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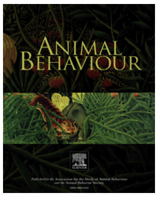

Density-related reproductive costs and natal conditions predict male life history in a highly polygynous mammal

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Polygynous males allocate substantial resources to sexual traits and behaviours to improve their chances of winning competitions for mates often at the cost of body maintenance. However, the degree to which males experience these trade-offs can be influenced by external conditions. Studies are needed that assess whether polygynous male resource allocation decisions about life history traits are density dependent. We tested for an influence of density on age-specific life history traits in male southern elephant seals, *Mirounga leonina*, using a 34-year data set collected at Marion Island. Specifically, we determine whether life history varied with density-related factors for survival, improved breeding success (measured as social status) and recruitment age. This was done by selecting linear models that tested biological hypotheses about density-dependent covariates related to competition intensity during breeding and natal conditions, while accounting for known intrinsic effects such as age and social status. Baseline mortalities were higher for males that had accumulated above average reproductive costs for their age than males with below average costs. This reproductive cost was determined by the number of females per harem relative to the population average. Thus, males likely allocated more resources to reproduction and less to body maintenance at all ages when defending and servicing relatively large harems, and this cost was compounding for males that dominated large harems at a young age. Males born in years with few pups were more likely to be dominant breeders and recruit at an earlier age than males born in years with many pups. Thus, breeding success and recruitment age likely depended on the population density experienced during early life, suggesting lasting effects of natal conditions in a long-lived animal. We show how density-dependent factors interact with intrinsic determinants of resource allocation to determine variation in polygynous male life history with long-term consequences.

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 most mammal species employ polygyny as a breeding strategy, males commonly experience stronger intrasexual reproductive competition than females (sexual selection theory; Clutton-Brock, 1989). 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 maximize their own lifetime reproductive success (prudent parent hypothesis; Drent & Daan, 1980; Martin & Festa-Bianchet, 2010). In polygynous males, reproductive costs mostly arise from trying to obtain and maintain social dominance rather than from actually breeding successfully (Festa-Bianchet et al., 2019; Lloyd et al., 2020).

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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 directly to parental care (Clutton-Brock, 1989), they cannot foist costs onto offspring like females. 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 appears to vary with (1) the number of male competitors, (2) the relative number of females to males 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., 2002) and could interact with density-independent factors in different ways (Coulson et al., 2001). Observations show that with high densities of males, the probability of a male challenging another male's social rank 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 may also be affected by the relative density of sexually mature females to males (i.e. 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 for males or even females (Le Galliard et al., 2005). More females relative to males provides more mating opportunities, which increases participation by 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 because 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 current 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 ecology (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 an 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 have influenced resource allocation decisions. Male elephant seals compete for dominance of female harems over an annual 3-month breeding season during which they do not supplement stored body reserves (Le Boeuf & Laws, 1994). Thus, males display an extreme form of capital breeding by allocating only stored body resources into an intense and relatively long breeding event (Soulsbury, 2019). Social dominance is often determined by body size (for winning fights) and resource-holding potential (for 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 small fraction of recruited males become dominant (Galimberti et al., 2002). Subordinate males may employ 'sneaking' tactics to mate with females, but this is relatively infrequent compared to dominant male paternity rates (Le Boeuf & Laws, 1994; Hoelzel et al., 1999; Wilkinson & Van Aarde, 1999). Thus, social status can be a reliable proxy of reproductive success for this species (Lloyd et al., 2020). Male elephant seal life history traits are structured according to age and social rank (Lloyd et al., 2020). Both subordinate and dominant males experience actuarial senescence concurrently with age-related breeding improvement after the age of first reproduction, suggesting that reproductive costs are experienced in this species (Lloyd et al., 2020). Specifically, costs of attempting to obtain dominance by subordinate males appear to be greater than costs of maintaining dominance (Lloyd et al., 2020). Furthermore, surviving dominant males are more likely to maintain their social status than subordinates are to obtain dominance over consecutive breeding events (Lloyd et al., 2020). Males also vary in the age of recruitment to the breeding population after becoming sexually mature at 4 years of age (Jones, 1981; Laws, 1956). However, none of these observations considered how density may alter patterns in male elephant seal life history traits.

We used 34 years of mark–recapture data of elephant seals at Marion Island, sub-Antarctic Indian Ocean, to test possible density-dependent causes of variation in male resource allocation decisions about life history traits. We evaluated the extent to which patterns in (1) actuarial senescence (or survival), (2) breeding improvement (measured as social status) and (3) recruitment age (from age 5 years in our study population) can be explained by several measures of density-dependent factors related to competition intensity during breeding and natal conditions. Given near perfect breeding season detection probabilities and similar tag loss rates among recruited males of this population (Lloyd et al., 2020), we used linear models to test biological hypotheses to determine whether male life history traits are density dependent.

