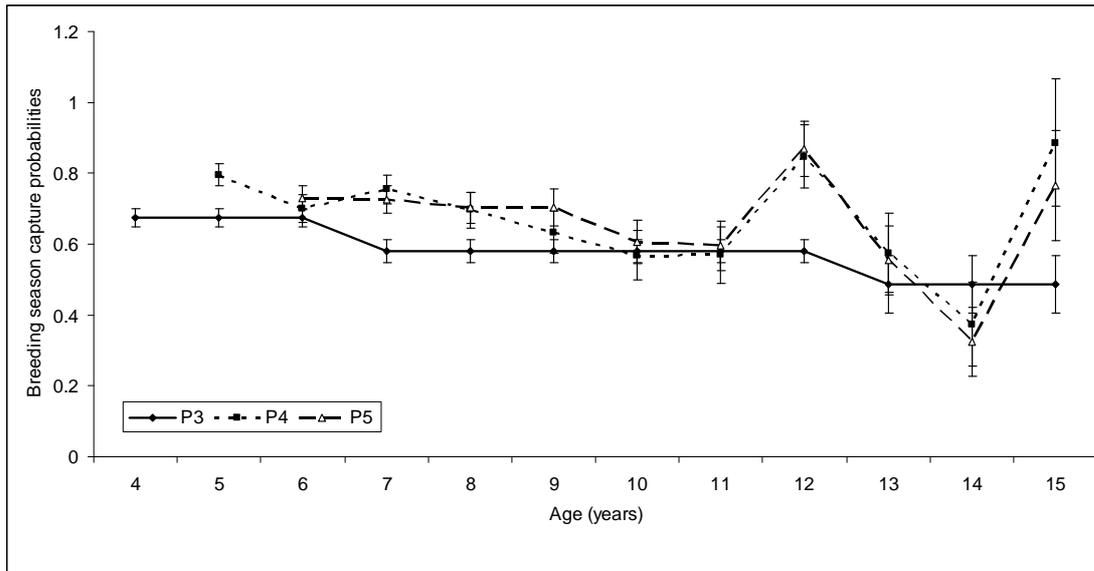


Fig. 5.2b. Capture probabilities (during breeding seasons) of pooled cohorts (1983 to 1992) of female southern elephant seals primiparous at different ages (P3 – age 3; P4 – 4 yrs; P5 – 5 yrs) shown as indices of breeding probabilities. Survival was modelled as constant through time.

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 3rd, 4th and 5th 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.

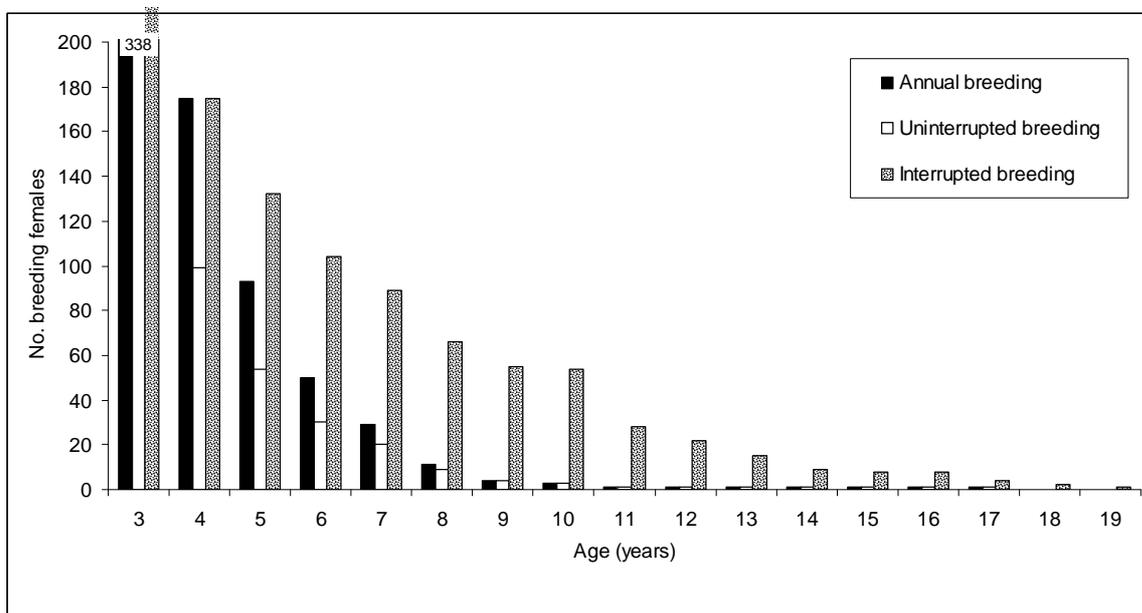


Fig. 5.3a. Fertility schedule of adult female southern elephant seals observed to be primiparous at age three. Annual breeding – females that bred in consecutive years before a sabbatical and a subsequent resumption of breeding. Uninterrupted breeding – females that bred annually from primiparity to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

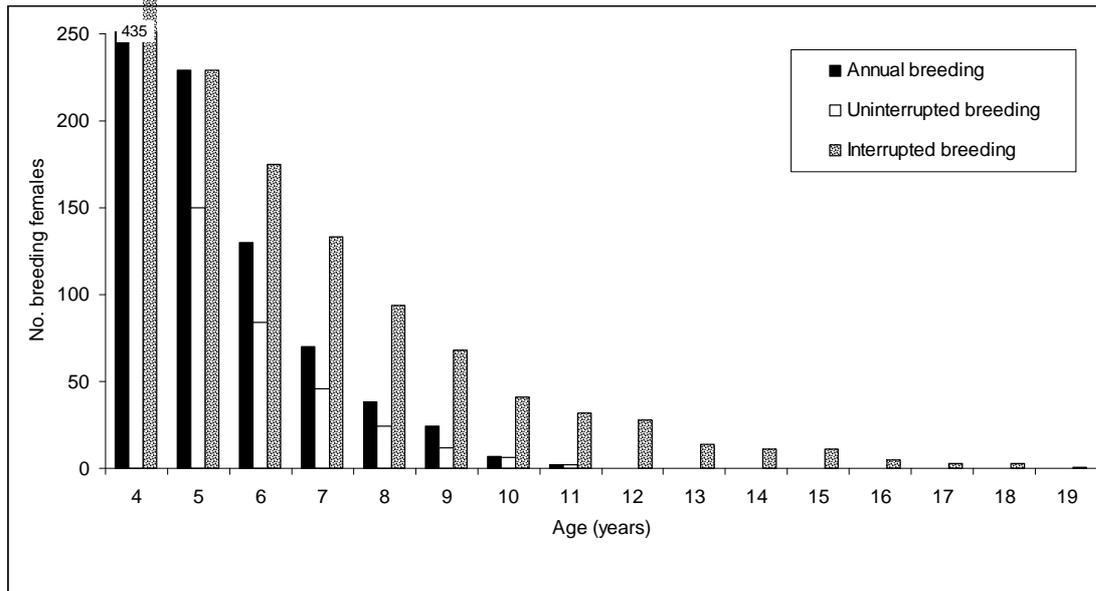


Fig. 5.3b. Fertility schedule of adult female southern elephant seals observed to be primiparous at age four.

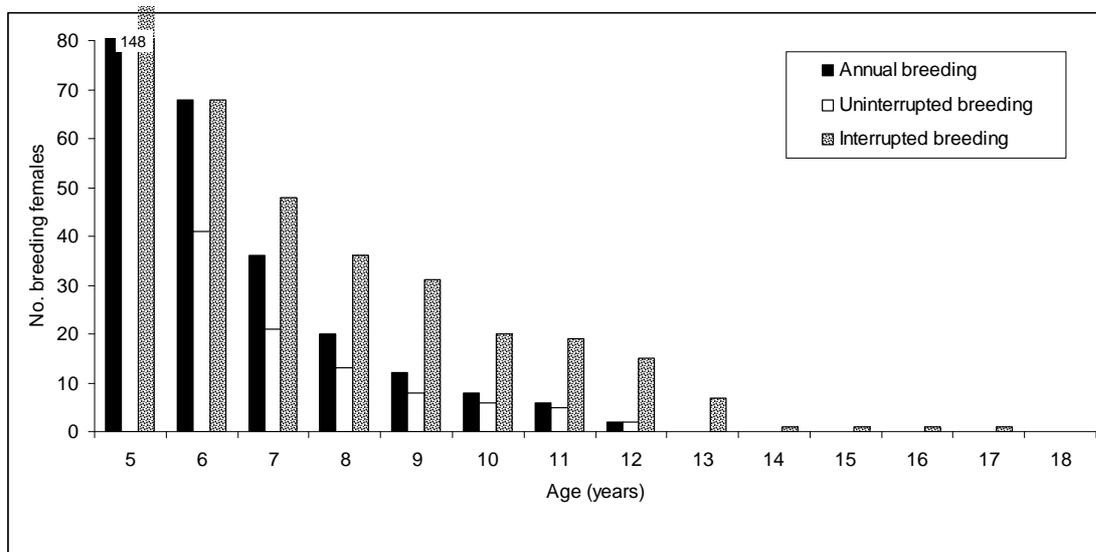


Fig. 5.3c. Fertility schedule of adult female southern elephant seals observed to be primiparous at age five.

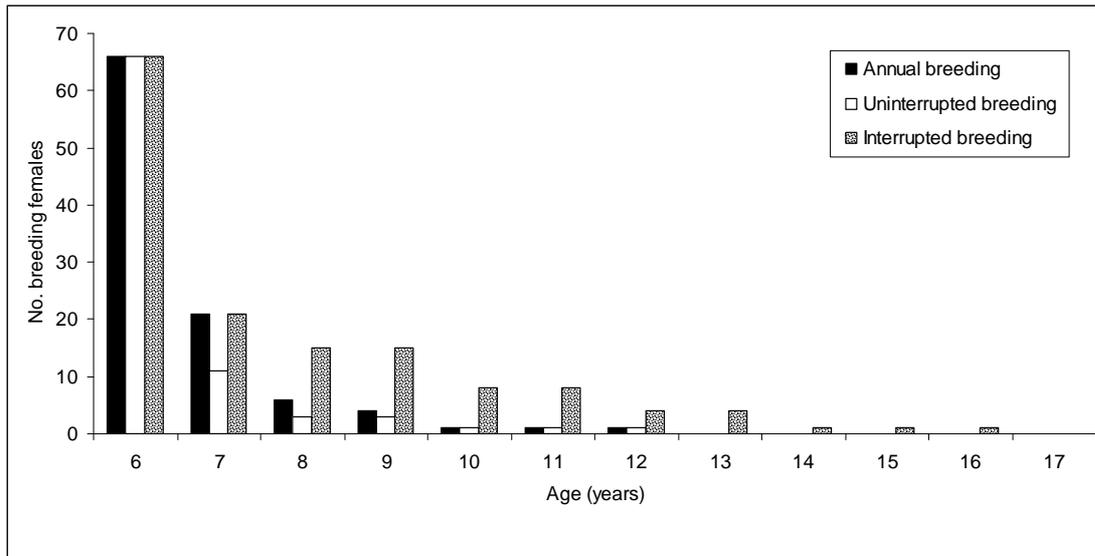


Fig. 5.3d. Fertility schedule of adult female southern elephant seals observed to be primiparous at age six.

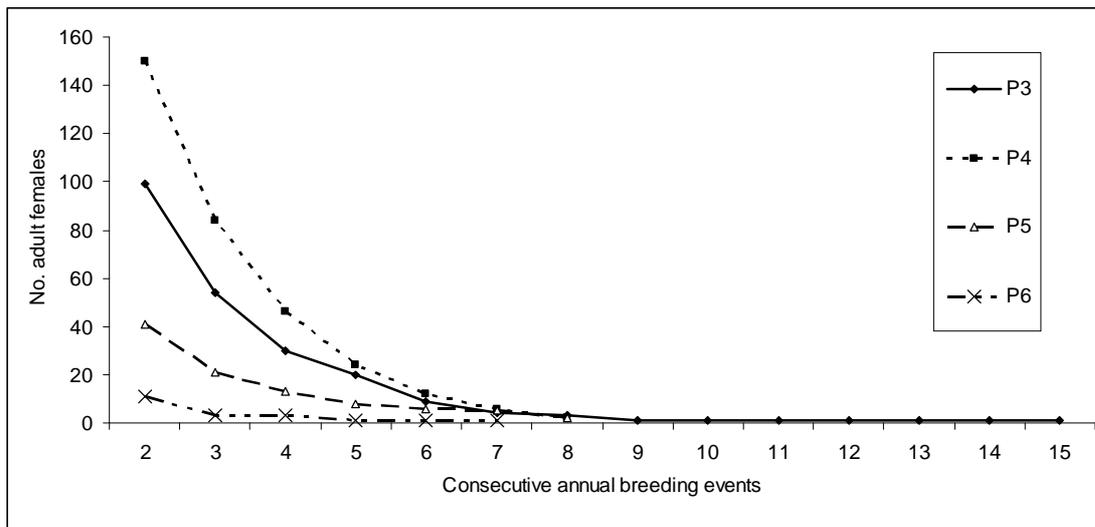


Fig. 5.4. Relative numbers of adult females participating in consecutive annual breeding events dependent on their age at primiparity (ages three - P3, four - P4, five - P5, and six - P6), from a total sample of 1032 individuals from 15 consecutive cohorts (1983 to 1997)

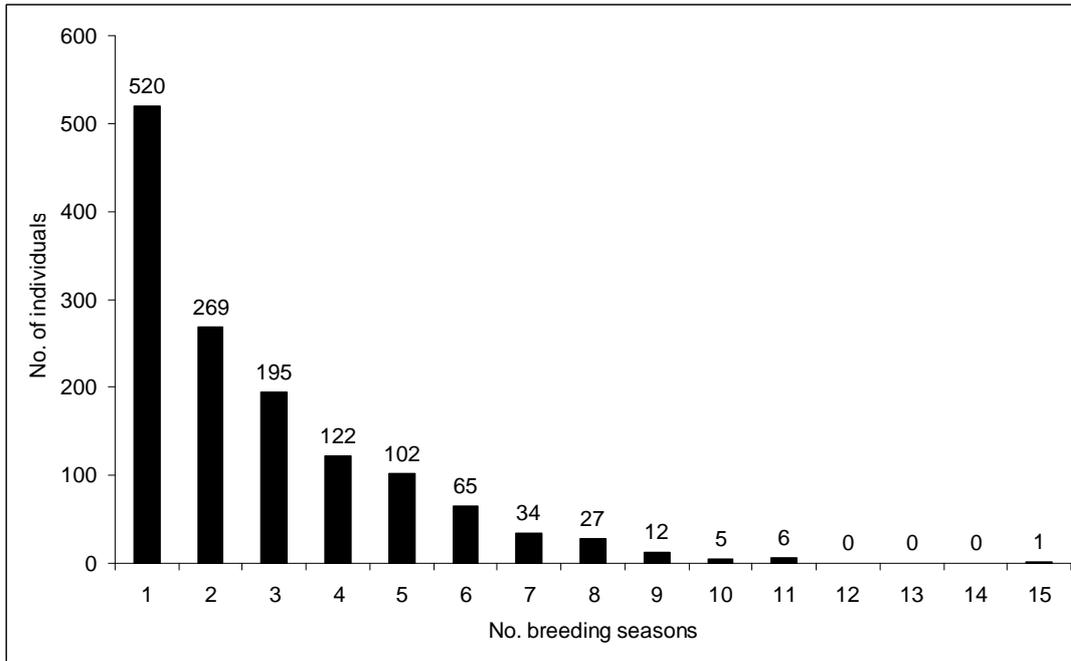


Fig. 5.5. Frequency distribution of the total observed number of breeding attempts (not necessarily consecutive) per individual female southern elephant seal ($n = 1358$) from 20 pooled cohorts (1983-2002) at Marion Island over the breeding periods from 1983 to 2007.

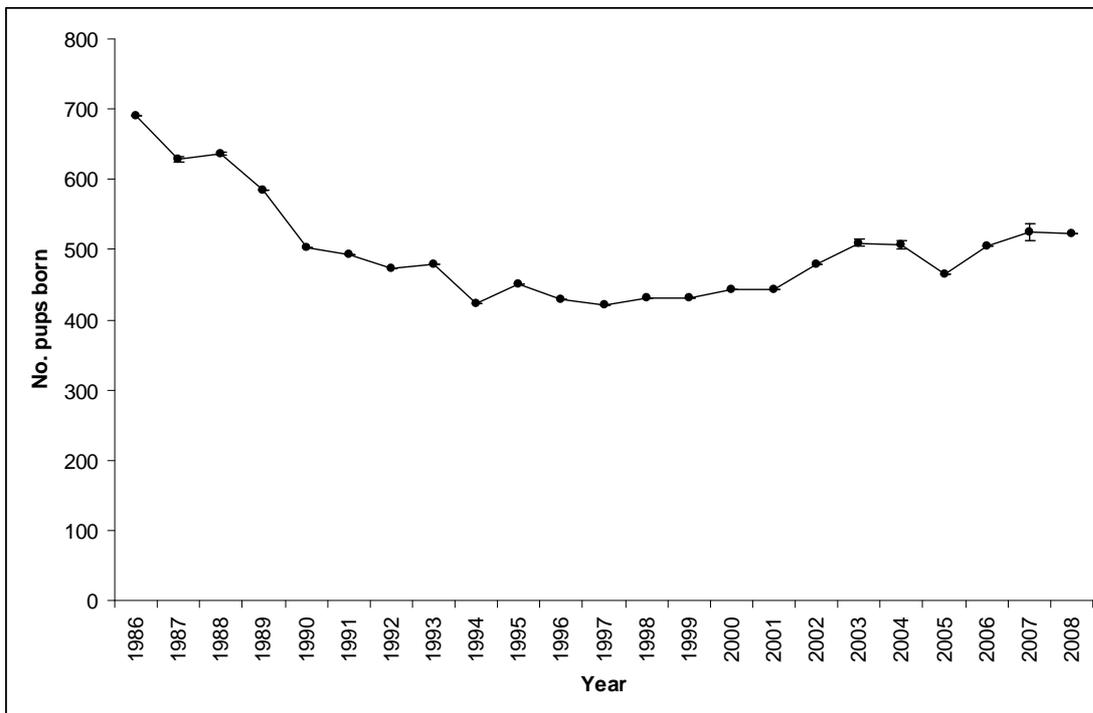


Fig. 5.6. Number of southern elephant seal pups born at Marion Island (1986 to 2008).

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.

