RECRUITMENT PROBABILITIES AND REPRODUCTIVE COSTS FOR WEDDELL SEALS IN EREBUS BAY, ANTARCTICA

by

Gillian Louise Hadley

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

of

Doctor of Philosophy

In

Biological Sciences

MONTANA STATE UNIVERSITY
Bozeman, Montana

April 2006

APPROVAL

of a dissertation submitted by

Gillian Louise Hadley

This dissertation has been read by each member of the thesis committee and has been found to be satisfactory regarding content, English usage, format, citations, bibliographic style, and consistency, and is ready for submission to the Division of Graduate Education.

Dr. Jay J. Rotella, Committee Chair

Approved for the Department of Ecology

Dr. David Roberts, Department Head

Approved for the Division of Graduate Education

Dr. Joseph J. Fedock, Graduate Dean

STATEMENT OF PERMISSION TO USE

Gillian Louise Hadley

April 2006

ACKNOWLEDGMENTS

This research was funded by a grant from the National Science Foundation to R. Garrott, J. Rotella, and D. Siniff (grant #OPP-0225110). Prior NSF grants to D. Siniff and J. Testa supported the collection of data used in this dissertation. I am grateful to the many individuals that collected data on the Erebus Bay Weddell seal population since the 1960s, particularly field team members from 2002-2004: C. Alfano, S. Ellison, D. Ireland, M. Johnston, K. Proffitt, T. Scheer, B. Stewart, and J. Warren. Michael Cameron helped me learn the ropes of doing science in Antarctica, assisted with fieldwork in 2002, and was constantly willing to help with database-related issues.

Members of BIOL 508 and Dr. Donald Siniff provided thoughtful comments on manuscripts in progress. I was fortunate to have Karen Newlon as an office-mate. Her clear thinking, careful editing, technical knowledge of Microsoft products, and ever-ready comic relief were a great help to me throughout my degree.

My graduate committee (Dr. Jay Rotella, Dr. Robert Garrott, Dr. Scott Creel, and Dr. Jim Nichols) provided useful advice during every phase of this research. I especially thank Bob, Jay, and Jim for their visits to the Ice which were a valuable time for me to view the Erebus Bay study system from a variety of perspectives and enjoy evening discussions on an array of topics both scientific and non-scientific. My major advisor, Jay Rotella, was helpful in every respect, and I have come to appreciate much more of what it is to be a scientist as a result of Jay’s knowledge, advice, thoughtful comments, and most importantly, sense of humor.

Finally, I thank my family and my husband-to-be, Jeffrey Warren, for their continued love, support, and interest in my work.

TABLE OF CONTENTS

TABLE OF CONTENTS - CONTINUED

LIST OF TABLES

LIST OF FIGURES

ABSTRACT

The study of life history traits such as age at first reproduction and the evaluation of recruitment probabilities and reproductive costs allow insight regarding the diverse factors and mechanisms shaping reproductive strategies. We investigated these mechanisms using a 26-year mark-resight dataset for Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica. Mean age at first reproduction was 7.62 years of age (SD=1.71), but varied from four to 14 suggesting the presence of important heterogeneity in quality among females. Survival rate was maximized for offspring of age-14 mothers ($\hat{\phi}$ =0.70 [$S\hat{E}$ =0.08]), whereas recruitment probability was highest for pups born to youngest-breeding mothers. For example, probability of recruitment at age 7 was an average of 43% lower for seals born to age-14 mothers than for seals born to age-6 mothers. These results suggest the influence of countervailing selection (where favored genotypes for reproductive success are generally those that are selected against as juveniles). Sea-ice extent affected annual recruitment rates, likely due to cascading effects of oceanographic conditions on marine primary productivity and fluctuations in food availability for female Weddell seals. Results from the reproductive cost analysis strongly supported the presence of reproductive costs to survival ($\overline{\hat{\phi}}$ was 0.91 for breeders versus 0.94 for nonbreeders). Costs to fecundity were present for first-time breeders (mean probability of breeding the next year was 0.20 lower for first-time breeders than for experienced breeders). Females that delayed breeding until later in life experienced highest reproductive costs to fecundity, possibly due to their inferiority relative to other individuals in the population, again suggesting the influence of heterogeneity in individual quality. From these analyses we have gained insight into 1) the extent of within-population variation in important life-history characteristics for a long-lived species, and 2) the sources of this variation and potential linkages with environmental variables. Keys to future research will be 1) explaining variation in individual quality with random effects models or by using mass as an indicator variable, and 2) more detailed exploration of appropriate climate and sea-ice indices to elucidate linkages between this top trophic level predator and variation in the Antarctic marine environment.

CHAPTER ONE.

INTRODUCTION

Introduction to Dissertation

In 1954, Lamont Cole stated that “there have been relatively few attempts to evaluate quantitatively the importance of specific features of life histories”. In the years since Cole made this observation, much has been learned about the variability of life history traits in different types of organisms and how this variability affects population growth rates. This growing body of work has allowed life-history theorists to make generalized predictions about the strategies of different types of organisms and the expected variability of various life-history parameters. Testing and refining these predictions with data gathered from wild populations has become a key area for investigation by ecologists. For long-lived species, long-term datasets are necessary for observing variation in life history traits. Population studies that began several decades ago are now revealing interesting trends and patterns in the life-history strategies of long-lived species. As these data become available, it is important for investigators to evaluate support for life-history predictions and compare and contrast the outcomes with results from other study systems.

The extent to which a species conforms to life history predictions is likely to be influenced by the type of environment it inhabits. Species in polar environments may exhibit life history strategies different from those in more temperate environments. The aim of this dissertation is to investigate variation in life history traits and vital rates for a long-lived species in an extreme environment. We utilized a 35-year dataset on individually marked Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica to evaluate predictions regarding 1) recruitment to the breeding population, and 2) investment in reproduction relative to survival.

For many species, when to begin reproduction is an important life-history decision that varies by individual and can have important implications for lifetime reproductive success and fitness. In Chapter 2, we estimated age-specific probabilities of first-time breeding and modeled variation in these rates to determine age at first reproduction and understand why it varies in a population of Weddell seals in Erebus Bay, Antarctica. We used multi-state mark-resight modeling methods and encounter histories of 4,965 known-age female seals to test predictions about age-related variation in probability of first reproduction and the effects of annual variation, cohort, and population density.

In Chapter 2, we discovered that some females did not begin reproduction until well beyond the mean age of first reproduction. We hypothesized that variation in maternal characteristics, birth location, and/or oceanographic conditions may explain the occurrence of such delayed reproduction. Therefore, in Chapter 3 we used 25 years of data on individually marked Weddell seals to evaluate a variety of hypotheses regarding how survival and recruitment probabilities of offspring vary as functions of maternal characteristics (age, experience, and age at first reproduction), location of birth, and oceanographic conditions (sea-ice extent and sea surface temperature). We predicted that offspring survival and recruitment probabilities would be positively related to maternal age and experience up to some threshold maternal age, and we evaluated three hypotheses for the shape of the relationship beyond the threshold age (steadily increasing, approaching an asymptote, or decreasing). We expected to find an inverse relationship between maternal age at first reproduction and offspring survival and recruitment probabilities, and additionally expected survival and recruitment probabilities to vary by location of birth. Highest survival and recruitment probabilities were predicted for either 1) seals born at more protected locations with stable sea-ice conditions, or 2) seals born at colonies with highest mean maternal age. Sea surface temperature and sea-ice extent were additionally expected to influence annual recruitment probabilities due to their influence on primary productivity.

Chapters 2 and 3 focused on understanding the mechanisms determining which female seals are recruited to the breeding population, and at what age this occurs. It was also important for us to investigate the life-history strategies of animals following their recruitment, and to evaluate the consequences of different strategies for lifetime reproductive output. Organisms balance current reproduction against future survival and fecundity, which results in life-history trade-offs. These trade-offs are also known as reproductive costs and may be significant factors shaping life history strategy for many species. Opportunities to test life-history predictions about reproductive costs in long-lived species are rare due to the need for long-term data. In Chapter 4, we again used multi-state mark-resight models and 26 years of mark-resight data (1979-2004) to estimate the costs of reproduction to survival and fecundity for Weddell seals. We evaluated whether this species 1) conformed to the fixed reproductive strategy predicted by life-history theory for long-lived species (individuals minimize survival costs and incur primarily costs to future reproduction) or 2) incurred costs to survival in order to reproduce in a variable environment (flexible-strategy hypothesis). We predicted that reproductive costs would be highest for young, inexperienced seals, but would not be influenced by age at first reproduction. We also expected costs to vary annually, and predicted that favorable oceanographic conditions would be correlated with decreased reproductive costs.

Finally, in Chapter 5 we briefly summarized major findings of the previous three chapters and addressed future research directions. Because this research was conducted in cooperation with several colleagues, the text was written in the first-person plural throughout the thesis to allow for the submission of individual chapters as journal articles with several co-authors.

Literature Cited

Cole, L.C. 1954. The population consequences of life history phenomena. The Quarterly Review of Biology 29:103-137.

CHAPTER TWO.

VARIATION IN AGE AT FIRST REPRODUCTION OF WEDDELL SEALS IN EREBUS BAY, ANTARCTICA

Introduction

For many mammal species, there is considerable variation in the age at which first reproduction occurs, among and within populations (Bengston and Laws 1985, Harvey and Zammuto 1985, Reiter and LeBoeuf 1991, others). The age at which an animal begins breeding has the potential to greatly influence individual fitness and lifetime reproductive output (Stearns 1976, 1992). Therefore, variation in age at first reproduction can be limited by trade-offs between current and future reproduction and between lifetime reproductive output and survival (Roff 2001). For example, a younger age at first reproduction will increase individual fitness if future survival and breeding probabilities remain constant. However, breeding at a younger age may reduce resources available for future growth and maintenance and consequently affect lifetime reproductive output (Gadgil and Bossert 1970, Roff 1992). Knowledge of the extent and sources of variation in age at first reproduction is critical for understanding these trade-offs and their potential fitness consequences.

Long lifespan combined with delayed maturity allows substantial variation in reproductive tactics for some species. Despite the importance of the topic, our knowledge of age at first reproduction in long-lived species has, in most cases, been limited by a lack of sufficient data, absence of appropriate analytical methods, or both.

Discerning when an individual first reproduces is often difficult in field situations and requires a study population that is readily observable during the reproductive season and for which the reproductive status of individuals is easily determined. Moreover, long generation times necessitate long-term studies (e.g., >10 years for many species) to observe the full range of natural variation in age at first reproduction.

Analytically, challenges with estimating age at first reproduction occur when 1) not all animals begin reproduction at the same age, and 2) detection probability for individuals that have not yet reproduced is <1.0 (Clobert et al. 1994, Spendelow et al. 2002). Open-model mark-resight methods allow researchers to estimate transition rates between breeding states for numerous age classes even when detection rates for animals are <1.0. However, these methods still require some potentially restrictive assumptions, such as the assumption of a maximum age by which all surviving individuals become breeders (Testa et al. 1990, Clobert et al. 1994, Spendelow et al. 2002). The multi-state mark-resight methods used in this paper are a recent extension of basic mark-resight models and allow us to estimate age-specific transition rates between reproductive states without assuming a maximum age by which all individuals begin reproduction (Nichols et al. 1994). Thus, the method widens the range of long-lived species and datasets for which age at first reproduction may be estimated.

The Erebus Bay population of Weddell seals (*Leptonychotes weddellii*) provides a unique opportunity for learning about age at first reproduction in a long-lived mammal inhabiting a harsh and extremely variable environment. This population of seals, located at approximately 77° South in McMurdo Sound in the Ross Sea region of Antarctica, is the southernmost population of breeding mammals in the world, and displays a life history that is highly dependent on sea-ice conditions (Stirling 1969, Hastings and Testa 1998). Reproductive states of Weddell seals are highly observable as female seals remain on the sea ice for several weeks during parturition and nursing of pups (Stirling 1969). Additionally, females are strongly philopatric (Stirling 1969, Cameron and Siniff 2004), allowing us to reasonably assume that females born at Erebus Bay colonies will, if they survive to breeding age, return to Erebus Bay to have their pups. Finally, a long-term dataset exists for the Erebus Bay Weddell seals, making it an ideal population for analysis of age at first reproduction in a multi-state mark-resight framework.

Our goal was to learn about age at first reproduction in Weddell seals by evaluating the extent and sources of variation in the probability of first-time reproduction. We defined age-specific recruitment as the age-specific rate of transition from 'prebreeder' (female that had not yet had a pup) to 'breeder' (female that had been determined to have had her first pup [by being sighted more than once with a pup in a given breeding season]), given that the seal had survived to the age in question and was present in the study population. For convenience and consistency with other literature, we used the term breeder to denote an individual that produced a pup, not just engaged in mating. Our analyses tested predictions based on *a priori* hypotheses about sources of variation in age at first reproduction and related demographic parameters.

Predictions

The analyses that generated age-specific recruitment rates for our dataset also generated annual survival probabilities. In keeping with life-history theory and previous empirical work on long-lived species (Eberhardt and Siniff 1977, Gaillard et al. 1998, Gaillard et al. 2000), we predicted lower and more variable survival rates for juveniles than for adults.

Age at first reproduction may be delayed in harsh environments where more time is necessary for individuals to attain breeding size or status (Roff 1992). Therefore, we predicted that mean age at first reproduction for the Erebus Bay population would be higher than for a population of Weddell seals at Signy Island, situated further north (60° South) in a more moderate environment (average temperature 14° C warmer) (Stroeve and Shuman 2004). Break-up of shore-fast ice occurs earlier at Signy Island, but this is compensated for by the fact that pupping takes place approximately 2 months earlier than in McMurdo Sound (Testa et al. 1990).

We evaluated two possible hypotheses for age variation in probability of first reproduction. If heterogeneity in individual quality existed, then the group of animals recruiting at the youngest ages would be expected to contain more high-quality individuals whereas those seals that had not recruited by older ages would be expected to contain successively greater proportions of poorer-quality animals. At later ages, the remaining unrecruited seals might be of such low quality that they would be unable to invest energy into reproduction (Cam et al. 2002), and we would observe recruitment probabilities decreasing with increasing age after age of peak reproduction. An alternative prediction, based on evolutionary theory but with no individual heterogeneity, was that selective pressure to maximize fitness would lead to breeding as early as physiologically possible (Cole 1954), and recruitment probabilities would increase with age until all viable members of a cohort were breeding.

For Weddell seals, environmental variability and population density are two potentially important drivers of variation in age at first reproduction. Of these two drivers, we expected that environmental variation was more important from year to year than was density variation because abundance of seals did not vary drastically in the period 1979-2003 (Testa and Siniff 1987). In contrast, environmental variability is likely because polar marine environments are characterized by the growth and retreat of annual sea ice, and the timing and magnitude of the sea-ice coverage fluctuates from year to year (Smith et al. 1998, Arrigo et al. 2002). Sea-ice conditions in Erebus Bay determine the seals' access to breeding sites as well as abundance of food resources. Annual variation in sea-ice conditions leads us to expect substantial variation in age at first reproduction among years.

We expected all age classes to increase or decrease together in response to environmental change but predicted that the magnitude of the response would differ. We expected greater year-to-year variation in recruitment probabilities for young seals than for older seals. Specifically, the temporal variance of recruitment probabilities should decrease with increasing age, as we expected older females to become less choosy and more willing to take risks in order to reproduce (Williams and Nichols 1984).

Finally, we hypothesized that cohort (as a surrogate for environmental conditions experienced early in life) may be an important predictor of variation in age-specific recruitment rates and thus, evaluated cohort as a possible source of variation. Because Weddell seals are capital breeders (that is, they depend on fat reserves to sustain themselves and do little foraging during lactation), adult body size, and therefore environmental conditions at birth, likely play substantial roles in determining breeding probability (Reiter and LeBoeuf 1991, Boyd 2000). Therefore, we expected recruitment probabilities to vary by cohort. Although we predicted little or no effect of density, we examined the possible influence of population density by evaluating two hypotheses: 1) cohorts born in years of high population density might delay reproduction as an outcome of high levels of competition early in life (Festa-Bianchet and Jorgenson 1998), and 2) years of high population density would be followed by years of low recruitment rates due to decreased breeding opportunities for young females (Reiter and LeBoeuf 1991).

Methods

Study Area and Population

The Erebus Bay study area is located at the southern end of McMurdo Sound, Antarctica (-77.62º to -77.87º South, 166.3º to 167.0º East; see Cameron and Siniff 2004 for description and map of study area). Eight to 14 Weddell seal breeding colonies are located within this study area (Stirling 1969). Each colony is associated with tidal cracks that create areas where adult female seals haul out to have their pups. Seals have been individually marked and resighted for each of the past 35 years. Over this period, both the proportion of the population that is marked and the proportion of marked animals that are of known age have gradually increased (Cameron and Siniff 2004). Currently, approximately 80% of the seals in this population are marked, and over 80% of marked animals are of known age. Each year, 300-600 pups are born at colonies in Erebus Bay, and most females surviving to reproductive age return to breed in Erebus Bay (Cameron and Siniff 2004). More detailed information about Weddell seal natural history can be found in Stirling (1969), Siniff et al. (1977), Testa and Siniff (1987), and Cameron and Siniff (2004).

Data Collection

Each year from 1969 until the present, Weddell seal pups born within the Erebus Bay study area have been individually marked with plastic livestock tags attached to the inter-digital webbing of each rear flipper. In addition, any seal with a broken or missing tag was retagged. The majority of the tagging effort occurred from approximately October 15 to November 15 each year, during the peak of parturition. Beginning in early November, six to eight surveys of the study area were carried out, usually separated by intervals of three to five days. Every individual that was sighted (marked or unmarked) was recorded in a database. For mother-pup pairs, the presence and tag number of a relative (mother or pup) was also recorded. All miscellaneous sighting or handling events were also recorded in the database.

Data Analysis

We used multi-state mark-resight models (Arnason 1972, 1973; Hestbeck et al. 1991; Brownie et al. 1993) to estimate age-specific recruitment, survival, and sighting probabilities for female seals. Seals included in the sample were tagged as pups and were thus of known age. Seals tagged prior to 1979 were not included in the sample as sample sizes for those years were too low. One of three breeding states was assigned to each seal for each year that it was sighted based on the number of sightings with a pup within that year's breeding season: 1) prebreeder (a seal not yet sighted with a pup more than once in any season), 2) breeder (a seal sighted with a pup more than once in the current breeding season), or 3) nonbreeder (a seal designated a breeder in a previous season but not sighted with a pup more than once in the current season). We required that a seal be seen with a pup more than once during the breeding season to be classified as a breeder for that year. This was done to avoid falsely conferring breeding status to a seal with an unrelated pup lying nearby during a survey. Finally, note that our definition of states based on sighting histories (e.g., designation of prebreeder is based on never having been sighted as a breeder, whereas designation of nonbreeder is based on previous detection as a breeder) is not a good general approach, but is reasonable in our case because of suspected very high sighting probabilities for breeders (see Results).

To evaluate predictions about recruitment, we developed a set of *a priori* models that included three types of parameters: apparent survival probability (ϕ), sighting probability (p), and conditional transition probability (ψ) (Table 2.1). Our primary interest was the age-specific probability of transition from prebreeder to breeder (ψ^{pb}), which represented probability of first-time breeding. However, it was important for us to adequately model the variation in other parameters included in our models. Therefore, we first evaluated a set of models in which (1) ψ^{pb} was modeled very generally (see below) and the general structure was held constant across all models and (2) ϕ and p were modeled with varying levels of complexity (Survival-and-sighting-probability suite, Table 2.1). This strategy allowed us to first determine the most parsimonious combination of effects for φ and p and to subsequently consider competing parameterizations of ψ (Recruitment-probability suite, Table 2.1).

Models in the survival-and-sighting-probability suite had two possible parameterizations of ϕ: 1) breeding-state and age effects or 2) breeding-state, age, and year effects. Breeding-state effects were included because 1) the majority of seals in the prebreeder state are young and previous studies found ϕ for juveniles to be lower and more variable with age than ϕ for adults (Testa 1987*a*, Hastings et al. 1999, Cameron 2001), and 2) a potential difference in ϕ has been hypothesized for breeding versus non-breeding Weddell seals (Siniff et al. 1977) and demonstrated for other pinniped species (Reiter and LeBoeuf 1991, Lunn et al. 1994). Based on age classes used in the best model in Cameron and Siniff (2004), prebreeder ϕ was modeled with 3 age classes: 1-, 2-, and ≥3-years old and breeder and nonbreeder ϕ were each modeled as one age class. However, because transition probabilities were not included in Cameron and Siniff (2004), and ϕ is conditional on state, we have also included models with age variation in ϕ for the breeder and nonbreeder classes. In these models, ϕ is modeled as a quadratic function of age for all individuals. Six age classes were used (1, 2, 3-6, 7-10, 11-14, and 15 and older), following Cameron and Siniff (2004) and Hastings et al. (1999). In order to capture annual variation in ϕ, year effects were included in some models in addition to the above age and breeding-state effects.

Table 2.1. Biological hypotheses for effects of different covariates on Weddell seal apparent survival (ϕ), sighting (p), and recruitment probabilities (ψ^{pb}) in Erebus Bay, Antarctica, and associated model structures. Breeding state (p = prebreeder, b = breeder, or n = nonbreeder) is indicated by superscript and model structure is indicated by subscript. Age effects differed by parameter type – a3 indicates a 3-class age effect (ages 1, 2, 3 and older), a4 indicates a 4-class age effect (ages 1, 2, 3-6, 7 and older), A indicates a quadratic 6-class age effect (ages 1, 2, 3-6, 7-10, 11-14, 15 and older), a9 indicates a 9-class age effect (ages 1-3, 4, 5, 6, 7, 8, 9, 10, 11 and older)), and a9T indicates a 9-class age effect with a linear trend. Other covariates were year (yr); cohort (co); and annual population density (dn). All models in the survival-and-sighting-probability suite had the same structure for modeling ψ^{pb} (a9*yr). All models in the recruitment-probability suite included the structure for ϕ and p taken from the best model in the survival-and-sighting-probability suite.

Hypothesis	Model structure
Survival-and-sighting-probability suite	
1) 3-class age effect on ϕ^p; 4-class age effect on p^p	ϕ^p_{a3} ϕ^b ϕ^n p^p_{a4} p^b p^n
2) 3-class age effect on ϕ^p; quadratic age effect on p^p	ϕ^p_{a3} ϕ^b ϕ^n $p^p_{a4+a4^2}$ p^b p^n
3) 3-class age effect on ϕ^p; 4-class age effect on p^p and year effect on p^p, p^b, and p^n	ϕ^p_{a3} ϕ^b ϕ^n p^p_{a4+yr} p^b_{yr} p^n_{yr}
4) 3-class age effect on ϕ^p; quadratic age effect on p^p and year effect on p^p, p^b, and p^n	ϕ^p_{a3} ϕ^b ϕ^n $p^p_{a4+a4^2+yr}$ p^b_{yr} p^n_{yr}
5) 3-class age effect on ϕ^p and year effect on ϕ^p, ϕ^b, and ϕ^n; 4-class age effect on p^p	ϕ^p_{a3+yr} ϕ^b_{yr} ϕ^n_{yr} p^p_{a4} p^b p^n
6) 3-class age effect on ϕ^p and year effect on ϕ^p, ϕ^b, and ϕ^n; quadratic age effect on p^p	ϕ^p_{a3+yr} ϕ^b_{yr} ϕ^n_{yr} $p^p_{a4+a4^2}$ p^b p^n
7) 3-class age effect on ϕ^p and year effect on ϕ^p, ϕ^b, and ϕ^n; 4-class age effect on p^p and year effect on p^p, p^b, and p^n	ϕ^p_{a3+yr} ϕ^b_{yr} ϕ^n_{yr} p^p_{a4+yr} p^b_{yr} p^n_{yr}
8) 3-class age effect on ϕ^p and year effect on ϕ^p, ϕ^b, and ϕ^n; quadratic age effect on p^p and year effect on p^p, p^b, and p^n	ϕ^p_{a3+yr} ϕ^b_{yr} ϕ^n_{yr} $p^p_{a4+a4^2+yr}$ p^b_{yr} p^n_{yr}

Table 2.1 cont.