METHODS

Male Southern Elephant Seals at Marion Island

Elephant seals at Marion Island, part of the Prince Edward Islands (46°54′S, 37°44′E), 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 every breeding season (austral September–November), with tags containing information about cohort and individual identity. Beaches were surveyed regularly inside (7-day intervals) and outside (10-day intervals) 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, all individuals at the island were tallied on 15 October, the peak haul-out date of this colony (Condy, 1979). The life history traits of males from the Marion Island population are structured according to age and breeding, dispersion from the natal colony is relatively low for both prebreeders ($\psi^{E}_{a\ 1-5} = 0.05$) and breeders ($\psi^{E}_{a\geq 6} = 0.14$) with approximately half the prebreeders returning, breeding season detection probabilities are high across years ($p = 0.95 \pm$ SD 0.05) and tag loss probabilities are constant for all adult ages (see Lloyd et al., 2020 for details). There is a low level of individual heterogeneity in survival probability between individuals of the same age and breeding state ($\sigma = 0.000017$), but larger interindividual differences in breeding success (i.e. the probability of being dominant; $\sigma = 0.23$; Lloyd et al., 2020). Therefore, individual heterogeneity in breeding success is likely prevalent and must be considered when making predictions (Vaupel & Yishiin, 1985; Cam et al., 2002).

Data Analysis

Only males that had recruited to the breeding population were considered. This provided a data set of 291 individuals with complete life histories (i.e. birth to ‘apparent’ death; see below) and 35 individuals with incomplete life histories (i.e. still alive at time of study). Base models were initially established to determine whether recruited male life history traits (i.e. survival probability, breeding success probability and recruitment age) were determined by intrinsic effects such as age, breeding state and individual heterogeneity among others (see Appendix: Base models and model hypotheses; Grueber et al., 2011; Lloyd et al., 2020).

Several density-dependent factors related to competition intensity during breeding and natal conditions were then investigated as covariates of these demographic traits (Table 1). Two weighted covariates that are not intuitive and require additional explanation are (1) relative breeding experience and (2) relative beach cost. (1) For each year a recruited individual was alive, the number of times it had previously been a subordinate and dominant male was tallied separately to gain some indication of past breeding experience. Thus, an individual had two measures of breeding experience for each year alive: one for past experience as a subordinate male and the other for past experience as a dominant male. Breeding experience as a subordinate and/or dominant male was then expressed as a relative measure compared to the population average of each age class. (2) The cost of hauling out at a particular beach was approximated by the average number of breeding females (Appendix Table A1), and associated number of subordinate challengers (Appendix Fig. A1), observed at each beach during the study period. Males were assigned weighted scores depending on their breeding state and whether they were dominant at beaches with below or above average harem sizes (11.27 females per harem being the population average). Beach cost was scored as follows: 1 = subordinate male, 2 = dominant male of beach with below average harem size (<12 females), 3 = dominant male of beach with above average harem size (≥ 12 females). These scores accumulated as an individual aged and were expressed as a relative measure compared to the population average of each age class. See Appendix: Relative beach cost for more about the substantiation and method of estimating relative beach cost.

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 (see Appendix: Base models and model hypotheses) were fitted and selected using an information-theoretic approach (Akaike's information criterion, $\mathrm{AIC_c}$) in R 3.5.2 (R Core Team, 2019). Where models were equivalent ($\Delta\mathrm{AIC} \leq 2$; Burnham & Anderson, 2004), the simpler model (fewer parameters) was favoured. Predicted estimates of the most parsimonious models are reported as the mean with lower and upper 95% confidence intervals.

Actuarial senescence

Generalized linear models were fitted to 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 (see goodness-of-fit Test 2.CT in Lloyd et al., 2020). Thus,

Table 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

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 of each age class
Recruitment age	Numeric	Individual	5–10 years	Known age of marked male first seen participating during a breeding season (austral 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 (SM) or dominant (DM) male relative to the population average of 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
Standardized number of breeding males/females	Numeric	Year	M: −0.78, −0.068, 0.52 F: −0.80, −0.13, 0.58	Number of males (M, subordinate and dominant) or females (F) counted on 15 October each breeding season (M: range 34–67; F: range 402–540). Counts were standardized 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 (range 421–700 pups)
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	Incorporates factors that vary annually from when first-marked males recruited to the breeding population
Cohort	Categorical	Cohort	27 cohorts	Incorporates factors that vary by cohort
Site	Categorical	Site	9 sites	Pebble beaches where male pups were weighed at weaning

Summary statistics represent quartiles (lower, median, upper), ranges or counts.

animals not seen for consecutive years were presumed dead and not temporarily emigrated. Given the findings of Lloyd et al. (2020), a base model was established by fitting survival data to models of 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 of each age class; Appendix Table A2). Because few age classes were examined (from ages 5 to 14 years), age was scaled in the quadratic model to prevent correlation between age and age^2.

Breeding improvement

Generalized linear mixed models (R package 'lme4'; Bates et al., 2014) were fitted to data coded as 1 (dominant) and 0 (subordinate) each annual breeding season for males with complete life histories. Given that dominant males at the study colony have very high paternity rates (Wilkinson & Van Aarde, 1999), breeding success was approximated as the probability of having a dominant social status. 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 year, particularly that 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 models of 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., 2020).

Recruitment age

Linear models 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 in this analysis. Recruitment age was defined as the age an individual was first seen participating in a breeding event, which ranged from 5 to 10 years of age. Prebreeders 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 at this time. A base model was established by comparing a recruitment age model that included no covariate effects (intercept only model) to models containing breeding state at recruitment, year of recruitment and birth cohort.

