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Optimizing lifetime reproductive output: Intermittent breeding as a tactic for females in a long-lived, multiparous mammal

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Abstract

1. In iteroparous species, intermittent breeding is an important life-history tactic that can greatly affect animal population growth and viability. Despite its importance, few studies have quantified the consequences of breeding pauses on lifetime reproductive output, principally because calculating lifetime reproductive output requires knowledge of each individual's entire reproductive history. This information is extremely difficult to obtain in wild populations.
2. We applied novel statistical approaches that account for uncertainty in state assessment and individual heterogeneity to an 18-year capture–recapture dataset of 6,631 female southern elephant seals from Macquarie Island. We estimated survival and breeding probabilities, and investigated the consequences of intermittent breeding on lifetime reproductive output.
3. We found consistent differences in females' demographic performance between two heterogeneity classes. In particular, breeding imbued a high cost on survival in the females from the heterogeneity class 2, assumed to be females of lower quality. Individual quality also appeared to play a major role in a female's decision to skip reproduction with females of poorer quality more likely to skip breeding events than females of higher quality.
4. Skipping some breeding events allowed females from both heterogeneity classes to increase lifetime reproductive output over females that bred annually. However, females of lower quality produced less offspring over their lifetime.
5. Intermittent breeding seems to be used by female southern elephant seals as a tactic to offset reproductive costs on survival and enhance lifetime reproductive output but remains unavoidable and driven by individual-specific constraints in some other females.

KEYWORDS

finite-mixture capture–recapture models, individual heterogeneity, life-history trade-offs, *Mirounga leonina*, reproductive costs, state uncertainty

1 | INTRODUCTION

That individuals make trade-offs between fitness-related traits is a central assumption in life-history theory (Stearns, 1992). Because energy is limited, allocating resources to any particular life-history trait inevitably results in less resources allocated to another trait. Consequently, traits competing for the same resources (e.g. longevity and fecundity) cannot be simultaneously maximized (Roff, 1992; Stearns, 1992). The most prominent of these trade-offs is manifest in the cost of reproduction in which a high allocation of resources to current reproduction may lead to reduced survival and/or a reduced probability of breeding in subsequent years (Williams, 1966). In long-lived iteroparous species, individuals are expected to value their own survival over that of their offspring as any reduction in adult survival inevitably leads to lower lifetime reproductive output (LRO) (Roff, 1992). Long-lived individuals are therefore more likely to adjust their breeding effort by skipping reproductive events rather than investing in reproduction at a cost to survival (Hamel et al., 2010).

Intermittent breeding has the potential to substantially affect an individuals' fitness and consequently the population's dynamics. Accordingly, how often individuals skip reproduction has been a central question in evolutionary ecology. The occurrence and frequency of intermittent breeding have been documented in various long-lived species and linked to many factors including age (Beauplet, Barbraud, Dabin, Küssener, & Guinet, 2006; Rughetti, Dematteis, Meneguz, & Festa-Bianchet, 2014; Zhang, Rebke, Becker, & Bouwhuis, 2015), reproductive experience (Desprez, Pradel, Cam, Monnat, & Gimenez, 2011; Pradel, Choquet, & Béchet, 2012), individual quality (Hamel, Cote, Gaillard, & Festa-Bianchet, 2009; Sanz-Aguilar et al., 2011) and population density (Hamel, Côté, & Festa-Bianchet, 2010). Reproductive skipping has also been reported to be an adaptive tactic to offset reproductive costs under severe environmental conditions (Cubaynes, Doherty, Schreiber, & Gimenez, 2011; Forcada, Trathan, & Murphy, 2008; Soldatini, Albores-Barajas, Massa, & Gimenez, 2016) or to be the unavoidable outcome of other events (e.g. breeding dispersal Danchin & Cam, 2002; Reed, Harris, & Wanless, 2015). However, the fitness consequences of skipping breeding have rarely been quantified in wild populations. This is because LRO, defined here as the number of young produced over an individual's life, requires knowledge of the animal's entire reproductive history to be estimated. This is difficult because of the inherent issue of imperfect detection and uncertainty in the assessment of reproductive state. Rouan, Gaillard, Guédon, and Pradel (2009) proposed a new method derived from multi-event capture–recapture models (Pradel, 2005) to estimate LRO when the reproductive status is uncertain or unknown. We used this method to investigate the consequences of intermittent breeding on LRO of female southern elephant seals (*Mirounga leonina*) from Macquarie Island. Previously, female southern elephant seals had been assumed to breed (pup and mate) annually from primiparity to death, but de Bruyn et al. (2011) recently showed that intermittent breeding occurs in the Marion Island population. However, the frequency and consequences of reproductive skipping in this species remain unknown.

Using a multi-event model that accounts for uncertainty in breeding state assessment and individual heterogeneity on an 18-year dataset of 6,631 female southern elephant seals, we investigated possible reproductive costs on survival and future reproduction and estimated the frequency of reproductive skipping. As a posteriori measure of individual heterogeneity may underestimate the overall individual differences and mask reproductive costs operating at the individual level (Cam, Link, Cooch, Monnat, & Danchin, 2002; Chambert, Rotella, Higgs, & Garrott, 2013; Weladji et al., 2008), we used a finite-mixture model (Pledger, Pollock, & Norris, 2003) to investigate the presence of overall individual heterogeneity in survival and breeding probabilities. In the case of southern elephant seals, individual heterogeneity is likely to be generated by variability in the seal's ability to forage successfully and to assimilate nutrients and synthesize fat content. Using the method developed by Rouan et al. (2009), we evaluated the long-term consequences of intermittent breeding on LRO while accounting for individual heterogeneity. We propose two contrasting predictions:

