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Population and individual life history consequences of polygyny in male southern elephant seals

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Population and individual life history consequences of polygyny in male southern elephant seals

by

Kyle John Lloyd

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Declaration

I, Kyle John Lloyd, declare that the thesis, which I hereby submit for the degree Ph.D. (Zoology) at the University of Pretoria, is my own work and has not previously been submitted by me for a degree at this or any other tertiary institution.

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DATE: 29 November 2019

Summary

Title: Population and individual life history consequences of polygyny in male southern elephant seals

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Degree: Doctor of Philosophy (Zoology)

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Our understanding of polygynous life history is biased towards females. Few studies investigate the processes governing male life history because of the difficulty in measuring male reproductive effort, and because population growth is thought to be limited only by females. Therefore, clarity is needed on the drivers and predictors of polygynous male life history and the long-term consequences this has for male fitness. My thesis achieves this overall aim by answering specific questions about the life history of male southern elephant seals at Marion Island using a 34-year mark-recapture dataset. The male elephant seal served as a model organism to investigate the most important life stages of polygynous males in general.

For pre-breeders that survived their first year of life, individual heterogeneity in survival probabilities was expressed from age 2. Males born in years with relatively few pups were more likely to be robust in quality than males born in years with many pups. Survival probabilities of robust individuals and the population average became more similar as pre-breeders aged, suggesting that frail individuals were preferentially removed from the population during development. Therefore, the majority of pre-breeders that survived to breed successfully were robust in quality.

Pre-breeder recruitment probabilities increased with age. In addition, pre-breeders of the same age often recruited as first-time subordinate breeders than as first-time dominant breeders. First-time subordinate breeders started recruiting from a younger age than first-time dominant breeders. Males likely need time to socially mature or require some breeding experience to outcompete older breeders. Pre-breeders expressed individual heterogeneity in recruitment probabilities, with robust individuals (i.e. higher survival) being more likely to recruit than frail individuals (i.e. lower survival). This supports the individual quality theory, which predicts that life-history traits are positively, rather than negatively, correlated. Pre-breeders born during low pup production years generally recruited at younger ages than pre-breeder born during high pup production years.

Males attending breeding events did not suffer lower survival probabilities than same aged males that were still pre-breeders, suggesting that there was no reproductive cost for attending breeding events for early recruits. However, all males attending breeding events experienced actuarial senescence from recruitment age, with subordinate males suffering higher baseline mortalities. Given that this coincided with breeding improvement (the probability of becoming dominant), males appear to pay a reproductive cost for attempting to obtain dominance. When comparing survival probabilities between individual dominant males, there was also a reproductive cost for breeding successfully that accumulated with age. Males that were dominant at beaches with above average harem sizes accumulated higher reproductive costs than males that were dominant at beaches with below average harem sizes. Nevertheless, dominant males still maintained higher survival probabilities than subordinate males of the same age. Therefore, individual quality (inferred from breeding state) may play an important role in modifying resource allocation trade-offs between reproduction and survival.

Future breeding success (measured as social status) increased with age for both subordinate and dominant males, but dominant males were more likely to remain dominant than subordinate males were in obtaining dominance. This apparent improvement in breeding success with age was predicted by birth cohort size, again suggesting that males born into cohorts with few conspecifics performed better as adults.

In conclusion, I provide support for several population theories and show how they shaped male elephant seal demographics from birth to death. My findings provide valuable insight into the drivers and predictors of male life history in a highly polygynous breeding system.

Disclaimer

My thesis has been structured as a series of chapters with a combined reference list presented at the end (excluding references from supplementary information). The research chapters are written and formatted as scientific articles to be published in peer-reviewed journals and are the product of my own original work. However, several collaborators contributed their expertise to the end product. Readers must please bear the use of different personal pronouns, repetition and overlap between chapters, for which I apologise.

Chapter 5 was intended to apply the results of preceding research chapters to answer the question of how male elephant seals affect the stable (asymptotic) population growth rate. This was accomplished using elasticity values derived from a two-sex population model. However, over the course of professional discussions following examination of this thesis, it has become evident that the methodology used to derive elasticities from the population model was incorrect. I mistakenly calculated the elasticities using conventional linear numeric perturbation rather than non-linear techniques. Chapter 5 serves as a cautionary example for population ecologists of not only how to construct and interpret two-sex population models, but also how analytical techniques differ from standard one-sex population models.

The project conducted to collect the data used in my thesis had ethics clearance from the Animal Ethics Committee of the Faculty of Veterinary Science, University of Pretoria, under AUCC 040827-022, AUCC 040827-023, AUCC 040827-024 and EC030602-016, and was carried out under permit from the Director-General: Department of Environment, Forestry and Fisheries (DEFF), South Africa. Funding for the project was obtained from the South African Department of Science and Technology (DST) through the National Research Foundation (NRF). The conclusions drawn and discussed are attributed to the author and not necessarily to the NRF. The DEFF provided logistical support for ongoing fieldwork at Marion Island, through the South African National Antarctic Programme (SANAP).

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Dedication

To my Oupa, Richard Benecke,

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You laid the foundations so that I could build.

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Chapter 1: *General Introduction*

Population and individual life history consequences of polygyny in male southern elephant seals

Sex-specific differences in life history

Life history describes an organism’s life cycle and the adaptive strategies used to maximise fitness over its lifetime (Stearns 1992). Life histories are bound by a number of evolved mechanisms, such as genetics, development, physiology and phylogeny (Flatt & Heyland 2011). The evolution of anisogamy (reproduction by means of two phenotypically dissimilar gametes) has led to males and females fulfilling different roles in sexual reproduction (Parker *et al*. 1972). Males and females of multicellular haploid species contribute different sized gametes to sexual reproduction. Males typically contribute abundant, smaller, motile sperm that are energetically inexpensive to produce; and females contribute few, large, non-motile eggs (ova) that are energetically expensive to produce (oogamy; Parker 1982). Sperm evolution has exploited female resource investment into egg cells by producing gametes that contain limited cytoplasmic resources. Large, resource-rich sperm cells would be less mobile and beaten by smaller sperm cells to fertilise female eggs (Pizzari & Parker 2009). Females are thought to be the limiting sex that determines reproductive success because a single male can produce many sperm cells to fertilise numerous female egg cells (Darwin 1871; Haigh & Hudson 1993). Thus, males generally compete for access to limited mating opportunities (precopulation) and to successfully fertilise female eggs (postcopulation), whilst females are generally concerned about mate choice (males that contribute high genetic quality) and, in some cases, parental care (Trivers 1972). As a result, males and females have evolved different primary and secondary adaptations to maximise their own reproductive success with consequences for sex-specific life-history traits (sexual selection; Fisher 1930).

Polygynous breeding systems

The intensity and direction of sexual selective pressure on life-history traits is a complex function of several breeding system parameters (Parker & Simmons 1996). It is often assumed that sexual selection is strongest in males because male reproductive success is most variable (i.e. mating and fertilisation are not guaranteed – Bateman's principle/gradient; Bateman 1948), but the distribution of mating opportunities within a population may also play a critical role (mate assortment; McDonald & Pizzari 2018). For example, the intensity of precopulatory competition may be less when males mate females that are highly polyandrous (a single female mates multiple males) because paternity is less certain (sperm competition; Wade & Shuster 2005). Or males may be involved in parental care (e.g. single-mate monogamous breeding systems) and so require more time and energy to raise offspring than compete for multiple mates (Jašarević *et al*. 2012). However, for the majority of vertebrate species, males employ polygyny as a breeding tactic: the mating of several females by a single male who provides little to no parental care. In mammals, up to 90% of species are polygynous (Clutton-Brock 1989). This is because the number of offspring produced by a male increases substantially with the number of females fertilised, whereas the number of offspring produced by a female is limited (Wilson 1975). Often a male can improve his reproductive success by mating and fertilising new females (i.e. re-mating) rather than investing in parental care (Trivers 1972). Female offspring quality rather than quantity improves when more than one male is mated, which explains the evolution of polyandry and extra-pair copulations in promiscuous monogamous species (Simmons 2005; see Bonduriansky *et al*. 2008 regarding sexual conflict). However, the potential for increasing reproductive success by re-mating females is still much higher for polygynous males (Arnqvist & Nilsson 2000).

Polygyny is broadly divided into two types depending on how females use space and resources (Emlen & Oring 1977). Mate-defence polygyny involves a dominant male defending access to a group or harem of females (Clutton-Brock 1989). The duration of mate-guarding by the dominant male can be seasonal or for extended periods of time until displaced by another male. Resource-defence polygyny involves a dominant male defending a resource used by females, such as in territorial species (Clutton-Brock 1989). Females utilise resources within a male’s territory and are subsequently mated by the resident male. Subordinate males that cannot outcompete dominant males may employ alternative breeding tactics to acquire some mating opportunities, but the reproductive success of these alternative strategies is almost always less than that used by dominant males (Repka & Gross 1995). For example, subordinate males may sneak into female harems when the dominant male is unaware, or intercept females moving between dominant male territories (Wolff 2009).

Processes governing polygynous male life history

In polygynous males, sexual selection is possible because of variation in individual competitive ability for limited mating opportunities and fertilisation success (Pizzari & Bonduriansky 2010). Sexual selection targets traits and behaviours the expression of which covaries with reproductive success (Pizzari & Bonduriansky 2010). Thus, polygynous males have evolved elaborate and exaggerated secondary sexual traits and behaviours that promote access to female mates and egg fertilisation, but are not necessarily needed for survival (Darwin 1871; Fisher 1930). Secondary sexual traits include large body size to physically dominate other males, weapons such as horns and antlers to compete in male-male contests, ornaments that signal a male's quality or social status, and large testes and sperm concentrations to ensure fertilisation (Bro-Jørgensen 2007; Ramm & Stockley 2010). Behaviours can include aggression, fighting, displaying, and scent-marking amongst others (McCann 1981). In social species, male-male contests (intraspecific competition) for female harems result in breeding hierarchies, where dominant males consistently outcompete subordinates and reproductive success is skewed towards the dominant minority (Clutton-Brock 1989; Galimberti *et al*. 2002). Consequently, female mate choice is restricted, but offspring quality is likely improved by inheriting the superior traits of dominant males (Reichard *et al*. 2005).

When intraspecific competition is intense, polygynous males are predicted to 'live fast and die young' in comparison to females (Bonduriansky *et al*. 2008). Because reproductive success is not guaranteed for all males in a population, males allocate substantial body resources to current reproduction to improve their chances of outcompeting other males and securing females (Crocker *et al*. 2012). This high-risk strategy is meant to yield high returns over short durations (Vinogradov 1998). In contrast, female reproductive success is more guaranteed, allowing them to pursue a low-risk strategy that provides moderate returns over longer periods of time (Bonduriansky *et al*. 2008). By allocating substantial body resources to current reproduction, males have fewer resources left to allocate to traits associated with survival and future reproduction (Bro-Jørgensen 2007). This principle of resource allocation (Cody 1966) is rooted in trade-off theory, which predicts that when two life-history traits share the same limited internal resource-pool, an increase in one trait that improves fitness results in a decrease in another trait that reduces fitness (Stearns 1992). This is referred to as the "Y" model of resource allocation (van Noordwijk & de Jong 1986; Zera & Harshman 2001) and is demonstrated when comparing polygynous and monogamous male aging rates.

Although males of both polygynous and monogamous species may experience the same amount of reproductive costs in their lifetime, the nature and timing of when these costs are experienced differ (Tidière *et al*. 2015). Senescence is the progressive deterioration of an organism with age, which leads to the loss of biological functions, decreased fertility and increased mortality risk (Monaghan *et al*. 2008). Polygynous males generally experience actuarial (survival) senescence at an earlier age after becoming sexually and socially mature than monogamous males who rather invest in having fewer offspring at a time over longer durations (Tidière *et al*. 2015). A similar pattern can be seen when comparing actuarial senescence rates between polygynous males and females, with females often aging at a slower rate or not at all (Clutton-Brock & Isvaran 2007). Allocating resources to growing secondary sexual traits during development can also detrimentally affect a male’s lifespan and reproductive performance later in life (Lemaître *et al*. 2018). For example, males that invest in reproduction during development are more likely to be dominant breeders, but may experience actuarial and reproductive senescence at faster rates than subordinate males (Lemaître *et al*. 2014). Therefore, life-history traits that depend on resource allocation decisions do not only differ between breeding systems and sexes, but also between males of the same population.

Contradictory findings about polygynous male life history

Most studies that investigate lifetime consequences of reproductive costs focus on the female component of polygynous populations (reviewed by Lemaître *et al*. 2015; Bleu *et al*. 2016; Lemaître & Gaillard 2017). Few studies have investigated the male component, likely due to uncertainty in paternity assignment (Lemaître *et al*. 2015). Those that have find results that contradict population theory (Festa-Bianchet 2012). For example, it is predicted that dominant males should suffer higher reproductive costs than subordinate males, because dominant males allocate more resources to developing secondary sexual traits and behaviours, and expend more energy securing, defending and mating females (trade-off theory; Stearns 1992). Therefore, dominant male survival and future reproduction should be lower than that of subordinate males following a successful breeding event. However, several demographic studies find that dominant males pay no additional reproductive costs for breeding successfully (McElligott *et* *al*. 2002; Pelletier *et al*. 2006; Bonenfant *et al*. 2009; Toïgo *et al*. 2013). Instead, dominant males perform consistently better than subordinate males throughout life.

Individual differences in resource acquisition and allocation may be one explanation for why dominant males show positive, rather than negative, covariances among life-history traits (van Noordwijk & de Jong 1986). Dominant males may be better at acquiring resources than subordinate males, and so have more resources available to allocate to both survival and reproduction (McElligott *et al*. 2002). Individual variation is inherent to any sexually reproducing population and is a central driver of population dynamics and evolution (Vindenes & Langangen 2015). Individual heterogeneity in life-history traits originates from resource allocation decisions that are based on an individual's genotype, somatic state (e.g. parental investment) and epigenetic state (e.g. environmental conditions; Lindström 1999; Wilson & Nussey 2009; Hill 2011). Individual heterogeneity includes between- and within-individual variation that is not explained by temporal and spatial heterogeneity alone (Gimenez *et al*. 2018). Some observable phenotypic attributes that differ between individuals include age, sex, social status, morphometrics, behaviour, and genotype (Gimenez *et al*. 2018). Advancements in finite-mixture models (Pledger *et al*. 2003) and random effect models (Gimenez & Choquet 2010) also allow for unobserved individual heterogeneity to be taken into account in analyses. Individual heterogeneity can be fixed with permanent effects throughout life (e.g. silver spoon effects from early-life conditions; Tuljapurkar *et al*. 2009), or dynamic being brought about only during certain life stages and/or conditions (Vindenes & Langangen 2015). What was previously treated as a nuisance variable that needed to be accounted for when estimating life-history traits (Vaupel *et al*. 1979) has now become an essential component to mark-recapture models for detecting life-history processes (van Noordwijk & de Jong 1986; Hamel *et al*. 2009).

Therefore, dominant polygynous males that perform better than subordinate males throughout life are thought to be high quality individuals that can afford additional reproductive costs with little to no consequences for life-history trade-offs (McElligott *et al*. 2002). Studies of polygynous male life history need to consider the long-term effects of individual heterogeneity during ontogeny, between breeding states, and within breeding states to confidently interpret results (van Noordwijk & de Jong 1986).

Why is clarity needed about polygynous male life history?

It is often assumed that only females affect population dynamics because they are the limiting sex (Caswell 2001). However, accumulating evidence suggests that even polygynous males are not redundant. Simply removing males frees up space and resources for female use with consequences for population dynamics (Clutton-Brock *et al*. 2002). But males also affect female fitness, and even male fitness, in more subtle ways. For females, this includes mate searching behaviour (sperm limitation), male resource use (relatively large males with secondary sexual traits consume more resources than females in sexually dimorphic species), sexual harassment (by reducing female fitness through male harm) and sexual segregation (when dominant males force females into suboptimal habitats due to resource competition or avoidance of sexual harassment; Rankin & Kokko 2007). For males, conspecific density and age structure influence competition for female mates. For example, young males participate earlier (Stevenson & Bancroft 1995) and more actively (Sæther *et al*. 2003) in breeding events when competition from older males is reduced. This in turn elevates reproductive costs for young males which may show reduced body growth (Clutton-Brock *et al*. 1985a). Male biased sex ratios also have similar effects by increasing intraspecific competition intensity (Solberg *et al*. 1999). These sex-specific life-history traits and behaviours result in nonrandom mating events which can alter the distribution of offspring phenotypes and ultimately population growth (Schindler *et al*. 2013). Clearly, males are non-trivial and their potential demographic effects should be considered. Therefore, more studies are needed to understand the processes governing polygynous male life history before we can consider how males affect population dynamics (Mysterud *et al*. 2002a; Rankin & Kokko 2007).

The male southern elephant seal as a model organism

The breeding cycle and behaviour of male southern elephant seals (*Mirounga leonina* L. 1758; hereafter elephant seals) is well suited for investigating drivers and predictors of polygynous male life history. Elephant seals are mesopredators (secondary consumers) that forage widely over the Southern Ocean (McMahon *et al*. 2005), feeding on krill (particularly by juveniles; Lübcker *et al*. 2017), cephalopods (demersal squid and benthic octopods; Clarke & MacLeod 1982) and fish at different ocean depths (McConnell *et al*. 1992). Their large size and numbers make them important consumers of Antarctic marine resources relative to other marine mammals, with the potential to impact prey dynamics (Bradshaw *et al*. 2003; Hindell *et al*.

2003). Populations breed on sub-Antarctic islands (mainly around the Antarctic Convergence Zone) and mainland South America, covering approximately 20° of latitude (Le Boeuf & Laws 1994). Five genetically distinct populations are recognized: the Peninsula Valdés (including Falkland Islands) population in Argentina, the South Georgia population in the southern Atlantic Ocean, the Îles Kerguelen (including Heard Island) and Îles Crozet (including Prince Edward Islands) population in the southern Indian Ocean, and the Macquarie population in the southern Pacific Ocean (Hoelzel *et al*. 2001; de Bruyn *et al*. 2016). Individuals display high site fidelity to the breeding colony where they were born or first reproduced (Fabiani *et al*. 2006; Hofmeyr *et al*. 2012). Populations were historically harvested for blubber during the eighteenth and nineteenth centuries, causing population numbers to decrease drastically (Le Boeuf & Laws 1994). Populations began to recover when the seal hunting industry ceased in 1909, but declined again between the 1950s and 1990s, with some populations decreasing by as much as 80% (Pistorius *et al*. 2004; McMahon *et al*. 2005). Food limitation due to changing environmental conditions is hypothesised to be the leading cause (McMahon *et al*. 2005; Pistorius *et al*. 2011). Currently, most populations are either increasing or remain stable (McMahon *et al*. 2005; de Bruyn *et al*. 2016), except for the Macquarie Island population (van den Hoff *et al*. 2014).

Unlike most species which fall somewhere between the income and capital breeding continuum, elephant seals display extreme capital breeding systems (Boyd 2000). This means that males and females do not supplement body resources during breeding events, but instead rely on stored body reserves to allocate to current reproduction. In elephant seals, this amounts to a clear separation between an aquatic phase of energy acquisition and a terrestrial breeding phase of energy consumption (Galimberti *et al*. 2007). During annual three-month breeding seasons, females return to colonies to give birth a few days after arriving and fast for 3-4 weeks while the pup suckles until being weaned. During the last 3-5 days of nursing, the female comes into oestrous (Le Boeuf & Laws 1994). Females clump together in groups forming a harem due to limited availability of breeding sites and display high oestrus synchrony (Laws 1956). Together with high breeding site fidelity (Fabiani *et al*. 2006), female behaviours accommodate mate-defence polygyny in males (Bartholomew 1970; Cassini 1999). Males arrive on land before females to establish territories on beaches and fast for the duration of the breeding season (~100 days) whilst they compete to monopolise harem mating rights (McCann 1981). The resident dominant male (or ‘beachmaster’) tries to mate with all of the oestrous females in the harem and shows no parental care (Le Boeuf & Laws 1994). Dominant males practise breeding behaviours known as ‘heading’ to determine if females are in oestrus, and ‘herding’ to ensure that females stay within harems (Laws 1956). Subordinate males try to either challenge dominant males or resort to alternative breeding strategies such as sneaking (Wolff 2009). Despite mating attempts by subordinate males, reproductive success is heavily skewed towards dominant males (Hoelzel *et al*. 1999; Wilkinson & van Aarde 1999; Galimberti *et al*. 2002). Pre-breeding (juvenile) males take four years to become sexually mature, but recruit to the breeding population once socially mature between ages 5 and 10 (Jones 1981). Pre-breeders are observable when they haul out onto land to rest during winter months and to moult in summer months (Condy 1979). Breeders haul out during breeding events and to moult shortly after recovering from breeding events (Condy 1979). Pre-breeders generally do not haul out during the breeding season (August-November).

In summary, male elephant seals are ideal model organisms to study how resource allocation decisions shape polygynous male life history for the following reasons:

- Elephant seal morphology and behaviour lends itself to mark-recapture techniques. Pup cohorts wean over a short period of time after which they are separated from the harem, making it easy to access and tag individuals on the webbing of their hind flippers (de Bruyn *et al*. 2008).
- Detection probabilities are high because the terrestrial phase of the elephant seal life cycle is predictable and follows an annual rhythm (Oosthuizen *et al*. 2019a). Marked individuals are easy to find as most are concentrated in groups along coastlines (Oosthuizen *et al*. 2012).
- Elephant seals are highly polygynous meaning that males allocate substantial resources to reproduction to secure and mate with females (Galimberti *et al*. 2007). In fact, elephant seals are proportionally the most sexually dimorphic mammal species, suggesting that the intensity of sexual selection pressure in males is strong (Clutton-Brock 1989). Male elephant seals are also capital breeders meaning that during breeding events resources are allocated to reproduction alone and not some unrelated activity such as foraging. Therefore, it is easier to identify and confidently interpret the causes and consequences of allocating resources to current reproduction.

- Male elephant seals almost always attend breeding events once recruited to the breeding population (pers. obs. from mark-recapture data). Therefore, the lifetime consequences of reproductive costs are easier to interpret because males do not skip breeding events to rest and recuperate.
- Male elephant seals display obvious behavioural cues during breeding events that enable researchers to confidently assign breeding states (social status) to individuals. High dominant male paternity rates mean that the true underlying reproductive success of an individual is closely related to its observed breeding state. Therefore, the cost of attending breeding events (pre-breeders *cf*. breeders) and the additional cost of breeding successfully (subordinate breeders *cf*. dominant breeders) can be distinguished using breeding states.
- The pre-breeder phase of development is particularly interesting in elephant seals because males take several years to reach sexual and social maturity unlike ungulate species (Lemaître *et al*. 2018). Therefore, males are exposed to various processes throughout development that may influence individual differences as they mature.

Marion Island elephant seal colony

Sub-Antarctic Marion Island (300 km^2) is one of two islands that form part of the Prince Edward Island archipelago in the southern Indian Ocean (46°54' S, 37°45' E); the nearest landmass being Îles Crozet 950 km to the east (Figure 1). The Prince Edward Islands are volcanic outcrops, separated by a shallow saddle of approximately 19 km (Lutjeharms & Ansorge 2008). The islands lie within the Antarctic Circumpolar Current with the Antarctic Polar Front in the south and Sub-Antarctic Front in the north (Lutjeharms & Valentine 1984). The frontal systems provide important feeding areas for a host of marine species (Bost *et al*. 2009). The Prince Edward Islands are also breeding grounds of several species of marine mammals, including elephant seals. A mark-recapture study of elephant seals at Marion Island was formally initiated in 1983 and has continued uninterrupted to present (Bester *et al*. 2011). Almost all weaned pups are tagged with two livestock tags on the hind flippers at the end of each breeding season and monitored by dedicated field researchers throughout the year (Figure 2; de Bruyn *et al*. 2008; Pistorius *et al*. 2011). The Marion Island elephant seal colony is relatively small compared to others, comprising only 0.1% of the world's total population (calculated from Le Boeuf & Laws 1994). Elephant seals breed mainly on the eastern half of the island at many (~54 beaches), small (<100m long), discrete, rocky beaches (Condy 1978; Oosthuizen *et al*. 2012). Thus, harems are distinct from one another and do not merge like in other larger colonies (Laws 1956). This allows for dominant and subordinate males to be easily identified at each harem during breeding events (Figure 3).

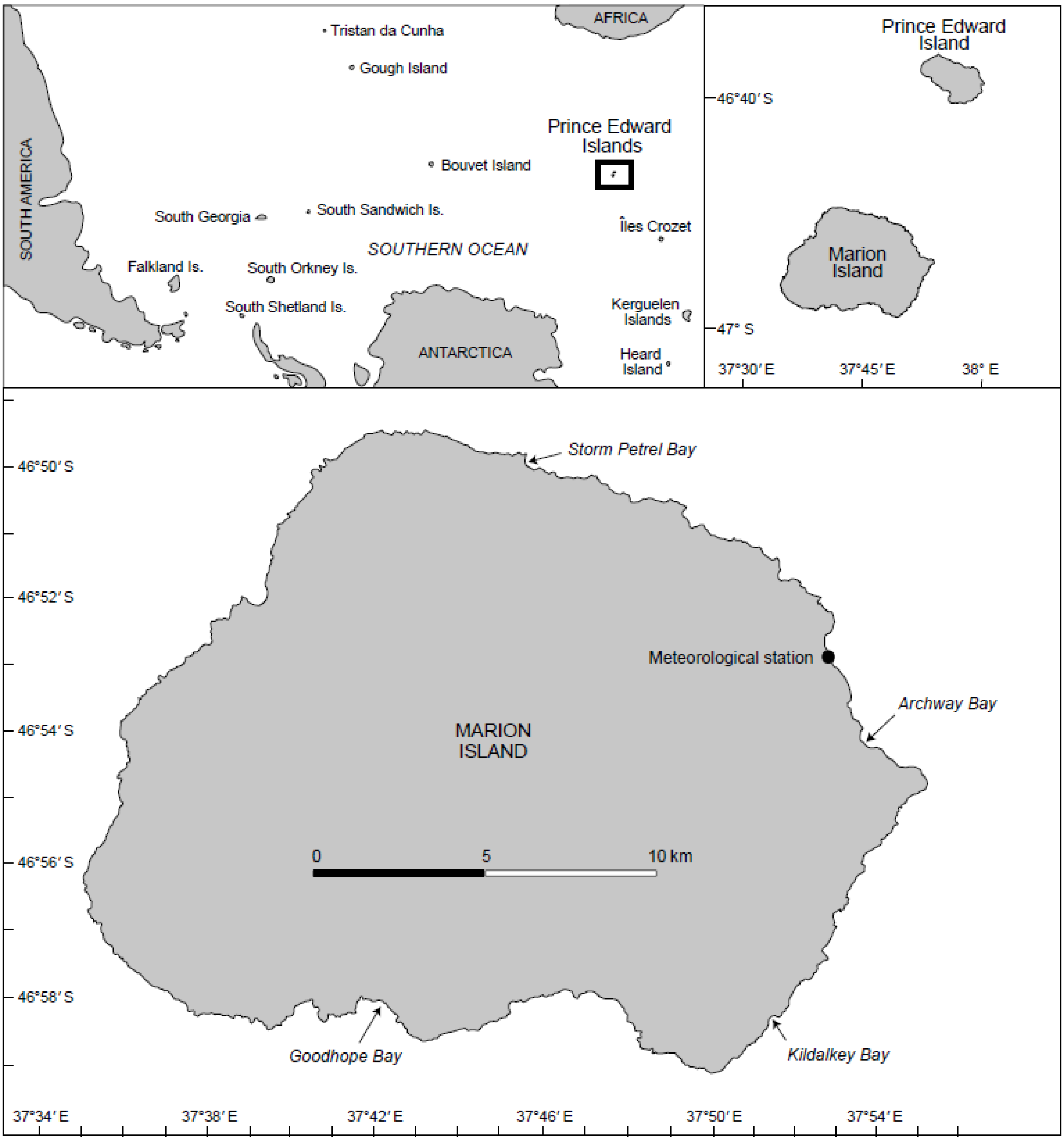

Figure 1: Map of Marion Island. Clockwise: position of the Prince Edward Islands in relation to surrounding landmasses; position of Marion Island in relation to Prince Edward Island; and Marion Island showing the extent of regular southern elephant seal haul-out sites on the eastern half of the island from Storm Petrel Bay to Goodhope Bay. Taken from Pistorius *et al*. 2011 with author permission.

Figure 2: Most southern elephant seals were tagged with two identical plastic Jumbo Rototags (Dalton Supplies Ltd.) shortly after weaning (de Bruyn *et al*. 2008; Pistorius *et al*. 2011). Cohorts were identified by the colour combination of tags and individuals were identified by unique three-digit numbers printed on each tag. Elephant seals were tagged on the right and left inner interdigital (between the second and third digit) of the hind flippers from 1983 to 1999 and on the outer interdigital (between the first and second digit) of the hind flippers from 2000 to 2009 (Oosthuizen *et al*. 2010). Photo: Sean Evans

Thesis aims and structure

The overarching aim of my thesis is to determine the drivers and predictors that shape polygynous male life history using the southern elephant seal as a model organism. In particular, I examine how resource allocation decisions to current breeding affect lifetime survival and future breeding probabilities. Whilst elephant seal studies to date have only examined the immediate effects of current breeding using a few individuals (Galimberti *et al*. 2007), I make use of a 34-year mark-recapture dataset that follows the fate of 27 cohorts, 6245 male pups, and 326 adult males at Marion Island (Pistorius *et al*. 2011). The reproductive success associated with dominating female harems has resulted in male elephant seals evolving a highly polygynous breeding system (Clutton-Brock 1989; Le Boeuf & Laws 1994). Therefore, male elephant seals are ideal representatives of a polygynous life cycle. In addition, recent studies of females from the same breeding colony provide an opportunity to formulate a comprehensive understanding of elephant seal population dynamics (Oosthuizen 2016). I incorporate individual heterogeneity into my chapter aims by comparing life-history traits between age classes, breeding states (social status), hidden states (quality groups) and individuals. I make use of mark-recapture models, linear models, population projection models and other techniques at the forefront of population ecology analyses to test working biological hypotheses and discuss my results within the context of current population theory. My thesis comprises three research chapters presented as stand-alone scientific articles followed by a final chapter that applies my findings to the population as a whole. I then proceed to establish how I have contributed to answering the overarching aim of my thesis. Each research chapter is the product of my own original work with assistance and input from several expert collaborators.

Chapter 2 – Life-history consequences of reproductive costs among breeding states

In my first research chapter, I make use of the behaviourally distinct breeding states of male elephant seals to distinguish between two types of reproductive costs: (1) the cost of attending breeding events and (2) the cost of breeding successfully. Pre-breeders have no accumulated reproductive costs, subordinate breeders pay a cost for attempting to breed, and dominant breeders pay an additional cost for breeding successfully. Variation in recruitment age allows me to compare same aged individuals of different breeding states. I assume that breeding state correlates closely with breeding success because dominant breeders sire many more offspring than subordinates (Hoelzel *et al*. 1999). I assess reproductive costs by comparing age-specific survival, recruitment and future breeding success probabilities among breeding states with the following testable predictions:

a) Males attending breeding events are expected to have lower survival than pre-breeders of the same age given that they allocate resources to breeding (hauling out on land, fasting and fighting), regardless of social rank. Pre-breeders, in contrast, do not haul out during the breeding season and therefore presumably do not incur these costs.

b) I also expected that most pre-breeders will recruit to the breeding population as subordinate breeders, but that older individuals will have a higher probability of recruiting as dominant breeders. By delaying attendance costs, pre-breeders that recruit at older ages may have more resources available than younger recruits to allocate to attaining competitive dominance and successfully securing females.

c) Breeding effort (weight loss, both in absolute and relative terms) of male elephant seals increases with dominance and breeding success (Galimberti *et al*. 2007), and therefore I expect dominant breeders to have lower survival (representing a cost of successfully securing and mating females) than subordinate breeders. In contrast, given their past breeding experience (and thus improved breeding skills; Dugdale *et al*. 2011) and social rank (and thus favourable phenotype for establishing dominance; Sanvito *et al*. 2007), I expect that dominant breeders surviving to the following breeding season are more likely to be dominant again.

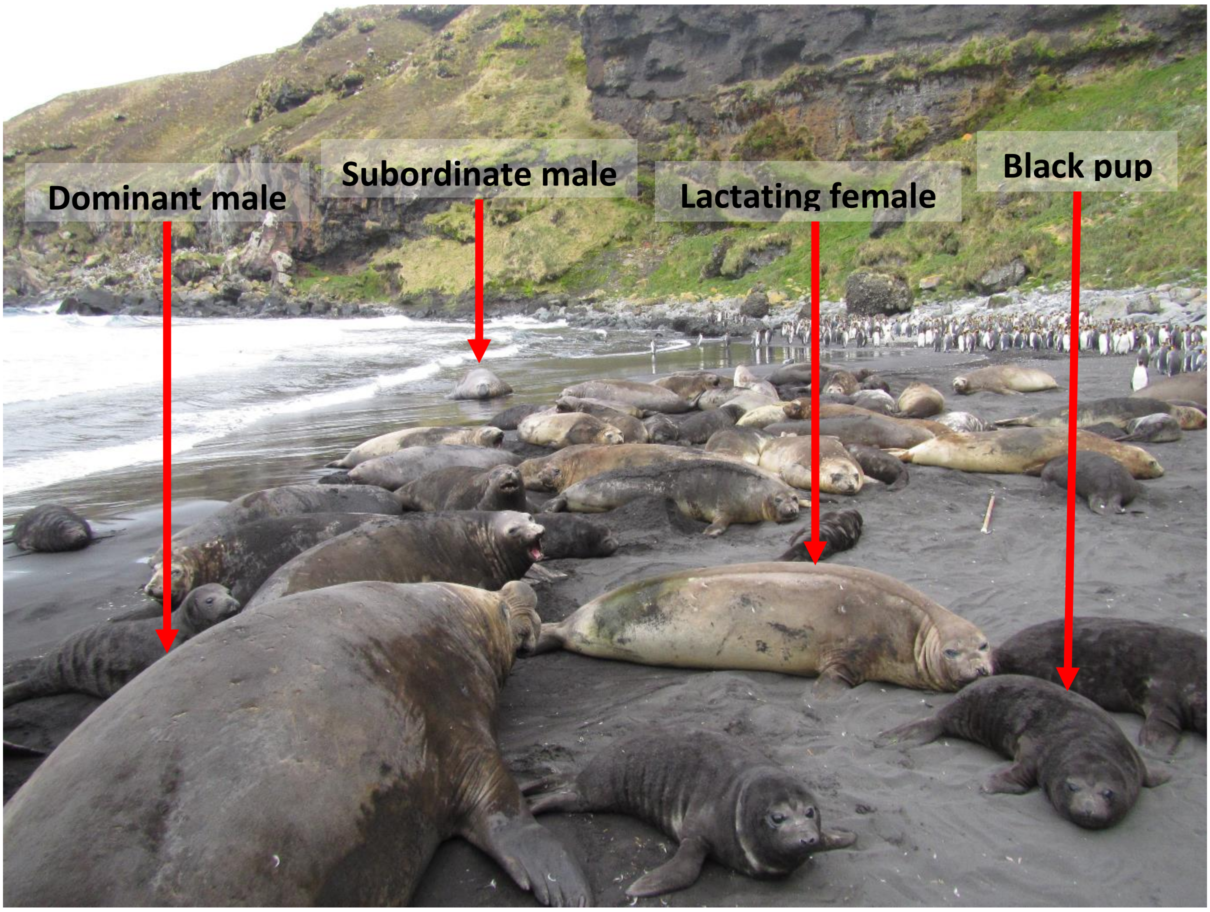

Figure 3: A typical southern elephant seal harem at Marion Island during an annual breeding season (August-November). The breeding state or social status of individual males is easily determined from behavioural cues and positioning within the harem. Dominant males are generally positioned at the centre of harems and display specific breeding behaviours such as vocalising and chasing subordinate males, or heading, herding and mating females. Subordinate males are generally positioned at the periphery of harems and display specific breeding behaviours such as monitoring the dominant male and sneaking towards females (Laws 1956; McCann 1981; Le Boeuf & Laws 1994; Modig 1996). Photo: Kyle J. Lloyd

Chapter 3 – Life-history consequences of individual heterogeneity among pre-breeders

In my second research chapter, I examine individual heterogeneity as a biological process in male elephant seals (Senner *et al*. 2015) and determine how it influences pre-breeder survival and recruitment probabilities. I make use of a recently refined technique called finite-mixture modelling that accounts for unobserved individual heterogeneity. Finite-mixture models assign individuals to a finite number of hidden states that represent different quality groups (McLachlan & Peel 2000; Wilson & Nussey 2010; Gimenez *et al*. 2018). I construct two hidden states that represent "robust" and "frail" individuals and compare the life-history traits of these two groups to that of the population response to answer the following questions:

a) Are robust and frail individuals distinguishable based on age-specific survival and recruitment probabilities? If individual heterogeneity is present in these demographic rates, models that specify differences between groups should perform better than models that do not (Fay *et al*. 2016).

b) At what age can individual heterogeneity be detected in survival and recruitment probabilities and for how long? Although individuals differ phenotypically at birth, fitness consequences may be transient, intermediate or permanent depending on current selective pressures (Oosthuizen *et al*. 2018).

c) How do differences between groups change with age relative to one another and the population response? Specific patterns in responses will elude to particular processes taking place (van de Pol & Verhulst 2006; Hamel *et al*. 2018b).

d) Does the probability of being robust or frail vary with conditions experienced in early-life? For example, cohorts born under high population density may suffer from lower demographic performance in adulthood (Pigeon *et al*. 2017). I investigate the relationship between population density during the year of birth and the probability of being robust or frail.

e) How does the composition of robust and frail individuals change within a cohort and carry-over into the breeding population? Using estimates obtained from mixture models and population matrix projection, I compare the proportion of robust and frail individuals that make up the population from weaning to age 11.

Chapter 4 – Life-history consequences of density-dependent drivers among breeders

In my third research chapter, I determine if patterns (variation) in breeder survival, breeding success and recruitment age are density-dependent. Polygynous males generally experience a higher degree of intraspecific competition to reproduce successfully than females (Clutton-Brock 1989). Therefore, male resource allocation decisions to current reproduction are likely influenced by the density of conspecifics either at breeding events when competing for mates or whilst developing secondary sexual traits when competing for resources (Loison *et al*. 1999; Coulson *et al*. 2001; Beirne *et al*. 2015). Based on my findings of Chapter 2, I specifically evaluate the extent to which patterns in (a) actuarial senescence, (b) breeding improvement (measured as social status), and (c) recruitment age are explained by several measures of density-dependent factors related to competition intensity and natal conditions. I also consider intrinsic effects, such as age, breeding state and experience, which may interact with density-dependent factors in different ways (Moorad *et al*. 2019). In many polygynous species, body mass at weaning is a strong intrinsic predictor of survival (McMahon *et al*. 2000; Oosthuizen *et al*. 2018), and may be correlated with other life history traits such as competitive performance which is linked to breeding success (Rödel & von Holst 2009). Because weaning masses were only available for a subsample of males from the study population, I perform a separate analysis to determine which density-dependent factors influence (d) pup weaning mass across cohorts.

Chapter 5 – Synthesis & Perspectives

My last chapter is divided into two parts. In collaboration with several researchers, I first investigate how male elephant seals affect population dynamics. A two-sex population model developed specifically for polygynous breeding systems is used to determine which male demographic parameters are sensitive to proportional changes (elasticity) at asymptotic lambda (i.e. population growth rate when not affected by stochastic events). Too often the male component of populations is ignored when using population projection models to answer theoretical and applied questions (Caswell 2001). This oversimplifies our understanding of population dynamics by not considering the variation that sexual reproduction contributes to male and female life-history traits (Jenouvrier *et al*. 2018). I present my results as a short note/communication. The second part summarises the main findings of each research chapter and how these relate to one another by discussing the most important life stages of male elephant seals in turn. This includes pre-breeder survival, pre-breeder recruitment, breeder survival, and breeder social status and fertility. I conclude with how the overarching aim of my thesis was achieved; and follow with recommendations for studies that can use the same elephant seal mark-recapture dataset to provide added insight into the determinants of polygynous male life history.

Chapter 2: *Life-history consequences of reproductive costs among breeding states*

Trade-offs between age-related breeding improvement and survival senescence in highly polygynous elephant seals: dominant males always do better

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Dominant male southern elephant seal roaring at Blue Petrel Bay (Marion Island, 2016). Photo: Kyle J. Lloyd

Abstract

1. Life history trade-off theory predicts that current reproduction can negatively affect survival and future reproduction. Few studies have assessed breeding costs for males of polygynous species compared to females, despite substantial variation in breeding success among individual males (e.g. subordinate *cf*. dominant breeders). Specifically, differentiating between the cost of attending breeding seasons, and the additional cost of successfully securing and mating females is lacking.
2. We investigated whether trade-offs are present in the highly polygynous male southern elephant seal (*Mirounga leonina*) using 34-years of individual-level data. We compare age-specific survival, recruitment and future breeding success probabilities of pre-breeders (males yet to recruit) and breeders (subordinate and dominant social ranks) using multievent models.
3. Pre-breeders and breeders of overlapping ages had similar survival probabilities, suggesting that there was no attendance cost for early recruits. In addition, the probability of recruiting as a dominant breeder never exceeded recruitment probability as a subordinate breeder of the same age. Therefore, older pre-breeders that delayed attendance costs generally did not improve their breeding success (probability of being dominant) at recruitment more than younger recruits. Rather, recruitment age may be a function of individual quality, with lower quality individuals requiring more time to socially mature.
4. When comparing subordinate and dominant breeders, we found clear evidence for survival senescence, with subordinate breeders having a higher baseline mortality. In contrast, age-specific future breeding success (probability of being dominant at *t*+1) increased with age, with dominant breeders maintaining higher subsequent breeding success than subordinate breeders.
5. The opposite trends in survival and future breeding success for both subordinate and dominant breeders may indicate a lifetime, population-level trade-off. However, we found no evidence to suggest that being a dominant breeder consecutively (and having a higher accumulated breeding cost) accelerated the rate of senescence when compared to individuals that were previously subordinate.
6. Thus, males experienced actuarial senescence regardless of social rank, with dominant (and possibly high quality) breeders showing a reduced trade-off between survival and

future breeding success. We make several novel contributions to understanding polygynous male life histories and southern elephant seal demography.

Keywords: actuarial senescence, breeding success, individual heterogeneity, life history trade-offs, *Mirounga leonina*, multievent models, recruitment, reproductive costs

Introduction

Trade-offs exist between life history traits when an increase in one trait that improves fitness results in a decrease in another trait that reduces fitness (Flatt & Heyland 2011). At the individual level, this often occurs as a result of two traits sharing the same limited internal resource pool to pay growth and maintenance costs (the "Y" model of resource allocation; van Noordwijk & de Jong 1986; Zera & Harshman 2001). Well established trade-offs include negative correlations between survival (somatic maintenance) and reproduction, current versus future reproduction, and number and size of offspring (Stearns 1992). Hence, trade-offs are central to understanding life history theory (Stearns 1992). While compelling evidence of reproductive trade-offs exist for vertebrate females, few studies assess reproductive trade-offs in free-ranging males (reviewed by Bleu *et al*. 2016). Thus, there is a need to investigate the role of trade-offs in the evolution of male life history strategies (Hamel *et al*. 2010).

Animals have evolved a diversity of breeding systems to maximize breeding success within the boundaries set by trade-offs (Stearns 1992; Roff & Fairbairn 2007), with the most common among mammals being polygyny (a male defends access to several females or a resource used by females; Clutton-Brock 1989). For many polygynous species, males and females contribute to the production of young in different ways. Males primarily contribute their gametes, whilst females are additionally responsible for parental care through gestation and lactation (Hoelzel *et al*. 1999). Thus, males and females experience different selective pressures in order to maximise reproductive fitness (Hoelzel *et al*. 1999). Males have evolved traits that promote access to females (precopulation), such as larger body size, ornaments, weapons and aggressive behaviour (Bro-Jørgensen 2007); as well as fertilisation (postcopulation), such as large testes and fast spermatogenesis rates to increase sperm production (Ramm & Stockley 2010). Intense sexual selection drives the production and maintenance of these costly secondary sexual traits and behaviours, resulting in polygynous males allocating a disproportionate amount of resources towards breeding (Crocker *et al*. 2012). Thus, sex differences in survival rates of polygynous species are generally greater than for monogamous species (Tidière *et al*. 2015).

Breeding costs for polygynous males can be identified as the cost of attending breeding events, and the additional cost of successfully securing and mating with females (Sedinger *et al*. 2001). Few studies have been able to differentiate between these two costs, as most studies only compare individuals that have already recruited to the breeding population (e.g. successful *cf*. failed breeders or breeders *cf*. non-breeders; Bleu *et al*. 2015). Strong sexual selection leads to considerable rank-related skew in breeding success among males of polygynous species, with dominant breeders siring most offspring born into a population (Galimberti *et al*. 2002). Subordinate breeders are often smaller, younger and otherwise frail compared to dominant breeders and, although alternative breeding tactics are employed (such as “sneaking”), they generally have lower breeding success (Hoelzel *et al*. 1999; Wilkinson & van Aarde 1999). Attendance at breeding grounds alone is therefore a weak determinant of male breeding success as only a small proportion of males actually secure and mate with females (Galimberti *et al*. 2002). Subordinate breeders could benefit from the experience of attending (information-gathering), which could enhance their future breeding success (Cam & Monnat 2000; Dugdale *et al*. 2011; Bosman *et al*. 2013). However, studies are needed that compare age-specific life history traits of males that differ in sustained breeding costs to determine effects on future breeding success.

We use over three decades of detailed individual life history data collected at Marion Island in the southern Indian Ocean to investigate reproductive trade-offs in male southern elephant seals (*Mirounga leonina* L. 1758; hereafter elephant seals). Unlike most species which fall somewhere between the income (maintain no energy reserves) and capital (stockpile energy reserves) breeding continuum, elephant seals display extreme capital breeding (Boyd 2000). This means that breeding males pour their stored energy reserves into an intense three month breeding season, during which they will fast and compete for dominance over female harems (Le Boeuf & Laws 1994). Breeding effort is energetically costly with males losing, on average, a quarter of their body mass (range 12-50%; mean 551 kg) by the end of the breeding season (Galimberti *et al*. 2007). The dominant breeder attempts to mate with all females in oestrus in the harem, whilst defending his mating rights from subordinate breeders (Le Boeuf & Laws

1994). Subordinate breeders copulate few females (McCann 1981; Hoelzel *et al*. 1999) with subordinates at Marion Island copulating less than at other colonies, likely as a result of harems being smaller and more defendable. For example, subordinates achieved only 1.9% of copulations observed over three breeding seasons at Marion Island (Wilkinson & van Aarde 1999). These factors have resulted in one of the most polygynous and competitive mating systems amongst vertebrates (Clutton-Brock 1989), driving the evolution of the greatest proportional difference in sexual size dimorphism among mammals (Le Boeuf & Laws 1994). Given the high energy expended in precopulatory sexual competition, foraging time lost and injury risk, we expect strong evidence for reproductive trade-offs in male elephant seals.

No studies have explored the life history traits of adult male elephant seals using data that spans several generations. Here, we study the relationship between current breeding social rank (breeding state at time *t*) and survival, recruitment, and future breeding success (at time *t*+1; direct fitness traits *sensu* Hamel *et al*. 2010; Bleu *et al*. 2015). We assume that social rank correlates closely with breeding success because dominant breeders sire many more offspring than subordinates (see Hoelzel *et al*. 1999). Thus, breeding success can be inferred by observation of social rank (i.e. both subordinate and dominant breeders attend breeding events whereas pre-breeders do not; but only dominant breeders consistently mate). We assess reproductive trade-offs by comparing age-specific survival, recruitment and future breeding success probabilities of pre-breeders (males yet to recruit to the breeding population) and breeding males (subordinate and dominant breeders), with the following testable predictions:

a) Males attending breeding events are expected to have lower survival than pre-breeders of the same age given that they allocate resources to breeding (hauling out on land, fasting and fighting), regardless of social rank. Pre-breeders, in contrast, do not haul out during the breeding season and therefore presumably do not incur these costs.
b) We also expected that most pre-breeders will recruit to the breeding population as subordinate breeders, but that older individuals will have a higher probability of recruiting as dominant breeders. By delaying attendance costs, pre-breeders that recruit at older ages may have more resources available than younger recruits to allocate to attaining competitive dominance and successfully securing females.
c) Breeding effort (weight loss, both in absolute and relative terms) of male elephant seals increases with dominance and breeding success (Galimberti *et al*. 2007), and therefore

we expect dominant breeders to have lower survival (representing a cost of successfully securing and mating females) than subordinate breeders. In contrast, given their past breeding experience (and thus improved breeding skills; Dugdale *et al*. 2011) and social rank (and thus favourable phenotype for establishing dominance; Sanvito *et al*. 2007), we expect that dominant breeders surviving to the following breeding season are more likely to be dominant again.