Pup weaning mass

Given the lack of literature investigating how male elephant seal demographics are determined by pup weaning mass, but its apparent importance in the life histories of female elephant seals (Oosthuizen et al., 2018) and other species of polygynous males (Rödel & von Holst, 2009), a supplementary analysis was performed to determine which density-dependent factors influence pup weaning mass across cohorts (see Appendix: Pup weaning mass). This was specifically done to aid result interpretation and was not a primary aim of the study.

Ethical Note

The project 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 Forestry, Fisheries and the Environment, South Africa. Marking involved tagging elephant seals shortly after weaning with two identical standard plastic Rototags (Dal 008 Jumbotags, Dalton Supplies Ltd, Henley-on-Thames, U.K. 45 × 17 mm) to the hind flippers ($N = 27$ cohorts, 6245 male pups; Pistorius et al., 2011). Tags were pierced through the inner interdigital webbing from 1983 to 1999 and outer interdigital webbing from 2000 to 2009 using an applicator. Disturbance was minimized when resighting tagged elephant seals on beaches by resighting exposed tags from a distance using binoculars or sneaking up to sleeping elephant seals to gently reveal tags concealed by the hind flippers.

RESULTS

Actuarial Senescence

Male survival decreased linearly (on the logit scale) with age from recruitment (Appendix Table A2) and depended on breeding state, with dominant males having higher survival probabilities than subordinate males. Relative beach cost explained additional variation in survival (model 3, Table 2). Individuals that had above average beach costs for their age experienced higher baseline mortalities than individuals with below average beach costs (Fig. 1). This meant that males that dominated 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.

Breeding Improvement

Breeding success (the probability of being dominant) increased with age according to a logarithmic form, likely because most old males obtained and maintained dominance for consecutive years (Appendix Table A2). Breeding success was also predicted by the natural log of cohort size at birth (model 17, Table 2). 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 than males born in years with many pups (Fig. 2). However, males of the same age, and therefore birth 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 $\omega_{17}/\omega_{13} = 2.55$). Males that recruited at older ages were more likely to be first-time dominant breeders than younger recruits (Appendix Fig. A5). As both age and individual heterogeneity were accounted for in model parameterization, 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.

Recruitment Age

Male recruitment age varied with the breeding state (i.e. social status) of the recruit at its first breeding event (Appendix Table A2). Males that were dominant at recruitment were generally older than males that recruited as subordinates. Like the most well-supported

Table 2
Intrinsic and density-dependent predictors of survival, breeding success, recruitment age and average pup weaning mass of male southern elephant seals at Marion Island

Model	Parameters	ΔAIC_c	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 + relative beach cost**	**0.00**	**0.61**	**4**	**−450.74**
4	age + breeding state + standardized 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) + relative subordinate male experience + relative dominant male experience + (1|id)	2.63	0.14	5	−367.81
10	log(age) + relative subordinate male experience + (1|id)	9.87	0.00	4	−372.44
11	log(age) + relative dominant male experience + (1|id)	7.61	0.01	4	−371.31
12	log(age) + recruitment age + relative subordinate male experience + relative dominant male experience + (1|id)	3.62	0.08	6	−367.28
13	log(age) + recruitment age + relative 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) + standardized 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 + standardized 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 + standardized number of breeding males + (1|year)	11.35	0.00	12	−3967.01
26	site + standardized 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

Symbol 1|variable indicates a random effect. 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 were used to derive estimates.

