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Population ecology

Age-specific cost of first reproduction in female southern elephant seals

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When to commence breeding is a crucial life-history decision that may be the most important determinant of an individual's lifetime reproductive output and can have major consequences on population dynamics. The age at which individuals first reproduce is an important factor influencing the intensity of potential costs (e.g. reduced survival) involved in the first breeding event. However, quantifying age-related variation in the cost of first reproduction in wild animals remains challenging because of the difficulty in reliably recording the first breeding event. Here, using a multi-event capture–recapture model that accounts for both imperfect detection and uncertainty in the breeding status on an 18-year dataset involving 6637 individuals, we estimated age and state-specific survival of female elephant seals (*Mirounga leonina*) in the declining Macquarie Island population. We detected a clear cost of first reproduction on survival. This cost was higher for both younger first-time breeders and older first-time breeders compared with females recruiting at age four, the overall mean age at first reproduction. Neither earlier primiparity nor delaying primiparity appear to confer any evolutionary advantage, rather the optimal strategy seems to be to start breeding at a single age, 4 years.

1. Introduction

When to begin breeding is a crucial life-history decision that greatly affects individual fitness and lifetime reproductive output [1]. Because reproduction is energetically expensive, the first breeding event can entail a cost that can be expressed through decreased survival and/or reduced future probability of reproduction [2]. This cost, referred to as the cost of first reproduction, plays a key role in the evolution of life-history strategies and can have fundamental demographic consequences on population dynamics [1].

In low-density, declining populations, individuals are predicted to breed earlier [3,4]. The age at which individuals first reproduce is known to be an important influence on the intensity of the reproductive cost experienced by individuals [5–7]. This is particularly the case in species where size differs greatly between age classes, with younger and thus generally smaller first-time breeders being more likely to face a higher cost than individuals delaying first reproduction [8].

In long-lived species, variations in adult survival consistently affect population growth rate [9]. Hence, quantifying age-related variation in the survival cost of first reproduction is essential to understanding population dynamics and predicting population responses to environmental change. Investigating these variations

requires long-term longitudinal monitoring of individuals of both known age and breeding experience. In practice, however, determining an individual's reproductive experience remains challenging because of the imperfect detection of individuals [10] and uncertainty in the assignment of reproductive status [11] inherent to studies of wild populations.

Using a multi-event capture–recapture model that accounts for uncertainty in the assignment of breeding state, we analysed 18 years of data collected from more than 6000 individually marked female elephant seals (*Mirounga leonina*). Female southern elephant seals are extreme capital breeders and rely entirely on their stored reserves while nursing offspring. They start breeding from 3 years of age while still undergoing somatic growth [12], making them an ideal model species to assess the cost of first reproduction. We incorporated breeding experience as a latent state to estimate age-specific survival probabilities of pre-breeders, first-time breeders and experienced breeders, and quantify age-related variation in the cost of first reproduction. Accordingly, we present the first successful investigation of the effects of age and reproductive experience on survival that explicitly accounts for uncertainty in breeding states.

2. Material and methods

(a) Study species and data collection

Southern elephant seals (*M. leonina*) have a circumpolar distribution in the Southern Ocean. During the breeding season, females gather in harems, and each female gives birth to a single pup which nurses for approximately 24 days while fasting. From 1993 to 1999, 6637 females were permanently marked after weaning at Macquarie Island (54°30' S, 158°50' E), a closed breeding population [13]. Until 2001, intensive searches were made for branded individuals but from 2002 resightings were opportunistic.

(b) Capture–recapture analyses

We considered four states representing four different steps of the species' life cycle: pre-breeder (PB), first-time breeder (B^1), experienced breeder (E) and dead (+), underlying the four possible observations made in the field when collecting data: (i) not seen, (ii) seen and assigned as pre-breeder, (iii) seen with an unknown breeding state and (iv) seen and assigned as adult (see [11] for details about breeding-state assignment). We built a multi-event capture–recapture model to deal with uncertainty in the assignment of breeding states and reproductive experience [11,14]. Our model included four different parameters: detection probability (p), state assignment probability (β), survival probability (ϕ) and probability of transition between breeding states (ψ). All first-time breeders became experienced in the following breeding season, and we fixed the transition probability from B^1 to E at 1. An experienced breeder could not return to the PB or B^1 state but remained experienced. Transition probabilities from E to PB and B^1 were thus fixed at 0, while the transition from E to E was fixed at 1 (electronic supplementary material).

To determine the best model structure, we compared models exhibiting various combinations of age- and breeding-state effects on each parameter. For pre-breeders, we considered only eight age classes (0, 1, 2, 3, 4, 5, 6 and ≥ 7 years old) as no individuals were recorded as pre-breeders after age 6 (females were recorded as 'unknown' or 'breeders' only). For the same reason, we considered only nine age classes for first-time breeders (0, 1, 2, 3, 4, 5, 6, 7 and ≥ 8 years old). We considered

annual variation on detection probability in all models to account for varying resighting effort over the study period.