Methods

Southern elephant seal biology

Southern elephant seals are circumpolar mesopredators in the Southern Ocean (McMahon *et al*. 2005), but display high site fidelity to their place of first reproduction (Hofmeyr 2012). The Marion Island population in the southern Indian Ocean declined by 87% between 1951 and 1993, but subsequently increased from a minimum of 421 pups born in 1997 to 557 pups born in 2016 (Pistorius *et al*. 2011). Males take approximately four years to become sexually mature and six to ten years to reach physical maturity in order to compete during the annual breeding season (Laws 1956). Females typically group together to form a harem at the beginning of the breeding season (Hoelzel *et al*. 1999). Males compete for the mating rights of a harem, with larger body size (and possibly increased fasting endurance) being associated with winning fights and achieving a dominant social rank (McCann 1981). Females give birth a few days after arriving at the colony and fast for four weeks while the pup suckles until weaned (Le Boeuf & Laws 1994). During the last days of nursing, the female enters oestrous and is mated by the resident dominant male (“beachmaster”; Le Boeuf & Laws 1994). Pre-breeders do not attend colonies during the breeding season and haul out in winter (April-August) and to moult in summer (November-March; Condy 1979). Adults haul out to breed (August-November) and to moult (December-March; Condy 1979).

Mark-recapture protocol

All elephant seal pups weaned at Marion Island from 1983 to 2009 were uniquely marked with two plastic livestock tags applied to the hind flippers (*n* = 27 cohorts, 6245 male pups; Figure S1.1; Pistorius *et al.* 2011). Pups were tagged in the inner interdigital webbing from 1983 to 1999 and in the outer interdigital webbing from 2000 to 2009. Tag loss was integrated into the analysis (Oosthuizen *et al*. 2010). From 1983 to 2016, all beaches where elephant seals bred were surveyed every seven days during the breeding season and every ten days outside of the breeding season. In total, 58 177 observations of marked male elephant seals were made over 34 years.

Model design

Multievent models were constructed to test predictions about reproductive trade-offs and the relative support for each model was evaluated using an information-theoretic approach. Multievent models are a class of hidden Markov models, which describe the transition of an individual among states conditional on the previous state, with unobservable (i.e. "hidden") states present (Pradel 2005, 2009). Multievent models have the added advantage that, together with imperfect detection, a probability of uncertainty in state assignment can be estimated, separating the true underlying state of an individual from the observation process where error may occur (Gimenez *et al*. 2012).

When a male elephant seal was resighted, one of nine events could be assigned to it: not seen (0); seen as a pre-breeder with two tags (1); seen as a pre-breeder with one tag (2); seen as a subordinate breeder with two tags (3); seen as a subordinate breeder with one tag (4); seen as a dominant breeder with two tags (5); seen as a dominant breeder with one tag (6); seen with an unknown breeding state and two tags (7); and seen with an unknown breeding state and one tag (8). Dominant breeders were identified as being associated with one or more females with pup(s), which they defended and mated (male often positioned within the harem). Subordinate breeders were either on the periphery of harems or on beaches not occupied by females. We assigned animals to events 7 and 8 when an individual was seen as both subordinate and dominant several times during the same breeding season. In such cases (*n* = 43), uncertainty existed about the true breeding state that the individual occupied during the breeding season. On only nine occasions were individuals that had previously participated in a breeding season not seen in a future breeding season, given that the individual was known to be alive through subsequent encounters. These nine individuals were also classified as having an unknown breeding status during absent years. A seal year began at the start of every breeding season and ended before the following breeding season.

An individual could occupy one of nine possible states during each seal year (Figure S1.3; Pradel 2005). The states were: pre-breeder with two tags (PB2, has not previously participated in a breeding season); pre-breeder with one tag (PB1); pre-breeder alive elsewhere with two tags (PBAE2, temporarily emigrated and last seen with two tags); pre-breeder alive elsewhere with one tag (PBAE1); subordinate breeder with two tags (SB2); subordinate breeder with one tag (SB1); dominant breeder with two tags (DB2); dominant breeder with one tag (DB1); and dead (D, an absorbing state representing death and permanent emigration). Pre-breeders alive elsewhere were hidden states constructed to account for temporary emigration from the study population (Schaub *et al*. 2004). Goodness-of-fit tests (Supp. S2) indicated that this behaviour was prevalent among pre-breeders, but not breeders. Introducing an unobservable state improved estimates of survival and detection probabilities of pre-breeders (Schaub *et al*. 2004).

Models were parameterised as matrices corresponding to initial state probabilities, transition probabilities and event probabilities (Supp. S3). All individuals entered the study as pre-breeders (weaned pups) and 99% were initially marked with two tags. Therefore, the initial state probability (π), which estimates the probability of being in a particular state when first encountered, was kept constant. Transitions between states were modelled in five steps with each step conditioning on preceding transitions: (1) tag loss probability from two to one tag (τ^{21}), (2) tag loss probability from one to zero tags (τ^{10}), (3) apparent survival probability (φ), (4) breeding probability (ψ, distinguished as recruitment – the probability to transition from pre-breeder to subordinate or dominant breeder states – and future breeding success – the probability to transition from subordinate or dominant breeder states to the dominant breeder state, the alternative being to transition to the subordinate breeder state), and (5) temporary migration probability out of (ψ^{E}, emigration) and into (ψ^{I}, immigration) the study area by native individuals. Event probabilities were modelled using detection (p) and state assignment probability (δ) matrices.

Model constraints and selection

Goodness-of-fit tests were conducted to determine if data met assumptions of the simpler Cormack-Jolly-Seber model (Supp. S2; Pradel *et al*. 2005). We performed model selection by determining the most parsimonious model in each parameter set in the following order:

$\delta, p, \tau^{21}, \tau^{10}, \psi^{E/I}, \varphi, \psi$. For each parameter set, the most complex model was specified initially and subsequently compared to simpler models (including null models) whilst keeping models of other parameters constant. The most parsimonious model identified in each set was carried forward in subsequent analyses. Models tested specific hypotheses (Supp. S4), with survival and breeding models focussing on breeding state and age effects. This included variants of interactions between fixed effects, and linear additive and polynomial effects, with a total of 14 age classes (maximum age recorded) and 34 sampling occasions (duration of study) being recognised. Terminal age classes of ≥10 and ≥11 years were specified for breeder survival and future breeding success, respectively, because of the sparseness of data at old ages (only 10 subordinate and 42 dominant breeders were observed past age 11; Figure S1.2); and confirmed in a separate analysis (Table S6.1). Similarly, a terminal age class of ≥6 years was specified for pre-breeder survival as only 14 pre-breeders were observed transitioning from age 7 to age 8 (Figure S1.1). As senescence was apparent in breeder survival probabilities, an analysis was performed to determine the onset age of actuarial senescence (Table S6.2) and semi-Markov models of various three parameter hazard functions were fitted to a single state encounter history matrix to confirm if mortality increased during the oldest ages (i.e. no terminal age class; Choquet *et al*. 2011).

With evidence of overdispersion in the data, the small sample corrected quasi-likelihood Akaike's Information Criterion ($QAIC_c$) was used to select models ($\log_e(L)/\hat{c}$, where $\hat{c} = 1.7$; Supp. S2; Anderson *et al*. 2001; see Choquet & Nogue 2011 for QAIC calculation details). The $QAIC_c$ value of each model within each parameter set was compared to the most parsimonious model in that set. We used $\Delta QAIC_c$, Akaike weights (ω_i; the strength of evidence of each model relative to other models in the set) and evidence ratios (ω_i/ω_j; the empirical support for model *i* relative to model *j* given the data) to compare models (Burnham & Anderson 2004). Where models were equivalent ($\Delta QAIC_c \leq 2$; Burnham & Anderson 2004), the simpler model (fewer parameters) was favoured. The most parsimonious models for survival and breeding probabilities were compared to models with an individual random effect using a likelihood-ratio test to determine if unexplained between-individual heterogeneity was present in these parameters (Supp. S7; Gimenez & Choquet 2010). Models were fitted in E-SURGE 2.1.4 (Choquet *et al*. 2009). Predicted estimates are reported as the mean followed by the lower and upper 95% confidence interval (CI).

Results

Pre-breeders vs Breeders

The best supported model (model 9, Table 1) treated age variation in pre-breeder survival as a fixed effect (assuming the parameters to be different and independent of each other at every age) and age variation in breeder survival as a continuous logit-linear relationship. Thus, there was a distinction between pre-breeder and breeder survival probabilities when compared to state-independent models (*cf.* models 5-7). However, differences among breeding states for overlapping age classes (ages 5, 6 and 7) were weak or non-existent (model 1 *cf.* models 2-4, Figure 1). First year survival of pre-breeders was low (0.56; CI: 0.54, 0.58), peaked during the second year (0.72; CI: 0.69, 0.75) and remained relatively similar thereafter (~0.68).

Recruitment from the pre-breeder state to the subordinate or dominant breeder states increased with age in a quadratic relationship (model 32, Table 2). For older pre-breeders, the age-specific probability of recruiting as a dominant breeder did not exceed recruitment as a subordinate breeder (Figure 3A). The only competitive model (model 27, ω_{32}/ω_{27} = 1.4) indicated that age-specific recruitment probabilities followed the same trends. Pre-breeders first recruited as subordinate breeders at age 5 and as dominant breeders at age 6, with recruitment probabilities peaking at age 8 for both subordinate (0.62; CI: 0.50, 0.72) and dominant (0.12; CI: 0.09; 0.18) breeders.

Subordinate vs Dominant breeders

Social ranks were correctly assigned to the majority of observed breeders (0.94; CI: 0.91, 0.96; Supp. S5). Age variation in survival was linear and decreasing on the logit scale from the age at recruitment onward (model 9, Table 1, Figure 1), suggesting senescence in breeder survival. This was supported by the decreasing trend in survival probabilities of the fully age-dependent model (model 5, Figure 2A) and the Reduced Additive Weibull model which best described the population's mortality rates (model 24, Figure 2B). The Reduced Additive Weibull model is expressed as the sum of two hazard functions of Weibull form, thus capturing juvenile, adult and old individual phases of mortality (bathtub shape; Xie & Lai 1996). The continuous logit-linear model that described subordinate and dominant breeder survival (model 9) is an approximation of the Gompertz model – a continuous function assuming an exponential increase of mortality rate with age (Gompertz 1825; Gaillard *et al*. 2004; Pardo *et al*. 2014; Blue *et al*. 2015). The onset age of actuarial senescence began when subordinate (age 5) and dominant (age 6) breeders first recruited to the breeding population (Table S6.2). The rate of senescence was independent of social rank, with subordinate breeders having a higher baseline mortality (Table S5.2). Competing Gompertz models of actuarial senescence ($\Delta QAIC_c \leq 2$) assumed that the rate of senescence was lower for dominant breeders (model 8); or that survival did not vary between subordinate or dominant breeders (model 10). However, the relative empirical support of the most parsimonious model was twice that of competing models.

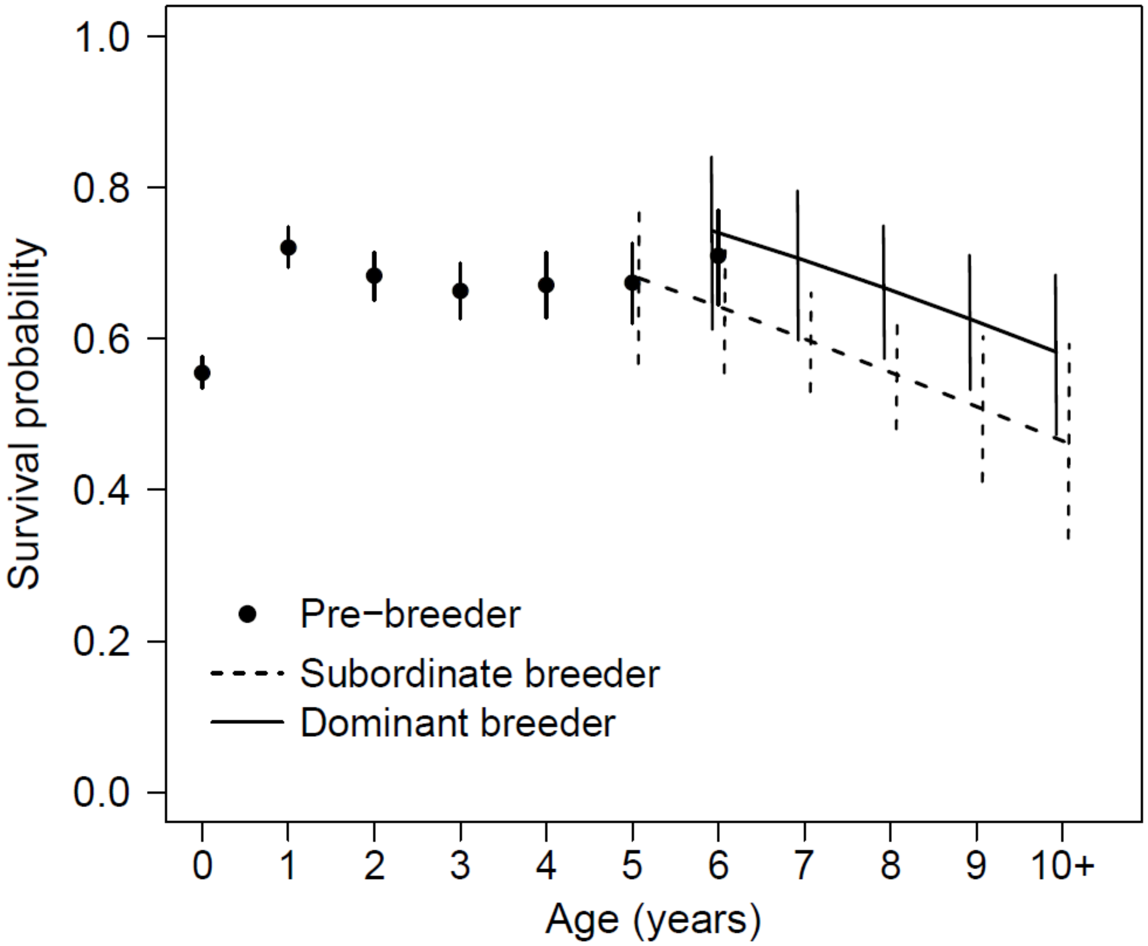

Figure 1: Mean predicted survival probabilities (95% confidence intervals) of male southern elephant seals at Marion Island. Subordinate and dominant breeders were sighted from age 5 and 6, respectively. Estimates were derived from model 9 (Table 1), which treated age variation in pre-breeder survival as a fixed effect and in breeder survival as a continuous logit-linear relationship. Subordinate breeders had a higher baseline mortality than dominant breeders, but the rate of senescence was independent of social rank.

Table 1: Multievent models representing reproductive trade-off hypotheses about survival probabilities (φ) of male southern elephant seals at Marion Island. Superscripts indicate variation ($\neq$) or equality (=) among pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states. Subscripts represent specific age classes (a) or continuous logit-linear and logit-quadratic regression. Small sample corrected quasi-likelihood Akaike's Information Criterion (QAIC_c; $\hat{c} = 1.7$) was used to select models, with the following measurements: ΔQAIC_c (difference in QAIC_c between the model with the lowest QAIC_c value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood). Models in bold font were used to derive estimates.

Model	Parameters	ΔQAIC_c	ω_i	K	Deviance
	Survival at breeding state level (multievent matrix)				
1	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB}}_{\text{a }5,6,7,8,9,\geq 10} + \varphi^{\text{DB}}_{\text{a }6,7,8,9,\geq 10}$	13.07	0.00	85	228.79
2	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,\geq 8} + \varphi^{\text{PB=SB}}_{\text{a }5,6,7} + \varphi^{\text{SB}}_{\text{a }8,9,\geq 10} + \varphi^{\text{DB}}_{\text{a }6,7,8,9,\geq 10}$	12.29	0.00	84	231.51
3	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 8} + \varphi^{\text{PB=DB}}_{\text{a }6,7} + \varphi^{\text{SB}}_{\text{a }5,6,7,8,9,\geq 10} + \varphi^{\text{DB}}_{\text{a }8,9,\geq 10}$	13.51	0.00	85	228.80
4	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,\geq 8} + \varphi^{\text{PB=SB=DB}}_{\text{a }5,6,7} + \varphi^{\text{SB}\neq\text{DB}}_{\text{a }8,9,\geq 10}$	8.55	0.00	82	237.11
5	$\varphi^{\text{PB=SB=DB}}_{\text{a }0,1,2,3,4,5,6,7,8,9,10,11,12,13}$	14.71	0.00	81	240.11
6	$\varphi^{\text{PB=SB=DB}}_{\text{a }0,1,2,3,4,5,6,7,8,9,\geq 10}$	11.51	0.00	78	249.30
7	$\varphi^{\text{PB=SB=DB}}_{\text{a }0,1,2,3,4,5,\geq 6}$	7.13	0.01	74	262.72
8	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB}}_{\text{a }5,6,7,8,9,\geq 10\ (\text{linear}^{\text{SB}})} + \varphi^{\text{DB}}_{\text{a }6,7,8,9,\geq 10\ (\text{linear}^{\text{DB}})}$	1.27	0.17	78	249.17
9	$\boldsymbol{\varphi}^{\mathbf{PB}}_{\mathbf{a\ 0,1,2,3,4,5,\geq 6}} + \boldsymbol{\varphi}^{\mathbf{SB\neq DB}}_{\mathbf{a\ 5,6,7,8,9,\geq 10\ (linear^{SB=DB})}}$	**0.00**	**0.31**	**77**	**252.39**
10	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB=DB}}_{\text{a }5,6,7,8,9,\geq 10\ (\text{linear}^{\text{SB=DB}})}$	1.37	0.16	76	255.73
11	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB}}_{\text{a }5,6,7,8,9,\geq 10\ (\text{quadratic}^{\text{SB}})}$ $+ \varphi^{\text{DB}}_{\text{a }6,7,8,9,\geq 10\ (\text{quadratic}^{\text{DB}})}$	3.85	0.05	80	242.98
12	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB}\neq\text{DB}}_{\text{a }5,6,7,8,9,\geq 10\ (\text{quadratic}^{\text{SB=DB}})}$	2.02	0.11	78	249.18
13	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB=DB}}_{\text{a }5,6,7,8,9,\geq 10\ (\text{quadratic}^{\text{SB=DB}})}$	3.39	0.06	77	252.44
14	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB}\neq\text{DB}}_{\text{cst}}$	5.26	0.02	76	255.78
15	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB=DB}}_{\text{a }5,6,7,8,9,\geq 10}$	9.30	0.00	80	243.04
16	$\varphi^{\text{PB}}_{\text{a }0,1,2,3,4,5,\geq 6} + \varphi^{\text{SB=DB}}_{\text{cst}}$	2.21	0.10	75	259.15
	Survival at population level (single-state matrix)				
17	$\varphi^{\text{PB=SB=DB}}_{\text{a }0,1,2,3,4,5,6,7,8,9,10,11,12,13}$	2.70	0.16	26.00	539.05
18	$\varphi^{\text{PB=SB=DB}}_{\text{cst}}$	100.61	0.00	16.00	882.08
19	$\varphi^{\text{PB=SB=DB}}_{\text{a }0,1,2,3,4,5,6,7,8,9,10,11,12,13\ (\text{linear}^{\text{PB=SB=DB}})}$	93.39	0.00	17.00	829.76
20	$\varphi^{\text{PB=SB=DB}}_{\text{a }0,1,2,3,4,5,6,7,8,9,10,11,12,13\ (\text{quadratic}^{\text{PB=SB=DB}})}$	46.76	0.00	18.00	781.08
21	Gompertz3+ function	89.61	0.00	19.00	742.22
22	Weibull3+ function	23.29	0.00	19.00	738.73
23	Flexible Weibull function	33.57	0.00	18.00	780.34
24	**Reduced Additive Weibull function**	**0.00**	**0.62**	**18.00**	**778.48**
25	Mixture of Flexible & Reduced Additive Weibull functions	2.13	0.21	21.00	667.37

26	Siler function	56.29	0.00	20.00	703.44

Table 2: Multievent models representing reproductive trade-off hypotheses about breeding probabilities (ψ) of male southern elephant seals at Marion Island. Superscripts indicate variation (≠) or equality (=) among pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states. Subscripts represent specific age classes (a) or continuous logit-linear and logit-quadratic regression. Small sample corrected quasi-likelihood Akaike's Information Criterion (QAIC$_c$; $\hat{c}$ = 1.7) was used to select models, with the following measurements: ΔQAIC$_c$ (difference in QAIC$_c$ between the model with the lowest QAIC$_c$ value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood). Models in bold font were used to derive estimates.

Model	Parameters	ΔQAIC$_c$	ω_i	K	Deviance
	*Recruitment (*PB-SB & PB-DB*)*				
27	$\psi^{PB-SB}_{a\ 5,6,7,\geq 8} + \psi^{PB-DB}_{a\ 6,7,\geq 8}$	0.67	0.42	77	252.39
28	$\psi^{PB-SB}_{a\ 5,6,7,\geq 8\ (\text{linear}^{PB-SB})} + \psi^{PB-DB}_{a\ 6,7,\geq 8\ (\text{linear}^{PB-DB})}$	30.93	0.00	74	263.03
29	$\psi^{PB-SB\neq PB-DB}_{a\ 5,6,7,\geq 8\ (\text{linear}^{PB-SB=PB-DB})}$	15.84	0.00	73	266.43
30	$\psi^{PB-SB=PB-DB}_{a\ 5,6,7,\geq 8\ (\text{linear}^{PB-SB=PB-DB})}$	101.12	0.00	72	271.31
31	$\psi^{PB-SB}_{a\ 5,6,7,\geq 8\ (\text{quadratic}^{PB-SB})} + \psi^{PB-DB}_{a\ 6,7,\geq 8\ (\text{quadratic}^{PB-DB})}$	28.33	0.00	75	259.49
32	$\boldsymbol{\psi^{PB-SB\neq PB-DB}_{a\ 5,6,7,\geq 8\ (\text{quadratic}^{PB-SB=PB-DB})}}$	**0.00**	**0.58**	**74**	**262.61**
33	$\psi^{PB-SB=PB-DB}_{a\ 5,6,7,\geq 8\ (\text{quadratic}^{PB-SB=PB-DB})}$	86.09	0.00	73	267.39
34	$\psi^{PB-SB\neq PB-DB}_{cst}$	212.61	0.00	72	272.86
35	$\psi^{PB-SB=PB-DB}_{a\ 5,6,7,\geq 8}$	90.15	0.00	74	263.83
36	$\psi^{PB-SB=PB-DB}_{cst}$	978.85	0.00	71	287.50
	*Future breeding success (*SB-DB & DB-DB*)*				
37	$\psi^{SB-DB}_{a\ 6,7,8,9,10,\geq 11} + \psi^{DB-DB}_{a\ 7,8,9,10,\geq 11}$	12.80	0.00	74	262.61
38	$\psi^{SB-DB}_{a\ 6,7,8,9,10,\geq 11\ (\text{linear}^{SB-DB})} + \psi^{DB-DB}_{a\ 7,8,9,10,\geq 11\ (\text{linear}^{DB-DB})}$	2.45	0.16	67	289.90
39	$\boldsymbol{\psi^{SB-DB\neq DB-DB}_{a\ 6,7,8,9,10,\geq 11\ (\text{linear}^{SB-DB=DB-DB})}}$	**0.00**	**0.56**	**66**	**294.25**
40	$\psi^{SB-DB=DB-DB}_{a\ 6,7,8,9,10,\geq 11\ (\text{linear}^{SB-DB=DB-DB})}$	8.78	0.01	65	298.91
41	$\psi^{SB-DB}_{a\ 6,7,8,9,10,\geq 11\ (\text{quadratic}^{SB-DB})} + \psi^{DB-DB}_{a\ 7,8,9,10,\geq 11\ (\text{quadratic}^{DB-DB})}$	5.34	0.04	69	281.54
42	$\psi^{SB-DB\neq DB-DB}_{a\ 6,7,8,9,10,\geq 11\ (\text{quadratic}^{SB-DB=DB-DB})}$	2.00	0.21	67	289.89
43	$\psi^{SB-DB=DB-DB}_{a\ 6,7,8,9,10,\geq 11\ (\text{quadratic}^{SB-DB=DB-DB})}$	10.74	0.00	66	294.42
44	$\psi^{SB-DB\neq DB-DB}_{cst}$	6.28	0.02	65	298.88
45	$\psi^{SB-DB=DB-DB}_{a\ 6,7,8,9,10,\geq 11}$	15.55	0.00	69	281.68
46	$\psi^{SB-DB=DB-DB}_{cst}$	32.30	0.00	64	303.95

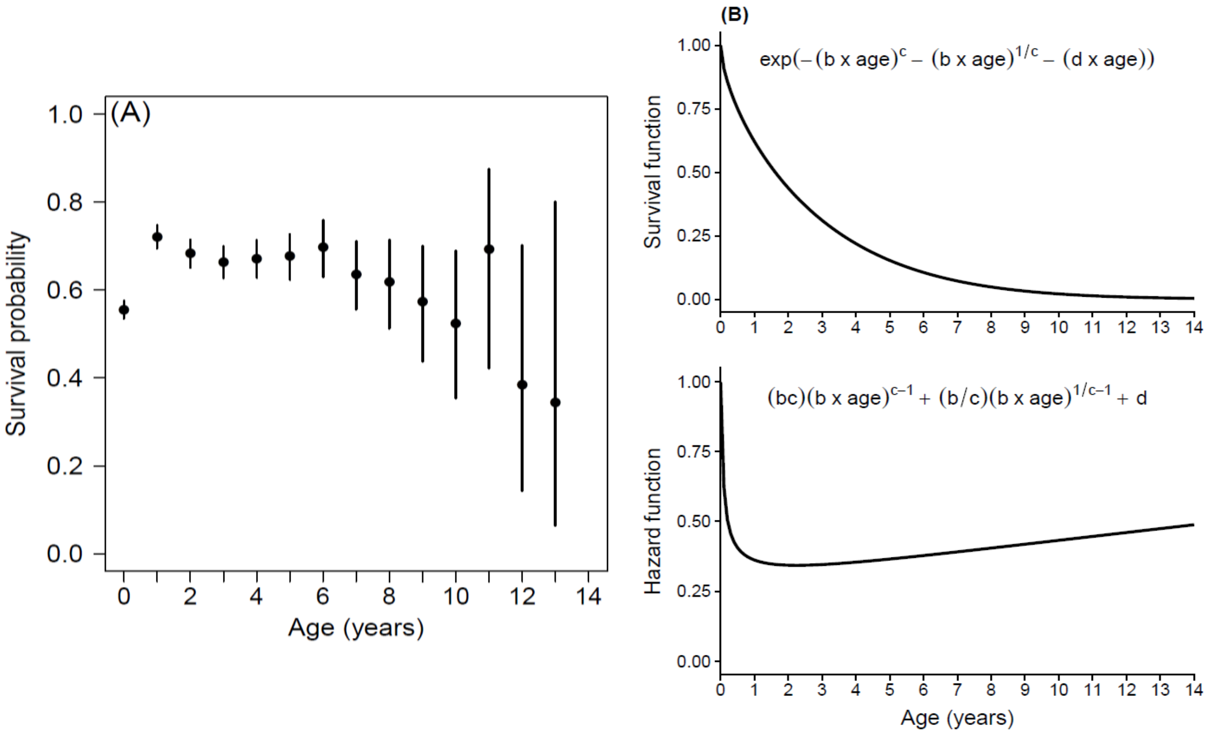

Figure 2: (A) Fully age dependent survival probabilities (95% confidence intervals) of male southern elephant seals independent of breeding state (model 5, Table 1). Individuals showed a general decreasing trend in survival from recruitment ages (6-8 years) to the oldest recorded age. (B) The Reduced Additive Weibull model (model 24) describing survival and mortality over the male southern elephant seal lifespan. Parameter estimates were b = 0.11 representing the scale parameter, c = 0.56 representing the shape parameter, and d = 0.17 representing mortality at age 0 (Choquet *et al*. 2011). According to the hazard function, mortality increased at the oldest age classes, substantiating evidence for actuarial senescence.

Future breeding success (i.e. the probability to transition to the dominant breeder state) increased according to a logit-linear relationship with age for both subordinate and dominant breeders, with an equal rate of increase for both breeding states (model 39, Table 2). Dominant breeders that survived to the next breeding season were more likely to remain dominant than become subordinate (Figure 3B). Results for other multievent predictions and parameters are given in Supp. S5. Models with individual random effects explained more variation in survival and breeding probabilities than breeding state and age alone (Supp. 7). However, individual variation was small and less for survival (σ = 0.000017) than breeding (σ = 0.23) probabilities, with similar parameter estimates for models with and without the individual random effect (Table S7.1).

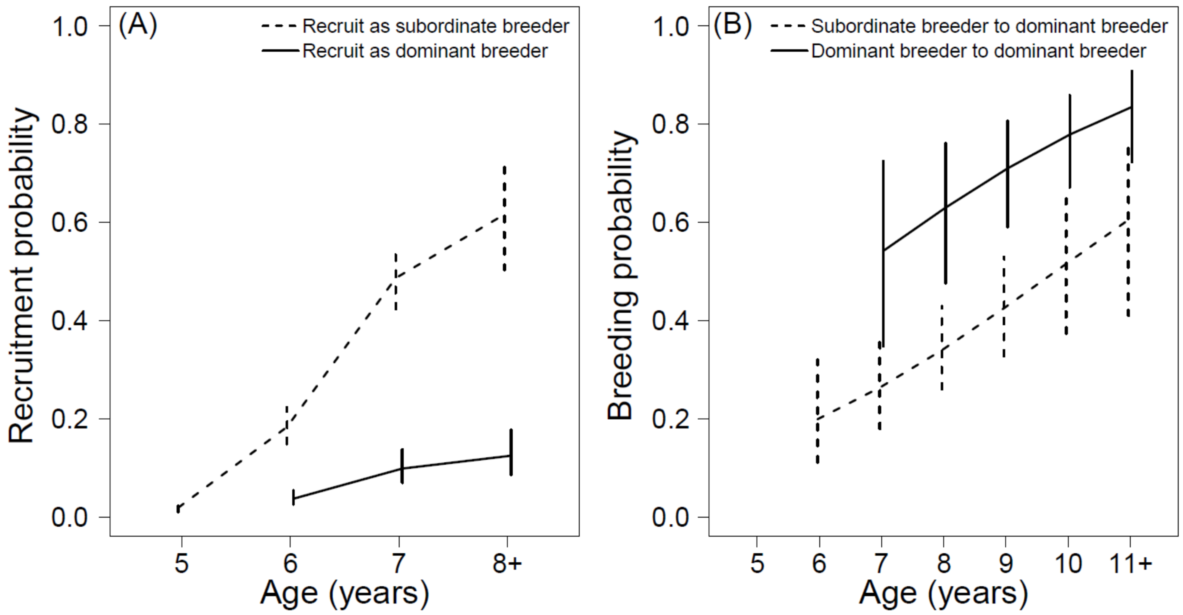

Figure 3: Predicted (A) recruitment and (B) future breeding success probabilities of male southern elephant seals at Marion Island. Mean probabilities (95% confidence intervals) were derived from models 32 and 39 (Table 2), which assumed that recruitment and future breeding success increased with age according to a logit-quadratic and logit-linear relationship, respectively. The rates of increase for recruitment and future breeding success were independent of breeding state.

Discussion

Allocating limited resources to current breeding results in trade-offs with other life history traits. In polygynous breeding systems, males allocate resources to attend breeding events, and to secure and mate with females. This study is the first to investigate lifetime demographic trade-offs in male southern elephant seals, one of the most sexually dimorphic and polygynous mammal species globally. We provide valuable insight into male southern elephant seal demography, and polygynous male life history in general, which has received much less attention than females (Pistorius *et al*. 1999; Pistorius *et al*. 2005). Our findings support recent studies of other polygynous systems that early male recruits do not pay a cost of attending breeding events (Markussen *et al*. 2019), and that breeding males pay a cost of attempting to be successful rather than actually being successful (Festa-Bianchet *et al*. 2019).

Pre-breeders vs Breeders

In males, the cost of reproduction to other life history traits has been demonstrated in studies that experimentally manipulate breeding effort (e.g. Kilpimaa *et al*. 2004). However, few studies have been able to compare naturally occurring mature males that have no history of reproductive costs with those that do. Here, we compared survival probabilities between male elephant seal pre-breeders that have acquired no cost of breeding in their lifetime with breeders of overlapping age classes. Contrary to our expectations, we found that pre-breeders and breeders had similar age-specific survival probabilities. In addition, the probability of recruitment as a dominant breeder was always lower than recruitment as a subordinate breeder of the same age, even when recruitment was delayed to older ages. In fact, the probability of being a subordinate rather than dominant breeder at recruitment was much higher at older ages. Therefore, pre-breeders that delayed attendance at breeding events did not have more resources available to improve their breeding success at recruitment (by recruiting directly as dominant breeders) when compared to younger recruits. Male elephant seals grow throughout their lives and show increased variability in growth rates among individuals with age (McLaren 1993). It may be that pre-breeders that delayed recruitment were of lower quality (e.g. smaller body size) than pre-breeders that recruited earlier (Becker & Bradley 2007), as access to females is determined by dominance relationships between males (McCann 1981). This may explain the slightly higher survival probabilities of dominant breeders (age 6) compared to pre-breeders of the same age. In such a scenario, it would be more beneficial for low quality pre-breeders to attend breeding events at an older age when they have obtained an adequate body size to compete for female harems (the restraint hypothesis; Pianka 1976). This is not to say that older recruits had a lower lifetime breeding success than younger recruits, given that the chances of obtaining and maintaining dominance increased with age.

Subordinate vs Dominant breeders

When comparing males that did attend breeding events, there was no support for a greater cost of breeding to survival in dominant breeders compared to subordinate breeders. However, both subordinate and dominant breeders displayed survival senescence, with subordinate breeders having a higher baseline mortality. This occurred concurrently with an age-related increase in the probability to be dominant (at t+1) for both subordinate and dominant breeders (at t). Thus, whereas the probability of becoming and remaining a dominant breeder increased with age, survival declined with age after recruitment. The opposing trends in age-specific patterns of survival and future breeding success highlights the possibility of a population-level trade-off for recruited males.

Contrary to our expectations, we found that dominant breeders maintained higher survival probabilities than subordinate breeders of the same age. This may initially seem surprising given that weight loss in male elephant seals increases with both successful competitions for and interactions with females (Galimberti *et al*. 2007). Apart from vocalising and (rarely) fighting subordinates, dominant breeders also spend energy herding and mating females (Galimberti *et al*. 2000). However, higher survival of successful, dominant breeders has also been observed among males of other polygynous species, with the common explanation being differences in individual quality among social ranks, which is reinforced by sexual selection (McElligott *et al*. 2002; Pelletier *et al*. 2006; Toïgo *et al*. 2013).

Age-related breeding improvement and survival senescence

Males bred at an earlier age at Marion Island compared to other colonies (Jones 1981), most likely due to low male density and many discrete, instead of extensive, beaches on the island (Supp. S5; Wilkinson & van Aarde 1999). For both subordinate and dominant breeders, there was an increase in the probability of future breeding success (i.e. attaining dominant social rank) with age after recruitment. Conversely, young dominant breeders were more likely to lose harem dominance (i.e. become subordinate) in subsequent breeding events than older dominant breeders. Age-related breeding improvement has been demonstrated in other groups of animals including mammals (Dugdale *et al*. 2011) and birds (Limmer & Becker 2010). Breeding experience is hypothesised as a cause, either due to the fine tuning of breeding behaviours or due to more efficient physiological pathways (Forslund & Pärt 1995; Riechert *et al*. 2012). Thus, young males may be constrained by behavioural and physiological aspects related to reproduction (the constraint hypothesis; Curio 1983; Nol & Smith 1987). For dominant breeders, previous experience may involve showing reduced aggression towards females but not males (Baxter & Dukas 2017), increased ability to detect females in oestrus, and the promotion of harem cohesion by reducing disturbance from subordinates (McCann 1981). For subordinate breeders, experience may also involve learning to establish territories at the correct beaches earlier in the breeding season (Haley 1994; Mulaudzi *et al*. 2008).

Alternatively, males may increase breeding effort with age by allocating resources to body size throughout life (McLaren 1993) to improve their competitive ability (McCann 1981) rather than only in some last event when their condition becomes critical (terminal investment hypothesis; Duffield *et al*. 2017).

The increasing trend in the probability to be dominant with age, with no sign of late decrease, was opposite to the decreasing trend in survival with age. Our study was observational and therefore relationships were based purely on correlation, which does not imply causation. However, the well-supported, contrasting slopes of survival and future breeding success for both subordinate and dominant breeders suggest a trade-off between the two life history traits (Nussey *et al*. 2008). In some species, individuals only show signs of decreasing survival probability at old ages (antagonistic pleiotropy theory; Williams 1957). However, actuarial senescence in male elephant seals began from the age of recruitment and persisted throughout life (disposable soma theory; Kirkwood 1977). In female elephant seals at Marion Island, survival and future breeding probabilities are similar for young and old breeders (Pistorius *et al*. 2004), with only low quality females experiencing an immediate survival cost of first reproduction (Oosthuizen *et al*. 2019b). Male elephant seals are short-lived relative to females (Pistorius *et al*. 1999) and, more generally, compared to other large mammals (Condit *et al*. 2013). Sexual selection for breeding dominance and male allocation to costly secondary sexual traits and behaviours is hypothesized to constitute one key driver of sex-biased mortality in polygynous vertebrates (lizards: Reedy *et al*. 2019; birds: Liker & Székely 2005; primates: Bronikowski *et al*. 2011; vertebrates: Clutton-Brock & Isvaran 2007; Bonduriansky *et al*. 2008; but see Lemaître & Gaillard 2012). Among polygynous male ruminants, for example, strong sexual selection advances the onset of survival senescence, leading to shorter longevity compared to socially monogamous male species (Tidière *et al*. 2015). Strong sexual selection may be driving survival senescence in male elephant seals, given their highly competitive breeding system (Clutton-Brock 1989). For example, mass loss at the end of the breeding season increases with age at a rate of 113 kg per year in male elephant seals (1.70%; Galimberti *et al*. 2007). Therefore, less resources are available with age to allocate to survival-related traits (e.g. immune response; Pelletier *et al*. 2005; Harshman & Zera 2007).

State-based heterogeneity in life history traits: dominant males always do better

Costs to breeder survival likely resulted from attempting to obtain dominance rather than from the consequences of breeding successfully (i.e. "the cost of trying"; Festa-Bianchet 2012; Festa-Bianchet *et al*. 2019), as we failed to find evidence of higher breeding costs in dominant breeders compared to subordinate breeders. Despite substantial energetic allocation to breeding through sexual competition, several studies have found that successful breeding does not incur a cost to survival in polygynous males (Festa-Bianchet 2012). This can be attributed to individual heterogeneity in phenotypic quality among social ranks (Wilson & Nussey 2010). For polygynous ungulates, phenotypic variability in quality among individuals of fallow deer (*Dama dama*; McElligott *et al*. 2002), bighorn sheep (*Ovis canadensis*; Pelletier *et al*. 2006), and alpine ibex (*Capra ibex*; Toïgo *et al*. 2013) resulted in no measurable breeding cost to survival. This would make sense for a group of polygynous mammals where higher quality males (having larger body and horn/antler size) monopolise mating events by outcompeting males of lesser quality over consecutive years (Pelletier *et al*. 2006).

Sexual selection theory predicts that sexual traits that win male-male competitions and successfully attract mates should be positively correlated to individual quality and thus life history traits (Hamilton & Zuk 1982). High quality males have a larger resource pool than low quality males allowing them to afford costs to both survival (immune response; Folstad & Karter 1992) and breeding (secondary sexual traits; Simmons 2011). Thus, male sexual traits serve as indicators of condition related to survival (immunocompetence: Gilbert *et al*. 2016) and future breeding success (dominance: McCann 1981). Dominant elephant seals are generally of a larger body size (and proboscis length) and have a greater resource holding potential (ability to compete) than subordinates (Sanvito *et al*. 2007). Although obtaining a high social rank comes at great energetic expense for dominant breeders in both absolute and relative weight loss, it does not appear to affect short-term survival (Galimberti *et al*. 2007) or, in this case, increase the rate of survival senescence compared to subordinates. Therefore, sexual selection may be creating a selective pressure for high quality males that reduces breeding costs (Adamo & Spiteri 2009).

Conclusion

Our individual-level, multidecadal data of male southern elephant seals and their evident social breeding structure allowed us to partition the costs of current breeding among breeders (dominant and subordinate) and pre-breeders. We successfully compared survival probabilities of pre-breeders with no accumulated breeding costs to breeders of overlapping ages and found that there was no cost to attending breeding events for early recruits. In addition, pre-breeders that delayed attendance costs did not improve their chances of being first-time dominant breeders more than subordinate breeders. We provide the first evidence of actuarial senescence in male southern elephant seals, and show that senescence occurred at ages when female elephant seals retain stable survival rates (Pistorius *et al*. 2004). In contrast, age-specific future breeding success (measured as social rank) increased with age, with dominant breeders maintaining higher subsequent breeding success than subordinates. These opposite trends in survival and future breeding success for both subordinate and dominant breeders point to a population-level trade-off. Nonetheless, we find no evidence to suggest that being a dominant breeder consecutively accelerated the rate of senescence when compared to subordinates, with individual quality being the likely explanation. Our results make several novel contributions to understanding polygynous male life histories, which can be further developed by exploring life history trait covariates at the individual-level.

Supporting Information

Supplement S1: Sample sizes and state transitions

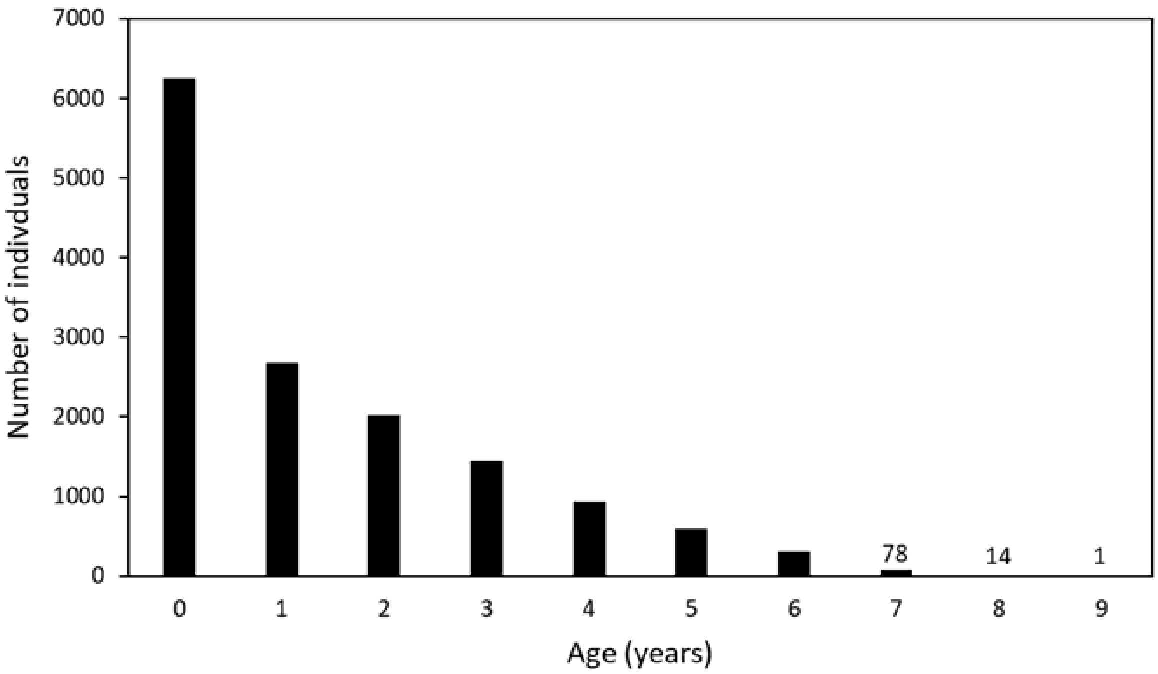

Figure S1.1: Total number of uniquely marked pre-breeding male southern elephant seals at Marion Island recorded per age class between 1983 and 2016.

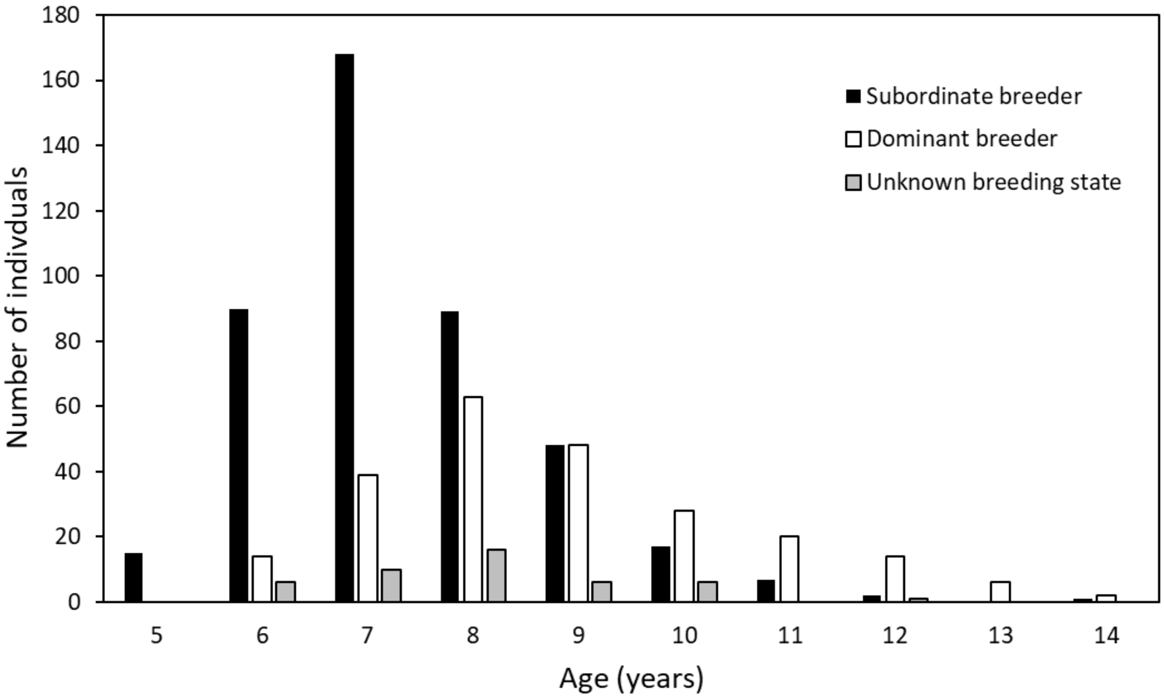

Figure S1.2: Total number of uniquely marked breeding male southern elephant seals at Marion Island recorded per age class between 1983 and 2016.

