
Southern Ocean sentinels: demographic insights into the declining population of Southern elephant seals at Macquarie Island

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Some of the clearest expressions of climate changes have been found in the Southern Ocean, one of the biggest marine ecosystems and a major component of the Earth's climate system. Top predators living in this ecosystem are considered to be one of the best indicators of these global changes as their population fluctuations reliably integrate and reflect prevailing environmental conditions. Southern elephant seals (*Mirounga leonina*) are pole-ward predators that feed throughout the Southern Ocean. In the past decades, their worldwide populations have been stable or increasing with the single exception of the Macquarie Island population that has been declining for unknown reasons over the past 50 years. This study, based on an 18-year capture-recapture dataset involving more than 6 000 individually marked females, aims to explore and understand the demographic mechanisms driving this decline and the potential impact of a changing environment on a key predator. Using models that deal with the issue of uncertainty in reproductive status, I showed that breeding is extremely costly in female elephant seals and results in a substantial decrease in survival of both first-time and experienced breeders. To offset this high reproductive cost to survival and maximize their reproductive success, female elephant seals tend to skip some reproductive events during their lifetime. Environmental conditions during the beginning of the post-moult foraging trip, which also corresponds to the beginning of females' pregnancy, play a critical role in this decision to skip reproduction or not. By incorporating this information into a matrix population model, I confirmed and reevaluated the decline of this population. Taken together, these results provide a detailed understanding of the southern elephant seals demography and give potential clues to the processes driving the decline of the Macquarie Island population. More broadly, my research contributes to a body of knowledge regarding the role of evolutionary and ecological processes in shaping life histories and population trajectories in long-lived species.

Declaration

The work in this thesis entitled "Southern Ocean sentinels: demographic insights into the declining population of Southern elephant seals at Macquarie Island" was carried out in the Marine Predator Research Group, Macquarie University. I certify that this work has not previously been submitted for a degree nor has it been submitted as part of requirements for a degree to any other university or institution other than Macquarie University.

I also certify that the thesis is an original piece of research and it has been written by me. Any help and assistance that I have received in my research work and the preparation of the thesis itself has been appropriately acknowledged.

In addition, I certify that all information sources and literature used are indicated in the thesis.

Marine Desprez

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Statement of publication and co-authorship

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Chapter	1	2	3	4	5	6
Conception	MD	MD	MD	MD	MD	MD
		CRM	CRM	CRM	CRM	
		MAH	MAH	MAH	JDL	
		OG	OG	OG	MAH	
		RH	RH	RH	OG	
			SC		RH	
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*Wisdom is to have dreams that are big enough
not to lose sight when we pursue them.*

*La sagesse c'est d'avoir des rêves suffisamment
grands pour ne pas les perdre de vue
lorsqu'on les poursuit.*

Oscar Wilde

Chapter 1

General introduction



Picture: M. Desprez

Life-history strategies and costs of reproduction

Animals display tremendous diversity in their patterns of growth, maturation, reproduction and survival. These patterns, or life-history strategies, result from a complex combination of demographic traits (size at birth, growth rate, age and size at maturity, number, size and sex-ratio of offspring, lifespan, etc) that should maximise individuals' reproductive success (*i.e.* the ability to pass on genes to the next generation) in a particular environment (Roff 1992; Stearns 1992). Reproductive success would obviously be maximal if individuals started reproducing immediately after birth, produced an infinite number of offspring and lived forever. Yet such "Darwinian demons" (Law 1979) do not exist in the real world because individuals dispose of limited resources that must be competitively allocated to the different vital functions. Allocating resources towards any particular life-history trait is always done to the detriment of another trait and consequently traits competing for the same resources (*e.g.* longevity and fecundity) cannot be simultaneously maximised. These constraints, or trade-offs, have led to the evolution of various patterns of life history that can be distributed along a slow-fast continuum that contrasts species with relative slow turnover to species with fast turnover (Gaillard *et al.* 1989; Promislow & Harvey 1990; Sæther & Bakke 2000). *Fast* species (also sometimes referred to as r-selected species) are generally characterized by a short life span, early maturity and high fecundity (*i.e.* produce many offspring *per* reproductive event). At the other end of the spectrum, *slow* species (or K-selected species) are associated with long life expectancy, delayed age at maturity and low fecundity. Two mammalian species commonly cited to illustrate the extremes of life-history strategies are the house mouse (*Mus musculus*) and the blue whale (*Balaenoptera musculus*). Mice live on average 2 years and reach maturity at 5-7 weeks. Once sexually mature, they produce 5 to 10 litters a year with an average of 5-6 young *per* litter. At the opposite extreme, blue whales are thought to live up to 80-90 years, maybe even longer. They become sexually mature between 5 to 15 years of age and give birth only every 2-6 years to a single offspring.

Variation in life history strategies not only exists between species but also within species. Even if all members of a species share a common broad life history (*e.g.* in a *slow* species: long life expectancy, delayed maturity and low fecundity), each individual may allocate its resources somewhat differently over its lifetime as a function of extrinsic and intrinsic factors. Individuals of the same species may therefore vary widely in their age at primiparity, the number of offspring they produce *per* breeding event, the number of reproductive events

they undertake over lifetime, etc. Once again, these different life-history decisions are all constrained by trade-offs, allocating energy towards one particular trait precluding allocation towards another (Roff 1992; Stearns 1992).

Stearns (1989) enumerated 45 possible trade-offs between 10 major life-history traits (Table 1.1). The most prominent of these trade-offs is the cost of reproduction (Williams 1966) in which a high allocation of resources to current reproduction may lead to reduced survival, a lower probability of breeding in subsequent years and/or decreased offspring quality. The occurrence and intensity of the cost of reproduction is influenced by (1) individual differences in resource acquisition and allocation (Van Noordwijk & de Jong 1986) and (2) variation in environmental conditions (*i.e.* the quantity and quality of resources available) (Erikstad *et al.* 1998). The ability of an individual to acquire resources at a given time depends on its 'state' at this time (McNamara & Houston 1996). This state can be defined by various features including, among others, age, body mass, reproductive experience, foraging skills, territory quality, state of immune system, dominance status, etc. Individuals able to obtain more resources are generally better able to cope with the costs of reproduction (Bonnet *et al.* 2002; Hamel *et al.* 2009). The way individuals then allocate the acquired resources between the competing functions may vary according to their species-specific strategy. In *fast* species, individuals are more likely to allocate high reproductive effort on each of their few reproductive occasions (Stearns 1992). On the contrary, in *slow* species, individuals have developed a conservative reproductive strategy and are less prone to trade their own survival for that of their offspring as, for them, longevity is the key to obtaining the greatest reproductive success (Clutton-Brock 1988; Newton 1989). Consequently, the costs of reproduction has mainly been reported in terms of future survival in *fast* species and in terms of future reproduction in *slow* species (Hamel *et al.* 2010b). However, the strategy of resource allocation may vary throughout an individuals' life. For example, according to the "restraint hypothesis" (Williams 1966; Pianka & Parker 1975), long-lived individuals should invest less in reproduction when young because of the associated cost and the increased risk of mortality. However, when older, they should increase their reproductive effort as their residual reproductive value decreases. The preferred trait towards which a long-lived individual allocates its resources may therefore depend on its age (survival when young and reproduction when old). Finally, the acquisition of resources and the strategy of allocation are influenced by environmental conditions. When resources are abundant, competition among life-history traits is minimized, survival and reproduction can be optimised and reproductive

costs are masked. However, when resources are scarce, individuals should favour one function over another in order to optimise their reproductive success. Costs of reproduction may therefore only be evident in unfavourable environmental conditions (e.g. harsh weather (Tavecchia *et al.* 2005), high density (Festa-Bianchet *et al.* 1998; Hamel *et al.* 2010a) or high levels of competition for resources (Lindström 2001)).

Trait 1		Trait 2								
		PS	FR	PG	PC	NO	SO	OG	OC	OS
Current reproduction	CR	1	2	3	4	<i>5</i>	<i>6</i>	<i>7</i>	<i>8</i>	<i>9</i>
Parental survival	PS	-	10	11	12	<i>13</i>	<i>14</i>	<i>15</i>	<i>16</i>	<i>17</i>
Future reproduction	FR		-	18	19	<i>20</i>	<i>21</i>	<i>22</i>	<i>23</i>	<i>24</i>
Parental growth	PG			-	25	<i>26</i>	<i>27</i>	<i>28</i>	<i>29</i>	<i>30</i>
Parental condition	PC				-	<i>31</i>	<i>32</i>	<i>33</i>	<i>34</i>	<i>35</i>
Number of offspring	NO					-	<i>36</i>	<i>37</i>	<i>38</i>	<i>39</i>
Size of offspring	SO						-	40	41	42
Offspring growth	OG							-	43	44
Offspring condition	OC								-	45
Offspring survival	OS									-

Table 1.1. An incomplete trade-off matrix for life-history traits. Parental survival and parental growth: from the current reproductive episode to the next. Parental condition: taken between this reproductive episode and the next, preferably on a standard date critical for survival (e.g. late winter). Size of offspring: to be reported as a series of sizes for species with parental care [birth, fledging, independence). Additional columns could be added to represent the trade-offs associated with maturation. Intra-individual trade-offs are indicated in bold type. Intergenerational trade-offs are indicated in italics (from Stearns 1989).

The existence of costs of reproduction is a central assumption in life-history theory (Roff 1992; Stearns 1992). These costs play a key role in the evolution of reproductive tactics and may have profound consequences on population dynamics (Proaktor *et al.* 2008). Accordingly, quantifying reproductive costs is a fundamental topic of research in ecology. However, their detection and measurement in wild populations is not straightforward.

Studying reproductive costs in wild populations

Reznick (1985) identified four different approaches for assessing costs of reproduction: (1) phenotypic correlations between life-history parameters, (2) experimental manipulations of a given reproductive trait in order to measure the cost-related response in other traits, (3)

genetic correlations between life-history components determined through quantitative genetic analysis and (4) selection experiments measuring the response of life-history components to changes in allocation. However, determining genetic costs and/or conducting experimental manipulations (approaches 2, 3 and 4) is often difficult or impractical in wild populations, especially in the case of large species. Consequently, phenotypic correlations may often be the only practical method available to estimate costs of reproduction. To be robust, phenotypic correlations need to be assessed from high-quality data collected from continual monitoring of individuals from birth to death, which may raise logistical and methodological issues. First, long-term individual-based studies are often complicated to run and difficult to maintain (Clutton-Brock & Sheldon 2010). Second, wild individuals are not always observable and their life histories are therefore only partially known raising some fundamental questions: what is the state of an unobserved individual? is it alive or dead? if alive, is it breeding or not? This issue of imperfect detection has long been ignored in evolutionary biology, unobserved individuals being sometimes considered as dead while they may just have dispersed from the study area. Yet ignoring this imperfect detection can lead to biases in demographic estimates and flawed inferences (Gimenez *et al.* 2008). Capture-recapture models have been specifically designed to avoid this issue by accounting for imperfect detection while estimating parameters of primary interest (Lebreton *et al.* 1992). In particular, the development of multi-state capture-recapture models has played a central role in studies of evolutionary trade-offs (*e.g.* Nichols *et al.* (1994); Nichols & Kendall (1995); Cam & Monnat (2000); Doligez *et al.* (2002); Yoccoz *et al.* (2002); Barbraud & Weimerskirch (2005); Hadley *et al.* (2007); Rotella (2009)). Besides dealing with the issue of imperfect detection, these models allow individuals to move within a finite number of 'states' throughout their life ('state' referring to any attribute of an individual). By casting reproductive status (*e.g.* breeders and nonbreeders) as states, multi-state models can be used to estimate breeding probabilities, corresponding to the transition probabilities between and among reproductive states, and state-specific vital rates. Investigating costs of reproduction is then possible by comparing the demographic parameters obtained for breeders with the ones estimated for nonbreeders.

Despite their usefulness in estimating reproductive costs, multi-state capture-recapture models present a major limitation: they assume that all detected individuals can be assigned to a particular reproductive status with certainty. This requirement may be difficult to meet in practice: what is the reproductive status of an individual detected outside the breeding season

(e.g. when feeding, moulting, etc), or detected without young during the breeding season? Uncertainty in state assignment is unavoidable in many situations, particularly when individuals are observed at a distance. To avoid censoring data that include uncertain or unknown states, often constituting the bulk of the information collected, Pradel (2005) proposed an extension of multi-state models, the multi-event models, that account for uncertainty in state assignment. The main idea behind this modelling approach is to separate what is directly observable in the field, called the 'events' and encoded in the capture histories, from the underlying biological states that must be inferred and are of primary interest. Multi-event models therefore describe two processes: the process of transition among states and the process of generation of events given the underlying state (Fig 1.1) (see Pradel (2005, 2009) for a formal description and technical details of these models).

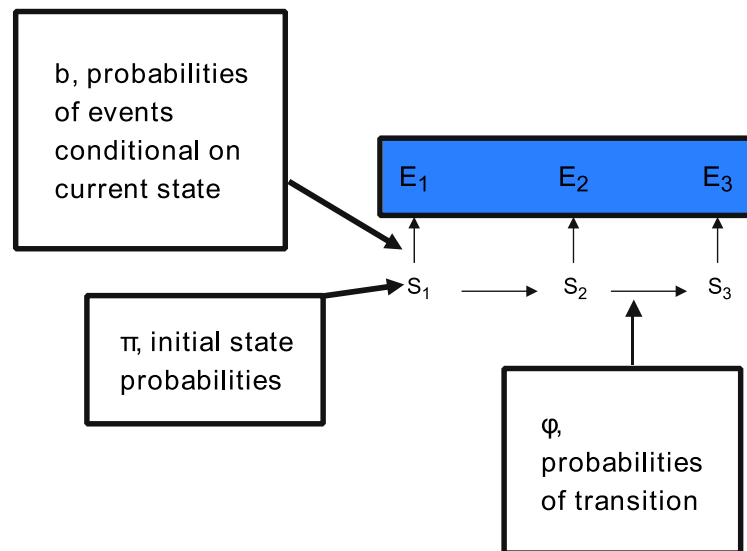


Fig. 1.1. A schematic representation of the rationale of multi-event models. The encounter history (or capture history) of a marked individual (blue box) is made of the observations (called events) E_i . The states S_i are related to the observed encounter history through the probabilities of generation of events given the states b (from Pradel et al 2009).

Multi-event modelling approach is widely applicable across all domains of ecological research (Pradel 2009; Gimenez *et al.* 2012). By dealing with uncertainty in reproductive status, these models can be particularly valuable for assessing costs of reproduction, especially in species whose life cycle is mostly unobservable. Marine mammals, for example, spend most or all of their life at sea and may only be observable on a restricted time period. Demographic data collected on these species are therefore very likely to include a high level of uncertainty.

Southern elephant seals

The southern elephant seal (*Mirounga leonina*) is an ideal species to test life-history predictions in long-lived species. Although elephant seals are predominantly marine foragers, they return to land twice each year to breed and to moult enabling access for marking and resighting. Elephant seals are extreme capital breeders, as lactating females rely entirely on their stored reserves for the 24-day pup-rearing period. The occurrence of pregnancy in pinniped capital breeders is thought to be very sensitive to body reserves (Boyd 2000) and so female elephant seals may only be able to reproduce when their body condition (defined here as the amount of available lipid relative to lean tissue) is above a threshold. Breeding in this species is therefore very likely to depend on both individual quality (*i.e.* the seal's ability to forage successfully and to assimilate nutrients and synthesize fat content) and environmental conditions during foraging trips. Variable life-history strategies are therefore likely to exist within the same population.

Elephant seals have a pole-ward migration feeding throughout the Southern Ocean, one of the biggest marine ecosystems and a major component of the Earth's climate system. By their position near the apex of the trophic system, elephant seals are considered to be indicators of environmental change, their population fluctuations reliably integrating and reflecting prevailing environmental conditions (Van den Hoff *et al.* 2014). Therefore, investigating variation in elephant seal life-history traits is important not only to understanding how these changes affect the population dynamics, but also for detecting and understanding changes in the Southern Ocean ecosystem.

Biology and life cycle

Southern elephant seals are the largest pinniped and one of the most polygynous and sexually dimorphic species of all mammals, some mature males weighing up to almost ten times more (1500-3700 kg) than females (400-800 kg) (Laws 1953; Campagna 2008). Elephant seals spend most of their life at sea, undertaking extensive foraging trips (often over 5000 km in a round trip) throughout the Southern Ocean (Hindell *et al.* 2003b; Biuw *et al.* 2007). They prey on deep-water squid and fish (Slip 1995; Daneri & Carlini 2002; Van den Hoff *et al.* 2003) and have developed the remarkable ability to dive to depths in excess of 2000m and for as long as 120 minutes (Hindell *et al.* 1992; McIntyre *et al.* 2010). While these values are the

extremes of those recorded, the average values remain impressive. Adult females routinely make multiple consecutive dives of 20 minutes reaching depths of 400-800m while males generally dive for longer periods (about 30 minutes) but to lesser depths, reflecting their tendency to feed over continental shelves (while females forage in deeper open water) (Hindell *et al.* 1991). These foraging trips are interrupted by two annual terrestrial haul-outs to breed (September-November) and to moult (during the austral summer). The breeding haul-out is replaced with a mid-year/winter haul-out (from March to August) in the case of sexually immature individuals (Carrick *et al.* 1962b; Hindell & Burton 1988b). The timing of the terrestrial phases is highly predictable but varies slightly according to the individuals' sex and age (Fig 1.2) (Carrick *et al.* 1962b; Hindell & Burton 1988b). In August, sexually mature males start coming ashore to establish territories marking the beginning of the breeding season. Male elephant seals reach sexual maturity at the age of 4 but become socially mature (*i.e.* large and experienced enough to compete with other males) at much older ages (around 10 years old) (Jones 1981). Pregnant females start returning to land in September and aggregate into 'harems' (sometimes consisting of more than a hundred females) controlled by dominant males ('beachmasters'). The number of females ashore increases until reaching a peak at mid-October. A few days after their return, females give birth to a single pup, weighing between 30 and 40 kg, which they nurse for approximately 24 days (Laws 1953). Age at first pupping in females ranges between 3 and 8 years of age. Because elephant seals are capital breeders in which males do not contribute to the care of pups, nursing results in extreme reduction in female body mass (35% on average over the 24-day lactation period) (Fedak *et al.* 1996; Arnborn *et al.* 1997). The pups are weaned when females abruptly abandon them and depart to sea to rebuild their energetic reserves. By this time, pups weigh approximately 120-130 kg.

The females become sexually receptive just prior to weaning and mate before leaving the harem. Although fertilization takes place at this time, the blastocyst does not implant until the end of the moult, approximately three months later (Fig. 1.3). Until recently, female southern elephant seals were assumed to breed (pup and mate) annually from primiparity to death but de Bruyn *et al.* (2011) reported that intermittent breeding occurs in the Marion Island population. The breeding season ends in late November when the last of the males and females return to sea.

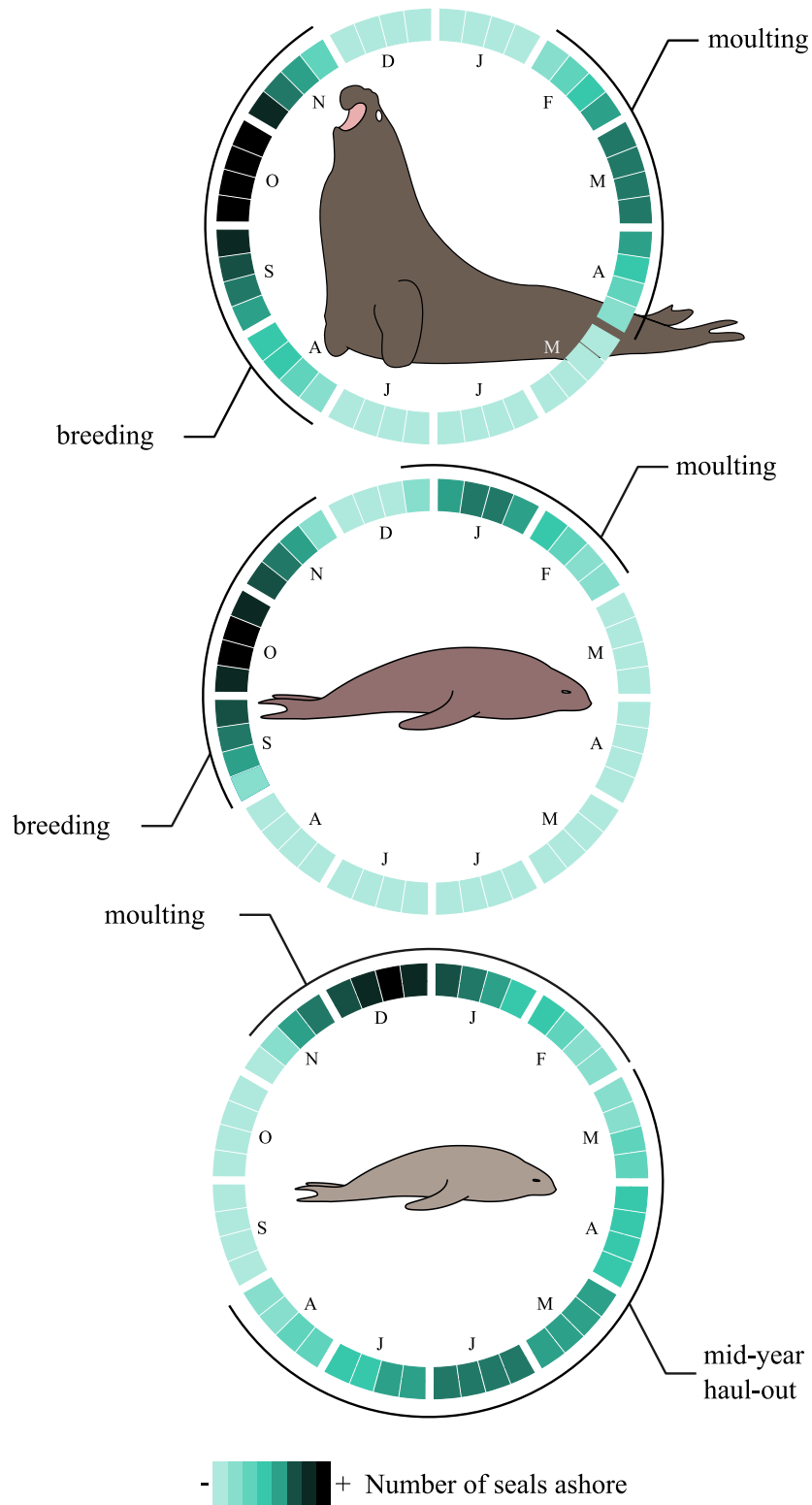


Fig. 1.2. A schematic representation of the annual cycle on land of breeding males (top), breeding females (middle) and juveniles (bottom) southern elephant seals at Macquarie Island. Capital letters represent the months.

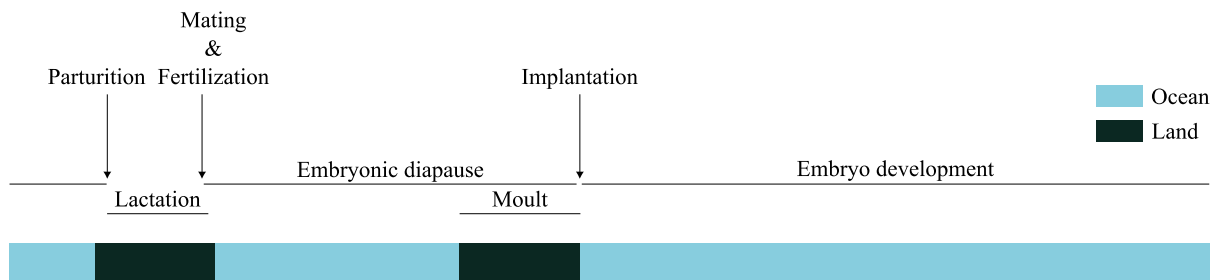


Fig. 1.3. A schematic representation of the reproductive cycle of breeding female southern elephant seals at Macquarie Island.

As the breeding season is ending, juveniles return to land for their annual moult. In elephant seals, the moult not only entails the shedding of the hair but also of the first layer of skin. The rich supplies of blood needed at the body surface for the new skin and hair require the seals to leave the water in order to conserve body heat. The duration of the moult varies from around 30 days for younger seals to around 55 days for older sub-adult males. While ashore, elephant seals do not feed and rely entirely on their stored reserves accumulated during the preceding foraging trip at sea. The number of juveniles ashore peak in mid-December before declining to a low level in February. Adult females begin hauling out in late December after a post-breeding foraging trip that lasts a minimum of 70 days (Hindell *et al.* 1991; Hindell *et al.* 2003b). Most females have completed their moult and left the area by the end of February. Finally, adult males come ashore to moult from mid-February to the end of April.

Distribution and population status

Southern elephant seals have a circumpolar distribution that ranges mainly between 35°S and 70°S (Laws 1994; McMahon *et al.* 2005a). While they travel long distances to forage (Hindell *et al.* 2003b; Biuw *et al.* 2007), elephant seals display a high level of philopatry returning to breed close to or at their natal sites (Nicholls 1970; Lewis *et al.* 1996). On the basis of their breeding locations, four genetically distinct populations have been identified (Slade *et al.* 1998; Hoelzel *et al.* 2001): the South Georgia population ($\approx 400\,000$ individuals) in the south Atlantic, the Îles Kerguelen population ($\approx 220\,000$ individuals) in the south Indian Ocean, the Macquarie Island population ($\approx 76\,000$ individuals) in the south Pacific Ocean and the Peninsula Valdés Population ($\approx 42\,000$ individuals) in Argentina (McMahon *et al.* 2005a). These four populations constitute about 98% of the global population of southern elephant

seals. The remaining 2% consists of small subpopulations scattered throughout the sub-Antarctic and adjoining regions (Laws 1994) (Fig 1.4).

Between the 1950s and 1990s, substantial declines in the southern Indian Ocean and the southern Pacific Ocean populations were observed (Laws 1994; McMahon *et al.* 2005a). The primary reason of these declines is still unclear but food limitation stands out as the most likely explanation (McMahon *et al.* 2005a). Recent studies suggest that the southern Indian Ocean population is now stable or increasing (Slip & Burton 1999; Pistorius *et al.* 2004; McMahon *et al.* 2009; Authier *et al.* 2011). However, the Macquarie Island population continues to decrease at a reported rate of 0.8% per year (Van den Hoff *et al.* 2014). While the southern elephant seal is classified as 'Least Concern' on the IUCN red list (Campagna 2008), the population decline at Macquarie Island has been of sufficient concern so that the southern elephant seal has been listed as 'Vulnerable' under the Australian Environment Protection and Biodiversity Conservation Act 1999 (Department of the Environment, Australia).

Population monitoring on Macquarie Island

Macquarie Island (54°30' S, 158°57' E) is home to a large population (~ 18 000 breeding females) of southern elephant seals. From 1993 to 1999, around 14 000 recently weaned seals (\approx 2 000 each year) were permanently marked by hot iron branding (McMahon *et al.* 2006b; McMahon *et al.* 2006c) on the isthmus of the island (Fig 1.5). Throughout the year, until 2001, daily searches for branded individuals were made on the Isthmus, the main study area. The top third of the island was searched every ten days while the rest of the coastline was searched monthly. From 2002, resightings were opportunistic. Each marked seal resighted was recorded along with its sex and reproductive status when identified.

Besides the data collection required for the capture-mark-recapture program, the population of elephant seals has been counted annually on the isthmus and almost every year on the entire island from 1988 (Fig 1.6). The count is done on the 15th October which corresponds to the peak haul-out date of breeding females (Hindell & Burton 1988b).