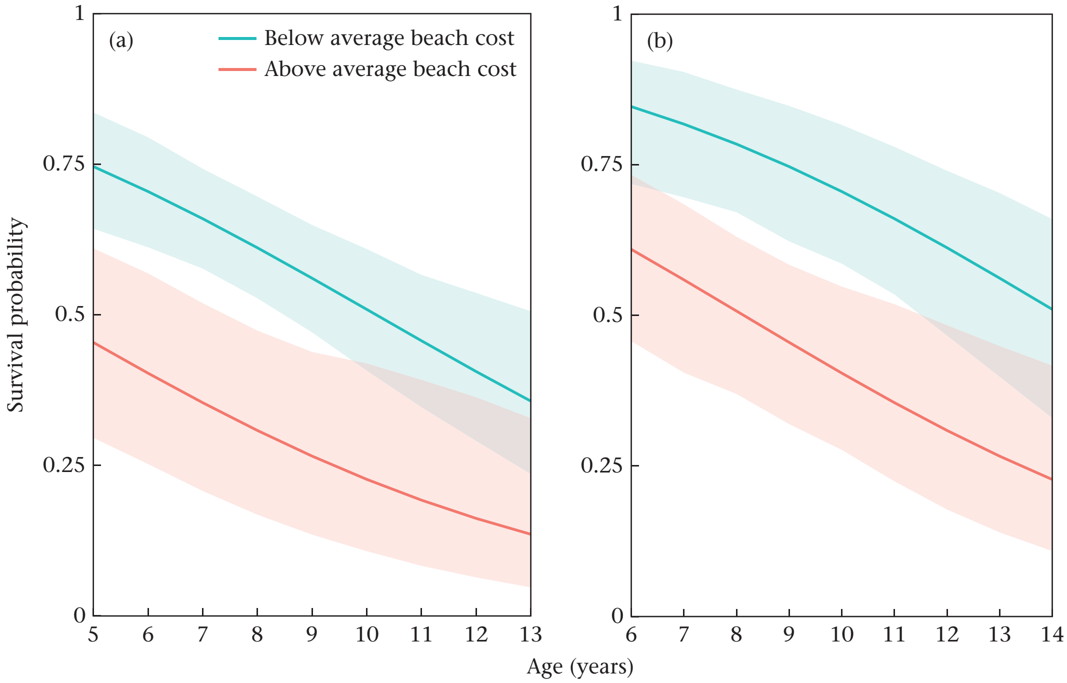

Figure 1. Mean predicted survival probabilities (±95% confidence interval) of male southern elephant seals at Marion Island. Estimates were derived from model 3 (Table 2), which treated age variation in (a) subordinate and (b) dominant male survival as a continuous logit-linear relationship. Beaches were assigned weighted scores based on average female harem size and associated numbers of subordinate males. Plotted data used the minimum (−1.99) and maximum (3.24) relative beach costs observed in the population. The survival model was described as: $logit\ (survival\ probability) = 1.64 - (0.21 \times age) + (0.84 \times breeding\ state) - (0.24 \times relative\ beach\ cost)$.

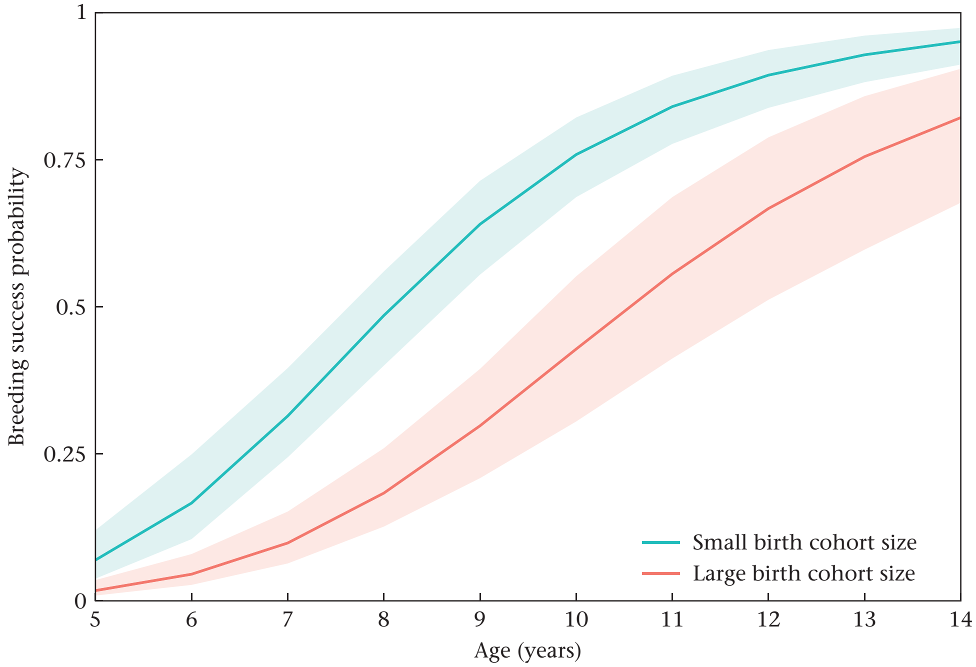

Figure 2. Mean predicted breeding success (probability of being dominant ±95% confidence interval) of male southern elephant seals at Marion Island. Estimates were derived from model 17 (Table 2), which treated age variation in breeding success as a continuous logit-log relationship. Plotted data used the minimum (420 pups) and maximum (700 pups) birth cohort sizes observed in the population. The breeding success model was described as: $logit(breeding\ success) = 5.71 + (5.40 \times log(age)) - (2.81 \times log(birth\ cohort\ size)) + 0.74$.

breeding improvement model, recruitment age also increased with the natural log of cohort size at birth (model 22, Table 2). First-time subordinate males were more likely to recruit at ca. age 6 when born in years with relatively few pups and at ca. age 7 when born in years with many pups (Fig. 3). First-time dominant males were more likely to recruit at ca. age 7 when born in years with relatively few pups and at ca. age 8 when born in years with many pups (Fig. 3).