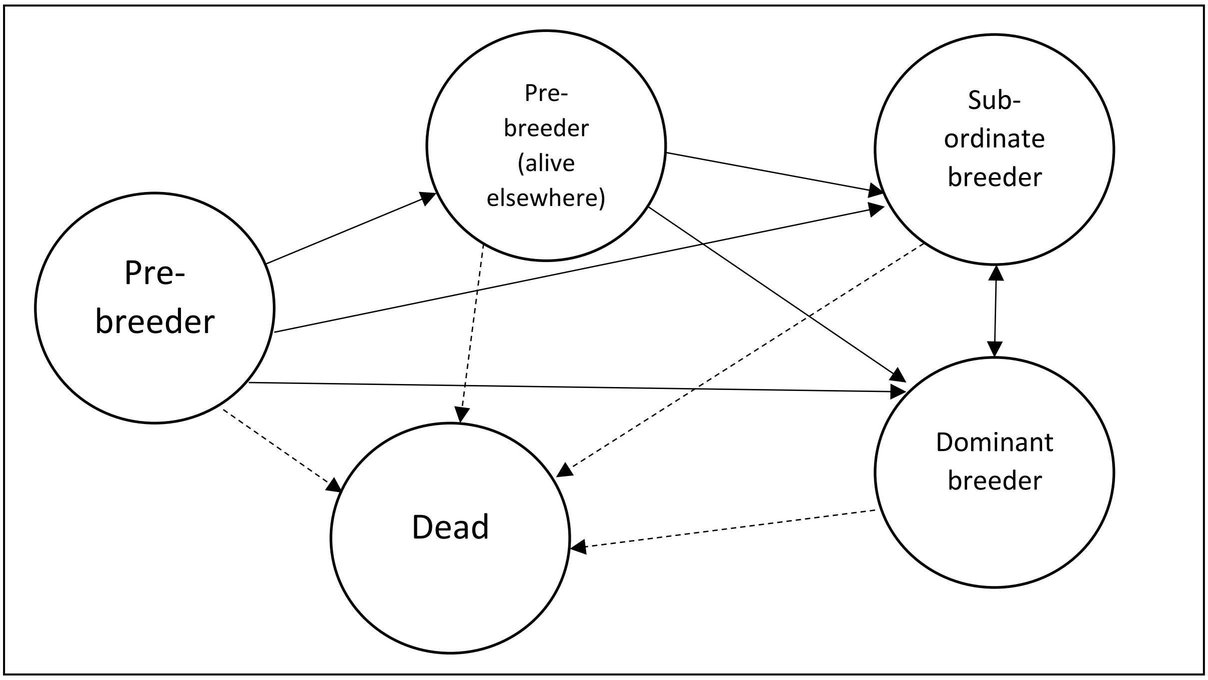

Figure S1.3: A simplified diagram illustrating possible transitions among breeding states for male southern elephant seals at Marion Island. Recruiting pre-breeders transition into becoming either a subordinate or dominant breeder, hence a unidirectional transition.

Supplement S2: Goodness-of-fit tests

No formal goodness-of-fit (GOF) tests exist for multievent mark-recapture models (Pradel *et al*. 2005). Nevertheless, we approximated whether the data fitted the assumption of the simpler Cormack-Jolly-Seber model that all marked individuals behave the same at any given time (Pradel *et al*. 2003). The multievent encounter history matrix was converted to a single state matrix (presence/absence) and separated into matrices for pre-breeders and breeders, as the two groups were likely to differ in encounter histories (Pradel *et al*. 2003). We did not consider multistate GOF tests to prevent overdispersion that may result from having too few observations per state and because multistate GOF tests are not optimal in the presence of unidirectional state transitions (i.e. breeders cannot return to the pre-breeder state). The test for transience (or effect of marking on immediate survival; Test 3.SR) for pre-breeders suggested that there were differences in the expected time of first recapture between newly marked and previously marked individuals ($\chi^2(26) = 203.84$; $P < 0.001$). When suppressing first encounters, the remaining heterogeneity was much weaker ($\chi^2(26) = 26.13$; $P = 0.43$; Pradel *et al*. 1997). The test for trap-dependence (or immediate trap response behaviour; Test 2.CT) showed that detection probabilities differed among pre-breeders ($\chi^2(29) = 256.73$; $P < 0.001$), indicating that individuals displayed large variability in their encounter history matrix. Therefore, temporary emigration was introduced into the study as hidden states, allowing for Test 2.CT to be dropped (Pradel *et al*. 2005). An adjusted inflation/overdispersion factor ($\hat{c}$) was calculated by (1) summing pre-breeder and breeder χ^2-statistics and degrees of freedom from Test3 and Test2; and (2) dividing the total χ^2-statistic by the total degrees of freedom. GOF tests were conducted using U-CARE 2.3.4 (Choquet *et al*. 2009).

Table S2.1: Testing the homogeneity assumptions of the Cormack-Jolly-Seber single-state model for mark-recapture data collected from male southern elephant seals at Marion Island. Goodness-of-fit tests follow approaches developed by Pradel *et al*. (1997, 2003) to derive an adjusted overdispersion factor ($\hat{c}$).

Breeding state	**Test**	**Degrees of freedom**	**χ^2-statistic**	**$\hat{c}$**
Pre-breeder	3.SR	28	78.88	2.82
	3.SM	27	70.66	2.62
	2.CT	Not applicable		
	2.CL	19	8.12	0.43
	Total	74	157.67	2.13
Breeder	3.SR	26	26.13	1.01
	3.SM	8	4.33	0.54
	2.CT	5	3.76	0.75
	2.CL	0	0	0
	Total	39	34.22	0.88
Overall		**113**	**191.89**	**1.70**

References

Choquet, R., Lebreton, J.D., Gimenez, O., Reboulet, A.M. & Pradel, R. 2009. U-CARE: Utilities for performing goodness of fit tests and manipulating capture-recapture data. *Ecography* 32: 1071-1074.

Pradel, R., Hines, J.E., Lebreton, J.D. & Nichols, J.D. 1997. Capture-recapture survival models taking account of transients. *Biometrics* 53: 60-72.

Pradel, R., Wintrebert, C. & Gimenez, O. 2003. A proposal for a goodness-of-fit test to the Arnason-Schwarz multisite capture-recapture model. *Biometrics* 59: 43-53.

Pradel, R., Gimenez, O. & Lebreton, J.D. 2005. Principles and interest of GOF tests for multistate capture–recapture models. *Animal Biodiversity and Conservation* 28: 189-204.

Supplement S3: Specifying elementary matrices

Multievent models were parameterised using initial state, transition and event matrices in the programme E-SURGE 2.1.4 (Choquet *et al*. 2009). Mark-recapture data were imported in Text format and the overdispersion factor was set to $\hat{c} = 1.7$. Under "Modify", the number of states (9), events (9) and age classes (14) were set in order to determine the number of rows and columns of each matrix. The following nine (biological) states were recognised:

PB2 – Pre-breeder with two tags (has not previously participated in a breeding season)

PB1 – Pre-breeder with one tag

PBAE2 – Pre-breeder alive elsewhere with two tags (temporarily emigrated and last seen with two tags)

PBAE1 – Pre-breeder alive elsewhere with one tag

SB2 – Subordinate breeder with two tags (attended breeding season but did not mate)

SB1 – Subordinate breeder with one tag

DB2 – Dominant breeder with two tags (attended breeding season and mated)

DB1 – Dominant breeder with one tag

D – Dead (an absorbing state representing death and permanent emigration)

Pre-breeders alive elsewhere are hidden states constructed to account for individuals not observed in a seal year that may have temporary emigrated from the study area (Schaub *et al*. 2004). Events relate in a probabilistic framework to nine possible breeding states that an individual can occupy during each seal year. The following nine (observed) events were recognised:

0 – Not seen

1 – Seen as a pre-breeder with two tags

2 – Seen as a pre-breeder with one tag

3 – Seen as a subordinate breeder with two tags

4 – Seen as a subordinate breeder with one tag

5 – Seen as a dominant breeder with two tags

6 – Seen as a dominant breeder with one tag

7 – Seen with an unknown breeding state and two tags

8 – Seen with an unknown breeding state and one tag

GEPAT (for GEnerator of PATtern of elementary matrices) was used to specify the matrices. Estimated parameters were assigned with alphabetical letters, "-" indicates that the corresponding parameter was set to 0, and "*" means (1 - Σ (all other parameters on the same row)). There was always only one "*" per row.

References

Choquet, R., Rouan, L. & Pradel, R. 2009. Program E-SURGE: a software application for fitting multievent models. In: D.L. Thomson, E.G. Cooch & M.J. Conroy (eds.), *Modeling demographic processes in marked populations*, pp. 845-865. Springer, New York.

Schaub, M., Gimenez, O., Schmidt, B.R. & Pradel, R. 2004. Estimating survival and temporary emigration in the multistate capture–recapture framework. *Ecology* 85: 2107-2113.

GEPAT matrices (in order of appearance in the interface)

Initial state matrix:

$$\begin{array}{c} \begin{array}{cccccccc} \text{PB2} & \text{PB1} & \text{PBAE2} & \text{PBAE1} & \text{SB2} & \text{SB1} & \text{DB2} & \text{DB1} \end{array} \\ \left(\begin{array}{cccccccc} \pi & * & - & - & - & - & - & - \end{array} \right) \end{array}$$

First tag loss matrix:

$$\begin{array}{cc} & \begin{array}{ccccccccc} \text{PB2} & \text{PB1} & \text{PBAE2} & \text{PBAE1} & \text{SB2} & \text{SB1} & \text{DB2} & \text{DB1} & \text{D} \end{array} \\ \begin{array}{c} \text{PB2} \\ \text{PB1} \\ \text{PBAE2} \\ \text{PBAE1} \\ \text{SB2} \\ \text{SB1} \\ \text{DB2} \\ \text{DB1} \\ \text{D} \end{array} & \left(\begin{array}{ccccccccc} * & \tau^{2-1} & - & - & - & - & - & - & - \\ - & * & - & - & - & - & - & - & - \\ - & - & * & \tau^{2-1} & - & - & - & - & - \\ - & - & - & * & - & - & - & - & - \\ - & - & - & - & * & \tau^{2-1} & - & - & - \\ - & - & - & - & - & * & - & - & - \\ - & - & - & - & - & - & * & \tau^{2-1} & - \\ - & - & - & - & - & - & - & * & - \\ - & - & - & - & - & - & - & - & * \end{array} \right) \end{array}$$

Second tag loss matrix:

$$
\begin{array}{cccccccccc}
 & \text{PB2} & \text{PB1} & \text{PBAE2} & \text{PBAE1} & \text{SB2} & \text{SB1} & \text{DB2} & \text{DB1} & \text{D} \\
\text{PB2} & * & - & - & - & - & - & - & - & - \\
\text{PB1} & - & * & - & - & - & - & - & - & \tau^{1-0} \\
\text{PBAE2} & - & - & * & - & - & - & - & - & - \\
\text{PBAE1} & - & - & - & * & - & - & - & - & \tau^{1-0} \\
\text{SB2} & - & - & - & - & * & - & - & - & - \\
\text{SB1} & - & - & - & - & - & * & - & - & \tau^{1-0} \\
\text{DB2} & - & - & - & - & - & - & * & - & - \\
\text{DB1} & - & - & - & - & - & - & - & * & \tau^{1-0} \\
\text{D} & - & - & - & - & - & - & - & - & *
\end{array}
$$

Survival matrix:

$$
\begin{array}{cccccccccc}
 & \text{PB2} & \text{PB1} & \text{PBAE2} & \text{PBAE1} & \text{SB2} & \text{SB1} & \text{DB2} & \text{DB1} & \text{D} \\
\text{PB2} & \varphi & - & - & - & - & - & - & - & * \\
\text{PB1} & - & \varphi & - & - & - & - & - & - & * \\
\text{PBAE2} & - & - & \varphi & - & - & - & - & - & * \\
\text{PBAE1} & - & - & - & \varphi & - & - & - & - & * \\
\text{SB2} & - & - & - & - & \varphi & - & - & - & * \\
\text{SB1} & - & - & - & - & - & \varphi & - & - & * \\
\text{DB2} & - & - & - & - & - & - & \varphi & - & * \\
\text{DB1} & - & - & - & - & - & - & - & \varphi & * \\
\text{D} & - & - & - & - & - & - & - & - & *
\end{array}
$$

Breeding matrix (representing recruitment and future breeding success):

$$
\begin{array}{cccccccccc}
 & \text{PB2} & \text{PB1} & \text{PBAE2} & \text{PBAE1} & \text{SB2} & \text{SB1} & \text{DB2} & \text{DB1} & \text{D} \\
\text{PB2} & * & - & - & - & \psi & - & \psi & - & - \\
\text{PB1} & - & * & - & - & - & \psi & - & \psi & - \\
\text{PBAE2} & - & - & * & - & \psi & - & \psi & - & - \\
\text{PBAE1} & - & - & - & * & - & \psi & - & \psi & - \\
\text{SB2} & - & - & - & - & * & - & \psi & - & - \\
\text{SB1} & - & - & - & - & - & * & - & \psi & - \\
\text{DB2} & - & - & - & - & * & - & \psi & - & - \\
\text{DB1} & - & - & - & - & - & * & - & \psi & - \\
\text{D} & - & - & - & - & - & - & - & - & *
\end{array}
$$

Temporary migration matrix:

$$\begin{array}{c|ccccccccc}
 & \mathrm{PB2} & \mathrm{PB1} & \mathrm{PBAE2} & \mathrm{PBAE1} & \mathrm{SB2} & \mathrm{SB1} & \mathrm{DB2} & \mathrm{DB1} & \mathrm{D} \\
\hline
\mathrm{PB2} & * & - & \psi^{E} & - & - & - & - & - & - \\
\mathrm{PB1} & - & * & - & \psi^{E} & - & - & - & - & - \\
\mathrm{PBAE2} & \psi^{I} & - & * & - & - & - & - & - & - \\
\mathrm{PBAE1} & - & \psi^{I} & - & * & - & - & - & - & - \\
\mathrm{SB2} & - & - & - & - & * & - & - & - & - \\
\mathrm{SB1} & - & - & - & - & - & * & - & - & - \\
\mathrm{DB2} & - & - & - & - & - & - & * & - & - \\
\mathrm{DB1} & - & - & - & - & - & - & - & * & - \\
\mathrm{D} & - & - & - & - & - & - & - & - & *
\end{array}$$

Detection matrix:

NS – Not seen

$$\begin{array}{c|ccccccc}
 & \mathrm{NS} & \mathrm{PB2} & \mathrm{PB1} & \mathrm{SB2} & \mathrm{SB1} & \mathrm{DB2} & \mathrm{DB1} \\
\hline
\mathrm{PB2} & * & p & - & - & - & - & - \\
\mathrm{PB1} & * & - & p & - & - & - & - \\
\mathrm{PBAE2} & * & - & - & - & - & - & - \\
\mathrm{PBAE1} & * & - & - & - & - & - & - \\
\mathrm{SB2} & * & - & - & p & - & - & - \\
\mathrm{SB1} & * & - & - & - & p & - & - \\
\mathrm{DB2} & * & - & - & - & - & p & - \\
\mathrm{DB1} & * & - & - & - & - & - & p \\
\mathrm{D} & * & - & - & - & - & - & -
\end{array}$$

State assignment matrix:

$$\begin{array}{c|ccccccccc}
 & 0 & 1 & 2 & 3 & 4 & 5 & 6 & 7 & 8 \\
\hline
\mathrm{NS} & * & - & - & - & - & - & - & - & - \\
\mathrm{PB2} & - & * & - & - & - & - & - & - & - \\
\mathrm{PB1} & - & - & * & - & - & - & - & - & - \\
\mathrm{SB2} & - & - & - & \delta & - & - & - & * & - \\
\mathrm{SB1} & - & - & - & - & \delta & - & - & - & * \\
\mathrm{DB2} & - & - & - & - & - & \delta & - & * & - \\
\mathrm{DB1} & - & - & - & - & - & - & \delta & - & *
\end{array}$$

Supplement S4: Specifying model constraints (in order of appearance in the Results)

Survival (φ): Our analyses took both Markovian transitions among stochastic breeding states and deterministic changes in age into account, and described patterns of reproductive trade-offs at the breeding state level. For survival probability, we specified a terminal age class for pre-breeders from age six years and for breeders from age ten years (because of sparseness of data at old ages; Supp. S1). This was confirmed in a separate analysis (Table S6.1). Models were fully age-dependent for pre-breeder survival, with three models testing for differences in survival probabilities between pre-breeders and breeders of overlapping ages (age 5, 6 and 7 years), and three models that were only age structured to determine if indeed breeding state differences in survival were well supported by the data. Age variation in breeder survival was treated as a fixed effect (assuming the parameters to be different and independent of each other at every age), and as continuous logit-linear and logit-quadratic regression. The logit-linear relationship between age and survival is an approximation of the Gompertz function (Gompertz 1825), which assumes an exponential increase of mortality rate ($\mu(x)$) with age (x) as $\mu(x) = A(\exp(bx))$ with A corresponding to the baseline mortality (the logit-linear intercept) and b representing the rate of senescence (the logit-linear slope; Loison *et al*. 1999; Péron *et al*. 2010; Pardo *et al*. 2014; Bleu *et al*. 2015; Tidière *et al*. 2017). Age variation in survival is constrained to be linear from the onset age of senescence (Gaillard *et al*. 2004). As there was evidence of senescence patterns, semi-Markov models with three parameter survival and hazard functions were fitted (Choquet *et al*. 2011). E-SURGE can only fit simple semi-Markov models; thus the encounter history matrix was reduced to a single state (presence/absence) and only transitions from age x to age $x + 1$ were considered (only initial state, survival and detection probabilities) for cohorts with complete survival histories (from birth to death).

Table S4.1: Candidate list of survival models (φ) with a description of the tested hypothesis.

Model	Parameters	Hypothesis
	Survival at breeding state level (multievent matrix)	
1	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,\geq 10} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,\geq 10}$	Different survival probabilities among breeding states. Age variation treated as a fixed effect.
2	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,\geq 8} + \varphi^{\mathrm{PB=SB}}_{\mathrm{a}\ 5,6,7} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 8,9,\geq 10} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,\geq 10}$	Equal pre-breeder and subordinate breeder survival for overlapping ages 5, 6 and 7.
3	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 8} + \varphi^{\mathrm{PB=DB}}_{\mathrm{a}\ 6,7} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,\geq 10} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 8,9,\geq 10}$	Equal pre-breeder and dominant breeder survival for overlapping ages 6 and 7.
4	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,\geq 8} + \varphi^{\mathrm{PB=SB=DB}}_{\mathrm{a}\ 5,6,7} + \varphi^{\mathrm{SB\neq DB}}_{\mathrm{a}\ 8,9,\geq 10}$	Equal pre-breeder, subordinate and dominant breeder survival for overlapping ages 5, 6 and 7.
5	$\varphi^{\mathrm{PB=SB=DB}}_{\mathrm{a}\ 0,1,2,3,4,5,6,7,8,9,10,11,12,13}$	Equal survival among breeding states. Fully age structured from ages 0 to 13.

6	$\varphi^{PB=SB=DB}_{a\ 0,1,2,3,4,5,6,7,8,9,\geq 10}$	Equal survival among breeding states. Age structured with terminal ages lumped at age 10 (general terminal age class for breeders).
7	$\varphi^{PB=SB=DB}_{a\ 0,1,2,3,4,5,\geq 6}$	Equal survival among breeding states. Age structured with terminal ages lumped at age 6 (general terminal age class for pre-breeders).
8	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB}_{a\ 5,6,7,8,9,\geq 10\ (\text{linear}^{SB})} + \varphi^{DB}_{a\ 6,7,8,9,\geq 10\ (\text{linear}^{DB})}$	Breeder age variation treated as a logit-linear relationship with different intercepts and gradients between subordinate and dominant breeders.
9	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB\neq DB}_{a\ 5,6,7,8,9,\geq 10\ (\text{linear}^{SB=DB})}$	Breeder age variation treated as a logit-linear relationship with different intercepts and equal gradients.
10	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB=DB}_{a\ 5,6,7,8,9,\geq 10\ (\text{linear}^{SB=DB})}$	Breeder age variation treated as a logit-linear relationship with equal intercepts and gradients.
11	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB}_{a\ 5,6,7,8,9,\geq 10\ (\text{quadratic}^{SB})} + \varphi^{DB}_{a\ 6,7,8,9,\geq 10\ (\text{quadratic}^{DB})}$	Breeder age variation treated as a logit-quadratic relationship with different intercepts and gradients.
12	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB\neq DB}_{a\ 5,6,7,8,9,\geq 10\ (\text{quadratic}^{SB=DB})}$	Breeder age variation treated as a logit-quadratic relationship with different intercepts and equal gradients.
13	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB=DB}_{a\ 5,6,7,8,9,\geq 10\ (\text{quadratic}^{SB=DB})}$	Breeder age variation treated as a logit-quadratic relationship with equal intercepts and gradients.
14	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB\neq DB}_{cst}$	Different survival between subordinate and dominant breeders with no age variation.
15	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB=DB}_{a\ 5,6,7,8,9,\geq 10}$	Equal survival between subordinate and dominant breeders with age variation treated as a fixed effect.
16	$\varphi^{PB}_{a\ 0,1,2,3,4,5,\geq 6} + \varphi^{SB=DB}_{cst}$	Equal survival between subordinate and dominant breeders with no age variation.
	Survival at population level (single-state matrix)	
17	$\varphi^{PB=SB=DB}_{a\ 0,1,2,3,4,5,6,7,8,9,10,11,12,13}$	Population model fully age structured from ages 0 to 13.
18	$\varphi^{PB=SB=DB}_{cst}$	Population model with no age variation.
19	$\varphi^{PB=SB=DB}_{a\ 0,1,2,3,4,5,6,7,8,9,10,11,12,13\ (\text{linear}^{PB=SB=DB})}$	Population model with age variation treated as a continuous logit-linear relationship.
20	$\varphi^{PB=SB=DB}_{a\ 0,1,2,3,4,5,6,7,8,9,10,11,12,13\ (\text{quadratic}^{PB=SB=DB})}$	Population model with age variation treated as a continuous logit-quadratic relationship.
21	Gompertz3+ function	See Gompertz (1825).
22	Weibull3+ function	See Weibull (1951).
23	Flexible Weibull function	See Bebbington, Lai & Zitikis (2007a).
24	Reduced Additive Weibull function	See Xie & Lai (1996).
25	Mixture of Flexible & Reduced Additive Weibull	See Bebbington, Lai & Zitikis (2007b).
26	Siler function	See Siler (1979).

Breeding (ψ): Similarly, we specified a starting and terminal age class for pre-breeder recruitment to the subordinate (age 5 to 8 years) and dominant (age 6 to 8 years) breeding states. Future breeding success probabilities were predicted from the age after subordinate and dominant breeders first attended breeding seasons and terminated at 11 years for all breeders. For age classes where breeding state transitions were impossible (ages < 5), probability values were fixed to zero to ensure that models did not contain redundant parameters. Recruitment and future breeding success probabilities were state and age structured, with age variation treated as a fixed effect, and as continuous logit-linear and logit-quadratic regression.

Table S4.2: Candidate list of breeding models (ψ, representing recruitment and future breeding success) with a description of the tested hypothesis.

Model	Parameters	Hypothesis
	Recruitment (ψ)	
27	$\psi^{PB-SB}_{a\ 5,6,7,\geq 8} + \psi^{PB-DB}_{a\ 6,7,\geq 8}$	Pre-breeder age variation treated as a fixed effect with different recruitment probabilities to subordinate and dominant breeder states.
28	$\psi^{PB-SB}_{a\ 5,6,7,\geq 8\ (\mathrm{linear}^{PB-SB})} + \psi^{PB-DB}_{a\ 6,7,\geq 8\ (\mathrm{linear}^{PB-DB})}$	Pre-breeder age variation treated as a logit-linear relationship with different intercepts and gradients to breeder states.
29	$\psi^{PB-SB\neq PB-DB}_{a\ 5,6,7,\geq 8\ (\mathrm{linear}^{PB-SB=PB-DB})}$	Pre-breeder age variation treated as a logit-linear relationship with different intercepts and equal gradients to breeder states.
30	$\psi^{PB-SB=PB-DB}_{a\ 5,6,7,\geq 8\ (\mathrm{linear}^{PB-SB=PB-DB})}$	Pre-breeder age variation treated as a logit-linear relationship with equal intercepts and gradients to breeder states.
31	$\psi^{PB-SB}_{a\ 5,6,7,\geq 8\ (\mathrm{quadratic}^{PB-SB})} + \psi^{PB-DB}_{a\ 6,7,\geq 8\ (\mathrm{quadratic}^{PB-DB})}$	Pre-breeder age variation treated as a logit-quadratic relationship with different intercepts and gradients to breeder states.
32	$\psi^{PB-SB\neq PB-DB}_{a\ 5,6,7,\geq 8\ (\mathrm{quadratic}^{PB-SB=PB-DB})}$	Pre-breeder age variation treated as a logit-quadratic relationship with different intercepts and equal gradients to breeder states.
33	$\psi^{PB-SB=PB-DB}_{a\ 5,6,7,\geq 8\ (\mathrm{quadratic}^{PB-SB=PB-DB})}$	Pre-breeder age variation treated as a logit-quadratic relationship with equal intercepts and gradients to breeder states.
34	$\psi^{PB-SB\neq PB-DB}_{cst}$	Different pre-breeder recruitment to subordinate and dominant breeder states. No age variation.
35	$\psi^{PB-SB=PB-DB}_{a\ 5,6,7,\geq 8}$	Equal pre-breeder recruitment to subordinate and dominant breeder states. Age variation treated as a fixed effect.
36	$\psi^{PB-SB=PB-DB}_{cst}$	Equal pre-breeder recruitment to subordinate and dominant breeder states. No age variation.
	Future breeding success (ψ)	
37	$\psi^{SB-DB}_{a\ 6,7,8,9,10,\geq 11} + \psi^{DB-DB}_{a\ 7,8,9,10,\geq 11}$	Breeder age variation treated as a fixed effect with different future breeding success probabilities between subordinate and dominant breeders.

38	$\psi^{\mathrm{SB-DB}}_{\mathrm{a\ 6,7,8,9,10,\geq 11\ (linear^{SB-DB})}} + \psi^{\mathrm{DB-DB}}_{\mathrm{a\ 7,8,9,10,\geq 11\ (linear^{DB-DB})}}$	Breeder age variation treated as a logit-linear relationship with different intercepts and gradients between subordinate and dominant breeders.
39	$\psi^{\mathrm{SB-DB\neq DB-DB}}_{\mathrm{a\ 6,7,8,9,10,\geq 11\ (linear^{SB-DB=DB-DB})}}$	Breeder age variation treated as a logit-linear relationship with different intercepts and equal gradients.
40	$\psi^{\mathrm{SB-DB=DB-DB}}_{\mathrm{a\ 6,7,8,9,10,\geq 11\ (linear^{SB-DB=DB-DB})}}$	Breeder age variation treated as a logit-linear relationship with equal intercepts and gradients.
41	$\psi^{\mathrm{SB-DB}}_{\mathrm{a\ 6,7,8,9,10,\geq 11\ (quadratic^{SB-DB})}} + \psi^{\mathrm{DB-DB}}_{\mathrm{a\ 7,8,9,10,\geq 11\ (quadratic^{DB-DB})}}$	Breeder age variation treated as a logit-quadratic relationship with different intercepts and gradients.
42	$\psi^{\mathrm{SB-DB\neq DB-DB}}_{\mathrm{a\ 6,7,8,9,10,\geq 11\ (quadratic^{SB-DB=DB-DB})}}$	Breeder age variation treated as a logit-quadratic relationship with different intercepts and equal gradients.
43	$\psi^{\mathrm{SB-DB=DB-DB}}_{\mathrm{a\ 6,7,8,9,10,\geq 11\ (quadratic^{SB-DB=DB-DB})}}$	Breeder age variation treated as a logit-quadratic relationship with equal intercepts and gradients.
44	$\psi^{\mathrm{SB-DB\neq DB-DB}}_{\mathrm{cst}}$	Different future breeding success between subordinate and dominant breeders with no age variation.
45	$\psi^{\mathrm{SB-DB=DB-DB}}_{\mathrm{a\ 6,7,8,9,10,\geq 11}}$	Equal future breeding success between subordinate and dominant breeders with age variation treated as a fixed effect.
46	$\psi^{\mathrm{SB-DB=DB-DB}}_{\mathrm{cst}}$	Equal future breeding success between subordinate and dominant breeders with no age variation.

State assignment (δ): The state assignment matrix estimates the probability of correctly recognising an individual as a subordinate or dominant breeder in the field given that it was encountered. The complementary probability was that a male hauled out during the breeding season and was observed with an ambiguous breeding state (social rank). For example, a breeding male may gain and lose dominance of a harem several times during a breeding season and thus be recorded as both a dominant and subordinate breeder. Uncertainty in state assignment could also arise from sampler assessment, which could vary among field researchers (Gimenez *et al*. 2012). Therefore, we fitted time and breeding state structured models.

Table S4.3: Candidate list of state assignment models (δ) with a description of the tested hypothesis.

Model	Parameters	Hypothesis
47	$\delta^{\mathrm{SB\neq DB}}_{\mathrm{t\ 1991-2016}}$	Time variation from when marked subordinate and dominant breeders were first seen together (1991) to account for sampler bias. Different state assignment probabilities between subordinate and dominant breeders account for different social cues used to assign states and behavioural differences (Laws 1956).
48	$\delta^{\mathrm{SB=DB}}_{\mathrm{t\ 1991-2016}}$	Time variation and equal state assignment between breeders.
49	$\delta^{\mathrm{SB\neq DB}}_{\mathrm{cst}}$	No time variation and different state assignment between breeders.
50	$\delta^{\mathrm{SB=DB}}_{\mathrm{cst}}$	Null model. No time variation and equal state assignment between breeders.

Detection (p): Detection probabilities may differ among field researchers, which may result in differences among years. Alternatively, male elephant seals in different breeding states may behave differently (e.g. haul out periods and duration of beach residency; Condy 1979; Mulaudzi *et al*. 2008). Therefore models specifying time and breeding state variation in detection probabilities were compared.

Table S4.4: Candidate list of detection models (p) with a description of the tested hypothesis.

Model	Parameters	Hypothesis
51	$p^{\mathrm{PB}}_{\mathrm{t\ 1984-2016}} + p^{\mathrm{SB}}_{\mathrm{t\ 1990-2016}} + p^{\mathrm{DB}}_{\mathrm{t\ 1992-2016}}$	Time variation from when marked pre-breeders (1984), subordinate breeders (1990) and dominant breeders (1992) were first resighted to account for sampler bias. Different detection probabilities among breeding states account for behavioural differences (Laws 1956).
52	$p^{\mathrm{PB=SB=DB}}_{\mathrm{t\ 1984-2016}}$	Time variation and equal detection among breeding states.
53	$p^{\mathrm{PB1 \neq PB2 \neq SB1 \neq SB2 \neq DB1 \neq DB2}}_{\mathrm{cst}}$	No time variation and different detection among breeding states and number of tags (two tags are easier to resight than one tag).
54	$p^{\mathrm{PB \neq SB \neq DB}}_{\mathrm{cst}}$	No time variation and different detection among breeding states.
55	$p^{\mathrm{PB \neq SB=DB}}_{\mathrm{cst}}$	No time variation and different detection between pre-breeders and breeders to account for different haul out periods on land (Condy 1979).
56	$p^{\mathrm{PB=SB=DB}}_{\mathrm{cst}}$	Null model. No time variation and equal detection among breeding states.

Tag loss (τ^{21}, τ^{10}): Tag loss probabilities were incorporated within the transition matrices to avoid post-hoc correction of survival estimates (Laake *et al*. 2014). Tag loss depends on the position of tag placement and tends to increase with age (Oosthuizen *et al*. 2010). Therefore, tag loss was group (inner *cf*. outer interdigital) and age structured in the umbrella model. We also considered several simpler age class models.

Table S4.5: Candidate list of tag loss models (τ^{21}, τ^{10}) with a description of the tested hypothesis.

Model	Parameters	Hypothesis
	First tag loss (τ^{21})	
57	$\tau^{\mathrm{IIT \neq OIT}}_{\mathrm{a\ 0,1,2,3,4,5,\geq 6}}$	Ages grouped according to general pre-breeder (younger individuals) and breeder (older individuals) age classes; but independent of breeding state (more likely to be a function of age than breeding state). Age variation among younger, but not older age classes. Different tag loss probabilities between inner and outer interdigital tag positions (Oosthuizen *et al*. 2010).

58	$\tau^{\mathrm{IIT}\neq\mathrm{OIT}}_{\mathrm{a}\ 0:5,6,7,8,9,10,11,12,13}$	Age variation among older, but not younger age classes. Different tag loss between tag positions.
59	$\tau^{\mathrm{IIT}\neq\mathrm{OIT}}_{\mathrm{a}\ 0:5,\geq 6}$	Age variation grouped according to general pre-breeder and breeder age classes. Different tag loss between tag positions.
60	$\tau^{\mathrm{IIT}\neq\mathrm{OIT}}_{\mathrm{cst}}$	No age variation. Different tag loss between tag positions.
61	$\tau^{\mathrm{IIT}=\mathrm{OIT}}_{\mathrm{a}\ 0:5,\geq 6}$	Age variation grouped according to general pre-breeder and breeder age classes. Equal tag loss between tag positions.
62	$\tau^{\mathrm{IIT}=\mathrm{OIT}}_{\mathrm{cst}}$	Null model. No age variation and equal tag loss between tag positions.
	Second tag loss (τ^{10})	
63	$\tau^{\mathrm{IIT}\neq\mathrm{OIT}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6}$	Age variation among younger, but not older age classes. Different tag loss probabilities between tag positions.
64	$\tau^{\mathrm{IIT}\neq\mathrm{OIT}}_{\mathrm{a}\ 0:5,6,7,8,9,10,11,12,13}$	Age variation among older, but not younger age classes. Different tag loss between tag positions.
65	$\tau^{\mathrm{IIT}\neq\mathrm{OIT}}_{\mathrm{a}\ 0:5,\geq 6}$	Age variation grouped according to general pre-breeder and breeder age classes. Different tag loss between tag positions.
66	$\tau^{\mathrm{IIT}\neq\mathrm{OIT}}_{\mathrm{cst}}$	No age variation. Different tag loss between tag positions.
67	$\tau^{\mathrm{IIT}=\mathrm{OIT}}_{\mathrm{a}\ 0:5,\geq 6}$	Age variation grouped according to general pre-breeder and breeder age classes. Equal tag loss between tag positions.
68	$\tau^{\mathrm{IIT}=\mathrm{OIT}}_{\mathrm{cst}}$	Null model. No age variation and equal tag loss between tag positions.

Temporary migration ($\psi^{\mathrm{E}}, \psi^{\mathrm{I}}$): Temporary migration was estimated as the probability of temporally transitioning from observable and unobservable states and vice versa for native individuals. Variation in temporary migration estimates may result from behavioural differences among recognised pre-breeder age groups (e.g. juvenile *cf*. sub-adult; McIntyre *et al*. 2012; Tosh *et al*. 2012).

Table S4.6: Candidate list of temporary emigration (ψ^{E}) and immigration (ψ^{I}) models with a description of the tested hypothesis.

Model	Parameters	Hypothesis
69	$\psi^{\mathrm{E}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \psi^{\mathrm{I}}_{\mathrm{a}\ 1,2,3,4,5,\geq 6}$	Age variation according to general pre-breeder age classes. Different temporary emigration and immigration probabilities.
70	$\psi^{\mathrm{E}}_{\mathrm{a}\ 0,1,2,3:5,\geq 6} + \psi^{\mathrm{I}}_{\mathrm{a}\ 1,2,3:5,\geq 6}$	Age variation grouped according to underyearling, yearling, juvenile and sub-adult pre-breeder age classes. Different temporary emigration and immigration probabilities.
71	$\psi^{\mathrm{E}}_{\mathrm{a}\ 0:5,\geq 6} + \psi^{\mathrm{I}}_{\mathrm{a}\ 1:5,\geq 6}$	Age variation grouped according to juvenile and sub-adult pre-breeder age classes. Different temporary emigration and immigration probabilities.
72	$\psi^{\mathrm{E}\neq\mathrm{I}}_{\mathrm{cst}}$	No age variation and different temporary emigration and immigration probabilities.
73	$\psi^{\mathrm{E}=\mathrm{I}}_{\mathrm{cst}}$	Null model. No age variation and equal temporary emigration and immigration probabilities.

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Supplement S5: Results and discussion of state assignment, detection, tag loss, and temporary migration probabilities, as well as recruitment age and parameter estimates

State assignment models dependent (model 49, Table S5.1) and independent (model 50) of breeding state were equivalent ($\Delta QAIC_c \leq 2$), with a weight ratio (ω_{49}/ω_{50}) of only 1.5. Thus, the simpler, null model was favoured and indicated that there was little uncertainty in social rank assignment throughout the study (0.94; CI: 0.91, 0.96). For the model dependent on breeding state, dominant breeders were correctly assigned slightly less (0.90; CI: 0.77, 0.96) than subordinates (0.95; CI: 0.86, 0.99), most likely as a result of dominant breeders losing control of harems several times during a breeding season (McCann 1981). Detection probabilities varied with time (model 52), meaning that resightings of marked individuals were not consistent each year, independent of breeding state. This was similar to the model describing detection probabilities of marked females of the same population in that detection varied with time, but also breeding state (Oosthuizen 2016). This was likely as a result of females having more distinct behavioural differences among breeding states than males. For example, females skip breeding seasons, whereas males almost never do (de Bruyn *et al*. 2011). Time variation in detection probabilities for both sexes likely resulted from having different field researchers conduct the mark-recapture study each year (Bester *et al*. 2011). However, male detection probabilities were high throughout the study (mean 0.95 ± SD 0.050, Figure S5.1).

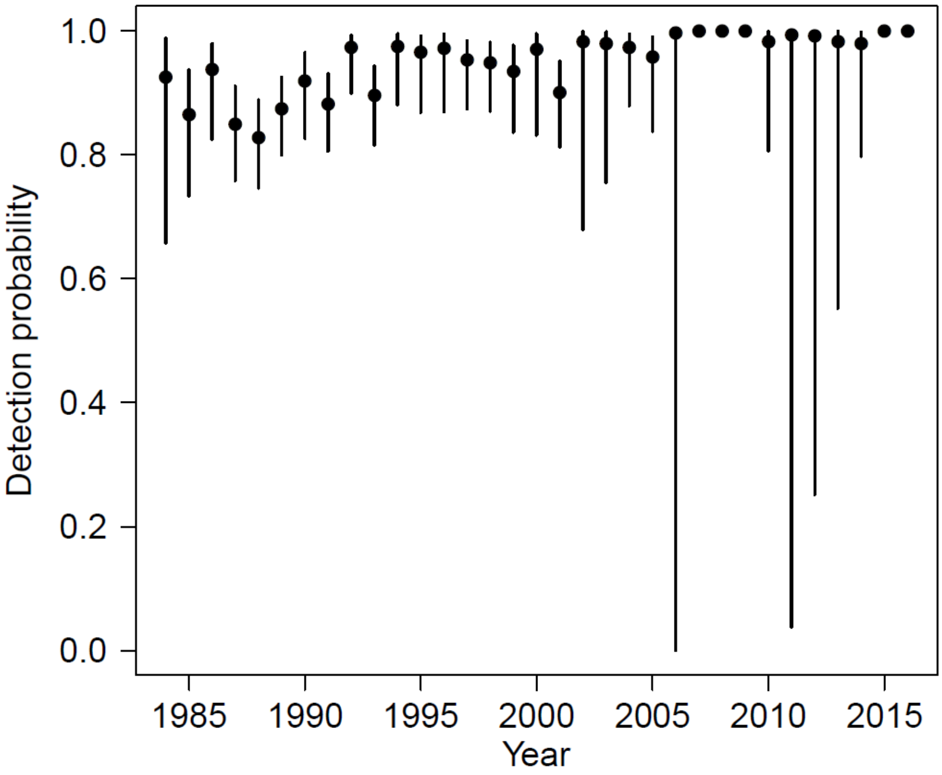

Figure S5.1: Mean detection probabilities (95% confidence intervals) of male southern elephant seals at Marion Island collected over 34 years. Estimates were derived from model 52 (Table S5.1) which treated time variation in detection as a fixed effect. Resights occurred after the first cohort was tagged in 1983. A seal year began at the start of every breeding season and ended before the following breeding season. Variation in confidence interval widths were likely the result of different observer effort or model convergence at the boundary.

Table S5.1: Multievent models for a mark-recapture study of male southern elephant seals at Marion Island collected over 34 years. Superscripts indicate variation (≠) or equality (=) among pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states, inner- (IIT) and outer- (OIT) interdigital tag positions, or temporary emigrant (E) and immigrant (I) hidden states. Subscripts indicate variation (−) or equality (cst or :) among specific age classes (a) and years (t). Small sample corrected quasi-likelihood Akaike's Information Criterion (QAIC$_c$; $\hat{c}$ = 1.7) was used to select models, with the following measurements: ΔQAIC$_c$ (the difference in QAIC$_c$ between the model with the lowest QAIC$_c$ value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood). Models in bold font were used to derive estimates.

Model	**Parameters**	**ΔQAIC$_c$**	$\boldsymbol{\omega_i}$	$\boldsymbol{K}$	**Deviance**
	State assignment (δ)				
47	$\delta^{SB\neq DB}_{t\,1991-2016}$	43.74	0.00	217	90.30
48	$\delta^{SB=DB}_{t\,1991-2016}$	9.27	0.01	191	102.41
49	$\delta^{SB\neq DB}_{cst}$	0.00	0.60	167	117.07
50	$\boldsymbol{\delta^{SB=DB}_{cst}}$	**0.84**	**0.39**	**166**	**117.78**

	Detection (p)				
51	$p^{\mathrm{PB}}_{\mathrm{t}\,1984-2016} + p^{\mathrm{SB}}_{\mathrm{t}\,1990-2016} + p^{\mathrm{DB}}_{\mathrm{t}\,1992-2016}$	83.65	0.00	166	117.78
52	$\boldsymbol{p^{\mathrm{PB=SB=DB}}_{\mathrm{t}\,1984-2016}}$	**0.00**	**0.98**	**112**	**173.82**
53	$p^{\mathrm{PB1\neq PB2\neq SB1\neq SB2\neq DB1\neq DB2}}_{\mathrm{cst}}$	11.90	0.00	85	229.17
54	$p^{\mathrm{PB\neq SB\neq DB}}_{\mathrm{cst}}$	11.00	0.00	82	237.55
55	$p^{\mathrm{PB\neq SB=DB}}_{\mathrm{cst}}$	10.61	0.00	81	240.47
56	$p^{\mathrm{PB=SB=DB}}_{\mathrm{cst}}$	9.25	0.01	80	243.46
	First tag loss (τ^{21}*)*				
57	$\tau^{\mathrm{IIT\neq OIT}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6}$	3.77	0.13	112	173.82
58	$\tau^{\mathrm{IIT\neq OIT}}_{\mathrm{a}\ 0:5,6,7,8,9,10,11,12,13}$	22.66	0.00	116	167.99
59	$\boldsymbol{\tau^{\mathrm{IIT\neq OIT}}_{\mathrm{a}\ 0:5,\geq 6}}$	**0.00**	**0.86**	**102**	**190.82**
60	$\tau^{\mathrm{IIT\neq OIT}}_{\mathrm{cst}}$	9.46	0.01	100	194.73
61	$\tau^{\mathrm{IIT=OIT}}_{\mathrm{a}\ 0:5,\geq 6}$	26.79	0.00	100	194.91
62	$\tau^{\mathrm{IIT=OIT}}_{\mathrm{cst}}$	32.19	0.00	99	196.93
	Second tag loss (τ^{10}*)*				
63	$\tau^{\mathrm{IIT\neq OIT}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6}$	16.74	0.00	102	190.82
64	$\tau^{\mathrm{IIT\neq OIT}}_{\mathrm{a}\ 0:5,6,7,8,9,10,11,12,13}$	24.46	0.00	106	183.70
65	$\tau^{\mathrm{IIT\neq OIT}}_{\mathrm{a}\ 0:5,\geq 6}$	1.96	0.15	92	211.40
66	$\tau^{\mathrm{IIT\neq OIT}}_{\mathrm{cst}}$	0.00	0.40	90	216.08
67	$\tau^{\mathrm{IIT=OIT}}_{\mathrm{a}\ 0:5,\geq 6}$	0.99	0.24	90	216.09
68	$\boldsymbol{\tau^{\mathrm{IIT=OIT}}_{\mathrm{cst}}}$	**1.26**	**0.21**	**89**	**218.52**
	Temporary migration ($\psi^{\mathrm{E}}, \psi^{\mathrm{I}}$*)*				
69	$\psi^{\mathrm{E}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \psi^{\mathrm{I}}_{\mathrm{a}\ 1,2,3,4,5,\geq 6}$	1.26	0.35	89	218.52
70	$\boldsymbol{\psi^{\mathrm{E}}_{\mathrm{a}\ 0,1,2,3:5,\geq 6} + \psi^{\mathrm{I}}_{\mathrm{a}\ 1,2,3:5,\geq 6}}$	**0.00**	**0.65**	**85**	**228.79**
71	$\psi^{\mathrm{E}}_{\mathrm{a}\ 0:5,\geq 6} + \psi^{\mathrm{I}}_{\mathrm{a}\ 1:5,\geq 6}$	67.47	0.00	80	243.93
72	$\psi^{\mathrm{E\neq I}}_{\mathrm{cst}}$	65.11	0.00	78	250.16
73	$\psi^{\mathrm{E=I}}_{\mathrm{cst}}$	156.04	0.00	77	254.59

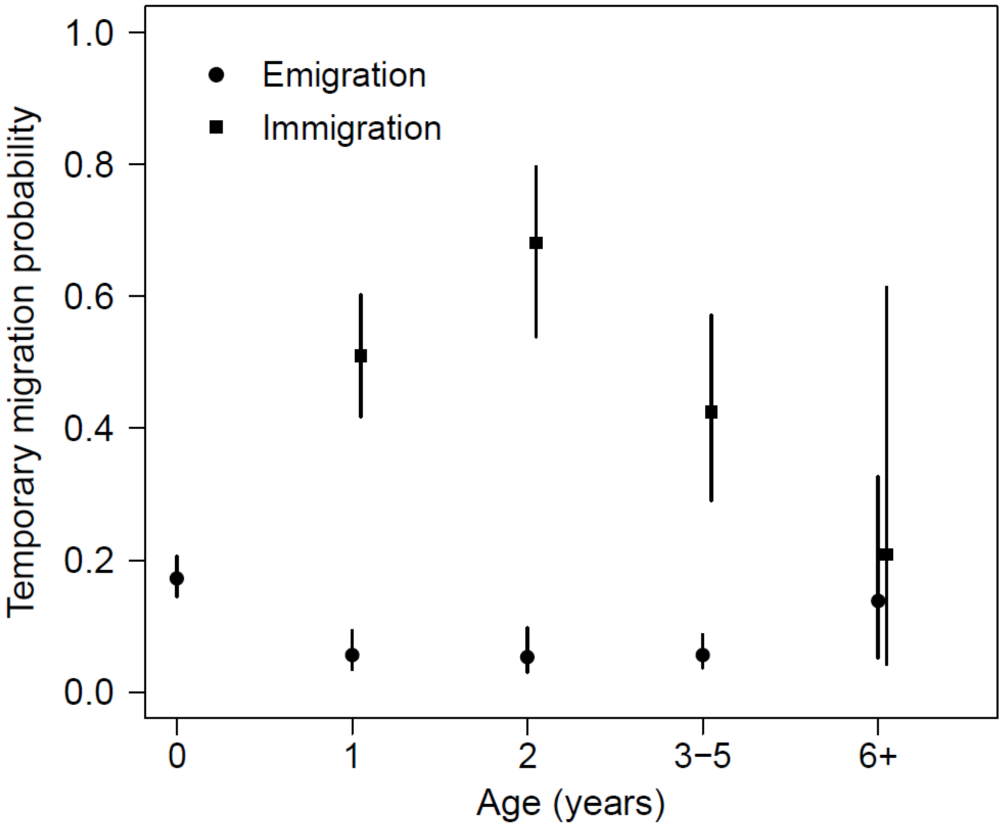

Figure S5.2: Mean temporary migration probabilities (95% confidence intervals) of male southern elephant seals native to Marion Island. Estimates were derived from model 70 (Table S5.1) which estimated temporary emigration and immigration probabilities separately with age treated as a fixed effect. Temporary immigration probabilities were estimated after the first temporary emigration event.