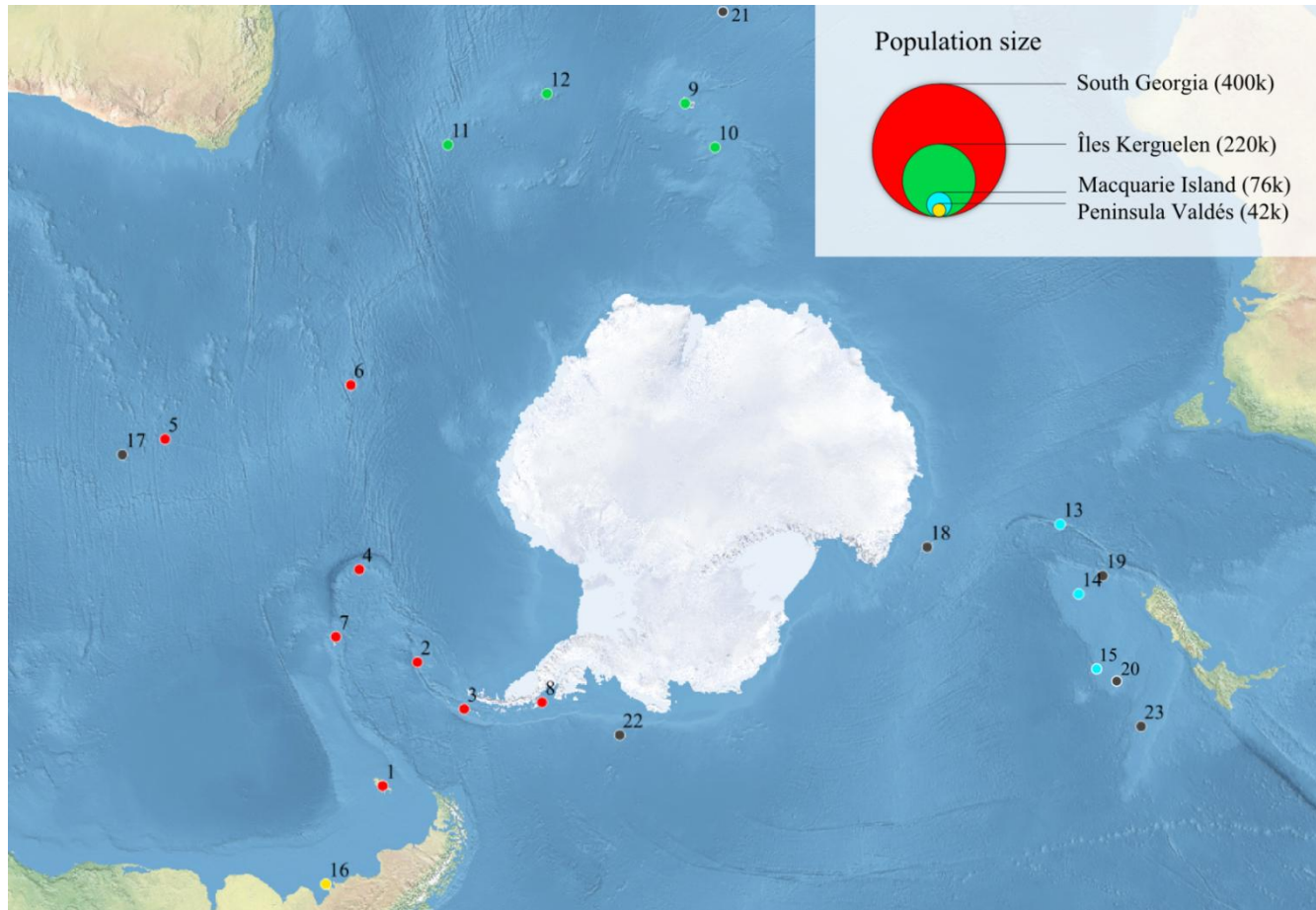


Fig. 1.4. Distribution of the populations of southern elephant seals. Antarctica is displayed in the centre of the map. Subpopulations constituting the South Georgia population, the Îles Kerguelen population, the Macquarie Island population and the Peninsula Valdés population are represented in red, green, blue and yellow respectively. The grey points represent other small subpopulations. 1: Falkland Islands, 2: South Orkney Islands, 3: South Shetland Islands, 4: South Sandwich Islands, 5: Gough Island, 6: Bouvet Island, 7: South Georgia, 8: Avian Island, 9: Îles Kerguelen, 10: Heard Island, 11: Marion Island and Prince Edward Islands, 12: Îles Crozet, 13: Macquarie Island, 14: Campbell Island, 15: Antipodes Island, 16: Peninsula Valdés, 17: Tristan da Cunha, 18: Balleny Islands, 19: Auckland Island, 20: Bounty Island, 21: Amsterdam and St Paul Islands, 22: Peter I Oy, 23: Chatham Island. (map by Guillaume de Boyer)

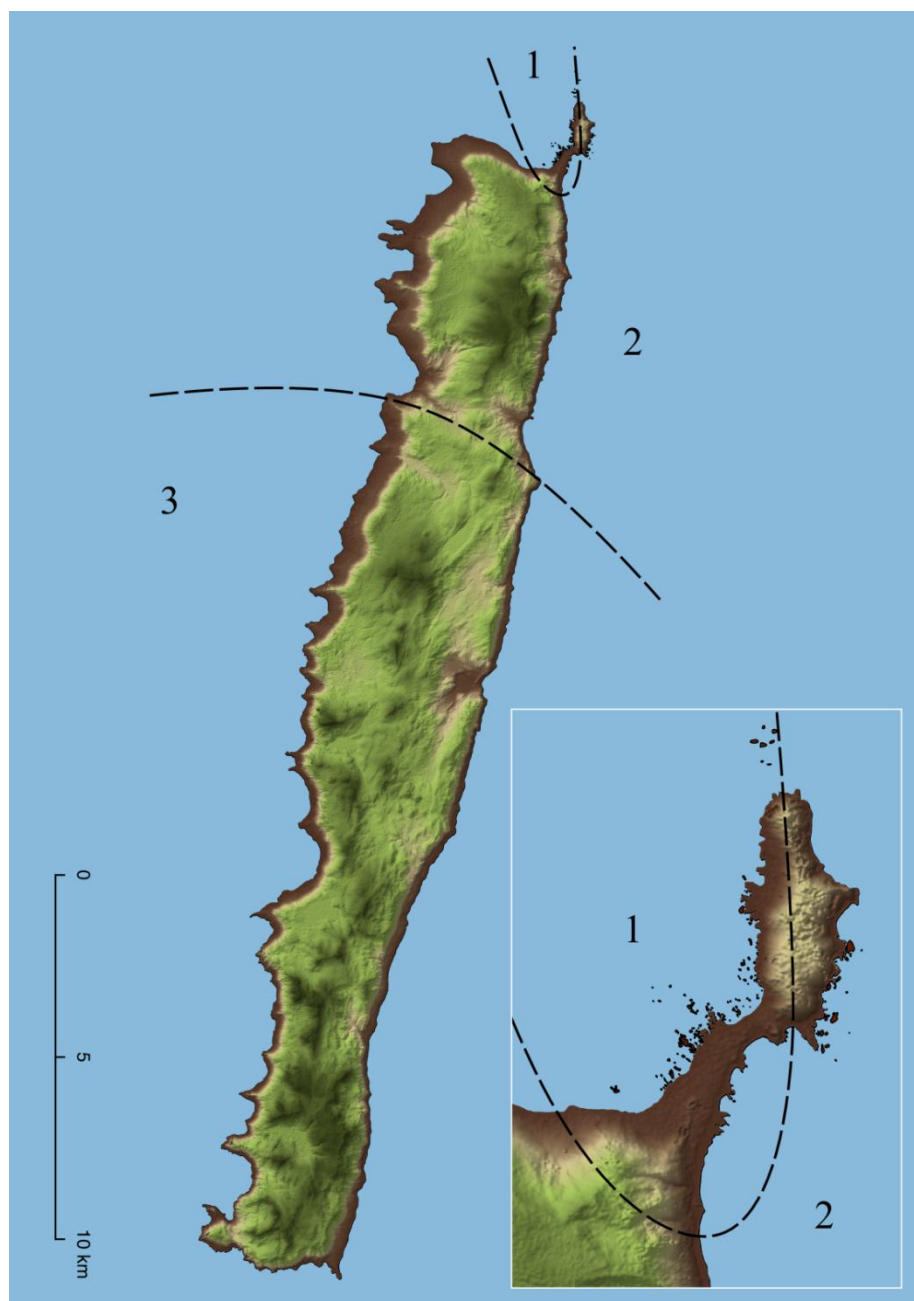


Fig. 1.5. Areas of fieldwork effort at Macquarie Island. All seals were branded in the area 1. Resightings were done 1- daily, 2- every ten days and 3- once a month. (map by Guillaume de Boyer)

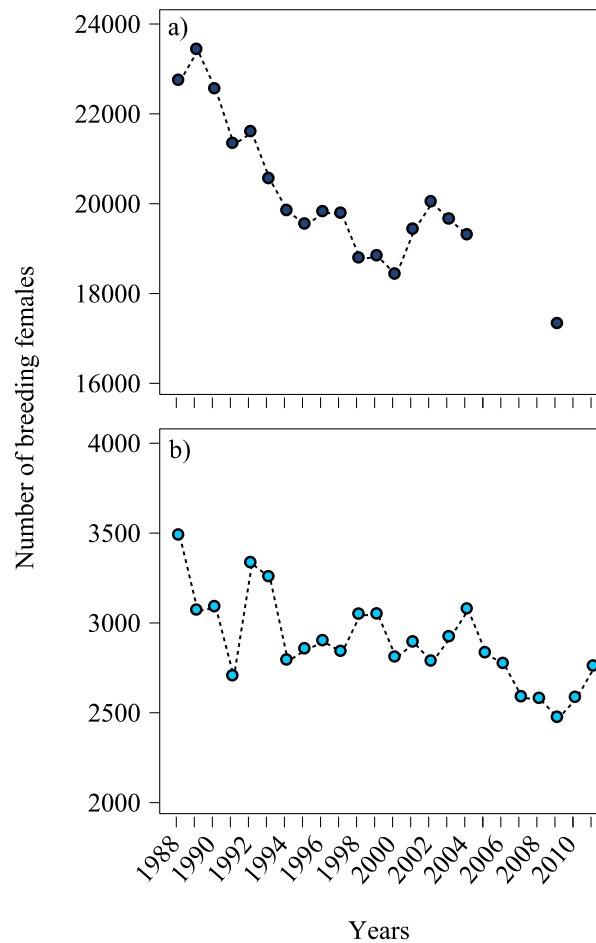


Fig. 1.6. Number of breeding females counted on the 15th October at Macquarie Island between 1988 and 2011 on a) the whole island and b) the Isthmus.

Sources of uncertainty in reproductive states assessment

The first obvious source of uncertainty in the assessment of an individual's reproductive status in a year is when a seal is detected outside the breeding season only (*i.e.* during its moult or mid-year haulout). In this case, it is impossible for the observer to know if the seal has been breeding or not during the current year. Sources of uncertainty can also arise during the breeding season. In males, with the exception of the beachmaster, assigning reproductive status is extremely difficult. Young sexually mature males, even if still too small and inexperienced to compete in harems, often stay nearby trying to mate with the females. Copulation events involving these males are rarely observed but may still be successful in producing offspring (Fabiani *et al.* 2004). In females, the presence of a pup in close proximity is often taken as a proof of their breeding status. However, because the end of the breeding season and the beginning of juvenile moulting period overlap, it is not always possible to

make the distinction between a seal coming ashore for its annual moult and a breeding female that may have recently lost her pup. This is particularly true for first-time breeders that are known to have a lower probability of breeding successfully than experienced individuals (Cam & Monnat 2000). At Macquarie Island, females often give birth on exposed beaches and pups may be washed away during storms. If this event happens before observers record the presence of pups, it is not possible to know with certainty if a female seen without a pup gave birth or not.

Uncertainty in reproductive status assignment was limited in females hauling-out on the Isthmus when daily resightings were made (and therefore multiple resightings within a year were generally available for each female limiting the risk of uncertainty in their reproductive status). However, the level of uncertainty was much higher for females detected elsewhere on the island, with some females detected only once during the entire breeding season. Female elephant seals are highly philopatric (Nicholls 1970; Lewis *et al.* 1996). Nevertheless, they may haul-out on different areas of the island throughout their life (*i.e.* females born on the isthmus do not automatically breed on the isthmus). Consequently, the number of females whose life-history included one or several occasions for which the reproductive status could not be ascertained represented a large percentage of the population.

Aims and thesis structure

The overarching aim of this thesis was to gain further insights into the demographic mechanisms that influence the population dynamics of southern elephant seals. Population dynamics depend on processes that affect the survival and reproduction and on the amount of variation in each of these processes. Therefore, I paid particular attention to the costs of reproduction that may affect survival and future reproduction and investigated how variation in individual traits (*i.e.* age, reproductive status, breeding experience) and environmental conditions influenced the occurrence and intensity of these costs. After confirming the decline of the Macquarie Island population of southern elephant seals, I also explored the life-history traits that most influenced the population growth. Understanding variation in life-histories between individuals and the intrinsic population dynamics may enable a better understanding of the proximate causes of the population decline at Macquarie Island.

This thesis has four main parts: (i) dealing with uncertainty in reproductive status, (ii) quantifying the costs of reproduction, (iii) confirming the population trend and finally (iv) synthesis and conclusion. Each part consists of one or two chapters, with each chapter discussing one specific research topic. In this thesis, I focus solely on the female segment of the population, assuming that female reproduction was not limited by male availability. This choice, a female-only focus, was mainly driven by the fact that most male southern elephant seals die before being able to compete in harems and having the opportunity to breed. For those few that lived long enough to breed, there is no data on actual reproductive success, only whether they attained beachmaster status. Consequently, studying reproductive costs in males was likely to be futile in the face of the extremely limited amount of data available.

Dealing with uncertainty in reproductive status

Demographic datasets often contain a large amount of uncertainty in reproductive status, especially in regard to the first breeding event. Censoring all capture histories that include uncertain reproductive states would substantially reduce the size of the dataset and therefore decrease the precision of the life-history parameter estimates making the study of evolutionary trade-offs difficult. As life-history parameter estimates were also used to parameterize the population model (chapter 5), these parameters needed to be estimated as precisely and accurately as possible. Consequently, before addressing any question about life-history strategies, I explored in **chapter 2** a multi-event modeling approach that could deal with uncertain reproductive status. In order to assess and quantify the gain in precision obtained by the use of this model, I compared the age-specific survival and recruitment probabilities estimated with the multi-event model to the ones obtained using a standard multi-state mark-recapture approach. The multi-event model described in this chapter served as a basis for the development of models used in chapter 3 and 4 to investigate variation in life-history strategies.

Quantifying the costs of reproduction

The age at which an individual first reproduces is the result of a trade-off between the benefits of early recruitment (*i.e.* increased breeding opportunities) against the benefits of delayed maturation (*i.e.* greater reproductive success). Age at first breeding can have crucial implications for lifetime reproductive success as breeding too early may lead to a premature

death and breeding too late may reduce the number of breeding opportunities over lifetime. In **chapter 3**, I examined the consequences, in terms of survival, of variation in age at first breeding by estimating the age-specific survival probabilities of first-time breeders and by comparing these estimates with age-specific survival of prebreeders and experienced females (*i.e.* those that had bred at least once in the past). Potential reproductive cost on survival of experienced females was investigated in **chapter 4**. In this chapter, I also explored reproductive costs in terms of future reproduction by estimating the probability to skip breeding the following year in relation to reproductive experience, age, temporal variation and environmental conditions. Finally, I evaluated the consequences of different strategies, in terms of intermittent breeding, on lifetime reproductive success.

Confirming the population trend

The trend of the Macquarie Island population of southern elephant seals has been estimated recently from annual count of breeding females (Van den Hoff *et al.* 2014). In **chapter 5**, I confirm and refine the decline of this population by estimating the population growth rate from a detailed matrix population model parameterized with the demographic estimates obtained in Chapter 4. From this matrix model, I also investigated the life-history trait(s) that has (have) the strongest relative effect on the population growth, information impossible to obtain from census data, in order to improve our understanding of the demographic mechanisms underlying the dynamics of this population.

Conclusions & perspectives

In **chapter 6**, I summarized the findings of my research and suggest several directions for future studies.

Each chapter of this thesis, except for the introductory and concluding chapters, has been written as a paper for publication in peer-reviewed journals. As such, there may be some repetition between the method sections of the various chapters.

Chapter 2

Dealing with uncertainty in reproductive status



Picture: M. Desprez

Published as: Desprez M., McMahon C. R., Hindell M. A., Harcourt R., & Gimenez O. (2013). Known unknowns in an imperfect world: incorporating uncertainty in recruitment estimates using multi-event capture–recapture models. *Ecology and evolution*, 3, 4658–4668.

Abstract

Studying the demography of wild animals remains challenging as several of the critical parts of their life history may be difficult to observe in the field. In particular, determining with certainty when an individual breeds for the first time is not always obvious. This can be problematic because uncertainty about the transition from a prebreeder to a breeder state – recruitment – leads to uncertainty in vital rate estimates and in turn in population projection models. To avoid this issue, the common practice is to discard imperfect data from the analyses. However, this practice can generate a bias in vital rate estimates if uncertainty is related to a specific component of the population and reduces the sample size of the dataset and consequently the statistical power to detect effects of biological interest. Here I compared the demographic parameters assessed from a standard multi-state capture-recapture approach to the estimates obtained from the newly developed multi-event framework that specifically accounts for uncertainty in state assessment. Using a comprehensive longitudinal dataset on southern elephant seals, I demonstrated that the multi-event model enabled us to use all the data collected (6 639 capture-recapture histories *vs.* 4 179 with the multi-state model) by accounting for uncertainty in breeding states, thereby increasing the precision and accuracy of the demographic parameter estimates. The multi-event model allowed us to incorporate imperfect data into demographic analyses. The gain in precision obtained has important implications in the conservation and management of species since limiting uncertainty around vital rates will permit predicting population viability with greater accuracy.

Keywords: breeding state assignment, multi-state capture-recapture models, primiparity, southern elephant seals, state uncertainty, vital rates.

Introduction

Estimating demographic parameters is fundamental to understand animal population dynamics and investigating life-history strategies (Caswell 2001; Morris & Doak 2002; Williams *et al.* 2002). Incorrect estimates of demographic parameters, in particular age of first reproduction, can lead to biased estimates of fitness, flawed inferences about population viability (Patterson & Murray 2008) and make the detection of evolutionary trade-offs difficult (Cam *et al.* 2002; Buoro *et al.* 2012). However, identifying an individual's reproductive status in the field is not always possible. In particular, determining when an individual breeds for the first time can be difficult when the probability of detection within a year is less than one (Buoro *et al.* 2010). In many birds and mammals, young and inexperienced individuals breeding for the first time have less chance of being successful compared to more experienced breeders or individuals that delay their first reproductive event to an older age (Cam & Monnat 2000; Hadley *et al.* 2006; Hadley *et al.* 2007; Sanz-Aguilar *et al.* 2008; Sanz-Aguilar *et al.* 2009; Limmer & Becker 2010). Consequently, young first-time breeders are likely to abort, abandon their offspring or give birth to offspring that do not survive long enough to be detected. Under these circumstances, individuals may be wrongly considered nonbreeders leading to a biased estimate of the age at first reproduction. To avoid making this error, the conservative approach is to analyze only data from individuals whose reproductive status has been determined with certainty and this has been the established practice. However, doing so reduces the sample size of the dataset thereby decreasing the statistical power to detect signals of biological importance and potentially introduces bias in the estimates of age of first reproduction.

Multi-state capture-recapture models (MSM) are widely used to estimate demographic parameters such as survival (Lebreton *et al.* 2009) and transition probabilities between breeding states (Nichols *et al.* 1994; Cam *et al.* 1998; Barbraud & Weimerskirch 2005; Crespin *et al.* 2006; Sanz-Aguilar *et al.* 2008) while accounting for the fact that the probability of detecting an individual in the wild is less than one. Ignoring imperfect detection can lead to biased estimates and flawed inference (Gimenez *et al.* 2008) but this is often not the only source of uncertainty in capture-recapture studies (Pradel 2009). Even when an individual is observed in the field, its status can still remain unknown or uncertain (*e.g.* sex (Nichols *et al.* 2004; Pradel *et al.* 2008; Genovart *et al.* 2012), epidemiologic status (Conn & Cooch 2009), reproductive status (Gimenez *et al.* 2012)). To deal with this issue and

to allow the use of imperfect field data, an extension of the multi-state capture-recapture framework, known as the multi-event model (MEM) (Pradel 2005), has been developed. Besides accounting for imperfect detection, this model also accounts for uncertainties in the assessment of state. The MEM therefore allows the use of all the data collected unlike the MSM that forces a reduction in the sample and potentially removes a whole segment of the population. The MEM framework has already been used to assess, among other things, the probability of skipping reproduction (Sanz-Aguilar *et al.* 2011), the influence of reproductive experience on breeding probabilities (Desprez *et al.* 2011) and to estimate demographic parameters while accounting for mark loss (Juillet *et al.* 2011) (see Gimenez *et al.* 2012 for a detailed review). To date however, no studies aiming to estimate recruitment probabilities while specifically accounting for uncertainty in breeding status have been undertaken.

Estimating demographic parameters from both MSM and MEM requires adequate capture-recapture data and annual observations of reproductive status. In this regard, the Macquarie island population of southern elephant seal (*Mirounga leonina*) provides an ideal study population as a large number of known-age animals have been uniquely marked and resighted. However, the first breeding event in an elephant seal's life remains difficult to observe and record with certainty. This is in part because the end of the breeding season overlaps with the beginning of the juvenile moulting period. Accordingly it is not always possible to distinguish between a young seal coming ashore for its first breeding event from a seal hauling out for its annual moult. Moreover, young sexually mature males, even if still too small and inexperienced to compete in harems (*i.e.* they are socially immature), often remain on the beaches trying to mate. Copulations involving these males are rarely observed but may still be successful, and produce offspring (Fabiani *et al.* 2004). For the females, the presence of a pup in close proximity is often taken as a proof of their breeding status but if first-time breeders lose their pup pre-partum or early post-partum, they may wrongly be considered nonbreeders due to the absence of a pup. Consequently, making the distinction between a juvenile (an individual that has not bred yet) and a first-time breeder is not always obvious.

Here, I used a MEM framework to assess survival and recruitment, from data including individuals for which the breeding state was unknown on one or several occasions. I compared these estimates to those obtained from a standard MSM capture-recapture analysis, in which data from individuals with known breeding status only (juveniles or adults) were analyzed. In particular, I quantified the gain in precision obtained from the use of data

including uncertainties by comparing the standard errors of the same parameter estimates obtained under MSM and MEM.

Material and methods

Introduction to the study species

Southern elephant seals (*Mirounga leonina*) have a circumpolar distribution in the Southern Ocean (McMahon *et al.* 2005a). While they spend most of their lives at sea foraging, they return to land biannually, once to moult (timing depending on sex and age (Hindell & Burton 1988b)) and once to breed (September-November).

Each year from 1993 to 1999, approximately 2 000 recently weaned southern elephant seals were permanently and uniquely marked with hot iron brands (McMahon *et al.* 2006c) at Macquarie Island (54°30'S, 158°50'E). Although elephant seals travel long distances to forage, the Macquarie Island population is considered a closed breeding population and is the only major Pacific sector breeding population in the Southern Ocean (McMahon *et al.* 2005a). Until 2001, intensive searches were made for branded individuals (daily searches on the isthmus, the main study area and the area to which most seals return (McMahon *et al.* 2003); every ten days around the top third of the island and once a month around the whole island). Despite this intensive effort, the first breeding event in an elephant seal's life remained difficult to observe and record with certainty. From 2001 onwards, re-sightings were opportunistic according to availability of personnel.

Our aim was to model the most uncertain part (first breeding events) of the life cycle of elephant seals. As a large proportion of the males die before reaching this step, I analyzed only the data from female seals. To coincide with the southern elephant seal life cycle, I considered that a year started in September and ended in August (*e.g.* the first year of our study runs from September 1993 to August 1994, hereafter referred to as 1993). I considered two breeding states: the juvenile state (individuals that have not bred yet) and the adult state (seals that have bred at least once). I determined the breeding state of a female according to a) the age (all females from 0 to 2 years old were considered juveniles because recruitment never occurred before 3 years of age (McMahon *et al.* 2003)), b) the presence of a pup with

the female (any individual seen with a pup was considered an adult) and c) the period during which the female was seen ashore (details in Appendix A). All females considered 'adults' on one occasion were then considered 'adults' for the rest of their life. An 'unknown' status was assigned each time a breeding state could not be assigned using one of the above criteria.

Multi-state capture-recapture model (MSM)

The standard capture-recapture model used to estimate recruitment probabilities while accounting for imperfect detection was a multi-state model (Lebreton *et al.* 2009) with three states: juveniles (J), adults (A) and dead individuals (D) underlying three observations or events: (1) not seen; (2) seen as juvenile; (3) seen as adult. The breeding status was known with certainty for each individual and each sampling occasion. This model included three parameters: re-sighting probability (p) that linked the observations made in the field to the breeding states, survival probability (ϕ) and transition probability between states (*i.e.* recruitment) (ψ). The observation process and the temporal dynamic of states could be summarized in the matrix of re-sighting probabilities P , with states at t in rows and observations at t in columns, and matrices of survival S and transition T , with states at t in rows and states at $t+1$ in columns:

$$P = \begin{pmatrix} 1 - p^J & p^J & 0 \\ 1 - p^A & 0 & p^A \\ 1 & 0 & 0 \end{pmatrix},$$

$$S = \begin{pmatrix} \phi^J & 0 & 1 - \phi^J \\ 0 & \phi^A & 1 - \phi^A \\ 0 & 0 & 1 \end{pmatrix},$$

$$T = \begin{pmatrix} 1 - \psi^{J \rightarrow A} & \psi^{J \rightarrow A} & 0 \\ 0 & 1 & 0 \\ 0 & 0 & 1 \end{pmatrix}.$$

For instance, a juvenile had a probability p^J of being re-sighted at time t (matrix P , 1st row, 2nd column) and the complementary probability $(1 - p^J)$ not to be seen (matrix P , 1st row, 1st column), whereas its probability of being re-sighted as an adult was null and fixed to 0 (matrix P , 1st row, 3rd column). Then, this individual could either survive from time t to $t+1$ with a probability ϕ^J (matrix S , 1st row, 1st column) or die with a probability $1 - \phi^J$ (matrix S , 1st row, last column). Finally, it could either breed with a probability of $\psi^{J \rightarrow A}$ and become an

adult at $t+1$ (matrix T , 1st row, 2nd column) or remain juvenile with a probability $1 - \psi^{J \rightarrow A}$ (matrix T , 1st row, 1st column). A dead individual however could not be seen. Its probability of being re-sighted was thus fixed to 0 (last row, 2nd and 3rd columns). Its survival probability from time t to $t+1$ was also null and fixed to 0 (matrix S , last row, 1st and 2nd columns) as well as its transition probability to another state (matrix T , last row, 1st and 2nd columns).

Multi-event capture-recapture model (MEM)

To account for uncertainties in the breeding status, I used a multi-event model (Pradel 2005) in which I considered all the possible observations made in the field during a breeding season: an individual may be missed (not seen); seen and assigned as a juvenile; seen with an unknown state; and seen and assigned as an adult. States remained the same as in the previous model, *i.e.* juvenile, adult and dead but, in contrast to the MSM in which there was a strict correspondence between observations and states, several observations might correspond to a single state in the MEM. In the observation process, in addition to the re-sighting probability, I included the probability of state assignment (β) defined as the probability that a reproductive status was assigned with certainty to an individual. The observation process was thus represented by the product of the re-sighting matrix (P) and the breeding state ascertainment matrix (A). Columns of the re-sighting matrix and rows of the breeding state ascertainment matrix corresponded to the events ‘individual not seen’, ‘juvenile detected’ and ‘adult detected’ whereas columns of the breeding state ascertainment matrix corresponded to the four possible observations made in the field (individual not seen; seen and assigned as a juvenile; seen with an unknown state; and seen and assigned as an adult):

$$A = \begin{pmatrix} 1 & 0 & 0 & 0 \\ 0 & \beta^J & 1 - \beta^J & 0 \\ 0 & 0 & 1 - \beta^A & \beta^A \end{pmatrix}.$$

When an individual was seen during a sampling occasion with an unknown breeding status, the model considered all the possible histories. For instance, let us assume that we have 4 sampling occasions, for simplicity, and all individuals are marked as juveniles. We consider an individual with the encounter history 1123 that was marked as a juvenile (1), re-sighted in the second occasion as juvenile (1), seen in the third occasion in an unknown state (2) and finally seen as adult (3). Because the breeding status of this individual was unknown during the second occasion, the time of its recruitment is uncertain. Two scenarios are possible: (i)

this individual was a juvenile when it was observed with an unknown status and the probability is $\phi^J(1-\psi^{J \rightarrow A})p^J\beta^J\phi^J(1-\psi^{J \rightarrow A})p^J(1-\beta^J)\phi^J\psi^{J \rightarrow A}p^A\beta^A$, (ii) it was an adult and the probability is $\phi^J(1-\psi^{J \rightarrow A})p^J\beta^J\phi^J\psi^{J \rightarrow A}p^A(1-\beta^A)\phi^A p^A\beta^A$. These two events being mutually exclusive, the probability for this particular history is the sum of the two possible probabilities.

GOF test

Goodness-of-fit (GOF) tests are not available for capture-recapture models with permanent transitions (from juveniles to adults for both models and from juveniles to unknown state and unknown state to adults for the MEM) (Pradel *et al.* 2005). I assumed that if there was some lack of fit in the MSM, it would affect the MEM in the same way and would not compromise the comparison.

Model selection

For the MSM, I used data consisting of capture-recapture histories from 4 179 individuals for which the breeding state was always known with certainty. In the MEM, I analyzed all the 6 639 capture-recapture histories including 2 460 histories with one or more occasions for which an observed seal's breeding status was unknown. For both MSM and MEM, I fitted a set of models incorporating relevant combinations of temporal and individual effects on each parameter (p , Φ , ψ and β when applicable) sequentially while constraints on remaining parameters were held constant. As the sampling design varied over the study period, I considered an effect of time (representing the temporal variation between sampling periods, *i.e.* 1 year) on the re-sighting and state assignment probabilities. I also investigated a state effect on the re-sighting probability given that juveniles avoid hauling-out during the breeding season (Hindell & Burton 1988b) and were thus less likely to be detected than adults. Assigning a breeding state to female elephant seals was particularly challenging for individuals between 3 and 5 years old. I thus considered, in addition to the temporal variation, an age and state effect on the state assignment probability. I also examined the state and age effect on the survival probability as I expected lower survival for young juveniles than for older individuals (McMahon *et al.* 2003). Regarding temporal effects on the survival and recruitment probabilities, I considered a year effect. As adult survival in long-lived

iteroparous species is more likely to remain stable over time than juvenile survival (Gaillard & Yoccoz 2003), I also examined the case in which only juvenile survival was affected by the time. Finally, I investigated the variability of recruitment probability according to the age of females. Once the main effect was determined for a parameter, I added each of the remaining effects in an additive and interactive fashion to assess if one of these combinations was relevant. I repeated this until no better model was selected. For the MSM, I started by identifying the most appropriate structure for p , then for Φ and finally for ψ using the structure for p and Φ selected in the previous step. For MEM, I proceeded in the same way starting by identifying the structure for β , then for p and Φ and finally for ψ . I selected the most parsimonious model using the Akaike Information Criterion AIC (Burnham & Anderson 2002). Analyses were performed using E-SURGE (Choquet *et al.* 2009b).

Results

The best combination of effects influencing survival, recruitment and resighting probabilities was the same in both MSM and MEM (Table 2.1). Using the method of Choquet and Cole (2012), I noticed that the recruitment parameter (varying with age and time) was not identifiable in the most parsimonious model for both MSM and MEM. Consequently, I considered the model in which recruitment depended only upon age but was identifiable. I checked that survival and resighting probabilities obtained from this model were comparable to the ones estimated from the initial best model.

All parameters (except recruitment) were influenced by temporal variation. In addition to this time effect, resighting and survival probabilities varied according to the breeding state of the seals. Both survival and recruitment probabilities also depended on the age of individuals. Importantly, the MEM allowed a gain in precision for the estimates of resighting and survival as the standard errors for these parameters were lower in the MEM than in the MSM (Fig. 2.1). For recruitment, the standard errors obtained for the older ages (5 and 6 year old) were also lower from the MEM but not for the younger ages (3 and 4 year old) (Fig. 2.1).

Table 2.1. Model selection results for (a) the standard multi-state capture-recapture model and (b) the multi-event capture-recapture model. The two best models selected for each model are in bold characters and the ones selected after checking parameters identifiability are highlighted in blue. Abbreviations: np = number of parameters; t = time effect; a = age effect, c = constant effect, t_{juv} = time effect only on the juvenile state.