1. As non-breeding females avoid the costs of reproduction, we expect them to have higher survival and probability of reproducing the following year than breeders ("prudent parent hypothesis" (Cam, Hines, Monnat, Nichols, & Danchin, 1998; Le Bohec et al., 2007)). Surviving for future reproductive opportunities being crucial in long-lived species, reproductive skipping may be an adaptive tactic that maximizes lifetime reproductive output. In this case, we expect that female elephant seals that skip some reproductive events will have a higher survival rate and produce more offspring over their lifetime than females breeding in each consecutive year.
2. Given non-breeding females might be females of lower reproductive potential (Reed et al., 2015; Robert, Paiva, Bolton, Jiguet, & Bried, 2012), we expect them to have both lower survival and breeding probabilities than females of higher reproductive potential (Cam et al., 2002; Chambert et al., 2013; Hamel, Cote, Gaillard, Festa-Bianchet, 2009). This hypothesis assumes that individuals with lower reproductive potential will be less able to bear the cost of reproduction than others. In this scenario, we expect females with lower reproductive potential to skip more breeding events as a result of individual-specific constraints and produce less offspring over their life span than other females.

2 | MATERIALS AND METHODS

2.1 | Study species and data collection

Southern elephant seals are the largest of the pinnipeds and one of the most polygynous and sexually dimorphic species of mammals (Laws, 1953). They spend most of their time at sea foraging but return to land twice annually: to breed (September–November) and to moult (timing depending on sex and age (Hindell & Burton, 1988)).

From 1993 to 1999, between October and December, 6,631 recently weaned female elephant seals were permanently and uniquely marked by hot iron branding at Macquarie Island (54°30′S, 158°57′E) (McMahon, Burton, van den Hoff, Woods, & Bradshaw, 2006). Throughout the year, from 1994 to 2001, daily searches for branded individuals were made on the Isthmus, the main study area. The top third of the island was searched every 10 days and the rest of the coastline was searched monthly. From 2002 to 2011, although there were fewer searches throughout the year a dedicated survey took place each year during the breeding season, the time that was most critical for determining the individual's breeding status. We defined a breeder as a seal engaged in breeding, irrespective of its success. Females were therefore considered breeders when seen with a pup or detected in a harem during the breeding season. Seals never observed as breeders on previous sampling occasions and seen on land between the end of the breeding season and the breeders' minimum return date for moult were considered pre-breeders (see Appendix 1 in Desprez, McMahon, Hindell, Harcourt, and Gimenez (2013) for more details about state assignment). Seals younger than 3 years old were also considered pre-breeders given recruitment never occurred before this age (McMahon, Burton, & Bester, 2003). Experienced non-breeders were assumed not to be present in harems during the breeding season (de Bruyn et al., 2011) but may have been resighted on land during their annual moult. In this case, it was impossible to determine if the observed individual was an actual non-breeder or a breeder not detected during the breeding season. Therefore, all experienced non-breeders, along with individuals for which we were not able to assign a breeding state, were recorded as "unknown".

2.2 | Multi-event model incorporating uncertain reproductive status and individual heterogeneity

We developed a multi-event capture–recapture model (Pradel, 2005) to quantify individual variation in survival and reproduction probabilities from observational data including individuals with uncertain reproductive status on one or more occasions (Appendix S1).

We defined five different events: 0 = seal not observed; 1 = seal observed and identified as a pre-breeder; 2 = seal observed with an uncertain reproductive status and never observed as a breeder on previous sampling occasions; 3 = seal observed and identified as a breeder and 4 = seal observed with an unknown reproductive status but observed as a breeder at least once in the past (i.e. experienced seal E). The underlying biological states considered were: pre-breeders (PB); first-time breeders (B1); experienced breeders (EB), for breeders with at least one previous reproductive event; experienced non-breeders (ENB), for non-breeders with at least one previous reproductive event; and dead (†). All females were initially marked as pre-breeders, consequently the probability of being encountered for the first time in the state PB was fixed to 1. The transition matrix combined both survival probabilities Φ and conditional probabilities to breed the following year ψ, whereas the event matrix included the detection probabilities p and conditional probabilities of assigning a reproductive status with certainty δ. We investigated the presence of individual heterogeneity in survival and breeding probabilities of experienced breeders and non-breeders by adding discrete classes of heterogeneity with specific survival and breeding probabilities into the model (finite-mixture models Pledger et al., 2003, Appendix S1).

2.3 | Goodness-of-fit test and model selection

Goodness-of-fit tests were performed using program U-CARE (Choquet, Lebreton, Gimenez, Reboulet, & Pradel, 2009) (Appendix S2). Model selection was based on prior knowledge of the studied population (Desprez et al., 2014) and followed a step-down approach with each parameter modelled sequentially while constraints on other parameters were held constant (Appendix S2).

Based on a prior study of this population (Desprez et al., 2014), survival probabilities of pre-breeders and first-time breeders were kept distinct and age-dependent. 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 six age classes for first-time breeders (3, 4, 5, 6, 7 and ≥8 years old). Recruitment probability was kept age-dependent (Desprez et al., 2014).

To test our first hypothesis stating that non-breeders had higher survival and breeding probabilities than breeders, we investigated a reproductive status effect on the transition probabilities. We also tested for the influence of reproductive experience in breeding probabilities as we suspected first-time breeders to suffer greater reproductive costs than experienced breeders and therefore to be more likely to skip the following reproductive occasion. The intensity of the reproductive costs experienced by individuals may vary between age classes. Therefore, we tested the influence of age on survival and breeding probabilities within each reproductive status. Finally, to test our second hypothesis, we investigated the presence of individual heterogeneity in survival and breeding probabilities by adding discrete classes of heterogeneity (finite-mixture models Pledger et al., 2003) in the most parsimonious model. We did not investigate temporal variation on survival and breeding probabilities in order to limit the number of parameters in the models tested and the number of alternative models. Models were ranked using Akaike information criterion corrected for over-dispersion (QAIC, Burnham and Anderson, 2002). Model selection was performed using program E-SURGE (version 1.9.0, Choquet, Rouan, and Pradel, 2009) and parameter identifiability was checked using the built-in tools (Choquet & Cole, 2012). Owing to parameter identifiability issues, we could not investigate the presence of individual heterogeneity in pre-breeders and first-time breeders.