The best supported model for first tag loss probability depended on tag position and age group (model 59, Table S5.1). Estimates for typical pre-breeder age classes were lower for the inner-interdigital (IIT: 0.043; CI: 0.036, 0.051) than outer-interdigital (OIT: 0.10; CI: 0.085, 0.12) tag position, but were similar for typical breeder age classes (IIT: 0.11; CI: 0.073, 0.16; OIT: 0.13; CI: 0.066, 0.23). The probability of losing the first tag for both tag positions increased as males matured, however this was much less for the outer-interdigital position. Likewise, first tag loss probabilities differ between positions in females, with the inner-interdigital position also having a lower probability of loss than the outer-interdigital position for all ages (Oosthuizen 2016). This suggests that tags in the outer-interdigital position were more likely to be lost and tagging should resume in the inner-interdigital position. The data were ambivalent about second tag loss probability being constant or varying between tag positions and age groups (models 66-68). Therefore, the simpler, null model was favoured (0.064; CI: 0.026, 0.15).

Temporary emigration and immigration probabilities of native individuals were estimated separately with models specifying variation among recognised pre-breeder age groups (model 70, Table S5.1) or across all pre-breeder age classes (model 69). The model with recognised pre-breeder age groups was simpler and received more support (ω_{70}/ω_{69} = 1.9). First year (underyearling) emigration probabilities were relatively high (0.17; CI: 0.15, 0.21), but decreased and remained stable thereafter with a slight increase in the oldest age group (sub-adults; Figure S5.2). Immigration probabilities indicated that approximately half of the emigrants of the first three age groups (under-yearlings, yearlings and juveniles) returned to the island, with fewer emigrants of the last age group (sub-adults) returning. Temporary migration patterns in native females are different as females have fewer pre-breeder age classes (females recruit from age 3; Laws 1956; Oosthuizen 2016). Recognised pre-breeder age groups reflect different periods in the male elephant seal life cycle that are associated with development (Ling & Bryden 1992). Therefore, differences in migration probabilities among age groups may be related to changes in energy requirements (and therefore foraging behaviour; see Pistorius *et al*. 1999). This requires further investigation to be interpreted confidently.

While social breeding maturity is only reached at around 10 years of age in some large populations of elephant seals (Jones 1981), a few males started to control harems at Marion Island from six years of age. The topography at Marion Island, where most breeding harems are relatively small and formed on discrete instead of extensive beaches, may enable younger males to achieve dominance status at sites unattended by older, larger and generally more competitive males. Landscape attributes may therefore influence a population's social structure and dynamics. Male population age structure also influences the age of first breeding in polygynous ungulates (Markussen *et al*. 2019); and an alternative explanation may be that Marion Island males were able to achieve dominant status at early ages because the number or proportion of older males was relatively low.

Table S5.2: Parameter estimates (maximum likelihood estimates and 95% confidence intervals on the logit scale) of the most parsimonious multievent models of a mark-recapture study of male southern elephant seals at Marion Island. Superscripts indicate pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states, inner- (IIT) and outer- (OIT) interdigital tag positions, or temporary emigrant (E) and immigrant (I) hidden states. Subscripts indicate specific age classes (a), years (t) or regression parameters.

Parameters	**Estimate**	**Lower 95% confidence interval**	**Upper 95% confidence interval**
Initial state (π)			
π	4.23	3.95	4.50
Survival at breeding state level (multistate, φ)			
$\varphi^{PB}_{a\,0}$	0.22	0.14	0.31
$\varphi^{PB}_{a\,1}$	0.95	0.82	1.09
$\varphi^{PB}_{a\,2}$	0.77	0.62	0.92
$\varphi^{PB}_{a\,3}$	0.68	0.52	0.85
$\varphi^{PB}_{a\,4}$	0.72	0.52	0.91
$\varphi^{PB}_{a\,5}$	0.73	0.49	0.97
$\varphi^{PB}_{a\,\geq 6}$	0.90	0.60	1.20
$\varphi^{SB}_{intercept}$	0.30	0.03	0.57
$\varphi^{DB}_{intercept}$	0.79	0.35	1.22
$\varphi^{SB=DB}_{slope}$	-0.31	-0.61	-0.02
Recruitment (ψ)			
$\psi^{PB-SB}_{intercept}$	-1.10	-1.37	-0.82
$\psi^{PB-DB}_{intercept}$	-2.69	-3.11	-2.27
$\psi^{PB-SB=PB-DB}_{slope}$	4.32	2.82	5.82
$\psi^{PB-SB=PB-DB}_{slope^2}$	-2.56	-4.06	-1.06
Future breeding success (ψ)			
$\psi^{SB-DB}_{intercept}$	-0.48	-0.86	-0.10
$\psi^{DB-DB}_{intercept}$	0.71	0.15	1.28
$\psi^{SB-DB=DB-DB}_{slope}$	0.62	0.19	1.06
State assignment (δ)			
$\delta^{SB=DB}_{cst}$	2.68	2.29	3.07
Detection (p)			
$p^{PB=SB=DB}_{t\,1984}$	2.52	0.65	4.39
$p^{PB=SB=DB}_{t\,1985}$	1.86	1.01	2.71
$p^{PB=SB=DB}_{t\,1986}$	2.72	1.55	3.88
$p^{PB=SB=DB}_{t\,1987}$	1.73	1.14	2.33
$p^{PB=SB=DB}_{t\,1988}$	1.58	1.08	2.08
$p^{PB=SB=DB}_{t\,1989}$	1.95	1.38	2.52
$p^{PB=SB=DB}_{t\,1990}$	2.44	1.56	3.32
$p^{PB=SB=DB}_{t\,1991}$	2.02	1.42	2.61
$p^{PB=SB=DB}_{t\,1992}$	3.60	2.19	5.02
$p^{PB=SB=DB}_{t\,1993}$	2.15	1.49	2.82
$p^{PB=SB=DB}_{t\,1994}$	3.71	2.00	5.42
$p^{PB=SB=DB}_{t\,1995}$	3.36	1.88	4.83
$p^{PB=SB=DB}_{t\,1996}$	3.58	1.89	5.26

$p_{\mathrm{t}\,1997}^{\mathrm{PB=SB=DB}}$	3.03	1.94	4.12
$p_{\mathrm{t}\,1998}^{\mathrm{PB=SB=DB}}$	2.95	1.91	3.99
$p_{\mathrm{t}\,1999}^{\mathrm{PB=SB=DB}}$	2.69	1.63	3.74
$p_{\mathrm{t}\,2000}^{\mathrm{PB=SB=DB}}$	3.49	1.60	5.37
$p_{\mathrm{t}\,2001}^{\mathrm{PB=SB=DB}}$	2.22	1.47	2.97
$p_{\mathrm{t}\,2002}^{\mathrm{PB=SB=DB}}$	4.07	0.75	7.40
$p_{\mathrm{t}\,2003}^{\mathrm{PB=SB=DB}}$	3.88	1.13	6.63
$p_{\mathrm{t}\,2004}^{\mathrm{PB=SB=DB}}$	3.63	1.98	5.28
$p_{\mathrm{t}\,2005}^{\mathrm{PB=SB=DB}}$	3.14	1.64	4.63
$p_{\mathrm{t}\,2006}^{\mathrm{PB=SB=DB}}$	5.84	-14.77	26.44
$p_{\mathrm{t}\,2007}^{\mathrm{PB=SB=DB}}$	15.16	13.13	17.19
$p_{\mathrm{t}\,2008}^{\mathrm{PB=SB=DB}}$	14.54	11.77	17.31
$p_{\mathrm{t}\,2009}^{\mathrm{PB=SB=DB}}$	11.32	9.18	13.45
$p_{\mathrm{t}\,2010}^{\mathrm{PB=SB=DB}}$	4.05	1.42	6.67
$p_{\mathrm{t}\,2011}^{\mathrm{PB=SB=DB}}$	5.26	-3.25	13.77
$p_{\mathrm{t}\,2012}^{\mathrm{PB=SB=DB}}$	4.85	-1.09	10.79
$p_{\mathrm{t}\,2013}^{\mathrm{PB=SB=DB}}$	4.07	0.21	7.93
$p_{\mathrm{t}\,2014}^{\mathrm{PB=SB=DB}}$	3.92	1.37	6.47
$p_{\mathrm{t}\,2015}^{\mathrm{PB=SB=DB}}$	12.92	11.71	14.13
$p_{\mathrm{t}\,2016}^{\mathrm{PB=SB=DB}}$	12.72	11.96	13.48
First tag loss (τ^{21})			
$\tau_{\mathrm{a}\,0:5}^{\mathrm{IIT}}$	-3.11	-3.29	-2.92
$\tau_{\mathrm{a}\,\geq 6}^{\mathrm{IIT}}$	-2.19	-2.37	-2.01
$\tau_{\mathrm{a}\,0:5}^{\mathrm{OIT}}$	-2.09	-2.54	-1.64
$\tau_{\mathrm{a}\,\geq 6}^{\mathrm{OIT}}$	-1.94	-2.65	-1.23
Second tag loss (τ^{10})			
$\tau_{\mathrm{cst}}^{\mathrm{IIT=OIT}}$	-2.69	-3.61	-1.76
Temporary migration ($\psi^{\mathrm{E}}, \psi^{\mathrm{I}}$)			
$\psi_{\mathrm{a}\,0}^{\mathrm{E}}$	-1.56	-1.77	-1.35
$\psi_{\mathrm{a}\,1}^{\mathrm{E}}$	-2.80	-3.33	-2.28
$\psi_{\mathrm{a}\,2}^{\mathrm{E}}$	-2.86	-3.49	-2.22
$\psi_{\mathrm{a}\,3:5}^{\mathrm{E}}$	-2.82	-3.28	-2.36
$\psi_{\mathrm{a}\,\geq 6}^{\mathrm{E}}$	-1.82	-2.92	-0.72
$\psi_{\mathrm{a}\,1}^{\mathrm{I}}$	0.04	-0.33	0.41
$\psi_{\mathrm{a}\,2}^{\mathrm{I}}$	0.76	0.16	1.37
$\psi_{\mathrm{a}\,3:5}^{\mathrm{I}}$	-0.30	-0.89	0.29
$\psi_{\mathrm{a}\,\geq 6}^{\mathrm{I}}$	-1.34	-3.13	0.46

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Supplement S6: Terminal age classes and onset age of actuarial senescence

Table S6.1: Terminal age class groupings for survival (φ) and future breeding success (ψ) probabilities of male southern elephant seals at Marion Island. Superscripts indicate pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states. Subscripts indicate specific age classes (a). Small sample corrected quasi-likelihood Akaike's Information Criterion (QAIC$_c$; $\hat{c} = 1.7$) was used to select models, with the following measurements: ΔQAIC$_c$ (the difference in QAIC$_c$ between the model with the lowest QAIC$_c$ value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood).

Model	Parameters	ΔQAIC$_c$	ω_i	*K*	Deviance
	Survival (φ)				
74	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,\geq 10} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,\geq 10}$	0.00	0.38	82	237.15
75	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,10,\geq 11} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,\geq 10}$	2.02	0.14	83	234.32
76	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,10,11,\geq 12} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,\geq 10}$	4.04	0.05	84	231.55
77	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,10,11,12,13} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,\geq 10}$	6.04	0.02	85	228.85
78	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,\geq 10} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,10,\geq 11}$	1.97	0.14	83	234.32

79	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,\geq 10} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,10,11\geq 12}$	1.33	0.20	84	231.52
80	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5,6,7,8,9,\geq 10} + \varphi^{\mathrm{DB}}_{\mathrm{a}\ 6,7,8,9,10,11,12,13}$	3.16	0.08	85	228.82
	Future breeding success (ψ)				
81	$\psi^{\mathrm{SB-DB}}_{\mathrm{a}\ 6,7,8,9,10,\geq 11} + \psi^{\mathrm{DB-DB}}_{\mathrm{a}\ 7,8,9,10,\geq 11}$	0.69	0.25	82	237.15
82	$\psi^{\mathrm{SB-DB}}_{\mathrm{a}\ 6,7,8,9,10,11,\geq 12} + \psi^{\mathrm{DB-DB}}_{\mathrm{a}\ 7,8,9,10,\geq 11}$	0.00	0.35	83	234.29
83	$\psi^{\mathrm{SB-DB}}_{\mathrm{a}\ 6,7,8,9,10,11,12,\geq 13} + \psi^{\mathrm{DB-DB}}_{\mathrm{a}\ 7,8,9,10,\geq 11}$	2.02	0.13	84	231.52
84	$\psi^{\mathrm{SB-DB}}_{\mathrm{a}\ 6,7,8,9,10,11,12,13,14} + \psi^{\mathrm{DB-DB}}_{\mathrm{a}\ 7,8,9,10,\geq 11}$	2.02	0.13	84	231.52
85	$\psi^{\mathrm{SB-DB}}_{\mathrm{a}\ 6,7,8,9,10,\geq 11} + \psi^{\mathrm{DB-DB}}_{\mathrm{a}\ 7,8,9,10,11,\geq 12}$	2.64	0.09	83	234.32
86	$\psi^{\mathrm{SB-DB}}_{\mathrm{a}\ 6,7,8,9,10,\geq 11} + \psi^{\mathrm{DB-DB}}_{\mathrm{a}\ 7,8,9,10,11,12,\geq 13}$	4.65	0.03	84	231.55
87	$\psi^{\mathrm{SB-DB}}_{\mathrm{a}\ 6,7,8,9,10,\geq 11} + \psi^{\mathrm{DB-DB}}_{\mathrm{a}\ 7,8,9,10,11,12,13,14}$	5.37	0.02	85	228.84

Adding additional age classes to predict survival and future breeding success probabilities of subordinate and dominant breeders did not improve model fit more than the initial terminal age classes of ≥10 (model 74) and ≥11 years (model 81), respectively ($\Delta\mathrm{QAIC}_c \leq 2$; Table S6.1).

Table S6.2: Onset age of actuarial senescence (φ) of male southern elephant seals at Marion Island. Superscripts indicate pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states. Subscripts indicate specific age classes (a). Small sample corrected quasi-likelihood Akaike's Information Criterion (QAIC_c; $\hat{c} = 1.7$) was used to select models, with the following measurements: $\Delta\mathrm{QAIC}_c$ (the difference in QAIC_c between the model with the lowest QAIC_c value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood).

Model	**Parameters**	**$\Delta\mathrm{QAIC}_c$**	**ω_i**	***K***	**Deviance**
9	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB \neq DB}}_{\mathrm{a}\ 5,6,7,8,9,\geq 10\ (\mathrm{linear}^{\mathrm{SB=DB}})}$	0.00	0.88	66	294.25
88	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB}}_{\mathrm{a}\ 5} + \varphi^{\mathrm{SB \neq DB}}_{\mathrm{a}\ 6,7,8,9,\geq 10\ (\mathrm{linear}^{\mathrm{SB=DB}})}$	4.49	0.09	67	289.93
89	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB \neq DB}}_{\mathrm{a}\ 5,6} + \varphi^{\mathrm{SB \neq DB}}_{\mathrm{a}\ 7,8,9,\geq 10\ (\mathrm{linear}^{\mathrm{SB=DB}})}$	7.80	0.02	69	281.57
90	$\varphi^{\mathrm{PB}}_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6} + \varphi^{\mathrm{SB \neq DB}}_{\mathrm{a}\ 5,6,7} + \varphi^{\mathrm{SB \neq DB}}_{\mathrm{a}\ 8,9,\geq 10\ (\mathrm{linear}^{\mathrm{SB=DB}})}$	10.40	0.00	71	273.68

The most parsimonious model predicted that age was constrained to be linear and decreasing on the logit scale from age 5 for subordinate breeders and age 6 for dominant breeders; the ages at which each breeding state first appeared in the breeding population (model 9, Table S6.2). Thus, predicting survival probabilities separately as fixed effects for young breeders did not improve model fit.

Supplement S7: Individual random effect

Fixed individual characteristics that are not measured in mark-recapture studies need to be accounted for and quantified as they may influence life history trade-off patterns (Cam *et al*. 2002) and parameter estimation (Barry *et al*. 2003). Unexplained residual variance was incorporated into our analysis using an individual random effect ($+ind$; Gimenez & Choquet 2010). The deviances of the most parsimonious models for survival (model 9, Table 1) and breeding (models 32 and 39, Table 2) probabilities were compared to models of the same parameterisation with the addition of an individual random effect to test for homogeneity (H_0: $\sigma^2_{\varphi/\psi} = 0$ *cf*. H_1: $\sigma^2_{\varphi/\psi} > 1$). This was done using a likelihood-ratio test in R 3.5.2 (R Core Team 2019). There was sufficient evidence to reject the null hypotheses (φ: $\chi^2(1) = 15.38$, $P < 0.001$; ψ: $\chi^2(1) = 15.34$, $P < 0.001$), suggesting that survival, recruitment and/or future breeding success probabilities differed between individuals of the same breeding state and age class. However, the variances (σ) of the individual random effects were small and less for survival (0.000017) than breeding (0.23) probabilities. In addition, parameter estimates for models with and without the individual random effect were equivalent or similar (Table S7.1). Therefore, future studies need to consider more sensitive or fine scale techniques (e.g. Bayesian analysis, finite-mixture models, individual covariates) to confidently detect between-individual differences in male elephant seal life history traits (Gimenez & Choquet 2010).

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Table S7.1: Parameter estimates on the logit scale of the most parsimonious models with and without an individual random effect. Absolute differences between parameter estimates were small or negligible. Superscripts indicate pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states. Subscripts indicate specific age classes (a) or regression parameters.

Parameters	Without individual random effect	With individual random effect	Difference
Survival (φ)			
$\varphi^{PB}_{a\ 0}$	0.22	0.22	0.00
$\varphi^{PB}_{a\ 1}$	0.95	0.95	0.00
$\varphi^{PB}_{a\ 2}$	0.77	0.77	0.00
$\varphi^{PB}_{a\ 3}$	0.68	0.68	0.00
$\varphi^{PB}_{a\ 4}$	0.72	0.72	0.00
$\varphi^{PB}_{a\ 5}$	0.73	0.74	0.01
$\varphi^{PB}_{a\ \geq 6}$	0.90	0.90	0.00
$\varphi^{SB}_{intercept}$	0.30	0.31	0.01
$\varphi^{DB}_{intercept}$	0.79	0.74	0.05
$\varphi^{SB=DB}_{slope}$	-0.31	-0.31	0.00
Recruitment (ψ)			
$\psi^{PB-SB}_{intercept}$	-1.10	-1.07	0.03
$\psi^{PB-DB}_{intercept}$	-2.69	-2.68	0.02
$\psi^{PB-SB=PB-DB}_{slope}$	4.32	4.30	0.02
$\psi^{PB-SB=PB-DB}_{slope^2}$	-2.56	-2.48	0.08
Future breeding success (ψ)			
$\psi^{SB-DB}_{intercept}$	-0.48	-0.53	0.04
$\psi^{DB-DB}_{intercept}$	0.71	0.61	0.11
$\psi^{SB-DB=DB-DB}_{slope}$	0.62	0.71	0.09

Chapter 3: *Life-history consequences of individual heterogeneity among pre-breeders*

Selective disappearance of frail juveniles: consequences for understanding social dominance in adult male elephant seals

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Pre-breeding southern elephant seals playing at Van Den Boogaard Bay (Marion Island, 2016).
Photo: Kyle J. Lloyd

Abstract

1. Individual heterogeneity is variation in trait expression observed among individuals of a population. Individual heterogeneity in the pre-breeder stage of development is of importance given its eventual contribution to the breeding population's overall reproductive performance. Yet most studies do not consider the role of individual heterogeneity in pre-breeders when investigating population processes.
2. We investigated individual heterogeneity in the survival and recruitment probabilities of pre-breeding male southern elephant seals (*Mirounga leonina*) using 34 years of data collected at Marion Island. Elephant seals are highly polygynous capital breeders, with few male offspring surviving to compete in breeding events and even fewer breeding successfully. Specifically, we fitted finite-mixture models with two hidden groups that represented "robust" and "frail" individuals and compared the demographic rates of these groups to that of the population.
3. Survival and recruitment as first-time subordinate breeders could be distinguished between groups. Survival of both robust and frail pre-breeders decreased from age 2, whilst differences between groups were maintained (ontogeny processes). The population-level survival rate showed a slower decrease with age, suggesting that frail individuals were preferentially removed from the population (selective disappearance). Differences in recruitment probabilities were apparent from age 5 (earliest recorded age) and increased until age 7, with most recruits comprising robust pre-breeders.
4. Male pre-breeders were more likely to be robust at age 2 when born in years with few conspecifics, suggesting that individual heterogeneity was determined, in part, by density-dependent effects.
5. A population projection model revealed that male breeders of every age class never consisted of more than 5% of frail recruits. Rather, the breeding population increasingly consisted of robust recruits that obtained social dominance with age.
6. We demonstrated that individual heterogeneity in male pre-breeder demographic rates was present and persistent throughout much of development and determined the proportion of adult males that obtained social dominance in a highly polygynous and competitive breeding system.

Keywords: delayed density dependence, finite mixture models, individual heterogeneity, individual quality, juvenile life history, Marion Island, *Mirounga leonina*, polygynous breeding system, viability selection

Introduction

Life-history studies regularly focus at the population level, thus assuming that all individuals of the same age, sex or cohort are equivalent (Hamel *et al*. 2018a). In reality, populations are composed of genetically and phenotypically heterogeneous individuals showing substantial variation in demographic rates (Senner *et al*. 2015). Recent empirical evidence shows that heterogeneity in demographic rates is highly structured with positive covariation between life-history traits. For instance, individuals frequently have both higher (or lower) survival and reproductive performance than the population-level average (Cam *et al*. 2002; Fay *et al*. 2016; Oosthuizen *et al*. 2019b).

Individual heterogeneity has traditionally been treated as a nuisance parameter that needed to be accounted for when estimating population size or demographic rates (Huggins 1991; Hamel *et al*. 2018a). However, individual variation in life-history traits that are linked to fitness components is the basis of any selection process and is thus biologically meaningful (Gomulkiewicz *et al*. 2018). Individual heterogeneity may generate selection processes within cohorts that reduce or increase the proportion of individuals with a particular trait over time (Figure 1A-F; Vaupel & Yashin 1985; van de Pol & Verhulst 2006, Hamel *et al*. 2018b). Cohort composition may also change if individuals with different initial traits pursue different life-history trajectories that maximise their own fitness (Figure 1G, H; Nussey *et al*. 2008). Thus, the amount of individual heterogeneity in a population is not constant (Gimenez *et al*. 2018) and can strongly affect the age-specific mean and variance of a population’s demographic rates (van de Pol & Verhulst 2006). Accumulating evidence suggests that individual heterogeneity plays an essential role in many biological processes that affect life history. For instance, individual variation in demographic rates may alter or even prevent the detection of life-history trade-offs (van Noordwijk & de Jong 1986; Gimenez *et al*. 2018). Similarly, age-specific variation in demographic rates including both early-life improvement and late-life senescence could not be fully understood without taking individual heterogeneity into account (Forslund & Pärt 1995; Nussey *et al*. 2008). Therefore, it is of fundamental importance to understand and quantify how individual heterogeneity affects age-specific demographic rates, especially survival and reproduction (Kendall & Fox 2002; Hughes *et al*. 2008; Smallegange *et al*. 2018).

The pre-breeder stage is of particular importance when assessing individual heterogeneity in life histories (Hamel *et al*. 2018a). At this developmental stage, the amount of individual heterogeneity is expected to be substantial and may affect population dynamics (Acker *et al*. 2014). For example, in long-lived species, pre-breeders may recruit at different ages if recruitment depends on traits such as body mass that vary among individuals (Lee *et al*. 2013; Oosthuizen *et al*. 2018; Markussen *et al*. 2019). Variation in genetics or early-life conditions influences pre-breeder initial trait values which may (1) persist throughout life *via* silver spoon effects (Figure 1A, B); (2) be accentuated through selective appearance (Figure 1C, D) or an accumulation of effects (e.g. individual experience and stochastic events; Figure 1H); or (3) may disappear with age through selective disappearance (Figure 1C, D) or compensatory effects (Figure 1G; Caswell 2001; van de Pol & Verhulst 2006; van de Pol *et al*. 2006; Nussey *et al*. 2007; Hamel *et al*. 2016, 2018b). These processes can occur concurrently with other population processes (Figure 1E, F) and at different stages of maturity, both within and between the individuals of a population (van de Pol & Verhulst 2006; Rebke *et al*. 2010). If individual heterogeneity persists throughout pre-breeder development, the effects can be revealed in the fitness components of the breeding population (Clutton-Brock 1988). Despite the high reproductive value of pre-breeders in long-lived species (Sæther *et al*. 2013), early-life stages remain poorly understood due to low survival, low detection and high dispersal probabilities (Cooper *et al*. 2008; Fay *et al*. 2017). Therefore, studies are needed that investigate individual heterogeneity throughout pre-breeder development to better understand processes governing breeder demographic rates.

Measuring the effect of individual heterogeneity on population demographic rates remains challenging, especially when individual heterogeneity is unobservable. Given the number of factors that influence the overall quality of an individual, it is not possible to account for the total amount of individual heterogeneity in a population by measuring even a large number of traits (Gimenez *et al*. 2018). However, long-term, individual-level, mark-recapture studies make it possible to test and quantify the presence of individual heterogeneity using finite-mixture modelling (Clutton-Brock & Sheldon 2010; Chevallier *et al*. 2013). These models arise from the notion that the individuals of a population can be placed on a low-high continuum of quality that is positively correlated with individual fitness (Wilson & Nussey 2010). Unlike random effect models, finite-mixture models do not assume that individual heterogeneity is normally distributed for a given trait. Rather, individual heterogeneity is taken into account by assigning individuals to a finite number of hidden groups (i.e. hidden states or sub-populations) based on their life history trajectory (McLachlan & Peel 2000; Supp. S1). By doing so, individual heterogeneity is studied at a broader scale as demographic rates are compared between groups and not individuals (Hamel *et al*. 2017).

The male southern elephant seal (hereafter elephant seal, *Mirounga leonina*) provides an ideal model species to investigate individual heterogeneity in the pre-breeding component of a population. In this long-lived mammal, male pre-breeders take several years to reach sexual and social maturity (unlike females which take only two to three years). Male elephant seals are thus exposed to various processes throughout pre-breeder development that may influence individual differences as they age. For example, variation in weaning mass influences juvenile survival after independence (McMahon *et al*. 2000; McMahon *et al*. 2017) and age at recruitment in females (Oosthuizen *et al*. 2018). The male pre-breeder stage is marked by a secondary growth spurt between ages 4-6 during which resource acquisition plays an important role in their survival (i.e. puberty; Pistorius *et al*. 2005). This is exemplified in the foraging strategy of pre-breeders, with individuals that develop a stable foraging strategy early in life living longer (Authier *et al*. 2012). The age of recruitment of males varies between 5 and 10 years and is expected to be negatively related to individual quality (particularly in body size), as breeding attempts are highly competitive (Laws 1956; Galimberti *et al*. 2007). Males compete for dominance of female harems, with only a few dominant males (or beachmasters) monopolising the majority of mating opportunities (Hoelzel *et al*. 1999; Galimberti *et al*. 2002). In addition, pre-breeders that recruit directly as dominant males are more likely to breed again in subsequent years than males that recruit initially as subordinates (Lloyd *et al*. 2019). Thus, individual heterogeneity is likely present and changing with age in male pre-breeder demographic rates, and is likely to carry over into the breeding population.

We investigate individual heterogeneity in male pre-breeder elephant seals at Marion Island using data from a continuous 34-year mark-recapture study (Pistorius *et al.* 2011). Few studies have investigated the effects of individual heterogeneity using finite-mixture models (Gimenez *et al*. 2018) and even fewer have considered the male component of a population (Gimenez & Gaillard 2018). We investigate individual heterogeneity in male elephant seals by constructing two hidden groups that represent “robust” and “frail” individuals and compare the demographic rates of these groups to that of the population response to answer the following questions:

a) Are robust and frail individuals distinguishable based on age-specific survival and recruitment probabilities? If individual heterogeneity is present in these demographic rates, models that specify differences between groups should perform better than models that do not (Fay *et al*. 2016).
b) At what age can individual heterogeneity be detected in survival and recruitment probabilities and for how long? Although individuals differ phenotypically at birth, fitness consequences may be transient, intermediate or permanent depending on current selective pressures (Oosthuizen *et al*. 2018).
c) How do differences between groups change with age relative to one another and the population response? Specific patterns in responses will elude to particular processes taking place (Figure 1; van de Pol & Verhulst 2006; Hamel *et al*. 2018b). As individuals were only marked as pups in this study, the process of selective appearance does not apply to pre-breeder survival, but does apply to recruitment as marked individuals transition into the breeding population.
d) Does the probability of being robust or frail vary with conditions experienced in early life? For example, cohorts born under high population density may suffer from lower demographic performance in adulthood (Pigeon *et al*. 2017). We investigate the relationship between population density during the year of birth and the probability of being robust or frail.
e) How does the composition of robust and frail individuals change within a cohort and carry over into the breeding population? Using estimates obtained from mixture models and population matrix projection, we compare the proportion of robust and frail individuals that make up the population from weaning to age 11.

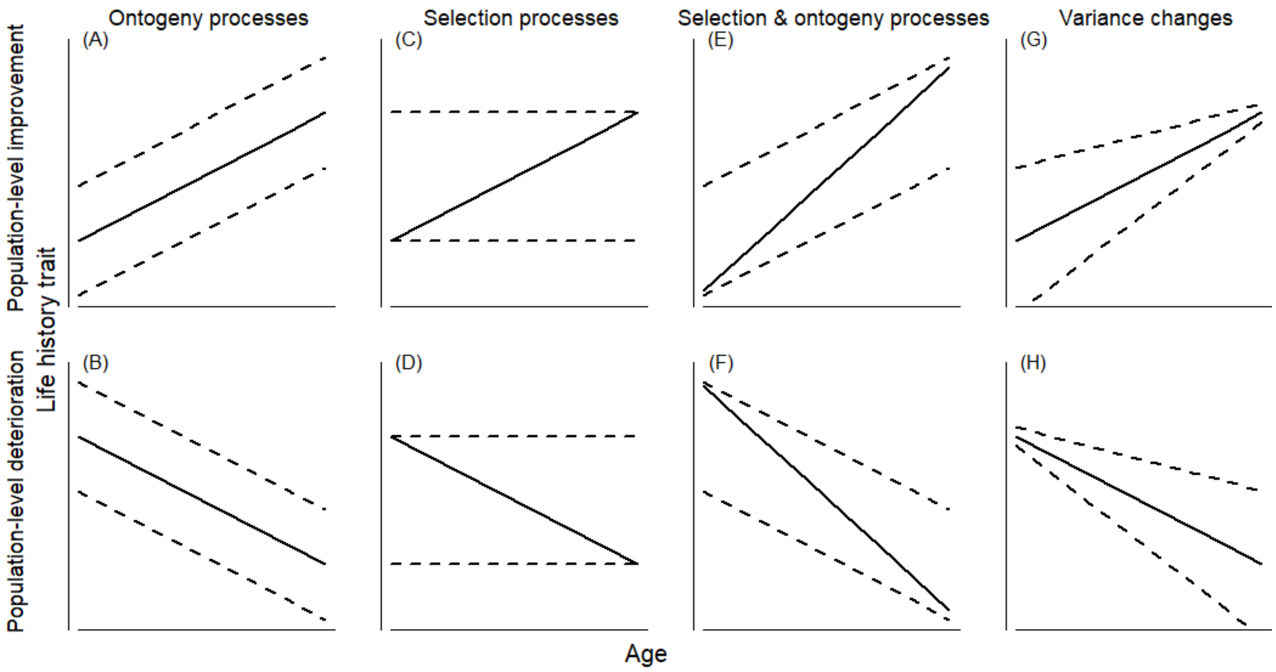

Figure 1: Scenarios of age-specific change in a life history trait distinguishing the mean population response (solid line) from the mean response of heterogeneous groups that make up the population (dashed lines). Processes acting on individual heterogeneity within (A, B, C, D, E, F) and between (G, H) groups change the position of the population response relative to group responses. The life-history trait represents a demographic rate (e.g. survival) or measurable characteristic (e.g. body mass). Ontogeny processes: (A) Improvement, such as experience, of all individuals whilst differences within groups are maintained (i.e. silver-spoon effects). (B) Deterioration, such as senescence, of all individuals whilst differences within groups are maintained. Selection processes: Selective appearance (e.g. fertility selection or immigration) or disappearance (e.g. viability selection or emigration) of individuals within groups skews the population response. (C) Selective appearance adds robust individuals or selective disappearance removes frail individuals. (D) Selective disappearance removes robust individuals or selective appearance adds frail individuals. Selection and ontogeny processes: (E, F) Selective appearance and disappearance of individuals with age whilst all individuals experience ontogenetic effects. Variance changes between groups: (G) Individual differences between groups are reduced (e.g. compensatory effects) with the frail group (lower intercept) improving at a faster rate relative to the robust group. (H) Individual differences between groups are amplified (e.g. accumulating effects) with the frail group deteriorating at a faster rate than the robust group. Adapted from van de Pol & Verhulst (2006) and Hamel *et al*. (2018b).

Methods

Model design

The population of male elephant seals at Marion Island was studied between 1983 and 2016, with almost all pups born on the island tagged at weaning (Pistorius *et al*. 2011). Details of the mark-recapture protocol can be found in Lloyd *et al*. (2019). The resulting dataset consisted of 27 cohorts, 6 245 marked pups, 326 marked breeders, and 58 177 observations made over 34 years. Finite-mixture multievent models (a variant of the hidden-Markov modelling framework) were used to model individual heterogeneity in pre-breeder demographic rates (Gimenez *et al*. 2018). Modelling individual heterogeneity in breeders using finite-mixture models was not possible because of small sample sizes which inhibit model convergence and parameter estimation. The finite-mixture component allows for unobserved individual heterogeneity to be accounted for by assigning individuals to a finite number of hidden states based on how individuals survive and transition between states throughout their lifetime (i.e. latent heterogeneity; Pledger *et al*. 2003). The multievent component allows for uncertainty in state assignment (Gimenez *et al*. 2012). The general model was based on the analysis of Lloyd *et al*. (2019), which consisted of nine events observed in the field relating in a probabilistic framework to nine states that an individual could occupy during each year (Pradel 2005; Supp. S2). Each year started at the beginning of the elephant seal breeding season and ended before the start of the next breeding season.

The possible events were: not seen (0); seen as a pre-breeder with two tags (1); seen as a pre-breeder with one tag (2); seen as a subordinate breeder with two tags (3); seen as a subordinate breeder with one tag (4); seen as a dominant breeder with two tags (5); seen as a dominant breeder with one tag (6); seen with an unknown breeding state and two tags (7); and seen with an unknown breeding state and one tag (8). Breeders were assigned to the unknown breeding state when an individual was seen as both a subordinate and dominant breeder several times during the same breeding season. The possible breeding states included: pre-breeder with two tags (PB-T2, has not previously participated in a breeding season); pre-breeder with one tag (PB-T1); pre-breeder alive elsewhere with two tags (PBAE-T2, temporarily emigrated and last seen with two tags); pre-breeder alive elsewhere with one tag (PBAE-T1); subordinate breeder with two tags (SB-T2); subordinate breeder with one tag (SB-T1); dominant breeder with two tags (DB-T2); dominant breeder with one tag (DB-T1); and dead (D, an absorbing state representing death and permanent emigration).

Individual heterogeneity was incorporated into matrices corresponding to initial state, transition and event probabilities by duplicating pre-breeder states (Supp. S1 & S2). Two hidden states or groups, representing robust and frail individuals on the quality continuum (Wilson & Nussey *et al*. 2010), are considered sufficient when individual heterogeneity is assumed to follow a unimodal distribution (Pledger 2005). The probability of being assigned to a group (π^{ind}) was initially kept constant and depended on the survival and recruitment probabilities of an individual (Fay *et al*. 2016). All individuals entered the population as pre-breeders, nearly all with two tags (π^{tag}; Lloyd *et al*. 2019). Transition probabilities between states were modelled in five steps with each step conditioning on preceding transitions: tag loss from two to one tag (τ^{21}), tag loss from one to zero tags (τ^{10}), apparent survival (φ), breeding (ψ, representing recruitment – the probability to recruit from the pre-breeder state to the subordinate or dominant breeder state – and future breeding state – the probability to transition from the subordinate or dominant breeder state to the dominant breeder state), and temporary migration out of (ψ^{E}) and into (ψ^{I}) the study population by native individuals. Event probabilities were modelled with detection (p) and breeding state assignment (δ) probabilities. Survival, recruitment and detection probabilities were parameterised using models that tested specific hypotheses about the structure of individual heterogeneity in the pre-breeder population (Supp. S3). Differences between robust and frail under-yearlings could not be assessed because group assignment was highly correlated with first-year survival (Fay *et al*. 2018). This meant that individual heterogeneity was only modelled in pre-breeders that survived their first year. Assignment to a group (π^{ind}) was further explored upon detecting individual heterogeneity in pre-breeder demographic rates by investigating time- and density-related effects (Supp. S3). Heterogeneity in tag loss, temporary migration, breeder survival, future breeding state and state assignment probabilities were parameterised using the most parsimonious models from Lloyd *et al*. (2019). Temporary migration probabilities were kept constant to reduce model complexity and promote model convergence. To summarise, the initial model was:

$$\pi^{\text{ind}}_{\text{cst}}\ \pi^{\text{tag}}_{\text{cst}}\ \tau^{21}_{\text{tag position}\cdot\text{age }0,1,2,3,4,5,\geq 6}\ \tau^{10}_{\text{cst}}\ \varphi^{\text{PB}}_{\text{ind}\cdot\text{age }0,1,2,3,4,5,\geq 6}\ \varphi^{\text{SB}\neq\text{DB}}_{\text{age }5,6,7,8,9,\geq 10(\text{linear}^{\text{SB}=\text{DB}})}$$

$$\psi^{\text{PB}-\text{SB}}_{\text{ind}\cdot\text{age }5,6,7,\geq 8}\ \psi^{\text{PB}-\text{DB}}_{\text{ind}\cdot\text{age }6,7,\geq 8}\ \psi^{\text{SB}-\text{DB}\neq\text{DB}-\text{DB}}_{\text{age }6,7,8,9,10,\geq 11(\text{linear}^{\text{SB}-\text{DB}=\text{DB}-\text{DB}})}\ \psi^{\text{E}\neq\text{I}}_{\text{cst}}\ p^{\text{PB}=\text{SB}=\text{DB}}_{\text{time }1984-2016}\ \delta^{\text{SB}=\text{DB}}_{\text{cst}}$$

Model selection and goodness-of-fit

Parameters were initially specified as the most complex model in each candidate set followed by simpler models, with the most parsimonious model being kept for each parameter. Models were fitted using a maximum likelihood approach in E-SURGE 2.1.4 (Choquet *et al.* 2009), with 14 age classes (maximum age recorded) and 34 occasions. Model convergence was checked by comparing the deviance of complex and simpler nested models. Small sample corrected quasi-likelihood Akaike's Information Criterion ($QAIC_c$) was used to select models and was supplemented with Akaike weights (ω_i) to give the strength of evidence of each model relative to other models in the candidate set (Burnham & Anderson 2004). An overdispersion factor of $\hat{c}$ = 1.7 was taken from Lloyd *et al*. (2019), who performed goodness-of-fit tests on the same data, to adjust AIC and parameter variance (Pradel *et al*. 2005; Péron *et al*. 2010). Probability estimates are reported as the mean followed by the lower and upper 95% confidence interval (CI). Where necessary, multiple random initial values were run for three iterations to assist model estimation. Additional results, including parameter estimates, are reported in the supplementary information (Supp. S5).

Population projection model

Age-specific proportions of robust and frail individuals of each breeding state were estimated using simple age- and stage-structured population projection models (Caswell 2001). A post-breeding census and annual projection interval were assumed. Two matrices were constructed representing the life-cycle of robust and frail pre-breeders from age 0 to 11 (Supp. S4). Age 11 was the oldest recorded age class with a meaningful number of observed subordinate breeders (*n* = 7). Thus, matrix elements differed in terms of pre-breeder survival and recruitment probabilities, but not breeder survival and future breeding state probabilities. Probabilities were estimated using the most parsimonious models from this study. Pups (*n* = 260, average number of male pups produced annually between 1985 and 2016 assuming 1:1 sex ratio; Pistorius *et al*. 2011) were divided between matrices based on the group assignment probability estimated by the constant model ($\pi_{\text{cst}}^{\text{ind}}$, model 30, Table S3.3). Pups were then projected through the matrix without replacement (i.e. no fertility estimates). The number of individuals that transitioned from $age\ x$ to $age\ x+1$ were recorded for each breeding state and converted to a proportion. Population matrices were projected in R 3.5.2 (R Core Team 2019).

Results

Individual heterogeneity was present in pre-breeder survival (model 1, Table 1) and recruitment to the subordinate breeder state (model 18). The best supported models depended on group (hidden states) with age treated as a fixed effect (assuming the parameters to be different and independent of each other at every age). However, the probability to recruit to the dominant breeder state could not be distinguished between robust and frail pre-breeders (model 18 *cf*. models 17 and 19), likely as a result of few pre-breeders making this transition. Fewer pre-breeders recruited directly as dominant breeders (*n* = 54) compared to subordinate breeders (*n* = 262) in the observed population.

By definition, the group with higher survival probabilities was regarded as robust. Differences in survival probabilities between robust and frail pre-breeders were apparent from age 2 onwards (model 5), with differences between yearling groups receiving less support ($\omega_{\text{model 5}}/\omega_{\text{model 1}}$ = 2.5). Thus, population-level survival was estimated separately for under-yearlings (0.57; CI: 0.55, 0.59) and yearlings (0.75; CI: 0.72, 0.77). Groups differed in recruitment probabilities from the earliest recorded age (age 5, model 24). However, robust and frail pre-breeders shared equivalent recruitment probabilities from age 8 onwards. Few pre-breeders remained to recruit at these older age classes (*n* = 15) in the observed population.

When investigating trends in robust and frail pre-breeder survival with age, survival was constrained to be linear and decreasing on the logit scale for both groups (model 15, Figure 2A). Frail individuals experienced a much lower baseline survival than robust individuals with differences between groups maintained throughout pre-breeder development (i.e. different intercepts, same slopes; Table. S5.2). However, there was some evidence to suggest that robust pre-breeder survival decreased at a faster rate than frail pre-breeders (model 15), although this model received less support ($\omega_{\text{model 15}}/\omega_{\text{model 14}}$ = 2.2). The population-level response also showed decreasing survival with age, but at a slower rate than both groups. The population average shared similar survival probabilities with robust pre-breeders at older ages (overlapping confidence intervals from age 5; Figure 2A), suggesting that processes removed frail pre-breeders from the population (Figure 1C).

Table 1: Finite-mixture multievent models for survival (φ), recruitment (ψ) and group assignment (π^{ind}) probabilities of male southern elephant seals at Marion Island. Pre-breeders were assigned to hidden states (PB1 & PB2) when entering the marked population at weaning. Superscripts and subscripts indicate variation or equality among pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states, age classes (a), and time- and density-related covariates. Small sample corrected quasi-likelihood Akaike's Information Criterion (QAIC$_c$; $\hat{c}$ = 1.7) was used to select models, with the following measurements: ΔQAIC$_c$ (the difference in QAIC$_c$ between the model with the lowest QAIC$_c$ value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood). Models in bold font were used to derive estimates.

Model	Parameters	ΔQAIC$_c$	ω_i	K	Deviance
	Survival (φ) – presence of individual heterogeneity				
1	$\boldsymbol{\varphi}^{\mathbf{PB1=PB2}}_{\mathbf{a\ 0}} + \boldsymbol{\varphi}^{\mathbf{PB1\neq PB2}}_{\mathbf{a\ 1,2,3,4,5,\geq 6}}$	**0.00**	**1.00**	**48**	**398.95**
2	$\varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 0,1,2,3,4,5,\geq 6}}$	110.48	0.00	42	458.57
3	$\varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{cst}}$	40.97	0.00	37	518.66
4	$\varphi^{\mathrm{PB1=PB2}}_{\mathrm{cst}}$	195.49	0.00	36	537.36
	Survival (φ) – onset age of individual heterogeneity detection & disappearance				
1	$\varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 0}} + \varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 1,2,3,4,5,\geq 6}}$	1.86	0.19	48	398.95
5	$\boldsymbol{\varphi}^{\mathbf{PB1=PB2}}_{\mathbf{a\ 0,1}} + \boldsymbol{\varphi}^{\mathbf{PB1\neq PB2}}_{\mathbf{a\ 2,3,4,5,\geq 6}}$	**0.00**	**0.49**	**47**	**407.40**
6	$\varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 0,1,2}} + \varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 3,4,5,\geq 6}}$	7.70	0.01	46	416.42
7	$\varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 0,1,2,3}} + \varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 4,5,\geq 6}}$	132.68	0.00	45	428.45
8	$\varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 0,1,2,3,4,5}} + \varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ \geq 6}}$	2.90	0.11	47	407.46
9	$\varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 0,1,2,3,4}} + \varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 5,\geq 6}}$	27.44	0.00	46	416.85
10	$\varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 0,1,2,3}} + \varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 4,5,\geq 6}}$	29.66	0.00	45	426.16
11	$\varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 0,1,2}} + \varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 3,4,5,\geq 6}}$	81.00	0.00	44	437.02
12	$\varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 0,1}} + \varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 2,3,4,5,\geq 6}}$	114.00	0.00	43	447.95
13	$\varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 0}} + \varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 1,2,3,4,5,\geq 6}}$	112.34	0.00	42	458.57
	Survival (φ) – trends in individual heterogeneity with age				
5	$\varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 0,1}} + \varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 2,3,4,5,\geq 6}}$	3.19	0.12	47	407.40
14	$\varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 0,1}} + \varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 2,3,4,5,\geq 6}\left(\mathrm{linear}^{\mathrm{PB1\neq PB2}}\right)}$	1.56	0.26	41	466.98
15	$\boldsymbol{\varphi}^{\mathbf{PB1=PB2}}_{\mathbf{a\ 0,1}} + \boldsymbol{\varphi}^{\mathbf{PB1\neq PB2}}_{\mathbf{a\ 2,3,4,5,\geq 6}\left(\mathbf{linear}^{\mathbf{PB1=PB2}}\right)}$	**0.00**	**0.57**	**40**	**478.61**
16	$\varphi^{\mathrm{PB1=PB2}}_{\mathrm{a\ 0,1}} + \varphi^{\mathrm{PB1\neq PB2}}_{\mathrm{a\ 2:\geq 6}}$	5.02	0.05	39	491.01
	Recruitment (ψ) – presence of individual heterogeneity				
17	$\psi^{\mathrm{PB1-SB\neq PB2-SB}}_{\mathrm{a\ 5,6,7,\geq 8}} + \psi^{\mathrm{PB1-DB\neq PB2-DB}}_{\mathrm{a\ 6,7,\geq 8}}$	3.78	0.11	40	478.61
18	$\boldsymbol{\psi}^{\mathbf{PB1-SB\neq PB2-SB}}_{\mathbf{a\ 5,6,7,\geq 8}} + \boldsymbol{\psi}^{\mathbf{PB1-DB=PB2-DB}}_{\mathbf{a\ 6,7,\geq 8}}$	**0.00**	**0.70**	**37**	**517.32**
19	$\psi^{\mathrm{PB1-SB=PB2-SB}}_{\mathrm{a\ 5,6,7,\geq 8}} + \psi^{\mathrm{PB1-DB\neq PB2-DB}}_{\mathrm{a\ 6,7,\geq 8}}$	10.91	0.00	36	531.99
20	$\psi^{\mathrm{PB1-SB=PB2-SB}}_{\mathrm{a\ 5,6,7,\geq 8}} + \psi^{\mathrm{PB1-DB=PB2-DB}}_{\mathrm{a\ 6,7,\geq 8}}$	2.66	0.19	33	580.10
	Recruitment (ψ) – onset age of individual heterogeneity detection & disappearance				
18	$\psi^{\mathrm{PB1-SB\neq PB2-SB}}_{\mathrm{a\ 5,6,7,\geq 8}}$	2.00	0.20	37	517.32
21	$\psi^{\mathrm{PB1-SB=PB2-SB}}_{\mathrm{a\ 5}} + \psi^{\mathrm{PB1-SB\neq PB2-SB}}_{\mathrm{a\ 6,7,\geq 8}}$	2.89	0.13	36	531.71
22	$\psi^{\mathrm{PB1-SB=PB2-SB}}_{\mathrm{a\ 5,6}} + \psi^{\mathrm{PB1-SB\neq PB2-SB}}_{\mathrm{a\ 7,\geq 8}}$	6.50	0.02	35	547.01
23	$\psi^{\mathrm{PB1-SB=PB2-SB}}_{\mathrm{a\ 5,6,7}} + \psi^{\mathrm{PB1-SB\neq PB2-SB}}_{\mathrm{a\ \geq 8}}$	9.29	0.01	34	563.18
24	$\boldsymbol{\psi}^{\mathbf{PB1-SB\neq PB2-SB}}_{\mathbf{a\ 5,6,7}} + \boldsymbol{\psi}^{\mathbf{PB1-SB=PB2-SB}}_{\mathbf{a\ \geq 8}}$	**0.00**	**0.53**	**36**	**531.63**
25	$\psi^{\mathrm{PB1-SB\neq PB2-SB}}_{\mathrm{a\ 5,6}} + \psi^{\mathrm{PB1-SB=PB2-SB}}_{\mathrm{a\ 7,\geq 8}}$	5.00	0.04	35	546.96

26	$\psi_{\text{a 5}}^{\text{PB1}-\text{SB}\neq\text{PB2}-\text{SB}} + \psi_{\text{a 6,7,}\geq 8}^{\text{PB1}-\text{SB}=\text{PB2}-\text{SB}}$	3.91	0.08	34	563.02
	Recruitment (ψ) – trends in individual heterogeneity with age				
24	$\boldsymbol{\psi_{\text{a 5,6,7}}^{\text{PB1}-\text{SB}\neq\text{PB2}-\text{SB}} + \psi_{\text{a }\geq 8}^{\text{PB1}-\text{SB}=\text{PB2}-\text{SB}}}$	**0.00**	**1.00**	**36**	**531.63**
27	$\psi_{\text{a 5,6,7(linear}^{\text{PB1}-\text{SB}\neq\text{PB2}-\text{SB}})}^{\text{PB1}-\text{SB}\neq\text{PB2}-\text{SB}} + \psi_{\text{a }\geq 8}^{\text{PB1}-\text{SB}=\text{PB2}-\text{SB}}$	69.07	0.00	34	564.93
28	$\psi_{\text{a 5,6,7(linear}^{\text{PB1}-\text{SB}=\text{PB2}-\text{SB}})}^{\text{PB1}-\text{SB}\neq\text{PB2}-\text{SB}} + \psi_{\text{a }\geq 8}^{\text{PB1}-\text{SB}=\text{PB2}-\text{SB}}$	68.07	0.00	33	582.02
29	$\psi_{\text{a 5:7}}^{\text{PB1}-\text{SB}\neq\text{PB2}-\text{SB}} + \psi_{\text{a }\geq 8}^{\text{PB1}-\text{SB}=\text{PB2}-\text{SB}}$	185.39	0.00	32	603.88
	Group assignment (π^{ind})				
30	π_{cst}	7.33	0.02	36	531.63
31	$\pi_{\text{cohort year}}$	32.46	0.00	62	309.09
32	$\pi_{1983:1997,1998:2009}$	6.26	0.04	37	517.23
33	$\boldsymbol{\pi_{\text{cohort size}}}$	**0.00**	**0.94**	**37**	**517.06**
34	$\pi_{\text{cohort sex ratio}}$	68.19	0.00	37	518.91

Changes in recruitment probabilities with age did not follow any linear trends (model 24 *cf.* models 27-29). Recruitment to the subordinate breeder state was fully age dependent with differences between robust and frail pre-breeders increasing from ages 5 to 7 (Figure 2B). No frail pre-breeders recruited at age 5. The population-level response was almost identical to that of robust recruits, with estimates of frail recruits having wide, overlapping confidence intervals.