(a)

No.	Resighting	Survival	Recruitment	np	AIC	ΔAIC
Modelling resighting probability						
1	t	c	c	19	38183.72	4070.35
2	$state$	c	c	4	37541.75	3428.38
3	$state + t$	c	c	20	35882.67	1769.30
4	$state . t$	c	c	34	35547.54	1434.17
Modelling survival probability						
5	$state . t$	t	c	50	35483.52	1370.15
6	$state . t$	a	c	50	35291.92	1178.55
7	$state . t$	$state$	c	35	35306.70	1193.33
8	$state . t$	$a + t$	c	66	35269.17	1155.80
9	$state . t$	$a . t$	c	186	35271.62	1158.26
10	$state . t$	$a + state$	c	51	34997.94	884.57
11	$state . t$	$a . state$	c	55	34871.81	758.44
12	$state . t$	$a . state + t$	c	88	34823.00	709.63
13	$state . t$	$a . state . t$	c	251	34878.34	764.97
14	$state . t$	$a . state + t_{juv}$	c	71	34834.19	720.83
15	$state . t$	$a . state . t_{juv}$	c	146	34884.66	771.30
Modelling recruitment probability						
16	$state . t$	$a . state + t$	t	102	34848.23	734.86
17	$state . t$	$a . state + t$	a	102	34300.64	187.27
18	$state . t$	$a . state + t$	$a + t$	118	34113.37	0
19	$state . t$	$a . state + t$	$a . t$	207	34128.83	15.47

(b)

No.	State ascertainment	Resighting	Survival	Recruitment	np	AIC	ΔAIC
Modelling state assignment probability							
1	t	c	c	c	19	82115.13	14639.87
2	$state$	c	c	c	5	76305.06	8829.80
3	a	c	c	c	18	78082.77	10607.51
4	$state + t$	c	c	c	22	75938.10	8462.84
5	$state . t$	c	c	c	33	75869.10	8393.84
6	$state + a$	c	c	c	19	75678.92	8203.66
7	$state . a$	c	c	c	22	74626.59	7151.33
8	$state . a + t$	c	c	c	56	74391.90	6916.64
9	$state . a . t$	c	c	c	177	74500.28	7025.02
Modelling resighting probability							
10	$state . a + t$	t	c	c	72	71506.77	4031.51
11	$state . a + t$	$state$	c	c	57	71939.31	4464.05
12	$state . a + t$	$t + state$	c	c	73	69179.87	1704.61
13	$state . a + t$	$t . state$	c	c	87	68793.74	1318.48
Modelling survival probability							
14	$state . a + t$	$t . state$	t	c	103	68769.08	1293.82
15	$state . a + t$	$t . state$	a	c	103	68722.04	1246.78
16	$state . a + t$	$t . state$	$state$	c	88	68421.34	946.08
17	$state . a + t$	$t . state$	$state + t$	c	104	68400.77	925.51
18	$state . a + t$	$t . state$	$state . t$	c	118	68378.39	903.13
19	$state . a + t$	$t . state$	$state + a$	c	104	68269.14	793.88
20	$state . a + t$	$t . state$	$state . a$	c	118	67949.92	474.66
21	$state . a + t$	$t . state$	$state . a + t$	c	150	67847.01	371.75
22	$state . a + t$	$t . state$	$state . a . t$	c	359	67902.75	427.49
23	$state . a + t$	$t . state$	$state . a + t_{juv}$	c	134	67906.55	431.29
24	$state . a + t$	$t . state$	$state . a . t_{juv}$	c	254	67961.76	486.50
Modelling recruitment probability							
25	$state . a + t$	$t . state$	$state . a + t$	t	164	67797.67	322.41
26	$state . a + t$	$t . state$	$state . a + t$	a	164	67542.05	66.79
27	$state . a + t$	$t . state$	$state . a + t$	$a + t$	180	67475.26	0
28	$state . a + t$	$t . state$	$state . a + t$	$a . t$	269	67504.51	29.25

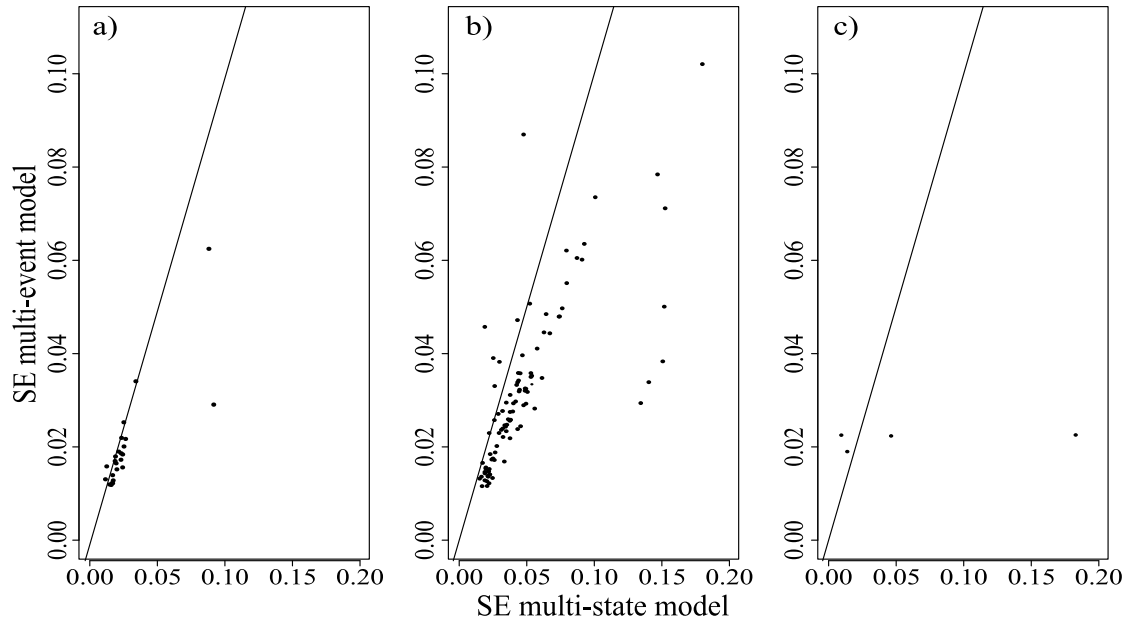


Fig. 2.1. Standard errors for a) resighting probabilities, b) survival probabilities and c) recruitment probabilities of female elephants seals: from the Multi State Model vs. the Multi Event Model. Data points correspond to parameter estimates. The solid line represents the situation in which the SEs are equal for both models parameters estimates.

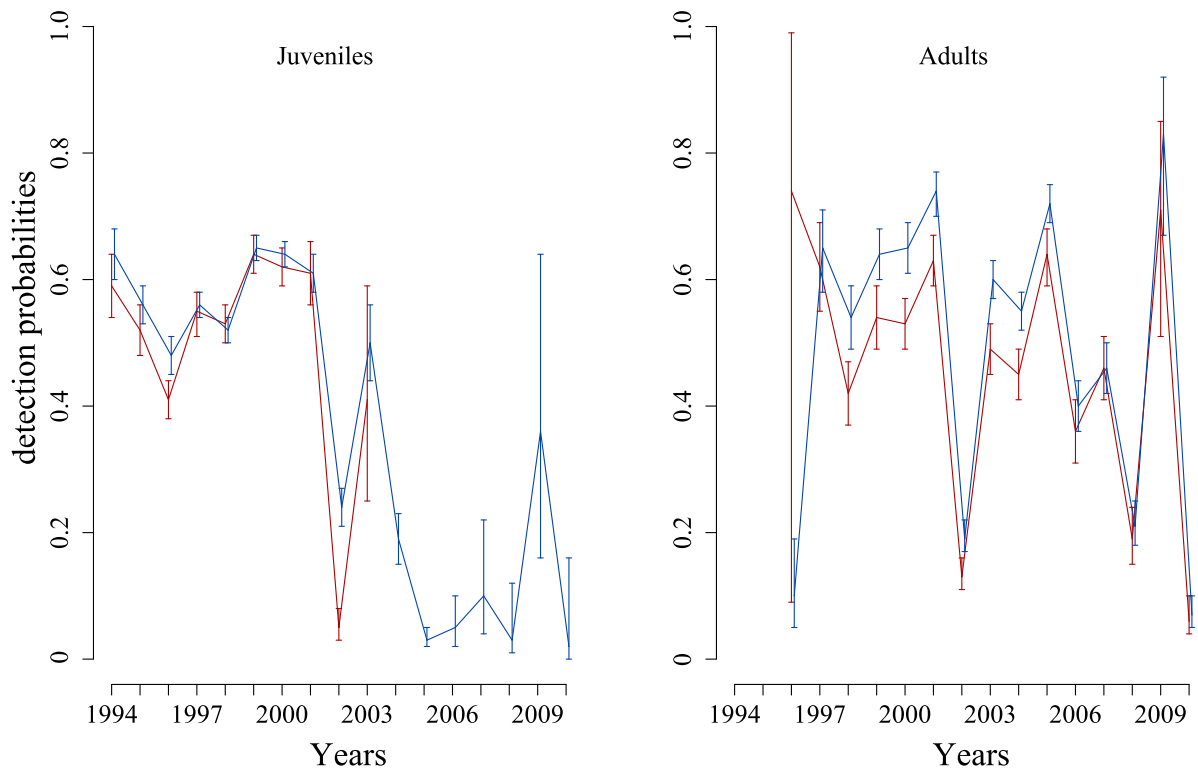


Fig. 2.2. Resighting probabilities of female elephant seals by state, time and type of capture-recapture model. The red line represents estimates from the MSM and the blue line represents estimates from the MEM. First resighting event occurred in 1994 for juveniles and 1996 for adults. Estimates on the boundary are not represented.

Resighting probabilities varied with both breeding state and time, with marked fluctuations over the study period. Estimates from the MEM were higher than the ones obtained from the MSM (except for the resighting probabilities of juveniles in 1998 and for adults in 1996) (Fig. 2.2). From the MSM, resighting probabilities of juveniles were estimated on the boundary from 2004 whereas they were assessed until 2010 from the MEM. For adult resighting probabilities, the trend over years was the same for both MSM and MEM (except in 1996) with very low probabilities in 2002, 2008 and 2010 (Fig. 2.2).

Survival probabilities depended on breeding state, age and time (Table 2.1). For the juveniles, probabilities were lower when estimated from the MSM (except for the 3 year old individuals) (Fig. 2.3). The use of the MEM enabled us to estimate the survival of juveniles until 2002 and for seals up to 8 years old whereas probabilities could not be estimated after 2001 or for seals older than 6 with the MSM (Fig. 2.3 and 2.4). However, the confidence intervals for the survival probabilities obtained from the MEM for seals of 7 and 8 years old were large. Concerning adult survival, the difference between the two models was smaller than for juveniles (Fig. 2.3) apart from the survival probability of the 3 year olds that could not be estimated in the MSM. For both models, no survival probabilities could be estimated in 2009 or for seals older than 14 years old.

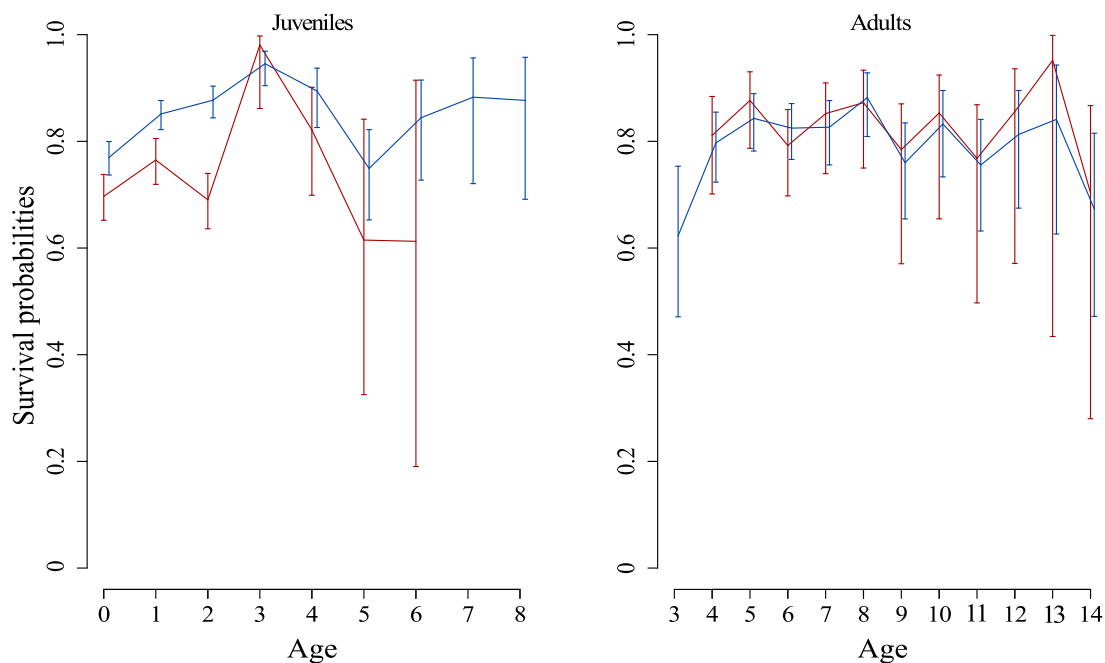


Fig. 2.3. Survival probabilities of female elephant seals by state, age and type of capture-recapture model. Each point shows the survival probability of a specific age averaged over the years. Estimates on the boundary are not represented. The red line represents estimates from the MSM and the blue line represents estimates from the MEM.

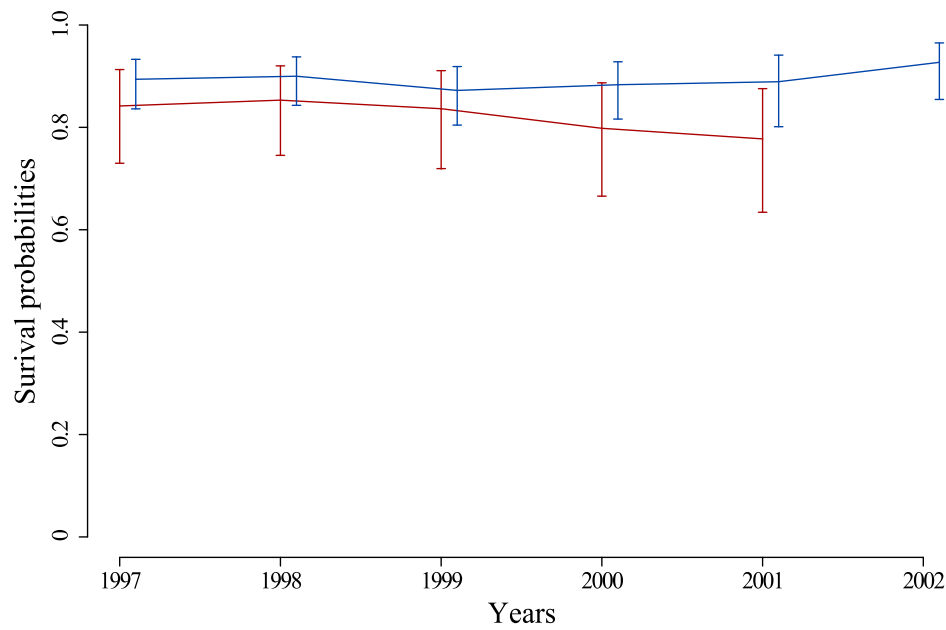


Fig. 2.4. Survival probabilities of the 4 year old female juveniles by year and type of capture-recapture model. Estimates on the boundary are not represented. The red line represents estimates from the MSM and the blue line represents estimates from the MEM.

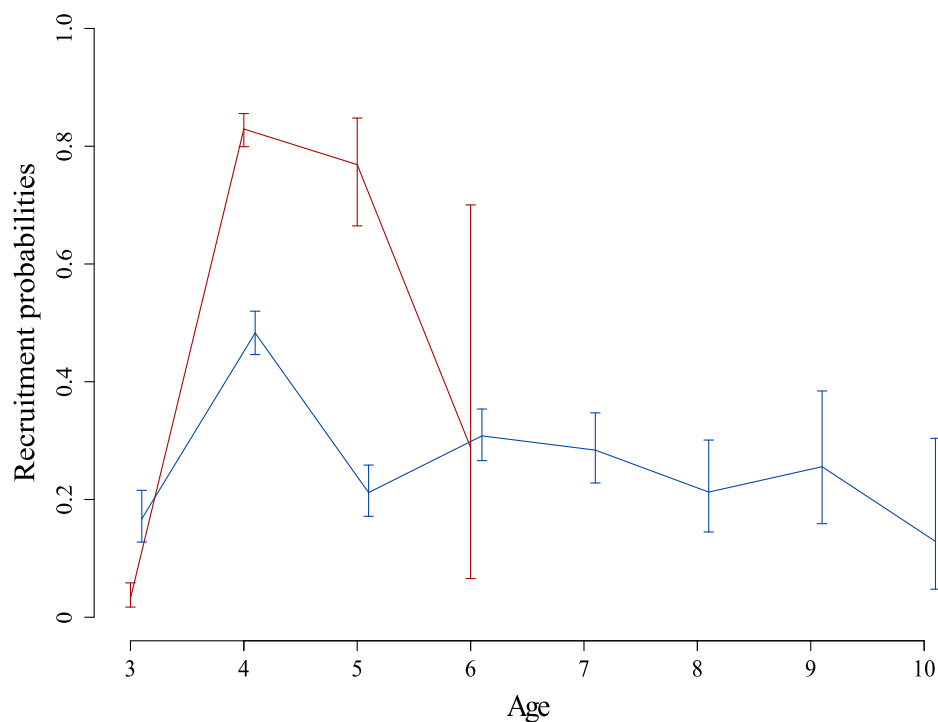


Fig. 2.5. Recruitment probabilities of female elephant seals by age and type of capture-recapture model. Each point shows the probability of recruiting at a particular age averaged over the years. Estimates on the boundary are not represented. The red line represents estimates from the MSM and the blue line represents estimates from the MEM.

Recruitment was influenced by age (Table 2.1). For both models, female elephant seals had the highest probability of recruiting at age 4 (Fig. 2.5). As for survival, the MEM made it possible to estimate recruitment probabilities for older individuals (10 year old *vs.* 6 year old, Fig. 2.5) than the MSM. Probabilities from the MEM were lower than the ones obtained from the MSM (except for the 3 year olds) with a pronounced difference for the recruitment estimates of the 4 and 5 year old seals (Fig. 2.5). Recruitment at 3 years old was low for both models.

State assignment probabilities were only estimated in the MEM and depended upon state, age and time. However, probabilities to assign the juvenile state were not identifiable. All adults detected and older than 5 years were recorded as 'adults' with certainty. Uncertainty about the adult state was very high for 3 year old individuals.

Discussion

Estimating precise demographic parameters, such as recruitment and survival, is of fundamental importance to the study of population dynamics and is needed to provide robust population projections (Lebreton *et al.* 1992; Caswell 2001). Here, by comparing estimates obtained from two different capture-recapture models, the recently developed multi-event model that explicitly accounts for uncertainty in the breeding state of the individuals, and the more standard multi-state model commonly used by ecologists, I show that exploiting data including uncertainty in breeding status can greatly improve the precision and accuracy of the estimates.

Accounting for uncertainty did not affect the structure of the most parsimonious model since the demographic parameters obtained from the MEM and the MSM were influenced by the same combination of effects. However, the precision of the survival and re-sighting probabilities was higher in the MEM. Indeed, as it has already been reported earlier (Pradel *et al.* 2008; Genovart *et al.* 2012), considering capture-recapture histories including both certain and uncertain states can raise the size of the sampled population leading to more precise and accurate estimates. The gain in precision was less obvious when estimating recruitment probability. This is probably due to the fact that uncertainties were directly related to the recruitment parameter and concentrated on the 3 and 4 year olds. Thus, addition of unknown

breeding states in the data slightly reduced the precision of the recruitment estimates for these ages. The difference in recruitment estimates between the two models was more pronounced for the 4 and 5 year olds with probability estimates much lower in the MEM than in the MSM. This is consistent with the fact that only two breeding states (juveniles and adults) were considered in the MSM and the number of seals assigned “juveniles” with certainty was low (<200 at 4 years old and <20 at 5 years old) while the number of adults recorded at these ages was comparatively high (≈ 1000 seals) leading to high probabilities of recruitment. In the MEM, the number of seals assigned to a breeding state was counterbalanced by the number of “unknown” seals (≈ 680 for the 4 years old and ≈ 430 for the 5 years old) that might still be juveniles. Recruitment estimates for the 4 and 5 year old seals were thus reduced in the MEM.

In real world datasets, uncertain field observations often constitute the bulk of the information collected (Nakagawa & Freckleton 2008; Pradel 2009) and particular statistical tools are therefore needed to exploit these data. The MEM, by accounting for uncertainties in breeding status, enabled us to use all the information available and to assess demographic parameters for longer periods and for more age classes than in the standard approach. This may be of particular importance in studies aiming to determine the influence of environmental factors on demographic parameters over time (Nevoux *et al.* 2010) or to investigate senescence or other trade-offs involving age (Hadley *et al.* 2006; Clutton-Brock & Sheldon 2010). However, it is important to note that even though using MEM improved the precision of most estimates, no accurate results could be obtained when the data only included individuals with uncertain breeding states or when resighting probabilities were very low. Consequently, determining and then maintaining an appropriate and constant sampling effort remains of paramount importance in demographic studies (Kendall *et al.* 2009; Clutton-Brock & Sheldon 2010; Magurran *et al.* 2010). This point is clearly illustrated in our study as a lot of uncertainties were induced by changes in the sampling effort for reasons beyond our control (McMahon *et al.* 2006b) (from an intense, systematic re-sighting effort to an opportunistic one, cessation of permanent marking in 1999 and severe restrictions imposed on resighting effort in 2002).

Despite this limitation, the present modelling greatly increased the precision of most of the demographic parameter estimates. This clearly illustrates the importance of including uncertainty in models for conservation and management of wildlife. Being able to include more precise demographic information in population projection models greatly enhances the

ability to produce precise and reliable projected population growth rates (Caswell 2001). This is especially important in the case of species of conservation concern such as the southern elephant seal, for which accurate assessment of population viability is critical but not straightforward. In fact, for many endangered or vulnerable populations, life-history datasets are incomplete, sparse and sporadic and this will lead to imprecise vital rate estimates and subsequently uncertain assessment of population viability. This in turn may lead to inappropriate or even deleterious management decisions. I suggest that using the MEM to improve the precision of demographic parameter estimates will limit uncertainty in population projection models and so improve the reliability of conservation measures.

In conclusion, the MEM increased the precision and accuracy of our demographic parameter estimates showing that imperfect data can be usefully and successfully incorporated into demographic analyses and should not be discarded. However, while using the MEM greatly enhances our ability to deal with uncertainty, such analytical advances cannot replace appropriate sampling effort, and this still remains of paramount importance for studies aiming to quantify vital rates.

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Appendix A. Females state assignment according to haul-out dates

Southern elephant seals have a predictable annual haul-out life cycle characterized by three periods ashore: the breeding season, the moulting period and the mid-year haul-out (mostly for juveniles). I represented the number of females resighted ashore from September to August (to coincide with the elephant seals life cycle) at Macquarie Island over a 60 years period (1951 - 2011) for each age from 3 (age at which the youngest breeding females are detected) to 12 years old. No representation was done for older seals because of the very low number of females resighted. The number of seals ashore during most haul-outs closely approximated a normal distribution (Hindell & Burton 1988b). I used a generalized additive model GAM (Wood 2006) to determine the curve that best fitted the data. I represented the upper and lower 95% confidence interval of this curve (Fig. A.1).

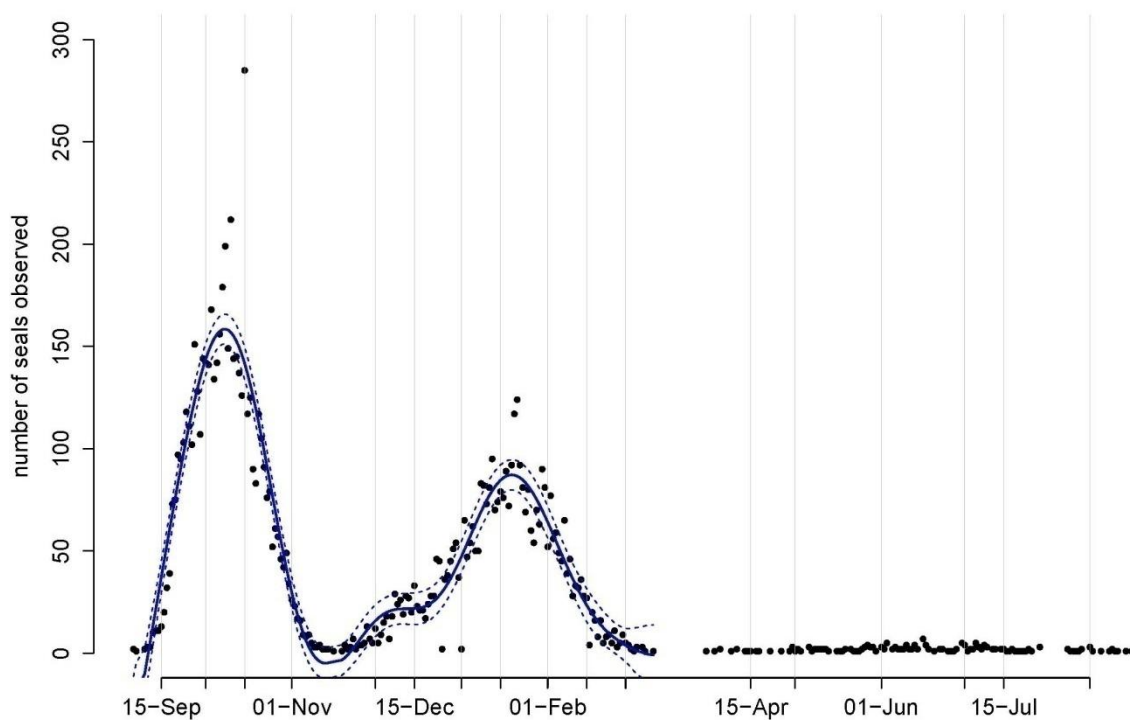


Fig. A.1. Number of female elephant seals of 4 years of age resighted ashore at Macquarie Island over a 60 years period (1951-2011). The solid line represents the curve generated by the generalized additive model and the dotted lines represent the upper and lower bounds of the confidence interval.

I used the lower limit of the confidence interval to determine the dates at which the breeding season and the moulting period started and ended. I considered that the date for which this curve passed through the point 0 (*i.e.* number of seals seen ashore = 0) was the date limiting the breeding season or the moulting period (respectively) (Fig. A.2, Table A.1).

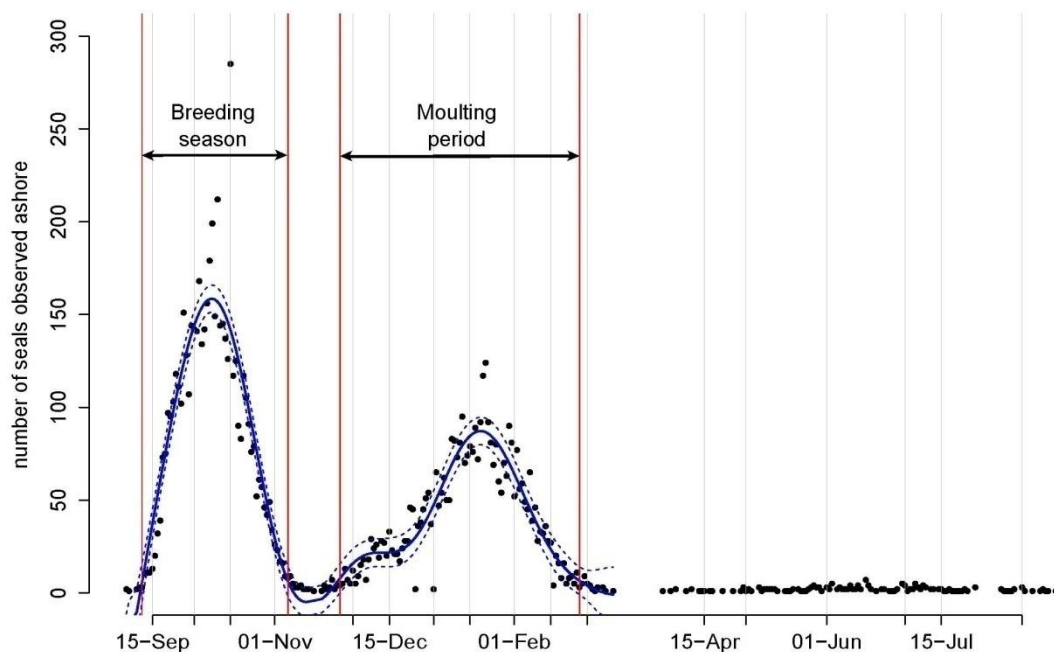


Fig. A.2. Breeding season and moulting period for 4-year old female elephant seals at Macquarie Island.

Age	Breeding season		Moulting period	
	Start	End	Start	End
3	-	-	02 / 11	14 / 02
4	11 / 09	06 / 11	26 / 11	26 / 02
5	08 / 09	15 / 11	07 / 12	26 / 02
6	10 / 09	18 / 11	08 / 12	26 / 02
7	10 / 09	17 / 11	12 / 12	27 / 02
8	09 / 09	13 / 11	20 / 12	23 / 02
9	11 / 09	07 / 12	28 / 12	21 / 02
10	11 / 09	16 / 11	18 / 12	23 / 02
11	13 / 09	14 / 11	21 / 12	18 / 02
12	14 / 09	16 / 11	26 / 12	20 / 02

Table A.1. Dates delimiting the breeding season and the moulting period of adult females elephant seals according to their age. Dates of the breeding season for the 3-year old females could not be determined because of the very low number of 3-year old adults resighted.

Female elephant seals give birth to their pups on average 4 days after their return to land. The minimum period of lactation before the pup weaning is 21.6 days (McMahon & Hindell 2003). Females need to spend a minimum of 70 days at sea before the start of their moult (Hindell *et al.* 1991) to rebuild their fat reserves. Consequently, the minimum return date to land for a breeder is the date of the beginning of the breeding season plus 96 days (Table A.2).

Age	Minimum return date to land for moulting
3	13 / 12
4	16 / 12
5	13 / 12
6	15 / 12
7	15 / 12

Table A.2. Minimum return date to land of adult females according to their age. I did not consider individuals older than 7 years because their minimum return date was before the beginning of the moulting season as determined previously.

For each age class, I considered that all individuals seen ashore during the breeding season were 'adults'. All individuals resighted on land between the end of the breeding season and the minimum return date to land were considered 'juveniles'. All individuals seen ashore outside of these periods were considered 'unknown'. All females considered 'adults' on one occasion were then considered 'adults' for the rest of their life.

For 3-year olds, only individuals seen with a pup were considered adults as I could not determine the dates of the breeding season. To determine the minimum return date to land, I used the minimum start date of the breeding season of all age classes (*i.e.* 08/09).

Individuals older than 7 years of age were only considered 'adults' or 'unknown'.

Chapter 3

Age-specific cost of first reproduction



Picture: B. Arthur

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Abstract

When to commence breeding is a crucial life-history decision that may be the most important determinant of an individual's lifetime reproductive output and can have major consequences on population dynamics. The age at which individuals first reproduce is an important factor influencing the intensity of potential costs (e.g. reduced survival) involved in the first breeding event. However, quantifying age-related variation in the cost of first reproduction in wild animals remains challenging because of the difficulty in reliably recording the first breeding event. Here, using a multi-event capture-recapture model that accounts for both imperfect detection and uncertainty in the breeding status on an 18-year dataset involving 6 637 individuals, I estimated age and state-specific survival of female elephant seals (*Mirounga leonina*) in the declining Macquarie Island population. I detected a clear cost of first reproduction on survival. This cost was higher for both younger first-time breeders and older first-time breeders compared with females recruiting at age four, the overall mean age at first reproduction. Neither earlier primiparity nor delaying primiparity appear to confer any evolutionary advantage, rather the optimal strategy seems to be to start breeding at a single age, four years.

Keywords: Primiparity, Survival, Life History, *Mirounga leonina*, Capture-Mark-Recapture, Demography

Introduction

When to begin breeding is a crucial life-history decision that greatly affects individual fitness and lifetime reproductive output (Stearns 1992). Because reproduction is energetically expensive, the first breeding event can entail a cost that can be expressed through decreased survival and/or reduced future probability of reproduction (Williams 1966). This cost, referred to as the cost of first reproduction, plays a key role in the evolution of life-history strategies and can have fundamental demographic consequences on population dynamics (Stearns 1992).

In low-density, declining populations, individuals are predicted to breed earlier (Eberhardt 1977, 2002). The age at which individuals first reproduce is known to be an important influence on the intensity of the reproductive cost experienced by individuals (Reiter & Le Boeuf 1991; Pyle *et al.* 1997; Tavecchia *et al.* 2001). This is particularly the case in species where size differs greatly between age classes, younger and thus generally smaller first-time breeders being more likely to face a higher cost than individuals delaying first reproduction (Proaktor *et al.* 2007).

In long-lived species, variations in adult survival consistently affect population growth rate (Gaillard & Yoccoz 2003). Hence, quantifying age-related variation in the survival cost of first reproduction is essential to understanding population dynamics and predicting population responses to environmental change. Investigating these variations requires long-term longitudinal monitoring of individuals of both known age and breeding experience. In practice, however, determining an individual's reproductive experience remains challenging because of the imperfect detection of individuals (Gimenez *et al.* 2008) and uncertainty in the assignment of reproductive status (Desprez *et al.* (2013), chapter 2) inherent to studies of wild populations.

Using a multi-event capture-recapture model that accounts for uncertainty in the assignment of breeding state, I analysed 18 years of data collected from more than 6 000 individually marked female elephant seals (*Mirounga leonina*). Female southern elephant seals are extreme capital breeders and rely entirely on their stored reserves while nursing offspring. They start breeding from 3 years of age while still undergoing somatic growth (Laws 1956), making them an ideal model species to assess the cost of first reproduction. I incorporated breeding experience as a latent state to estimate age-specific survival probabilities of

prebreeders, first-time breeders and experienced breeders and quantify age-related variation in the cost of first reproduction. Accordingly, I present the first successful investigation of the effects of age and reproductive experience on survival that explicitly accounts for uncertainty in breeding states.

Material and methods

Study species and data collection

Southern elephant seals (*Mirounga leonina*) have a circumpolar distribution in the Southern Ocean. During the breeding season, females gather in harems and each female gives birth to a single pup which nurses for approximately 24 days while fasting. From 1993 to 1999, 6 637 females were permanently marked after weaning at Macquarie island (54°30'S, 158°50'E), a closed breeding population (McMahon *et al.* 2005a). Until 2001, intensive searches were made for branded individuals but from 2002 resightings were opportunistic.