2.4 | Lifetime reproductive output (LRO)

There are a number of metrics for quantifying an individual's lifetime reproductive effort including: (1) lifetime reproductive success (LRS) which refers to the total number of offspring an individual produces over its entire life span after some critical stage has been successfully passed (Rouan et al., 2009) (see Clutton-Brock 1988 for case studies); (2) lifetime reproductive output (LRO), i.e. the total number of offspring born to a female over the female's lifetime;

and (3) lifetime breeding success (LBS) which like LRO is the enumeration of the total number of offspring produced over a female's lifetime (Kruuk, Clutton-Brock, Rose, & Guinness, 1999). Here we use LRO as our measure of reproductive performance (see Caswell, 2011 for a similar choice).

We defined LRO as the total number of offspring born to a female over the study period. As most female southern elephant seals die before reaching 14 years old (Carrick & Ingham, 1962) and that resightings were done until 2011, we were confident that our study period covers the life span of most branded females and that the number of offspring produced over the study period corresponds to their real lifetime reproductive output.

Elephant seals typically give birth to a single pup (McMahon & Hindell, 2003). Therefore, we assumed that all breeding females produced one pup and that LRO corresponded to the number of times a female bred over her lifetime. To deal with the issue of uncertainty in reproductive status when females were not detected or could not be assigned to a reproductive state, we estimated LRO using the Generalized Viterbi Algorithm (Rouan et al., 2009). Based on the demographic parameters obtained from the best-supported model (Table 1), this approach provided all the possible sequences of states with their associated probabilities for a particular encounter history. For each sequence, we counted the number of times a female was a breeder and weighted this number by the associated sequence probability. We summed the results obtained for all sequences of one particular encounter history to estimate the LRO of each female. Rouan et al.'s (2009) approach to compute the LRO reconstitutes the most probable sequence of states, including the dead state and the number of reproductive attempts, while accounting for non-detections due to detectability <1. This concurs with the method recently proposed by Gimenez & Gaillard (2017). Therefore, it is possible to calculate the number of reproductive attempts for any individual, whether it dies during the study period or not. We proceeded in the same way to estimate the number of times a female skipped reproduction (i.e. the number of times a female was in the state "experienced non-breeder") over her lifetime. Then, we calculated the skipping frequency over a female's lifetime as the proportion of breeding life span (equal to the sum of the number of times a female was a breeder and the number of times she skipped reproduction over lifetime) when the female did not breed. This measure allowed us to control for the fact that female elephant seals with longer life span had more occasions to skip reproduction than females with shorter life span.

Finally, we used GLMs fitted with a negative binomial distribution (log-link function) to quantify the effects of the heterogeneity class, skipping frequency and skipping frequency squared (to account for potential quadratic effects) on the lifetime reproductive output. Because the maximum LRO and number of breeding pauses potentially reached by a female over the study period varied between cohorts (e.g. females born in 1993 cumulated a greater number of breeding attempts over the study period than females born in 1999), we considered each cohort separately. Statistical analyses were computed using R version 3.2.3 (R Core Team, 2015) and candidate models were compared using Akaike information criterion (AIC, Burnham & Anderson, 2002). When ΔAIC between models was <2 (i.e. the models were equally good at describing the data), we estimated the parameters using model averaging. Whenever an interaction term was retained in the best model, separate models were run for each level of heterogeneity class.

TABLE 1 List of the four best-supported model structures for survival and reproduction in female southern elephant seals at Macquarie Island (see Appendix S2 for complete model selection). The best-supported model is in bold. For each model, QAIC, the number of parameters (np) and the difference in the number of QAIC units from the best model (ΔQAIC) are provided

Model	Survival	Reproduction	QAIC	np	ΔQAIC
(a) Without individual heterogeneity					
1	**PB.a$_{(0-7+)}$; B1.a$_{(3-8+)}$; EB; ENB**	**PB.a$_{(3-8+)}$; B; ENB**	**35692.87**	**109**	**0.00**
2	PB.a$_{(0-7+)}$; B1.a$_{(3-8+)}$; EB; ENB	PB.a$_{(3-8+)}$; B1; EB; ENB	35694.13	110	1.26
3	PB.a$_{(0-7+)}$; B1.a$_{(3-8+)}$; EB.a$_{(4-5+)}$; ENB	PB.a$_{(3-8+)}$; B; ENB	35694.346	110	1.476
4	PB.a$_{(0-7+)}$; B1.a$_{(3-8+)}$; EB; ENB	PB.a$_{(3-8+)}$; B.a$_{(4-5+)}$; ENB	35694.79	110	1.92
(b) With individual heterogeneity					
5	**PB.a$_{(0-7+)}$; B1.a$_{(3-8+)}$; EB(1);EB(2);ENB(1);ENB(2)**	**PB.a$_{(3-8+)}$; B(1); B(2); ENB(1); ENB(2)**	**35682.811**	**114**	**0.00**
6	PB.a$_{(0-7+)}$; B1.a$_{(3-8+)}$; EB(1).a$_{(4-5+)}$;EB(2).a$_{(4-5+)}$;ENB(1);ENB(2)	PB.a$_{(3-8+)}$; B(1); B(2); ENB(1); ENB(2)	35686.096	116	3.28
7	PB.a$_{(0-7+)}$; B1.a$_{(3-8+)}$; EB(1);EB(2);ENB(1);ENB(2)	PB.a$_{(3-8+)}$; B1; EB(1); EB(2); ENB(1); ENB(2)	35686.318	115	3.51
8	PB.a$_{(0-7+)}$; B1.a$_{(3-8+)}$; EB(1);EB(2);ENB(1);ENB(2)	PB.a$_{(3-8+)}$; B(1).a$_{(4-5+)}$; B(2).a$_{(4-5+)}$; ENB(1); ENB(2)	35686.622	116	3.81