Hypothesis	Model structure
9) 6-class quadratic age effect on ϕ^p, ϕ^b, and ϕ^n; 4-class age effect on p^p	ϕ^p_A ϕ^b_A ϕ^n_A p^p_{a4} p^b p^n
10) 6-class quadratic age effect on ϕ^p, ϕ^b, and ϕ^n; quadratic age effect on p^p	ϕ^p_A ϕ^b_A ϕ^n_A $p^p_{a4+a4^2}$ p^b p^n
11) 6-class quadratic age effect on ϕ^p, ϕ^b, and ϕ^n; 4-class age effect on p^p and year effect on p^p, p^b, and p^n	ϕ^p_A ϕ^b_A ϕ^n_A p^p_{a4+yr} p^b_{yr} p^n_{yr}
12) 6-class quadratic age effect on ϕ^p, ϕ^b, and ϕ^n; quadratic age effect on p_P and year effect on p^p, p^b, and p^n	ϕ^p_A ϕ^b_A ϕ^n_A $p^p_{a4+a4^2+yr}$ p^b_{yr} p^n_{yr}
13) 6-class quadratic age effect and year effect on ϕ^p, ϕ^b, and ϕ^n; 4-class age effect on p^p	ϕ^p_{A+yr} ϕ^b_A ϕ^n_A p^p_{a4} p^b p^n
14) 6-class quadratic age effect and year effect on ϕ^p, ϕ^b, and ϕ^n; quadratic age effect on p^p	ϕ^p_{A+yr} ϕ^b_A ϕ^n_A $p^p_{a4+a4^2}$ p^b p^n
15) 6-class quadratic age effect and year effect on ϕ^p, ϕ^b, and ϕ^n; 4-class age effect on p^p and year effect on p^p, p^b, and p^n	ϕ^p_{A+yr} ϕ^b_A ϕ^n_A p^p_{a4+yr} p^b_{yr} p^n_{yr}
16) 6-class quadratic age effect and year effect on ϕ^p, ϕ^b, and ϕ^n; quadratic age effect on p^p and year effect on p^p, p^b, and p^n	ϕ^p_{A+yr} ϕ^b_A ϕ^n_A $p^p_{a4+a4^2+yr}$ p^b_{yr} p^n_{yr}
Recruitment-probability suite	
1) Variable effect of age (constant after age 11)	ψ^{pb}_{a9}
2) Linear trend effect of increasing age	ψ^{pb}_{a9T}
3) Cohort effect (variable effect of birth year)	ψ^{pb}_{co}
4) Negative effect of density in birth year	$\psi^{pb}_{dn(birth)}$
5) Variable effect of year (representing changing environmental conditions)	ψ^{pb}_{yr}
6) Negative effect of previous season's density as temporal covariate	ψ^{pb}_{dn}

Table 2.1 cont.

Hypothesis	Model structure
7) Negative quadratic effect of density	$\psi^{pb}_{dn+dn^2}$
8) Variable effect of age (constant after age 11); additive effect of cohort	ψ^{pb}_{a9+co}
9) Variable effect of age (constant after age 11); additive effect of density	ψ^{pb}_{a9+dn}
10) Variable effect of age (constant after age 11); additive effect of density in birth year	$\psi^{pb}_{a9+dn(birth)}$
11) Variable effect of age (constant after age 11); additive effect of year	ψ^{pb}_{a9+yr}
12) Variable effect of age (constant after age 11); interactive effect of year	ψ^{pb}_{a9*yr}

Sighting probabilities were also allowed to vary by breeding state in all models due to a documented difference in p for animals of different reproductive status (Siniff et al. 1977, Croxall and Hiby 1983, Testa 1987*b*). We incorporated age-related variation in p for prebreeders by considering four age-classes (1-, 2-, 3-6, and ≥7-yrs old) based on Cameron and Siniff's (2004) reported age structure for p in our study population. We included a quadratic effect of age on p in some models (as did Cameron and Siniff 2004), and allowed p to vary by age class without constraint in other models. As with ϕ, both additive and interactive effects of year and age on p were considered in some models. Because we knew that all or nearly all reproductive females were detected each year, we expected sighting probabilities for breeders (p^b) to be close to 1.0, but allowed these rates to be estimated by the models to confirm our prediction.

Because we designated three breeding states, our models included nine transition probabilities. We fixed parameter values at zero for the three transitions that were impossible: 1) prebreeder to nonbreeder (ψ^{pn}), 2) breeder to prebreeder (ψ^{bp}), and 3) nonbreeder to prebreeder (ψ^{np}). Three transition probabilities were estimated in the multi-state models: 1) ψ^{pb}, which represents recruitment probability, 2) ψ^{bn}, and 3) ψ^{nb}. The remaining three transition probabilities ($\psi^{pp}, \psi^{bb}, \psi^{nn}$, i.e., probabilities of remaining in the same state from one year to the next) were obtained by subtraction based on the fact that the sum of the three transition probabilities for any starting breeding state must equal 1 (e.g., $\psi^{pp} + \psi^{pb} + \psi^{pn} = 1$; $\psi^{pp} = 1 - \psi^{pb} - \psi^{pn}$, where $\psi^{pn} = 0$).

Because our modeling effort was focused on recruitment probability, ψ^{pb}, we held the transition probabilities involving breeders (ψ^{bn} and ψ^{nb}) constant for this analysis. Variation in recruitment probability was modeled with various combinations of age, year, cohort, and population density effects. Because no seals recruited before age four, we fixed ψ^{pb} to zero for seals aged <4-yrs old. For older seals, we estimated ψ^{pb} for eight age classes in all models (4-, 5-, 6-, 7-, 8-, 9-, 10-, and $\geq$11-yrs old). To evaluate predictions made above about importance of cohort variation and the nature of annual variation in ψ_{PB}, some models included cohort or year effects.

Finally, some models evaluated the relationship between ψ^{pb} and population density in a seal's year of birth or in the year a seal had her first pup in the study area. The density values used in these models were annual estimates of the number of females $\geq$3-yrs old ($\hat{N}$) on the study area for 1979-2003 (Table 2.2). The estimates were based on open-population models using the multiple sampling occasions within each season. We used Cameron's (2001) estimates of N for the years 1979-2000 and estimated N for 2001-2003 with Program JOLLY (Pollock et al. 1990) and the method described in Cameron (2001). This method was originally developed by Jolly (1965) and Seber (1965) with the following modification by Siniff et al. (1977). To account for the facts that all animals were not necessarily available for detection at all sampling periods (some may have departed the area before the final sampling occasion) and not every individual seen in a survey was tagged (some were released without marks), annual abundance estimates ($\hat{N}^k$, where *k* is year) were obtained by estimating the superpopulation size (Schwarz and Arnason 1996) where superpopulation refers to the total number of animals in the sampled area during at least one sampling occasion, 2 through *j*, where *j* is the final occasion of the year. Superpopulation size for year *k*, N^k, was estimated as the sum of the initial population size estimate, $\hat{N}_2^k$, and the estimated number of new animals (recruits, $\hat{B}_i^k$) added to the population between the multiple sighting occasions occurring within years. The number of recruits was estimated as suggested by Jolly (1965):

$$\hat{B}_i^k = \hat{N}_{i+1}^k - \hat{\phi}_i^k \hat{N}_i^k$$

where $\hat{N}_i^k$ was the population size estimated by Program JOLLY on occasion *i* in year *k*, and $\hat{\phi}_i^k$ was the probability of surviving the period from occasion *i* to *i*+1 in year *k*, and remaining in the study area, also estimated by Program JOLLY. Annual abundance, $\hat{N}^k$, was then calculated as

$$\hat{N}^k = \hat{N}_2^k + \sum_{i=2}^{j-1} \hat{B}_i^k \ .$$

To prevent failure of the numerical optimization algorithm used to estimate multi-state model parameters, all abundance estimates were standardized (mean = 0, SD = 1) prior to being used as covariates in subsequent analyses.

Table 2.2. Abundance estimates (number of females age three and older, $\hat{N}$) used as temporal covariates in models containing a density effect (dn). Estimates for 1979-2000 are from Cameron (2001) and estimates for 2001-2003 were calculated using Program JOLLY (Pollock *et al*. 1990) and the method described in Cameron (2001).

Year	$\hat{N}$	$\hat{SE}(\hat{N})$
1979	841.0	55.2
1980	807.2	37.3
1981	680.3	32.6
1982	608.1	36.6
1983	873.5	29.8
1984	888.1	33.7
1985	625.1	16.6
1986	625.6	27.4
1987	713.4	25.3
1988	812.6	32.8
1989	637.4	23.2
1990	628.2	17.9
1991	679.6	18.8
1992	579.7	19.7
1993	646.4	18.3
1994	565.3	17.7
1995	750.0	29.3
1996	609.9	22.4
1997	811.9	21.4
1998	665.0	13.7
1999	709.2	20.4
2000	707.1	14.7
2001	483.2	5.9
2002	547.3	9.9
2003	882.6	15.7

Multi-state models were constructed and estimates of model parameters generated using Program MARK (White and Burnham 1999). Akaike's Information Criterion (AIC_c) (Akaike 1973), corrected for small sample bias (Hurvich and Tsai 1989) was used to evaluate the relative support in the data for models in our *a priori* set (Burnham and Anderson 1998). We used the AIC_c value associated with each model to obtain the difference in AIC_c (ΔAIC_c) between the model in question and the model with the minimum AIC_c. Annual estimates of age-specific recruitment probability from the top-ranked model were further analyzed using the variance components module in Program MARK (e.g., see Burnham et al. 1987). This allowed us to separate sampling and temporal process variation to calculate coefficients of variation and evaluate hypotheses about differences among age classes in variability of age-specific recruitment rates. We calculated the amount of possible variation for each age class (VR or variance ratio) as the ratio between observed variance and maximum variance (maximum variance is ϕ *(1-* ϕ*)*, where ϕ is the mean survival rate) (Gaillard and Yoccoz 2003).

We evaluated goodness of fit (GOF) using the newly-available median-$\hat{c}$ method in Program MARK and additionally investigated model ranking under various scenarios, using $\hat{c}$ set to 1.0, 2.0, 3.0 and 4.0 (encompassing average levels of overdispersion (Burnham and Anderson 1998)) to detect the degree of change in model ranking. AIC_c values were converted to $QAIC_c$ values in an attempt to correct for overdispersion, (Burnham and Anderson 1998).

For our study population, it is known that tag loss occurs at a low rate (probability that a female seal will retain at least one of two tags ranged from 0.971 to 0.998; Cameron and Siniff 2004). Therefore, we used the tag-retention rates ($\hat{\theta}$) estimated for this population by Cameron and Siniff (2004) to adjust $\hat{\phi}$ ($\hat{\phi}_{adj} = \hat{\phi}/\hat{\theta}$; Arnason and Mills 1981). This was necessary because if some animals lost both tags, $\hat{\phi}$ represents the product of the underlying survival rate and the tag retention rate (Nichols et al. 1992). Transition probabilities are conditional on survival (Williams et al. 2002) – that is, they are the estimated rates of movement from one state to another, assuming that the animal has survived to the current year and is available on the study area to potentially make the transition. Therefore, transition probability estimates did not need to be corrected for tag loss.

Results

Analyses were performed using encounter histories of 4,965 known-age females that were born within the study area from 1979 to 2003. Of these, 1,212 were known to return to the study area at least once after their year of birth, and 3,753 were never resighted following their year of birth. These data provided us with useful estimates of ϕ, p, and ψ^{pb} which allowed us to gain valuable insights into various hypotheses regarding age at first reproduction.

Goodness of Fit and Model Selection

For the most complex model in our model set (Table 2.1, Survival-and-sighting-probability suite, Model 7), ĉ was 1.807 (based on median-ĉ goodness-of-fit test), and this value was subsequently used to adjust for overdispersion and convert $\mathrm{AIC_c}$ values to $\mathrm{QAIC_c}$ values. Model rankings were robust to changes in ĉ for values of ĉ ≤ 2.3. The top-ranked model from the survival-and-sighting-probability suite included age- and year-effects on both ϕ and p (Table 2.3). $\mathrm{QAIC_c}$ weight for this model was 0.995, indicating that the data strongly supported this model. No other models received any substantial support from the data ($\Delta\mathrm{QAIC_c} \geq 10.98$). Accordingly, the model structure for ϕ and p in the top-ranked model was used as a starting point for our subsequent modeling of ψ^{pb}.

Within the recruitment suite (Table 2.3), model-selection results strongly supported a model that included additive effects of year and age on ψ^{pb} (QAIC$_c$ weight = 0.99; ΔQAIC$_c$ for all other models $\geq$15.00). Given the model-selection results, a single model that contained age and year effects for ϕ, p, and ψ^{pb} was strongly supported by the data and used for estimating parameter values.

Survival and Sighting Probability

Given the structure of our best model, we were able to estimate ϕ and p for prebreeders in 22 different years (1980-2001), for breeders in 19 years (1984-2002), and for nonbreeders in 18 years (1985-2002; Table 2.4). For the last year of the study (2003), ϕ was inestimable for each group. We do not report $\hat{\phi}$ for prebreeders in 2002 because of potential bias in $\hat{\phi}$ from non-random temporary emigration of young age classes (i.e., probability of presence in the sampled area during one year depends on presence in the study area the previous year) (Kendall et al. 1997). Because all females in this dataset were first tagged as pups in 1979 or later and because of the delayed maturity in the species, we could not estimate ϕ and p for breeders until 1984 or for nonbreeders until 1985.

Table 2.3. Model-selection results for initial modeling of $\hat{\phi}$ and $\hat{p}$ and subsequent modeling of $\hat{\psi}^{pb}$ in Program MARK. Transition probabilities from breeding to non-breeding state ($\hat{\psi}^{bn}$) and from non-breeding to breeding state ($\hat{\psi}^{nb}$) were held constant in all models. QAIC$_c$, ΔQAIC$_c$ (difference in QAIC$_c$ value between the top model and each subsequent model), w_i ("weight of evidence" in favor of each model *i*), w_i/w_1 (weight of model *i* relative to that of top-ranked model 1), *k* (number of estimated parameters), and deviance are shown for each of the models in both suites that had $w_i > 0$.

Model structure	**QAIC$_c$**	**ΔQAIC$_c$**	w_i	w_i/w_1	***k***	**Deviance**
Survival and sighting probability models						
1) ϕ^{p}_{a3+yr} ϕ^{b}_{yr} ϕ^{n}_{yr} p^{p}_{a4+yr} p^{b}_{yr} p^{n}_{yr}	13514	0	0.9954	1.00	206	5800.14
2) ϕ^{p}_{a3+yr} ϕ^{b}_{yr} ϕ^{n}_{yr} $p^{p}_{a4+a4^2+yr}$ p^{b}_{yr} p^{n}_{yr}	13525	10.98	0.0041	0.00	205	5813.21
3) ϕ^{p}_{a3} ϕ^{b} ϕ^{n} p^{p}_{a4+yr} p^{b}_{yr} p^{n}_{yr}	13529	15.39	0.0005	0.00	183	5863.43
Recruitment models						
4) ϕ^{p}_{a3+yr} ϕ^{b}_{yr} ϕ^{n}_{yr} p^{p}_{a4+yr} p^{b}_{yr} p^{n}_{yr} ψ^{pb}_{a9+yr}	13338	0	0.9990	1.00	87	5869.52
5) ϕ^{p}_{a3+yr} ϕ^{b}_{yr} ϕ^{n}_{yr} p^{p}_{a4+yr} p^{b}_{yr} p^{n}_{yr} ψ^{pb}_{a9}	13353	15.00	0.0006	0.00	67	5925.16
6) ϕ^{p}_{a3+yr} ϕ^{b}_{yr} ϕ^{n}_{yr} p^{p}_{a4+yr} p^{b}_{yr} p^{n}_{yr} $\psi^{pb}_{a9+dn(birth)}$	13355	16.64	0.0002	0.00	68	5924.77
7) ϕ^{p}_{a3+yr} ϕ^{b}_{yr} ϕ^{n}_{yr} p^{p}_{a4+yr} p^{b}_{yr} p^{n}_{yr} ψ^{pb}_{a9+dn}	13355	16.89	0.0002	0.00	68	5925.02

Table 2.4. Annual ϕ and p estimates and standard error estimates for female Weddell seals in Erebus Bay, Antarctica, obtained from Program MARK. Estimates were generated from the top-ranked model (Model 4 in Table 2.3), and ϕ estimates were corrected for tag loss. Estimates of p^b are not included in the table as all rounded to 1.000.

	Survival probability ($\hat{\phi}$)					**Sighting probability ($\hat{p}$)**				
	prebreeder			*breeder*	*nonbreeder*	*prebreeder*				*nonbreeder*
Year	***age 1***	***age 2***	***age 3+***	***all ages***	***all ages***	***age 1***	***age 2***	***ages 3-6***	***age 7+***	***all ages***
1980	0.57 (0.25)					0.02 (0.02)				
1981	0.27 (0.07)	0.32 (0.11)				0.15 (0.06)	0.27 (0.09)			
1982	0.66 (0.15)	0.71 (0.12)	0.97 (0.03)			0.06 (0.02)	0.12 (0.04)	0.41 (0.10)		
1983	0.41 (0.08)	0.47 (0.09)	0.90 (0.03)			0.34 (0.07)	0.52 (0.07)	0.85 (0.04)		
1984	0.47 (0.08)	0.53 (0.09)	0.92 (0.03)	0.89 (0.03)		0.20 (0.04)	0.35 (0.06)	0.73 (0.05)		
1985	0.57 (0.11)	0.63 (0.09)	0.95 (0.03)	0.93 (0.03)	0.95 (0.02)	0.10 (0.02)	0.19 (0.04)	0.55 (0.05)		0.88 (0.03)
1986	0.46 (0.08)	0.52 (0.10)	0.92 (0.03)	0.89 (0.03)	0.93 (0.03)	0.04 (0.01)	0.08 (0.02)	0.31 (0.05)	0.57 (0.06)	0.73 (0.05)
1987	0.58 (0.10)	0.64 (0.10)	0.95 (0.02)	0.93 (0.03)	0.96 (0.02)	0.07 (0.01)	0.14 (0.03)	0.44 (0.05)	0.70 (0.05)	0.83 (0.03)
1988	0.50 (0.09)	0.56 (0.08)	0.93 (0.02)	0.91 (0.02)	0.94 (0.02)	0.11 (0.02)	0.20 (0.03)	0.56 (0.04)	0.79 (0.04)	0.89 (0.02)
1989	0.45 (0.07)	0.51 (0.09)	0.91 (0.02)	0.88 (0.03)	0.92 (0.03)	0.07 (0.01)	0.13 (0.02)	0.43 (0.04)	0.69 (0.05)	0.82 (0.03)
1990	0.61 (0.08)	0.67 (0.08)	0.96 (0.02)	0.94 (0.02)	0.96 (0.02)	0.09 (0.02)	0.17 (0.03)	0.51 (0.04)	0.75 (0.04)	0.86 (0.02)
1991	0.54 (0.08)	0.60 (0.08)	0.94 (0.02)	0.92 (0.02)	0.95 (0.02)	0.06 (0.01)	0.13 (0.02)	0.42 (0.04)	0.68 (0.04)	0.82 (0.03)
1992	0.55 (0.09)	0.61 (0.08)	0.94 (0.02)	0.92 (0.02)	0.95 (0.02)	0.03 (0.01)	0.08 (0.01)	0.30 (0.04)	0.56 (0.05)	0.73 (0.04)
1993	0.52 (0.08)	0.58 (0.08)	0.94 (0.02)	0.91 (0.02)	0.94 (0.02)	0.06 (0.01)	0.13 (0.02)	0.43 (0.04)	0.69 (0.04)	0.82 (0.03)
1994	0.59 (0.08)	0.65 (0.08)	0.95 (0.02)	0.93 (0.02)	0.96 (0.02)	0.04 (0.01)	0.06 (0.01)	0.26 (0.03)	0.50 (0.05)	0.68 (0.04)
1995	0.51 (0.08)	0.57 (0.08)	0.93 (0.02)	0.91 (0.02)	0.94 (0.02)	0.06 (0.01)	0.13 (0.02)	0.43 (0.04)	0.69 (0.04)	0.82 (0.03)
1996	0.47 (0.07)	0.53 (0.07)	0.92 (0.02)	0.89 (0.02)	0.93 (0.02)	0.05 (0.01)	0.11 (0.02)	0.38 (0.04)	0.64 (0.04)	0.79 (0.03)
1997	0.51 (0.06)	0.57 (0.08)	0.93 (0.02)	0.91 (0.02)	0.94 (0.02)	0.08 (0.02)	0.16 (0.03)	0.49 (0.04)	0.73 (0.04)	0.85 (0.02)
1998	0.68 (0.07)	0.73 (0.07)	0.97 (0.01)	0.96 (0.01)	0.97 (0.01)	0.05 (0.01)	0.10 (0.02)	0.35 (0.04)	0.61 (0.05)	0.77 (0.03)
1999	0.61 (0.07)	0.67 (0.07)	0.96 (0.01)	0.94 (0.02)	0.96 (0.01)	0.07 (0.01)	0.14 (0.02)	0.44 (0.04)	0.70 (0.04)	0.83 (0.03)
2000	0.60 (0.08)	0.66 (0.07)	0.96 (0.01)	0.94 (0.02)	0.96 (0.01)	0.06 (0.01)	0.11 (0.02)	0.39 (0.04)	0.65 (0.04)	0.80 (0.03)
2001	0.59 (0.09)	0.65 (0.08)	0.95 (0.02)	0.93 (0.02)	0.96 (0.02)	0.02 (0.00)	0.05 (0.01)	0.19 (0.02)	0.41 (0.04)	0.60 (0.04)
2002				0.85 (0.03)	0.89 (0.03)				0.39 (0.05)	0.57 (0.04)

For prebreeders, $\hat{\phi}$ increased with age and was less variable for animals >3-yrs old than for animals 1- and 2-yrs old: $\hat{\bar{\phi}}$ for 1-yr olds was 0.53 ($\hat{SE} = 0.02$, σ (square root of true temporal variance) = 0.07); $\hat{\bar{\phi}}$ for 2-yr olds was 0.59 ($\hat{SE} = 0.02$, $\sigma = 0.07$); and $\hat{\bar{\phi}}$ for animals $\geq$3-yrs olds was 0.94 ($\hat{SE} < 0.01$, $\sigma = 0.01$). Breeders had lower $\hat{\phi}$ relative to nonbreeders: $\hat{\bar{\phi}}$ for breeders was 0.92 ($\hat{SE} < 0.01$, range = 0.85 [$\hat{SE} = 0.03$] to 0.96[$\hat{SE} = 0.01$]) and $\hat{\bar{\phi}}$ for nonbreeders was 0.94 ($\hat{SE} < 0.01$, range = 0.89 [$\hat{SE} = 0.03$] to 0.97 [$\hat{SE} = 0.01$]). Prebreeder $\hat{p}$ varied across years in this model and increased with age: $\hat{\bar{p}}$ for 1-yr olds was 0.08 ($\hat{SE} = 0.01$, range = 0.02 [$\hat{SE} < 0.01$] to 0.34 [$\hat{SE} = 0.07$]); $\hat{\bar{p}}$ for 2-yr olds was 0.16 ($\hat{SE} = 0.02$, range = 0.05 [$\hat{SE} = 0.01$] to 0.52 [$\hat{SE} = 0.07$]); $\hat{\bar{p}}$ for 3- to 6-yr olds was 0.4 ($\hat{SE} = 0.03$, range = 0.19 [$\hat{SE} = 0.02$] to 0.85 [$\hat{SE} = 0.04$]); and $\hat{\bar{p}}$ for seals $\geq$ 7-yrs old was 0.65 ($\hat{SE} = 0.02$, range = 0.39 [$\hat{SE} = 0.05$] to 0.79 [$\hat{SE} = 0.04$]). Nonbreeder $\hat{\bar{p}}$ was 0.78 ($\hat{SE} = 0.02$, range = 0.57 [$\hat{SE} = 0.04$] to 0.89 [$\hat{SE} = 0.02$]) and breeder $\hat{p}$ was 0.99 or 1.0 ($\hat{SE} < 0.0001$) in all years.