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CHAPTER SIX:
**USING COMPLEX ECOLOGICAL MODELLING SOFTWARE REQUIRES
CAREFUL THOUGHT, A THOROUGH UNDERSTANDING OF THE SOFTWARE
AND METICULOUS EXPERIMENTAL DESIGN**

Abstract

An incomplete understanding of sophisticated modelling software can camouflage inappropriate experimental design. Capture-mark-recapture (CMR) data is increasingly being used to address ecologically important questions. Various sophisticated software packages have made access to complex analytical procedures user-friendly, one such tool is the Program MARK. More than 1400 published studies have cited the use of MARK in less than 10 years and clearly the software has had a significant impact in ecology. We consider how well ecologists (that apply sophisticated analytical software, but are not necessarily expert biometrists/statisticians) understand what can- and cannot be accomplished in ecological studies with such complex software, using MARK as example. Using a long-term demographic study on southern elephant seals (*Mirounga leonina*) we illustrate how poor experimental design could be veiled due to the complexity of such software. We discuss one potentially hidden encumbrance in the MARK analytical process that can result in incorrect analyses. We suggest that users cultivate a thorough understanding of the software programmes they use, and that relevant experts are proposed as potential reviewers for their work, to increase the rigor with which published results report on the use of such analytical tools. This will help to ensure that flawed analyses are not published to the detriment of ecological theory advancement or wildlife management, and that students are not misled by published, but erroneous use of such powerful tools.

Introduction

Being able to reliably identify animals individually throughout their lives is the cornerstone of sound life-history and demographic work, given that individual identity forms the basis for long-term capture-mark-recapture studies (CMR). CMR experiments provide vital data for the advancement of animal population studies for a range of taxa and under various field scenarios. Such a variety of applications of the technique (including related adaptations such as mark-resight experiments) resulted in a great deal of research aimed at reducing bias and increasing the technique's scientific rigor. A progression of sophisticated software packages (e.g. POPAN, SURGE, DENSITY, CAPTURE) has become available to collate the significant analytical developments of the past decades into interfaces that have boosted the applicability of CMR. One particularly user-friendly application that has gained considerable popularity for specialists and non-specialists alike is Program MARK (White and Burnham 1999). To date more than 1400 published (1999 – 2009, Scopus®, Fig. 6.1) wildlife/biometric studies have cited the founding paper for this program, clearly with significant advances in our knowledge of animal populations throughout the world.

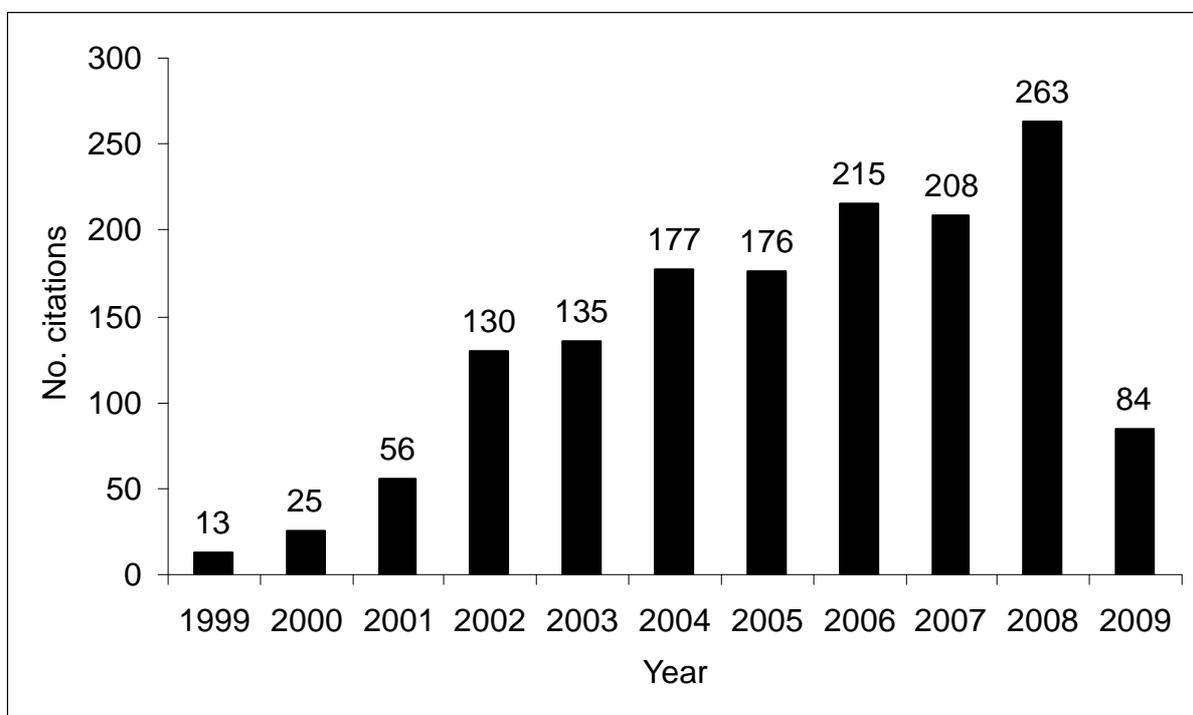


Fig. 6.1. Illustrating the impact of the founding paper for the capture-mark-recapture analytical program MARK (White and Burnham 1999). The number of published papers (up to 08 July 2009), to have cited White and Burnham (1999) *per year* are shown (Scopus®).

The Cormack-Jolly-Seber (CJS) (Cormack 1964; Jolly 1965; Seber 1965) modelling approach for estimating fundamental population parameters (e.g. survival) is central to MARK. Given the complexities of wildlife population systems, the CJS approach requires various assumptions to be made, e.g. (1) that every marked animal present in the population at time (i) has the same probability of recapture (p); (2) Every marked animal in the population immediately after time (i) has the same probability of surviving to time ($i+1$) (Burnham et al. 1987; Lebreton et al. 1992). Although we do not review the multitude of works pertaining to the moderation/elimination of these biases, one assumption, namely individual capture heterogeneity (Lebreton et al. 1992) forms the core of this study. Life history studies using mark-recapture experiments are dependent on, among others, choosing marking methods that do not compromise recapture and survival probability estimates. Unequal catchability or individual capture heterogeneity can have a number of sources, including marker loss and incorrect marker identification (Carothers 1979; Pledger and Efford 1998). Errors associated with: tag-loss, tag visibility and tag readability (including correct colour identification) can compromise individual identification and hence the estimation of vital life-history parameters (e.g. Curtis 2006). We attempt to address the question of marker resighting heterogeneity using program MARK and show how poorly designed experiments can be veiled by incomplete understanding of the software's complexity and functionality. We suggest that such software complexity not only blinds researchers but may also blind journal referees to fundamental flaws in experimental design for two reasons. Firstly, important analytical procedures involved in the correct use of MARK are hidden from the referees of such work. Secondly, referees tend to assume (erroneously) that poor or flawed experimental design has been accounted for by such hidden analytical procedures within the software programme.

We provide a case study using southern elephant seals to illustrate how an experimental design initiated for purposes other than (but related to) that applied in this study, appeared useable for the detection of variation in marker sightability. Herewith we aim to initiate discussion regarding the potential pitfalls in using sophisticated analytical tools by non-specialist users, and the veiled dangers of such user-friendly programmes. We contend that the illustrated scenario may not be

uncommon in ecological papers reporting on results gleaned from MARK (or other complex CMR software).

Southern elephant seal case study

Pinnipeds are among the more easily marked vertebrates owing to relatively unrestricted access to weaned animals (Bester 1988; McMahon et al. 2006; see Chapter 3 – de Bruyn et al. 2008). Tags, inserted in the flippers of pinnipeds, have been one of the more popular means of marking seals (e.g. Erickson et al. 1993; see Chapter 3 – de Bruyn et al. 2008), however certain errors, such as the loss of tags (e.g. Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009) is associated with this method. To effectively correct for capture heterogeneity in estimates of survival, knowledge of not only tag-loss but also tag sightability are required. The visibility of marks is an important factor in the development and design of animal marks (Trippensee 1941). The CMR dataset of southern elephant seals at Marion Island (spanning two decades) is ideal for investigating the long-term readability of tags. This long-term study has resulted in a plethora of papers on population demography, however, none assessed the possible effect of tag-dependent heterogeneity on results (aside from tag-loss; Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009), although Wilkinson and Bester (1997) did mention the potential for confusion between certain tag colours from field observations. We applied the Cormack-Jolly-Seber (CJS) and associated models (Lebreton et al. 1992) to the long-term mark-resighting data of female southern elephant seals at Marion Island to assess whether tag-dependent heterogeneity, ultimately affecting capture probability, exists in this population.

We chose adult females as study subjects because: (1) there is a comprehensive 19 year CMR dataset available for adult female seals, (2) they are philopatric and return annually to known and well surveyed study beaches, whereas adult males and juveniles of both sexes are less philopatric (Hofmeyr 2000) and (3) females show low and constant tag-loss over time (Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009)

Material and methods

Tagging and resighting of seals

An intensive tagging program of southern elephant seals commenced in 1983 at sub-Antarctic Marion Island (46°54'S, 37°45'E). From 1983 to 1999, 4059 (average: 239 annually, range: 179–344) newly weaned female pups were double tagged in their hindflippers using Dal 008 Jumbotags® (Dalton Supplies Ltd., Henley-on-Thames, U.K.). The self-piercing tags were uniquely embossed with a three-digit number, and colour-coded to denote the year of application (Table 6.1).

Beaches were checked for tagged seals every seven days during the breeding season (mid-Aug to mid-Nov, all years) 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). For each seal that was resighted, the tag number, tag colour combination (Table 6.1), number of tags remaining (one or two), location and date of the sighting were noted. Two trained observers *per* research season (April to April) were used concurrently to search for tagged seals from 1983 to 2004 (except during 1995, 1996 & 2001 when only one observer was available).

Table 6.1. Tagging regime for different cohorts of southern elephant seals at Marion Island, 1983 - 1999.

Year tagged	Code	Outer tag colour	Inner tag colour
1983	OO	Orange	Orange
1984	BB	Blue	Blue
1985	YY	Yellow	Yellow
1986	RR	Red	Red
1987	PP	Pink	Pink
1988	GW	Green	White
1989	BF	Black	Flame (Bright orange)
1990	LB	Lemon (Pale yellow)	Dark brown
1991	OB	Orange	Royal blue
1992	YP	Yellow	Pink
1993	GR	Green	Red
1994	WB	White	Black
1995	OY	Orange	Yellow
1996	BP	Blue	Pink
1997	WR	White	Red
1998	PO	Pink	Orange
1999	GG	Green	Green

Analysis of tag resightability

To clarify tag resighting heterogeneity by cohort (i.e. colour) multiple resights of each individual within any given year was limited to include only the last resight in each research season. All seals were assumed to age on 15 October, which is the peak adult female haul-out date at Marion Island (Condy 1978). Encounter (resighting) history matrices were constructed for adult female seals (1842 of the 4059 female individuals tagged as weanlings) using the resighting data from the fourth year of life (mean age at first breeding; Pistorius et al. 1999; see Chapter 5) to “death” and treating age three as the “initial release” occasion. In effect, the resighting data available up to 2004 thus allowed 19 years of resighting history for the 1983 cohort (from “initial release” at age 3) and therefore 2 years for the 1999 cohort. These capture-history matrices (depicting absence or presence of individuals per year as 0 or 1 respectively, over time) were condensed to a single input file (staggered, to represent the different “release” occasions for each cohort) for the software package MARK.

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: ϕ_i = the survival probability for all animals between the i th and $(i+1)$ th sample ($i = 1, \dots, k-1$), and ρ_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. The median \hat{c} GOF method was used to test the model assumptions including; equal catchability, that marked animals are not missed or marks lost, that every marked animal at time (i) has the same chance of surviving to time $(i+1)$, and that all samples are instantaneous between times (i) and $(i+1)$ (Lebreton et al. 1992). The most parsimonious model was selected using the small sample corrected Akaike Information Criterion (AIC_c) (Lebreton et al. 1992). Overdispersed data, as a result of violation of one or more of the CJS model assumptions, requires \hat{c} (variance inflation factor) adjustments to AIC_c estimates ($QAIC_c$) for the CJS and nested models. AIC_c model selection was used to test

hypotheses regarding capture heterogeneity of adult female southern elephant seals. Because assessment of survival probabilities were not of primary concern in this study, the findings of Pistorius et al. (1999) were used to depict biologically realistic survival estimates for seals in the models. Models were parameterised using the matrix design in MARK. The encounter history data type is herewith defined and various models can be structured by manipulating numbers in edit boxes within a matrix. In so doing the matrix design depicts a numerical indexing scheme as substitute for the individual survival and recapture (or resighting) values, respectively. Parameter index matrices were structured to be time but not age dependent for survival. Models with capture probability as constant over time but not between cohorts, and as constant over both time and cohort were considered. The lower the AIC_c value, the more parsimonious the model (Burnham and Anderson 1998), and we considered two models to be significantly different when the ΔAIC_c was greater than two (Anderson and Burnham 1999).

Results

The GOF tests indicated some overdispersion in the data set ($\hat{c} = 1.440$) and as a consequence AIC_c values were adjusted accordingly. Relative parsimony supported the fully time dependent CJS model rather than that depicting capture heterogeneity between cohorts (model A) (Table 6.2). Cohort dependent capture heterogeneity in the dataset was not supported and confusion of different coloured tags appears unimportant in the dataset.

Table 6.2. Elimination of nonsignificant effects from the fully time-dependent Cormack-Jolly-Seber (CJS) in modelling recapture probability in adult female southern elephant seals from Marion Island. For each model the Quasi-Akaike Information Criterion ($QAIC_c$), $QAIC_c$ weight, Model Likelihood (mL), number of estimable parameters (NP) and Quasi-Deviance (QDEV) are given. Apparent survival probabilities are referred to as ϕ and recapture probabilities as p . The figures in the model refer to age dependence up to a particular year of life; t – time dependent; c – constant per cohort; _c – constant for all cohorts over time. Model selection based on median $\hat{c} = 1.440$. Model A depicts constant recapture probability within each cohort after age 3; while model B depicts constant recapture probability across all cohorts after age 3.

Model	$QAIC_c$	$QAIC_c$ Weight	mL	NP	QDEV
CJS	8495.034	0.999	1.000	37.000	1734.965
A ($\phi_{\varnothing 3t}; p_{\varnothing 3c}$)	8533.319	0.000	0.000	36.000	1775.273
B ($\phi_{\varnothing 3t}; p_{\varnothing 3_c}$)	8568.029	0.000	0.000	20.000	1842.272

Discussion

We found no significant differences in resight probability among cohorts of adult female southern elephant seals at Marion Island and hence conclude that all seals had the same chance of being resighted during the study. Factors that could potentially affect sightability or accurate individual animal identification can be divided into two broad categories, namely, observer bias and marker bias. Observer bias centres around observer effort and/or ability (e.g. training, visual impairment) on correct mark identification. Marker bias includes a myriad of factors under two main categories; permanent and temporary illegibility. Permanent illegibility factors include worn lettering, marker breakage, marker discolouration, and marker loss. Temporary illegibility factors include soiling, physical obstruction and weather conditions (e.g. light levels). Such a plethora of potential prejudiced variables make studies aimed at quantifying any one factor difficult.

Although cohort, tag age and tag colour are indistinguishable i.e. confounded in this experimental design, the use of adult females can provide some insight into potential marker confusion issues because the age effect on survival and especially capture probability is known to be minor for this sector of the population (Pistorius et al. 1999, 2004, 2008). Differences observed in recapture probabilities can likely be ascribed to other issues such as temporary emigration from the study site (see Chapter 4). There is corroborating evidence which suggests that confusion in documenting tag colours is of little consequence e.g.: (1) Field workers are tested for colour blindness before appointment. (2) The tag colour combinations are known to the field staff and in all cases only one or two colours have to be identified per seal. (3) Seal sex, age and size often serve as indicators of seal identity once records are checked. (4) Observer bias is reduced by random application of uniquely numbered tags to both sexes within a cohort. (5) We assume that consistently (a) misreading a particular tag and (b) noting it as a specific other tag, is minimized given the design of the resighting schedule that allows multiple resights of the same tags over a relatively short period (one month) of time (see Methods section). (6) At the inception of this mark-resighting program, tag colour combinations (inner and outer tag components) were chosen to minimize the likelihood of confusion between cohorts.

All tags used in this study were manufactured by the same company with the same materials (see Methods section). While it is not known if the manufacturing procedure was identical for each tag or cohort of tags, based on the manufacturers assurance we assume that breakage and inscription wear would be constant amongst tag colours and would follow a similar age related trend. Tag colour should clearly not result in inconsistent tag-loss over time between cohorts (Pistorius et al. 2000; see Appendix 2 – Oosthuizen et al. 2009). We expect that certain temporary tag illegibility factors (e.g. physical visual obstruction) would affect resightability of any tags regardless of their colour, while other temporary factors (e.g. soiling) could affect some colours more than others. For example, white tag components exposed to muddy water would appear pinkish. However, the resighting schedule, allows for repeated encounters of individual seals regardless of the state of their tags. Unlike permanent illegibility factors (e.g. tag colour, breakage) that cannot be corrected no matter how often the tag is sighted, temporary illegibility factors (e.g. soiling) would not persist over time and frequency of sighting would eliminate such temporary illegibility problems. We thus disregard temporary illegibility factors as an important source of tag-dependent sighting heterogeneity.

Long-term mark recapture/resighting datasets, particularly for large mammals, are rare and undoubtedly beset with variables, such as temporary emigration, which affect capture heterogeneity in a CMR context. Consequently, analyses based on even the most rigorously designed mark-recapture experiments require certain assumptions to be made. Of course, the species under investigation and the objective of the study will dictate which of the assumptions within the modelling approach will be more crucial than others if models are to be properly assessed. For example, in elephant seals temporary emigration from island study sites can introduce significant confounding arguments without certain assumptions made. Clearly, assuming zero temporary emigration does not make biological sense (also see Chapter 4), while modelling in an “open CMR” context introduces other sources of heterogeneity (Pledger et al. 2003), where further assumptions are required that perhaps do not align with the study scenario. Mitigating against as many of these assumptions as possible is therefore highly desirable for estimating life-history such as survival rigorously. Here we suggest that tag colour confusion and its resulting

effects on estimates of survival in this elephant seal dataset is unlikely, thus, lending confidence to previous estimates of survival based on this dataset (e.g. Pistorius et al. 1999, 2004, 2008; McMahon et al. 2003, 2005).

