ENVIRONMENTAL CORRELATES OF REPRODUCTION, PATTERNS OF MATERNAL ALLOCATION, AND VARIATION IN ADULT FEMALE VITAL RATES IN THE WEDDELL SEAL

by

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A dissertation submitted in partial fulfillment
of the requirements for the degree

of

Doctor of Philosophy

in

Ecology and Environmental Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

November 2017

ACKNOWLEDGEMENTS

I am grateful to Dr. Jay Rotella, my graduate advisor, for his patient help over the course of my graduate work. Jay is a relentless advocate for his students, and helped me become a better writer, scientist, and manager of people. Jay is an exemplar and role model for me as a scientist and teacher. I would also like to thank Dr. Robert Garrott for his guidance. Bob was instrumental in helping to frame the ideas for each one of my chapters and provided critical insights at multiple stages of my work, in addition to helping me become better at teaching, writing, and managing people both in the field and out. Dr. William Link helped develop the analyses for my third chapter, and provided a much-needed sounding board for the ideas therein. I would also like to thank Dr. Matt Lavin for his help at different stages of my work, and unfailing positivity. Dr. Donald Siniff is responsible for initiating the long-term research project on Weddell seals that was the core of my Ph.D. research, and I am grateful for his foresight in helping make this a long-term study.

This study runs on the efforts of dozens of field technicians who have collected data for decades, and I am grateful for their efforts. I would like to acknowledge Kaitlin Macdonald, whose efforts as a field technician, and then support as a colleague, made my work and life possible on the ice. Additionally, the employees of the National Science Foundation, as well as hundreds of contractors both in Antarctica and stateside, make this work possible through their tireless efforts to support science. This project was funded by the National Science Foundation, Division of Polar Programs.

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ABSTRACT

The dynamics of populations are the integrated result of multiple processes affecting variation in vital rates. Using a long-term mark-recapture dataset from a population of Weddell seals (*Leptonychotes weddellii)* in Erebus Bay, Antarctica, I investigated three processes related to population dynamics: environmental correlates of reproduction, sources of variation in maternal allocation to offspring, and sources of variation in the vital rates of adult females. First, I assessed the strength of the association between primary production in the McMurdo Sound and Ross Sea polynyas and the number of pups born in Erebus Bay. I demonstrated both a strong coupling between trophic levels and a surprising timing in the relationship. Pup numbers were most strongly associated with primary production in the months after birth, consistent with a response by mothers to take advantage of the environment of relative abundance. Second, I showed that the patterns of maternal allocation to offspring differ in the prenatal and post-parturition periods. Maternal and pup masses at parturition increased with maternal age (maximum near age 16) prior to declining for older animals, consistent with both restraint and senescence. In contrast, maternal allocation to offspring continued to increase with maternal age during the post-parturition period. Together, these patterns are strong evidence for terminal allocation. Furthermore, I found extensive among-individual heterogeneity, such that some mothers consistently produce heavier pups and allocate more resources during lactation. Finally, I assessed the sources of variation in the vital rates of adult females, using a multistate model to jointly estimate the probabilities of survival and reproduction. Survival rates steadily declined with age, consistent with the onset of senescence at the age of first reproduction, whereas reproductive rates increased for young animals to a maximum 8 years after the age of first reproduction before exhibiting a senescent decline. I found extensive among-individual and yearly variation in reproductive rates, coupled to minimal variation in survival rates. This dissertation adds novel information to the understanding of the complex demography of Weddell seals by revealing an association between trophic levels and patterns of variation in both the allocation of resources to offspring as well as vital rates of adult females. Together, these results shed further light on the flexible life-history patterns of a long-lived marine mammal.

CHAPTER ONE

INTRODUCTION TO THE DISSERTATION

Seeking to understand the nature and causes of dynamics in populations is a central motivation of ecology, and changes in the size and structure of a population are the integrated result of a variety of factors including environmental, temporal, and within- and among-individual processes (Gaillard, Festa-Bianchet & Yoccoz 1998; Vindenes, Engen & Sæther 2008; Jenouvrier, Péron & Weimerskirch 2015). Evaluating the strength of these processes is critical to furthering our understanding of life-history evolution (Clutton-Brock 1988; Stearns 1992), and relevant to the management of wild populations as well as the conservation of species at risk (e.g., Caughley 1994; Beissinger & Westphal 1998). Increasingly, understanding the effects of such a diversity of processes on wild animal populations relies on long-term studies of marked populations, and sophisticated modeling techniques, to properly assess the strength of multiple factors (Clutton-Brock & Sheldon 2010). In particular, such long-term studies are critical for assessing variation in population size associated with environmental and/or temporal processes as they are often the only method of evaluating both age-related changes in life-history traits and the influence of among-individual variation arising from the latent traits of individuals.

The population of Weddell seals in Erebus Bay, in the Ross Sea of Antarctica, is ideal for assessing potential sources of variation in within- and among-individual processes related to population dynamics. The study population forms pupping and breeding colonies during the austral spring, from October to December of each year. Females are highly philopatric and, once recruited to this population, have a very low probability of producing pups elsewhere (Cameron *et al.* 2007; Hadley *et al.* 2007). Colonies form on the frozen ocean near tidal cracks that allow females to enter and exit the water. During 4 to 6 weeks of lactation, each mother remains closely associated with her pup, which allows crews to reliably determine annual pup production, assign each female's annual reproductive state, and measure the mass of a targeted sample of mothers and pups (Proffitt *et al.* 2007; Hadley *et al.* 2007). Long-term monitoring has resulted in a multi-decadal time-series for population abundance and production, and an extensive mark-resight database of known-aged individuals that includes reproductive histories for all females born in the study area. Previous work on the study population's vital rates has demonstrated large inter-annual and among-individual variation in multiple vital rates (Cameron & Siniff 2004; Hadley *et al.* 2006; Hadley, Rotella & Garrott 2007; Proffitt, Garrott & Rotella 2008; Garrott *et al.* 2012; Stauffer 2012; Stauffer, Rotella & Garrott 2013), investigated ecological correlates of such variation (Hadley *et al.* 2007; Proffitt *et al.* 2007; Chambert, Rotella & Garrott 2012; Garrott *et al.* 2012; Stauffer *et al.* 2014), proposed the mass dynamics of mothers and pups as a mechanism for linking environmental variation to variation in vital rates (Proffitt *et al.* 2007), documented the importance of incorporating individual heterogeneity (Chambert *et al.* 2013; Chambert, Rotella & Garrott 2014), and shed light on fundamental processes that shape life histories (Rotella *et al.* 2009, 2012).

However, there are several key areas in which our understanding of the processes affecting the population dynamics of Weddell seals is incomplete. A relationship between vital rates and variation in biotic components of the ecosystem has not been found. Moreover, important questions remain regarding the patterns of 1) mass dynamics of mothers and pups and 2) variation in rates of adult female survival and reproduction and how those patterns vary among years and individuals. The objectives of this dissertation were to evaluate diverse hypotheses regarding these three processes and potential sources of variation in those processes with the goals of 1) assessing the strength and timing of the coupling between primary production in the Ross Sea and number of pups born in Erebus Bay, which could provide useful information about the strength of evidence for bottom-up processes on vital rates of an upper trophic-level consumer, 2) evaluating support for a series of hypotheses regarding the allocation of maternal resources to offspring and how allocation might change with female change and among individuals, and 3) estimating the magnitude of variation in the vital rates of adult females while incorporating multiple potential sources of heterogeneity. In each chapter, I took advantage of recent advances in Bayesian model comparison and evaluation to ensure that inferences were drawn from a rigorous statistical framework.

Although the trophic structure of many Antarctic marine ecosystems in thought to be simple, with relatively few trophic levels, the coupling between variation in these trophic levels is poorly known (Smith, Ainley & Cattaneo-Vietti 2007). The Ross Sea is one of the most productive areas on the planet, with phytoplankton blooms during the austral summer that represents tremendous within- and among-year variation in primary production (Smith & Gordon 1997; Arrigo, Weiss & Smith 1998). Polynyas, areas of open ocean surrounded by sea ice, are the first locations to receive direct sunlight in the austral spring, are important sources of primary production during the year, and have long been associated with the abundance of consumers (Stirling 1980, 1997). A common model for trophic-level interactions would suggest time lags between these changes in resource availability at the base of the food web and commensurate changes in the abundance of consumers at higher trophic levels (Schmidt & Ostfeld 2008), or a bottom-up model for the trophic web. However, the strength of bottom-up coupling in Antarctic ecosystems is poorly known (Smith *et al.* 2007), and the connection between variation in primary production and the abundance of Weddell seals, a consumer of mid-trophic level consumers, is unknown. In the few cases wherein bottom-up regulation of the vital rates of upper trophic-level consumers has been investigated in Antarctic ecosystems, results have been mixed (Arrigo & van Dijken 2003; Dugger *et al.* 2014). Moreover, other work has suggested the presence of top-down regulation in the Ross Sea (Testa *et al.* 1985; Ainley *et al.* 2004; Ainley, Ballard & Dugger 2006), such that both the degree and direction of coupling between trophic levels in the Ross Sea is poorly understood. In Chapter 2, I investigate a potential connection between annual primary production in two polynyas in the Ross Sea and the number of Weddell seal pups in Erebus Bay each year. I evaluate the evidence for a bottom-up coupling of trophic levels by estimating the strength of the association between primary production and pup numbers as well as the timing of the association.

In Chapter 3, I evaluate the sources of variation in the allocation of maternal resources to offspring. The allocation of resources from mother to offspring is a key component of an individual’s life history, and among- and within-individual variation in allocation has consequences to the fitness of both offspring and parent that can affect the dynamics of populations (Roff 1992; Stearns 1992). In particular, maternal allocation has been linked to offspring development and survival (Côté & Festa-Bianchet 2001; Skibiel, Dobson & Murie 2009; Skibiel, Speakman & Hood 2013; Baron *et al.* 2010), with potentially long-lasting effects on offspring vital rates (Hackman *et al.* 1983; Kruuk *et al.* 1999; Lummaa 2003; Bateson *et al.* 2004). Reproduction is also costly for the mother (Gittleman & Thompson 1988; Robbins 1993), and the degree to which she can allocate resources to her offspring is ultimately limited by her body reserves (King, Roff & Fairbairn 2011), which may directly reflect resource availability in the environment (Schubert *et al.* 2009). However, the relationship between maternal body reserves and allocation to offspring is thought to be mediated through multiple factors including maternal age, reproductive experience, variability in the environment, and among-individual heterogeneity arising from latent traits. Previous work in this system has separately evaluated sources of variation in maternal mass near parturition and pup mass near weaning (Proffitt *et al.* 2007, 2008). Recent work has demonstrated large among-individual differences in allocation even after taking into account environmental conditions and characteristics of the mother such as age and reproductive experience (Weladji *et al.* 2010; Hamel, Craine & Towne 2012). Thus, important questions remain regarding how individual heterogeneity influences the patterns of allocation in Weddell seals. Using a hierarchical modeling approach, I evaluated the sources of variation in four key metrics of maternal allocation (maternal mass at parturition, pup mass at parturition, pup mass gain during early lactation, and pup mass gain during late lactation) with the goal of estimating the relative effects from a variety of maternal characteristics while also incorporating random effects for year and individual mothers.

Finally, in Chapter 4, I focused on the most comprehensive analysis to date of sources of variation in the vital rates of adult females. The fitness of organisms is sensitive to differences in life history traits such as lifespan and lifetime reproductive output (Williams 1966; Newton 1989), and some differences in observed life history traits might simply be the result of the stochastic nature of survival and reproduction (Tuljapurkar, Steiner & Orzack 2009). However, among-individual differences in the underlying vital rates of survival and reproduction is also known to affect life history traits (Clutton-Brock 1988; Cam *et al.* 2002), and several hypotheses from life-history theory predict specific patterns of variation in vital rates (Roff 1992; Stearns 1992). Such variation in fitness-related traits is known to have consequences for population dynamics (Kendall & Fox 2002; Vindenes *et al.* 2008; Vindenes & Langangen 2015). Previous investigations in this system have demonstrated significant variation in the probabilities of reproduction associated with breeding state, age, and individual heterogeneity, as well as suggested a high degree of year-to-year variation (Hadley *et al.* 2006; Hadley, Rotella & Garrott 2007; Rotella *et al.* 2012; Chambert *et al.* 2013). Separately, the probabilities of survival have been shown to be associated with breeding state of individuals, though there was little evidence for age-related changes and no estimation of individual heterogeneity (Cameron & Siniff 2004; Hadley *et al.* 2007). I used a 33-year dataset containing the reproductive histories of 1,274 individual known-aged females in a multistate modeling framework to jointly estimate the probabilities of survival and reproduction. I evaluated a variety of hypotheses from life-history theory regarding the patterns of variation in vital rates by incorporating effects due to maternal age, reproductive state, and temporal variation into a small set of competing models. Finally, I employed recent advances in Bayesian model comparison and assessment to estimate model performance over multiple metrics to make inference from within a rigorous framework.

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CHAPTER TWO

TIGHT COUPLING OF PRIMARY PRODUCTION AND MARINE MAMMAL REPRODUCTION IN THE SOUTHERN OCEAN

Contribution of Authors and Co-Authors

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Contributions: Collected data and conducted statistical analyses. Wrote the manuscript.

Co-Author: Jay J. Rotella

Contributions: Supervised the project and collected data. Provided expertise and feedback on the statistical analysis. Provided expertise and comments on drafts of the manuscript.

Co-Author: Kevin R. Arrigo

Contributions: Provided remotely-sensed data. Provided expertise and comments on drafts of the manuscript.

Co-Author: Robert A. Garrott

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

Manuscript Information Page

J. Terrill Paterson, Jay J. Rotella, Kevin R. Arrigo, Robert A. Garrott
Proceedings of the Royal Society B

Status of Manuscript:
____ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
_x__ Published in a peer-reviewed journal

Published in the Proceedings of the Royal Society B on April 8, 2015. Issue 282.
Citation style has been changed to be more consistent throughout this document.

Abstract

Polynyas are areas of open water surrounded by sea ice and are important sources of primary production in high-latitude marine ecosystems. The magnitude of annual primary production in polynyas is controlled by the amount of exposure to solar radiation and sensitive to changes in sea-ice extent. The degree of coupling between primary production and production by upper-trophic-level consumers in these environments is not well understood, which prevents reliable predictions about population trajectories for species at higher trophic levels under potential future climate scenarios. In this study, we find a strong, positive relationship between annual primary production in an Antarctic polynya and pup production by ice-dependent Weddell seals. The timing of the relationship suggests reproductive effort increases to take advantage of high primary production occurring in the months after the birth pulse. Though the proximate causal mechanism is unknown, our results indicate tight coupling between organisms at disparate trophic levels on a short time scale, deepen our understanding of marine ecosystem processes, and raise interesting questions about why such coupling exists and what implications it has for understanding high latitude ecosystems.

Key Words: polynyas; primary production; Antarctica; trophic levels; Weddell seal

Introduction

High-latitude marine environments are subject to extreme variations in both photoperiod and amount of open water as the extent of sea ice seasonally expands and contracts (Parkinson *et al.* 1992; Zwally *et al.* 2002; Clarke & Harris 2003; Meier, Stroeve & Fetterer 2007). Primary production (the amount of organic carbon produced by photosynthetic organisms at the base of the food chain) is highly dependent upon the amount of available light (Field *et al.* 1998). Though localized increases in primary production have been documented under first-year sea ice in the Arctic and Antarctic (Arrigo *et al.* 1997, 2012), the majority of primary production associated with phytoplankton blooms occurs in areas of open water. The extremes of the photoperiod and changes in the amount of open water exposed to solar radiation in these environments help to explain the large variation in intra-annual primary production. The maximum amount of production occurs during the polar spring and early summer when photosynthetic organisms take advantage of the increase in incident solar radiation and decline in sea ice cover and form `blooms' (Smith Jr *et al.* 2000; Pabi, van Dijken & Arrigo 2008).

In the sea-ice zones of both polar oceans, polynyas are recurrent regions of open water surrounded by ice (Williams, Carmack & Ingram 2007). They have long been associated with large numbers of marine mammals and birds and increased amounts of primary production relative to proximal ice-covered areas (Stirling 1980, 1997). Many polynyas in the Arctic occur well south of the Arctic Circle and receive sunlight throughout the year and can thereby remain productive. In contrast, all polynyas in the Antarctic occur south of the Antarctic Circle, experience minimal sunlight and are non-productive during the polar winter (Karnovsky, Ainley & Lee 2007). In both polar oceans, they remain biologically important even as the surrounding sea ice melts in the polar spring. During this time, polynyas are the first areas exposed to the increasing sunlight, and are a comparatively localized source of increased primary production in polar oceans (Stirling 1997; Arrigo & van Dijken 2003).

Polynyas form through two, non-mutually exclusive, forcing processes. Mechanically forced polynyas form as a result of wind stress or ocean currents advecting sea ice, whereas localized high-oceanic-heat-flux, or upwelling ocean currents, form convectively forced polynyas (Williams *et al.* 2007). The formation mechanism partially controls primary production in a polynya by influencing factors such as water-column stratification, nutrient availability and temperature (Arrigo 2007). Phytoplankton assemblages vary considerably between polynyas and reflect the diverse interaction of formation mechanisms and environmental conditions (Moisan & Mitchell 1999; Tremblay & Smith Jr 2007). Previous work has revealed a rich interplay among regulatory mechanisms that act on these primary producers and influence the timing and magnitude of primary production in polar oceans (Arrigo, Weiss & Smith 1998; Ainley *et al.* 2004; Ainley, Ballard & Dugger 2006; Olli *et al.* 2007). The strength of connections between primary production and vital rates of upper-trophic-level consumers such as birds, seals and whales that are known to take advantage of polynyas remains unclear (Ainley *et al.* 1991, 2007; Smith, Ainley & Cattaneo-Vietti 2007a; Dugger *et al.* 2014) given contrasting results from previous work in Antarctica. For example, one study indicated that enhanced primary production in the Ross Sea polynya does not appear to translate into increased biomass of upper-trophic-level predators such as whales and penguins (Tremblay & Smith 2007), whereas another study using different methods suggested that the colony size of Adélie penguins (*Pygoscelis adeliae*) is positively associated with primary production in polynyas where penguin rookeries are strongly associated with local polynyas (Arrigo & van Dijken 2003).

The Ross Sea overlies the continental shelf in eastern Antarctica (Figure 2-1) and is the most biologically productive area in the Southern Ocean (Smith & Gordon 1997; Arrigo *et al.* 1998), though the expansion of sea ice and reduced photoperiod inhibits large-scale primary production during the austral winter. There is debate on the relative contribution of mechanical and convective forcing mechanisms to the formation of the eponymous polynya (Zwally, Comiso & Gordon 1985; Jacobs & Comiso 1989). Recent work suggests both synoptic-scale winds and warm-water upwelling from the Modified Circumpolar Deep Water current contribute to the formation of the Ross Sea polynya (Reddy, Arrigo & Holland 2007). The haptophyte *Phaeocystis antarctica* dominates the phytoplankton assemblage in the Ross Sea polynya, with smaller abundances of various diatoms. The former prefer the comparatively poorly stratified waters of the central Ross Sea, and the latter the well-stratified waters along the edge of the ice (Karnovsky *et al.* 2007).

The McMurdo Sound polynya is one of several coastal polynyas that form along the western edge of the Antarctic continent. Like other coastal polynyas in the region, its areal extent and total primary production are much lower than that of the Ross Sea polynya (Arrigo & van Dijken 2003). In general, the coastal polynyas are formed by katabatic winds advecting ice away from the coast (Maqueda, Willmott & Biggs 2004). High rates of sea-ice melting in the austral spring and summer induce a strong stratification of the water column later in the season (Arrigo & van Dijken 2004). Previous work has suggested that the stratification in turn favors the dominance of diatoms in the phytoplankton assemblages in many coastal polynyas (Arrigo *et al.* 2000; Goffart, Catalano & Hecq 2000; Tagliabue & Arrigo 2003; Arrigo & van Dijken 2003). The Ross Sea and McMurdo Sound polynyas form via different forcing mechanisms that differentially influence the phytoplankton assemblages responsible for primary production.

The responsiveness of consumers to variation in primary production in the Ross Sea is relatively poorly known (Smith *et al.* 2007a). In general, consumer response to changes in resource abundance is complex and dependent upon a variety of characteristics of both the ecosystem and organism (reviews in Ostfeld & Keesing 2000; Solan *et al.* 2006). A common model for consumer-resource interaction envisions time-lags of varying lengths between changes in resource availability and the response of consumers, presumably to allow energy transfer up through trophic levels or the spatial rearrangement of consumers (e.g. Holt 2008; Schmidt & Ostfeld 2008). Intriguingly, however, studies in several taxa have suggested that consumers use unknown cues to anticipate future resources and increase current reproductive effort to take advantage of anticipated abundances (Lindström 1988; Boutin *et al.* 2006; Bergeron *et al.* 2011;

Korpimäki & Hakkarainen 2012). Using a lengthy time series of vital rates for a well-studied carnivore, we report on previously unknown connections between primary productivity in the two Antarctic polynyas studied here and the number of Weddell seal (*Leptonychotes weddellii*) pups born nearby each year during 1997 to 2012. Moreover, we suggest the differential results found for each polynya are due to the different physical forcing mechanisms responsible for the development of each polynya and their influences on assemblages of primary producers. We are the first to investigate a potential connection between a high-trophic-level, fish-eating predator and the magnitude of primary production in different types of polynyas.

Methods

Primary production was estimated for each polynya from 1997 to 2012 using satellite ocean- color data from the Sea-viewing Wide Field-of-view Sensor (SeaWiFS) and MODerate Resolution Imaging Spectrometer (MODIS) (Arrigo & van Dijken 2004). Total primary production per year for each polynya was calculated by first converting chlorophyll a (Chl α) concentrations to primary productivity rates at each pixel (Arrigo *et al.* 1998) and then integrating the rates over the length of the growing season. The estimates of primary production were first standardized to yield values with a mean of zero and unit variance.

Breeding colonies of Weddell seals along the western edge of Ross Island are the subject of a long-term mark-recapture study (1971 to present (Siniff *et al.* 1977)). Each year during the austral spring (October and November), all pups born are individually marked during repeated visits to the colonies every 2-3 days. Between 5 and 8 complete surveys of the entire area are also conducted each field season. The intense sampling effort allows for a high degree of confidence in the number of pups born into the colonies. For this study, we used the numbers of pups born per year from a subset of the long-term data (1997 to 2012) that matches the years for which satellite-based estimates of primary production are available in the two polynyas and that also encompassed large annual variation in pup numbers (Chambert, Rotella & Garrott 2012).

These two long-term datasets were used to evaluate potential relationships between the number of pups born in Erebus Bay and primary production in the Ross Sea and McMurdo Sound polynyas (Figure 2-2). In light of the uncertainties regarding the coupling of primary production and the vital rates of upper trophic-level consumers in this system, we developed a series of models (Table 2-1) for the relationship between pup numbers and standardized values of primary production. We proposed models to investigate potential differences in the strength of the association between primary production in either or both of the two polynyas and the number of pups by comparing models utilizing primary production at different time lags. Preliminary analyses of the relationship used a variety of time lags for standardized values of primary production to model the number of pups born each year, and suggested the most support for models with time lags of 0 years (primary production in year *t*) and 1 year (primary production in year *t*-1). Accordingly, models with time lags of 0 and 1 year are presented in detail here. Models that regress the number of pups in year t on the magnitude of primary production in year *t* propose that the number of Weddell seal pups is associated with primary production in the same year, whereas those using primary production in year *t*-1 propose a 1-year lag in the association.