"a$_{(x-y)}$" indicates an age class effect (e.g. "a$_{(0-7+)}$" denotes a 8 age classes effect (from age 0 to age 7+) with the last age class (7+) grouping the individuals older than 6 years of age); "." denotes an interactive effect. "PB", "B1", "EB", "B" and "ENB" correspond to the states pre-breeders, first-time breeders, experienced breeders, breeders (first-time and experienced breeders grouped) and experienced non-breeders respectively. "E(N)B(1)" and "E(N)B(2)" indicate the two different classes of heterogeneity for experienced (non)breeders and "B(1)", "B(2)" indicate the two different classes of heterogeneity for breeders (first-time breeders and experienced breeders grouped together).

3 | RESULTS

From 1993 to 1999, between 897 and 975 newly weaned females were marked every year. Out of the 6,631 branded females, 4,623 were seen again during the study period and 2,400 were detected at least once with a pup. For 2,249 females, the reproductive status could not be determined for at least one resight.

3.1 | Model selection and demographic parameters

Goodness-of-fit tests indicated that the CJS model did not fit the data correctly (Appendix S2). We corrected for over-dispersion using a variance inflation factor ($\hat{c}$ = 2.01).

We first investigated the best model structure without considering the presence of individual heterogeneity. Detection probabilities showed marked fluctuations over the study period. As expected, the probability of detecting a breeder was higher than the probability of detecting a non-breeder (i.e. pre-breeder and experienced non-breeder) (Appendices S2 and S3). The probability of positively identifying a pre-breeder, when detected, decreased with age. From age 5, most pre-breeders resighted (≥96%) were recorded with an unknown reproductive status (Appendix S3). By contrast, the probability of identifying a breeder as such, given that the female has bred, was low at age 3 (0.14, *SE* = 0.06) but constant and close to 1 for older females.

Survival rate and probability of breeding the following year depended on the females' current reproductive state (Table 1, Appendix S2). We did not detect an influence of age on the survival and breeding probabilities of experienced non-breeders. However, the difference in QAIC between the models assuming no age variation in the survival or breeding probabilities of breeders (model 1 and 2) and the models including a two-age class effect (model 3 and 4) was <2 (Table 1), indicating that these models were equally good at describing the data (Burnham & Anderson, 2002). Similarly, the model differentiating the breeding probabilities of first-time breeders and experienced breeders (model 1) and the model assuming equal breeding probabilities between breeders (i.e. no effect of the reproductive experience on the breeding probability, model 2) both fitted the data (Table 1).

We tested the presence of individual heterogeneity in survival and/or breeding probabilities in the most parsimonious model and all models with ΔAIC < 2 (Appendix S1). The model including heterogeneity in both survival and breeding probabilities was better supported than any other model (Table 1; Appendix S2) suggesting a difference between two classes of individuals. In this model, age was not retained as a variable influencing the survival and reproduction of experienced breeders and non-breeders. Similarly, there was no difference in breeding probabilities between first-time and experienced breeders. Experienced breeders from the heterogeneity class 1 (70% of females) had similar survival to experienced non-breeders from the same heterogeneity class (Figure 1) suggesting an absence of reproductive costs on survival in this class of individuals. By contrast, experienced breeders from the heterogeneity class 2 (30% of females) had lower survival than both the experienced non-breeders from the same heterogeneity class and the females from the heterogeneity class 1 (Figure 1). This difference revealed that female elephant seals from the heterogeneity class 2 bred at a substantial cost to survival. Age-dependent survival estimates for pre-breeders and first-time breeders supported results from a previous study that suggest that first-time breeders suffer a high cost to survival (Desprez et al., 2014; Appendix S3). However, bigger confidence intervals in the survival probabilities of the 3-year old first-time breeders made the cost of first reproduction experienced by females from this age class less clear in this study. This loss of precision was likely due to the higher complexity of the model used in this study compared to the model used in Desprez et al. (2014).

In both heterogeneity classes, female elephant seals skipping a reproductive event (i.e. in the state "non-breeders") in year *t* had

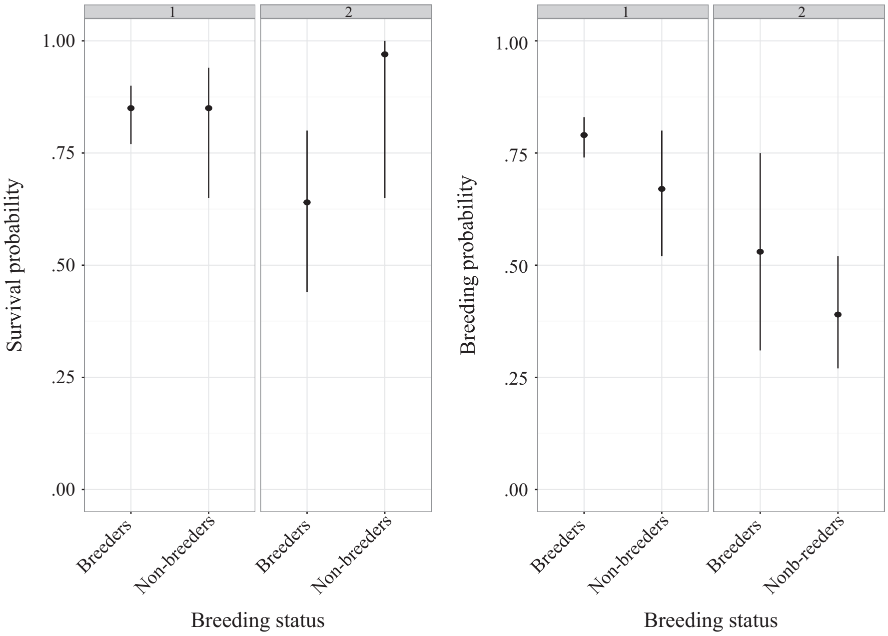

FIGURE 1 Survival and breeding probabilities of female elephant seals by breeding states and heterogeneity classes. "1" and "2" denotes the heterogeneity classes 1 and 2 respectively. "Breeders" corresponds to the state experienced breeders in the survival graph and to the state breeders (no breeding experience considered) in the breeding graph. "Non-breeders" corresponds to the state experienced non-breeders in both graphs