The Argument

An expanded version of this seal example was originally accepted by two reviewers to be publishable. A third reviewer identified the confounding effect of tag colour, with seal age (and hence tag age and wear) which cannot be teased apart and as a consequence, the manuscript was not acceptable for publication. The only way to overcome the confounding effects of tag colour, seal age and tag age would be to place different coloured tags on seals within the same cohort (year). While this issue is not a CMR or MARK issue but a basic experimental design issue, one referee's expertise in MARK allowed for easy detection of the confounding problem, knowing immediately that the confounding flaw could not be accounted for in the analysis using this software contrary to that assumed by the other reviewers.

We had tried to overcome this issue of the covariates being indistinguishable within the study design by manipulating the PIM tables in MARK to reduce the confounding bias and using only adult females as study subjects (see above). Parameter index matrix (PIM) structuring for model design within MARK is an invisible component of the analytical procedure to manuscript reviewers. While authors describe their model structuring in the results of papers, this does not always translate to the actual PIMs being structured to depict the intended model, particularly if users do not fully understand the PIM manipulation process (White and Burnham 1999). This is especially relevant when complex permutations of biological parameters are envisaged to be at play in a system (see Fig. 6.2 and also Lebreton et al. 1992) and allows for ambiguity when researchers attempt to repeat the methods. Reviewers not familiar with the functionality of MARK may have difficulty in visualising the structuring of PIMs, unless the PIMs are presented as part of the manuscript and thus available for scrutineering. PIMs are bulky additions to manuscripts and as a consequence rarely available to reviewers or readers. This also pertains to the design matrix, which is an additional (and more complex) means to constrain models defined by the PIMs.

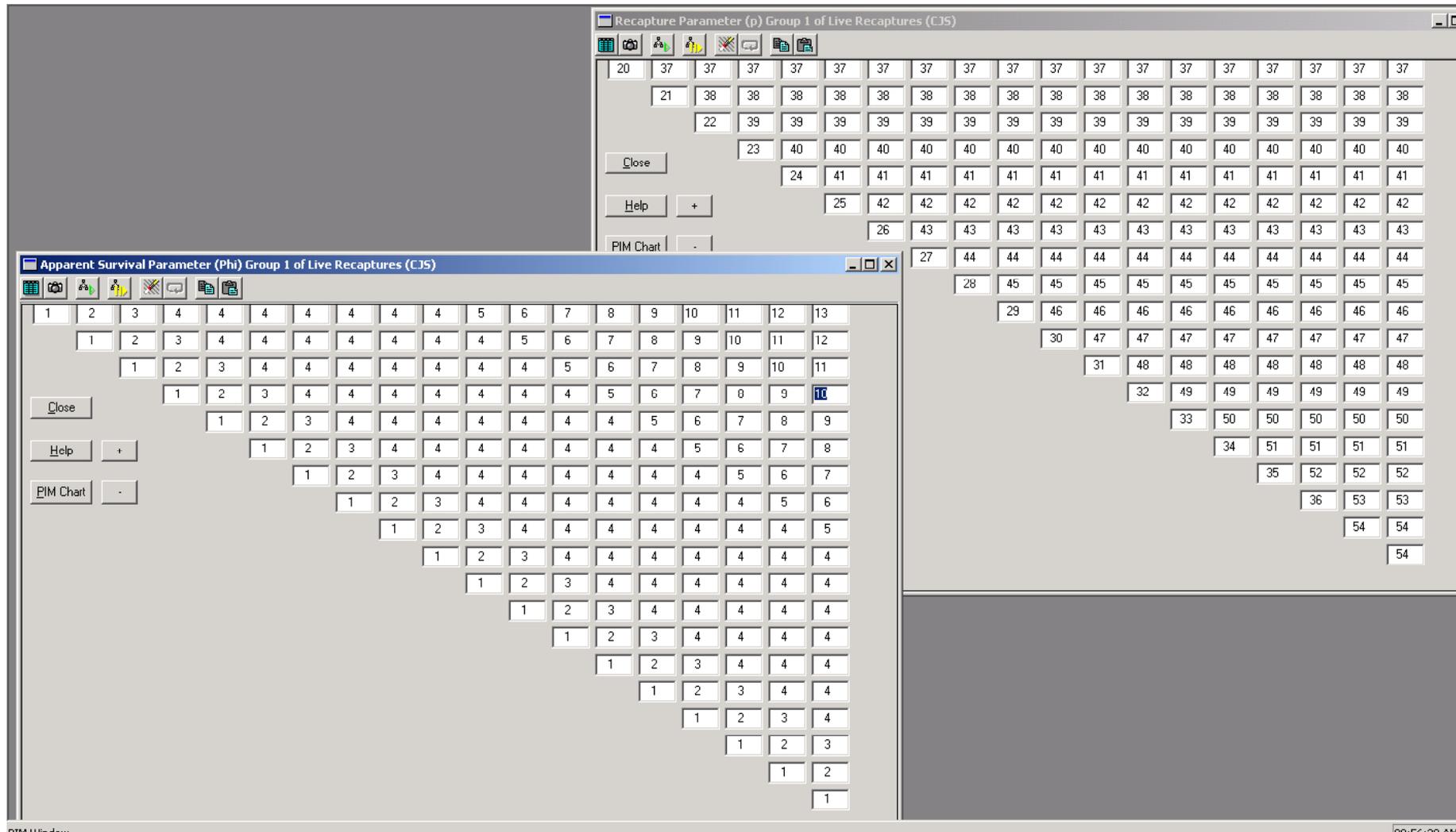


Fig. 6.2. An example of a more complex Parameter Index Matrix (PIM) setup for survival and recapture estimation of one group (e.g. sex) of animals from different cohorts over a temporal scale, within the Program MARK (White and Burnham 1999).

The approach to model construction in MARK essentially encompasses three steps (excluding additive effects/ covariate inclusive hypotheses), greatly simplified as follows (specific details in White and Burnham 1999). First, the collected data is condensed to biologically meaningful 0's (absence) and 1's (presence), to be used as input files for MARK. Secondly, the user interacts with these input files via PIMs, i.e. the parameter space for a data type is defined in the PIMs. At this stage the user structures various models by manipulating numbers in edit boxes within a matrix (Fig. 6.2), i.e. substituting a numerical indexing scheme for the individual survival and recapture (or resighting) values, respectively. Thirdly, these models are then weighted according to quality of fit and precision by way of Information Criterion, usually Akaike's, but sometimes Bayesian (Burnham and Anderson 2004). The most parsimonious model, i.e. the model that best describes the quality of fit (deviance) of the data as related to the number of estimable parameters (precision) (Lebreton et al. 1992), is then used to draw biological conclusions from. Because, the analytical steps are "hidden" within the programme some referees erroneously assume that fundamental experimental design imperfections may have been taken into consideration within these "hidden" steps. The recent advent of "online supplementary material" for journals could provide an avenue for publication of some of these previously "hidden" steps and help to alleviate this problem.

Multitudes of published works have their origin within a mark-recapture framework, but in many cases the published study was not initially envisaged to arise from the CMR data. Indeed this broad applicability is one of the fundamental strengths of CMR experiments. However, CMR experiments are not all things, to all studies all of the time and do have limitations as shown here. Thus understanding the limitations of original experimental design is crucial to effective data analyses. It is our aim here to highlight the need for researchers to think very carefully about their data and not to assume too readily that sound design for one study, albeit a study of very broad scope as is the case in CMR studies, will satisfy all the needs for a related study e.g. the quantification of tag colouration of recapture as described above. The need for careful experimental design in biological studies is clear and well established (e.g. Anderson 2001). However, strong experimental design and a solid analytical foundation do not always guarantee unbiased results in the face of user-friendly, yet sophisticated analytical software as described here. Ecologists and

wildlife managers are increasingly required to provide rapid answers and input into global ecological problems, and often answers are sought from datasets that are not specifically structured to address that specific question. A case in point is a published study by Loehle et al. (2005) that used radiotelemetry experiments for assessing survival (Franklin et al. 2006). Several MARK experts critiqued the Loehle et al. (2005) study, identifying conceptual errors of the details of the analytical procedures (Franklin et al. 2006). They therefore addressed the two issues raised here; that of conceptually opaque use of powerful analytical tools and poor research design. Given the two examples highlighted here (Loehle et al. 2005, this study) it follows that there is a likelihood of at least some of the >1400 published papers citing MARK (Fig. 6.1) containing flaws due to poor study design and/or an inadequate understanding of software/programme functionality. The latter study and our example of SES illustrates the need for researchers to consider carefully their study design prior to commencement of field work and to be visionary in how studies are designed i.e. to trawl the current state of knowledge carefully and thoroughly to identify knowledge gaps which can be addressed. Researchers also need to be cautious when using new software packages and have a responsibility to fully understand how they work before submitting work for peer review.

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CHAPTER SEVEN: **GENERAL CONCLUSION**

Synthesis

The long-term Marion Island southern elephant seal mark-recapture programme has provided an authoritative foundation for understanding the population dynamics of a long-lived marine top-predator. Extensive mark-recapture and population trend analyses over the past decade have elucidated much about the life history traits and their demographic consequences in this species. Notwithstanding these advancements, important facets of the regulation of the Marion Island population have remained contentious. Particularly, the roles of juvenile (McMahon et al. 2003, 2005) and adult female survival (Pistorius et al. 1999a, 2004, 2008a) in the recent recovery of the population from decline to increase (McMahon et al. 2009), has fuelled considerable debate. The exact timing of population trend inflexion (1994 or 1997/8) has also seen continuing debate (Pistorius et al. 1999b, 2001; Bradshaw et al. 2002; McMahon et al. 2009). The nature of the drivers of these life history parameters, and ultimate population trends, have been explored and density dependent and density independent regulating factors have been proposed (Pistorius et al. 2001, 2008b; Bradshaw et al. 2002; McMahon et al. 2009) to be important in the Marion Island population. However, given the complexity of the relationship between these intrinsic and extrinsic population regulating drivers (de Little et al. 2007), researchers must guard against oversimplification in their efforts to explain these drivers (McMahon et al. 2008). To heed such caution the need arises for holistic approaches to life history studies, whereby numerous ecological factors are explored and field methodology improvements are sought to further explicate relevant ecological parameters.

Individual body condition and its established relationship with various life history processes require methodology that allows for accurate body condition estimation. In seals the relevant measure of body condition, central to further understanding of population demography, is mass (e.g. Proffitt et al. 2007). In Chapter two the importance of body mass estimation in seal population demographic studies are acknowledged and the current challenges elucidated. Building on the foundation of photogrammetric work that has been done on seals, I aimed to

establish a photogrammetric method for body mass estimation that would be widely applicable to phocids (and potentially other vertebrates) in a range of field scenarios. By focusing attention on the substrate surrounding the seal to create a three-dimensional space within which the seal shape can then be 'built', rather than building a model based solely on features of the seal itself, a robust and widely applicable method resulted. Consequently, this novel three-dimensional photogrammetric method for estimation of body volume and mass can be implemented in areas hitherto impossible with existing weighing or photogrammetric methods. In so doing, body mass estimates of large samples of individuals over extensive study areas can now be achieved with obvious incentive to future covariate analyses in demographic studies. The field effort required to weigh seals for providing a benchmark to test the photogrammetric techniques against, highlighted some challenges associated with chemical immobilisation. While the current protocol on Marion Island is sufficient for our needs, I was interested in examining if improvements, specifically related to the recovery time experienced by immobilised seals, could be made. A prospective experimental protocol was thus structured and is presented in Appendix one.

The ability to relate the body mass of any particular individual to genetically related individuals (e.g. mother and pup) has palpable advantages in demographic research. However, to model body mass as a covariate with survival or reproductive effort as related to kin, one first needs to be able to identify appreciable numbers of related individuals over time. To address this current gap in the long-term mark-recapture experiment at Marion Island was the specific aim of Chapter three. The polygynous breeding system of southern elephant seals results in crowded breeding harems on beaches, making access to individuals difficult. Compounding the difficulty of access to individuals is the inability to identify the mothers of pups once they have weaned and moved out of crowded harems, because adult females abruptly break the maternal tie to their then weaned pups. Consequently, a repeatable procedure involving; a quick intrusion into the harem, placement of a marker on an unweaned pup, identification of the mother, and withdrawal from the harem is required. Supersmall® Dalton lamb tags proved to be the most effective marker type for use in harems smaller than 60 cows (maximum for Marion Island harems). In the testing phase of this temporary marking technique more than half of all known aged mother's

pups could be marked prior to weaning. Clearly, a continuation of this field effort over time, will provide a large sample of relatedness information applicable to cumulative studies of for example, maternal investment, inbreeding avoidance and sociality at haul-out sites.

Methodological advances within a mammalian mark-recapture framework (Chapters two and three) are unfortunately initially constrained by the lag-time involved in accumulating sufficient temporal samples. The opportunities for such advancements would however not have been highlighted, had there not existed a long-term dataset that could be built upon. Therefore, the 25-year longitudinal mark-resighting southern elephant seal dataset at Marion Island remains extremely valuable for demographic studies even without these latest accompaniments. In Chapter four this dataset is used to assess the survivorship schedule of elephant seals at this locality to extend upon the 15-year mark-recapture dataset used by Pistorius et al. (1999a). In Appendix two, we addressed tag-loss for the entire 25-year mark-recapture experiment, for correction of survival estimates presented in Chapters four and five. A comparable approach to the Pistorius et al. (1999a) study was adopted in Chapter four, given the pivotal role that study played in the subsequent demographic discussion of this population of seals, and for re-assessment of the survivorship conclusions drawn from that study. The Pistorius et al. (1999a) study did not, however, correctly address the extra-binomial variation observed in the data, although this possibly would not have altered the conclusions drawn there. However, in Chapter four, extra-binomial variation in the current dataset was too large to ignore and was thus adjusted as a parallel analysis to the unadjusted analysis. These overdispersed results indicated departures of the data from particularly the “recapture homogeneity” assumption. This finding initiated discussion of the hitherto assumed “negligible” migration of elephant seals into and out of this population, both temporarily and permanently. Notwithstanding this extra-binomial variation in the data for most cohorts, meaningful survival estimates could be gleaned from program MARK. Blurred distinction in categorisation of age-classes and demographic terminology seems to have augmented some of the contention related to earlier findings for this population. The additional 10 years of marking and resighting data used here elucidated the relative importance of juvenile and adult female survival in regulation of this population. A comparative increase in juvenile

survival appears to have preceded an increase in adult female survival, lending support to the McMahon et al. (2003, 2005) contention that this sector was important in the population recovery. However, this change in survivorship appeared to be centred around three-year olds (a proportion of which pup every year – Bester and Wilkinson 1994) that were classified as adult females by Pistorius et al. (1999a, 2004, 2008a), but as part of the juvenile age-group according to McMahon et al. (2003, 2005). Similarly, an apparent 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 (1st, 2nd and 3rd year age-classes) around 1994 related to increased survival (thus breeding potential) of 4th, 5th and 6th year adult females around 1998. Notwithstanding the important findings reported, a multistate modelling approach with an ‘unobservable’ state should be considered to further clarify survivorship findings. The addition of environmental covariates in model design would further improve our knowledge of regulation in this population. In particular, seal movement (and survival) relationships with Southern Oscillation Index, Antarctic circumpolar waves, frontal system shifts and pack ice extent, among others, could enhance our understanding of the importance of extrinsic population drivers. While not within the scope of this thesis, the findings gleaned here can improve future assessments of southern elephant seal biology and indeed general mammalian population ecology in establishing the relative importance of environmental and biological covariates on these populations. A hasty leap into assessments of the importance of environmental covariates in population regulation, without a clear understanding of fundamental life-history parameters in the context of the relevant population/species is risky. Unless hypotheses regarding the fundamental biological traits of the species are quantitatively assessed, erroneous assumptions could become entrained in the published literature and in time are accepted as truth, as illustrated in Chapter five.

In Chapter five, attention was directed at the adult female sector of the population to gain a clearer understanding of the potential influence of longevity, fertility and senescence on population demography. Predicted longevity estimates of adult females based on survival estimates gleaned from Chapter four, indicated that a far greater number of post 20-year old individuals should persist than has been observed. This is likely a function of the large number of young animals from the

increasing post 1994 period of the population included in the estimates, and it remains to be seen if such a large number of very old individuals will persist within the next decade if the population trend remains relatively stable. The commonly preferred state-dependent modelling approach was used to investigate senescence. Analogous with the Pistorius and Bester (2002) study, there was no evidence for actuarial senescence in this population of southern elephant seals, despite a much larger sample of aged individuals. Contrary to the previous study's findings however, reproductive senescence was evident in post 12-year old individuals. Additionally, females primiparous at age three indicated reduced breeding success later in life compared with four- and five-year old primiparous individuals. This suggests that while survivorship of young adult females (3-, 4- and 5-year-olds) may have increased (Chapter four), allowing a greater absolute number of females to breed (thereby augmenting population growth) these animals reduce their breeding efforts in later life and those that became primiparous at age three even more so. The "prudent parent" hypothesis predicts that a female will invest somatically before investing in offspring, and this seems to apply to southern elephant seals, with significant implications on population growth as compared to per capita foraging pressure. Contrary to assumptions hitherto expressed, southern elephant seals do not generally breed every year after primiparity and this is unrelated to age at primiparity. Conclusions of numerous previous papers have in part rested upon some of these assumptions and will need re-evaluation.

The complexity in identification of the drivers of elephant seal population regulation necessitates extensive research questions based on various facets of seal ecology. In light thereof, the resident Marion Island killer whale population has been identified as a potentially important top-down driver of the southern elephant seal population. However, very little is known about this population of killer whales and no work has been done on their sociality and the importance of their prey preferences on this social organisation. We thus initiated a fundamental sociality study to launch subsequent studies of prey preference, temporal and spatial predation rates and killer whale population dynamics. The preliminary results pertaining to the sociality of killer whales here (Appendix 3) will hopefully initiate studies to address the relative importance of killer whales as drivers of elephant seal populations.

Chapter six was in fact intended as an antecedent to chapters four, five and Appendix two in the analytical process. Initially, I attempted to establish if confusion in identification of markers attached to different cohorts of elephant seals was evident in this mark-recapture programme. However, during the process of analyses, further literature perusal and in the course of professional discussions it became evident that the analyses were confounded to address this research question. I considered the intricacies of the analytical procedure and realised that my unfortunate lack of prescience may in fact serve as a cautionary discussion for ecologists as users of complex analytical software. This Chapter can therefore be seen as the “Ph” in “PhD”. The recognition of appropriate experimental design in mark-recapture experiments in the face of sophisticated software packages is illustrated. Meticulous perusal of available literature and careful thought of the available data and the software to be used is discussed.

