INDIVIDUAL AND ENVIRONMENTAL VARIABILITY IN A POPULATION OF LONG-LIVED MARINE MAMMALS

by

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of the requirements for the degree

of

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ABSTRACT

Environmental fluctuations and individual heterogeneity are two interacting sources of population variation affecting demographic and evolutionary processes. While environmental variation has traditionally been at the core of population ecology, individual heterogeneity has received relatively little attention. Using long-term mark-recapture data, I investigated some specifics of environmental and individual variation in a population of Weddell seals. First, I assessed the impact of an extreme environmental perturbation (occurrence of gigantic icebergs in the vicinity of seal breeding area) on colony attendance, survival, and reproductive rates of females. As expected for long-lived species, survival rates were unaffected by the perturbation. Reproductive rates dropped by ~40% during this iceberg event but rapidly re-increased afterwards. The seal population thus appeared to be resilient and relatively unaffected by this isolated perturbing event, but if such events were to occur too frequently, the effects on reproduction could have important demographic impacts. Second, I showed that individual heterogeneity was an important source of variation in female reproductive rates. Accounting for this heterogeneity allowed detection for the first time of an important cost of reproduction on future breeding probability. This reproductive cost was expressed as a 10% higher probability of reproduction a given year if a female skipped reproduction the previous year. Further, I found that individual differences were relatively consistent over time, although their expression seemed slightly amplified in disturbed conditions. Finally, I addressed the evolutionary consequences of this individual heterogeneity in female reproductive rates. Females reproducing at high frequency produced female offspring with average chances of recruitment, suggesting no trade-off between progeny number and quality. Using simulations, I showed that such females with high reproductive rates were consequently expected to produce more grandchildren through their female progeny and thus potentially have higher fitness, although the contribution of male progeny could not be investigated here. Female reproductive rates also displayed some heritability, although very low, as expected for a fitness-related trait. Taken together, these results suggest that, in this population, traits associated with the observed individual reproductive heterogeneity could be under natural selection.

CHAPTER ONE

INTRODUCTION TO DISSERTATION

Variation is a central feature of life that is prevalent at all levels of biological organization, from genes to ecosystems (Campbell and Reece 2005, Begon et al. 2009). Diversity stems from temporal, spatial and individual variation, which is the product of intrinsic (e.g., genetics, aging) or environmental factors (e.g., abiotic: physical environment; biotic: competition, prey resources). Population ecology has traditionally focused on the temporal dynamics of wild populations. Understanding what environmental forces cause animal populations to vary in size or composition (e.g., age structure) is not only of fundamental interest to ecologists (Begon et al. 1996, Gotelli 2008, Rockwood 2009) but is also crucial for management and conservation (Williams et al. 2002, Mills 2006).

Individual heterogeneity is ubiquitous in natural populations and should not be discounted as a source of variation. In its broader sense, individual variation refers to any phenotypic differences underlaid by genetic factors and represents the raw material of natural selection (Darwin 1859, Endler 1986). In population ecology, individual heterogeneity derives from latent differences in vital rates (Cam et al. 2002), which can be equally linked to innate (Foerster et al. 2003, Hunt et al. 2004) or acquired phenotypic traits (Bergeron et al. 2011, Lailvaux and Kasumovic 2011). Individual heterogeneity influences the magnitude of demographic stochasticity and can therefore affect the dynamics and persistence of a population (Conner and White 1999, Vindenes et al. 2008, Kendall et al. 2011). It can also induce bias in estimators of population parameters

(Johnson et al. 1986) and hamper the detection of life history patterns resulting from individual trade-offs, such as reproductive cost or senescence (Vaupel and Yashin 1985, Service 2000, Nussey et al. 2008, Weladji et al. 2008).

Though environmental and individual heterogeneity are generally addressed separately, these two types of variation may interact to affect demographic and evolutionary processes (van Noordwijk 1989). Indeed, realized phenotypes result from a combination of inherent individual characteristics (genetics) and environmental conditions (Falconer 1989, van Noordwijk 1989), such that the expression of individual heterogeneity can vary across environments. For instance, individuals may perform similarly well in optimal conditions such that apparent individual heterogeneity is small. Major differences in individual performance may be revealed in poor conditions (e.g., Tavecchia et al. 2005), increasing the level of variation observed and exposing the limits of the species' phenotypic range. Quantifying individual and environmental variation separately and together should improve our understanding of the evolutionary forces acting on a population and its potential to adapt to a changing environment.

This dissertation addresses both environmental and individual variability in the vital rates of a population of free-ranging Weddell seals breeding in Erebus Bay, Antarctica. This population has been subject to a long-term mark-recapture monitoring program since the 1970's (Siniff et al. 1977) and previous studies have highlighted substantial inter-annual variability in several vital rates, including juvenile and adult survival (Cameron and Siniff 2004, Hadley et al. 2006, 2007a, Stauffer et al. 2013b), recruitment and reproductive rates (Hadley et al. 2006, 2007b, Garrott et al. 2012, Rotella

et al. 2012) as well as temporary emigration (Stauffer et al. 2013a). In an attempt to explain this variability, the effects of local sea-ice conditions and several large-scale climatic indices have been investigated (Hadley et al. 2007a, Proffitt et al. 2007, Garrott et al. 2012, Stauffer et al. 2013b). Although no simple pattern emerged, the results suggested that seasonal and annual fluctuations of sea-ice extent were responsible of some of the demographic variation. The most favorable conditions seem to occur when sea-ice extent is low in the summer and large in the winter. The negative influence of extensive summer sea-ice has been attributed to the consequent reduction in open water and thus in spring phytoplankton bloom (Smith and Gordon 1997, Arrigo and van Dijken 2004), which is hypothesized to reduce prey availability (Proffitt et al. 2007). On the other hand, the positive effect of sea-ice extent in the winter could be due to its favorable influence on ice-obligate microbial primary productivity (Arrigo and Thomas 2004) and krill abundance (Loeb et al. 1997), which can positively affect fish stocks (Hadley et al. 2007a). Furthermore, because Weddell seals are one of the few top-predators in the Ross Sea able to forage beneath extensive areas of consolidated sea-ice (Smith et al. 2007), they may face less competition and predation during years with extensive winter sea-ice (Garrott et al. 2012). Most interpretations about environmental influences on the demography of these seals have centered on bottom-up trophic processes (Hadley et al. 2007a, Proffitt et al. 2007, Garrott et al. 2012), but it has been suggested that top-down processes might be very prevalent in the Ross Sea ecosystem (Ainley et al. 2006, 2007). The potential for direct abiotic influences of sea-ice dynamics have also been suggested (Cameron and Siniff 2004). Specifically, the late-winter configuration of local sea-ice can

determine the amount of favorable breeding habitat and ease of access to Erebus Bay colonies, affecting immigration, emigration and reproduction (Cameron and Siniff 2004).

While previous investigations have laid a solid base for better understanding environmental fluctuations in the Erebus Bay population of Weddell seals, we do not presently understand the role and relative importance of individual heterogeneity in this population and how it interacts with environmental variation. The quantification of individual heterogeneity in wild populations is a challenging task (Nichols 2002), but our ability to address this issue has been greatly improved by recent developments in mixed-effects mark-recapture modeling and its implementation (Cam et al. 2002, Royle 2008, Gimenez and Choquet 2010, Ford et al. 2012). These statistical advances, along with the comprehensive longitudinal dataset available for this seal population, enable us to address individual heterogeneity and therefore to enhance our comprehension of selective pressures and trends potentially at work in this population.

This dissertation focuses on three topics. First, I assess the relative importance of yet-unexplored environmental factors on the temporal variation of population size and vital rates. Using a 29-year mark-recapture dataset, I evaluate the impact of an extreme environmental perturbation represented by the occurrence of a gigantic iceberg. This extreme event is of primary interest because it had the potential to push individual seals to their phenotypic limits. Next, I quantify individual heterogeneity in female reproductive probabilities and investigate how this heterogeneity interacts with the extreme environmental perturbation. In particular, I evaluate whether individual differences in reproduction were amplified during the perturbed period as a result of low-

quality females having a harder time coping with challenging environmental conditions. Finally, I assess the evolutionary significance of individual heterogeneity in female reproductive rates by investigating its fitness consequences and heritability.

CHAPTER TWO

ENVIRONMENTAL EXTREMES VERSUS ECOLOGICAL EXTREMES: IMPACT OF A MASSIVE ICEBERG ON THE POPULATION DYNAMICS OF A HIGH-LEVEL ANTARCTIC MARINE PREDATOR

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Contributions: Supervised the long-term project and collected data. Provided expertise and comments on drafts of the manuscript.

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British spelling is used in this chapter to conform to the journal requirements.

Reference citations and figure numbering were modified for more consistency throughout the dissertation.
The Electronic Supplementary Material of this article has been included here as an Appendix (Appendix A). The original files are freely available online at http://rspb.royalsocietypublishing.org/content/suppl/2012/09/14/rspb.2012.1733.DC1.html.

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Abstract

Extreme events have been suggested to play a disproportionate role in shaping ecological processes, but our understanding of the types of environmental conditions that elicit extreme consequences in natural ecosystems is limited. Here, we investigated the impact of a massive iceberg on the dynamics of a population of Weddell seals. Reproductive rates of females were reduced, but survival appeared unaffected. We also found suggestive evidence for a prolonged shift towards higher variability in reproductive rates. The annual number of females attending colonies showed unusual swings during the iceberg period, a pattern that was apparently the consequence of changes in sea-ice conditions. In contrast to the dramatic effects that were recorded in nearby populations of emperor penguins, our results suggest that this unusual environmental event did not have an extreme impact on the population of seals in the short-term, as they managed to avoid survival costs and were able to rapidly re-achieve high levels of reproduction by the end of the perturbation. Nevertheless, population projections suggest that even this modest impact on reproductive rates could negatively affect the population in the long run if such events were to occur more frequently, as is predicted by models of climate change.

Key Words: Catastrophic event, Demography, Iceberg B-15, Vital rates, *Leptonychotes weddellii*.

Introduction

Extreme events are thought to play a disproportionate role in shaping ecological and evolutionary processes (Parmesan et al. 2000, Gutschick and BassiriRad 2010). Previous empirical and theoretical work suggests that: (i) in many situations, maximum values taken by environmental covariates are better predictors of ecological patterns than are means and variances (Gaines and Denny 1993); and (ii) strong episodes of natural selection principally occur during extreme events (Gutschick and BassiriRad 2003). Since the intensification of extreme climatic events has been recognized as one of the most important facets of climate change (Easterling et al. 2000, Meehl et al. 2000), increasing attention has been dedicated to research on extreme events (i.e., "event-focused" in contrast to "trend-focused") (Jentsch et al. 2007). Many aspects of this emerging field are however still poorly understood and deserve further investigation (Smith 2011a). Climate extremes do not necessarily translate into an *extreme ecological response* (thereafter, *EER*), and one of the big challenges for ecologists will be to identify which conditions might potentially induce extreme reactions in biological systems (Smith 2011a). An *EER* occurs when organisms cannot acclimate, at a relatively low fitness cost, to extreme or rare environmental conditions (Gutschick and BassiriRad 2010). At the population level, a negative *EER* can thus be identified when conditions induce a strong reduction of the most important vital rates, which would otherwise be buffered against environmental variability (Pfister 1998, Gaillard and Yoccoz 2003, Morris and Doak 2004), thus negatively affecting the growth and chances of persistence of the population. So far, our comprehension of the link between environmental extremes and *EER* remains

very limited and case- or taxon-specific, with a predominance from studies on plants (Gutschick and BassiriRad 2010, Smith 2011a, b). Most observational studies that have investigated the effects of climate extremes have reported an *EER* (e.g., animals (Wilson and Peach 2006, Altwegg et al. 2006, Frederiksen et al. 2008), plants (Allen and Breshears 1998, Breshears et al. 2005)). On the other hand, results of a number of recent experiments indicate that the response to climate extremes of numerous biological systems remains within their range of regular variability (see (Smith 2011a, b) and references therein), suggesting that *EERs* might occur less frequently than suggested by observational studies.

Extreme climatic events are usually thought of in terms of extreme values of a continuous environmental variable (Gutschick and BassiriRad 2010) (e.g., extreme temperatures, precipitation levels), but they can also take the form of discrete perturbations (Turner and Dale 1998), such as unusually big fires (Moritz 1997), hurricanes (Ackerman et al. 1991), floods (Parsons et al. 2005, Wilson and Peach 2006) or rain-on-snow events (Hansen et al. 2011). In polar regions, calving of massive icebergs, which are known to be influenced by worldwide weather systems (MacAyeal et al. 2006) and expected to occur more frequently due to global climate change (Scambos et al. 2000), are events that can strongly impact local ecosystems (Arrigo et al. 2002). For instance, the occurrence of the unusually large iceberg B-15 (~10,000km²), which calved from the Ross Ice Shelf, Antarctica, in March 2000 (MacAyeal et al. 2008), is known to have strongly disturbed the Ross Sea ecosystem, from primary productivity to upper levels of the trophic web (Arrigo et al. 2002, Seibel and Dierssen 2003, Arrigo and van

Dijken 2004, Kooyman et al. 2007, Thrush and Cummings 2011). In particular, local colonies of emperor penguins (*Aptenodytes forsteri*) experienced unusually high levels of breeding failure and of adult and chick mortality (Kooyman et al. 2007). However, the potential impact of this iceberg event on a local population of Weddell seals (*Leptonychotes weddellii*), another long-lived marine vertebrate, has not been investigated yet. This population has been continuously monitored since 1969, including years of iceberg presence (2001-2005), and the data provide a unique opportunity to assess changes in local abundance and demographic rates in relation to the iceberg event and to compare the findings with responses seen in other local species. For that purpose, we estimated annual abundance of female seals in colonies (local abundance), as well as a complete set of annual vital rates (survival and reproduction probabilities), for a 29-year period and evaluated how the mean and variance of those demographic parameters changed during and after the onset of the iceberg. By doing so, we were able to assess whether this event induced an *EER* in a marine mammal species as it did in nearby populations of emperor penguins. Potential effects on process variance were explicitly considered in this study because any increase in the variability of demographic parameters decreases the long-term growth rate of a population, hence reducing its chances of persistence (Lewontin and Cohen 1969). We then assessed by simulations how the growth rate of the population changed during the iceberg episode.

Here, the iceberg event is defined as the period from 2001 to 2005 during which four massive fragments of iceberg B-15 (Appendix A, figure A1) were in the vicinity of the seals' breeding area. We expect the presence of these icebergs to have impacted the

seal population through two different mechanisms. First, by creating challenging sea-ice conditions (Dugger et al. 2010) (large extent of sea-ice and thick ice with massive pressure ridges likely making access to the ice surface difficult) these icebergs might have hampered access of seals to breeding colonies. We thus predict that local abundance was reduced during iceberg years. Second, because there is evidence that primary productivity and abundance of primary consumers were reduced during the perturbed period (Arrigo et al. 2002, Seibel and Dierssen 2003, Thrush and Cummings 2011), the absolute amount of food available to seals might have been lower than usual. We therefore predict a negative impact on vital rates due to a limitation of available energy resources. However, because under such limiting conditions long-lived iteroparous species are expected to allocate more energy to survival than reproduction (Erikstad et al. 1998), we predict a more dramatic reduction in reproductive rates compared to survival rates (Lescroël et al. 2009). Lastly, during challenging conditions, one might expect seals to emigrate and breed in colonies outside Erebus Bay, where ice and food conditions might be more favourable. However, previous evidence suggests that Weddell seals are highly philopatric and seals breeding in Erebus Bay are very rarely observed breeding outside the primary study area (only 2% of all recorded breeding events occurred outside the study area) (Cameron and Siniff 2004, Hadley et al. 2007b). We therefore do not expect seals to have massively emigrated and bred in other colonies although we do assess this possibility based on results of survey efforts conducted outside the study area during the iceberg event.

Material and Methods

Study Area and Study Population

Erebus Bay is located in the south western part of Ross Sea, Antarctica (77.62^0 to 77.87^0S, 166.3^0 to 167.0^0 E). Each year in spring, Weddell seal pupping colonies form on the fast ice within this study area. Pupping occurs from mid-October to late-November, and each mother remains on the ice with its pup for 1–2 weeks. Seals have been annually marked and resighted since 1969, and since 1982 every pup born in the study area has been individually marked shortly after birth. Mother-pup pairs are detected with probability 1.0 on the ice (Hadley et al. 2006), and many of the females that do not produce a pup in a given year (i.e., pre-breeders and skip-breeders; see below for details), also haul out in the study area and are highly detectable (Rotella et al. 2009).

Data Collection and Data Analyses

Each year, during the pupping season, colonies were visited every two to three days to tag newborn pups and any other untagged seals. Also, beginning in early November of each year, five to eight surveys typically separated by three to five days were conducted throughout the study area. Every encountered animal (marked or unmarked) was recorded along with its sex and breeding state, which can be determined with certitude. Intense searching effort has also been conducted since 1997 outside the study area (Cameron and Siniff 2004), and especially during years of iceberg presence, to record breeding events occurring outside of Erebus Bay.

The statistical analysis consisted of three components. In a first step, using mark-recapture data collected over the 29-years period (1982-2010), we estimated two types of

annual demographic parameters: local abundance and vital rates (survival and reproductive rates). Annual estimates of local abundance were obtained using within-season resight data and the superpopulation approach of Schwarz & Arnason (Schwarz and Arnason 1996), while annual vital rates were estimated under a multi-state modelling approach (Williams et al. 2002) based on inter-annual resight data. Here, we define "local abundance" as the number of females that were present in Erebus Bay colonies in a given year. As in any long-lived species, changes in abundance due to deaths and births are relatively slow, while immigration and emigration events can produce rapid and large annual changes. In our system, where local abundance is spatially defined by breeding colonies and temporally defined by the breeding season, annual variations are mainly linked to the pattern of utilization of colonies by females. In particular, some locally born seals may be absent from colonies during one or a few consecutive breeding seasons while some seals born outside the study area may temporarily attend colonies. Whereas information on variation in death and birth processes is accurately investigated through the multi-state analyses of mark-recapture data (see below) on locally born individuals, annual variation in local abundance primarily informs us about possible changes in inter-annual utilization patterns.

In the second step, we estimated the mean and the process variance of the different demographic parameters, for different relevant periods, based on the decomposition of the total variance (Burnham et al. 1987, Burnham and White 2002). Two different pairs of periods were considered to make relevant comparisons: (i) non-iceberg years (1982-2000 & 2006-2010) vs. iceberg years (2001-2005); and (ii) years

before iceberg (period 1982-2000) vs. years after iceberg (period 2001-2010). In the third step, we used simulations to estimate the population growth rate for the non-iceberg and the iceberg periods.

Estimation of Annual Local Abundance

Estimates of annual local abundance were obtained using methods recently developed for this population (Rotella et al. 2009), based on data collected during multiple within-year surveys on both known-age females (tagged as pups) and unknown-age females (tagged as adults or untagged). Three different breeding classes were distinguished in this analysis: (i) pre-breeders (P), i.e., females not breeding that year and that never had a pup before; (ii) breeders, (B) i.e., females known to have had a pup that year; and (iii) skip-breeders (S), i.e., females without a pup that year but that were known to have produced a pup in a previous year. We first estimated the size of each class for known-age females, for which the breeding state can be assigned each year given that the complete breeding history is known. Then, estimates of numbers in states P and S for known-age females were used to help inform the analysis of data from unknown-age females, for which states P and S are undistinguishable until a reproductive event has been observed. Full details of the estimation process were recently presented (Rotella et al. 2009). Estimates from data of known-age and unknown-age females were finally combined to obtain the total local abundance in each breeding class each year. Variances and model-selection uncertainty were carried forward at each step of this analysis, and when initial estimates were transformed into other quantities of interest, we used the delta method (Seber 1982) to estimate variances of the new quantities.

Estimation of Annual Vital Rates

A multi-state mark-recapture approach (Williams et al. 2002) was used to estimate apparent survival probabilities (ϕ) and reproductive rates (ψ; i.e., transition probabilities, conditional on survival from year t to $t+1$, from any state in year t into an active breeder state in year $t+1$), while accounting for imperfect detection. Four breeding states were distinguished in this analysis: (i) pre-breeder (P); (ii) first-time breeder (F); (iii) experienced breeder (E); and (iv) skip-breeder (S). Recruitment was defined as the transition from state P to F (ψ^{PF}) and reproduction as transition from state F, E or S to state E (ψ^{FE}, ψ^{EE}, ψ^{SE}). Several combinations of age and year effects were considered for each reproductive status (Hadley et al. 2006, 2007b, Rotella et al. 2012) and evaluated with the Akaike Information Criterion (AIC) corrected for sample size (AICc) and overdispersion (QAICc). The estimates that were subsequently used in the analysis come from the most supported of these models. More details about the model selection procedure are provided in Appendix A (Text A1, Table A1). A total of 6,373 individual histories from female Weddell seals, consisting in 5,810 known-age individuals (i.e., tagged as newborn pups in the study area) and 563 unknown-age seals, were available and used in the analysis.

Decomposition of Variance Components

We used the method of moments (Burnham et al. 1987, Burnham and White 2002) to (i) derive estimates of means and process variation and (ii) obtain shrunk annual estimates, along with their standard errors and 95% confidence intervals, of local abundance and vital rates for each of the ensembles of years considered. For annual vital

rates, which were all estimated simultaneously in the same multistate models, this was done using the random effects module of Program MARK (White et al. 2001). Because vital rates are probabilities, their maximum possible variance is a function of the mean (Morris and Doak 2004). Therefore, following previous authors (Gaillard and Yoccoz 2003, Morris and Doak 2004, Frederiksen et al. 2008, Rotella et al. 2012), we scaled the process variance by the maximum possible variance for the corresponding mean before making comparisons among different periods. For local abundance estimates, which were obtained independently for each year, the method of moments was performed in program R (version R.2.12.0, (R Development Core Team 2010)), using the generalized weighted procedure (Burnham et al. 1987). No scaling of process variance was necessary as local abundances are not probabilities.

Estimation of Population Growth Rates

Using estimates of the mean and process variance of vital rates, we estimated population growth rates for the non-iceberg and the iceberg periods. For each period, we randomly drew 5,000 sets of vital rate values from their estimated distributions and calculated the dominant eigen value (Caswell 2001), or asymptotic population growth rate (λ), for each set. We then compared the distributions of λ between the two periods. The values of survival used in these simulations were adjusted for tag loss (Hadley et al. 2006, Rotella et al. 2012). Because all vital rates are probabilities and thus belong to the interval [0;1], random values were generated at the scale of log odds using random normal deviates based on the estimated mean and variance of the log odds of each vital rate.

Results

We predicted that the challenging sea-ice conditions created by the presence of the icebergs would hamper the access of seals to breeding colonies and thus decrease local abundance. Moreover, in relation to a probable reduction in food resources, we also expected seals to adopt a strategy in keeping with conserving and allocating more energy to survival at the expense of reproduction. We therefore also predicted a decrease in reproductive rates, but not in survival, during the iceberg period. To test these predictions, we estimated local abundance as well as rates of survival and reproduction for a series of 29 years of available data and assessed how these parameters changed during the iceberg episode. Moreover, given that we expected that the temporal variability of these demographic parameters might also have been affected by the iceberg event, we assessed potential changes in process variance.

Local Abundance

We found suggestive evidence for a reduction of total local abundance during iceberg years (figure 2-1a; see also Appendix A, Table A2), although the details of this reduction were not as simple as predicted. Indeed, while the number of breeders was consistently lower than usual during all iceberg years (figure 2-1a, figure 2-2), the number of pre-breeders and skip-breeders was more variable within this period (figure 2-2). In fact, for these two latter classes of seals, the estimated local abundance for a single year (2003) was in strong contrast with estimates for all other iceberg years. Local abundance in 2003 was the largest of the entire time series ($\widehat{N}_{tot}^{2003}$ = 1,028.9, SE = 24.2; Appendix A, Table A3) and was associated with peaks in the estimated numbers of skip-

breeders and pre-breeders (figure 2-2). Nevertheless, of females that attended the breeding grounds in 2003, only ~33% produced a pup, which is the smallest proportion of breeders ever estimated. In contrast, the subsequent year (2004) had the lowest estimate of both total local abundance ($\widehat{N}_{tot}^{2004}$ = 290.0, SE = 2.1) and number of breeders ever recorded ($\widehat{N}_{br}^{2004}$ = 158.0, SE = 0.0).

There is also some evidence that process variance in local abundance changed over the years of study (figures 1b, 1c; Appendix A, Table A4). The estimated process standard deviation ($\hat{\sigma}_{process}$) of total local abundance, as well as $\hat{\sigma}_{process}$ of skip-breeder and pre-breeder numbers, were higher during the iceberg episode than in other years (figure 2-1b). This increased variance was due to the large difference in local abundance between 2003 and other iceberg years (see above). When estimates for the pre-iceberg period were compared with those for all years following the iceberg onset (2001-2010), we found evidence that $\hat{\sigma}_{process}$ increased for all population components (figure 2-1c), and especially for breeders (figure 2-2).

To summarize, the iceberg event seems to have impacted both the mean and variance of local abundance, but in a more complex way than predicted. It reduced the mean number of breeders, increased $\hat{\sigma}_{process}$ for the non-breeding components of the population during iceberg years and increased $\hat{\sigma}_{process}$ for breeders for a more prolonged period (figures 1 and 2).

Vital Rates

As predicted, probabilities of recruitment and probabilities of reproduction substantially decreased during iceberg years (figure 2-3a; see also figures 4a and 4b and

Appendix A, Table A5). In particular, the reduction of recruitment rates (ψ^{PF}) ranged from 42% for 10-yr-old females (a drop from 0.54 to 0.31) to 59% for 5-yr-old females (from 0.03 to 0.01), and the reduction of reproductive rates ranged from 27% for ψ^{EE} (from 0.69 to 0.50) to 37% for ψ^{FE} (from 0.52 to 0.33). It was however unclear whether rates declined more for younger or less-experienced animals than for others (figure 2-3a). The temporal projection of annual reproduction and recruitment rates (figure 2-4a, b) shows that these parameters followed a decreasing trend until 2004, when they reached the lowest values ever recorded in 29 years, but then rebounded and stayed relatively high after the icebergs were gone.

Process variation of recruitment and reproduction did not appear to be different in iceberg years versus non-iceberg years (figure 2-3b). However, when estimates were compared for the pre-iceberg period versus the period after iceberg onset (2001-2010), we found evidence of increased process variation (figure 2-3c). Despite the substantial uncertainty associated with estimates, due to the small number of iceberg years, the evidence is relatively strong for probabilities of reproduction, for which $\hat{\sigma}_{process}$ increased by 42%, 65% and 73% for ψ^{FE}, ψ^{EE} and ψ^{SE}, respectively, after the onset of the iceberg (Appendix A, Table A6).

Finally, as predicted, we found no evidence of change in the mean and the process variance of survival rates during or after the iceberg event (figures 3 and 4c). These results indicate that the iceberg event did not have extreme consequences on the dynamic of this population, as females managed to avoid survival costs and were able to achieve high reproductive rates immediately after the iceberg episode.

Population Growth Rate

For the non-iceberg period, the average value of population growth rate (λ) was 1.00, and λ was greater than 1.0 in about 37.7% of simulations (Appendix A, figure A2). For the iceberg period, λ averaged 0.96 and only 1.3% of simulated λ were greater than 1.0. Therefore, we conclude that, while the population was typically stable during the non-iceberg period, it was most likely in a declining phase ($\lambda<1$) during the iceberg episode, because of the decrease in vital rates.