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

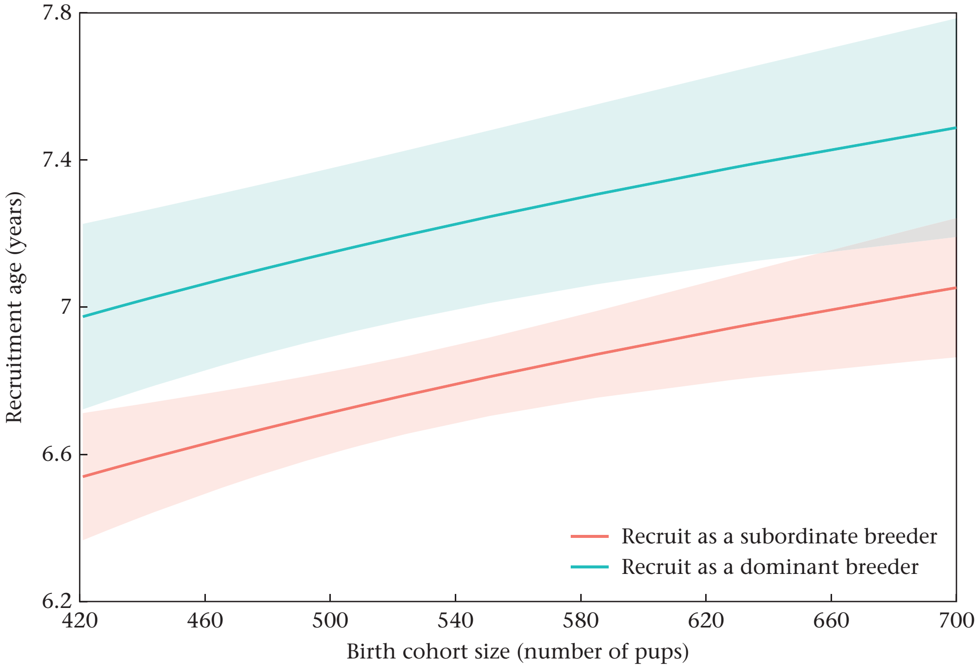

Figure 3. Mean predicted recruitment age (±95% confidence interval) of male southern elephant seals at Marion Island across observed birth cohort sizes. Estimates were derived from model 22 (Table 2), which predicted that recruitment age increased linearly with the natural log of cohort size at birth (number of pups produced annually). The recruitment age model was described as: $recruitment\ age = 0.43 + (0.44 \times breeding\ state) + (1.01 \times log(birth\ cohort\ size))$.

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 with 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 relatively large harems that likely required more energy to defend and service than others. Males born of relatively small cohort sizes were more likely to breed as a dominant male than males born of large cohort sizes. Similarly, males recruited to the breeding population at younger 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.

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 cost of attempting to breed is experienced by all males recruited to the breeding population (Lloyd et al., 2020). However, subordinate males have lower survival probabilities than dominant males, likely because of individual quality (Lloyd et al., 2020). Our new finding suggests that actuarial senescence differs not only between but also within breeding states, likely because of long-term reproductive costs from breeding successfully.

Males that defended and serviced relatively 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).

Our findings support the disposable soma theory of senescence, which predicts that males increase resource allocation to optimize reproduction under harsh environmental conditions (here in the form of competition intensity) at a greater cost to self-maintenance (Kirkwood & Rose, 1991). While mild environmental stressors may improve fitness by mobilizing 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 fertilizing female eggs (postcopulatory competition); both of which covary positively when maximizing 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 vocalizations (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 with a female), males across taxa allocate more sperm to each ejaculation to improve fertilization rates (Parker, 2016). Dominant male elephant seals must contend with subordinate males attempting to mate with 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 whether this pattern is universal among polygynous males or specific to breeding systems with intense male–male aggression such as those of elephant seals (Loison et al., 1999).

Cohort Level Natal Effects of Conspecific Density

Males born in relatively low pup production years were more likely to recruit at a younger age and become dominant breeders. A similar trend may occur in female elephant seals of the same population, whereby females recruit earlier and fecundity increases with decreasing population size (Pistorius et al., 2001, but see Oosthuizen et al., 2021). The effect of birth cohort size appears to have 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 birth year (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 while 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 as well

(Appendix: Pup weaning mass; 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, 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 a younger 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 and Comiso, 2009), and may become limiting for prebreeding 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 (Barry, 2013; Descamps et al., 2008; Engels & Sauer, 2007; Fay et al., 2015). Polygynous males generally have higher mortality rates after independence than females (Clutton-Brock et al., 1985) because more resources are required to maintain larger body sizes (Toïgo & Gaillard, 2003). Polygynous males are also 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 years when juveniles experience a secondary growth spurt (Laws, 1984; Ling & Bryden, 1981; McLaren, 1993). Thus, juvenile males experiencing favourable conditions may have more resources available to allocate towards secondary sexual traits that promote earlier recruitment and social dominance with age (Lloyd et al., 2020).

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 (or social statuses). First-time dominant breeders generally recruited 1 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, prebreeders 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., 2020; 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 the extent to which an individual can maximize breeding success in an environment that limits optimal functionality (Monaghan, 2008).

Conclusions

We have shown that density-dependent drivers likely affecting competition intensity during breeding and natal conditions accounted for variation observed in male southern elephant seal vital rates. Resource allocation decisions about survival made by a relatively long-lived, polygynous animal were determined not only by its intrinsic state, but also by implicit measures of density experienced during breeding. The cost of reproduction to survival was greater for dominant males of large harems than dominant males of smaller harems, especially when having defended and serviced females at a young age. In addition, the overwhelming effect of cohort size at birth on breeding success and recruitment age demonstrates how early life experiences may have lasting consequences for male fitness. Our case study is one of few to provide valuable insight into how polygynous male demographics vary with density by affecting resource allocation decisions. 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.

Author Contributions

Kyle J. Lloyd: Conceptualization, Formal analysis, Funding acquisition, Investigation, Methodology, Visualisation, Writing – original draft, review & editing; **W. Chris Oosthuizen:** Data curation, Methodology, Supervision, Writing – review & editing; **Jay J. Rotella:** Methodology, Validation, Writing – review & editing; **Marthán N. Bester:** Data curation, Methodology, Project administration, Writing – review & editing; **P.J. Nico de Bruyn:** Data curation, Funding acquisition, Methodology, Project administration, Resources, Supervision, Writing – review & editing.