The probability of being robust was negatively correlated with the number of pups produced during a male's birth year (model 33). Males born in years of relatively small cohort sizes were more likely to be robust at age 2 than males born in years of relatively large cohort sizes (Figure 3). Years with the largest birth cohort sizes were grouped chronologically (1985-1989), which coincided with a period during which the population growth rate was decreasing. However, the model comparing group assignment probabilities between periods of decreasing and increasing population growth rates received little support (ω_{33}/ω_{32} = 23.5).

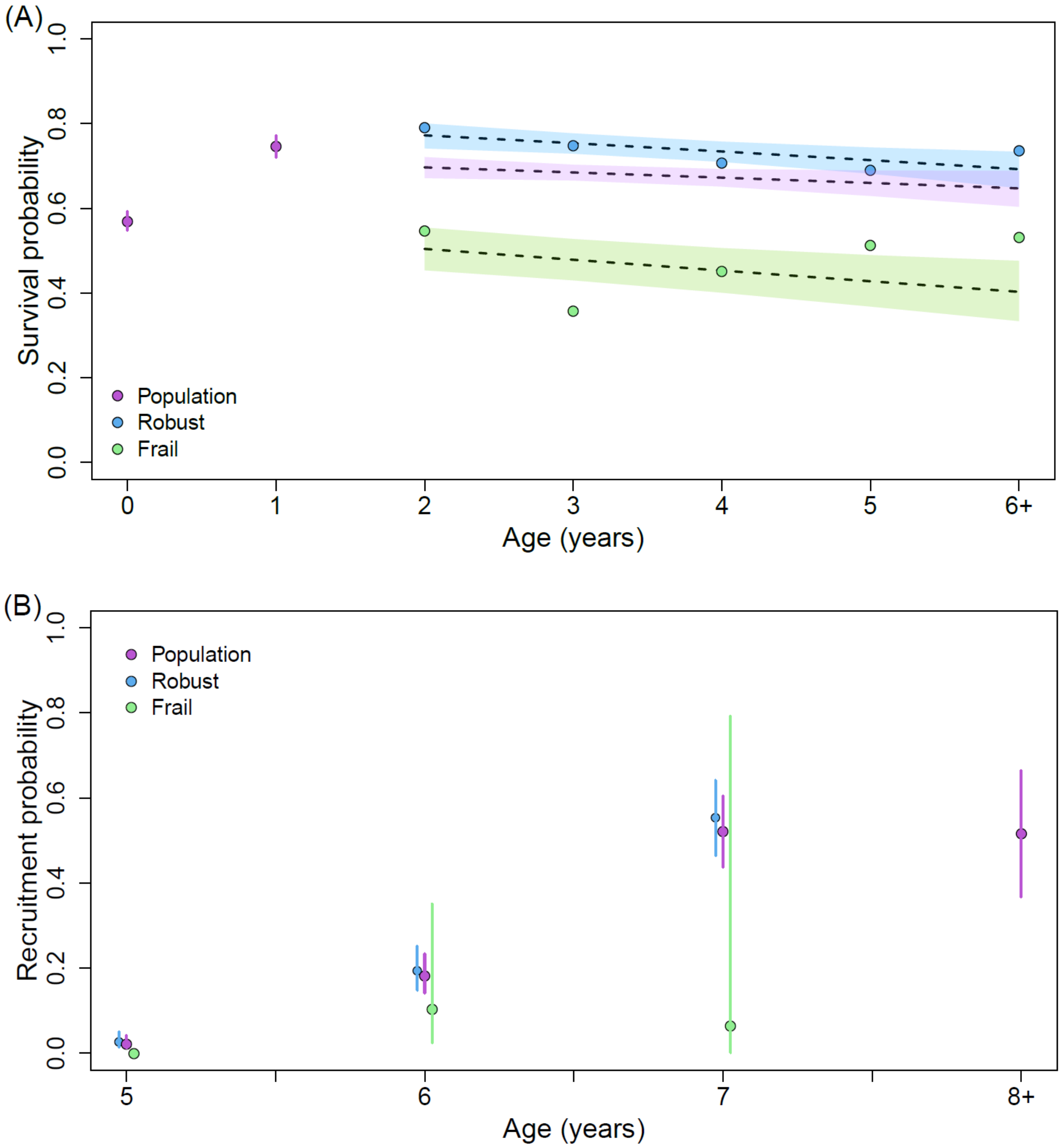

Figure 2: Mean (A) survival and (B) recruitment probabilities (± 95% confidence intervals) of male southern elephant seal pre-breeders at Marion Island. Estimates were derived for population and group (hidden states representing robust and frail individuals) responses. Differences in survival probabilities between robust and frail pre-breeders were expressed from age 2 as a continuous logit-linear relationship (model 15, Table 1). Age-specific recruitment probabilities were estimated for robust and frail individuals transitioning into the breeding population as subordinate breeders from ages 5 to 7 (model 24).

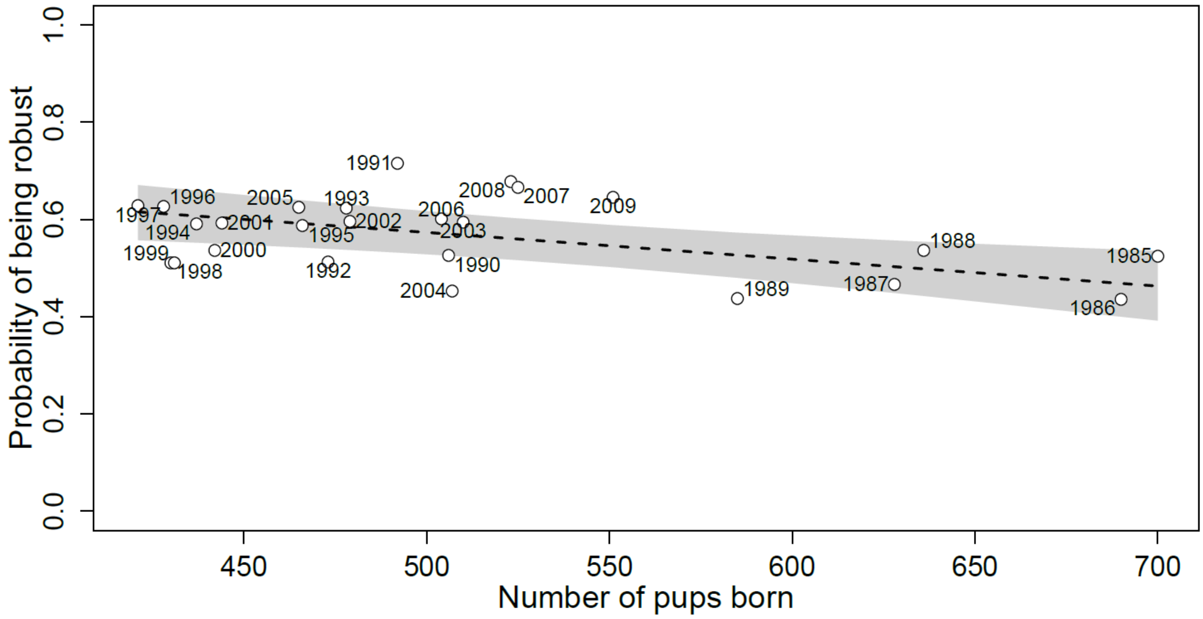

Figure 3: The mean probability (± 95% confidence intervals) of a male southern elephant seal being robust between 1985 and 2009 was negatively correlated with the number of pups born at Marion Island during the male's birth year (model 33). Independent annual estimates (∘) followed this general trend (model 31).

Approximately 56% of males born at Marion Island between 1983 and 2009 were robust in the population projection model (π^{ind}, model 30, Table 1). Thus, 146 of 260 male pups were assigned as robust, and 114 of 260 male pups were assigned as frail. After age 2, the pre-breeder component of the population increasingly consisted of robust individuals, whilst the proportion of frail individuals decreased (Figure 4). However, a small proportion of frail pre-breeders survived to recruitment ages, with the first frail pre-breeders recruiting as subordinate breeders at age 6 and as dominant breeders at age 7. Conversely, a large proportion of robust pre-breeders survived to recruitment ages, with the first robust pre-breeders recruiting earlier as subordinate breeders at age 5 and as dominant breeders at age 6. Changes in the proportion of robust and frail pre-breeders with age had consequences for the breeding component of the population. Both frail subordinate and frail dominant breeders never made up more than 5% of any age class. Most notable was that the proportion of breeders were increasingly robust and dominant with age. By the oldest age class, robust dominant breeders comprised 74% of the population, likely siring the majority of pups at the island. In contrast, frail dominant breeders made up only 4% of breeders at age 11.

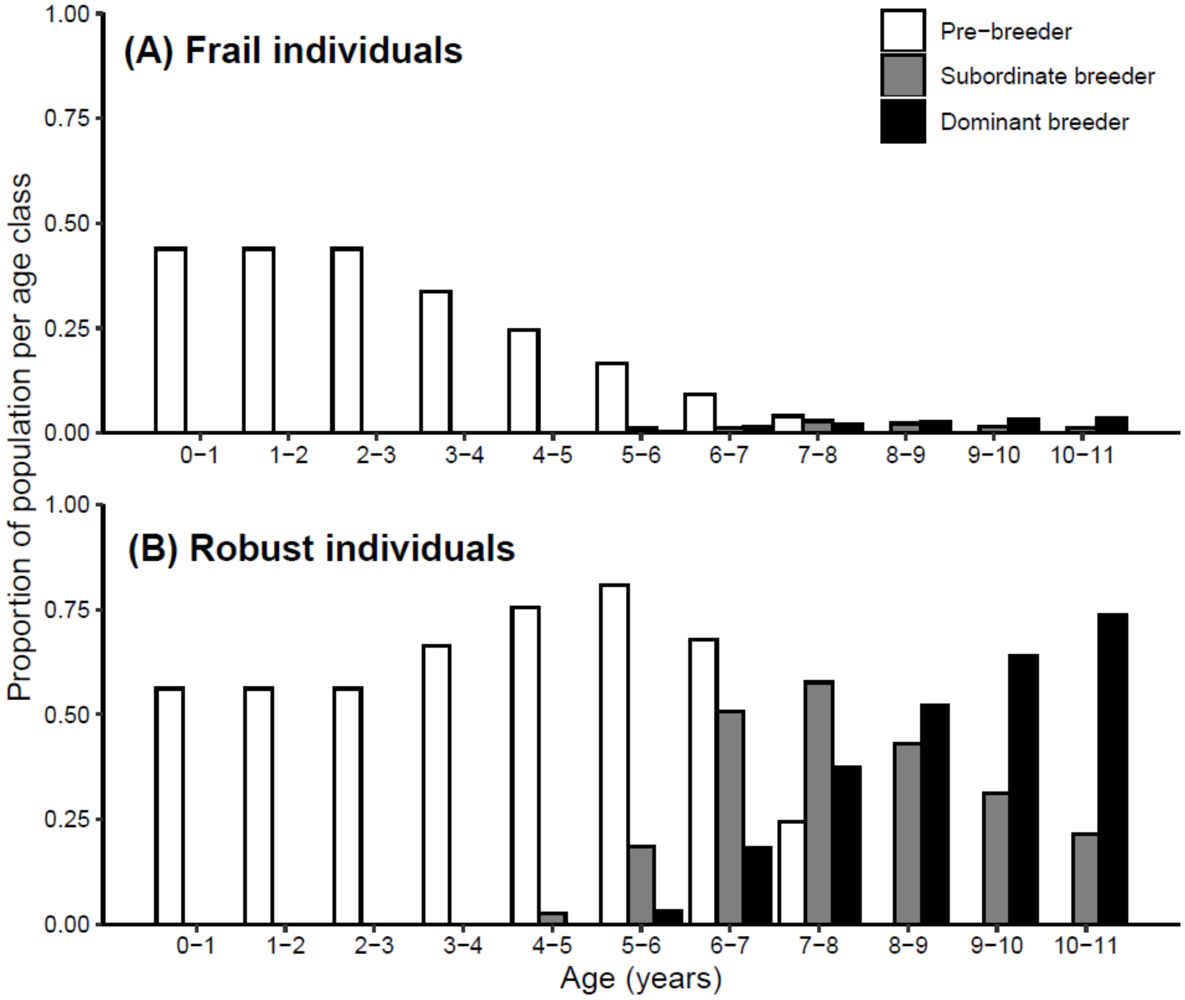

Figure 4: Proportion of robust and frail male southern elephant seals when 260 male pups were projected through population matrices from ages 0 to 11. Pups had a 56% chance of being robust (model 30, Table 1). Matrix elements were parameterised using probability estimates of the most parsimonious survival (model 15) and recruitment (model 24) models. The breeding population consisted primarily of recruited robust pre-breeders.

Discussion

Few studies have investigated individual heterogeneity in pre-breeder demographic rates since most focus on the breeder component of a population (Hamel *et al*. 2018b). Here, we compared pre-breeder demographic rates between robust and frail individuals of the highly polygynous male southern elephant seal and predict consequences for the breeding population. For pre-breeders that survived their first year of life, we show that individual heterogeneity in survival probabilities was expressed from age 2 and that frail individuals were preferentially removed from the population as pre-breeders matured. Pre-breeder survival was positively correlated with recruitment as robust individuals were more likely to transition into the breeding population than frail individuals from a younger age. Birth cohort size was a likely predictor of individual quality in pre-breeders. Differences in pre-breeder survival and recruitment probabilities meant that most breeders that obtained dominance were robust in quality from an early age.

Individual heterogeneity in male pre-breeder survival and recruitment

We found support for the presence of individual heterogeneity in male elephant seal pre-breeders. Using finite-mixture models, we investigated individual heterogeneity as unobservable individual differences that were assumed to be fixed (Cam *et al*. 2016; *cf*. individual stochasticity; Jenouvrier *et al*. 2018). Age-specific survival and recruitment probabilities to the subordinate breeder state (hereafter recruitment) were distinguishable between robust and frail pre-breeders. Frailty would otherwise have gone unnoticed if pre-breeder demographic rates were modelled only at the population level (Vaupel & Yashin 1985; Lloyd *et al*. 2019). Consequently, we were able to detect hidden processes governing pre-breeder population dynamics and describe how they affected groups differently.

Finite-mixture models are unique in that they categorise an individual by evaluating its entire life history (latent heterogeneity; McLachlan & Peel 2000). In our study, this meant that pre-breeder survival probabilities were correlated with recruitment probabilities (van de Pol & Verhulst 2006). We found that robust pre-breeders (i.e. individuals with above average survival) were more likely to recruit to the breeding population than frail pre-breeders. This positive covariance between survival and recruitment supports the individual quality hypothesis (Wilson & Nussey 2010), and not the trade-off hypothesis which predicts lower pre-breeder survival when individuals invest in reproductive traits during early life (Stearns 1992). Positive correlations between survival and reproductive traits as a result of fixed heterogeneity are widespread among mark-recapture studies (reviewed by Gimenez *et al*. 2018; Vedder & Bouwhuis 2018). This makes sense in a breeding system where allocation to body growth and maintenance during development is equivalent to allocation to secondary sexual traits that are used to obtain dominance.

To compete for mates, polygynous males need to be sexually and socially mature (Jones 1981). For most polygynous males, including elephant seals, this often takes the form of body size and mass. Larger males generally outcompete competitors and maintain a mating monopoly (Galimberti *et al*. 2007). In capital breeders especially, reproduction relies on energy stores (Stephens *et al*. 2009). Thus, the ability with which pre-breeders acquire food (including competitive ability and metabolic efficiency) to increase body size for reproduction may also coincidentally maintain survival during development (van Noordwijk & de Jong 1986; Authier *et al*. 2012). Male pre-breeders can use these stockpiles during periods of resource limitation by catabolising blubber lipids and body protein for metabolic energy (Slip *et al*. 1992). Elephant seal pre-breeders also endure periods of fasting on land during annual moult for 25-30 days (Condy 1979) and shorter rest periods during winter months (Kirkman *et al*. 2001). Conversely, breeding systems where dominance is determined by early allocation to weapons support the trade-off hypothesis (Lemaître *et al*. 2014; Gaillard *et al*. 2017). Weapons do not provide any immediate survival benefits, although they may act as honest indicators of high survival at old ages (Lemaître *et al*. 2018). Therefore, investment in high quality weapons during early development may cost current survival. For example, in male red deer (*Cervus elaphus*), allocation to larger antlers relative to body mass in the first year has short-term survival costs to second-year survival (Lemaître *et al*. 2018). Therefore, the consequences of resource allocation decisions must be interpreted within the context of a species' life history and biology (e.g. Vedder & Bouwhuis 2018).

Survival probabilities were distinguishable between robust and frail pre-breeders from age 2 and less so at age 1. Male elephant seal growth rates accelerate with age from weaning followed by a growth spurt at puberty (ages 4-6; McLaren 1993). In addition, age-specific body size variability between individuals increases as males age; a trend which is absent among females (McLaren 1993). Therefore, fitness consequences may be more pronounced at older pre-breeder ages when between-level differences in body size are greater. Alternatively, model specification suggests that yearling pre-breeder survival was not correlated with robust and frail pre-breeder recruitment probabilities. Pre-breeders that are small in body size at weaning are generally less likely to survive and may be rapidly removed from the population (McMahon *et al*. 2000). Consequently, most frail under-yearlings and yearlings may not even survive to age 2 and would not affect recruitment estimates.

Both robust and frail pre-breeder survival decreased at the same rate from age 2, suggesting that all pre-breeders were exposed to the same unavoidable sources of mortality independent of quality. By growing throughout life (McLaren 1993), male elephant seals are particularly prone to food limitation (Pistorius *et al*. 2005) and likely suffer some cost to survival. However, silver spoon effects predict that the state of an individual at $age\ x$ will be positively related to its state at $age\ x + 1$ (Grafen 1988). Therefore, a cascading effect results whereby individuals that start poorly remain frail throughout life in the absence of compensatory effects (Caswell 2001; Beckerman *et al*. 2002; Cam *et al*. 2016). Food requirements increase during puberty (Ling & Bryden 1981; Laws 1984), making it unlikely for frail pre-breeders to improve survival rates. The population-level response also decreased at a slower rate and showed similar survival probabilities to robust pre-breeders at recruitment ages. Thus, the discrepancy in survival probabilities between robust pre-breeders and the population response decreased over time, suggesting that frail pre-breeder phenotypes were preferentially removed from the population with age (i.e. selective disappearance; Cam *et al*. 2002; van de Pol & Verhulst 2006). This process, known as viability selection, favours phenotypes that ensure reproduction (or at least participation in breeding events; Fisher 1930) and in so doing reduces the amount of pre-breeder heterogeneity in the population. Further support for the removal of frail pre-breeders from the population were shown in recruitment probabilities as the population response was nearly identical to that of robust pre-breeders. Robust pre-breeders also started recruiting at an earlier age than frail pre-breeders. This pattern is common among long-lived species (restraint hypothesis; Pianka 1976; Hadley *et al*. 2006; Fay *et al*. 2016) and supports earlier speculations from this population (see Lloyd *et al*. 2019). Thus, individuals of different phenotypes started to enter the breeding population at different ages.

Effects of early-life conditions on individual heterogeneity

Annual variation in early-life conditions had long-term fitness consequences for male elephant seal pre-breeders. Apart from intrinsic factors that determine an individual's quality (i.e. genetics), extrinsic factors such as early-life conditions contribute substantially to permanent demographic variation among individuals (Lindström 1999; van de Pol *et al*. 2006; Cam & Aubry 2011; Oosthuizen *et al*. 2018). For example, red-billed choughs (*Pyrrhocorax pyrrhocorax*) raised under favourable environmental conditions are more likely to survive to breeding age and recruit than offspring raised under poor conditions (Reid *et al*. 2003). Silver spoon effects that persist throughout much of an individual's life are known to also occur in mammals (Pigeon *et al*. 2017), reptiles (Madsen & Shine 2000) and fish (Baudron *et al*. 2014). The probability of seals being robust or frail at age 2 varied by cohort, which implies that individuals of the same cohort were more similar on average than individuals of other cohorts (Beckerman *et al*. 2003). The cohort effect was pervasive in the population likely as a result of males being sensitive to extrinsic factors during early development (Rose *et al*. 1998). Thus, the pre-breeder component of the population consisted of cohorts with different survival and recruitment potentials which may have delayed consequences for population dynamics.

Results suggested that population density at birth may partly explain future individual differences in pre-breeder demographic rates. Males born into small cohort sizes were more likely to be robust and thus have higher pre-breeder survival and recruitment probabilities than males born into large cohort sizes. The number of pups born per breeding season could be both a measure of how many pregnant females competed with one another during gestation which influences resource availability during maternal dependency (i.e. foetal intrauterine development and lactation); and a measure of the number of conspecifics competing for limited resources during juvenile independency (Garrott *et al*. 2012). Resource limitation during ontogeny, whether through indirect (maternal-dependency phase) or direct (juvenile-independency phase) means, is known to affect pre-breeder phenotype (Monaghan 2008). Resource limitation during maternal dependency in another large mammal, the African elephant (*Loxodonta africana*), reduces survival and delays age at first reproduction in males (Lee *et al*. 2013). High birth-year population densities are associated with lower offspring growth and survival (Pacoureau *et al*. 2017), lower adult body mass (Mysterud *et al*. 2002b), and lower reproductive performance (Pigeon *et al*. 2017; Fay *et al*. 2018). Juvenile males frequently suffer higher mortality rates than females after weaning, especially when conditions are poor (Clutton-Brock 1985), likely due to males maintaining larger body sizes (Toigo & Gaillard 2003) and developing secondary sexual traits (Milner *et al*. 1999). Thus, individual heterogeneity in male elephant seal pre-breeders may originate from density-dependent effects with long-term consequences for survival and recruitment probabilities.

Consequences of individual heterogeneity for the breeding population

To adequately study population dynamics, important sources of heterogeneity (e.g. age, breeding state and individual quality) need to be incorporated into population models (Jenouvrier *et al*. 2018). Although our population projection model provided only approximations of population proportions based on mean demographic estimates, it illustrated the long-term consequences of pre-breeder individual heterogeneity on breeder composition. Because frail individuals were preferentially removed from the population, the pre-breeder component increasingly consisted of robust individuals with each age step (i.e. within-cohort selection; Vaupel & Yashin 1985). Thus, few frail pre-breeders recruited to the breeding population and made up only a small proportion of dominant males.

However, breeding inequality was still prevalent even among robust recruits and is a common feature in observed elephant seal populations (Galimberti *et al*. 2002). Processes operating on pre-breeders that select for survival and recruitment are likely different from those operating on breeders that select for breeding success (which includes traits such as aggression, competitive ability, fasting endurance, and other breeding behaviours; McCann 1981; Haley 1994; Mulaudzi *et al*. 2008). Although robust and frail pre-breeders were differentiated based on survival and recruitment probabilities, this does not imply that most robust recruits obtain dominance and breed successfully. Future studies need to examine individual heterogeneity throughout the life history of male elephant seals to determine if pre-breeder individual heterogeneity has life-long effects on breeder survival and reproductive performance.

Conclusion

Polygynous mammals take several years to become sexually and socially mature in competitive breeding systems. Thus, pre-breeders constitute a substantial part of most long-lived populations. And yet, little is known about processes governing pre-breeder demographic rates during development and the implications for population dynamics. Using finite-mixture models, we detected frailty in male pre-breeder survival and recruitment probabilities that was not observed at the population-level (Lloyd *et al*. 2019). If pre-breeder survival had not incorporated individual heterogeneity, the apparent rate of decrease in survival would have mistakenly been interpreted as being lower than what was described by robust and frail pre-breeders. Frail pre-breeders also comprised a substantial proportion of each cohort from early ages and yet barely contributed to the reproductive value of the breeding population. Thus, ignoring individual-level effects can lead to erroneous conclusions about population dynamics with population management implications (Caudill *et al*. 2017). Advances in techniques such as integral projection models can allow us to combine individual-level processes with population dynamics to predict more accurate demographic traits and interactions with density-dependent and -independent factors (Plard *et al*. 2019).

Supporting Information

Supplement S1: State transitions

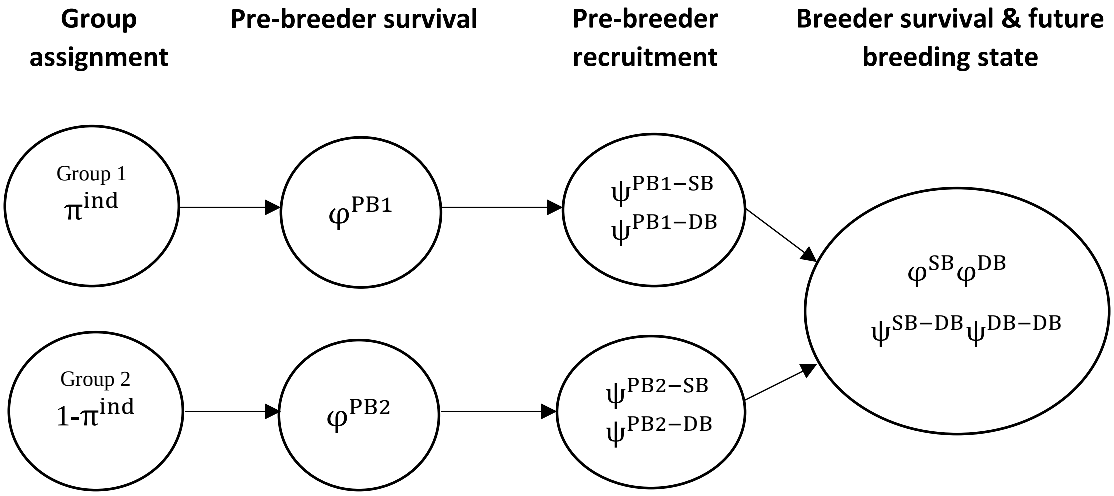

Figure S1.1: Possible transitions among breeding states when male elephant seal pre-breeders were assigned to hidden states (Group 1 - PB1 and Group 2 - PB2). Group assignment was based on how pre-breeders survived and recruited to the breeding population.

Supplement S2: Specifying elementary matrices

Finite-mixture multievent models were parameterised using initial state, transition and event matrices in the programme ESURGE 2.1.4 (Choquet *et al*. 2009). Mark-recapture data were imported in Text format and the overdispersion factor was set to $\hat{c} = 1.7$. Under “Modify”, the number of states along with hidden states (13), events (9) and age classes (14) were set in order to determine the number of rows and columns of each matrix. Pre-breeder states were duplicated to make two hidden states represented as Group 1 (PB1) and Group 2 (PB2; Pledger *et al*. 2003). Pre-breeders alive elsewhere (PBAE) was also a hidden state constructed to account for individuals not observed in a particular year that may have temporary emigrated from the study population (Schaub *et al*. 2004). The following thirteen (biological) states were recognised:

PB1-T2 – Group 1 pre-breeder with two tags (had not previously participated in a breeding event)

PB2-T2 – Group 2 pre-breeder with two tags

PB1-T1 – Group 1 pre-breeder with one tag

PB2-T1 – Group 2 pre-breeder with one tag

PBAE1-T2 – Group 1 pre-breeder alive elsewhere with two tags (temporarily emigrated and last seen with two tags)

PBAE2-T2 – Group 2 pre-breeder alive elsewhere with two tags

PBAE1-T1 – Group 1 pre-breeder alive elsewhere with one tag

PBAE2-T1 – Group 2 pre-breeder alive elsewhere with one tag

SB2 – Subordinate breeder with two tags (attended breeding season but did not mate)

SB1 – Subordinate breeder with one tag

DB2 – Dominant breeder with two tags (attended breeding season and mated)

DB1 – Dominant breeder with one tag

D – Dead (an absorbing state representing death and permanent emigration)

Events related in a probabilistic framework to the nine possible breeding states that an individual could occupy each year. The following nine (observed) events were recognised:

0 – Not seen

1 – Seen as a pre-breeder with two tags

2 – Seen as a pre-breeder with one tag

3 – Seen as a subordinate breeder with two tags

4 – Seen as a subordinate breeder with one tag

5 – Seen as a dominant breeder with two tags

6 – Seen as a dominant breeder with one tag

7 – Seen with an unknown breeding state and two tags

8 – Seen with an unknown breeding state and one tag

GEPAT (for GEnerator of PATtern of elementary matrices) was used to specify the matrices. Estimated parameters were assigned with alphabetical letters, "-" indicates that the corresponding parameter was set to 0, and "*" means (1 - Σ (all other parameters on the same row)). There was always only one "*" per row.

References

Choquet, R., Rouan, L. & Pradel, R. 2009. Program E-SURGE: a software application for fitting multievent models. In: *Modeling demographic processes in marked populations*. Thomson D.L., Cooch, E.G. & Conroy, M.J. (eds), pp. 845-865. Springer, New York.

Pledger, S., Pollock, K.H. & Norris, J.L. 2003. Open capture-recapture models with heterogeneity: I. Cormack-Jolly-Seber model. *Biometrics* 59: 786-794.

Schaub, M., Gimenez, O., Schmidt, B.R. & Pradel, R. 2004. Estimating survival and temporary emigration in the multistate capture–recapture framework. *Ecology* 85: 2107-2113.

GEPAT matrices (in order of appearance in the interface)

Group assignment matrix:

Group1	Group2
π^{ind}	*

Initial breeding state and number of tags matrix:

	PB1-T2	PB2-T2	PB1-T1	PB2-T1	PBAE1-T2	PBAE2-T2	PBAE1-T1	PBAE2-T1	SB2	SB1	DB2	DB1
Group 1	π^{tag}	*	-	-	-	-	-	-	-	-	-	-
Group 2	-	-	π^{tag}	*	-	-	-	-	-	-	-	-

First tag loss matrix:

	PB1-T2	PB1-T1	PB2-T2	PB2-T1	PBAE1-T2	PBAE1-T1	PBAE2-T2	PBAE2-T1	SB 2	SB 1	DB 2	DB 1	Dead
PB1-T2	*	τ^{2-1}	-	-	-	-	-	-	-	-	-	-	-
PB1-T1	-	*	-	-	-	-	-	-	-	-	-	-	-
PB2-T2	-	-	*	τ^{2-1}	-	-	-	-	-	-	-	-	-
PB2-T1	-	-	-	*	-	-	-	-	-	-	-	-	-
PBAE1-T2	-	-	-	-	*	τ^{2-1}	-	-	-	-	-	-	-
PBAE1-T1	-	-	-	-	-	*	-	-	-	-	-	-	-
PBAE2-T2	-	-	-	-	-	-	*	τ^{2-1}	-	-	-	-	-
PBAE2-T1	-	-	-	-	-	-	-	*	-	-	-	-	-
SB2	-	-	-	-	-	-	-	-	*	τ^{2-1}	-	-	-
SB1	-	-	-	-	-	-	-	-	-	*	-	-	-
DB2	-	-	-	-	-	-	-	-	-	-	*	τ^{2-1}	-
DB1	-	-	-	-	-	-	-	-	-	-	-	*	-
Dead	-	-	-	-	-	-	-	-	-	-	-	-	*

Second tag loss matrix:

	PB1-T2	PB1-T1	PB2-T2	PB2-T1	PBAE1-T2	PBAE1-T1	PBAE2-T2	PBAE2-T1	SB 2	SB 1	DB 2	DB 1	Dead
PB1-T2	*	-	-	-	-	-	-	-	-	-	-	-	-
PB1-T1	-	*	-	-	-	-	-	-	-	-	-	-	τ^{1-0}
PB2-T2	-	-	*	-	-	-	-	-	-	-	-	-	-
PB2-T1	-	-	-	*	-	-	-	-	-	-	-	-	τ^{1-0}
PBAE1-T2	-	-	-	-	*	-	-	-	-	-	-	-	-
PBAE1-T1	-	-	-	-	-	*	-	-	-	-	-	-	τ^{1-0}
PBAE2-T2	-	-	-	-	-	-	*	-	-	-	-	-	-
PBAE2-T1	-	-	-	-	-	-	-	*	-	-	-	-	τ^{1-0}
SB2	-	-	-	-	-	-	-	-	*	-	-	-	-
SB1	-	-	-	-	-	-	-	-	-	*	-	-	τ^{1-0}
DB2	-	-	-	-	-	-	-	-	-	-	*	-	-
DB1	-	-	-	-	-	-	-	-	-	-	-	*	τ^{1-0}
Dead	-	-	-	-	-	-	-	-	-	-	-	-	*

Survival matrix:

	PB1-T2	PB1-T1	PB2-T2	PB2-T1	PBAE1-T2	PBAE1-T1	PBAE2-T2	PBAE2-T1	SB 2	SB 1	DB 2	DB 1	Dead
PB1-T2	φ	-	-	-	-	-	-	-	-	-	-	-	*
PB1-T1	-	φ	-	-	-	-	-	-	-	-	-	-	*
PB2-T2	-	-	φ	-	-	-	-	-	-	-	-	-	*
PB2-T1	-	-	-	φ	-	-	-	-	-	-	-	-	*
PBAE1-T2	-	-	-	-	φ	-	-	-	-	-	-	-	*
PBAE1-T1	-	-	-	-	-	φ	-	-	-	-	-	-	*
PBAE2-T2	-	-	-	-	-	-	φ	-	-	-	-	-	*
PBAE2-T1	-	-	-	-	-	-	-	φ	-	-	-	-	*
SB2	-	-	-	-	-	-	-	-	φ	-	-	-	*
SB1	-	-	-	-	-	-	-	-	-	φ	-	-	*
DB2	-	-	-	-	-	-	-	-	-	-	φ	-	*
DB1	-	-	-	-	-	-	-	-	-	-	-	φ	*
Dead	-	-	-	-	-	-	-	-	-	-	-	-	*

Breeding matrix (representing recruitment and future breeding state):

	PB1-T2	PB1-T1	PB2-T2	PB2-T1	PBAE1-T2	PBAE1-T1	PBAE2-T2	PBAE2-T1	SB2	SB1	DB2	DB1	Dead
PB1-T2	*	-	-	-	-	-	-	-	ψ	-	ψ	-	-
PB1-T1	-	*	-	-	-	-	-	-	-	ψ	-	ψ	-
PB2-T2	-	-	*	-	-	-	-	-	ψ	-	ψ	-	-
PB2-T1	-	-	-	*	-	-	-	-	-	ψ	-	ψ	-
PBAE1-T2	-	-	-	-	*	-	-	-	ψ	-	ψ	-	-
PBAE1-T1	-	-	-	-	-	*	-	-	-	ψ	-	ψ	-
PBAE2-T2	-	-	-	-	-	-	*	-	ψ	-	ψ	-	-
PBAE2-T1	-	-	-	-	-	-	-	*	-	ψ	-	ψ	-
SB2	-	-	-	-	-	-	-	-	*	-	ψ	-	-
SB1	-	-	-	-	-	-	-	-	-	*	-	ψ	-
DB2	-	-	-	-	-	-	-	-	*	-	ψ	-	-
DB1	-	-	-	-	-	-	-	-	-	*	-	ψ	-
Dead	-	-	-	-	-	-	-	-	-	-	-	-	*

Temporary migration matrix:

	PB1-T2	PB1-T1	PB2-T2	PB2-T1	PBAE1-T2	PBAE1-T1	PBAE2-T2	PBAE2-T1	SB2	SB1	DB2	DB1	Dead
PB1-T2	*	-	-	-	ψ^E	-	-	-	-	-	-	-	-
PB1-T1	-	*	-	-	-	ψ^E	-	-	-	-	-	-	-
PB2-T2	-	-	*	-	-	-	ψ^E	-	-	-	-	-	-
PB2-T1	-	-	-	*	-	-	-	ψ^E	-	-	-	-	-
PBAE1-T2	ψ^I	-	-	-	*	-	-	-	-	-	-	-	-
PBAE1-T1	-	ψ^I	-	-	-	*	-	-	-	-	-	-	-
PBAE2-T2	-	-	ψ^I	-	-	-	*	-	-	-	-	-	-
PBAE2-T1	-	-	-	ψ^I	-	-	-	*	-	-	-	-	-
SB2	-	-	-	-	-	-	-	-	*	-	-	-	-
SB1	-	-	-	-	-	-	-	-	-	*	-	-	-
DB2	-	-	-	-	-	-	-	-	-	-	*	-	-
DB1	-	-	-	-	-	-	-	-	-	-	-	*	-
Dead	-	-	-	-	-	-	-	-	-	-	-	-	*

Detection matrix:

NS – Not seen

	NS	PB2	PB1	SB2	SB1	DB2	DB1
PB1-T2	*	p	-	-	-	-	-
PB1-T1	*	-	p	-	-	-	-
PB2-T2	*	p	-	-	-	-	-
PB2-T1	*	-	p	-	-	-	-
PBAE1-T2	*	-	-	-	-	-	-
PBAE1-T1	*	-	-	-	-	-	-
PBAE2-T2	*	-	-	-	-	-	-
PBAE2-T1	*	-	-	-	-	-	-
SB2	*	-	-	p	-	-	-
SB1	*	-	-	-	p	-	-
DB2	*	-	-	-	-	p	-
DB1	*	-	-	-	-	-	p
Dead	*	-	-	-	-	-	-

Breeding state assignment matrix:

	0	1	2	3	4	5	6	7	8
NS	*	-	-	-	-	-	-	-	-
PB2	-	*	-	-	-	-	-	-	-
PB1	-	-	*	-	-	-	-	-	-
SB2	-	-	-	δ	-	-	-	*	-
SB1	-	-	-	-	δ	-	-	-	*
DB2	-	-	-	-	-	δ	-	*	-
DB1	-	-	-	-	-	-	δ	-	*

Supplement S3: Specifying model constraints (in order of appearance in Results)

Survival (φ) *and Recruitment* (ψ): The analysis of pre-breeder survival and recruitment probabilities considered hidden states, representing robust and frail individuals, and deterministic changes in age. In addition, recruitment probabilities always depended on breeding state (i.e. the transition to subordinate and dominant breeder states) given the results of Lloyd *et al*. (2019). The majority of pre-breeders that survived from age 7 to 8 recruited to the breeding population, with only 14 pre-breeders recorded at age 8 and 1 pre-breeder at age 9. Age classes were lumped at ages ≥6 for survival and ages ≥8 for recruitment as there was a large enough sample size to estimate recruitment at age 7, but not survival. Robust and frail pre-breeder survival at age 0 was correlated with group assignment and so could not be estimated. Therefore, first-year survival was constrained to be equal between robust and frail pre-breeders in the base model, meaning that only heterogeneity remaining in the population at age 1 was considered (Fay *et al*. 2018). The first candidate set of models tested if groups differed in survival and recruitment probabilities (i.e. presence of individual heterogeneity), whilst treating age variation as a fixed effect (assuming the parameters to be different and independent of each other at every age). The second candidate set of models investigated at what age observed differences in survival and recruitment probabilities between groups became apparent or disappeared (i.e. onset age of individual heterogeneity detection & disappearance). This was done by constructing models independent of hidden states at various ages. Survival models testing for the onset of individual heterogeneity expression at older ages (4, 5 and ≥6) did not converge. The third candidate set of models tested hypotheses developed by van de Pol & Verhulst (2006) and modified by Hamel *et al*. (2018) for identifying within- and between-individual changes in heterogeneity (i.e. trends in individual heterogeneity with age). Age variation in survival and recruitment was treated as a continuous logit-linear relationship with different intercepts and slopes between groups (testing for individual heterogeneity changes between groups); with different intercepts and equal slopes between groups (testing for ontogenetic processes, or selection and ontogenetic processes depending on the population response); and constant (testing for selection processes only). To determine the population response, the most parsimonious survival and recruitment models were run without hidden states.

Table S3.1: Candidate list of survival (φ) models with a description of the tested hypothesis. Southern elephant seals at Marion Island were assigned to hidden states (PB1 & PB2) when entering the marked population at weaning. Superscripts and subscripts indicate variation or equality among pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states, and ages (a).

Model	Parameters	Hypothesis
	Survival (φ) – presence of individual heterogeneity	
1	$\varphi_{\mathrm{a}\ 0}^{\mathrm{PB1=PB2}} + \varphi_{\mathrm{a}\ 1,2,3,4,5,\geq 6}^{\mathrm{PB1\neq PB2}}$	Different survival probabilities between groups with age variation treated as a fixed effect.
2	$\varphi_{\mathrm{a}\ 0,1,2,3,4,5,\geq 6}^{\mathrm{PB1=PB2}}$	Equal survival probabilities between groups with age variation treated as a fixed effect.
3	$\varphi_{\mathrm{cst}}^{\mathrm{PB1\neq PB2}}$	Different survival probabilities between groups with no age variation.
4	$\varphi_{\mathrm{cst}}^{\mathrm{PB1=PB2}}$	Equal survival probabilities between groups with no age variation. Null model
	Survival (φ) – onset age of individual heterogeneity detection & disappearance	
5	$\varphi_{\mathrm{a}\ 0,1}^{\mathrm{PB1=PB2}} + \varphi_{\mathrm{a}\ 2,3,4,5,\geq 6}^{\mathrm{PB1\neq PB2}}$	Differences in survival probabilities between groups expressed from age 2.

6	$\varphi^{PB1=PB2}_{a\ 0,1,2} + \varphi^{PB1\neq PB2}_{a\ 3,4,5,\geq 6}$	Differences in survival probabilities between groups expressed from age 3.
7	$\varphi^{PB1=PB2}_{a\ 0,1,2,3} + \varphi^{PB1\neq PB2}_{a\ 4,5,\geq 6}$	Differences in survival probabilities between groups expressed from age 4.
8	$\varphi^{PB1\neq PB2}_{a\ 0,1,2,3,4,5} + \varphi^{PB1=PB2}_{a\ \geq 6}$	Differences in survival probabilities between groups disappear from age 6.
9	$\varphi^{PB1\neq PB2}_{a\ 0,1,2,3,4} + \varphi^{PB1=PB2}_{a\ 5,\geq 6}$	Differences in survival probabilities between groups disappear from age 5.
10	$\varphi^{PB1\neq PB2}_{a\ 0,1,2,3} + \varphi^{PB1=PB2}_{a\ 4,5,\geq 6}$	Differences in survival probabilities between groups disappear from age 4.
11	$\varphi^{PB1\neq PB2}_{a\ 0,1,2} + \varphi^{PB1=PB2}_{a\ 3,4,5,\geq 6}$	Differences in survival probabilities between groups disappear from age 3.
12	$\varphi^{PB1\neq PB2}_{a\ 0,1} + \varphi^{PB1=PB2}_{a\ 2,3,4,5,\geq 6}$	Differences in survival probabilities between groups disappear from age 2.
13	$\varphi^{PB1\neq PB2}_{a\ 0} + \varphi^{PB1=PB2}_{a\ 1,2,3,4,5,\geq 6}$	Differences in survival probabilities between groups disappear from age 1.
	Survival (φ) – trends in individual heterogeneity with age	
14	$\varphi^{PB1=PB2}_{a\ 0,1} + \varphi^{PB1\neq PB2}_{a\ \mathbf{2,3,4,5,\geq 6}(\text{linear}^{PB1\neq PB2})}$	Age variation treated as a logit-linear relationship from age 2 with different intercepts and slopes between groups. Variance changes between groups (Fig. 1G, H).
15	$\varphi^{PB1=PB2}_{a\ 0,1} + \varphi^{PB1\neq PB2}_{a\ \mathbf{2,3,4,5,\geq 6}(\text{linear}^{PB1=PB2})}$	Age variation treated as a logit-linear relationship from age 2 with different intercepts and equal slopes between groups. Ontogenetic processes (Fig. 1A, B), or selection and ontogenetic processes (Fig. 1E, F).
16	$\varphi^{PB1=PB2}_{a\ 0,1} + \varphi^{PB1\neq PB2}_{a\ 2:\geq 6}$	Different survival probabilities between groups from age 2 with no age variation. Selection processes only (Fig. 1C, D).

Table S3.2: Candidate list of recruitment (ψ) models with a description of the tested hypothesis. Southern elephant seals at Marion Island were assigned to hidden states (PB1 & PB2) when entering the marked population at weaning. Superscripts and subscripts indicate variation or equality among pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states, and ages (a).