Recruitment Probability

In the best model, $\hat{\psi}^{pb}$ was estimated separately for animals in eight different age classes (4-, 5-, 6-, 7-, 8-, 9-, 10-, and $\geq$11-yrs old) and allowed to vary by year (Table 2.5). Estimates from this model provided strong evidence of age-related variation in probability of recruiting to the breeding population. No female $\leq$3-yrs old was ever

Table 2.5. Annual recruitment probability estimates ($\hat{\psi}^{pb}$) for female Weddell seals in Erebus Bay, Antarctica. Standard error estimates (in parentheses) include sampling and temporal variation of the annual estimates. *VR* represents the ratio between observed temporal variance and maximum variance (maximum variance is ϕ *(1-* ϕ*)*, where ϕ is the mean survival rate) and was calculated from means and standard errors generated by the variance components module in Program MARK for ages six and older. Estimates were generated from the top-ranked model (Model 4 in Table 2.3). Recruitment estimates for age 4 are not presented as they were <0.003 for all years.

Year	**age 5**	**age 6**	**age 7**	**age 8**	**age 9**	**age 10**	**age 11+**
1984	0.09 (0.11)						
1985	0.06 (0.04)	0.27 (0.15)					
1986	0.01 (0.01)	0.07 (0.05)	0.16 (0.11)				
1987	0.04 (0.02)	0.23 (0.08)	0.42 (0.10)	0.45 (0.11)			
1988	0.08 (0.03)	0.36 (0.08)	0.58 (0.09)	0.62 (0.09)	0.62 (0.10)		
1989	0.03 (0.01)	0.14 (0.05)	0.29 (0.08)	0.32 (0.09)	0.32 (0.10)	0.35 (0.12)	
1990	0.05 (0.02)	0.25 (0.06)	0.45 (0.07)	0.49 (0.08)	0.49 (0.09)	0.52 (0.11)	0.42 (0.12)
1991	0.05 (0.02)	0.24 (0.05)	0.43 (0.08)	0.47 (0.08)	0.47 (0.09)	0.50 (0.11)	0.41 (0.12)
1992	0.01 (0.01)	0.08 (0.03)	0.18 (0.06)	0.20 (0.07)	0.21 (0.07)	0.23 (0.09)	0.17 (0.08)
1993	0.03 (0.01)	0.18 (0.04)	0.35 (0.06)	0.38 (0.07)	0.39 (0.08)	0.42 (0.10)	0.33 (0.11)
1994	0.03 (0.01)	0.14 (0.04)	0.29 (0.06)	0.32 (0.07)	0.32 (0.08)	0.35 (0.10)	0.27 (0.10)
1995	0.04 (0.01)	0.19 (0.04)	0.36 (0.06)	0.40 (0.07)	0.40 (0.08)	0.43 (0.10)	0.34 (0.11)
1996	0.02 (0.02)	0.10 (0.03)	0.21 (0.05)	0.24 (0.06)	0.24 (0.07)	0.27 (0.09)	0.20 (0.08)
1997	0.05 (0.02)	0.26 (0.05)	0.46 (0.06)	0.50 (0.07)	0.51 (0.08)	0.54 (0.10)	0.44 (0.11)
1998	0.05 (0.02)	0.24 (0.05)	0.43 (0.07)	0.47 (0.07)	0.47 (0.09)	0.51 (0.11)	0.41 (0.11)
1999	0.05 (0.02)	0.26 (0.05)	0.47 (0.07)	0.51 (0.07)	0.51 (0.09)	0.54 (0.11)	0.44 (0.12)
2000	0.07 (0.02)	0.31 (0.06)	0.52 (0.07)	0.56 (0.08)	0.56 (0.09)	0.59 (0.11)	0.50 (0.12)
2001	0.01 (0.01)	0.07 (0.03)	0.15 (0.05)	0.17 (0.06)	0.17 (0.07)	0.19 (0.08)	0.14 (0.07)
2002	0.04 (0.01)	0.21 (0.05)	0.40 (0.07)	0.44 (0.07)	0.44 (0.08)	0.47 (0.11)	0.38 (0.11)
2003	0.03 (0.01)	0.15 (0.03)	0.29 (0.06)	0.33 (0.07)	0.33 (0.08)	0.36 (0.10)	0.28 (0.10)
Mean ($\hat{SE}$ ***)***	**0.04 (0.02)**	**0.20 (0.08)**	**0.36 (0.13)**	**0.40 (0.13)**	**0.40 (0.13)**	**0.42 (0.12)**	**0.34 (0.11)**
VR (x 100)†		**2.78**	**4.85**	**4.73**	**5.07**	**4.40**	**4.17**

† The values in this row have been multiplied by 100.

known to have a pup. Only two 4-yr olds were documented to have pups; accordingly, $\hat{\bar{\psi}}^{pb}$ for this age class was 0.0009 ($S\hat{E}$ = 0.00054). For animals >4-yrs old, $\hat{\bar{\psi}}^{pb}$ steadily increased from 0.04 ($S\hat{E}$ = 0.02) for 5-yr olds (n = 40) to a high of 0.42 ($S\hat{E}$ = 0.10) for 10-yr olds (n = 19) (Table 2.5). We did not observe a threshold age by which all females in the population had become breeders. To the contrary, age-specific $\hat{\bar{\psi}}^{pb}$ did not exceed 0.42 for any age, and $\hat{\bar{\psi}}^{pb}$ for females ≥11-yrs old was 0.34 ($S\hat{E}$ = 0.10), providing some evidence of a decline in $\hat{\bar{\psi}}^{pb}$ after age 11.

Our estimates of annual variation in $\hat{\psi}^{pb}$ supported our prediction that reproductive behavior in Weddell seals would vary over time due to yearly fluctuations in environmental conditions. Only four of the 20 model parameters for year effects had confidence intervals that did not include zero, providing little evidence of temporal variation in $\hat{\psi}^{pb}$ for most years. In the four unusual years (1988, 1997, 1999, and 2000) $\hat{\psi}^{pb}$ was higher than average (estimate of year effect ($\hat{\beta}$), which compared year-specific estimates to the overall mean, was > 0 in these years). Additionally, the amount of annual variation depended on age class. Variance components could not be separated for 4- and 5-yr olds as high sampling variance prevented accurate estimation of true temporal variance. Contrary to our prediction, annual variation in age-specific $\hat{\psi}^{pb}$ did not always decrease with age and was in fact highest for seals age 9 (Table 2.5). However, our ability to detect age-specific differences in temporal variance was constrained by our selected model. Ideally, a model with an age and year interaction would be used to compare temporal variance among age classes but this model contained too many parameters and was not well-supported for our dataset. Models with cohort or population density effects were not well-supported by the data (best cohort model: $QAIC_c$ weight=0.0, $\Delta QAIC_c$=42.23; best population-density model: $QAIC_c$ weight=0.0002, $\Delta QAIC_c$=16.46) (Table 2.3). In general, these results suggest that the annual variation in ψ^{pb} resulted from sources beyond just variation in density on the study area.

Discussion

A unique long-term database provided us with extensive information on sightings and reproductive status for a population of highly-philopatric, long-lived pinnipeds. These data combined with advances in mark-resight analyses allowed us to evaluate a diverse array of competing models that estimated age-specific probabilities of first breeding. From this process, we were able to gain novel insights into life-history decisions made by Weddell seals and hypotheses regarding variation in age at first reproduction.

In the process of conducting the requisite analyses for estimating age at first reproduction, we also estimated apparent survival and sighting probabilities. Although these parameters were not the focus of this paper, our results indicated interesting patterns of variation in these rates, and so these are presented briefly prior to discussion of age at first reproduction. As expected from previous work on Weddell seals (Testa 1987*a*, Hastings et al. 1999, Cameron and Siniff 2004), and on long-lived species in general (Eberhardt and Siniff 1977, Gaillard et al. 1998, Gaillard et al. 2000), survival for juveniles was lower and displayed more annual variation than adult survival. Similarly, sighting probabilities increased with age for prebreeders, and varied substantially from year to year for young age classes. Less annual variation was displayed in nonbreeder sighting probability and almost no annual variation was detected in breeder sighting probabilities. As expected, sighting probability for breeders was estimated close to 1.0 (average = 1.0, $S\hat{E} < 0.0001$) in all years. Female seals breeding in our study area were readily observable as they remained on the sea ice to nurse their pups for several weeks, which provided us with excellent data for precisely estimating age-specific probabilities of first breeding. This high detection probability for breeders was necessary for our approach of defining pre-breeding and non-breeding states based on sighting history data.

Our analysis focused on estimation of age-specific recruitment rates ($\hat{\psi}^{pb}$) as a basis for determining age at first reproduction. When viewing the estimates of ψ^{pb} (Table 2.5), it is important to keep in mind that the age-specific rates were based on those individuals that were still alive and that had not yet recruited to the breeding population by the age in question. Our estimates of ψ^{pb} increased sharply between ages five and seven, then remained consistently high through age 10 (Table 2.5). However, in each successive age class, there were fewer survivors that had not yet recruited to the breeding population. Although the respective proportion of animals breeding for the first time after age eight remained somewhat constant, the actual number of seals making the transition to breeding for the first time was getting smaller with each successive age as some seals died and others became breeders.

The proportion of a cohort of females that recruits to the breeding population at various ages and the average age at first reproduction can be calculated deterministically as follows. We used our best estimates of age-specific ϕ and ψ^{pb} (average rates derived from our top-ranked model) to calculate the number of seals out of a hypothetical cohort of 1,000 new-born females that would be expected to survive and breed for the first time at each age. The results of the exercise indicate that (1) approximately 215 females of the original 1,000 would eventually be recruited to the breeding population, (2) the largest number of females (approximately 63) would recruit to the breeding population at age 7, and (3) the mean age of first reproduction was 7.62 (SD = 1.71) (Table 2.6). Finally, approximately 19 of these females would be still alive and unrecruited at age 11.

Table 2.6. Age-specific ϕ^{p} and ψ^{pb} estimates generated from best model were averaged over years and applied to a hypothetical group of 1000 female Weddell seals beginning at age 0 in order to obtain total number of seals recruited at each age. N_I is the number of prebreeders originally present in the previous age class. N_S is the number of prebreeders in N_I that survived to the current age class. N_R is the number recruited at the current age, which was then subtracted from N_S in order to obtain N_I for the next age class. Age-specific proportion of seals recruited at each age is shown in the final column.

Age	N_1	$\hat{\phi}^{p}$	N_S	$\hat{\psi}^{pb}$	N_R	***Proportion***
1	1000.00	0.53	530.00	0.00	0.00	0.0000
2	530.00	0.59	312.70	0.00	0.00	0.0000
3	312.70	0.94	293.94	0.00	0.00	0.0000
4	293.94	0.94	276.30	0.00	0.00	0.0000
5	276.30	0.94	259.72	0.04	10.39	0.0104
6	249.33	0.94	234.37	0.20	46.87	0.0469
7	187.50	0.94	176.25	0.36	63.45	0.0635
8	112.80	0.94	106.03	0.40	42.41	0.0424
9	63.62	0.94	59.80	0.40	23.92	0.0239
10	35.88	0.94	33.73	0.42	14.17	0.0142
11	19.56	0.94	18.39	0.34	6.25	0.0063
12	12.14	0.94	11.41	0.34	3.88	0.0039
13	7.53	0.94	7.08	0.34	2.41	0.0024
14	4.67	0.94	4.39	0.34	1.49	0.0015
				Total	***215.24***	***0.2154***

Our results demonstrate the gradual nature of the recruitment process for Weddell seals. Earliest recruitment took place at four years of age and females continued to enter the breeding population beyond age 11. Relative to other pinniped species (Stewart 1986, Reiter and LeBoeuf 1991, Lunn et al. 1994, Bowen et al. 2003), Erebus Bay Weddell seals have an older mean age at first reproduction (7.62 years) and display more variability in this trait. Mean age at first reproduction for Weddell seals at Signy Island was 4-5 years (Croxall and Hiby 1983), a difference which may be attributed to the more northerly location of this population at approximately 61º South latitude. For moose (*Alces alces*), Sand (1996) concluded that in northern populations that are situated in climatically harsh or more seasonal environments, reproduction constituted a higher risk than in southern populations. The harsh environment the Erebus Bay seals inhabit at 77º South may require that 1) more resources be accumulated before reproduction, and/or 2) a longer time is needed to accrue the necessary resources for reproduction. These results suggest that age at first reproduction may be affected by whether a population inhabits the core or periphery of the species' range and reveal an interesting topic for further study in other long-lived species.

The delayed reproduction that we observed in Weddell seals is common among long-lived species and likely results from a life-history trade-off between current and future reproduction (Gadgil and Bossert 1970, Roff 1992, 2001). Reproduction at the earliest physiologically possible age is selected against because costs are high and outweigh potential benefits. However, as an individual ages, willingness to take a risk in order to reproduce should increase because fewer and fewer reproductive opportunities remain (Williams and Nichols 1984). Moreover, after an animal has spent additional years accumulating resources and foraging skills, the benefit of a reproductive attempt will be higher and potential cost to survival and future reproduction will have decreased (Goodman 1981). Because of their long lifespan, these species have the luxury of making such a tradeoff and delaying reproduction. Thus, delayed reproduction is an important adaptive feature in the life-history of long-lived species.

We have demonstrated that some female Weddell seals delay first reproduction until far beyond the mean age. A possible explanation for this variation in breeding strategy is the presence of inherent differences in fitness among individuals in the population that are not accounted for in age or cohort groups used in modeling (see Clutton-Brock 1988 for review). Individual seals in this population may differ substantially in terms of their intrinsic fecundity and vigor, with some individuals better at surviving and reproducing than others (Cam et al. 2002, Cooch et al. 2002, Link et al. 2002). In each successive age class, there may be a higher and higher proportion of lower-quality animals left which still have not recruited to the breeding population (Cam et al. 2002). These females may invest their more limited resources into surviving to the next year and may not have enough remaining resources to reproduce.

Another possible explanation of the apparent delayed reproduction is that seals recruiting to the Erebus Bay population have previously reproduced outside of our study area. However, female Weddell seals are strongly philopatric (Stirling 1969, 1974; Croxall and Hiby 1983; Cameron and Siniff 2004) and seals born in Erebus Bay generally return there to breed. Although survey effort outside the Erebus Bay study area has been variable over the duration of the study, it has increased in recent years (Cameron 2001). Of the females sighted outside the study area each year from 1997 through 2000, an average of 6.5% were born in Erebus Bay study area, and an average of only 0.4% were born in Erebus Bay *and* sighted with a pup during surveys outside Erebus Bay (M.F. Cameron, personal communication). Given what we know of female movement patterns, we expect that the occurrence of reproduction outside the study area has extremely minimal impact on the estimated recruitment rates presented here.

Of the covariates we evaluated, year was most important for modeling variation in age-specific recruitment rates and extensive variation in annual recruitment estimates was apparent (Table 2.5). Annual variation in population density did not appear to be a substantial driver of the annual variation in age-specific recruitment that we observed, a result that is consistent with previous findings for Weddell seals (Testa and Siniff 1987). When populations are at or near equilibrium or carrying capacity, vital rates are expected to be much more sensitive to environmental changes that affect resource availability than when numbers are well below carrying capacity (Eberhardt 1977, Fowler 1981). This interaction of density-dependent and density-independent mechanisms suggests that relatively stable populations such as the Erebus Bay Weddell seal population (Testa and Siniff 1987) are likely more influenced by environmental factors.

Moreover, life-history literature regarding long-lived mammals predicts that because population growth rates are less likely to be influenced by changes in age at first reproduction than by changes in any other life history parameter (Eberhardt and Siniff 1977, Goodman 1981), age at first reproduction should be the first trait affected by varying environmental conditions. This was observed for crabeater seals (*Lobodon carcinophagus*) where age at first reproduction decreased following harvest of baleen whales that competed with the seals for Antarctic krill (*Euphausia superba*) (Bengston and Laws 1985). Additionally, mean age at first reproduction increased for northern elephant seals on the South Farallon Islands following an El Niño event that severely impacted resource availability for pinnipeds. Consequently, proportion of females giving birth was reduced, with the biggest impact on young females (Huber et al. 1991). Results of these previous studies are not always easy to interpret, because of the difficulty in drawing strong inferences about age at first reproduction. Nevertheless, they appear to be consistent with a hypothesis of environmental variation in resource availability leading to temporal variation in age at first reproduction. Similar environmental mechanisms may explain the annual variation we observed for Weddell seals. A goal of future analyses is to incorporate information about resource availability and annual sea-ice covariates into age-specific recruitment models to better explain the observed annual variation and understand potential population responses to environmental changes related to global climate change.

Contrary to our prediction, young females displayed the least amount of annual variation in recruitment probabilities. However, interactive age and year effects would be required to allow different age classes to display substantially different amounts of variation. Due to the number of years and age classes in our analysis, the model with parameters for interactions is large and complex (209 parameters). Unless the effect of year on recruitment rate differed extensively among age classes, a model of this size would be less likely to be supported by the data than would simpler models. The model results regarding interaction of age and year effects may reflect the model complexity resulting from a large number of years and age classes. Some potentially important biological mechanisms may not be detected due to the number of parameters contained in representative models.

This paper presents a novel approach for estimating age-specific recruitment rates and determining age at first reproduction for a long-lived species. There are few species for which this has been accomplished and the resulting insights augment our knowledge of population processes and life-history traits for pinnipeds in particular and for long-lived species in general. The findings from this paper additionally suggest areas for further investigation. Survival estimates from our analysis indicated survival was higher for non-breeding females than for breeding females, which raises questions about potential costs to survival associated with breeding state. These costs may also affect future breeding performance. As well as exhibiting delayed reproduction, some long-lived species additionally show a tendency to be intermittent breeders and to abandon reproduction under unfavorable circumstances (Goodman 1981). Based on data indicating that a female seal's probability of pupping in consecutive years was lower than probability of pupping after a year without pupping, Siniff (1981) suggested that reproductive performance in one year can influence the next year's performance. In a similar analysis, Testa (1987*b*) limited the data to females age eight and older to avoid biasing the results with newly mature females, and found instead that pupping in the previous year may actually increase probability of pupping in the current year. Testa suggested that Siniff's (1981) findings of a reproductive cost may apply only to inexperienced mothers. The use of multi-state models, which has allowed us to answer questions in this study about the transition from prebreeder to breeder, can also provide us with insight about annual transitions a seal makes between breeding and non-breeding states following recruitment. This modeling approach will be used in a forthcoming paper to investigate questions about reproductive costs that may be faced by Weddell seals and potential differences in survival and subsequent breeding probabilities that may result from breeding.

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B.N. Petran and F. Csàaki , editors. International Symposium on Information Theory. Second edition. Akadèemiai Kiadi, Budapest, Hungary.

Arnason, A.N. 1972. Parameter estimates from mark-recapture experiments on two populations subject to migration and death. Research in Population Ecology 13:97-113.

Arnason, A.N. 1973. The estimation of population size, migration rates, and survival in a stratified population. Research in Population Ecology 15:1-8.

Arnason, A.N. and K.H. Mills. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Canadian Journal of Fisheries and Aquatic Sciences 38:1077-1095.

Arrigo, K.R., G.L. van Dijken, D.G. Ainley, M.A. Fahnestock, and T. Markus. 2002. Ecological impact of a large Antarctic iceberg. Geophysical Research Letters 29:10-29.

Bengston, J.L. and R.M Laws. 1985. Trends in crabeater seal age at maturity: an insight into Antarctic marine interactions? Antarctic Nutrient Cycles and Food Webs (eds. W.R. Siegfried, P.R. Condy, and R.M. Laws), pp. 669-675. Springer-Verlag, Berlin, Germany.

Bowen, W.D., S.L. Ellis, S.J. Iverson, and D.J. Boness. 2003. Maternal and newborn life-history traits during periods of contrasting population trends: implications for explaining the decline of harbour seals (*Phoca vitulina*), on Sable Island. Journal of Zoology, London 261:155-163.

Boyd, I.L. 2000. State-dependent fertility in pinnipeds: contrasting capital and income breeders. Functional Ecology 14:623-630.

Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock, and J.B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transition probabilities. Biometrics 49:1173-1187.

Burnham, K.P. and D.R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer, New York, New York, USA.

Burnham, K.P., D.R. Anderson, G.C. White, C. Brownie, and K.P. Pollock. 1987.

Design and analysis of methods for fish survival experiments based on release-recapture. American Fisheries Society Monograph 5. 437pp.

Cam, E., W.A. Link, E.G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. American Naturalist 159:97-105.

Cameron, M.F. 2001. Dynamics of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Dissertation. University of Minnesota, Minneapolis, Minnesota, USA.

Cameron, M.F. and D.B. Siniff. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Canadian Journal of Zoology 82:601-615.

Clobert, J., J.-D. Lebreton, D. Allainé, and J.M. Gaillard. 1994. The estimation of age-specific breeding probabilities from recaptures or resightings in vertebrate populations: II. Longitudinal models. Biometrics 50:375-387.

Clutton-Brock, T.H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA.

Croxall, J.P. and L. Hiby. 1983. Fecundity, survival and site fidelity in Weddell seals, *Leptonychotes weddellii*. Journal of Applied Ecology 20:19-32.

Cooch, E.G., E. Cam, and W. Link. 2002. Occam's shadow: levels of analysis in evolutionary ecology. Journal of Applied Statistics 29:19-48.

Cole, L.C. 1954. The population consequences of life history phenomena. Quarterly Review of Biology 29:103-137.

Eberhardt, L.L. 1977. Optimal policies for conservation of large mammals with special reference to marine ecosystems. Environmental Conservation 4:205-212.

Eberhardt, L.L. and D.B. Siniff. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183-190.

Festa-Bianchet, M. and J.T. Jorgenson. 1998. Selfish mothers: reproductive expenditure and resource availability in bighorn ewes. Behavioral Ecology 9:144-150.

Fowler, C.W. 1981. Density-dependence as related to life history strategy. Ecology 62:602-610.

Gadgil, M. and W.H. Bossert. 1970. Life historical consequences of natural selection. American Naturalist 104:1-24.

Gaillard, J.-M., M. Festa-Bianchet, and N.G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.

Gaillard, J.-M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Gaillard, J.-M., and N.G. Yoccoz. 2003. Temporal variation in survival of mammals: a case of environmental canalization? Ecology 84: 3294-3306.

Goodman, D. 1981. Life history analysis of large mammals. Pages 415-436 *in* C.W. Fowler and T.D. Smith, editors. Dynamics of Large Mammal Populations. John Wiley and Sons, New York, New York, USA.

Harvey, P.H. and R.M. Zammuto. 1985. Patterns of mortality and age at first reproduction in natural populations of mammals. Nature 315:319-320.

Hastings, K.K. and J.W. Testa. 1998. Maternal and birth colony effects on survival of Weddell seal offspring from McMurdo Sound, Antarctica. Journal of Animal Ecology 67:722-740.

Hastings, K.K., J.W. Testa, and E.A. Rexstad. 1999. Interannual variation in survival of juvenile Weddell seals (*Leptonychotes weddellii*) from McMurdo Sound, Antarctica: effects of cohort, sex, and age. Journal of Zoology, London 248:307-323.

Hestbeck, J.B., J.D. Nichols, and R.A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523-533.

Huber, H.R., A.C. Rovetta, L.A. Fry, and S. Johnston. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. Journal of Mammalogy 72:525-534

Hurvich, C.M. and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.

Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration - Stochastic model. Biometrika 52:225-247.