Interpreting individual coefficients of a model in which collinearity exists between the predictors is a recognized and long-standing problem in ecological modeling (Graham 2003). Our study depends on interpreting both the magnitude (to judge the relative strength of the relationship between primary production in the two polynyas and the number of pups born in Erebus Bay) and the sign of the regression parameters. However, collinearity among predictor variables makes a comparative assessment of regression parameters problematic insofar as it inflates the variance of the estimated parameters, potentially obscuring relationships in the data. In this study, primary production in McMurdo Sound and Ross Sea polynyas in the same year were moderately correlated ($\rho = 0.51$) in our data. We addressed the collinearity issue by utilizing a Bayesian perspective on classical ridge regression that shrank our regression coefficients towards zero to appropriately penalize for multicollinearity (Hoerl & Kennard 1970; Hsiang 1975; Congdon 2007). We assumed exchangeability for the regression coefficients for primary production and assigned the prior distribution: $\beta_i \sim$ Normal (0, ρ) and $\rho \sim$ Gamma (0.001, 0.001) for i=1,2,3,4. Model comparison was done using the WAIC (Widely Applicable Information Criterion), a fully Bayesian information criterion (Gelman, Hwang & Vehtari 2014) whose interpretation is similar to AIC, i.e. lower values indicate a more parsimonious model (Watanabe 2010; Hooten & Hobbs 2014). Relative support for models is based on the comparison of WAIC values to the top model

(ΔWAIC = WAIC(model) - WAIC(top model)), similar to the interpretation of ΔAIC values. R-squared values were calculated using the mean of the variance of the (posterior) simulations for residuals to estimate the expected value for the variance of the residuals (proportional to the residual sum of squares in classical regression);

$$R^2 = 1 - \frac{\mathrm{E}(\mathrm{Var}\,\boldsymbol{\epsilon})}{\mathrm{Var}\,\boldsymbol{C}},$$

where $\boldsymbol{\epsilon} = \epsilon_1, \ldots, \epsilon_{15}$ and $\boldsymbol{C} = (C_1, \ldots, C_{15})$ are the vectors of residuals and counts of pups for i=1 to 15 years (1997 to 2012) (Gelman & Pardoe 2006).

Results

The time series used for this model represent a wide range of values for both primary production and the number of pups (Figure 2-3), as well as annual variation in the extent of sea ice (see Discussion). Model-selection results (Table 2-1) strongly suggest that model 7 is the most parsimonious model and much better supported than all other model (ΔWAIC > 4.84 for all other models). Model 7 explained a considerable amount of the variation in the number of pups born in the study area ($R^2 = 0.62$) based on primary production in the McMurdo Sound and Ross Sea polynyas. In model 7, the number of pups in year *t* has a positive association with the total primary production in the McMurdo Sound polynya in year *t* and a negative association with total primary production in the Ross Sea polynya in year *t* (Figure 2-4). Model results suggest that the number of pups for a year with average productivity in both polynyas is approximately 441 (95% credible interval: 396.54 to 483.96). An increase of one standard deviation in primary production within the McMurdo Sound polynya is associated with a sizeable increase of 108 pups (95% credible interval: 0.07 to 163.34); the same increase in primary productivity in the Ross Sea polynya is associated with a more moderate decrease of 49 pups (95% credible interval: -101.59 to 3.88). Thus, it appears that pup production in Erebus Bay is more tightly linked to primary production in the smaller but closer McMurdo Sound polynya than to production in the larger but more distant Ross Sea polynya.

The pattern of positive association between the magnitude of primary production in the McMurdo Sound polynya and the number of pups born in Erebus Bay is consistent across less-supported models (Table 2-1 and Figure 2-4), e.g., the second most-supported model (Model 3, ΔWAIC=4.84, $R^2 = 0.47$), despite being a considerably poorer model than model 7, includes the same positive association for the McMurdo Sound polynya but ignores production in the Ross Sea polynya.

Models that included data on primary production in year *t*-1 in either or both polynyas performed much worse than did models that included information on primary production in the current year. For example, a model containing information from both polynyas in year *t*-1 (model 6, Table 2-1) had a ΔWAIC value of 11.36 and explained little of the variation ($R^2 = 0.09$) in annual pup production. Thus, our results provide much stronger support for the hypothesis that current-year production is related to pup production than for the idea that pup production lags primary production by a year.

Discussion

The difference between the association of primary production in the Ross Sea and McMurdo Sound polynyas to the number of pups born in Erebus Bay is stark. Our results suggest the number of pups is strongly, positively associated with primary production in the McMurdo Sound polynya and less strongly, negatively associated with the Ross Sea polynya. In the Ross Sea polynya the surge in phytoplankton abundance each spring, which is responsible for increased primary production, is thought to be effectively decoupled from the grazing pressure exerted by zooplankton (Arrigo *et al.* 2000; Tagliabue & Arrigo 2003). The phytoplankton assemblage is dominated by *P. Antarctica* (Tagliabue & Arrigo 2003), a species that forms colonies consisting of hundreds of individual cells (Rousseau *et al.* 2007). Previous work has suggested that zooplankton are incapable of effectively grazing the colonies due either to their large size (Smith Jr *et al.* 2003) or their high growth rates (Tagliabue & Arrigo 2003). For either hypothesis, the increase in *P. antarctica* may not be matched by an increase in the abundance of consumers such as krill, birds, seals and whales. The various coastal polynyas, including McMurdo Sound, are primarily mechanically forced by intense katabatic winds. These winds are several times stronger than the synoptic-scale wind that drives the Ross Sea polynya. The strength of the katabatic winds in the early spring induces deep mixing of the water column and inhibits phytoplankton blooms (Arrigo *et al.* 1998). By the time the winds have diminished to the point that melting sea ice can induce stratification, the upper layers of the water column are consistently exposed to increased solar radiation (Arrigo *et al.* 1998, 2000), which is comparatively inhospitable to the shade-adapted *P. Antarctica* (Tagliabue & Arrigo 2003). Diatoms dominate these well-stratified waters and prior work has demonstrated that the diatom assemblages are more effectively grazed by zooplankton (Haberman, Ross & Quetin 2003). The results from our study are partially consistent with a view of ecosystem functioning whereby a high degree of coupling exists between trophic levels in the diatom-dominated McMurdo polynya. However, this traditional description of the ecosystem would also suggest little to no influence of primary production in the *P. antarctica* – dominated Ross Sea polynya on the number of pups due to the decoupling between trophic levels, which is in contrast with the negative association suggested by our top model. Though further work is needed to characterize the coupling of trophic levels in the Ross Sea, our results certainly suggest that primary production is not completely decoupled from the upper trophic levels.

Moreover, model-selection results are somewhat surprising given the timing of pupping (October and November of year *t*) and the measurements of total primary production (October of year *t* through March of year *t*+1). Specifically, we find evidence that more pups tend to be born in October and November when primary production at that time and in the following few months is higher in the McMurdo Sound polynya and lower in the Ross Sea polynya (Model 7). Because linkages between abiotic and biotic processes in the Ross Sea ecosystem are poorly understood, we currently lack an obvious proximate causal mechanism that could explain the surprising timing of the relationship. Accordingly, we are forced to speculate about the potential mechanisms that are responsible for the strong correlation we detected between primary production in a polynya and reproduction of a high-trophic level predator. Given the lack of a time lag between variations in primary production and the number of pups born, it seems unlikely that a transfer of primary production upwards through the food chain, *sensu stricto*, within the same season is responsible. Rather, we hypothesize that the relationship is due to spatial rearrangement of the members of the differing trophic levels such that increases in primary production attract fish that are common prey of Weddell seals. When the increase is in the McMurdo Sound polynya, we speculate that individual adult female Weddell seals somehow anticipate the conditions associated with high primary productivity and respond by increasing their probability of producing a pup. Conversely, when primary productivity increases in the much larger Ross Sea polynya the spatial rearrangement of prey items dilutes the relative amount of food available in McMurdo Sound and seals respond by reducing the probability of producing a pup.

This surprising finding is not completely without precedent, as evidence for so-called anticipatory reproduction (Boutin *et al.* 2006) has been found in several species including the red fox (*Vulpes vulpes*) (Lindström 1988), squirrels (*Tamiasciurus hudsonicus* and *Sciurus vulgaris*) (Boutin *et al.* 2006), boreal owls (*Aegolius funereus*) (Korpimäki & Hakkarainen 2012), and eastern chipmunks (*Tamias striatus*) (Bergeron *et al.* 2011). For these studies, actual causal mechanisms are unknown, hypothesized proximate causal mechanism vary, and anticipatory reproductive responses to future resource abundance is proposed as an adaptation for increasing juvenile survival (but see (Descamps *et al.* 2008)). In the case of the Weddell seal, the largest cohorts of pups tend to be produced in years with abundant resources, which ought to increase their chances of avoiding starvation and predation upon gaining nutritional independence several months after being born. Recent work on Weddell seals reported that female pups from the largest birth cohorts have the greatest chance of eventually recruiting to the breeding population and provided evidence that recruitment probability was more tightly associated with environmental conditions experienced by the mothers months earlier when their pups were in utero than with conditions during the subsequent period of juvenile independence (Garrott *et al.* 2012). The results reported here suggest a possible avenue for extending those findings: specifically, future studies should evaluate whether environmental conditions during the juvenile-independence period, as measured by primary productivity in the McMurdo Sound polynya, relate to survival of young during their first two years of life when the majority of deaths occur in a given birth cohort (Hastings, Testa & Rexstad 1999). Whereas analyses that assessed factors associated with eventual recruitment by females, which typically occurs at age 8 (Hadley *et al.* 2006), integrate processes occurring over multiple years, an analysis aimed specifically at juvenile survival ought, we speculate, to be more powerful for identifying the short-term environmental conditions that are tied more directly to annual variation in juvenile survival rates, which appears to be a key determinant of cohort strength and variation in long-term population trajectories (Eberhardt & Siniff 1977). In order for mothers to reliably place pups into environments with favorable conditions during the juvenile-independence period, females need to have reliable cues to the year's polynya production level many months in advance given the species' long gestation period and the fact that females alter whether they give birth in a given year but not the general location where they give birth. We don't know what cues are available or used but do suspect that seals might gain information on sea-ice conditions during late-summer forays, from sensing the degree of mixing in the water column related to the strength of katabatic winds during late summer-early winter, and/or from some other yet-to-be determined source. However, given that pup production does indeed seem to vary according to the magnitude of primary production in the current year, these results should stimulate future work on the topic.

Trophic-level interactions in the Antarctic are of considerable interest for understanding marine ecosystem processes. Although there are relatively few trophic levels in the food chain in the Ross Sea ecosystem, the temporal responsiveness and the strength/direction of interaction between the trophic levels is comparatively poorly understood (Smith *et al.* 2007). Recent work has found some evidence for the within-season, top-down regulation of prey abundance through predation, e.g., Antarctic toothfish (*Dissostichus mawsoni*) by Weddell seals (Testa *et al.* 1985) and fish and krill by Adélie penguins (Ainley *et al.* 2004, 2006), and there is evidence for overlap between the trophic levels for some consumers that share prey items (Zhao *et al.* 2004). The degree of coupling between variations in primary production and vital rates of upper-trophic level consumers in Antarctic marine ecosystems is comparatively unknown (Smith, Ainley & Cattaneo-Vietti 2007). Penguin colony size has been demonstrated to be associated with the magnitude of primary production (Arrigo & van Dijken 2003). In contrast, recent work (Dugger *et al.* 2014) has suggested a lack of connection between variation primary production in the Ross Sea Polynya and reproductive parameters of Adélie penguin colonies on Ross Island.

High-latitude ecosystems are particularly susceptible to impacts of climate change. We have demonstrated a coupling between primary production in a coastal polynya and vital rates of an upper trophic-level consumer over a comparatively short time scale. The magnitude of primary production in a polynya is largely dependent on the extent of open water and, for coastal polynyas, the extent of open water is partially dependent on the strength of katabatic winds (Arrigo *et al.* 1998). Conditional on the relationship between the vital rates of Weddell seals and primary production suggested here, changes in the amount of open water in coastal polynyas could have an impact on the population by influencing the number of pups born into the nearby colonies. In March of 2000, an extremely large iceberg calved from the eastern Ross Ice Shelf fragmented, with pieces drifting into the southwestern Ross Sea. The accumulation of iceberg fragments prevented the normal advection of sea ice northward from the Ross Sea, which greatly diminished the amount of open water and reduced the magnitude of primary production for areas in the Ross Sea by as much as 95% (Arrigo *et al.* 2002). The reduction in primary production is associated with a dramatic drop in the number of Weddell Seal pups born into the same colonies studied here. The regional extent of sea ice and the future of the Ross Ice Shelf in the face of a changing climate are uncertain. Though sea ice extent has increased in recent years, recent work indicates that the increases are likely short-lived and predicts greatly diminished summer sea-ice extent in the future (Comiso *et al.* 2011; Smith *et al.* 2014). The impact of reduced sea-ice cover on primary production in polynyas is unique to each polynya as the timing and mechanism of polynya formation influences the degree of water-column stratification, composition of phytoplankton assemblage, and resulting timing and magnitude of primary production. Given the sensitivity of the number of pups to variation in primary productivity, we need to study how polynya productivity might relate (or not) to other aspects of population dynamics such as survival rates, movement in and out of the area, and to other species with different life histories. With such information, we can develop an ecosystem view and make broader predictions about responses to annual changes in ice dynamics, something that will be important to predicting high-latitude marine ecosystem responses to possible climate change.

Acknowledgements

Logistical support for fieldwork in Antarctica was provided by Lockheed Martin, Raytheon Polar Services Company, Antarctic Support Associates, the United States Navy and Air Force, and Petroleum Helicopters Incorporated. Animal handling protocol was approved by Montana State University's Animal Care and Use Committee (Protocol #2011-38).

Models: Pups ~ N(μ, σ^2)	ΔWAIC	R^2	α, intercept	McM_{t-1}, β_1	McM_t, β_2	Ross_{t-1}, β_3	Ross_t, β_4
1: $\mu = \alpha$	12.85	0.00	437.18 (366.65,504.95)				
2: $\mu = \alpha + \beta_1\ \mathrm{McM}_{t-1}$	9.92	0.21	438.53 (372.01, 502.86)	43.03 (-4.18, 121.04)			
3: $\mu = \alpha + \beta_2\ \mathrm{McM}_t$	4.84	0.47	440.72 (384.68,493.23)		79.95 (-0.15, 138.80)		
4: $\mu = \alpha + \beta_3\ \mathrm{Ross}_{t-1}$	12.99	0.00	437.12 (363.75, 506.92)			5.00 (-16.78, 56.19)	
5: $\mu = \alpha + \beta_4\ \mathrm{Ross}_t$	12.98	0.00	437.67 (366.48, 507.94)				0.83 (-30.58, 37.03)
6: $\mu = \alpha + \beta_1\ \mathrm{McM}_{t-1} + \beta_3\ \mathrm{Ross}_{t-1}$	11.36	0.09	437.94 (368.34, 505.33)	27.84 (-7.43, 116.94)		-0.36 (-51.05, 43.26)	
7: $\mu = \alpha + \beta_2\ \mathrm{McM}_t + \beta_4\ \mathrm{Ross}_t$	0	0.62	441.13 (396.54, 483.96)		108.17 (0.07, 163.34)		-49.54 (-101.59, 3.89)
8: $\mu = \alpha + \beta_1\ \mathrm{McM}_{t-1} + \beta_4\ \mathrm{Ross}_t$	11.21	0.13	438.90 (370.12, 502.04)	27.96 (-5.50, 111.21)			4.74 (-34.05, 56.92)
9: $\mu = \alpha + \beta_2\ \mathrm{McM}_t + \beta_3\ \mathrm{Ross}_{t-1}$	7.22	0.34	439.90 (383.07, 495.25)		63.60 (-1.74, 129.86)	7.86 (-38.04, 56.66)	

Table 2-1. Based on the fully Bayesian WAIC (Widely Applicable Information Criterion), the data strongly indicate that the number of pups produced in year *t* is best modeled as a function of primary productivity in the McMurdo polynya (McM) and Ross Sea polynya (Ross) at year *t*, Model 7 (ΔWAIC scores are calculated by subtracting the lowest score from all other scores [$\mathrm{WAIC}_{\mathrm{Model\ 7}} = 178.62$] such that the best-supported model has a ΔWAIC score of 0 and more poorly supported models have larger values.).

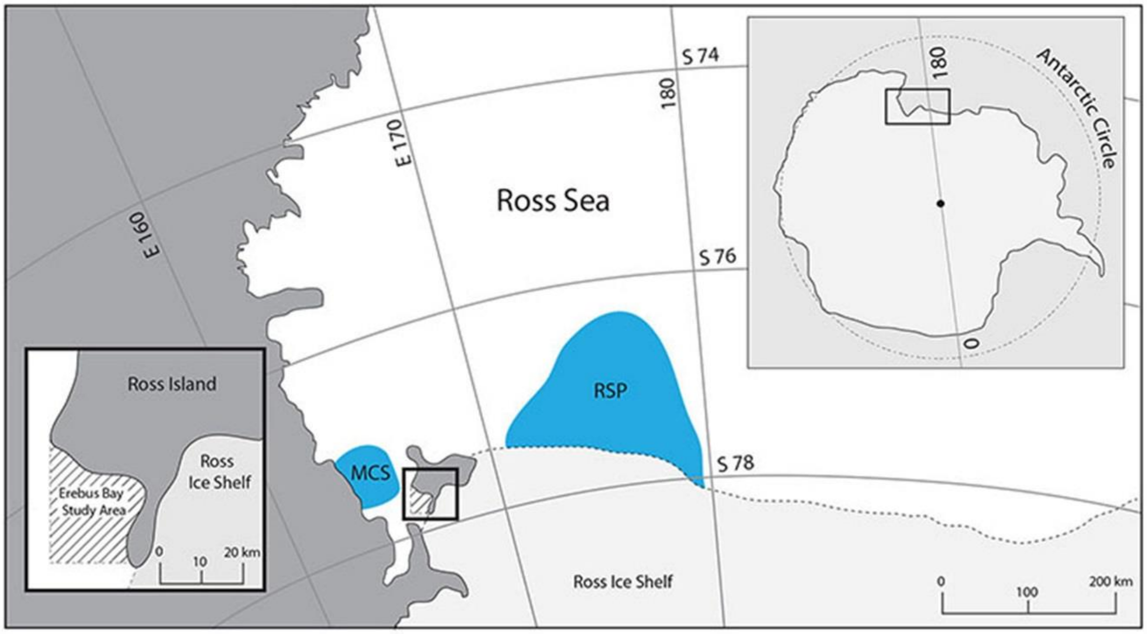

Figure 2-1. The Ross Sea hosts both the Ross Sea polynya (RSP) and McMurdo Sound polynya (MCS). Locations above are approximate as the areal extent of the polynyas demonstrates significant amounts of inter-annual variation. The long-term mark-recapture study has focused on the breeding colonies of Weddell seals in Erebus Bay, proximal to the Ross Ice Shelf and Ross Island.

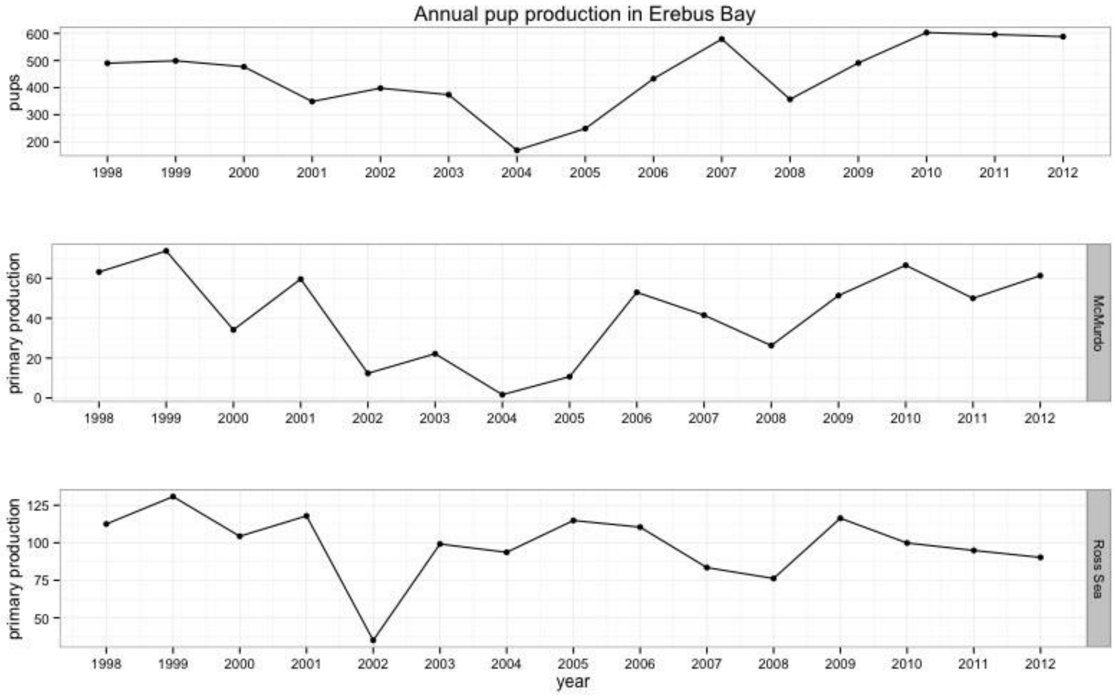

Figure 2-2. The number of pups born in the Erebus Bay seal colonies between 1997 and 2012 ranges from 169 (2004) to 603 (2007). Primary production (g C m^{-2} yr^{-1}.) in both the McMurdo Sound polynya and Ross Sea polynya demonstrates a high degree of inter-annual variability.

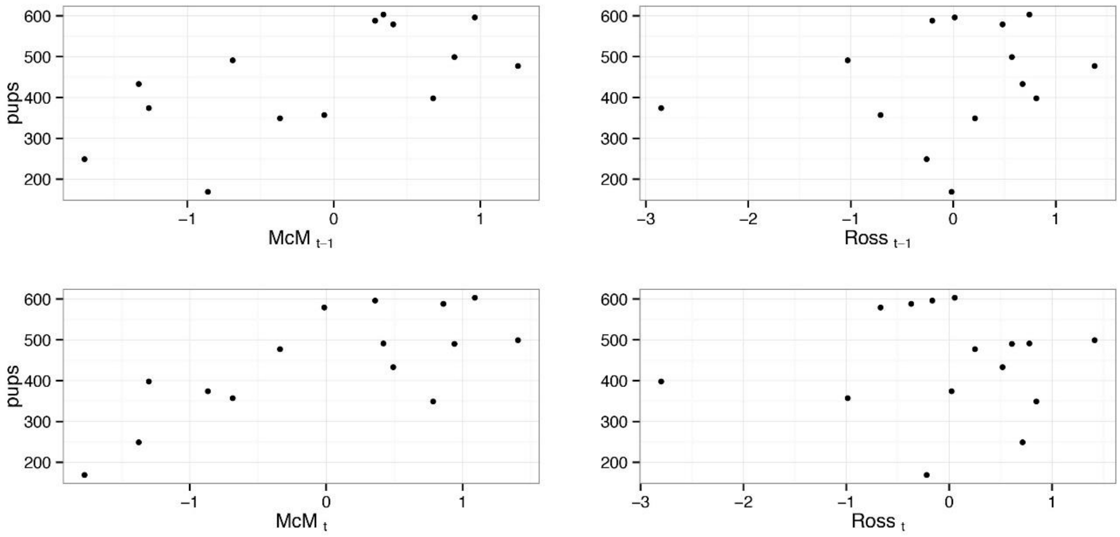

Figure 2-3. Scatterplots of standardized values of primary production in the McMurdo Sound (McM) and Ross Sea (Ross) polynyas for two time lags (year *t*-1 and *t*) against the number of Weddell seal pups born in year *t*.