Discussion

In this study, we assessed whether a large-scale environmental perturbation, represented by the occurrence of massive icebergs, had extreme consequences on a population of Weddell seals breeding in the South-western Ross Sea. Previous studies of this well-known iceberg event reported dramatic effects on lower-level taxa (Arrigo et al. 2002, Seibel and Dierssen 2003) and on two local populations of emperor penguins (Kooyman et al. 2007), but the potential impact on the population of Weddell seals was unknown. Our goal was to evaluate whether this event would (i) exceed the acclimation capacity of the species and (ii) be a threat for the population at a mid-term time scale. The comparison of our results for seals with those from a previous study on emperor penguins (Kooyman et al. 2007) allowed us to compare the responses of two high-level predators that depend on similar food resources but have substantial differences in their feeding and breeding habits. Of particular note, female Weddell seals store resources in the months before giving birth and then essentially stop feeding and remain at the breeding colony for the entire pup-rearing period. In contrast, to successfully rear their chick, emperor

penguin parents have to maintain movements between breeding colonies and foraging areas, and these movements were known to have been hampered by the presence of the icebergs (Kooyman et al. 2007).

First, our results on vital rates reveal that seals were much less affected than emperor penguins in the short-term. Indeed, Weddell seals did not suffer any apparent cost of survival, while emperor penguin colonies incurred very high adult and chick mortality (Kooyman et al. 2007). Moreover, the magnitude of the decline in reproductive rates was lower for this population of seals than for nearby populations of emperor penguins (e.g., 100% of breeding attempts failed at the Cape Crozier colony in 2001, (Kooyman et al. 2007)). The impact on penguins' reproduction was partly linked to the fact that their traveling routes from breeding colonies to foraging areas were partially blocked by the presence of the iceberg (Kooyman et al. 2007), making chick feeding much more difficult. Seals probably avoided such a large impact on their reproduction because, as lactating mammals and capital breeders, they are not dependent on such foraging trips to feed their pups. Second, as mature seals were able to survive at high rates during perturbed years, both local abundance and breeding rates returned to previous levels by the end of this episode, and they have remained relatively high since then. We therefore conclude that this iceberg event did not represent an *EER* for this population, as it does not appear to have exceeded the acclimation abilities of individual seals or to have represented a threat for the persistence of the population at a mid-term time scale.

In terms of local abundance, we found a substantial reduction during most iceberg years, but in contrast with our predictions, this pattern was not consistent across the entire period. Indeed, the most extreme positive and negative peaks ever recorded occurred during this event, in 2003 and 2004, respectively. These large fluctuations in colony attendance contrast with the consistent pattern of low reproductive rates within the iceberg period, indicating that these two demographic parameters probably responded to different environmental factors. On one hand, because Weddell seal females strongly depend on stored energy reserves during the pup-rearing period (Boness and Bowen 1996, Wheatley et al. 2008), we can hypothesize that the consistent decrease in reproductive rates might have primarily been a consequence of the overall reduction in primary production and prey availability (Arrigo et al. 2002, Seibel and Dierssen 2003, Thrush and Cummings 2011). On the other hand, it seems that variations in local abundance, and notably the contrast between 2003 and other iceberg years, primarily resulted from changes in sea-ice conditions (Cameron and Siniff 2004). Indeed, while most iceberg years were characterized by extensive sea ice, in 2003 open water extended far south, close to Erebus Bay colonies, and sea-ice extent was low (Appendix A, figure A1). It is also interesting to note that the high local abundance observed in 2003 was associated with unusually low reproductive rates, a pattern in contrast with the positive correlation observed between these two demographic parameters in all other years (figure 2-5). Therefore, seals massively attended Erebus colonies in 2003, but not principally to breed. Moreover, the detection rate of skip-breeders, which provides a relevant measure of colonies utilization (figure A3) given that resighting effort is high and consistent every

year, displays the same temporal pattern as local abundance (figure A4). It indicates that skip-breeders have a flexible pattern of colony utilization, depending on current environmental conditions, and clearly shows that such females were much more likely to be in Erebus Bay colonies in 2003 than in other iceberg years. Furthermore, the high local abundance of 2003 was associated with an upsurge in the number of untagged and unknown-age adult females (i.e., females that were born outside the study area), indicating the presence of many temporary immigrants this year (Appendix A, figure A5). These observations suggest that environmental conditions might have forced seals to move further south and thus massively attend Erebus Bay in 2003 but not primarily for the purpose of giving birth. This environmental forcing was probably linked to the large extent of open water to the North for the following reasons. First, Erebus Bay, which is the southern-most breeding site for the species, might have been one of the few available places suitable for hauling out in the Ross Sea this year. Second, the reduced sea-ice extent allowed the formation of the McMurdo Polynya, thus providing a relatively abundant source of food near colonies this year. Finally, the distribution of seals' competitors and predators, which cannot occupy areas of consolidated ice, might have been shifted further south in the Ross Sea (Smith et al. 2007), such that Weddell seals could have moved further south to reduce inter-specific competition and predation risk. In contrast, the sea-ice conditions that prevailed in all other iceberg years could have prevented a large number of seals from using Erebus Bay because (i) the access to colonies might have been relatively hard; and (ii) sites further north had more food available, enough fast ice for hauling out, and relatively few competitors and predators.

This pattern might have been particularly strong in 2004, when both local abundance and reproductive rates reached the lowest values ever recorded. However, although the extent of sea-ice cover was indeed particularly large this year, it was not dramatically different from 2002 or 2005 (figure A1). We thus speculate that these physical conditions have acted in combination to particularly unfavourable food conditions (Thrush and Cummings 2011) to cause such a poor situation in 2004.

Taken together, the results of the present study suggest that Weddell seals were able to handle the challenging conditions created by the iceberg mainly by skipping reproduction and occupying the most favourable available environment, probably balancing between energy expenditure (reproductive effort, availability of haul-out sites), resource intake (proximity of food resources and competitors) and predation risk. An alternative explanation would be that seals massively emigrated from Erebus Bay, except in 2003, to breed elsewhere. However, this appears unlikely, as during all surveys conducted outside the study area at other seal-aggregation sites during iceberg years, almost no females known to have been born in Erebus Bay were found with pups outside the study area despite intensive searches (Hadley et al. 2007b). Moreover, given the unusually high local abundance, but still relatively low level of reproduction, recorded in 2003, such a hypothesis seems untenable. The apparent behavioural response of seals is in keeping with a strategy of saving and allocating a larger proportion of energy to survival, as would be expected in a long-lived organism (Erikstad et al. 1998, Gaillard and Yoccoz 2003). The ability to buffer adult survival against environmental variability by adjusting reproductive effort has already been shown in this population (Rotella et al.

2012), but previous work did not investigate the particulars of the iceberg event. Here, by explicitly assessing how demography during the iceberg period contrasted with that recorded in years with typical conditions, we demonstrated that the iceberg event had a substantial impact on reproduction, but that survival was well buffered from environmental variation. Two previous studies on Adélie penguins (*Pygoscelis adeliae*) (Lescroël et al. 2009, Dugger et al. 2010) reported similar results, as they showed that this iceberg event induced an increase in foraging effort and of dispersal rates of these birds but had no apparent effect on their survival. It is however important to recognise that all these analyses, including ours, are based on a single event, such that their scope of inference remains limited to this particular event, and as a consequence, any extrapolation must be considered with caution.

Although we found a moderate impact, in the short- and mid-term, of this single perturbing event on the seal population, more substantial negative effects might be expected in the long-term, especially as the frequency of such events is predicted to increase (Scambos et al. 2000, Arrigo et al. 2002). First, we found that the average population growth rate dropped from 1.00 during non-iceberg years to 0.96 during iceberg years, meaning that the population was temporarily in a declining phase. A higher frequency of such events would therefore be detrimental for the population in the long run. Second, our results also suggest that the process variance of reproduction and recruitment probabilities might have been increased for a prolonged period after the iceberg onset. Although analyses of data of future years will be required to assess the consistency and potential persistence of this pattern, this is in direct contrast with the

long-lasting stability of vital rates that was observed pre-iceberg. It is especially interesting to note the quick rebound, in 2006 and 2007, in the abundance of breeders on colonies and in rates of reproduction and recruitment, after a decreasing trend during the iceberg period. By skipping reproduction or delaying recruitment for several years during the iceberg period, many females avoided a major energy expense. Therefore, when conditions went back to normal after 2005, these 'resting' females were likely in good condition to recruit or reproduce again. The temporary decline in these variables the following year (2008) might indicate that fewer inexperienced females recruited that year, perhaps because many had recruited the previous two years, as well as that many females that produced pups in 2006 and 2007 were unable to compensate for energy expenditures made in those two years and breed again in 2008. After 2008, reproductive rates went back to high values again. This post-iceberg pattern suggests that the delay in reproduction and recruitment of many individuals caused by the perturbation could have shifted the reproductive regime of the population towards greater variation, a pattern that would have negative consequences on the long-term growth rate of the population (Lewontin and Cohen 1969). These types of regime-shift patterns have indeed been suggested as one of the main consequences of extreme events (Scheffer and Carpenter 2003, Holmgren et al. 2006, Smith 2011b).

Our understanding of the potential ecological importance of extreme environmental events is still in its infancy but can be expected to rapidly improve given growing interest in the topic among ecologists (Jentsch et al. 2007, Smith 2011a), especially in relation to climate change predictions (Easterling et al. 2000, Meehl et al.

2000). Extreme events have often been considered as necessarily having immediate and overwhelming effects (Arrigo et al. 2002, Wilson and Peach 2006, Kooyman et al. 2007), but growing evidence suggests that their effects might often be more complicated and more indirect than previously assumed (Smith 2011a). As illustrated in this study and previous ecological studies on the same iceberg, some events might induce *EER* in some species but not in others. Moreover, even if they do not cause an immediate *EER*, extreme events might still have important longer-term consequences through cumulative or recurring effects. The investigation of extreme events is, by definition, relatively difficult, as such events occur rarely in nature, but the growing number of long-term ecological monitoring programmes, as well as the development of experiments directly imposing extreme conditions on a biological system, should allow for improved understanding.

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protocol was approved by Montana State University's Animal Care and Use Committee (Protocol no. 41-05).

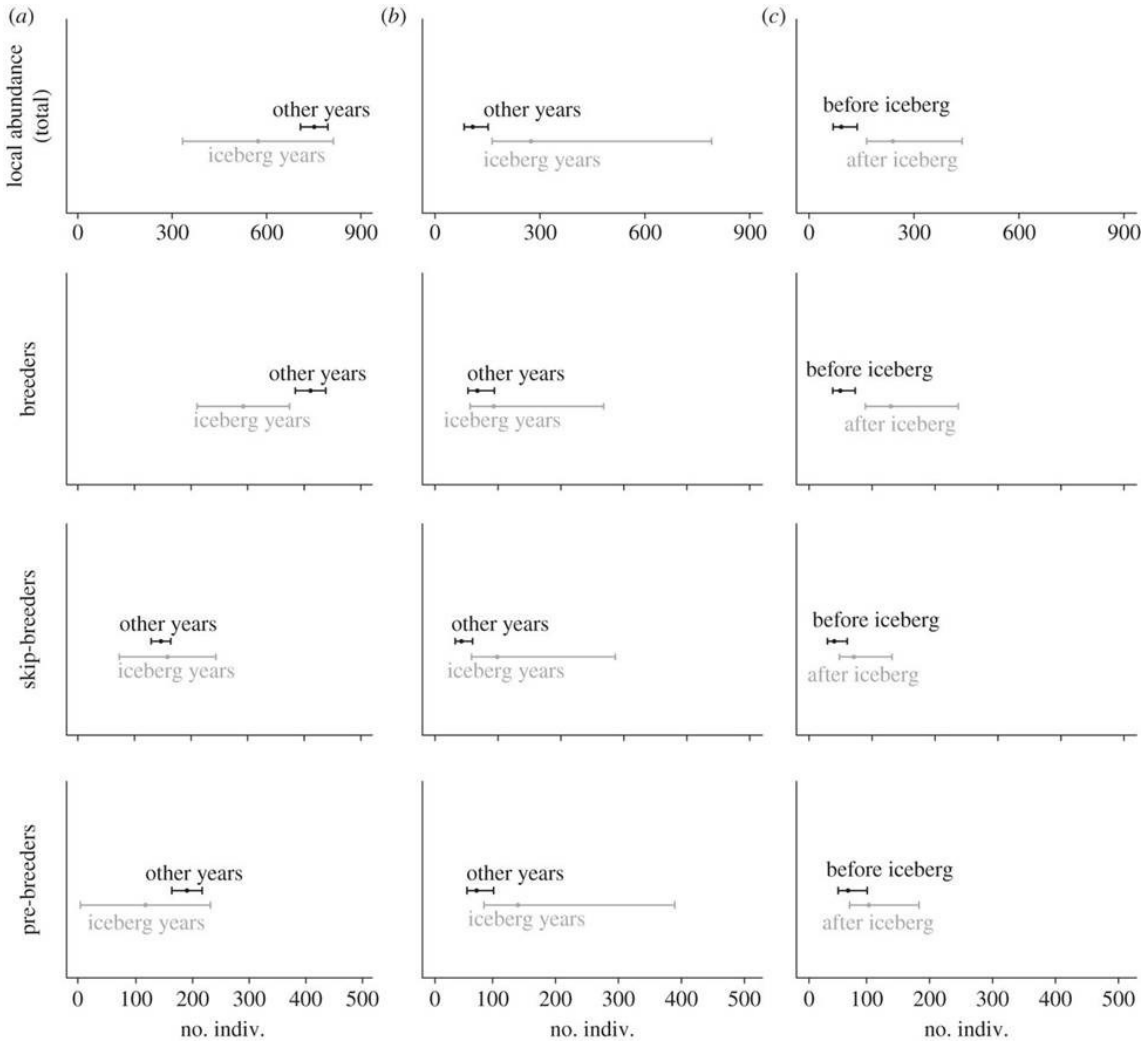

Figure 2-1.Summary of the results obtained for the mean and process s.d. of the different components (breeding classes) of local abundance.
(a) Comparison of the mean between iceberg years and during other years; (b) comparison of process s.d. between iceberg and non-iceberg years; and (c) comparison of process s.d. after and before the iceberg event. Error bars represent 95% CIs (i.e. error due to sampling variation). Note that for optimal scaling of CIs, x-axis ranges are not necessarily the same among individual graphs.

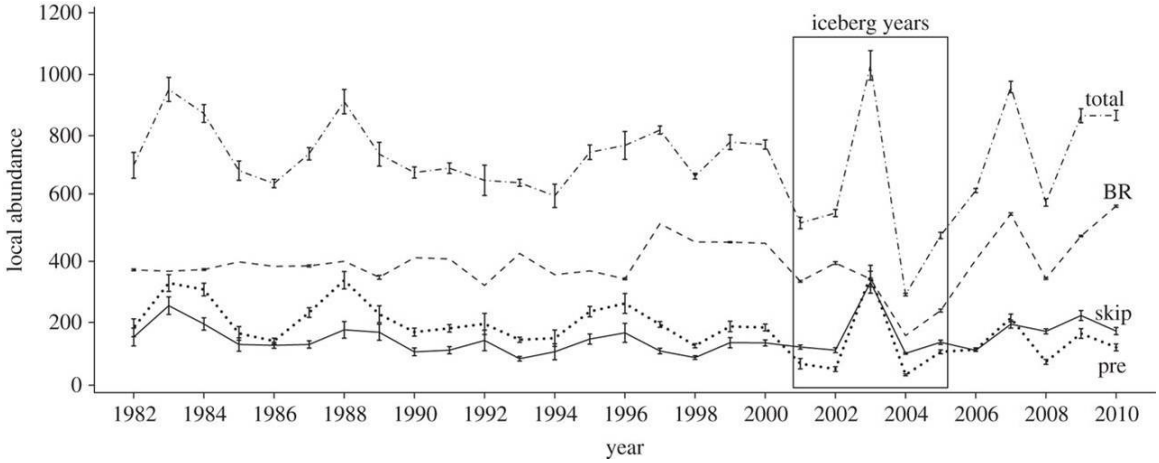

Figure 2-2. Temporal variation in the size of the different breeding classes occupying colonies from 1982 to 2010.
The dashed-dotted line represents the total local abundance (total), the dashed line represents the number of breeders (BR), the solid line represents the number of skip-breeders (skip) and the dotted line represents the number of pre-breeders (pre). The period during which the iceberg was present in the vicinity of seal colonies is showed by a solid frame. Error bars represent 95% CIs (i.e. error due to sampling variation).

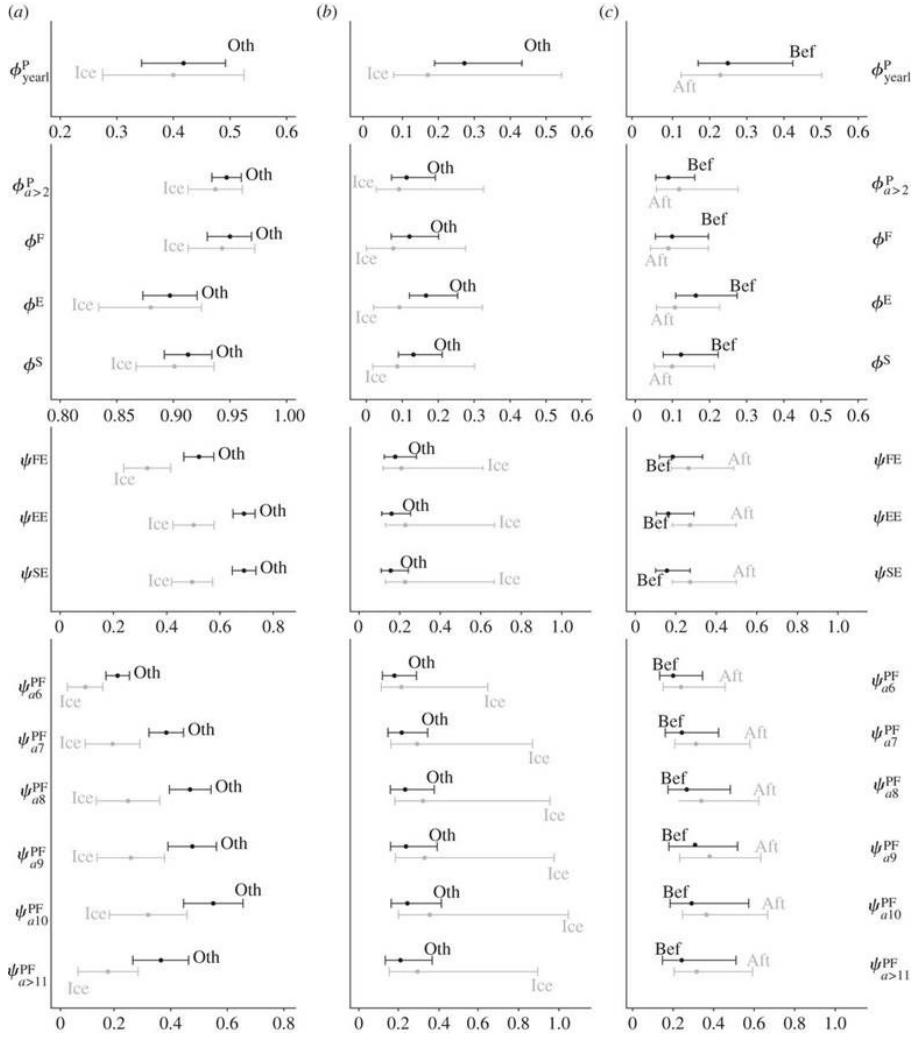

Figure 2-3. Summary of the results obtained for the mean and process s.d. of vital rates. (*a*) Comparison of the mean between iceberg years (Ice) and during other years (Oth); (*b*) comparison of process s.d. between iceberg and non-iceberg years; and (*c*) comparison of process s.d. after (Aft) and before (Bef) the iceberg event. Error bars represent 95% CIs (i.e. error due to sampling variation). Note that for optimal scaling of CIs, *x*-axis ranges are not necessarily the same among individual graphs. Demographic parameters are represented by lowercase Greek letters: 'ϕ' (survival) and 'ψ' (reproductive rates, i.e. transition among breeding states). Superscripts represent states specificities of these parameters: 'P' (pre-breeder), 'F' (first-time breeder), 'E' (experienced breeder) and 'S' (skip-breeder). For transition parameters ψ, the first superscript represents state of departure (at time t) and the second superscript represents state of arrival (at $t + 1$). Subscripts represent age-specificity for the pre-breeder state: '*yearl*' (yearling), '$a \geq 2$' (older than two), '$a5$', '$a6$', '$a7$', '$a8$', '$a9$' and '$a10$' (age 5, 6, 7, 8, 9 and 10, respectively), and '$a \geq 11$' (older than eleven). Note that yearling survival corresponds to survival from 1-year-old to 2-year-old.

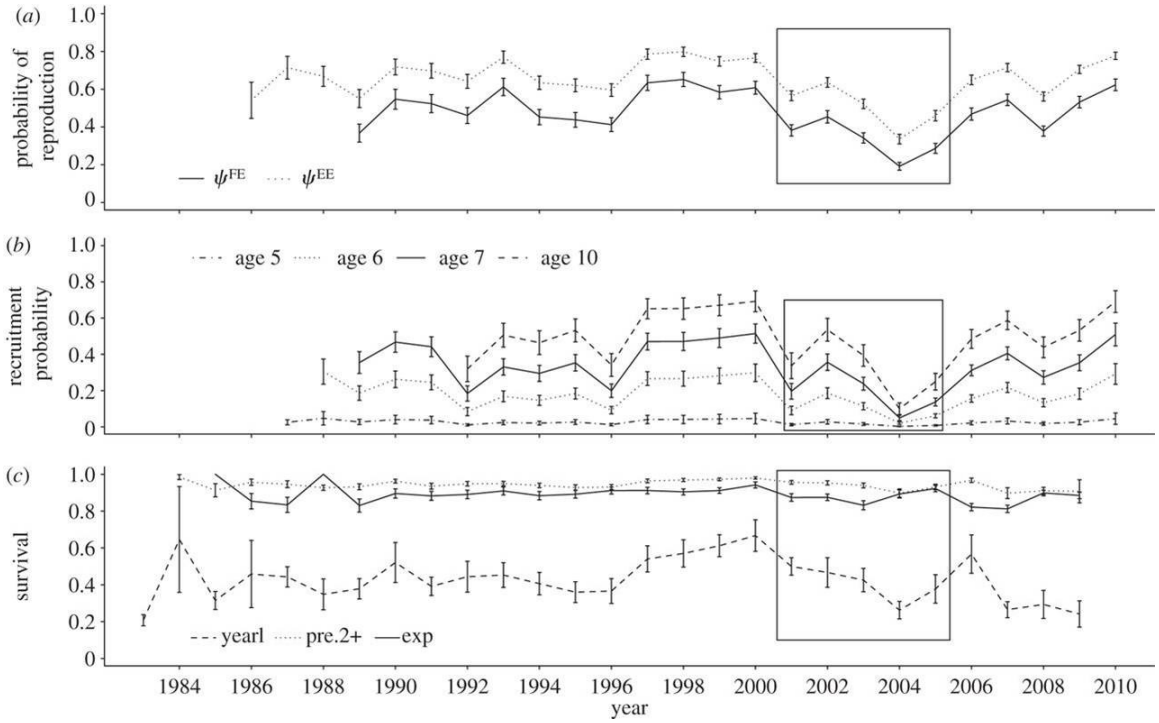

Figure 2-4. Temporal variation of probabilities of (*a*) reproduction (ψ^{FE}, ψ^{EE}), (*b*) recruitment (ψ^{PF}) and (*c*) survival.
The iceberg period is represented by a solid frame. Error bars represent s.e. (i.e. error due to sampling variation). Not all states and age classes are displayed on these graphs for better readability. 'yearl', yearling, which corresponds to second-year survival (i.e. survival from age 1 to age 2); 'pre2+', pre-breeders of age ≥ 2; 'exp', experienced breeders.

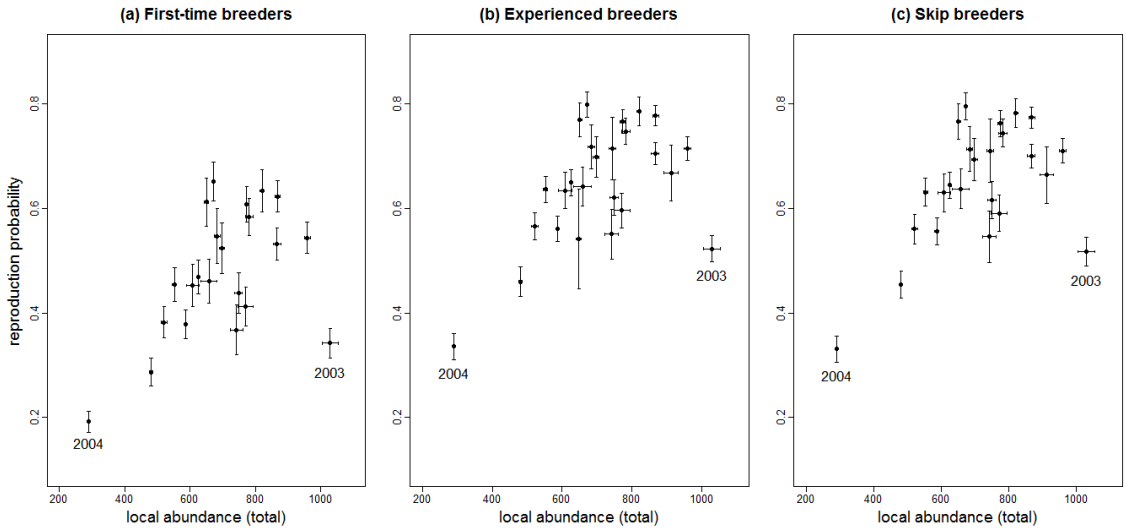

Figure 2-5. Relationship between local abundance (*x-axis*) and the three state-specific reproductive rates (*y-axis*).
(*a*) first-time breeders (ψ^{FE}), (*b*) experienced-breeders (ψ^{EE}) and (*c*) skip-breeders (ψ^{SE}). Years 2003 and 2004 are marked on each graph. Error bars represent s.e. (i.e. error due to sampling variation).

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CHAPTER THREE

INDIVIDUAL HETEROGENEITY IN REPRODUCTIVE RATES AND COST OF REPRODUCTION IN A LONG-LIVED VERTEBRATE

Contribution of Authors and Co-Authors

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Abstract

Individual variation in reproductive success is a key feature of evolution, but also has important implications for predicting population responses to variable environments. Although such individual variation in reproductive outcomes has been reported in numerous studies, most analyses to date have not considered whether these realized differences were due to latent individual heterogeneity in reproduction or merely random chance causing different outcomes among like individuals. Furthermore, latent heterogeneity in fitness components might be expressed differently in contrasted environmental conditions, an issue that has only rarely been investigated. Here, we assessed (i) the potential existence of latent individual heterogeneity and (ii) the nature of its expression (fixed vs. variable) in a population of female Weddell seals (*Leptonychotes weddellii*), using a hierarchical modeling approach on a 30-year mark-recapture dataset consisting of 954 individual encounter histories. We found strong support for the existence of latent individual heterogeneity in the population, with 'robust' individuals expected to produce twice as many pups as 'frail' individuals. Moreover, the expression of individual heterogeneity appeared consistent, with only mild evidence that it might be amplified when environmental conditions are severe. Finally, the explicit modeling of individual heterogeneity allowed us to detect a substantial cost of reproduction that was not evidenced when the heterogeneity was ignored.

Key Words: Bayesian statistics, Individual variation, Life history theory, Marine mammals, Population dynamics, Posterior predictive checks.