We compared models based on Akaike information criterion (AIC) [15]. Analyses were performed using the software E-SURGE [16].

Currently, no goodness-of-fit tests are available for multi-event models. However, to test model robustness, we compared model ranking under different levels of over-dispersion with a variance inflation factor \hat{c} of 1.0, 1.5, 2.0, 2.5 and 3.0 (encompassing average levels of over-dispersion [17]).

3. Results

Model rank was robust to changes in \hat{c} values (table 1). The top-ranked model showed age- and breeding-state effects on survival, state assignment and detection probabilities. Estimates of detection probability also varied annually and recruitment probability depended on age (table 1; electronic supplementary material).

Only 10% (s.e. = 0.01) of females recruited into the breeding population at 3 years old (figure 1). The mean age at first reproduction was 4 years with 34% (s.e. = 0.02) of females first breeding at this age. Some individuals delayed their first breeding attempt to older ages but more than 60% of the population that bred at least once in their life had recruited by age 4 (figure 1).

We detected a large cost of first reproduction on survival, with first-time breeders invariably having lower survival probabilities than pre-breeders of the same age (–31%, –19% and –17% for the 3-, 4- and 5-year-old first-time breeders, respectively) and experienced breeders of the same age (–22% and –23% for the 4- and 5-year-old first-time breeders, respectively; figure 2). This cost was higher for females breeding for the first time at 3 years old compared with those commencing breeding at 4 or 5 years old.

Survival of first-time breeders peaked at 4 years old. Survival probabilities of the 3- and 5-year-old first-time breeders were 9% and 6%, respectively, lower than survival of females recruiting at age four (figure 2). Survival of experienced seals was higher than survival of first-time breeders for all age classes (figure 2).

4. Discussion

Breeding for the first time is costly for female southern elephant seals, a prime example of a capital breeder, at Macquarie Island. No matter which age they commence breeding, first-time breeders always have lower survival than pre-breeders. This suggests that there is considerable selection pressure on first-time breeders, particularly on individuals in poor condition (i.e. low quality) that are consequently removed from the population [18,19]. The first breeding event acts like a powerful filter selecting higher quality individuals [5,7,20]. This is further evident from our finding that experienced seals have higher survival than first-time breeders of the same age.

In this population, the intensity of the cost to survival varied with age and was higher for younger first-time breeders than for females delaying their first breeding event to 4 or 5 years of age. Female elephant seals are still undergoing somatic growth until the age of six; therefore, first-time breeders must allocate energy to both growth and

Table 1. List of all models considered in model selection. The model selected is in italic. np, number of parameters; s, breeding-state effect; a, age effect; t, time effect; cst, constant.

no.	parameters				AIC					ΔAIC	
	detection	state assignment	survival	recruitment	np	$\hat{c} = 1$	$\hat{c} = 1.5$	$\hat{c} = 2$	$\hat{c} = 2.5$	$\hat{c} = 3$	$\hat{c} = 1$
1	<i>s.a + t</i>	<i>s.a</i>	<i>s.a</i>	<i>a</i>	112	66387.35	44328.90	33302.67	26686.94	22276.45	0.00
2	s.a + t	s.a	s.a	cst	107	66646.10	44502.10	33430.05	26786.80	22358.03	264.75
3	s.a + t	s.a	a	a	102	66668.10	44513.40	33436.05	26789.64	22358.70	286.75
4	s.a + t	s.a	s	a	88	66906.15	44662.76	33541.07	26868.06	22419.38	524.80
5	s.a + t	s	s.a	a	105	67098.03	44802.02	33654.01	26965.21	22506.01	716.68
6	t.a	s.a	s.a	a	194	67562.94	45135.29	33921.47	27193.18	22707.65	1181.59
7	s.a + t	a	s.a	a	108	67640.16	45165.44	33928.08	27185.66	22690.72	1258.81
8	t.s	s.a	s.a	a	88	67703.80	45194.53	33939.90	27187.12	22685.27	1322.45
9	t + a	s.a	s.a	a	75	67713.87	45192.58	33931.94	27175.55	22671.29	1332.53
10	t.(PB, B ¹ E)	s.a	s.a	a	74	67779.72	45235.82	33963.86	27200.69	22691.91	1398.38
11	t.(PB B ¹ E)	s.a	s.a	a	73	68048.83	45414.55	34097.41	27307.13	22780.28	1667.48
12	t.(PB E, B ¹)	s.a	s.a	a	74	68084.39	45438.93	34116.20	27322.56	22793.46	1703.05
13	t + (PB, B ¹ E)	s.a	s.a	a	60	68170.25	45486.83	34145.12	27340.10	22803.42	1788.90
14	t + s	s.a	s.a	a	61	68170.52	45487.68	34146.26	27341.41	22804.84	1789.17
15	t + (PB E, B ¹)	s.a	s.a	a	60	68179.45	45492.97	34149.72	27343.78	22806.48	1798.10
16	t.(PB B ¹ , E)	s.a	s.a	a	60	68182.96	45495.31	34151.48	27345.18	22807.65	1801.61
17	t	s.a	s.a	a	59	68184.35	45495.56	34151.17	27344.54	22806.78	1803.00