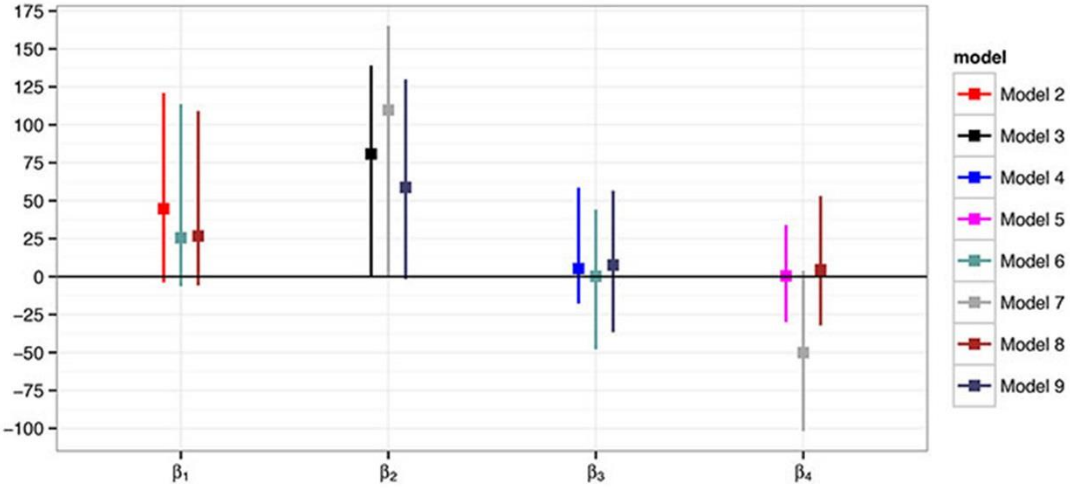

Figure 2-4. Model results comparing the different 95% credible intervals for the approximate distributions of the regression coefficients suggest a positive association between standardized values of primary productivity in McMurdo at time t-1 (β_1) and t (β_2) and the number of pups born in Erebus Bay at time t. There is comparatively little evidence for a relationship between the number of pups born in Erebus Bay and primary production in the Ross Sea polynya in year *t*-1 (β_3) and year *t* (β_4).

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CHAPTER THREE

PATTERNS OF AGE-RELATED CHANGE IN REPRODUCTIVE EFFORT DIFFER IN THE PRENATAL AND POSTNATAL PERIODS IN A LONG-LIVED MAMMAL

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Manuscript Information Page

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Journal of Animal Ecology

Status of Manuscript:
____ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
_x__ Published in a peer-reviewed journal

Published in the Journal of Animal Ecology on September 7, 2016. Issue 85.

Abstract

1. Age-related changes in maternal reproductive allocation for long-lived species are a key prediction from life-history theory.

2. Theoretical and empirical work suggests allocation may increase with age due to constraint (increases with experience) or restraint (increases with age in the face of declining residual reproductive value), and may decrease among the oldest-aged animals due to senescence in reproductive function.

3. Here we use a hierarchical modeling approach to investigate age-related patterns of change in maternal reproductive effort in the Weddell seal, a long-lived marine mammal with a protracted period of maternal care during which mothers allocate a large proportion of body mass while feeding little.

4. We find maternal allocation increases with age for young mothers during both the prenatal and postnatal periods. In contrast, older mothers demonstrate a senescent decline in prenatal allocation but allocate more of their declining resources to their offspring during the postnatal period. We also find strong evidence for the importance of individual effects in reproductive allocation among mothers: some mothers consistently produce heavier (or lighter) pups than expected.

5.Our results indicate that maternal allocation changes over a mother's reproductive lifespan and that age-specific differences differ in notable ways in prenatal and postnatal periods.

Key Words: Antarctica; Ross Sea; senescence; terminal allocation; reproductive allocation; Weddell seal

Introduction

The allocation of energy to reproduction is a central component of an organism's life-history, and has consequences for the fitness of both offspring and parent (Smith & Fretwell 1974; Roff 1992; Stearns 1992). Maternal allocation is linked to the growth and development of offspring and strongly associated with early survival (Skibiel, Dobson & Murie 2009; Skibiel, Speakman & Hood 2013; Baron *et al.* 2010). Moreover, the effects of early maternal allocation may be long-lasting. Empirical work suggests an association between the level of allocation and an offspring's future survival, recruitment and reproduction (Hackman *et al.* 1983; Kruuk *et al.* 1999; Lindström 1999; Lummaa & Clutton-Brock 2002; Lummaa 2003; Bateson *et al.* 2004), a connection likely mediated through the permanent response of critical body systems, e.g. the immune system, to the level of provisioning early in life (Lucas 1991; Hales & Barker 2001; Gluckman *et al.* 2005; McMullen *et al.* 2012). The amount of energy allocated to offspring is ultimately limited by the finite resources of the mother, and her ability to acquire and allocate those resources to reproduction (King, Roff & Fairbairn 2011). Therefore, environmental conditions may directly affect allocation strategies by varying resource availability (Schubert *et al.* 2009). However, there is ample evidence to suggest maternal allocation further varies according to maternal characteristics, such that the amount of energy allocated to offspring varies over the reproductive lifespan of the mother independently of the environment.

There is evidence for both within-individual increases (Gadgil & Bossert 1970; Curio 1983; Forslund & Pärt 1995) and decreases (Kirkwood & Austad 2000; Mysterud *et al.* 2001) in allocation over an individual's reproductive lifespan, and a series of non-mutually exclusive hypotheses relate the potential mechanisms at work. As individuals age, they commonly improve in reproductive performance as they acquire experience and skills, i.e., the constraint hypothesis (Curio 1983; Bowen *et al.* 2006). The reproductive restraint hypothesis (Gadgil & Bossert 1970; Pianka & Parker 1975) predicts that the degree of allocation is driven by the residual reproductive value (expected future fecundity) of an individual. Therefore, as individuals age, they should allocate more resources to current offspring in the face of fewer expected future reproductive events, i.e., the "terminal investment" hypothesis. When increases in reproductive allocation are not necessarily associated with fitness costs, the pattern of increasing allocation with age is "terminal allocation" (Weladji *et al.* 2010). In contrast, declines in reproductive performance for older animals may be driven by senescence (Medawar 1946; Williams 1957; Kirkwood 1981). These patterns are not mutually exclusive. Individuals undergoing senescent declines in some measures of reproduction or survival can demonstrate simultaneous increases in other measures of reproductive performance, e.g., in female moose (*Alces alces*) (Ericsson *et al.* 2001), and reindeer (*Rangifer tarandus*) (Weladji *et al.* 2010). Moreover, senescent declines in reproductive effort can be followed by increases in the same component of effort for the terminal breeding attempt

(Froy *et al.* 2013), or when the immune system of individuals is compromised (Velando, Drummond & Torres 2006). In addition to broad changes in patterns of allocation over the life of individuals, allocation may also vary over the shorter-term. In the face of finite resources, parental allocation is constrained by the canonical life-history trade-off between allocation to current offspring and potential consequences to survival and future reproduction (Stearns 1989, 1992; Roff 1992), leading to costs of reproduction. Thus, individuals' previous reproductive experience (either in terms of number of reproductive events or relative allocation of energy to those events (Creighton, Heflin & Belk 2009; Martin & Festa-Bianchet 2011) may affect current and future allocation independently from age-related patterns.

Variation in reproductive allocation at the population level is likely the result of within-individual changes in maternal allocation due to senescence, restraint, or constraint as well as between-individual differences due to selection, reproductive experience, and individual quality. When frail individuals die at higher rates with increasing age such that higher-quality individuals dominate at older ages, the average reproductive performance of survivors increases with age (Vaupel, Manton & Stallard 1979). The possibility that apparent increases with age might be due to selection underscores the importance of accounting for individual heterogeneity in the population. There is also compelling evidence for individual variation in reproductive traits, with females of similar life histories differing in key traits (Pol & Verhulst 2006; Stopher *et al.* 2008). Moreover, given that reproductive allocation might incur a cost, allocation patterns can also be mediated by the degree to which an individual can meet, and recover from, the energetic demands of current reproduction (van Noordwijk & de Jong 1986; Stearns 1989). Hence, latent variation in individual reproductive ability, and viability selection that preserves high-quality individuals can influence patterns of observed reproductive allocation, which highlights the need to account for individual effects when assessing reproductive allocation (Clutton-Brock 1984; Hamel *et al.* 2009).

In long-lived polygynous organisms, reproductive allocation can vary depending on offspring sex (Hewison & Gaillard 1999), maternal attributes such as age and experience (Derocher & Stirling 1998; Bowen *et al.* 2006), and environmental conditions (Garroway & Broders 2007). Moreover, prior work suggests that patterns of reproductive allocation within individuals may differ in the prenatal and postnatal periods (Lock *et al.* 2007; Weladji *et al.* 2010). In mammals, these two periods reflect the different physiological processes of gestation and lactation (Oftedal 1985). Prenatal allocation during gestation is reflected in litter size and offspring mass at birth (Millar 1977; Oftedal 1985; Gittleman & Thompson 1988; Boyd & McCann 1989; Ochoa-Acuña, Francis & Boness 1998), whereas offspring mass gains from birth through weaning should reflect postnatal maternal allocation during lactation (Gittleman & Thompson 1988; Pomeroy *et al.* 1999). Consequently, analyses of variation in offspring mass from parturition through weaning should be useful for evaluating hypotheses related to individual variation in allocation during two different periods (Robbins & Robbins 1979; Kovacs & Lavigne 1986; Derocher & Stirling 1998; Georges & Guinet 2000; Bowen *et al.* 2001).

The Weddell seal (*Leptonychotes weddelli)*, which inhabits the fast ice around the coast of Antarctica, is a model organism with which to investigate variation in maternal allocation. Females are large bodied, long-lived, have flexible reproductive schedules, produce a single offspring, and raise their young without assistance from males. They are highly philopatric to natal sites where they raise young in predictable colonies on the shore-fast ice during the austral spring (Stirling 1969). During the inferred 5- to 6-week lactation period, which is one of the longest among phocid seals (Schulz & Bowen 2005), females stay in close proximity to their pups and are readily approached by humans, which provides an excellent opportunity to assess maternal masses for a large sample of mothers. Females largely fast through the lactation period, implying postnatal allocation of energy to offspring is predominately derived from body reserves acquired prior to parturition (Wheatley *et al.* 2006). Moreover, energy transfer from mom to pup is both dramatic and variable with females losing, on average, 40% of their post-partum mass, and pups more than tripling their birth weight during the lactation period (Wheatley *et al.* 2006).

Here, we used the mass of mothers and pups soon after parturition, and the rate of mass gain during early lactation (parturition to ~ 20 days) and late lactation (~ 20 to ~ 35 days) to assess patterns of reproductive energy allocation during both the prenatal and postnatal periods. In doing so, we evaluated the relative support for a variety of evolutionary hypotheses regarding allocation of energy to offspring. Reproductive constraint will be supported if reproductive allocation increases with reproductive experience and/or age for the younger mothers. Senescence will be supported if reproductive allocation decreases with age for older mothers. In contrast, an increase in reproductive allocation with age would support terminal allocation. We used a large sample of pups from known-age mothers, and a separate, smaller sample of known-age mothers from approximately the same period. We evaluated the functional relationship between maternal post-parturition mass and maternal age (updating previous work (Proffitt *et al.* 2007) with a larger data set). We then compared the pattern of maternal masses with age to the pattern of pup parturition masses and mass gains during early and late lactation with maternal age. Furthermore, while controlling for key offspring characteristics, we assessed the influence of maternal breeding experience and reproductive experience the previous year on post-parturition pup masses and daily gains during early and late lactation to test for more complicated patterns of prenatal and postnatal allocation separate from maternal age.

Materials and Methods

Study System

This study was conducted on the population of Weddell seals that inhabits Erebus Bay, located on the west coast of Ross Island, Antarctica. Sea ice accumulation in Erebus Bay during the austral winter covers the bay with thick sea ice. During the austral spring, Weddell seals use tidal cracks to haul out onto the sea ice to give birth in 8-14 pupping colonies (Stirling 1969). These animals are highly philopatric, and the probability of a female who recruited to the breeding population subsequently breeding elsewhere is extremely low (Cameron *et al.* 2007; Hadley, Rotella & Garrott 2007). Moreover, the on-ice detection rate is extremely high (~1.0), ensuring that all mother-pup pairs are detected each year (Hadley *et al.* 2006). Each year ~400-500 pups are born during the pupping season from mid-October through November (Cameron & Siniff 2004). Since 1969 newborn Weddell seal pups have been marked with individually numbered tags in the inter-digital webbing of each hind flipper (Siniff *et al.* 1977). Broken and missing tags of adult seals have been replaced throughout the years to maintain a database of known-age animals. Since 1973, six to eight mark-resight surveys have been conducted throughout the study area each year, beginning in early November. At the time of tagging and during each survey, the date, location, tag numbers and relative's tag numbers were recorded into the long-term database.

Pup and Maternal Mass Measurements

Pup mass measurements were obtained during the 2004 through 2014 field season (October 10 through December 10). Pupping colonies were surveyed every 24 to 48 hours to identify newborn pups. Pups from known-age females were opportunistically selected for mass measurements with an attempt to distribute the sample throughout the pupping season and among as broad a distribution of maternal ages as possible, with priority given to known-age females with pups already in the mass study. Pups judged to be 24 to 72 hours old, based on the presence of a frozen placenta and condition of the umbilicus, were selected for sampling and weighed. Considerable effort was made to locate these pups again at 20 and 35 days post-parturition for additional mass measurements, near the middle and end of the lactation period, respectively (Wheatley *et al.* 2006). However, due to weather and logistical constraints in the study area, not all pups were weighed at exactly 20 and 35 days. As a result, early lactation mass measurements were obtained from 16-26 days; late lactation masses were obtained from 29 to 41 days. Only pups with all three measurements are included in this study (n=856 animals over 11 years). Preweaning survival in these pups is very high (0.79 to 0.98, depending on birth timing and maternal characteristics (Proffitt, Rotella & Garrott 2010), thus pups that were missing measurements were most likely simply not observed during surveys, rather than dead. Daily mass gains from parturition to early lactation were calculated as the difference in mass measurements divided by the number of days between the measurements; daily mass gains from early lactation to late lactation were similarly calculated. This method explicitly linearizes the mass gains during the lactation period. Maternal mass measurements were made close to parturition (within two days) over the same period (2004 to 2014, excluding 2013) on a subset of mothers (n=321 measurements on 214 animals) using a digital weighing platform and subject to the same survey protocols, i.e. sampling frequency and age stratification.

Maternal Attributes

We investigated a variety of dynamic and static features of mothers. Maternal age was a covariate of central interest and we investigated its relationship to maternal and pup mass using a variety of functional forms. A female's reproductive status in one season may affect reproductive allocation to future reproduction either negatively through reproductive costs (Hirshfield & Tinkle 1975; Guinness, Albon & Clutton-Brock 1978; Festa-Bianchet, Gaillard & Jorgenson 1998; Hadley *et al.* 2007) or positively if females that reproduce often are also those that are better at acquiring resources for recovering from past reproduction and preparing for future reproduction (Clutton-Brock 1984). We therefore developed two measures of breeding experience. The first covariate was a categorical measure of a female's maternal state in the previous year using the categories: prebreeder (never reproduced: individual ages ranging from 5 to 14), first-time breeder (reproduced for the first time last year, ages 6 to 13), an experienced breeder who pupped (ages 7 to 31), or an experienced breeder who skipped reproduction (ages 7 to 29). This covariate was used to assess a potential relationship between allocation in the previous year and allocation in the current year. The second covariate, number of previous pups, was a measure of the number of pups born to a mother in all previous years. Initial work on this data set suggests parity is highly correlated with maternal age, making the results of regression difficult to interpret. Therefore, we developed this metric as an age-specific measure of reproductive experience (and therefore useful as an index of individual quality), constructed by centering a female's number of previous pups using the mean number of previous pups for that maternal age.

Pup Attributes

The timing of parturition within a season has been shown to be associated with offspring mass in seals (Boltnev & York 2001; Bowen *et al.* 2001, 2004). In particular, unpublished work from this study suggests that the largest pups are born near the mean date of birth (October 28) with smaller pups born earlier and later. We thus used a quadratic form for the influence of the timing of birth on pup mass. Similar to the maternal age covariate, we centered parturition dates using the mean, and then squared it to produce thxe quadratic term. We included a binary variable that indicated if a pup was female or not. Offspring parturition mass is considered an indicator of pre-natal maternal allocation (Oftedal 1985; Kovacs & Lavigne 1986; Ochoa-Acuña *et al.* 1998) and has been positively correlated with post-parturition mass gain and weaning mass (Hill 1987). To more clearly partition potential maternal effects associated with in-utero maternal allocation from those associated with post-parturition maternal allocation through lactation, we included pup parturition mass (centered using the mean) as a covariate in analyses of early and late lactation daily mass gains. Finally, because Weddell seal pups gain mass rapidly throughout the lactation period (Wheatley *et al.* 2006) and weather and logistical delays sometimes forced us to weigh pups 1-3 days after parturition, we used deviation from the target age (DTA, or days since birth) to account for variation in pup weight due to the timing of weighing.

Random Effects

Individual phenotypic variation can have profound effects on the degree of maternal allocation in seals (Lunn, Boyd & Croxall 1994; Mellish, Iverson & Bowen 1999) and for many mothers considered here, we had multiple measures of post-parturition maternal mass at different ages and mass data from multiple offspring. To account for phenotypic variation and the unbalanced repeated-measures data structure, we included a random effect for maternal identity in models of post-parturition pup mass, and both early and late lactation daily mass gain (simple adjustment to the intercept). We also included a random effect of year (simple adjustment to the intercept) to model inter-annual variation in maternal allocation that may reflect changing environmental conditions. We did not have a sufficient number of repeated maternal mass measurements across years to support a random effect for maternal identity in models of post-parturition maternal mass, and we treated each observation as independent.

Statistical Analysis

We utilized a Bayesian hierarchical modeling approach to investigate patterns of maternal and pup masses in relation to static and dynamic attributes of both the mother and pup. We were primarily interested in evaluating the relative support for each of five functional forms for maternal age in each of the four model suites, conditional on the inclusion of a modest number of maternal and pup characteristics as covariates in each model. For comparison, we included a null model that included all covariates except maternal age. We evaluated the relative support for linear, quadratic, logarithmic, single threshold, and double threshold models. Linear models allow for a constant positive, negative or no relationship between the response and maternal age. In contrast, quadratic and logarithmic models allow for changes in the response with age such that the magnitude of the change (slope of the curve) itself varies, with the former allowing for an initial improvement with age followed by a subsequent decline and the latter allowing for an increase with maternal age for the youngest animals followed by more modest increases with age. In contrast to the smooth curves implied by the quadratic and logarithmic models, threshold models (also known as piecewise, or segmented models) allow for different relationships on either side of the threshold (or breakpoint), e.g., Weladji et al. (2010). Here, we used single threshold and double threshold models with linear relationships on either side of each threshold. The former allows for a linear increase/decrease in the response variable with maternal age up to the threshold, followed by a separate linear increase/decrease. Double threshold models allow for similar relationships between two thresholds, and could, for example, be used to model a steady increase in a trait, to a plateau, and subsequent decline. *A priori*, we restricted the different linear relationships to be continuous at the thresholds such that the slope of the lines changed on either side of a threshold, but not the intercept, i.e. we did not allow for disjointed line segments in our models. A strength of our Bayesian approach is that the thresholds are themselves treated as model parameters to be estimated from the data, yielding a straightforward measure of uncertainty that is easy to incorporate into model selection and prediction.

We used a similar approach for the four distinct suites of mass measurements: post-parturition maternal mass, post-parturition pup mass, and daily mass gains during early and late lactation were each separately modeled using a Gaussian error structure (with variance σ^2) with the mean a function of maternal and pup characteristics (Appendix 1, Supporting Information). We investigated the use of shrinkage priors on all model coefficients and their effect on our inference, specifically Bayesian interpretations of ridge (Hoerl & Kennard 1970), lasso (Park & Casella 2008) and horseshoe (Carvalho, Polson & Scott 2010) regularization methods. The results were nearly identical, and we present here the results using comparatively diffuse priors. For each of the regression coefficients for the fixed effects (maternal and pup characteristics), we used independent, vague normal priors. We assumed the random effects were drawn from independent normal distributions with means equal to 0 and standard deviations (σ_{mother}, σ_{year}). We used independent inverse-gamma priors for each variance parameter within each model ($\sigma^2_{mother,}$ σ^2_{year}, and σ^2). For the single threshold models we assigned uniform priors for the threshold, defined from maternal age 6 to 29. For double threshold model, it is necessary to specify two ranges for potential thresholds, and we used uniform priors defined from ages 6 to 17 for the first threshold and from ages 17 to 29 for the second threshold.

We fit all models using the runjags package (Denwood *et al.* 2016), which serves as an interface to the JAGS software (Plummer 2003), to implement MCMC sampling in the R programming environment (R Core Team 2015). Four chains were run for each model with 60 000 samples per chain, and 10 000 samples discarded as burn-in, resulting in 50 000 samples per chain used for posterior inference. Posterior convergence was assessed both graphically and with the Gelman-Rubin statistic (Gelman & Rubin 1992), $\hat{R}$ (convergence assumed for values $\hat{R} < 1.01$). Model fit was assessed using: 1) a posterior predictive check comparing the sum of squared residuals for the observed data to that for replicated data generated under the model, and 2) a graph of the residuals plotted against maternal age to check if model fit was driven by the comparatively larger number of young animals or if model fit was reasonable across maternal ages.

We used the fully Bayesian Watanabe-Akaike information criterion (WAIC) to estimate the relative predictive ability of each model in the four model suites (Watanabe 2010;

Hooten & Hobbs 2015). There is some question as to what constitutes predictive ability (as assessed by various information criteria) in the presence of within- and between-individual variation and imbalanced data (Vaida & Blanchard 2005; Gelman, Hwang & Vehtari 2014), and we acknowledge we are using WAIC to compare models across all levels of variation. We assessed the relative support for each model using ΔWAIC values, similar in interpretation to ΔAIC values. We also assessed model fit using a hierarchical implementation of the classical R^2 (Nakagawa & Schielzeth 2013).

Results

We found strong evidence that both maternal and pup masses near parturition initially increased with maternal age and then declined for older mothers (Table 3-1). Specifically, we found that as maternal age increased post-parturition masses initially increased and then eventually decreased for both mothers (quadratic form: $\beta_{\mathrm{MaternalAge}}=6.02$, se=0.83; $\beta_{\mathrm{MaternalAge}^2} = -0.54$, se=0.12) and pups (quadratic form: $\beta_{\mathrm{MaternalAge}}=0.22$, se=0.05; $\beta_{\mathrm{MaternalAge}^2} =-0.024$, se=0.006) (Table 3-2). Based on results from the fixed effects, post-parturition maternal mass for an experienced mother who had a pup last year and had an average amount of breeding experience is expected to average 395 kg (90% credible interval, CI: 376, 414) at age 7, peak at 480 kg (469, 490) at age 20, and decline to a minimum of 442 kg (412, 471) at age 28. Similarly, predicted post-parturition masses for pups increased from 29 kg (28, 30) for 7-year old mothers (with a predicted mass of 395 kg (376, 414)), peak at 32 kg (31, 33) for 18-year old mothers (with a predicted mass of 479 kg (468, 489)), and decline to 28 kg (25, 30) by the maternal age of 31 (with a predicted mass of 410 kg (365, 454)). Furthermore, we found that pups born to experienced mothers who skipped reproduction last year had slightly higher parturition masses compared to pups born to experienced mothers who had a pup last year, suggesting a potential cost of reproduction. The close correspondence in the patterns of change (increase, peak, and decline with increasing maternal age) for post-parturition masses of mothers and pups strongly suggest early-life improvements in maternal allocation, which is consistent with the constraint hypothesis, and senescent declines in energy allocation late in life.

In striking contrast, results for the postnatal period indicate that old mothers allocate proportionally more of their body reserves than younger, heavier mothers. The most heavily supported functional form of maternal age in models of daily gains during early lactation was the single-threshold model. Daily mass gains during early lactation increased with maternal age rapidly among the youngest mothers up to the threshold of approximately 12 years (threshold=11.9, se=0.84) ($\beta_{\mathrm{MaternalAge}}$=0.09, se=0.02), then continued to increase with maternal age at a diminished rate ($\beta_{\mathrm{MaternalAge}}$=0.01, se=0.006). During the late-lactation period, the most supported model used the logarithm of maternal age and suggests daily gains increase with maternal age to a pseudo-threhold ($\beta_{\mathrm{log(MaternalAge)}}$=0.16, se=0.05). Pups born to younger (and therefore lighter) mothers are predicted to have lower post-parturition masses than prime-aged mothers and the *lowest* daily gains throughout lactation, whereas pups born to older (and also lighter) mothers also have lower post-parturition masses but have the *highest* daily gains throughout lactation (Figure 3-1). It is the combination of post-parturition mass and daily mass gain through late lactation that determines weaning mass. Thus, based on predictions from the fixed effects portion of models for parturition through late lactation, we find evidence that pups born to older mothers experience increased gains throughout lactation such that the gap in birth masses is diminished by late lactation.