Introduction

Differences in the reproductive and survival abilities of individuals in a population have long been considered a key feature of life (Darwin 1859). The investigation of the prevalence, nature, and underlying mechanisms of such individual heterogeneity in fitness components is relevant to both evolutionary ecology (Wilson and Nussey 2010, Bergeron et al. 2011) and population dynamics (Lomnicki 1978, Kendall et al. 2011). First, inter-individual variability associated with fitness differences is, with heritability, one of the fundamental principles of the theory of natural selection (Darwin 1859, Endler 1986). Further, we know that the detection *in natura* of reproductive trade-offs and senescence patterns, expected from life history theory, can be hampered when consistent individual differences are ignored in demographic studies (Vaupel and Yashin 1985, Van Noordwijk and De Jong 1986, Service 2000, Cam et al. 2002, Nussey et al. 2008, Weladji et al. 2008). Finally, it has been shown that heterogeneity in vital rates could change the magnitude of demographic stochasticity and thus affect population dynamics and persistence (Lomnicki 1978, Conner and White 1999, Vindenes et al. 2008, Kendall et al. 2011). In terms of mechanisms, individual heterogeneity has been related to genetic characteristics (Foerster et al. 2003, Hunt et al. 2004), as well as to innate and acquired phenotypic traits, such as physical features (e.g., Andersson 1989, Zuk et al. 1990, Festa-Bianchet et al. 1997, Bérubé et al. 1999, Vanpé et al. 2007), physiology (Burton et al. 2011, Pryke et al. 2012), and behavior (Dall et al. 2004, Smith and Blumstein 2008). Alternatively, individual heterogeneity may also be explained by variations in conditions and resources during early development (Lindström 1999, Festa-

Bianchet et al. 2000, Metcalfe and Monaghan 2001, Lummaa and Clutton-Brock 2002, Hamel et al. 2009), in environmental conditions throughout life (Landis et al., 2005), in parental care (Hunt and Simmons 2000, Schwagmeyer and Mock 2008) and in other maternal effects (Mousseau and Fox 1998, Fox et al. 2006).

Although among-individual variability in fitness is generally assumed to be ubiquitous in nature (Bergeron et al. 2011, Kendall et al. 2011), the extent to which it is actually prevalent in wild populations remains poorly understood, as evidenced by recent attention to the topic in the literature (Cam and Monnat, 2000; Cam et al., 2002; Aubry et al., 2009; Hamel et al., 2009a; Tuljapurkar et al., 2009; Hamel et al., 2009b; Steiner et al., 2010; Aubry et al., 2011; Orzack et al., 2011; Hamel et al., 2012a; Cam et al., 2012, Plard et al., 2012). Individual heterogeneity in wild populations of vertebrates was first conceived and investigated through the 'fixed heterogeneity' hypothesis (Cam et al. 2002, Bergeron et al. 2011). The two key features of this hypothesis are that (i) differences among individuals in performance are linked to some latent individual characteristics, and (ii) these latent differences are expressed in a constant (fixed) fashion over individuals' lifetimes (i.e., across ages and the various environmental conditions experienced). The importance of the first of these features, i.e., the existence of underlying differences in vital rates among individuals, has recently been questioned by the formulation of an alternative 'dynamic heterogeneity' hypothesis (Tuljapurkar et al. 2009, Steiner et al. 2010, Orzack et al. 2011). This hypothesis recognizes that an individual's breeding and survival status can change (be dynamic) over a lifetime due to random chance alone. Thus, individuals with the same underlying vital rates can realize

different life-history-trajectory outcomes and underlying heterogeneity in individual vital rates need not be invoked to explain variability in realized fitness, unless observed levels of variation exceed those that can be generated by random chance and other sources of variation in individual vital rates and lifetime success, such as environmental conditions, individual's age, prior breeding experience, and current reproductive status. The relevant question with regard to the existence of latent heterogeneity in fitness components is thus: after accounting for these sources of variation, can the residual variability in realized fitness be explained solely by random chance or is there evidence for additional, unobserved, and perhaps unaccountable for, sources of variation tied to individuals?

The second key feature of the 'fixed heterogeneity' hypothesis could also be questioned, and an alternative view is that the expression of the underlying heterogeneity is variable, rather than fixed, over time. Indeed, individuals might differ in their ability to survive and reproduce, but such differences might not be consistently expressed across ages or environmental conditions (Lomnicki 1978, Hamel et al. 2009, Lailvaux and Kasumovic 2011). This feature of individual heterogeneity in fitness components is especially relevant to the theory of natural selection, as the relative success of alternative phenotypes or genotypes also depends on the environmental conditions experienced (e.g., van Noordwijk 1989). Such interaction between environment and latent heterogeneity could have two consequences: (1) the hierarchy of individuals, in terms of robustness, could change with environmental conditions, or (2) the hierarchy could be maintained, but the expression of underlying individual heterogeneity could be amplified in certain conditions (Lomnicki 1978), such that the amount of realized heterogeneity might vary

across contrasted environments (Lescroël et al. 2009, Hamel et al. 2009). For instance, it has been suggested that individual differences could be primarily, or only, expressed in unfavorable and stressful situations (Tavecchia et al. 2005, Barbraud and Weimerskirch 2005), while in favorable conditions, individuals would all perform similarly well. This idea is also supported by the fact that the strength of selective pressures at play in wild populations is generally quite variable over time (Siepielski et al. 2009) and seems to be dominated by rare episodes of very strong selection (Gould and Eldredge 1993).

In this study, using 30 years of mark-recapture data from a population of female Weddell seals (*Leptonychotes weddellii*, figure 3-1), we investigated (i) the relative support for the existence of unidentified (latent) sources of IH in reproductive rates, and (ii) the nature (fixed vs. variable) of the expression of underlying sources of variation across contrasting environmental conditions. Although as suggested elsewhere (Cam et al. 2002), individual heterogeneity in fitness components likely concerns both reproduction and survival here we focus on reproductive rates because we expect them to display more heterogeneity given that, at the population level, they vary much more than do adult survival rates, which are very high and stable (Rotella et al. 2012). In these analyses, we focused on females that recruited to the breeding part of the population and did not include adult females that never produced a pup. Estimates of individual heterogeneity presented here thus pertain to the breeding portion of the population and are therefore conservative (i.e., represent minimum levels of heterogeneity in the whole population). To investigate the two questions of interest, the following three competing hypotheses were confronted: (H1) ‘no individual heterogeneity’: there is no substantial

difference in reproduction probabilities among individuals; (H2) 'fixed individual heterogeneity': there is substantial individual heterogeneity in reproduction probabilities, and it is consistently expressed across contrasted environmental conditions; and (H3) 'variable individual heterogeneity': there is substantial individual heterogeneity in reproduction probabilities, and its expression varies with environmental conditions. Hypothesis H1 corresponds to a 'null' model, as defined by Tuljapurkar et al. (2009), in which the observed differences in individual reproductive outputs are solely the result of the probabilistic nature of individual state transitions ('dynamic heterogeneity' hypothesis), while H2 corresponds to the 'fixed heterogeneity' hypothesis (Cam et al. 2002). In H3, which corresponds to an additional alternative hypothesis (Hamel et al. 2009), we contrasted the level of individual heterogeneity in 'normal years' with that in a 'perturbed period' of years when massive icebergs were present in the vicinity of seal colonies (2001-2005). This unusual perturbing event represented an episode of unfavorable conditions for the seals as evidenced by reduced reproductive rates (Chambert et al., 2012).

Material and Methods

Study Population and Data Collection

The population of Weddell seals breeding in Erebus bay (South-western Ross Sea, Antarctica [77.62^0-77.87^0S, 166.3^0-167.0^0E]) has been the subject of a mark-recapture program since 1971 (Siniff et al. 1977), and since 1982, every pup born in the study area has been systematically marked shortly after birth. Each year, during the pupping season (October-November), seal colonies were visited every two to three days to tag newborn

pups and untagged mothers, and five to eight surveys were conducted throughout the entire study area. During surveys, every encountered animal was recorded along with its sex and reproductive status. Animal handling involved in the collection of these data followed a protocol that was approved by Montana State University's Animal Care and Use Committee (Protocol #2011-38).

In this study, we used data from 1982 through 2011 to build encounter histories of individually marked females that were (i) of known-age (i.e., tagged as pups inside the study area), (ii) part of the breeding population (i.e., females that had bred at least once) and (iii) resighted at least once after their year of first reproduction (recruitment) to provide information on reproductive rates (here defined as the 'probability of producing a pup subsequent to recruitment'). The detection rate of mother-pup pairs is virtually 1.0 on the ice (Hadley et al. 2006), such that every year all females giving birth in Erebus Bay are detected. Moreover, female Weddell seals display strong philopatry, making it extremely rare for a female recruited inside the study area to later reproduce outside the study area (Hadley et al. 2007b, Cameron et al. 2007). Here, we restricted our analyses to data collected on females born inside Erebus Bay and known to have given birth there. Thus, we could reasonably assume that all reproductive events of this sub-population of seals were recorded in our data, and any female not seen in a given year could be assumed to have skipped reproduction that year.

Statistical Modeling

Encounter histories started at the first reproductive event (state F) of an individual and thereafter consisted of two possible states: experienced breeder (E; as opposed to 'first-time breeder F'), and skip-breeder (S). Probabilities of reproduction were defined as rates of transition from any state *k* (F, S or E), in year *t*, into state E in year *t+1* (ψ^{kE}). The complementary transition rates into state S corresponded to probabilities of skipping reproduction ($1 - \psi^{kE}$). Based on previous analyses and knowledge of this population of seals (Hadley et al., 2007a; Rotella et al., 2009, Chambert et al., 2012), we modeled ψ^{kE} as a function of reproductive state in year *t-1* (δ_{t-1}^{k}) and year *t* (η_t). We also included the standardized age of individual *i* in year *t* ($A_{i,t}$) as a covariate in our models, but given that this study did not focus on age effects, our primary goal in doing so was to account for the potential confounding effect of age when considering our competing hypotheses about individual heterogeneity. We thus decided to model the age effect as a quadratic relationship because of its generality and biological relevance, and did not test alternative simpler age effects (e.g., linear trend, no trend). In order to investigate our three *a priori* hypotheses (H1, H2 and H3), we considered the influence of two types of individual random effects: (i) a 'baseline' individual effect (α_i) expressed in 'normal' environmental conditions; and (ii) an individual effect (β_i) expressed in 'iceberg' years. Accordingly, we built a set of three competing models:

$$H1: logit\left(\psi_{i,t}^{kE}\right) = \mu + \delta_{t-1}^{k} + \eta_t + \gamma_1 . A_{i,t} + \gamma_2 . A_{i,t}^2$$

$$H2: logit\left(\psi_{i,t}^{kE}\right) = \mu + \delta_{t-1}^{k} + \eta_t + \gamma_1 . A_{i,t} + \gamma_2 . A_{i,t}^2 + \alpha_i$$

$$H3: logit\left(\psi_{i,t}^{kE}\right) = \mu + \delta_{t-1}^{k} + \eta_t + \gamma_1 . A_{i,t} + \gamma_2 . A_{i,t}^2 + (1 - X_t).\alpha_i + X_t.\beta_i$$

Here, μ represents a theoretical mean reproductive rate (on the logit scale), γ_1 and γ_2 are the two parameters of the quadratic age effect, and X_t is a binary covariate indicating whether year t was an iceberg year ($X_t = 1$) or not ($X_t = 0$). We also note that in model H2 α_i corresponds to a unique random intercept for each individual i that is expressed in all years in keeping with the fixed heterogeneity hypothesis. On the other hand, in model H3, α_i represents the individual effect in non-iceberg years (i.e., 'normal' years), and β_i corresponds to the individual effect expressed during iceberg years (i.e., 'disturbed' years).

In the analyses presented here, modeling was focused on the sequence of reproductive states during the time an individual was known to have been alive, i.e., between its first reproductive event (state F) and its last encounter (in state E or S), a period we refer to here as the 'minimal lifetime window' (MinLifeWin) of the animal. Models were thus conditional on the first and the last detection of each individual and did not include a survival parameter. This approach was sensible for our objective of evaluating possible differences among individuals in their frequency of reproduction, and not in their survival rates. Given the very high detection rates inside colonies (Hadley et al., 2007a; Rotella et al., 2009, Chambert et al., 2012) and the high philopatry of locally born animals in colonies (Cameron and Siniff 2004, Cameron et al. 2007), estimates of reproductive rates appeared to be very robust to this right-censoring of encounter histories. Indeed, when we performed analyses (not presented in this paper) using non-right-censored data in which survival and detection were explicitly modeled, we found that estimates of model parameters were the same. For ease of interpretation, we thus

decided to present the results of the simpler approach focusing solely on reproductive rates. Furthermore, as noted before, any non-detection event inside an individual's MinLifeWin necessarily corresponded to the skip-breeding state. Reproductive states were thus known for all years within an individual's MinLifeWin, such that we did not need to include a detection parameter in our models.

A Bayesian approach was used for inference and implemented in the software program OpenBUGS (Lunn et al. 2009). Markov chain Monte Carlo (MCMC) methods were used to sample, and thus approximate, the posterior distributions of the parameters of interest. The year and individual varying parameters η_t, α_i, and β_i were modeled hierarchically following independent normal distributions with mean 0 and model- and parameter-specific standard deviations: $\eta_t \sim N(0, \sigma_\eta)$, $\alpha_i \sim N(0, \sigma_\alpha)$ and $\beta_i \sim N(0, \sigma_\beta)$. Standard deviations σ_α and σ_β are measures of the magnitude of inter-individual variability in reproductive rates, for their respective environmental condition, and are thus of primary interest to our question. We chose to model the two individual effects (α_i and β_i) as independent between the two time periods, rather than assume a common correlation applied to all individuals by explicitly including it as a parameter of a multivariate normal distribution. If explicitly modeled, the magnitude of the estimated correlation is driven by the individuals behaving similarly in iceberg and non-iceberg years, and does not represent the contrasted individual reproductive patterns seen for some individuals. This specification allowed model H3 to be as distinct as possible from the fixed heterogeneity hypothesis represented in model H2. We investigated and

quantified correlation under this independence assumption by calculating a correlation coefficient ($\rho_{\alpha,\beta}$) directly from the joint posterior distribution of the $\alpha_i's$ and $\beta_i's$.

A prior for μ was specified through a uniform U(0,1) distribution on the mean of ψ on the original scale (i.e., $\bar{\psi} = logit^{-1}(\mu)$). Parameters δ_{t-1}^{k}, γ_1 and γ_2 were assigned diffuse normal prior distributions N(0,1000) on the logit scale. Uniform prior distributions U(0,10) were used for hyperparameters σ_ε, σ_α, and σ_β. To assess the sensitivity of inferences of the standard deviation of individual effects (σ_α) to the choice of prior, we compared these results to those obtained using an inversegamma(4, 0.05) prior on variance σ_α^2 (see Appendix B). This latter prior distribution has a very high density in values close to zero and thus strongly penalizes high values of variance. This prior therefore penalizes, *a priori*, the heterogeneity hypothesis (H2), which is a way to assess the support for this hypothesis in a conservative way.

For each of the three competing models, we ran 2 chains in parallel with different sets of initial values. The first 5,000 MCMC samples were discarded (burn-in period), after having checked that convergence was satisfactory. Convergence was visually assessed using sample path plots in conjunction with the Brooks-Gelman-Rubin diagnostic 'R' (Brooks and Gelman 1998), with values close to 1.00 indicating adequate convergence. A total of 150,000 MCMC samples after burn-in were used for inference. All parameters described above were defined on the logit scale in the models, but summaries of the posterior distributions provided later in the text, figures, and tables were transformed back to the scale of a probability of reproduction (i.e., interval [0,1]) to ease interpretation. Back-transformed values are hereafter denoted with a star (e.g., σ_α^*).

Model Comparison and Hypothesis Selection

In addition to making inference directly from parameter posterior distributions, we adopted a model-comparison approach. In ecology, the evaluation and comparison of competing models, generally analyzed under a likelihood approach, has traditionally been based on generic criteria of model accuracy (Burnham and Anderson 2002), dominated by the use of the Akaike Information Criterion (AIC). In Bayesian statistics, there currently is no consensus on the best way to select and compare competing models (Link and Barker 2010). Generic criteria, such as AIC, BIC (Bayesian Information Criterion) and DIC (Deviance Information Criterion) are used (Spiegelhalter et al. 2002, Barnett et al. 2010, Cubaynes et al. 2012), but are also widely criticized, especially in the context of hierarchical (random effects) models (Link and Barker 2010). Here, we chose to implement posterior predictive checking to compare the performance of our three competing models (Gelman et al. 2004, Schofield and Barker 2011). The principle of posterior predictive checking (see Gelman et al. 2004, p.159) is straightforward: if a given model represents a good approximation of the true process that generated the data, then replicated data generated under this model should have very similar features to the observed data. This approach allows assessment of the goodness-of-fit of each model and provides an explicit tool for model comparison.

For each particular model, the implementation of posterior predictive checking took place as follows. First, 10,000 replicate datasets (y^{rep}) were simulated under different draws from the joint posterior distribution of all parameters to account for uncertainty. As in the statistical models used to analyze the data (see above), the simulation of each individual's reproductive history (i) was conditional on its first and

last encounters (i.e., its MinLifeWin was fixed) and (ii) started with state F. Subsequent states were simulated using year- and individual-specific reproductive rates calculated from the set of parameters relevant to each model, thus including the effects of state, age and year for all models. Second, a relevant function of the data ($T(.)$) was derived for each replicate ($T(y^{rep})$), and the distribution of $T(y^{rep})$, called the posterior predictive distribution, was compared to the observed value $T(y^{obs})$ derived from the observed dataset (y^{obs}). One-sided posterior predictive p-values (i.e., $Pr[T(y^{rep}) \geq T(y^{obs})]$ or $Pr[T(y^{rep}) \leq T(y^{obs})]$) were then calculated as a summary statistic of the lack of fit between replicated and observed data.

We chose to derive and compare data features directly related to our question of interest. Notably, it has been emphasized in the recent literature that the existence of underlying individual heterogeneity should not be claimed if the observed level of variation in individual performance (e.g., lifetime reproductive success or temporal persistence in a given reproductive state) is not larger than that simply predicted by random chance alone (Tuljapurkar et al. 2009). We therefore decided to explicitly compare the competing models in predicting the observed level of realized inter-individual variation in (i) reproductive success and (ii) measures of temporal persistence in the experienced breeder state (E). As a measure of individual reproductive success, we used the observed reproductive output (RepOutput), i.e. the number of pups produced by an individual within its MinLifeWin. The measures of individual persistence in the breeder state were defined as follows: (i) the longest time of persistence in the reproductive state (PersistRep), defined as the maximum number of consecutive years an

individual remained in state E without skipping a year of reproduction (i.e., length of the longest series of E's for each individual); and (ii) the number of consecutive reproductive events (ConsecRep), defined as the total number of two-year sequences 'EE' in an individual's history. These measures of reproductive performance were calculated for each individual and the level of variability across individuals was investigated through two statistics of interest: (i) the standard deviation (SD) and (ii) the maximum value (Max). To summarize, we thus investigated the SD and Max of the distribution of these 3 variables (RepOutput, PersistRep and ConsecRep) over all individuals for each posterior replicate of simulated data (i.e., 10,000 SD's and Max's).

Within each individual's reproductive history, the number of stochastic state transitions is a direct function of the MinLifeWin of this particular individual. Therefore, the level of discrepancy between simulated and observed data is better informed by individuals with long MinLifeWin. To better expose potential lack-of-fit of each model, the comparison between $T(y^{rep})$ and $T(y^{obs})$ was thus based on the 645 individuals (out of a total of 954) having a MinLifeWin of at least 5 years, which we considered a reasonable compromise between sample size and amount of informative data from each individual. Nevertheless, we note that comparisons from samples defined by a different MinLifeWin threshold (e.g., including all individuals) gave similar results and led to the same conclusions.

Simulations of Expected Reproductive Output

To further investigate the biological meaning of the estimated level of latent individual heterogeneity, we predicted the expected number of descendants, using simulations of individual reproductive trajectories, for three hypothetical types of individuals: (i) a 'frail individual' $\left(logit\left(\bar{\psi}_{frail}\right) = \mu - 2\sigma_{\alpha}\right)$, (ii) an 'average individual' $\left(logit\left(\bar{\psi}_{avg}\right) = \mu\right)$, and (iii) a 'robust individual' $\left(logit(\bar{\psi}_{robust}) = \mu + 2\sigma_{\alpha}\right)$. In each individual trajectory, a female started as an 8-year-old first-time breeder (the mean age at first reproduction being 7.62 years in the data) and was allowed to live 10 additional years, which represents the expected future lifespan for an 8-year old female. The projections consisted of simulating the stochastic sequence of reproductive states over this fixed time frame, based on posterior means obtained from the best heterogeneity model (H2 or H3) with random year effects drawn $[\eta_t \sim N(0, \sigma_{\eta})]$ at each time step and applied to the three types of individuals such that they were exposed to the same annual conditions. Results are based on 5,000 simulated trajectories for each type of individual.

Results

Encounter histories from 954 females provided a total of 6,792 known-state observations (i.e., 'individual-years'), with 954 observations in state F, 3,667 in state E, and 2,171 in state S. In this dataset, individual MinLifeWin (i.e. number of informative years of data, from first reproduction to last sighting) ranged from 2 to 25 years, with an average of 7.1 years per female, and more than 67% of individuals had a MinLifeWin of

at least 5 years. The number of pups produced by a female (RepOutput) within its MinLifeWin ranged from 1 to 19, with an average of 4.8 and a standard deviation of 3.2. The two measures of reproductive persistence (ConsecRep and PersistRep) ranged from 0 to 16, and respectively averaged 2.1 (with SD = 2.5) and 2.7 (with SD = 2.1).

Parameter Posterior Distributions

The posterior means of the age parameters (γ_1^* and γ_2^*) were consistent among the three models (table 3-1). The shape of the estimated quadratic trend, imposed in the model, suggests that reproductive rates increased up to age 14-15 and then decreased at older ages (figure 3-2).

We found clear evidence for the presence of heterogeneity in this population, as the estimated level of 'baseline' inter-individual standard deviation in reproductive rates σ_α^* (measured on the interval [0,1]) was distinctly greater than 0 in both model H2 (posterior mean of σ_α^* = 0.15; 95% credible interval = [0.13, 0.18]) and model H3 (posterior mean of σ_α^* = 0.13; 95% credible interval = [0.10, 0.16], table 3-1). It is also interesting to note that the posterior means of σ_α^* from both models H2 and H3 were of the same order of magnitude as the estimated level of inter-annual variability σ_η^* (table 3-1). The estimated magnitude of σ_α^* was the same when a restrictive inverse-gamma prior, penalizing high values, was used (Appendix B), highlighting the fact that the data provide strong support for this level of underlying individual heterogeneity. In model H3, the posterior mean of σ_β^* (0.18; 95% credible interval = [0.13, 0.23]) was marginally greater than that of σ_α^*, suggesting that inter-individual differences might have been amplified during iceberg years. However, the difference between σ_α^* and σ_β^* was relatively small

(posterior mean of $(\sigma_{\alpha}^{*} - \sigma_{\beta}^{*})$ = 0.04, 95% credible interval [-0.01, 0.10]). Hence, we do not make any strong inference about the biological importance of the estimated difference. The estimated correlation between α_i and β_i ($\rho_{\alpha,\beta}$) was positive but relatively weak (posterior mean of $\rho_{\alpha,\beta}$ = 0.11; 95% credible interval = [0.01, 0.20], see also figure 3-3), providing suggestive, although inconclusive, evidence of some degree of consistency in individual robustness between normal and iceberg years. For instance, individuals that appeared to be very robust [frail] in normal years were never very frail [robust] in perturbed years (figure 3-3).

Another noteworthy aspect of our results concerns the estimated effect of reproductive state at $t-1$ (table 3-1) on current probabilities of reproduction. All models consistently produced posterior means of $\psi_{i,t}^{EE}$ near 0.67 (SD = 0.03), but posterior means of $\psi_{i,t}^{SE}$ varied by model: model H1 provided a much lower value (about 0.67 [SD = 0.03] and exactly equal to the posterior mean of $\psi_{i,t}^{EE}$) than did models H2 and H3 (about 0.76 [SD = 0.03] and 0.74 [SD = 0.03], respectively). Therefore, when individual heterogeneity was explicitly taken into account (models H2 and H3), we found evidence of a cost of reproduction on subsequent reproductive probability that was not detected when this heterogeneity was ignored. Specifically, models H2 and H3 indicated that a female was more likely to reproduce in a given year if she had skipped reproducing the year before.

Posterior Predictive Checks

Overall, the comparison of observed data to simulated data from each model, incorporating uncertainty in all parameters, revealed that the homogeneity model (H1)

substantially under-predicted the extent of inter-individual differences (measured by SD and Max) in reproductive performance in the observed data, and that better predictions were provided by the fixed individual heterogeneity model (H2) than by the variable individual heterogeneity model (H3).

More specifically, we found that individual variability in RepOutput was poorly predicted by model H1: indeed, only 0.7% of the simulated data sets (y^{rep}) obtained from model H1 produced SDs of RepOutput as large as the observed SD (figure 3-4: P = 0.007). Model H1 also tended to under-predict the Max value of RepOutput (figure 3-5: P = 0.115). The poor performance of model H1 at accounting for the observed level of individual heterogeneity was even more evident when considering measures of reproductive persistence (SD of ConsecRep: $P < 0.001$; SD of PersistRep: $P = 0.001$; and Max of ConsecRep: $P = 0.036$; Max of PersistRep: $P = 0.032$). In contrast, the fixed heterogeneity model (H2) provided predictions that were well distributed around the observed values of all these features (all p-values between 0.347 and 0.491). The posterior predictive performance of the variable heterogeneity model (H3) appeared to be intermediate, with a slight under-prediction of the SD (figure 3-4), and to a lesser extent, of the Max (figure 3-5) of the different measures of reproductive performance.

These results clearly show that individual heterogeneity in reproductive rates must be accounted for to explain the level of individual variability observed in reproductive performance. Moreover, it seems that this heterogeneity is better represented as a fixed feature than as a variable feature. Finally, when individual heterogeneity in reproductive rates was incorporated, costs of reproduction to future reproduction were detected.

Simulations of Expected Reproductive Output

The approximate expected reproductive output (±SD) was 4.4 (±1.3) pups for 'frail' females, 6.9 (±1.3) pups for 'average' females and 8.8 (±1.0) pups for 'robust' females (figure 3-6). A 'robust' individual is thus expected to produce on average twice as many pups as a 'frail' individual over a 10-year period, a result that strongly suggests that the estimated level of individual heterogeneity in reproductive probabilities translates into substantial differences in terms of expected reproductive output.

Discussion

We investigated three competing hypotheses concerned with the existence and the temporal expression of individual heterogeneity in reproductive rates of females in a population of Weddell seals. Results provided strong support for the presence of latent individual heterogeneity in reproduction and the expression of this heterogeneity seemed relatively independent from environmental conditions. We also detected a substantial cost of reproduction when individual heterogeneity was explicitly accounted for in the models, which is a novel finding for this species and has important implications for future studies of reproductive costs in other species.