TABLE 2 Model selection to determine the model structure that best explains lifetime reproductive output variability in female southern elephant seals at Macquarie Island. Only the three best-supported model structures for each model selection are reported. Final selected models are in bold. When ΔAIC between models was <2, parameters were estimated using model averaging. For each model, AIC and the difference in the number of AIC units from the best model (ΔAIC) are provided

Models per cohorts					Models per cohorts and heterogeneity classes				
Cohort	No.	Fixed effects	AIC	ΔAIC	Heterogeneity class	No.	Fixed effects	AIC	ΔAIC
1	**1**	**HeteroClass × SkipFreq + SkipFreq^2**	**1713.50**	**0.00**	1	**1**	**SkipFreq + SkipFreq^2**	**1257.30**	**0.00**
						2	1	1419.30	162.00
	2	HeteroClass + SkipFreq + SkipFreq^2	1887.10	173.60		3	SkipFreq	1421.20	163.90
					2	**1**	**SkipFreq**	**437.90**	**0.00**
	3	HeteroClass × SkipFreq	1915.20	201.70		**2**	**SkipFreq + SkipFreq^2**	**439.60**	**1.70**
						3	1	459.70	21.80
2	1	**HeteroClass × SkipFreq + SkipFreq^2**	**1385.50**	**0.00**	1	**1**	**SkipFreq + SkipFreq^2**	**933.19**	**0.00**
						2	1	1083.10	149.91
	2	HeteroClass + SkipFreq + SkipFreq^2	1530.90	145.40		3	SkipFreq	1084.00	150.81
					2	**1**	**SkipFreq**	**451.50**	**0.00**
	3	HeteroClass × SkipFreq	1571.60	186.10		**2**	**SkipFreq + SkipFreq^2**	**452.60**	**1.10**
						3	1	467.40	15.90
3	1	**HeteroClass × SkipFreq + SkipFreq^2**	**1231.90**	**0.00**	1	**1**	**SkipFreq + SkipFreq^2**	**855.72**	**0.00**
						2	SkipFreq	990.58	134.86
	2	HeteroClass + SkipFreq + SkipFreq^2	1357.20	125.30		3	1	991.50	135.78
					2	**1**	**SkipFreq**	**371.90**	**0.00**
	3	HeteroClass + SkipFreq	1397.50	165.60		2	SkipFreq + SkipFreq^2	374.00	2.10
						3	1	384.60	12.70
4	1	**HeteroClass × SkipFreq + SkipFreq^2**	**1463.80**	**0.00**	1	**1**	**SkipFreq + SkipFreq^2**	**977.35**	**0.00**
						2	SkipFreq	1154.70	177.35
	2	HeteroClass + SkipFreq + SkipFreq^2	1622.30	158.50		3	1	1153.00	175.65
					2	**1**	**SkipFreq**	**488.00**	**0.00**
	3	HeteroClass × SkipFreq	1668.50	204.70		**2**	**SkipFreq + SkipFreq^2**	**488.70**	**0.70**
						3	1	502.00	14.00

(Continues)

TABLE 2 (Continued)

Models per cohorts					Models per cohorts and heterogeneity classes				
Cohort	No.	Fixed effects	AIC	ΔAIC	Heterogeneity class	No.	Fixed effects	AIC	ΔAIC
5	1	**HeteroClass × SkipFreq + SkipFreq^2**	**1591.40**	**0.00**	1	**1**	**SkipFreq + SkipFreq^2**	**1162.10**	**0.00**
						2	1	1349.90	187.80
	2	HeteroClass + SkipFreq + SkipFreq^2	1730.10	138.70		3	SkipFreq	1351.50	189.40
					2	**1**	**SkipFreq**	**429.90**	**0.00**
	3	SkipFreq + SkipFreq^2	1798.20	206.80		**2**	**SkipFreq + SkipFreq^2**	**431.60**	**1.70**
						3	1	436.70	6.80
6	1	**HeteroClass × SkipFreq + SkipFreq^2**	**1303.30**	**0.00**	1	**1**	**SkipFreq + SkipFreq^2**	**960.28**	**0.00**
						2	SkipFreq	1069.70	109.42
	2	HeteroClass + SkipFreq + SkipFreq^2	1366.20	62.90		3	1	1070.20	109.92
					2	**1**	**SkipFreq**	**343.20**	**0.00**
	3	HeteroClass + SkipFreq	1424.80	121.50		**2**	**1**	**345.10**	**1.90**
						3	**SkipFreq + SkipFreq^2**	**345.20**	**2.00**
7	1	**HeteroClass × SkipFreq + SkipFreq^2**	**1262.60**	**0.00**	1	**1**	**SkipFreq + SkipFreq^2**	**934.96**	**0.00**
						2	1	1004.40	69.44
	2	HeteroClass + SkipFreq + SkipFreq^2	1290.30	27.70		3	SkipFreq	1005.90	70.94
					2	**1**	**1**	**326.80**	**0.00**
	3	HeteroClass	1337.70	75.10		**2**	**SkipFreq**	**328.00**	**1.20**
						3	SkipFreq + SkipFreq^2	329.90	3.10

"HeteroClass" corresponds to the heterogeneity classes and "BP" corresponds to the number of breeding pauses over lifetime.