A mother's age-specific breeding experience had a strong, positive relationship with her pup's post-parturition mass ($\beta_{NPreviousPups}$=0.28, se=0.10) but not to subsequent daily gains during early or late lactation. Thus, mothers with greater-than-average reproductive experience for their age give birth to heavier pups but do not allocate more resources to their offspring in the post-natal period. In contrast, a mother's reproductive status in the previous year was strongly associated with the daily gain during both early and late lactation. Notably, pups born to mothers who were prebreeders last year had daily mass gains during early lactation that were lower than those for mothers of any other reproductive class. During late lactation, both mothers who were prebreeders or first-time breeders last year had lower mass gains than experienced mothers who either pupped or skipped last year (Table 3-2). The estimated differences in gains have a marked impact on pup mass late in lactation. For example, a pup born to an inexperienced mother who was a prebreeder last year is predicted to weigh 3.3 kg and 7.9 kg less than a pup born to an experienced mother who pupped last year by 20 and 35 days post-parturition, respectively.

Pup characteristics were also related to parturition mass and mass gain. There was a quadratic effect of deviation from the mean birthdate of October 28 in this data set

($\beta_{\text{Birthdate}}$=0.11, se=0.03; $\beta_{\text{Birthdate}}{}^{2}$=-0.012, se=0.004), suggesting pups born earlier in October and later in November were born smaller than those near the mean birthdate. However, birth date was not associated with subsequent mass gains. Pups that were heavier than the mean at birth also had slightly higher daily gains through the early lactation period ($\beta_{\text{PaturitionMass}}$=0.03, se=0.004) such that the mass discrepancy at birth widened during early lactation. For a pup with a particularly heavy post-parturition mass (5 kg above the mean), this would translate into a gain of an extra 3 kg during early lactation. We did not find evidence that parturition mass or mass gains differed between male and female pups.

We found compelling evidence for high variance of individual maternal effects (Figure 3-2). Estimated standard deviations for the random effect of maternal identification (simple additive effect) were large for models of post-parturition pup mass (σ_{mom}=1.89 kg) as well as for daily gains made during early lactation (σ_{mom}=0.28 kg/day) and late lactation (σ_{mom}=0.28 kg/day). These effects translate into substantial differences in pups born to mothers with different identities but that were alike in other respects. For example, pups born to mothers with the 95th percentile (1.86 kg) and 5th percentile (-1.62 kg) estimated random effects for maternal identity on post-parturition pup mass are estimated to have a birth mass difference of 3.48 kg, or approximately 12% of the mean parturition mass (30.06 kg). Similarly, the difference between the 95th percentile and 5th percentile point estimates for the effect of maternal identity on early and late lactation daily gains correspond to differences of 0.64 kg/day and 0.55 kg/day, respectively, which results in differences in pup masses of approximately 12.8 kg over 20 days, and 8.25 kg from 20 days to 35 days. In comparison, we found evidence that expected values for pup mass and mass gain were quite consistent among years (post-parturition maternal mass - σ_{year}=11.59 kg; post-parturition pup mass - σ_{year}=0.83 kg; daily gains in early lactation - σ_{year}=0.06 kg/day; daily gains during late lactation - σ_{year}=0.13 kg/day). The inclusion of the two random effects explained as much or more of the variance compared to the fixed effects alone (Table 3-1).

The residuals plotted against maternal age (Figure A1, Appendix A) indicate that the top models for each response variable were appropriate: no pattern in the residuals (particularly at older ages) suggests that the model fit across maternal ages. The more general posterior predictive check (Figure A2, Appendix A) also indicates that the top models had an appropriate fit to the data.

Discussion

The pattern of energy allocation in the prenatal period demonstrated here provides clear evidence for age-related increases in reproductive energy allocation for younger mothers and senescent declines for older mothers. We demonstrated that the masses of both mothers and pups soon after parturition increased early in a mother’s reproductive life, peaked in the late-teens, and then decreased in old age. The increase in maternal mass early in a mother’s reproductive lifespan is consistent with previous work in pinnipeds and other species (McLaren 1993; Arnbom, Fedak & Rothery 1994; Festa-Bianchet *et al.* 1996; Bowen *et al.* 2006; Weladji *et al.* 2010; Hamel, Craine & Towne

2012) and likely reflects the continued somatic growth after first reproduction, as well as increased experience consistent with the constraint hypothesis. The senescent decline in maternal mass documented here is consistent with that demonstrated for some ungulates (Weladji *et al.* 2010; Nussey *et al.* 2011), but contrasts with previous results for grey seals (Bowen *et al.* 2006), which found senescent declines in several measures of reproductive energy allocation but no evidence for a decrease in maternal mass close to parturition. The proximate causes of a senescent decline in maternal body mass could be due to diminished foraging efficiency connected to age-related declines in muscle function (Hindle *et al.* 2009a; b), and the resultant difficulty of meeting the higher maintenance costs associated with a larger mass (Innes *et al.* 1987; Pomeroy *et al.* 1999).

Regardless of the causes of age-related improvements and declines in maternal body mass, our results indicate that these changes transfer over to the birth mass of offspring, i.e., pup mass close to birth in relation to maternal age follows the same pattern that maternal mass does close to birth. This finding is consistent with previous work on a diversity of species indicating maternal condition near parturition is a strong correlate of offspring size (Fedak, Arnbom & Boyd 1996; Pomeroy *et al.* 1999; Keech *et al.* 2000; Parker & Loiselle 2002; Adams 2005; Bowen *et al.* 2006). The amount of energy a mother can allocate to her offspring in the prenatal period may be sharply limited by in-utero physiological constraints (Clutton-Brock 1984), such as an allometric relationship between body weight and metabolic rate (Loison & Strand 2005), which limits the ability of an organism to increase allocation. However, we also found strong evidence for individual effects on prenatal allocation, which suggests that individuals vary in terms of how they allocate resources. These individual effects are likely the combination of both static and dynamic traits *sensu* Cam and Monnat (2000), with the former (a measure of quality) potentially influencing the latter (time-varying, unmeasured covariates such as maternal mass or body length). The modest, positive relationship between post-parturition pup mass and age-specific breeding experience suggests that more experienced individuals allocate more energy than less experienced individuals of the same age (consistent with the constraint hypothesis), though we cannot rule out changes in metabolic efficiency. Moreover, we found very strong evidence for strong individual maternal effects on pup masses near parturition. The heaviest pups, therefore, tend to be born to prime-aged mothers with above-average breeding experience and a large, positive individual effect.

The pattern of variation in reproductive energy allocation with maternal age is sharply different in the postnatal period than that found in the prenatal period. The data strongly suggest that the amount of mass gained each day by pups during early lactation and late lactation increases with maternal age, increasing sharply among the youngest mothers and more modestly among older mothers. The increase in postnatal allocation early in maternal life likely reflects increases in maternal body mass and energy transfer to the pup (Wheatley *et al.* 2006). The fact that the single-threshold model was most supported for daily gains during early lactation, whereas the logarithmic model was most supported for the late lactation period, most likely reflects a more dramatic increase in daily gains with maternal age during early lactation, i.e. the improvement in reproductive performance is larger than can be well-modeled using the more gradual logarithmic model. Biologically, we can speculate that the reproductive performance of younger, lighter females improves more dramatically during early lactation with age as their own mass increases. As the body reserves of mothers continues to decline through late-lactation, the improvement in performance with age is more gradual and reflects the ability of mothers to nurse a pup through the long lactation period. In contrast to results for younger mothers, the senescent decline in maternal body mass near parturition for older mothers demonstrated here, combined with the increased allocation for the oldest ages indicates that older (and thereby lighter) mothers are allocating proportionally more energy to their offspring than prime-age or younger mothers, consistent with terminal allocation. This cross-sectional study could not directly assess the presence of a cost of reproduction associated with this increased allocation, which, if present, would support the terminal investment hypothesis (Weladji *et al.* 2010). In addition to the age-related pattern of postnatal energy allocation, we demonstrated strong evidence for individual effects on the allocation during the postnatal period. Together, these results indicate that older mothers with above-average individual effects are the females that allocate the most resources to their offspring.

The influence of the reproductive status of the mother in the previous year strongly suggests that postnatal energy allocation is higher for experienced mothers but not appreciably different for experienced mothers that either skipped reproduction or had a pup last year. Reproductive skipping has been proposed as an adaptive tactic for low-quality individuals (Cam *et al.* 1998), i.e., skipping allows a mother to acquire or conserve resources necessary to support offspring lactation, and found to help avoid the survival-reproduction trade off (Cubaynes *et al.* 2011). In our study population, some individuals simply breed more often and yet still produce pups of typical quality (Chambert *et al.* 2013). Our work demonstrates that postnatal energy allocation to pups is roughly equal for experienced mothers who skipped reproduction in the previous year and those that had pups. Interestingly, we have some evidence that pups born to experienced mothers who skipped last year have a slightly higher post-parturition mass, compared to mothers who pupped last year. Together, these results suggest that skipping might be a means to ensure that a female has sufficient reserves to produce a pup, i.e., some females require additional time to acquire resources to support lactation.

We have shown a stark contrast in reproductive energy-allocation patterns during the prenatal and postnatal periods. Though younger mothers increase allocation with age during both periods, we find that older mothers have senescent declines in allocation during the prenatal period, followed by an increase in postnatal energy allocation, which is consistent with terminal allocation. In contrast to energy allocation in the prenatal period (which may be tightly constrained), allocation in the postnatal period appears to be more flexible and a function of breeding experience and maternal age. This could reflect more opportunities for differences due to variation in maternal care attributes, e.g., characteristics of lactation such as efficiency or milk quality (Anderson & Fedak 1987; Arnbom, Fedak & Boyd 1997; Mellish *et al.* 1999), which this study cannot address. Moreover, the importance of individual maternal effects shown here suggests individual-level variation in postnatal energy allocation performance, a result reported previously in other pinnipeds (Mellish *et al.* 1999; Lang, Iverson & Bowen 2009) as well ungulates

(Wolcott, Reitz & Weckerly 2015). This increase in postnatal allocation amongst the oldest mothers results in pup weaning masses commensurate with those from prime-aged mothers, implying that older mothers are compensating for diminished birth masses by increasing their energy allocation during lactation. This indicates that reproductive allocation changes over the length of a mother's reproductive lifespan as well as within a single reproductive cycle as a function of age.

The age-related variation in energy allocation that we have shown in Weddell seal mothers has important consequences for population dynamics. Previous work across a variety of species has demonstrated that offspring weaning mass is positively associated with both juvenile survival (Wauters, Bijnens & Dhondt 1993; McMahon, Burton & Bester 2000; Côté & Festa-Bianchet 2001; Ailsa, Bernie & Barker 2001; Proffitt, Garrott & Rotella 2008) and future reproductive success (Festa-Bianchet, Jorgenson & Réale 2000; Bowen *et al.* 2015). Our results imply that the pups with the highest weaning mass are born to experienced, prime-aged and older mothers with above-average individual effect on parturition masses and daily mass gains through the lactation period. Such pups would be expected to survive better than others given previous results that indicate that pup survival increases with maternal age in a pseudo-threshold form in our study population (Hadley *et al.* 2007). However, nursing and weaning a heavy pup during a senescent decline has implications for maternal survival; the increased allocation could cause mortality to increase in addition to the actuarial senescence arising from declining physiological function.

Acknowledgments

We thank the many graduate students and field technicians who have collected data on this project. This project was supported by the National Science Foundation, Division of Polar Programs (grant no. ANT-1141326 to J.J.R., R.A.G. and Donald B. Siniff) and prior NSF Grants to R.A.G., J.J.R., D.B.S. and J. Ward Testa. Logistical support for fieldwork in Antarctica was provided by Lockheed Martin, Raytheon Polar Services Company, Antarctic Support Associates, the United States Navy and Air Force, and Petroleum Helicopters Incorporated.

Model	**Form**	**ΔWAIC**	**R^2_m**	**R^2_c**
Post-parturition maternal mass				
	Null	46.54	0.13	0.18
	Linear	22.01	0.21	0.23
	Quadratic	0	0.24	0.30
	Logarithm	7.45	0.23	0.27
	1-threshold	7.11	0.24	0.28
	2- threshold	6.95	0.24	0.29
Post-parturition pup mass				
	Null	27.19	0.12	0.36
	Linear	18.58	0.13	0.37
	Quadratic	0	0.15	0.40
	Logarithm	7.46	0.14	0.39
	1-threshold	9.89	0.17	0.40
	2- threshold	3.67	0.15	0.39
Early-lactation gain				
	Null	49.68	0.24	0.54
	Linear	22.34	0.28	0.57
	Quadratic	14.81	0.29	0.57
	Logarithm	6.72	0.29	0.58
	1-threshold	0	0.30	0.58
	2- threshold	0.83	0.30	0.58
Late-lactation gain				
	Null	10.89	0.09	0.34
	Linear	4.20	0.11	0.35
	Quadratic	5.62	0.11	0.36
	Logarithm	0	0.11	0.36
	1-threshold	1.92	0.11	0.36
	2- threshold	1.73	0.11	0.36

Table 3-2. Model comparison results using ΔWAIC (Widely Applicable Information Criterion, which has a similar interpretation to ΔAIC scores) and both marginal R^2 (fixed effects) and conditional R^2 (fixed and random effects) values. Lower ΔWAIC scores suggest more parsimonious and better-predicting models.

	Post-parturition maternal mass (kg)	**Post-parturition pup mass (kg)**	**Early-lactation gain (kg/day)**	**Late-lactation gain (kg/day)**
Intercept	**463.61 (6.27)**	**30.96 (0.41)**	**2.31 (0.05)**	**1.50 (0.13)**
Maternal age[‡]	**6.02 (0.83)**	**0.22 (0.05)**		
(Maternal age)^2	**-0.54 (0.12)**	**-0.024 (0.006)**		
log(Maternal age) [‡]				**0.16 (0.05)**
threshold model				
Maternal age[‡]**, age < threshold**			**0.09 (0.02)**	
Maternal age[‡]**, age ≥ threshold**			**0.01 (0.006)**	
threshold‡			**11.91 (0.84)**	
First-time last year[*]	6.57 (14.14)	-0.09 (0.65)	-0.06 (0.08)	**-0.27 (0.10)**
Prebreeder last year	-2.18 (12.19)	-0.80 (0.57)	**-0.17 (0.07)**	**-0.30 (0.09)**
Experienced, skipped last year	-3.87 (6.59)	**0.66 (0.32)**	0.07 (0.04)	-0.03 (0.05)
No. previous pups	3.44 (2.07)	**0.28 (0.098)**	-0.02 (0.01)	-0.006 (0.02)
DTA		**1.81 (0.48)**		
Birthdate[‡]		**0.11 (0.030)**	0.002 (0.003)	-0.004 (0.005)
(Birthdate)^2		**-0.012 (0.004)**	0.00 (0.00)	0.00 (0.001)
Post-parturition pup mass			**0.031 (0.004)**	0.001 (0.005)
Sex – female		0.12 (0.26)	0.02 (0.03)	0.00 (0.04)
σ_{mother}		**1.89 (0.21)**	**0.28 (0.02)**	**0.28 (0.03)**
σ_{year}	**11.51 (6.10)**	**0.83 (0.35)**	**0.06 (0.03)**	**0.13 (0.05)**
σ	**46.89 (1.93)**	**3.26 (0.12)**	**0.35 (0.01)**	**0.50 (0.02)**

Table 3-3. Regression coefficient estimates (mean of the approximate posterior distribution, standard error in parentheses) for factors influencing post-parturition maternal mass, post-parturition pup mass, daily gain through early lactation, and daily gain from early through late-lactation. Coefficients in bold are those for which the 95% credible interval does not include zero. [‡]The linear predictor was first centered and then squared to produce quadratic covariates; maternal ages were transformed by subtracting the minimum age and adding a small constant for the logarithmic form. ‡All models were fit using centered maternal ages, this threshold has been back-transformed to the original scale to aid interpretation. [*] The reference level for reproductive experience is a mother who was experienced and had a pup last year.

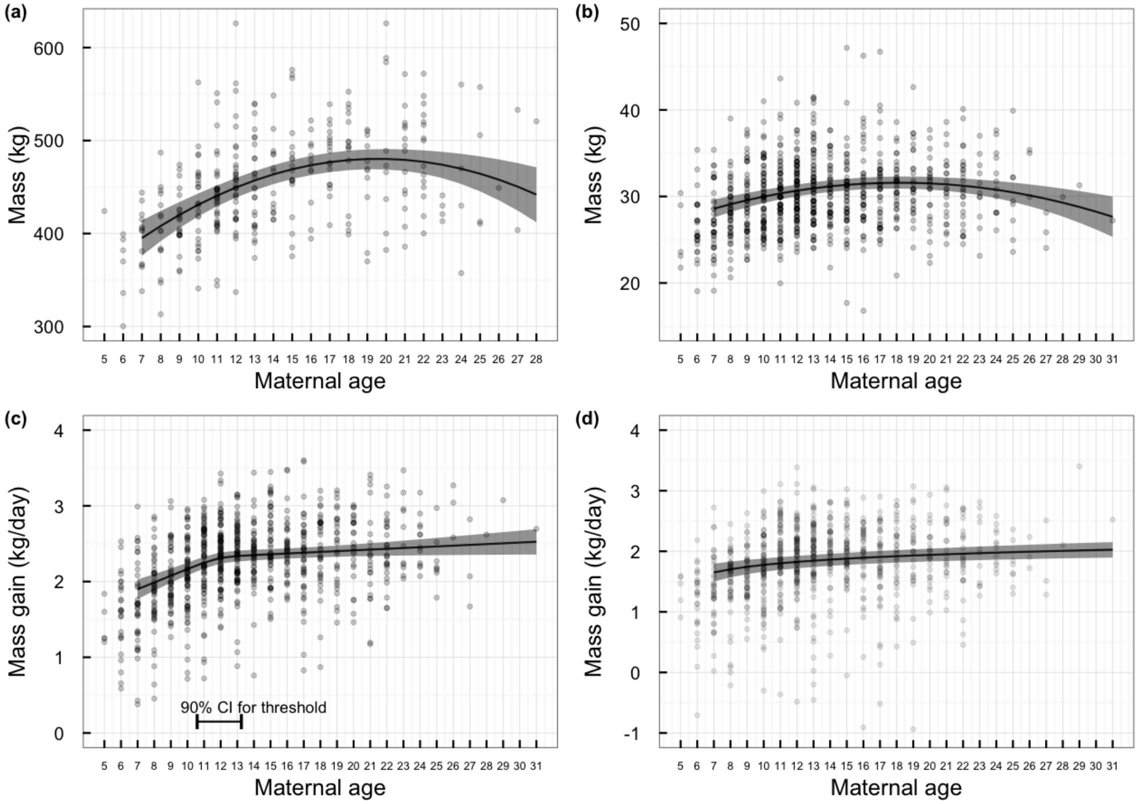

Figure 3-1. Posterior credible intervals (90%) for the mean response (using approximate posterior distributions for fixed-effects regression parameters) for: (a) post-parturition maternal mass, (b) post-parturition pup mass, (c) daily gains during early lactation, and (d) daily gains during late lactation. The predicted intervals are for an experienced mother who pupped last year (minimum age of 7 years in this data set) and a male pup (b through d), with all other variables held to the mean (0).

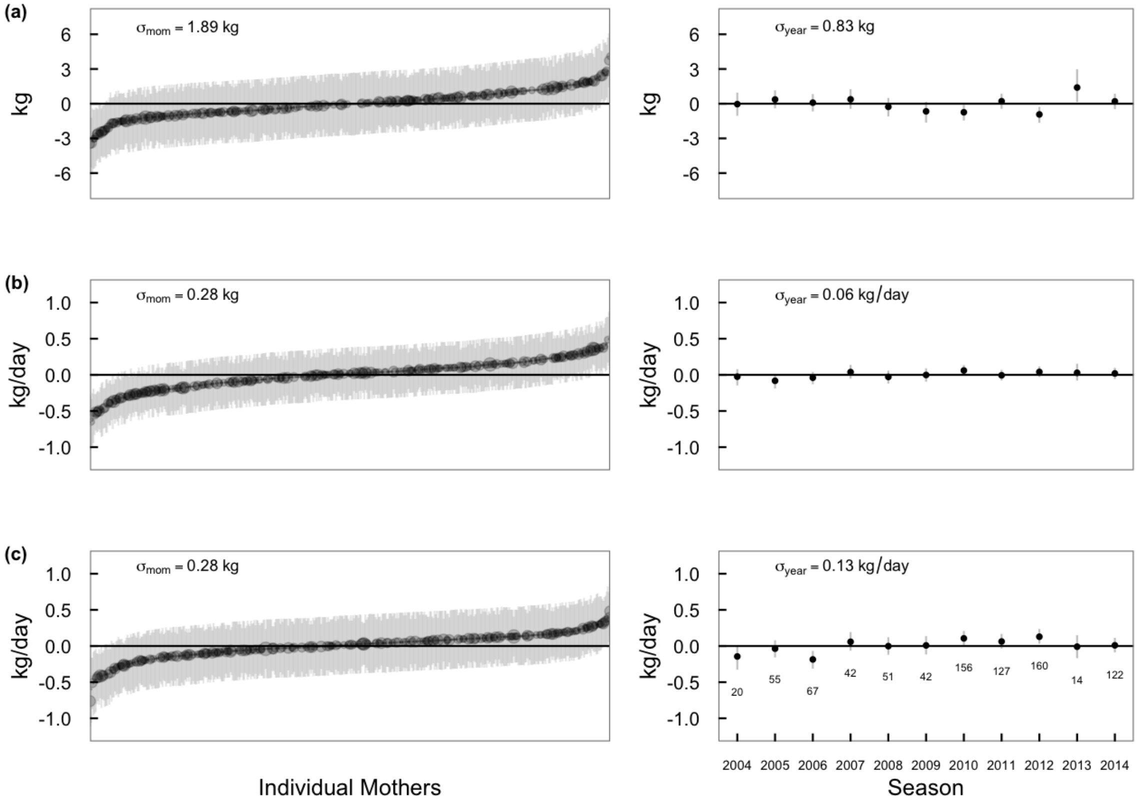

Figure 3-2. Approximate distributions (mean and 90% credible interval) of random effects for maternal identity and year from models for post-parturition pup mass (a), daily gains during early lactation (b), and daily gains during late lactation (c). For random effects from maternal identity, the point size represents the number of repeated measures from an individual mom with the largest point representing n=6, and the smallest n=1. For yearly random effects, the number below the 90% credible interval is the sample size within each year.

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CHAPTER FOUR

VARIATION IN THE VITAL RATES OF AN ANTARCTIC MARINE PREDATOR: REPRODUCTIVE COSTS, AGE-RELTAED CHANGES, AND INDIVIDUAL HETEROGENEITY

Contribution of Authors and Co-Authors

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Manuscript Information Page

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Journal of Animal Ecology

Status of Manuscript:
_x__ Prepared for submission to a peer-reviewed journal
____ Officially submitted to a peer-review journal
____ Accepted by a peer-reviewed journal
____ Published in a peer-reviewed journal

Ecology.