Model	**Parameters**	**Hypothesis**
	Recruitment (ψ) – presence of individual heterogeneity	
17	$\psi^{PB1-SB\neq PB2-SB}_{a\ 5,6,7,\geq 8} + \psi^{PB1-DB\neq PB2-DB}_{a\ 6,7,\geq 8}$	Different recruitment probabilities between groups for subordinate and dominant first time breeders.
18	$\psi^{PB1-SB\neq PB2-SB}_{a\ 5,6,7,\geq 8} + \psi^{PB1-DB=PB2-DB}_{a\ 6,7,\geq 8}$	Different recruitment probabilities between groups for subordinate but not dominant first time breeders.
19	$\psi^{PB1-SB=PB2-SB}_{a\ 5,6,7,\geq 8} + \psi^{PB1-DB\neq PB2-DB}_{a\ 6,7,\geq 8}$	Different recruitment probabilities between groups for dominant but not subordinate first time breeders.
20	$\psi^{PB1-SB=PB2-SB}_{a\ 5,6,7,\geq 8} + \psi^{PB1-DB=PB2-DB}_{a\ 6,7,\geq 8}$	Equal recruitment probabilities between groups for subordinate and dominant first time breeders. Null model.
	Recruitment (ψ) – onset age of individual heterogeneity detection & disappearance	
21	$\psi^{PB1-SB=PB2-SB}_{a\ 5} + \psi^{PB1-SB\neq PB2-SB}_{a\ 6,7,\geq 8}$	Differences in recruitment probabilities between groups expressed from age 6.

22	$\psi_{\mathrm{a}\ 5,6}^{\mathrm{PB1-SB=PB2-SB}} + \psi_{\mathrm{a}\ 7,\geq 8}^{\mathrm{PB1-SB\neq PB2-SB}}$	Differences in recruitment probabilities between groups expressed from age 7.
23	$\psi_{\mathrm{a}\ 5,6,7}^{\mathrm{PB1-SB=PB2-SB}} + \psi_{\mathrm{a}\ \geq 8}^{\mathrm{PB1-SB\neq PB2-SB}}$	Differences in recruitment probabilities between groups expressed from age 8.
24	$\psi_{\mathrm{a}\ 5,6,7}^{\mathrm{PB1-SB\neq PB2-SB}} + \psi_{\mathrm{a}\ \geq 8}^{\mathrm{PB1-SB=PB2-SB}}$	Differences in recruitment probabilities between groups disappear from age 8.
25	$\psi_{\mathrm{a}\ 5,6}^{\mathrm{PB1-SB\neq PB2-SB}} + \psi_{\mathrm{a}\ 7,\geq 8}^{\mathrm{PB1-SB=PB2-SB}}$	Differences in recruitment probabilities between groups disappear from age 7.
26	$\psi_{\mathrm{a}\ 5}^{\mathrm{PB1-SB\neq PB2-SB}} + \psi_{\mathrm{a}\ 6,7,\geq 8}^{\mathrm{PB1-SB=PB2-SB}}$	Differences in recruitment probabilities between groups disappear from age 6.
	Recruitment (ψ) – trends in individual heterogeneity with age	
27	$\psi_{\mathrm{a}\ 5,6,7(\mathrm{linear}^{\mathrm{PB1-SB\neq PB2-SB}})}^{\mathrm{PB1-SB\neq PB2-SB}} + \psi_{\mathrm{a}\ \geq 8}^{\mathrm{PB1-SB=PB2-SB}}$	Age variation treated as a logit-linear relationship up to age 7 with different intercepts and slopes between groups. Variance changes between groups (Fig. 1G, H).
28	$\psi_{\mathrm{a}\ 5,6,7(\mathrm{linear}^{\mathrm{PB1-SB=PB2-SB}})}^{\mathrm{PB1-SB\neq PB2-SB}} + \psi_{\mathrm{a}\ \geq 8}^{\mathrm{PB1-SB=PB2-SB}}$	Age variation treated as a logit-linear relationship up to age 7 with different intercepts and equal slopes between groups. Ontogenetic processes (Fig. 1A, B), or selection and ontogenetic processes (Fig. 1E, F).
29	$\psi_{\mathrm{a}\ 5:7}^{\mathrm{PB1-SB\neq PB2-SB}} + \psi_{\mathrm{a}\ \geq 8}^{\mathrm{PB1-SB=PB2-SB}}$	Different recruitment probabilities between groups up to age 7 with no age variation. Selection processes only (Fig. 1C, D).

Group assignment (π^{ind}): Assignment as robust or frail individual was further explored upon detecting individual heterogeneity in pre-breeder survival, recruitment and detection probabilities. Correlations between group assignment probabilities and various time- and density-related covariates were investigated.

Table S3.3: Candidate list of group assignment (π^{ind}) models with a description of the tested hypothesis. Southern elephant seals at Marion Island were assigned to hidden states when entering the marked population at weaning. Subscripts indicate time- and density-related covariates.

Model	**Parameters**	**Hypothesis**
30	π_{cst}	Group assignment probability constant. Null model.
31	$\pi_{\mathrm{cohort\ year}}$	Group assignment probabilities vary annually. This serves as a proxy for any annual variation in environmental effects.
32	$\pi_{1983:1997,1998:2009}$	Group assignment probabilities vary between 1983-1997 (population decrease) and 1998-2009 (population increase; Pistorius *et al*. 2011).
33	$\pi_{\mathrm{cohort\ size}}$	Group assignment probabilities depend on cohort size (number of pups produced per breeding season).
34	$\pi_{\mathrm{cohort\ sex\ ratio}}$	Group assignment probabilities depend on cohort sex ratio (proportion of male to female pups; Trivers-Willard hypothesis; Trivers & Willard 1973).

Detection (p): Resight abilities may differ among field researchers, which would result in detection differences among years. Seals grouped according to a particular state may behave more similarly than seals of another state. These behavioural differences may translate into different detection probabilities. However, subordinate and dominant breeders likely have the same detection probabilities given the results of Lloyd *et al.* (2019). Individuals with one tag are less likely to be resighted as a marked animal than individuals with two tags. Therefore, detection models were structured according to year, state (hidden and breeding) and number of tags.

Table S3.4: Candidate list of detection (p) models with a description of the tested hypothesis. Southern elephant seals at Marion Island were assigned to hidden states (PB1 & PB2) when entering the marked population at weaning. Superscripts and subscripts indicate variation or equality among pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states, pre-breeders with two tags (T2) and one tag (T1), and years (t).

Model	Parameters	Hypothesis
35	$p_{\mathrm{t\ 1984-2016}}^{\mathrm{PB1=PB2=SB=DB}}$	Differences in detection probabilities across years but not among breeding states, hidden states and number of tags.
36	$p_{\mathrm{cst}}^{\mathrm{PB1-T2\neq PB1-T1\neq PB2-T2\neq PB2-T1\neq SB=DB}}$	Differences in detection probabilities among breeding states, hidden states and number of tags but not years.
37	$p_{\mathrm{cst}}^{\mathrm{PB1\neq PB2\neq SB=DB}}$	Differences in detection probabilities among breeding states and hidden states but not number of tags and years.
38	$p_{\mathrm{cst}}^{\mathrm{PB1=PB2\neq SB=DB}}$	Differences in detection probabilities among breeding states but not hidden states, number of tags and years.
39	$p_{\mathrm{cst}}^{\mathrm{PB1=PB2=SB=DB}}$	Equal detection probabilities among breeding states, hidden states, number of tags and years. Null model.

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Supplement S4: Projecting the population model

Age- and stage-structured population matrix ***A*** assumed a post-breeding census and annual projection interval for male elephant seals. As this was a single-sex matrix, individuals entered the matrix at weaning (age 0) without replacement (i.e. no fertility estimates). The pre-breeder (PB) component was age structured from age 0 to 7, with recruitment to the subordinate (PB–SB) and dominant (PB–DB) breeder states starting at age 5 and 6, respectively. Pre-breeders that did not recruit by age 8 were removed from the matrix (i.e. 0 survival probability from age 7 to age 8), as only n = 14 pre-breeders were recorded at age 8 in the observed population (Lloyd *et al*. 2019). The subordinate breeder (SB) component was age structured from age 5 to 11 and the dominant breeder (DB) component from age 6 to 11. Subordinate breeders could become dominant (SB–DB) from age 6, whilst dominant breeders could lose their status and become subordinate (1 – DB–DB) from age 7. Diagonal elements represented the probability of surviving (φ) and remaining in the same breeding state (1 – ψ). Sub-diagonal elements represented the probability of surviving (φ) and transitioning (ψ) to a different breeding state. Probabilities were derived from estimates of the most parsimonious survival and recruitment (including future breeding state) models from this study. Two separate population matrices were constructed for robust and frail pre-breeders. A total of 260 pups (average number of male pups produced annually from 1985 to 2016 assuming a 1:1 sex ratio; Pistorius *et al*. 2011) were divided between matrices according to the group assignment probability (π^{ind}) estimated in model 30 (Table S3.3). The population matrix was projected in R 3.5.2 (R Core Team 2019).

$$\left[\begin{array}{ccccccccccc}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
\varphi_0^{\mathrm{PB}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & \varphi_1^{\mathrm{PB}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & \varphi_2^{\mathrm{PB}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & \varphi_3^{\mathrm{PB}} & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \varphi_4^{\mathrm{PB}}(1 - \psi_5^{\mathrm{PB-SB}}) & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \varphi_5^{\mathrm{PB}}(1 - \psi_6^{\mathrm{PB-SB}})(1 - \psi_6^{\mathrm{PB-DB}}) & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \varphi_6^{\mathrm{PB}}(1 - \psi_7^{\mathrm{PB-SB}})(1 - \psi_7^{\mathrm{PB-DB}}) & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \varphi_4^{\mathrm{PB}}\psi_5^{\mathrm{PB-SB}} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \varphi_5^{\mathrm{PB}}\psi_6^{\mathrm{PB-SB}} & 0 & 0 & \varphi_5^{\mathrm{SB}}(1 - \psi_6^{\mathrm{SB-DB}}) & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \varphi_6^{\mathrm{PB}}\psi_7^{\mathrm{PB-SB}} & 0 & 0 & \varphi_6^{\mathrm{SB}}(1 - \psi_7^{\mathrm{SB-DB}}) & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \varphi_7^{\mathrm{PB}}\psi_8^{\mathrm{PB-SB}} & 0 & 0 & \varphi_7^{\mathrm{SB}}(1 - \psi_8^{\mathrm{SB-DB}}) \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \varphi_5^{\mathrm{PB}}\psi_6^{\mathrm{PB-DB}} & 0 & 0 & \varphi_5^{\mathrm{SB}}\psi_6^{\mathrm{SB-DB}} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & \varphi_6^{\mathrm{PB}}\psi_7^{\mathrm{PB-DB}} & 0 & 0 & \varphi_6^{\mathrm{SB}}\psi_7^{\mathrm{SB-DB}} & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & \varphi_7^{\mathrm{PB}}\psi_8^{\mathrm{PB-DB}} & 0 & 0 & \varphi_7^{\mathrm{SB}}\psi_8^{\mathrm{SB-DB}} \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0
\end{array}\right.$$

$$\left.\begin{matrix}
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \varphi_6^{DB}(1 - \psi_7^{DB-DB}) & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \varphi_7^{DB}(1 - \psi_8^{DB-DB}) & 0 & 0 & 0 & 0 \\
\varphi_8^{SB}(1 - \psi_9^{SB-DB}) & 0 & 0 & 0 & 0 & 0 & \varphi_8^{DB}(1 - \psi_9^{DB-DB}) & 0 & 0 & 0 \\
0 & \varphi_9^{SB}(1 - \psi_{10}^{SB-DB}) & 0 & 0 & 0 & 0 & 0 & \varphi_9^{DB}(1 - \psi_{10}^{DB-DB}) & 0 & 0 \\
0 & 0 & \varphi_{10}^{SB}(1 - \psi_{11}^{SB-DB}) & 0 & 0 & 0 & 0 & 0 & \varphi_{10}^{DB}(1 - \psi_{11}^{DB-DB}) & 0 \\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & \varphi_6^{DB}(\psi_7^{DB-DB}) & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & \varphi_7^{DB}(\psi_8^{DB-DB}) & 0 & 0 & 0 & 0 \\
\varphi_8^{SB}\psi_9^{SB-DB} & 0 & 0 & 0 & 0 & 0 & \varphi_8^{DB}(\psi_9^{DB-DB}) & 0 & 0 & 0 \\
0 & \varphi_9^{SB}\psi_{10}^{SB-DB} & 0 & 0 & 0 & 0 & 0 & \varphi_9^{DB}(\psi_{10}^{DB-DB}) & 0 & 0 \\
0 & 0 & \varphi_{10}^{SB}\psi_{11}^{SB-DB} & 0 & 0 & 0 & 0 & 0 & \varphi_{10}^{DB}(\psi_{11}^{DB-DB}) & 0
\end{matrix}\right]$$

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Supplement S5: Additional results

Table S5.1: Finite-mixture models for detection probabilities (p) of male southern elephant seals at Marion Island. Pre-breeders were assigned to hidden states (PB1 & PB2) when entering the marked population at weaning. Superscripts and subscripts indicate variation or equality among pre-breeder (PB), subordinate breeder (SB) and dominant breeder (DB) states, number of tags (-T2 & -T1) and years (t). Small sample corrected quasi-likelihood Akaike's Information Criterion (QAIC$_c$; $\hat{c}$ = 1.7) was used to select models, with the following measurements: ΔQAIC$_c$ (the difference in QAIC$_c$ between the model with the lowest QAIC$_c$ value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood). The model in bold font was used to derive estimates.

Model	Parameters	ΔQAIC$_c$	ω_i	K	Deviance
35	$p_{\mathrm{t\ 1984-2016}}^{\mathrm{PB1=PB2=SB=DB}}$	346.95	0.00	67	290.99
36	$\boldsymbol{p}_{\mathbf{cst}}^{\mathbf{PB1-T2\neq PB1-T1\neq PB2-T2\neq PB2-T1\neq SB=DB}}$	**0.00**	**1.00**	**48**	**398.95**
37	$p_{\mathrm{cst}}^{\mathrm{PB1\neq PB2\neq SB=DB}}$	15.96	0.00	45	425.90
38	$p_{\mathrm{cst}}^{\mathrm{PB1=PB2\neq SB=DB}}$	366.91	0.00	36	542.12
39	$p_{\mathrm{cst}}^{\mathrm{PB1=PB2=SB=DB}}$	368.00	0.00	35	557.64

Detection probabilities were dependent on hidden states and breeding states, as well as number of tags (model 36, Table S5.1). Robust pre-breeders with two tags (0.97; CI: 0.96, 0.98) and one tag (0.97; CI: 0.94, 0.98) were more likely to be detected than frail pre-breeders with two tags (0.41; CI: 0.34, 0.48) and one tag (0.17; CI: 0.10, 0.28). Subordinate and dominant breeders had a similarly high detection probability as robust pre-breeders (0.95; CI: 0.90, 0.97).

Table S5.2: Parameter estimates (maximum likelihood estimate with 95% confidence intervals) on the logit scale of the most parsimonious survival (φ, model 15), recruitment (ψ, model 24), group assignment (π^{ind}, model 33) and detection (p, model 36) models. Superscripts indicate pre-breeder (PB1 – robust, PB2 – frail), subordinate breeder (SB) and dominant breeder (DB) states, and number of tags (T2 – two tags, T1 – one tag). Subscripts indicate specific ages (a), years (t) or regression parameters.

Parameters	**Estimate**	**Lower 95% confidence interval**	**Upper 95% confidence interval**
Survival (φ)			
$\varphi_{\mathrm{a}\ 0}^{\mathrm{PB1=PB2}}$	0.47	0.33	0.60
$\varphi_{\mathrm{a}\ 1}^{\mathrm{PB1=PB2}}$	1.34	1.16	1.52
$\varphi_{\mathrm{intercept}}^{\mathrm{PB1}}$	1.02	0.89	1.14
$\varphi_{\mathrm{intercept}}^{\mathrm{PB2}}$	-0.19	-0.40	0.02
$\varphi_{\mathrm{slope}}^{\mathrm{PB1=PB2}}$	-0.15	-0.24	-0.05
Recruitment (ψ)			
$\psi_{\mathrm{a}\ 5}^{\mathrm{PB1-SB}}$	-3.60	-4.26	-2.95
$\psi_{\mathrm{a}\ 6}^{\mathrm{PB1-SB}}$	-1.39	-1.72	-1.06
$\psi_{\mathrm{a}\ 7}^{\mathrm{PB1-SB}}$	0.44	0.05	0.82
$\psi_{\mathrm{a}\ 5}^{\mathrm{PB2-SB}}$	-69.17	-69.17	-69.17
$\psi_{\mathrm{a}\ 6}^{\mathrm{PB2-SB}}$	-2.12	-3.65	-0.58
$\psi_{\mathrm{a}\ 7}^{\mathrm{PB2-SB}}$	-2.47	-6.49	1.56
$\psi_{\mathrm{a}\ \geq 8}^{\mathrm{PB1-SB=PB2-SB}}$	0.75	-0.02	1.52
$\psi_{\mathrm{a}\ 6}^{\mathrm{PB1-DB=PB2-DB}}$	-3.32	-4.04	-2.59
$\psi_{\mathrm{a}\ 7}^{\mathrm{PB1-DB=PB2-DB}}$	-1.42	-2.04	-0.81
$\psi_{\mathrm{a}\ \geq 8}^{\mathrm{PB1-DB=PB2-DB}}$	-0.06	-0.96	0.85
Group assignment (π^{ind})			
$\pi_{\mathrm{intercept}}^{\mathrm{ind}}$	0.24	0.07	0.42
$\pi_{\mathrm{slope}}^{\mathrm{ind}}$	-0.20	-0.33	-0.07
Detection (p)			
$p_{\mathrm{cst}}^{\mathrm{PB1-T2}}$	3.52	3.08	3.95
$p_{\mathrm{cst}}^{\mathrm{PB1-T1}}$	3.40	2.67	4.13
$p_{\mathrm{cst}}^{\mathrm{PB2-T2}}$	-0.37	-0.66	-0.08
$p_{\mathrm{cst}}^{\mathrm{PB2-T1}}$	-1.57	-2.19	-0.95
$p_{\mathrm{cst}}^{\mathrm{SB=DB}}$	2.87	2.19	3.54

Chapter 4: *Life-history consequences of density-dependent drivers among breeders*

Density-dependent drivers of male actuarial senescence, breeding improvement and recruitment age in a highly polygynous marine mammal

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Dominant male southern elephant seal vocalising at Ship's Cove (Marion Island, 2016).
Photo: Kyle J. Lloyd

Abstract

1. Polygynous males allocate substantial resources to secondary sexual traits and behaviours to improve their chances of winning male-male interactions for mates. Competition intensity for mating opportunities is often determined by local densities of males and females. Yet few studies assess whether polygynous male resource allocation decisions are density-dependent.
2. We investigated density-dependent drivers of age-specific life-history traits in male southern elephant seals (*Mirounga leonina*) using a 34-year dataset collected at Marion Island. Specifically, we determine whether density-dependent factors affect actuarial (survival) senescence, breeding improvement (measured as social status) and recruitment age. Linear models that tested biological hypotheses were fitted to the data and selected using an information theoretic approach.
3. Actuarial senescence depended on relative beach costs accumulated by individual males with age. Beach costs were higher for males that dominated harems with more females than the population average. Males that had accumulated above average beach costs for their age had higher baseline mortalities than males with below average beach costs. This suggests that males allocated more resources to reproduction and less to body maintenance at all ages when defending and servicing large harems. Thus, in addition to attempting to obtain dominance, males also paid a reproductive cost for breeding successfully that depended on harem size.
4. Males born in years with relatively few pups were more likely to be dominant breeders than males born in years with many pups. Similarly, males were more likely to recruit to the breeding population at an earlier age when their birth cohort size was small. Thus, breeding success and recruitment age depended on population density during early life.
5. We provide valuable insight into how density-dependent factors interact with intrinsic determinants of resource allocation, such as age and breeding state, to determine variation in polygynous male demographic traits.

Keywords: breeding social status, cohort size, intrinsic state, male life history, Marion Island, reproductive costs, southern elephant seal, trade-off hypothesis

Introduction

Senescence is the within-individual deterioration of body condition and function with age, and is widespread among different taxa (Nussey *et al*. 2013). Life-history theory predicts that one mechanism of senescence involves trade-offs in resource allocation between reproduction and body maintenance (disposable soma theory; Kirkwood 1977; Stearns 1992). Selection should optimize life-history trade-offs under prevailing external conditions so as to maximise reproductive success (Roff & Fairbairn 2007). Therefore, environmental and demographic factors that affect costs of reproduction will influence resource allocation decisions and, potentially, senescence patterns (Rodríguez-Muñoz *et al*. 2019). Variation in senescence rates has been shown to occur among metapopulations (Holand *et al*. 2016) and between individuals (Beirne *et al*. 2015) that experience different external conditions. The sensitivity and magnitude of these extrinsic effects depend on the intrinsic state of an organism (Moorad *et al*. 2019). For example, males and females often differ in senescence rates (Lemaître *et al*. 2015), likely as a result of differences in the intensity of intra-sexual reproductive competition (Williams 1957). The sex that experiences stronger competition will suffer higher costs to body maintenance, because more resources are allocated to reproduction (Bonduriansky *et al*. 2008). Mortality risk also increases as more confrontations occur between individuals of the same sex, which reduces selective pressure against deleterious alleles at old ages (mutation accumulation theory; Medawar 1952; antagonistic pleiotropy theory; Williams 1957). The sex experiencing stronger competition should then also show greater variation in senescence patterns when environmental and demographic factors alter competition intensity (Beirne *et al*. 2015) or prevent somatic repair (e.g. natal conditions; Lemaître *et al*. 2014). Investigating changes in the relationship between external conditions and resource allocation to reproduction are essential to understand how life-history evolution is shaped (Gaillard & Lemaître 2017).

As the majority of mammal species employ polygyny as a breeding strategy, males commonly experience stronger intra-sexual reproductive competition than females (sexual selection theory; Clutton-Brock 1989). For example, polygynous males often show earlier onset and steeper rates of senescence than females when compared to monogamous species (“live fast, die young” strategy; Clutton-Brock & Isvaran 2007; but see Bonduriansky *et al*. 2008). In females of polygynous species, reproductive costs mostly result from lactation rather than gestation (Froy *et al*. 2016). However, potential costs from lactation may instead be borne by immediate offspring through the manipulation of milk quality and quantity (Lavigne *et al*.

1982), thus allowing mothers to reduce trade-offs and maximise their own lifetime reproductive success (prudent parent hypothesis; Drent & Daan 1980; Martin & Fest-Bianchet 2010). In polygynous males, reproductive costs mostly arise from trying to obtain dominance than from actually breeding successfully (Festa-Bianchet *et al*. 2019; Lloyd *et al*. 2019). Males allocate substantial resources to the growth and maintenance of secondary sexual traits and behaviours to better their chances of winning male-male competitions for mates, but with no guarantee of success (Preston *et al*. 2003). As polygynous males do not contribute to parental care (Clutton-Brock 1989), they cannot foist costs to offspring. Therefore, male resource allocation decisions are generally sensitive to external conditions affecting competition intensity and natal origins (Loison *et al*. 1999; Coulson *et al*. 2001; Beirne *et al*. 2015), which can perpetuate sex-biased vital rates (Toïgo & Gaillard 2003). Understanding how and why polygynous male resource allocation decisions vary is paramount to conservation and management initiatives that often assume sexes are equivalent in life-history traits (Rankin & Kokko 2007).

In mate-defence polygyny, density-dependent factors determine the amount of effort required by males to obtain and maintain social dominance of female harems. This is because competition intensity for mates varies with (1) the number of male competitors, (2) the relative number of males to females, and (3) male age structure. Although related, all three measures of density need to be considered because they are not necessarily correlated (Mysterud *et al*. 2002a) and could interact with density-independent factors in different ways (Coulson *et al*. 2001). With high densities of males, the probability for males to interfere with one another’s dominance is greater (Kokko & Rankin 2006), meaning that more energy is expended in male-male interactions and the risk of injury increases (Beirne *et al*. 2015). Competition intensity is also affected by the relative density of females to males (adult/tertiary/operational sex ratio). Few females relative to males increases aggression among males competing for limited mating opportunities, resulting in increased mortality and emigration, and decreased breeding success of males or even females (Le Galliard *et al*. 2005). More females relative to males provides more mating opportunities, which increases participation of young males (earlier recruitment) and male breeding success (Stevenson & Bancroft 1995), and reduces rates of actuarial senescence (Rodríguez-Muñoz *et al*. 2019). Lastly, long-lived species often have strongly age-structured populations meaning that competition intensity can vary according to the density of individuals per age class (Festa-Bianchet *et al*. 2003). Generally, the competitive ability of males increases with age as a result of selection for high-quality individuals (selection hypothesis; Forslund & Pärt 1995) and/or individual improvement due to experience (restraint and constraint hypotheses; Pianka 1976; Curio 1983; Nol & Smith 1987). Therefore, competition intensity is reduced when older, experienced males are removed from the population (e.g. through trophy hunting), causing younger, inexperienced males to allocate more resources to participate in breeding events (Milner *et al*. 2007).

Despite accumulating evidence that male resource allocation decisions are density-dependent, population theory remains strongly female biased. More studies that focus on males are needed to establish the sex-specific role of density-dependence in male population theory (reviewed by Hamel *et al*. 2010; Lemaître & Gaillard 2017). The highly polygynous and competitive life history of male southern elephant seals (*Mirounga leonina*, hereafter elephant seals) provides a unique opportunity to investigate how density-dependent factors affect reproductive costs and, thus, resource allocation decisions of polygynous males in general. Fluctuations in global elephant seal population trends over recent decades (McMahon *et al*. 2005) provide natural variation in density-dependent factors that may influence resource allocation decisions. Male elephant seals compete for dominance of female harems over an annual three-month breeding season during which they do not supplement stored body reserves (Le Boeuf & Laws 1994). Thus, dominance is often determined by body size (winning fights) and resource holding potential (fasting endurance; McCann 1981; Modig 1996; Galimberti *et al*. 2007). Dominant males defend their mating rights from subordinate males and service oestrus females regularly (Laws 1956). Competition for mates is generally intense as only a fraction of recruited males become dominant (Galimberti *et al*. 2002). Subordinate males may employ “sneaking” tactics to mate females, but this is relatively infrequent compared to dominant male paternity rates (Le Boeuf & Laws 1994; Hoelzel *et al*. 1999; Wilkinson & van Aarde 1999). Male elephant seal vital rates are age- and breeding state-structured (Lloyd *et al*. 2019). Both subordinate and dominant males experience actuarial senescence concurrently with age-related breeding improvement after the age of first reproduction, which suggests that reproductive costs occur (Lloyd *et al*. 2019). Specifically, costs of attempting to obtain dominance by subordinate males appear to be greater than costs of maintaining dominance (Lloyd *et al*. 2019). Furthermore, surviving dominant males are more likely to maintain their social status than subordinates are in obtaining dominance in the following breeding event (Lloyd *et al*. 2019). Males also show variation in recruitment age after becoming sexually mature at age 4 (Laws 1956; Jones 1981).

None of these observations consider how density may alter patterns in male elephant seal life-history traits.

We use 34 years of mark-recapture data of elephant seals at Marion Island to investigate possible density-dependent causes of variation in male resource allocation decisions. We evaluate the extent to which patterns in (a) actuarial senescence, (b) breeding improvement (measured as social status), and (c) recruitment age can be explained by several measures of density-dependent factors related to competition intensity and natal conditions. Given near perfect detection probabilities and similar tag loss rates among recruited males of this population (Lloyd *et al*. 2019), we use linear models testing biological hypotheses to determine if male life-history traits are density-dependent. We also consider intrinsic effects, such as age, breeding state and experience, which may interact with density-dependent factors in different ways. In many polygynous species, body mass at weaning is a strong intrinsic predictor of survival (Oosthuizen *et al*. 2018), and may be correlated with other life-history traits such as competitive performance which is linked to breeding success (Rödel & von Holst 2009). Because weaning masses were only available for a subsample of males from our study population, we perform a separate analysis to determine which density-dependent factors influence (d) pup weaning mass across cohorts.

Methods

Male southern elephant seals at Marion Island

Elephant seals at Marion Island have been monitored at an individual (mark-recapture) and population (census counts) level since 1983 (Pistorius *et al*. 2011). Almost all pups born at the island were tagged with two livestock tags on the hind flippers each breeding season, with tags containing information about cohort and individual identity. Beaches were surveyed regularly inside (7-day intervals) and outside (10-day intervals) of breeding seasons, during which both tagged and untagged individuals were recorded according to age group and breeding state (or social status). For each breeding season, the sum total of all individuals at the island were tallied on 15 October – the peak haul-out date for this colony (Condy 1979). Life-history traits of males from the Marion Island population are age- and breeding state-structured, detection probabilities are high across years (p = 0.95 ± SD 0.05) and tag loss probabilities are constant for all adult ages and similar between tagging positions (see Lloyd *et al*. 2019 for details). Individuals of the same age and breeding state do not differ much in survival probabilities (σ = 0.000017), but do show differences in breeding success (i.e. the probability of being dominant; σ = 0.23; Lloyd *et al*. 2019). Therefore, individual heterogeneity in breeding success is likely prevalent and needs to be taken into account when making predictions.

Data analysis

Only males that had recruited to the breeding population were considered when predicting (a) actuarial senescence, (b) breeding improvement and (c) recruitment age. This provided a dataset of 291 individuals with complete life histories (i.e. birth to 'apparent' death) and 35 individuals with incomplete life histories (i.e. still alive at time of study). Several density-dependent factors related to competition intensity and natal conditions were investigated as covariates of these demographic traits (Supp. S1).

Two covariates that are not intuitive and require additional explanation include (1) relative breeding experience and (2) relative beach cost. (1) For each year an individual was alive, the number of times it had previously been a subordinate and dominant male was tallied separately for each breeding state to gain some indication of past breeding experience. Breeding experience as a subordinate and/or dominant male was then expressed as a relative measure compared to the population average at each age class. (2) The cost of hauling out at a particular beach was determined by the average number of breeding females (Table S1.2) and associated number of subordinate challengers (Figure S1.1) observed at each beach during the study period. Males were assigned weighted scores depending on their breeding state and if they were dominant at beaches with below or above average harem sizes (11.27 females being the population average). Beach cost was scored as follows: 1 = subordinate male, 2 = dominant males of beaches with below average harem sizes (<12 females), 3 = dominant males of beaches with above average harem sizes (≥12 females). These scores accumulated as an individual aged and were expressed as a relative measure compared to the population average at each age class.

Intrinsic effects that may interact with density-dependent factors were included as well. Multicollinearity was checked using variance inflation factors, with a threshold of 5 (O'Brien 2007). Linear models representing biological hypotheses about the structure of male life-history traits (Table S2.2) were fitted and selected using an information-theoretic approach (Akaike's Information Criterion, AIC_c) in R 3.5.2 (R Core Team 2019). Where models were equivalent ($\Delta AIC \leq 2$; Burnham & Anderson 2004), the simpler model (fewer parameters) was favoured. Predicted estimates of the most parsimonious models were reported as the mean, and lower and upper 95% confidence interval.

a) *Actuarial senescence*

Generalized linear models (R package 'stats') were fitted to mark-recapture data coded as 1 (alive) and 0 (dead) each "seal year" for males with complete life histories. A seal year began at the beginning of a breeding season and ended before the start of the following breeding season. Few males skipped breeding seasons ($n = 43$ of 726 cases) and adult males were equally detectable (goodness-of-fit Test 2.CT in Lloyd *et al*. 2019). Thus, animals not seen for consecutive years were presumed to have died and not temporarily emigrated. Given the findings of Lloyd *et al*. (2019), a base model was established by fitting survival data to age (linear), polynomials of age (quadratic), logarithm of age, breeding state (subordinate and dominate) and relative dominance (number of times previously and currently dominant relative to the population average at each age class; Table S2.1). As few age classes were examined (between ages 5 to 14), age was scaled in the quadratic model to prevent correlation between age and age^2.

b) *Breeding improvement*

Generalised linear mixed models (R package 'lme4'; Bates *et al*. 2015) were fitted to mark-recapture data coded as 1 (dominant) and 0 (subordinate) each annual breeding season for males with complete life histories. Thus, breeding success was measured as the probability to be dominant. Males seen as both dominant and subordinate during the same breeding season were assigned the breeding state that the individual most frequently occupied during that breeding event. Particular attention was paid to the breeding state occupied during the middle and late breeding season when dominant males most likely impregnate oestrus females (Le Boeuf & Laws 1994). A base model was established by fitting breeding success data to age (linear), polynomials of age (quadratic) and logarithm of age. An individual random effect was included to account for any unobservable individual variation not explained by age alone (Caswell & Vindenes 2018; Lloyd *et al*. 2019).

c) *Recruitment age*

Linear models (R package 'stats') were used to fit covariates that may explain the age at which males recruited to the breeding population. Individuals with complete and incomplete life histories were included. Recruitment age was determined when an individual was first seen participating in a breeding season, which ranged from 5 to 10 years of age. Pre-breeders generally do not haul out at Marion Island during the breeding season (Condy 1979). Therefore, each individual had an assigned recruitment age with several associated covariates that may explain why the individual recruited then. A base model was established by fitting recruitment age to no covariate affect (intercept only model), breeding state at recruitment, year of recruitment, and cohort of recruit.

d) *Pup weaning mass*

Elephant seal pups along a specific stretch of coastline were weighed shortly after weaning (1-3 days) between 1998 and 2018 (except for the 2000, 2001 and 2008 breeding seasons); providing a sample size of n = 887 male pups from 18 cohorts (mean = 120.24 kg ± SD 22.38 kg). Pups were rolled into a sling net and weighed with a calibrated scale suspended on a pole between two field researchers (Oosthuizen *et al*. 2015). Pup mass was calculated by subtracting the mass of the net taken directly after weighing. Predictors of weaning mass for individuals of the same study population include site, sex, female population size and chlorophyll-a concentration with year treated as a random effect (see Oosthuizen *et al*. 2015). Given our aims, we used linear mixed models (R package 'lme4') to fit weaning mass to site as a fixed effect and year as a random effect in the base model. Sites differ in quality as breeding areas (Mulaudzi *et al*. 2008) and available sample size as some harems are generally larger than others across years. Year as a random effect separated between-year variance from within-year variance in weaning mass (Oosthuizen *et al*. 2015). We used the standardised (mean = 0, SD = 1) number of females per breeding season instead of the total number of females per breeding season; although birth cohort size was strongly correlated with the latter as females mostly give birth to a single pup (r = 0.98). Sex was not considered in the base model as only males were of interest. Density-independent factors, such as chlorophyll-a concentrations, were not investigated in this study.

Results

a) *Actuarial senescence*

The base model described male survival as decreasing linearly with age from recruitment (Table S2.1). Survival also depended on breeding state, with dominant males having higher survival probabilities than subordinate males for each respective age class. Relative beach cost explained additional variation in actuarial senescence patterns (model 3, Table 1). For both subordinate and dominant males, individuals that had above average beach costs for their age experienced higher baseline mortalities than individuals with below average beach costs (Figure 1). This means that males that were dominant of large harems (≥12 females) at some point in their breeding history accumulated higher reproductive costs than males that dominated small harems (<12 females). However, dominant males still had higher survival probabilities than subordinate males of the same age and relative beach cost. Therefore, subordinate and dominant male survival was a function of competition intensity expressed as weighted scores that captured the cumulative reproductive costs associated with defending and servicing female harems of different sizes.

b) *Breeding improvement*

The base model described male breeding success (the probability of being dominant) as increasing with age according to a logarithmic form, likely as a result of most old males obtaining and maintaining dominance for consecutive years (Table S2.1). Breeding success was also predicted by the natural log of cohort size at birth (model 17, Table 1). Cohort size was estimated by counting the total number of male and female pups born at Marion Island each breeding season. The natural log of cohort size was used because the number of females available to produce pups is finite, and thus the effects of cohort size may decrease with incremental increases in the number of pups (Stauffer *et al*. 2013). Males born in years with relatively few pups were more likely to be dominant at all adult ages than males born in years with many pups (Figure 2). However, males of the same age and cohort size still displayed sufficient variation in breeding success to suggest that individual heterogeneity was prevalent in this life-history trait ($\sigma = 0.74$).

There was some support for breeding success depending on recruitment age and relative dominant male breeding experience (model 13, but ω_{17}/ω_{13} = 2.55). Males that recruited at older ages were more likely to be first-time dominant breeders than younger recruits (Figure S3.1). As both age and individual heterogeneity were accounted for in model parametrisation, the increase in breeding success with age can be confidently attributed to breeding experience. Males with above average breeding experience for their age class were more likely to be dominant again than males with below average experience.

c) *Recruitment age*

The base model described male recruitment age as depending on the breeding state of the recruit at their first breeding event (Table S2.1). Males that were dominant at recruitment were generally older than males that recruited as subordinates. Similar to breeding improvement, recruitment age also increased with the natural log of cohort size at birth (model 22, Table 1). First-time subordinate males were more likely to recruit at ~age 6 when born in years with relatively few pups and at ~age 7 when born in years with many pups (Figure 3). First-time dominant males were more likely to recruit at ~age 7 when born in years with relatively few pups and at ~age 8 when born in years with many pups.

d) *Pup weaning mass*

Annual variation in average pup weaning mass was explained by the natural log of cohort size at birth, in addition to fixed (site) and random (year) effects of the base model (model 28, Table 1). Across all sites, pup weaning mass decreased with increasing pup production (Figure S3.2). In other words, weaned males were heavier on average when born in years with relatively few pups and lighter on average when born in years with relatively many pups. Predicted average pup weaning masses at the largest harem (or beach site) matched observed values (Figure 4).

Table 1: Intrinsic and density-dependent predictors of survival, breeding success, recruitment age and average pup weaning mass of male southern elephant seals at Marion Island. Small sample Akaike's Information Criterion (AIC_c) was used to select models, with the following measurements: ΔAIC_c (the difference in AIC_c between the model with the lowest AIC_c value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood). Models in bold font were used to derive estimates.

Model	Parameters	ΔAICc	ω_i	K	Deviance
	Survival				
1	age + breeding state	2.98	0.14	3	-453.24
2	age + breeding state + recruitment age	3.07	0.13	4	-452.27
3	**age + breeding state + rel. beach cost**	**0.00**	**0.61**	**4**	**-450.74**
4	age + breeding state + std number of breeding males	4.94	0.05	4	-453.20
5	age + breeding state + operational sex ratio	5.00	0.05	4	-453.24
6	age + breeding state + log birth cohort size	7.54	0.01	3	-455.52
7	age + breeding state + birth sex ratio	9.94	0.00	3	-456.72
	Breeding success				
8	log(age) + (1|id)	17.46	0.00	3	-377.25
9	log(age) + rel. subordinate male experience + rel. dominant male experience + (1|id)	2.63	0.14	5	-367.81
10	log(age) + rel. subordinate male experience + (1|id)	9.87	0.00	4	-372.44
11	log(age) + rel. dominant male experience + (1|id)	7.61	0.01	4	-371.31
12	log(age) + recruitment age + rel. subordinate male experience + rel. dominant male experience + (1|id)	3.62	0.08	6	-367.28
13	log(age) + recruitment age + rel. dominant male experience + (1|id)	1.87	0.20	5	-367.43
14	log(age) + recruitment age + (1|id)	4.72	0.05	4	-369.87
15	log(age) + std number of breeding males + (1|id)	13.93	0.00	4	-374.47
16	log(age) + operational sex ratio + (1|id)	7.13	0.01	4	-371.07
17	**log(age) + log birth cohort size + (1|id)**	**0.00**	**0.51**	**4**	**-367.51**
18	log(age) + birth sex ratio + (1|id)	18.35	0.00	4	-376.68
	Recruitment age				
19	breeding state	9.62	0.01	3	-427.50
20	breeding state + std number of breeding males	6.48	0.03	4	-424.90
21	breeding state + operational sex ratio	5.33	0.06	4	-424.33
22	**breeding state + log birth cohort size**	**0.00**	**0.86**	**4**	**-421.66**
23	breeding state + birth sex ratio	6.20	0.04	4	-424.76
	Pup weaning mass				
24	site + (1|year)	11.04	0.00	11	-3967.88
25	site + std number of breeding males + (1|year)	11.35	0.00	12	-3967.01
26	site + std number of breeding females + (1|year)	7.97	0.02	12	-3965.32
27	site + operational sex ratio + (1|year)	12.28	0.00	12	-3967.47
28	**site + log birth cohort size + (1|year)**	**0.00**	**0.93**	**12**	**-3961.33**
29	site + birth sex ratio + (1|year)	5.91	0.05	12	-3964.29

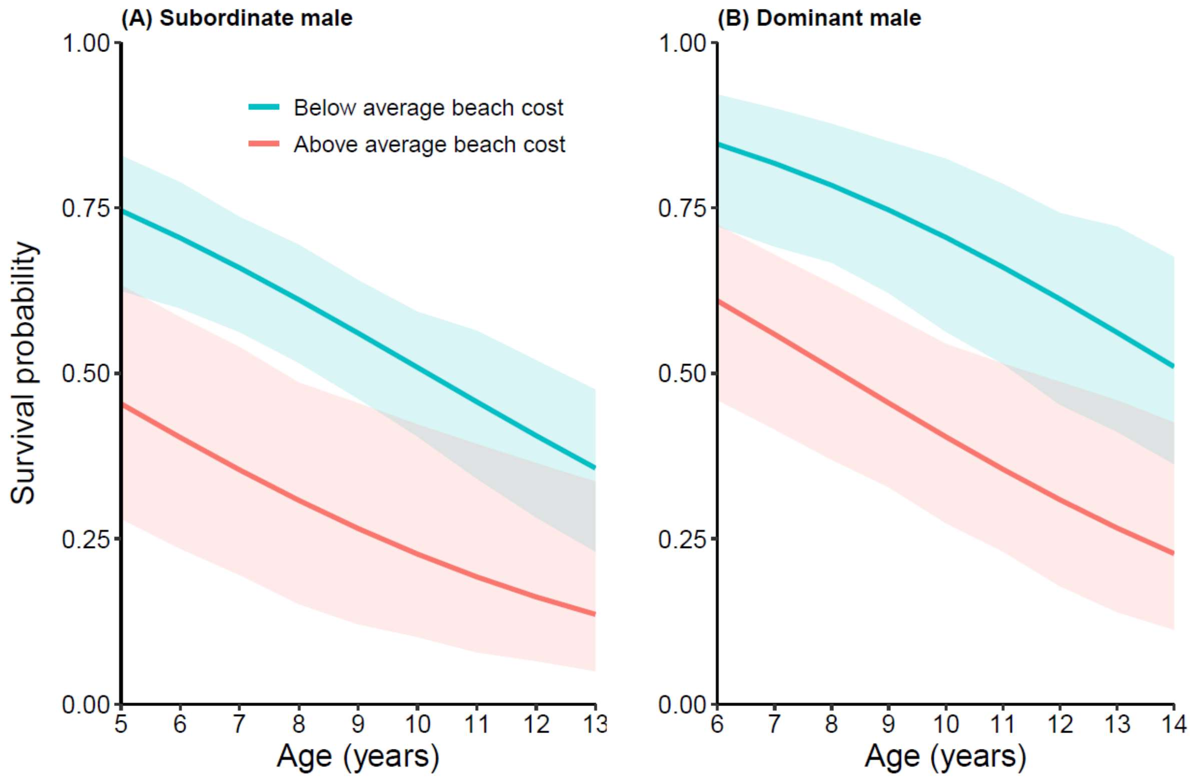

Figure 1: Mean predicted survival probabilities (±95% confidence interval) of male southern elephant seals at Marion Island. Estimates were derived from model 3 (Table 1), which treated age variation in subordinate and dominant male survival as a continuous logit-linear relationship. Survival also depended on relative beach costs accumulated by individuals with age. Beaches were assigned weighted scores based on average female harem size and associated numbers of subordinate males. Males with above average beach costs for their age class had higher baseline mortalities than males with below average beach costs. Plotted data used the minimum (-1.99) and maximum (3.24) relative beach costs observed in the population. The survival model was described as:
$logit(survival\ probability) = 1.64 - (0.21 \times age) + (0.84 \times breeding\ state) - (0.24 \times relative\ beach\ cost)$

Discussion

The general direction of resource allocation decisions may be predetermined through the evolution of specific life-history strategies, such as polygyny (Bonduriansky *et al*. 2008). Sexual selection in competitive breeding systems has driven males to allocate substantial resources to reproduction to secure mating opportunities at the cost of body maintenance. Hence, competing polygynous males often experience life-history trade-offs that are unavoidable. However, density-dependent factors can influence the extent to which males allocate resources towards attempting to secure and mate females. Conspecific density can influence the intensity of competition for mates among adult males, or competition for resources needed for growth and development among juveniles. We provide valuable insight into which density-dependent factors drive resource allocation decisions in the highly polygynous male southern elephant seal. Baseline mortalities increased when males accumulated costs from dominating harems that required more energy to defend and service than others. Males born of relatively small cohort sizes were more likely to breed consecutively as a dominant male than males born of large cohort sizes. Similarly, males recruited to the breeding population at earlier ages when born in years with low pup production. We discuss the possible mechanisms behind these density-dependent factors and the consequences for polygynous male life histories.