Kendall, W.L., J.D. Nichols, and J.E. Hines. 1997. Estimating temporary emigration using capture-recapture data with Pollock's robust design. Ecology 78:563-578.

Link, W.A., E.G. Cooch, and E. Cam. 2002. Model-based estimation of individual fitness. Journal of Applied Statistics 29:207-224.

Lunn, N.J., I.L. Boyd, and J.P. Croxall. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. Journal of Animal Ecology 63:827-840.

Nichols, J.D., J. Bart, R.J. Limpert, W.J.L. Sladen, and J.E. Hines. 1992. Annual survival rates of adult and immature eastern population tundra swans. Journal of Wildlife Management 56:485-494.

Nichols, J.D., J.E. Hines, K.H. Pollock, R.L. Hinz, and W.A. Link. 1994. Estimating breeding proportions and testing hypotheses about costs of reproduction with capture-recapture data. Ecology 75:2052-2065.

Pollock, K.H., J.D. Nichols, C. Brownie, and J.E. Hines. 1990. Statistical inference for capture-recapture experiments. Wildlife Monographs 107. 97pp.

Reiter, J. and B.J. LeBoeuf. 1991. Life-history consequences of variation in age at primiparity in northern elephant seals. Behavioral Ecology and Sociobiology 28:153-160.

Roff, D.A. 1992. The Evolution of Life Histories: Theory and Analysis. Chapman and Hall, New York, New York, USA.

Roff, D.A. 2001. Age and size at maturity. Pages 99-112 *in* C.W. Fox, D.A. Roff, and D.J. Fairbairn, editors. Evolutionary Ecology: Concepts and Case Studies. Oxford University Press, Oxford, England.

Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity, and environmental conditions. Oecologia 106:212-220.

Schwarz, C.J. and A.N. Arnason. 1996. A general methodology for the analysis of capture-recapture experiments in open populations. Biometrics 52:860-873.

Seber, G.A.F. 1965. A note on the multiple-recapture census. Biometrika 52:249-259.

Siniff, D.B., D.M. DeMaster, R.J. Hofman, and L.L. Eberhardt. 1977. An analysis of the dynamics of a Weddell seal population. Ecological Monographs 47:319-335.

Siniff, D.B. 1981. Seal population dynamics and ecology. Journal of the Royal Society of New Zealand 11:317-327.

Smith, R.C., K.S. Baker, and S.E. Stammerjohn. 1998. Exploring sea ice indexes for polar ecosystem studies. BioScience 48:83-93.

Spendelow, J.A., J.D. Nichols, J.E. Hines, J.-D. Lebreton, and R. Pradel. 2002. Modelling postfledgling breeding probabilities in species with delayed maturity: a case study of Roseate Terns at Falkner Island, Connecticut. Journal of Applied Statistics 29:385-405.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quarterly Review of Biology 51:3-47.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.

Stewart, R.E.A. 1986. Energetics of age-specific reproductive effort in female Harp seals, *Phoca groenlandica*. Journal of Zoology, London 208:503-517.

Stirling, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. Ecology 50:573-586.

Stirling, I. 1974. Movements of Weddell seals in McMurdo Sound, Antarctica. Australian Journal of Zoology 22:39-43.

Stroeve, J. and C. Shuman. 2004. Historical Arctic and Antarctic Surface Observational Data. Boulder, CO: National Snow and Ice Data Center. Digital media.

Testa, J.W. 1987*a*. Juvenile survival and recruitment in a population of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Canadian Journal of Zoology 65:2993-2997.

Testa, J.W. 1987*b*. Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddellii*). Canadian Journal of Zoology 65:1091-1099.

Testa, J.W. and D.B. Siniff. 1987. Population dynamics of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Ecological Monographs 57:149-165.

Testa, J.W., D.B. Siniff, J.P. Croxall, and H.R. Burton. 1990. A comparison of reproductive parameters among three populations of Weddell seals (*Leptonychotes weddellii*). Journal of Animal Ecology 59:1165-1175.

White, G.C. and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):120-138.

Williams, B.K. and J.D. Nichols. 1984. Optimal timing in biological processes. American Naturalist 123:1-19.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California, USA.

CHAPTER THREE.

VARIATION IN SURVIVAL AND RECRUITMENT PROBABILITIES OF FEMALE WEDDELL SEALS: INFLUENCE OF MATERNAL CHARACTERISTICS, BIRTH LOCATION, AND OCEANOGRAPHIC VARIABLES

Introduction

For all animal populations, recruitment of young into the breeding population is an essential population process that directly affects population growth rate. An individual's probability of recruitment may be influenced by many factors: individual characteristics unique to each animal in the population, environmental factors that affect all individuals similarly but vary in strength over time, or interactions of both. Some individual characteristics change over an individual's lifetime (age or breeding state), while others remain constant (location of birth or maternal characteristics). An individual's probability of eventually joining the breeding population is also clearly affected by the probability of surviving to potential recruitment age. The term 'recruitment' often refers to the combined probabilities of 1) surviving to reproductive age, and 2) successfully reproducing, and few studies have been able to separate these two components (Reed et al. 2003). However, studies that separately estimate survival and recruitment probabilities allow researchers to distinguish the factors influencing these two disparate processes. In the remainder of this paper, the term recruitment will refer to the probability of beginning reproduction at a given age, assuming survival to that age.

Recruitment is difficult to study for some species (e.g., marine mammals) because longevity and delayed maturity dictate that long-term data sets be available. Moreover, separately estimating survival and recruitment probabilities requires adequate mark-resight data and annual observations of reproductive status. In this regard, the Erebus Bay population of Weddell seals (*Leptonychotes weddellii*) provides an ideal study population as large numbers of animals have been uniquely marked and resighted since 1969. Females are strongly philopatric (Stirling 1969, Cameron and Siniff 2004), allowing us to reasonably assume that females born at Erebus Bay colonies will, if they survive to breeding age, return to Erebus Bay to have their pups. Furthermore, it is the world's southernmost breeding-mammal population (Dearborn 1965), and the harsh and highly variable environment may lead to high variability of vital rates (Barbraud and Weimerskirch 2001). Finally, the Erebus Bay population is spatially structured with numerous pupping colonies (Stirling 1969), allowing evaluation of whether a seal's colony of birth affects its subsequent survival and recruitment probabilities.

In a recent investigation (previous chapter, Hadley et al. 2006), the mean age of first reproduction for female Weddell seals in the Erebus Bay population was estimated as 7.62 years (SD = 1.71), with a range of 4 to 14 years of age. This study provided strong evidence that some females produced their first pup many years beyond the mean age of first reproduction. Therefore, understanding differences between females that recruited early and those that recruited late was a goal for future research on the Erebus Bay Weddell seal population. Several studies have linked maternal characteristics such as age and breeding experience to offspring mass, growth, or survival probability (Arnbom et al. 1993, Iverson et al. 1993, Bowen et al. 1994, Lunn et al. 1994, Hastings and Testa 1998), but none that we are aware of have linked these characteristics to offspring recruitment probability. A possible link between fluctuations in Weddell seal reproductive indices and large-scale oceanographic processes has been proposed (Testa et al. 1990, Testa et al. 1991), but the mechanism for these effects is not known. This paper investigates the potential influence of maternal characteristics and location of birth on a female Weddell seal's probability of 1) survival to ages where recruitment is possible, and 2) age-specific recruitment to the breeding population. We additionally explore the use of oceanographic variables to explain annual variation in recruitment probability.

Predictions

In this study, we evaluated numerous hypotheses regarding the effects of maternal characteristics and birth location on both offspring probability of survival to recruitment age, and offspring's probability of recruitment. Previous work on Weddell seals (Hastings and Testa 1998) reported that offspring survival rate was positively related to the age of the mother at the time of the offspring's birth. However, the dataset used in that analysis only included mothers age 11 and younger. Resighting data for known-age seals in Erebus Bay indicate that females can live to age 30. Because many seals do not produce a first pup until age 9 or older, Hasting and Testa's (1998) analysis encompassed only the beginning of a female seal's reproductive lifespan. Research on Antarctic fur seals (*Arctocephalus gazella*; Lunn et al. 1994) suggests that maternal experience positively affects pups' probability of survival to weaning. When considering the full range of ages and levels of maternal experience that occur in a population of mothers, we expected that offspring survival and recruitment probabilities would display one of three relationships: (1) increase linearly with increasing maternal age and experience, (2) increase linearly to some threshold level, and then continue to increase, but only very slowly due to diminishing returns of increasing age/experience (pseudo-threshold relationship, Franklin et al. 2000), or (3) increase linearly to some threshold level, and then decrease due to senescence of mothers (quadratic relationship with optimal maximum at some intermediate maternal age or experience level).

In addition to age and experience, the age at which a mother had her first pup (i.e., maternal age at first reproduction) may be related to offspring survival and recruitment probabilities. A female able to begin reproduction at a young age may have inherently higher survival or reproductive capabilities (Cam et al. 2002, Hadley et al. 2006), whereas lower-quality females may be more likely to delay primiparity. If these reproductive capabilities are heritable, offspring of females primiparous at young ages may display higher probabilities of survival and recruitment. Northern elephant seal (*Mirounga angustirostris*) females that were primiparous at age 3 were found to be superior in mass and condition to females primiparous at age 4 (Reiter and LeBoeuf 1991), supporting the idea that females beginning reproduction early are high-quality females. In an earlier study, the same authors observed that females producing the most offspring in a lifetime were those that began breeding early in life (LeBoeuf and Reiter 1988). Hastings and Testa (1998) found that the age when mothers have their first pup did not affect survival rate of offspring, but allowed that variation in age of first reproduction in their sample (approximately 225 known-age mothers) may have been insufficient to detect such a relationship. For our larger dataset (1,372 known-age mothers), we predicted that maternal age at first reproduction would be inversely related to offspring survival and recruitment probability (females that began reproduction at the youngest ages would have pups with highest survival and recruitment probabilities). This was expected based on the hypothesized relationship between age at first reproduction and individual quality.

Environmental conditions during juvenile years are likely to affect early growth and development, and some studies have specifically linked environmental conditions at time of birth with future reproductive success (Albon et al. 1987, Forchammer et al. 2001). Therefore, variation in birth site quality may influence survival and recruitment probabilities. Weddell seals use spatially distinct breeding colonies (Stirling 1969), and thus, if breeding sites vary in quality, location of a seal's birth may explain some variation in survival and recruitment probabilities. Several investigators have related variation in breeding site attributes to parental reproductive success or offspring survival rate (Sǽther and Heim 1993, Hastings and Testa 1998, Kokko et al. 2004), but we are unaware of studies that have estimated variation in recruitment probabilities associated with birth site. In some years, breeding colonies for Weddell seals vary dramatically in terms of ice conditions. Some colonies lose fast ice earlier than others, which forces pups into the water earlier in the year (Hastings and Testa 1998) and exposes them to marine-based predators. Breeding colonies may also vary in the availability of prey and distance to productive foraging areas for Weddell seals. Hastings and Testa (1998), working with a somewhat-limited dataset, found evidence of colony-specific differences in juvenile survival in one of five cohorts. Based on these findings, we predicted that survival and recruitment probabilities would be higher for animals born at colonies close to a large island with protected bays than for those born near smaller, less-protected, offshore islands. However, because (1) we previously predicted that maternal characteristics would affect the future of their offspring and (2) maternal characteristics differ among colonies, we developed the alternative prediction that seals born at offshore colonies would have higher survival and recruitment probabilities than seals born elsewhere due to the older average age of mothers pupping at those locations (unpublished data).

A recent analysis of data for the Erebus Bay population of Weddell seals found annual variation in survival and recruitment probabilities (Hadley et al. 2006), but did not attempt to elucidate the causes of that variation. The mechanisms underlying this annual variation are likely related to the effect of large-scale climate or sea-ice conditions on prey abundance. Although little is known of the drivers of annual variation in prey abundance for Weddell seals, the sensitivity of Southern ocean ecosystems, and especially upper trophic level predators, to climate change has been noted in numerous recent studies (Weimerskirch et al. 2003, Beauplet et al. 2005, McMahon and Burton 2005). During El-Niño Southern Oscillation (ENSO) events, sea surface temperatures (SSTs) in the Southern Ocean decrease and lead to higher concentrations of sea ice in the Ross Sea (Kwok and Comiso 2002). High winter sea-ice extent leads to a higher abundance of ice algae which utilize the underside of the ice as a substrate (Ross and Quetin 1991). When the ice breaks up in spring and early summer, the ice algae are released into the water column and form the basis of an overall increase in marine productivity (Brierley and Thomas 2002). Heavy winter ice cover may also increase abundance of krill (*Euphausia crystallorophias*), as was suggested by Ainley et al. (1998) after observing increased prevalence of krill in Adélie penguin (*Pygoscelis adeliae*) diets in years of heavy ice cover. Because of these relationships with marine primary productivity, annual measures of ENSO strength, SST, or seasonal measures of sea-ice extent in the Ross Sea region may explain annual variability in recruitment probabilities for females Weddell seals in Erebus Bay. We expected that heavy sea-ice years (high ENSO index, low SST, and high maximum (winter) sea-ice extent) would lead to increased foraging success for female Weddell seals and would therefore be correlated with higher recruitment probabilities. We focused on applying these covariates to recruitment probabilities because life history theory predicts that for long-lived species, recruitment will be more sensitive to environmental fluctuations than survival (Eberhardt 1977). We expected that winter sea-ice conditions would play the strongest role in determining whether young female seals obtained the resources necessary to begin reproduction the following year, but we also investigated the effect of summer sea-ice conditions (minimum sea-ice extent) due to a hypothesized negative impact of summer sea-ice extent on foraging success (Proffitt et al. unpublished).

Methods

Study Area and Population

The Erebus Bay study area is located at the southern end of McMurdo Sound in the Ross Sea region of Antarctica (-77.62º to -77.87º South, 166.3º to 167.0º East; see Cameron and Siniff 2004 for description and map of study area). Eight to 14 Weddell seal breeding colonies are located within this study area (Stirling 1969). Each colony is associated with tidal cracks that create areas where adult female seals haul out to have their pups. Seals have been individually marked and resighted for each of the past 35 years. Over this period, both the proportion of the population that is marked and the proportion of marked animals that are of known age have gradually increased (Cameron and Siniff 2004). As of 2004, approximately 80% of the seals in this population were marked, and over 80% of marked animals are of known age. In most years, 300-600 pups are born at colonies in Erebus Bay, and females surviving to reproductive age are strongly philopatric, returning to breed in Erebus Bay (Stirling 1969, 1974; Croxall and Hiby 1983; Cameron and Siniff 2004). More detailed information about Weddell seal natural history can be found in Stirling (1969), Siniff et al. (1977), Testa and Siniff (1987), and Cameron and Siniff (2004).

Data Collection

Each year from 1969 until the present, Weddell seal pups born within the Erebus Bay study area have been individually marked with plastic livestock tags attached to the inter-digital webbing of each rear flipper. In addition, any seal with a broken or missing tag was retagged. The majority of the tagging effort occurred from approximately October 15 to November 15 each year, during the peak of parturition. Beginning in early November, six to eight surveys of the study area were carried out, usually separated by intervals of three to five days. Every individual that was sighted (marked or unmarked) was recorded in a database. For mother-pup pairs, the presence and tag number of a relative (mother or pup) was also recorded. All miscellaneous sighting or handling events were also recorded in the database.

Annual climate and sea-ice covariates were obtained online through various resources. The annual ENSO value was an estimate of ENSO strength obtained from Golden Gate Weather Services (http://ggweather.com/enso/years.htm). Data from various sources (Western Regional Climate Center, National Ocean and Atmospheric Administration (NOAA) Climate Diagnostics Center, and NOAA Climate Prediction

Center) were used to derive the ENSO score, which represented a consensus on the strength of El Niño or La Niña events each year. Monthly mean SSTs for 110 locations covering the region from 156° to 174° East and 70° to 80° South were obtained from NOAA (http://iridl.ldeo.columbia.edu/). The mean of these values was calculated for each year from 1984 to 2003, generating annual mean SST for the Eastern McMurdo Sound region. Monthly SIE for the Ross Sea Sector (160° East to 130° West) was provided by the National Snow and Ice Data Center (http://nsidc.org) (Comiso 1990), and monthly values for September (sepSIE) and February (febSIE) were used in models to represent winter and summer (roughly maximum and minimum) sea-ice extent for each year from 1984-2003.

Data Analysis

We used multi-state mark-resight models (Arnason 1972, 1973; Hestbeck et al. 1991; Brownie et al. 1993) to estimate age-specific recruitment, survival, and sighting probabilities for female seals. Seals included in the sample were 1) tagged as pups and thus of known age, and 2) born to mothers tagged as pups to allow inclusion of maternal characteristics as covariates. One of three breeding states was assigned to each seal for each year that it was sighted based on the number of sightings with a pup within that year's breeding season: 1) prebreeder (P) - a seal not yet sighted with a pup more than once in any season, 2) breeder (B) - a seal sighted with a pup more than once in the current breeding season, or 3) nonbreeder (N) - a seal designated a breeder in a previous season but not sighted with a pup more than once in the current season. For convenience and consistency with other literature, we used the term breeder to denote an individual that produced a pup, not just engaged in mating. We required that a seal be seen with a pup more than once during the breeding season to be classified as a breeder for that year to avoid falsely conferring breeding status to a seal with an unrelated pup lying nearby during a single survey. The associated risk of using this criterion was misclassifying a breeder if her pup died after the initial sighting of the mother-pup pair. Based on females in our dataset that we considered "known breeders" (nursing or lying in proximity to newborn pups), we calculated ~1% were seen only once with a pup and therefore would have been misclassified.

To evaluate predictions about the effects of birth location and maternal characteristics on recruitment, we developed a set of *a priori* models that included three types of parameters: apparent survival probability (ϕ), sighting probability (p), and conditional transition probability (ψ). This study focused on ϕ^p (where superscript indicates breeding state), the survival probability for prebreeders, and ψ^{pb}, the age-specific probability of transition from prebreeder to breeder. ψ^{pb} represented the probability that an animal that was alive and had not yet produced a pup, would recruit to the pup-producing population of females (hereafter, breeding population). Regardless of their survival rate, females that reach a particular age and have not yet begun reproduction have some specific probability of beginning reproduction at that age, and this probability is the recruitment probability. Therefore, we evaluated a set of models in which survival and recruitment probabilities, as well as sighting probability, were related to various combinations of covariates.

Covariates included age, breeding state, three maternal characteristics (age, experience, and age at first reproduction), and location of birth. Maternal age and age at first reproduction were determined from the known histories of the mothers of each seal in our sample. Maternal age was defined as the age of the mother when the individual seal was born, whereas maternal age at first reproduction was the age at which the mother's first pup was born. Maternal experience was measured as the number of pups she had previously given birth to on the study area prior to the current pup. One of three regions of the study area was assigned to each seal in our sample as its location of birth (Fig 3.1). Individual pupping colonies were not used because there would be too few individuals in some categories. Birth location was designated as North of Erebus Glacier Tongue (EGT), South of EGT, or Delbridge Islands (less protected, offshore islands).

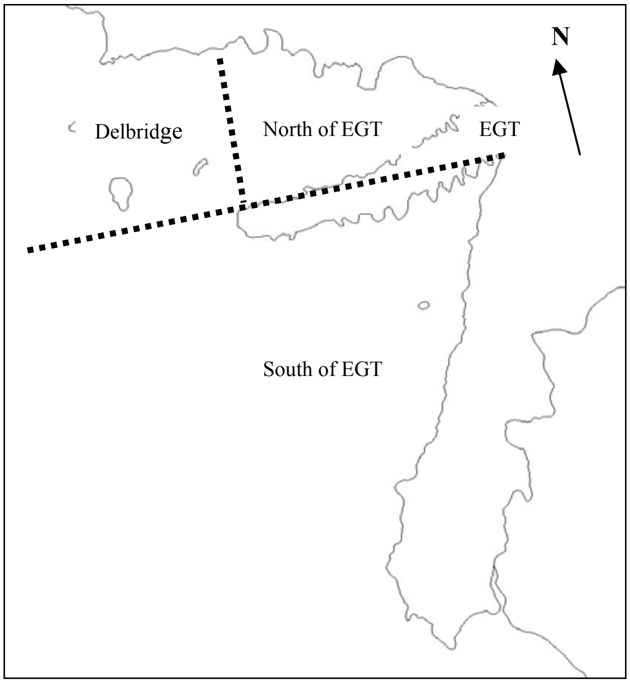

Figure 3.1. Map of Erebus Bay Study Area in eastern McMurdo Sound, Antarctica. Solid lines represent study area and colony boundaries. Dashed lines represent boundaries between birth locations used in this analysis: Delbridge Islands, North of Erebus Glacier Tongue (EGT), and South of EGT.

We conducted our modeling in two steps. First, survival probabilities were modeled, with recruitment probability varying with age and birth location in all models. The second step involved modeling recruitment probabilities using survival covariates selected in step one. Additional models were evaluated to confirm that the order of the parameters in this sequential process did not affect the final overall ranking of top models. All models in our model set allowed ϕ to vary by breeding state because 1) the majority of seals in the prebreeder state are young and previous studies found $\hat{\phi}$ for juveniles to be lower and more variable with age than $\hat{\phi}$ for adults (Testa 1987*a*, Hastings et al. 1999, Cameron 2001, Hadley et al. 2006), and 2) a potential difference in ϕ has been hypothesized for breeding versus non-breeding Weddell seals (Siniff et al. 1977) and demonstrated for other pinniped species (Reiter and LeBoeuf 1991, Lunn et al. 1994). ϕ^p was modeled using 3 age classes: 1-, 2-, and ≥3-years old (based on age classes used in Cameron and Siniff 2004), whereas ϕ^b and ϕ^n were modeled without age variation.

Sighting probabilities were also allowed to vary by breeding state and age in all models due to a documented difference in p for animals of different reproductive status (Siniff et al. 1977; Croxall and Hiby 1983; Testa 1987*b,* Hadley et al. 2006). We incorporated age-related variation in p^p by considering four age-classes (1-, 2-, 3-6, and ≥7-yrs old) based on Cameron and Siniff's (2004) reported age structure for p in our study population. We fixed p^b to 1.0 because we knew that all or nearly all reproductive females were detected each year (Hadley et al. 2006).

Because we designated three breeding states, our models included nine transition probabilities. We fixed parameter values at zero for the three transitions that were impossible: 1) prebreeder to nonbreeder (ψ^{pn}), 2) breeder to prebreeder (ψ^{bp}), and 3) nonbreeder to prebreeder (ψ^{np}). Three transition probabilities were estimated in the multi-state models: 1) ψ^{pb}, which represents recruitment probability, 2) ψ^{bn}, and 3) ψ^{nb}. The remaining three transition probabilities ($\psi^{pp}, \psi^{bb}, \psi^{nn}$, i.e., probabilities of remaining in the same state from one year to the next) were obtained by subtraction based on the fact that the sum of the three transition probabilities for any starting breeding state must equal 1 (e.g., $\psi^{pp} + \psi^{pb} + \psi^{pn} = 1$; $\psi^{pp} = 1 - \psi^{pb} - \psi^{pn}$, where $\psi^{pn} = 0$). Because our modeling effort was focused on recruitment probability (ψ^{pb}) we held the transition probabilities involving breeders (ψ^{bn} and ψ^{nb}) constant for this analysis. Because no seals recruited before age four, we fixed ψ^{pb} to zero for seals aged <4-yrs old. For older seals, we estimated ψ^{pb} for eight age classes in all models (4-, 5-, 6-, 7-, 8-, 9-, 10-, and ≥11-yrs old).

Annual variation in recruitment probability was expected based on results from previous analyses (Hadley et al. 2006). However, when separating the data according to year, age, breeding state, and maternal characteristics, sample sizes for this study were too small to allow estimation of all annual survival and transition probabilities. Therefore, we did not consider models with individual year effects. We did, however, investigate sources of annual variation in ψ^{pb} by including models with annual environmental covariates (ENSO, SST, sepSIE, febSIE). Representing individual years with the associated environmental covariates required a single parameter estimating slope for the covariate, rather than 20 individual parameters, one for each year. This allowed us to build simpler models that evaluated our predictions of annual variation in ψ^{pb}. Six additional models were constructed in which each covariate was incorporated with a 0, 1, or 2 year lag. This allowed for the possibility of climate and/or ice conditions in a previous year affecting ψ^{pb} in the current year.