Abstract

Life-history traits such as lifespan and reproductive output can vary greatly among individuals within a species because individuals differ in their inherent abilities and because of the stochastic events they experience. Improved understanding of life-history evolution and population dynamics critically depends on properly identifying sources of variation in the probabilities of survival and reproduction. Here, we used a 33-year data set with reproductive histories for 1,274 female Weddell seals from Erebus Bay, Antarctica, to assess diverse predictions regarding variation in survival and reproductive rates including: 1) costs of reproduction, 2) age-related changes, 3) individual heterogeneity, and 4) annual variation. Our analysis used recent advances in Bayesian model selection techniques and diagnostics to assess the strength of evidence for competing predictions. We found strong evidence for costs of reproduction to both survival and future reproduction, with breeders having rates of survival and subsequent reproduction that were 3% and 6% lower than rates for non-breeders. We detected age-related changes in the rates of survival and reproduction but the patterns differed for the two rates. Survival rates steadily declined from 0.91 at primiparity to 0.81 at the maximal age of 31 years. In contrast, reproductive rates increased from 0.68 to 0.78 over the 8 years after primiparity and then steadily declined to 0.28 for the oldest females. Models that included individual effects explained more variation in life-history traits than those that did not: latent traits of individuals explained a substantial amount of variation in reproductive rates but minimal variation in survival rates, which contrasts with findings from other studies that simultaneously assessed variation in survival and reproduction. As

predicted for this long-lived species with a flexible breeding strategy, we found more annual variation in the rate of reproduction (mean = 0.67; range = 0.48, 0.79) than survival (mean = 0.91; range = 0.88, 0.93). Our study found variation in vital rates consistent with a series of predictions from life-history theory, and is the first to provide a thorough assessment of variation in important vital rates for a long-lived, high-latitude marine mammal while taking full advantage of recent developments in model evaluation.

Introduction

Within a species, individual fitness can vary due to differences in important life-history traits, such as lifespan, onset and pace of reproduction, and total reproductive output (Roff 1992; Stearns 1992). Such differences can result from random chance in survival and reproductive outcomes for animals with identical underlying vital rates (Tuljapurkar, Steiner & Orzack 2009). Among-individual differences in underlying vital rates are also generated by a host of processes acting on individuals that differ with respect to their genetics, phenotypes, ages, reproductive histories and the environmental conditions they experienced from early life to their current age (Kendall & Fox 2002; Vindenes, Engen & Sæther 2008; Vindenes & Langangen 2015). Moreover, among-individual differences in observed vital rates might arise from innate characteristics that reflect unmeasured aspects of individuals (Cam, Aubry & Authier 2016). Fundamentally, the sources and patterns of variation in demographic rates (specifically, survival and reproduction) within a species are of evolutionary importance, given the relationship between these demographic rates and fitness (Fisher 1930; Sæther *et al.* 2013).

Given that an individual has access to a finite pool of resources, the principle of allocation posits that organisms should strive to balance the allocation of resources to reproduction and survival so as to maximize fitness (Fisher 1930; Cody 1966; Williams 1966). Physiological trade-offs between survival and reproduction are a consequence of allocating resources in a zero-sum game (Stearns 1992), especially because reproduction is costly (Gittleman & Thompson 1988; Robbins 1993), but critical to fitness. The cost of reproduction can be paid by decreased probability of survival and/or future reproduction due to diminished allocation of reserves to somatic maintenance and repair necessary to preserve both (Bell 1980; Reznick, Nunney & Tessier 2000). A key prediction is that breeders should have a lower survival and/or future reproductive rate than non-breeders, or a negative covariation between survival and future reproduction (Nichols *et al.* 1994). However, empirical results provide mixed evidence for these expected trade-offs, with some researchers reporting the expected negative covariation (Huber *et al.* 1999; Koivula *et al.* 2003; Hadley, Rotella & Garrott 2007), no covariation (Festa-Bianchet, Gaillard & Jorgenson 1998), and/or a positive covariation between survival and future reproduction (Cam *et al.* 1998; Yoccoz *et al.* 2002; Beauplet *et al.* 2006; Weladji *et al.* 2008; Hamel *et al.* 2009a; Hamel, Craine & Towne 2012). Apparently contrasting results are partly due to the fact that the detection of trade-offs is complicated by a variety of factors, including unaccounted-for differences among individuals (Van Noordwijk & de Jong 1986), the life speed of the organism (Hamel *et al.* 2010), whether the species is a capital or income breeder (Jönsson 1997), and temporal variation in the environment (Reznick 1985). Moreover, the effect size of such trade-offs can be affected by among-individual differences that might exist due to differences in age and reproductive history (Viallefont, Cooke & Lebreton 1995; Tavecchia *et al.* 2005; Froy *et al.* 2013; Rughetti *et al.* 2015; Fay *et al.* 2016). Together, these results dictate that studies aimed at measuring trade-offs will need to study multiple individual traits, while accounting for diverse sources of heterogeneity.

Two different life-history theories predict that the optimal allocation of resources should change with age. The restraint hypothesis predicts that individuals will increase their allocation to reproduction with age as the expected number of future reproductive events decreases, and each event becomes more valuable to fitness (Williams 1966; Pianka & Parker 1975). Age-related improvements in reproduction-related traits, which are a consequence of the prediction, have been found in field studies of diverse taxa (Forslund & Pärt 1995; Bérubé, Festa-Bianchet & Jorgenson 1999; Newton, Rothery & Grubb 2002; Blas, Sergio & Hiraldo 2009). The increasing allocation to reproduction comes at the expense of allocation to survival, and a classic prediction from life-history theory is that survival is expected to decline from the onset of reproduction (Hamilton 1966). The senescence hypothesis suggests that the allocation of resources to reproduction earlier in life comes at the expense of somatic maintenance (Kirkwood & Rose 1991), which causes later-life declines in physiological function (senescence) such that both survival and reproductive rates decline with age (Bouwhuis *et al.* 2012; Lemaître *et al.* 2015; Lemaître & Gaillard 2017). These two theories are not mutually exclusive (Weladji *et al.* 2010). The former is predicated on the cost of reproduction being paid by diminished survival and/or future reproductive rates, whereas the latter posits a physiological decline in function that may not translate into fitness costs. Critically, much of the theory predicting senescence is specific to survival, and the extent to which age-related patterns of reproduction match patterns for survival remains an open question (Lemaître *et al.* 2015). Empirical work supports the co-occurrence of the two processes (Rebke *et al.* 2010), and has demonstrated that patterns of senescence are highly variable both across species and between intra-specific traits, including rates and ages of onset (Nussey *et al.* 2008, 2009; Evans, Gustafsson & Sheldon 2011; Bouwhuis *et al.* 2012). Understanding the trajectories of senescence across multiple traits remains a key challenge in understanding life-history evolution (Bouwhuis *et al.* 2012).

To properly evaluate factors influencing survival and reproductive events, it is crucial to consider possible variation among individuals that might exist even after reproductive state and age are accounted for. Unaccounted-for differences among individuals are known to obscure state- or age-dependent patterns of variation in survival and/or reproduction, and bias estimation of population-level patterns when individuals differ in their probabilities of reproduction and survival (Vaupel & Yashin 1985; Zens & Peart 2003; van de Pol & Verhulst 2006; Bouwhuis *et al.* 2009). In the classic example of “heterogeneity’s ruses”, a population comprised of frail and robust individuals will tend to have its frail individuals die earlier in life such that the population-level survival rate can appear to increase with age even if the underlying survival rates of individuals do not (Vaupel & Yashin 1985; Cam *et al.* 2002). One metric of among-individual differences is the age at first reproduction. Both theory (Stearns 1976) and empirical work (Krüger 2005) suggest that fitness is sensitive to changes in this parameter, and there are two contrasting predictions for the pattern of survival and reproduction. Individuals who begin breeding at a young age might be of higher quality, and if age at first reproduction is a metric of individual quality, we would expect both survival and reproduction to be higher for individuals that began breeding earlier compared to individuals of the same age that began breeding later (Wilson & Nussey 2010). In contrast, if a trade-off between survival and future reproduction exists, individuals that begin breeding later should have higher survival rates (Fay *et al.* 2016).

Ideally, we would be able to perfectly document which traits are associated with an individual's probability of survival and reproduction, and variation in vital rates could be perfectly accounted for. However, imperfect knowledge of individual traits exists in most studies, even after accounting for variation arising from genetics (Merilä & Sheldon 2000; Wilson & Nussey 2010), maternal effects (Stover, Kendall & Fox 2012), or the environmental conditions experienced during early development (Lindström 1999; Metcalfe & Monaghan 2001; Hamel *et al.* 2009b). Individual heterogeneity has come to represent the variation in survival and reproduction that results from these unobserved (latent) traits of individuals (Cam *et al.* 2016), with significant evolutionary implications (Wilson & Nussey 2010; Bergeron *et al.* 2011; Cam *et al.* 2016). Positive covariation in rates of survival and reproduction is generally interpreted as evidence for the individual-quality hypothesis wherein some individuals live long lives and produce many young whereas others live shorter lives and produce fewer young (Hamel *et al.* 2009a; Lescroël *et al.* 2009). In contrast, negative covariation between survival and reproduction, wherein some individuals survive poorly but achieve high reproductive output while alive whereas others live long lives but breed sparingly, indicates that different individuals have different reproductive tactics for maximizing fitness (Descamps *et al.* 2006; Pettorelli & Durant 2007; Reid *et al.* 2010). Understanding the nature of covariation between rates of survival and reproduction is important as the pattern has strong consequences for possible heterogeneity in the importance of different individuals to the population's dynamics, specifically the extent to which dynamics might depend on high-quality individuals (Clutton-Brock 1988; Hamel *et al.* 2009a) versus individuals with diverse life-history tactics and associated portfolio effects (Greene *et al.* 2010). Although empirical evidence for such individual heterogeneity has rapidly accumulated with statistical techniques that allow a direct estimation of individual contributions to vital rates via hierarchical modeling, the patterns of covariation between survival and reproduction remain unclear (Cam *et al.* 2016).

A contrasting, though not mutually exclusive, explanation for observed variation among individuals contends that it results from the stochastic nature of life histories, i.e., observed variation results from the probabilistic nature of survival and reproduction (Tuljapurkar *et al.* 2009; Steiner & Tuljapurkar 2012). In this case, differences in life-history trajectories and life-history traits need not reflect underlying variation in individuals' ability to survive and reproduce. The debate thus far centers on evaluating the ability of models to predict observed life histories, in particular lifespan and lifetime reproductive output. However, recent work has suggested that even models that do not represent the underlying data-generating process can reproduce observed patterns of variation (Authier, Aubry & Cam 2017, but see Chambert *et al.* 2013). Resolution to the conundrum requires work with high-quality datasets for many individuals to properly determine sources of apparent among-individual differences in life-history traits, a carefully thought out set of competing models, and multiple methods of model assessment and comparison that are appropriate for hierarchical modeling (Link & Barker 2009; Authier *et al.* 2017).

Environmental variation produced by both periodic and stochastic processes also plays a key role in shaping life histories (Gaillard *et al.* 2000; Orzack & Tuljapurkar 2001; Boyce *et al.* 2006; Metcalf & Koons 2007). For individuals living in the same location, their survival and reproductive outcomes could vary due to temporal variation in resources or conditions. Theory predicts that population growth rates and fitness are negatively correlated with temporal variance in these vital rates (Cohen 1966; Lewontin & Cohen 1969); however, the impacts of proportional changes in survival or reproduction on populations growth rates and fitness are not expected to be the same (Goodman 1971; Caswell 1978; Morris & Doak 2004). According to the demographic buffering hypothesis, life histories should evolve to minimize the effects of environmental variation on fitness by favoring traits that buffer important vital rates from temporal environmental variation (Gaillard, Festa-Bianchet & Yoccoz 1998; Gaillard *et al.* 2000; Pfister 1998). In long-lived species, population growth and fitness are most sensitive to variations in adult survival (Gaillard *et al.* 1998; Sæther & Bakke 2000; Reid *et al.* 2010; Rotella *et al.* 2012). Consequently, demographic buffering would result in the canalization of traits associated with high adult survival, and one would expect lower variation in adult survival than in reproductive performance (Gaillard & Yoccoz 2003). Some theoretical and empirical work has challenged the demographic buffering hypothesis, with results allowing for the possibility that selection could, under some circumstances, favor positive covariation between temporal variation and population growth such that changes in important vital rates are not buffered against (Payne & Wilson 1999; Doak *et al.* 2005; Metcalf & Koons 2007; Koons *et al.* 2009).

In this study, we used 33 years of mark-recapture data from a population of female Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica to evaluate variation in the probabilities of survival and reproduction arising from: costs of reproduction associated with breeding state, effects of age, latent traits of individuals, and temporal variation. Weddell seals are long-lived, predominantly capital breeders producing a single pup per reproductive event, and have shown a flexible reproductive strategy ideal for investigating sources of variation in life-history traits among individuals (Hadley *et al.* 2006; Stauffer, Rotella & Garrott 2013; Chambert, Rotella & Garrott 2015). The population has been intensively monitored since 1968, and contains a large number of known-aged individuals with known breeding histories (Stirling 1969; Siniff *et al.* 1977), which is possible due to the fact that females display strong site fidelity and are readily detectable, especially in years when they produce a pup (Hadley *et al.* 2006). By simultaneously assessing both survival and reproduction, we are able to contrast patterns of variation and assess the strength of evidence for several predictions from life-history theory. If there are physiological trade-offs between the allocation of resources to survival and reproduction, we would expect rates of survival and reproduction to be lower after reproductive events. Furthermore, we can evaluate how vital rates change with age as predicted by both the restraint and senescence hypotheses. If the latent traits of individuals are associated with survival and reproduction, then competing models that incorporate individual heterogeneity as well as breeding state and age should explain more variation in observed life-histories than do models that rely only on state- and age-based transitions. Finally, we can evaluate the prediction from demographic buffering that survival rates should be high and demonstrate low variability in response to environmental canalization; a prediction that was supported by an earlier analysis that ignored possible individual heterogeneity in latent traits (Rotella *et al.* 2012).

Methods

Study Population and Data Collection

The study population of Weddell seals forms pupping and breeding colonies in Erebus Bay, Antarctica (77.62°-77.87°S, 166.3°-167.0°E) during the austral spring, from October to December of each year. Females are highly philopatric and, once recruited to this population, have a very low probability of producing pups elsewhere (Cameron *et al.* 2007; Hadley *et al.* 2007). The colonies form in close proximity to tidal cracks in the frozen ocean, which allow females to access the ice surface and render them accessible to field crews. Since 1973, six to eight mark-resight surveys have been conducted in the study area each year, beginning in early November. During surveys, the identity and reproductive status of each animal was recorded. Because of the high detectability of mothers with pups, we were able to reliably assign each female to the following reproductive states: pre-breeder, first-time mother, experienced breeder (female with a pup who has also produced a pup in at least one previous year), skip-breeder attending the colonies (female without a pup but who has produced a pup in at least one previous year), or a skip breeder who was not observed in the colonies. Given the high on-ice detection rates and site fidelity, a female who was not seen in the colonies was assumed to have not produced a pup that year and to have temporarily emigrated from the breeding population (Hadley *et al.* 2007).

Our data set consisted of encounter histories for 1,274 female Weddell seals, from 1984 to 2016. We restricted our analyses to those individuals that were tagged as pups and subsequently recruited to the breeding population (thus, known-aged individuals who bred at least once). An individual entered the dataset in the year she first gave birth, and each individual's annual reproductive state was recorded that year and all subsequent years.

Modeling Approach

Our goal was to assess the strength of evidence for: reproductive costs incurred by tradeoffs, age-related changes in vital rates, among-individual heterogeneity and temporal variation in vital rates using a modest set of competing models. A natural framework to test these ideas is a multistate approach (Nichols *et al.* 1994; Lebreton & Pradel 2002) using 5 states (first-time breeder = F, experienced breeder = E, skip breeder attending the colonies = S, and skip breeder who was away = A, are the 4 reproductive states for live females, and the fifth state was a dead state). We used a Bayesian approach to model the probabilities of transition between each state that allowed us to readily incorporate state- and age-related effects, effects due to individual heterogeneity, and temporal effects on both survival and reproduction. Furthermore, this flexible modelling approach allowed us to very specifically assess the goodness of fit for each model, as well as estimate the predictive ability of each model in two ways: a general estimate of predictive ability over the entire data set, and an estimate of the predictive ability for each model specific to the oldest aged-animals.

To address demographic questions, we decomposed the probabilities of transitioning between states F, E, S, and A, and to the dead state, using the constituent state-dependent probabilities of: (1) survival (φ), (2) temporarily emigrating from the population (γ), (3) the probability of reproduction (ψ), and (4), the probability of returning to the colonies once emigrated, ρ (Table 4-1). For example, the probability of transitioning between a first-time breeder and an experienced breeder was the product of the probabilities that a female will survive the year after she first gives birth, φ_F, be present in the study area the following year, $(1-\gamma_F)$, and reproduce in year *t*+1, ψ_F. The central focus of our work was to evaluate the diverse sources of variation in survival and reproduction and comparing the estimated patterns against predictions from several key life-history theories. Thus, we modeled the log-odds of survival and reproduction as functions of linear combinations of covariates hypothesized to be related to each rate. First, we included intercept terms for the survival from year t to year $t+1$ for an individual in state *f* in year t, α_f^{φ} with *f* = F, E, S or A, and reproduction conditional on survival in year *t*, α_f^{ψ}. With all other covariates being held equal, these terms correspond to the state-dependent probabilities of survival and reproduction. The estimated terms provide direct measures of possible costs of reproduction to rates of survival and reproduction. Costs of reproduction are in evidence if probabilities of survival and/or reproduction are lower for individuals who reproduced in year *t*, when compared to rates for individuals who skipped reproduction. We allowed costs of reproduction to differ for first-time breeders and experienced breeders by estimating these terms separately. We set the intercept terms for the survival rate of females in states S and A to be the same (Kendall 2004).

We considered quadratic and logarithmic functional forms for possible relationships between age and survival, and age and reproduction. These forms allow a variety of relationships between age and the probabilities of survival and reproduction, including linear (if the coefficient for the quadratic term was estimated near zero), concave or convex (allowing increases, decreases and attendant maxima and minima for the quadratic form), as well as increases/decreases for younger animals and a plateau at older ages. We allowed each form to vary separately for survival and reproduction, resulting in four total combinations. Moreover, we used a within-individual centering approach (van de Pol & Verhulst 2006; van de Pol & Wright 2009) in which we subtracted and individual’s age at first reproduction from each subsequent age for that animal. This rescales an individual’s true age (years since birth) to a reproductive age (years since first reproduction). Hereafter, “age” is used to represent this transformed quantity, and all estimated effects from age are specific to years since first reproduction. This allowed an accurate estimation of a true within-subject effect of aging, rather than a between-subject effect that would result from using raw ages, and allowed us to assess the strength of evidence for age-related changes in vital rates (van de Pol & Verhulst 2006). We predicted that senescence in survival would result in lower probabilities of survival for older animals. The various functional forms that we considered allowed us to evaluate evidence for diverse possibilities for the pattern of age-related changes in the probability of survival and reproduction for which multiple possible changes seemed plausible: a steady decrease (senescence after first reproduction), a steady increase (improvements in accordance with the restraint hypothesis), increase to a maximum followed by a decrease (initial improvement early in life and eventual senescence), or an increase to a plateau of high adult survival and/or reproduction (initial improvement followed by consistently high survival and/or reproduction).

Third, we included both the age at first reproduction for each individual, as well as individual random effects on the probabilities of survival and reproduction to address variation due to among-individual differences. We predicted that age at first reproduction would be a useful metric of individual quality, such that the probabilities of survival, reproduction, or both would be lower for animals that begin breeding later. For Weddell seals in particular, age at first reproduction might be a useful indicator of individual quality, given that they are capital breeders that rely heavily on extensive body reserves to meet the demands of reproduction and lactation (Wheatley *et al.* 2006). Findings that some animals can acquire the body reserves earlier in life could be evidence of variation in innate characteristics or individual quality. There is a variety of patterns predicted for the relationship between the individual random effects on survival, ζ_i^{φ}, and reproduction, ζ_i^{ψ}. The individual quality hypothesis predicts a positive covariation between individual random effects for the probabilities of survival and reproduction, as superior animals are able to breed, and recover from breeding, at higher rates than others. In contrast, if costs of reproduction are present, we predicted a negative covariation between the individual random effects for survival and reproduction. Moreover, environmental canalization against variability in survival and/or differences in resource acquisition and allocation are predicted to result in no relationship between the individual random effects. An alternative explanation for among-individual differences in life-history traits is that they arise from the stochastic nature of survival and reproduction, and do not reflect adaptive individual characteristics (Tuljapurkar *et al.* 2009; Cam *et al.* 2016). To evaluate this possibility, we ran models that included state- and age-related effects, but not individual random effects, and we considered these to be appropriate null models for testing the need to consider individual heterogeneity. If latent traits of individuals are associated with survival and reproduction, models that incorporate them should explain more variation in observed life histories than models that rely on state- or age-related effects alone.

Finally, we included a random effect for year on both survival, ξ_y^{φ}, and reproduction ξ_y^{ψ}, to account for temporal variation in vital rates. Taken together, we assessed the strength of evidence for these ideas using the following formulation for the probabilities of survival and reproduction:

$$\text{logit}\left(\varphi_{ify}\right) = \alpha_f^{\varphi} + f^{\varphi}\left(\text{age}_{iy}\right) + \text{age.at.first}_i + \zeta_i^{\varphi} + \xi_y^{\varphi}$$

$$\text{logit}\left(\psi_{ify}\right) = \alpha_f^{\psi} + f^{\psi}\left(\text{age}_{iy}\right) + \text{age.at.first}_i + \zeta_i^{\psi} + \xi_y^{\psi}$$

We evaluated eight different models that considered four combinations of two possible functional forms for the effects of age since first reproduction ($f^{\varphi}\left(\text{age}_{iy}\right)$ for survival, and $f^{\psi}\left(\text{age}_{iy}\right)$ for reproduction), each of which was run either including (IH) or excluding (Null) individual random effects.

To accurately assess the strength of evidence for each of these ideas, we accounted for variation in the probabilities of temporarily emigrating from the study area, and returning from a temporary emigrant state. Previous work in this system has established that these probabilities are both Markovian (depending on whether the female is seen in the colonies or not the previous year, which is correlated with reproductive state in this system), and highly variable among years (Hadley *et al.* 2007; Stauffer *et al.* 2013). More generally, if temporary emigration is non-random (i.e., Markovian), it can result in biased estimates of survival (Kendall, Nichols & Hines 1997). We therefore included intercepts to allow these probabilities to vary by state, α_f^{γ} for *f* = F, E, and S, and used a separate intercept for the probability of returning, α^{ρ}. We accounted for temporal variation using random effects for year on the probabilities of temporary emigration, ξ_y^{γ}, and the probability of returning, ξ_y^{ρ}:

$$\text{logit}\left(\gamma_f\right) = \alpha_f^{\gamma} + \xi_y^{\gamma}$$

$$\text{logit}(\rho) = \alpha^{\rho} + \xi_y^{\rho}$$

Uncertain Transitions

For individuals that went missing and were never seen again during the study (n = 935), their fate after the last observation was unknown: they may have died (state 5), or temporarily emigrated (state 4). For example, an individual last seen in 2014 could have died in 2015, or temporarily emigrated in 2015 and died in 2016, or temporarily emigrated in 2014 and stayed away through 2016. To account for these uncertain transitions, we adjusted the likelihood for the year of last observation by using the sum of all these possible transitions. This approach was computationally more tractable for this large data set compared to a state-space formulation (Kéry & Schaub 2011; King 2012), and it explicitly accounts for the probability of never being seen again by accounting for all the possible years in which an individual could have died (King 2012).

Model Fitting

A Bayesian approach was used to fit these models using the software program JAGS, Version 4.3.0, (Plummer 2015), using the runjags package (Denwood 2016) as an interface in the R computing environment (R Core Team 2015). Markov chain Monte Carlo (MCMC) methods were used to approximate the posterior distribution of the parameters of interest. All random effects of year were assumed to be independent, and modeled hierarchically using mean-zero normal distributions with unique standard deviations. Standard deviations were given uniform priors, U(0,10). We modeled the individual random effects on survival and reproduction using a mean-zero multivariate normal distribution. The covariance matrix was given a scaled inverse-Wishart prior, with an identity matrix for the scale and degrees of freedom set to 3 (Gelman *et al.* 2014). The latter constraint imposed a uniform prior on the correlation between the two random effects. Reported standard deviations for the individual random effects and correlation between them were derived from the estimated covariance matrix. All regression coefficients for the functional forms for age and age at first reproduction were assigned diffuse normal priors, N(0, 1000), on the logit scale. State-dependent effects, e.g., α_f^{φ}, were given diffuse priors, U(0,1), on the probability scale. We carried out a prior-sensitivity analysis by comparing inferences across choices of prior, particularly for the hierarchical standard deviations, including both diffuse and restrictive priors. Our resulting inferences were invariant to the choice of prior.