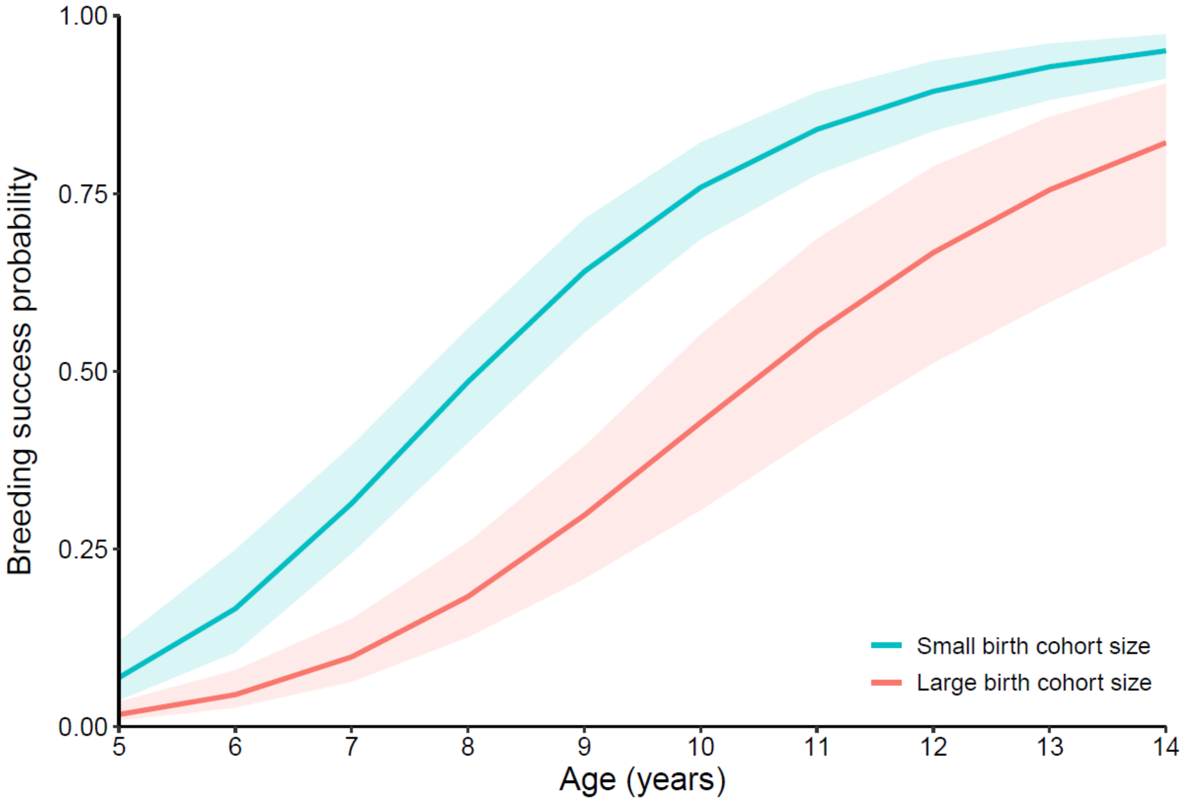

Figure 2: Mean predicted breeding success (probability of being dominant; ±95% confidence interval) of male southern elephant seals at Marion Island. Estimates were derived from model 17 (Table 1), which treated age variation in breeding success as a continuous logit-log relationship. Breeding success also depended on the natural log of cohort size at birth (number of pups produced annually). Males born of small cohort sizes were more likely to be dominant at all adult ages than males born of large cohort sizes. Plotted data used the minimum (420 pups) and maximum (700 pups) birth cohort sizes observed in the population. The breeding success model was described as:

$$logit(breeding\ success) = 5.71 + (5.40 \times log(age)) - (2.81 \times log(birth\ cohort\ size)) + 0.74$$

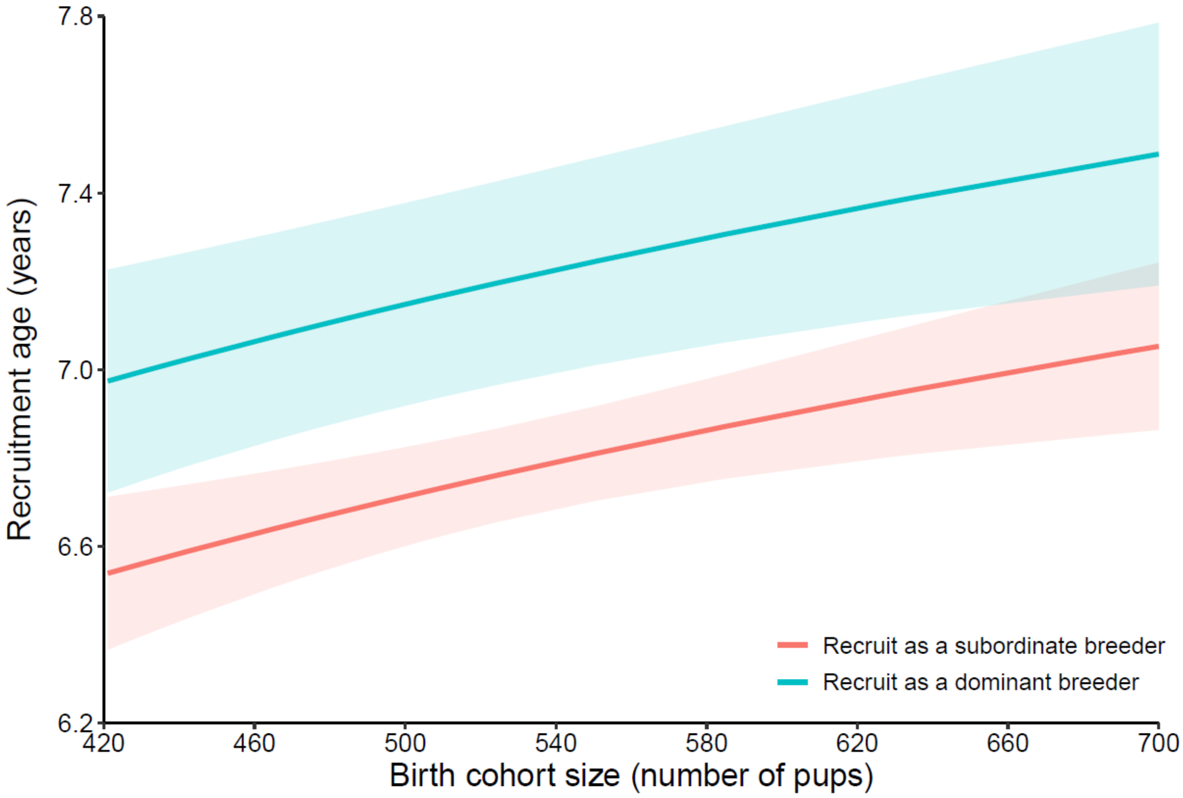

Figure 3: Mean predicted recruitment age (±95% confidence interval) of male southern elephant seals at Marion Island. Estimates were derived from model 22 (Table 1), which predicted that recruitment age increased linearly with the natural log of cohort size at birth (number of pups produced annually). For males born of the same birth cohort size, recruitment as first-time dominant breeders occurred at older ages than recruitment as first-time subordinate breeders. The recruitment age model was described as: $recruitment\ age = 0.43 + (0.44 \times breeding\ state) + (1.01 \times log(birth\ cohort\ size))$

Cumulative long-term reproductive costs of breeding successfully

Actuarial senescence depended on breeding state and accumulated reproductive costs associated with site-specific competitiveness. The short-term reproductive cost of attempting to breed is experienced by all breeding males (Lloyd *et al*. 2019). However, subordinate males have lower survival probabilities than dominant males, likely as a result of individual quality (Lloyd *et al*. 2019). Our new finding suggests that actuarial senescence not only differ between breeding states, but also within breeding states as a result of long-term reproductive costs from breeding successfully. Males that defended and serviced large harems at some point in their reproductive past accumulated above average reproductive costs as they aged. This “invest now, pay later” reproductive tactic resulted in higher baseline mortalities regardless of a male’s current breeding state (cumulative reproductive cost hypothesis; Aubry *et al*. 2009). Few studies such as ours have simultaneously tested for both short-term and cumulative long-term reproductive costs, especially in males (Kroeger *et al*. 2018). Although the cost of attempting to breed contributes to current survival trade-offs (Festa-Bianchet *et al*. 2019), defending and servicing females also comes at an energetic and physiological cost to polygynous males, including elephant seals. In terms of energetic costs, absolute and relative weight loss is positively related to the number of interactions with male challengers and receptive females, and time spent on land defending females (Galimberti *et al*. 2007). The rate of agonistic behaviour also increases with harem size (Modig 1996). In northern elephant seals (*Mirounga angustirostris*), dominant males lose more energy, blubber reserves and body water content than subordinate males when controlling for body size (Crocker *et al*. 2012). Although physiological costs have not been assessed in male elephant seals, prolonged exposure to stress hormones that peak during reproductive events (e.g. glucocorticoids; Romero 2002) impair immune response and the general health of other polygynous species (Girard-Buttoz *et al*. 2014).

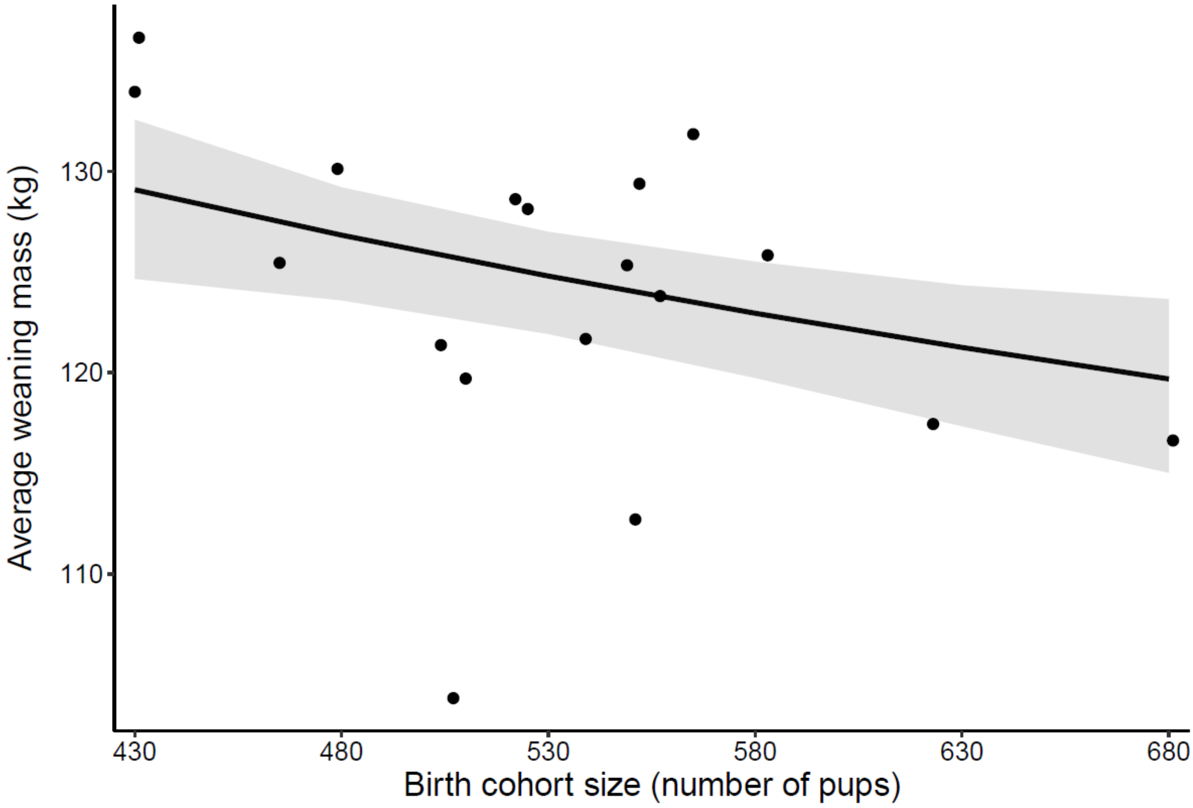

Figure 4: Mean predicted average pup weaning mass (±95% confidence interval) of male southern elephant seals born at Archway beach (MM007) as a representative example. Estimates were derived from model 28 (Table 1), which predicted pup weaning mass decreasing linearly with the natural log of cohort size at birth (number of pups produced annually). Points represent actual average pup weaning masses of each observed birth cohort size.

Our findings support the disposable soma theory of senescence, which predicts that males increase resource allocation to optimise reproduction under harsh environmental conditions (here in the form of competition intensity) at a greater cost to self-maintenance (Kirkwood & Rose 1991). Whilst mild environmental stressors may improve fitness by mobilising body resources (Girard-Buttoz *et al*. 2014), the elephant seal breeding season is highly stressful for a prolonged period of fasting (Laws 1956). Reproductive costs for polygynous males involve winning male-male interactions for mating opportunities (precopulatory competition) and successfully fertilising female eggs (postcopulatory competition); both of which covary positively when maximising breeding success (McDonald *et al*. 2017). Dominant male elephant seals are most active both aggressively and sexually when the number of oestrus females is greatest (McCann 1981). As harem size appears to be positively correlated with the number of associated males, dominant males of large harems may spend more energy patrolling beaches (depending on beach topography; Crocker *et al*. 2012) and lose more water through increased antagonistic vocalisations (respiratory evaporative water loss: Deutsch 1990; cutaneous water loss: Norris *et al*. 2010) against subordinate challengers. Not only is mating rate increased by the number of females per harem (Parker & Ball 2005), but under increasing risk of sperm competition (i.e. when more than one male can potentially mate a female), males across taxa allocate more sperm to each ejaculation to improve fertilisation rates (Parker 2016). Dominant male elephant seals must contend with subordinate males attempting to mate females on the periphery of harems and when intercepting departing females (McCann 1981). Thus, dominant males may increase sperm allocation to each mating event in the presence of subordinate competitors (e.g. delBarco-Trillo & Ferkin 2004), which consequently demands a higher energetic cost in the form of ejaculate expenditure (Dewsbury 1982). Thus, multiple environmental stressors in the form of pre- and postcopulatory competition can form synergies that accelerate senescence (Watson *et al*. 2015). Studies are needed to confirm if this pattern is universal among polygynous males or specific to particular breeding systems with intense male-male aggression (Loison *et al*. 1999).

Cohort-level natal effects of conspecific density

Males born during lower pup production years were more likely to recruit earlier and become dominant breeders. A similar trend occurs in female elephant seals of the same population, whereby females recruit earlier and fecundity increases with decreasing population size

(Pistorius *et al*. 2001). The effect of birth cohort size had long-term consequences for the demographic performance of breeding males (silver spoon hypothesis; Grafen 1988; Lindström 1999; Beckerman *et al*. 2003; Cam & Aubry 2011). This occurred at the cohort-level, meaning that similar resource allocation decisions were made among individuals of the same age (Beckerman *et al*. 2003). Cohort effects are observed in several taxa including insects (Kelly & Tawes 2013), mites (Beckerman *et al*. 2003), reptiles (Baron *et al*. 2010), birds (Lindström 1999), and mammals (Pigeon *et al*. 2017). Cohort size at birth is a density-dependent measure that could affect cohort resource allocation decisions at two distinct stages in male elephant seal life history: maternal dependency and juvenile independency (Garrott *et al*. 2012). Adulthood (i.e. participating in breeding events) is another distinct life-history stage, but density-dependent measures operating at this time were less likely to affect recruitment age and breeding success. Indeed, early-life environmental conditions typically explain up to 35-55% of variation in individual performance in large mammals (Hamel *et al*. 2009).

The number of pups produced per breeding season provides an indication of how many breeding females were competing for resources whilst pregnant and storing body resources for lactation (capital breeding system; Laws 1956; Hindell & Slip 1997). With fewer breeding females competing for limited resources, more resources may be made available to wean heavier pups (Oosthuizen *et al*. 2015; but see Bradshaw *et al*. 2002). In fact, we found that average male pup weaning mass decreased with increasing cohort size; a similar trend found in other polygynous species (Nussey *et al*. 2005; Pacoureau *et al*. 2017). Apart from intrinsic maternal factors such as age, breeding experience and breeding success, resource allocation to offspring varies according to prevailing environmental conditions that affect the mother's body condition and recovery (Fischer *et al*. 2011; Griffen 2018). Therefore, female elephant seals may allocate more resources to offspring in low competitive environments as they have sufficient resources to pay current reproductive costs (Pacoureau *et al*. 2017). Body mass at the time of weaning strongly influences male juvenile survival (McMahon *et al*. 2000; McMahon *et al*. 2017), and may be correlated with other adult life-history traits (Rödel & von Holst 2009). For example, heavier female elephant seal pups are more likely to survive and recruit at an earlier age, even though this effect does not extend into adulthood (Oosthuizen *et al*. 2018).

Alternatively, males of small cohort sizes compete with fewer individuals of the same age throughout development (Coulson *et al*. 2001; Forchhammer *et al*. 2001). Resources are variable in time and space in elephant seal foraging areas (Smith *et al*. 2009), and may become limiting for pre-breeding males (Pistorius *et al*. 2005). Laboratory experiments and field observations show that resource limitation during early male development affects juvenile survival, age of recruitment, size at maturity, and breeding success in other groups of animals (Engels & Sauer 2007; Descamps *et al*. 2008; Barry 2013; Fay *et al*. 2015). Polygynous males generally have higher mortality rates after independence than females (Clutton-Brock *et al*. 1985b) because more resources are required to maintain larger body sizes (Toïgo & Gaillard 2003). Polygynous males are generally more sensitive to changes in resource acquisition during development because they grow costly secondary sexual traits (Rose *et al*. 1998). Resource acquisition is particularly important for male elephant seals at ages 4-6 when juveniles experience a secondary growth spurt (McLaren 1993; Ling & Bryden 1981; Laws 1984). Thus, juvenile males experiencing favourable conditions may have more resources available to allocate towards secondary sexual traits that promote earlier recruitment and dominance with age (Lloyd *et al*. 2019).

Despite these cohort-level responses, male elephant seals still showed individual heterogeneity in recruitment age and breeding success. For recruitment age, individual differences were observed between breeding states. First-time dominant breeders generally recruited one year later than first-time subordinate breeders of the same birth cohort size. In other words, individuals of the same birth cohort size that delayed recruitment were more likely to be dominant (and thus breed successfully) at their first breeding event. By delaying recruitment, pre-breeders have more time to allocate resources to secondary sexual traits that win male-male interactions (‘late-breeding hypothesis’ *cf*. ‘early-breeding hypothesis’; Serrano *et al*. 2003; Azpillaga *et al*. 2018). However, delaying recruitment does not guarantee breeding success and early first-time subordinate males may benefit from gaining breeding experience (e.g. information-gathering; Schjørring *et al*. 1999; Lloyd *et al*. 2019; this study). For breeding success, individual differences were observed between individuals of the same age and birth cohort size. Cohort effects can diminish with age through the accumulation of individual-level experience, stochastic events, reduced selective pressure and latent expression of genotypes (Caswell 2001; Caswell & Vindenes 2018). These individual-level factors determine to what extent an individual can maximise breeding success in an environment that limits optimal functionality (Monaghan 2008).

Conclusion

We show that density-dependent drivers affecting competition intensity during breeding events and natal conditions explained variation in male southern elephant seal vital rates. Our study is one of few to provide valuable insight into how polygynous male demographics vary with density by affecting resource allocation decisions to survival, breeding success and recruitment age. This has immediate implications for wildlife management of polygynous mammal species, as well as long-term implications for evolutionary models that predict how populations will respond to unprecedented extremes.

Supporting Information

Supplement S1: Covariate summary

Table S1.1: Summary of the covariates used to predict survival probability, breeding success probability, recruitment age and average pup weaning mass of male southern elephant seals at Marion Island. Summary statistics represent quartiles (lower, median, upper), ranges or counts.

Category	Covariate	Data type	Level	Summary statistics	Description
Intrinsic	Age	Numeric	Individual	5-14 years	Known age of marked males of the breeding population.
	Breeding state	Categorical	Individual	261 subordinates, 129 dominants	Observed social status during breeding seasons: 0 = subordinate male, 1 = dominant male.
	Relative dominance	Numeric	Individual	-0.51, -0.40, 0.56	Number of times previously and currently dominant relative to the population average at each age class.
	Recruitment age	Numeric	Individual	5-10 years	Known age of marked male first seen participating during a breeding season (August-November).
	Relative subordinate/dominant male breeding experience	Numeric	Individual	SM: -0.60, -0.33, 0.38 DM: -0.40, -0.22, 0.00	Number of times previously (but not currently) a subordinate or dominant male relative to the population average at each age class.
Density-dependent: competition intensity	Relative beach cost	Numeric	Individual	-0.73, -0.51, 0.51	Beaches were scored (weighted) according to the average number of breeding females (and associated number of subordinate males) counted at each beach every breeding season. *See text for details.
	Standardised number of breeding males/females	Numeric	Year	M: -0.78, -0.068, 0.52 F: -0.80, -0.13, 0.58	Number of males (subordinate and dominant) or females counted on 15 October each breeding season. Counts were standardised across years.
	Operational sex ratio	Numeric	Year	8.68, 9.26, 10.66 females per male	Number of breeding females per breeding male (subordinate and dominant) counted on 15 October each breeding season.
Density-dependent: natal condition	Log birth cohort size	Numeric	Cohort	6.12, 6.22, 6.34 pups	Natural log of male and female pups born each breeding season.
	Birth sex ratio	Numeric	Cohort	0.9, 0.94, 1.05	Number of male pups per female pup born each breeding season.
Proxy	Year	Categorical	Year	1989-2017	Captures factors that vary annually from when first marked males recruited to the breeding population.
	Cohort	Categorical	Cohort	27 cohorts	Captures factors that vary by cohort.
	Site	Categorical	Site	9 sites	Pebble beaches were male pups were weighed at weaning.

* Relative beach cost: Male elephant seals expend more energy (measured as weight loss) with increasing interactions with male challengers and receptive females (Galimberti *et al*. 2007). These costs likely accumulate over time resulting in accelerated somatic deterioration with age (Bonduriansky *et al*. 2008). For example, male elephant seals almost never skip breeding events once recruited to the breeding population (Lloyd *et al*. 2019) and only have a short recovery period before hauling out onto land to moult (Condy 1979). Although long-term reproductive costs have rarely been investigated, there is some evidence that female mammals with long-term above average reproductive costs experience life-history trade-offs (Kroeger *et al*. 2018). In addition, early investment in reproduction can have downstream effects for polygynous male survival and future reproductive performance (Lemaître *et al*. 2014). Given that dominant males defend and service female harems of different sizes, we hypothesised that males dominating larger harems would incur greater reproductive costs than males dominating smaller harems. We also postulated that larger harems would attract more subordinate challengers that would try to copulate peripheral females and so require more time and effort to defend (Modig 1996). Indeed, we found that the average number of males observed per weekly census was positively correlated with the average number of females at each beach (Person's $r = 0.62$; Figure S1.1). Therefore, beaches were assigned weighted scores according to the average number of breeding females counted at each beach during peak haul-out (15 October) between 1992 and 2016 (Condy 1979). The year 1992 represents the 10th year after the first cohort of elephant seal pups were tagged (marked); which is sufficient time for all surviving males and females to recruit to the breeding population. We assumed that subordinate males spend the least amount of energy during breeding events as most do not mate successfully (Galimberti *et al*. 2002) and are chased away by vocalising dominant males (McCann 1981). Population counts estimated that the average number of breeding females per harem was 11.27. Therefore, beach cost was scored as follows: 1 = subordinate male, 2 = dominant males of beaches with below average harem sizes (<12 females), 3 = dominant males of beaches with above average harem sizes (≥12 females). Scores accumulated (added) each consecutive breeding season until an individual was presumed dead. Cumulative scores were then expressed as a relative measure by comparing it to the population average at each age class (Figure S1.2).

Table S1.2: Average number of breeding female southern elephant seals per harem (or beach site) at Marion Island counted on 15 October (peak haul-out date) between 1992 and 2016; and the associated average number of males observed at each harem per week during annual breeding seasons (September-November; Condy 1979). SD – standard deviation, NA – not applicable (beaches with long stretches of coastline provide subordinate males with resting areas and so do not threaten local dominant males).

Beach code	Beach name	Average number of females per harem (SD)	Average number of males per week (SD)
MM001	Boulder Beach	6 (3)	0.95 (0.22)
MM002	Trypot Beach	22 (7)	1.01 (0.14)
MM003	Macaroni North	1 (0)	0.71 (0.41)
MM004	Macaroni Bay	15 (6)	0.98 (0.17)
MM006	The Arch/Archway Beach	2 (1)	0.50 (0.35)
MM007	Archway Bay	38 (7)	1.05 (0.13)
MM009	Hansen Point	4 (3)	0.71 (0.26)
MM011	Bullard North	19 (5)	0.99 (0.08)
MM012	Bullard South	7 (3)	0.87 (0.12)
MM013	Killer Whale Cove	5 (3)	0.83 (0.19)
MM014	Waterfall Beach	4 (3)	0.54 (0.32)
MM015n	Landfall North	12 (5)	0.93 (0.10)
MM015r	Landfall River	4 (3)	NA
MM016	Sealers' Cave	11 (7)	0.89 (0.14)
MM017	Whale Bird Point	2 (1)	0.75 (0.12)
MM018n	Funk North	40 (8)	0.99 (0.07)
MM018r	Funk River	4 (3)	NA
MM018s	Funk South	3 (2)	NA
MM019	Kildalkey Rocks/Point	1 (0)	NA
MM020	Kildalkey Bay	43 (8)	0.97 (0.10)
MM025	Watertunnel River	5 (4)	NA
MM026	Goodhope Bay	21 (6)	0.88 (0.19)
MM046	Cape Davis Main Beach	1 (0)	NA
MM051	Rope Beach	3 (4)	0.65 (0.28)
MM052	Fork Beach	4 (4)	0.48 (0.08)
MM053e	Goney East	18 (6)	0.95 (0.10)
MM053w	Goney West	34 (8)	0.99 (0.12)
MM054	Toothpick	5 (5)	0.40 (0.41)
MM055	Log Beach	4 (4)	0.82 (0.20)
MM056L	King Penguin Long	17 (4)	0.92 (0.11)
MM056m	King Penguin Main	41 (11)	0.97 (0.11)
MM056mi	King Penguin Middle	3 (1)	0.84 (0.13)
MM056w	King Penguin West	7 (5)	0.76 (0.21)
MM057	Pinnacle to King Penguin	3 (2)	NA
MM058	Pinnacle Beach	22 (7)	0.94 (0.10)
MM059	Sea Elephant Bay	3 (2)	0.78 (0.19)
MM060	Blue Petrel Bay	13 (6)	0.93 (0.15)

MM061	Sealers' to Blue Petrel Bay	2 (0)	NA
MM062e	Sealers' East	34 (7)	0.79 (0.30)
MM062w	Sealers' West	3 (2)	0.81 (0.13)
MM063	Sealers' South	5 (5)	0.83 (0.20)
MM064d	Deep Beach	3 (2)	NA
MM064t	Third Beach	2 (1)	NA
MM065	Ship's Cove	25 (8)	0.98 (0.12)
MM066	Duikers' Point	1 (0)	NA
MM067	Van Den Boogaard	5 (3)	0.88 (0.15)
MM068	Rockhopper Bay	6 (6)	NA

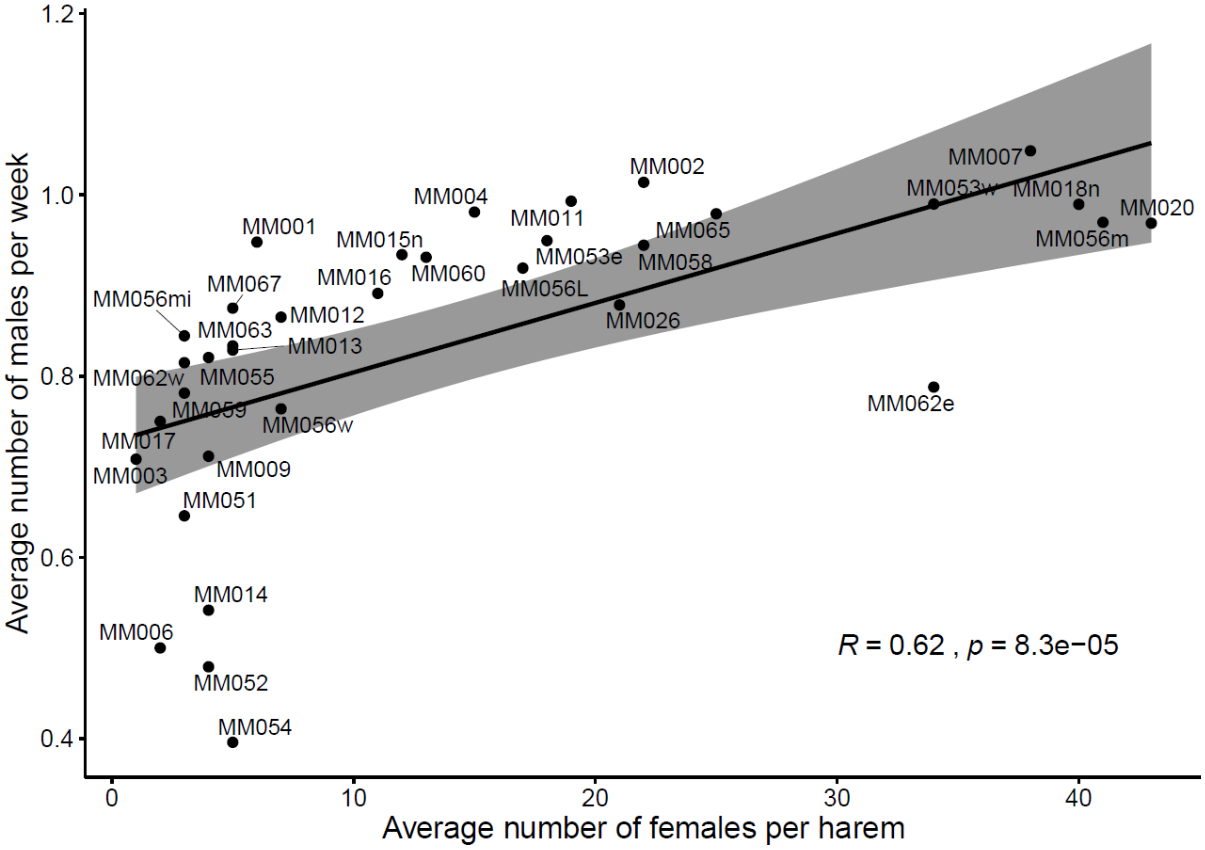

Figure S1.1: Average number of breeding female southern elephant seals per harem (or beach site) at Marion Island counted on 15 October (peak haul-out date) between 1992 and 2016; and the associated average number of males observed at each harem per week during annual breeding seasons (September-November). Pearson's coefficient (r = 0.62) estimated a relatively strong correlation between harem size and number of associated males.

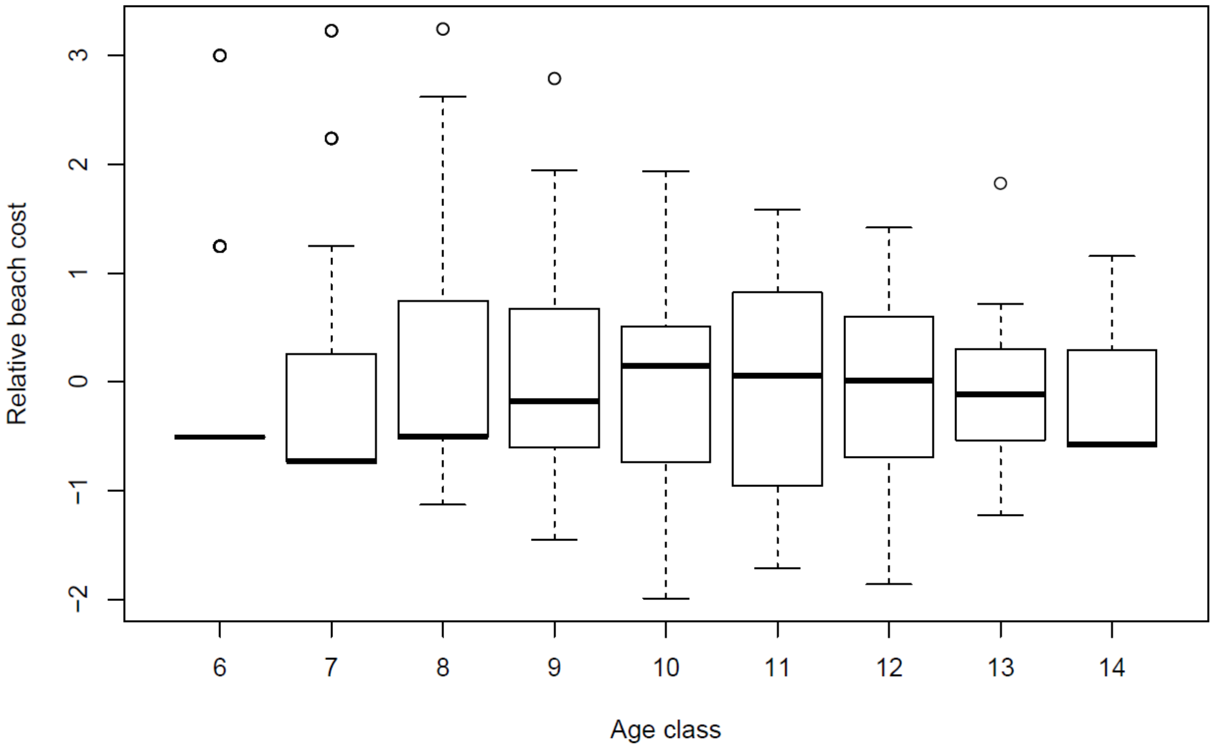

Figure S1.2: The distribution of relative beach costs experienced by male southern elephant seals at Marion Island between 1992 and 2018 expressed per age class.

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Supplement S2: Base models and model hypotheses

Table S2.1: Base models for survival probability (generalised linear models), breeding success probability (generalised linear mixed models) and recruitment age (linear models) of male southern elephant seals at Marion Island. Breeding success models had an individual random effect term (1|id). Small sample Akaike's Information Criterion (AIC$_c$) was used to select models, with the following measurements: ΔAIC$_c$ (the difference in AIC$_c$ between the model with the lowest AIC$_c$ value and the relevant model), ω_i (Akaike weight), K (number of parameters), Deviance (-2 multiplied by log likelihood). Models in bold font were carried forward to include density-dependent covariates.

Model parameters	**ΔAICc**	ω_i	***K***	**Deviance**
Survival probability				
age + breeding state	**0.00**	**0.42**	**3**	**-453.24**
age + relative dominance	5.10	0.03	3	-455.79
age + age^2 + breeding state	1.70	0.18	4	-453.08
age + age^2 + relative dominance	6.64	0.02	4	-455.55
log(age) + breeding state	0.54	0.32	3	-453.51
log(age) + relative dominance	5.48	0.03	3	-455.98
Breeding success probability				
age + (1|id)	3.94	0.09	3	-379.22
age + age^2 + (1|id)	1.39	0.30	4	-376.93
log(age) + (1|id)	**0.00**	**0.61**	**3**	**-377.25**
Recruitment age				
intercept term only	6.39	0.04	2	-431.71
breeding state	**0.00**	**0.96**	**3**	**-427.50**
year	13.69	0.00	30	-404.24
cohort	35.54	0.00	28	-417.59

Table S2.2: Candidate list of models with a description of the tested hypothesis.

Model	**Parameters**	**Hypothesis**
	Survival	
1	age + breeding state	Survival decreases linearly with age and differs between subordinate and dominant males.
2	… + recruitment age	Reproductive costs increase with earlier participation in breeding events.
3	… + rel. beach cost	Reproductive costs increase with increasing accumulated interactions with challengers and females.
4	… + std number of breeding males	Reproductive costs increase overall during breeding events with greater potential for male-male fights.

5	… + operational sex ratio	Reproductive costs increase with fewer mating opportunities available per male.
6	… + log birth cohort size	Reproductive costs increase with increasing competition for limited resources during development (e.g. growth of secondary sexual traits).
7	… + birth sex ratio	Reproductive costs increase with increasing competition for limited resources among same aged males (e.g. secondary growth spurt at ages 4-6).
	Breeding success	
8	log(age) + (1|id)	Logistic increase in breeding improvement with age accounting for individual differences.
9	… + rel. subordinate male experience + rel. dominant male experience	Breeding improvement increases with above average experience as a subordinate and dominant male.
10	… + rel. subordinate male experience	Breeding improvement increases with above average experience as a subordinate male (e.g. naïve first-time breeders).
11	… + rel. dominant male experience	Breeding improvement increases with above average experience as a dominant male (e.g. skills such as site-information, aggression, vocalising, herding and detecting oestrus females).
12	… + recruitment age + rel. subordinate male experience + rel. dominant male experience	Breeding improvement increases with earlier participation in breeding events and above average breeding experience as a subordinate and dominant male.
13	… + recruitment age + rel. dominant male experience	Breeding improvement increases with earlier participation in breeding events and above average breeding experience as a dominant male (having likely already been a subordinate male at the first breeding event).
14	… + recruitment age	Breeding improvement increases with earlier participation in breeding events.
15	… + std number of breeding males	Breeding improvement increases overall during breeding events with fewer male competitors.
16	… + operational sex ratio	Breeding improvement increases with more mating opportunities available per male.
17	… + log birth cohort size	Breeding improvement increases with decreasing competition for limited resources during development (e.g. growth of secondary sexual traits).
18	… + birth sex ratio	Breeding improvement increases with decreasing competition for females among same aged males (e.g. at old ages when most males are dominant).
	Recruitment age	
19	breeding state	Recruitment age differs between first-time subordinate and dominant males due to intense competitive mating hierarchy.
20	… + std number of breeding males	Recruiting males participate earlier during breeding events with fewer competing males.
21	… + operational sex ratio	Recruiting males participate earlier with more mating opportunities available per male.

22	… + log birth cohort size	Recruiting males participate earlier with decreasing competition for limited resources during development (e.g. growth of secondary sexual traits).
23	… + birth sex ratio	Recruiting males participate earlier with decreasing competition for females among same aged males after becoming sexually mature.

Supplement S3: Additional results

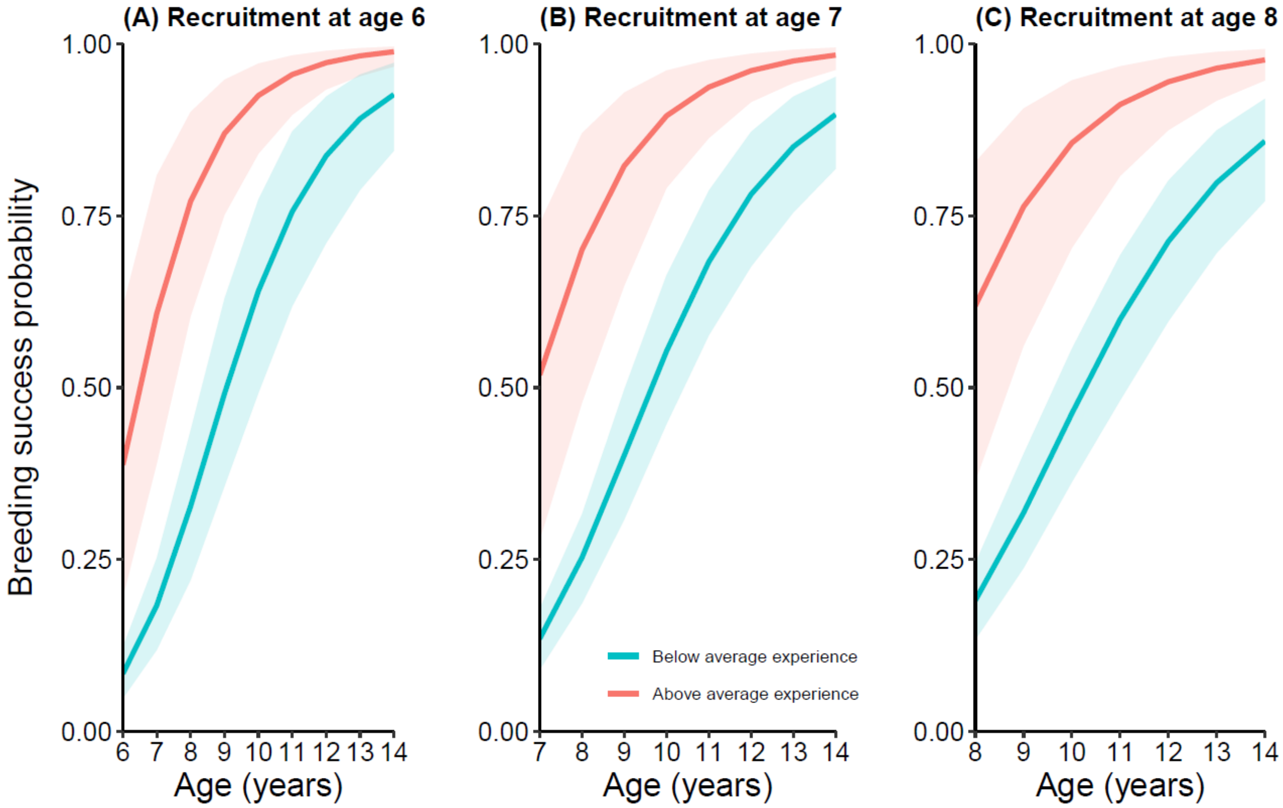

Figure S3.1: Mean predicted breeding success (probability of being dominant; ±95% confidence interval) of male southern elephant seals at Marion Island. Estimates were derived from model 13 (Table 1), which treated age variation in breeding success as a continuous logit-log relationship. Breeding success also depended on recruitment age and relative dominant male breeding experience. Older recruits were more likely to be dominant at their first breeding event than younger recruits. Males with above average experience as a dominant breeder for their age class were more likely to be dominant again. Most males recruited at ages 6, 7 and 8 in the observed population with a minimum and maximum relative breeding experience of -1.5 and 4.3, respectively.

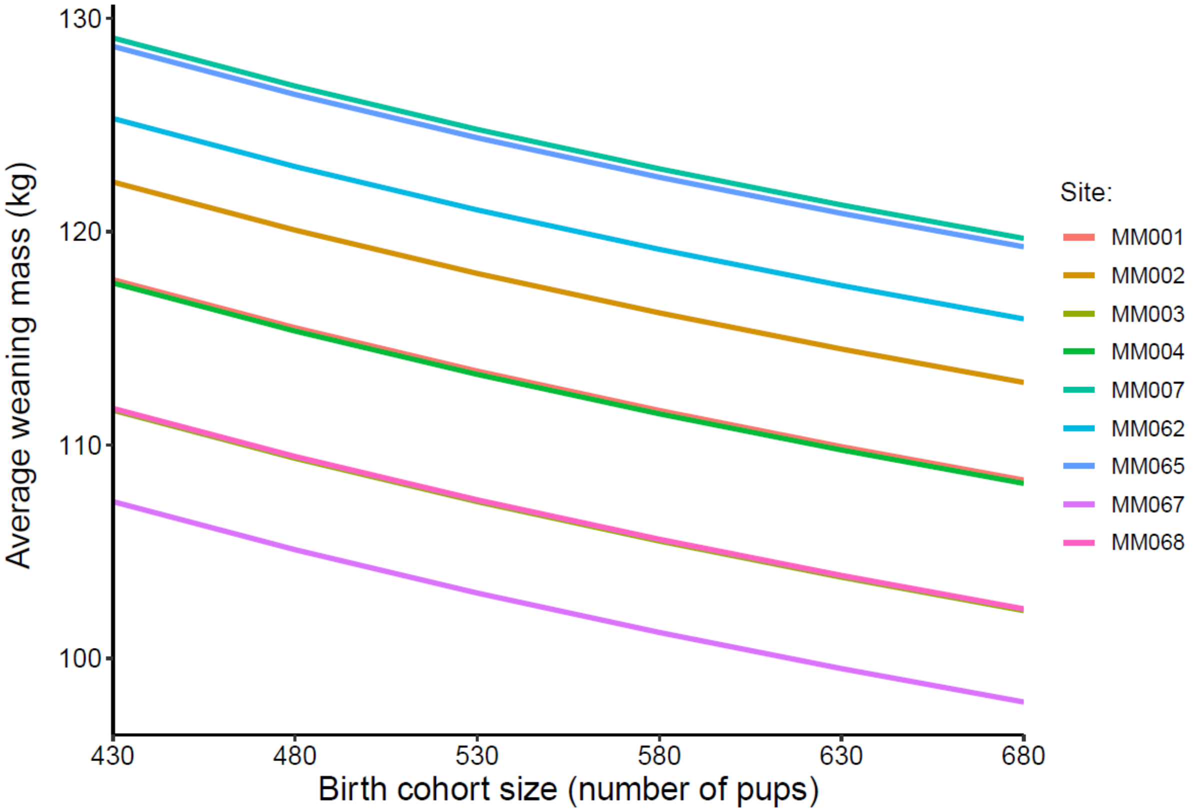

Figure S3.2: Mean predicted average pup weaning mass (±95% confidence interval) of male southern elephant seals at Marion Island. Estimates were derived from model 28 (Table 1), which predicted that average pup weaning mass decreased linearly with the natural log of cohort size at birth (number of pups produced annually). Site codes correspond to specific beaches where male pups were weighed at weaning. Sites with higher intercept terms generally had larger harem sizes each breeding season.

Chapter 5: *Synthesis and Perspectives*

Males matter in polygynous breeding systems: predictions from a two-sex population projection model

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Dominant male southern elephant seal at Macaroni Bay warning me not to approach (Marion Island, 2016). Photo: Travis Duck

Introduction

Population ecology deals specifically with the factors that control growth rates, abundances and distributions of populations (Sutherland *et al*. 2013). This has application for many disciplines ranging from theoretical (e.g. evolutionary biology) to applied (e.g. wildlife conservation; Benton & Grant 1999). Population projection models provide a means of elucidating which life-history traits are the most important in determining individual fitness and population growth (Caswell 2001). However, population projection models generally do not consider sexual reproduction despite males and females having sex-specific life-history traits (Miller & Inouye 2011). Focus is placed on the female component of populations, whilst the presence/absence of males is ignored (Shyu & Caswell 2018). Single-sex models assume that (1) male and female life-history traits are equivalent, (2) sex ratios are equal, and (3) males do not affect population growth (Lindström & Kokko 1998; Engen *et al*. 2003; Toïgo & Gaillard 2003; Rankin & Kokko 2007).

Male and female life-history traits differ substantially in polygynous breeding species (Clutton-Brock & Isvaran 2007). Polygynous males experience stronger sexual selection pressure and suffer higher reproductive costs resulting in earlier and steeper rates of senescence compared to females (survival: Lemaître *et al*. 2015; reproduction: Lemaître *et al*. 2017; body mass: Douhard *et al*. 2017). Sex-specific life-history traits also result from different developmental periods (Caswell 2001), dispersal patterns (Miller *et al*. 2011), responses to environmental and demographic variation (Coulson *et al*. 2001), and resource use (Clutton-Brock *et al*. 2002). Consequently, male and female densities and sex ratios change as cohorts age (Miller & Inouye 2011). Changing male densities and sex ratios can affect population dynamics in various direct and indirect ways (Mysterud *et al*. 2002a). For example, mean parturition dates can be delayed when more inexperienced young males breed which reduces offspring body mass (Sæther *et al*. 2003); oestrus can be induced or inhibited depending on the frequency and intensity of male stimuli (McComb 1987; McComb 1991); and males can limit fertilisation rates when sex ratios are female biased (i.e. sperm limitation; Wedell *et al*. 2002). Therefore, males matter to population dynamics and should be included in population projection models where applicable (Rankin & Kokko 2007).

When the assumptions of single-sex models do not hold, it is imperative that two-sex population models with parameters that link male and female components are developed (Gerber & White 2014). One way in which this can be accomplished is by using fertility functions (also known as marriage or mating functions; Caswell 2001). Fertility functions describe the demographic interactions between males and females, with matings being limited by the harmonic mean of male and female abundances (Miller & Inouye 2011). The harmonic fertility function is effective for populations that employ polyandry, monogamy or polygyny (Shyu & Caswell 2018).

Here, we assess how the life-history traits of male southern elephant seals (*Mirounga leonina*; hereafter elephant seal) at Marion Island influence population dynamics. Elasticity values are derived from a two-sex population model to determine which male demographic parameters are the most important in contributing to (1) male fitness, and (2) asymptotic lambda (λ, population growth rate at stable age distribution; Benton & Grant 1999). Detailed elephant seal demographic estimates are available for both males and females from a 34-year mark-recapture dataset (Oosthuizen 2016; Lloyd *et al*. 2019). Male elephant seals are highly polygynous and are thought to not limit female fertility (paucity-of-males hypothesis; Wilkinson & van Aarde 1999). However, rather than using absolute numbers and observed male behaviour, we compare the elasticities of male and female demographic traits at different ages and life stages.