This entire thesis has been structured with the additional purpose of illuminating potential future research directions in life history studies and population demographic research.

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Appendix I:
PROTOCOL FOR FUTURE DRUG EXPERIMENTATION DURING
IMMOBILISATION OF SOUTHERN ELEPHANT SEALS AT MARION
ISLAND

PJN de Bruyn & MN Bester

Introduction

Many aspects of wildlife research require intensive work that necessitates physical contact with the study animals. These animals are thus often restrained through the use of certain immobilizing chemical compounds. Chemical restraint of any wild animal should be dependent on a drug or drug combination that adheres to the following principles, namely, potency (drug volume needs to be kept low), rapid induction, safety for the animal, minimum of side effects and is reversible (Meltzer et al. 2004). The difficulties with finding such a drug for any one species are numerous in that the drugs themselves vary in efficacy and effect, the species that are targeted may respond differently to each drug, and each species differs in their response to each drug. It is therefore necessary to investigate/test different drugs and drug combinations for each species, in order to identify the best form of chemical immobilization for the wellbeing of the study animal.

Pinnipeds are one such group of wild animals where researchers require the use of chemical compounds to immobilize their study animals for either superficial, non-painful work (such as attachment of tags) or more intrusive, often painful work (such as surgery) (Lynch et al. 1999). Some research has been done to test the adequacy of various drugs for use with numerous pinniped species (Gales 1989). One species that has enjoyed a large amount of interdisciplinary scientific treatment is the southern elephant seal (*Mirounga leonina*). A great deal of research has in recent years been aimed at demographic aspects of the southern elephant seal populations throughout the Southern Ocean. At Marion Island (as with many other locations), the focus has in particular been on changes in population sizes (Bester and Wilkinson 1994; Pistorius et al. 1999a), and causal factors

contributing to these changes, both proximate and ultimate (Bester and Wilkinson 1994; Pistorius et al. 1999b). The Marion Island elephant seal population has declined by 83% since 1951 (Laws 1994) and by 37.2% between 1986 and 1994 at an annual rate of change of 5.8%, which was linear over the period (Pistorius et al. 1999a). Pistorius et al. (1999b) suggested low adult female survival due to food limitation, to be the proximate cause of the decline in the Marion Island population. In order to investigate these and other questions, seals often need to be weighed (see Chapter 2 – de Bruyn et al. 2009) at various ages, satellite or other tracking devices deployed on the animals, or dietary or physiological studies need to be done. Since these animals are large and potentially dangerous research subjects, such studies require the seals to be immobilized and/or anaesthetised temporarily. McMahon et al. (2005, 2008) showed that such handling and intensive research does not affect either short or long-term survival of elephant seals.

Elephant seals of all ages have been routinely immobilized in the past (Gales 1989). Several experimental procedures have been conducted to assess the usefulness of various drugs for southern elephant seal immobilization, sedation, anaesthesia, and mitigation and reversal of side effects while the animal is drugged (e.g. Ling and Nicholls 1963; Gales and Burton 1987; Bester 1988; Erickson and Bester 1993; Woods et al. 1994, 1995, 1996a, 1996b; Ramdohr et al. 2001; Field et al. 2002). Ketamine-hydrochloride appears to have been among the more successful drugs for the immobilization of southern elephant seals for a number of decades (Ryding 1982; Gales 1989; Woods et al. 1996a). The primary difficulty with the use of ketamine is that this drug is irreversible. This can be potentially problematic for two main reasons where seals are concerned, 1) the animal may return to the sea before induction takes place and can then become immobile in the water, 2) seals are adapted physiologically to live in extreme environments (Kooyman et al. 1981) and when sedated/immobilized often suffer side effects such as apnoea or hypothermia (Gales 1989; Woods et al. 1994) which, if any particular case is severe under the influence of ketamine, cannot be treated by reversal. Most workers have attempted to circumvent this problem by

combining the “knockdown” properties of ketamine with reversible sedatives such as diazepam, midazolam and xylazine (Gales and Burton 1987; Woods et al. 1994, 1995). The α -2 adrenergic receptor agonist, medetomidine, has only been tested once to our knowledge on 12 adult female southern elephant seals (Woods et al. 1996) although the ketamine-medetomidine cocktail has been extensively and successfully used on terrestrial herbivores (e.g. reindeer; Ryeng et al. 2001), carnivores (e.g. mink, Arnemo and Sølvi 1992) and primates (e.g. red howler monkeys, Vié et al. 1998). Other drugs such as tiletamine and zolazepam have been used with success and are preferred over ketamine by some, particularly with intravenous administering (Woods et al. 1994; McMahon et al. 2000). Opioid drugs have been tested for elephant seal immobilization and have rendered erratic results (Ramdohr et al. 2001), however, a key benefit (when the results are not erratic) in using these drugs is their fast induction and complete and quick reversal, both properties treasured by wildlife biologists in the field. Neuromuscular blockers such as succinylcholine chloride proved to have fatal consequences when used to immobilise some southern elephant seals (Ling et al. 1967).

Aims and Objectives

At present we use only ketamine on Marion Island with no added sedatives and while results have been consistent, our aims in this study are particularly focussed on finding at least partially reversible alternatives:

- 1) Combine the α -2 agonist medetomidine and the opioid antagonist butorphanol with ketamine at various ratios, increasing the medetomidine/butorphanol to appropriate levels in order to minimise reversal time using atipamezol while still attaining adequate immobilization for non-painful work. The medetomidine/ketamine cocktail has been used on adult female southern elephant seals but some problems of vomiting and respiratory depression were seen (Woods et al. 1995). The addition of butorphanol to this mixture has shown a decreased tendency for vomiting and respiratory depression in other species (e.g. red wolves, Larsen et al. 2002).
- 2) Assess the usefulness of the opioid drug, thiafentanil (A3080), for the immobilization of elephant seals. The small volume and fast induction

of this drug, and complete reversal with naltrexone may provide a suitable method of immobilization. This relatively new drug has rendered good results in the few tests done on terrestrial species (e.g. nyala antelope, Cooper et al. 2005). This drug has not been tested on any pinnipeds to our knowledge although related morphine derivatives such as etorphine have delivered variable results (Ramdohr et al. 2001).

- 3) Determine the efficacy of intramuscular administering of nalorphine or naltrexone after ketamine immobilization to test for any reversal effect, since recent work with terrestrial animals have given indications of limited reversal of cyclohexylamines by these opioid antagonists (pers. comm. D. Meltzer). Concurrently to test if these drugs assist in alleviation of respiratory depression if administered intramuscularly, intravenously or sublingually. The more commonly used respiratory stimulant doxapram has been shown to have limited, or no effect in alleviating apnoea in southern elephant seals although it did speed recovery times after ketamine immobilisation (Woods et al. 1996b).

Materials and Methods

The study area

Southern elephant seals will be primarily immobilized for purposes of weighing and deployment of satellite and other tracking devices, mostly along the eastern coast of sub-Antarctic Marion Island (46°54'S, 37°45'E) (Fig. 1.2 in Chapter 1). It is primarily during these sessions that the drug effects will be tested.

Field techniques and Data collection

The desired dose will be administered intramuscularly in the dorsal hip area using a handheld syringe or a modified version of the remote injection method (tubing between needle and syringe [Bester 1988 as described by Ryding 1982]). A 100-150 mm, 13–18 gauge needle with sealed tip and lateral hole will be used for injection. Where seals are logistically impossible to weigh, masses will be estimated using the photogrammetric technique initially developed in this thesis (see Chapter 2 – de Bruyn et al. 2009).

Accurate morphological measurements of standard length and maximum girth length will be taken.

An attempt will be made to sample at least 10 different animals per aimed experiment (see Aims and Objectives section - this Appendix) (i.e. total $n \geq 30$). An effort will be made to obtain an even representation of sex – and age classes of seals for the experiments. Each experiment will require certain monitoring procedures to ascertain the response to each drug dose/mixture. The responses monitored will include heart rate, respiratory rate, head response, palpebral response, fore-flipper withdrawal response, hind-flipper response and if possible rectal temperature. If possible a pulse-oximeter will be attached to the immobilized animals' tongue to detect changes in blood oxygen saturation and pressure/pulse. The level of anaesthesia/sedation will be scored according to the eight-point scale developed by McMahon et al. (2000) or the six-point scale developed by Woods et al. (1996) at constant time intervals. The dosages utilized will depend upon initial visual pre-anaesthetic assessment, but will follow the guidelines documented by other authors as far as possible. Where tests on variable doses of the same drug/drug mixtures are to be performed, an effort will be made to keep age – and sex variables as constant as possible. Animals that are visibly excited, injured or in poor condition will not be included in the experiments.

For objective 1:

A small sample of animals will initially be immobilised with only ketamine (2-4 mg/kg) as a control procedure. Thereafter initial drug doses will follow Woods et al. (1996) for ketamine (1.5-2.0 mg/kg) in combination with medetomidine (0.01-0.027 mg/kg). Butorphanol will be added to this mixture at similar doses to medetomidine, i.e. 1:1. Atipamezole will be administered at approximately 0.4 mg/kg to reverse the medetomidine. The total dose of medetomidine will not exceed 10 mg/animal (possibly excluding very large bulls) as this has been shown to cause severe heart rate depression and apnoea in adult females (Woods et al. 1996). Further experiments will follow whence the dose of medetomidine and butorphanol will increase while the dose of ketamine decreases, in order to evaluate whether higher doses of the

reversible drug medetomidine could attain adequate immobilisation for non-painful work.

For objective 2:

The dosages of etorphine used by Ramdohr et al. (2001) will allow a guideline of initial doses of thiafentanil since the two drugs have similar potency (1 : 1.5 – etorphine : thiafentanil) although the induction time of the latter is shorter (Meltzer et al. 2004). Therefore our initial dose of thiafentanil will be at approximately 0.0009 mg/kg and reversal with naltrexone at 25-40 times the total thiafentanil dose.

For objective 3:

Initial ketamine doses will vary between 2-5 mg/kg in order to attain heavy immobilization (score = 5, Woods et al. 1996). Thereafter the naltrexone/naloxone will be administered at doses ranging from 0.01 to 0.02 mg/kg (naloxone) and 0.05 to 0.15 mg/kg (naltrexone), but keeping the dose and frequency of administration constant per individual to assess recovery time and level accurately (Higgins et al. 2002).

In so doing, we intend to provide data that could alleviate the constraints imposed by the non-reversible use of ketamine-hydrochloride in isolation.

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Appendix II:
**COHORT AND TAG-SITE SPECIFIC TAG-LOSS RATES IN MARK-
RECAPTURE STUDIES: A SOUTHERN ELEPHANT SEAL CAUTIONARY
CASE**

WC Oosthuizen, PJN de Bruyn, MN Bester & M Girondot

Abstract

Marker-loss is a common feature of mark-recapture studies and important as it may bias parameter estimation. A slight alteration in tag-site of double tagged southern elephant seals (*Mirounga leonina*) marked at Marion Island from 1983 – 2005 in an ongoing mark-recapture program, had important consequences for tag-loss. We calculated age-specific tag-retention rates and cumulative tag-retention probabilities using a maximum likelihood model selection approach in the software application TAG_LOSS 3.2.0. Under the tag-loss independence assumption, double tag-loss of inner interdigital webbing tags (IIT; 17 cohorts) remained below 1% in the first 5 years and increased monotonically as seals aged, with higher tag-loss in males. Lifetime cumulative IIT tag-loss was 11.9 % for females and 18.4 % for males, and equivalent for all cohorts. Changing the tag-site to the outer interdigital webbing (OIT; 6 cohorts) resulted in increased and cohort dependent tag-loss, although the variation (mean \pm 95% CI) in cumulative tag-loss probabilities never exceeded 5.3% between cohorts at similar age. Although different studies may homogenize techniques, we advocate the importance of dataset-specific assessment of tag-loss rates to ensure greatest confidence in population parameters obtained from mark-recapture experiments. Permanent marking should be implemented where feasible.

Introduction

Mark-recapture studies are frequently used by ecologists and wildlife managers to estimate demographic parameters of wildlife populations. These parameters provide insight into population processes and allow implementation of appropriate management policies. Mark-recapture data analyses have largely been based on Cormack-Jolly-Seber (CJS) parameterizations (Lebreton et al. 1992). However, violations of the

assumptions of the CJS model can severely bias parameter estimates (Arnason and Mills 1981; McDonald et al. 2003). Fundamental assumptions are that marks do not affect future survival, are not lost or missed during resights (Seber 1982), and are correctly identified (Stevick et al. 2001). However, these assumptions are potentially violated by many marking techniques and may be inherent to all long term tagging regimes. Marker-loss and marker-induced mortality result in population size overestimates through negatively biased survival rates, since individuals that have lost their marks cannot be identified anymore and appear 'dead' to the observer (Arnason and Mills 1981; Pollock et al. 1990; McDonald et al. 2003). Additionally, if recaptured, such individuals appear to be immigrants, biasing recruitment rates upward (Cowen and Schwarz 2006). Time or group dependent marker-loss may additionally result in non-uniform biases in survival estimates through heterogeneous recapture probabilities among groups or over time (Pollock et al. 2001). Therefore, knowledge of violations of fundamental assumptions such as marker-loss is crucial to obtain robust information of life-history data that allows informed decision making (McMahon and White 2009).

The extensive use of non-permanent markers to identify individuals in mark–recapture studies for investigations of life-history, demographics, dispersal, growth and behavior makes estimation of marker-loss rates widely applicable to numerous ecological research disciplines and wildlife authorities across a wide range of species. An increasing number of studies incorporate quantitative estimates of marker-loss rates in conjunction with analytical advances in this field (Barrowman and Meyers 1996; Conn et al. 2004; Cowen and Schwarz 2006). These include tag-loss in invertebrates (Kneib and Huggler 2001), terrestrial and marine vertebrates, (Stobo and Horne 1994; Diefenbach and Alt 1998; Adam and Kirkwood 2001; Casale et al. 2007) and neckband failure (Johnson et al. 1995) and band loss in birds (Spendelov et al. 1994). Marker-loss is usually estimated by double marking individuals and approximating marker-loss by following subjects through time and noting whether one or two marks are retained. In the absence of a permanent mark (in addition to the two temporary markers), marker-loss independence is

assumed, where the probability of losing the second marker is independent of the probability of losing the first marker. This assumption is difficult to test because permanent marking is not easily accomplished. However, in cases where permanent marks facilitated assessment of the assumption, assuming independence has been shown to underestimate tag-loss (e.g., Diefenbach and Alt 1998; Bradshaw et al. 2000; McMahon and White 2009). However, aside from the potential errors associated with the independence assumption, researchers should attempt to quantify inconsistent marker-loss over time or variation therein between groups of marked animals (Spendelow et al. 1994). Failure to account for marker-loss differences between juveniles and adults for example, may lead to erroneous conclusions about the importance of juvenile and adult survival as population growth determinants. Similarly, a false indication of processes such as density dependent survival may be indicated when marker-loss differs according to the population density, physical environment or tagger proficiency at specific colonies or study sites.

Many pinniped species are ideal mark-recapture study subjects due to their ubiquitous terrestrial phases, generally high site fidelity and thus their temporal and spatial accessibility to researchers. Individuals are usually marked by double tagging in the connective tissue of the interdigital webbing of each hind flipper in true seals (Phocidae) or in the trailing edge of both front flippers in fur seals and sea lions (Otariidae) (Erickson et al. 1993). However, in contrast to permanent markings such as branding or tattoos, tag-loss can be substantial (e.g., Stobo and Horne 1994; McMahon and White 2009) and if left uncorrected may severely bias survival estimates. On sub-Antarctic Marion Island (46°54'S, 37°45'E), southern elephant seals *Mirounga leonina* L. have been subject to a 25-year (1983 – 2008) ongoing mark-recapture study. The mark-recapture program forms the foundation of investigations into life-history, demography, dispersal and philopatry of southern elephant seals at Marion Island (e.g., Bester 1989; Pistorius et al. 1999, 2004; Kirkman et al. 2003, 2004; McMahon and Burton 2005; McMahon et al. 2005). Two previous studies have estimated tag-loss for this population, to incorporate tag-loss adjustments into demographic data. Wilkinson and Bester (1997) used a ratio method to calculate tag-loss over the period 1983 to 1990 and Pistorius et al.

(2000) improved on this method, estimating linear tag-loss (1983 – 1993) based on the time at liberty of tagged seals in a maximum likelihood framework. Age and sex specific tag-loss rates from Pistorius et al. (2000) were subsequently used to correct mark-recapture survival estimates of southern elephant seals at Marion Island.

The physical placement of markers can be central to the accuracy of estimates gained from mark-recapture experiments. Incorrect tag placement can result in increased mortality (Kneib and Huggler 2001) or reduced apparent survival as a consequence of increased tag-loss. Tag placement has nonetheless received limited attention in studies beyond fisheries management (e.g., Brennan et al. 2007). Limpus (1992), however, evaluated tag placement in turtles, where tag-loss was higher in the more distal tagging positions on the front flipper. The hind flipper tag-site used to mark elephant seals at Marion Island changed in 2000 from the inner interdigital webbing (between digits two and three or three and four; 1983 – 1999) to the upper, outer interdigital webbing of the hind flippers (between digits one and two; 2000 – 2008). The tag-site adjustment aimed at improving tag visibility for resighting, because the tags placed in the inner interdigital webbing are often obscured by the flipper digits when animals are hauled out on land (WCO, PJNdB, MNB personal obs.). The effect of tag-site on tag-loss has not been quantified here or directly for other pinnipeds and such an adjustment may have important consequences for demographic analyses.

We estimate and compare tag-loss rates for 17 cohorts of southern elephant seals double tagged in the inner interdigital webbing (inner interdigital tags: IIT), and six cohorts double tagged in the upper, outer interdigital webbing (outer interdigital tags: OIT). Variation in tag-loss due to seal age and sex, tagging protocol (tag-site, i.e., IIT and OIT) and tagging proficiency by different personnel (resulting in cohort specific tag-loss rates) are considered.

Methods

Mark-resight framework

Data from cohorts of southern elephant seals born on Marion Island from 1983 - 2005 and resighted up to April 2008 were used. During each breeding season, virtually all recently weaned southern elephant seal pups born on Marion Island were sexed and double tagged in the interdigital webbing of the hind flippers with identical, uniquely numbered, color-coded plastic Dal 008 Jumbotags[®] (Dalton Supplies Ltd., Henley-on-Thames, United Kingdom). These two-piece self-piercing tags are applied with an applicator, and have favorable retention rates as compared to other tag types (Testa and Rothery 1992). The male component of all tags was positioned on the outer surface of the flipper (i.e., the point of this component protrudes from the inner surface). From 1983 to 1999 tags were applied to the center of either of the two inner sections of interdigital webbing of the hind flipper (webbing between digits two and three or three and four; IIT). From 2000 – 2005, tags were applied to the center of the upper interdigital webbing of the hind flipper (between the first and second digit; OIT). At tagging, one third of the tag extended past the trailing edge of the interdigital webbing. During all years tags were applied by two dedicated field personnel, all of whom were trained by MNB (except from 1986 to 1988 when up to six pairs of trained field personnel tagged pups). Further details regarding the tagging procedure appear in Wilkinson and Bester (1997) and Chapter 3 (de Bruyn et al. 2008).