For each model, we ran four separate chains in parallel with different starting values. Model convergence was determined by the visual assessment of trace plots, with convergence assumed upon good mixing of the chains and consistent approximate posterior distributions. Models were run for 50,000 iterations, with the first 10,000 discarded for adaptation and burn-in. Due to computational restrictions, we thinned each chain by keeping every 4th sample, resulting in 40,000 samples for inference.

Model Comparison and Assessment

Our goal was to determine which combination of functional form for age and inclusion/exclusion of random effects for individuals best explained variation in observed life histories for our data set. As our biological inferences are based on the comparison of multiple competing models, we utilized three levels of model comparison and assessment to ensure inferences were drawn from within a rigorous framework.

First, we assessed the fit of each model to our data set using posterior predictive checks (Gelman *et al.* 2014) in a manner very similar to previous work in this system (Chambert *et al.* 2013). After fitting a model, we used the approximate posterior distribution of all parameters to generate 10,000 replicate data sets using the same number of individuals, years and data structure, with each replicate representing a simulated life-history for the specific individuals and years in our study. For each replicate, we calculated the mean number of pups produced per mom (hereafter, NP), as well as mean persistence in the breeder state (PB, the number of consecutive breeding events). The resulting distribution of these two statistics generated under replication, the posterior predictive distribution, was compared to the actual values in the data set using three statistics: the mean, maximum and variance, resulting in six total comparisons. For each posterior predictive check, we calculated a one-sided Bayesian p-value as the proportion of times the observed statistic was greater than that the posterior predictive distribution (Gelman *et al.* 2014).

After establishing that models were at least a reasonable fit to our data, we then assessed their estimated out-of-sample predictive ability using the Widely Applicable Information Criterion, also known as the Watanabe-Akaike Information Criterion, hereafter WAIC (Watanabe 2013). WAIC is similar to the Akaike Information Criterion (AIC) in interpretation: in theory, lower values would suggest a better predictive model (Gelman, Hwang & Vehtari 2014; Hooten & Hobbs 2015). Moreover, WAIC easily generalizes to models with random effects. However, we are aware of two issues with the use of WAIC. First, the approximation to the predictive ability of a model may be unreliable under two conditions: if the effective number of parameters exceeds half the sample size, or if the contribution of any single parameter is estimated to be greater than one, both of which can be easily checked after model fitting (Gelman *et al.* 2014). Our second concern was a practical one. In condensing the fit of a complicated hierarchical model to a large data set down to a single number (such as a WAIC score), we ran the risk of averaging the fit of a model across different parts of the data set. Specifically, one of our main goals was to assess variation in survival and reproduction with age, in particular for the oldest age classes of animals, where data are less abundant. We were particularly concerned about selecting models that might fit the data well for younger ages, where data are more abundant, but that might have fit more sparse data from older ages poorly, e.g., a quadratic model might do well at predicting an increase in a vital rate early in life but erroneously predict senescent declines late in life merely as a consequence of the quadratic functional form and provide misleading inferences at ages for which data are sparse.

We therefore used a second measure of assessing the predictive ability of each model. One of our main goals was to assess variation in survival and reproduction with age, in particular for the oldest age classes of animals. A practical method of assessing the predictive performance of each model at older ages would have been to use a leave-one-out cross validation approach and estimate the probability of each observed state transition, y_l, for older animals when the model is fit to a data set excluding that state transition, $\mathbf{y}_{-l}$. This value is known as the conditional predictive ordinate for any observation *l*, $\mathrm{CPO}_l = [\mathrm{y}_l|\mathbf{y}_{-l}]$ (Geisser 1993; Hooten & Hobbs 2015). We note that in the case of our study, that quantity was not a true out-of-sample estimate as the remainder of that individual's life-history informs parameter estimates. However, the CPO for any transition in our data set does provide a metric of model fit, and it is one that can be selectively targeted to specific sections. This method of calculation of a CPO requires a separate model run for each desired estimate of a conditional predictive ordinate. Thus, for even modest sample sizes, the computational demands render the approach impractical. However, the CPO for any point is equivalent to the harmonic mean of its predictive distribution resulting from fitting the model to the entire data set (Lewis *et al.* 2013; Hooten & Hobbs 2015), and is easily approximated for any point from the output of an MCMC algorithm (Chen, Shao & Ibrahim 2012):

$$\mathrm{CPO}_l = \frac{1}{T}\left(\sum_{t=1}^{T}\frac{1}{[\mathrm{y}_l|\boldsymbol{\theta}_t]}\right)^{-1},$$

where *l* represents any point in the data set, $t = 1, \ldots, T$ is the iteration of the Markov chain, $\boldsymbol{\theta}_t$ is the vector of parameters estimated at the t^{th} iteration, and $[\mathrm{y}_l|\boldsymbol{\theta}_t]$ is the probability of observation y_l conditional on the estimated parameters. Thus, we were able to use values of the CPO to evaluate the fit of our model to specific sections of our data without resorting to multiple model runs, and as a supplement to a general measure of predictive performance such as WAIC. For our purposes, we approximated the CPO for every state transition past 20 years of age for individuals who were 20 or older at the time of last observation (n = 139). We then used the negative of the sum of the logarithms of the CPO values,

$$-\sum_{l=1}^{L} \log(\mathrm{CPO}_l)\,,$$

as a summary statistic for the predictive performance of each model for the oldest individuals (Hooten & Hobbs 2015).

Results

We evaluated patterns of variation in the probabilities of survival and reproduction, incorporating state-, age-, and individual metrics while also accounting for year-to-year variation with a multistate approach. Encounter histories from 1,274 individual Weddell seal females yielded a total of 8,652 individual state transitions. The data included 1,274 observations in the first-time breeder state, 5,025 observations in the experienced breeder, 1,972 observations in the skip breeder, seen state, and 720 observations in the skip breeder, away state. Individual reproductive histories ranged from a single observation (n = 169) to 25 observations (n = 2), with a median value of 6 observations per individual. Age at first reproduction ranged from 4 years to 16, with a median value of 7. The distribution of ages in these data was asymmetrical (range = 4-31 years, 25% quantile = 9 years, median = 12 years, 75% quantile = 15 years), due to both right censoring of these longitudinal data and the smaller number of individuals that were observed beyond 20 years of age (n = 139, 11%).

Model Assessment: Goodness of Fit and Prediction

Goodness-of-fit assessment revealed two important patterns (Table 4-2). First, across functional forms for age, one-sided *p*-values suggested that the models without individual random effects fit the data more poorly than did those that included individual heterogeneity (IH). Null models typically over- or under-predicted the mean, variance and maximum for the number of pups per mom (NP) and persistence in the breeder state (PB), compared to IH models. Second, though the *p*-values for IH models were roughly comparable across the functional form of the effects of age on survival and reproduction, which suggested that these models were coarsely consistent in predicting the observed variation in number of pups per mom and persistence in the breeder state, the model with quadratic effects of age on survival and reproduction was the best fit to the data. However, there is no absolute scale on which to gauge the meaning of *p*-values, i.e. a reject or fail-to-reject criterion. Thus, while we noted the relative goodness of fit for each model and the strength of the models that incorporate individual heterogeneity, we did not find cause to reject any model prior to assessing the predictive ability.

Results from WAIC scores revealed two models as competitors for the best single model. The structure of both models was similar: both had a quadratic effect of age on the probability of reproduction and included individual heterogeneity (IH). They differed in that one model had a logarithmic form of age on the probability of survival, whereas the other had a quadratic effect. Further evaluation with the targeted use of the CPO provided an important additional insight. The model with quadratic effects of age on survival outperformed every other model for our oldest animals. Given that a central focus of this work was patterns of reproduction and survival with age, particularly for the oldest-aged animals, we chose the model with quadratic effects of age on survival and reproduction as the single model from which to draw inference (though we note inference was very similar to the model with a logarithmic effect of age on survival, see Appendix A). These results also suggested that all models incorporating individual heterogeneity out-perform the equivalent null model in terms of both WAIC and CPO scores.

To aid interpretation, we have back-transformed several key parameter estimates to the probability scale (hereafter denoted by a * prefix), unless otherwise noted, using the following covariate conditions: age at first reproduction (state F) of 7 years (the median value), and age for experienced mothers and mothers who skipped reproduction (states E, S and A) of 12 years (the median value). Moreover, our estimates are for an individual with the average value for random effects for survival and reproduction in a year, with average annual effects on each vital rate. Survival rates were corrected for tag loss by dividing estimated rates by the tag retention rate, estimated to be approximately 99% in this study system (Cameron & Siniff 2004; Hadley *et al.* 2007).

Evidence for State-Dependent Variation

The resulting approximate posterior distributions for parameters under the top model strongly suggested that reproduction is costly to both survival and reproduction in the year after a female produces a pup (Table 4-3). Using our reference values, estimated survival rates for a first-time mother (*$\widehat{\varphi_F}$ = 0.91; 90% CI: 0.89, 0.93) and an experienced mother with a pup (*$\widehat{\varphi_E}$ = 0.91; 90% credible interval: 0.90, 0.92) were similar and lower than the estimate for a skip breeder ($*\widehat{\varphi_S} = 0.94$; 90% CI: 0.93, 0.95), which indicated that the cost of reproduction was similar for first-time mothers and those with previous experience. Probabilities of reproduction in the next breeding season were markedly lower for first-time breeders ($*\widehat{\psi_F} = 0.69$; 90% CI: 0.64, 0.74), and experienced breeders ($*\widehat{\psi_E} = 0.77$; 90% CI: 0.74, 0.79), than for females who skipped reproduction regardless of whether they were in colony attendance ($*\widehat{\psi_S} = 0.83$; 90% CI: 0.81, 0.86), or not ($*\widehat{\psi_A} = 0.80$; 90% CI: 0.76, 0.84). In contrast to results for survival, our results for reproduction indicated that the cost of reproduction to subsequent reproduction was greater for primiparous mothers than for experienced mothers. In addition, we estimated that the probability of temporarily emigrating from the study area to be approximately three times higher for first-time breeders ($*\hat{\gamma}_F = 0.18$; 90% CI: 0.14, 0.24) than for either experienced breeders ($*\hat{\gamma}_E = 0.06$; 90% CI: 0.05, 0.09), or skip breeders attending the colonies ($*\hat{\gamma}_S = 0.05$; 90% CI: 0.04, 0.07).

Evidence for Age-Dependent Variation

Our results supported three hypotheses from life-history theory regarding patterns of age-related variation. First, in our best-supported model, we had clear evidence for survival senescence: the linear term was estimated to be negative ($\hat{\beta}_{\text{age}} = -0.03$; 90% CI: -0.05, -0.02), whereas the quadratic effect of age on survival was estimated to be zero ($\hat{\beta}_{\text{age}^2} < 10^{-5}$; 90% CI: $-2\times10^{-4,}$ 1×10^{-4}). For our reference values, this translated into a decline in survival for breeders from 0.92 (90% CI: 0.91, 0.93) at age 7 to 0.82 (90% CI: 0.78, 0.86) by age 31. Second, this decline began at the age of first reproduction, which is consistent with the restraint hypothesis, i.e., a decline in the probability of survival with age as residual reproductive value decreases (Figure 4-1). In contrast, the effects of age on reproduction ($\hat{\beta}_{\mathrm{age}}$ = 0.13; 90% CI: 0.09, 0.17 and $\hat{\beta}_{\mathrm{age}^2}$ = -0.008; 90% CI: -0.01, -0.006) indicated that the probability of reproduction initially increases after primiparity, reaches its maximum value approximately 8 years later (corresponding to 15 years of age for an animal that began breeding at 7), and then declines (Figure 4-1). For our reference values, this translated into a probability of consecutive reproductive events increasing from 0.68 (90% CI: 0.64, 0.72) for a 7-year-old female, to 0.78 (90% CI: 0.75, 0.81) for a 15-year-old, and declining to 0.30 (90% CI: 0.17, 0.45) for a 31-year-old, which provides strong evidence for both a gradual improvement with age consistent with a decline in residual reproductive value, and a decline consistent with a senescent deterioration in physiological function.

Evidence for Individual Variation

A female's age at first reproduction was found to be negatively and linearly related to both her probability of survival ($\hat{\beta}_{\mathrm{age.first}}$ = -0.05; 90% CI: -0.09, -0.004), and of reproduction in the subsequent year ($\hat{\beta}_{\mathrm{age.first}^{\mathrm{t}}}$ = -0.06; 90% CI: -0.10, -0.02), which is consistent with the prediction that females who begin reproduction earlier in life are of higher individual quality (Table 4-3). We note that although these estimated effects are modest in size, they might have nontrivial implications for expected lifetime output of long-lived organisms. Using the approximate posterior distributions of our parameters, we simulated 20,000 reproductive histories for two individuals (one that began breeding at 5 and another that began at age 9) while holding the yearly effects on survival, reproduction, temporary emigration and returning, as well as individual effects on survival and reproduction, to their estimated mean values. A female who began breeding at age 5 would be expected to produce 7.9 (sd = 5.5) pups over a 11.5-year reproductive lifespan (sd = 8.9), whereas a female with primiparity at age 9 would be expected to produce 6.7 pups (sd = 4.9) over a 10.1-year reproductive lifespan (sd = 8.2).

Our results also provided strong evidence for individual heterogeneity in reproductive rates arising from unobserved traits of individuals. Based on our estimated standard deviation of the normal distribution of individual random effects for reproduction ($\hat{\sigma}_{\mathrm{i}}^{\psi}$ = 0.66; 90% CI: 0.58, 0.75), 90% of females would have random effects between -1.32 and 1.32. Such effect sizes are considerable on the logit scale, and imply that the distribution of individual probabilities of reproduction is wide. Based on 20,000 simulated reproductive histories for three individuals that started reproduction at age 7 and that had individual effects of -1.32, 0, or 1.32 and mean values for temporal random effects, the expected number of pups over the expected lifespan are 4.8 (sd = 3.4), 6.8 pups (sd = 5.0) and 7.9 pups (sd = 6.0) for individuals with low, average and high random effects, respectively. The difference of 3.1 pups over the 90% CI range of values was almost three times greater than the difference of 1.1 pups found across the 90% CI range of values for the observable trait of age at first reproduction. In sharp contrast, we found little evidence for strong individual effects on the survival rate. The standard deviation of the normal distribution for these effects ($\hat{\sigma}_{\mathrm{i}}^{\varphi}$= 0.14; 90% CI: 0.01, 0.31), corresponds to a distribution of effects with 90% of individuals between -0.23 and

0.23. Given the high survival rates of even older individuals and the nonlinear logit transformation, these effects had negligible impact on among-individual differences in survival. We found no strong evidence for a relationship between an individual's random effect for reproduction and survival (Figure 4-2). Although the mean of correlation between the two random effects was estimated to be negative (correlation = -0.34; 90% CI: -0.82, 0.24), the wide credible interval for the correlation, which overlaps zero, prevents strong inference.

Evidence for Temporal Variation in Vital Rates

As predicted by the demographic buffering hypothesis, yearly variation in survival was very low, compared to yearly variation in reproduction (Figure 4-3). Averaged across all estimated values for individual random effects, the estimated survival rate for a 12-year-old, experienced mother that first reproduced at age 7, was estimated to be both high, (mean = 0.91; 90% CI: 0.89, 0.92) and to have little annual variation (range: 0.87 to 0.93). In contrast, the probability of reproduction for such a female was estimated to be more modest (mean = 0.76; 90% CI: 0.65, 0.83), and to be much more variable (range: 0.59 to 0.86). These results are consistent with survival being environmentally canalized against high variation, and support our prediction that individuals show a flexible reproduction strategy to maintain high survival. Moreover, our results also supported our prediction that the probability of temporary emigration was typically low (mean for an experienced breeder = 0.08; 90% CI: 0.02, 0.18), but highly variable in response to short-term environmental fluctuations (range: 0.02 to 0.43): the maximum occurred during the years in which mega-icebergs greatly affected the study area’s ice conditions and ecosystem function. The estimated probability of returning to the area after having temporarily emigrated was typically high (mean = 0.70; 90% CI: 0.48, 0.85) with similar variation (range: 0.32 to 0.87), which we also interpreted as evidence for both the philopatric nature of Weddell seals and the flexible patterns of colony attendance previously demonstrated for this species.

Discussion

Our work investigated variation in the probabilities of survival and reproduction for female Weddell seals, key vital rates that work in concert to shape among-individual heterogeneity in observed life-history traits. By simultaneously modeling survival and reproduction as functions of reproductive state, age, age at first reproduction, including individual variation arising from latent traits and temporal processes, and accounting for the probabilities of movement out of the study area, we were able to assess the relative support for several hypotheses from life-history theory. Our results provide strong evidence that life-history tradeoffs arise due to the co-occurrence of costs of reproduction to both survival and future reproduction, and age-related changes that support both the restraint and senescence hypotheses. After accounting for the effects of reproductive state and age, we found evidence for high residual variation in life-history traits. The negative relationship that we identified between the age at first reproduction and both survival and reproduction supports the individual quality hypothesis. Moreover, we detected a substantial amount of individual heterogeneity in the probabilities of reproduction, which contrasts strongly with the small amount of individual heterogeneity that we estimated in survival rates. We demonstrated that models that incorporate individual heterogeneity due to latent traits explained more variation in observed life-history traits than did models that relied only on reproductive state and age covariates. Finally, after accounting for a wide variety of sources of variation on underlying vital rates, our results strongly support the hypothesis that underlying vital rates in this long-lived species are environmentally canalized against temporal variation in survival.

Co-occurrence of Costs of
Reproduction to Survival and Future Reproduction

Our study is the first comprehensive evaluation of potential costs of reproduction in this system, considering multiple sources of variation in a simultaneous evaluation of survival and reproductive rates. We found conclusive evidence for a cost of reproduction to both future reproduction and survival in female Weddell seals. The probability of subsequent reproduction was markedly lower for first-time breeders, a result consistent with prior work in this system suggesting the first reproductive event is particularly costly (Hadley *et al.* 2007; Chambert *et al.* 2013). Moreover, the cost to future reproduction also exists for experienced breeders after accounting for individual heterogeneity in underlying vital rates and accounting for Markovian temporary emigration. These results are similar to an earlier analysis of reproductive costs in this system (Chambert *et al.* 2013) that included individual heterogeneity in reproductive rates, but not survival, and did not separate the probabilities of breeding from temporary emigration. We conclude that the minor amount of individual heterogeneity in survival, coupled with the small probability of temporary emigration in any given year, does not significantly bias the estimation of reproductive costs based on analyses focused on reproduction alone. Our work contradicts a weakly supported suggestion that the cost of reproduction to survival is higher for first-time breeders than experienced breeders (Hadley *et al.* 2007), by demonstrating that the survival rates for both first-time and experienced breeders are the same. Moreover, the difference between rates for breeders and non-breeders is large for such a long-lived animal.

For long-lived species, true fitness is particularly sensitive to lifespan (Williams 1966; Newton 1989), which is correlated with the number of reproductive events, and particularly important for Weddell seals (Rotella *et al.* 2012). The prudent parent hypothesis predicts that organisms should allocate resources so as to maintain high survival rates, and reproduce when physiological or environmental conditions allow them to obviate costs (Drent & Daan 1980; Cam *et al.* 1998). Facultative responses to this differential allocation include skipped reproduction (Dhondt 1985; Le Bohec *et al.* 2007; Bouwhuis *et al.* 2009; Reed, Harris & Wanless 2015), though empirical results suggest the probabilities of skipping and subsequent costs to reproduction and survival are entangled with individual quality (Cam *et al.* 1998; Reed *et al.* 2015). However, our results, which represent one of very few cases of costs being paid to both survival and reproduction, contradict this prediction, and suggest that even for a long-lived organism with a flexible breeding strategy, the costs to survival and future reproduction remain after accounting for other sources of heterogeneity. Moreover, these results differ from other long-lived capital breeders with flexible breeding strategies that did not find costs of reproduction (Madsen & Shine 1999; Toigo *et al.* 2002). We suggest that the co-occurrence of reproductive costs to both survival and reproduction in female Weddell seals demonstrated here, one of very few cases of costs being paid to both survival and reproduction, reflect underlying magnitudes of variation in resource allocation and acquisition (Van Noordwijk & de Jong 1986). Weddell seal females depend heavily on stored body resources to meet the demands of intensive energetic investment of lactation (Stirling 1969; Wheatley 2006; Wheatley *et al.* 2008b; a): individuals lose from 2.1 to 5.9 kilograms of body mass per day (Wheatley *et al.* 2006) over the course of the lactation period, 28 to 53 days (Kaufman, Siniff & Reichle 1975; Wheatley *et al.* 2006). When among-individual differences in resource allocation exceed those of resource acquisition, we would expect to detect trade-offs between reproduction and survival (Van Noordwijk & de Jong 1986), and previous work in this system has documented large among-individual variation in resource allocation to offspring during the lactation period (Mannas 2011*;* Paterson *et al.* 2016). Our study system provides a useful example of the connection between resource allocation and the detection of trade-offs, and suggests that further evaluation of similar relationships across the continuum of capital/income breeding strategies is needed to better discern the patterns and magnitudes of such trade-offs across taxa.

Age-related Changes in Vital Rates

We found both survival and reproduction rates to be strongly related to age. Our finding of survival senescence contrasts with previous findings for the study population in which evidence of senescence in survival rates was not found (Cameron & Siniff 2004; Hadley *et al.* 2007). This previous work estimated survival rates for age classes of animals in a non-hierarchical framework, and we attribute the difference in results to our use of a hierarchical model with random effects, using functional forms for age rather than discrete age classes, and the use of a within-individual centering approach to correctly estimate within-individual processes. Additionally, our thorough model assessment has demonstrated that the fit of the best-supported quadratic functional form for reproductive rates is not driven by early-life improvements, broadly supporting previous work (Chambert *et al.* 2013).

We found that the patterns and timing of age-related changes for the two vital rates differ in striking ways. Whereas the probability of reproduction peaked approximately 8 years after a female's first reproductive event and then declined for older females, we found strong evidence that the probability of survival steadily declined after primiparity. Improvements in reproductive output during the early reproductive years is consistent with the restraint hypothesis (Williams 1966; Pianka & Parker 1975; Forslund & Pärt 1995). An alternative hypothesis to explain the improvement with age during the early years of an individual's life suggests that younger individuals are constrained from investing too heavily in reproduction owing to ongoing somatic investment or a lack of skills and/or experience that are related to age (Curio 1983). Although improvements related to increasing body mass or experience are common in empirical work (Pärt 1995, 2001; Bowen *et al.* 2006; Reid *et al.* 2010), under the constraint hypothesis, and for long-lived species, we would expect to see a commensurate increase in the probabilities of survival. The co-occurrence of immediate declines in survival rates and early increases in reproductive rates estimated in this study corresponds well with the hypothesis that the ongoing trade-off between reproduction and survival changes as realized reproductive value increases with age. This study is one of very few that has been able to separate the possible causes of age-related improvements in reproduction. However, these age-related increases in the probability of reproduction do not persist into older age. For these oldest-aged animals, the simultaneous decline in both survival and reproductive probabilities strongly argues against the idea that declines are due to increased reproductive effort with age (the restraint hypothesis) (Nussey *et al.* 2008; Jones *et al.* 2008). Although a decline in survival can be explained by both increasing reproductive investment with age (trade-offs) and a senescent decline in physiological function (Pianka & Parker 1975; Blarer, Doebeli & Stearns 1995), the simultaneous decline in the probabilities of reproduction with age suggest that reproductive performance for old animals is governed by a decline in physiological function**.** Previous work on Weddell seals has demonstrated that muscular function changes with age in a manner that may reduce foraging efficiency (Hindle *et al.* 2009), and we speculate that physiological senescence might be one mechanism underlying the declines in survival and reproductive rate shown here. Our work is consistent with the growing consensus for senescence in vital rates (Clutton-Brock & Sheldon 2010; Nussey *et al.* 2013; Lemaître *et al.* 2015), and further demonstrates that age-related patterns of variation differ between survival and reproduction.