Methods

Two-sex population matrix

Age- and stage-structured population projection matrix $\boldsymbol{A}$ assumed a post-breeding census and annual projection interval. For males, the pre-breeder (Pm) component of the matrix was age structured from age 0 to 7, with recruitment to the subordinate (Pm-Sm) and dominant (Pm-Dm) breeding states starting at age 5 and 6, respectively. Male pre-breeders that did not recruit by age 8 were removed from the matrix (i.e. 0 survival probability from age 7 to age 8), as only n = 14 marked pre-breeders were recorded at age 8 in the observed population between 1983 and 2016 (Figure S1.1). The subordinate breeder (Sm) component was age structured from age 5 to 11 and the dominant breeder (Dm) component from age 6 to 12 (Figure S1.2). Subordinate breeders could become dominant (Sm-Dm) from age 6, whilst dominant breeders could lose their status and become subordinate ($1 - Dm\text{-}Dm$) from age 7. For females, the pre-breeder (Pf) component was age structured from age 0 to 6, with recruitment as breeding adults (Af) starting at age 3. Female pre-breeders that did not recruit by age 6 were removed from the matrix along with adult females that survived beyond age 21 (Figures S1.1 & S1.3). Fertility depended upon the harmonic means of male and female abundances (Caswell & Weeks 1986; Lindström & Kokko 1998) and was modified specifically for a polygynous breeding system by setting a lower sex-specific per capita fertility rate (Gerber & White 2014). Female elephant seals mostly give birth to one pup each breeding season and therefore only contribute half a pup genetically per year. Polygynous males, however, can mate with multiple females and produce more than half a pup per year. Males are limited rather by the minimum number of females that they can mate with each breeding season. Therefore, the frequency-dependent modified harmonic fertility function was described as follows:

$$Ff = \min(0.5, \frac{K \times Nm}{Nm \times (Nf/h)})$$

$$Fm = \min(\frac{0.5 \times Nf}{Nm}, \frac{K \times Nf}{Nm \times (Nf/h)})$$

where, Nm and Nf are the sex-specific abundances of males and females, respectively; K is the number of offspring produced per adult female (set to 1 weaned pup per female); and h is the average harem size (set to 11 females per harem based on the observed average between 1992 and 2016). A breeding-state only summary matrix was described as follows:

$$\begin{bmatrix} 0 & 0 & Fm \cdot \rho \cdot \varphi^{\mathrm{Af}} & 0 & Cf \cdot Ff \cdot \rho \cdot \varphi^{\mathrm{Af}} \\ \varphi^{\mathrm{Pm}} \cdot (1 - \psi^{\mathrm{Pm-Sm}}) \cdot (1 - \psi^{\mathrm{Pm-Dm}}) & 0 & 0 & 0 & 0 \\ \varphi^{\mathrm{Pm}} \cdot \psi^{\mathrm{Pm-Sm}} & \varphi^{\mathrm{Sm}} \cdot (1 - \psi^{\mathrm{Sm-Dm}}) & \varphi^{\mathrm{Dm}} \cdot (1 - \psi^{\mathrm{Dm-Dm}}) & 0 & 0 \\ \varphi^{\mathrm{Pm}} \cdot \psi^{\mathrm{Pm-Dm}} & \varphi^{\mathrm{Sm}} \cdot \psi^{\mathrm{Sm-Dm}} & \varphi^{\mathrm{Dm}} \cdot \psi^{\mathrm{Dm-Dm}} & 0 & 0 \\ 0 & 0 & Fm \cdot (1 - \rho) \cdot \varphi^{\mathrm{Af}} & 0 & Cf \cdot Ff \cdot (1 - \rho) \cdot \varphi^{\mathrm{Af}} \\ 0 & 0 & 0 & \varphi^{\mathrm{Pf}} \cdot (1 - \psi^{\mathrm{Pf-Af}}) & 0 \\ 0 & 0 & 0 & \varphi^{\mathrm{Pf}} \cdot \psi^{\mathrm{Pf-Af}} & \varphi^{\mathrm{Af}} \end{bmatrix}$$

where, ρ is the birth sex ratio (set to 1:1 males to females based on the observed average of 0.99:1 between 1983 and 2016); and Cf is the probability a female will breed. The top rows above the male and female components of the matrix represent fertility rates (i.e. the number of male and female pups produced each breeding season). Diagonal elements represent the probability of surviving (φ) and remaining in the same breeding state ($1 - \psi$). Sub-diagonal elements represent the probability of surviving (φ) and transitioning (ψ) to a different breeding state. Demographic parameter estimates were derived from mark-recapture studies of the Marion Island elephant seal population (Oosthuizen 2016; Lloyd *et al*. 2019).

Matrix projection and analysis

Population projection matrix $\boldsymbol{A}$ was multiplied by an abundance matrix that represented the number of individuals in each age class and breeding state. A breeding-state only summary matrix was described as follows:

$$n(t+1) = \boldsymbol{A} \times \begin{bmatrix} N_{Wm} \\ N_{Pm} \\ N_{Sm} \\ N_{Dm} \\ N_{Wf} \\ N_{Pf} \\ N_{Af} \end{bmatrix} (t)$$

where, t is the number of time steps (i.e. annual breeding season or year); and N is the number of individuals per breeding state, with N_W representing the number of weaned pups. The two-sex population model was projected 200 time steps forward to obtain asymptotic lambda (λ) using the statistical programme R 3.5.2 (R Core Team 2019). The degree of sensitivity of each male demographic parameter to proportional changes was calculated to obtain elasticity values.

Results and Discussion

Male demographic traits contributed to the asymptotic population growth rate (λ = 1.1) in terms of pre-breeder survival, pre-breeder recruitment and dominant breeder fertility. Similarly, the general population model for large marine mammals predicts that the most important life stages for regulating population growth include juvenile mortality followed by age of first reproduction and then reproductive rates of adult females (Eberhardt 1977; Eberhardt & Siniff 1977; Pendleton *et al*. 2006; Jounela *et al*. 2019). When comparing male pre-breeder survival probabilities, proportional changes at ages 0, 4 and 5 had the greatest effect on λ (Figure 1). First-year survival is low for most polygynous species (reviewed by Galliard *et al*. 2000 for ungulates), including male elephant seals (Pistorius *et al*. 1999; Lloyd *et al*. 2019), likely due to under-yearlings being naïve and vulnerable to extrinsic sources of mortality (e.g. predation: Reisinger *et al*. 2011). Ages 4 and 5 coincide with puberty and early recruitment in male elephant seals (McLaren 1993; Lloyd *et al*. 2019), suggesting that many more individuals recruited to the breeding population and bred successfully when survival was improved at these ages. Male pre-breeder recruitment probabilities contributed to λ the most when transitioning as first-time subordinate breeders at age 5 and as first-time dominant breeders at age 6 (Figure 2). These were the earliest ages males were seen participating in breeding events, but only a few pre-breeders recruited at such a young age ($Pm\text{-}Sm_{\text{age5}}$: 0.019; $Pm\text{-}Dm_{\text{age6}}$: 0.037; Lloyd *et al*. 2019). Improved dominant breeder fertility rates increased population growth the most at age 8 (Figure 3). Similarly, the total number of marked dominant breeders recorded in each age class between 1983 and 2016 also peaked at age 8 (Figure S1.2). Age 8 may be the "prime age" of male elephant seals at Marion Island – an age after which the cost of trying to obtain dominance (expressed as actuarial senescence) outweighs the benefits of breeding successfully (Lloyd *et al*. 2019).

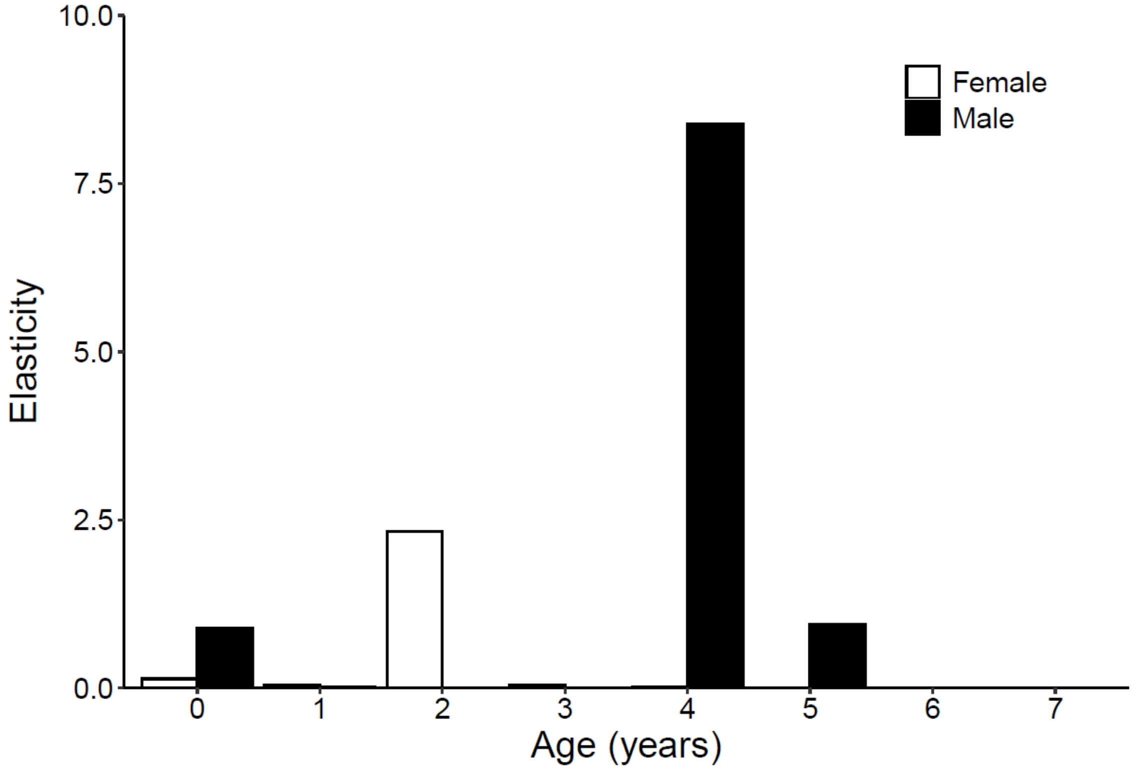


Figure 1: Elasticities of southern elephant seal survival probabilities during pre-breeder development. Values were derived from a two-sex population projection model.

However, subsequent investigations into how the demographic parameters of two-sex population models influence λ revealed that the importance of males may have been overstated. We made the mistake of using linear sensitivity (perturbation) analyses that are commonly used for one-sex population models (Caswell 2001). The complexity of performing sensitivity analyses for two-sex population models is illustrated by the few examples available in the literature (Jenouvrier *et al*. 2010). Fertility functions in two-sex population models depend on population structure (i.e. demographic parameters are interdependent), meaning that a change in one parameter will alter another parameter in the model. Therefore, numeric perturbation of a single parameter while keeping all other parameters constant is not possible. As demographic parameters can affect λ both directly and indirectly in two-sex population models, nonlinear perturbation analyses are instead required. This involves a two-sex population model converging on a stable equilibrium population structure ($\hat{p}$) and growing at an exponential asymptotic population growth rate ($\hat{\lambda}$) given by the dominant eigenvalue of the population projection matrix $\hat{\boldsymbol{A}}[\hat{p}]$. More details can be found in Caswell (2008).

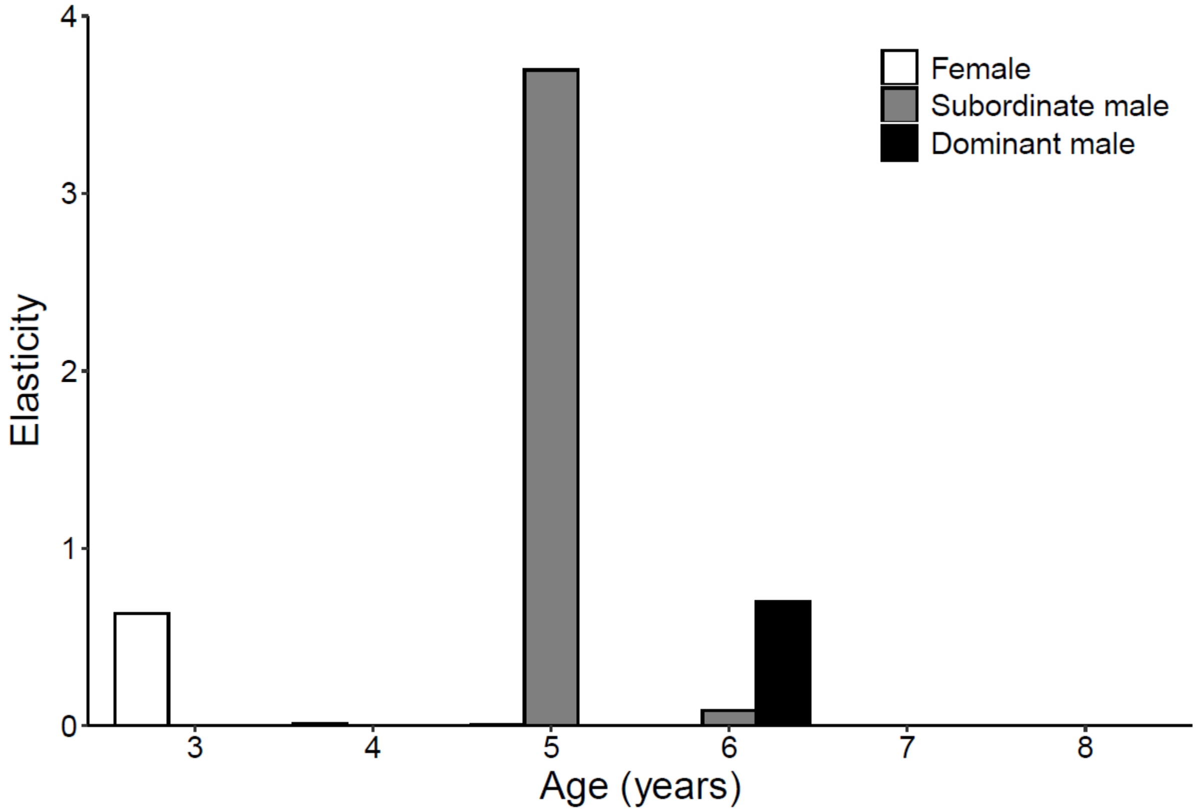


Figure 2: Elasticities of southern elephant seal recruitment probabilities derived from a two-sex population projection model. Males transitioned into the breeding population as first-time subordinate breeders (ages 5-8) or as first-time dominant breeders (ages 6-8). Females recruited from age 3.

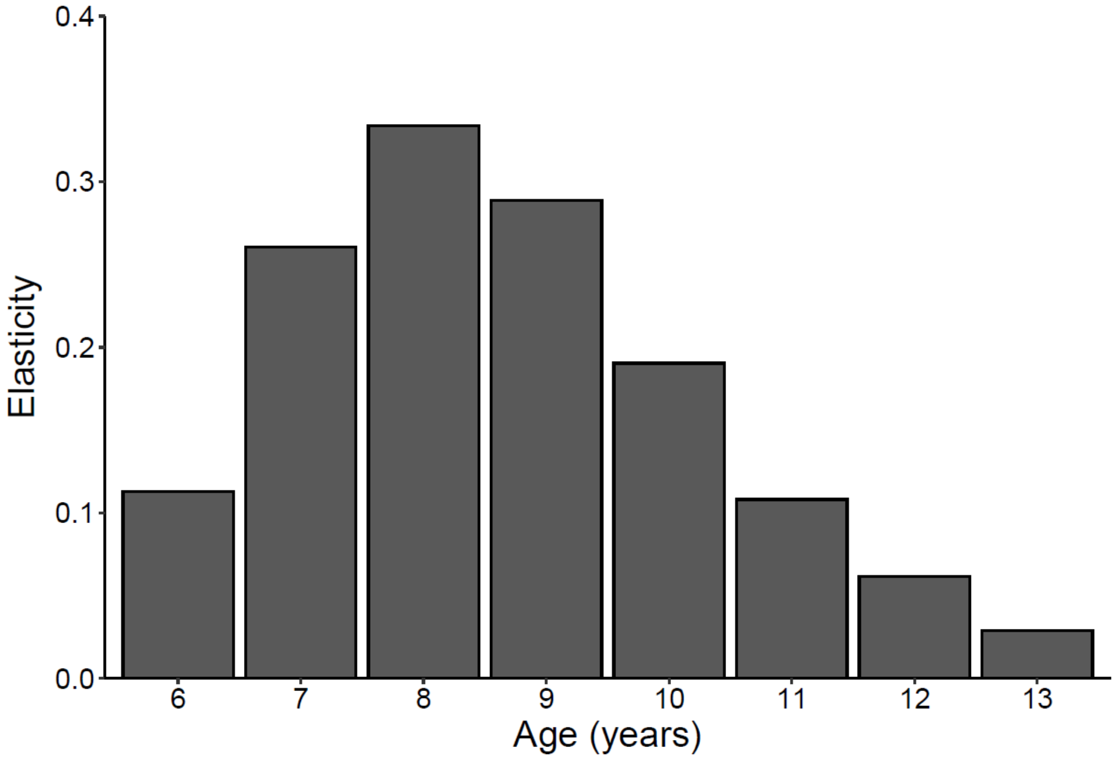


Figure 3: Elasticities of dominant male southern elephant seal fertility rates derived from a two-sex population projection model.

Conclusion

Two-sex models are essential for studying how the interaction of males and females affect population growth. Preliminary elasticity values of elephant seal demographic traits showed that males can influence population growth, particularly through pre-breeder survival and recruitment at young ages. However, the importance of these demographic traits may be overstated following reanalysis of the two-sex population model using nonlinear perturbation techniques that take fertility functions into account. Regardless, we have provided new perspectives in constructing, analysing and interpreting age- and state- (social status and sex) structured population models – an otherwise rare case in the field of population ecology.

Supplementary Information

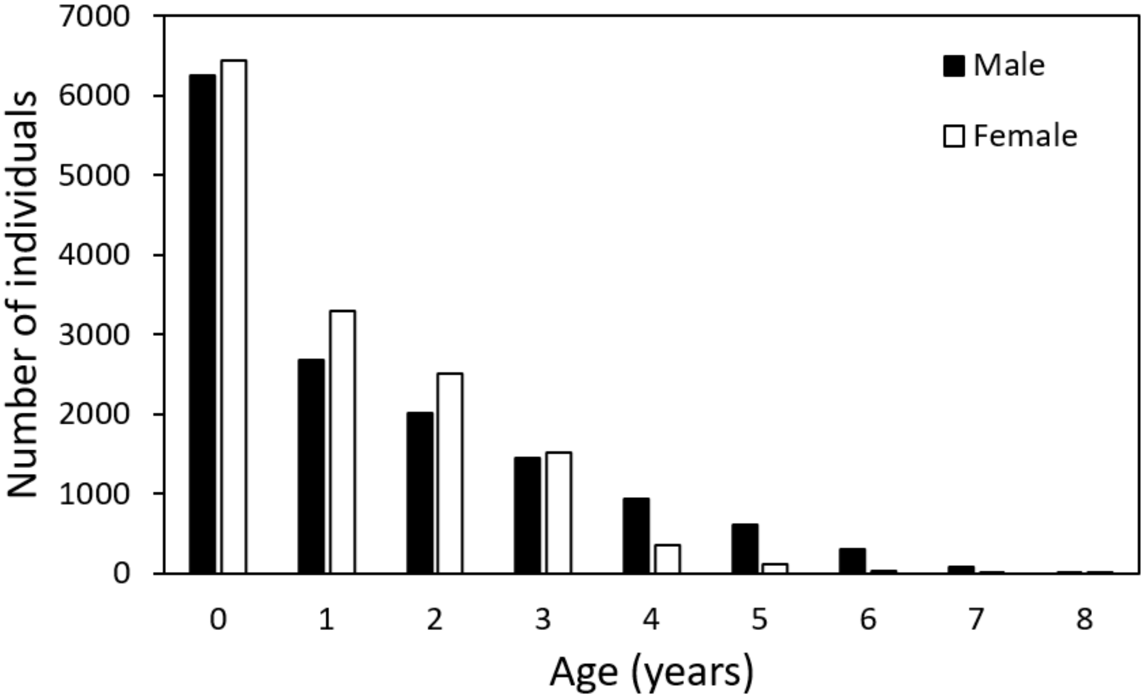


Figure S1.1: Total number of uniquely marked pre-breeding male (1983-2016) and female (1983-2013) southern elephant seals at Marion Island recorded per age class.

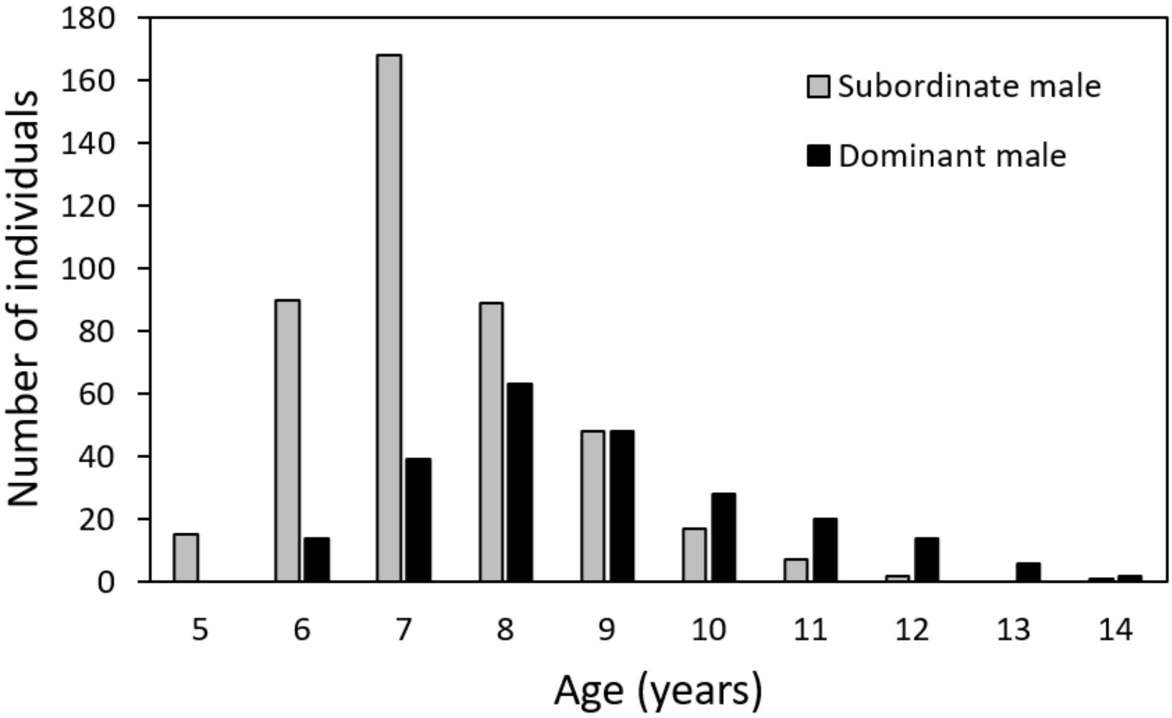


Figure S1.2: Total number of uniquely marked breeding male southern elephant seals at Marion Island recorded per age class and breeding state between 1983 and 2016.

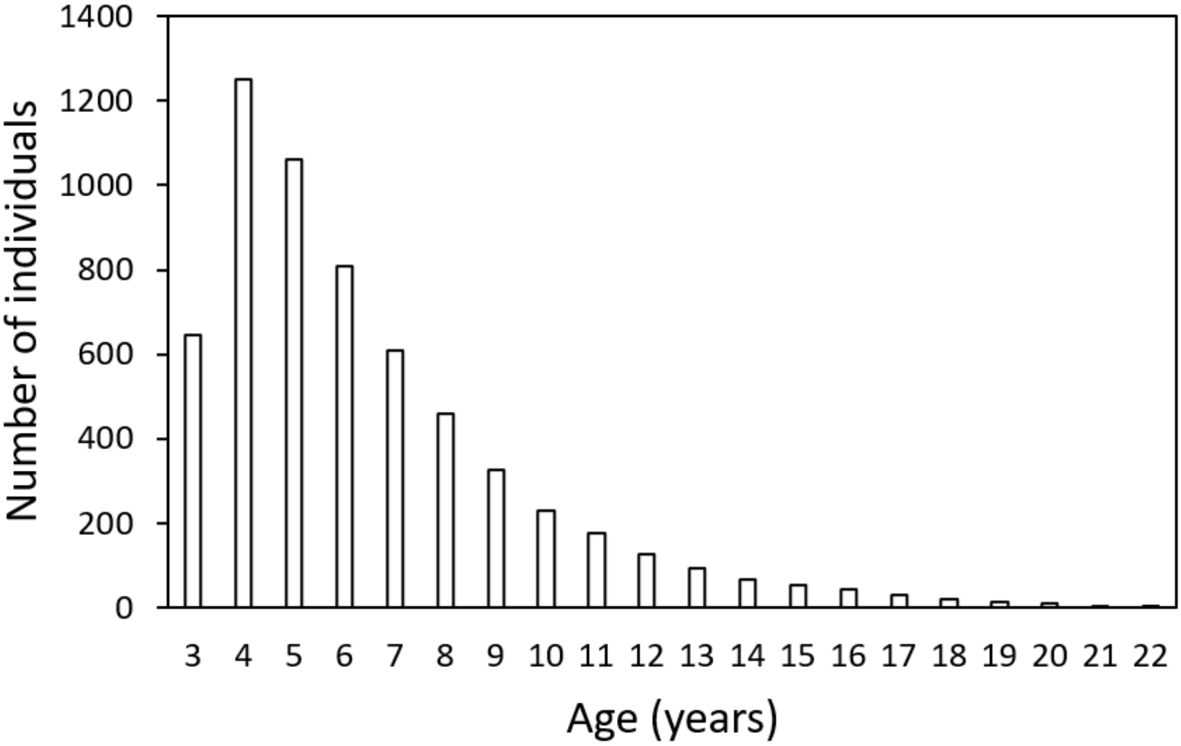


Figure S1.3: Total number of uniquely marked breeding female southern elephant seals at Marion Island recorded per age class between 1983 and 2013.

Synthesis and Conclusion

Our knowledge of polygynous life history is biased towards the female component of populations (Lemaître *et al*. 2015; Bleu *et al*. 2016; Lemaître & Gaillard 2017). Less is known about the processes governing polygynous male life history. Mark-recapture studies struggle to accurately determine the social status or paternity rates of individual males and therefore do not have measures of reproductive effort (Festa-Bianchet 2012; Lemaître *et al*. 2015). This is problematic because polygynous males invest substantial resources towards reproduction to maximise their chances of breeding successfully (Crocker *et al*. 2012). Male life history also does not receive much attention because polygynous males are believed to be redundant in sexual reproduction and assumed to have no discernible effect on population growth (Caswell 2001; Rankin & Kokko 2007). Therefore, clarity is needed on the drivers and predictors of polygynous male life history to properly understand how males affect population dynamics. The chapters of my thesis achieve this overall aim by answering specific questions about the life history of the male southern elephant seals at Marion Island using a 34-year mark-recapture dataset (Pistorius *et al*. 2011). The male elephant seal served as a model organism to test biological hypotheses about the most important life stages of polygynous male life history in general (Clutton-Brock 1989; Figure 4).

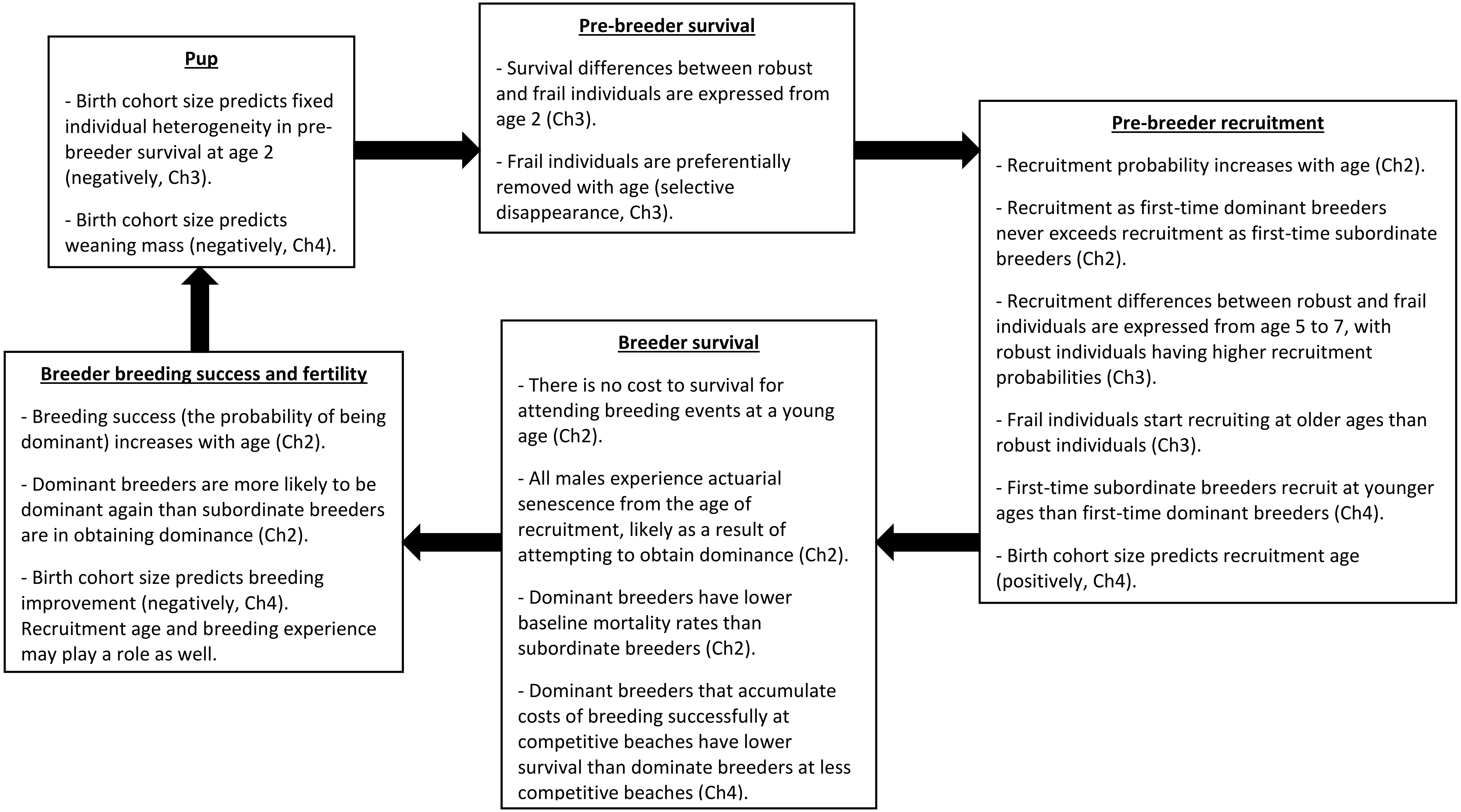
For male pre-breeders that survived their first year of life, individual heterogeneity in survival probabilities was expressed from age 2 when using finite-mixture models (Chapter 3). Males born in years with relatively few pups were more likely to be robust in quality than males born in years with many pups. Survival probabilities of robust individuals and the population average became more similar as pre-breeders aged. This implies that frail individuals were preferentially removed from the population and that the amount of individual heterogeneity within the frail quality group was reduced as pre-breeders matured (selective disappearance; van de Pol & Verhulst 2006; Hamel *et al*. 2018b). Therefore, the majority of pre-breeders that survived to recruitment age were robust in quality. Being able to detect and describe how individual heterogeneity changes with age informs us of which males are more likely to be dominant in competitive breeding systems. For example, using the life-history traits estimated for robust and frail pre-breeders, we showed that very few frail pre-breeders ever bred successfully.

The probability of a pre-breeder recruiting to the breeding population increased with age (Chapter 2). In addition, pre-breeders were more likely to recruit as first-time subordinate breeders than first-time dominant breeders when compared to individuals of the same age (Chapter 2). First-time subordinate breeders also started recruiting from a younger age than first-time dominant breeders (Chapters 2 & 4). This makes sense in a highly competitive breeding system where males require time to socially mature (e.g. grow in body size and mass) or require some breeding experience before outcompeting older breeders (Chapter 4; Pianka 1976; Jones 1981). Male pre-breeders also displayed individual heterogeneity in recruitment probabilities, with robust individuals (i.e. higher survival) being more likely to recruit than frail individuals (i.e. lower survival) between ages 5 and 7 (Chapter 3). Therefore, contrary to what trade-off theory predicts (Stearns 1992), robust pre-breeders that allocated resources to ensure survival during development were not limited in their ability to recruit when compared to frail pre-breeders. In fact, robust pre-breeders started recruiting from a younger age than frail pre-breeders (Chapter 3). This supports the individual quality theory, which predicts that life-history traits are positively, rather than negatively, correlated (Wilson & Nussey 2010). Recruitment age was also predicted by birth cohort size (Chapter 4). Pre-breeders born during low pup production years generally recruited at younger ages than pre-breeders born during high pup production years.

In mate-defence polygyny, males allocate substantial resources to reproduction to improve their chances of dominating female harems (Crocker *et al*. 2012; Bro-Jørgensen 2007). We found that males attending breeding events did not suffer lower survival probabilities when compared to same aged males that were still pre-breeders (Chapter 2). This suggested that there was no reproductive cost for attending breeding events, at least for early recruits. However, all males attending breeding events experienced actuarial senescence from their respective age of recruitment, with subordinate males suffering higher baseline mortalities (Chapter 2). Given that this coincided with breeding improvement (the probability of becoming dominant), males appeared to pay a reproductive cost for attempting to obtain dominance. This “cost of trying” has only recently emerged from polygynous male studies (Festa-Bianchet 2012; Festa-Bianchet *et al*. 2019). Dominant males always survived better than subordinate males of the same age (Chapter 2), which led to initial speculation that there was no additional reproductive cost for breeding successfully. Dominant males were likely high quality individuals that had sufficient resources to secure, defend and mate females without much cost to survival. However, when we compared survival probabilities between individual dominant males, we found that there was a reproductive cost for breeding successfully that accumulated with age (Chapter 4). Males that were dominant at beaches with above average harem sizes accumulated higher reproductive costs than males that were dominant at beaches with below average harem sizes. Larger harems may take more energy to service and defend against subordinate challengers (Galimberti *et al*. 2007). Regardless of this additional reproductive cost, dominant males still maintained higher survival probabilities than subordinate males of the same age (Chapter 4). Therefore, individual quality (inferred from breeding state or social status) may play an important role in modifying resource allocation trade-offs between survival and reproduction in male elephant seals.

The probability of being a dominant male served as a measure of breeding success, because dominant male paternity rates are high for elephant seals (Hoelzel *et al*. 1999), particularly at Marion Island (Wilkinson & van Aarde 1999). Future breeding success increased with age for both subordinate and dominant males; but dominant males were more likely to maintain their social status than subordinate males were in obtaining dominance (Chapter 2). This apparent improvement in breeding success with age was predicted by birth cohort size (Chapter 4). Clearly, birth cohort size was an important measure of density that affected several male elephant seal life-history traits throughout an individual's lifetime. Recruitment age and breeding experience may also play a role in determining breeding success (Chapter 4). Males that recruited at older ages were more likely to be dominant at their first breeding event, and males with experience as a dominant breeder were more likely to breed again (also supported by Chapter 2).

In conclusion, I provide support for several population theories and show how they shaped male elephant seal life history from birth to death. I examined how life-history trade-offs affected resource allocation decisions in breeders (Chapter 2), how individual heterogeneity during pre-breeder development determined which individuals were more likely to survive and recruit to the breeding population (Chapter 3), how density-dependent measures of competition intensity and natal conditions caused variation in breeder life-history traits (Chapter 4), and how polygynous males can affect population growth (Chapter 5). My findings provide valuable insight into the drivers and predictors of polygynous male life history. I have also improved our understanding of male southern elephant demography by assessing the lifetime consequences of processes operating at both the population- and individual-level. This could only be accomplished using the long-term, mark-recapture study of elephant seals at Marion Island. It is my hope that both researchers and practitioners will see that males matter to population dynamics and that more attention be given to male life history in future.



Pup

- Birth cohort size predicts fixed individual heterogeneity in pre-breeder survival at age 2 (negatively, Ch3).

- Birth cohort size predicts weaning mass (negatively, Ch4).

Pre-breeder survival

- Survival differences between robust and frail individuals are expressed from age 2 (Ch3).

- Frail individuals are preferentially removed with age (selective disappearance, Ch3).

Pre-breeder recruitment

- Recruitment probability increases with age (Ch2).

- Recruitment as first-time dominant breeders never exceeds recruitment as first-time subordinate breeders (Ch2).

- Recruitment differences between robust and frail individuals are expressed from age 5 to 7, with robust individuals having higher recruitment probabilities (Ch3).

- Frail individuals start recruiting at older ages than robust individuals (Ch3).

- First-time subordinate breeders recruit at younger ages than first-time dominant breeders (Ch4).

- Birth cohort size predicts recruitment age (positively, Ch4).

Breeder survival

- There is no cost to survival for attending breeding events at a young age (Ch2).

- All males experience actuarial senescence from the age of recruitment, likely as a result of attempting to obtain dominance (Ch2).

- Dominant breeders have lower baseline mortality rates than subordinate breeders (Ch2).

- Dominant breeders that accumulate costs of breeding successfully at competitive beaches have lower survival than dominate breeders at less competitive beaches (Ch4).

Breeder breeding success and fertility

- Breeding success (the probability of being dominant) increases with age (Ch2).

- Dominant breeders are more likely to be dominant again than subordinate breeders are in obtaining dominance (Ch2).

- Birth cohort size predicts breeding improvement (negatively, Ch4). Recruitment age and breeding experience may play a role as well.

Figure 4: Summary of the main findings of Chapters 2, 3, and 4 of this thesis. Information is arranged according to the life cycle of male southern elephant seals at Marion Island.

Perspectives

There are several research questions that stem from the findings of my thesis which can provide added insight into the determinants of polygynous male life history. These questions relate specifically to the southern elephant seal population at Marion Island.

Body size and mass

The discussions of Chapters 2, 3, and 4 hypothesise that body size is an important proxy of individual quality in male elephant seals. Male elephant seals have a long developmental period compared to other polygynous mammals (*cf*. ungulates: Lemaître *et al*. 2018), because sufficient time is required to obtain a body size that can contend in breeding events (i.e. males need to socially mature; Jones 1981). This is illustrated by a secondary growth spurt that males experience after sexual maturity at age 4 (McLaren 1993). Differences in body size between individuals of the same cohort increase throughout pre-breeder development (McLaren 1993), likely resulting in variation in competitive ability among recruited males. Dominant males are often larger in both size and mass than subordinate males (McCann 1981). A larger body size and mass affords males a physical advantage in fights and provides a greater resource holding potential while fasting during breeding events (Galimberti *et al*. 2007). Dominant males lose more absolute and relative body mass than subordinate males by the end of the breeding season (Galimberti *et al*. 2007), but this does not appear to affect actuarial senescence and breeding improvement rates when comparing breeding states (Lloyd *et al*. 2019). Weaning mass may even determine pre-breeder survival and recruitment rates (Chapter 3; McMahon *et al.* 2000; McMahon *et al*. 2017; Oosthuizen *et al*. 2018), recruitment age, and breeding success (Chapter 4).

Photogrammetry provides a means of estimating body size and mass (de Bruyn *et al*. 2009). Photogrammetry involves taking photographs of a relatively inert individual from different angles with standardised camera settings. Reference points and a measuring rod with markings at regular intervals are placed around the photographed individual to provide scale and context. Photographs are compiled to build a 3D model of the individual with accurate dimensions. Photogrammetry projects of elephant seals at Marion Island have been conducted since 2006. Marked individuals are photographed regularly during pre-breeder and breeder life stages, allowing for growth trajectories to be tracked throughout an individual's lifetime. Breeding males are photographed at the beginning (August) and end (November) of the breeding season to estimate mass loss, and again in the moulting season (December-March) to determine how individuals recover after participating in breeding events. In capital breeders such as elephant seals, reproductive effort can be estimated directly from changes in mass (Galimberti *et al*. 2007). Thus, several questions relating to my thesis can be answered using the photogrammetry dataset:

1. Are differences in growth trajectories related to pre-breeder survival and recruitment probabilities? This will establish if body size or mass predicts individual quality and the presence of between-individual differences in life-history traits (Chapter 3). No studies have tracked changes in growth patterns of individual male elephant seals throughout pre-breeder development (*cf*. McLaren 1993).

2. Do pre-breeders that are relatively larger or heavier than individuals of the same cohort recruit at an earlier age? Does body size or mass at recruitment confer a fitness advantage in terms of social status (subordinate *cf*. dominant first-time breeders)? Apart from extrinsic, population-level processes such as birth cohort size (Chapter 4), intrinsic, individual-level processes such as body size or mass may explain why pre-breeders vary in recruitment age and competitive ability.

3. Does a breeding male's relative body mass decrease from a particular age (i.e. body mass senescence), and does this depend on breeding state (Chapter 2) or competition intensity (Chapter 4)? Does body mass senescence explain why males experience actuarial senescence (Chapter 2)? Male elephant seals may have a prime age after which body condition progressively deteriorates. If this is the case, it will explain how reproductive costs are experienced with lifetime consequences for breeder survival.

4. How do males differ in their ability to recover from breeding events? Dominant males may lose more weight than subordinate males during the breeding season (Galimberti *et al*. 2007), but they may be better at recovering lost condition before the moulting season begins. This will determine if dominant males are better at acquiring resources than subordinate males, allowing them to live longer and repeatedly breed (i.e. higher individual quality; Chapter 2).

Reproductive senescence

In Chapter 2, I assessed how resource allocation to current reproduction affected survival and future breeding probability. Future breeding probability was measured as observed social status, which assumed that dominant males mated and subordinate males did not (or at least at low frequencies). I found that investing resources in current reproduction had no cost on future breeding probability. Instead, future breeding probability increased with age. However, future breeding probability only served as a proxy for whether a male mated successfully at the next breeding event. It did not measure whether a male successfully fertilised females at the next breeding event. Reproduction for polygynous males involves securing females to mate (precopulation) and fertilising female eggs (postcopulation). Therefore, while male elephant seals did not display reproductive senescence in precopulatory traits, they may still show reproductive senescence in postcopulatory traits as a result of current reproductive costs. Reproductive senescence in postcopulatory traits have been observed in males of other species (reviewed in Lemaître & Gaillard 2017). These traits include testes circumference (soay sheep *Ovis aries*; Hayward *et al*. 2015), testes size (ringed seal *Phoca hispida*; Chambellant 2010), sperm performance (barn swallow *Hirundo rustica*; Møller *et al*. 2009) and ejaculate quality (blue-footed booby *Sula nebouxii*; Velando *et al.* 2011). Reduced male fertilisation success with age can have serious implications for female fitness (Lemaître & Gaillard 2017). Dominant male elephant seals not only have to produce many ejaculations throughout the breeding season while fasting, but may also be under sexual selective pressure to allocate many sperm to each ejaculation to ensure fertilisation (Parker 2016). Subordinate males are known to sneak into harems to mate with females (McCann 1981), thus creating competition to fertilise female eggs (i.e. sperm competition). Male elephant seal ejaculations may be energetically expensive to produce, and may deteriorate in quality and quantity during current and subsequent breeding events. Male elephant seal postcopulatory traits can be measured as mating duration and frequency (behavioural observations), sperm fertility (livestock sampling techniques) and paternity tests (genetic samples).

Maternal effects

Birth cohort size appeared to play an important role in determining several male elephant seal life-history traits (Chapters 3 & 4). Support from trends in average male weaning mass (Chapter 4) and other studies of both males and females (Oosthuizen *et al*. 2015; McMahon *et al*. 2017) suggest that elephant seal mothers are able to manipulate the amount of resources allocated to pups either through gestation or lactation. Thus, maternal effects may be a source of individual heterogeneity for male elephant seals. The Trivers-Willard hypothesis predicts that mothers in good condition will invest more in male offspring (relative to female offspring) and mothers in poor condition will invest more in female offspring (relative to male offspring; Trivers & Willard 1973). This includes manipulating offspring sex, resource allocation or other forms of parental care. In polygynous breeding systems, a male pup that survives to adulthood and breeds successfully sires many more offspring than a female pup will in her lifetime. Therefore, mothers in good condition are predicted to invest more in male pups to improve their own lifetime reproductive success; whilst mothers in poor condition are already resource limited and cannot afford to invest resources into male pups that will likely be frail and subordinate (Trivers & Willard 1973). For elephant seals, it is already established that mothers manipulate resource allocation to offspring depending on prevailing environmental conditions and that this affects first-year survival (McMahon *et al.* 2000; McMahon *et al*. 2017). However, what is not known is whether maternal effects have lifetime consequences for male life-history traits (i.e. silver-spoon effects; see Oosthuizen *et al*. 2018 for females). Mother-pup pairs are individually identified at Marion Island (de Bruyn *et al*. 2008), thus providing the maternal effects associated with each male pup (e.g. maternal body size and mass, maternal age, maternal cohort, and maternal breeding experience). However, mother-pup identification only began in 2006 and so more time is needed to allow tagged males to mature and breed before the lifetime consequences of maternal effects can be thoroughly investigated.

Breeder experience

Breeding experience may play a role in determining breeding success in male elephant seals (Chapter 4). Apart from participating in breeding events as either a subordinate or dominant male, other measures of breeding experience include arrival date (territory establishment), haul-out site (site-specific reproductive potential, information-gathering, familiarity), harem size (frequency of male-female and male-male interactions) and changes in social status (competitive ability) during breeding events. This information is collected for tagged males during weekly censuses and annual population counts (Pistorius *et al*. 2011). A study can be conducted to determine if these measures of breeding experience explain breeding improvement with age (Chapter 4).

Prince Edward Island and other breeding colonies as a comparative study

Expeditions to mark elephant seals born at neighbouring Prince Edward Island (~19 km from Marion Island) would provide an opportunity to compare the life histories of males weaned under different natal conditions. Whilst density-independent factors at birth are likely the same for Prince Edward Island (PEI) and Marion Island (MI) elephant seals, density-dependent factors will differ. The PEI breeding colony (386 pups in 1977) is smaller than the MI breeding colony (mean of 1049 pups between 1973 and 1976) and has fewer beaches available for females to form harems (Condy 1978). However, if birth cohort size is related to competition intensity (Chapters 3 & 4), males and females of both PEI and MI likely compete for resources in the same foraging area (Jonker & Bester 1998; McIntyre *et al*. 2012; Tosh *et al*. 2012). MI mark-recapture data could also be compared to demographic information from other elephant seal colonies that are larger in size, such as Macquarie Island (McMahon *et al*. 2003), or similar in size but positioned within a different environmental context, such as the Falkland Islands (Galimberti *et al*. 1999).

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Postgraduate Activities

The following activities were completed during my Ph.D. candidature (2017-2019).

Peer-reviewed publications

1. Lloyd, K.J., Oosthuizen, W.C., Bester, M. & de Bruyn, P.J.N. 2020. Trade-offs between age-related breeding improvement and survival senescence in highly polygynous elephant seals: dominant males always do better. *Journal of Animal Ecology* in press. https://doi.org/10.1111/1365-2656.13145
2. Lloyd, K.J. & Vetter, S. 2019. Generalist trophic ecology in a changing habitat: the case of the four-striped mouse in a woody-encroached savannah. *African Journal of Ecology* 57: 371-381. https://doi.org/10.1111/aje.12613
3. Lloyd, K.J., Altwegg R., Doutrelant C. & Covas R. 2017. Factors affecting the foraging distance and duration of a colonial bird, the sociable weaver, in a semi-arid environment. *African Journal of Ecology* 56: 659-663. https://doi.org/10.1111/aje.12484
4. Horak, I.G., Pearcy, A. & Lloyd, K.J. 2017. Parasites of domestic and wild animals in South Africa. LI. Ticks infesting leopard tortoises *Stigmochelys pardalis*, hingeback tortoises *Kinixys zombensis* and angulate tortoises *Chersina angulata*. *Onderstepoort Journal of Veterinary Research* 84: a1303. https://doi.org/10.4102/ojvr.v84i1.1303

Conference presentations

1. 2nd World Marine Mammal Conference, Barcelona, December 2019. *Trade-offs between age-related breeding improvement and survival senescence in highly polygynous elephant seals*.
2. 39th Zoological Society of Southern Africa conference, Skukuza, July 2019. *Trade-offs between age-related breeding improvement and survival senescence in highly polygynous elephant seals*.
3. 5th African Marine Mammal Colloquium, Port Elizabeth, August 2018. *Dominant males pay only a participatory cost to reproduce*.
4. South African National Antarctic Programme, Hermanus, August 2018. *Dominant males pay only a participatory cost to reproduce*.

Postgraduate short-courses

1. Global Perspectives on Adaptive Wildlife Management (Swedish University of Agricultural Sciences, 2019).
2. Study Design and Data Analysis for Scientists (University of Cape Town, 2018).
3. Statistics for Biological Sciences with distinction (University of Pretoria, 2018).

Qualifications

1. Qualified SAFRING A-Ringer for ringing/banding small passerines in southern Africa.
2. Qualified field guide with competency at iSimangaliso/Greater St. Lucia Wetlands Park, Hluhluwe/Imfolozi Game Reserve, Enseleni Nature Reserve, and Tala Nature Reserve (CATHSSETA, NQF 2).

Workshops

1. Avian Medicine workshop (Southern Africa Wildlife Disease Association, 2019).
2. General Natural and Agricultural Sciences Tutor Training (University of Pretoria, 2019).
3. 1st International Ant Identification Course (Soil Fauna in Africa Consortium, 2018).
4. Introduction to Bat Biology, Ecology, Conservation and Identification workshop (AfricanBats, 2017).

Volunteer work

1. Zoological Gardens of South Africa working with African Penguins (SANBI, 2019).
3. African Bird Fair exhibitor for BirdLife Northern Gauteng (BirdLife South Africa, 2019).
4. Two environmental awareness presentations at schools (Bozeman High School & Arcadia Primary School, 2019).
5. Sociable Weaver Project at Benfontein Nature Reserve (FitzPatrick Institute of African Ornithology, 2018).
6. SA Agulhas II Open Day exhibitor for Marion Island Marine Mammal Programme (SANAP, 2018).