During the entire study period (1983 - 2008), the resighting effort remained constant and included all beaches along a 51.9km coastline where southern elephant seals can haul out, except during the early period (1983 - 1988) when no resights were made during winter (mid-April – mid-August). During the molting and winter periods (mid-November - mid-August), all beaches were searched for tagged seals every ten days, but in the breeding season (mid-August – mid-November) this was done on a seven-day cycle to allow for increased seal numbers and harem density. For every tagged seal that was resighted, the date and locality of the sighting, tag color combination and three-digit number, number of tags remaining (one or two), and the sex of the seal (if identified) were recorded. We assume similar and accurate resight

rates of single and double tags owing to the high and constant resight effort by trained personnel on Marion Island, where both flippers of each animal was always inspected for the presence of tags. This was done to prevent different reporting rates for single or double tags which may bias estimates (Adam and Kirkwood 2001). The haulout pattern of elephant seals (Kirkman et al. 2003, 2004) allowed for confirmation of recorded tag data with subsequent resights, often several times over a season. Shed tags were not replaced.

Estimation of tag-loss

We estimated tag-loss using a maximum likelihood method for individually identifiable mark-resight study subjects in the software application TAG_LOSS (Version 3.2.0; http://www.esu.u-psud.fr/epc/conservation/Tag_Loss/Tag_Loss.html) as presented by Rivalan et al. (2005). This program provides quasi-continuous tag-loss probabilities and incorporates assessment of different trends in tag-loss rates over time. Quasi-continuous tag-loss probabilities based on exact time at liberty remove bias associated with pooled observations (Xiao 1996; Diefenbach and Alt 1998). Model functions described the time-dependent daily probability of tag-loss $p(t)$ (see Rivalan et al. 2005). Model selection was based on Akaike's Information Criteria (AIC), where the model with the smallest AIC value provided the most parsimonious fit (Burnham and Anderson 1998). AIC weights (w_i) provided the relative support for each model. Pups initially tagged with only one tag, seals of unknown sex and pups double tagged, but never resighted, were excluded from analyses. Tagged seals that were not resighted most likely died during their first pelagic foraging trip (60 – 65% first year mortality; McMahon et al. 1999; Pistorius and Bester 2002) or emigrated from the study area (Bester 1989; MNB unpublished data). Double tag-loss within the first year is suggested to be minimal (see Results and Discussion).

The annual haulout cycle of elephant seals, combined with the continuous high resight effort in the current study permits calculation of reliable estimates of tag time at liberty, in contrast to studies where few resights are possible (e.g., leatherback sea turtles *Dermodochelys coriacea*, Rivalan et al. [2005] and loggerhead sea turtles *Caretta caretta*, Casale et al.

[2007]). We constructed individual capture histories for all individuals tagged on day zero (at weaning), and subsequently resighted ($n = 7849$, cohort range $n = 228 - 479$). Three sets of capture histories were considered, following Rivalan et al. (2005): (1) The individual was resighted with two tags intact for the duration of its presence in the study, to estimate the minimum number of days without tag-loss (N_{22} ; $n = 6786$). (2) We initially observed the individual with two remaining tags (N_{22}), but subsequently with only one tag intact (N_{21}). This capture history calculates both the minimum number of days without tag-loss (N_{22}) and the interval length (mean = 212 days) during which one tag was lost (N_{21} ; $n = 952$). (3) Subsequent to double tagging, we only observed the individual with one tag intact for the duration of its presence in the study (N_{21} ; $n = 111$). Because permanent marks were absent, we could not reliably identify animals that had lost both tags (N_{20} or N_{10} ; known $n = 10$), and therefore did not consider such cases. This necessitated the assumption of tag-loss independence, where the probability of losing one tag did not affect the probability of losing the second tag.

We tested three different trends in daily tag-loss over time: constant rate, monotonic increase/decrease and a two-step function (e.g., rapid initial tag-loss, followed by a decreased continuous loss pattern and then a further increase or decrease with varying slope; this function can adjust to many different daily tag-loss rate modalities over time). Tag-loss patterns were assessed separately for each sex and cohort and also for cohorts and sexes pooled over time. We used the best fitting trend to test for a sex, cohort and tag-site effect on tag-loss. For the sex and cohort variables, we compared the AIC model fit for separate sex/cohort models, compared to a single model grouping sexes/cohorts. Constructing models that separated IIT and OIT and subsequently evaluating model fit assessed tag-site variability. TAG_LOSS 3.2.0 converted parameter estimates from the best model to daily tag-loss probabilities, age-specific tag-loss probabilities and cumulative tag-loss rates (Rivalan et al. 2005). Age-specific tag-loss is the conditional probability that a tag is lost during one year among the tags that were still present at the beginning of that year. Standard errors of parameters were calculated by the square-root of the inverse of the Fisher information matrix (Abt and Welch

1998). The proportion of animals retaining at least one tag is presented as identification probabilities (1 - cumulative tag-loss probability). Identification probabilities therefore represent the proportion of individuals still identifiable (retaining either one or two tag/s) for each age group.

Results

Tag-loss was best described by a monotonic increase of tag-loss rate with time for both male and female groups (AIC w_i (monotonic) = 1) (Table 1). Although several cohorts showed support for the constant model or two-step function, few of these cohorts showed substantial support against the monotonic increasing model. Males from cohort 17 deviated most from the monotonic trend (Δ AIC = 17.01), while only one other cohort (cohort 10 females) with a Δ AIC value > 4 (Δ AIC = 7.95) indicated some support for an alternate model. Both these groups received support for the two-step function model, indicating initial high tag-loss soon after tagging, but leveling off over time.

Tag-site had a significant effect on tag-loss rates, with cohort and sex differences in tag-loss also dependent on the tag-site. Tag-loss did not differ between cohorts with IIT, and the model with a general estimate calculated over all 17 cohorts received the most AIC support (Table 2). In contrast, strong support for variable tag-loss rate between cohorts was found for OIT (cohorts grouped, Δ AIC_{18 - 23} = 190.03) (Fig. 1). Cohort dependent OIT tag-loss was not unexpected, as field observations indicated that cohort 23 showed uncharacteristically high initial tag-loss associated with suboptimal (shallow - tag extends more than one third past the trailing edge of the flipper webbing) tagging. In addition, we suspected that cohorts 19 and 20 might show different tag-loss rates that could lead to inter-cohort variation as these tags were sometimes tagged too deep (tag not extending by one third past the trailing edge of the flipper webbing). We subsequently removed cohorts 19, 20 and 23 from the OIT model, to test whether cohort variability existed among the remaining three cohorts. Cohort specific variability persisted (cohorts grouped Δ AIC_{18, 21, 22} = 59.34, cohorts separate Δ AIC = 0), and we continued analyses considering all OIT cohorts separately. Separate sex models, with

increased tag-loss in males, improved model fit for IIT (Table 3). Conversely, a single model for males and females combined was sufficient to describe tag-loss for OIT cohorts.

Table 1. Model selection results for tests of southern elephant seal tag-loss trend over time, at Marion Island.

Cohort	Tag-site	Males				Females			
		Model of change of tag-loss rate				Model of change of tag-loss rate			
		Constant	Monotonic	direction	2 steps	Constant	Monotonic	direction	2 steps
1	IIT	119.52	112.51	+	116.50	171.85	169.18	+	173.17
2	IIT	120.48	117.53	+	121.41	200.60	201.12	+	205.12
3	IIT	278.71	273.20	+	277.20	300.49	291.10	+	295.10
4	IIT	170.28	173.42	-	177.44	257.17	254.50	+	258.50
5	IIT	227.20	224.72	+	228.70	221.33	216.38	+	219.98
6	IIT	245.02	237.28	+	240.87	258.25	256.04	+	259.28
7	IIT	258.11	257.76	+	261.74	247.33	251.28	+	255.26
8	IIT	239.07	234.04	+	238.04	229.30	230.17	+	234.16
9	IIT	214.48	213.38	+	217.38	327.08	322.64	+	326.64
10	IIT	222.12	220.40	-	219.05^a	400.89	404.89	=	396.93^b
11	IIT	248.59	248.45	+	252.38	288.61	285.10	+	284.12
12	IIT	134.55	134.05	+	138.05	278.11	277.29	+	280.93
13	IIT	153.06	155.56	+	156.82	177.04	175.69	+	179.17
14	IIT	162.68	158.19	+	156.42^b	378.33	367.55	+	371.54
15	IIT	219.67	199.89	+	203.88	215.89	205.05	+	209.05
16	IIT	175.11	178.12	+	181.36	318.64	319.25	+	323.20
17	IIT	167.68	171.69	=	154.68^a	210.59	205.46	-	202.98^c
18	OIT	224.71	199.69	+	203.69	243.94	218.45	+	221.40
19	OIT	189.52	180.91	+	184.91	305.19	289.70	+	293.70
20	OIT	268.39	265.37	+	269.37	324.18	325.70	+	328.43
21	OIT	345.78	339.70	+	343.70	483.32	486.05	+	490.04
22	OIT	89.64	90.72	+	93.55	167.01	169.35	+	171.97
23	OIT	378.02	378.56	-	381.46	393.78	397.78	-	401.28
Total AIC		4852.39	4765.10		4818.59	6398.92	6319.70		6381.97
Δ AIC		87.25	0.00		53.45	79.22	0.00		62.27
AIC w_i		0.00	1.00		0.00	0.00	1.00		0.00

^a High rate just after tagging and it becomes null after 1500 days

^b High rate just after tagging

^c Rate becomes null after 2000 days

Age-specific tag-loss rates (Fig. 1) were derived for cohorts 1 – 17 (IIT; grouped), and cohorts 18 – 23 (OIT; separately). IIT showed low initial tag-loss rates that increased monotonically over time. Age-specific tag-loss of adult females followed a slight convex curve, with tag-loss increasing at a low rate for adult females above age five. Cumulative IIT tag-loss rates (double tag-loss; Fig. 2) were less than 1% up to age five for both sexes. Tag-loss in males increased more as they aged when compared with females, although older age classes are represented by fewer males than females (e.g., 13 males and 106 females above age 12), leading to greater confidence in female retention rates to this age. Near the maximum life expectancy, close to 81% of males, and 88% of females were expected to remain identifiable under the tag-loss independence assumption. Age-specific tag-loss rates for OIT were generally higher than those of IIT and predominantly increased over time, apart from cohort 23 in which tag-loss declined after high initial loss. Cumulative tag-loss rates increased from cohort 18 to 23 (Fig. 2), with the exception of cohort 22 (cumulative tag-loss cohort 18 < 19 < 22 < 20 < 21 < 23), *i.e.*, apart from cohort 22, tag-loss increased as resight time decreased. The variation in cumulative tag-loss rates between individual OIT cohorts and between grouped OIT and grouped IIT cohorts was relatively small, despite model-supported separation. The maximum difference observed between IIT and OIT cohorts was for cohort 23, indicating a 5.2% lower identification probability at age 2 as compared to cohorts with IIT. When cohort 23 was not considered, OIT inter-cohort variation did not differ by more than 0.16% \pm 0.16 (mean \pm 95%CI) for ages 0-2. Cohort variation for OIT increased as animals aged (age 3-7), but 95% confidence intervals never spanned more than 5.3% for any age (Fig. 3).

Table 2. Model performance based on AIC for cohort dependent and independent tag-loss rates in southern elephant seals at Marion Island.

Cohort grouping	Males	Δ AIC	AIC w_i
1,...,23	4765.14	25.59	0.00
1-17, 18,...,23	4739.55	0.00	1.00
1,...,17, 18-23	4860.33	120.78	0.00
1-17, 18-23	4834.75	95.19	0.00
1-23	4910.24	170.68	0.00

Cohort grouping	Females	Δ AIC	AIC w_i
1,...,23	6319.70	0.00	0.93
1-17, 18,...,23	6324.90	5.19	0.07
1,...,17, 18-23	6421.61	101.91	0.00
1-17, 18-23	6426.81	107.10	0.00
1-23	6511.57	191.87	0.00

Cohort grouping	M+F	Δ AIC	AIC w_i
1,...,23	11084.85	12.06	0.00
1-17, 18,...,23	11072.78	0.00	1.00
1,...,17, 18-23	11274.87	202.09	0.00
1-17, 18-23	11262.81	190.03	0.00
1-23	11431.83	359.05	0.00

Table 3. Model selection for a sex-effect, dependent on tag-site, for southern elephant seal tag-loss from Marion Island. Males in cohorts 1-17 showed higher tag-loss rates than females.

Cohorts	Sexes separated	Sexes grouped	Δ AIC	AIC w_i
1-17	7722.49	7730.82	8.333	0.98
18-23	3539.07	3531.99	7.073	0.97

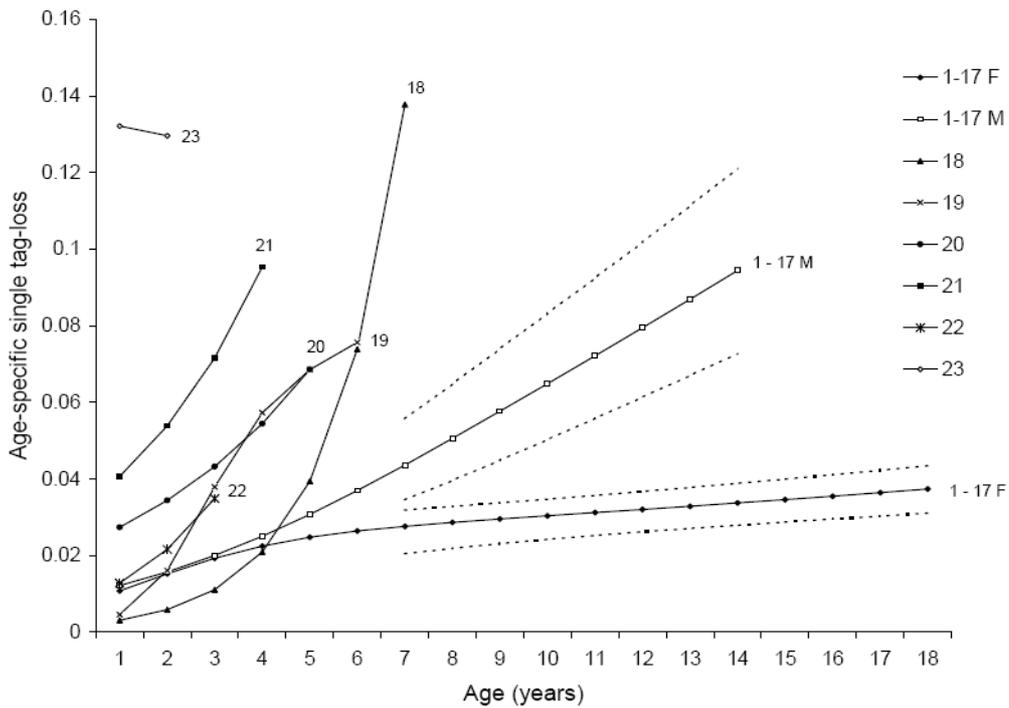


Fig. 1. Maximum likelihood functions for age-specific single tag-loss rates over time. Inner interdigital tags (IIT; cohorts 1-17) are represented by two general functions for males and females. Standard errors (tag-loss probability \pm 2SE) are presented for IIT tags above age 7.

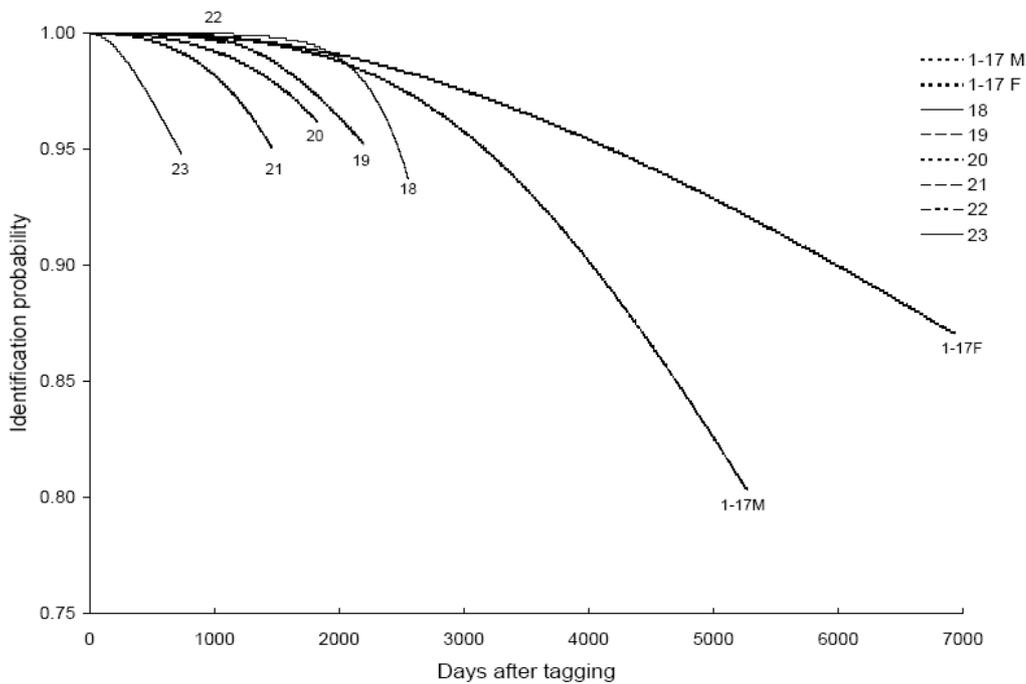


Fig. 2. Identification probabilities of double tagged southern elephant seal cohorts at Marion Island. An individual is rendered unidentifiable when both tags are lost.