Capture-recapture analyses

I considered four states representing four different steps of the species' life cycle: prebreeder (PB), first-time breeder (B^1), experienced breeder (E) and dead (\dagger), underlying the four possible observations made in the field when collecting data: (1) not seen, (2) seen and assigned as prebreeder, (3) seen with an unknown breeding state and (4) seen and assigned as adult (See Desprez *et al.* (2013), Appendix A Chapter 2, for details about breeding state assignment). I built a multi-event capture-recapture model to deal with uncertainty in the assignment of breeding states and reproductive experience (Pradel (2005); Desprez *et al.* (2013), chapter 2). Our model included four different parameters: detection probability (p), state assignment probability (β), survival probability (ϕ) and probability of transition between breeding states (ψ). All first-time breeders became experienced the following breeding season and I fixed the transition probability from B^1 to E at 1. An experienced breeder could not return to the PB or B^1 state but remained experienced. Transition probabilities from E to PB and B^1 were thus fixed at 0 while the transition from E to E was fixed at 1 (Appendix A).

To determine the best model structure, I compared models exhibiting various combinations of age and breeding state effects on each parameter. For prebreeders, I considered only 8 age classes (0, 1, 2, 3, 4, 5, 6 and ≥ 7 years old) as no individuals were recorded as prebreeders after age 6 (females were recorded as 'unknown' or 'breeders' only). For the same reason I considered only 6 age classes for first-time breeders (3, 4, 5, 6, 7 and ≥ 8 years old). I considered annual variation on detection probability in all models to account for varying resighting effort over the study period. I compared models based on Akaike Information Criterion (AIC) (Burnham & Anderson 2002). Analyses were performed using the software E-SURGE (Choquet *et al.* 2009b).

Currently, no goodness-of-fit (GOF) tests are available for multi-event models. However, to test model robustness I compared model ranking under different levels of over-dispersion with a variance inflation factor \hat{c} of 1.0, 1.5, 2.0, 2.5 and 3.0 (encompassing average levels of over-dispersion (Lebreton *et al.* 1992)).

Results

Model rank was robust to changes in \hat{c} values (Table 3.1). The top-ranked model showed age and breeding state effects on survival, state assignment and detection probabilities. Estimates of detection probability also varied annually and recruitment probability depended on age (Table 3.1, Appendix B and C).

Only 10% (SE= 0.01) of females recruited into the breeding population at 3 years old (Fig. 3.1). The modal age at first reproduction was 4 years with 34% (SE=0.02) of females first breeding at this age. Some individuals delayed their first breeding attempt to older ages but more than 60% of the population that bred at least once in their life had recruited by age 4 (Fig. 3.1).

I detected a large cost of first reproduction on survival, with first-time breeders invariably having lower survival probabilities than prebreeders of the same age (-31%, -19% and -17% for the 3, 4 and 5 year old first-time breeders respectively) and experienced breeders of the same age (-22% and -23% for the 4 and 5 year old first-time breeders respectively) (Fig. 3.2). This cost was higher for females breeding for the first time at 3 years old compared to those commencing breeding at 4 or 5 years old.

Table 3.1. List of all models considered in model selection. The model selected is in bold characters. Abbreviations: *np*, number of parameters; *s*, breeding state effect; *a*, age effect; *t*, time effect; *cst*, constant.

No.	Parameters				<i>np</i>	AIC					Δ AIC
	detection	State assignment	Survival	Recruitment		$\hat{c}=1$	$\hat{c}=1.5$	$\hat{c}=2$	$\hat{c}=2.5$	$\hat{c}=3$	
1	<i>s . a + t</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	112	66381.35	44328.90	33302.67	26686.94	22276.45	0.00
2	<i>s . a + t</i>	<i>s . a</i>	<i>s . a</i>	<i>cst</i>	107	66646.10	44502.10	33430.05	26786.80	22358.03	264.75
3	<i>s . a + t</i>	<i>s . a</i>	<i>A</i>	<i>a</i>	102	66668.10	44513.40	33436.05	26789.64	22358.70	286.75
4	<i>s . a + t</i>	<i>s . a</i>	<i>S</i>	<i>a</i>	88	66906.15	44662.76	33541.07	26868.06	22419.38	524.80
5	<i>s . a + t</i>	<i>s</i>	<i>s . a</i>	<i>a</i>	105	67098.03	44802.02	33654.01	26965.21	22506.01	716.68
6	<i>t . a</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	194	67562.94	45135.29	33921.47	27193.18	22707.65	1181.59
7	<i>s . a + t</i>	<i>a</i>	<i>s . a</i>	<i>a</i>	108	67640.16	45165.44	33928.08	27185.66	22690.72	1258.81
8	<i>t . s</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	88	67703.80	45194.53	33939.90	27187.12	22685.27	1322.45
9	<i>t + a</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	75	67713.87	45192.58	33931.94	27175.55	22671.29	1332.53
10	<i>t . (PB, B^l E)</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	74	67779.72	45235.82	33963.86	27200.69	22691.91	1398.38
11	<i>t . (PB B^l, E)</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	73	68048.83	45414.55	34097.41	27307.13	22780.28	1667.48
12	<i>t . (PB E, B^l)</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	74	68084.39	45438.93	34116.20	27322.56	22793.46	1703.05
13	<i>t + (PB, B^l E)</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	60	68170.25	45486.83	34145.12	27340.10	22803.42	1788.90
14	<i>t + s</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	61	68170.52	45487.68	34146.26	27341.41	22804.84	1789.17
15	<i>t + (PB E, B^l)</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	60	68179.45	45492.97	34149.72	27343.78	22806.48	1798.10
16	<i>t . (PB B^l, E)</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	60	68182.96	45495.31	34151.48	27345.18	22807.65	1801.61
17	<i>t</i>	<i>s . a</i>	<i>s . a</i>	<i>a</i>	59	68184.35	45495.56	34151.17	27344.54	22806.78	1803.00

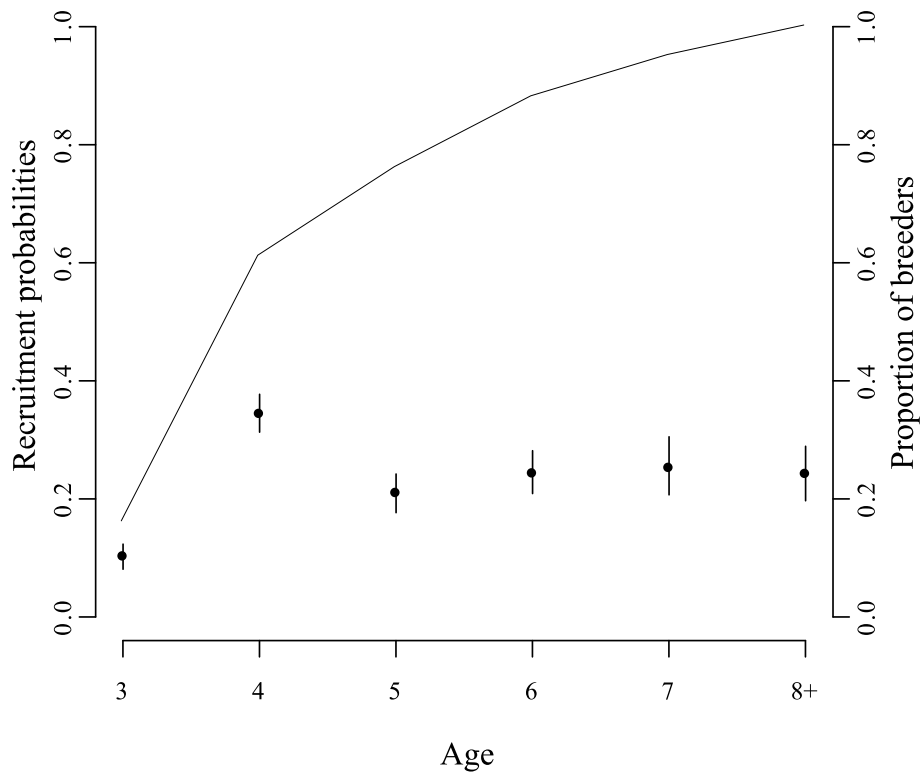


Fig. 3.1. Recruitment probabilities (points) and cumulative proportion of first-time breeders in the breeding population (solid line) according to age.

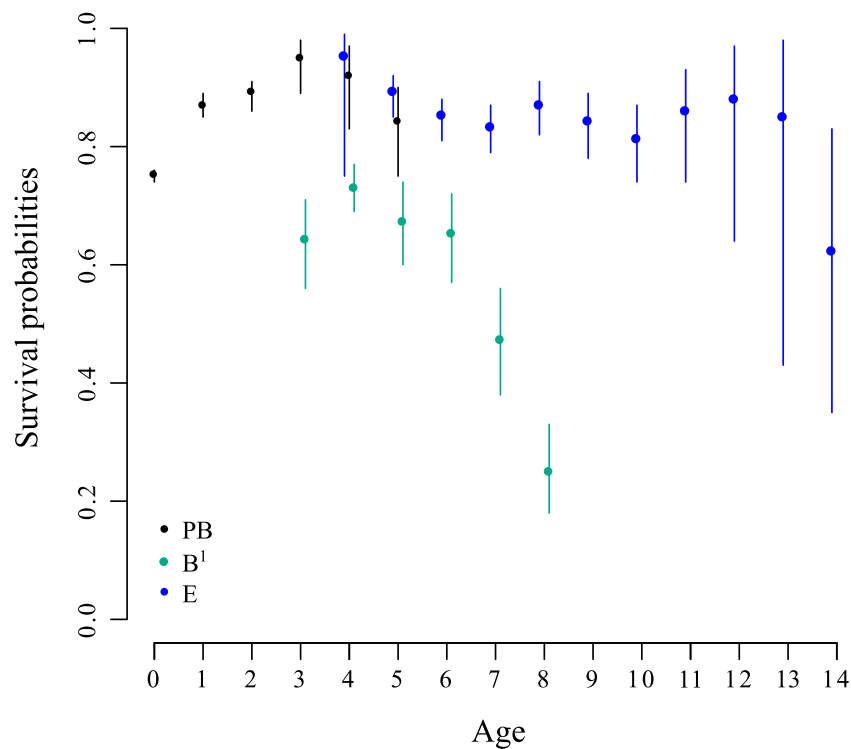


Fig. 3.2. Survival probabilities of female elephant seals by breeding state and age. For first-time breeders, last estimate represents survival probability for the age class ≥ 8 years old. No estimates could be obtained for PB and E older than 5 and 14 years old respectively because of small sample sizes. Estimates on the boundary are not represented.

Survival of first-time breeders peaked at 4 years old. Survival probabilities of the 3- and 5-year old first-time breeders were 9% and 6% lower than survival of females recruiting at age 4 (Fig. 3.2). Survival of experienced seals was higher than survival of first-time breeders for all age classes (Fig. 3.2).

Discussion

Breeding for the first time is costly for female southern elephant seals, a prime example of a capital breeder, at Macquarie Island. No matter which age they commence breeding, first-time breeders always have lower survival than prebreeders. This suggests that there is considerable selection pressure on first-time breeders, particularly on individuals in poor condition (*i.e.* low quality) that are consequently removed from the population (Cam & Monnat 2000; Cam *et al.* 2002). The first breeding event acts like a powerful filter selecting higher quality individuals (Pyle *et al.* 1997; Tavecchia *et al.* 2001; Barbraud & Weimerskirch 2005). This is further evident from our finding that experienced seals have higher survival than first-time breeders of the same age.

In this population, the intensity of the cost to survival varied with age and was higher for younger first-time breeders than for females delaying their first breeding event to four or five years of age. Female elephant seals are still undergoing somatic growth until the age of six, therefore first-time breeders must allocate energy to both growth and reproduction (Laws 1956). Because elephant seals are capital breeders, nursing results in extreme reduction in body mass (35% on average over the 24 day lactation period) (Fedak *et al.* 1996). Consequently, younger and generally smaller individuals with lower reserves are likely to face a higher total energetic cost of first reproduction and to suffer greater mortality. This being true, I expected older first-time breeders to be buffered against this energetic cost and to exhibit higher survival (Proaktor *et al.* 2007). In contrast, I found that survival of first-time breeders decreased from age five and that the optimal age to start breeding in this population appeared to be four. Reproducing earlier substantially reduces the chance of survival but delaying the first reproduction also increases the risk of dying before any reproduction could occur. Seals delaying reproduction are thus likely to be seals in poorer condition. Primiparity at age four seems thus to be the optimal strategy to maximize survival.

Life-history theory predicts that the age at first breeding should decrease in a declining population (Eberhardt 2002). Despite the long-term decline in the Macquarie Island population (Van den Hoff *et al.* 2014), our study shows that a mechanism for safely reducing the age of primiparity does not seem to exist. Instead, I found that the cost of first reproduction at age three remained very high. It is likely that selection acts against earlier primiparity given the small proportion (10%) of the female population recruiting at three years of age and that, while animals can breed earlier in response to low densities, there is little to be gained of such changes to the age of first breeding. Therefore, I appear to have detected a floor effect for primiparity, whose mechanism is as yet unknown. Such a floor effect may act as an absolute barrier to plasticity in life history strategies for populations under stress.

Acknowledgements

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Appendix A. Model structure

At a given sampling occasion, a seal may be prebreeder (PB), first-time breeder (B^I), experienced breeder (E) or dead (\dagger). In the field, the possible observations made were: '0' (not detected), '1' (detected and assigned as a prebreeder), '2' (detected with an unknown breeding state) and '3' (detected and assigned as an adult A) (See Appendix A Chapter 2 for more information about state assignment).

All seals were prebreeders when first captured and the initial state vector Π was thus defined as:

$$\Pi = \begin{array}{c|cccc} & PB & B^I & E & \dagger \\ \hline & 1 & 0 & 0 & 0 \end{array}$$

I defined the survival matrix S, the transition between breeding states matrix T (conditional on survival), the detection matrix P and the breeding state assignment matrix SA as:

$$S = \begin{array}{c|cccc} & PB & B^I & E & \dagger \\ \hline PB & \phi & 0 & 0 & 1-\phi \\ B^I & 0 & \phi & 0 & 1-\phi \\ E & 0 & 0 & \phi & 1-\phi \\ \dagger & 0 & 0 & 0 & 1 \end{array}$$

$$T = \begin{array}{c|cccc} & PB & B^I & E & \dagger \\ \hline PB & 1-\psi & \psi & 0 & 0 \\ B^I & 0 & 0 & 1 & 0 \\ E & 0 & 0 & 1 & 0 \\ \dagger & 0 & 0 & 0 & 1 \end{array}$$

$$P = \begin{array}{c|ccc} & '0' & PB & A \\ \hline PB & 1-p & p & 0 \\ B^I & 1-p & 0 & p \\ E & 1-p & 0 & p \\ \dagger & 1 & 0 & 0 \end{array}$$

$$SA = \begin{array}{c|cccc} & '0' & '1' & '2' & '3' \\ \hline '0' & 1 & 0 & 0 & 0 \\ PB & 0 & \beta & 1-\beta & 0 \\ A & 0 & 0 & 1-\beta & \beta \end{array}$$

To simplify notation, I did not distinguish probabilities in matrices. However, transitions are not all equal. According to effects I wanted to test, I differentiated some probabilities from the others. For example, if I considered that survival probabilities of prebreeders and breeders were different, I differentiated the probability ϕ in the first row from the second and third rows. This comment is valid for all matrices.

Appendix B. Detection probabilities

Table B.1. Detection probabilities according to breeding state, years and age.

Breeding state	Year	Age	Estimates	CI-	CI+	SE
Juveniles	1993	0	1.00	1.00	1.00	0.00
	1994		0.64	0.60	0.67	0.02
	1995		0.62	0.59	0.65	0.02
	1996		0.56	0.53	0.59	0.01
	1997	1	0.68	0.65	0.70	0.01
	1998		0.67	0.64	0.69	0.01
	1999		0.79	0.77	0.81	0.01
	2000		0.79	0.77	0.81	0.01
	1995		0.51	0.48	0.54	0.02
	1996		0.45	0.42	0.48	0.01
	1997		0.58	0.55	0.60	0.01
	1998	2	0.57	0.54	0.59	0.01
	1999		0.71	0.68	0.73	0.01
	2000		0.71	0.69	0.73	0.01
	2001		0.73	0.71	0.76	0.01
	1996		0.26	0.23	0.29	0.01
	1997		0.37	0.34	0.40	0.02
	1998		0.36	0.33	0.39	0.02
	1999	3	0.51	0.47	0.54	0.02
	2000		0.51	0.48	0.54	0.02
	2001		0.54	0.51	0.57	0.02
	2002		0.25	0.22	0.29	0.02
	1997		0.24	0.21	0.27	0.02
	1998		0.23	0.20	0.26	0.01
	1999		0.36	0.32	0.39	0.02
	2000	4	0.36	0.33	0.40	0.02
	2001		0.39	0.35	0.43	0.02
	2002		0.15	0.13	0.18	0.01
	2003		0.45	0.40	0.50	0.03
	1998		0.21	0.18	0.24	0.02
	1999		0.33	0.29	0.37	0.02
	2000	5	0.34	0.30	0.38	0.02
	2001		0.36	0.32	0.40	0.02
	2002		0.14	0.12	0.17	0.01
	2003		0.42	0.37	0.47	0.03
	2004		0.21	0.17	0.26	0.02
	1999	6	0.22	0.18	0.26	0.02
	2000		0.22	0.19	0.26	0.02

(Table B.1. Continued)

Breeding state	Year	Age	Estimates	CI-	CI+	SE
Juveniles	2001	6	0.24	0.20	0.29	0.02
	2002		0.08	0.07	0.11	0.01
	2003		0.29	0.24	0.34	0.03
	2004		0.13	0.10	0.17	0.02
	2005		0.03	0.02	0.06	0.01
	2000	7+	0.15	0.11	0.18	0.02
	2001		0.16	0.13	0.20	0.02
	2002		0.05	0.04	0.07	0.01
	2003		0.19	0.16	0.24	0.02
	2004		0.08	0.06	0.11	0.01
	2005		0.02	0.01	0.04	0.01
	2006		0.04	0.02	0.07	0.01
First-time breeders	1996	3	1.00	1.00	1.00	0.00
	1997		1.00	1.00	1.00	0.00
	1998		1.00	0.99	1.00	0.00
	1999		1.00	0.99	1.00	0.00
	2000		1.00	1.00	1.00	0.00
	2001		1.00	1.00	1.00	0.00
	2002		1.00	0.88	1.00	0.00
	1997	4	1.00	1.00	1.00	0.00
	1998		0.85	0.68	0.93	0.06
	1999		0.99	0.01	1.00	0.06
	2000		0.88	0.75	0.95	0.05
	2001		1.00	1.00	1.00	0.00
	2002		0.21	0.13	0.31	0.04
	2003		0.86	0.73	0.93	0.05
	1998	5	0.84	0.67	0.93	0.07
	1999		0.99	0.01	1.00	0.06
	2000		0.88	0.75	0.94	0.05
	2001		1.00	1.00	1.00	0.00
	2002		0.20	0.11	0.35	0.06
	2003		0.86	0.71	0.94	0.06
	2004		0.77	0.59	0.89	0.07
	1999	6	0.99	0.01	1.00	0.06
	2000		0.87	0.69	0.95	0.06
	2001		1.00	1.00	1.00	0.00
	2002		0.19	0.09	0.34	0.06
	2003		0.85	0.66	0.94	0.07
	2004		0.75	0.57	0.87	0.08
	2005		1.00	1.00	1.00	0.00
	2000	7	0.65	0.42	0.83	0.11
	2001		1.00	1.00	1.00	0.00

(Table B.1. Continued)

Breeding state	Year	Age	Estimates	CI-	CI+	SE
First-time breeders	2002	7	0.06	0.03	0.13	0.02
	2003		0.61	0.40	0.78	0.10
	2004		0.46	0.30	0.63	0.09
	2005		1.00	1.00	1.00	0.00
	2006		0.45	0.27	0.65	0.10
	2001	8+	1.00	1.00	1.00	0.00
	2002		0.08	0.03	0.16	0.03
	2003		0.66	0.43	0.84	0.11
	2004		0.52	0.33	0.70	0.10
	2005		1.00	1.00	1.00	0.00
	2006		0.51	0.32	0.70	0.10
	2007		0.51	0.31	0.72	0.11
Experienced breeders	1997	4	0.84	0.64	0.94	0.07
	1998		0.75	0.60	0.86	0.07
	1999		0.88	0.78	0.94	0.04
	2000		0.89	0.79	0.94	0.04
	2001		0.92	0.84	0.96	0.03
	2002		0.40	0.25	0.57	0.09
	2003		0.83	0.70	0.91	0.05
	1998	5	0.61	0.53	0.68	0.04
	1999		0.79	0.73	0.84	0.03
	2000		0.80	0.75	0.84	0.02
	2001		0.85	0.81	0.88	0.02
	2002		0.25	0.21	0.30	0.02
	2003		0.71	0.65	0.76	0.03
	2004		0.69	0.63	0.74	0.03
	1999	6	0.75	0.69	0.80	0.03
	2000		0.75	0.70	0.80	0.03
	2001		0.81	0.77	0.85	0.02
	2002		0.20	0.17	0.24	0.02
	2003		0.65	0.60	0.70	0.02
	2004		0.63	0.58	0.68	0.03
	2005		0.79	0.75	0.83	0.02
	2000	7	0.74	0.69	0.79	0.03
	2001		0.80	0.76	0.84	0.02
	2002		0.19	0.16	0.23	0.02
	2003		0.64	0.59	0.68	0.02
	2004		0.62	0.57	0.66	0.02
	2005		0.78	0.74	0.81	0.02
	2006		0.43	0.38	0.48	0.03
	2001	8	0.79	0.74	0.83	0.02
	2002		0.18	0.15	0.22	0.02

(Table B.1. Continued)

Breeding state	Year	Age	Estimates	CI-	CI+	SE
Experienced breeders	2003	8	0.61	0.56	0.66	0.03
	2004		0.59	0.55	0.64	0.02
	2005		0.76	0.72	0.80	0.02
	2006		0.41	0.36	0.46	0.02
	2007		0.55	0.49	0.60	0.03
	2002	9	0.22	0.19	0.27	0.02
	2003		0.68	0.63	0.72	0.02
	2004		0.66	0.61	0.70	0.02
	2005		0.81	0.77	0.84	0.02
	2006		0.48	0.43	0.53	0.03
	2007	10	0.61	0.56	0.66	0.03
	2008		0.30	0.25	0.36	0.03
	2003		0.58	0.52	0.63	0.03
	2004		0.56	0.50	0.61	0.03
	2005		0.74	0.69	0.78	0.02
	2006		0.37	0.32	0.43	0.03
	2007		0.51	0.46	0.57	0.03
	2008	11	0.22	0.18	0.27	0.02
	2009		0.88	0.82	0.93	0.03
	2004		0.56	0.49	0.62	0.03
	2005		0.73	0.68	0.78	0.03
	2006		0.37	0.32	0.43	0.03
	2007		0.51	0.45	0.57	0.03
	2008	12	0.22	0.18	0.27	0.02
	2009		0.88	0.81	0.93	0.03
	2010		0.14	0.10	0.19	0.02
	2005		0.64	0.56	0.71	0.04
	2006		0.28	0.22	0.34	0.03
	2007	13	0.40	0.33	0.48	0.04
	2008		0.16	0.12	0.20	0.02
	2009		0.83	0.73	0.89	0.04
	2010		0.09	0.06	0.13	0.02
	2006		0.20	0.14	0.27	0.03
	2007	14	0.30	0.23	0.40	0.04
	2008		0.11	0.07	0.16	0.02
	2009		0.76	0.62	0.86	0.06
	2010		0.06	0.04	0.10	0.01
	2007		0.30	0.19	0.43	0.06
	2008	15	0.10	0.06	0.18	0.03
	2009		0.75	0.57	0.87	0.08
	2010		0.06	0.03	0.11	0.02
	2008	15	0.12	0.06	0.24	0.04

(Table B.1. Continued)

Breeding state	Year	Age	Estimates	CI-	CI+	SE
Experienced breeders	2009	15	0.78	0.58	0.90	0.08
	2010		0.07	0.03	0.15	0.03
	2009	16	0.69	0.40	0.88	0.13
	2010		0.05	0.01	0.14	0.03
	2010	17	0.04	0.01	0.15	0.03

Appendix C. State assignment probabilities

Table C.1. Breeding state assignment probabilities according to state and age.

State	Age	Estimates	CI-	CI+	SE
Prebreeder	0-2	1.00	1.00	1.00	0.00
	3	0.58	0.54	0.62	0.02
	4	0.27	0.23	0.31	0.02
	5	0.04	0.03	0.06	0.01
	6	0.03	0.01	0.07	0.01
	7+	0.00	0.00	0.00	0.00
Breeder	0-2	0.00	0.00	0.00	0.00
	3	0.05	0.03	0.09	0.01
	4	0.83	0.79	0.87	0.02
	5	1.00	1.00	1.00	0.00
	6	1.00	1.00	1.00	0.00
	7+	1.00	1.00	1.00	0.00

Chapter 4

Consequences of intermittent breeding on lifetime reproductive output



Picture: M. Desprez

Under review in *Journal of Animal Ecology*: Desprez M., Gimenez O., McMahon C. R., Hindell M. A., & Harcourt R. Optimising lifetime reproductive output: skipping breeding as survival strategy for female southern elephant seals in a declining population.

Abstract

In iteroparous species, intermittent breeding is considered an important life-history strategy that can greatly affect population growth and viability. However, few studies have quantified the consequences of breeding pauses on lifetime reproductive output, mainly because lifetime reproductive output calculation requires the knowledge of each individual's entire reproductive history, information that is extremely difficult to obtain in wild populations. In this study, I applied recently developed statistical approaches that account for uncertainty in state assessment to an 18 year capture-recapture dataset involving 6 631 female southern elephant seals from the declining Macquarie Island population. I estimated survival and breeding probabilities, and investigated the consequences of intermittent breeding on lifetime reproductive output. I found that breeding imbued a high cost on survival in this population of elephant seals, non-breeding females having a 10% higher chance of surviving to the next breeding season than breeding females. However, breeding females were less likely to skip reproduction the following year than non-breeding females suggesting that heterogeneity in female quality strongly influenced intermittent breeding. Environmental conditions also played an important role in females' decisions to skip reproduction as breeding probabilities were positively associated with the Southern Annular Mode (SAM) during the first trimester of pregnancy. Finally, our results showed that lifetime reproductive output was maximal for females skipping 2 to 4 breeding events over their lifetime. In this population of elephant seals, intermittent breeding seems to be an important strategy to offset high reproductive costs on survival and to optimize lifetime reproductive output.

Keywords: intermittent breeding, life-history, *Mirounga leonina*, multi-event capture-recapture models, reproduction, reproductive cost, Southern Annular Mode, state uncertainty.

Introduction

The existence of trade-offs between fitness-related traits is a central assumption in life-history theory (Stearns 1992). Because energy is limited, individuals should allocate resources between various vital functions (e.g. growth, maintenance, production of offspring) in a way that maximizes their fitness (Roff 1992; Stearns 1992). Reproduction and survival, as well as current and future reproduction, are considered to be distinct functions competing for the same resources. Consequently, a high allocation of resources to current reproduction may lead to a reduced survival and/or a reduced probability of breeding in subsequent years. In long-lived iteroparous species, individuals should almost always value their own survival over that of their offspring as any significant reduction in adult survival will lead to lower lifetime reproductive output (LRO) (Roff 1992). Long-lived individuals are thus more likely to adjust their breeding effort by skipping reproductive events than to invest in reproduction at a cost to survival.

Accordingly, how often and when individuals skip reproduction have been central questions in evolutionary ecology. Reproductive skipping has been linked to many factors including age (Beauplet *et al.* 2006; Rughetti *et al.* 2014; Zhang *et al.* 2015), reproductive experience (Desprez *et al.* 2011; Pradel *et al.* 2012), individual quality (Hamel *et al.* 2009), population density (Hamel *et al.* 2010a) and environmental conditions (Hadley *et al.* 2007; Cubaynes *et al.* 2011). However, the consequences of intermittent breeding on LRO have rarely been quantified mainly because there is imperfect detection and uncertainty in the assessment of reproductive state in most studies of wild populations. As lifetime reproductive output, defined here as the number of young produced over the lifespan, requires knowledge of an individuals' entire reproductive history to be estimated, any incomplete encounter history makes its exact calculation impossible.

Recently, Rouan *et al.* (2009) proposed a new method derived from multi-event capture-recapture models (Pradel 2005) to estimate LRO when the reproductive status is uncertain or unknown (see also Gimenez *et al.* (2012)). Here, I used this new method to investigate the consequences of intermittent breeding on LRO of female southern elephant seals (*Mirounga leonina*) in the declining Macquarie Island population. During the breeding season, mature female elephant seals return to land to give birth to a single pup that they nurse for approximately 24 days (Laws 1953). Females become sexually receptive just prior to

weaning and leave the breeding colony after mating. Although fertilization takes place at this time, the blastocyst does not implant until the end of the moult several months later. Until recently, female southern elephant seals were assumed to breed (pup and mate) annually from primiparity to death but de Bruyn *et al.* (2011) showed that intermittent breeding does occur in the Marion Island population. However, the frequency, environmental drivers and consequences of reproductive skipping in southern elephant seals are still completely unknown. Southern elephant seals undertake extensive foraging trips throughout the Southern Ocean (Hindell *et al.* 2003b; Biuw *et al.* 2007) to rebuild their energetic reserves after their annual fasting periods (during the breeding season and the moult). Environmental conditions during these provisioning trips are crucial and climatic variability, by affecting biological productivity and the quantity and quality of resources available, is assumed to play an important role in an individual's decision to skip reproduction.

Using a multi-event model that accounts for uncertainty in breeding state assessment and an 18 year-dataset involving 6 631 female southern elephant seals, I estimated the frequency of reproductive skipping and investigated possible reproductive costs on survival and future reproduction. I also examined the influence of environmental variability on seals' vital rates and on the intensity of reproductive costs. Finally, using the method developed by Rouan *et al.* (2009) and nonlinear quantile regression, I evaluated the long-term consequences of intermittent breeding on LRO. I propose two contrasting predictions:

(1) Because non-breeding females may avoid potential costs of reproduction, I expect them to have higher survival and probability of reproducing the following year than breeders ('prudent parent hypothesis' (Cam *et al.* 1998)). Surviving to future reproductive opportunities being crucial in long-lived species, reproductive skipping may be considered a breeding strategy that maximizes lifetime reproductive output. Therefore, I expect that female elephant seals skipping some reproductive events (*e.g.* when conditions are not favourable) will live longer and produce more offspring over their lifetime than females breeding in each consecutive year.

(2) Individuals of high intrinsic quality both survive and reproduce with a higher probability than females of poorer quality, irrespective of the environmental conditions (Cam *et al.* 2002). This hypothesis assumes that higher quality individuals incur smaller reproductive costs than others for equal reproductive investment. Under this scenario I expect that females that skip fewer breeding events are higher quality females and produce more offspring over their lifespan than other females.

Material and methods

Study species and data collection

Southern elephant seals (*Mirounga leonina*) are the largest pinniped and one of the most polygynous and sexually dimorphic species of mammals (Laws 1953). They spend most of their time at sea foraging but return to land thrice annually: to breed (September-November), to moult (austral summer) and for a winter haulout (mostly undertaken by juveniles)(Hindell & Burton 1988b). While ashore, elephant seals do not feed and rely entirely on the stored reserves accumulated during the preceding foraging trip at sea.