Strong Evidence for the Presence of Latent Individual Heterogeneity

Overall, we found conclusive evidence for the existence of latent individual heterogeneity in reproductive rates. The estimated magnitude of inter-individual variability (σ_α^*, σ_β^*) from models H2 and H3 was high and clearly distinct from zero, even when a penalizing prior was used (Appendix B). Moreover, heterogeneity models,

especially model H2, provided predictions of realized among-individual variability in reproductive performances that were similar to the observed levels, whereas estimators ignoring underlying individual heterogeneity (from model H1) tended to substantially under-predict the degree of realized among-individual variability. This latter result reveals that the magnitude of 'residual' (i.e., after having accounted for age, year and breeding state) inter-individual variability observed in the population cannot be adequately explained as the simple result of a chance mechanism (stochastic nature of individual trajectories; Tuljapurkar et al., 2009). These findings provide good support for the existence of latent individual heterogeneity in this population. Although the sources of this individual variation in reproductive performance remain unidentified so far, a relevant speculation is that individual seals probably differ in their ability to acquire, store and conserve energy resources (Van Noordwijk and De Jong 1986). In Weddell seals, which mainly feed on fish and squids (Burns et al. 1998), individual differences in resource acquisition might be directly linked to physical, physiological or behavioral attributes that determine diving and hunting abilities (Williams et al. 2004, Costa et al. 2004). Different individuals might also adopt different strategies regarding the timing, duration, and location of foraging bouts (K. Goetz and D. Costa; A. Hindle, J.-A. Mellish and M. Horning, pers. comm.). Given the probable spatial and temporal variability in food availability and competitor abundance in the Ross Sea (Guglielmo et al. 1998, 2009, Saggiomo et al. 1998, Smith et al. 2007), different strategies could have an influence on the foraging efficiency of individual seals. On the other hand, differences might also be linked to physiological and metabolic functions that influence the efficiency of storage,

consumption, and/or conservation of energy resources (Kooyman et al. 1973, Castellini et al. 1992, Wheatley et al. 2006, 2008a,b). Furthermore, differences might exist in phenotypic attributes that directly affect fecundity, such as oocyte quality or success of embryo implantation (Atkinson 1997). We however hypothesize that attributes affecting the efficiency of acquisition and conservation of energy resources play a much more important role in determining the observed level of individual heterogeneity, especially as female Weddell seals are essentially capital breeders for which reproductive success heavily depends on body fat reserves (Boness and Bowen 1996, Wheatley et al. 2008a,b).

The estimated extent of among-individual variability appeared to be of the same order of magnitude as the estimated level of inter-annual variability, which is known to be a major component of vital-rate variation in this population (Hadley et al., 2007b; Rotella et al., 2012; Chambert et al., 2012). Inter-individual differences are thus responsible for a non-negligible amount of variation in reproductive rates. This novel result reveals that individual heterogeneity should not be ignored (Weladji et al. 2008, Gimenez and Choquet 2010, Hamel et al. 2012) in modeling exercises aiming at capturing the major sources of vital-rate variation of this population. Our simulation work also reveals that the amount of individual reproductive heterogeneity found in this population translates into substantial differences in terms of expected reproductive output. Although reproductive output is only one of the several components of true fitness, this result suggests that fitness might vary quite substantially among individuals of this population. Differences in the survival and future reproductive success of offspring will however need to be investigated in order to obtain a more thorough

measure of individual heterogeneity in fitness. Producing more offspring is not necessarily a better strategy, especially in species with high parental care investment, as a female might have to trade-off the quality (i.e., less maternal investment) of each offspring to produce more of them. On the other hand, if maternal investment is relatively homogeneous, then the fate of any offspring is relatively independent from its particular mother, and therefore, a female that produces more offspring will have a higher expected fitness. Overall, this is an important result of the present study because the quantification of fitness variation in natural populations (Link et al., 2002) is a crucial step to better understand broad evolutionary processes. At present, there are few examples of such direct quantification of individual variation in fitness components of animals in the wild, and they remain limited to a small number of highly detectable species (e.g., *Rissa tridactyla*: Cam et al., 2002; *Marmota flaviventris*: Oli & Armitage, 2003).

Marginal Evidence for a Temporally Variable Expression of Latent Individual Heterogeneity

From the results of model H3, we were able to investigate whether, during 'perturbed' environmental conditions, (i) the hierarchy in robustness among individuals would change and (ii) the magnitude of individual heterogeneity would be amplified. First, we found mild support for our prediction that the hierarchy among individuals would be maintained across the two contrasted environmental conditions. Indeed, the posterior mean correlation between individual effects in the two contrasted conditions was positive, as predicted, but still relatively low ($\rho_{\alpha,\beta}$ = 0.11). Nevertheless, even though the relative hierarchy certainly changed among many individuals, there was still some consistency in the robustness, as no individuals went from one extreme to the other

(figure 3-3). This result suggests that the most robust individuals in normal years tend to also be more robust than average in perturbed years (and vice-versa), in support with the fixed heterogeneity hypothesis (Cam et al., 2002). Concerning the potential amplification of the magnitude of individual heterogeneity in perturbed conditions, we also found only suggestive evidence for the predicted pattern, as the estimate of inter-individual variability appeared to be only marginally larger in the perturbed period than in normal years. In spite of the inconclusive evidence provided by these data, we note that the results were in the predicted direction, suggesting that inter-individual differences might be more apparent when environmental conditions are harsh. This trend is in accordance with theoretical predictions (Lomnicki, 1978) and empirical results from previous work on seabirds (Barbraud and Weimerskirch, 2005) and ungulates (Tavecchia et al., 2005).

On the other hand, the posterior predictive performance of model H3 appeared to be poorer than that of the simpler model H2, a result that highlights the relevance of the 'fixed heterogeneity' hypothesis for representing the key aspect of the individual heterogeneity that prevails in the study population. As other studies have suggested that interactions between individual heterogeneity and environmental conditions might be relatively common in nature (Lomnicki 1978, Hamel et al. 2009), we can wonder why we might have failed to find clear evidence of such an interaction here. This might be due to the fact that the 5-year iceberg event (MacAyeal et al 2008) used here as a proxy of perturbed environmental conditions might have been too brief to allow a precise assessment of how it affected the expression of individual heterogeneity. Indeed, even though the investigation of such unique large-scale perturbations can be very informative

(Carpenter 1990), the detection of complex interactive effects, such as the ones predicted here, might require longer periods of contrasted environments. Overall, we therefore conclude that, because our data could not strongly support hypothesis H3, the 'fixed heterogeneity' hypothesis (H2) remains the best representation of the individual heterogeneity in reproductive probabilities existing in this population.

Evidence of a Cost of Reproduction

In these analyses, we also shed light on the relatively important cost of current reproduction on future reproduction, and revealed this is only detected when individual heterogeneity is accounted for in the model (Vaupel and Yashin 1985, Weladji et al. 2008). In a previous study of the same population, Hadley et al. (2007a) found no evidence for such a reproductive cost in recruited individuals, and even observed a pattern opposite to what had been expected, as the estimated probability of reproduction in year t was slightly lower for individuals having skipped reproducing the previous year ($\hat{\psi}^{SE}$ = 0.65) than for those having bred the previous year ($\hat{\psi}^{EE}$ = 0.67). In the present study, posterior means similar to the latter estimates were obtained from model H1 (table 3-1), but posterior means from models H2 and H3 provided clear evidence of a reproductive cost (e.g., model H2: ψ^{SE} = 0.76 vs. ψ^{EE} = 0.67). Models ignoring individual heterogeneity failed to detect the difference between ψ^{SE} and ψ^{EE} because these state-specific estimates were averaged over all types of individuals. As frail females skip reproduction more often than other females, they provide more data to transitions from state S (either toward state E, with probability ψ^{SE}, or toward state S, with probability $\psi^{SS} = 1 - \psi^{SE}$) and thus have a greater influence on the estimation of ψ^{SE};

and because frail females have lower reproductive rates (more transitions 'S to S' than average), they tend to pull the averaged value of ψ^{SE} down. Including individual heterogeneity in the model disentangles the influence of reproductive state at $t-1$ (e.g., influence of energy expenditure/allocation), which is common to all females, from the influence of individual robustness, which is specific to each female. The magnitude of the estimated cost is such that, on average, when a female reproduces in a given year, she is about 10% less likely to breed the next year than if she had skipped reproduction. This is one of the first evidence of such a reproductive cost in a population of long-lived marine mammal living in a polar environment, and it supports findings of previous studies that have shown the necessity of accounting for individual heterogeneity to highlight, in demographic data, these types of life history trade-offs occurring at the individual scale (Vaupel and Yashin 1985, Van Noordwijk and De Jong 1986, Service 2000, Cam et al. 2002, Nussey et al. 2008, Weladji et al. 2008).

Conclusion and Perspectives

The growing number of demographic studies using individual-level models and explicitly investigating individual heterogeneity will certainly allow improvement in our understanding of the prevalence, the magnitude and the nature of inter-individual differences in fitness components, as well as in our comprehension of the expression of life history trade-offs in wild populations (Service 2000, Weladji et al. 2008). Furthermore, given that individual heterogeneity can have an influence on demographic stochasticity (Kendall et al. 2011), the accounting of individual effects in population

dynamics models should enhance the accuracy of demographic projections, especially for small and threatened populations.

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Table 3-1. Summary of the posterior distributions of relevant parameters for the three competing models.

Parameters	H1. No IH			H2. Fixed IH			H3. Variable IH		
	Mean	2.5% LCI	97.5% LCI	Mean	2.5% LCI	97.5% LCI	Mean	2.5% LCI	97.5% LCI
$\bar{\psi}^{kE}$	0.62	0.55	0.67	0.66	0.59	0.72	0.65	0.58	0.71
ψ^{FE}	0.50	0.42	0.57	0.54	0.45	0.62	0.52	0.43	0.60
ψ^{EE}	0.67	0.62	0.72	0.67	0.61	0.73	0.67	0.60	0.72
ψ^{SE}	0.67	0.61	0.72	0.76	0.70	0.81	0.74	0.68	0.79
γ_1^*	-0.06	-0.10	-0.03	-0.06	-0.10	-0.01	-0.06	-0.10	-0.02
γ_2^*	-0.08	-0.12	-0.04	-0.10	-0.15	-0.06	-0.09	-0.14	-0.05
σ_η^*	0.12	0.09	0.18	0.14	0.10	0.19	0.13	0.09	0.19
σ_α^*	--	--	--	0.15	0.13	0.18	0.13	0.10	0.16
σ_β^*	--	--	--	--	--	--	0.18	0.13	0.23
$\rho_{\alpha,\beta}$	--	--	--	--	--	--	0.11	0.01	0.20

The acronym 'IH' stands for 'individual heterogeneity'. The mean, and the lower (2.5%) and upper (97.5%) limits of a 95% credible interval (LCI), of the posterior distribution are shown. Symbols with a star (e.g., γ_1^*) correspond to parameters which value has been transformed back to the more interpretable scale of a probability of reproduction (i.e., in the interval [0,1]). The parameters displayed in this table are: (i) $\bar{\psi}^{kE}$, mean reproductive rate, corresponding to a theoretical value ($logit^{-1}(\mu)$) averaging across states (k), ages, years and individuals; (ii) rates of reproduction, specific to the reproductive state k at $t-1$ and averaged across ages, years and individuals: first-time breeders (ψ^{FE}), experienced breeders (ψ^{EE}) and skip-breeders (ψ^{SE}); (iii) first-order (γ_1^*) and second-order (γ_2^*) age-effect parameters; we note that both posterior means of γ_1^* and γ_2^* are negative, but the quadratic trend is still parabolic concave (figure 3-2) because age values were standardized (see Methods); (iv) standard deviation of the normal distribution of random year effects (σ_η^*), of random 'baseline' individual effects (σ_α^*), and of random individual effects expressed during iceberg years (σ_β^*); (v) the correlation between the two types of individual effects ($\rho_{\alpha,\beta}$).

Figure 3-1. Female Weddell seal (Leptonychotes Weddellii) with her pup, in Erebus Bay.

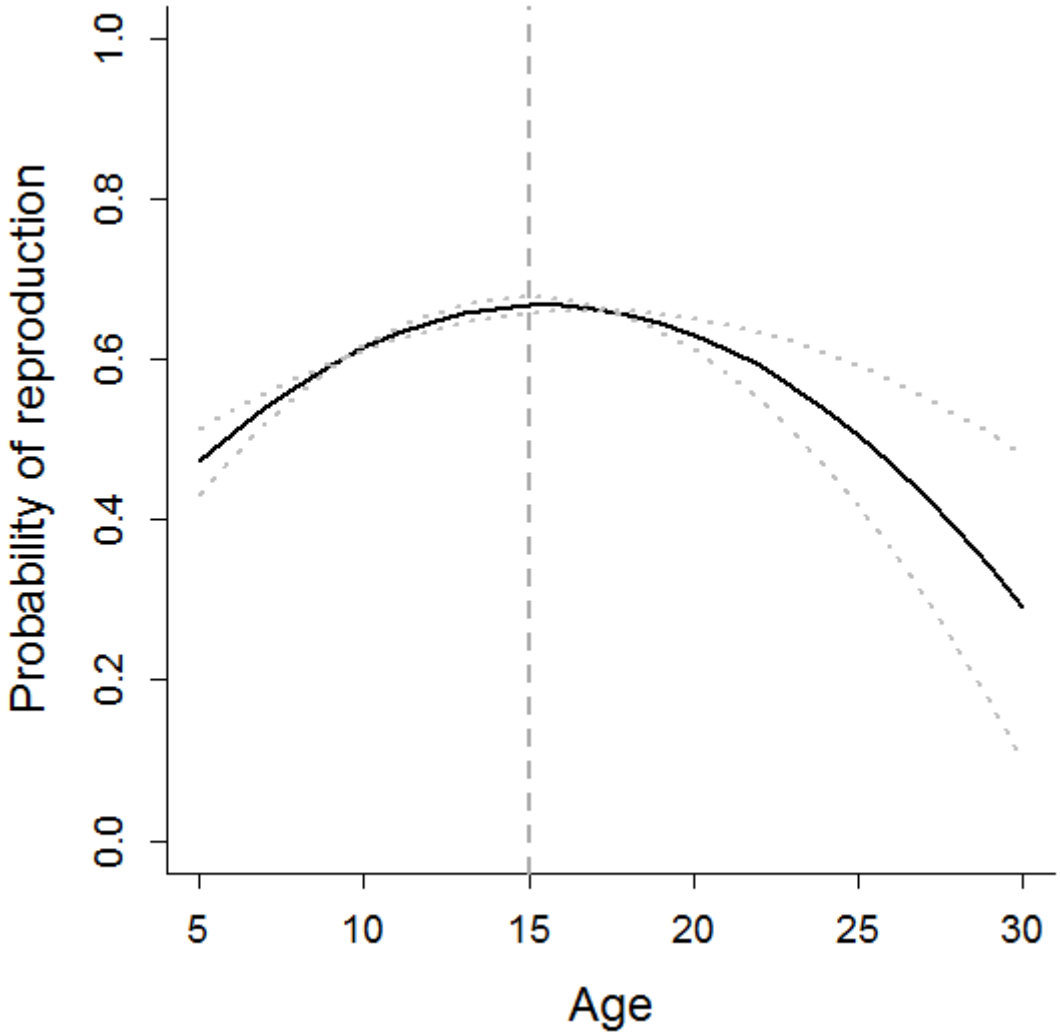

Figure 3-2. Estimated age-related trend in reproductive rates.
The quadratic curve displayed on this graph has been obtained by using posterior means of γ_1 and γ_2 from model H2. The curve obtained by using posterior means of parameters from models H1 and H3 is extremely similar. The black solid curve represents the mean estimated trend, while the grey dotted curves represent the 95% credible interval. The age at which the probability of reproduction is maximum (age 15) is shown by the grey dashed vertical line.

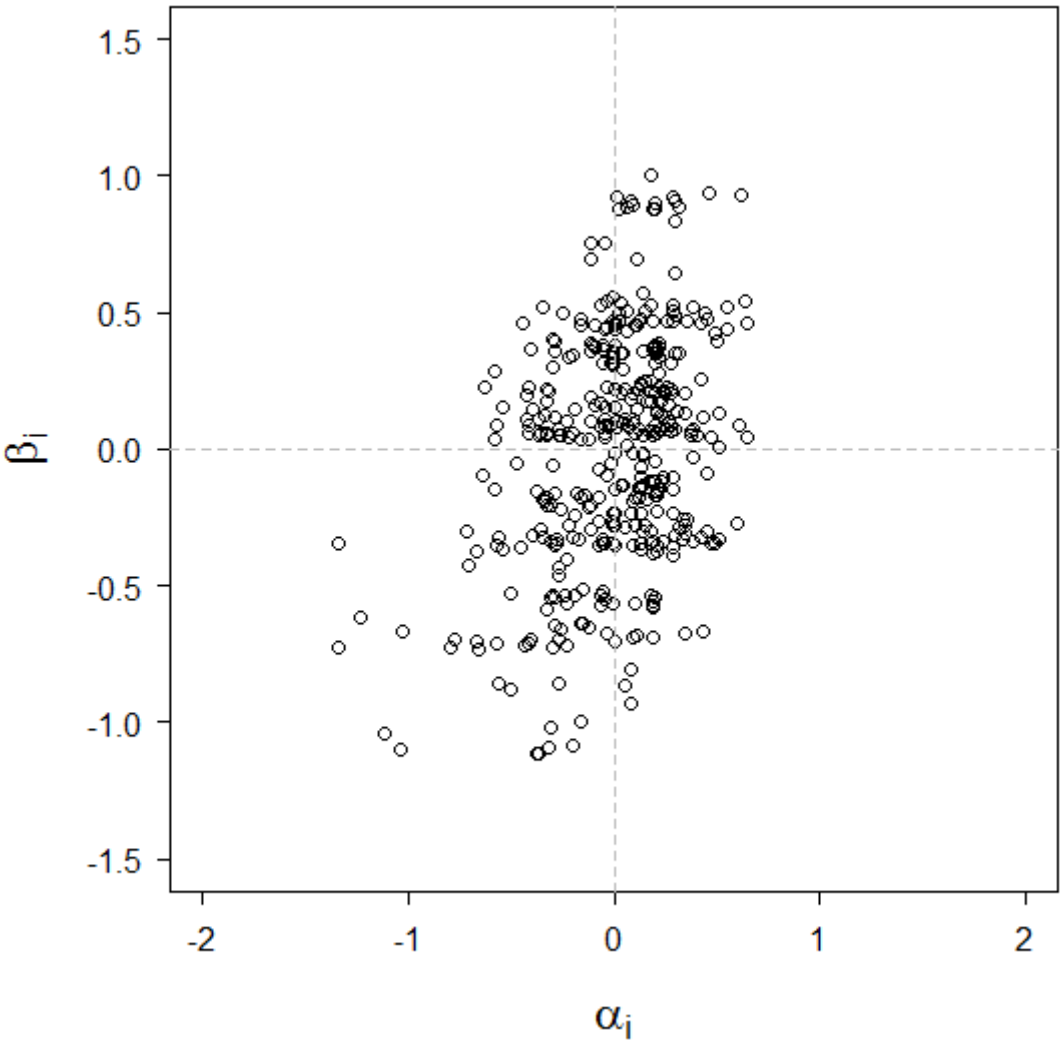

Figure 3-3. Relationship between the posterior means of individual effects in 'normal years' ($\boldsymbol{\alpha_i}$) and in 'iceberg years' ($\boldsymbol{\beta_i}$).
The overall relationship appears to be positive, but relatively weak. However we can clearly note the lack of points in 'extreme values' of the lower-right and upper-left corners, indicating that no individuals with a high α_i value have a very low β_i value, and no individuals with a high β_i value have a very low α_i value.

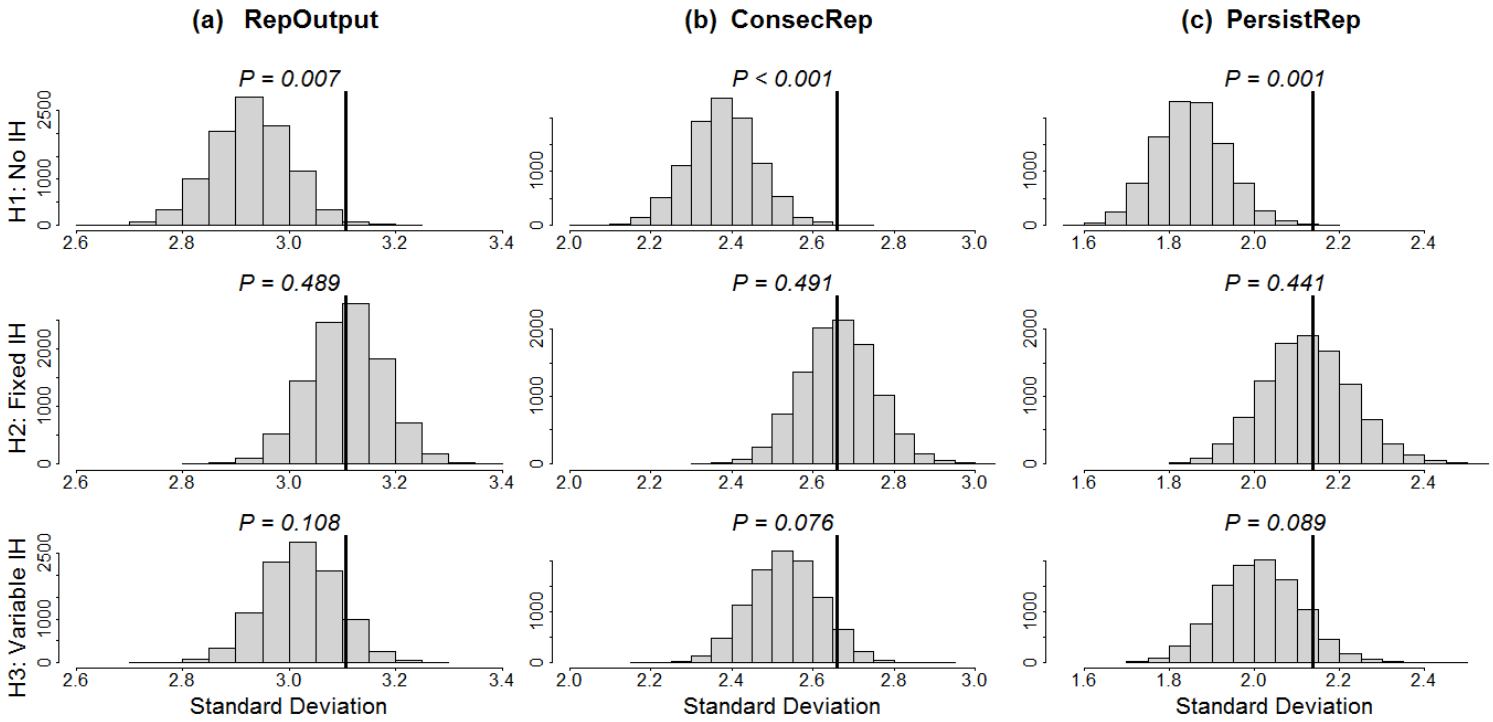

Figure 3-4. Posterior predictive distributions of the inter-individual standard deviation of (a) observed reproductive output (RepOutput), (b) number of transitions from state E to state E (ConsecRep) and (c) maximum persistence in state E (PersistRep), for each model (each row).
The standard deviation value from observed data is shown by the vertical black line and the posterior predictive one-sided p-value is also displayed above each plot. This posterior predictive analysis was restricted to individuals having a minimum lifetime window of at least 5 years.

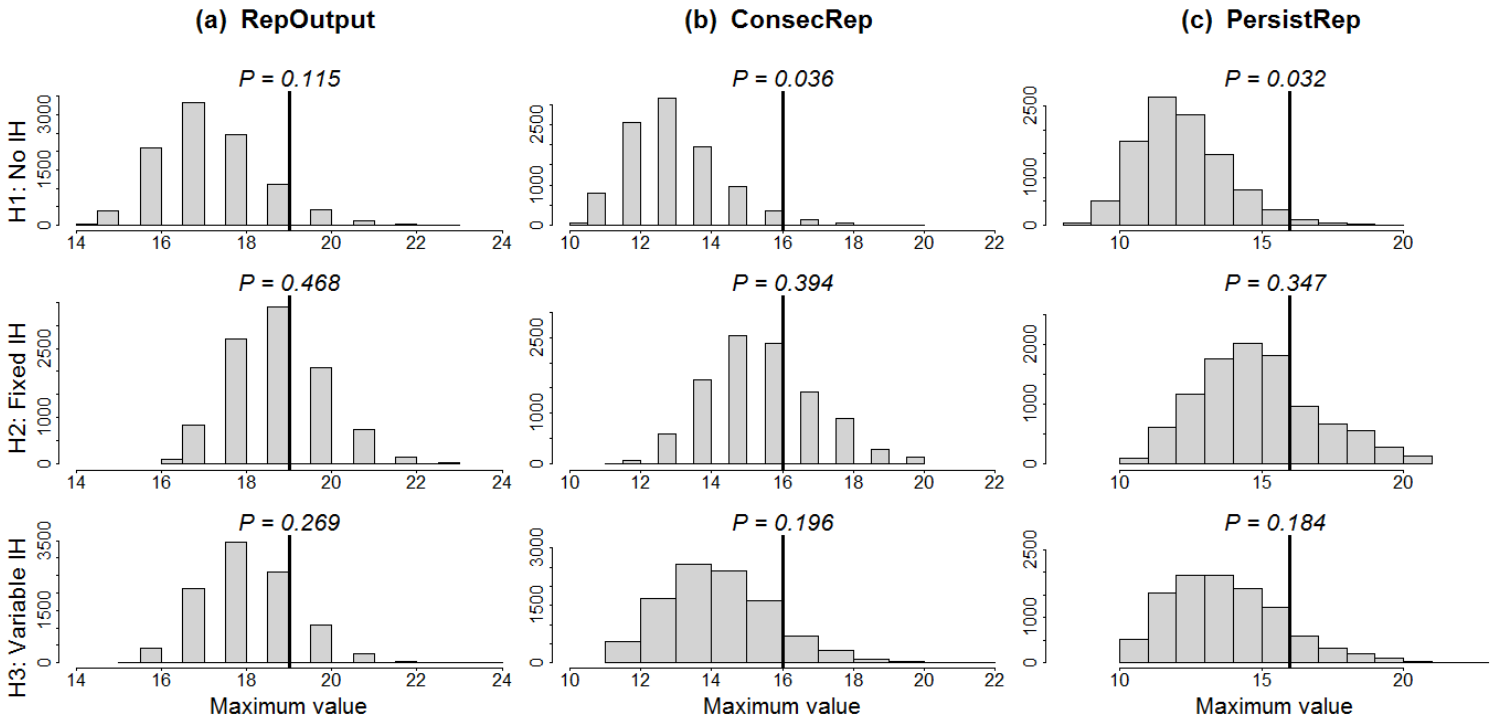

Figure 3-5. Posterior predictive distribution of the maximum value among all individuals of (a) observed reproductive output (RepOutput), (b) number of transitions from state E to state E (ConsecRep) and (c) maximum persistence in state E (PersistRep), for each model (each row).
The maximum value from observed data is shown by the vertical black line and the posterior predictive one-sided p-value is also displayed above each plot. This posterior predictive analysis was restricted to individuals having a minimum lifetime window of at least 5 years.