Among-individual Heterogeneity in Vital Rates

We found strong evidence that among-individual heterogeneity exists in vital rates and that it is associated with a measurable trait (age at first reproduction) as well as latent traits of individuals. These results confirm speculations from previous work on this study population that the age at first reproduction is negatively correlated with the probabilities of future reproduction (Hadley *et al.* 2007). We attribute our ability to confirm the result to the fact that we incorporated individual random effects, which allowed us to better estimate several distinct measures of individual quality. We do, however, note that our use of within-individual centering of age based on the age at first reproduction, which transformed age from years since birth to years since first reproduction, differs from what was done in prior work. Although this parameterization allows us to estimate a true within-individual process (van de Pol & Wright 2009), it does emphasize age at first reproduction such that it might have been easier to detect associations between survival and reproductive rates. For long-lived species, individuals are expected to delay reproduction until sufficient somatic development allows them to at least partially mitigate the costs of reproduction (Viallefont *et al.* 1995; Oli, Hepp & Kennamer 2002; Kim *et al.* 2011), and early recruitment may therefore be a metric of individual quality (Wilson & Nussey 2010; Fay *et al.* 2016). Our finding that individuals that begin reproducing earlier in life are likely to have a higher lifetime reproductive output adds to a small number of studies reporting similar associations (Descamps *et al.* 2006; Dugdale *et al.* 2011; Aubry *et al.* 2011; Fay *et al.* 2016), which supports the hypothesis that this trait is a valid indicator of individual quality. We believe that age at first reproduction is particularly relevant for Weddell seals because females vary in their age at primiparity (Hadley *et al.* 2006), begin reproduction while still investing in somatic growth (Paterson *et al.* 2016), and depend heavily on large body reserves to meet the demands of reproduction and lactation (Wheatley *et al.* 2006).

Although our results broadly support those from previous work estimating heterogeneity in reproductive probabilities in the study population (Chambert *et al.* 2013), we estimated a level of among-individual heterogeneity in reproduction that is approximately four times greater than what was previously estimated ($\hat{\sigma}_{\mathrm{i}}^{\psi}$ = 0.15 in the previous work, compared to $\hat{\sigma}_{\mathrm{i}}^{\psi}$ = 0.66 in the current work). We are quite certain that the change is the result of further decomposing the probabilities of transitioning to states as the product of the probability of colony attendance and the probability of reproduction. Moreover, our data include all individuals who reproduced at least once, whereas the previous work focused on individuals who were seen at least once after the year of first reproduction. The updated estimates have important consequences due to the strong attendant increases in the magnitude of variation for lifetime reproductive output and emphasizes the importance of carefully incorporating sources of individual heterogeneity in reproduction in Weddell seals and other species in which reproductive strategies are flexible.

In what is one of only a handful of studies to simultaneously assess heterogeneity in both reproduction and survival (Cam *et al.* 2002, 2013; Royle 2008), we estimated very little individual heterogeneity in survival rates, and found no strong evidence for a correlation between an individual's estimated probability of survival and reproduction. The lack of evidence for correlation is notable, as it strongly suggests that regardless of costs of reproduction in this species, individual heterogeneity in survival is trivial compared to that in reproduction. We view this result as a reflection of Fisher's fundamental theorem insofar as the theorem predicts little among-individual variation in traits that are most closely associated with fitness (Fisher 1930), and Weddell seal fitness is thought to be strongly associated with adult survival and lifespan (Rotella *et al.* 2012). In such a situation, it will be difficult to detect correlations between individual random effects if the variance of one component is close to zero due to vital rate canalization. Furthermore, we speculate that the difference in magnitudes between individual effects of survival and reproduction indicates a flexible breeding strategy (Reid 1987; Erikstad *et al.* 1997). Given the relationship between longevity and fitness, individuals should attempt to forego reproduction when the cost to survival exceeds that already documented in this work. We therefore interpret the high among-individual variation in breeding probabilities as evidence that some individuals are consistently able to meet the demands of reproduction. This level of heterogeneity among individuals is particularly large, given that Weddell seals have already gone through a strong filter such that, on average, only 1 in 5 females survives from birth to first reproduction (Garrott *et al.* 2012). Such residual variation among individuals may reflect underlying among-individual differences in physiological, or metabolic functions (Wheatley *et al.* 2008a; b), in addition to differences in resource acquisition. High levels of among-individual heterogeneity in prey consumption have been documented in Weddell seals (Goetz 2015), and recent work has suggested that breeding probabilities might be sensitive to the consumption of Antarctic toothfish (*Dissostichus mawsoni*), an energy-dense prey item (Salas *et al.* 2017), such that individuals that consume more toothfish are more able to meet the demands of reproduction and lactation.

Based on posterior predictive checks, WAIC, and a targeted calculation of the conditional predictive ordinate, models that included individual random effects explained more variation in our data set and had better estimated predictive power as a whole, compared to models without such random effects. This is particularly relevant to testing such neutral theories (Tuljapurkar *et al.* 2009) given recent work that suggests that mis-specified models can reproduce variation in observed life histories and that correctly assessing the strength of evidence for neutral processes and/or individual heterogeneity requires the comparison of the predictive power of models in a multi-model framework (Cam *et al.* 2016; Authier *et al.* 2017). To our knowledge, our study is the first to compare models with individual heterogeneity against neutral models using such rigorous model assessment criteria, and we strongly support the recommendations of Cam *et al.* (2016) in the use of a multi-model inference framework in which to evaluate the strength of evidence for these hypotheses.

Temporal Variation

Knowledge of temporal variation in vital rates provides important insights into life-history evolution and is critical for population dynamics (Gaillard *et al.* 2000), in particular for species at risk (Nichols & Hines 2002). The year-to-year variation in underlying vital rates reveals patterns that are predicted for Weddell seals, which is a long-lived, capital breeder with a flexible breeding strategy. The work presented here provides the first comprehensive look at temporal variation in rates of reproduction, survival and temporary emigration in this southern-most breeding mammal population and strongly supports the hypothesis that adult survival rates, in contrast to reproductive rates, exhibit low variability in the face of significant variation in environmental conditions (Chambert, Rotella & Garrott 2012; Rotella *et al.* 2012; Stauffer *et al.* 2014). Our work provides new insights into temporary emigration by adult females and indicates that temporary emigration rates vary by year. Previous work has documented the dispersal of post-lactating females to the north of the study area (Testa 1994; Ainley & Siniff 2009; Goetz 2015) and suggested that consumption of toothfish after reproduction is critical for regaining body mass and allowing reproduction to occur in the subsequent year (Goetz 2015; Shero *et al.* 2015; Goetz *et al.* 2017). We speculate that temporary emigration is a strategy that allows female Weddell seals to access more foraging opportunities to the north while foregoing opportunities that may exist by returning to the colonies such as the evaluation of mating opportunities, avoidance of predation, and the ability to learn from conspecifics (Stauffer *et al.* 2013). Furthermore, our work represents a baseline framework of temporal variation in vital rates that should prove useful as a reference for future work in this system, particularly in the face of potential challenges induced by both climate change (Beltran, Testa & Burns 2017) and commercial fishing (Ainley & Siniff 2009; Blight *et al.* 2010; Salas *et al.* 2017).

Conclusion

We simultaneously addressed diverse potential sources of variation in several vital rates in Weddell seals using multi-decadal data on individually marked females with known reproductive histories. Through our use of rigorous model comparison in a multi-model framework, we identified important life-history tradeoffs and metrics of individual quality and measured temporal variation in multiple vital rates. Our results make several novel contributions to our understanding of the evolutionary processes that shape life histories. These findings make it possible to assess the importance of among-individual heterogeneity to population dynamics, as well as lay the groundwork for future investigations into other sources of among-individual heterogeneity in life-history traits, e.g., maternal effects, cohort effects, and genetics.

Acknowledgments

We thank the many graduate students and field technicians who have collected data on this project. We also thank J.D. Nichols for helpful comments on the manuscript. This project was supported by the National Science Foundation, Division of Polar Programs (grant no. ANT-1141326 to J.J.R., R.A.G. and Donald B. Siniff) and prior NSF Grants to R.A.G., J.J.R., D.B.S. and J. Ward Testa. Logistical support for fieldwork in Antarctica was provided by Lockheed Martin, Raytheon Polar Services Company, Antarctic Support Associates, the United States Navy and Air Force, and Petroleum Helicopters Incorporated. Animal handling protocol was approved by Montana State University's Animal Care and Use Committee (Protocol #2011-38).

		To state, year t+1				
		F	E	S	A	dead
From state, year t	first-time breeder, F	0	$\varphi_F(1-\gamma_F)\psi_F$	$\varphi_F(1-\gamma_F)(1-\psi_F)$	$\varphi_F\gamma_F$	$1-\varphi_F$
	experienced breeder, E	0	$\varphi_E(1-\gamma_E)\psi_E$	$\varphi_E(1-\gamma_E)(1-\psi_E)$	$\varphi_E\gamma_E$	$1-\varphi_E$
	skip breeder seen, S	0	$\varphi_S(1-\gamma_S)\psi_S$	$\varphi_S(1-\gamma_S)(1-\psi_S)$	$\varphi_S\gamma_S$	$1-\varphi_S$
	skip breeder, away, A	0	$\varphi_A(\rho)\psi_A$	$\varphi_A(\rho)(1-\psi_A)$	$\varphi_A(1-\rho)$	$1-\varphi_A$
	dead	0	0	0	0	1

Table 4-1. Transition matrix for the multi-state model of reproductive histories with five states: first-time breeder, F, experienced breeder, E, skip breeder who was seen in the colonies, S, skip breeder who was not seen in the colonies, A, and a dead state. The probabilities of transitioning between each state were decomposed into the probability of survival out of each state, φ, the probability of temporarily emigrating, γ, the probability of returning to the colonies, ρ, and the probability of reproduction, ψ.

Models		Predictive Criteria		Goodness of Fit					
Functional Forms		ΔWAIC	CPO	NP_{avg}	NP_{var}	NP_{mx}	PB_{avg}	PB_{var}	PB_{max}
$f^{\phi}(age) =$ quad	**IH**	**1.0**	**788.9**	**0.48**	**0.58**	**0.58**	**0.43**	**0.42**	**0.48**
$f^{\psi}(age) =$ quad	Null	190.5	808.4	0.46	0.50	0.36	0.35	0.16	0.15
$f^{\phi}(age) =$ quad	IH	19.9	796.9	0.46	0.49	0.28	0.43	0.41	0.39
$f^{\psi}(age) =$ log	Null	218.3	817.7	0.72	0.68	0.23	0.85	0.69	0.36
$f^{\phi}(age) =$ log	IH	0	793.4	0.47	0.66	0.58	0.39	0.43	0.48
$f^{\psi}(age) =$ quad	Null	195.8	811.2	0.45	0.56	0.34	0.33	0.18	0.16
$f^{\phi}(age) =$ log	IH	20.5	801.8	0.46	0.57	0.27	0.40	0.43	0.40
$f^{\psi}(age) =$ log	Null	223.3	820.5	0.71	0.75	0.23	0.82	0.72	0.37

Table 4-2. Model assessment and comparison results representing a series of competing hypotheses about patterns of variation in vital rates associated with state, age, individual heterogeneity (IH), and temporal variability. The goodness-of-fit of each model was assessed using posterior predictive distributions of the mean, variance, and maximum of (i) number of pups per mom (NP), and (ii) the persistence in the experienced breeder state (PB, representing back-to-back breeding events). The posterior predictive P-value for each model and metric is a measure of model fit. Those models with values closer to 0.5 suggest a better fit to the data. We estimated the predictive ability for each model using the Widely Applicable Information Criterion (WAIC), which has a similar interpretation to the Akaike Information Criterion (AIC) in that models with a lower score are more supported. We also combined in-sample and out-of-sample approaches to assess how well each model fit for our oldest aged animals using the conditional predictive ordinate (CPO). We calculated the CPO for each observed transition for animals aged 20 and older (n = 139), and took the $-\sum \log(CPO)$ for all individual values. Similar to WAIC, lower values suggest better predictive ability.

Survival, φ		**Reproduction, ψ**		**Transition out/in: γ , ρ**	
	Mean (90% CI)		Mean (90% CI)		Mean (90% CI)
$*\varphi_F$	0.91 (0.89, 0.93)	$*\psi_F$	0.69 (0.64, 0.74)	$*\gamma_F$	0.18 (0.14, 0.24)
$*\varphi_E$	0.91 (0.90, 0.92)	$*\psi_E$	0.77 (0.74, 0.79)	$*\gamma_E$	0.06 (0.05, 0.09)
$*\varphi_S$	0.94 (0.93, 0.95)	$*\psi_S$	0.83 (0.81, 0.86)	$*\gamma_S$	0.05 (0.04, 0.07)
$*\varphi_A$	0.94 (0.93, 0.95)	$*\psi_A$	0.80 (0.76, 0.84)	$*\rho$	0.72 (0.64, 0.79)
$\beta_{age.first}$	-0.05 (-0.09, -0.004)	$\beta_{age.first}$	-0.06 (-0.10,-0.02)		
β_{age}	-0.03 (-0.05, -0.02)	β_{age}	0.13 (0.09, 0.17)		
$\beta_{age}{}^2$	$< 10^{-5}$ (-2×10^{-4}, 1×10^{-4})	$\beta_{age}{}^2$	-0.008 (-0.01, -0.006)		
σ_i^{φ}	0.14 (0.01, 0.31)	σ_i^{ψ}	0.66 (0.58, 0.75)	σ_y^{γ}	1.00 (0.77, 1.28)
σ_y^{φ}	0.20 (0.09, 0.0.32)	σ_y^{ψ}	0.39 (0.29, 0.50)	σ_y^{ρ}	0.88 (0.56, 1.26)

Table 4-3. Summary of the posterior distributions of parameters from top model, which included a quadratic functional form for age and individual random effects on the probabilities of survival and reproduction. The parameters in this table are: (i) mean state-dependent survival, φ, (ii) mean state-dependent reproduction conditional on survival, ψ, (iii) the mean state-dependent probabilities of temporarily emigrating (γ) and probability of returning (ρ), (iv) the regression coefficients for the functional form of age, β_{age} and $\beta_{age}{}^2$, and age at first reproduction, $\beta_{age.first}$, and (v) the standard deviation of the random effects of individual for survival (σ_i^{φ}) and reproduction (σ_i^{ψ}), random effects of year for survival (σ_y^{φ}) and reproduction (σ_y^{ψ}), and random effect of year on the probabilities of temporarily emigrating (σ_y^{γ}) and returning (σ_y^{ρ}). Symbols preceded by an asterisk (e.g., $*\varphi$) have been transformed back to the probability scale. For survival (φ) and reproduction (ψ), these values represent the probabilities for a 12-year old, average individual who first reproduced at age 7 (the population averages for these two numbers) in an average year. The probabilities of survival have been corrected for tag loss. The probabilities of temporarily emigrating (γ) and returning to the study area (ρ) are for an average year. States are: F = First-time breeder, E = Experienced breeder, S = Skip breeder, seen, and A = Skip breeder, away.

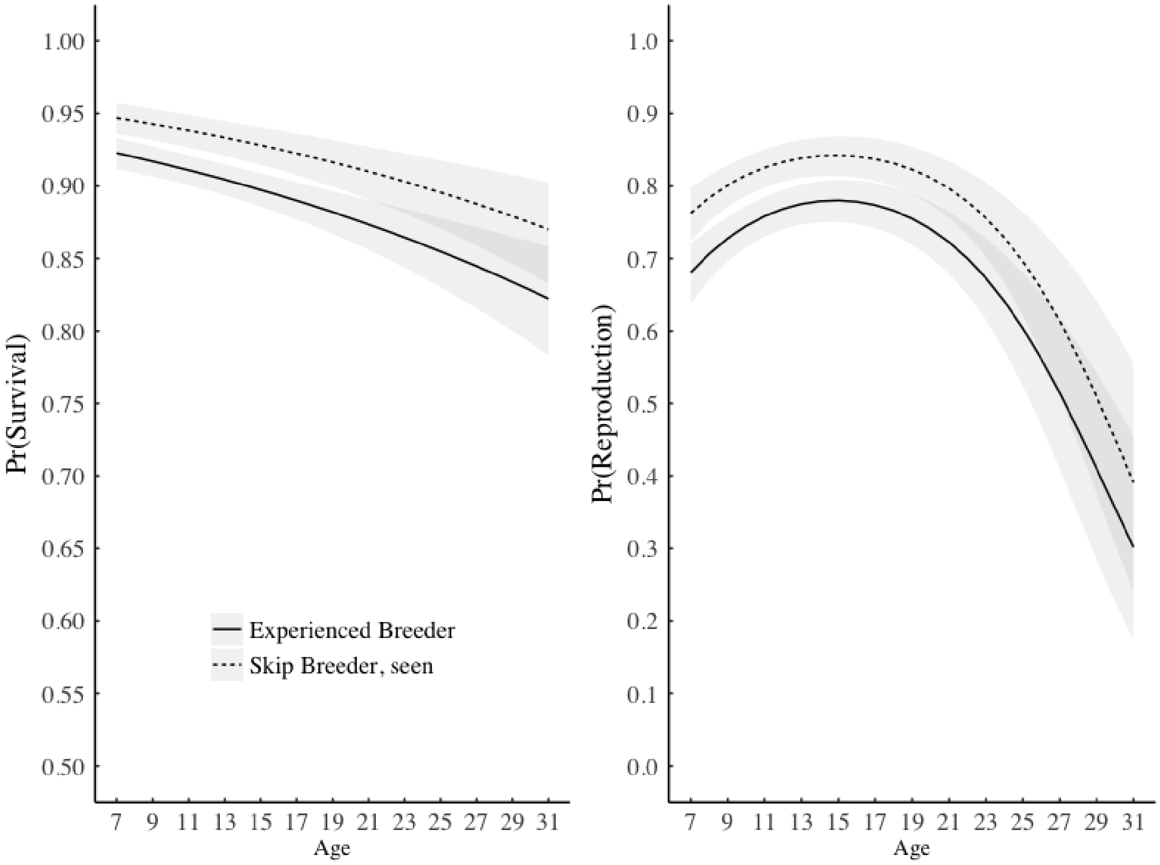

Figure 4-1. Estimated trends in survival and reproductive rates as a function of age and state from the top model, for an average individual who began breeding at age 7 and averaged across year effects. This model included a quadratic form for the effects of age on both survival and reproduction. On the logit scale, the coefficient for the quadratic term for age was estimated to be zero for survival rates, and negative for reproductive rates. Thus, survival declines as a linear function of age at first reproduction, whereas reproduction increases to a maximum near 15 years of age before declining.

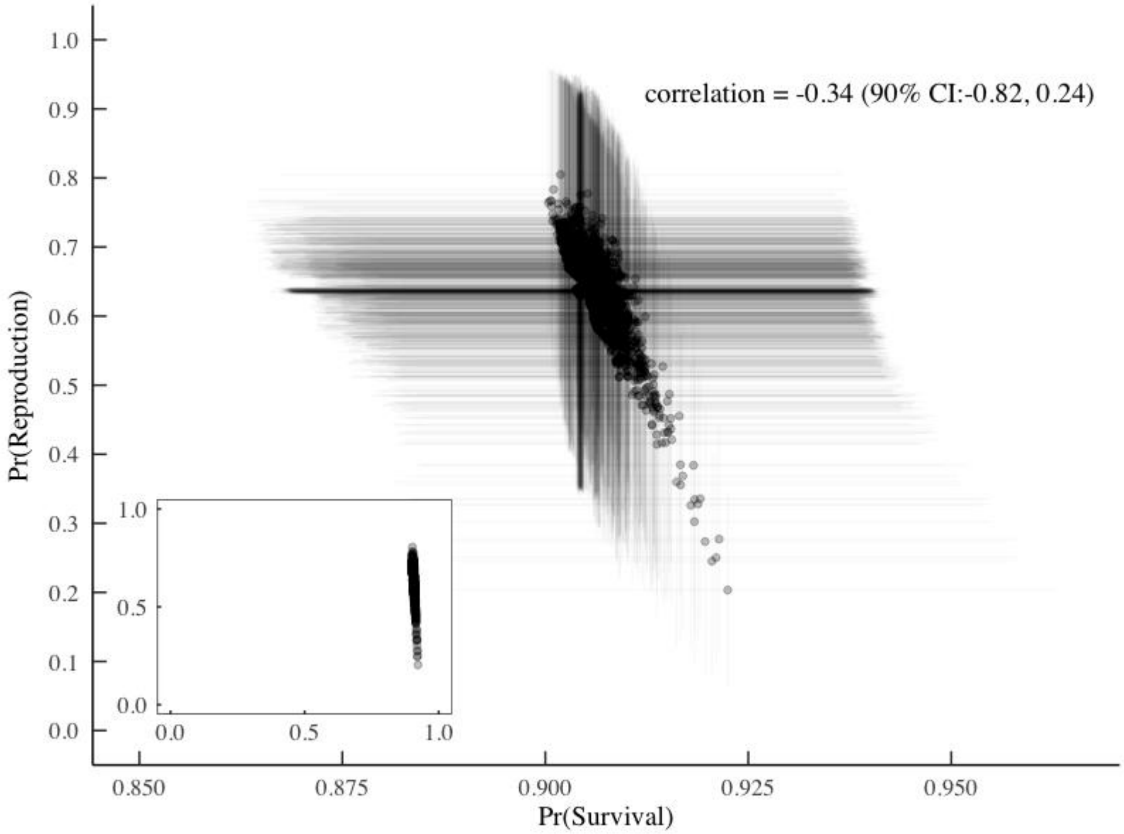

Figure 4-2. Estimated individual random effects for the probabilities of survival and reproduction. These have been transformed from the logit scale to probability by assuming each applies to a 12-year old individual in the Experienced Breeder state, who began breeding at age 7 (the median values in this data set), in an average year. The larger graph is presented on unequal scales to show the distribution of points; the inset graph is on equal axes. We note there is substantially more variation in the probabilities of reproduction, compared to survival. The mean of the correlation between the two random effects (-0.34, 90% CI: -0.82, 0.24) is negative, though the width of the credible interval prevents strong inference.