less chance of breeding the following breeding season ($t + 1$) compared to females that bred in year t (Figure 1). For a given breeding state, there was a clear difference between heterogeneity classes. Specifically, females from the heterogeneity class 1 had a higher probability of breeding the following breeding season than females from the heterogeneity class 2 (Figure 1). Recruitment estimates (i.e. probability to breed for the first time) supported results obtained in Desprez et al. (2014) that suggest that the mean age at first reproduction is 4 (Appendix S3). However, the recruitment estimate for the 3-year old was underestimated. The sample size of females starting to breed at 3 is small compared to the other age classes and included a fair amount of uncertainty. We assume that the additional complexity of the model used in this study compared to the one used in Desprez et al. (2014) lead to a loss of statistical power that affected the precision and accuracy of the parameters estimated for this age class. However, this bias affected the reproductive trajectories in both heterogeneity class the same way and therefore did not impact our final conclusions.

3.2 | Lifetime reproductive output

We estimated LRO and the skipping frequency over a seal's lifetime from the demographic parameters obtained in model 5 (Table 1, Model 73 in Table B3, Appendix S2).

For all cohorts, we found that the most parsimonious model explaining LRO retained the skipping frequency, the heterogeneity class and the interaction between those variables as explanatory variables (Table 2). In the heterogeneity class 1, we observed a nonlinear relationship between reproductive output (number of pups born) and the skipping frequency so that pup production initially increased in concert with the skipping frequency before decreasing as the skipping frequency kept increasing (quadratic effect, Table 2, Figure 2). In the heterogeneity class 2, the number of pups produced increased with the skipping frequency Table 2, Figure 2). Importantly, the maximal values of LRO achieved in heterogeneity class 1 were always higher and associated with fewer breeding pauses than in the heterogeneity class 2 (Figure 2). Specifically, the predicted maximum number of pups produced by females from the heterogeneity class 1 was 4.13 to 2.23 times higher than the predicted maximum number of pups produced by females from the heterogeneity class 2. Moreover, females from the heterogeneity class 1 never skipped more than half of the breeding seasons during their lifetime, while females from the heterogeneity class 2 had to skip more than half of their reproductive opportunities to reach the highest values of LRO (Figure 2). Importantly though, even in females from the heterogeneity class 1, the maximum LRO was reached when females skipped some reproductive events during their breeding life span.

4 | DISCUSSION

Life-history theory suggests that survival of long-lived individuals should be buffered against reproductive costs with individuals favouring their own survival by restricting reproductive effort (Gaillard & Yoccoz, 2003). However in some iteroparous long-lived species, some individuals use a flexible reproductive tactic and may invest in reproduction at a cost to their own survival (Erikstad, Fauchald, Tveraa, & Steen, 1998; Hadley, Rotella, & Garrott, 2007). Capital breeding and reproduction in fluctuating environments have been suggested as potential causes for reduced survival of breeders. In a truly capital breeding species, the southern elephant seal, we found that the ongoing cost of reproduction on survival was a function of individual heterogeneity and had long-term consequences on each female's LRO.

Finite-mixture capture–recapture models do not provide information about the underlying mechanisms. However, as female elephant seals from heterogeneity class 1 consistently outperformed females from heterogeneity class 2, our results suggest that individual heterogeneity was related to variation in individual quality (Chambert et al., 2013; Lescroël, Dugger, Ballard, & Ainley, 2009; Lewis et al., 2006), i.e. a property of the phenotype that is positively correlated with fitness (Wilson & Nussey, 2010). We hypothesize that such variation in individual quality was mainly generated by variability in the female's ability to forage successfully and to assimilate nutrients in the form of blubber (Hindell et al., 2017; McMahon, Harcourt, Burton, Daniel, & Hindell, 2017). Female elephant seals from heterogeneity class 1 were likely to be better foragers and to have better body condition (i.e. a high proportion of lipid relative to lean tissue) than females from heterogeneity class 2. This interpretation is supported by the finding that no apparent costs on both survival and future reproduction were detected in females from the heterogeneity class 1, while, by contrast, females from the heterogeneity class 2 invested in reproduction at a significant cost to their survival. Long-lived species are expected to adopt a conservative reproductive tactic and avoid potential reproductive costs on survival, as a small reduction in adult survival will reduce the number of subsequent breeding events and substantially affect the individual fitness (Curio, 1988; Shaw & Levin, 2013). Elephant seals are true capital breeders and nursing results in extreme reduction in female body mass (35% on average over the 24-day lactation period) (Arnbom, Fedak, & Boyd, 1997; Fedak, Arnbom, & Boyd, 1996). Therefore, survival of female elephant seals is likely to be strongly dependent on a females' ability to rebuild her energetic reserves during the post-breeding foraging trip. In the heterogeneity class 1, female breeders and non-breeders had similar survival rates suggesting that females from this heterogeneity class were able to bear the energetic costs induced by the pup rearing without compromising their own survival. By contrast, females from heterogeneity class 2 suffered a substantial reproductive cost on survival. The apparent survival cost in these females, likely to be less successful foragers than females from the heterogeneity class 1, may be a result of their inability to restore their nutrient reserves during the post-breeding foraging trip.