Data Availability

Data to reproduce manuscript analyses are available on figshare: https://doi.org/10.6084/m9.figshare.21790016 (Lloyd et al., 2022).

Declaration of Interest

The authors have no conflicts of interest.

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Appendix

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., 2020) 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 hypothesized 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 with peripheral females and so require more time and effort for the dominant male 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 (Pearson $r = 0.62$; Table A1, Fig. A1). 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 was tagged (marked), which is sufficient time for all surviving males and females to have recruited 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 vocalizing dominant males (McCann, 1981). From population counts we estimated that the average number of breeding females per harem was 11.27 (Table A1). Therefore, beach cost was scored as follows: 1 = subordinate male, 2 = dominant male of beach with below average harem size (<12 females), 3 = dominant male of beach with above average harem size (≥ 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 for each age class (Fig. A2).

Table A1
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 events (September–November; Condy, 1979)

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)

(*continued on next page*)

Table A1 (*continued*)

Beach code	Beach name	Average number of females per harem (SD)	Average number of males per week (SD)
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

NA: not applicable (beaches with long stretches of coastline provide resting areas for subordinate males and so do not challenge local dominant males).

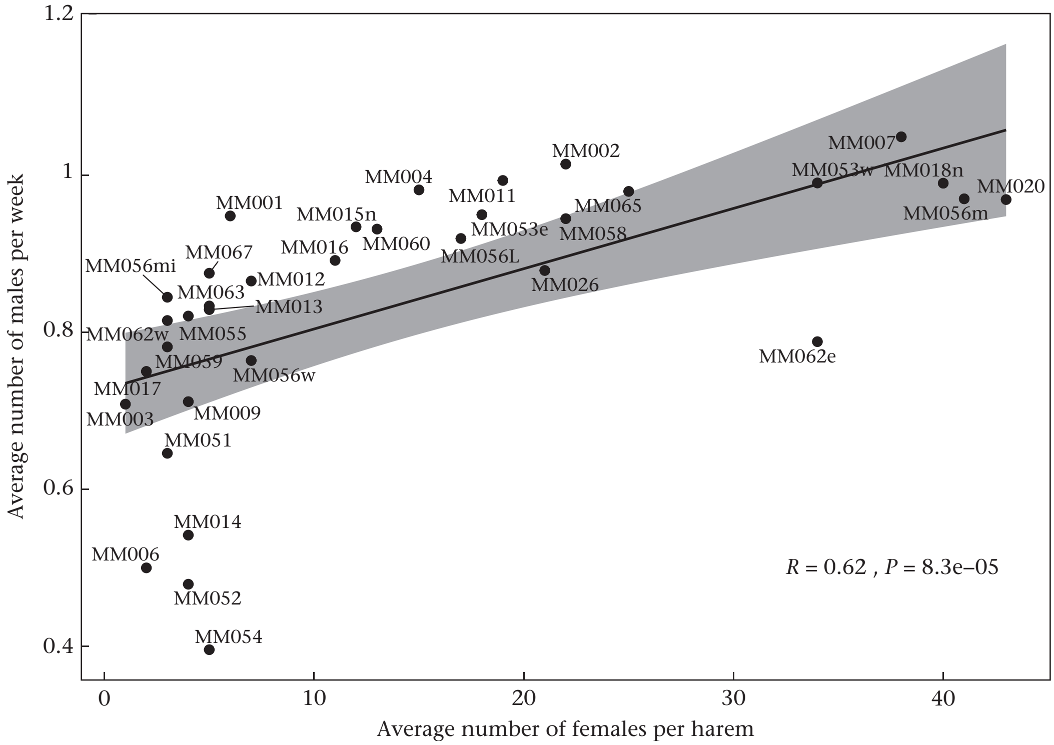

Figure A1. Average number of breeding female southern elephant seals per harem (or beach site) at Marion Island counted on 15 October (peak haul-out date) between 1992 and 2016, and the associated average number of males observed at each harem per week during annual breeding events (September–November).

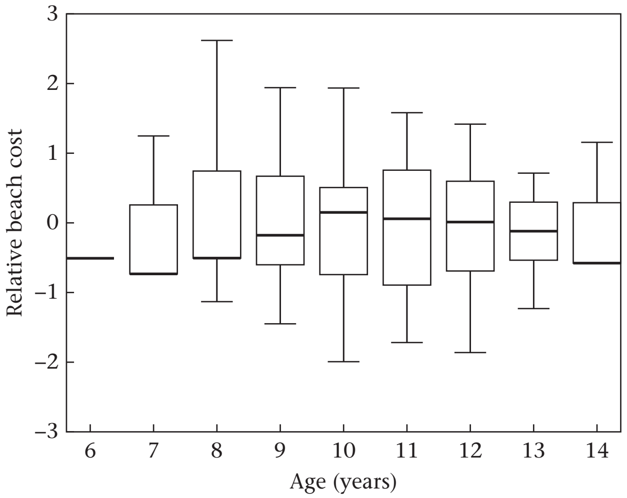

Figure A2. The range (whiskers), first and third quartiles (box edges) and median (bold line) of relative beach cost experienced by male southern elephant seals at Marion Island between 1992 and 2016 expressed per age class.