Multi-state models were constructed and estimates of model parameters generated using Program MARK (White and Burnham 1999). Akaike's Information Criterion (AIC_c) (Akaike 1973), corrected for small sample bias (Hurvich and Tsai 1989) was used to evaluate the relative support in the data for models in our *a priori* set (Burnham and Anderson 1998). We used the AIC_c value associated with each model to obtain the difference in AIC_c (ΔAIC_c) between the model in question and the model with the minimum AIC_c. Models with $\Delta AIC_c < 2$ were considered strongly supported by the data, and models with $\Delta AIC_c < 7$ were moderately supported. In addition, normalized Akaike weights (w_i, for each model i) were used as a measure of relative plausibility of various models. To describe the support for each of our predictions, we presented results from the highest-ranked model that addresses each particular hypothesis, along with the weight of evidence in favor of that particular model. For predictions regarding maternal covariates, we presented results only from models that showed improved fit relative to a model without maternal effects. In many studies, model averaging may be used to incorporate model selection uncertainty into estimates of parameters of interest. However, we did not use model averaging here because we were interested in describing the particular functions that best approximated the relationships between various covariates and survival or recruitment probability (see Blums et al. 2005).

We were unable to estimate c (a measure of overdispersion), as no currently available estimation technique allows testing goodness-of-fit for multi-state models with individual covariates. To assess the influence of possible lack of fit, we investigated model ranking under various scenarios, using $\hat{c}$ set to 1.0, 2.0, 3.0 and 4.0 (encompassing average levels of overdispersion (Burnham and Anderson 1998)) to detect the degree of change in model ranking.

For our study population, it is known that tag loss occurs at a low rate (probability that a female seal retained at least one of two tags for one year ranged from 0.977 to 0.998; Cameron and Siniff 2004). Therefore, we used the tag-retention rate ($\hat{\theta}$) estimated for this population by Cameron and Siniff (2004) to adjust $\hat{\phi}$ ($\hat{\phi}_{adj} = \hat{\phi}/\hat{\theta}$; Arnason and Mills 1981). This was necessary because if some animals lost both tags, $\hat{\phi}$ represented the product of the underlying survival rate and the tag retention rate (Nichols et al. 1992). Transition probabilities did not need to be corrected for tag loss as they are conditional on survival (Williams et al. 2002). That is, they are the estimated rates of movement from one state to another, assuming that the animal had survived to the current year and was available on the study area to potentially make the transition.

Results

Analyses were performed using encounter histories for 1,372 known-age females that were born on the study area from 1980 to 2004. Of these, 102 returned and had at least one pup on the study area prior to 2005, whereas 1,116 had not returned to the study area, and 154 had returned but not been recruited to the breeding population. Of the 102 breeding females, more than half (*n* = 66) were observed as breeders in multiple years. The average maternal age for animals in this dataset was 10.82 (SD = 3.78) and mothers of seals in our dataset had produced an average of 2.54 (SD = 2.56) pups in prior years. On average, these mothers had their first pup at age 7.22 (SD = 1.34).

The effects of lack of fit were assessed by evaluating our model set under various levels of overdispersion, and we found that model rankings did not change substantially when we varied $\hat{c}$ from 1.0 to $\hat{c}$ = 4.0. Thus, we feel confident drawing inference from these models. All but two of the models in our a priori set were at least weakly supported by the data ($\Delta \mathrm{AIC}_c < 10$) (Table 3.1). We provide estimates of recruitment probabilities for prebreeders (Table 3.2) from the top-ranked model (Table 3.1) to convey the general nature of the parameter estimates. When estimates were a function of the age of an animal's mother at the time of birth, we present estimates calculated using a maternal age of 10.82 yrs (the average maternal age for our dataset). Sighting probabilities estimated from the top-ranked model (Table 3.1) were low for young prebreeders ($\hat{p}^{p}_{age-1} = 0.04$ [$\hat{SE} = 0.01$]; $\hat{p}^{p}_{age-2} = 0.07$ [$\hat{SE} = 0.01$]) but increased with age ($\hat{p}^{p}_{age-3-6} = 0.31$ [$\hat{SE} = 0.02$], and $\hat{p}^{p}_{age-7+} = 0.41$ [$\hat{SE} = 0.05$]).

Table 3.1. Models representing hypotheses about covariate effects on estimated survival ($\hat{\phi}$) and recruitment ($\hat{\psi}^{pb}$) probabilities for female Weddell seals in Erebus Bay, Antarctica. ϕ was modeled first, with ψ^{pb} varying with age and birth location in all models. The second step involved modeling ψ^{pb} using survival covariates selected in step one. In both steps, sighting probability (p) varied with breeding state and four age classes, based on previous analyses (Cameron and Siniff 2004, Hadley et al. 2006). Covariates are indicated in parentheses and include ***st*** (breeding state), ***a3*** (age; modeled as three groups: age 1, age 2, age 3 and older), ***a9*** (age; modeled as nine groups: 1-3, 4, 5, 6, 7, 8, 9, 10, 11 and older), ***gr*** (group; determined by birth location), ***ma*** (maternal age), ***me*** (maternal experience), and ***mafr*** (maternal age at first reproduction). Logarithms of maternal covariates (ln(***ma***) and ln(***me***)) were used to create pseudothreshold models. Results from model selection are included: *k* (number of parameters), Dev (model deviance), QAIC$_c$, Δ_i (difference in QAIC$_c$ value between the overall top model and each subsequent model *i*), ws Δ_i (within-suite Δ_i; difference in QAIC$_c$ value between the top model in the model suite and each subsequent model *i*), and w_i ("weight of evidence" in favor of each model *i*).

Model	***k***	**Dev**	**AIC$_c$**	**Δ_i**	**ws Δ_i**	**w_i**
Survival probability suite						
$\phi(st)$	20	4257.27	4297.69	93.81	88.86	0.00
$\phi(st + a3)$	22	4164.67	4209.17	5.29	0.34	0.02
$\phi(st + gr + a3)$	24	4163.12	4211.72	7.84	2.89	0.00
$\phi(st + ma + a3)$	23	4163.03	4209.58	5.70	0.75	0.01
$\phi(st + ma + gr + a3)$	25	4161.76	4212.41	8.53	3.58	0.00
$\phi(st + ma + ma^2 + a3)$	**24**	**4160.23**	**4208.83**	**4.95**	**0.00**	**0.02**
$\phi(st + ma + ma^2 + gr + a3)$	26	4159.02	4211.73	7.85	2.90	0.00
$\phi(st + \ln(ma) + a3)$	23	4162.51	4209.06	5.18	0.23	0.02
$\phi(st + \ln(ma) + gr + a3)$	25	4161.38	4212.03	8.15	3.20	0.00
$\phi(st + me + a3)$	23	4163.81	4210.36	6.48	1.53	0.01
$\phi(st + me + gr + a3)$	25	4162.48	4213.13	9.25	4.30	0.00
$\phi(st + me + me^2 + a3)$	24	4163.72	4212.32	8.44	3.49	0.00
$\phi(st + me + me^2 + gr + a3)$	26	4162.37	4215.07	11.19	6.24	0.00
$\phi(st + \ln(me) + a3)$	23	4164.51	4211.07	7.19	2.24	0.01
$\phi(st + \ln(me) + gr + a3)$	25	4163.22	4213.87	9.99	5.04	0.00
$\phi(st + mafr + a3)$	23	4162.91	4209.46	5.58	0.63	0.01
$\phi(st + mafr + gr + a3)$	25	4161.44	4212.09	8.21	3.26	0.00
Recruitment probability suite						
$\psi^{pb}(a9)$	22	4164.29	4208.80	4.92	4.92	0.02

Table 3.1 continued

Model	***k***	**Dev**	**AIC$_c$**	**Δ_i**	**ws Δ_i**	**w_i**
$\psi^{pb}(ma + a9)$	23	4158.53	4205.08	1.20	1.20	0.12
$\psi^{pb}(ma + gr + a9)$	**25**	**4153.23**	**4203.88**	**0.00**	**0.00**	**0.22**
$\psi^{pb}(ma + ma^2 + a9)$	24	4158.45	4207.05	3.17	3.17	0.05
$\psi^{pb}(ma + ma^2 + gr + a9)$	26	4153.20	4205.90	2.02	2.02	0.08
$\psi^{pb}(\ln(ma) + a9)$	23	4158.67	4205.22	1.34	1.34	0.11
$\psi^{pb}(\ln(ma) + gr + a9)$	25	4153.27	4203.92	0.04	0.04	0.21
$\psi^{pb}(me + a9)$	23	4163.89	4210.44	6.56	6.56	0.01
$\psi^{pb}(me + gr + a9)$	25	4159.15	4209.80	5.92	5.92	0.01
$\psi^{pb}(me + me^2 + a9)$	24	4163.80	4212.40	8.52	8.52	0.00
$\psi^{pb}(me + me^2 + gr + a9)$	26	4159.15	4211.85	7.97	7.97	0.01
$\psi^{pb}(\ln(me) + a9)$	23	4163.27	4209.82	5.94	5.94	0.01
$\psi^{pb}(\ln(me) + gr + a9)$	25	4158.75	4209.4	5.52	5.52	0.02
$\psi^{pb}(mafr + a9)$	23	4162.62	4209.18	5.30	5.30	0.02
$\psi^{pb}(mafr + gr + a9)$	25	4158.80	4209.45	5.57	5.57	0.01

Table 3.2. Estimates of age- and birth-location-specific recruitment probabilities ($\hat{\psi}^{pb}$) and standard errors ($S\hat{E}$) generated from top-ranked model (see Table 3.1). The age of an animal's mother when the animal was born was also found to be related to $\hat{\psi}^{pb}$ (see Results). When estimates were a function of the age of an animal's mother at the time of birth, we present estimates calculated using a maternal age of 10.82 yrs (the average maternal age for our dataset.

	North of EGT		South of EGT		Delbridge Islands	
Age	$\hat{\psi}^{pb}$	$S\hat{E}$	$\hat{\psi}^{pb}$	$S\hat{E}$	$\hat{\psi}^{pb}$	$S\hat{E}$
4	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
5	0.04	0.02	0.05	0.01	0.07	0.02
6	0.14	0.04	0.17	0.03	0.25	0.04
7	0.24	0.06	0.27	0.05	0.38	0.06
8	0.16	0.06	0.18	0.06	0.27	0.08
9	0.13	0.07	0.15	0.07	0.22	0.10
10	0.16	0.10	0.18	0.10	0.27	0.14
11 and older	0.14	0.12	0.17	0.13	0.25	0.17

Maternal Characteristics

Results indicated that maternal characteristics do influence offspring survival and recruitment probabilities. We found the most evidence for the effect of maternal age. For survival probability, we found evidence supporting our prediction that mothers of intermediate age would produce offspring with the highest survival probability. In the top-ranked survival model (within-suite $w_i = 0.16$, Table 3.1), ϕ^p was positively related to maternal age ($\beta_{MA} = 0.12$; $\hat{SE} = 0.06$) and negatively related to maternal age squared ($\beta_{MA^2} = -0.07$; $\hat{SE} = 0.04$). Accordingly, estimates of offspring survival probability increased with increasing maternal age up to a maternal age of 14, beyond which further increases in maternal age led to a decrease in offspring survival rate (Figure 3.2). A specific scenario with one-year-old prebreeders illustrates the magnitude of the maternal effect on survival probability. For offspring born to age-6 mothers, $\hat{\phi}^p_{age-1}$ was 0.48 ($\hat{SE} = 0.11$). The rate increased to 0.56 ($\hat{SE} = 0.11$) for seals born to age-14 mothers, but decreased back to 0.48 ($\hat{SE} = 0.14$) for seals born to age-22 mothers. Interestingly, the pseudo-threshold model (representing our alternative prediction that offspring survival probability would continue to increase at older maternal ages, but would increase more slowly) was nearly as well-supported (within-suite $w_i = 0.14$). These two models were the only maternal effects models that explained variation in survival probability better than a model without maternal effects (within-suite $w_i = 0.13$).

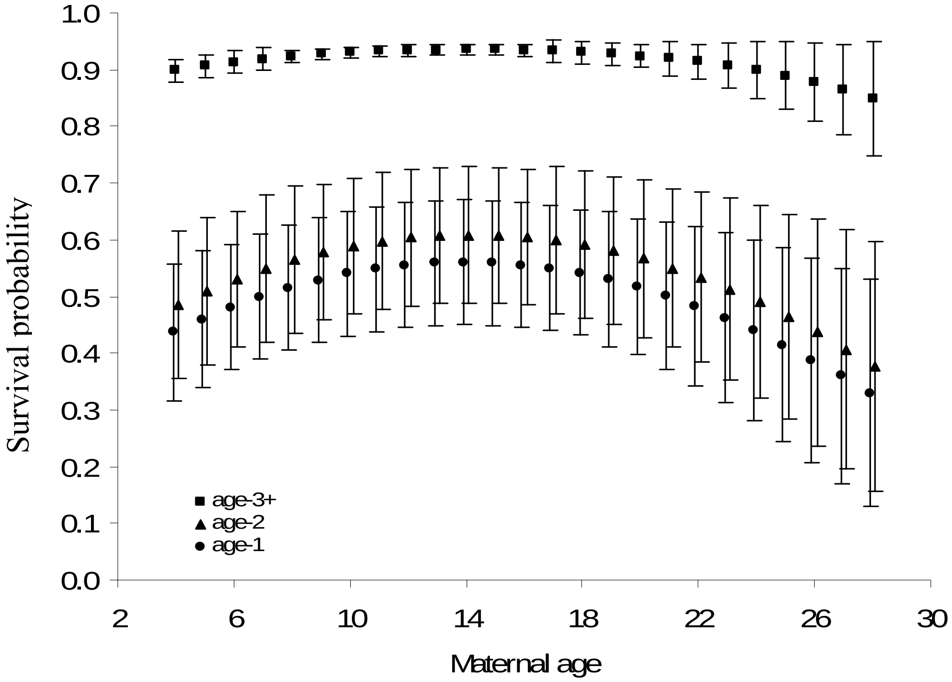

Figure 3.2. The quadratic relationship displayed between maternal age (x-axis) and offspring survival probability (y-axis) for female Weddell seals in Erebus Bay, Antarctica in three age classes of prebreeders (age-1, age-2, and ≥ age-3). Error bars represent 1 $\hat{SE}$.

Recruitment probability appeared to decrease with increasing maternal age (Figure 3.3), which disagreed with all of our hypothesized relationships. In the top-ranked model from the recruitment probability suite (within-suite $w_i = 0.22$; Table 3.1), recruitment probability displayed a negative linear relationship with maternal age (β_{MA} = -0.41; $\hat{SE} = 0.16$). For example, $\hat{\psi}^{pb}$ for an age-7 seal born in the Delbridge Islands (birth location also influences $\hat{\psi}^{pb}$ in this model) was 0.51 ($\hat{SE} = 0.08$) for maternal age of 6 and 0.30 ($\hat{SE} = 0.06$) for maternal age of 14. Again, there was nearly equal support (within-suite $w_i = 0.21$) for the pseudo-threshold model. In this case, the negative effect of maternal age on $\hat{\psi}^{pb}$ (β_{MA} = -0.36; $\hat{SE}$ = 0.15) lessened as maternal age increased. A negative effect of maternal age on recruitment probability was supported by all models including this covariate.

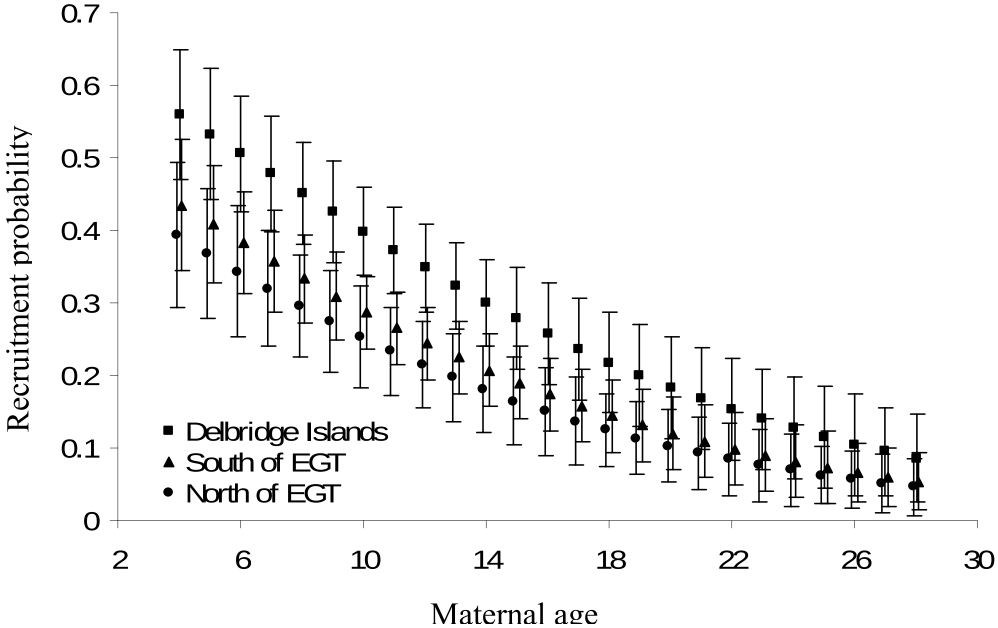

Figure 3.3. The relationship displayed between maternal age (x-axis) and offspring recruitment probability (y-axis) for female Weddell seals born at three different locations (Delbridge Islands, North of EGT, South of EGT) in Erebus Bay, Antarctica. Error bars represent 1 $\hat{SE}$. Results displayed are for probability of recruitment at age 7 only. Age-specific recruitment probabilities were estimated for younger and older age classes as well (Table 3.2).

We predicted that maternal experience, as well as maternal age, would influence survival and recruitment probabilities. However, models with maternal experience were ranked lower than models with no maternal covariates (Table 3.1). Given that the results of other studies (Weimerskirch 1990, 1992; Wooller 1990) have suggested that breeding experience is only important up to a point, we evaluated an exploratory model using only data for seals born to mothers of ages < 10 yrs. With this subset of data (n = 725), maternal experience was a strong predictor of variation in offspring recruitment probability (β_{ME} = 0.35; $S\hat{E}$ = 0.16) and the corresponding model was more strongly supported than a model with effect of maternal age (w_i = 0.89 versus w_i = 0.11). The results from this exploratory model supported our prediction that maternal experience would positively influence offspring recruitment probability, but demonstrated that this effect is only observed up to a maternal age of 10.

Location of Birth

We detected variation in $\hat{\psi}^{pb}$ that was related to location of birth, supporting our general prediction that location of birth would influence recruitment probability. However, the underlying mechanism for this variation is still unclear. Our prediction based on the physical characteristics of the various locations was not supported because age-specific $\hat{\psi}^{pb}$ was an average of 47% *higher* for seals born at the smaller, less protected, offshore islands (Delbridge Islands location) (Table 3.2, Figure 3.3). Our alternative prediction was that higher-than-average maternal age at Delbridge Islands would lead to higher $\hat{\psi}^{pb}$ for seals born there. We did find higher $\hat{\psi}^{pb}$ for seals born at Delbridge Islands, however this could not be explained by maternal age due to the inverse relationship between maternal age and $\hat{\psi}^{pb}$ that was described in the preceding paragraph.

Oceanographic Variables

As we predicted, annual variation in ψ^{pb} was strongly correlated with annual fluctuation in winter sea-ice extent (sepSIE). When four models including environmental covariates were added to our model set, the model including sepSIE was found to substantially improve model fit over the model without an annual covariate. This model was strongly supported ($w_i = 0.97$) relative to the previously top-ranked model (Table 3.3). In the best model, annual $\hat{\psi}^{pb}$ was positively related to the sea-ice extent in September of the previous year (roughly the maximum sea-ice extent) ($\hat{\beta}_{sepSIE} = 0.40$; $S\hat{E} = 0.11$). The second-ranked model ($w_i = 0.01$) provided weak evidence for the opposite relationship between annual $\hat{\psi}^{pb}$ and sea-ice extent the preceding February (roughly the minimum sea-ice extent ($\hat{\beta}_{febSIE} = -0.25$, $S\hat{E} = 0.13$). The annual measure of ENSO strength also resulted in a slightly improved model fit relative to the model without an annual covariate ($\Delta_i = 11.73$ vs $\Delta_i = 11.79$), and ENSO strength was positively related to $\hat{\psi}^{pb}$ ($\hat{\beta}_{ENSO} = 0.12$, $S\hat{E} = 0.08$), as predicted.

Table 3.3. Models representing hypotheses about effects of oceanographic variables (ENSO, SST, febSIE, sepSIE) on estimated recruitment probabilities ($\hat{\psi}^{pb}$) for female Weddell seals in Erebus Bay, Antarctica. Models in bold resulted in improved fit of the data relative to previous top-ranked model (from Table 3.1).

Model	***k***	**Dev**	**AIC$_c$**	**Δ_i**	**w_i**
$\psi^{pb}(ma + gr + a9 + sepSIE)$	**26**	**4139.39**	**4912.09**	**0.00**	**0.97**
$\psi^{pb}(ma + gr + a9 + febSIE)$	**26**	**4149.85**	**4202.55**	**10.46**	**0.01**
$\psi^{pb}(ma + gr + a9 + ENSO)$	**26**	**4151.13**	**4203.83**	**11.73**	**0.01**
$*\psi^{pb}(ma + gr + a9)$	25	4153.23	4203.88	11.79	0.01
$\psi^{pb}(ma + gr + a9 + SST)$	26	4151.60	4204.31	12.21	0.00

* Previously top-ranked model from Table 3.1 (no annual climate or sea-ice covariates)

Discussion

In this study, we successfully separated survival and recruitment processes and discovered several novel findings regarding sources of variation in each. In support of our prediction, we found that offspring survival probability was positively related to maternal age up to a threshold age of 14, and then either declined with further increase in maternal age, or continued to increase, but more slowly. A possible explanation for the nearly equal support for these two contrasting models is that an intermediate relationship best describes the relationship between survival probability and maternal age. Survival probability may level off after maternal age of 14 yrs rather than increasing or decreasing, and thus may not be well described by either of our two top-ranked models.

For pinnipeds in general, older females are expected to be larger when they give birth (Hill 1987, Crocker et al. 2001), and therefore produce larger pups (Kovacs and Lavigne 1986, Hill 1987, McCann et al. 1989, Arnbom et al. 1997). Large size at weaning likely confers a survival advantage to a pup for its juvenile years but this effect may play a lesser role beyond a maternal age of 14, when body size is not increasing as rapidly with age. Maternal reproductive senescence, which has been shown to occur in long-lived animals (e.g., Clutton-Brock 1988) may also play a role in explaining declining survival of offspring beyond a maternal age of 14. For northern fur seals (*Callorhinus ursinus*), maximum pup size was attained by females of intermediate age (12-13 years), and further increase in maternal age or size did not result in larger pups (Boltnev and York 2001). Boltnev and York (2001) suggested that the amount of energy allocated to a pup may decrease after a certain age, such that further increases in maternal size do not translate into larger pup size. We hypothesize that for Weddell seals, senescence-related declines in body condition translate into lower weaning weights and survival probabilities for pups born to females older than 14 yrs. A mass dynamics study of the Erebus Bay Weddell seals is currently underway and will eventually yield annual mother and pup parturition and weaning mass for a substantial portion of the population. This will allow us to evaluate 1) whether females display senescent decline in mass beyond some threshold age, and 2) whether the proportion of maternal mass that is invested in the pup is reduced beyond some threshold maternal age.