Regardless of their quality or breeding status, female elephant seals at Macquarie Island had a high probability of skipping the following breeding event (between 20% and 60%). The occurrence of pregnancy in pinniped capital breeders is thought to be very sensitive to body reserves (Boyd, 2000) and so female elephant seals may

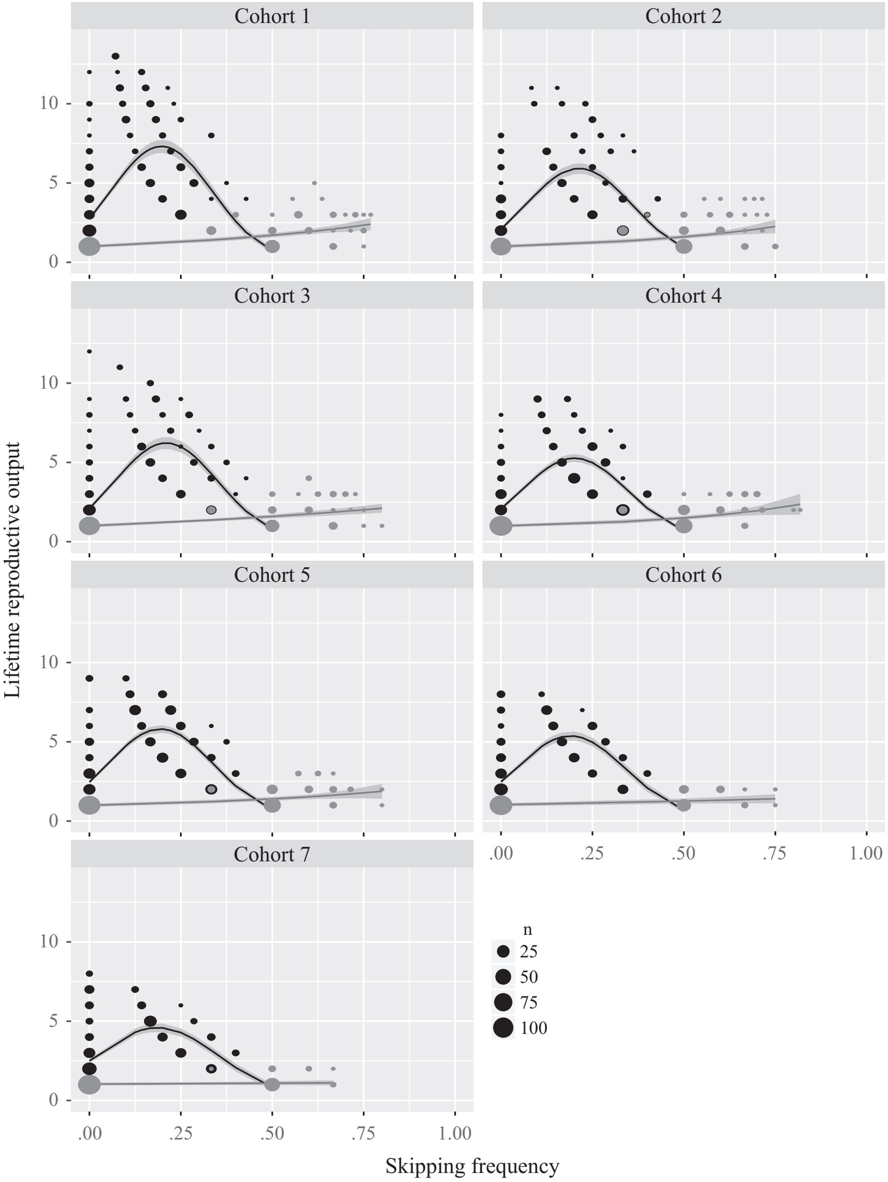

FIGURE 2 Relationship between the estimated Lifetime reproductive output (LRO) (i.e. number of young produced over life span) and the number of breeding pauses over lifetime in the seven studied cohorts of female southern elephant seals at Macquarie Island. Estimates for individuals from the heterogeneity classes 1 and 2 are represented in black and grey, respectively. Solid circles correspond to the estimates obtained using the Generalized Viterbi Algorithm. The size of the circles is relative to the number of female seals *n*. The solid lines represent the predictive curves obtained from the most parsimonious GLM models (see Table 2). The shaded areas represent the 95% confidence intervals

only be able to reproduce when their body condition (defined here as the amount of available lipid relative to lean tissue) is above a certain threshold. Breeding in this species is therefore likely to depend on individual quality, experience (Paterson, Rotella, Mannas, & Garrott, 2016) and environmental conditions during foraging trips (Hindell et al., 2017; McMahon et al., 2017). Overall, females from the heterogeneity class 2, assumed to be lower quality females, had lower breeding probabilities than females from the heterogeneity class 1. In these females, reproductive skipping may be unavoidable and mainly driven by individual-specific constraints (Reed et al., 2015). In the heterogeneity class 1, while we did not detect any reproductive cost on survival, 20% of breeders skipped the following breeding event. This suggested that reproductive costs may also exist for these females. When under a certain threshold of body condition, females from the heterogeneity class 1 may use reproductive skipping as an adaptive response to avoid jeopardizing their own survival, as predicted by the prudent parent hypothesis (Cam et al., 1998; Le Bohec et al., 2007). We did not investigate the influence of environmental conditions on the probability to skip breeding in this study due to the already high complexity of our model that accounted for individual heterogeneity on top of imperfect detection and state assignment probabilities. However, we suspect intermittent breeding to be closely associated with unfavourable environmental conditions as reported in other long-lived species (Cubaynes et al., 2011; Forcada et al., 2008; Soldatini et al., 2016). In particular, Van den Hoff et al. (2014) showed that, in this population of elephant seals, the number of breeding seals varied substantially between years and that this variation was related to environmental conditions.

Contrary to the prudent parent hypothesis, breeding probabilities were lower for non-breeders than for breeders. Individuals skipping reproductive events are expected to have an increased probability of breeding in a subsequent season because they are able to regain lost condition (Le Bohec et al., 2007; Pomeroy, Fedak, Rothery, &

Anderson, 1999). We suggest that in female elephant seals, a cost to reproductive skipping may exist as non-breeding females absent from the terrestrial mating harems had limited access to mating partners. Consequently, females skipping reproduction in year *t* were unlikely to give birth—and therefore to return to land and mate again—in year *t* + 1. We do note that elsewhere, opportunistic mating at sea away from the breeding colonies has been observed in southern elephant seals (de Bruyn et al., 2011) and may provide opportunities for the non-breeders to re-enter the breeding population.