Base models and model hypotheses

Base models were initially established to determine whether recruited male life history traits (i.e. survival probability, breeding success probability and recruitment age) were determined by intrinsic effects such as age, breeding state and individual heterogeneity among others (Table A2; Grueber et al., 2011; Lloyd et al., 2020). Biological hypotheses about the structure of male life history traits were fitted according to various density-dependent covariates related to competition intensity and natal conditions (Table A3).

Pup weaning mass

In many polygynous species, body mass at weaning is a strong intrinsic predictor of juvenile 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 performed a

Table A2
Base models for survival probability (generalized linear models), breeding success probability (generalized linear mixed models) and recruitment age (linear models) of male southern elephant seals at Marion Island

Model parameters	ΔAIC$_c$	ω_i	*K*	Deviance
Survival				
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				
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

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 were used to test for density-dependent covariates.

Table A3
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	… + relative beach cost	Reproductive costs increase with increasing accumulated interactions with challengers and females
4	… + standardized 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 while accounting for individual differences (i.e. individual random effect)
9	… + relative subordinate male experience + relative dominant male experience	Breeding improvement increases with above average experience as a subordinate and dominant male
10	… + relative subordinate male experience	Breeding improvement increases with above average experience as a subordinate male (e.g. naïve first-time breeders)
11	… + relative dominant male experience	Breeding improvement increases with above average experience as a dominant male (e.g. skills such as site information, aggression, vocalizing, herding and detecting oestrus females)
12	… + recruitment age + relative subordinate male experience + relative 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 + relative 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	… + standardized 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	… + standardized 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

separate analysis to determine which density-dependent factors influence pup weaning mass across cohorts.

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 887 male pups from 18 cohorts (mean ± SD = 120.24 ± 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 to fit weaning mass to site, treated as a fixed effect, and year, treated 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 treated as a random effect separated between-year variance from within-year variance in weaning mass (Oosthuizen et al., 2015). We used the standardized (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.

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 which were a priori included in all models (model 28, Table 2). Pup weaning mass decreased with increasing pup production (Fig. A3). 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 (e.g. Fig. A4).

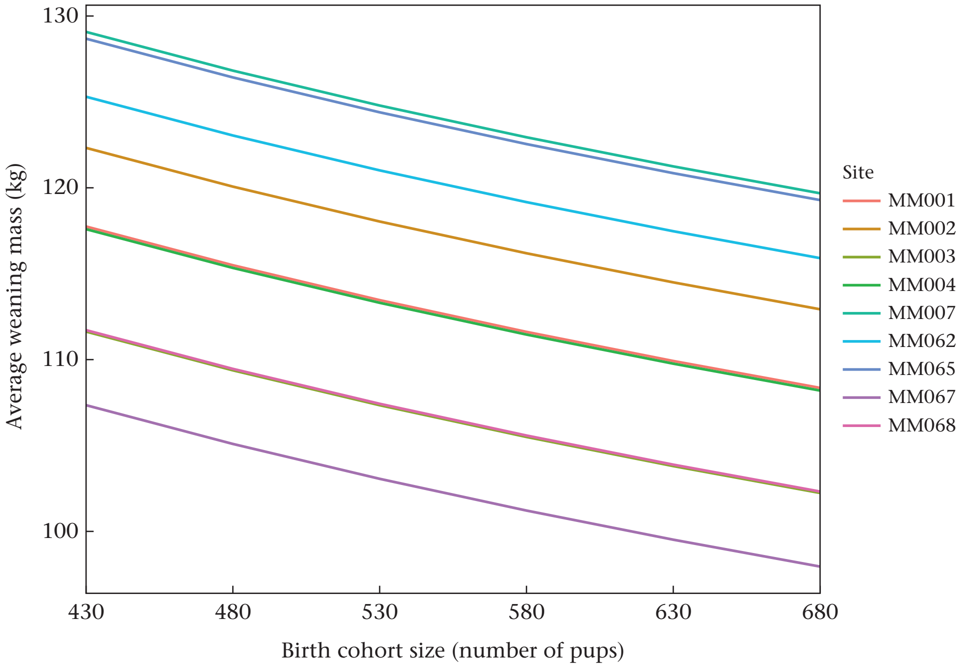

Figure A3. Mean predicted average pup weaning mass of male southern elephant seals at Marion Island. Estimates were derived from model 28 (Table 2), which predicted that average pup weaning mass decreased linearly with the natural log of cohort size at birth (number of pups produced annually). Site codes correspond to specific beaches where male pups were weighed at weaning (Table A1). Sites with higher intercept terms generally had larger harem sizes each breeding season.

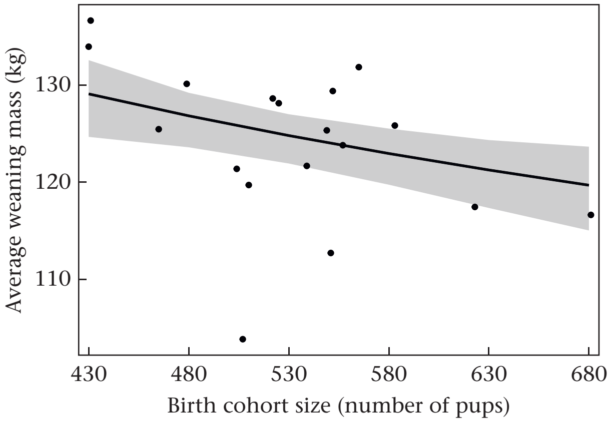

Figure A4. Mean predicted average pup weaning mass (±95% confidence interval) of male southern elephant seals born at Archway beach (MM007) as a representative example. Estimates were derived from model 28 (Table 2), which predicted pup weaning mass decreasing linearly with the natural log of cohort size at birth (number of pups produced annually). Points represent actual average pup weaning masses of each observed birth cohort size.