In contrast to our prediction, offspring recruitment probability displayed a negative relationship with maternal age – seals born to young females were more likely to join the breeding population than were seals born to older females. One reason we may have observed this relationship is that female seals may vary in individual quality. The high-quality females, which are able to begin reproduction at a young age, may pass this ‘reproductive superiority’ on to their offspring, making them more likely to become breeders than seals born to older females (Hadley et al. 2006). At first, this seems to somewhat contradict the quadratic relationship we observed above between maternal age and offspring survival probability. However, we propose that there are two different processes of interest: being born to an older female is advantageous for a pup’s survival, but once the pup has survived to potential recruitment age, seals that were born to young females are most likely to recruit to the breeding population, possibly due to heritability of reproductive superiority. Thus, a more competitive or highly fit female may pass heritable traits conferring higher fitness to her progeny, but this advantage may not be displayed during all life stages. A pup born to a young, highly fit mother may be at a disadvantage for early survival due to its mother's smaller size and hence, its lower weaning weight. However, if this pup reaches recruitment age, it may then display the high-quality traits of its mother and experience higher than average recruitment probability. This type of countervailing selection at different life stages has been documented in evolutionary studies (Price 1984, Price and Grant 1984, Schluter and Smith 1986, Pemberton et al. 1991). In these studies, the favored genotypes for reproductive success were generally those that were selected against as juveniles. Red deer females of one particular genotype had exceptionally low survival rates as juveniles, but if they did survive they went on to calve early and often (Pemberton et al. 1991). Countervailing selection is a common force that maintains genetic diversity in natural populations, and may also explain how fitness components may have high heritability while overall fitness does not (Pemberton et al. 1991).

We had predicted that maternal experience would display a similar relationship with survival and recruitment probabilities as did maternal age. However, the data only weakly supported models with maternal experience. Interestingly, the relationship was much stronger when modeled with an exploratory dataset of only seals born to females age 10 and younger. Again, this suggests the influence of heterogeneity in individual quality on recruitment probability. We hypothesize that the females that have produced the largest number of pups (and are thus most experienced by age 10) are the females that began reproduction at a young age and were able to produce pups in consecutive years due to their superior reproductive capabilities. Their offspring have likely inherited a genetic tendency for high reproductive output and therefore display higher recruitment probability. Because maternal age and experience are correlated, the maternal-age-related decline in offspring recruitment probability that we observed may mask any relationship with maternal experience beyond a maternal age of 10, explaining why we did not observe the effect of maternal experience with our full dataset.

In light of the inverse relationship between maternal age and offspring recruitment probability, the higher recruitment probability of seals born at Delbridge Islands (where mean maternal age is highest) is an unexpected result. We infer that there is some unknown benefit to recruitment that seals gained from being born at this location, and that this benefit outweighs the apparent negative effect of being born to older-than-average females. Little is known about differences in food availability at the various breeding colonies, and preliminary steps are currently being taken to use sonar equipment to detect abundance of Weddell seal prey items at various locations in McMurdo Sound. The bathymetry of the area surrounding the Delbridge Islands may cause this to be a more profitable foraging area for Weddell seals than other breeding colonies in the study area.

Recruitment probability has less influence than other life history parameters on population growth rates of marine mammals (Eberhardt and Siniff 1977, Goodman 1981), but traits to which population growth rate is less sensitive are typically the traits that are most variable in real populations (Fisher 1958, Eberhardt 1977, Gaillard et al. 2000). As such, recruitment probability may be responsible for much of the temporal variability in population growth rates (Gaillard et al. 1998). Moreover, the amount of variability among individuals is of interest as it describes the flexibility of individuals for adjusting to environmental change within the constraints of their life histories. Annual variation in recruitment probability for Weddell seals has been demonstrated (Testa

1987*b*,) and a possible link to large-scale oceanographic processes proposed (Testa et al. 1990, Testa et al. 1991), but the particular mechanism underlying this variation was not previously known. We have shown that sea-ice extent plays a strong role in explaining this annual variation. Years of higher recruitment probabilities were associated with high sea-ice extent in the previous winter, most likely due to the positive linkage between sea ice and primary productivity. Additionally, extensive winter sea-ice cover may favor krill recruitment and survival (Loeb et al. 1997) and benefit species such as *Pleuragramma antarcticum*, a primary food item for Weddell seals (Dearborn 1965). Female seals breeding for the first time may profit from this increased abundance of prey items in the winter preceding breeding, and may be more likely to successfully implant an embryo and carry their offspring to term, thereby increasing recruitment probabilities the following pupping season. The weak negative effect of summer sea-ice extent that we observed may be explained by the relationship between summer sea-ice extent and open-water primary productivity. Summer sea-ice extent determines the amount of open water available for phytoplankton blooms and therefore may determine foraging success of Weddell seals during the summer. Summer foraging success for females is likely an important predictor of pup weaning mass the following year (Proffitt et al. unpublished), but may not be as important as winter foraging success in determining whether an unrecruited female achieves the body condition necessary to breed and successfully implant an embryo for the first time.

In conclusion, our work shows that recruitment is influenced by many factors working together in complex relationships. Results from this study, along with results from a previous study on this population (Hadley et al. 2006), strongly suggest the presence of variation in quality among individuals. When individuals exhibit substantial differences in inherent probabilities of survival and reproduction, relationships between vital rates or life-history components observed at the population level do not necessarily reflect patterns at the individual level (Vaupel and Yashin 1985, Cooch et al. 2002). Thus, it will be important in future studies to attempt to account for individual variation either using some index of quality such as weight or body condition, or by estimating ‘latent fitness’ (underlying individual potential for survival and reproduction) using a random effects modeling approach (Cam et al. 2002, Link et al. 2002). We have also found evidence for countervailing selection in this population of Weddell seals – factors that enhance juvenile survival probability (i.e., being born to a young mother) result in reduced recruitment probability. The mechanisms through which maternal age exerts its influence may be better understood when maternal and offspring parturition and weaning masses have been measured for a substantial proportion of the population. Mass measurements will also shed light on linkages between oceanographic conditions and Weddell seal demographic rates. In this study, we have additionally found evidence of a correlation between annual recruitment probability and oceanographic conditions, which may assist future efforts to predictively model the response of Weddell seal populations to climate change.

Literature Cited

Ainley, D.G., P.R. Wilson, K.J. Barton, G. Ballard, N. Nur, and B. Karl. 1998. Diet and foraging effort of Adélie penguins in relation to pack-ice conditions in the southern Ross Sea. Polar Biology 20:311-319.

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B.N. Petran and F. Csàaki, editors. International symposium on information theory. Second edition. Akadèemiai Kiadi, Budapest, Hungary.

Albon, S.D., T.H. Clutton-Brock, and F.E. Guinness. 1987. Early development and population dynamics in red deer. II. Density-independent effects and cohort variation. Journal of Animal Ecology 56:69-81.

Arnason, A.N. 1972. Parameter estimates from mark-recapture experiments on two populations subject to migration and death. Research in Population Ecology 13:97-113.

Arnason, A.N. 1973. The estimation of population size, migration rates, and survival in a stratified population. Research in Population Ecology 15:1-8.

Arnason, A.N., and K.H. Mills. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Canadian Journal of Fisheries and Aquatic Sciences 38:1077-1095.

Arnbom, T., M.A. Fedak, I.L. Boyd, and B.J. McConnell. 1993. Variation in weaning mass of pups in relation to maternal mass, postweaning fast duration, and weaned pup behaviour in southern elephant seals (*Mirounga leonine*) at South Georgia. Canadian Journal of Zoology 71:1772-1781.

Arnbom, T., M. Fedak, and I.L. Boyd. 1997. Factors affecting maternal expenditure in southern elephant seals during lactation. Ecology 78:471-483.

Barbraud, C., and H. Weimerskirch. 2001. Emperor penguins and climate change. Nature 411: 183-186.

Beauplet, G., C. Barbraud, M. Chamballant, and C. Guinet. 2005. Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate, and oceanographic conditions. Journal of Animal Ecology 74:1160-1172.

Blums, P., J.D. Nichols, J.E. Hines, M.S. Lindberg, and A. Mednis. 2005. Individual quality, survival variation and patterns of phenotypic selection on body condition and timing of nesting in birds. Oecologia 143:365-376.

Boltnev, A.I., and A.E. York. 2001. Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. Journal of Zoology – London 254:219-228.

Bowen, W.D., O.T. Oftedal, D.J. Boness, and S.J. Iverson. 1994. The effect of maternal age and other factors on birth mass in the harbour seal. Canadian Journal of Zoology 72:8-14.

Brierley, A.S., and D.N. Thomas. 2002. Ecology of southern ocean pack ice. Advances in Marine Biology 43:171-276.

Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock, and J.B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transition probabilities. Biometrics 49:1173-1187.

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: a practical information-theoretic approach. Springer, New York, New York, USA.

Cam, E., W.A. Link, E.G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. American Naturalist 159:97-105.

Cameron, M.F. 2001. Dynamics of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Dissertation. University of Minnesota, Minneapolis, Minnesota, USA.

Cameron, M.F., and D.B. Siniff. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Canadian Journal of Zoology 82:601-615.

Clutton-Brock, T.H. 1988. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA

Comiso, J. 1990; updated 2004. DMSP SSM/I daily polar gridded sea ice concentrations, 1982 to 2004. Edited by J. Maslanik and J. Stroeve. Boulder, CO: National Snow and Ice Data Center. Digital media.

Cooch, E.G., E. Cam, and W. Link. 2002. Occam's shadow: levels of analysis in evolutionary ecology – where to next? Journal of Applied Statistics 29:19-48.

Crocker, D.E., J.D. Williams, D.P. Costa, and B.J. LeBoeuf. 2001. Maternal traits and reproductive effort in northern elephant seals. Ecology 82:3541-3555.

Croxall, J.P., and L. Hiby. 1983. Fecundity, survival and site fidelity in Weddell seals, *Leptonychotes weddellii*. Journal of Applied Ecology 20:19-32.

Dearborn, J.H. 1965. Food of Weddell seals at McMurdo Sound, Antarctica. Journal of Mammalogy 46:37-43.

Eberhardt, L.L. 1977. Optimal policies for conservation of large mammals with special reference to marine ecosystems. Environmental Conservation 4:205-212.

Eberhardt, L.L., and D.B. Siniff. 1977. Population dynamics and marine mammal management policies. Journal of the Fisheries Research Board of Canada 34:183-190.

Fisher, R.A. 1958. The genetical theory of natural selection. Second edition. Dover Publications, Inc., New York, New York, USA.

Forchammer, M.C., T.H. Clutton-Brock, J. Lindström, and S.D. Albon. 2001. Climate and population density induce long-term cohort variation in a northern ungulate. Journal of Animal Ecology 70:721-729.

Franklin, A.B., D.R. Anderson, R.J. Gutierrez, and K.P. Burnham. 2000. Climate, habitat quality, and fitness in northern spotted owl populations in northwestern California. Ecological Monographs 70:539-590.

Gaillard, J.-M., M. Festa-Bianchet, and N. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology and Evolution 13:58-63.

Gaillard, J.-M., M. Festa-Bianchet, N.G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components of large herbivores. Annual Review of Ecology and Systematics 31:367-393.

Goodman, D. 1981. Life history analysis of large mammals. Pages 415-436 *in* C. W. Fowler and T. D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA

Hadley, G.L., J.J. Rotella, R.A. Garrott, and J.D. Nichols. 2006. Variation in probability of first reproduction of Weddell seals. Journal of Animal Ecology. *In press*.

Hastings, K.K., and J.W. Testa. 1998. Maternal and birth colony effects on survival of Weddell seal offspring from McMurdo Sound, Antarctica. Journal of Animal Ecology 67:722-740.

Hastings, K.K., J.W. Testa, and E.A. Rexstad. 1999. Interannual variation in survival of juvenile Weddell seals (*Leptonychotes weddellii*) from McMurdo Sound, Antarctica: effects of cohort, sex, and age. Journal of Zoology London 248:307-323.

Hestbeck, J.B., J.D. Nichols, and R.A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523-533.

Hurvich, C.M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.

Hill, S.E.B. 1987. Reproductive ecology of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Dissertation. University of Minnesota, Minneapolis. Minnesota, USA.

Iverson, S.J., W.D. Bowen, D.J. Boness, and O.T. Oftedal. 1993. The effect of maternal size and milk energy output on pup growth in grey seals (*Halichoerus grypus*). Physiological Zoology 66:61-88.

Kokko, H., M.P. Harris, and S. Wanless. 2004. Competition for breeding sites and site-dependent population regulation in a highly colonial seabird, the common guillemot *Uria aalge*. Journal of Animal Ecology 73:367-376.

Kovacs, K.M., and D.M. Lavigne. 1986. Maternal investment and neonatal growth in the phocid seals. Journal of Animal Ecology 55:1035-1051.

Kwok, R., and J. C. Comiso. 2002. Southern ocean climate and sea ice anomalies associated with the southern oscillation. Journal of Climate 15:487-501.

LeBoeuf, B.J., and J. Reiter. 1988. Lifetime reproductive success in northern elephant seals. Pages 344-362 *in* T.H. Clutton-Brock, editor. Reproductive success: studies of individual variation in contrasting breeding systems. University of Chicago Press, Chicago, Illinois, USA.

Link, W.A., E.G. Cooch, and E. Cam. 2002. Model-based estimation of individual fitness. Journal of Applied Statistics 29:207-224.

Loeb, V., V. Siegel, O. Holm-Hansen, R. Hewitt, W. Fraser, W. Trivelpiece, and S. Trivelpiece. 1997. Effects of sea-ice extent and krill or salp dominance on the Antarctic food web. Nature 387:897-900.

Lunn, N.J., I.L. Boyd, and J.P. Croxall. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. Journal of Animal Ecology 63:827-840.

McCann, T.S., M.A. Fedak, and J. Harwood. 1989. Parental investment in southern elephant seals, *Mirounga leonine*. Behavioral Ecology and Sociobiology 25:81-87.

McMahon, C.R., and H.R. Burton. 2005. Climate change and seal survival: evidence for environmentally-mediated changes in elephant seal, *Mirounga leonina*, pup survival. Proceedings of the Royal Society B 272:923-928.

Nichols, J.D., J. Bart, R.J. Limpert, W.J.L. Sladen, and J.E. Hines. 1992. Annual survival rates of adult and immature eastern population tundra swans. Journal of Wildlife Management 56:485-494.

Pemberton, J.M., S.D. Albon, F.E. Guiness, and T.H. Clutton-Brock. 1991. Countervailing selection in different fitness components in female red deer. Evolution 45:93-103.

Price, T.D. 1984. The evolution of sexual size dimorphism in Darwin's finches. American Naturalist 123:500-518.

Price, T.D., and P.R. Grant. 1984. Life history traits and natural selection for small body size in a population of Darwin's finches. Evolution 38:483-494.

Reed, E.T., G. Gauthier, R. Pradel, J.-D. Lebreton. 2003. Age and environmental conditions affect recruitment in Greater Snow Geese. Ecology 84:219-230.

Reiter, J., and B.J. LeBoeuf. 1991. Life-history consequences of variation in age at primiparity in northern elephant seals. Behavioral Ecology and Sociobiology 28:153-160.

Ross, R.M., and L.B. Quetin. 1991. Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiaceae). Memoirs of the Queensland Museum 31:321-333.

Sǽther, B.E., and M. Heim. 1993. Ecological correlates of individual variation in age at maturity in female moose (*Alces alces*): the effects of environmental variability. Journal of Animal Ecology 62:482-489.

Schluter, D., and J.M.N. Smith. 1986. Natural selection on beak and body size in the song sparrow. Evolution 40:221-231.

Siniff, D.B., D.M. DeMaster, R.J. Hofman, and L.L. Eberhardt. 1977. An analysis of the dynamics of a Weddell seal population. Ecological Monographs 47:319-335.

Stirling, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. Ecology, 50:573-586.

Stirling, I. 1974. Movements of Weddell seals in McMurdo Sound, Antarctica. Australian Journal of Zoology 22:39-43.

Testa, J.W. 1987*a*. Juvenile survival and recruitment in a population of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Canadian Journal of Zoology 65:2993-2997.

Testa, J.W. 1987*b*. Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddellii*). Canadian Journal of Zoology 65:1091-1099.

Testa, J.W., and D.B. Siniff. 1987. Population dynamics of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Ecological Monographs 57:149-165

Testa, J.W., D.B. Siniff, J.P. Croxall, and H.R. Burton. 1990. A comparison of reproductive parameters among three populations of Weddell seals (*Leptonychotes weddellii*). Journal of Animal Ecology 59:1165-1175.

Testa, J.W., G. Oehlert, D.G. Ainley, J.L. Bengston, D.B. Siniff, R.M. Laws, and D. Rounsevell. 1991. Temporal variability in Antarctic marine ecosystems: periodic fluctuations in the phocid seals. Canadian Journal of Fisheries and Aquatic Science 48:631-639.

Vaupel, J.W., and A.I. Yashin. 1985. Heterogeneity's ruses: some surprising effects of selection on population dynamics. The American Statistician. 39:176-185.

Weimerskirch, H. 1990. The influence of age and experience on breeding performance of the Antarctic fulmar, *Fulmarus glacialoides*. Journal of Animal Ecology 59:867-875.

Weimerskirch, H. 1992. Reproductive effort in long-lived birds: age-specific patterns of condition, reproduction and survival in the wandering albatross. Oikos 64:464-473.

Weimerskirch, H., P. Inchausti, C. Guinet, and C. Barbraud. 2003. Trends in bird and seal populations as indicators of a system shift in the Southern Ocean. Antarctic Science 15:249-256.

White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):120-138.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California, USA.

Wooller, R. D., J. S. Bradley, I. J. Skira, and D. L. Serventy. 1990. Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. Journal of Animal Ecology 59:161-170.

CHAPTER FOUR.

EVALUATION OF REPRODUCTIVE COSTS FOR WEDDELL SEALS IN EREBUS BAY, ANTARCTICA

Introduction

An organism's evolutionary success is determined by its lifetime reproductive output, which in turn depends on its life history strategy. For most species, maximizing individual lifetime reproductive output is not as simple as maximally investing in reproduction – the individual must also ensure its own survival to future reproductive opportunities. Producing and caring for offspring may reduce an individual's longevity, thereby decreasing potential for future offspring. Moreover, investing energy in reproduction may decrease energy available for subsequent reproductive opportunities, thereby directly impacting lifetime reproductive output. Thus, organisms balance current reproduction against future survival and fecundity (Williams 1966). This trade-off is known as reproductive cost and may be a significant factor shaping life history strategy for many species (Roff 1992, Stearns 1992).

Reproductive costs have been documented for several long-lived vertebrates (birds: Reid 1987, Jacobsen et al. 1995, Golet et al. 1998; mammals: Testa 1987, Huber et al. 1991, Reiter and LeBoeuf 1991, Sydeman et al. 1991, Boyd et al. 1995). In contrast, other studies have noted the apparent absence of reproductive costs (Saether and Haagenrud 1983, Festa-Bianchet 1989, Green and Rothstein 1991). However, studies that failed to detect costs either to survival or future reproduction, typically did document costs of some sort, such as lowered offspring quality for females that reproduced in successive years (Green and Rothstein 1991) or decreased resistance to parasites (Festa-Bianchet 1989).

Diverse factors may affect the occurrence and size of reproductive costs. Age has been shown to be important in studies of ungulates (Clutton-Brock 1984) and birds (Viallefont et al. 1995, Tavecchia et al. 2005), as well as pinnipeds. Relative to older females, young female northern fur seals (*Callorhinus ursinus*) had higher levels of reproductive effort (measured as relative mass of pup), which investigators hypothesized would affect future survival and reproduction (Boltnev and York 2001). For Antarctic fur seals (*Arctocephalus gazella*), young females were less likely than older females to reproduce in consecutive years (Lunn et al. 1994).

Other studies have suggested that the occurrence of reproductive costs may depend on previous breeding experience (Weimerskirch 1990, Clutton-Brock et al. 1996, Barbraud and Weimerskirch 2005). Numerous studies have evaluated whether first-time breeders incur greater costs to survival and future reproduction than do experienced breeders. Lesser Snow Geese (*Chen caerulescens caerulescens*) breeding for the first time had lowered nesting probabilities in the following season, an effect which was most severe for birds first breeding at the youngest age (Viallefont et al. 1995).

The age at which reproduction begins may also influence the extent of reproductive costs faced later in life. Increased reproductive costs for individuals that begin reproduction at a young age, relative to those that begin at an older age, have been documented for seabirds (Viallefont et al. 1995) and pinnipeds (Reiter and LeBoeuf 1991, Lunn et al. 1994). However, for bighorn sheep (*Ovis canadensis*) and bison (*Bison*

bison), females that began reproduction early had equal or improved survival and reproductive success later in life relative to those that delayed first reproduction (Festa-Bianchet 1989, Green and Rothstein 1991). The extent to which reproductive costs are affected by age at first reproduction may depend on the level of heterogeneity in individual quality in a population. In cases where female quality varies substantially, those that begin reproduction early may be high-quality females that are less likely to display reproductive costs due to higher intrinsic survivorship and fecundity (Cam et al. 2002). Pistorius et al. (2004) documented a reproductive cost to female southern elephant seals (*Mirounga leonina*) in the form of 5-10% lower survival in the year following reproduction, but found no evidence that this cost varied according to age at first reproduction. The authors proposed a 'mass threshold hypothesis', suggesting that for capital breeders in general, attainment of a threshold mass is the central factor governing the age at which reproduction begins. They hypothesized that once this mass is reached, no further delay or trade-off between current reproduction and survival or future reproduction occurs. This hypothesis may be consistent with the presence of heterogeneity in individual quality, which could likely result in high-quality females (with superior foraging efficiency) attaining the threshold mass at the youngest age.

If mass is a crucial determinant of breeding behavior for capital breeders, then environmental or population conditions that affect mass may play a role in how reproductive costs vary. For some species, reproductive costs may only be present under scenarios of population density or resource scarcity that lower survival rates beyond some threshold ('survival threshold hypothesis') (Festa-Bianchet 1989, Stearns 1992, Tavecchia et al. 2005). For bighorn ewes, reproductive costs were present only during periods of resource scarcity. When resources were abundant, females more easily regained energy invested in reproduction. As a result, they experienced survival and breeding probabilities in the year following reproduction that were comparable to those for females that did not reproduce (Festa-Bianchet et al. 1998). In harsh climates with seasonal fluctuations in resource abundance, reproduction is risky and constitutes a potential for high costs, relative to milder climates (Sand 1996). Therefore, reproductive costs may be more strongly linked to environmental conditions in harsh environments where difficult conditions will occur more frequently. To fully understand how reproductive costs depend on environmental and population conditions, it is essential to study breeding effort under varying levels of resource availability.

Long-term studies are especially valuable to demonstrate how reproductive costs vary with changing ecological circumstances (Festa-Bianchet 1989). The Erebus Bay population of Weddell seals (*Leptonychotes weddellii*) is a model system for learning about costs of reproduction in a long-lived mammal inhabiting a harsh and extremely variable environment. This population of seals, located at approximately 77º South in McMurdo Sound in the Ross Sea region of Antarctica, is the southernmost breeding mammal population in the world and has been the subject of an ongoing mark-resight research program since 1969 (Stirling 1969, Siniff et al. 1977, Testa and Siniff 1987, Cameron and Siniff 2004). Data from this population provide researchers with a unique, long-term dataset for a long-lived marine mammal. Weddell seals are intermittent breeders, and some individuals may breed annually for many consecutive years, while others may remain nonbreeders for several years in between breeding years. Such variation makes the species an excellent subject for learning about life-history decisions and reproductive costs in long-lived animals that are capital breeders.