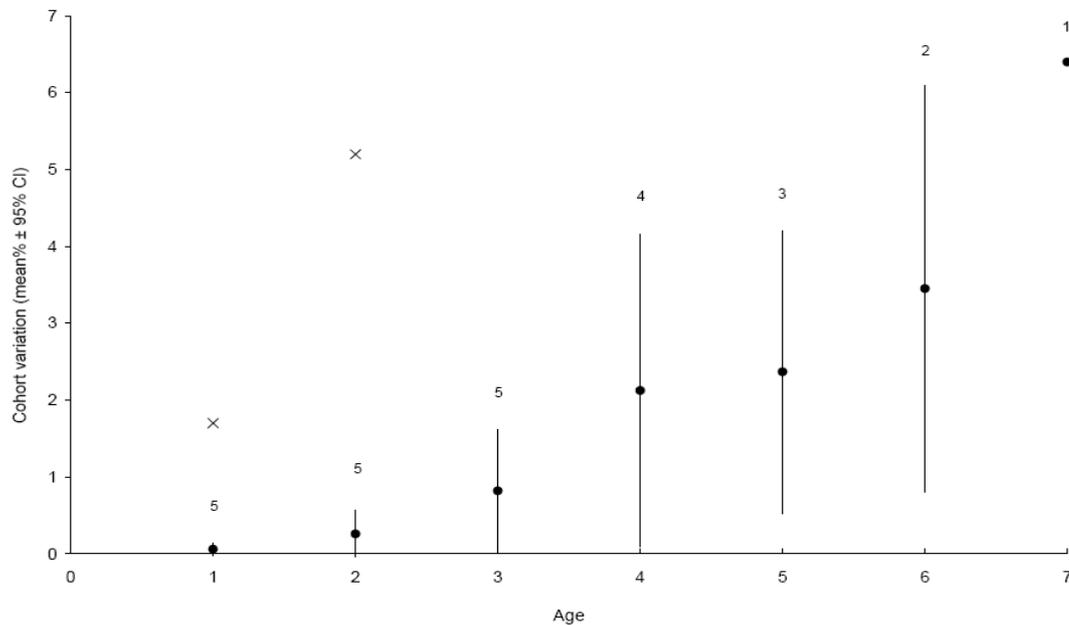


Fig. 3. Variation in southern elephant seal tag-loss rates between cohorts 18 – 23, double tagged in the outer interdigital webbing of the hind flipper (OIT). Points represent the mean tag-loss rate over cohorts 18 - 22, with numerical values indicating the available sample size (number of cohorts). Cohort 23 (x at ages 1 and 2) is not included in the calculation of mean cohort differences.

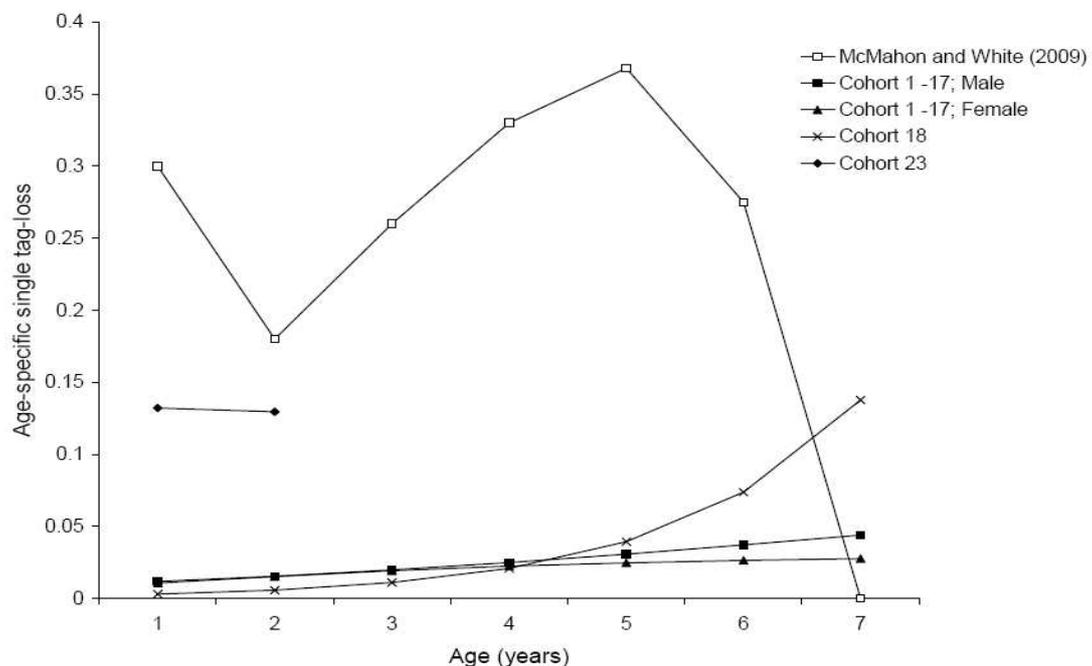


Fig. 4. Age-specific single tag-loss (N_{21}) in southern elephant seals from Macquarie Island (McMahon and White 2009) and Marion Island (data shown for IIT [cohort 1-17 males and females] and OIT cohorts 18 [longest OIT time-series] and 23 [cohort with greatest tag-loss measured]). Tag-transition from two to one tag is accurately measured at both locations, and not influenced by the independence of tag-loss assumption

Discussion

Tag-loss for both IIT and OIT cohorts of southern elephant seals is best described by a monotonic increase over time, although the pattern of tag-loss did deviate in some cohorts. Because all tags were applied to recently weaned individuals (~23 - 30 days old; see Chapter 3 – de Bruyn et al. 2008), tag-time and seal age cannot be differentiated. The increase in tag-loss rates over time is assumed to be generally related to an increase in seal- and flipper size and webbing thickness, rather than tag failure due to breakage (Pistorius et al. 2000). Extreme sexual dimorphism is present in adult elephant seals and the higher tag-loss rates in males tagged with IIT reflect this. Age-specific IIT tag-loss probabilities of males increased relative to those of females from age 3 to 4 onwards. Sexual body size differences become evident at age 3, whereas extreme sexual dimorphism manifests after male elephant seals undergo a secondary growth spurt between ages 4 and 6 (Laws 1984). In contrast, model selection favored a combined male and female model for OIT cohorts. The lack of a sex effect for the OIT cohorts may possibly be explained by a lack of statistical power, due to fewer years post-tagging (maximum = 7 years) to detect such effects. For IIT, model selected support for different sex models was only present when all cohorts were grouped, and not for individual cohorts (results not shown). Therefore, there may be insufficient statistical power to detect sex differences when using individual cohorts, or only a few combined cohorts (OIT, $n = 6$). However, seals tagged in the outer webbing of the hind flipper at Macquarie Island, similarly did not show sex differences in tag-loss (McMahon and White 2009). This may indicate that the influence of flipper size may be important for IIT-loss, but less so for tags applied to the outer webbing (OIT).

Cumulative tag-loss rates for both IIT and OIT are low in comparison with other phocid studies (e.g., Stobo and Horne 1994, McMahon and White 2009) and with previous assessments for a shorter time-series of this same mark-recapture program (Pistorius et al. 2000). Cumulative tag-loss rates from birth to age 15 computed by Pistorius et al. (2000) were 35% and 17% for males and females respectively, which is higher than those reported here. Pistorius et al. (2000) included 11 cohorts (1983 – 1993), with resighting data

up to 1998. Our data included an additional 6 cohorts with IIT, and a further 10 years of resighting data. The added cohorts, and more importantly the longer resighting time period would modify the tag-loss estimation. This may be especially important for the adult age categories (e.g., 13 males over age 12 in this study vs. only 2 males in Pistorius et al. 2000). The different analytical approach between this study and Pistorius et al. (2000) furthermore resulted in these differences. The Pistorius et al. (2000) function constrained tag-loss to be a straight line, with the younger age categories (the region in the graph that has the more weight in the likelihood output, because more individuals are included) guiding the initial slope of the linear trend line. Age-specific IIT tag-loss (this study) did not fit the linear function exactly, but were rather slightly concave up (males) or convex down (females), leading to lower cumulative loss.

Outer interdigital tags were shed at a higher rate than IIT. In aquatic mammals, body and fin/flipper undulations pass water posterior along the body with increasing force, creating body-bound vorticity. This vorticity is transmitted along the body to the trailing edge of the fin, or flipper, where it is shed in a thrust jet (Fish et al. 2008). In swimming phocids, the center of the flipper is in addition more rigid than the flipper extremities (Fish et al. 1988). While swimming, OIT may thus be subjected to increased drag and movement, leading to increased tag-loss. On land, IIT are usually protected from the substrate and environmental variables (e.g., ultraviolet light) because the tag is typically enclosed in the folds of the resting flipper (between adjacent flipper digits). OIT visibly protrude more, improving tag visibility for resighting and reducing disturbance to seals during tag resighting (the objective of the change in tag-placement in this study program). However, OIT are therefore also more likely to make contact with the substrate, plausibly leading to more abrasion and snagging, and potential loss from the flipper. Additionally, OIT exposed to more UV radiation than the enclosed IIT may become weakened over time and result in increased tag breakage, although we rarely observed such breakage.

McMahon and White (2009) compared tag-loss at Macquarie Island to Marion Island, and suggested that tag placement may affect tag-loss as tag-loss was much greater at Macquarie Island (OIT) than at Marion Island (IIT, from Pistorius et al. 2000). Our results support their interpretation. However, the large difference in tag-loss between the OIT from Macquarie Island (McMahon and White 2009) and Marion Island (this study) indicate that other factors are also important. We suggest that the timing of tagging is a critical determinant in life-time retention rates. At Marion Island, pups are always tagged post-weaning (age ~ 23 – 30 days), while pups on Macquarie Island were tagged at birth. McMahon and White (2009) rejected this hypothesis, as they calculated tag-loss from weaning (when pups were branded) only; and not birth. However, it is probable that flipper damage from tagging at birth may lead to increased tag-loss post-weaning and not necessarily only during the pre-weaning period as assumed by McMahon and White (2009). For example, newborn pups may be more immuno-compromised than weaned pups. Tag-loss due to immune reaction may, however, only occur in a few months time, rather than within the 3 – 4 week pre-weaning age. Weaned pups, in contrast, may be less susceptible to infection of the tag-site than newborn pups, leading to lower tag-loss. We recommend that pups are tagged at weaning only and suggest an alternative method to identify pre-weaned pups (see Chapter 3 – de Bruyn et al. 2008). On Marion Island, pre-weaned pups are marked with temporary Supersmall[®] tags (Dalton Supplies Ltd., Henley-on-Thames, U.K.) that are designed to minimize injury to the tag-site on the pre-weaned pup's delicate hind flipper. These tags are applied to the inner interdigital webbing of the hind flipper. At weaning (when hind flippers are sturdier), pups are tagged in the outer webbing of the hind flipper with the more robust Jumbotags[®]. This tagging protocol allows identification of pre-weaned pups (see Chapter 3 – de Bruyn et al. 2008), while postponing marking with long-lasting tags to a period when; a) the pup flipper is stronger; b) the pup is generally in better condition and has greater immunity than at birth; and c) tagging of weaned pups occurs well outside the harem (without the need to return the pup to the harem) that enable the precise placing of tags, which is required for low loss rates. The correlation between tag-loss, tag-site and time of tagging between Marion Island and Macquarie Island may

further be influenced by different tag types used (Dal 008 Jumbotags[®] [Marion] vs. Supertag[®] Size 1 [Macquarie]; Dalton Supplies Ltd., Henley-on-Thames, United Kingdom) and possibly the practice of cutting and filing the tag pin on Macquarie Island. If this procedure puts any strain on the tag itself (e.g., holding the tag to file it down, while the pup tries to move the flipper), tag-loss may be increased due to damage/enlargement of the tag-site during this procedure.

Differences in tagging proficiency of personnel may lead to heterogeneous tag-loss. Tag-loss in South African fur seals *Arctocephalus pusillus pusillus*, for example, varied between 6.8 - 33.8% for different tagging personnel (Shaughnessy 1994). Stobo and Horne (1993) reported cohort variation in tag-loss among year-old grey seals *Halichoerus grypus* which varied between 7.2 – 18.8%. In the present study, interannual variation in tagging proficiency may result in cohort specific tag-loss rates, despite stringent efforts to maintain constant tagging technique. Wilkinson and Bester (1997) compared tag-loss of one-year old elephant seals at Marion Island, and found no significant variation amongst 8 cohorts. This trend continued for all age groups in the 17 IIT cohorts, and no important variation in tag-loss between cohorts was evident. Conversely, OIT tag-loss varied by cohort. Field observation indicated that tag placement in three of the OIT cohorts were marginally suboptimal. It thus appears as if tag placement for OIT needs to be even more exact (~ 5mm) as compared with IIT, as only a slight misplacement of the tags (OIT) at tagging may render tags attached too deep (cohorts 19 and 20) or too shallow (cohort 23). Tags applied too deep in the webbing may increase infection and tissue necrosis of the tag-site as the flippers grow while tags applied too shallow are more likely to tear out of the trailing edge of the flipper. The outer webbing of the hind flipper also provides a smaller surface area in which to place a tag as compared to the neighboring inner webbings between digits two and three and three and four. This may therefore explain the cohort dependence observed (and the suggested need for more precise tag placement) for OIT, but not IIT.

Although tag location on the outer interdigital webbing may lead to a lower retention rate, it is assumed that loss of tags should occur randomly among cohorts when they are similarly tagged. Yet, even when we removed cohorts that we a priori believed might have been responsible for the observed bias, the remaining three cohorts still could not be grouped. The estimates of OIT are hampered by a lower sample size (6 cohorts) for a maximum time at liberty of 7 years, compared to 17 cohorts at a maximum time at liberty of over 24 years for IIT cohorts. As such, OIT resight data exists for only five cohorts of adult females, and two cohorts of adult males (based on the age at maturity for this species at Marion Island; Kirkman et al. 2003). Tag-loss probabilities are based on the time at liberty of tags: the time from application of the tag, to the last occasion that the individual was seen with two tags (N_{22}) or first seen with one tag (N_{21}). However, cohorts have different maximum times at liberty (maximum resight time decreases by one year for successive cohorts) which could influence parameter estimates, especially when the time at liberty is relatively short. This potential bias is apparent in the current study, significantly more so for OIT with shorter time at liberty and few sexually mature cohorts. For example, cohort 23 tags have a maximum time at liberty of around 900 days, in comparison with the first OIT cohort (18) at liberty for more than 2700 days. Inter-cohort variation should be more pronounced when the data are sparse, and a few random cases of tag-loss could potentially help to drive cohort specific differences. For five of the six OIT cohorts (cohort 22 being the exception), tag-loss estimates increased as absolute cohort age was younger. Therefore, we attribute at least part of the cohort specific tag-loss rates observed for OIT as an effect of fewer days to maximum time at liberty (specifically the time-span of N_{22}). We suspect that as more data becomes available, tag-loss of OIT should become more homogenous among cohorts, although at higher rates than the IIT cohorts.

The cohort effect observed for OIT necessitates caution when deriving life-history parameter estimates (such as age-specific survival rates) from these cohorts. Because animals from separate OIT cohorts lose tags at different rates, the proportion of marked animals in the population at any period will differ between cohorts, and not represent a homogenous group

with respect to tag-loss. An increase in tag-loss rate between IIT and OIT per se does not present considerable analytical drawbacks as survival rate corrections may simply be structured to represent the two different tag-sites. Extreme cohort variability, however, would negate the implementation of survival models structured at a population level (rather than a cohort level) as population level survival trends might be influenced by cohort specific tag-loss rates.

To demonstrate the differences in tag-loss rates between OIT cohorts, we considered an arbitrary cohort of 500 double tagged pups, a good approximation of the number of pups born annually on Marion Island in recent years (MNB unpublished data). On average, at age 2, cumulative tag-loss will render all individuals identifiable for three of the OIT cohorts (and all of the IIT cohorts). Tag-loss in cohort 20 and 21 will result in double tag-loss in 2 and 4 pups respectively, while tag-loss in cohort 23 rendered 26 pups unidentifiable. Therefore, in a mark-recapture framework, within the first two years of life, only cohort 23 had biologically meaningful variation in tag-loss rates – which may lead to a decrease of 5% in apparent survival rate [$1 - (26/500) = 0.948$]. The maximum variance in OIT loss was present at age 4, where one (cohort 18) or 25 (cohort 21) pups out of 500 are expected to lose both tags, leading to a 4.8% decrease in apparent survival rate of cohort 21 at this age. Survivorship is chiefly responsible for population regulation at Marion Island (see Pistorius et al. 1999, 2004), and indeed in many mammal populations where immigration and emigration is limited; accurate estimates of these rates are therefore invaluable. In this case, apparent survival rates for juveniles should not be biased by tag-loss even if IIT and OIT cohorts were combined in survival analysis (excluding cohort 23). However, variation in tag-loss between cohorts can negatively bias estimates for sub-adult male and adult age classes if such cohorts are pooled.

Assumption of independent tag-loss

The results presented assume tag-loss independence. Violations of the independence assumption will result in a greater proportion of animals retaining two or losing two tags, with few animals retaining only one tag. This

would result in an overestimate in tag retention rates, and negative bias in survival rates. Testing for dependence in tag-loss requires the permanent marking of study subjects. Permanent marking of southern elephant seals at Marion Island is not possible to facilitate testing of this assumption. Tattoos for example (Diefenbach and Alt 1998), although useful in a mark-recapture framework, are not realistic in our mark-resight design. Southern elephant seals have been successfully branded on Macquarie Island with no long-term influence on survival or condition (McMahon et al. 2006a). This protocol has allowed testing of the independent assumption for the period where flipper tagging and branding overlapped (McMahon and White 2009). However, branding is logistically impractical at Marion Island and this technique incorporates animal welfare concerns (Jabour Green and Bradshaw 2004) that resulted in the termination of the Macquarie Island southern elephant seal monitoring program (McMahon et al. 2006b, 2007). Passive Integrated Transponder (PIT tags) have been successfully used to mark numerous species (Gibbons and Andrews 2004) including southern elephant seals (Galimberti et al. 2000). PIT tags facilitate reliable long-term identification of elephant seals up to adult age-classes for both sexes (F. Galimberti personal communication). However, in contrast to external hind flipper tags which can be sighted from a distance, PIT tags require scanning each seal from a close distance (<20cm) with an electronic reader. This is often impossible to achieve, in particular for breeding females within harems, and aggregations of seals during the molt haulout (F. Galimberti personal communication). PIT tags are additionally more invasive than external tags, may itself incur tag-loss (Gibbons and Andrews 2004) and are expensive. Therefore, by comparison, double tagging with plastic tags remains the preferred choice of marking in elephant seals. Still, where PIT tags can be used in combination with double-tagging to provide an additional mark this method will be useful to improve tag-loss estimates. Previously tagged animals can in some cases be identified through scarring, and Bradshaw et al. (2000) used flipper scarring in New Zealand fur seal *Arctocephalus forsteri* pups to address dependence in tag-loss estimates. Such scarring (tag punctures in the flipper) is sometimes visible in elephant seals, but it is virtually impossible to regularly and

accurately distinguish seals that have lost both tags from untagged seals (e.g., transients/immigrants).