Additional results

There was some support for breeding success depending on recruitment age and relative dominant male breeding experience (Table 2, model 13, but $\omega_{17}/\omega_{13} = 2.55$). Older recruits were more likely to be dominant at their first breeding event than younger recruits and males with above average experience were more likely to be dominant again (Fig. A5).

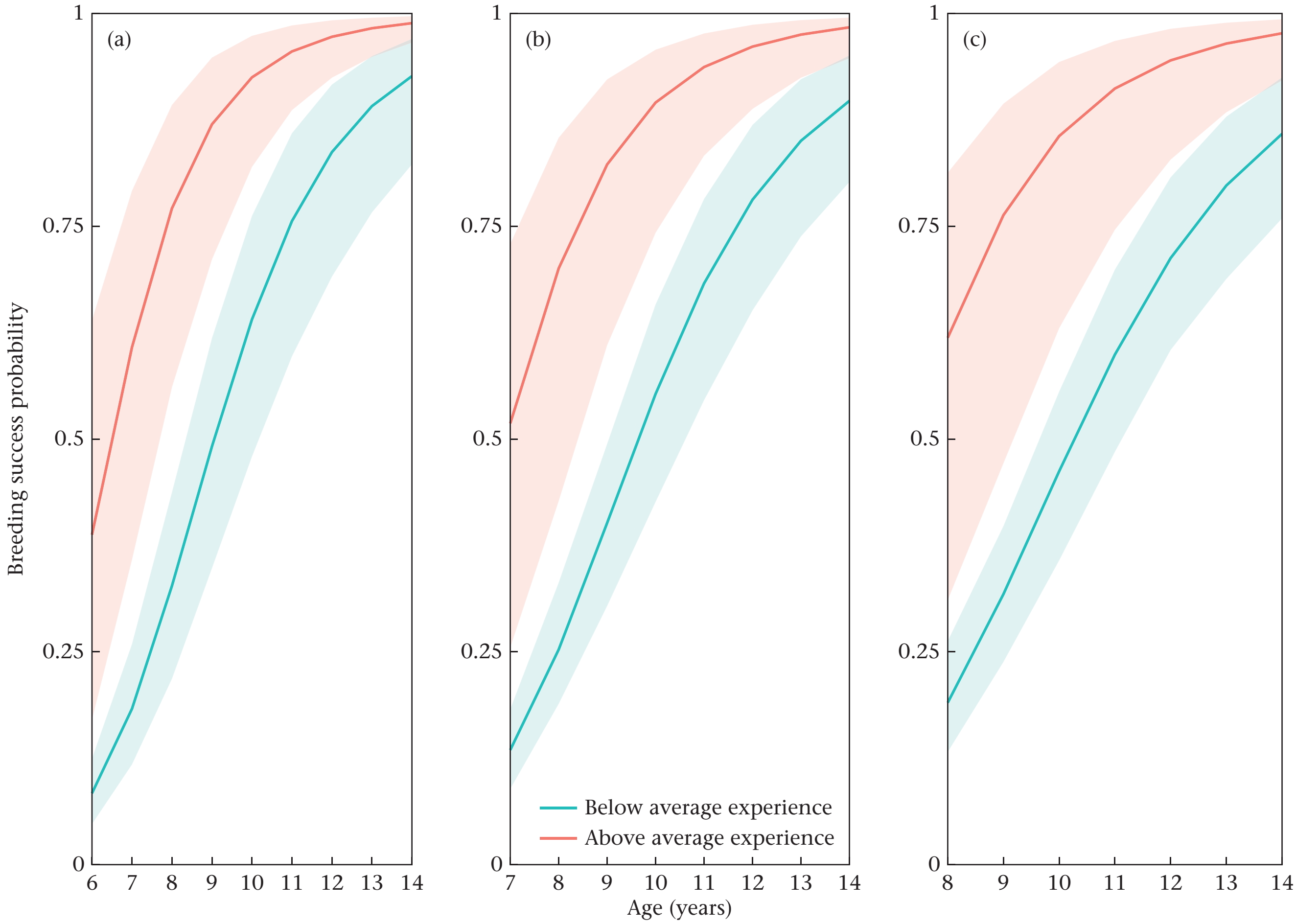

Figure A5. Mean predicted breeding success (probability of being dominant ±95% confidence interval) of male southern elephant seals at Marion Island that recruited at (a) age 6, (b) age 7 and (c) age 8. Estimates were derived from model 13 (Table 2), which treated age variation in breeding success as a continuous logit-log relationship. Older recruits were more likely to be dominant at their first breeding event than younger recruits. Breeding success also depended on relative breeding experience as a dominant male, with above average experience likely resulting in males being 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.