Contrasting predictions have been made regarding reproductive costs for long-lived species in variable environments. Life-history theory predicts that costs to survival should be strongly selected against in species with a long reproductive lifespan. Reproductive output for long-lived species is determined by the outcomes of numerous breeding attempts throughout life, whereas species with short lifespan may benefit from maximal investment in one reproductive bout. Therefore, surviving to future reproductive opportunities is critical to maximizing lifetime reproductive output for long-lived species (Williams 1966, Goodman 1974, Charlesworth 1980) and individuals should be less prone to trade their own survival for that of their offspring because any reduction in adult survival would greatly lower lifetime reproductive success (‘prudent parent’ reproductive strategy). However, numerous studies of long-lived seabirds in harsh environments have demonstrated that large variations in breeding conditions favor flexibility of reproductive effort (i.e., occasional investment in reproduction at a cost to survival, or ‘flexible-strategy hypothesis’) (Reid 1987, Erikstad et al. 1997, 1998, Jacobsen et al. 1995, Golet et al. 1998). Moreover, for long-lived species that breed only once per year, costs to survival may be more apparent than costs to fecundity because the period of critical survival follows the period of parental investment more closely than the next potential reproductive bout, allowing more time to recover lost reserves and avoid detriment to subsequent reproductive efforts (Daan et al. 1996). Thus, there is a need for research that addresses these contrasting life-history predictions for long-lived species and evaluates the relative magnitude of costs of reproduction to survival and fecundity.

Predictions

In this study, we evaluated both costs to survival and costs to fecundity for female Weddell seals in Erebus Bay, Antarctica. Despite the lower costs to survival generally predicted for long-lived species (the prudent parent hypothesis), the variability of the polar environment may require that seals occasionally invest in reproduction at a cost to survival (the flexible-strategy hypothesis). Therefore, we expected that both types of costs would be apparent. Life history strategy and lifetime reproductive output are also influenced by the manner in which reproductive costs vary during an individual's lifetime. Numerous studies have demonstrated that younger animals conceive, implant, or give birth later in life, and have lower natality rates than do older animals (Sæther and Haagenrud 1983, Lunn et al. 1994). For Weddell seals, we therefore predicted that both survival and fecundity costs would vary with age, with young seals exhibiting larger costs.

Animals breeding for the first time are also thought to experience higher reproductive costs than are experienced breeders, regardless of age (Weimerskirch 1990, Viallefont et al. 1995). However, separating the effects of age and breeding experience may be difficult in practice. Many investigators lack detailed information about individual reproductive histories or age of animals in their study population (Barbraud and Weimerskirch 2005), while others may not have adequate sample sizes or variation in their datasets to examine animals of equal age with varying levels of experience, or animals of various ages with equivalent experience. Our dataset included seals with and without breeding experience for every age from 4 to 14, and we were thus able to separately investigate the effects of age and breeding experience. Several studies have found higher reproductive costs for inexperienced breeders while controlling for age (Lunn et al. 1994, Viallefont et al. 1995), and we therefore predicted higher reproductive costs for inexperienced seals in our study.

In accordance with Pistorius et al.'s (2004) mass threshold hypothesis, we predicted that age of first reproduction would not affect reproductive costs. However, based on variation in age at first reproduction for Weddell seals reported in a previous analysis (Hadley et al. 2006), we expected that substantial heterogeneity in individual quality was present in this population. Therefore, we also proposed an alternative prediction that if reproductive costs did vary with age at first reproduction, highest costs would be experienced by those individuals that delayed primiparity. We hypothesized that such individuals were of lower quality and thus expected them to suffer higher costs of reproduction relative to high-quality seals of the same age that had begun reproduction at the mean age or even earlier (Cam et al. 2002).

Based on the survival threshold hypothesis supported by studies of bighorn sheep (Festa-Bianchet et al. 1998), we expected reproductive costs to both survival and fecundity to vary annually due to changing environmental conditions The sensitivity of marine ecosystems, and especially upper trophic level predators, to climate change has been noted in numerous recent studies (Beauplet et al. 2005, McMahon and Burton 2005). During El-Niño Southern Oscillation (ENSO) events, lower pressure is evident in the Southern Ocean, leading to cooler sea surface temperatures (SSTs) and larger sea-ice extent (Kwok and Comiso 2002). In the Ross Sea, phytoplankton blooms occurred later and were less extensive following winters with high maximum sea-ice extent (Arrigo and vanDijken 2004). Summer sea-ice extent determines the amount of open water available for phytoplankton blooms and therefore may determine foraging success of Weddell seals during the summer. Because of this relationship with marine primary productivity, annual measures of ENSO strength, SST, or seasonal measures of sea-ice extent in the Ross Sea region may explain annual variability in the magnitude of reproductive costs experienced by females Weddell seals in Erebus Bay. We expected that heavy sea-ice years (high ENSO index, low SST, and high maximum (winter) or minimum (summer) sea-ice extent) would lead to decreased foraging success for female Weddell seals and would therefore be correlated with increased reproductive costs. Based on the principles of the prudent parent hypothesis (that long-lived species should incur costs to reproduction before they incur costs to their own survival), we predicted that climate and sea-ice fluctuations would induce greater variability in fecundity costs than in survival costs.

Methods

Study Area and Population

The Erebus Bay study area is located at the southern end of McMurdo Sound, Antarctica (-77.62º to -77.87º South, 166.3º to 167.0º East; see Cameron and Siniff 2004 for description and map of study area). Eight to 14 Weddell seal breeding colonies are located within this study area (Stirling 1969). Colonies are associated with tidal cracks that form in the sea ice each austral spring, creating areas where adult female seals haul out to have pups. Most of these cracks form along the coast of Ross Island or smaller offshore islands. Colony size ranges from a few animals up to 250 animals and varies among years. Marking and resighting of this population has occurred for 35 years. Over this period, both the proportion of the population that is marked, and the proportion of marked animals that are of known age have gradually increased (Cameron and Siniff 2004). Currently, approximately 80% of the seals in this population are marked and over 80% of marked individuals are of known age. Each year, 300 - 600 pups are born at colonies in Erebus Bay, and most females surviving to reproductive age return to breed in Erebus Bay (Cameron and Siniff 2004). More detailed information about Weddell seal natural history and the Erebus Bay study area can be found in Stirling (1969), Siniff et al. (1977), Testa and Siniff (1987), and Cameron and Siniff (2004).

Data Collection

Each year from 1969 until the present, Weddell seal pups born within the Erebus Bay study area have been individually marked with plastic livestock tags attached to the inner inter-digital webbing of each rear flipper. In addition, any seal with a broken or missing tag was retagged and untagged adults were tagged opportunistically. The majority of the tagging effort occurred from approximately October 15 to November 15 each year, during the peak of parturition. Beginning in early November, six to eight resighting surveys of the study area were carried out, usually separated by intervals of three to five days. Every individual that was sighted (marked or unmarked) was recorded. For mother-pup pairs, the presence and tag number of a relative (mother or pup) was also recorded. These resighting records along with all miscellaneous sighting or handling events were recorded in a database maintained in Microsoft® Access format and records were checked by a customized error checking program (Cameron unpublished) before being added to the permanent database.

Annual climate and sea-ice covariates were obtained online through various resources. The annual ENSO value was an estimate of ENSO strength obtained from Golden Gate Weather Services (http://ggweather.com/enso/years.htm). Data from various sources (Western Regional Climate Center, National Ocean and Atmospheric Administration (NOAA) Climate Diagnostics Center, and NOAA Climate Prediction Center) were used to derive the ENSO score, which represented a consensus on the strength of El Niño or La Niña events each year. Monthly mean SSTs for 110 locations covering the region from 156° to 174° East and 60° to 80° South were obtained from NOAA (http://iridl.ldeo.columbia.edu/). The mean of these values was calculated for each year from 1984 to 2003, generating annual mean SST for the Eastern McMurdo Sound region. Monthly SIE for the Ross Sea Region was provided by the National Snow and Ice Data Center (http://nsidc.org) (Comiso 1990), and monthly values for September (sepSIE) and February (febSIE) were used in models to represent winter and summer (roughly maximum and minimum) sea-ice extent for each year from 1984-2003.

Data Analysis

Seals included in this study were females tagged as pups in the Erebus Bay study area since 1979 and were thus of known age. Based on subsequent observations made from 1979 through 2004, we built encounter histories for all known-age females that were known to have begun reproduction (sighted with a pup) by 2004. To reduce the complexity of our analysis and eliminate the necessity for modeling age-specific juvenile survival rates, we included observations of seals only after first reproduction. The minimum breeding age for seals in our dataset was four. Because a seal born in 1980 began reproduction in 1984, the first year included in the encounter histories was 1984, and encounter histories ended in 2004. Seals were partitioned into three groups based on age at first reproduction. Estimated mean age at first reproduction for female Weddell seals was 7.6 (Hadley et al. 2006), thus seals first breeding at ages 6 – 8 were considered 'average breeders', while 'early breeders' were those that first reproduced at ages 4 – 5 and 'late breeders' at ages 9 – 14.

Multi-state modeling (Arnason 1972, 1973; Hestbeck et al. 1991; Brownie et al. 1993) is a relatively recent extension of basic mark-resight modeling that holds great potential for answering questions of interest to evolutionary ecologists (Nichols and Kendall 1995). Multi-state modeling allows investigators to account for variation in detection probability associated with breeding state and permits the estimation of survival and breeding probabilities specific to yearly breeding state. Here, we used multi-state mark-resight models to examine 1) differences in apparent survival (hereafter, survival) for adult female seals in breeding (B) and nonbreeding (N) states and 2) variation in transition rates between breeding and nonbreeding states for adult female seals. We required that a seal be seen with a pup more than once during the breeding season in order to be classified as a breeder (state B) for that year. For convenience and consistency with other literature, we used the term breeder to denote that an individual produced a pup, and thus, as used here, the term does not simply indicate that the seal engaged in breeding activity. A seal was classified as nonbreeder (state N) for any year in which she was observed with a pup only once or not at all. This was done to avoid falsely conferring breeding status to a seal with an unrelated pup lying nearby during a single survey. The associated risk of using this criterion was misclassifying a breeder if she was only seen once with her pup (i.e., her pup died early in life). Based on females in our dataset that we considered "known breeders" (nursing or lying in proximity to newborn pups), we calculated ~1% were seen only once with a pup and therefore would have been misclassified.

To evaluate our predictions about reproductive costs, we developed a set of *a priori* models that included three types of parameters: survival (ϕ), sighting (p), and transition (ψ) probabilities (Appendices A and B). Transition probabilities were conditioned on survival and thus defined as follows: ψ^{bb} represented the probability of a breeder in year t becoming a breeder again in year t+1, given that the seal survived to year t+1, and ψ^{nb} represented the probability of a nonbreeder in year t becoming a breeder in year t+1, assuming survival to year t+1. Presence of costs to survival would be indicated by lowered breeder versus nonbreeder survival rate estimates ($\hat{\phi}^{b} < \hat{\phi}^{n}$), and presence of costs to fecundity would be suggested by lowered breeding probability estimates for breeders in the subsequent year relative to nonbreeders ($\hat{\psi}^{bb} < \hat{\psi}^{nb}$). In both cases we estimated immediate costs of reproduction in the form of reductions to survival or breeding probability for the year following reproduction. These parameters (ϕ^{r}, p^{r}, and ψ^{rs}, where r is breeding state at time t and s is breeding state at time t+1) were modeled with various covariates to represent our hypotheses about survival and fecundity costs (Appendices A and B).

To determine the combination of covariates that best explained variation in ϕ^r, p^r, and ψ^{rs}, we fit a series of effects to each parameter sequentially while constraints on remaining parameters were held constant (Appendices A and B). This process began with modeling various effects on p while a relatively complex structure (breeding state, group, and year effects with interactions) was applied to ϕ and ψ. Models of p included five possible combinations of breeding state, age, and year effects, and a quadratic effect of age (based on Cameron and Siniff 2004). Once the most appropriate structure for p was selected (in this case, only the effect of breeding state), we repeated the process for ϕ using 1) the selected structure for p determined in the process above, and 2) the relatively complex structure (breeding state, group, and year effects with interactions) for ψ. Finally, various models of ψ were evaluated using the structures for p and ϕ selected in previous steps (Appendix A). To avoid bias resulting from the order in which we modeled ϕ and ψ, we conducted a second model selection process where p was modeled first, followed by ψ and finally ϕ (Appendix B). Results from these two separate processes were combined into one table of top model results (Table 4.1).

Table 4.1. Model selection results for models representing hypotheses about reproductive costs to survival and fecundity of female Weddell seals in Erebus Bay, Antarctica. Results are presented for all models < 10 QAIC$_c$ units from top-ranked model after combining results from two model suites (Appendices A and B). Model parameters are state-dependent survival (ϕ^r), sighting (p^r), and transition (ψ^{rs}) probabilities where r and s are breeding states at times t and t+1. Covariates are indicated with model subscripts and include a (age), be (breeding experience; modeled by constraining survival and breeding probabilities following first breeding to differ from all subsequent breeding events), g (group; determined by age at first reproduction: 4-5, 6-8, or 9-14), and t (year; representing annual variation). Annual environmental covariates included ENSO (El-Niño Southern Oscillation score), SST (sea-surface temperature), sepSIE and febSIE (winter and summer sea-ice extent). Results from model selection are included: k (number of parameters), Dev (model deviance), QAIC$_c$, w_i ("weight of evidence" in favor of each model i), and ΔQAIC$_c$ (difference in QAIC$_c$ value from top model).

Model	k	Dev	QAIC$_c$	w_i	ΔQAIC$_c$
$\phi^r_t, p^r, \psi^{rs}_{be,t}$	47	2605.27	2700.75	0.47	0.00
$\phi^r_t, p^r, \psi^{rs}_{g,be,t}$	49	2603.15	2702.76	0.17	2.01
$\phi^r_{be,t}, p^r, \psi^{rs}_{be,t}$	48	2605.23	2702.77	0.17	2.02
$\phi^r_{g,t}, p^r, \psi^{rs}_{be,t}$	49	2604.53	2704.14	0.09	3.39
$\phi^r_t, p^r, \psi^{rs}_{g*,be,t}$	51	2602.21	2705.95	0.04	5.21
$\phi^r_{g.be.t}, p^r, \psi^{rs}_{be,t}$	50	2604.51	2706.18	0.03	5.43
$\phi^r_{g*,t}, p^r, \psi^{rs}_{be,t}$	51	2604.16	2707.90	0.01	7.15
$\phi^r_{a,SST}, p^r, \psi^{rs}_{be,t}$	52	2650.40	2708.97	0.01	8.22
$\phi^r_{SST}, p^r, \psi^{rs}_{be,t}$	28	2652.57	2709.10	0.01	8.36
$\phi^r_{g*,be,t}, p^r, \psi^{rs}_{be,t}$	52	2604.13	2709.94	0.00	9.19

* indicates an interaction between designated variable and breeding state.

Our specific predictions regarding reproductive costs to survival and fecundity were evaluated with models that used various combinations of breeding state, age, age at first reproduction, breeding experience, and year to explain variation in ϕ and ψ (Appendix A). In general, we expected to estimate higher ϕ and ψ for nonbreeders than for breeders, supporting our prediction of reproductive costs to both survival and fecundity. Support for our prediction regarding the influence of breeding experience was evaluated by examining models that included the effect of breeding experience, thus partitioning seals into three groups: first-time breeders, experienced breeders, and nonbreeders. We predicted larger differences between breeder and nonbreeder ϕ and ψ for inexperienced seals.

Average age of marked animals in our dataset increased throughout the study as a result of our restriction to using known-age seals. In order to know age, seals must be marked as pups and in the early years of the study, the only known-age seals had been marked relatively recently and were thus young in age. As these marked animals have aged, the mean age of seals in our sample increased with time. Thus, we evaluated models that included an interactive effect of age and year but did not consider models with additive effects of age and year because the two effects were strongly correlated. We did evaluate models that combined age effects with annual climate and sea-ice covariates in an attempt to separate the effects of age and environmental variation. Additionally, if a top-ranked model included a year effect, we replaced the year effect with a set of annual climate and sea-ice covariates (ENSO, SST, sepSIE, febSIE) in an attempt to improve model fit and learn the mechanism underlying the observed annual variation.

Multi-state models were constructed and estimates of model parameters generated using program MARK (White and Burnham 1999). In order to compare ψ^{bb} with ψ^{nb} and be able to constrain both of these parameters in our models, we changed the parameter definition setting in program MARK to allow direct estimation of ψ^{bb} and ψ^{nb}, with ψ^{bn} and ψ^{nn} obtained by subtraction. Akaike's Information Criterion (Akaike

1973), corrected for small sample bias (AIC_c, Hurvich and Tsai 1989), was used to evaluate the relative support in the data for models in our *a priori* set (Burnham and Anderson 1998). We used the AIC_c value associated with each model to obtain the difference in AIC_c (ΔAIC_c) between the model in question and the model with the minimum AIC_c. Models with ΔAIC_c less than 2 are considered to have substantial support in the data, those with values of ΔAIC_c between 4 and 7 have weak support, and those with values greater than 10 have essentially no support in the data (Burnham and Anderson 1998). We also used normalized Akaike weights (w_i, for each model *i*) as an index of relative plausibility of each model (Burnham and Anderson 1998). To determine how well our most general model fit the data, we implemented the recently-developed goodness-of-fit (GOF) test for multi-state models available in Program U-CARE (Choquet et al. 2003). The sum of multi-site tests was performed for each of our three groups (early, average, and late breeders) independently and the highest (most conservative) estimated overdispersion coefficient ($\hat{c}$) was used to adjust model selection results in Program MARK and convert AIC_c values to quasi-AIC_c ($QAIC_c$) values (Burnham and Anderson 1998).

For our study population, it is known that tag loss occurs at a low rate (probability that a female seal retained at least one of two tags for one year ranged from 0.977 to 0.998; Cameron and Siniff 2004). Therefore, we used the tag-retention rate ($\hat{\theta}$) estimated for this population by Cameron and Siniff (2004) to adjust $\hat{\phi}$ ($\hat{\phi}_{adj} = \hat{\phi} / \hat{\theta}$; Arnason and Mills 1981). This was necessary because if some animals lost both tags, $\hat{\phi}$ represented the product of the underlying survival rate and the tag retention rate (Nichols et al. 1992). Transition probabilities did not need to be corrected for tag loss as they are conditional on survival (Williams et al. 2002). That is, they are the estimated rates of movement from one state to another, assuming that the animal had survived to the current year and was available on the study area to potentially make the transition.

Results

Goodness of Fit and Model Selection

Between 1979 and 2004, 5,051 females were tagged as pups and therefore of known age. Of these, 607 returned to breed at least once between 1984 and 2004 and were included in our analysis of reproductive costs. Forty females were considered early breeders (age four or five), 462 were average breeders (first breeding at age six, seven, or eight), and 105 were late breeders (first breeding at age nine or older). State-specific sighting probabilities were estimated using the top-ranked model (Table 4.1) and were high for breeders ($\hat{p} > 0.99$, SE < 0.01) and nonbreeders ($\hat{p} = 0.76$, SE = 0.01). We were able to estimate all parameters of interest for a 17-year time period (1986-2003) (Table 4.2). Sample sizes for the first two occasions (1984, 1985) were too low for accurate estimation, and sighting and survival probabilities for the final interval (2003-2004) were not individually identifiable.

Results of the GOF test for our general model, applied to each of the three groups independently, provided evidence of overdispersion for the average and late breeding groups (average breeders: $\hat{c} = 2.63$, $\chi^2 = 242.03$, df = 92, $P < 0.01$; late breeders: $\hat{c} = 1.22$, $\chi^2 = 47.76$, df = 39, $P < 0.01$), and underdispersion for early breeders ($\hat{c} = 0.73$, $\chi^2 =$

21.87, df = 30, $P = 0.86$). To conservatively adjust for overdispersion and avoid over-fitting our models, we applied the highest ĉ value (2.63) to inflate variances on estimated parameters and to adjust AIC_c values prior to model selection and hypothesis evaluation.

Table 4.2. Estimates of state-specific apparent survival (ϕ^b and ϕ^n) and breeding probabilities (ψ^{bb} and ψ^{nb}) from the top-ranked model of reproductive costs for female Weddell seals in Erebus Bay, Antarctica (Table 4.1). Sighting probability was estimated as constant among years ($\hat{p}^b > 0.99$ [$\hat{SE} < 0.01$] and $\hat{p}^n = 0.76$ [$\hat{SE} = 0.01$]). Standard errors associated with each estimate are in parentheses, except for means where standard deviations are presented in parentheses. Estimates of survival probability and standard errors were corrected for tag loss. Breeding probabilities varied with breeding experience and estimates are presented for first-time and experienced breeders.

Year	$\hat{\phi}^b$	$\hat{\phi}^n$	$\hat{\psi}^{bb}_{first-time}$	$\hat{\psi}^{bb}_{\text{experienced}}$	$\hat{\psi}^{nb}$
1986	0.84 (0.17)	0.90 (0.12)	0.35 (0.21)	0.57 (0.23)	0.56 (0.23)
1987	0.88 (0.08)	0.93 (0.06)	0.38 (0.11)	0.60 (0.12)	0.59 (0.12)
1988	0.87 (0.06)	0.92 (0.04)	0.44 (0.08)	0.65 (0.07)	0.64 (0.08)
1989	0.96 (0.04)	0.98 (0.02)	0.57 (0.08)	0.76 (0.06)	0.75 (0.06)
1990	0.91 (0.03)	0.95 (0.02)	0.51 (0.06)	0.72 (0.05)	0.71 (0.05)
1991	0.98 (0.02)	0.99 (0.01)	0.45 (0.05)	0.66 (0.05)	0.65 (0.05)
1992	0.91 (0.03)	0.94 (0.02)	0.59 (0.06)	0.78 (0.04)	0.77 (0.04)
1993	0.90 (0.03)	0.94 (0.02)	0.43 (0.05)	0.65 (0.04)	0.64 (0.04)
1994	0.92 (0.02)	0.95 (0.02)	0.34 (0.04)	0.56 (0.04)	0.54 (0.04)
1995	0.88 (0.03)	0.92 (0.02)	0.34 (0.04)	0.56 (0.04)	0.55 (0.04)
1996	0.90 (0.02)	0.94 (0.02)	0.59 (0.05)	0.78 (0.03)	0.77 (0.03)
1997	0.94 (0.02)	0.97 (0.01)	0.59 (0.04)	0.78 (0.03)	0.77 (0.03)
1998	0.89 (0.02)	0.94 (0.02)	0.52 (0.04)	0.72 (0.03)	0.71 (0.03)
1999	0.92 (0.02)	0.95 (0.01)	0.57 (0.04)	0.76 (0.03)	0.75 (0.03)
2000	0.93 (0.02)	0.96 (0.01)	0.35 (0.03)	0.57 (0.03)	0.55 (0.03)
2001	0.88 (0.02)	0.92 (0.02)	0.47 (0.04)	0.68 (0.03)	0.67 (0.03)
2002	0.92 (0.02)	0.95 (0.02)	0.28 (0.03)	0.49 (0.03)	0.47 (0.03)
Mean	0.91 (0.03)	0.94 (0.02)	0.46 (0.04)	0.66 (0.05)	0.65 (0.05)

Of the five different parameterizations for sighting probability that were considered, the model in which p varied with breeding state was most strongly supported by the data (Appendix A). No other model was within 1.75 QAIC_c units, thus we chose to apply only breeding state effects to p for all subsequent modeling. Twenty-seven different combinations of covariates were used to model both ϕ and ψ, and when results from both model suites were combined, the data most strongly supported a model that included the effects of breeding state and year on ϕ and effects of breeding state, breeding experience, and year on ψ (Table 4.1). This model (w_i = 0.47, Table 4.1) was ranked highest in both the 'survival-first' and 'fecundity-first' model suites (Appendices A and B), and hence was used to generate most parameter estimates presented in this paper. However, we presented results from other models when they were < 10 QAIC$_c$ units from the top model and were the only models addressing a specific prediction.