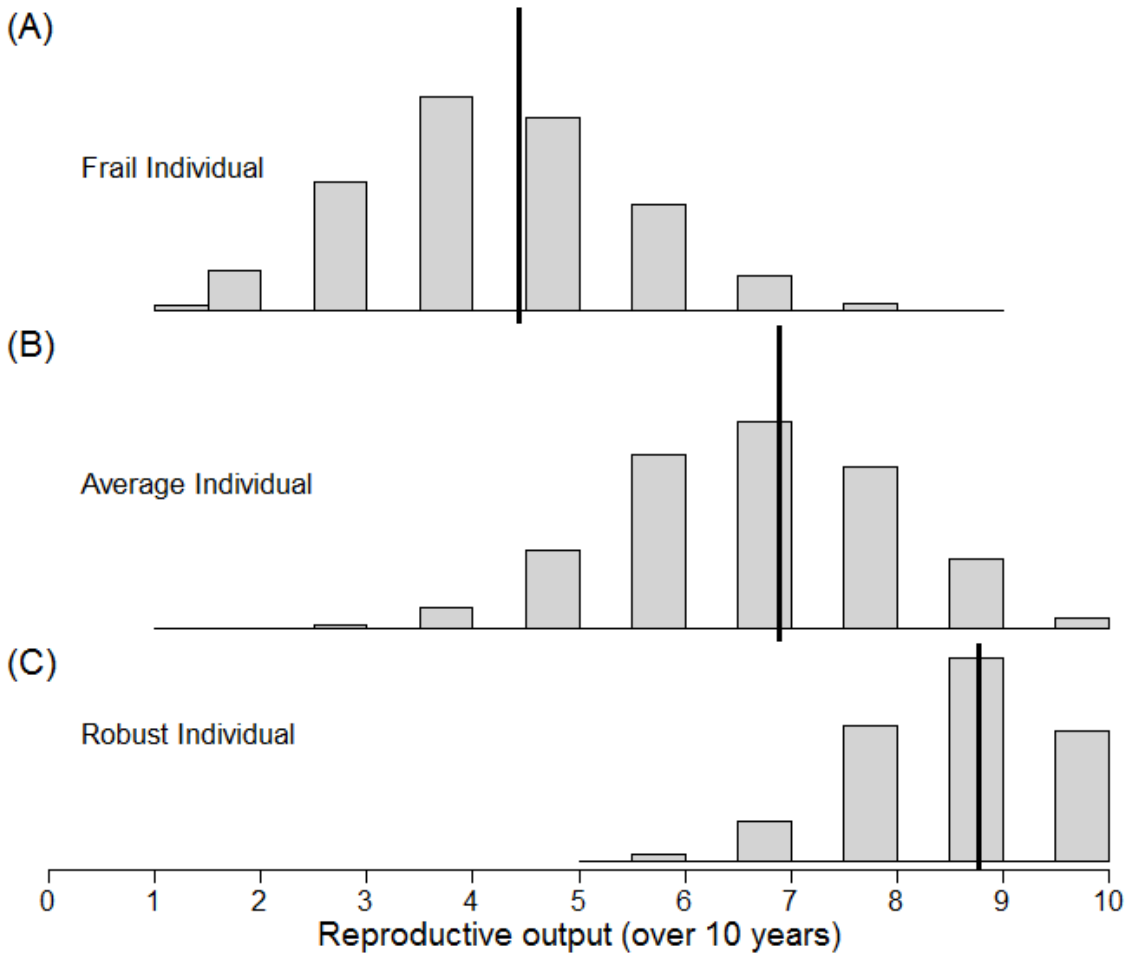

Figure 3-6. Approximated distributions of the expected reproductive output for three types of individuals.
(A) 'frail' individual; (B) 'average' individual; and (C) 'robust' individual (see text for details). These results are based on 5,000 simulated trajectories for each type of individual. The mean of each distribution is shown by a black vertical line.

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CHAPTER FOUR

AN EVOLUTIONARY PERSPECTIVE ON REPRODUCTIVE INDIVIDUAL HETEROGENEITY IN A MARINE VERTEBRATE

Contribution of Authors and Co-Authors

Manuscript in Chapter 4

Author: Thierry Chambert

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Co-Author: Jay J. Rotella

Contributions: Supervised the long-term project and collected data. Provided feedback on statistical analyses and comments on drafts of the manuscript.

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Contributions: Supervised the long-term project and collected data. Provided expertise and comments on drafts of the manuscript.

Manuscript Information Page

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Abstract

1. Although the quantification of individual heterogeneity in wild populations' vital rates has recently attracted growing interest among ecologists, the investigation of its evolutionary consequences remains limited, mainly because of the difficulties in assessing fitness and heritability from field studies on free-ranging animals. In the presence of individual variability, evaluation of fitness consequences can notably be complicated by the existence of trade-offs among different vital rates.

2. In this study, to further assess the evolutionary significance of previously quantified levels of individual heterogeneity in female Weddell seal (*Leptonychotes weddellii* Lesson) reproductive rates (Chambert et al. 2013), we investigated how several life history characteristics of female offspring were related to their mother's reproductive rate, as well as to other maternal traits (age and experience) and environmental conditions at birth.

3. The probability and age of first reproduction (recruitment) of female offspring was not related to their mother's reproductive rate, suggesting the absence of a maternal trade-off between the number and quality of offspring a female produces. Evidence of a positive, but relatively weak, relationship between the reproductive rates of a mother and her female offspring was found, suggesting some degree of heritability in this trait.

4. Using a simulation approach based on these statistical findings, we showed that substantial differences in the number of grandchildren, produced through female progeny can be expected among females with different reproductive rates.

5. Despite the presence of substantial stochastic variability, due to environmental fluctuations and other unidentified mechanisms, and in light of the fact that the metrics obtained do not provide a full measure of real fitness, our results do suggest that the individual reproductive variability found in female Weddell seals could potentially have important fitness consequences.

Introduction

The investigation of among-individual differences in phenotypic quality, survival and reproduction in wild populations is gathering more and more attention in the ecology literature (e.g., Aubry et al. 2011; Bergeron et al. 2008, 2011; Cam & Monnat 2000; Cam et al. 2012, 2002; Steiner, Tuljapurkar, & Orzack 2010). At first, ecologists were mainly interested in controlling for latent individual heterogeneity in population studies because it can hamper the detection of individual life history trade-offs, such as reproductive costs or senescence (Cam et al. 2002; Service 2000; Weladji et al. 2008). More recently, there has been a growing interest in the evolutionary significance of individual variability in wild populations (Bergeron et al. 2011; Wilson & Nussey 2010). Investigating how individual heterogeneity relates to fitness and assessing whether it has heritable bases are important steps to better understand the extent to which this variability can be under selective pressure. Fisher's fundamental theorem of natural selection postulates that the rate of change in fitness in a population is equal to the additive genetic variance in fitness (Fisher 1958). From this theory, it is predicted that traits strongly associated with fitness, such as life history traits, will exhibit low additive genetic variance and therefore low heritability (Charlesworth 1987; Mousseau & Roff 1987). Therefore, the potential for

current action of natural selection in wild populations is generally expected to be low as a result of past selective filtering (Kruuk et al. 2000), and some empirical studies have provided direct support to this prediction (Gustafsson 1986; Mousseau & Roff 1987; Roff & Mousseau 1987). On the other hand, some mechanisms, such as environment fluctuation or frequency-dependent selection, can be responsible for the maintenance of substantial levels of genetic variance in traits closely linked to fitness (Charlesworth 1987). The existence of such patterns has been found in some field studies (e.g., Van Noordwijk et al. 1980) and is supported by empirical evidence for the existence of natural selection bouts, often attributed to environmental variation, in the wild (Siepielski, DiBattista, & Carlson 2009). Further investigation involving different taxa and various environmental and historical contexts are therefore needed to strengthen our empirical knowledge of the prevalence and dynamics of natural selection in nature (Kruuk et al. 2000; Mousseau & Roff 1987; Siepielski et al. 2009).

Here, we investigate several aspects of the potential evolutionary consequences of individual reproductive heterogeneity in a population of Weddell seals (*Leptonychotes weddellii*). In a previous study, Chambert et al. (2013) were able to quantify the amount of latent individual variation in female reproductive rates; based on their results, they suggested that females of high quality (here, defined by the magnitude of an individually varying effect pertaining to reproductive rates) could be expected to have a lifetime reproductive output twice as large as that of low-quality females. This finding suggests the among-female variability in reproductive rates quantified in this population could yield important fitness differences. However, a female's fitness does not simply depend

on the number of offspring she produces, but also on the reproductive success of her offspring, which will ultimately determine her genetic contribution to the population through her number of grandchildren (Hunt et al. 2004). Therefore, a thorough assessment of the fitness consequences of the quantified level of individual heterogeneity must also consider how a female's reproductive rate may be related to her offsprings' lifetime reproductive success. First of all, one must consider potential trade-offs between offspring quantity and quality, which are expected to occur at the individual level (Lack 1947; Stearns 1992). If there is more variation in resource allocation than acquisition, a negative relationship between reproductive rates and offspring quality will be expressed at the among-individual level (Van Noordwijk & De Jong 1986). Females producing more offspring than average will do so at the cost of lower offspring quality, such that they will not necessarily have larger fitness. On the other hand, if among-individual variance primarily concerns resource acquisition (Van Noordwijk & De Jong 1986), a positive relationship is expected between offspring quantity and quality (Reznick, Nunney, & Tessier 2000), and a female's fitness should be positively related to her reproductive rates.

The relationship between a female's reproductive performance and the success of her offspring can also be affected by other maternal factors (Mousseau & Fox 1998), both environmental and genetic. First, environmental conditions early in life can be an important determinant of survival and future reproductive success (Lindström 1999; Lummaa & Clutton-Brock 2002). Therefore, in fluctuating environments, females can directly influence their offspring's fate through the choice of which years they reproduce

in. This type of flexible strategy is more prevalent in iteroparous species where investment in any reproductive event is highly costly (Erikstad et al. 1998), but also requires the environment to be sufficiently predictable. Fitness will be maximized for individuals who are able to spread their reproductive effort across years with the most favourable conditions. In the study population of Weddell seals, large annual fluctuations in cohort size (i.e., number of pups born each year) have been observed (Garrott et al. 2012), varying from 169 to 603 pups within the last 10 years. This pattern suggests females use a flexible reproductive strategy, varying both age at recruitment (Hadley et al. 2006) and frequency of subsequent reproduction to cope with important annual variations in environmental conditions (Chambert, Rotella, & Garrott 2012; Garrott et al. 2012; Hadley, Rotella, & Garrott 2007b; Rotella et al. 2009). Second, offspring quality can be positively influenced by maternal quality through the effects of heritable factors, either genetic or epigenetic. In such a case, individual variation in female reproductive rates will produce similar variation in fitness, and because there is heritability, traits involved should be under natural selection. But because heritability of reproductive frequency is expected to be very low (Charlesworth 1987), such a scenario seems very unlikely.

In this study, we addressed the evolutionary consequences of individual reproductive heterogeneity in female Weddell seals through three successive analyses. First, we investigated the relationship between female reproductive rates and several life history characteristics of their female offspring. In this first analysis, we also assessed the influence of other maternal traits (age, breeding experience) and environment at birth on

offspring reproductive success. Next, using a mother-daughter regression approach, we quantified the degree of heritability in female reproductive rates. Finally, using a simulation approach based on the results of the first two analyses, we calculated the expected number of grandchildren (proxy of fitness) produced by females with different reproductive rates. Because we do not have information on male reproduction, our inferences on fitness were limited to the contribution of female progeny. We acknowledge and discuss the fact that in a polygynous species such as the Weddell seal (Stirling 1969), maternal resource allocation could potentially be biased towards male progeny (Hewison & Gaillard 1999; Trivers & Willard 1973), a mechanism potentially having important fitness consequences. Despite this limitation, our endeavour at further investigating cross-generational influences of individual reproductive heterogeneity in females provides important insights regarding the evolutionary consequences of individual reproductive heterogeneity in wild animal populations.

Material and Method

Study Population and Data Collection

The study population forms colonies in Erebus Bay (Ross Sea, Antarctica [77.62^0-77.87^0S, 166.3^0-167.0^0E]), and each reproductive female births a single pup during October-November. Females typically start breeding at age 7 or 8 and reproduce in 65% of years thereafter, but substantial disparities in reproductive frequency have been shown (Chambert et al. 2013). This population has been monitored through a mark-recapture program for more than four decades (Siniff et al., 1977). Each year, colonies are frequently visited during the pupping season to tag pups and unmarked adults, and

five to eight population surveys are conducted. During surveys, all tagged and untagged seals encountered are recorded, along with their sex and reproductive status. Since 1982, virtually every pup born in the study population has been tagged and, currently, virtually all resident females and more than 85% of adults hauling out in the area each year are marked. Each female with a pup is detected (Hadley et al. 2006), and non-reproductive females attending the study area are also highly detectable (Rotella et al. 2009). Males are also detected on the ice, but information about their reproductive contribution cannot be directly obtained from field observations. Thanks to the intensive monitoring of the population and the strong female philopatry of this species (Cameron et al. 2007; Hadley, Rotella, & Garrott 2007a), we are able to precisely track the reproductive history of locally born females and their offspring (Chambert et al. 2013; Garrott et al. 2012; Rotella et al. 2012).

Statistical Modeling

First, we investigated the potential effects of several maternal covariates and cohort size (as a surrogate of annual environmental conditions) on female offspring's probability of recruitment and age at first reproduction. As defined in this study (see below), probability of recruitment, i.e., first reproductive event, is a combination of (i) survivorship from birth to age at reproductive maturity and (ii) probability of first reproduction by age 10 conditional on having survived the juvenile period. Second, we quantified the relationship between a mother's and daughter's individual reproductive effects. These variables, denoted 'MomIRE' for mothers and 'OffspIRE' for adult female offspring, corresponded to individually varying parameters pertaining to reproductive

rates from Chambert et al. (2013). To incorporate the uncertainty associated with these parameters, we used a subset of 2,000 values picked at regular intervals from the collection of MCMC draws used to approximate their posterior distributions.

We used a Bayesian approach for inferences, based on both parameter posterior distributions and model comparison. All models were implemented in program OpenBUGS (Lunn et al. 2009), using a Gibbs sampling algorithm and Markov Chain Monte Carlo (MCMC) to sample the posterior distribution of parameters. To perform model comparison, we incorporated binary inclusion variables w_k (Link & Barker 2006; Royle & Dorazio 2008), used as multipliers on each of the k parameters. With this approach, competing models can be defined by the combination of values (0 or 1) for each w_k, given that the *kth* parameter is present in the model only when $w_k = 1$. Because vague priors were used on all regression coefficients, total prior uncertainty was maintained constant across competing models by properly scaling the variance of priors as explained by Link and Barker (2006). A uniform U(0,100) distribution was specified for total prior variance V and all regression coefficients were assigned a normal prior with mean 0 and scaled variance equal to V/K_m, where K_m is the number of parameters in model m. We assumed no prior knowledge and thus specified equal prior probability for all competing models, which resulted in a prior probability of 0.5 for each inclusion variable w_k. The posterior probabilities of competing models provided a measure of model support and allowed derivation of the posterior probabilities of each w_k. The support of a covariate was assessed from the extent to which the posterior probability of the associated inclusion parameter w_k was larger than its prior probability of 0.5. For each

analysis, we ran 2 parallel chains from different sets of initial values, had a burn-in period of 5,000 iterations, and used the subsequent 1,000,000 iterations for inference. Adequate convergence was checked using visual examination of sample path plots. We also checked that all competing models were visited during the MCMC procedure (Table 4-1).

Probability of Recruitment and Age at First Reproduction

For the analysis on probability of recruitment, the binary response variable of interest (Y) was the occurrence (Y=1) or not (Y=0) of a first reproductive event, by age 10, of a female offspring. This variable Y was modelled as a Bernoulli trial, with a probability π of recruiting by age 10. We used age 10 as a threshold age for recruitment as did Garrott et al. (2012) because more than 96% of females that ever recruited have done so by age 10. This threshold allowed us to include as many cohorts as possible while minimizing errors due to ignoring females that recruited later than the threshold. The data set of interest consisted of 1,154 females born before 2003, 283 of which had recruited by age 10 at the end of the study (2012). Age at first reproduction was considered for the sample of 283 individuals born before 2003 and recruited by age 10. As a discrete positive variable, age at first reproduction was modelled with a Poisson distribution with theoretical mean and variance λ. We rescaled the response variable by subtracting the minimum age of recruitment (age 5) from the actual age of recruitment of an individual. This discrete variable appeared adequately characterized by a Poisson random variable (min = 0, mean = 2.63, var = 1.98, Poisson dispersion test: $\chi^2 = 213$, df = 282, $P = 0.99$, dispersion estimate = 0.76).

The same set of covariates representing maternal and environmental effects was considered in both analyses. To account for environmental conditions at birth, we used the size of the cohort in which an offspring was born. This covariate (CohSize) was defined as the standardized value of the total number of pups born that year and was believed to represent a good proxy of environmental conditions, as more pups are expected to be produced when environmental conditions are favourable (Garrott et al. 2012). For maternal traits, we considered the age (MomAge) and experience (MomExp) of the mother at offspring's birth. The covariate MomAge was defined as the standardized value of true age, and its effect was modelled as quadratic, which was chosen to capture more variability than a linear trend and because it represents several alternative biologically relevant age trends (e.g., senescence effects, terminal investment). Although the experience of a female can be defined as the number of pups she previously produced, this variable is intimately connected with age. Therefore, we defined a new variable MomExp corresponding to the standardized value of experience for each specific age. The values of this metric can be defined and biologically interpreted as the relative deviation of a female's experience from the population average experience across all females still alive at a given age. A potential relationship among covariates was checked graphically (Appendix C, Fig. C1) and the absence of any apparent pattern indicated that independence could be assumed.

We first assessed the support for each of these covariates and then investigated the support for MomIRE, the covariate of primary interest. This approach allowed making inference on MomIRE conditional on a model including only relevant covariates.

The relative support for each covariate was assessed from the posterior probability of the associated inclusion parameter w_k. We also used the posterior distributions, both conditional on specific models and averaged across models (unconditional), of the regression parameters β_k associated with each covariate k to assess their support. Interaction effects of cohort size and maternal covariates on offspring vital rates have never been evidenced in this population (Hadley et al. 2007b), and given the time delay between birth and recruitment, we did not expect any such interaction on offspring recruitment. Therefore, for the ease of interpretation and because they were not of primary interest here, covariate interactions were not considered. Probability of recruitment (by age 10) π was thus modelled as follows:

$$logit(\pi) = \mu_\pi + w_{coh}.\beta_{coh}.CohSize + w_{exp}.\beta_{exp}.MomExp + w_{age}.(\beta_{age1}.MomAge + \beta_{age2}.MomAge^2)$$

Similarly, for age at first reproduction, the parameter λ of the Poisson distribution was modelled as follows:

$$log(\lambda) = \mu_\lambda + w_{coh}.\beta_{coh}.CohSize + w_{exp}.\beta_{exp}.MomExp + w_{age}.(\beta_{age1}.MomAge + \beta_{age2}.MomAge^2)$$

The support of MomIRE was conditional on the best model identified in the previous analysis step and based on the mean posterior distribution of an inclusion variable w_{IRE} and the posterior distribution of a regression parameter β_{IRE}. The models were defined as follows:

$$logit(\pi) = \theta_\pi + w_{IRE}.\beta_{IRE}.MomIRE$$

$$log(\lambda) = \theta_\lambda + w_{IRE}.\beta_{IRE}.MomIRE$$

where, θ_π and θ_λ represent the intercept (μ_π or μ_λ), relevant parameters β_k and covariates *k* of the most supported model identified in the previous step, for each analysis respectively.

Relationship Between Mother and
Offspring Reproductive Individual Effect

From a sample of 264 offspring-mother pairs, we investigated the relationship between individual reproductive effects of offspring (OffspIRE) and their mother (MomIRE), while incorporating uncertainty associated with both these variables through use of their posterior distributions, instead of single point estimates, in the analysis. For comparison, we also performed analyses using only the mean of the posterior distribution as point estimates. The relationship between the two variables was investigated by a linear regression, where OffspIRE was the response variable and MomIRE the explanatory variable:

$$OffspIRE = \beta_0 + w_{IRE}\beta_{IRE}.MomIRE + \varepsilon$$

$$\varepsilon \sim N(0, \sigma_\varepsilon)$$

As in previous models, parameters w_{IRE} and β_{IRE} correspond respectively to an inclusion and a regression slope parameters. The mean value of OffspIRE is represented by β_0 and ε is an error term with residual standard error σ_ε.

Expected Reproductive Contribution
from Different Types of Females

Simulations were used to predict the expected reproductive contribution, measured as (i) number of offspring and (ii) number of grandchildren, of females having low, average and high reproductive rates (thereafter, 'quality'). Low- and high-quality females were defined by a posterior mean MomIRE value of 2 SD below and above average, respectively. Average quality females were defined by a posterior mean MomIRE value equal to the average value in the population. We performed 20,000 simulations for each type of female, and each simulation consisted of four steps. First, the number of offspring produced over the expected post-recruitment lifespan of 9 years was simulated using individual-specific annual reproductive rates. In addition to the effect of MomIRE, reproductive rates varied by year and as a function of an individual's reproductive state the previous year and age (quadratic trend), as described in Chambert et al. (2013), and the values of associated parameters we used here corresponded to the posterior means obtained in the same study. Given that the mean age at recruitment is 7.62 years, recruitment was assumed to occur at age 8 for all females. With a post-recruitment lifespan of 9 years, the last reproductive occasion was at age 17 and each female could thus produce between a minimum of one (because all females considered here were recruited to the breeding population) and a maximum of ten offspring. These features were representative of the study population, as in our data about 75% of females had recruited by age 8, 97% were not seen alive after age 17 and 93% produced a total of 10 or fewer pups. In a second step, among the total number of offspring produced, we calculated the expected number of females using a pup sex ratio of 0.50 estimated from

the data (SE = 0.01). This sex ratio was assumed constant in the simulations because we did not find any evidence of variation among cohorts or mothers, based on their age, experience or reproductive rate. In a third step, we simulated the number of female offspring expected to recruit. Sources of variation and parameter values pertaining to recruitment probability were based on the findings of the present study (see Results; Tables 3-1 and 3-2). Finally, the expected number of grandchildren produced by these recruited female offspring was calculated using individual-specific reproductive rates similar to those used in the first step, varying as a function of reproductive state, age and individual reproductive value (estimated OffspIRE; see Results) but averaged across year conditions. Reproductive occasions were assumed to occur within the same age span (8-17) as the one used in the first step for mother's reproduction. Cumulative probabilities and distribution summary statistics, calculated from the 20,000 simulations, were used to compare the expected values of reproductive contribution among the three types of female considered.

Results

Probability and Age at Recruitment

Results of model selection from the first step of the analysis (Table 4-1) indicate that CohSize was the only covariate to receive strong support (posterior probability of inclusion = 0.988) in the analysis of probability of recruitment. The estimated relationship between CohSize and probability of recruitment was found to be positive (Table 4-2; β_{coh}: model-averaged posterior mean = 0.26, 95% CI = [0.13; 0.40]; see also Appendix C, Table C1, for model-conditional posteriors), suggesting that pups from

larger cohorts had greater chances of recruiting by age 10. The effect of CohSize is in fact quite large (Fig. 4-1) given that, over the range of cohort sizes that occurred between 1983 and 2003, values of recruitment probabilities are expected to vary from 0.19 [0.16, 0.23] to 0.34 [0.30, 0.39]. None of the other considered covariates had any substantial effect on either recruitment probability or age at first reproduction (Table 4-1). MomAge seemed to receive marginal support in the recruitment probability analysis, but we note that: (i) the posterior probability of inclusion of this covariate (0.404) was actually lower than its prior probability (0.5); and (ii) posterior distributions of both MomAge effects (β_{age1} and β_{age2}) largely overlapped zero (Table 4-2; Appendix C, Table C1). Based on these results, the only covariate included in the second step of the recruitment probability analysis was thus CohSize. Concerning age at first reproduction, as no covariate had any apparent substantial effect (Tables 3-1 and 3-2; Appendix C, Table C2), the second step of the analysis was based on the constant model, which clearly received the most support (model posterior probability = 0.827).

We found no support for a relationship between MomIRE and either probability of recruitment (posterior of w_{IRE} = 0.21) or age at first reproduction (posterior of w_{IRE} = 0.03). Prior odds of 1:1 were converted to posterior odds of (i) 3.75:1 in favour of the simple model, including only covariate CohSize, in the analysis of recruitment probability and (ii) 29.35:1 in favour of the constant model for age at recruitment. Moreover, the posterior distributions of the slope β_{IRE} associated with MomIRE clearly overlapped zero (Probability of recruitment: β_{IRE} = 0.22 [-0.12, 0.56]; Age at first reproduction: β_{IRE} = 0.01 [-0.13, 0.15], respectively). These results suggest that the

females with different reproductive rates produced pups with similar recruitment characteristics (overall probability and age of primiparity).

Relationship Between Individual Reproductive Effects of Mother and Offspring

We found suggestive support for a positive relationship between MomIRE and OffspIRE, as the posterior probability of inclusion of MomIRE (w_{IRE} = 0.65) was larger than its prior probability of 0.5. The estimated regression slope β_{IRE} was relatively weak (mean = 0.05), but the estimated 95 % credible interval (0.04; 0.06) included only positive values, which is evidence of a positive relationship. We also emphasize that the uncertainty in MomIRE and OffspIRE values was fully taken into account here, resulting in conservative estimates of the relationship. Indeed, a regression analysis based on the posterior means of MomIRE and OffspIRE (i.e., with no uncertainty associated; Fig. 4-2a) provides a larger estimate of the regression slope (0.12 [0.03, 0.21]) and good support for the effect of MomIRE (P = 0.008). We also note the estimated correlation (standardized regression slope; Fig. 4-2b) between the two variables is 0.16 [0.04, 0.28]. Furthermore, a closer look at OffspIRE values or offspring from the same mothers (represented by vertical lines in Fig. 4-2) reveals that mothers with a high MomIRE tend to consistently produce pups with a high OffspIRE. This pattern is however not very strong, given that many vertical lines cross the averaged regression line, further supporting the idea of a low, but non-null, heritability of reproductive rates.

Expected Reproductive Contribution
from Different Types of Females

In the simulations, we included only the covariate effects found to be relevant in the statistical analyses described above. Therefore, offspring age at recruitment was assumed to be constant among females and cohorts given that none of the covariates we considered received any support. For recruitment probability, the estimated effect of cohort size (β_{coh} = 0.26) was included (Table 4-2). To depict realistic annual variability, standardized values of cohort size, and corresponding reproductive year effect, were randomly drawn from the observed distribution. Finally, because we found support for a weak correlation between OffspIRE and MomIRE, offspring individual effects were calculated from the mother's value MomIRE using the posterior means of regression coefficients (β_0= -0.02; β_{IRE} = 0.05) and were applied to offspring reproductive rates.

Substantial differences in expected number of descendants among females of different quality were found (Tables 3-3 and 3-4). A female with a high reproductive rate is expected to produce 2.0 times as many recruited females and 2.1 times as many grandchildren as a female with a low reproductive rate. Indeed, although stochastic variation is quite large (Table 4-3), the number of grandchildren expected to be produced through the female progeny is 3.6, 5.8 and 7.5 for females with low, average and high reproductive rates, respectively. The distribution of number of grandchildren (Fig. 4-3) is zero-inflated and multimodal because it corresponds to a mixture of distributions for each possible realized value for the number of recruited female offspring (0, 1, 2, 3 …) produced by the grandparent female. The quantiles of the distribution (Table 4-3) and upper tail probabilities (Table 4-4, Fig. 4-4), which are more appropriate statistics in the

case of such a multimodal distribution, also provide support for substantial differences among females. In particular, the probability of having no grandchildren is 76% higher for a low-quality female (0.58) relative to that for a high-quality female (0.33). Further, the chances of having a large number of grandchildren are much greater for a high quality female (Table 4-4, Fig. 4-4). For instance, the probability of having ≥ 10 grandchildren is about three times larger for a female of high quality (0.29) than for one of low quality (0.10), and for the probability of having ≥ 20 grandchildren this relative difference in odds reaches 7:1 (0.07 *vs.* 0.01). Overall these simulation results suggest that observed levels of individual heterogeneity in reproductive rates translate into substantial differences in terms of number of grandchildren expected to be produced through the female progeny.

Discussion

Environmental and Maternal Influences on Offspring Recruitment

Offspring recruitment was more influenced by cohort size than any of the maternal traits considered (age, experience and reproductive rate). Although birth cohort conditions did not appear to affect age at recruitment, it was positively related to recruitment probability. Interestingly, cohort effects on recruitment rates have been suggested to be mainly linked to environmental conditions prevailing during in utero foetal development rather than after birth (Garrott et al. 2012). It is likely these early-life conditions influence recruitment rates primarily by affecting survival at very young ages, when seals are the most vulnerable and mortality is the highest (Rotella et al. 2012),

although cohort effects on pre-recruitment survival appear to persist for approximately 6 years after birth (Stauffer, Rotella, & Garrott 2013). We did not find any influence of maternal age and breeding experience on offspring's recruitment probability and recruitment age. Evidence of a negative influence of mother's age on the probability of offspring recruitment conditional on survival was reported previously (Hadley et al. 2007b). However, the same study also found that pre-recruitment survival was affected by maternal age in the opposite direction and therefore tended to be higher in offspring born to older females. Because in our analysis, the recruitment variable was unconditional on survival, it is probable that these two opposite maternal effects cancelled each other out yielding no difference in overall recruitment chances. Regarding the lack of influence of maternal experience, our findings are in accordance with previous studies on this population (Hadley et al. 2007b). The novelty of our approach was to standardize the values of reproductive experience by age to eliminate the correlation between these two covariates. Despite this effort of standardization, we still did not detect any effect, which strengthens previous conclusions (Hadley et al. 2007b).