Overall, females from the heterogeneity class 2, assumed to be lower quality females, had lower demographic performance than females from the heterogeneity class 1. Such consistent differences between the two groups of females may arise from environmental conditions experienced during early-life (i.e. maternal care and/or environmental conditions) (Festa-Bianchet, Jorgenson, & Réale, 2000; Hamel, Gaillard, Festa-Bianchet, & Côte, 2009; Kendall, Fox, Fujiwara, & Nogeire, 2011; Lindström, 1999; Metcalfe & Monaghan, 2001; Schwagmeyer & Mock, 2008). In elephant seals in particular, maternal care has been reported to influence the pups weaning mass, a strong predictor of juvenile survival and future reproduction (McMahon, Burton, & Bester, 2000; McMahon et al., 2017; Oosthuizen, Bester, Altwegg, McIntyre, & Bruyn, 2015; Postma, Bester, & de Bruyn, 2013). Permanent variation in individual quality may also result from persistent differential habitat selection by individuals (Griffen & Norelli, 2015). Female elephant seals forage in two main areas: the Inter-Frontal zone or the Antarctic zone (Bailleul et al., 2010; Hindell, Bradshaw, Harcourt, & Guinet, 2003; Hindell et al., 2016) (but, see McIntyre et al., 2011 for the exception of the population from Marion Island). Individuals foraging in the Inter-Frontal zone are exposed to different environmental conditions and consume different prey from females foraging in the Antarctic zone (Banks, Lea, Wall, McMahon, & Hindell, 2014). At Îles Kerguelen, female elephant seals foraging in the Antarctic zone wean bigger pups than females foraging in the Inter-Frontal zone (Authier, Dragon, Richard, Cherel, & Guinet, 2012). Females of higher reproductive potential most likely adopt superior foraging tactics. Finally, consistent differences in demographic performance between females may be related to genetic factors (Stover, Kendall, & Fox, 2012). However, the relative influence of the genetic component on individual heterogeneity has been subject to debate and remains to be quantified (Cam et al., 2013; Tuljapurkar, Steiner, & Orzack, 2009).

In the heterogeneity class 2, females that never skipped breeding suffered from survival cost and produced less offspring over their lifetime than females skipping some reproductive events. Intermittent breeding seems to allow these females to maximize their survival and thereby accumulate a greater number of breeding events over their life span. Skipping breeding in some years (i.e. adaptive phenotypic plasticity in breeding propensity) was therefore advantageous and used by female southern elephant seals from the heterogeneity class 2 as a tactic to maximize LRO (Reed et al., 2015). Our results suggest that intermittent breeding may also have been used as an adaptive reproductive tactic by females from the heterogeneity class 1 to offset a potential survival cost. However, we could not draw any firm conclusion, as reproductive costs were not apparent in this class of females. Besides, alternative hypothesis may also explain the observed relationship between LRO and skipping frequency in the heterogeneity class 1. Indeed, the individual quality hypothesis predicts that high-quality individuals consistently outperform other individuals throughout their life, showing positive covariation between demographic parameters. Under this hypothesis, females of higher quality are likely to have a longer life span and therefore more occasions to skip breeding but more breeding pauses may not allow them to have higher LRO.

Nonetheless, higher quality females reached much higher LRO values than lower quality females suggesting that in lower quality females the incurred reproductive cost on survival could not be offset by intermittent breeding. Negative long-term consequences of reproductive cost on survival have also been reported in Weddell seals where a small difference in survival between breeders and non-breeders, i.e. 3%, led to substantial differences in life span (17 years vs. 10 years), and therefore lifetime reproductive output (Hadley et al., 2007).

Our results highlight the coexistence of different reproductive trajectories within the population of southern elephant seals at Macquarie Island as also suggested by McMahon et al. (2017). For poorer quality females, reproductive skipping seemed to be both adaptive and driven by individual-specific constraints. It is likely that females from the heterogeneity class 1 produce the majority of offspring that recruit into the breeding population. Similarly, at Amsterdam Island, high-quality female subantarctic fur seals (*Arctocephalus tropicalis*), only represent one-third of the studied population but produce more than two-thirds of the viable offspring (Beauplet & Guinet, 2007). The existence of a similar skew in the population of elephant seals at Macquarie Island has important implications for population dynamics and evolutionary processes. Our dataset did not include enough cohorts of individuals to fully investigate this question as such information can only be obtained from extremely scarce extensive long-term datasets that include several generations of individuals (Clutton-Brock & Sheldon, 2010).

In conclusion, both initial hypotheses received empirical support. Female elephant seals at Macquarie Island seemed to use reproductive skipping as a tactic to offset reproductive costs on survival and enhance LRO as predicted by the prudent parent hypothesis. However, a female's decision to skip reproduction was also dependent on individual-specific constraints as some females skipped more frequently than others while still suffering from a substantial reproductive cost on survival. Individual differences in reproduction are likely to be carried over to following breeding seasons as females with higher reproductive potential were more likely to breed during consecutive breeding seasons than seals of poor reproductive potential. It appears that seals successfully recruited into the population are likely to be produced by a subset of females and this may have profound implications for evolutionary processes given they will contribute disproportionally to future generations.

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AUTHORS' CONTRIBUTIONS

M.D., O.G., C.M., M.H. and R.H. designed the study; M.D. and O.G. developed the model; and M.D. performed the statistical analyses. M.D. wrote the first draft of the manuscript and all authors contributed to revisions.

DATA ACCESSIBILITY

The Sightings database, where the capture–mark–recapture data are curated, for the Macquarie Island Elephant Seals are available from the Australian Antarctic Data Centre, https://data.aad.gov.au/metadata/records/TAGS_Elephant_Seals (Burton, Van Den Hoff, & Hindell, 2017).

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Additional Supporting Information may be found online in the supporting information tab for this article.

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