From 1993 to 1999, between October and December, 6 631 recently weaned female elephant seals were permanently and uniquely marked by hot iron branding at Macquarie Island (54° 30' S, 158° 57' E)(McMahon *et al.* 2006c). Throughout the year, until 2001, daily searches for branded individuals were made on the Isthmus, the main study area. The top third of the island was searched every ten days while the rest of the coastline was searched monthly. From 2002, resightings were opportunistic. Each marked seal resighted was recorded along with its reproductive status when identified. I defined a breeder as a seal engaged in breeding activity, irrespective of its success. Females were therefore considered breeders when seen with a pup or detected in the harem during the breeding season. I considered that a seal never observed as a breeder on previous sampling occasions and seen on land between the end of the breeding season and the breeders' minimum return date for moult was a prebreeder (see Appendix A in Desprez *et al.* (2013), Chapter 2, for more details about state assignment). Seals younger than 3 years old were also considered prebreeders as recruitment never occurred before this age (McMahon *et al.* 2003). Experienced nonbreeders were assumed not to be present in harems during the breeding season (de Bruyn *et al.* 2011) but may be resighted on land during their annual moult. However, in this latter case, it was impossible to determine if the observed individual was an actual nonbreeder or a breeder not detected during the breeding season. Therefore, all experienced nonbreeders, along with individuals for which I was not able to assign a breeding state, were recorded as 'unknown'.

To coincide with the southern elephant seal life cycle, I considered that a year started in September and ended in August (e.g. the first year of the study, hereafter referred to as 1993, runs from September 1993 to August 1994).

Environmental data

I used a global climate index, the Southern Annular Mode (SAM), as a broad-scale proxy for Southern Ocean productivity to investigate the effects of environmental variability on the seals' demographic parameters. The SAM describes the relative atmospheric anomalies between the mid and high southern latitudes and positive SAM anomalies have been linked to higher primary productivity (Lefebvre *et al.* 2004; Forcada & Trathan 2009). SAM has also been positively associated with reproduction and survival of a population of Antarctic fur seals (*Arctocephalus gazella*, Schwarz *et al.* (2013)). I converted monthly SAM data (available at: <http://www.nerc-bas.ac.uk/icd/gjma/sam.html>) into an annual index by averaging values from November in year t (start of the post-breeding foraging trip for most females) to October in year $t+1$ (peak of females ashore for the breeding season). I also examined the influence of the SAM at four separate stages: (1) the post-breeding foraging trip (November-January), (2) the first trimester of pregnancy and the beginning of the post-moult foraging trip (February-April), (3) the second trimester of pregnancy and post-moult foraging trip (May-July) and (4) the last trimester of pregnancy and post-moult foraging trip (August-October).

Multi-event model design

I developed a multi-event capture-recapture model (Pradel 2005) to investigate individual and temporal variation in survival and reproduction probabilities from data including individuals with uncertain reproductive status on one or more occasions. The multi-event framework related the observations made in the field (called 'events' and encoded in the capture histories) to the underlying biological states of the individuals, not always directly observable in the field.

In this study, I considered five different events: 0- seal not observed; 1- seal observed and identified as a prebreeder; 2- seal observed with an uncertain reproductive status and never observed as a breeder on previous sampling occasions; 3- seal observed and identified as a breeder and 4- seal observed with an unknown reproductive status but observed as a breeder at least once in the past (*i.e.* experienced seal E). The underlying biological states considered were: prebreeders (PB); first-time breeders (B1); experienced breeders (EB), for breeders with at least one previous reproductive event; experienced nonbreeders (ENB), for

nonbreeders with at least one previous reproductive event, and dead (\dagger). The multi-event model was parameterised by the initial vector Π , the transition matrix $\Phi\psi$ and the event matrix B . All females were initially marked as prebreeders, consequently the probability of being encountered for the first time in the state PB was fixed to 1. The transition matrix combined both survival probabilities Φ and conditional probabilities to breed the following year ψ whereas the event matrix included the detection probabilities p and conditional probabilities of assigning a reproductive status with certainty δ . The transition and event matrices were defined as:

$$\Phi\psi = \begin{pmatrix} \Phi^{PB}(1 - \psi^{PB \rightarrow B1}) & \Phi^{PB}\psi^{PB \rightarrow B1} & 0 & 0 & 1 - \Phi^{PB} \\ 0 & 0 & \Phi^{B1}\psi^{B1 \rightarrow EB} & \Phi^{B1}(1 - \psi^{B1 \rightarrow EB}) & 1 - \Phi^{B1} \\ 0 & 0 & \Phi^{EB}\psi^{EB \rightarrow EB} & \Phi^{EB}(1 - \psi^{EB \rightarrow EB}) & 1 - \Phi^{EB} \\ 0 & 0 & \Phi^{ENB}\psi^{ENB \rightarrow EB} & \Phi^{ENB}(1 - \psi^{ENB \rightarrow EB}) & 1 - \Phi^{ENB} \\ 0 & 0 & 0 & 0 & 1 \end{pmatrix},$$

$$B = \begin{pmatrix} 1-p^{PB} & p^{PB}\delta^{PB} & p^{PB}(1-\delta^{PB}) & 0 & 0 \\ 1-p^{B1} & 0 & p^{B1}(1-\delta^{B1}-\delta^E) & p^{B1}\delta^B & p^{B1}\delta^E \\ 1-p^{EB} & 0 & p^{EB}(1-\delta^{EB}-\delta^E) & p^{EB}\delta^B & p^{EB}\delta^E \\ 1-p^{ENB} & 0 & p^{ENB}(1-\delta^E) & 0 & p^{ENB}\delta^E \\ 1 & 0 & 0 & 0 & 0 \end{pmatrix}$$

where rows of both matrices and columns of the matrix $\Phi\psi$ represent the biological states PB, B1, EB, ENB and \dagger , respectively, and columns of the matrix B correspond to the 5 events 0, 1, 2, 3 and 4, respectively. I compared this general state-dependent model to a set of models where parameters were constrained equal between reproductive states (see 'model selection' section).

Goodness-of-fit test

No goodness-of-fit (GoF) tests are yet available for multi-event models. Nevertheless, I evaluated the fit of the Cormack-Jolly-Seber (CJS) model (full time-dependence in survival and recapture probabilities) after transforming the observations into a single-state code ('1' for encountered individuals and '0' for not encountered individuals) and removing the first encounter (Pradel *et al.* 2005). This approach was conservative as the CJS model is a coarser model with stronger assumptions than our model (*e.g.* CJS model does not include

reproductive state or age differences). Goodness-of-fit tests were performed using program U-CARE (Choquet *et al.* 2009a).

Model selection

Model selection followed a step-down approach with each parameter modelled sequentially while constraints on other parameters were held constant. I first investigated the most parsimonious structure for detection probabilities p while a relatively complex combination of effects (reproductive state and age effects with interaction) was applied on other parameters. I then performed model selection on state assignment probabilities δ using the best-selected structure for p . Following the same process, I modelled the survival probabilities Φ and finally the reproduction probabilities ψ . In a final check, I conducted another model selection on Φ using the selected structure for p , δ and ψ to make sure that the order I chose to model the transition probabilities did not affect the model selection.

Regarding detection probabilities, I considered annual variation to account for varying resighting effort over the study period. I investigated a reproductive status effect given that prebreeders and experienced nonbreeders were known to avoid hauling out during the breeding season (Hindell & Burton 1988b; de Bruyn *et al.* 2011) and were thus less likely to be detected than breeders. I also tested for equality in detection probabilities between first-time breeders and experienced breeders. Finally, due to the results of goodness-of-fit tests, I considered that the probability of detecting a breeder varied according to its main location on the island. The probability of identifying a female reproductive status was kept state dependent. However, I investigated several combinations of age effects as it was more challenging to assign a breeding state to females aged between 3 and 7 years old. Females strictly younger than 3 years old were automatically assigned prebreeders. The probability of assigning the state prebreeder to females from 0 to 2 years old was thus fixed at 1 and the probability to assign the state breeder for the same age classes was fixed at 0. No prebreeders were identified with certainty after 6 years old, the probability to assign the state prebreeder from age 7 was thus fixed at 0. In order to limit the number of parameters, I did not investigate age effects on the detection probabilities and temporal variation in the probability of assigning a reproductive state. I proceeded in two steps to perform model selection on transition probabilities. First, I tested for age and reproductive state effects. Then, once the

best structure was identified, I investigated temporal variation. This approach limited the number of parameters in the models tested and the number of alternative models.

Based on a prior study of this population (Desprez *et al.* (2014), Chapter 3), survival probabilities of prebreeders and first-time breeders were kept distinct and age dependent. For prebreeders, I considered only eight age classes (0, 1, 2, 3, 4, 5, 6 and ≥ 7 years old) as no individuals were recorded as prebreeders after age 6 (females were recorded as 'unknown' or 'breeders' only). For the same reason, I considered only six age classes for first-time breeders (3, 4, 5, 6, 7 and ≥ 8 years old). Recruitment probability was kept age-dependent (Desprez *et al.* (2014), Chapter 3). Models were ranked using Akaike's information criterion corrected for overdispersion (QAIC; Burnham & Anderson (2002), see paragraph 'Goodness of-fit-test' in the section 'Results' for details about the calculation of the overdispersion coefficient \hat{c}). Model selection was performed using program E-SURGE (version 1.9.0; Choquet *et al.* (2009b)) and identifiability issues were checked using the diagnostic tool incorporated in the software (Choquet & Cole 2012).

Once I had selected the structure of the transition probabilities that minimized the QAIC, I tested the effect of the environmental covariate on the time-dependent parameters. To determine whether the variability of the environmental covariate could explain part of the temporal variability observed, I performed an analysis of deviance (ANODEV) that compares the deviance of the model including the environmental covariate with the deviance of the constant model and the time-dependent model (Grosbois *et al.* 2008). The proportion of variation explained by the covariate (R^2_{Dev}) was estimated as :

$$R^2_{\text{Dev}} = \frac{(\text{Dev}_{\text{Fcst}} - \text{Dev}_{\text{Fco}})}{(\text{Dev}_{\text{Fcst}} - \text{Dev}_{\text{Ft}})}$$

where Dev_{Fcst} was the deviance for the constant model, Dev_{Fco} the deviance for the model including the covariate and Dev_{Ft} the deviance for the time-dependent model.

Lifetime Reproductive Output

I defined LRO as the number of offspring produced over a lifetime. Elephant seals typically give birth to a single pup (McMahon & Hindell 2003). Therefore, I assumed that all breeding females produced one pup and that LRO corresponded to the number of times a female bred over a lifetime. To deal with the issue of uncertainty in reproductive status when females were not detected or could not be assigned to a reproductive state, I estimated LRO using the Generalized Viterbi Algorithm as described by Rouan *et al.* (2009). Based on the

demographic parameters obtained from the best-supported model, this approach provided all the possible sequences of states with their associated probabilities for a particular encounter history. For each sequence, I counted the number of times a female was a breeder and weighted this number by the associated sequence probability. I summed the results obtained for all sequences of one particular encounter history to estimate the LRO of each female. I proceeded the same way to estimate the number of times a female skipped reproduction (*i.e.* the number of times a female was in the state 'experienced nonbreeder') over her lifetime. I then investigated the relationship between LRO and the number of breeding pauses. Because the maximum LRO and number of breeding pauses potentially reached by a female over the study period varied between cohorts (*e.g.* females born in 1993 cumulated a greater number of breeding attempts over the study period than females born in 1999), I considered each cohort separately. I fitted nonlinear quantile regression to investigate the variability in the distribution of lifetime reproductive output. Quantile regression allows the study of changes in one or several portion(s) of a response variable distribution and provide a more complete picture of the relationships between variables than standard regression (Cade & Noon 2003). These analyses were performed using the *quantreg* package (v.5.05; Koenker (2013)) in program R (v.3.1.0; R Core Team (2014)).

Results

Goodness-of-fit test

GoF tests were performed to evaluate if our model adequately fitted the data. The overall goodness-of-fit test of the CJS model was statistically significant ($\chi^2 = 1516.30$, $df=123$, $p\text{-value}<0.001$; See Appendix A). Most of the lack of fit was due to strong transience and trap-dependence effects (3.SR test: $\chi^2 = 415.67$, $df = 15$, $p\text{-value} < 0.001$; 2.CT test: $\chi^2 = 796.85$, $df = 14$, $p\text{-value} < 0.001$). The transient effect was likely due to changes in survival with age whereas the trap-dependence effect could be explained by uneven observation effort. Female elephant seals faithful to the Isthmus of the Island -where observation effort was the most frequent- tended to be re-observed more often, leading to a spurious trap-happiness effect. I suspect this resighting heterogeneity to be less important for females that had not yet started breeding.

To quantify lingering trap-dependence effects when accounting for the different locations of resightings, I conducted separate GoF tests on the resighting histories of (i) breeders mainly located on the isthmus over their lifetime, (ii) breeders mainly located on the top third of the island and (iii) breeders mainly located on the rest of the island. The trap-dependence effect was still significant for the first group of breeders although much weaker ($\chi^2 = 68.82$, $df = 12$, $p\text{-value} < 0.001$; Appendix A). To account for this resighting heterogeneity, I introduced a location effect on the breeders resighting probabilities and corrected the remaining heterogeneity with a variance inflation factor (see below and Appendix A). The trap-dependence test was also significant for the prebreeder part of the resight ($\chi^2 = 32.82$, $df = 7$, $p\text{-value} < 0.001$; Appendix A) and I adjusted for this heterogeneity with the variance inflation factor (see Appendix A for more details).

The remaining significant transient effect was accounted for by including an age effect on the survival of both prebreeders and first-time breeders. I calculated an overall variance inflation factor ($\hat{c}=2.01$) to account for any remaining lack of fit (Appendix A).

Demographic parameters

Detection probabilities showed marked fluctuations over the study period. As expected, the probability of detecting a breeder was higher than the probability of detecting a nonbreeder (*i.e.* prebreeder and experienced nonbreeder) (Table 4.1; Appendix C). The probability of positively identifying a prebreeder, when detected, decreased with age. From age 5, almost all prebreeders resighted ($\geq 96\%$) were recorded with an unknown reproductive status (Appendix C). By contrast, the probability of identifying a breeder was low at age 3 (0.16, $SE=0.08$) but constant and close to 1 for older females.

Remarkably, survival of experienced breeders (0.80, $SE=0.01$) was almost ten percent lower than that of experienced nonbreeders (0.90, $SE=0.02$). The difference in QAIC between the model assuming no age variation in the survival of experienced females (breeders and nonbreeders, model 11) and the model including a two-age class effect (4 years old and older) on the survival of experienced breeders (model 12) was < 2 (Table 4.1), indicating that these two models were equally good at describing the data (Burnham & Anderson 2002). I retained the lowest QAIC model (with no age effect) since the survival estimated for the additional age class in the model 12 had large confidence intervals (0.64 – 0.96) and did not make any difference in the interpretation. Age-dependent survival estimated for prebreeders and

Table 4.1. List of the five best-supported models for each parameter (see Appendix B for complete model selection). The best-supported model is in bold. For each model, QAIC, the number of parameters (np) and the difference in the number of QAIC units from the best model (Δ AIC) are provided.

Model structure	QAIC	np	Δ AIC
<i>Detection</i>			
1. (PB; B.loc; ENB).t	35807.89	201	0.00
2. (PB; (B1,EB).loc; ENB).t	35829.21	243	21.32
3. (NB; B.loc).t	35852.98	187	45.09
4. (PB; (B1,EB).loc; ENB)+t	35885.47	149	77.58
5. (NB; (B1,EB).loc).t	35898.18	229	90.29
<i>State assignment</i>			
6. PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	35739.62	163	0.00
7. PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₆₊₎	35741.63	164	2.00
8. PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB}	35747.82	162	8.20
9. PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB.a}	35763.62	175	24.00
10. PB.a ₍₃₋₆₎ ; E ^{ENB} .a; B.a ₍₃₋₄₊₎ ; E ^B .a ₍₄₋₅₊₎	35765.04	176	25.41
<i>Survival</i>			
11. PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	35507.98	186	0.00
12. PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.a ₍₄₋₅₊₎ ; ENB	35509.26	187	1.29
13. PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.a; ENB	35511.59	198	3.62
14. PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; E	35518.69	185	10.71
15. PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; E.a ₍₄₋₅₊₎	35519.97	186	11.99
<i>Reproduction</i>			
16. (PB.a₍₃₋₈₊₎; B1; EB; ENB).t	35507.98	186	0.00
17. (PB.a ₍₃₋₈₊₎ ; B; ENB).t	35518.02	173	10.04
18. (PB.a ₍₃₋₈₊₎ ; B.a ₍₄₋₅₊₎ ; ENB).t	35527.83	179	19.85
19. (PB.a ₍₃₋₈₊₎ ; B1; EB).t; ENB	35555.18	174	47.20
20. (PB.a ₍₃₋₈₊₎ ; B).t; ENB	35562.82	161	54.85

List of abbreviations: 't' denotes a year effect; 'a' represents a full age effect whereas 'a_(x-y)' indicates an age class effect (e.g. 'a₍₀₋₇₊₎' denotes a 8 age classes effect (from age 0 to age 7+) with the last age class (7+) grouping the individuals older than 6 years of age); 'loc' assumes different detection probabilities in the 3 main location of resightings; '+' denotes an additive effect whereas '.' denotes an interactive effect. 'PB', 'B1', 'EB', 'B', 'ENB', 'E' and 'NB' correspond to the states prebreeders, first-time breeders, experienced breeders, breeders (first-time and experienced breeders grouped), experienced nonbreeders, experienced females (experienced breeders and nonbreeders grouped) and nonbreeders (prebreeders and experienced nonbreeders grouped) respectively. In section 'Assignment', 'E^B' ('E^{ENB}') indicates that a resighted breeder (experienced nonbreeder) is assigned 'experienced seal with unknown current reproductive status' (event 4).

first-time breeders supported results obtained in a previous study (Desprez *et al.* (2014), Chapter 3) although bigger confidence intervals in the survival probabilities of first-time breeders made the cost of first reproduction experienced by the 3-year old females less clear (Table 4.2). Models including annual variation in survival rates did not outperform the best-supported model without temporal variation suggesting no clear differences in survival rates between years (Table 4.1; Appendix B).

Parameters	Mean estimates with 95% confidence intervals
Prebreeders age 0	0.77 [0.75 - 0.79]
Prebreeders age 1	0.86 [0.83 - 0.88]
Prebreeders age 2	0.89 [0.86 - 0.91]
Prebreeders age 3	0.88 [0.84 - 0.90]
Prebreeders age 4	0.87 [0.82 - 0.91]
Prebreeders age 5	0.80 [0.74 - 0.86]
Prebreeders age 6	0.89 [0.78 - 0.95]
Prebreeders age 7+	0.92 [0.82 - 0.97]
First-time breeders age 3	0.92 [0.62 - 0.99]
First-time breeders age 4	0.80 [0.74 - 0.85]
First-time breeders age 5	0.77 [0.69 - 0.84]
First-time breeders age 6	0.69 [0.58 - 0.78]
First-time breeders age 7	0.54 [0.41 - 0.66]
First-time breeders age 8+	0.33 [0.24 - 0.45]
Experienced breeders	0.80 [0.77 - 0.83]
Experienced nonbreeders	0.90 [0.86 - 0.92]

Table 4.2. Annual survival estimates for females southern elephant seals at Macquarie Island, 1993-2010. Estimates were obtained from the best-supported model (Table 4.1).

Female elephant seals skipping a reproductive event in year t had less chance of breeding in year $t+1$, (except in 2002), than breeders (first-time and experienced) in year t (Fig. 4.1). Generally, first-time breeders had a lower probability of breeding again the following year than experienced breeders (Fig. 4.1). The probability of skipping reproduction ranged between 15% and 62 % for first-time breeders and between 11% and 77% for experienced breeders. I did not detect an influence of age on the breeding probabilities of breeders (first-time and experienced) or experienced nonbreeders. However, breeding probabilities varied greatly between years (Table 4.1, Fig. 4.1). Recruitment estimates supported results obtained in a previous study (Appendix D, Desprez *et al.* (2014), Chapter 3).

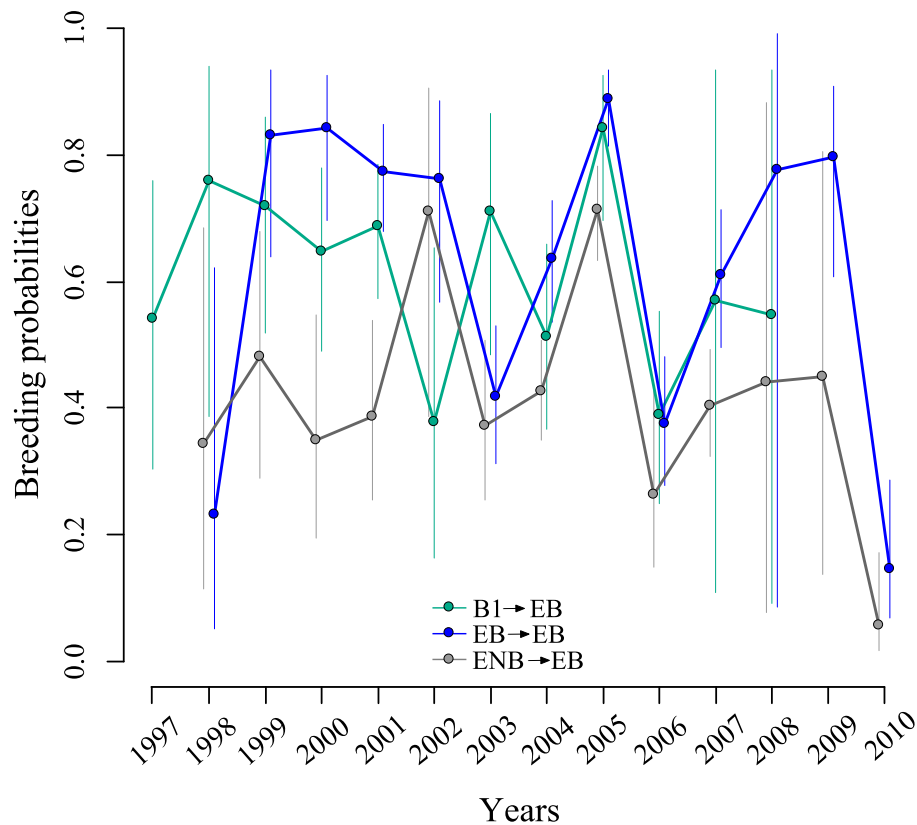


Fig. 4.1. Breeding probabilities of first-time breeders (green line), experienced nonbreeders (grey line) and experienced breeders (blue line) by years.

Environmental influence

I found a positive relationship between SAM values during the February-April period in year t and reproduction of female elephant seals in year $t+1$ (ANODEV = 3.077, p -value= 0.004). None of the other combinations of SAM tested had a significant effect on the breeding probabilities (Table 4.3).

	<i>np</i>	Deviance	Anodev	P_{ANODEV}	R^2_{Dev}
<i>SAM effect:</i>					
Annual	116	71274.71	0.41	0.93	0.05
Post-breeding	116	71226.21	1.19	0.31	0.14
Post-moult trimester 1	116	71139.08	3.08	0.004	0.29
Post-moult trimester 2	116	71281.28	0.31	0.97	0.04
Post-moult trimester 3	116	71203.63	1.61	0.13	0.18

Table 4.3. Models tested to investigate the influence of the SAM at time t on the reproduction probabilities of female elephant seals at Macquarie Island at time $t+1$. np is the number of parameters, P_{ANODEV} is the p -value and R^2_{Dev} indicates the proportion of variation explained by the covariate.

Variation in SAM values during the February-April period in year t , corresponding to the first trimester of pregnancy, explained 29% of the temporal variability in the breeding probabilities in year $t+1$. The relationship between SAM and reproduction was positive for all reproductive states (Fig. 4.2) suggesting that when SAM was high, females had a better chance of breeding in the following year. Survival was not influenced by temporal variation (Table 4.1) and accordingly I did not test the effect of the SAM on it.

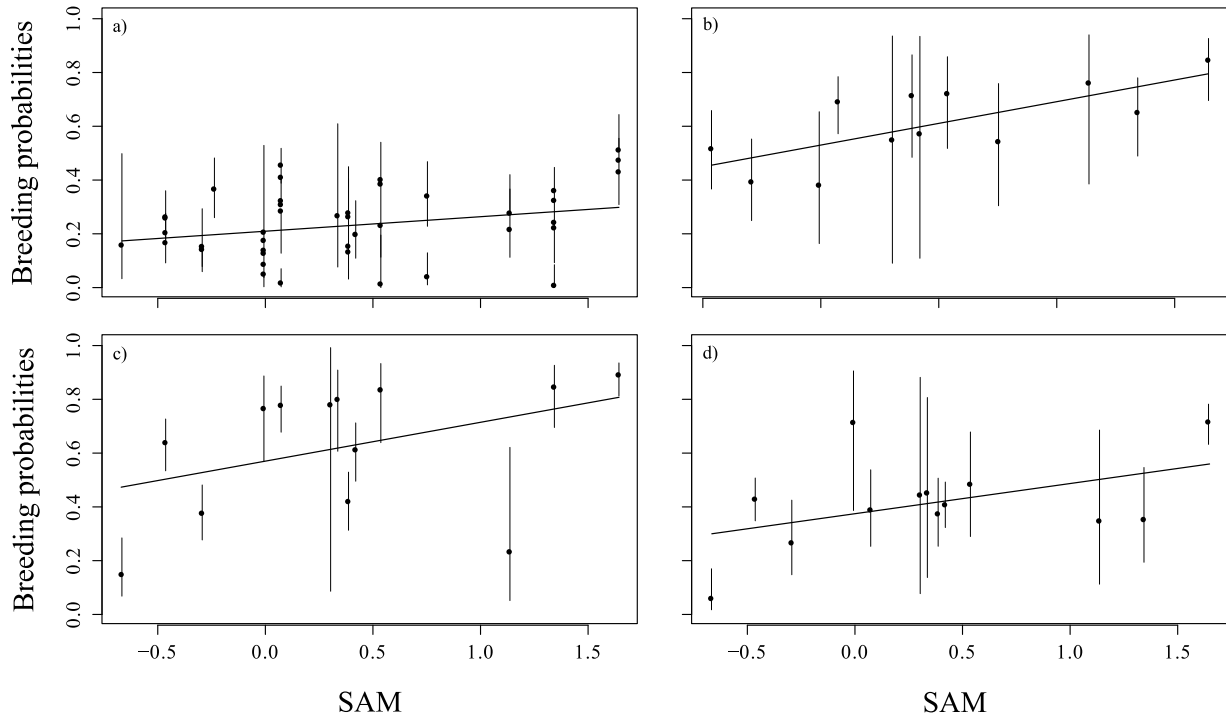


Fig. 4.2. Relationship between the breeding probabilities in year $t+1$ and the average SAM values between February and April in year t for a) prebreeders, b) first-time breeders, c) experienced breeders and d) experienced nonbreeders.

Lifetime Reproductive Output

For all cohorts and quantiles, the highest values of LRO were associated with 2 to 4 breeding pauses (Fig. 4.3; Appendix E). Both a higher and a lower number of non-breeding events were associated with lower values of LRO. While estimated LRO for each female was highly variable, a modified Ricker function (Cade & Guo 2000) fitted LRO changes well (Fig. 4.3). I considered the linearized form of the model:

$$\log(\text{LRO}) = \log(\alpha) + \beta \cdot \log(\text{BP}) + \gamma \cdot \text{BP} + \log(\epsilon)$$

where BP corresponded to the number of breeding pauses over lifespan and α , β and γ to the constants to estimate. All quantiles had a similar pattern: LRO increased with the number of

breeding pauses to a certain point and then went down as the number of breeding pauses rose (Fig. 4.3). The effect of reproductive skipping on LRO was better revealed at the higher LRO associated with upper quantiles ($\tau \geq 0.75$).

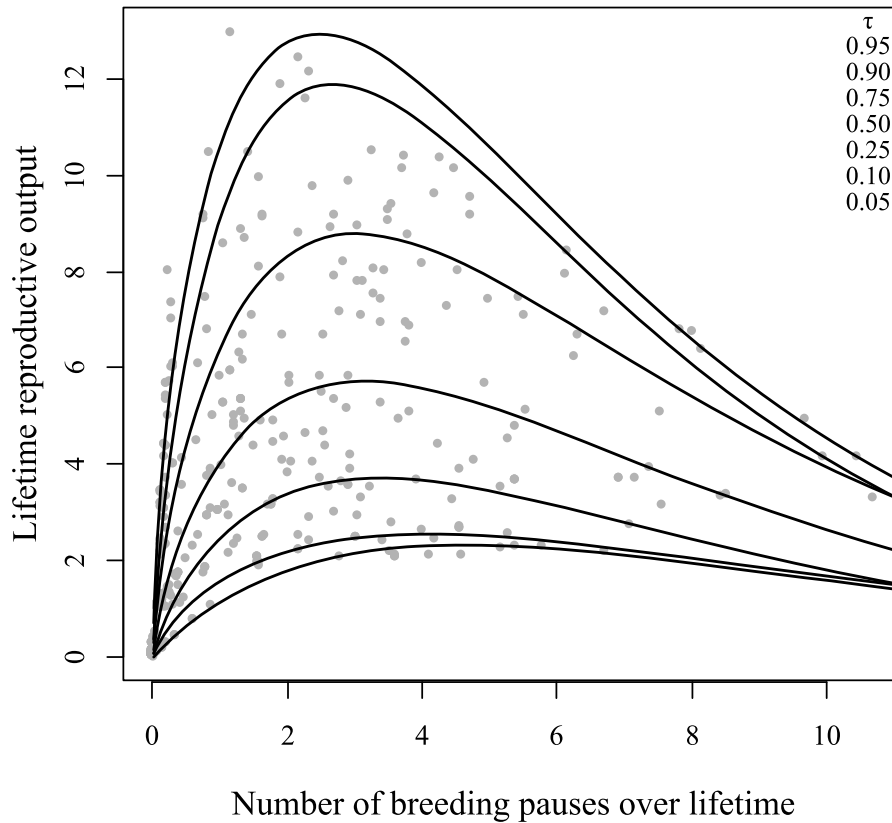


Fig. 4.3. Relationship between the LRO (i.e. number of young produced over lifespan) and the number of breeding pauses over lifetime in female southern elephant seals at Macquarie Island. Only results from the first cohort of females (i.e. born in 1993) are represented in this graph. Lines represent the quantile regressions for the 0.05, 0.10, 0.25, 0.50, 0.75, 0.90 and 0.95 quantiles.

Discussion

In this study, I addressed the life-history consequences of intermittent breeding in female southern elephant seals in the declining Macquarie Island population.

Contrary to the prudent parent hypothesis, female elephant seals skipping a reproductive event in year t had less chance of breeding in year $t+1$ than females that reproduced at time t . The reduced probability of breeding the following year may be explained by limited access to mating partners. Because non-breeding females were absent from the terrestrial mating harems, they had a lower probability of encountering mature males and mating.

Consequently, females skipping reproduction in year t were unlikely to give birth -and therefore to return to land and mate again- in year $t+1$. However, opportunistic mating at sea has been observed and may offset the missed mating opportunities in breeding harems (de Bruyn *et al.* 2011). An alternative explanation of the positive covariance between reproductive skipping in year t and $t+1$ may be the existence of heterogeneity in individual quality, whereby females in good condition (*i.e.* females with a high proportion of lipid relative to lean tissue) have a higher probability of breeding annually than those in poor condition (Cam *et al.* 1998; Barbraud & Weimerskirch 2005; Beauplet *et al.* 2006; Hamel *et al.* 2009). It is important to note that while breeders had a higher probability of breeding the following year than nonbreeders, this does not rule out the possibility of a cost of current reproduction on future reproduction. Such a cost, if existent, was insufficient to overcome the heterogeneity among individuals in this population (Cam *et al.* 1998; Cam *et al.* 2002). Clearly though, our results support the existence of a reproductive cost on future reproduction for first-time breeders as they were more likely to skip the following breeding event than experienced breeders. Given that most primiparous females are still undergoing somatic growth when they first breed, they must bear the cost of both growth, which continues to age six (Laws 1956), and breeding. Consequently, first-time breeders are likely to face a higher total energetic cost when reproducing. Reproductive skipping may therefore be associated with their inability to restore nutrient reserves sufficiently to breed the following year without compromising their survival.