Overall, cohort effects seemed to have a larger influence on recruitment than maternal age and experience. Studies directly comparing the effect of environment at birth versus maternal traits on offspring recruitment are scarce, but a similar pattern to what we report here has been found in other large mammals (e.g., bighorn sheep *Ovis canadensis :* Jorgenson et al. 1993; moose *Alces*: Sæther & Heim 1993). In birds and mammals, persistent influences of early-life environment on offspring survival and future reproduction are often mediated by parental conditions (Lindström 1999). Therefore,

environmentally driven maternal traits, as well as maternal care and behaviour, could still have important effects on offspring success (Maestripieri & Mateo 2009).

Offspring recruitment also appeared independent of maternal reproductive rates. Individual trade-offs between offspring number and quality are theoretically predicted (Smith & Fretwell 1974; Stearns 1992) and have been demonstrated in a broad range of taxa (Schroderus et al. 2012), including several primates and also humans (Gillespie, Russell, & Lummaa 2008; Walker et al. 2008). Our result does not necessarily indicate the absence of such a trade-off at the individual level in Weddell seals, but rather suggests among-female variation in resource acquisition (Van Noordwijk & De Jong 1986). Larger variation in reproductive frequency versus offspring quality implies that females engage in reproduction only with sufficient resources to successfully rear their pup. A similar conservative maternal care strategy exists in ungulates (Albon, Mitchell, & Staines 1983; Sand 1996) and is likely a common feature of species with low potential fecundity and high maternal investment (Erikstad et al. 1998).

Relationship Between Mother and Offspring Reproductive Rates

We found evidence for a positive, but weak correlation between reproductive rates of mothers and their female offspring. This result suggests weak heritability of this fitness-related trait and is in accordance with theoretical predictions (Charlesworth 1987; Fisher 1958), as well as previous empirical evidence in *Drosophila* (Roff & Mousseau 1987), collared flycatchers *Ficedula albicollis* (Gustafsson 1986) and 75 other wild populations of vertebrates and invertebrates (Mousseau & Roff 1987). The low heritability in female reproductive rates could also be linked to the fact that it is a

complex trait determined by a multitude of phenotypic characteristics not necessarily heritable and heavily influenced by the environment, as shown in red deer *Cervus elaphus* (Kruuk et al. 2000). When considering that only about 24% of all female seals ever born survive the pre-recruitment period, it is noteworthy that we still detected some heritability in this subset of 'good quality' individuals which already went through a strong selective filter (pre-recruitment survival).

Evolutionary Perspective of Heterogeneity in Reproductive Rates

Despite substantial stochastic variability, simulations reveal important differences in the expected number of grandchildren, produced via female progeny, among females with contrasting reproductive rates. Higher expected number of grandchildren result from higher frequency of reproduction, no difference in offspring recruitment and a slight heritability of reproductive rates. Together, our results indicate that maternal fitness is more influenced by the number than the quality of offspring produced. Similar patterns have been found in other mammal species with expanded maternal care. For instance, in Eurasian red squirrels (*Sciurus vulgaris)*, a mother's fitness is mainly explained by the number of litters she produces and is directly linked to her access to food resources (Wauters & Dhondt 1995). In pre-industrial humans (Gillespie et al. 2008), maternal fitness was shown to be positively related to fecundity in resource-rich families but not in resource-poor families, indicating that producing more children was a good strategy only for mothers having access to sufficient resources. The capacity for higher frequency of reproduction in female Weddell seals is also likely linked to their ability to access resources, presumably prey (Hadley et al. 2007b). Varied resource acquisition is also

expected to affect offspring quality (Smith & Fretwell 1974) and might similarly influence pup provisioning among mothers and therefore pup's condition at weaning (Wheatley et al. 2006). The lack of offspring recruitment variation among mothers could be a consequence of the stochasticity of post-weaning offspring's survival (Stauffer et al. 2013) negating maternal investment differences.

A major limitation in our study regarding conclusions about fitness is the non-integration of the reproductive contribution of male progeny. In polygynous species, male reproductive success can greatly vary and maternal investment of high-quality mothers is expected to be higher in sons (Trivers & Willard 1973). However, because Weddell seals display low sexual dimorphism and relatively low variation in male reproductive contribution for a polygynous species (Harcourt et al. 2007), the fitness differences among sexes, and therefore, the potential bias in maternal investment are probably small (Hewison & Gaillard 1999). Despite this limitation, our findings regarding heritability and cross-generational effects of female reproductive rates represent a first important step in better understanding the fitness consequences, and more broadly, the evolutionary significance of individual reproductive heterogeneity. To pursue this effort, future studies will need to decipher the role of differential maternal investment between male and female progeny, male reproductive contribution and potential heterogeneity in survival.

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Table 4-1. Model selection results from the first step of analyses of offspring probability of recruitment and age at first reproduction.

Model	Probability of Recruitment		Age at First Reproduction	
	Model Posterior Probability	MCMC Sample Size*	Model Posterior Probability	MCMC Sample Size*
Constant	0.009	18336	0.827	1653290
CohSize	0.555	1109849	0.068	136878
MomExp	0.000	513	0.086	171494
MomAge	0.003	5574	0.008	15163
CohSize + MomExp	0.032	63206	0.008	15667
CohSize + MomAge	0.354	707846	0.002	3815
MomExp + MomAge	0.000	595	0.001	2902
CohSize + MomExp + MomAge	0.047	94081	0.000	791

Covariate	Posterior Probability of Covariate Inclusion	
	Probability of Recruitment	Age at First Reproduction
Mother Age	0.404	0.011
Cohort Size	0.988	0.079
Mother Experience	0.079	0.095

The top part of the table shows the posterior probability of each competing model, while the bottom part shows the posterior probability of inclusion of each covariate. Note that non-informative priors were assumed, such that each covariate had a prior probability of inclusion of 0.5 and the prior model probabilities were equal among all competing models (0.125). The covariates considered were cohort size (CohSize), mother age (MomAge) and mother experience (MomExp) at the time of offspring birth.
*MCMC Sample Size corresponds to the number of MCMC draws, among 1,000,000 iterations, in which the model was picked. We see that all models were explored during the MCMC procedure. Models with better support were logically explored more often.

Table 4-2. Summary of parameter posterior distributions from analyses of offspring recruitment probability and age at first reproduction.

Parameter	Probability of recruitment			Age at first reproduction		
	mean	LCI	UCI	mean	LCI	UCI
β_{coh}	0.26	0.13	0.40	0.06	-0.01	0.14
β_{exp}	0.05	-0.08	0.17	-0.07	-0.14	0.00
β_{age1}	0.00	-0.54	0.47	0.14	-0.06	0.32
β_{age2}	-0.31	-0.73	0.08	0.05	-0.13	0.21

The mean, lower (2.5% quantile) and upper (97.5% quantile) limits of a 95% credible interval (LCI and UCI, respectively) are shown. Parameters are regression coefficients associated to the covariates considered in the models: cohort size (β_{coh}), mother experience (β_{exp}) and a first- (β_{age1}) and second-order (β_{age2}) mother age effects. Posterior summaries presented here are averaged across competing models (see Table 1) and therefore incorporate model uncertainty. We note that for all parameters model-conditional posterior distributions (see Appendix C, Tables C1 and C2) were similar to the model-averaged ones.

Table 4-3. Summary statistics of simulation results.

Distribution summaries	Expected number of offspring		
	Low Quality	Average	High Quality
Mean	4.4	6.9	8.8
SD	1.3	1.3	1.0
Quant. 2.5%	2	4	7
Quant. 97.5%	7	9	10

Distribution summaries	Expected number of grandchildren (from female progeny)		
	Low Quality	Average	High Quality
Mean	3.6	5.8	7.5
SD	5.0	6.3	7.2
Quant. 2.5%	0	0	0
Quant. 97.5%	16	21	24

The expected number of offspring (top) and grandchildren (bottom) were simulated for three types of parent females defined by their rate of reproduction and denoted as low (2SD below average), average and high (2SD above average) quality (see Material and Methods for details). The expected number of grandchildren concerns only offspring produced through the female progeny of the grandparent female. The distribution summaries shown are the mean, standard deviation (SD) and the 2.5% and 97.5% quantiles (Quant.).

Table 4-4. Upper tail probabilities of the expected number of grandchildren for each type of female.

Number of grandchildren	Low Quality female	Average Quality female	High Quality female	Relative difference $(P_{HQ}-P_{LQ})/P_{LQ}$
None	0.58	0.42	0.33	-43%
≥ 1	0.42	0.58	0.67	58%
≥ 5	0.41	0.57	0.66	61%
≥ 10	0.10	0.21	0.29	192%
≥ 15	0.04	0.11	0.17	305%
≥ 20	0.01	0.04	0.07	638%

Three types of grandparent female are defined based on their rate of reproduction, respectively denoted as low (2SD below average), average and high (2SD above average) quality (see Material and Methods for details). The relative difference is calculated as the proportional change in probability for the high quality (HQ) female relative to the low quality (LQ) female (Relative difference = $(P_{HQ}-P_{LQ})/P_{LQ}$). All the metrics shown were obtained from simulation results.

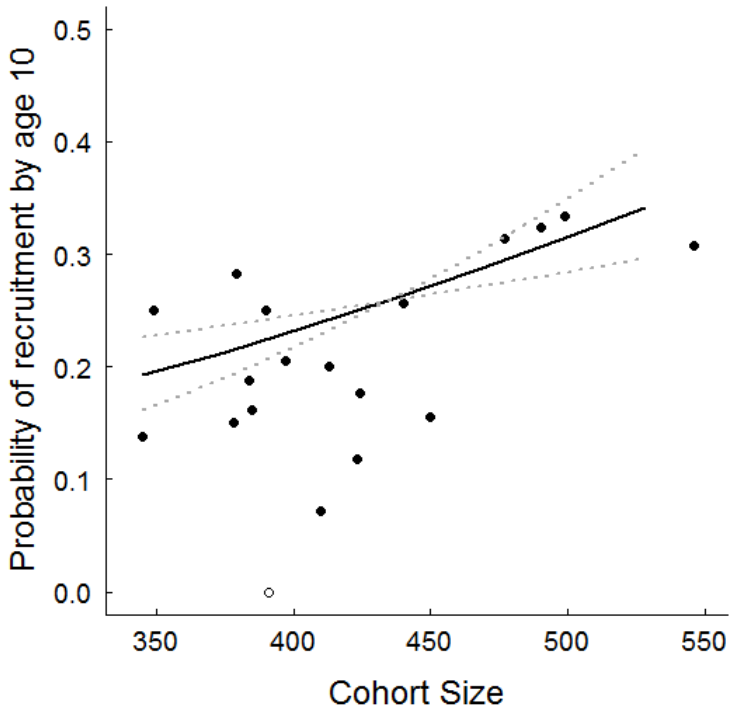

Figure 4-1. Observed and estimated relationship between birth cohort size and probability of recruitment by age 10.
The size of a cohort is defined as the total number of pups born in that particular year. From the estimated trend (β_{coh}: model-averaged posterior mean = 0.26, 95% CI = [0.13; 0.40]), values of recruitment probabilities are expected to vary from 0.19 [0.16, 0.23] to 0.34 [0.30, 0.39] across the range of cohort sizes observed between 1982 and 2003 (represented on the graph). The points represent the observed proportion of seals from each cohort that recruited by age 10. We note that the outlier value (proportion = 0.0; open circle) is due to a small sample size effect (n = 2) and do not represent the true recruitment proportion of the corresponding cohort (1983). The black solid line represents the estimated mean trend, while the grey dotted lines represent the 95% credible interval (2.5% and 97.5% quantiles).

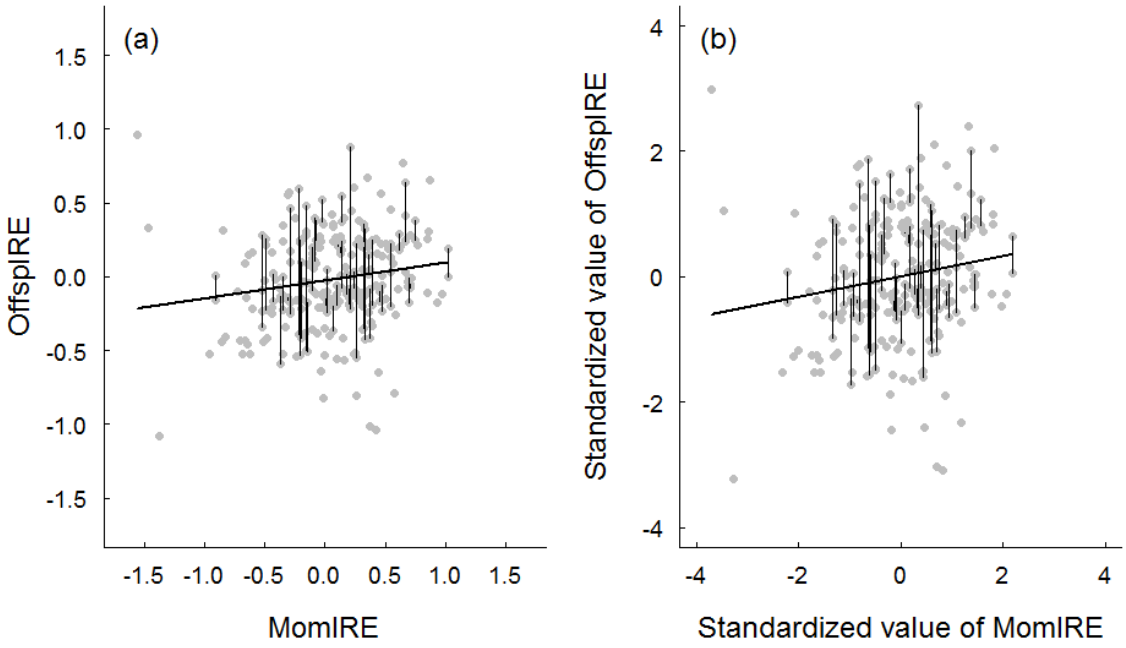

Figure 4-2**.** Relationship between mother and offspring estimated individual effects pertaining to reproductive rates.
(a) Plot of the posterior means of OffspIRE against MomIRE, with the estimated regression slope ($\hat{\beta}_{IRE} = 0.12$) represented by the black line. (b) Plot of the standardized posterior means of OffspIRE against MomIRE, with the estimated correlation slope (0.16) represented by the black line. Points pertaining to a same mother are linked by a vertical line. Most vertical lines cross the regression line, suggesting independence between mother and offspring, but several mothers with a high MomIRE seem to consistently produce pups with a high OffspIRE. This intermediate pattern of independence/non-independence is in accordance with the low heritability estimated.

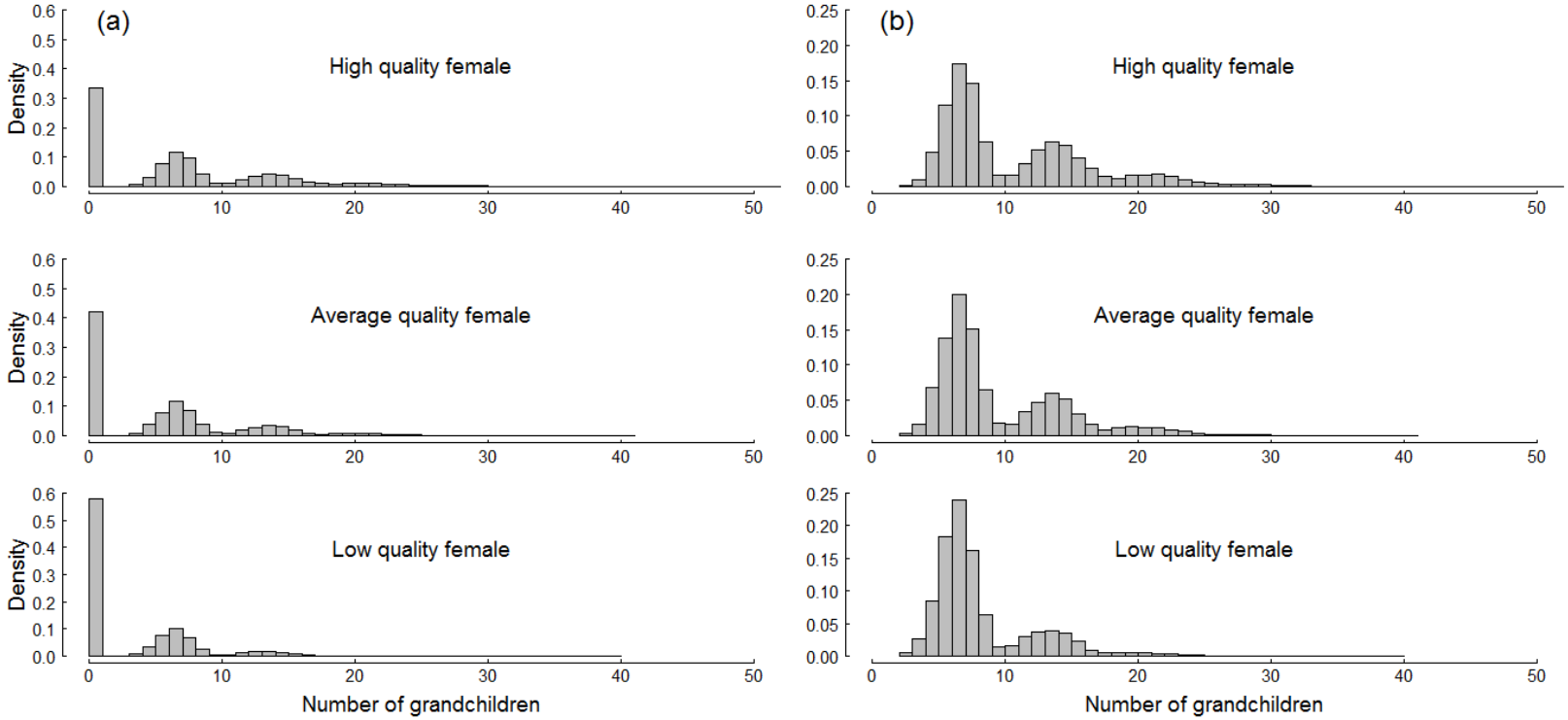

Figure 4-3. Histogram of the expected number of male and female grandchildren (x-axis), produced through the female progeny, for the 3 types of grandparent females considered (low, average and high quality).
(a) Full histogram including the density at x = 0; (b) histogram excluding density at x = 0 for a better readability of the distribution at x > 0. The distributions are zero-inflated (left panel) and multimodal because the number of grandchildren is determined by the realized number of recruited female offspring, which takes discrete values (0, 1, 2, 3 …). Therefore, the expected number of grandchildren corresponds to a mixture of distributions around each possible discrete value of recruited offspring.

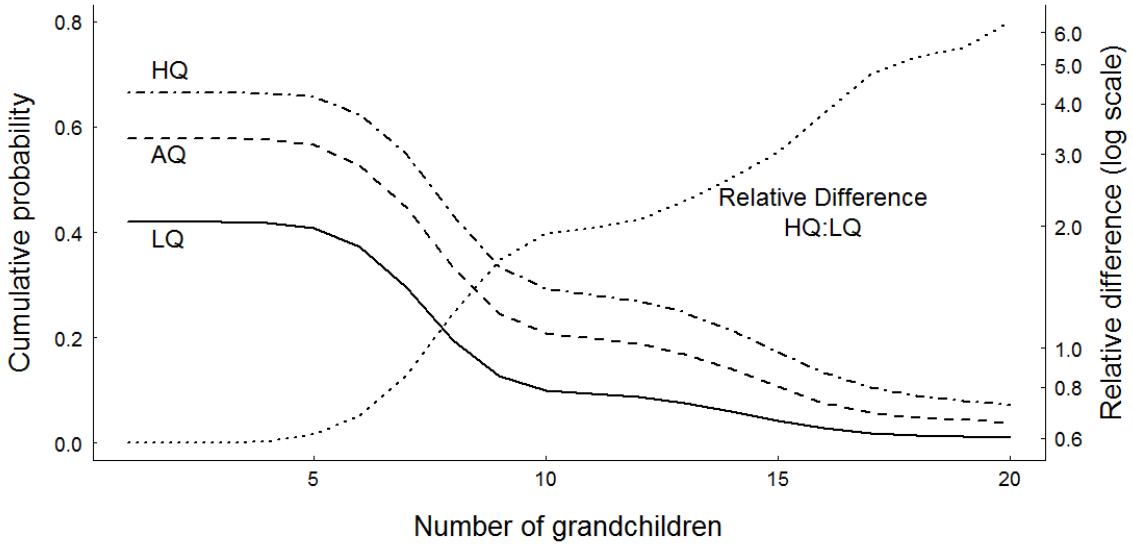

Figure 4-4. Upper tail probabilities of increasing expected number of grandchildren [Pr(x≥N)], for each type of female and relative difference in these probabilities between high and low quality females.
Tail probabilities are displayed as smoothed curves over the range of possible number of grandchildren (x-axis). The three types of female considered vary in terms of reproductive rates and are denoted as high quality (HQ), average quality (AQ) and low quality (LQ). The relative difference is defined as the proportional change in probability for the high quality female relative to the low quality female ($[Pr_{HQ}-Pr_{LQ}]/Pr_{LQ}$). These results were obtained from simulations.

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CHAPTER FIVE

CONCLUSION OF THE DISSERTATION

This dissertation addressed several aspects of environmental and individual variability in a population of Weddell seals breeding in Erebus Bay, Antarctica. Overall, I showed these two types of variation are prevalent and equivalently important features of the population reproductive output. Individual heterogeneity appears to be responsible for as much variation in reproductive rates as temporal fluctuations of the environment. This result has important implications for future demographic analyses on this population as it reveals that individual variation should not be ignored to accurately estimate reproductive rates and underlying individual trade-offs (Weladji et al. 2008). For instance, by explicitly including individual variation in the mark-recapture model, I was able to detect an important cost of reproduction that had never previously been shown (Hadley et al. 2007b).

The mechanisms underlying individual heterogeneity in female reproductive rates in this population remain unknown. The existence of physiological or physical differences directly affecting female fecundity (Atkinson 1997) could explain some of this variation, but phenotypic differences affecting resource acquisition are more likely. In Weddell seals, reproduction requires important maternal investment (Boness and Bowen 1996), so any trait affecting a female's ability to forage efficiently (Williams et al. 2004, Costa et al. 2004, Hindle and Horning 2010) and build body mass reserve is likely an important determinant of her success (Proffitt et al. 2007, Wheatley et al. 2008).

This hypothesis of substantial variation in resource acquisition (Van Noordwijk and De Jong 1986) is also supported by the absence of any apparent trade-off, expressed at the population level, between a female's frequency of reproduction and the recruitment rate of her female offspring (see chapter 4). Because such a trade-off between offspring quantity and quality probably exist at the individual level (Roff 1992, Stearns 1992), females reproducing more often than others must support that effort with additional energy intake to produce offspring of average quality (Reznick et al. 2000). Under this assumption of important individual variability in resource acquisition, individual differences in reproductive performance are likely amplified under limited resource conditions. The iceberg perturbation in the Ross Sea from 2001 to 2005 had negative cascading impacts on the regional trophic system (Arrigo et al. 2002, Seibel and Dierssen 2003) probably affecting food resource availability for seals and, therefore, it represented an interesting natural experiment to address this prediction. First, I found that female reproductive rates were substantially reduced during the five-year iceberg event, while survival remained unchanged (chapter 2). This result was in accordance with theoretical predictions (Pfister 1998, Morris and Doak 2004) for such a long-lived species (Rotella et al. 2012). Female seals likely suffered unusual resource limitation forcing them to allocate a larger ratio towards survival at the expense of reproduction. Second, I found mild evidence that the expression of individual reproductive heterogeneity increased during this extreme event (chapter 3). While firm conclusions cannot be drawn, this last result suggests individual heterogeneity may be amplified when resource limitations intensify.

The finding of substantial intrinsic individual variation in a population naturally raises the question of its evolutionary significance, as such variability represents the raw material of natural selection (Endler 1986). For adaptive evolution to occur, phenotypic variability must be heritable and correlate to fitness variation. I addressed both aspects of variation in female reproductive rates (chapter 4), initially by showing the independence of mother reproductive rates from female offspring recruitment probability and age. Consequently, reproductive rates appeared to positively affect the number of grandchildren born to the female progeny, indicating the potential for a direct influence on a female's fitness. An important limitation of this analysis is the non-integration of the reproductive contribution of male progeny, which can actually be a major source of fitness variation for mothers. Indeed, in a polygynous species like the Weddell seal (Stirling 1969), there usually is a large variability of reproductive contribution among males, such that a mother benefits from producing males of high quality (Trivers and Willard 1973, Clutton-Brock 1991, Hewison and Gaillard 1999). Next, I found a positive, but weak, correlation between reproductive rates of mothers and their female offspring, indicating some degree of heritability. Low heritability was not surprising because such fitness-related traits are expected to retain low additive genetic variance (Charlesworth 1987), as a result of historical selective processes acting in wild populations (Kruuk et al. 2000). Taken together, substantial individual variability, relationship to fitness and heritability of female reproductive rates suggest that natural selection might be acting in this seal population, although the selective pressure is probably very low.

This work suggests several avenues for future investigations. The ecological and demographic roles of bottom-up (Arrigo and Thomas 2004) versus top-down biotic processes (Arrigo and Thomas 2004, Ainley et al. 2006, 2007), as well as physical mechanisms related to sea-ice dynamics (Arrigo et al. 2002), clearly need continuing investigation. In particular, identifying limiting resources for Weddell seals will be important to thoroughly understand the causes of both temporal and individual variability observed in this population. Analyzing available mass and behavioral data will also provide critical insights about phenotypic traits associated with individual variation. Finally, future studies should address variation in male reproductive contributions (e.g., using genetic data) and the genetic determinants of heritability to advance our understanding of the evolutionary consequences of individual heterogeneity.