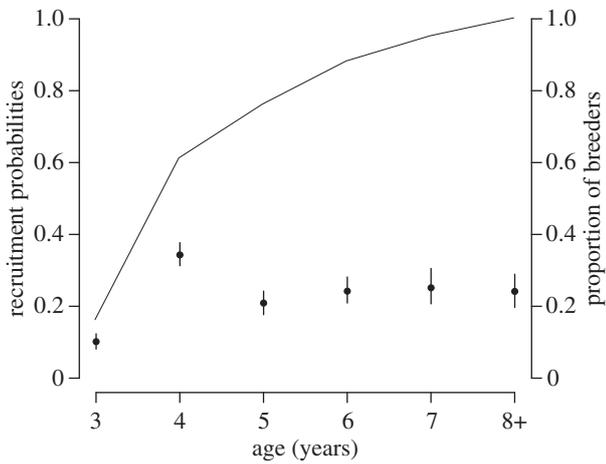


Figure 1. Recruitment probabilities (points) and cumulative proportion of first-time breeders in the breeding population (solid line) according to age.

reproduction [12]. Because elephant seals are capital breeders, nursing results in extreme reduction in body mass (35% on average over the 24-day lactation period) [21]. Consequently, younger and generally smaller individuals with lower reserves are likely to face a higher total energetic cost of first reproduction and to suffer greater mortality. This being true, we expected older first-time breeders to be buffered against this energetic cost and to exhibit higher survival [8]. By contrast, we found that survival of first-time breeders decreased from age five and that the optimal age to start breeding in this population appeared to be four years. Reproducing earlier substantially reduces the chance of survival but delaying the first reproduction also increases the risk of dying before any reproduction could occur. Seals delaying reproduction are thus likely to be seals in poorer condition. Primiparity at age four seems thus to be the optimal strategy to maximize survival.

Life-history theory predicts that the age at first breeding should decrease in a declining population [4]. Despite the long-term decline in the Macquarie Island population [22], our study shows that a mechanism for safely reducing the age of primiparity does not seem to exist. Instead, we found that the cost of first reproduction at age three remained very high. It is likely that selection acts against earlier

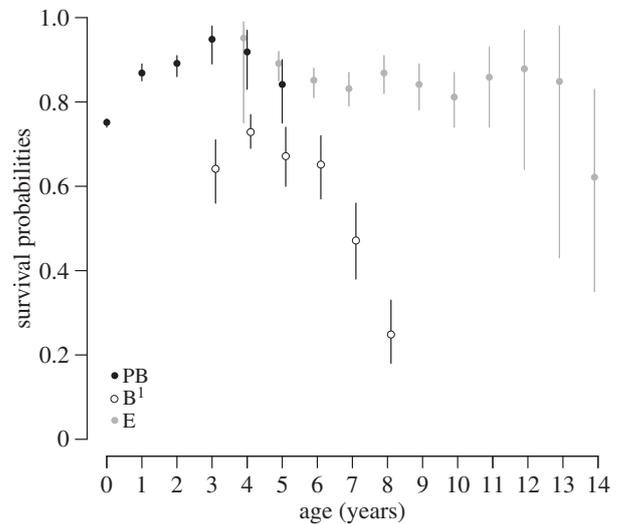


Figure 2. Survival probabilities of female elephant seals by breeding state and age. For first-time breeders, last estimate represents survival probability for the age class ≥ 8 years old. No estimates could be obtained for PB and E older than 5 and 14 years old, respectively, because of small sample sizes. Estimates on the boundary are not represented.

primiparity given the small proportion (10%) of the female population recruiting at 3 years of age, and that, while animals can breed earlier in response to low densities, there is little to be gained of such changes to the age of first breeding. Therefore, we appear to have detected a floor effect for primiparity, whose mechanism is as yet unknown. Such a floor effect may act as an absolute barrier to plasticity in life-history strategies for populations under stress.

This research was approved and cleared by the Australian Antarctic Animal Ethics Committee.

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Data accessibility. Southern elephant seal sightings data are available from <https://data.aad.gov.au> (entry ID: AADC-00102).

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