The probability to breed in year $t+1$ varied strongly among years, irrespective of the female reproductive state in year t . I found that a higher probability to breed in year $t+1$ was associated with high Southern Annular Mode (SAM) values during the February-April period in year t . Positive SAM anomalies are associated with higher primary productivity (Lefebvre *et al.* 2004; Forcada & Trathan 2009) and resources available during these periods are therefore likely to be more abundant. The February-April period corresponds to the end of the mature females moult and the beginning of their post-moult foraging trip (Hindell & Burton 1988b). This period also corresponds to the embryo implantation (Laws 1953). Our results showed that environmental conditions during this period play a critical role on intermittent breeding: if environmental conditions were poor (*i.e.* SAM values were low), a females' pregnancy was more likely to be interrupted. The extended fast undertaken by female elephant seals during the moult results in significant body mass loss (Boyd *et al.* 1993; Hindell *et al.* 1994). Females may not be able to bear energetic costs induced by gestation

when under a certain threshold of body condition. Breeding pauses may therefore be a strategy to offset reproductive costs under severe environmental conditions following the moult (Cubaynes *et al.* 2011). This may be the case even if heterogeneity in individual quality is also expected to play an important role in intermittent breeding, with lower quality individuals skipping reproduction more frequently than higher quality females independent of environmental conditions.

At Macquarie Island, breeding in female elephant seals produced a high cost to survival (see also Desprez *et al.* (2014), Chapter 3). Survival of experienced breeders was almost 10% lower than that of experienced nonbreeders. This result contradicts the prediction from life-history theory that survival of long-lived individuals should be buffered against reproductive costs with individuals favouring their own survival by restricting reproductive effort (Roff 1992). Female elephant seals at Macquarie Island invested in reproduction at a significant cost to their survival. This cost to survival has been observed in another long-lived pinniped, the Weddell seal (*Leptonychotes weddellii*, Hadley *et al.* (2006)), and capital breeding has been suggested as being a reason for the reduced survival of breeding females in that population. Elephant seals are extreme capital breeders and nursing induces high energetic costs (Arnbom *et al.* 1997). By avoiding the energetic costs of gestation and lactation, females skipping reproduction increased their chances of surviving to the following year.

In this population of elephant seals, breeding pauses seem to be used as a strategy to maximize LRO. For all cohorts and quantiles, female elephant seals skipping reproduction 2 to 4 times over their lifetime achieved the highest values of LRO. Given the high cost of breeding for female elephant seals, skipping reproduction on a few occasions may allow females to maximize their survival and thereby accumulate a greater number of breeding events over their lifespan. Our results also highlight the existence of two extreme strategies. Some females, represented by the upper quantiles ($\tau = 0.90$ and 0.95), were able to reach the highest values of LRO with few breeding pauses while poor mothers, represented by the lower quantiles ($\tau = 0.05$ and 0.10), produced the lowest numbers of offspring over lifespan irrespective of the number of breeding pauses. This supports the hypothesis of heterogeneity in female quality. "Supermums" producing the highest number of offspring over their lifespan with no or few breeding pauses appear to be females of higher quality able to cope with reproductive costs. At the opposite end of the spectrum, females skipping a high number of breeding events and producing a low number of pups were probably females in perpetually poorer condition.

In conclusion, both initial hypotheses received empirical support. Female elephant seals at Macquarie Island seem to use reproductive skipping as a strategy to offset reproductive costs on survival, females skipping reproduction having a higher chance to survive until the next year, and to optimize LRO. Breeding pauses were influenced by environmental conditions during the first trimester of pregnancy with females more prone to skip reproduction under unfavourable conditions. However, individual quality also seemed to play a major role in females' decision to skip reproduction, with high-quality females likely to breed more frequently than females in poorer condition.

The next step in addressing the consequences of intermittent breeding on individual fitness will be to look at the number of offspring produced by females that recruit into the breeding population. Our dataset did not include enough cohorts of individuals to investigate this question. Such information can only be obtained from extremely scarce extensive long-term datasets that include several generations of individuals (Clutton-Brock & Sheldon 2010).

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Appendix A. Goodness-of-fit-tests

A.1. Goodness-of-fit test performed on the entire dataset

Female southern elephant seals were marked from 1993 to 1999 and resighted from 1994 to 2010. The fit of the Cormack-Jolly-Seber (CJS) model was evaluated after transforming the observations into a single-state code ('1' for encountered individuals and '0' for not encountered individuals) and the first encounter removed.

	χ^2	df	p-value
Test 3.SR	415.67	15	<0.001
Test 3.SM	147.97	42	<0.001
Test 2.CT	796.85	14	<0.001
Test 2.CL	155.81	52	<0.001
Overall	1516.30	123	<0.001

Table A.1. Results of the goodness-of-fit test to the CJS model performed on the entire dataset.

I assumed the strong transient effect (test 3.SR) to be due to changes in survival with age and the trap-dependence effect (test 2.CT) to be due to an unequal effort of observation. I suspected the resighting heterogeneity to be less important for females that have not started breeding yet. To check these assumptions, I conducted separate GOF tests on different part of the resight histories (see below).

A.2. Goodness-of-fit test to the CJS model performed on the prebreeder part of the resight histories

	χ^2	df	p-value
Test 3.SR	610.01	8	<0.001
Test 3.SM	1.65	7	0.976
Test 2.CT	32.82	7	<0.001
Test 2.CL	2.252	6	0.895
Overall	646.74	28	<0.001

Table A.2. Results of the goodness-of-fit test to the CJS model performed on the prebreeder part of the resight histories after removing the first encounter.

The test 3.SR indicated a strong transient effect. Macquarie Island is considered as a closed breeding population (McMahon *et al.* 2006c) and the presence of transient seals is therefore

highly unlikely. I assumed the transient effect to be due to variation in survival with age and accounted for this heterogeneity by incorporating an age effect on the survival of prebreeders. Though still significant, the trap-dependence effect was much weaker than in section A.1. I adjusted for the remaining lack of fit with a variance inflation factor (see calculation below).

A.3. Goodness-of-fit tests to the CJS model performed on the breeder part of the resight histories.

In order to determine whether the trap-dependence effect was due to an unequal effort of observation, I conducted separate GoF tests on the resight histories of (i) the breeders mainly located on the isthmus over their lifetime, (ii) the breeders mainly located on the top third of the island and (iii) the breeders mainly located on the rest of the island.

	χ^2	df	p-value
Test 3.SR	196.07	13	<0.001
Test 3.SM	68.57	26	<0.001
Test 2.CT	68.82	12	<0.001
Test 2.CL	47.87	20	<0.001
Overall	381.34	71	<0.001

Table A.3.1. Results of the goodness-of-fit test to the CJS model performed on breeders mainly observed in location 1 (= Isthmus).

	χ^2	df	p-value
Test 3.SR	58.72	13	<0.001
Test 3.SM	12.40	13	0.495
Test 2.CT	18.07	11	0.080
Test 2.CL	8.87	10	0.545
Overall	98.05	47	<0.001

Table A.3.2. Results of the goodness-of-fit test to the CJS model performed on breeders mainly observed in location 2 (= top third of the Island).

	χ^2	df	p-value
Test 3.SR	12.02	9	0.212
Test 3.SM	0	4	1
Test 2.CT	0	8	1
Test 2.CL	1.64	7	0.977
Overall	13.66	28	0.989

Table A.3.3. Results of the goodness-of-fit test to the CJS model performed on breeders mainly observed in location 3 (= rest of the Island).

Only the test 2.CT conducted on the resight histories of the breeders in location 1 was still significant. The trap-dependence effect was however much weaker. To account for this resighting heterogeneity, I included a location effect on the resighting probabilities of breeders and adjusted for the remaining heterogeneity with a variance inflation factor (see calculation below).

Test 3.SR were statistically significant for the two first groups of breeders. I assumed this result to be due to the cost of first reproduction on survival (Desprez *et al.* (2014), Chapter 3). To account for this effect, I included an age effect on the survival of first-time breeders.

A.4. Calculation of the overall variance inflation factor from GoF tests A.2 and A.3.

After discarding the components of the test 3.SR of each GoF test (Pradel *et al.* 2005), I estimated the overall inflation factor as:

$$\hat{c} = \frac{\chi^2_{\text{test3.SM(A.2)}} + \chi^2_{\text{test2.CT(A.2)}} + \chi^2_{\text{test2.CL(A.2)}} + \chi^2_{\text{test3.SM(A.3.1)}} + \chi^2_{\text{test2.CT(A.3.1)}} + \chi^2_{\text{test2.CL(A.3.1)}} + \chi^2_{\text{test3.SM(A.3.2)}} + \chi^2_{\text{test2.CT(A.3.2)}} + \chi^2_{\text{test2.CL(A.3.2)}} + \chi^2_{\text{test2.CL(A.3.3)}}}{\text{df}_{\text{test3.SM(A.2)}} + \text{df}_{\text{test2.CT(A.2)}} + \text{df}_{\text{test2.CL(A.2)}} + \text{df}_{\text{test3.SM(A.3.1)}} + \text{df}_{\text{test2.CT(A.3.1)}} + \text{df}_{\text{test2.CL(A.3.1)}} + \text{df}_{\text{test3.SM(A.3.2)}} + \text{df}_{\text{test2.CT(A.3.2)}} + \text{df}_{\text{test2.CL(A.3.2)}} + \text{df}_{\text{test2.CL(A.3.3)}}}$$

$$\hat{c} = \frac{1.65 + 32.82 + 2.25 + 68.57 + 68.82 + 47.87 + 12.40 + 18.07 + 8.87 + 1.64}{7 + 7 + 6 + 26 + 12 + 20 + 13 + 11 + 10 + 4 + 8 + 7} = 2.01$$

Appendix B. Model selection

List of all models considered in model selection. The best model is in bold. For each model, QAIC, the number of parameters (np) and the difference in the number of QAIC units from the best model (ΔAIC) are provided. *List of abbreviations:* 't' denotes a year effect; 'a' represents a full age effect whereas 'a_(x-y)' indicates an age class effect (*e.g.* 'a₍₀₋₇₊₎' denotes a 8 age classes effect (from age 0 to age 7+) with the last age class (7+) grouping the individuals older than 6 years of age); 'loc' assumes different detection probabilities in the 3 main location of resightings; '+' denotes an additive effect whereas '.' denotes an interactive effect. 'PB', 'B1', 'EB', 'B', 'ENB', 'E' and 'NB' correspond to the states prebreeders, first-time breeders, experienced breeders, breeders (first-time and experienced breeders grouped), experienced nonbreeders, experienced females (experienced breeders and nonbreeders grouped) and nonbreeders (prebreeders and experienced nonbreeders grouped) respectively. In column 'Assignment', 'E^B'('E^{ENB}') indicates that a resighted breeder (experienced nonbreeder) is assigned 'experienced seal with unknown current reproductive status' (event 4).

Table B.1. List of all models considered in the first model selection

Model	detection	Assignment	Survival	Reproduction	AIC	np	ΔAIC
1	(PB; B.loc; ENB).t	PB.a₍₃₋₆₎; B.a₍₃₋₄₊₎; E^B; E^{ENB}.a₍₄₋₅₊₎	PB.a₍₀₋₇₊₎; B1.a₍₃₋₈₊₎; EB; ENB	(PB.a₍₃₋₈₊₎; B1; EB; ENB).t	35507.98	186	0.00
2	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B; ENB).t	35518.02	173	10.04
3	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B.a ₍₄₋₅₊₎ ; ENB).t	35527.83	179	19.85
4	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB).t; ENB	35555.18	174	47.20
5	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B).t; ENB	35562.82	161	54.85
6	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B.a ₍₄₋₅₊₎).t; ENB	35572.27	167	64.30
7	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B1; ENB).t; EB	35577.68	174	69.71
8	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B1).t; EB; ENB	35596.93	162	88.96
9	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; ENB).t; B1; EB	35602.44	161	94.47

(Table B.1. Continued)

Model	detection	Assignment	Survival	Reproduction	AIC	np	ΔAIC
10	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; ENB).t; B	35609.34	160	101.37
11	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; ENB).t; B.a ₍₄₋₅₊₎	35610.94	161	102.97
12	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ .t; B1; EB; ENB	35613.95	149	105.98
13	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ .t; B; ENB	35619.02	148	111.05
14	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ .t; B.a ₍₄₋₅₊₎ ; ENB	35620.45	149	112.48
15	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; B; ENB	35692.87	109	184.89
16	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; B1; EB; ENB	35694.13	110	186.15
17	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; B.a ₍₄₋₅₊₎ ; ENB	35694.79	110	186.82
18	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; ENB.a; B	35696.22	121	188.25
19	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; ENB.a; B1; EB	35697.36	122	189.39
20	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; B.a; ENB	35699.98	122	192.01
21	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; B1.a; EB; ENB	35701.27	115	193.30
22	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; (B; ENB).a	35702.19	134	194.21
23	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB).a; ENB	35708.77	127	200.79
24	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35709.78	139	201.81
25	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.a ₍₄₋₅₊₎ ; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35711.78	140	203.81
26	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB.t	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35717.39	151	209.42
27	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; E	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35720.76	138	212.79
28	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; E. ₍₄₋₅₊₎	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35721.86	139	213.89
29	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.a; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35722.39	151	214.42
30	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.t; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35722.64	151	214.67
31	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB.a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35727.34	151	219.36

(Table B.1. Continued)

Model	detection	Assignment	Survival	Reproduction	AIC	np	Δ AIC
32	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.a ₍₄₋₅₊₎ ; ENB.a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35729.33	152	221.36
33	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; (B1; E).a	35730.48	126	222.50
34	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; B1; E	35732.80	109	224.83
35	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ .t; EB; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35732.82	177	224.84
36	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ .t; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35733.34	190	225.36
37	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).t	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35733.65	163	225.67
38	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; B&E	35735.85	108	227.88
39	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; (B&ENB).a ₍₄₋₅₊₎	35736.30	109	228.32
40	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB	PB.a ₍₃₋₈₊₎ ; B1.a; E	35737.83	114	229.86
41	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; E.a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35738.33	150	230.36
42	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35739.62	163	231.65
43	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; ENB).t; B1.a ₍₃₋₈₊₎ ; EB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35740.19	202	232.21
44	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₆₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35741.63	164	233.65
45	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; (B1.a ₍₃₋₈₊₎ ; EB).t; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35744.67	189	236.70
46	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; (B1.a ₍₃₋₈₊₎ ; EB; ENB).t	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35745.62	201	237.64
47	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB}	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35747.82	162	239.84
48	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎).t; EB; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35753.23	228	245.26
49	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B.a; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35758.53	146	250.55
50	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; ENB).t; EB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35761.23	240	253.25
51	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB).t	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35763.43	252	255.46
52	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB.a}	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35763.62	175	255.65
53	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; E ^{ENB} .a; B.a ₍₃₋₄₊₎ ; E ^B .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35765.04	176	257.06

(Table B.1. Continued)

Model	detection	Assignment	Survival	Reproduction	AIC	np	Δ AIC
54	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB).t; ENB	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35765.37	240	257.40
55	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; (B; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35776.58	158	268.61
56	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; (E ^B ; E ^{ENB}).a; B.a ₍₃₋₄₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35783.89	188	275.91
57	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; (E ^B ; E ^{ENB}).a; B.a ₍₃₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35785.89	189	277.91
58	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; (B; E ^B ; E ^{ENB}).a	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35807.89	201	299.91
59	(PB; (B1,EB).loc; ENB).t	PB.a ₍₃₋₆₎ ; (B; E ^B ; E ^{ENB}).a	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35829.21	243	321.23
60	(NB; B.loc).t	PB.a ₍₃₋₆₎ ; (B; E ^B ; E ^{ENB}).a	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35852.98	187	345.01
61	(PB; (B1,EB).loc; ENB)+t	PB.a ₍₃₋₆₎ ; (B; E ^B ; E ^{ENB}).a	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35885.47	149	377.50
62	(NB; (B1,EB).loc).t	PB.a ₍₃₋₆₎ ; (B; E ^B ; E ^{ENB}).a	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35898.18	229	390.21
63	(PB; B.loc; ENB)+t	PB.a ₍₃₋₆₎ ; (B; E ^B ; E ^{ENB}).a	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	35955.46	146	447.48
64	(NB; B.loc)+t	PB.a ₍₃₋₆₎ ; (B; E ^B ; E ^{ENB}).a	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	36278.13	145	770.15
65	(NB; (B1,EB).loc)+t	PB.a ₍₃₋₆₎ ; (B; E ^B ; E ^{ENB}).a	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	PB.a ₍₃₋₈₊₎ ; (B1; EB; ENB).a	36281.72	148	773.75

Table B.2. List of all models considered in the second model selection

Model	detection	Assignment	Survival	Reproduction	AIC	np	Δ AIC
66	(PB; B.loc; ENB).t	PB.a₍₃₋₆₎; B.a₍₃₋₄₊₎; E^B; E^{ENB}.a₍₄₋₅₊₎	PB.a₍₀₋₇₊₎; B1.a₍₃₋₈₊₎; EB; ENB	(PB.a₍₃₋₈₊₎; B1; EB; ENB).t	35507.98	186	0.00
67	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.a ₍₄₋₅₊₎ ; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35509.26	187	1.29
68	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.a; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35511.59	198	3.62
69	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; E	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35518.69	185	10.71
70	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; E.a ₍₄₋₅₊₎	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35519.97	186	11.99
71	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.t; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35523.59	198	15.61

(Table B.2. Continued)

Model	detection	Assignment	Survival	Reproduction	AIC	np	ΔAIC
72	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB.t	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35526.99	198	19.02
73	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).a	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35527.80	210	19.82
74	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB.a	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35528.22	198	20.25
75	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; E.a	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35529.64	197	21.66
76	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB.a ₍₄₋₅₊₎ ; ENB.a	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35529.65	199	21.68
77	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ .t; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35532.83	224	24.85
78	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; (EB; ENB).t	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35536.24	210	28.26
79	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ .t; B1.a ₍₃₋₈₊₎ ; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35543.01	237	35.03
80	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; (B1.a ₍₃₋₈₊₎ ; EB).t; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35545.70	236	37.73
81	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; (B1.a ₍₃₋₈₊₎ ; EB; ENB).t	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35560.40	248	52.42
82	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; ENB).t; B1.a ₍₃₋₈₊₎ ; EB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35561.25	249	53.28
83	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎).t; EB; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35575.57	275	67.60
84	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; B.a; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35577.13	193	69.16
85	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB).t; ENB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35588.78	287	80.80
86	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	PB.a ₍₀₋₇₊₎ ; (B; ENB).a	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35591.25	205	83.27
87	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; ENB).t; EB	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35595.06	287	87.08
88	(PB; B.loc; ENB).t	PB.a ₍₃₋₆₎ ; B.a ₍₃₋₄₊₎ ; E ^B ; E ^{ENB} .a ₍₄₋₅₊₎	(PB.a ₍₀₋₇₊₎ ; B1.a ₍₃₋₈₊₎ ; EB; ENB).t	(PB.a ₍₃₋₈₊₎ ; B1; EB; ENB).t	35607.11	299	99.13

Appendix C. Detection and state assignment probabilities

Table C.1. Detection probabilities by reproductive state, year and main resighting location over the lifetime of a seal. For each estimate, the lower (CI-) and upper (CI+) limits of the confidence interval and the standard error (SE) are provided. 'PB', 'B' and 'ENB' correspond to the states prebreeder, breeder (first-time and experienced breeder grouped together) and experienced nonbreeder, respectively. Locations '1', '2' and '3' correspond to the Isthmus, the top-third of the Island and the rest of the Island respectively. The location effect was not tested on the detection of prebreeders and experienced nonbreeders. Detection probabilities of breeders were constrained to be low in 2002 to reflect the severe restrictions imposed on resighting effort during this year.

Parameter	Year	Location	Estimate	CI-	CI+	SE
Detection PB	1994	-	0.63	0.57	0.68	0.03
Detection PB	1995	-	0.56	0.52	0.60	0.02
Detection PB	1996	-	0.49	0.45	0.53	0.02
Detection PB	1997	-	0.55	0.52	0.59	0.02
Detection PB	1998	-	0.51	0.48	0.55	0.02
Detection PB	1999	-	0.63	0.60	0.66	0.02
Detection PB	2000	-	0.61	0.58	0.64	0.02
Detection PB	2001	-	0.56	0.53	0.60	0.02
Detection PB	2002	-	0.20	0.16	0.23	0.02
Detection PB	2003	-	0.38	0.34	0.43	0.03
Detection PB	2004	-	0.15	0.11	0.19	0.02
Detection PB	2005	-	0.03	0.01	0.07	0.01
Detection PB	2006	-	0.05	0.02	0.11	0.02
Detection PB	2007	-	0.05	0.02	0.13	0.02
Detection PB	2008	-	0.02	0.00	0.13	0.02
Detection PB	2009	-	0.23	0.07	0.53	0.12
Detection PB	2010	-	0.01	0.00	0.19	0.02
Detection B	1996	1	0.09	0.03	0.25	0.05
Detection B	1997	1	0.93	0.14	1.00	0.15
Detection B	1998	1	0.87	0.29	0.99	0.16
Detection B	1999	1	0.86	0.66	0.95	0.07
Detection B	2000	1	0.87	0.70	0.95	0.06
Detection B	2001	1	1.00	0.01	1.00	0.00
Detection B	2002	1	0.18	0.18	0.18	0.00
Detection B	2003	1	1.00	1.00	1.00	0.00
Detection B	2004	1	1.00	1.00	1.00	0.00
Detection B	2005	1	1.00	1.00	1.00	0.00
Detection B	2006	1	0.96	0.02	1.00	0.14
Detection B	2007	1	1.00	1.00	1.00	0.00
Detection B	2008	1	0.34	0.10	0.71	0.18
Detection B	2009	1	0.92	0.57	0.99	0.08
Detection B	2010	1	0.59	0.14	0.93	0.27
Detection B	1996	2	0.35	0.11	0.71	0.18

(Table C.1. Continued)

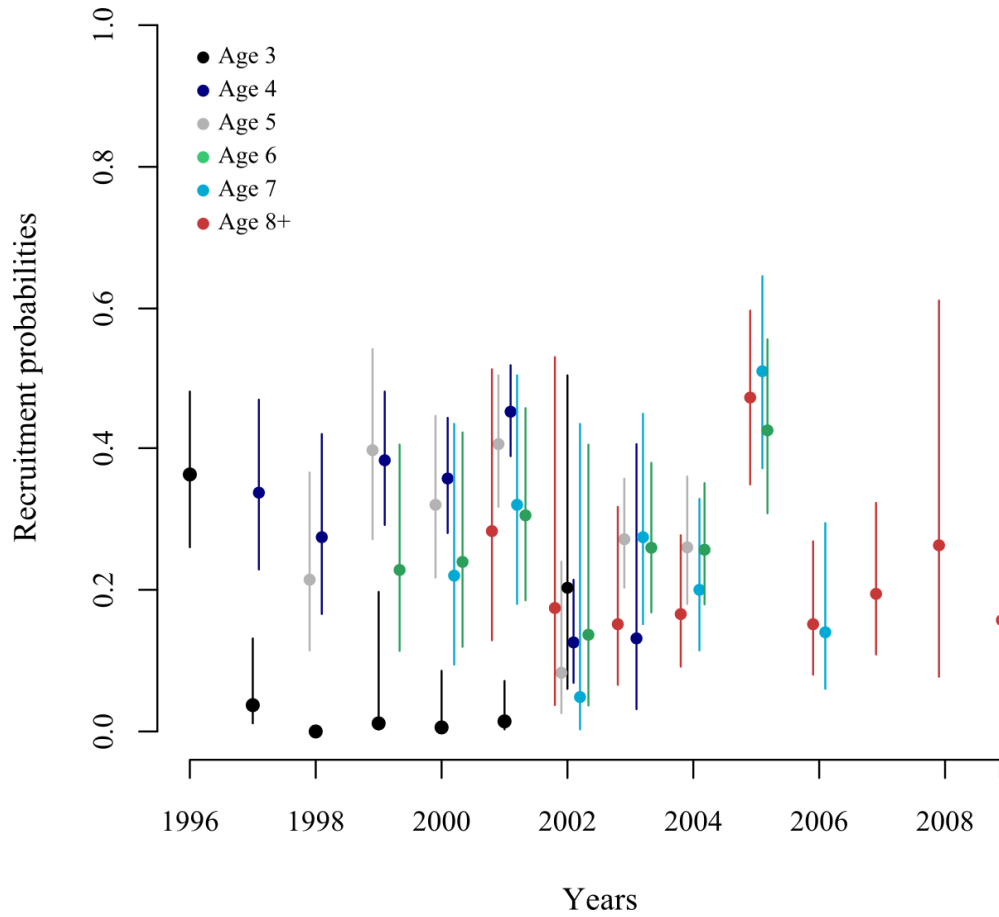
Parameter	Year	Location	Estimate	CI-	CI+	SE
Detection B	1997	2	1.00	1.00	1.00	0.00
Detection B	1998	2	0.79	0.20	0.98	0.23
Detection B	1999	2	0.82	0.48	0.96	0.12
Detection B	2000	2	0.82	0.48	0.96	0.12
Detection B	2001	2	0.97	0.18	1.00	0.08
Detection B	2002	2	0.21	0.21	0.21	0.00
Detection B	2003	2	0.65	0.43	0.83	0.11
Detection B	2004	2	0.83	0.52	0.96	0.11
Detection B	2005	2	0.88	0.68	0.96	0.07
Detection B	2006	2	1.00	1.00	1.00	0.00
Detection B	2007	2	0.56	0.31	0.79	0.13
Detection B	2008	2	0.32	0.10	0.67	0.16
Detection B	2009	2	0.80	0.32	0.97	0.18
Detection B	2010	2	1.00	1.00	1.00	0.00
Detection B	1996	3	0.78	0.16	0.98	0.25
Detection B	1997	3	1.00	1.00	1.00	0.00
Detection B	1998	3	0.54	0.08	0.94	0.33
Detection B	1999	3	0.69	0.27	0.93	0.19
Detection B	2000	3	0.39	0.17	0.66	0.14
Detection B	2001	3	0.52	0.30	0.73	0.12
Detection B	2002	3	0.05	0.05	0.05	0.00
Detection B	2003	3	0.49	0.27	0.73	0.13
Detection B	2004	3	0.37	0.17	0.63	0.13
Detection B	2005	3	0.30	0.17	0.48	0.08
Detection B	2006	3	0.69	0.21	0.95	0.23
Detection B	2007	3	0.17	0.05	0.46	0.10
Detection B	2008	3	0.09	0.02	0.40	0.08
Detection B	2009	3	0.37	0.13	0.71	0.17
Detection B	2010	3	0.25	0.01	0.89	0.30
Detection ENB	1997	-	0.00	0.00	0.00	0.00
Detection ENB	1998	-	0.14	0.07	0.27	0.05
Detection ENB	1999	-	0.29	0.17	0.46	0.08
Detection ENB	2000	-	0.38	0.25	0.53	0.07
Detection ENB	2001	-	0.35	0.26	0.46	0.05
Detection ENB	2002	-	0.22	0.13	0.34	0.06
Detection ENB	2003	-	0.43	0.36	0.51	0.04
Detection ENB	2004	-	0.25	0.20	0.32	0.03
Detection ENB	2005	-	0.02	0.01	0.08	0.02
Detection ENB	2006	-	0.10	0.07	0.15	0.02
Detection ENB	2007	-	0.15	0.10	0.21	0.03
Detection ENB	2008	-	0.02	0.00	0.11	0.02
Detection ENB	2009	-	0.69	0.21	0.95	0.24
Detection ENB	2010	-	0.01	0.00	0.04	0.01

Table C.2. *Breeding state assignment probabilities by reproductive state and age. For each estimate, the lower (CI-) and upper (CI+) limits of the confidence interval and the standard error (SE) are provided.*

Probability to assign the state:	Age	Estimate	CI-	CI+	SE
Prebreeder	1	1	1	1	0
Prebreeder	3	0.48	0.44	0.52	0.02
Prebreeder	4	0.21	0.17	0.25	0.02
Prebreeder	5	0.04	0.02	0.08	0.01
Prebreeder	6	0.03	0.01	0.09	0.02
Prebreeder	7+	0	0	0	0
Breeder	3	0.16	0.06	0.38	0.08
Breeder	4+	1.00	1.00	1.00	0.00
Experienced (given the female is a breeder)	-	0.00	0.00	0.00	0.00
Experienced (given the female is a nonbreeder)	4	0.06	0.00	0.67	0.10
Experienced (given the female is a nonbreeder)	5+	1.00	1.00	1.00	0.00

Appendix D. Recruitment probabilities

Fig. D.1. Recruitment probabilities by age and years. The vertical bars indicate the 95% confidence intervals around the mean estimates (closed circles).



Appendix E. Relationship between the lifetime reproductive output and the number of breeding pauses over lifetime

Lines on figures represent the quantile regressions for the 0.05, 0.10, 0.25, 0.50, 0.75, 0.90 and 0.95 quantiles.

Fig. E.1. Relationship between the lifetime reproductive output and the number of breeding pauses over lifetime in female southern elephant seals from the second cohort (i.e. born in 1994).

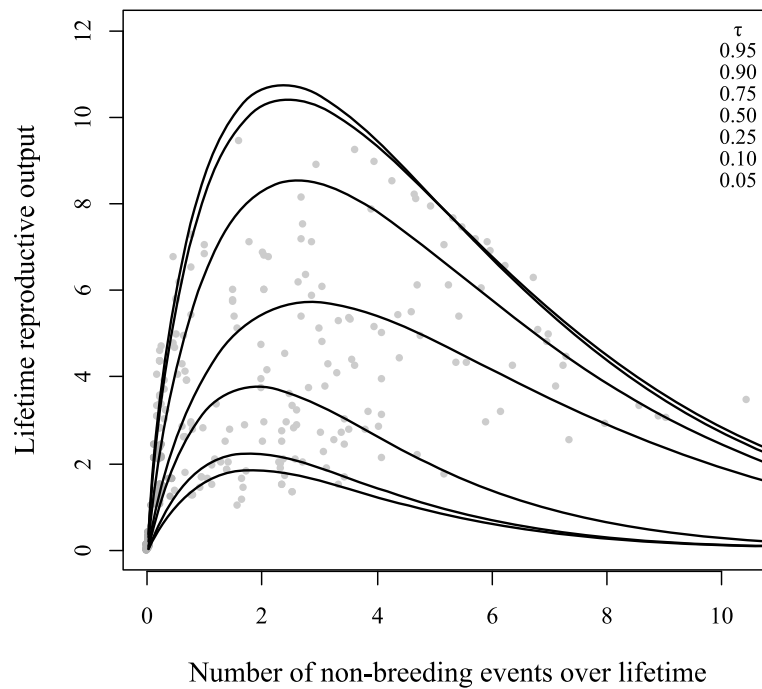


Fig. E.2. Relationship between the lifetime reproductive output and the number of breeding pauses over lifetime in female southern elephant seals from the third cohort (i.e. born in 1995).