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APPENDICES

APPENDIX A

SUPPLEMENTARY MATERIAL OF THE SECOND CHAPTER

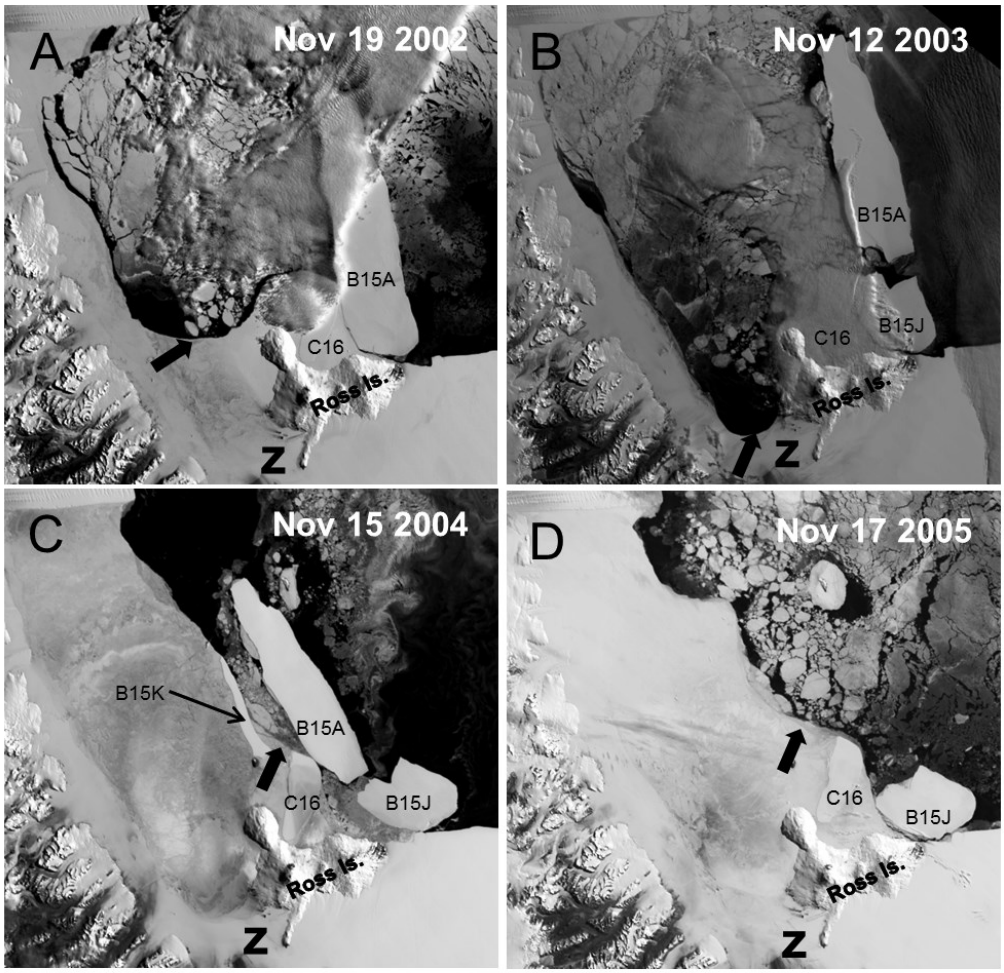

Figure A1. Configuration of the sea-ice in mid-November (Antarctic spring) for four of the iceberg years: A. year 2002; B. year 2003; C. year 2004; and D. year 2005. Seal colonies are located next to the Ross Island and are indicated by a "Z" on images. The location of the ice edge (i.e., limit between sea-ice and open water) is indicated by the big bold arrow. It is worth noting that the ice edge was very far from seal colonies in 2004 and 2005, relatively far from them in 2002 also, but very close to them in 2003 (year when abundance of seals at colonies was surprisingly high). The presence of the four icebergs (B-15A, B-15J, B-15K and C-16) is also indicated. Three of these icebergs are fragments of B-15 (B-15A, B-15J and B-15K), and the iceberg C-16 was formed in 2000 by the collision of B-15A with the ice front.
Source: National Snow and Ice Data Center, University of Colorado, Boulder (http://nsidc.org/data/iceshelves_images/ross_west.html).

Text A1. Model selection procedure of the multi-state modelling of vital rates

The multi-state mark-recapture modelling of vital rates was based on previous results and recent analyses for this population (Hadley et al. 2006, 2007b, Rotella et al. 2012). Using the Akaike Information Criterion (AIC) corrected for sample size (AICc) and overdispersion (QAICc), we confronted and evaluated several relevant combinations of multi-state structures identified in these previous analyses. Multi-state models include three types of parameters: (i) apparent survival probability (ϕ); (ii) detection probability (p); and (iii) transition probability (ψ), conditional on survival, from one state to another. Four breeding states were considered: (i) pre-breeder (P); (ii) first-time breeder (F); (iii) experienced breeder (E); and (iv) skip-breeder (S). Recruitment was defined as the transition from state P to F (ψ^{PF}) and reproduction as transition from state F, E or S to state E (ψ^{FE}, ψ^{EE}, ψ^{SE}). The following transitions are impossible and were thus fixed to zero in analyses: ψ^{PE}, ψ^{PS}, ψ^{FP}, ψ^{FF}, ψ^{EP}, ψ^{EF}, ψ^{SP}, ψ^{SF}.

The following age structure was considered for females in state P [1]: three age classes for parameter ϕ (newborn, yearling, ≥2 years old); $\phi_{newborn}$ represents survival from birth year to 1 year old, $\phi_{yearling}$ represents survival from 1 year old to 2 year old, and $\phi_{\geq 2}$ represents annual survival, for an individual in state P, from any age ≥2 to any age > 2;four age classes for p (1, 2, 3 to 6, ≥7 years old) and seven age classes for ψ (5, 6, …, 10, ≥11 years old). No age structure was considered for other states and detection probability was constrained to be the same for first-time and experienced breeders (Hadley et al. 2006, 2007b, Rotella et al. 2012). Because our primary interest was on temporal variation of ϕ*'s* and ψ*'s* and according to previous analyses' results (Rotella et al. 2012), we considered annual variation in these two parameters and tested for both additive and interactive effects of year among states and among pre-breeder age classes.

In this analysis, we used data of known-age and unknown-age females that were tagged from 1982 forward. For unknown-age females, as we do not know the entire breeding history, states P and S cannot be unambiguously assigned before a first reproduction event is observed. Moreover, for the first reproductive event observed, one cannot disentangle states F and E. Therefore, the encounter history of unknown-age individuals started the next observation following the first observed breeding event (i.e., when only states E or S were possible).

The relevant goodness-of-fit tests performed in program U-CARE indicated a modest level of overdispersion in the data ($\hat{c}$ = 1.67). We used this $\hat{c}$ value as a variance inflation factor and to convert AIC_c values to $QAIC_c$ values prior to conducting model selection. Estimates of vital rates were based on the most-supported model of a model suite (Table S1) that evaluated various scenarios of temporal variation (i.e., interactive or additive effects) for survival, recruitment and reproduction parameters. In the most-supported model, the pattern of annual variation (on the logit scale) in ϕ and ψ was shared (additive structure) among all age classes for pre-breeders (but effects for ϕ were separate from effects for ψ). Similarly, annual variation in ϕ and ψ was shared among recruited individuals, i.e., among females in states F, E and S. Patterns of annual variation were however allowed to differ for pre-breeders and recruited individuals.

Table A1. Model selection results of the multistate approach used for vital rates estimates.

Model Structure			Num. Par.	QAICc	ΔQAICc	QAICc Weight
Detection	Survival	Transition				
(P(a4),S)+yr, (F,E)(.)	P(a3+yr), (F,E,S)+yr	P(a7+yr), (F,E,S)+yr	152	21872.11	0.00	1.00
(P(a4),S)+yr, (F,E)(.)	P(a3+yr), (F,E,S)+yr	P(a7+yr), F(yr), E(yr), S(yr)	200	21923.27	51.16	0.00
(P(a4),S)+yr, (F,E)(.)	P(a3+yr), F(yr), E(yr), S(yr)	P(a7+yr), F(yr), E(yr), S(yr)	247	21970.60	98.49	0.00
(P(a4),S)+yr, (F,E)(.)	P(a3+yr), F(yr), E(yr), S(yr)	P(a3+yr), F(yr), E(yr), S(yr)	243	21975.99	103.88	0.00
(P(a4),S)+yr, (F,E)(.)	P(a3+yr), F(yr), E(yr), S(yr)	P(a3*yr), F(yr), E(yr), S(yr)	286	22015.37	143.26	0.00
(P(a4),S)+yr, (F,E)(.)	P(a3+yr), F(yr), E(yr), S(yr)	P(a7*yr), F(yr), E(yr), S(yr)	364	22091.68	219.57	0.00
(P(a4),S)+yr, (F,E)(.)	P(a3*yr), F(yr), E(yr), S(yr)	P(a7*yr), F(yr), E(yr), S(yr)	415	22138.40	266.29	0.00
P(a4+yr), (F,E)(.), S(yr)	P(a3*yr), F(yr), E(yr), S(yr)	P(a7*yr), F(yr), E(yr), S(yr)	440	22185.99	313.88	0.00

The structure of each parameter (detection, survival and transition probabilities) is given for the eight models evaluated. Four individual states are considered: P (pre-breeder), F (first-time breeder), E (experienced breeder) and S (skip-breeder). The sources of variation are: (i) state; (ii) year ('yr'); and (iii) age, for state P only. Age effects are denoted as follows: a3 indicates a three-class age effect (newborn, yearling and ≥2 years old), a4 indicates a four-class age effect (1, 2, 3 to 6, ≥7 years old) and a7 indicates a seven-class age effect (5, 6, 7, 8, 9, 10, ≥11 years old). Interactive effects are denoted by '*' entries, additive effects by '+' entries and constant parameters by '.' (dot) entries. When two states are inside the same parentheses, it means that they share a common year additive effect (e.g., '(F,E,S)+yr' means that states F, E and S are different but share the same year effect).

Table A2. Estimates of mean local abundance, for the different population components, for the two sets of years: (i) non-iceberg years (1982-2000 & 2006-2010); and (ii) iceberg years (2001-2005). Standard errors (SE), as well as 95% lower (LCL) and upper (UCL) confidence limits are provided.

Population component	Non-iceberg years				Iceberg years			
	Mean	SE	95% LCL	95% UCL	Mean	SE	95% LCL	95% UCL
Total population	751.6	22.2	708.1	795.1	572.8	122.3	333.0	812.5
Breeders	411.1	13.7	384.1	438.0	292.3	41.7	210.6	374.0
Skip-breeders	146.9	8.8	129.6	164.1	158.5	43.5	73.2	243.8
Pre-Breeders	192.8	13.6	166.0	219.5	119.4	58.6	4.5	234.2

Table A3. Estimates of annual local abundance obtained after shrinkage. Standard errors (SE) correspond to root mean square errors (*rmse*) of shrunk estimates.

Year	Total abundance		Pre-breeders		Breeders		Skip-breeders	
	estimate	SE	estimate	SE	estimate	SE	estimate	SE
2010	867.4	8.3	120	5.7	575	1.7	172.5	5.8
2009	866.5	11.5	164.8	8	478.8	1.2	222.5	8.1
2008	586.8	6	73.3	4	342	1.5	171.5	4.2
2007	958.9	9.4	214.6	6.4	549.6	2	194.7	6.5
2006	625.2	3.3	112.9	2.9	402	0	110.4	1.7
2005	480.6	5.3	105.5	3.1	238.7	2.4	136.5	3.4
2004	290	2.1	31.4	1.5	158	0	100.6	1.4
2003	1028.9	24.2	349.8	17.6	340.3	1.6	329.9	18
2002	552.6	5.9	50	3.8	391.7	2.2	111.1	4
2001	520.9	9.4	67.4	8.5	332.9	1.5	120.9	3.4
2000	773.7	7.5	184	5.6	455.5	0	134.3	5
1999	781.4	12.1	187.4	8.6	459	0.8	135.2	8.4
1998	671.7	4.6	125.2	3.5	459.5	0	87.1	3
1997	820.3	6.6	193.8	4.8	518.5	0	108.2	4.5
1996	770.9	23	261.4	16.3	340.7	1.4	166.8	15.5
1995	748.8	12	235.3	8.6	366.5	0	146.8	8.3
1994	608.3	19.1	149.5	13.4	354	0	105.8	13.2
1993	650.3	5.6	144.6	4.2	422.5	0	83.4	3.7
1992	658.2	24.9	195.7	17.4	319.5	0	142.3	16.9
1991	697.3	8.6	181.5	6.2	405	0	111	5.9
1990	683.4	9.2	169.3	6.6	409	0	105.4	6.3
1989	742.4	19.6	226.8	13.8	345.9	3.2	168.6	13.2
1988	912	20.1	336.3	14.3	397.5	0	176.4	13.8
1987	743.9	10.1	232.2	8	382.4	1.5	129.2	6
1986	647.9	6.9	140.3	4.8	381	0	126.7	4.9
1985	689.4	15.9	165.1	11.2	395.5	0	129.3	11
1984	873.8	14.6	306.4	10.3	370.8	1.4	195.4	10.1
1983	951.2	19.8	327.3	13.7	365.5	0	254.4	14.3
1982	706.7	21.2	183.1	14.7	369.8	1.5	153.4	14.7

Table A4. Estimated process standard deviation ($\hat{\sigma}_{process}$) of the size of the different population components for four sets of years: (i) non-iceberg years (1982-2000 & 2006-2010) vs. (ii) iceberg years (2001-2005); (iii) before iceberg period (1982-2000) vs. (iv) after iceberg period (2001-2010). LCL and UCL respectively represent the lower and upper limits of the 95% confidence interval of the estimated $\hat{\sigma}_{process}$.

Set of years	Total population			Breeders			Skip-breeders			Pre-breeders		
	$\hat{\sigma}_{process}$	LCL	UCL	$\hat{\sigma}_{process}$	LCL	UCL	$\hat{\sigma}_{process}$	LCL	UCL	$\hat{\sigma}_{process}$	LCL	UCL
Non-iceberg	107.9	83.4	151.9	67.3	52.3	94.4	42.0	32.1	59.7	66.1	50.9	93.3
Iceberg	274.5	163.7	790.6	93.2	55.8	267.8	98.8	58.0	286.5	131.8	78.0	380.9
Before	92.1	68.7	137.4	49.6	37.4	73.3	40.0	29.3	60.5	61.9	46.1	92.4
After	239.5	164.4	437.7	129.8	89.3	237.0	71.2	48.1	131.6	94.9	64.5	174.5

Table A5. Estimates of mean vital rates for the two sets of years: (i) non-iceberg years (1982-2000 & 2006-2010); and (ii) iceberg years (2001-2005). The relative difference between the two periods (i.e., change of mean during the iceberg period relative to the non-iceberg period) is also provided and 95% lower (LCL) and upper (UCL) confidence limits for all these estimates are shown.

Parameter	Non-iceberg years			Iceberg years			Relative Difference		
	Estimate	LCL	UCL	Estimate	LCL	UCL	Estimate	LCL	UCL
ϕ^{P}_{yearl}	0.42	0.34	0.49	0.4	0.27	0.52	-0.04	-0.39	0.3
$\phi^{P}_{a\geq 2}$	0.95	0.93	0.96	0.94	0.91	0.96	-0.01	-0.04	0.02
ϕ^{F}	0.95	0.93	0.97	0.94	0.91	0.97	-0.01	-0.04	0.03
ϕ^{E}	0.9	0.87	0.92	0.88	0.83	0.92	-0.02	-0.08	0.04
ϕ^{S}	0.91	0.89	0.93	0.9	0.87	0.94	-0.01	-0.06	0.03
Ψ^{FE}	0.52	0.46	0.58	0.33	0.24	0.41	-0.37	-0.55	-0.19
Ψ^{EE}	0.69	0.65	0.73	0.5	0.42	0.58	-0.27	-0.39	-0.15
Ψ^{SE}	0.69	0.65	0.73	0.5	0.42	0.57	-0.28	-0.4	-0.16
Ψ^{PF}_{a5}	0.03	0.01	0.04	0.01	0	0.02	-0.59	-1.07	-0.12
Ψ^{PF}_{a6}	0.2	0.16	0.24	0.09	0.03	0.15	-0.56	-0.88	-0.24
Ψ^{PF}_{a7}	0.37	0.31	0.44	0.19	0.09	0.28	-0.51	-0.78	-0.24
Ψ^{PF}_{a8}	0.46	0.39	0.53	0.24	0.13	0.35	-0.48	-0.74	-0.22
Ψ^{PF}_{a9}	0.47	0.38	0.55	0.25	0.13	0.37	-0.47	-0.74	-0.19
Ψ^{PF}_{a10}	0.54	0.44	0.65	0.31	0.17	0.45	-0.42	-0.7	-0.15
$\Psi^{PF}_{a\geq 11}$	0.36	0.26	0.45	0.17	0.06	0.28	-0.53	-0.85	-0.2

Table A6. Estimated relative process standard deviation ($\hat{\sigma}_{process}$) of vital rates for four sets of years: (i) non-iceberg years (1982-2000 & 2006-2010) vs. (ii) iceberg years (2001-2005); (iii) before iceberg period (1982-2000) vs. (iv) after iceberg period (2001-2010). LCL and UCL respectively represent the lower and upper limits of the 95% confidence interval of the estimated $\hat{\sigma}_{process}$. See Figure 3 (main text) for the meaning of parameter symbols.

Parameter	Non-iceberg			Iceberg years			Before Iceberg			After Iceberg		
	$\hat{\sigma}_{process}$	LCL	UCL	$\hat{\sigma}_{process}$	LCL	UCL	$\hat{\sigma}_{process}$	LCL	UCL	$\hat{\sigma}_{process}$	LCL	UCL
ϕ^P_{yearl}	0.27	0.19	0.43	0.17	0.08	0.54	0.25	0.17	0.42	0.23	0.12	0.50
$\phi^P_{a\geq 2}$	0.11	0.07	0.19	0.09	0.03	0.33	0.09	0.05	0.16	0.12	0.06	0.28
ϕ^F	0.12	0.07	0.20	0.07	0.00	0.28	0.10	0.05	0.20	0.09	0.04	0.20
ϕ^E	0.17	0.12	0.25	0.09	0.02	0.32	0.16	0.11	0.27	0.11	0.06	0.23
ϕ^S	0.13	0.09	0.21	0.09	0.02	0.30	0.12	0.08	0.22	0.10	0.05	0.21
Ψ^{FE}	0.18	0.12	0.28	0.21	0.12	0.61	0.19	0.12	0.33	0.26	0.18	0.49
Ψ^{EE}	0.16	0.11	0.25	0.23	0.13	0.67	0.16	0.10	0.29	0.27	0.18	0.50
Ψ^{SE}	0.16	0.11	0.24	0.23	0.13	0.67	0.16	0.10	0.27	0.27	0.18	0.50
Ψ^{PF}_{a5}	0.08	0.03	0.15	0.09	0.04	0.30	0.08	0.04	0.17	0.10	0.05	0.23
Ψ^{PF}_{a6}	0.17	0.12	0.28	0.21	0.11	0.64	0.19	0.12	0.33	0.23	0.14	0.44
Ψ^{PF}_{a7}	0.21	0.14	0.34	0.29	0.16	0.86	0.23	0.15	0.41	0.30	0.20	0.57
Ψ^{PF}_{a8}	0.23	0.15	0.37	0.32	0.18	0.94	0.25	0.16	0.47	0.33	0.22	0.61
Ψ^{PF}_{a9}	0.23	0.15	0.38	0.32	0.18	0.96	0.26	0.17	0.50	0.33	0.22	0.62
Ψ^{PF}_{a10}	0.24	0.16	0.41	0.35	0.19	1.03	0.28	0.17	0.56	0.35	0.23	0.65
$\Psi^{PF}_{a\geq 11}$	0.20	0.13	0.36	0.29	0.15	0.88	0.23	0.13	0.50	0.30	0.19	0.58

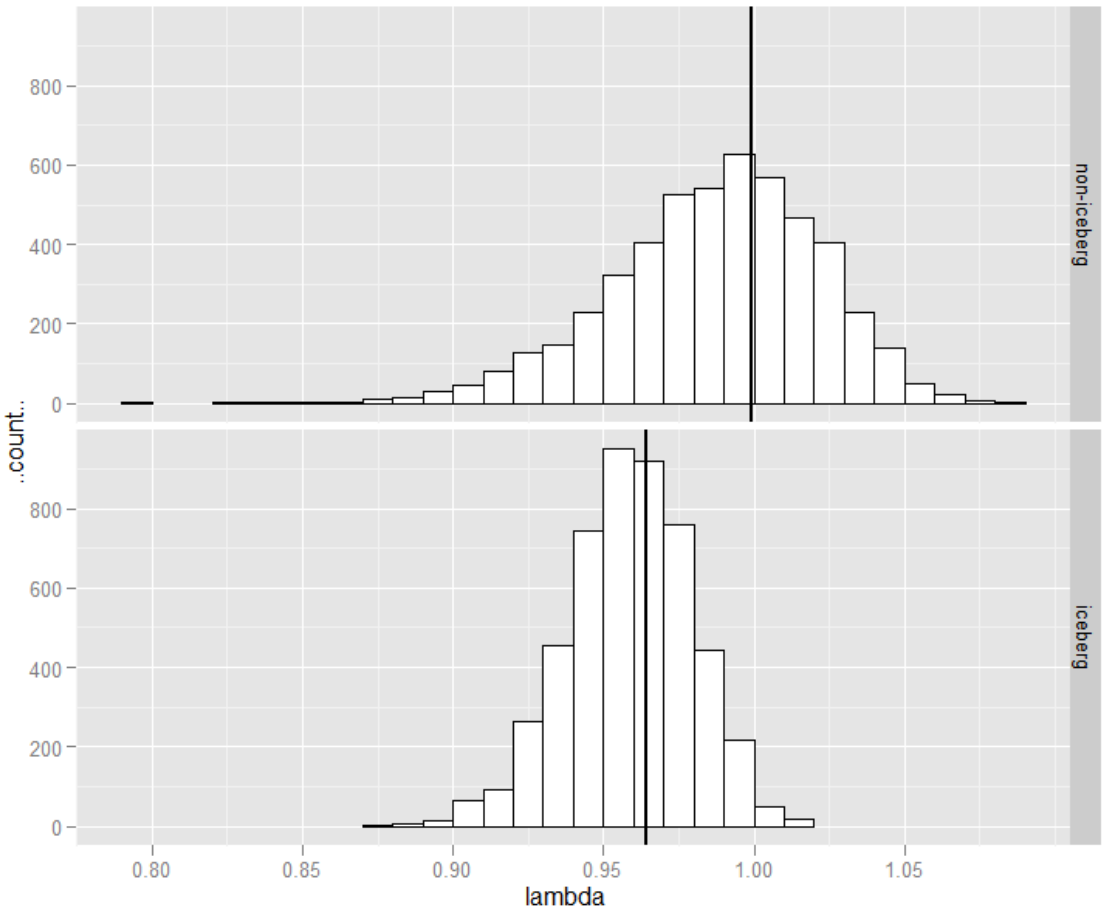

Figure A2. Approximation of the distribution of the asymptotic population growth rates λ for the non-iceberg (top panel) and the iceberg (bottom panel) periods. For each period, the distribution of λ was approximated from 5,000 sets of vital rates, randomly drawn from their estimated distribution (estimated mean and process variance). The vertical black line represents the average value of λ. See main text (methods) for details.

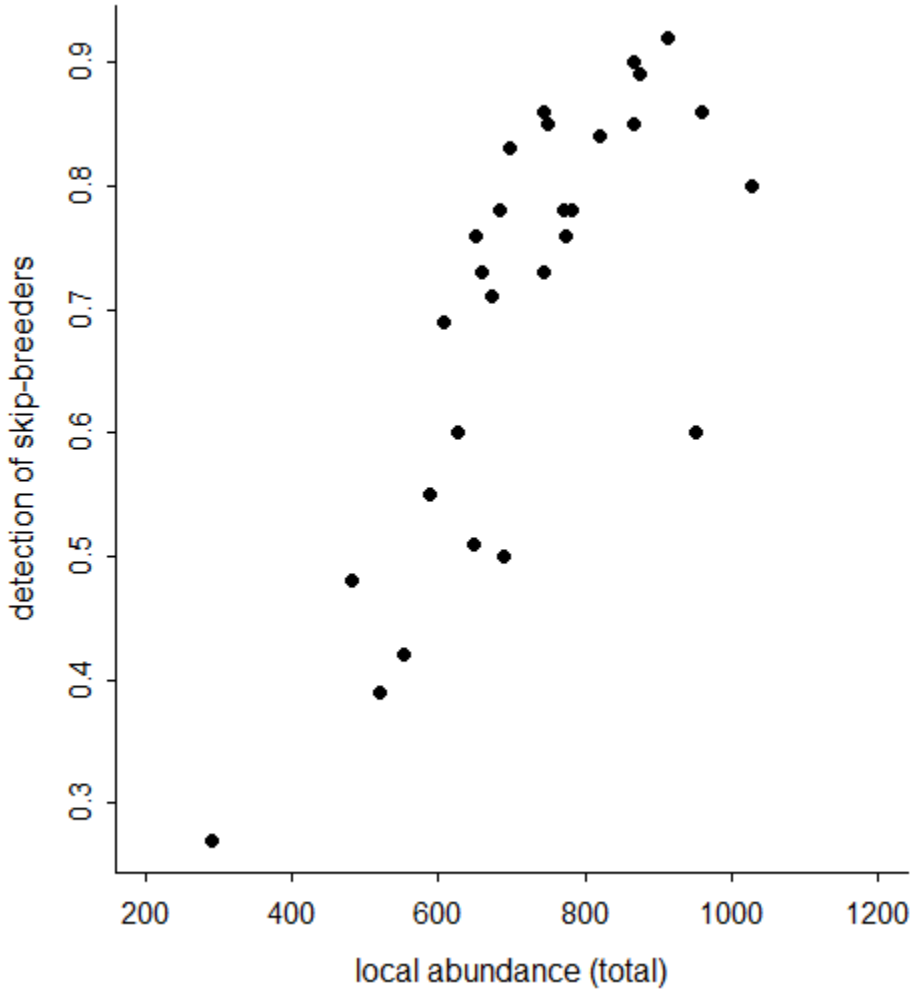

Figure A3. Relationship between local abundance (*x-axis*) and the detection rate of skip-breeders (*y-axis*). As the resighting effort on breeding colonies is high and consistent every year, the detection rate provides a good measure of colony utilization, as shown by the positive correlation between these two parameters.

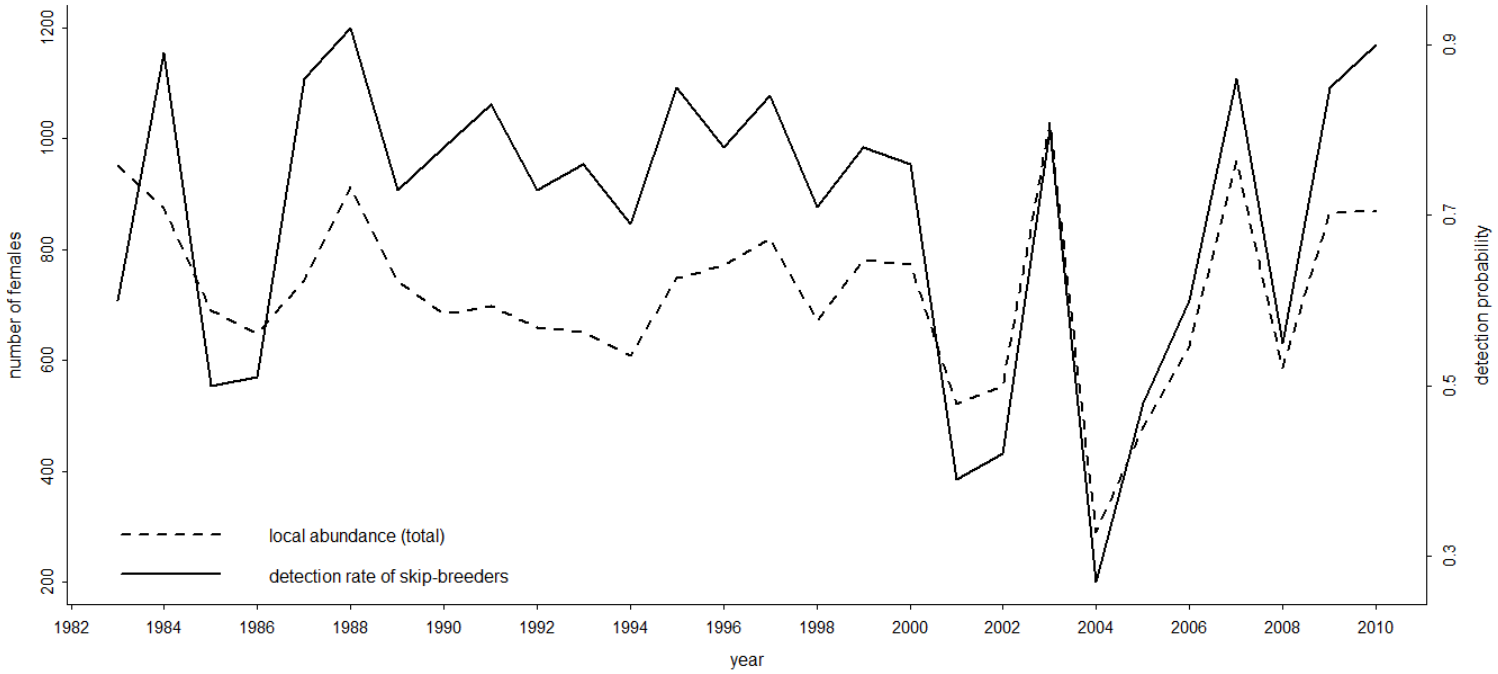

Figure A4. Temporal variation of local abundance on colonies (dashed line) and the detection rate of skip-breeders (solid line) from 1982 to 2010. Both measures display a very similar pattern of temporal variation, and it is especially interesting to note the similar peak in 2003, indicating that skip-breeders were more likely to attend colonies, and thus also more likely to be detected, in 2003 than in other iceberg years.