Several studies have provided evidence of dependent tag-loss, and the assumption of independence appears to be biologically unrealistic. Double ear tag-loss in sea otters *Enhydra lutris* (Siniff and Ralls 1991) and black bears *Ursus americanus* (Diefenbach and Alt 1998), and flipper tag-loss in fur seal pups (Bradshaw et al. 2000) and leatherback sea turtles (Rivalan et al. 2005) were all greater than expected under the independence assumption. Similar results for elephant seals from Macquarie Island have been shown (McMahon and White 2009), and the expectation is therefore that tag-loss at Marion Island would also be dependent. Dependent tag-loss varies according to individual attributes, leading to heterogeneous tag-loss probabilities (McMahon and White 2009). In black bears, individual behavior such as fighting, mother-pup grooming or playing probably influences tag-loss (Diefenbach and Alt 1998). In fur seal pups, mechanical abrasion is thought to induce tag-loss, which is likely influenced by substrate, pup behavior and condition (Bradshaw et al. 2000). Dependent tag-loss in leatherback sea turtles is probably related to individual immunity, as the majority of tags are lost as a result of tissue necrosis. Individuals prone to infection may therefore be more likely to lose the second tag if the first tag was already lost (Rivalan et al. 2005). Tag-loss in elephant seals at Macquarie Island seems to be more dependent on pup wean mass. Lower wean mass concurrent with lowered immuno-competence is suggested to result in a greater incidence of dependent tag-loss, while larger pups generally exhibit independent tag-loss (McMahon and White 2009). To what extent observations from different species or different marking protocols can be used to infer dependent tag-loss in individual elephant seals at Marion Island is unsure. Even species-specific comparison is intricate due to the large difference in age-specific single tag-loss rates between Marion Island (0.0 - 0.14, this study) and Macquarie Island (0.0 – 0.364, McMahon and White 2009). Ideally, because the degree of tag-loss heterogeneity varies among study species, physical environment and tagging protocol, with the bias associated with assuming tag-loss

independence reliant on the magnitude of tag-loss, dataset-specific assessment of this assumption will be of greatest value.

Pistorius et al. (2000) expected a low degree of bias caused by dependent tag-loss for the Marion Island tagging regime owing to; a) an observed increase in tag-loss rate over time instead of an apparent decline (see Xiao et al. 1999); b) low absolute tag-loss rates resulting in modest bias; c) high resight frequency, where most animals are seen multiple times per year, reducing the probability of missing tag transition from N_{22} - N_{20} (i.e., not seeing the seal changing tag status from two to one tag), and d) the relatively high proportion of resightings of seals with one tag remaining for extended periods. Diefenbach and Alt (1998) predicted from observations of permanently marked animals that low tag-loss and frequent resightings should result in little bias from dependent tag-loss. Therefore, as the rate of tag-loss from two tags to one tag (N_{21}) is markedly lower at Marion Island than at Macquarie Island (Fig. 4), dependence of tag-loss should result in a smaller bias of survival rate at Marion Island, and results should be fairly robust in dealing with these violations, especially for IIT. However, we acknowledge the potential bias in our results and agree that the tag-loss estimates provided here will be underestimated due to partial dependence of tag-loss in individuals. In cohorts with relatively high tag-loss (cohort 23 for example), the bias in survival rates will be higher.

Conclusion

Generally, small shifts in demographic rates of large-mammal populations, especially adult female survival, are able to produce a change in population growth (Eberhardt and Siniff 1977; Pistorius et al. 1999; McMahon et al. 2005). This illustrates the importance of accurate estimation of survival rates in mark-recapture studies, as biased estimates of demographic rates may result in erroneous conclusions and implementation of inappropriate management strategies leading to failure in management objectives (Brook et al. 1997; McMahon and White 2009). Tag-loss corrections in mark-recapture studies improve accuracy by adjusting survival estimates upwards. Double tagging with high retention tags, in conjunction with permanent marking

(where possible) should be used, while frequent resight/recapture occasions should improve life-history estimates (McDonald et al. 2003). Fluctuation in tag-loss rates between years, tag-site and other variables (e.g., colony and habitat differences) must be considered. We illustrate that small changes in tagging methodology can have potentially serious consequences for life-history estimates of a population if such changes are not investigated and, ideally, quantified. While homogenizing techniques for extensive use across study locations are appropriate for comparative purposes, we advocate the importance of dataset-specific assessment of tag-loss rates to ensure greatest confidence in population parameters obtained from mark-recapture experiments.

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Supplementary material.

Table S1. Estimated cumulative age specific tag retention probabilities for elephant seals at Marion Island. Cohort independent, sex specific probabilities are given for inner interdigital tags (IIT; cohorts 1 to 17), while outer interdigital tags are separated by cohort (OIT; cohorts 18,..., 23).

Age	1-17 F	1-17 M	18	19	20	21	22	23
1	1.000	1.000	1.000	1.000	0.999	0.998	1.000	0.983
2	0.999	0.999	1.000	1.000	0.996	0.992	0.999	0.948
3	0.998	0.998	1.000	0.997	0.990	0.977	0.995	
4	0.996	0.995	0.998	0.988	0.979	0.950		
5	0.992	0.991	0.994	0.973	0.962			
6	0.988	0.984	0.979	0.952				
7	0.983	0.974	0.936					
8	0.977	0.961						
9	0.970	0.944						
10	0.962	0.924						
11	0.954	0.900						
12	0.945	0.874						
13	0.935	0.846						
14	0.925	0.816						
15	0.915							
16	0.904							
17	0.893							
18	0.881							

Appendix III:

PRELIMINARY ANALYSIS OF THE SOCIAL STRUCTURE OF KILLER WHALES, *Orcinus orca*, AT SUB-ANTARCTIC MARION ISLAND

CA Tosh, PJN de Bruyn & MN Bester

Abstract

Studies of social differentiation between populations of killer whales (*Orcinus orca*) are important due to the cosmopolitan nature of the species, both in terms of distribution and feeding habits. The following research provides preliminary findings describing the social structure of the killer whale population at sub-Antarctic Marion Island. We provide evidence for consistent, observable patterns of social interactions with animals associating and disassociating in non-random patterns. We show that the social structure of this population may follow a new pattern of association, displaying a blend of the traditional resident/transient model displayed in the Northern Hemisphere. However, we emphasize the critical need for further studies related to the sociality, biology and life history of Southern Ocean killer whales.

Introduction

Social structure in cetaceans has been extensively described and analysed (Matkin et al. 1999; Baird and Whitehead 2000; Mann et al. 2000; Gowans et al. 2001; Weinrich et al. 2006) however, it is acknowledged that intra-specific generalizations can not be made in animals of advanced social structure (Di Fiore and Rendall 1994; Costa and Fitzgerald 1996). An ideal example is the differences in diet, behaviour and social organization of “transient” and “resident” killer whales in the North Pacific (Heimlich-Boran 1988; Bigg et al. 1990; Felleman et al. 1991; Baird et al. 1992; Ford et al. 1998; Baird and Whitehead 2000). It is thus particularly valuable to document the variability in such factors for different populations. The degree of social organization and the ability of animals to “learn” from individuals within the same population has implications for long-term survival, especially in marine environments (Boran and Heimlich 1999; Whitehead 2007a). Knowledge of the social differentiation between different populations of killer whales is vital

for conservation since different strategies will apply to distinct populations that may react to similar threats in diverse ways (Whitehead et al. 2004).

Killer whale social behaviour and organization are poorly understood in the Southern Indian and Atlantic Oceans. There is even uncertainty of the number of species and degree of ecological specialization for killer whales around the Antarctic continent (Pitman and Ensor 2003). Killer whales at Marion Island have been studied at a population level and local movements have been preliminarily analysed (Condy et al. 1978, Keith et al. 2001; Pistorius et al. 2002). Killer whale sightings occur regularly throughout the year, peaking between October and December (Keith et al. 2001; Pistorius et al. 2002). This peak presence coincides with the breeding season of southern elephant seals (*Mirounga leonina*) and numerous penguin species (Condy et al. 1978; de Bruyn et al. 2007). This pattern has also been observed at Iles Crozet (Guinet 1991) and Punta Norte, Argentina (Hoelzel 1991). Scant record of the diet of Marion Island killer whales exists (Condy et al. 1978; Keith et al. 2001; Pistorius et al. 2002; Kock et al. 2006). Indications from these publications and the personal observations of numerous field personnel suggest that Marion Island killer whales include a combination of seal, penguin and fish in their diet. Killer whales at Marion Island have been observed to participate in active searching and hunting, feeding and resting activities (Condy et al. 1978). To date, no comprehensive research has been done on the social organization, distribution patterns and ranging behaviour of sub-Antarctic killer whales. Hoelzel (1991) described behavioural and social factors of the southern killer whale population around Punta Norte, Argentina (latitudinally 5° north of Marion Island, not classified as sub-Antarctic).

This study aims to reveal the potential social structures of killer whales at Marion Island and provide a basis for future studies. We suggest that continued and focussed long-term data collection would provide valuable information about killer whale sociality at Marion Island.

Methods

Marion Island (46°54'S, 37°45'E) is the larger (296 km²) of a pair of islands comprising the Prince Edward Islands group. It is situated in the Southern Indian Ocean with the nearest landmass being the Iles Crozet (950km to the east) (Fig. 1). Oceanographically, Marion Island lies in the direct route of turbulent water masses (eddies) originating in the Thomas Bain fracture zone, a component of the South West Indian Ridge (Ansorge and Lutjeharms 2005). The interplay between the Antarctic Circumpolar Current and the prominent bottom topography of the South-West Indian Ridge results in productive turbulent water masses around the Prince Edward Islands (Ansorge and Lutjeharms 2005), sustaining the numerous mammal and bird species that use Marion Island as a breeding ground.

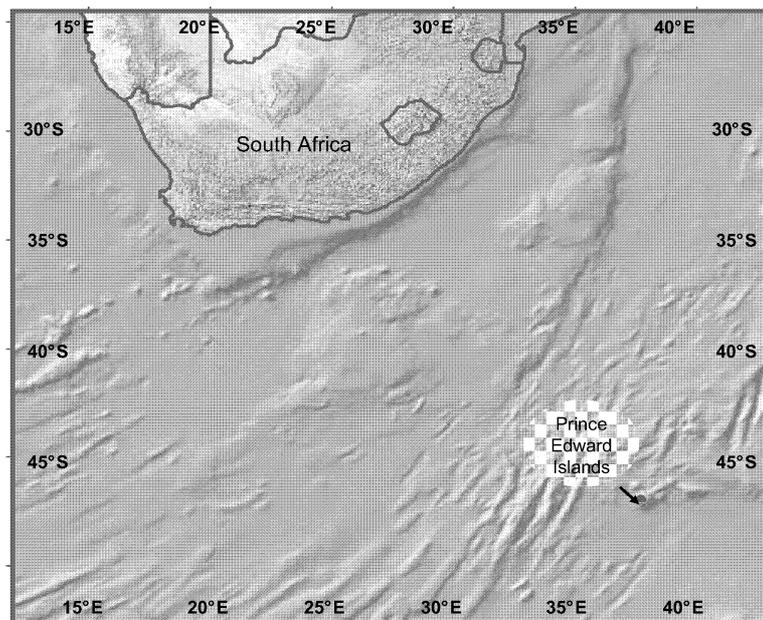


Fig. 1. The position of the Prince Edward Islands in relation to South Africa

Opportunistic land-based observations of killer whales around Marion Island were made from April 2006 - April 2007. As many individuals as possible at each sighting were photographed using digital cameras of various makes and capabilities by 25 different observers. Most observations were made within 0 – 100m of the shore and were 0 – 10 minutes in duration. The height of the observer varied depending on the locality of the sighting and varies between 0 - 15m above the subject. All identified individuals observed

in an encounter were considered to be associated. Individuals were identified based on unique dorsal fin markings, cuts or scratches on the body and any other unique markings. Each identified animal was assigned a unique name code, following the protocol established by the Dolphin Biology Research Institute (DBRI, Urian and Wells 1996), detailing its sex and unique number (e.g. MF001, **M**arion **F**emale number **001**). Subsequent identifications were only considered if there was certainty about the identity of the animal. Matching of photographs was only done by an experienced individual, using restrictive criteria. If any uncertainty existed, a second opinion was sourced and if the uncertainty persisted then the photograph was rejected. Sex and age was assigned to each animal based on dorsal fin size and shape (Leatherwood et al. 1976). For this study, three classes were identified, namely adult female, adult male and sub-adult/juvenile, the last category denoted with a **U** (unknown sex). Date and time of observation, direction of movement, observation site and group structure information (sex and age class of each individual) were also collected.

Quantitative analysis was performed in two steps. Preliminary data analysis described the number of sightings made throughout the year, the number of photographed sightings and the number of identified individuals in those sightings. The average group size, percentage of the group that was identified, the average number of males, females, sub-adults and calves associated with each identified individual are also given. A preliminary social analysis, calculating the degree of social differentiation, was first run with all identified individuals ($n=21$) and then with individuals that were identified four times or more ($n=11$). All identified animals seen three times or less were excluded from further analyses in order to lend strength to the analysis for which substantial data exists. The potential implications of these animals on pod identification are discussed. The analysis was thus limited to 11 individuals that were seen repeatedly throughout the sampling period (13 months). All encounters in which known animals occurred were used in the analyses. Associations were analysed using SOCPROG 2.3 for MATLAB 7.4 (Whitehead 2007b).

The degree of societal differentiation is displayed as the coefficient of variation (CV) of the true association indices, which is equated to the proportion of time dyads spend together. The coefficient of variation also depicts how varied the population is in terms of social structure (<0.3 representing homogenous societies; >0.5 representing well differentiated societies and >2.0 extremely differentiated societies). The strength of the analysis was displayed as an estimate of the correlation coefficient (CC) between the true association indices and the calculated association indices [0 (poor analysis) – 1 (strong analysis)]. Both the aforementioned values were calculated using likelihood methods with a resolution of integration = 0.001 (Whitehead 2007b). Standard errors were calculated using bootstrap with 100 replicates.

The basic procedure outlined in Baird and Whitehead (2000) was followed with a simple-ratio index being calculated to estimate the proportion of time each pair spent associating for all animals identified four times or more. The simple-ratio index does not overestimate associations between pairs as is the case between half-weight and twice-weight indices (Ginsberg and Young 1992). This resulted in the creation of an association matrix that is displayed as a cluster diagram (individuals are presented on the y-axis and strength of association on the x-axis) and a sociogram (individuals are arranged around a circle and associations are represented by lines of varying thickness/strength of association). Pods were assigned if animals spent 50% or more of their time associating (Bigg et al. 1990). A test for preferred and avoided associations was also run, based on the method suggested by Bedjer et al. (1998) and modified according to constraints based on testing associations within samples (Whitehead 1999, Whitehead 2007b). This test can only detect long-term preferred/avoided associations and tests the null hypothesis that there are no preferred companions between sampling periods.

Results

From start-April 2006 to end-April 2007, a total of 243 killer whale observations were made at various locations around Marion Island. Of these, 110 observations were photographed, with 56 encounters producing

identifiable individuals. The proportion of individuals identified within groups varied between sightings (Fig. 2), with 100% of individuals observed in 43% of the observations. There was a slight bias towards more individuals being observed in smaller groups (Fig. 3). Within this period 21 individuals (13 females, 5 males and 3 sub-adults) were identified according to unique characters and markings. The killer whale society at Marion Island is well differentiated ($CV_{21}=1.36\pm0.23$; $CV_{11}=0.80\pm0.1$) based on a strong analysis ($CC_{21}=0.63\pm0.05$; $CC_{11}=0.63\pm0.11$), there is thus a strong relationship between calculated and true association indices in the present study (Whitehead 2007b), irrespective of the sample used.

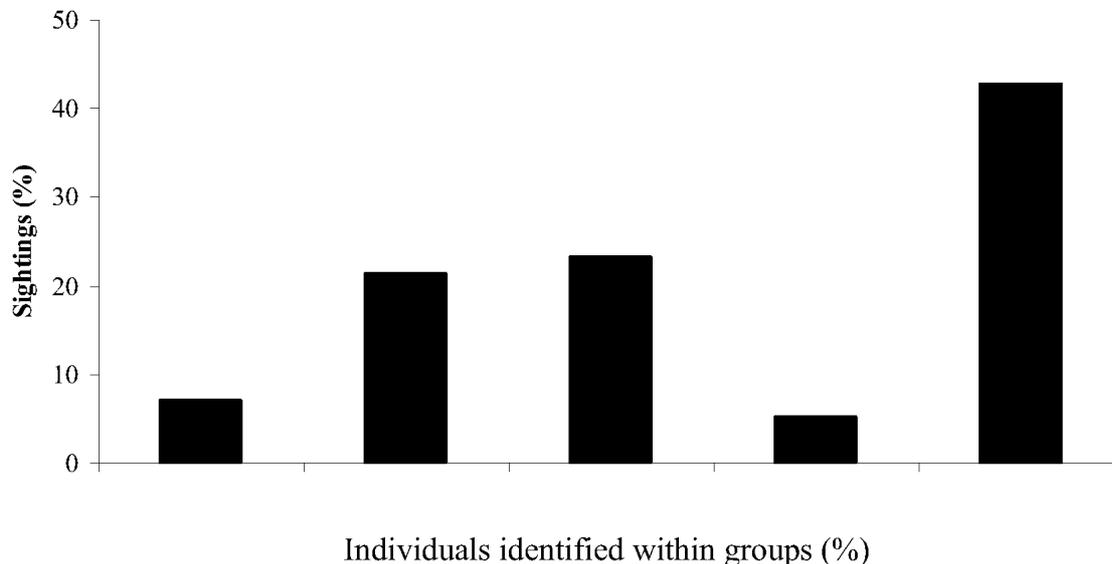


Fig. 2. The proportion of individuals identified within groups at each sighting

The average (standard deviation) group size for all identified animals was 3.43(0.87) whales, with group sizes ranging from 7 to 1 individual (Table 1). Within the groups, $74.97\% \pm 16.25\%$ of individuals were identified (Table 1). The average number animals sighted with each individual varied between 1 and 2 males, 1 and 3 females, 1 and 2 sub-adults and 1 calf (Table 1).

Table 1. Group information for all identified individuals (n=21).