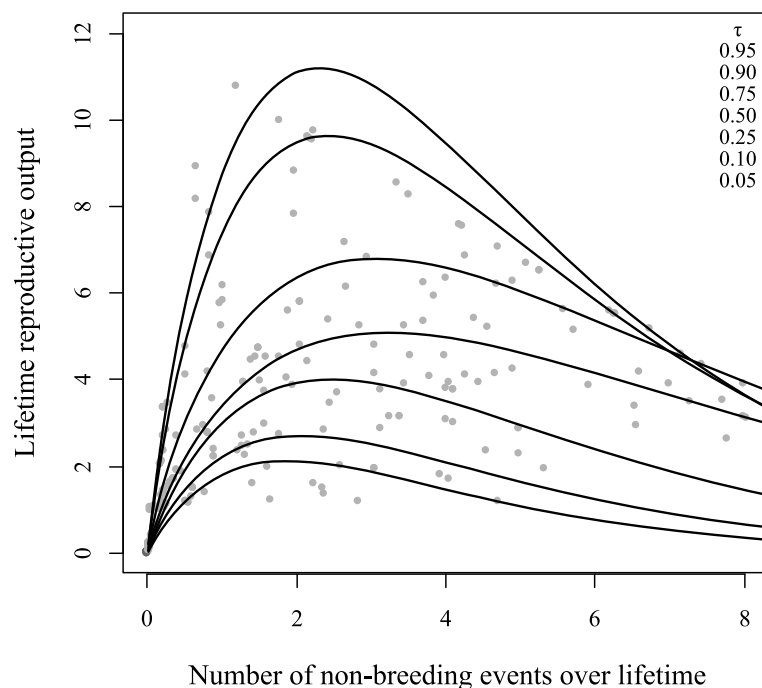


Fig. E.3. Relationship between the lifetime reproductive output and the number of breeding pauses over lifetime in female southern elephant seals from the forth cohort (i.e. born in 1996).

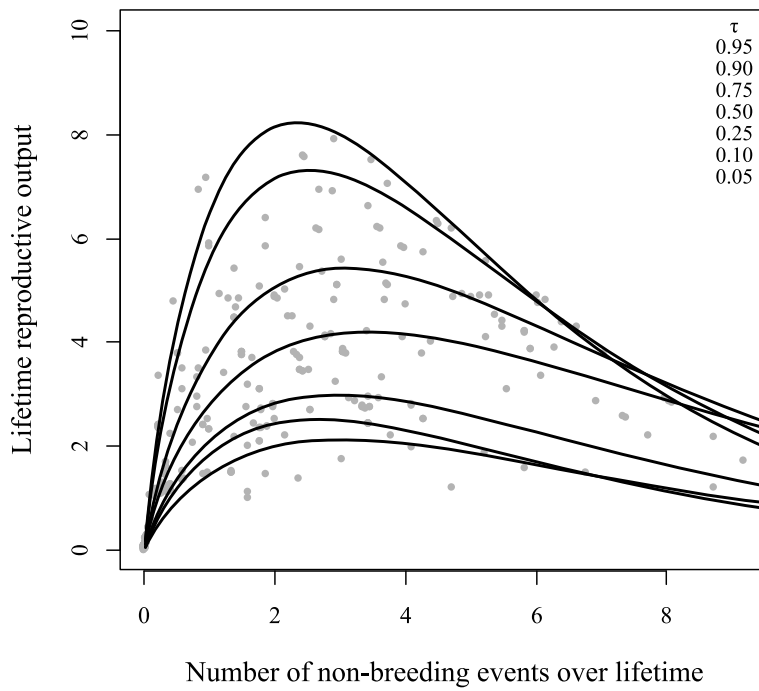


Fig. E.4. Relationship between the lifetime reproductive output and the number of breeding pauses over lifetime in female southern elephant seals from the fifth cohort (i.e. born in 1997).

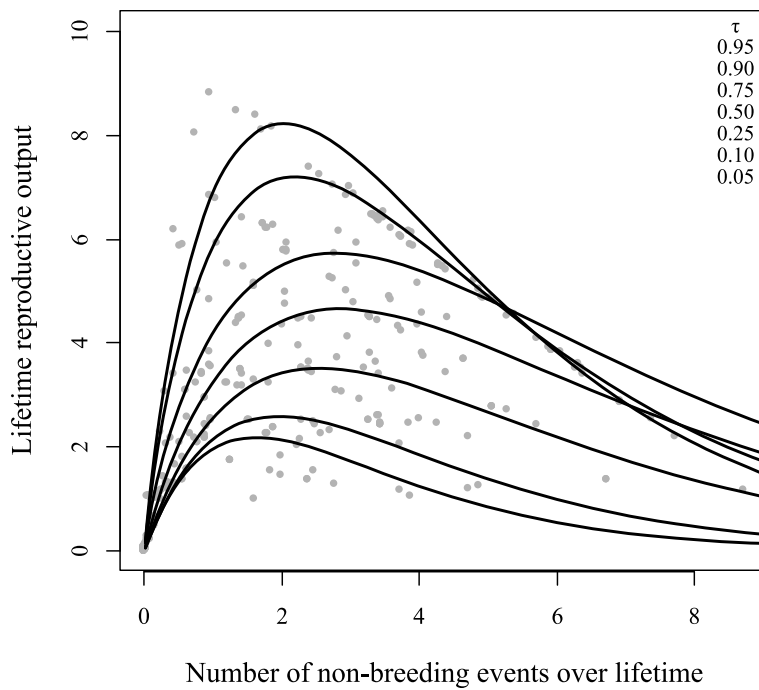


Fig. E.5. Relationship between the lifetime reproductive output and the number of breeding pauses over lifetime in female southern elephant seals from the sixth cohort (i.e. born in 1998).

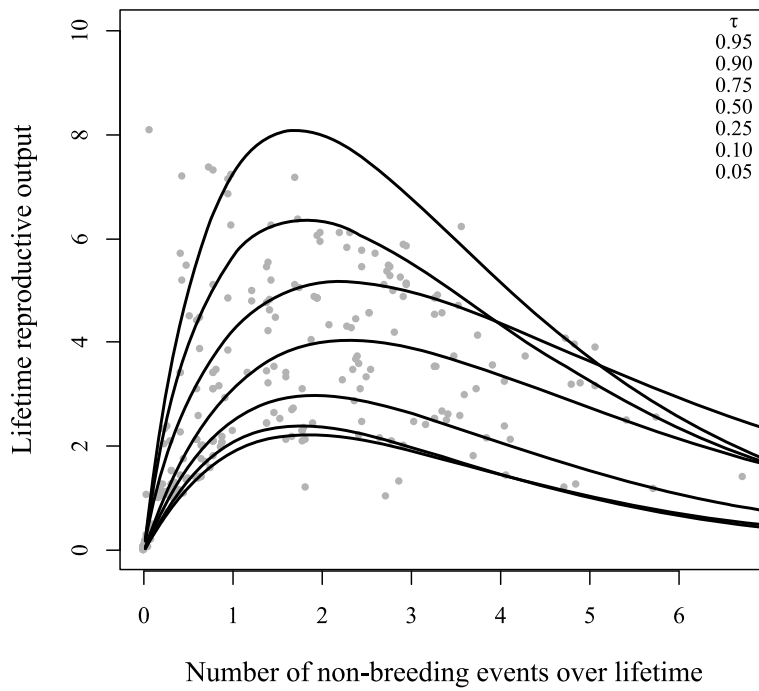
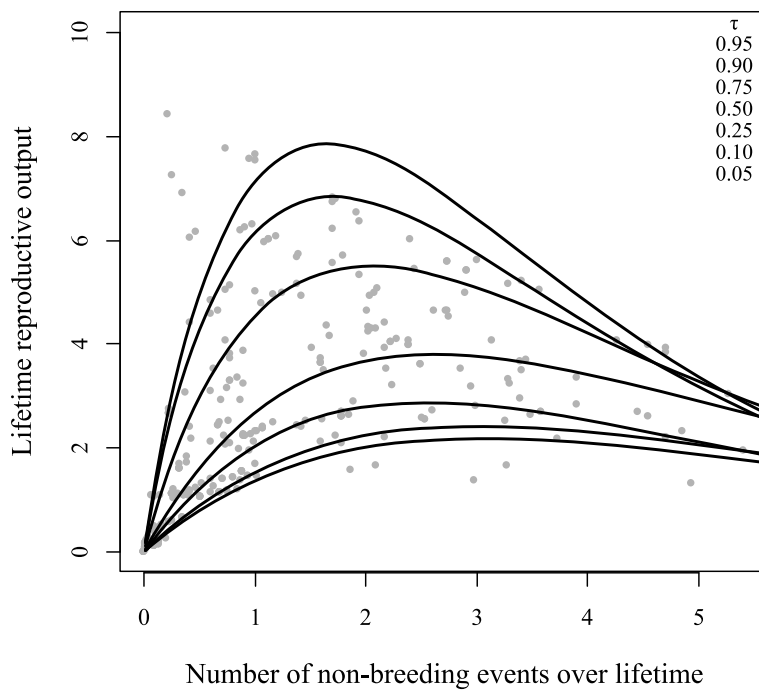


Fig. E.6. Relationship between the lifetime reproductive output and the number of breeding pauses over lifetime in female southern elephant seals from the seventh cohort (i.e. born in 1999).



Chapter 5

Population trend and prospects



Picture: M. Desprez

In preparation: Desprez M., McMahon C.R., Gimenez O., Harcourt R., Hindell M. A., & Lebreton J.-D.
Southern elephant seals at Macquarie Island, population trend and prospects.

Abstract

The Southern Ocean has exhibited spatially variable expressions of climate change that have resulted in contrasting responses by populations of predators inhabiting this ecosystem. Populations of southern elephant seals (*Mirounga leonina*) have all been stable or increasing with the exception of the Macquarie Island population that has decreased over the past 50 years. Here, I reevaluated the trend of this population by estimating the population growth rate using a matrix population model structured by age and reproductive state. I also estimated the demographic parameter elasticities in order to identify those parameters that have the most potential to influence the population growth rate. The matrix modelling approach, by contrast to the census-based approach that was recently used to estimate the growth rate of this population, has improved our understanding of the potential mechanisms driving the dynamics of the population. Our results confirmed the ongoing decline of the population of southern elephant seals at Macquarie Island. However, the modelled population growth rate was significantly lower than the population growth rate estimated from annual census data. The long generation time, high reproductive cost to survival and variable probability of breeding in female elephant seals are potential clues to this population decline but further investigation are required to fully understand the processes that drive population changes.

Keywords: *Mirounga leonina*, marine predator, population dynamics, matrix population model, census data, Southern Ocean.

Introduction

The Southern Ocean, one of the most extensive marine ecosystems globally and a major component of the Earth's climate system, has exhibited some of the clearest expressions of climate change (including increases in atmospheric temperatures, warming of the Antarctic Circumpolar current waters, regionally contrasting changes in the extent and seasonality of sea ice, strengthening of westerly winds, poleward shift of ocean fronts) over the past 50 years (*e.g.* Levitus *et al.* (2000); Marshall (2003); Vaughan *et al.* (2003); Comiso *et al.* (2011)). These changes are likely to have profound consequences on the structure and productivity of the Southern Ocean food webs and ecosystems (Montes-Hugo *et al.* 2009; Constable *et al.* 2014; Smith *et al.* 2014). However, measuring the extent and impact of these changes at the level of primary and secondary production is extremely difficult as it requires the monitoring of large areas of ocean for long periods of time, something near impossible in practice, especially during the Antarctic winter. By contrast, Southern Ocean top predators, such as seabirds and seals, can be relatively easily monitored at their natal colonies to which they dependably return (Hindell *et al.* 2003a). As they feed on prey such as krill, fish or squid that are themselves directly influenced by abiotic components, these predators are thought to reliably integrate and reflect variability in environmental conditions, so that changes in population trends are likely to be indicative of large-scale changes in ecosystem structure and/or function (Croxall *et al.* 2002; Jenouvrier *et al.* 2003; Weimerskirch *et al.* 2003). A number of long-term studies have successfully documented changes in top predator demographic traits, such as survival and breeding success, and/or population sizes in relation to climate variation (*e.g.* Barbraud & Weimerskirch (2001); Jenouvrier *et al.* (2003); Ainley *et al.* (2005); Forcada *et al.* (2005); Jenouvrier *et al.* (2005b); Hadley *et al.* (2007); Barbraud *et al.* (2011); Pardo *et al.* (2013); Van den Hoff *et al.* (2014)). Changes in population processes of top predators are therefore seen as one of the best indicators of global change impact in the Southern Ocean ecosystem.

Signals of climate change are not monotonic and vary considerably across the Southern Ocean (Trathan *et al.* 2007; Constable *et al.* 2014). Pertinent examples of this spatial variation are the differences in the northerly extent and temporal duration of the sea-ice around Antarctica. The Ross Sea is undergoing a significant positive trend in sea-ice extent and duration of the ice season (Comiso *et al.* 2011; Stammerjohn *et al.* 2012). By contrast, other regions in Antarctica, like the Weddell Sea, have experienced warmer surface

temperatures and, as a consequence, reduced sea-ice extent and extensive collapses of large ice shelves (Cook & Vaughan 2010; Stammerjohn *et al.* 2012). As a result of these contrasting physical conditions, the distribution and abundance of species of lower trophic levels varies across the Southern Ocean and different regions are dominated by different food webs (Trathan *et al.* 2007). This spatial variability in food webs may lead to contrasting responses to environmental changes among populations of the same species of marine predator inhabiting different areas of the Southern Ocean (Trathan *et al.* 2007; Constable *et al.* 2014). One such predator is the southern elephant seal (*Mirounga leonina*) where all but one population, the Macquarie Island population, is increasing or stable.

Southern elephant seals are marine predators of the Southern Ocean. While they travel long distances to forage (often over 5000 km in a round trip) (Hindell *et al.* 2003b; Biuw *et al.* 2007), elephant seals display a high level of philopatry returning to breed close to or at their natal sites (Nicholls 1970; Lewis *et al.* 1996). On the basis of their breeding locations, four genetically distinct populations of southern elephant seals have been identified (Slade *et al.* 1998; Hoelzel *et al.* 2001): the South Georgia population in the South Atlantic, the Îles Kerguelen population in the South Indian Ocean, the Macquarie Island population in the South Pacific Ocean and the Peninsula Valdés Population in Argentina (McMahon *et al.* 2005a). All populations of southern elephant seals were heavily harvested for their oil in the 19th century leading to a substantial decline in the number of individuals (Carrick & Ingham 1960; Hindell & Burton 1988a). Following the cessation of sealing, seal stocks appeared to recover (Carrick & Ingham 1960) before dramatically decreasing again in the South Indian and South Pacific Oceans between the 1950's and 1990's (McMahon *et al.* 2005a). Recent studies suggest that the southern Indian Ocean subpopulations are now stable or increasing (Slip & Burton 1999; Pistorius *et al.* 2004; McMahon *et al.* 2009; Authier *et al.* 2011). However, the Macquarie Island population appears to still be declining (Van den Hoff *et al.* 2014). Although the southern elephant seal is one of the best-studied pinnipeds, the reason for the ongoing decrease at Macquarie Island is still unclear (McMahon *et al.* 2005a). Currently the prevailing hypothesis is that it is in response to an ecosystem regime shift affecting the Southern Ocean (Weimerskirch *et al.* 2003; McMahon *et al.* 2005a).

Van den Hoff *et al.* (2014) used annual censuses of female elephant seals to assess the trend of the population of southern elephant seals at Macquarie Island. Detailed demographic information for this population is also available through a long-term capture-mark-recapture program that started in 1993 (McMahon *et al.* 2003). Here, I propose to estimate the growth

rate of this population using a matrix population model parameterized with demographic parameters obtained from that capture-recapture study. Such an approach presents a major advantage over the census-based approach as it identifies, through elasticity analysis, the life-history trait(s) that has (have) the strongest relative effect on the population growth rate, potentially providing important information on the demographic mechanisms underlying population changes (Caswell 2001). Such information is critical to propose effective conservation and management measures (Caughley 1994). By estimating the population growth rate from a matrix model, I aim to improve our understanding of the intrinsic dynamics of the population of southern elephant seals at Macquarie Island and confirm the direction and extent of the observed population trend. I compare this demographically derived estimate to the growth rate estimated from annual censuses over the same period as the capture-recapture study (1993-2011). I also estimate the elasticities of each demographic parameter in order to determine the contribution of each parameter to population growth. Finally I discuss the potential causes of the decline in the context of environmental changes and in light of recent studies of southern elephant seal foraging behaviour.

Material and methods

Data collection

Southern elephant seals (*Mirounga leonina*) have a predictable annual life cycle that includes two terrestrial haul-outs: to breed (September-November) and to moult (austral summer). During the breeding season, female elephant seals aggregate in dense harems controlled by few dominant males, and give birth to a single pup that they nurse for approximately 24 days while fasting. Once their pup is weaned, females mate and return to sea. From 1993 to 1999, 6 631 recently weaned female elephant seals were permanently and individually marked by hot iron branding (McMahon *et al.* 2006b; McMahon *et al.* 2006c) on the isthmus of Macquarie Island (54°30' S, 158°57' E). Throughout the year, until 2001, resighting surveys of branded individuals were conducted: (i) daily on the isthmus, (ii) every ten days on the top third of the island and (iii) once a month on the rest of the island. From 2002 onwards, resightings were opportunistic. Each marked seal resighted was recorded along with its reproductive status when identified.

In addition to the resighting data collection, breeding females present on the isthmus were counted annually from 1988 to 2011. Censuses of breeding females on the whole island were also undertaken from 1988 to 2004 and in 2009. The counts were done on the 15th October which corresponds to the peak haul-out date of breeding females (Hindell & Burton 1988b). Seals were counted at least twice by two or more observers and, if observer estimates differed by more than 5%, further counts were undertaken until the estimates were within the margin of error. The mean of the counts was used as the count estimate (Van den Hoff *et al.* 2007).

Demographic parameter estimates

Local demographic parameters (*i.e.* survival, recruitment and breeding probabilities) were estimated using a multi-event capture-recapture model (Pradel 2005) that accounted for uncertainty in reproductive status (see Chapter 4 for more details about the model and the model selection).

Population modelling

Our model was based on the female segment of the population only, as I assumed that, in this extreme polygynous system in which males do not contribute to the care of pups, the population dynamics would be principally determined by females. I modelled the population dynamics of the southern elephant seals using a linear time-invariant matrix model:

$$N_{t+1} = A * N_t$$

where A is the population projection matrix and N_t the population vector that describes the number of individuals in each class at time t (Caswell 2001).

Based on the results of previous capture-recapture studies (Desprez *et al.* (2014), Chapter 3; Chapter 4), I structured the population projection matrix A by age and reproductive state. At Macquarie Island, female elephant seals start to reproduce at 3 years of age (*i.e.* there is no recruitment into the breeding population before this age) (McMahon *et al.* 2003). The probability of recruiting varied from age 3 to age 8 and was considered constant and independent of age for females aged 8 years and older (Desprez *et al.* (2014), Chapter 3). Once recruited, female elephant seals may breed every year or skip some reproductive events (Chapter 4). I defined the fecundity as the number of weaned females produced *per* female

per breeding season. Survival of juveniles was age dependent from weaning (age 0) to age 7 and fixed as constant for individuals aged 7 years and older. I considered 6 age classes for the survival of first-time breeders (age 3 to age 8 and older) (Desprez *et al.* (2014), Chapter 3). Survival of experienced breeders and experienced nonbreeders were distinct and independent of age (Chapter 4). Assuming a pre-breeding census, I represent the life-cycle graph and the projection matrix corresponding to this population model in Fig. 5.1.

Demographic parameters, estimated from the capture-recapture model, were used to parameterize the population model (Table 5.1). I used the average values of time-dependent recruitment and breeding probabilities (Chapter 4). In long-lived species, reproductive parameters generally have low sensitivities (Sæther & Bakke 2000), therefore the use of average values for these parameters was assumed to not bias the estimate of the population growth rate. Fecundity corresponded to the product of sex-ratio by the number of pups produced per female. Elephant seals typically giving birth to a single pup (McMahon & Hindell 2003) and producing roughly even numbers of males and females (Carrick & Ingham 1962), I fixed the fecundity at the constant value of 0.5 ($f = 1 * 0.5$).

From the matrix model, I calculated the population growth rate λ (the dominant eigenvalue of the projection matrix A), the stable class distribution (right eigenvector of A) and the elasticities of the growth rate λ to variation in demographic rates (Caswell 2001). Analyses were performed in MATLAB (MATLAB 2013) and using the popbio package (Stubben & Milligan 2007) in R (R Core Team 2014).

The sampling variance of the asymptotic growth rate was estimated by simulating 10 000 matrix models replicates based on the parameter estimates and their sampling variance-covariance matrix, assuming a normal distribution (Houllier *et al.* 1989).

Census-based population growth rate

The number of breeding females on the isthmus is highly correlated to the number of breeding females on the whole island (Van den Hoff *et al.* 2014) and because censuses of the whole island were only available for a limited number of years, I used the continuous series

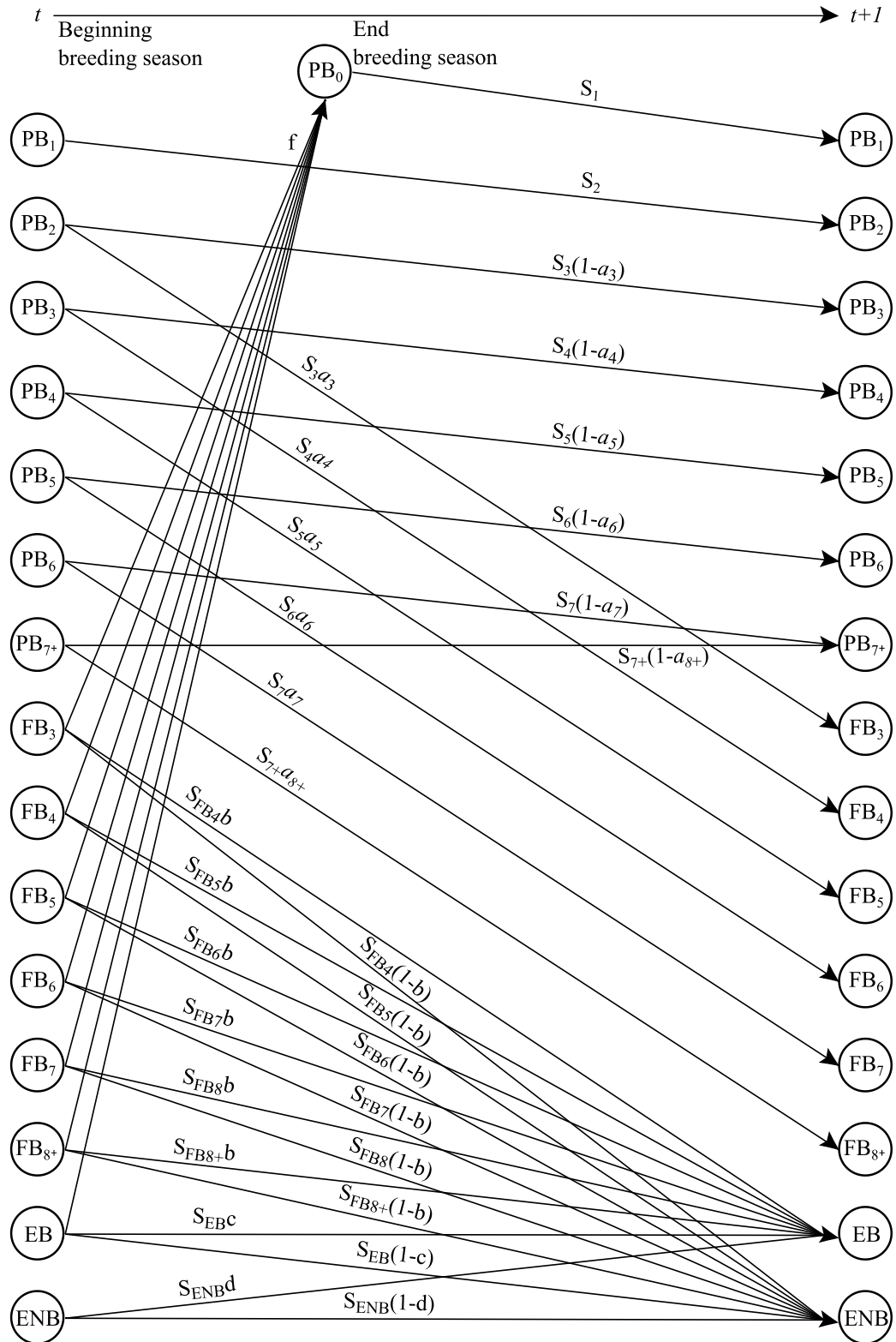


Fig. 5.1. Life-cycle of the female southern elephant seals at Macquarie Island. Transitions between classes (nodes) are indicated by arrows. Transition labels indicate the probability of individuals at one stage (start of arrow) moving or contributing to the node at the end of the arrow over the projection interval. I assume transitions occur over the time scale of 1 year. The population projection matrix corresponding to this life-cycle graph and the list of abbreviations are on the following page.

$$\begin{pmatrix}
 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_1f & S_1f & S_1f & S_1f & S_1f & S_1f & S_1f & 0 \\
 S_2 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & S_3(1-a_3) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & S_4(1-a_4) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & S_5(1-a_5) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & S_6(1-a_6) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & S_7(1-a_7) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & S_3a_3 & 0 & 0 & 0 & 0 & S_{7+}(1-a_{8+}) & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & S_4a_4 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & S_5a_5 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & S_6a_6 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & S_7a_7 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & S_{7+}a_{8+} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{FB4}b & S_{FB5}b & S_{FB6}b & S_{FB7}b & S_{FB8}b & S_{FB8+}b & S_{EB}c & S_{ENB}d \\
 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_{FB4}(1-b) & S_{FB5}(1-b) & S_{FB6}(1-b) & S_{FB7}(1-b) & S_{FB8}(1-b) & S_{FB8+}(1-b) & S_{EB}(1-c) & S_{ENB}(1-d)
 \end{pmatrix}$$

List of abbreviations:

Nodes PB_i and FB_i refer to prebreeders and first-time breeders at age i respectively (age $i+$ group all age classes from age i); nodes EB and ENB refer to experienced breeders and experienced nonbreeders respectively. Parameters ' S_i ' and ' S_{FBi} ' correspond to the survival probability of prebreeders and first-time breeders from age $i-1$ to age i respectively; ' S_{7+} ' and ' S_{FB8+} ' refer to the survival of prebreeders from age 7 and first-time breeders from age 8 respectively; ' S_{EB} ' and ' S_{ENB} ' correspond to the survival of experienced breeders and experienced nonbreeders respectively; 'f' refer to the fecundity, a_i denotes the probability to recruit at age i ; ' a_{8+} ' correspond to the probability to recruit from age 8; 'b', 'c' and 'd' correspond to the probability for a first-time breeder, experienced breeder and experienced nonbreeder respectively to breed the following year.

Parameters	Estimates	SE
S ₁	0.7718	0.01
S ₂	0.8554	0.01
S ₃	0.8870	0.01
S ₄	0.8757	0.02
S ₅	0.8724	0.02
S ₆	0.8049	0.03
S ₇	0.8921	0.04
S ₇₊	0.9181	0.04
S _{FB4}	0.9168	0.07
S _{FB5}	0.7986	0.03
S _{FB6}	0.7746	0.04
S _{FB7}	0.6895	0.05
S _{FB8}	0.5408	0.07
S _{FB8+}	0.3332	0.05
S _{EB}	0.8012	0.01
S _{ENB}	0.8968	0.02
a ₃	0.0907	0.03
a ₄	0.2942	0.04
a ₅	0.2795	0.05
a ₆	0.2649	0.06
a ₇	0.2444	0.07
a ₈₊	0.2006	0.07
f	0.5000	0
b	0.5932	0.07
c	0.6220	0.12
d	0.4153	0.10

Table 5.1. Estimates of demographic parameters used to parameterize the population projection matrix. These estimates were obtained from a multi-event capture-recapture model (Chapter 4). Parameters 'S_i' and 'S_{FBi}' correspond to the survival probability of prebreeders and first-time breeders from age $i-1$ to age i respectively; 'S₇₊' and 'S_{FB8+}' refer to the survival of prebreeders from age 7 and first-time breeders from age 8 respectively; 'S_{EB}' and 'S_{ENB}' correspond to the survival of experienced breeders and experienced nonbreeders respectively; 'f' refer to the fecundity, a_i denotes the probability to recruit at age i ; 'a₈₊' correspond to the probability to recruit from age 8; 'b', 'c' and 'd' correspond to the probability for a first-time breeder, experienced breeder and experienced nonbreeder respectively to breed the following year. Parameters a_i , b, c and d were average of annual values.

of annual isthmus counts to estimate the population growth rate. I considered the data available over the capture-recapture study period only (1993-2011). I estimated the observed population growth rate using two alternative estimates that are more appropriate in the case of random environment (λ_{obs1}) and demographic stochasticity (λ_{obs2}) (Lebreton 1982), variability commonly experienced by populations of wild animals:

$$\lambda_{\text{obs1}} = (1/n) * \sum (N_{t+1}/N_t) \text{ and } \lambda_{\text{obs2}} = \sum(N_{t+1}) / \sum(N_t)$$

where n is the number of years, N_t the population size at time t and N_{t+1} the population at time $t+1$. A 5% coefficient of variation (CV) was assumed to exist in female counts (see *data collection* section). However, the number of females present on the Island at the time of the censuses was likely to vary annually compared to the total number of females in the

population and a 5% CV may underestimate the size of the population. To remain conservative, I considered both a CV of 5% and 10%. The sampling variance of the growth rate was estimated by simulating 1 000 replicates, assuming a normal distribution.

Results

The number of breeding female elephant seals counted on the isthmus at Macquarie Island decreased from 3 232 in 1993 to 2 734 in 2011. The mean annual growth rates estimated from female annual counts were <1 at the exception of λ_{obs1} with a 10% CV that was equal to 1.0031 (Table 5.2). By comparison, the matrix model gave an annual growth rate λ of 0.9649 (95% CI: 0.9568 - 0.9729) over the same period indicating that the population was decreasing at an average rate of 3.51% (SE = 0.0041) per year. The predicted population growth rate λ was significantly lower than the observed population growth rates λ_{obs1} and λ_{obs2} (Wald test, Table 5.2).

	CV	Mean estimates with 95% confidence intervals	SE	z	p-value
$\lambda_{\text{modelled}}$	-	0.9649 [0.9568 - 0.9729]	0.0041	-	-
λ_{obs1}	0.05	0.9950 [0.9874 - 1.0031]	0.0041	-5.19	<0.01
	0.10	1.0031 [0.9857 - 1.0223]	0.0092	-3.79	<0.01
λ_{obs2}	0.05	0.9903 [0.9823 - 0.9982]	0.0042	-4.33	<0.01
	0.10	0.9905 [0.9734 - 1.0071]	0.0085	-2.71	<0.01

Table 5.2. Population growth rate estimated from matrix population model ($\lambda_{\text{modelled}}$) and census data (λ_{obs1} and λ_{obs2}) for southern elephant seals at Macquarie Island over the period 1993 -2011. z corresponds to the value obtained from a Wald test that compares the predicted annual growth rate ($\lambda_{\text{modelled}}$) to the census-based population growth rate (λ_{obs1} and λ_{obs2}). CV corresponds to the coefficient of variation and SE to standard errors.

The generation time, mean age of mothers at childbirth (Lebreton 2005), was estimated to be 11.3 years. Elasticity analysis indicated that the growth rate was most sensitive to changes in adult survival (first-time breeders, experienced breeders and nonbreeders grouped together,

elasticity = 0.54) and more specifically to changes in the survival of experienced breeders and nonbreeders (elasticities: 0.24 and 0.23 respectively) (Table 5.3). Elasticity of the survival of juveniles was low for all age classes (between 0.088 and 0.014) (Table 5.3). However, the overall elasticity of juvenile survival (all age classes grouped together) was relatively high (elasticity = 0.46) indicating that the juvenile component of this population has an important influence on the population growth rate. Fecundity and breeding probabilities had very low elasticities, as expected in a long-lived species (Table 5.3).