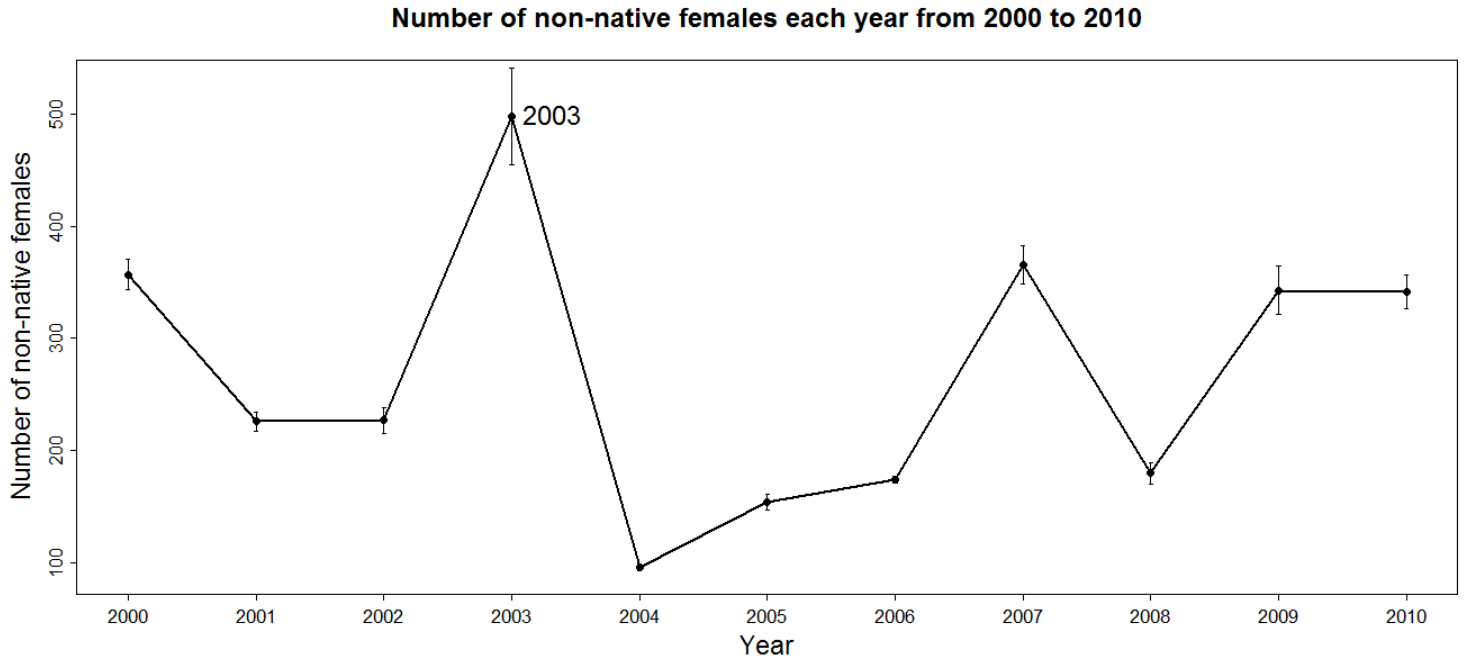

Figure A5. Number of unknown-age and unmarked females (i.e., tagged as adults) that attended Erebus Bay colonies each year from 2000 to 2010. Because we have tagged 100% of the pups born in the study area since 1982, we know that these females were not born in Erebus Bay. The upsurge of this type of females in 2003 indicates that there was a pulse of temporary immigration, probably linked to the sea-ice conditions that prevailed this year. Error bars represent 95% confidence intervals.

Table A7. Estimates of annual detection rates (and standard errors) of the four pre-breeder age-classes.

Year	Yearling		2-year-old		3 to 6 year old		Age ≥ 7 year old	
	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
1983	0.01	0.01	--	--	--	--	--	--
1984	0.05	0.03	0.13	0.05	--	--	--	--
1985	0.01	0.00	0.02	0.01	0.11	0.05	--	--
1986	0.01	0.00	0.02	0.01	0.12	0.04	--	--
1987	0.04	0.01	0.10	0.02	0.44	0.05	--	--
1988	0.07	0.02	0.17	0.03	0.60	0.04	--	--
1989	0.02	0.00	0.04	0.01	0.25	0.03	--	--
1990	0.02	0.01	0.06	0.01	0.31	0.04	0.60	0.05
1991	0.03	0.01	0.08	0.02	0.38	0.04	0.68	0.04
1992	0.02	0.00	0.04	0.01	0.26	0.03	0.54	0.05
1993	0.02	0.00	0.05	0.01	0.28	0.03	0.58	0.05
1994	0.01	0.00	0.04	0.01	0.22	0.03	0.49	0.05
1995	0.04	0.01	0.09	0.02	0.41	0.04	0.71	0.04
1996	0.02	0.01	0.06	0.01	0.32	0.03	0.62	0.04
1997	0.03	0.01	0.08	0.02	0.40	0.04	0.70	0.04
1998	0.02	0.00	0.04	0.01	0.24	0.03	0.52	0.05
1999	0.02	0.01	0.06	0.01	0.31	0.03	0.61	0.04
2000	0.02	0.00	0.05	0.01	0.28	0.03	0.58	0.04
2001	0.00	0.00	0.01	0.00	0.07	0.01	0.22	0.03
2002	0.00	0.00	0.01	0.00	0.08	0.01	0.24	0.03
2003	0.03	0.01	0.07	0.01	0.34	0.03	0.64	0.03
2004	0.00	0.00	0.01	0.00	0.04	0.01	0.14	0.02
2005	0.01	0.00	0.02	0.00	0.11	0.01	0.29	0.03
2006	0.01	0.00	0.03	0.01	0.16	0.02	0.40	0.04
2007	0.04	0.01	0.10	0.02	0.44	0.04	0.73	0.04
2008	0.01	0.00	0.02	0.00	0.13	0.02	0.35	0.04
2009	0.04	0.01	0.09	0.02	0.42	0.05	0.72	0.04
2010	0.05	0.02	0.13	0.05	0.52	0.10	0.79	0.07

Table A8. Estimates of annual detection rates (and standard errors) of skip-breeders and breeders (experienced and first-time breeders have the same detection probability). In all top-ranked models, the detection rate of breeders was constant over years.

Year	SKP-BREEDER		BREEDER	
	Estimate	SE	Estimate	SE
1983	0.60	0.23	0.97	0.01
1984	0.89	0.05	0.97	0.01
1985	0.50	0.13	0.97	0.01
1986	0.51	0.09	0.97	0.01
1987	0.86	0.03	0.97	0.01
1988	0.92	0.01	0.97	0.01
1989	0.73	0.04	0.97	0.01
1990	0.78	0.04	0.97	0.01
1991	0.83	0.03	0.97	0.01
1992	0.73	0.04	0.97	0.01
1993	0.76	0.04	0.97	0.01
1994	0.69	0.04	0.97	0.01
1995	0.85	0.02	0.97	0.01
1996	0.78	0.03	0.97	0.01
1997	0.84	0.03	0.97	0.01
1998	0.71	0.04	0.97	0.01
1999	0.78	0.03	0.97	0.01
2000	0.76	0.03	0.97	0.01
2001	0.39	0.04	0.97	0.01
2002	0.42	0.04	0.97	0.01
2003	0.80	0.02	0.97	0.01
2004	0.27	0.03	0.97	0.01
2005	0.48	0.03	0.97	0.01
2006	0.60	0.04	0.97	0.01
2007	0.86	0.02	0.97	0.01
2008	0.55	0.04	0.97	0.01
2009	0.85	0.03	0.97	0.01
2010	0.90	0.04	0.97	0.01

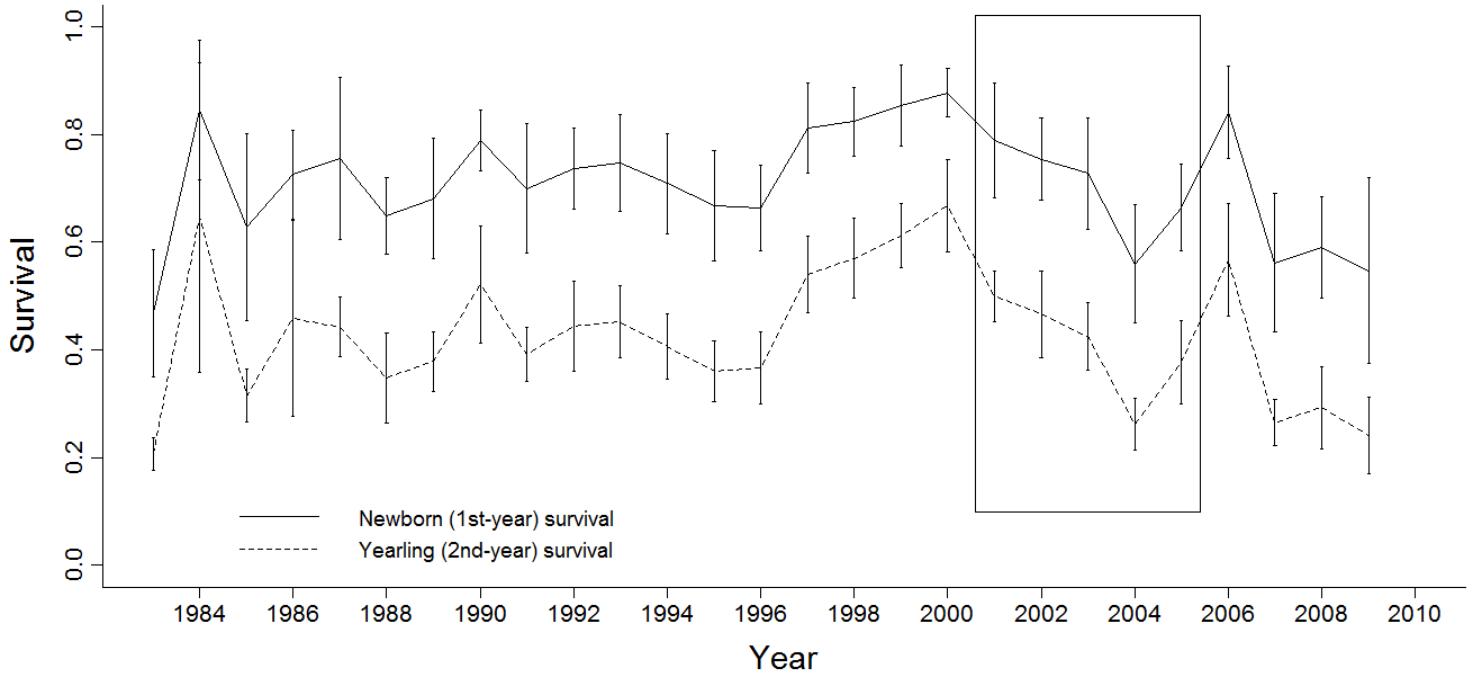

Figure A6. Estimates of first-year (newborn) survival rate (i.e., survival from birth year to 1 year old) for each year. Estimates of yearling survival (i.e., from age 1 to age 2) are also shown for comparison (see main text, Fig 4.c). The iceberg period is represented by a solid frame. Error bars represent standard errors (i.e., error due to sampling variation). We can see that the temporal trend for newborn survival rate is the same as that for yearling survival rate. This is due to the fact that these parameters share the same 'year effect' (i.e., additive structure) in our best models. Because of the very low detection rates of individuals of age 1 and age 2, there is little data to inform the proportion of individuals that actually died during their first vs. their second year of life. We therefore note that the estimates of first-year (newborn) survival rate contain substantial uncertainty and should be interpreted with caution.

APPENDIX B

SUPPLEMENTARY MATERIAL OF THE THIRD CHAPTER

Text B1. Estimation of the magnitude of the variance of individual random effects with a restrictive and penalizing prior

Here, we present the results from model H2 (see main text, Material and Methods - *Statistical modeling*) obtained when we used an inverse-gamma(4, 0.05) prior distribution for the variance of α_i (σ_α^2) instead of the uniform prior U(0,10) on the standard deviation σ_α that was used to obtain the results presented in the main mauscript. Although the U(0,10) distribution was used as a weakly informative prior, the inverse-gamma(4, 0.05) prior used here strongly penalizes high values of σ_α^2, and therefore, allows a more stringent assessment of the degree of support of the 'fixed heterogeneity' hypothesis (H2). This comparison aimed to assess the sensitivity of our estimates of σ_α to the choice of its prior, thus evaluating the strength of our inference regarding the magnitude of this parameter.

The characteristics of the inverse-gamma(4, 0.05) distribution are the following: the mean of the distribution is 0.017, the mode is 0.010 and the standard deviation is about 0.012. In terms of quantiles, 95% of the values are below 0.037, and 99% are below 0.061 (see Figure B1). The integrated probability of values greater than the H2 posterior mean, 0.462, is 7.e-06. These properties clearly illustrate that this inverse-gamma prior distribution strongly penalizes high variance values, and therefore, the 'fixed heterogeneity' hypothesis H2.

We ran 2 parallel MCMCs of 200,000 iterations, after a burn-in period of 5,000 iterations, to sample the posterior distribution of model parameters. The convergence of the MCMC chains was checked in the same way as were other models (see main text, Material and Methods).

The posterior distributions of all parameters were virtually identical to those obtained from the original model H2 using a U(0,10) prior (Table B1). Using the IG(4,0.05) prior, the posterior mean of the standard deviation of α_i , on original scale, is 0.14 (posterior SD = 0.01; 95% credible interval: [0.12, 0.17]) , compared to 0.15 (posterior SD = 0.01; 95% credible interval [0.13, 0.18]) for the original model using a U(0,10) prior. This comparison demonstrates the amount of information in the data was able to overcome the penalizing prior. This result strengthens our conclusions regarding the relatively high magnitude of among-individual variability in reproductive rates and thus the relevance of the 'heterogeneity hypothesis' H2 versus the homogeneity hypothesis H1.

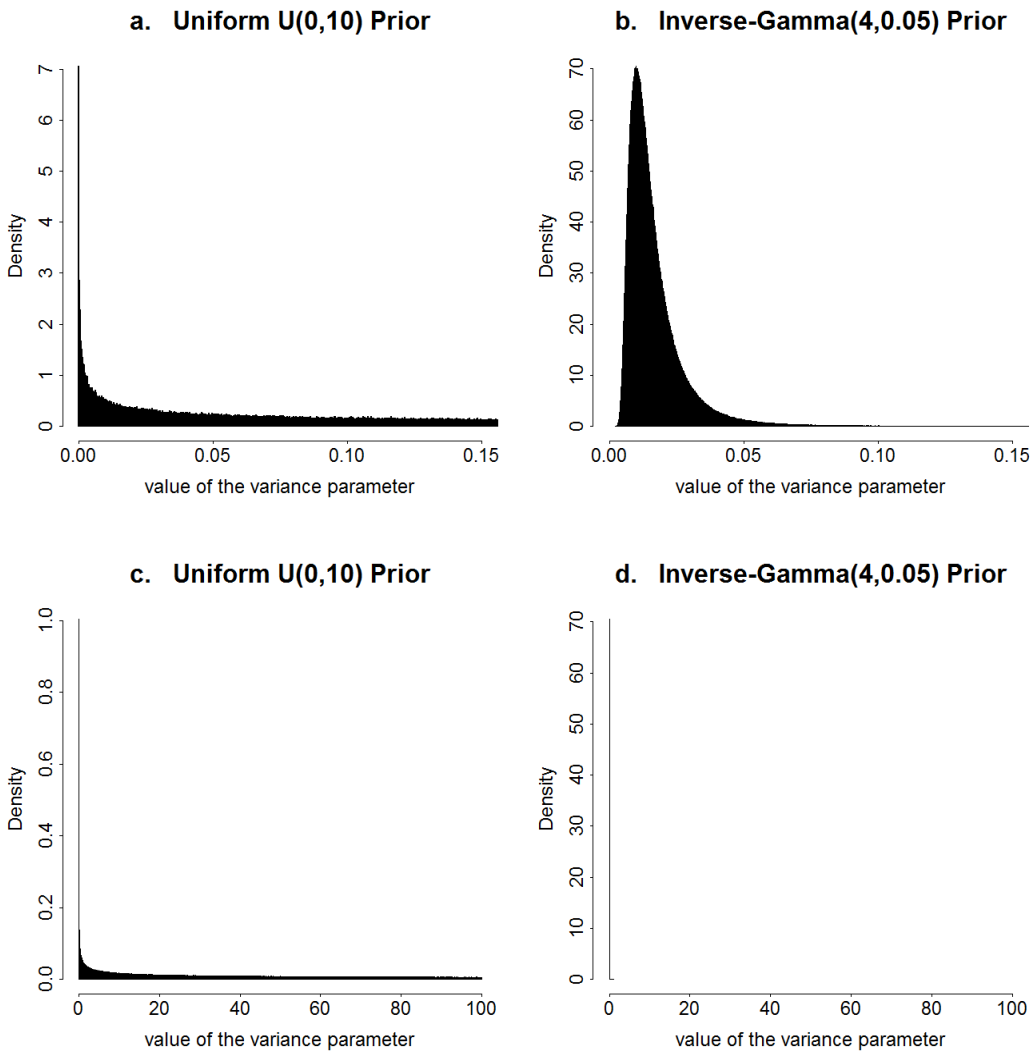

Figure B1. Histograms representing the probability density of the variance (σ_α^2) for the two different priors used for model H2: (a) & (c) uniform U(0,10) distribution on the corresponding standard deviation σ_α; (b) & (d) inverse-gamma(4,0.05) distribution on σ_α^2. For better readability, we show the densities on two different x-axis scales: histograms (a) and (b) are scaled on [0;0.15], where the density of σ_α^2 values under the inverse-gamma prior (b) can more easily be interpreted; histograms (c) and (d) are scaled on [0;100], where the full extent of the density of σ_α^2 values under the uniform prior (c) can be better seen. We see that the density of σ_α^2 values is heavily shifted towards very small values in the case inverse-gamma(4,0.05) prior distribution compared to the case of the uniform U(0,10) prior distribution. On the [0;100] scale, the density of the inverse-gamma(4;0.05) distribution looks as a single peak at zero.

Table B1. Summary of the parameter posterior distributions from model H2 ('fixed heterogeneity' hypothesis; see main text) using two contrasted priors on the variance (σ_α^2) of random individual effects: (i) the inverse-gamma(4,0.05) distribution on σ_α^2 which puts a lot of weight on very small values (close to zero), and thus strongly penalizes high values; (ii) the uniform U(0,10) distribution on the corresponding standard deviation σ_α, which is a very vague prior and has more weight on high values of variance. The mean, the standard deviation (SD), 2.5% and 97.5% percentiles (perc.) of the posterior distribution are shown. Symbols with a star (e.g., γ_1^*) correspond to parameters back-transformed to the more interpretable scale of a probability of reproduction (i.e., in the interval [0,1]). See main text for more details.

Parameters	MODEL H2 with Inverse-Gamma prior				MODEL H2 with Uniform prior			
	Mean	SD	2.5% perc.	97.5% perc.	Mean	SD	2.5% perc.	97.5% perc.
$\bar{\psi}^{kE}$	0.66	0.03	0.59	0.72	0.66	0.03	0.59	0.72
ψ^{FE}	0.53	0.04	0.45	0.62	0.54	0.04	0.45	0.62
ψ^{EE}	0.67	0.03	0.6	0.73	0.67	0.03	0.61	0.73
ψ^{SE}	0.75	0.03	0.69	0.8	0.76	0.03	0.7	0.81
γ_1^*	-0.06	0.02	-0.1	-0.01	-0.06	0.02	-0.1	-0.01
γ_2^*	-0.1	0.02	-0.15	-0.06	-0.1	0.02	-0.15	-0.06
σ_η^*	0.13	0.02	0.1	0.19	0.14	0.03	0.1	0.19
σ_α^*	0.14	0.01	0.12	0.17	0.15	0.01	0.13	0.18

APPENDIX C

SUPPLEMENTARY MATERIAL OF THE FOURTH CHAPTER

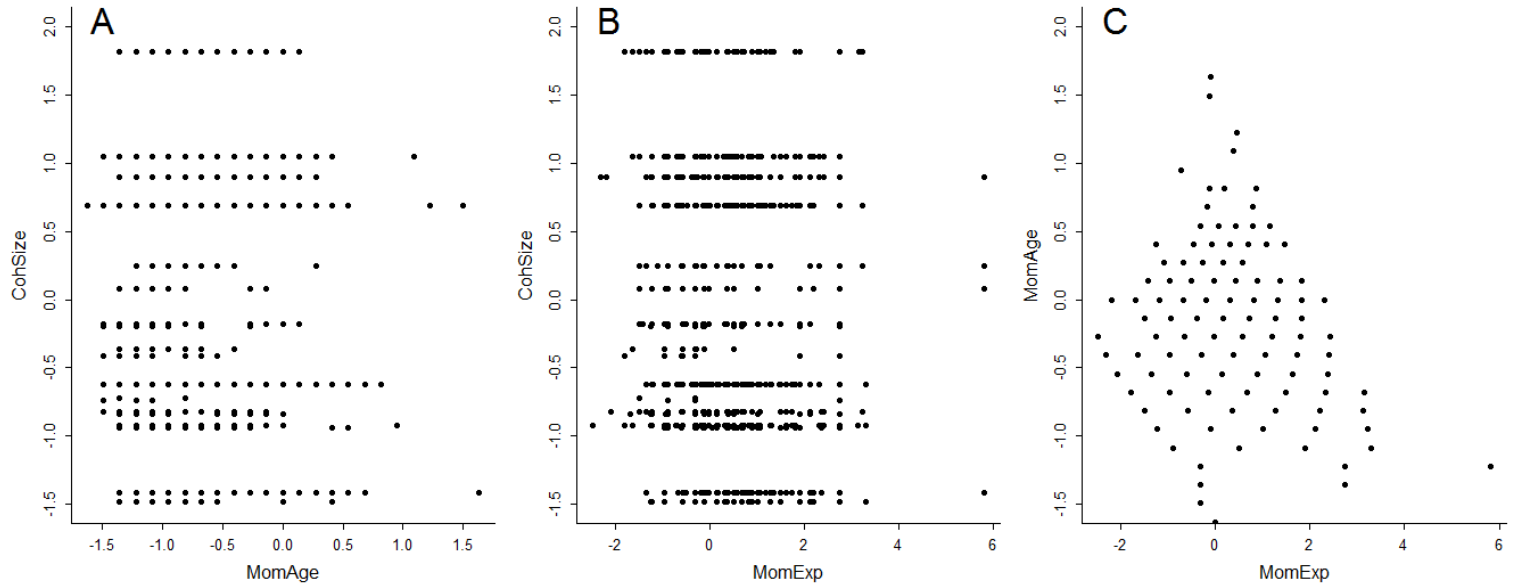

Figure C1. Plots of the relationship among covariates used to assess independence. The three covariates considered are: cohort size (CohSize), mother age (MomAge) and mother experience (MomExp). The three graphs respectively represent: (A) CohSize against MomAge; (B) CohSize against MomExp; and (C) MomAge against MomExp. There is no apparent relationship between any of the covariates, indicating that independence can be assumed.

Table C1. Summary of model-specific posterior distributions of each parameter of the recruitment probability analysis. The mean, lower (2.5% quantile) and upper (97.5% quantile) limits of a 95% credible interval (LCI and UCI, respectively) are shown. Parameters are regression coefficients associated to the covariates considered in the model: cohort size (β_{coh}), mother experience (β_{exp}) and a first- (β_{age1}) and second-order (β_{age2}) mother age effects. Each parameter appears in four of the eight models.

Parameter	Model	Mean	LCI	UCI
β_{coh}	Model 2	0.27	0.13	0.40
β_{coh}	Model 5	0.27	0.13	0.40
β_{coh}	Model 6	0.26	0.12	0.39
β_{coh}	Model 8	0.26	0.13	0.39
β_{exp}	Model 3	0.03	-0.07	0.15
β_{exp}	Model 5	0.04	-0.08	0.16
β_{exp}	Model 7	0.03	-0.08	0.15
β_{exp}	Model 8	0.05	-0.07	0.17
β_{age1}	Model 4	-0.05	-0.60	0.44
β_{age1}	Model 6	0.00	-0.54	0.47
β_{age1}	Model 7	-0.03	-0.58	0.41
β_{age1}	Model 8	0.02	-0.50	0.48
β_{age2}	Model 4	-0.35	-0.76	0.05
β_{age2}	Model 6	-0.31	-0.73	0.08
β_{age2}	Model 7	-0.35	-0.74	0.01
β_{age2}	Model 8	-0.30	-0.71	0.08

The eight models are defined as follows:
Model 1: No covariate;
Model 2: CohSize; *Model 3:* MomExp; *Model 4:* MomAge;
Model 5: CohSize + MomExp; *Model 6:* CohSize + MomAge; *Model 7:* MomExp + MomAge; *Model 8:* CohSize + MomExp + MomAge

Table C2. Summary of model-specific posterior distributions of each parameter of the age at recruitment analysis. The mean, lower (2.5% quantile) and upper (97.5% quantile) limits of a 95% credible interval (LCI and UCI, respectively) are shown. Parameters are regression coefficients associated to the covariates considered in the model: cohort size (β_{coh}), mother experience (β_{exp}) and a first- (β_{age1}) and second-order (β_{age2}) mother age effects. Each parameter appears in four of the eight models.

Parameter	Model	mean	LCI	UCI
β_{coh}	Model 2	0.07	-0.01	0.14
β_{coh}	Model 5	0.06	-0.02	0.13
β_{coh}	Model 6	0.07	0.00	0.14
β_{coh}	Model 8	0.06	-0.02	0.13
β_{exp}	Model 3	-0.07	-0.14	0.00
β_{exp}	Model 5	-0.06	-0.13	0.01
β_{exp}	Model 7	-0.06	-0.13	0.00
β_{exp}	Model 8	-0.05	-0.12	0.02
β_{age1}	Model 4	0.14	-0.06	0.33
β_{age1}	Model 6	0.15	-0.04	0.33
β_{age1}	Model 7	0.13	-0.07	0.31
β_{age1}	Model 8	0.13	-0.05	0.32
β_{age2}	Model 4	0.05	-0.13	0.21
β_{age2}	Model 6	0.04	-0.13	0.21
β_{age2}	Model 7	0.04	-0.12	0.21
β_{age2}	Model 8	0.04	-0.12	0.19

The eight models are defined as follows:
Model 1: No covariate;
Model 2: CohSize; *Model 3:* MomExp; *Model 4:* MomAge;
Model 5: CohSize + MomExp; *Model 6:* CohSize + MomAge; *Model 7:* MomExp + MomAge; *Model 8:* CohSize + MomExp + MomAge