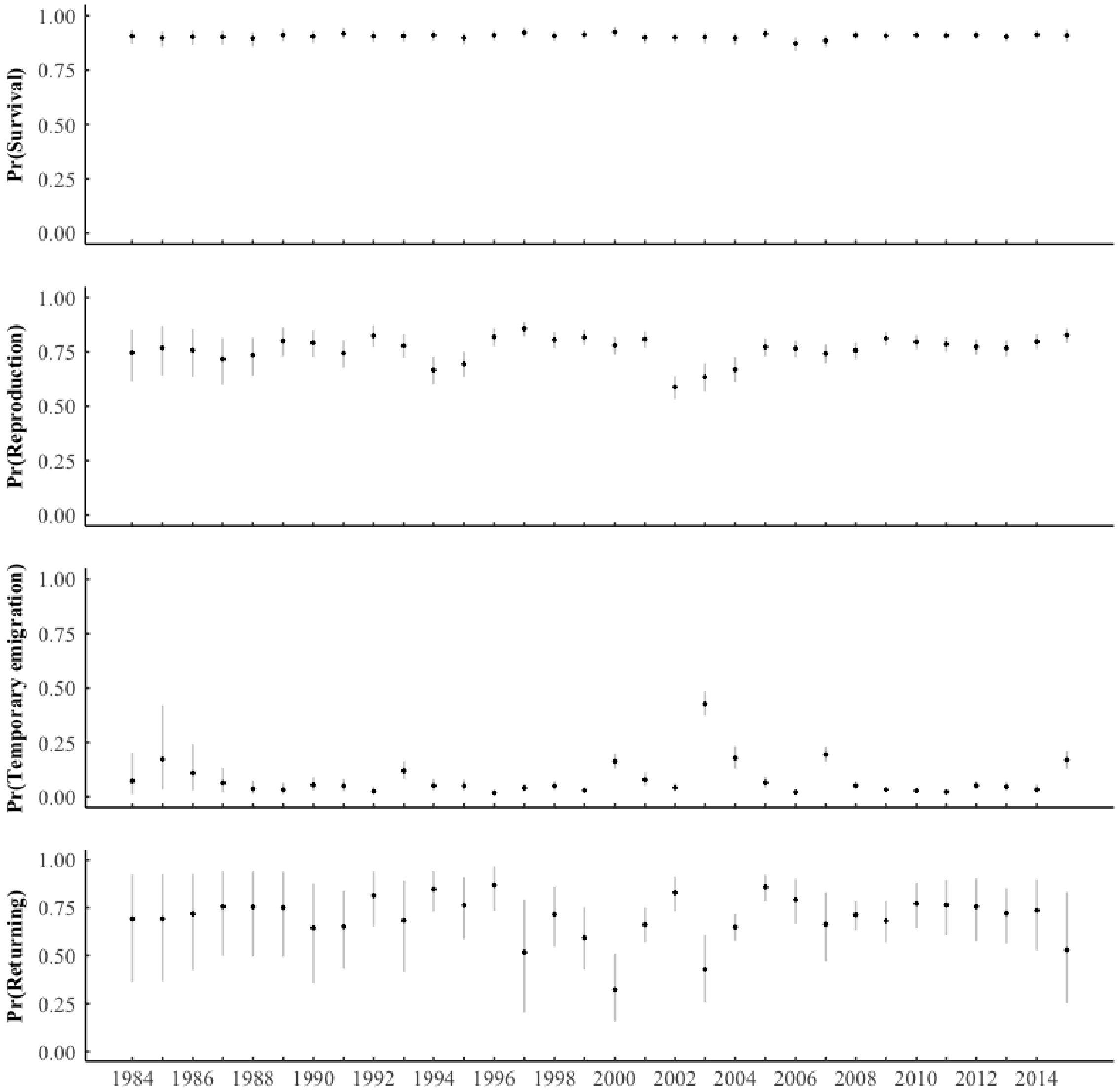

Figure 4-3. Estimated influence of yearly random effects on the probabilities of survival, reproduction, temporary emigration, and returning to the area once emigrated. These effects have been transformed from the logit scale to the probability scale by assuming each applies to a 12-year old individual, who began breeding at age 7, with an average individual random effect of survival and reproduction. Probabilities of survival have been corrected for tag loss. We note the relative difference in the variation among these effects. Year-to-year survival is high and less variable than reproduction. The probabilities of temporarily emigrating are low, and those of returning are high.

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CHAPTER FIVE

CONCLUSION AND DIRECTIONS FOR FUTURE RESEARCH

Conclusion

The long-term data on the population of Weddell seals in Erebus Bay has proven to be ideal for assessing the sources of variation in population features that are important to the dynamics of populations of long-lived mammals. Results from previous analyses of the data from the long-term research effort have resulted in diverse insights into the life history of Weddell seals, population dynamics, and associations between the population's dynamics and abiotic environmental fluctuations. Previous work has also identified body mass as a potential mechanism to link environmental processes to variation in vital rates, and documented extensive variation in the vital rates of adult females associated with breeding state, age, and individual heterogeneity. I have made new contributions to our understanding of the complex demography of this upper-trophic-level species by investigating several novel sources of heterogeneity in processes that Weddell seal population dynamics. Specifically, the results presented in this dissertation add novel information regarding 1) how Weddell seals may respond to environmental variability through bottom-up coupling of the trophic levels, 2) the dynamics of the maternal allocation of resources to offspring, and 3) the sources and magnitudes of variation in the vital rates of adult females.

Chapter 2 reports an association between the amount of annual primary production in two local polynyas and the total number of pups produced in the Erebus

Bay colonies. Polynyas, areas of open water surrounded by sea ice, are often the first areas to receive sunlight in the austral spring and are important sources of primary production in high-latitude marine ecosystems. As a result, polynyas serve as an important connection between larger-scale atmospheric and oceanographic conditions and the trophic structure of the ecosystem. By investigating the relationship at multiple time lags, Chapter 2 documented a surprising relationship that suggested more pups are born in the months prior to high primary production, i.e. pups numbers appear to increase to take advantage of an environment of relative abundance for the pups after weaning. This contrasted with the hypothesis that predicted pup numbers should be more closely associated with primary production in the year prior to birth, when the female may take advantage of higher primary production (and the implied spatial distribution of fish), to gain the body reserves required for reproduction. The results emphasize that the proximate causal mechanism of this relationship is unknown, but it does demonstrate a tight coupling between disparate trophic levels in a high-latitude environment.

Chapter 3 evaluated the patterns of variation in four response variables (adult female body mass soon after parturition, pup mass soon after parturition, and daily pup mass gains during both the early and late lactation periods) to assess the strength of evidence for several predictions from life history theory. Both the constraint and restraint hypotheses predicted that allocation of maternal resources should increase with reproductive experience and/or age. For older-aged animals, the senescence hypothesis predicted a decline in allocation commensurate with a decline in physiological function. Chapter 3 utilized a hierarchical modeling approach to more clearly estimate the magnitude of variation due to age effects, individual identity of the mother, and yearly effects. Results indicate that the body mass of mothers near parturition showed initial improvement with age, followed by senescent declines for the oldest mothers. The maternal pattern was mirrored for the parturition mass of pups, which suggests that pup mass is linked to maternal mass, and that allocation during the pre-natal phase is allometrically constrained by maternal mass. In contrast, results of Chapter 3 indicate that the allocation of resources from mothers to pups during the lactation period, demonstrated by daily mass gains for pups, continued to increase with maternal age such that pups born to the oldest mothers were experiencing the highest rates of daily gain. Taken together, these patterns are consistent with terminal allocation, wherein older females allocate more of a declining resource to their offspring. The results of Chapter 3 indicate that maternal allocation changes over a mother’s reproductive lifespan and that age-specific differences differ in remarkable ways in prenatal and postnatal periods. Moreover, the hierarchical modeling approach used in Chapter 3 estimated that the among-individual heterogeneity in the allocation of resources to offspring was much larger than the yearly variation in pup mass at parturition and pup mass gains over lactation, such that some mothers can repeatedly produce heavier pups at birth and allocate more resources during lactation.

Chapter 4 investigated the sources of variation in vital rates by decomposing the probabilities of transitioning between four reproductive states, and to one dead state, into the probabilities of survival, reproduction, and movement from and to the study area. Furthermore, each constituent probability of survival and reproduction was modeled as a function of female age, age at first reproduction, as well as both individual latent traits and effects due to year to evaluate the relative support for a variety of hypotheses from life history theory. Chapter 4 adopted a multi-model approach and used cutting-edge statistical techniques to rigorously evaluate the fit of each model to the data, as well as the predictive ability of each model over two scales of the data. Doing so allowed for a confident and direct evaluation of model performance for specific hypotheses that provided compelling evidence for reproductive costs to both survival and future reproduction, with breeders having lower rates of survival and subsequent reproduction than non-breeders. Chapter 4 detected age-related changes in the rates of survival and reproduction, though the patterns differed for the two rates. Consistent with the onset of senescence at primiparity, survival rates steadily declined from the age of first reproduction. In contrast, reproductive rates initially increased with age from primiparity to a maximum approximately 8 years later, then declined with age, a pattern that is broadly consistent with restraint affecting reproduction early in life coupled with a senescent decline later in life. Models that included individual effects explained more variation in life-history traits than those that did not, which strongly suggests that observed variation in life-history traits is associated with the latent traits of individuals in addition to the stochastic nature of life histories. Chapter 4 estimated the variation in individual heterogeneity in reproductive rates to be approximately four times higher than that found in previous studies, such that, all else being equal, the probabilities of reproduction range from less than 0.20 to more than 0.80. In contrast, Chapter 4 found a comparatively trivial amount of individual heterogeneity in survival, and no compelling evidence for a correlation between the two effects. As predicted for this long-lived species with a flexible breeding strategy, annual variation in the rate of reproduction was greater than that in the survival rate.

Directions for Future Research

Throughout this dissertation, variation in several processes associated with population dynamics have been documented, which suggests multiple avenues for future research. First, the proximate causal mechanism for the linkage between primary production in polynyas and pup numbers in Erebus Bay clearly needs further investigation. In particular, understanding the surprising timing of the relationship requires a better understanding of not only the environmental cues that may signal future high primary production, but also the physiological mechanism that allows the accommodation of such information. Moreover, as suggested in Chapter 2, the surprising timing of the relationship might be driven by females taking advantage of an environment of abundance, a suggestion with some precedent from other species (Lindström 1988; Boutin *et al.* 2006; Bergeron *et al.* 2011) as a way of increasing juvenile survival. Juvenile survival in Weddell seals is also thought to be low (Hastings, Testa & Rexstad 1999; Garrott *et al.* 2012), and an interesting direction for future research would be an analysis of the relationship between primary production in nearby polynyas in the post-parturition period and juvenile survival, though this is not without methodological challenges.

Second, the allocation of maternal resources to offspring during both the prenatal and post-parturition periods can have profound consequences on the lifetime success of offspring. Increasingly, researchers are finding connections between the conditions experienced early in life, and the probabilities of survival and reproduction throughout the lifetime of an organism (Kruuk *et al.* 1999; Lindström 1999; Lummaa & Clutton-Brock 2002; Lummaa 2003; Hayward, Rickard & Lummaa 2013). Although the mechanisms remain unclear in many studies, recent work has suggested that the prenatal environment experienced by organisms may permanently affect the expression of the fetal genome and have long-term physiological consequences for metabolism and immune system function (Lucas 1991, 1998; Hales & Barker 2001; Gluckman *et al.* 2005). Additionally, the postnatal environment (both preweaning and the postweaning juvenile period) has been shown to directly affect future survival and reproduction, though there are conflicting results in pinnipeds (McCann, Fedak & Harwood 1989; Bowen, Stobo & Smith 1992; McMahon, Burton & Bester 2000; Ailsa, Bernie & Barker 2001; Proffitt, Garrott & Rotella 2008). The relative influence of these two periods on the lifetime success of individuals is currently unknown (Beauplet *et al.* 2005), as are the potential interactions between them and possible compensation during the postnatal period for a “bad start” (Metcalfe & Monaghan 2001). The Weddell seal project is ideally positioned to assess the consequences of variation during the prenatal and postnatal periods to offspring survival and reproductive success. Maintaining the mass dynamics study into the future should ensure enough cohorts with mass measurements have had a chance to recruit to the breeding population to accurately assess the relative influence of maternal allocation in early life on the probabilities of juvenile survival and recruitment.

In ecology, it is canonical that reproductive success is not uniformly distributed among individuals. The findings presented here provide evidence of strong among-individual variation in the probabilities of reproduction arising from the latent traits of individuals, such that, all else being equal, some individuals might be several times more likely to breed than other, lower-quality individuals. The consequences of such variation for population dynamics should be directly assessed. In particular, integral projection models (IPMs) are ideal for assessing the impact of the combination of variation in vital rates arising from both discrete characteristics, e.g. age class, and continuously-distributed characteristics, such as estimated individual latent effects, on population growth rates (Ellner & Rees 2006; Rees & Ellner 2009). IPMs have been used to assess the consequences to population growth for species with complicated demography, incorporating variation in vital rates due to costs of reproduction, discrete life stages, and temporal variation (Ramula, Rees & Buckley 2009; Zuidema *et al.* 2010; Merow *et al.* 2014). To my knowledge, IPMs have not been used for population projections accounting for all the sources of variation in vital rates addressed in this dissertation. The Weddell seal project is therefore positioned to make novel contributions to the understanding of the population dynamics of long-lived species by making the most comprehensive assessment to date of the impacts of multiple sources of heterogeneity in vital rates on population growth rates.

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APPENDICES

APPENDIX A

SUPPLEMENTARY MATERIAL FOR THE THIRD CHAPTER

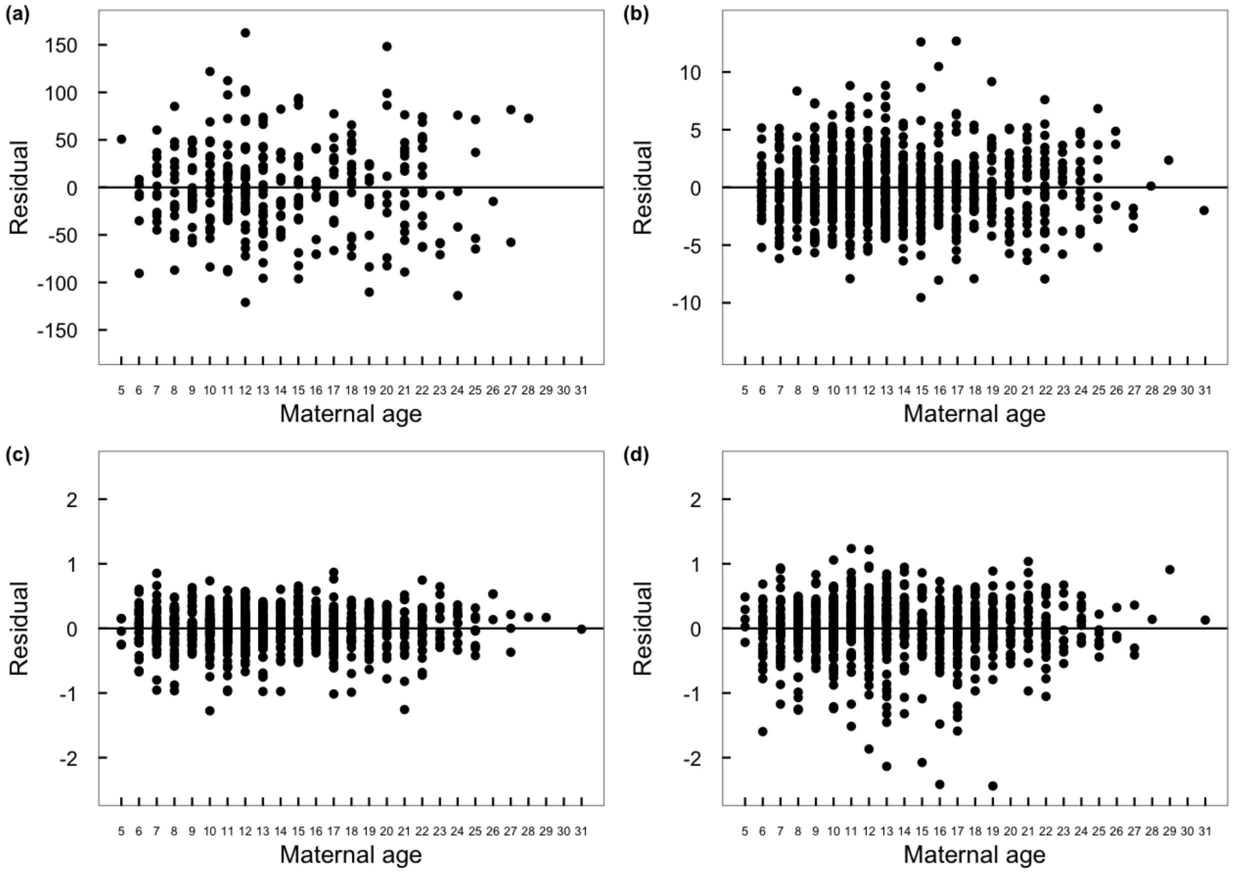

Figure A1. Residuals from each top model plotted against maternal age: (a) maternal masses near parturition with a quadratic form, (b) pup masses near parturition with a quadratic form, (c) daily mass gains during early lactation using a logarithmic form, and (d) daily mass gains during late lactation using a logarithmic form. The lack of structure from the residuals suggests the models fit reasonably well and, in the case of the quadratic models, are not driven by the more numerous data from younger animals.

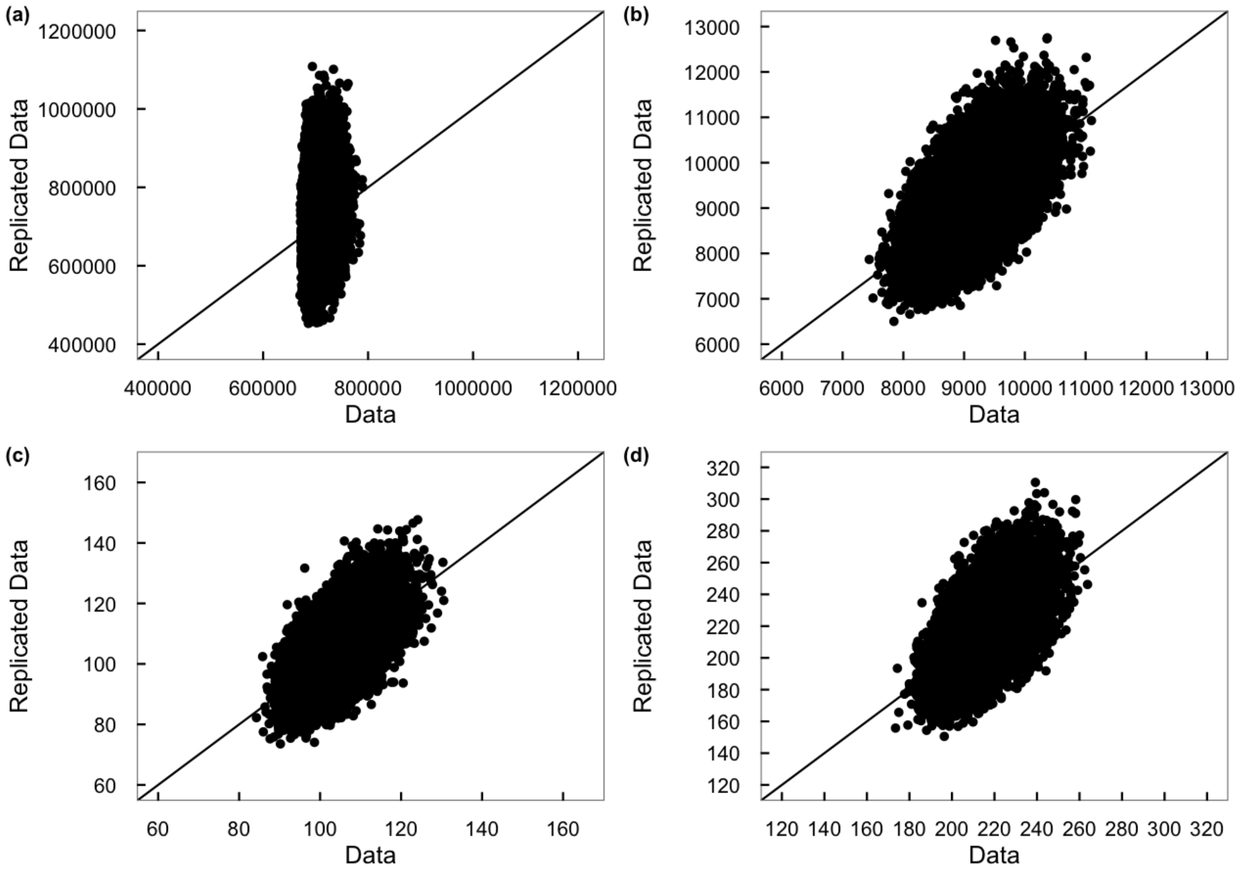

Figure A2. Posterior predictive check that compares the sum of squared residuals for the observed data against that for replicated data generated from the posterior distribution for each of the top models: (a) maternal masses near parturition with a quadratic form, (b) pup masses near parturition with a quadratic form, (c) daily mass gains during early lactation using a logarithmic form, and (d) daily mass gains during late lactation using a logarithmic form. The broad agreement suggests the top model is a reasonable fit to the data.

Text A1. Modeling Approach

Our modeling approach was to investigate the relative amount of support for different functional forms for maternal age, conditional on the inclusion of a small number of covariates common to each model. Our functional forms allowed for a variety of different relationships between maternal age and each response:

Functional form, $f(\text{MaternalAge})$

Null	$f(\text{MaternalAge}) = 0$
Linear	$f(\text{MaternalAge}) = \text{Maternal Age}^{*}$
Quadratic	$f(\text{MaternalAge}) = \text{Maternal Age}^{*} + \text{Maternal Age}^{*2}$
Logarithm	$f(\text{MaternalAge}) = \log(\text{Maternal Age}^{+})$
Single-threshold	$f(\text{MaternalAge})=(\text{Maternal Age} - \Delta)I_{\text{Maternal Age} \leq \Delta}(\text{Maternal Age}^{*}) + (\text{Maternal Age} - \Delta)I_{\text{Maternal Age} > \Delta}(\text{Maternal Age}^{*})$
Double-threshold	$f(\text{MaternalAge}) = (\text{Maternal Age} - \Delta)I_{\text{Maternal Age} \leq \Delta}(\text{Maternal Age}^{*}) + (\text{Maternal Age} - \Delta)I_{\text{Maternal Age} > \Delta}(\text{Maternal Age}^{*}) +$ $(\text{Maternal Age} - \Delta_2)I_{\text{Maternal Age} > \Delta_2}(\text{Maternal Age}^{*})$

The superscript '$*$' denotes a covariate was centered using its mean; the '$+$' superscript denotes the covariate was transformed by subtracting the minimum and adding a small constant. For the threshold models, the functions $I_{\Delta < \text{Maternal Age}}(\text{Maternal Age}^{*})$ are indicator functions such that, for example:

$$I_{\text{Maternal Age} \leq \Delta}(\text{Maternal Age}^{*}) = \begin{cases} 1, & \text{Maternal Age}^{*} \leq \Delta \\ 0, & \text{Maternal Age}^{*} > \Delta \end{cases},$$

where Δ is the estimated threshold. These define the domains over which each piece of the function is defined. It is important to note that for practical reasons of MCMC convergence and estimability, we parameterized the single threshold models using two separate linear segments, centered on the threshold itself. Hence, the estimated intercept for these models is the predicted response at the value of the threshold. For the double threshold models, we added a small adjustment to the slope for values of maternal age exceeding the second threshold, rather than estimate a separate slope over this domain. For the models of maternal mass near parturition, we modeled the response as:

$$(\text{Maternal mass at parturition})_{iy} \sim N(\mu_{iy}, \sigma^2),$$

$$\mu_{iym} = \alpha + f(\text{MaternalAge}) + \beta(\text{PreviousState}_{ym}) + \beta(\text{NPreviousPups}^{*}_{ym}) + \gamma_y,$$

for individual i (i=1,..,321), year y (y=1,…,11).

We used the same approach for models of pup mass near parturition, daily gains during early lactation, and daily gains during late lactation:

$$(\text{Pup mass at parturition})_{\mathrm{iym}} \sim N(\mu_{\mathrm{iym}},\sigma^2)$$

$$\mu_{iym}=\alpha + f(\text{MaternalAge}) + \beta(\text{PreviousState}_{ym}) + \beta(\text{NPreviousPups}^*_{ym}) + \beta(\text{DTA}_i) + \beta(\text{Birthdate}^*_i) + \beta(\text{Female}_{\mathrm{i}}) + \eta_{\mathrm{m}} + \gamma_{\mathrm{y}}$$

$$(\text{Daily gains during early lactation})_{iym} \sim N(\mu_{iym},\sigma^2)$$

$$\mu_{iym}=\alpha + f(\text{MaternalAge}) + \beta(\text{PreviousState}_{ym}) + \beta(\text{NPreviousPups}^*_{ym}) + \beta(\text{PartMass}^*_i) + \beta(\text{Birthdate}_i) + \beta(\text{Female}_{\mathrm{i}}) + \eta_{\mathrm{m}} + \gamma_{\mathrm{y}}$$

$$(\text{Daily gains during late lactation})_{iym} \sim N(\mu_{iym},\sigma^2)$$

$$\mu_{iym}=\alpha + f(\text{MaternalAge}) + \beta(\text{PreviousState}_{ym}) + \beta(\text{NPreviousPups}^*_{ym}) + \beta(\text{PartMass}^*_i) + \beta(\text{Birthdate}^*_i) + \beta(\text{Female}_{\mathrm{i}}) + \eta_{\mathrm{m}} + \gamma_{\mathrm{y}},$$

for individual i (i=1,..,856), year y (y=1,…,11), mother (m=1,…,460). The random effects in all models were assumed to be normally distributed with zero mean and estimated variance component, e.g. random effects for individual mothers: $\eta_{\mathrm{m}} \sim N(0, \sigma^2_{\mathrm{mother}})$ We centered our covariates when possible to aid in interpretation and model-fitting, using the mean from the data.