Parameters	Elasticity
S_1	0.088
S_2	0.088
S_3	0.088
S_4	0.075
S_5	0.043
S_6	0.024
S_7	0.014
S_{7+}	0.039
Total Juveniles	0.461
S_{FB4}	0.011
S_{FB5}	0.025
S_{FB6}	0.015
S_{FB7}	0.007
S_{FB8}	0.004
S_{FB8+}	0.006
S_{EB}	0.240
S_{ENB}	0.232
Total Adults	0.539
a_3	0.006
a_4	0.014
a_5	0.009
a_6	0.005
a_7	0.002
a_{8+}	0.002
f	0.088
b	0.007
c	0.024
d	0.016

Table 5.3. Elasticities of the population growth rate λ to demographic traits. Parameters ' S_i ' and ' S_{FBi} ' correspond to the survival probability of prebreeders and first-time breeders from age $i-1$ to age i respectively; ' S_{7+} ' and ' S_{FB8+} ' refer to the survival of prebreeders from age 7 and first-time breeders from age 8 respectively; ' S_{EB} ' and ' S_{ENB} ' correspond to the survival of experienced breeders and experienced nonbreeders respectively; ' f ' refer to the fecundity, a_i denotes the probability to recruit at age i ; ' a_{8+} ' correspond to the probability to recruit from age 8; ' b ', ' c ' and ' d ' correspond to the probability for a first-time breeder, experienced breeder and experienced nonbreeder respectively to breed the following year. Parameters a_i , b , c and d were average of annual values.

Discussion

Our results confirm the decline of the population of southern elephant seals at Macquarie Island over the period 1993-2011. However, the population growth rate estimated from the matrix model was lower than the population growth rates estimated from the annual censuses. Such discrepancies between survey-based and modelled population growth rates have been explained in several studies by the existence of individual migration between populations (Jenouvrier *et al.* 2003; Doxa *et al.* 2013). Macquarie Island is the major breeding site for southern elephant seals in the South Pacific Ocean. While breeding seals are also observed at Campbell and Antipodes Islands (Laws 1994) and movements of individuals between these islands have been documented (Van den Hoff 2001), permanent migration of elephant seals to and from Macquarie Island have been shown to be negligible (Van den Hoff 2001) and therefore unlikely to cause a bias in the estimates. A potential alternative explanation for the discrepancy between the population growth rate estimates may be intra-island movements. Females have been recorded to move between Macquarie Island breeding sites from one year to another (Carrick *et al.* 1962a). These movements are often a result of male harassment that females try to avoid by returning at sea or moving along the beach to another harem (Carrick *et al.* 1962a). Females may also move to other breeding sites as they get older and more experienced, favouring larger and more stable harems than when young and inexperienced (McMahon & Bradshaw 2004). Finally, direct competition for space with the king penguin (*Aptenodytes patagonicus*) has been suggested as another potential cause of elephant seal movements on the Island (Van den Hoff *et al.* 2007). Even when most females remained on the same part of the Island, some individuals moved considerable distances between two successive breeding localities (Carrick *et al.* 1962a). These movements between different areas of the Island might well induce a bias in the demographic estimates, as the probability of detecting an individual would vary according to its location. On the Isthmus, the main study area, daily surveys for branded seals were conducted during this study, but resighting effort was more limited for the rest of the Island. Females breeding outside the Isthmus had therefore less chance of being detected. I was able to account for this resighting heterogeneity in the capture-recapture study (Chapter 4), but the spurious trap-dependence effect resulting from the uneven observation effort may not have been entirely corrected. The permanent or temporary migration of female elephant seals out of the Isthmus may therefore have lead us

to slightly underestimate survival and reproduction probabilities (Rotella 2009) and in turn the modelled population growth rate (Fletcher *et al.* 2012).

The generation time I estimated from the matrix population model was longer than the one estimated by McMahon *et al.* (2005b) (11.3 years *vs.* 7.9 years, respectively). Generation times have critical implications for conservation decisions given they are an integrated signal of how fast a population is able to replace itself. The importance of generation time is borne out by longer generation times translating to slower turn-over rates and hence greater rates of population decrease. Given that rates of change are an important consideration when determining the conservation status of a species (*e.g.* IUCN categories), it follows that changes in generation times can be important for the conservation of a species in terms of the status it is assigned to and the consequent protection or management intervention afforded to that population. The two different generation times were estimated from different population models. McMahon *et al.* (2005b) used a Leslie-matrix model structured by age classes only, with females considered to become adult at 6 years old and breeding every year from then. Based on previous studies (Desprez *et al.* (2014), Chapter 3; Chapter 4), I estimated the generation time from a more detailed matrix population model that was structured by both age and stage. This model was more biologically appropriate as in this population vital rates depend on individual reproductive states (*i.e.* prebreeders, first-time breeders, experienced breeders and nonbreeders). The use of this model showed that the turn-over of this population was much slower than previously thought and highlight the important implications that different modelling methods can have on conservation decisions. Nilsen *et al.* (2009) suggested that in a population facing an increased overall mortality, slow generation time and decrease of the population growth rate may result from the inability of the individuals to increase their reproductive effort in early life. This pattern may apply to the population of southern elephant seals at Macquarie Island as female elephant seals starting to reproduce earlier have been shown to face a higher cost of first reproduction to survival (Desprez *et al.* (2014), Chapter 3) likely preventing females in this population speeding up their life cycle.

The use of a matrix population model also allowed us to estimate the demographic parameter elasticities providing a deeper insight into the dynamics of the population of southern elephant seals at Macquarie Island. As expected in a long-lived species, adult survival had the largest potential impact on the projected population growth rate. However, in this population of elephant seals, a strong survival cost of reproduction has recently been detected, with breeding females having a lower chance of surviving than nonbreeders (Desprez *et al.* (2014),

Chapter 3; Chapter 4). Condit *et al.* (2014) suggested that the increasing growth rate of the population of northern elephant seals (*Mirounga angustirostris*) at Año Nuevo was due to higher survival of adult females. The reduced survival of breeding females in the Macquarie Island population may therefore be a key factor in the decline of this population. However this contradicts the general prediction that, in a declining population, adult survival should increase as a result of a lower density of individuals (Eberhardt 2002; Bonenfant *et al.* 2009). Elephant seals are extreme capital breeders in which reproduction induces high energetic costs and massive body mass loss (Arnborn *et al.* 1997). While nursing their pups, females completely rely on stored reserves (in the form of blubber) accumulated during the preceding foraging trip. Foraging behaviour and environmental conditions (*i.e.* the quantity and quality of resources available) in foraging grounds may therefore have great leverage on the survival of breeding individuals. Female elephant seals forage in two main areas: the inter-Frontal zone (pelagic waters between the Subantarctic and Polar fronts) and the Antarctic zone (area south of the southern Antarctic Circumpolar Current Front) (Bradshaw *et al.* 2003; Hindell *et al.* 2003b; Bailleul *et al.* 2007b; Bailleul *et al.* 2010). At Îles Kerguelen, the proportion of females committed to the pelagic strategy is estimated to be around 75% and 25% for the Antarctic strategy (Authier *et al.* 2012). This proportion is thought to be similar at Macquarie Island (Hindell *et al.* In press). While female elephant seals at Îles Kerguelen mainly feed on myctophid fish (Cherel *et al.* 2008; Bailleul *et al.* 2010), the diet of female elephant seals at Macquarie Island varies depending on the location of the foraging grounds, with pelagic and Antarctic feeders having a squid or fish-dominated diet respectively (Bradshaw *et al.* 2003; Newland *et al.* 2009; Field *et al.* 2011; Banks *et al.* 2014; Walters *et al.* 2014). The difference between the main prey consumed by female elephant seals in the pelagic waters of the South Indian Ocean and the South Pacific Ocean may be due to spatial variability in food webs (Trathan *et al.* 2007; Barbraud *et al.* 2012). The Southern Ocean, though oceanographically interconnected, is not a single ecosystem and different areas are dominated by different food webs. In the southern Indian Ocean, the lower trophic levels are dominated by myctophid fishes (Cherel *et al.* 2008; Barbraud *et al.* 2012). In the South Pacific Ocean, the food web has been poorly studied but the squid-dominated diet of Macquarie Island elephant seals may reflect the dominant prey available for the seals in this area. However, squid are likely to be a less profitable prey for female elephant seals as their content in fat and protein is lower than in myctophid fishes (Authier *et al.* 2012). Hence, the diet of elephant seals in the South Pacific Ocean may be less optimal, in terms of rate of energy gain, than the diet of other populations of elephant seals.

Elephant seals are faithful to their foraging areas (Bradshaw *et al.* 2004; Authier *et al.* 2012). Despite leading to high inter-annual variability in foraging success, long-term fidelity to foraging grounds was presumed to be a strategy that allowed females to maximize net energy gain over their lifetime (Bradshaw *et al.* 2004). Yet this strategy may have evolved in an environment where resource distribution and abundance were more predictable and years of poor environmental conditions relatively rare. Over the last century, some of the clearest expressions of climate change have been found in the Southern Ocean and these changes are highly likely to affect the composition of food webs (Trathan *et al.* 2007). In the context of this changing environment, long-term fidelity to foraging grounds may have adverse consequences on the survival and breeding success of elephant seals and in turn on the population trend. An expression of these negative consequences has been documented for the population of elephant seals at Macquarie Island by Van den Hoff *et al.* (2014). Female elephant seals foraging in Antarctic waters exploit the Antarctic continental shelf but retreat with the expansion of the Antarctic sea-ice as winter approaches, shifting from a benthic foraging strategy to a pelagic one (Bailleul *et al.* 2007a). Foraging on the Antarctic shelf is more profitable than foraging in pelagic waters (Thums *et al.* 2011; Hindell *et al.* In press) and as a result, those female seals foraging in the Antarctic zone generally wean bigger pups than females foraging in the inter-Frontal zone (Authier *et al.* 2012). As the survival of pups is directly linked to their size at weaning (McMahon & Burton 2005), the Antarctic strategy, while riskier, may be associated with a better fitness. However, given that the northerly sea-ice extent and duration have been increasing in the region south of Macquarie Island (Stammerjohn *et al.* 2012), they have been excluding female elephant seals from the high-quality foraging grounds for longer periods. Van den Hoff *et al.* (2014) suggested that the poor foraging success of Antarctic foragers during high sea-ice years negatively affected the number of females recruiting into the population a few years later, likely due to a higher mortality of Antarctic foragers' offspring. Consequently, weaning smaller pups with lower chance of post-weaning survival may have a negative effect on the population trend. A mother's fidelity to a particular foraging strategy may therefore play an important role in the population decline at Macquarie Island.

Both juvenile and adult survival had a large potential impact on the population growth rate at Macquarie Island. However, survival of juveniles and adults have remained constant over the study period (Chapter 4) while the observed population size has been fluctuating (with an overall decline) between years. The absence of temporal variability in demographic traits that

have the greatest effect on the projected population growth is a common pattern among wild populations (Sæther & Bakke 2000; Gaillard & Yoccoz 2003; Morris & Doak 2004). Consequently, traits with greater elasticities are often not those that contribute the most to the observed fluctuations in population size between years (Cooch *et al.* 2001; Gaillard & Yoccoz 2003; Jenouvrier *et al.* 2005a). In the population of elephant seals at Macquarie Island, the temporal variability of recruitment and breeding probabilities (Chapter 4) may therefore have the strongest impact on the observed fluctuations in the population size. In Chapter 4, I showed that recruitment and breeding probabilities were positively associated with the Southern Annular Mode (SAM) during the first trimester of females' pregnancy. At first glance, the overall declining trend of the elephant seals population observed at Macquarie Island runs counter to expectation as, since the late 1970's, SAM has become more positive and this should therefore have a positive impact on the population reproduction. However, SAM explained only 29% of the temporal variability in breeding probabilities (Chapter 4) and many other environmental factors also influence seals' reproduction. The decline of the population of elephant seals at Macquarie Island is therefore likely to be the consequence of a complex combination of factors.

The favoured foraging areas (inter-Frontal zone and Antarctic zone) of elephant seals from Macquarie Island extend across a vast area (120°E - 220°W between 40 and 75°S) that displays various and sometimes contrasting responses to climate change. Some of the most important changes that have been experienced by elephant seals from Macquarie Island are: (1) a pole-ward shift of oceanographic frontal positions (Gille 2008; Sokolov & Rintoul 2009). Elephant seals foraging on the frontal areas must therefore expend more of their energy reserves to reach these areas; (2) an increase of sea-ice extent and duration in the Ross Sea and a decrease of sea-ice extent and duration in both East and West Antarctica (Stammerjohn *et al.* 2012). While an increased sea-ice field may have negative consequences on females' foraging success, a reduced one may facilitate access to optimal foraging grounds (Van den Hoff *et al.* 2014); (3) a persistent increase of SAM over the last 30 years attributed to the development of the ozone hole (Marshall 2003). Positive SAM values have been linked to higher primary productivity (Lefebvre *et al.* 2004; Forcada & Trathan 2009) and finally (4) an increase in ocean temperatures (Levitus *et al.* 2000) that have been associated with lower levels of krill (Trathan *et al.* 2003).

All these changes are suspected to have affected the composition of the food web (Trathan *et al.* 2007). Based on the location of their foraging grounds, elephant seals from Macquarie

Islands are likely to experience various environmental conditions and therefore to be differently affected by climate change. Nonetheless, some reasonable predictions can be made for this population of elephant seals. Warming of the Southern Ocean is predicted to continue and to negatively affect sea-ice conditions in Antarctica (Bracegirdle *et al.* 2008). The Ross Sea is expected to reverse its present trend with a decrease in summer sea ice concentration of more than half by 2050 (Smith *et al.* 2014). Positive effects from the reduced sea-ice field on the population dynamics of elephant seals may first appear as a result of a facilitated access to the Antarctic foraging grounds. At the same time though, reduced sea-ice extent and warmer water temperatures negatively affect krill survival and recruitment (Loeb *et al.* 1997; Trathan *et al.* 2003). This may in turn lead to changes in the structure of the ecosystem and potentially to an ecosystem regime shift. Such a shift is suspected to have caused the decline of many marine predators between the 1960 and 1980's (Weimerskirch *et al.* 2003). These changes may therefore eventually negatively impact the population dynamics of elephant seals. Further southward shift in ocean frontal positions may also compromise the survival of weaned pups, juveniles and post-breeding females as they will have to travel longer distances using up their limited energy reserves before reaching their foraging grounds (McConnell *et al.* 2002; Field *et al.* 2005; Van den Hoff *et al.* 2014). Finally, elephant seals are known to forage within regions managed by the Commission for the Conservation of Antarctic Marine Living Resources (CCAMLR) (Bradshaw *et al.* 2003; Hindell *et al.* 2003b). Even if the direct competition between elephant seals and fisheries is considered minimal at present, an increasing exploitation of Antarctic marine resources paired with a potential alteration in prey quantity and quality due to environmental changes may add another threat on the population of elephant seals (Bradshaw *et al.* 2003; Hindell *et al.* 2003b).

In conclusion, our study confirms the ongoing decrease of the population of elephant seals at Macquarie Island. By using a matrix population model, I gained valuable insights into the dynamics of this population and the mechanisms driving this population decline (*i.e.* slow generation time, high cost of reproduction to survival and temporal fluctuations in the probability of breeding). The next step of this study is to develop a time-dependent matrix model and to investigate if the fluctuations of the population growth rate can be explained by climate variability (*e.g.* SAM anomalies, sea-ice extent, etc). A retrospective analysis (*i.e.* LTRE, Caswell (2001)) will also provide valuable information about the contribution of each demographic parameter to the past observed changes in the population growth rate. Beyond

that, I aim to predict the responses of the southern elephant seal population at Macquarie Island to future climate change by linking the population model to oceanographic forecasts from the IPCC models.

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Conclusions & perspectives



Picture: M. Desprez

Overall summary

The aim of this thesis was to improve our understanding of the demographic mechanisms underlying the decline of the population of southern elephant seals at Macquarie Island, and to a broader extent, to contribute to a body of knowledge regarding the role of evolutionary and ecological processes in shaping life histories and population trajectories in long-lived species.

Population dynamics depend directly on the survival and reproduction of individuals, and therefore estimating these two vital rates and identifying those factors that affect them are the first steps of any demographic study (Caswell 2001). In long-lived species, estimating survival and reproductive rates requires adequate long-term dataset. In this regard, the Macquarie Island population of southern elephant seals provides an ideal study population as a large number of known-age animals have been uniquely marked and resighted over time. However, unbiased estimation of demographic parameters remains challenging to obtain for wild populations because some components of life-history (*e.g.* reproduction, dispersal, etc) are difficult to observe and record with certainty in the field. This is especially true for marine mammals like elephant seals that spend most of their lives at sea when it is almost impossible to observe them and collect fine scale life-history information. At Macquarie Island in particular, the reproductive status of a large proportion of the marked female elephant seals could not be ascertained at each sampling occasion. This uncertainty, if not accounted for, can give rise to large errors in demographic estimates and subsequent population projections. I showed that multi-event capture-recapture modelling can reliably estimate demographic parameters in studies where an individuals' reproductive status is not always known (Desprez *et al.* (2013), **Chapter 2**). This modelling approach, by allowing the use of all the data collected and therefore by increasing the size of the dataset that can be used in the analyses, greatly improves the precision and accuracy of the demographic parameter estimates compared to the standard multi-state mark-recapture approach. Using this modelling framework, I determined how the survival and reproduction of female elephant seals at Macquarie Island were affected by variability in individual traits (age, reproductive status, breeding experience) and environmental conditions. I found that survival depended on female reproductive status (*i.e.* prebreeder, breeder, nonbreeder) and breeding experience (*i.e.* first-time breeder or experienced seal) and varied with age for prebreeders and first-time breeders. While survival of elephant seals seemed not to be affected by environmental

variability, breeding probabilities showed marked fluctuations over the years. Besides this temporal variation, the probability of breeding again the following year was influenced by females current reproductive state and experience. Finally, the probability that a female began breeding (*i.e.* recruitment) depended on the seal's age.

The age at primiparity may be one of the most important determinants of a female's reproductive success (Stearns 1992), and this in turn can have major consequences on population dynamics. Therefore, I investigated variation in the age at which females start breeding at Macquarie Island and the consequences of this variability on vital rates. In **Chapter 3**, I showed that the youngest females recruited at 3 years of age but that most females delayed their first breeding attempt until age 4 (Desprez *et al.* 2014). Theoretically, individuals should start to reproduce as soon as possible in order to maximise their lifetime reproductive success. However, long-lived individuals often delay their first breeding event well after physiological maturity suggesting that breeding too early may have a cost that outweighs the benefit of an early recruitment (Williams 1966; Stearns 1992; Descamps *et al.* 2006). I found that first reproduction imbued a high cost on a female's survival, no matter at which age females started to breed, but this cost was higher for females recruiting at age 3 compared to females that started reproducing at age 4. Given females are still undergoing substantial somatic growth when they first breed, first-time breeders must allocate energy to both growth and reproduction (Laws 1956). Younger female elephant seals are generally smaller, with lower energetic reserves to offset the fast associated with the lactation period, and are therefore more likely to face a higher relative energetic cost of first reproduction and to die than females recruiting at age 4. Interestingly, I found that the survival of individuals delaying their first reproduction until they were older than four decreased with age. This suggests that seals delaying recruitment after 4 years of age were most likely to be seals in poorer condition that were compelled to 'do the best of a bad job' (Descamps *et al.* 2006). In this population of elephant seals, substantial heterogeneity in individual quality seems therefore to exist and the first-breeding event appears to act as a powerful filter selecting for higher quality females. This hypothesis was further supported by the fact that experienced females (*i.e.* those that have bred at least once in the past) had higher survival than first-time breeders of the same age, suggesting that individuals in poorer condition were being selectively removed from the population.

The first reproduction event in southern elephant seals not only imposed a cost on survival but also on future reproduction so that surviving primiparous females were more likely to

skip the following breeding event than experienced breeders (**Chapter 4**). As mentioned previously, female elephant seals must bear the energetic costs related to both growth and reproduction. Growth is particularly fast, and energetically demanding, during the first few years of life (≈ 5 years) (McLaren 1993; Bell *et al.* 2005). First-time breeders, mainly aged 4 or 5 years (Desprez *et al.* (2014), **Chapter 3**) and still experiencing substantial growth, are therefore likely to face a higher relative energetic cost than experienced females, generally older than 5 years of age and for which the growth is slower. Higher reproductive costs on survival and future reproduction in first-time breeders may also be due to their lack of experience and efficiency in various activities. Inexperienced breeders may, for example, use more of their stored body reserves to wean a viable pup than experienced females. Fedak *et al.* (1996) showed that lighter mothers (likely younger and less experienced seals), used 43-85% of their stored body fat during lactation compared to 44-49% for heavier females. Reproductive skipping in first-time breeders may therefore be a result of their inability to restore nutrient reserves sufficiently to breed without compromising their survival.

Nonetheless, breeding was also costly for experienced females. In **Chapter 4**, I showed that experienced breeders had a 10% less chance of surviving to the next breeding season than non-breeding seals. Female elephant seals at Macquarie Island therefore invest in reproduction at some cost to their survival. This cost may have critical implications on the population dynamics as the survival of experienced breeding females has a large impact on population growth (**Chapter 5**). In contrast to first-time breeders, I did not detect a cost of current reproduction on future reproduction in experienced females as a seal breeding in year t was more likely to breed again the following year than a seal skipping the reproductive event. The apparent absence of a cost to future reproduction, expressed at a population level, again strongly supports the existence of individual heterogeneity among females of this population, whereby individuals of poor condition are more likely to skip reproduction than females in good condition (Cam *et al.* 2002).

Recruitment and breeding probabilities showed marked fluctuations between years suggesting that environmental conditions affect a female's reproductive behaviour. In particular, higher probabilities to recruit or breed in year $t+1$ were associated with higher Southern Annular Mode (SAM) values during the February-April period in year t , corresponding to the first trimester of females' pregnancy (**Chapter 4**). This period also corresponds to the time when female seals return to sea to replenish their energetic reserves after a month-long fast associated with the moult. The quantity and quality of the food

available at this time is therefore critical. Positive SAM values have been associated with higher primary productivity (Lefebvre *et al.* 2004; Forcada & Trathan 2009) and resources available for seals during these periods are likely to be more abundant. In contrast, negative SAM values are likely to be associated with poorer environmental conditions. My results showed that breeding in female elephant seals from Macquarie Island is extremely costly as it results in a substantial reduction in survival. Under severe environmental conditions (*i.e.* low SAM values), the risk of dying from the high energetic costs related to the reproduction is likely to be worse and skipping reproduction during these years may be a strategy to offset reproductive costs and increase longevity. This naturally raises the question: Did females that skip reproductive events when conditions were unfavourable produce a larger number of offspring over their lifetime than females that bred each consecutive year?

At Macquarie Island, the highest values of lifetime reproductive success (*i.e.* number of pups produced over lifetime) were achieved by females that skipped between 2 and 4 breeding occasions over their lifespan. However, my results also suggested that lifetime reproductive success depended upon each females' quality. The best females were able to produce the highest numbers of offspring over their lifespan with no or only a few breeding pauses, whereas by contrast, the least successful females produced the lowest numbers of offspring despite frequently skipping breeding. I suggest that the females that reached the highest values of lifetime reproductive success were likely to be females of higher quality who were therefore able to cope with reproductive costs while females that produced the lowest numbers of offspring were most likely females in perpetually poor condition.

In **Chapter 5**, I used all the demographic information obtained in the previous chapters to build a detailed matrix population model and estimate the population growth rate of the population of southern elephant seals at Macquarie Island. My results confirmed the decline of this population although the population growth rate estimated by the matrix model was significantly lower than the population growth rates estimated from annual censuses. This discrepancy between the population growth rate estimates may be due to a slight bias in the demographic estimates used to parameterize the matrix model as a result of uncorrected resighting heterogeneity in the capture-recapture analysis and/or to bias in the census data. However, this work is still ongoing and additional analysis will refine our conclusions.

In a declining population, theory predicts that age at first reproduction should decrease and that the reproductive rate of adult females, as well as adult survival, should increase as a

result of a lower density of individuals (Eberhardt 2002). Interestingly, I did not observe such trends in the Macquarie Island population. Despite the long-term decline evident in this population, selection seems to act against a younger age at first reproduction (< 4 years) given the high reproductive cost to survival that younger primiparous females experience. I also showed that, contrary to the predicted increase in reproductive rate, female elephant seals from Macquarie Island actually skip a number of reproductive events in order to maximise their lifetime reproductive success. Moreover, survival of adult breeding females from this declining population is low compared to the survival estimated in the increasing population of northern elephant seals at Año Nuevo (Condit *et al.* 2014). Overall, my results do not support the paradigm proposed by Eberhardt (2002). However, this study was only based on seven cohorts of individuals and this may have been insufficient to detect the predicted changes in vital rates. It is possible that, given the decline of Macquarie Island population started 50 years ago, the age at primiparity, for example, decreased from age 5 to 4 and that, while still low, the reproductive rates and survival of adult females increased. Such changes in vital rates require long-term datasets that include several generations of individuals to be detected. The generation time of the population of southern elephant seals at Macquarie Island was estimated to be 11.3 years (**Chapter 5**), and so the dataset used in this study, while of many years duration, was still too short to investigate such changes.

Perspectives

This study provides insights into the demography of the population of southern elephant seals at Macquarie Island. The high reproductive costs to survival and the temporal fluctuations of the breeding probabilities in female elephant seals give potential clues to the processes driving the decline of this population. To refine these conclusions, I aim to improve the population dynamics analysis started in Chapter 5. I will develop a time-dependent matrix model and investigate whether the fluctuations of the population growth rate over time can be explained by variation in environmental conditions. I also aim to predict the responses of this population to future climate change by linking the population model to oceanographic forecasts from the IPCC models.

As presented, my research has raised many new questions and further investigation will be required to fully understand the reason(s) for the ongoing decline of the population of

southern elephant seals at Macquarie Island. In particular, my results strongly suggest the existence of a substantial heterogeneity in female elephant seal quality that was not accounted for by the fixed effects included in the capture-recapture models (*i.e.* reproductive status, reproductive experience and age). Such heterogeneity may mask the existence of trade-offs operating at the individual level (Van Noordwijk & de Jong 1986; Cam *et al.* 2002; Chambert *et al.* 2013) and therefore explain the positive relationship detected between the probability of breeding at time t and $t+1$ in female elephant seals of this population when a negative relationship was expected. Incorporating individual heterogeneity into population models is therefore an important follow-up of this study. Capture-recapture mixture models (Pledger *et al.* 2003; Gimenez & Choquet 2010; Péron *et al.* 2010) or random effects models within a Bayesian framework (Cam *et al.* 2002; Royle 2008; Buoro *et al.* 2010) could be used to account for the latent heterogeneity in vital rate estimates, although such models do not provide information about the mechanisms underlying the individuals' heterogeneity. However, adding another level of complexity to the models to account for individual heterogeneity in addition to the imperfect detection and uncertainty in state assignment may raise issues in terms of parameter redundancy and computation time. An easier alternative might be to include proxies of individual quality that can be directly measured in the field as covariates into the capture-recapture model. In the case of southern elephant seals, variation in individual quality is likely to be generated by variability in the seal's ability to forage successfully and to assimilate nutrients and synthesize fat content, which is ultimately expressed by individuals' body mass. Incorporating body mass relative to age or length and/or foraging success into these models will therefore provide valuable information about the influence of individual quality on life-history strategies and will be illuminating in answering some fundamental questions around the influence of energetics on this population's dynamics (*e.g.* do females have to reach a threshold in body mass to start breeding? Are the females that delay their first breeding event smaller than females breeding at an earlier age? Do bigger females breed more often over their lifetime than smaller females? etc) (Boyd 2002). It would also be insightful to investigate how females' individual quality affects their offspring survival and recruitment. My study showed that some females produce many more offspring over their lifetime than others. However, the available data did not allow me to investigate whether the pups produced by these two different categories of females had different probabilities of survival or of recruiting into the breeding population. At Amsterdam Island, high-quality female subantarctic fur seals (*Arctocephalus tropicalis*), representing only one third of the studied population, produced more than two-thirds of the viable offspring

(Beauplet & Guinet 2007). The existence of a similar skew in the population of elephant seals at Macquarie Island is not unlikely and therefore, estimating the contribution of female elephant seals to the next generation relative to their body mass and investigating how variation in the proportion of females of high and poor quality influences population growth will provide important information on the intrinsic dynamics of this population. However, undertaking a study of this nature requires the collection of a large sample of repeated measures of seals' body mass. This raises logistical issues for a species like the southern elephant seal (*i.e.* adult seals must be captured and anaesthetized to take the measurements). The development and refinement of techniques such as photogrammetry, which allow body mass to be estimated with a high degree of precision without having to manipulate individual seals, may considerably facilitate the collection of such data in the future (de Bruyn *et al.* 2009).

The next crucial step will be to determine the sources of heterogeneity in individual quality. Permanent underlying differences among individuals may arise from consistent differences among habitats selected by individuals over their life (Kendall *et al.* 2011). Female elephant seals forage in two main areas: the Inter-Frontal zone and the Antarctic zone and are faithful to their individual foraging grounds (Bradshaw *et al.* 2003; Hindell *et al.* 2003b; Bailleul *et al.* 2007b; Bailleul *et al.* 2010; Hindell *et al.* In press). Individuals foraging in the Inter-Frontal zones experience different environmental conditions and have a different diet composition than females foraging in the Antarctic zone (Bradshaw *et al.* 2003; Banks *et al.* 2014). At Îles Kerguelen, female elephant seals foraging in the Antarctic zone wean bigger pups, that will have higher survival probabilities (McMahon *et al.* 2000), than females foraging in the Inter-Frontal zone (Authier *et al.* 2012). Linking females' foraging strategy to females' body mass, vital rates (*i.e.* survival and reproduction) and number of viable pups produced over lifetime, by combining demographic data and bio-logging data, will determine if one or the other foraging strategy is associated with females of higher quality and is therefore superior/more profitable in terms of reproductive success. Moreover, an improved understanding of the link between the seals' foraging behaviour and the population dynamics and growth will also improve predictions about the response of this population to future climate change.

Genetic differences are thought to contribute widely to individual variation in demographic performance (Kendall *et al.* 2011; Stover *et al.* 2012). However the relative influence of this genetic component on the heterogeneity in individual quality has been subject to significant

discussion and remains to be quantified (Tuljapurkar *et al.* 2009; Steiner & Tuljapurkar 2012; Cam *et al.* 2013). By combining capture-recapture data and pedigree information from Macquarie Island population (Papaïx *et al.* 2010), it would be possible to investigate the heritable component of the variation in body mass, foraging behaviour and vital rates. Such information will allow us to model more precisely the pattern of variation of the population structure and growth.

Identifying sources of individual heterogeneity in the population of southern elephant seals at Macquarie Island will improve our understanding of the intrinsic dynamics of this population. Combining this information with studies that evaluate the impact of past and present environmental fluctuations on demographic parameters will also improve our ability to predict the response of this population to future climate changes and may contribute to resolving the mystery behind the decline of this population. However, the cessation of the research program on southern elephant seals at Macquarie Island prevents the collection of additional data (body mass, bio-logging data, genetic data and demographic data) and represents a major obstacle to the research perspectives discussed previously (Green & Bradshaw 2004; McMahon *et al.* 2006a; McMahon 2007; McMahon *et al.* 2007). Another way to determine the mechanisms behind the decline of Macquarie Island population would be to compare the outcomes of this study with the results from demographic studies conducted in other, stable or increasing populations of southern elephant seals. The population of southern elephant seals at Marion Island, in the South Indian ocean, seems to be the most appropriate population for such a comparative study as census data and detailed demographic information from a long-term capture-mark-recapture program is also available for this population (Pistorius *et al.* 2011).

Conclusion

After showing that imperfect data could be a valuable input into capture-recapture models that could improve the precision and accuracy of the demographic parameter estimates, my research provided insights into the demography of the population of southern elephant seals at Macquarie Island. I have found that breeding is extremely costly in female elephant seals and results in a substantial decrease in survival. To offset this high reproductive cost and to maximise their lifetime reproductive success, female elephant seals tend to skip some

reproductive events over their lifetime. In particular, environmental conditions during the beginning of the post-moult foraging trip, which also corresponds to the beginning of females' pregnancy, seem to play a critical role in seals' decision to breed or not. These findings give potential clues to the processes driving the decline of this population and suggest several directions for future investigations.

To be continued...

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