ID	Pod	Number of times observed	Average group size (range)	Percentage of group identified (average \pm SD)	Number of adult ♂ 's observed within groups (average)	Number of adult ♀ 's observed within groups (average)	Number of sub-adults observed within groups (average)	Number of calves observed within groups (average)
MF001	M1	8	4.25 (7-2)	61.79 \pm 37.71	1.00	2.38	1.00	1.00
MF014	M1	11	3.82 (7-2)	75.11 \pm 31.93		2.00	1.00	1.00
MF020	M1	6	3.83 (6-3)	96.67 \pm 8.16		2.33	1.00	1.00
MU021	M1	6	3.83 (6-3)	96.67 \pm 8.16	2.33	1.00	1.00	
MF002	M2	9	3.67 (5-2)	59.07 \pm 26.31	1.00	1.78	1.50	1.00
MM005	M2	5	4.00 (7-2)	62.38 \pm 35.25	1.00	1.75	1.33	1.00
MF003	M3	14	2.64 (6-1)	89.88 \pm 21.73	1.33	1.80	1.00	1.00
MM007	M3	5	2.80 (4-2)	61.67 \pm 26.09	1.00	1.33	1.00	
MU004	M3	12	3.25 (7-2)	88.99 \pm 21.18	1.00	2.00	1.00	1.00
MF010	-	5	2.60 (5-1)	57.33 \pm 39.33	1.00	1.80		1.50
MF012	-	5	3.80 (5-2)	53.00 \pm 13.04	1.00	2.00	1.40	1.00
MF006	-	2	4.50 (7-2)	46.43 \pm 5.05		1.00		
MF009	-	1	4.00 (4)	50.00	1.00	3.00		
MF013	-	3	2.33 (4-1)	83.33 \pm 28.87	1.00	2.00		
MF015	-	2	5.50 (7-4)	64.29 \pm 50.51	1.00	3.00	1.00	1.00
MF017	-	2	3.00 (3)	100.00		2.00	1.00	
MF018	-	2	3.00 (3)	100.00		2.00	1.00	
MM008	-	2	2.50 (4-1)	75.00 \pm 35.35	1.00	2.00		
MM011	-	3	1.67 (3-1)	77.78 \pm 38.49	1.00		2.00	
MM019	-	1	4.00 (4)	75.00	1.00	2.00	1.00	
MU016	-	2	3.00 (3)	100.00		2.00	1.00	

Table 2. Social characteristics of 11 identified killer whales used in the present study.

Individual (ID)	Sex	Number of observations	Mean level of association	Maximum level of association	Pod ID
MF001	F	8	0.34	1	M1
MF002	F	9	0.16	0.67	M2
MF003	F	14	0.28	1	M3
MF010	F	5	0.03	0.25	--
MF012	F	5	0.07	0.67	--
MF014	F	11	0.34	1	M1
MF020	F	6	0.33	1	M1
MM005	M	5	0.12	0.67	M2
MM007	M	5	0.27	0.5	M3
MU004	U	12	0.28	1	M3
MU021	U	6	0.33	1	M1

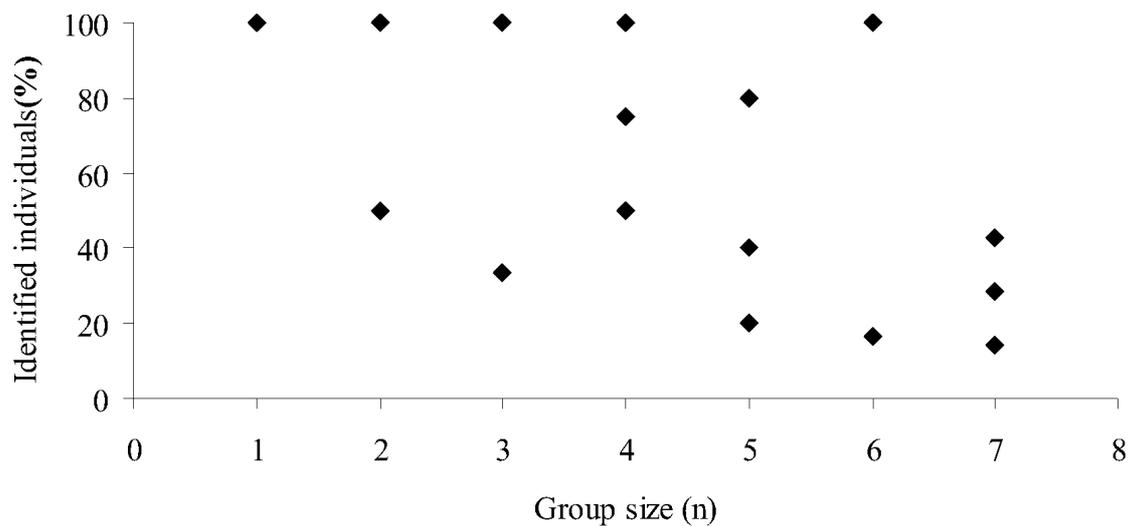


Fig. 3. Relationship between group size and the number of individuals identified within the group.

Eleven individuals (7 females, 2 males and 2 sub-adults) were seen on more than 3 occasions (Mean = 7.64; Range = 4-13), and were thus used for the data analysis (Table 2). There was a total of 84 identifications within the study period, mean number of interactions between dyads (pairs) = 0.75, and mean number of associations per individual = 7.45. Nine of the 11 frequently identified animals could be assigned to pods (Fig. 4). The grouping of animals into pods is also supported by the sociogram (Fig. 5). Strong relationships around the perimeter of the circle and the asymmetry of linkages through the axes of the circle indicate non-random associations. The varying thicknesses of the lines in the sociogram show different levels of association between dyads. The sociogram also supports weak or temporary associations made within the population. The thinner lines crossing the centre of the sociogram show weak or temporary associations. Pod M1 consists of 4 individuals (MF020, MU021, MF014 and MF001) spending 67% of their time together; within this pod MF020 and MU021 are seen to associate 100% of the time possibly due to a parent-offspring relationship. MF014 and MF001 are also closely associated with a strong association index of 1.0. Two individuals (MF002 and MM005) associated 67% of the time, these two animals were only seen alone once and the rest of the time as part of a larger group consisting mainly of females. These two animals are possibly part of a larger group, which could be classified as M2. MF010 and MF012 were not assigned to pods but did display loose relationships with other of animals in the study, namely MF002. Further observations are needed in order to identify if these animals could potentially be the missing members of pod M2. Pod M3 consists of three individuals; MF003 and MU004 (which are associated 100% of the time owing to a possible parent-offspring relationship), and MM007. The addition of MM007 is based on a small sample size; he was only seen 5 times and of these on two occasions with MF003 and MU004 (20/12/2006 and 08/01/2007) (Fig. 6). There was some interaction between pod M1 and M3 (Fig. 6). On 14 December 2006, all the individuals from pod M1 and M3 (except for MM007) were seen together in a group of 6 individuals and there was movement by MF001 from pod M1 to pod M3 on occasion.

Preferred and avoided associations were detected using the Bedjer et al. (1998) test. Constant results were obtained using 1000 random permutations with 100 flips /permutation. Long term preferred associations were indicated by high standard deviation and coefficient of variation (SD=0.20; CV=1.8) of real association indices when compared to randomly generated association indices (SD=0.11; CV=1.5). Avoided associations were also indicated by a lower proportion of non-zero elements in the real data (proportion = 0.49) when compared to the randomly generated data (proportion = 0.53).

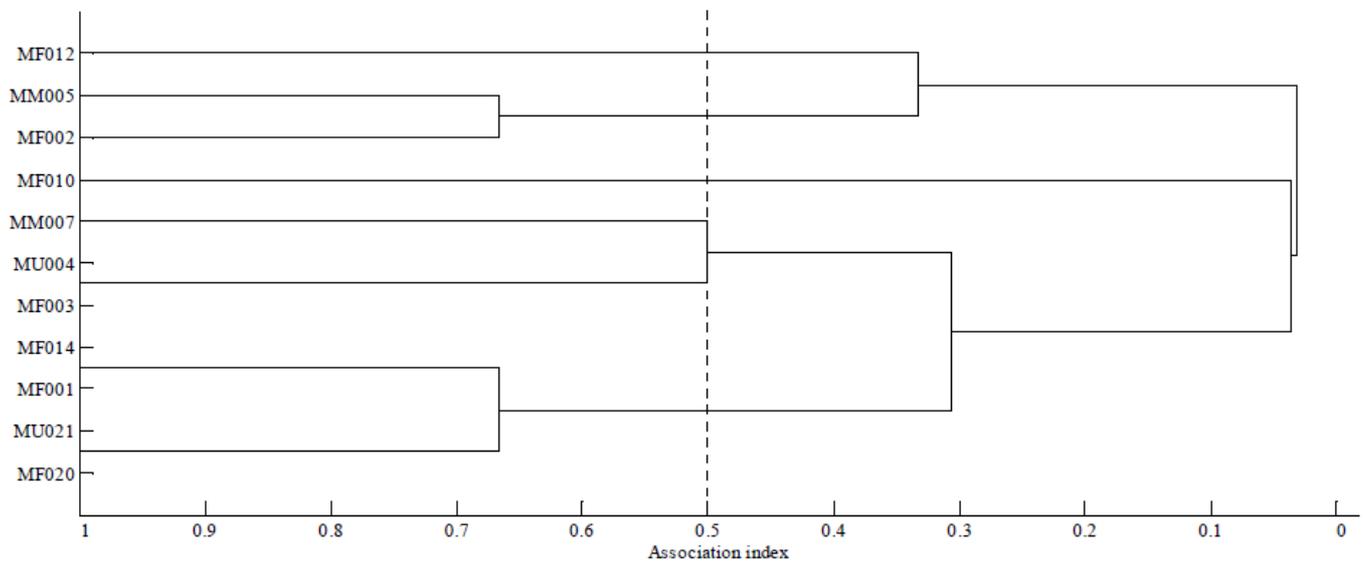


Fig. 4. Cluster diagram showing the association indices between identified individuals. Any association with an index greater than 0.5 (dotted line; Baird and Whitehead 2000) delineates a pod.

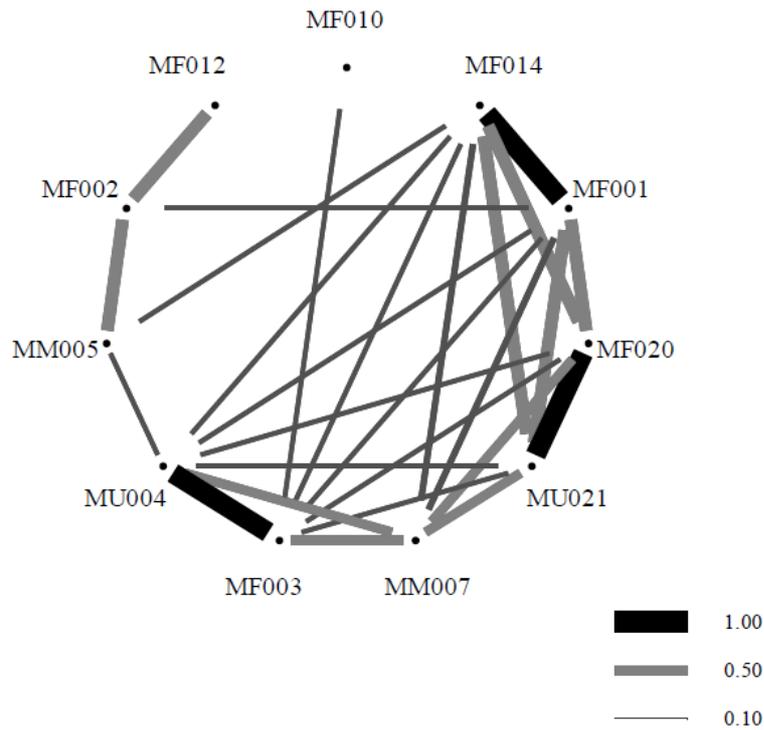


Fig. 5. Sociogram for the 11 individuals in this study. The key shows line thickness for three values, the linkages between individuals vary according to association indices (Association = 1.00 is highest).

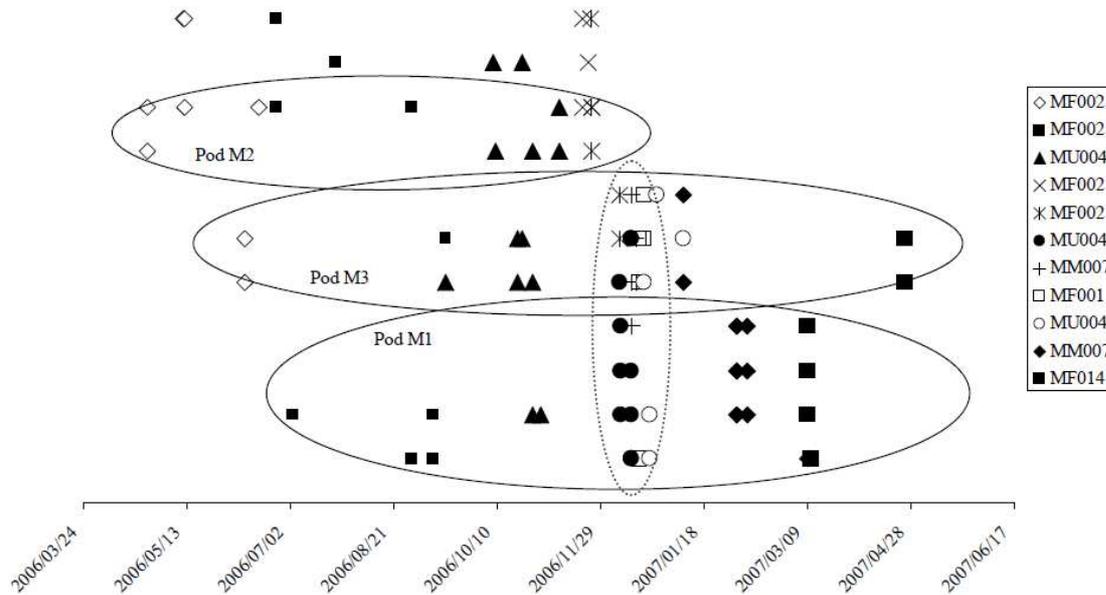


Fig. 6. Timeline of observations within the study period showing pod delineations as defined by association indices ≥ 0.5 (Bigg et al. 1990), The shaded area shows a period when Pod M1 and M2 were observed in the same group.

Discussion

Killer whale research on Marion Island is limited by land based data collection methods. This restricts the ability of the observer to identify all animals within the groups and makes the description of interactions between individuals within groups difficult. The Marion Island population is relatively small; with approximations of between 25 and 30 individuals in 2000 (Pistorius et al. 2002). Small population size limits the number of possible sightings of animals and therefore identifications. Although observations were limited to land based methods of a small population, this study is still based on 53% of all identified individuals. The exclusion of animals identified fewer than 3 times may have implications for the present study, but given that those animals sighted more than 3 times were often seen in smaller groups where all individuals were identified, basic pod composition is not affected. A bias exists against larger groups where not all individuals were identified (Fig. 3). Identification is constrained by poor visibility (weather and distance from shore), lack of identifiable marks and the opportunistic nature of the sightings, factors that affect all studies based on photographic methods (Friday et al. 2000). In the present study, we adopted the criteria as suggested by the IWC (1990) and used only experienced personnel, restrictive criteria and double confirmations if any doubt existed for the matching of individuals in order to reduce false-negative errors where two sightings of the same animal are marked as different (Stevick et al. 2001).

These factors notwithstanding, this study describes a well-differentiated killer whale society with certain individuals clearly associating with specific other individuals. The society seems to be female dominated, supporting findings for killer whales in the northern hemisphere (Brault and Caswell 1993), with females associating with their offspring foremost and then with other females. The role of male killer whales, at this stage, is difficult to define as there is no readily available relatedness information. Condy et al. (1978) describes a male biased composition of the Marion Island adult killer whale population, however, no correction for repeat identifications of the same animals was done. Our results indicate adult female biased (72%) composition among the 18 identified adult killer whales within the population,

which is more aligned with findings by Keith et al. (2001) for the Marion Island population. Difficulty in comparisons between studies arise due to the problems associated firstly with identification of individuals and secondly, distinguishing adult females and sub-adult males.

The relationships between Marion Island - and Antarctic killer whales are as yet unknown, but it seems that they share common characteristics with the type-B killer whales as described by Pitman and Ensor (2003), with a large eye-patch and dorsal cape. Further research is needed to reveal if the killer whale population around Marion Island appear to display similar social organisation to northern hemisphere transient killer whales as described by Baird and Whitehead (2000) or if they display a typically resident social structure (Heimlich-Boran 1986). Small groups (Marion Island: mean = 3.56 individuals (Keith et al. 2001), British Columbia: mean = 2.4 individuals (Baird and Whitehead 2000)), and females that are gregarious (high average association rates) seem to be common between populations. Baird and Whitehead (2000) attributed the social structure of transient killer whales in British Columbia to ecological factors, with energetic constraints imposed by foraging on other marine mammals limiting group size to 3 or less individuals (Baird and Dill 1996). Marion Island killer whales could potentially be displaying a small-group resident model, with animals showing a high degree of philopatry but with group size being energetically constrained. Long term residence in an area, or repeated visits to a site over many years has been shown for killer whales from Marion Island (Condy et al. 1978, Keith et al. 2001) and from Punte Norte (Hoelzel 1991). The presence of killer whales at Punte Norte is limited to a set period of high quality food availability and their behaviour is constrained by the need to maximise prey intake at beaches where hunting success is maximised (Hoelzel et al. 1991). The tendency to patrol beaches of varying topography (Condy et al. 1978, Pistorius et al. 2002), the varied food sources and the temporal variability in food sources may all be factors contributing to observed patterns at Marion Island. Further research is needed to draw conclusions on the link between social structure and diet/foraging at Marion Island, as can be done for killer whales at other localities (e.g. Hoelzel 1991, Baird and Dill 1996).

With the development of a killer whale identikit, further research detailing the temporal changes in associations and the strengths of associations between different classes will be possible. Given the paucity of knowledge about killer whales in the Southern Ocean, where uncertainty exists even at species level (Pitman and Ensor 2003), the current study proves that killer whales can be researched successfully and productive conclusions drawn over a relatively short time using shore-based observation data. Marion Island may serve as a focal point for observations of killer whales in the Southern Ocean, providing research opportunities difficult elsewhere.

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**“I don’t see much sense in that,” said Rabbit
“No,” said Pooh humbly, “there isn’t. But there was going to
be when I began it. It’s just that something happened to it
along the way.”**

Winnie the Pooh by *A. A. Milne*