Evidence for Reproductive Costs to Survival

The results strongly supported our prediction that breeding imposes an immediate cost to survival probability. In the top-ranked model, the coefficient estimating the effect of being a breeder on ϕ was negative and the confidence interval did not include zero ($\hat{\beta}_{state}$ = -0.48, SE = 0.15 , CI = -0.79 to -0.19). For breeding females, mean annual survival probability (0.91, SD = 0.03, n=17) was lower than mean annual survival probability for nonbreeders (0.94, SD = 0.02, n=17) (Table 4.2). This important result was further supported by the fact that, in all models within 7 QAIC$_c$ units from the top model, the effect of being a breeder on $\hat{\phi}$ was negative and the confidence interval did not include zero.

Our prediction that breeding experience would influence costs to survival was moderately supported by the 3rd-ranked model in our set (w_i = 0.17). The point estimate for the effect of first-time breeding was negative ($\hat{\beta}_{first-time}$ = -0.06), suggesting a higher cost of reproduction to first-time breeders, but the confidence interval included zero (CI =

-0.39 to 0.28) and thus, strong inference could not be drawn from this result. Our prediction that age of first reproduction would not strongly influence reproductive costs to survival was supported by the absence of an interaction between age at first reproduction and breeding state in models < 7 $\mathrm{QAIC_c}$ from the top-ranked model. We did, however, find weak support for a model suggesting that costs to survival varied with age and first reproduction (7th-ranked mode, $w_i = 0.01$), and that early breeders showed the largest reduction in survival probability (5.3%) associated with reproduction.

We found that survival probabilities did vary substantially by year, but our prediction of annual variation in reproductive costs to survival was not supported, because the amount of variation was the same for breeders and nonbreeders (the top-ranked model forced parallel trajectories for these probabilities over time). For breeding females, annual survival probability estimates ($\hat{\phi}_i$, for each year *i* from 1986 - 2002) ranged from 0.84 (SE=0.17) to 0.98 (SE=0.02) and in nonbreeders $\hat{\phi}_i$ ranged from 0.90 (SE=0.12) to 0.98 (SE=0.02) (Table 4.2). When environmental covariates were substituted for year effects in the top-ranked model, there was weak evidence that sepSIE explained some of the annual variation in survival probabilities. The 4th- and 5th-ranked models ($w_i = 0.04$ and $w_i = 0.01$, respectively) in the environmental effects suite (Table 4.3) suggested that years with heavy winter sea-ice were followed by years of higher survival. In the 5th-ranked model, the interaction between sepSIE and breeding state suggested reduced reproductive costs to survival following years with high winter sea-ice extent. In this model, following the year with highest sepSIE (2003), breeders and nonbreeders had similar survival probabilities ($\hat{\phi}^b = 0.94$ [SE = 0.01], $\hat{\phi}^n = 0.95$ [SE =

0.01]). When sepSIE was at its lowest (2000), $\hat{\phi}^b$ was 0.79 (SE = 0.03) and $\hat{\phi}^n$ was 0.84 (SE = 0.04), suggesting a cost of reproduction to survival under these conditions.

Table 4.3. Model selection results for models representing hypotheses about influence of climate and sea-ice covariates on reproductive costs to survival and fecundity of female Weddell seals in Erebus Bay, Antarctica. Results are presented for all models < 10 QAIC$_c$ units from top-ranked model. Covariates are indicated with model subscripts and include ENSO (El-Niño Southern Oscillation score), SST (sea-surface temperature), sepSIE and febSIE (winter and summer sea-ice extent). Results from model selection are included: *k* (number of parameters), Dev (model deviance), QAIC$_c$, w_i ("weight of evidence" in favor of each model *i*), and ΔQAIC$_c$ (difference in QAIC$_c$ value from top model).

Model	*k*	Dev	QAIC$_c$	w_i	ΔQAIC$_c$
$\phi^r_t, p^r, \psi^{rs}_{be,t}$	47	2605.27	2700.75	0.39	0.00
$\phi^r_t, p^r, \psi^{rs}_{be,febSIE}$	28	2644.45	2700.98	0.34	0.24
$\phi^r_t, p^r, \psi^{rs}_{be,febSIE*}$	29	2643.57	2702.13	0.19	1.39
$\phi^r_{sepSIE}, p^r, \psi^{rs}_{be,t}$	28	2648.71	2705.24	0.04	4.50
$\phi^r_{sepSIE*}, p^r, \psi^{rs}_{be,t}$	29	2648.69	2707.26	0.02	6.51
$\phi^r_t, p^r, \psi^{rs}_{be,sepSIE*}$	29	2650.47	2709.04	0.01	8.29
$\phi^r_{SST}, p^r, \psi^{rs}_{be,t}$	28	2652.57	2709.10	0.01	8.36
$\phi^r_t, p^r, \psi^{rs}_{be,sepSIE}$	28	2653.14	2709.67	0.00	8.92

* indicates an interaction between designated variable and breeding state.

Evidence for Reproductive Costs to Fecundity

Two of our predictions regarding costs to fecundity were strongly supported by results from the overall top-ranked model, which provided evidence that costs to fecundity were present and that they varied with breeding experience. In this model, mean annual probability of breeding ($\bar{\hat{\psi}}$) for surviving first-time breeders from the previous year ($\bar{\hat{\psi}}^{bb}$=0.46, SD = 0.10, *n*=17) was much lower than for experienced breeders ($\bar{\hat{\psi}}^{bb}$=0.66, SD = 0.09, *n*=17). Experienced breeders that had a pup in the previous year had breeding probabilities that were comparable to those of seals that did not produce a pup the previous year ($\overline{\hat{\psi}}^{nb}=0.65$, SD = 0.10, n=17) (Table 4.2). These results provided evidence that there was an immediate cost of reproduction to the subsequent year's fecundity, but that this cost was only observed for first-time breeders.

As with survival costs, our prediction of no influence of age at first reproduction on fecundity costs was supported by the absence of this covariate in the most-supported model. However, again there was moderate support for the influence of age at first reproduction in a lower-ranked model (w_i = 0.03, Table 4.1). According to results from this model, seals that were late breeders (began reproduction at age 9 or older) experienced a 39.1% reduction in breeding probability after first-time breeding, relative to average and early breeders, whose breeding probabilities lowered by 28.8% and 20.3%, respectively. These costs were reduced for experienced breeders in all three categories: late breeders still had 7.8% lower mean annual breeding probabilities following reproduction, but average breeders displayed no cost, and early breeders were in fact more likely to breed in subsequent years than to abstain. These results offered weak support for our prediction that late breeders experience higher reproductive costs due to their inferiority relative to other individuals in the population, but confidence intervals on the effect sizes for age at first reproduction in this model included zero and thus, strong inference could not be drawn from this result.

Contrary to our prediction, reproductive costs to fecundity did not appear to vary substantially year to year. We detected annual variation in breeding probabilities (Table 4.2) and all models < 10 QAIC_c units from the top model included an effect of year on breeding probabilities (Table 4.1), but the amount of annual variation in breeding probabilities was not different for breeders and nonbreeders. After substituting environmental covariates for year effects in the top-ranked model, a model indicating that summer sea-ice extent influenced breeding probabilities was nearly as well supported (w_i = 0.34 versus w_i = 0.39 for top-ranked model, Table 4.3). Breeding probabilities increased following years with low febSIE ($\hat{\beta}_{febSIE}$ = -0.25, SE = 0.04, CI = -0.33 to -0.16). There was also moderate support (w_i = 0.19) for the influence of febSIE on the magnitude of reproductive costs. Contrary to our prediction, reproductive costs to fecundity did not increase following years with high summer sea-ice conditions. Breeding probabilities for both breeders and nonbreeders were negatively affected by high summer sea-ice extent, but surprisingly, breeders were less affected than nonbreeders. However, the coefficient for the interaction term describing this relationship was estimated with low precision ($\hat{\beta}_{st*febSIE}$ = 0.14, SE = 0.09, CI = -0.04 to 0.32), and thus our ability for inference from this result is limited.

Discussion

Factors that influence the presence and/or magnitude of reproductive costs are of substantial interest in life-history theory and population ecology (Roff 1992, Stearns 1992). Investigating reproductive costs for long-lived species that reproduce intermittently allows the evaluation of life-history predictions regarding relative investment in survival versus reproduction (i.e., minimizing cost to survival to allow for many reproductive opportunities [Williams 1966, Goodman 1974, Charlesworth 1980] versus occasional investment in reproduction at a cost to survival [Reid 1987, Erikstad et al. 1997, 1998, Jacobsen et al. 1995, Golet et al. 1998]). The study of reproductive costs in long-lived species also provides the opportunity to determine the effect of varying ages of first reproduction on future survival and reproductive success.

Our results for female Weddell seals strongly indicate the presence of reproductive costs to both survival and fecundity. Although survival probabilities varied annually, nonbreeder survival was consistently approximately 3% higher than breeder survival (Table 4.2). This seemingly small difference in survival probability translates into a substantial difference in mean life span. The extreme case of a female that produced a pup every year would yield a mean lifespan of approximately 10.6 years (Mean Life Span = $-1/\ln(\hat{\phi})$, where $\hat{\phi} = 0.91$). In contrast, a female that was a nonbreeder every year had a mean survival probability of 0.94, and as a result, a longer mean life span of approximately 16.2 years. The reproductive cost to survival that was experienced by female Weddell seals may have meaningful consequences for life span, and as a result, lifetime reproductive output. Weddell seals evidently follow the ‘flexible-strategy’ hypothesis (Reid 1987, Erikstad et al. 1997, 1998), investing in reproduction at an ongoing cost to their own survival, rather than minimizing survival costs and restricting breeding effort, as is generally predicted by life-history theory for long-lived animals (Charlesworth 1980). This may be partly attributed to the fact that they are capital breeders. Successfully producing a pup requires transferring a large proportion of body reserves to the pup while feeding only opportunistically during the lactation period, which typically lasts 6-7 weeks (Hill 1987, Testa et al. 1989). The extreme reduction in body mass resulting from fasting may be a primary reason for lowered survival probability following reproduction.

Reproductive costs to a Weddell seal female's fecundity were only apparent for first-time breeders. Testa (1987) found a cost of pupping for Weddell seals equivalent to a 0.05 drop in the probability of pupping the following year but found that this cost was not evident for females over 7 years old. Because many seals breeding before age 7 are first-time breeders, our results lend support to Testa's (1987) finding and additionally suggest a mechanism explaining the absence of costs beyond age 7. Our finding of fecundity costs only for first-time breeders again contrasts with the 'prudent parent' strategy expected for long-lived species. Rather than minimizing reproductive costs to survival and experiencing costs chiefly to future fecundity, Weddell seals seem to endure ongoing costs of reproduction to their own survival, but only suffer reduced fecundity after first reproduction. Once a seal was experienced, her annual breeding probability was similar whether or not she produced a pup the previous year. The fact that first-time breeders are 20-40% less likely to breed the subsequent year than experienced breeders (Table 4.2) may in part be attributed to breeding strategy, as with survival costs. As capital breeders, Weddell seal females must rely on fat reserves to produce milk for their pups. First-time breeders are primarily young, relatively small seals, and thus the reduction in body mass following successful weaning of a pup likely takes a larger toll than for larger, experienced seals. As a result, first-time breeders may be much less likely to regain their own body mass and additionally store enough energy to produce a pup again in the following year. Similar cases of inexperienced individuals requiring a longer 'recovery time' following a breeding season have been found for numerous species (Wooller and Coulson 1977, Ollason and Dunnet 1988, Weimerskirch 1990, Viallefont et al. 1995). For Antarctic fur seals (Lunn et al. 1994), which are income breeders, the greater failure of primiparous females to pup the next season was attributed to their inability to regain body condition prior to implantation of a fertilized egg.

In addition to breeding experience, age at first reproduction may influence reproductive costs to fecundity for Weddell seals. Although evidence for this effect came from a less-supported model (Table 4.1) and results were imprecise, reproduction did result in a cost for experienced breeders if they were late breeders (first reproduction after age 8). This cost was non-existent for average breeders, and reproduction was actually associated with *higher* breeding probability estimates the subsequent year for early breeders (first reproduction at age 4 or 5). A previous analysis revealed that age at first reproduction varied from four to 14 and suggested that individual heterogeneity exists among females in this population (Hadley et al. 2006). Beginning reproduction at age four or five may only be possible for high-quality females that are good reproductive performers and don’t experience reduced breeding probabilities as a result of reproduction. In contrast, females that do not have a first pup until age nine or older may be poor reproductive performers for whom reproduction is more costly (Cam et al. 2002).

An alternate explanation for apparent delayed reproduction is that females breeding for the first time in our study area have previously reproduced outside the study area. However, female Weddell seals are strongly philopatric (Stirling 1969, 1974; Croxall and Hiby 1983; Cameron and Siniff 2004) and seals born in Erebus Bay generally return there to breed. Although survey effort outside the Erebus Bay study area has been variable over the duration of the study, it has increased in recent years. During extensive surveys from 1997 to 2000, between 368 and 567 adult females were sighted each year within 100 km of Erebus Bay (see Cameron and Siniff (2004), Fig. 1 for survey locations). Of the females sighted in each of these four years, an average of 6.5% were born in Erebus Bay study area, and an average of only 0.4% were born in Erebus Bay *and* sighted with a pup during surveys outside Erebus Bay (M.F. Cameron, personal communication). Given what we know of female movement patterns, we expect that the occurrence of reproduction outside the study area has extremely minimal impact on the estimates of survival probability, breeding probability, and reproductive costs presented here.

The annual variation in reproductive costs that we expected to observe was not evident from results of our top-ranked model. Survival and breeding probabilities varied annually in a similar manner for breeders and nonbreeders, hence the magnitude of reproductive costs was relatively consistent across time for the duration of our study (1986-2002). Models that included unique coefficients for the individual effects of each year on each breeding state required the addition of 20 parameters, and thus the amount of year-to-year variation in reproductive costs would need to be substantial in order to support this level of model complexity. Representing individual years with the associated annual climate and sea-ice covariates required fewer parameters and thus allowed us to build simpler models that evaluated our prediction of annual variation in reproductive costs. Further, these models allowed us to assess the relative strength of correlations between reproductive costs and ENSO, SST, and SIE. We found evidence that sea-ice conditions may determine magnitude of reproductive costs to both survival and fecundity. Although not as well supported as the model with unique coefficients for each year, these models revealed an interesting relationship between the amount of sea ice in the Ross Sea sector of the Southern Ocean and the magnitude of reproductive costs for Weddell seals, and supported our prediction that fecundity costs would be more tied to environmental variation than survival costs. We found strong evidence that breeding probabilities depended on extent of sea-ice the previous summer, supporting our prediction that heavy sea-ice conditions in summer would lead to decreased foraging success. A probable explanation is the reduced amount of open water available for phytoplankton blooms and the consequent reduction in maternal foraging success. In support of this explanation, Proffitt et al. (unpublished) demonstrated that foraging success of pregnant Weddell seals (reflected by weaning mass in the following year) increased during summers characterized by reduced sea-ice cover. In contrast, we found weak evidence that survival probability was influenced by winter, rather than summer, sea-ice conditions and this effect was in the opposite direction of the effect on breeding probability. Survival probability increased and reproductive costs to survival were reduced in years following winters of high sea-ice extent. High winter sea-ice extent leads to a higher abundance of ice algae which utilize the underside of the ice as a substrate (Ross and Quetin 1991). When the ice breaks up in summer, the ice algae are released into the water column and form the basis of an overall increase in marine productivity (Brierly and Thomas 2002). This sea-ice algal production plays a lesser role than open-water phytoplankton production (Lizotte 2001), but may explain the weak positive effect on survival probability that we observed.

Reproductive costs have been measured in various ways. Reznick (1985) argues that unambiguously detecting a cost of reproduction requires genetic correlation or experimental manipulations to demonstrate a genetic basis for the inverse relationship or trade-off between two life history traits. Our study utilized phenotypic correlation (statistical association between life history traits) and thus may not have accurately reflected genetic costs of reproduction due to naturally occurring variation in reproductive effort and the possibility that environmental heterogeneity in the study system will lead to variation in life history traits unrelated to reproductive effort. However, phenotypic correlation is still valuable in situations where experimental manipulation of some aspect of reproduction or genetic correlation of reproductive effort and cost are not possible. Phenotypic correlations allow assessment of the ecological costs of reproduction (reproductive costs that take into account interaction with the environment instead of solely evolutionary tradeoffs) as well as the consequences of these costs for population dynamics. Although a genetic basis for reproductive costs has not been established, studies such as ours may still estimate the overall consequences of current reproduction on survival and future reproduction (Reznick 1992, Festa-Bianchet et al. 1998).

In conclusion, our results show that female Weddell seals pay a cost for reproduction, in the form of reduced survival during years following reproduction, and reduced fecundity following first reproduction. It is possible that these costs depend on age at first reproduction. Seals primiparous at younger ages may be high-quality individuals and as a result, may not experience reduced fecundity following reproduction as do the presumably lower-quality seals primiparous at older ages. It will be critical to further explore the possible role of individual heterogeneity suggested by the differential fecundity costs we observed for various ages at first reproduction. Mass data collected during an ongoing study of mass dynamics in the Erebus Bay Weddell seal population may be useful as a surrogate variable representing individual quality and could reveal the extent to which reproductive costs are influenced by heterogeneity among individuals. This study detected moderate support for an interesting relationship between sea-ice extent and magnitude of reproductive costs to fecundity. Stronger relationships between reproductive costs and environmental condition may exist but will require more study to determine the relevant resolution for annual environmental covariates. Moreover, Weddell seal vital rates may not be linked to a single climate variable, and may instead respond to some combination of factors. More detailed exploration of appropriate climate and sea-ice indices may elucidate such linkages.

Literature Cited

Akaike, H. 1973. Information theory and an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petran and F. Csàaki, editors. International Symposium on Information Theory. Akadèemiai Kiadi, Budapest, Hungary.

Arnason, A.N. 1972. Parameter estimates from mark-recapture experiments on two populations subject to migration and death. Research in Population Ecology 13:97-113.

Arnason, A.N. 1973. The estimation of population size, migration rates, and survival in a stratified population. Research in Population Ecology 15:1-8.

Arnason, A.N., and K.H. Mills. 1981. Bias and loss of precision due to tag loss in Jolly-Seber estimates for mark-recapture experiments. Canadian Journal of Fisheries and Aquatic Sciences 38:1077-1095.

Arrigo, K. R. and G.L. van Dijken. 2004. Annual changes in sea-ice, chlorophyll *a*, and primary production in the Ross Sea, Antarctica. Deep Sea Research II 51:117-138.

Barbraud, C., and H. Weimerskirch. 2005. Environmental conditions and breeding experience affect costs of reproduction in blue petrels. Ecology 86:682-692.

Beauplet, G., C. Barbraud, M. Chamballant, and C. Guinet. 2005. Interannual variation in the post-weaning and juvenile survival of subantarctic fur seals: influence of pup sex, growth rate, and oceanographic conditions. Journal of Animal Ecology 74:1160-1172.

Boltnev, A.I., and A.E. York. 2001. Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. Journal of Zoology – London 254:219-228.

Boyd, I.L., J.P. Croxall, N.J. Lunn, and K. Reid. 1995. Population demography of Antarctic fur seals: the costs of reproduction and implications for life-histories. Journal of Animal Ecology 64:505-518.

Brierly, A.S., and D.N. Thomas. 2002. Ecology of southern ocean pack ice. Advances in Marine Biology 43:171-276.

Brownie, C., J.E. Hines, J.D. Nichols, K.H. Pollock, and J.B. Hestbeck. 1993. Capture-recapture studies for multiple strata including non-Markovian transition probabilities. Biometrics 49:1173-1187.

Burnham, K.P., and D.R. Anderson. 1998. Model selection and inference: A practical information-theoretic approach. Springer, New York, New York, USA.

Cam, E., W.A. Link, E.G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. American Naturalist 159:97-105.

Cameron, M.F., and D.B. Siniff. 2004. Age-specific survival, abundance, and immigration rates of a Weddell seal (*Leptonychotes weddellii*) population in McMurdo Sound, Antarctica. Canadian Journal of Zoology 82:601-615.

Charlesworth, B. 1980. Evolution in an age-structured population. Cambridge University Press, Cambridge, England.

Choquet, R., A.M. Reboulet, R. Pradel, O. Giminez, and J.-D. Lebreton. 2003. User's manual for U-CARE. CEFE/CNRS, Montpelier, France.

Clutton-Brock, T.H. 1984. Reproductive effort and terminal investment. American Naturalist 123:212-229.

Clutton-Brock, T.H., I.R. Stevenson, P. Marrow, A.D. MacColl, A.I. Houston, and J.M. McNamara. 1996. Population fluctuations, reproductive costs and life-history tactics in female Soay sheep. Journal of Animal Ecology 65:675-689.

Comiso, J. 1990 (updated 2004). DMSP SSM/I daily polar gridded sea ice concentrations, 1982 to 2004. Edited by J. Maslanik and J. Stroeve. Boulder, CO: National Snow and Ice Data Center. Digital media.

Croxall, J.P., and L. Hiby. 1983. Fecundity, survival and site fidelity in Weddell seals, *Leptonychotes weddellii*. Journal of Applied Ecology 20:19-32.

Daan, S., C. Deerenberg, and C. Dijkstra. 1996. Increased daily work precipitates natural death in the kestrel. Journal of Animal Ecology 65:539-544.

Erikstad, K E., M. Asheim, P. Fauchald, L. Dalhaug, and T. Tveraa. 1997. Adjustment of parental effort in the Puffin: the role of adult body condition and chick size. Behavioral Ecology and Sociobiology 40:95-100.

Erikstad, K.E., P. Fauchald, T. Tveraa, and H. Steen. 1998. On the cost of reproduction in long-lived birds: the influence of environmental variability. Ecology 79:1781-1788.

Festa-Bianchet, M. 1989. Individual differences, parasites, and the costs of reproduction for bighorn ewes (*Ovis canadensis*). Journal of Animal Ecology 58:785-795.

Festa-Bianchet, M., J.-M. Gaillard, and J.T. Jorgenson. 1998. Mass- and density-dependent reproductive success and reproductive costs in a capital breeder. American Naturalist 152:367-379.

Golet, G.H., D.B. Irons, and J.A. Estes. 1998 Survival costs of chick rearing in black-legged kittiwakes. Journal of Animal Ecology 67:827-841.

Goodman, D. 1974. Natural selection and a cost ceiling on reproductive effort. American Naturalist 108:247-267.

Green, W.C.H., and A. Rothstein. 1991. Trade-offs between growth and reproduction in female bison. Oecologia 86:521-527.

Hadley, G.L., J.J. Rotella, R.A. Garrott, and J.D. Nichols. 2006. Variation in probability of first reproduction of Weddell seals. Journal of Animal Ecology. *In press*.

Hestbeck, J.B., J.D. Nichols, and R.A. Malecki. 1991. Estimates of movement and site fidelity using mark-resight data of wintering Canada geese. Ecology 72:523-533.

Hill, S.E.B. 1987. Reproductive ecology of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Ph.D. dissertation. University of Minnesota, Minneapolis, Minnesota, USA.

Huber, H.R., A.C. Rovetta, L.A. Fry, and S. Johnston. 1991. Age-specific natality of northern elephant seals at the South Farallon Islands, California. Journal of Mammalogy 72:525-534.

Hurvich, C.M., and C.-L. Tsai. 1989. Regression and time series model selection in small samples. Biometrika 76:297-307.

Jacobsen, K.-O., K.E. Erikstad, and B.-E. Sǽther. 1995. An experimental study of the costs of reproduction in the Kittiwake *Rissa tridactyla*. Ecology 76:1636-1642.

Kwok, R., and J.C. Comiso. 2002. Southern ocean climate and sea ice anomalies associated with the southern oscillation. Journal of Climate 15:487-501.

Lizotte, M. 2001. The contributions of sea-ice algae to Antarctic marine primary production. American Zoologist 41:57-73.

Lunn, N.J., I.L. Boyd, and J.P. Croxall. 1994. Reproductive performance of female Antarctic fur seals: the influence of age, breeding experience, environmental variation and individual quality. Journal of Animal Ecology 63:827-840.

McMahon, C.R., and H.R. Burton. 2005. Climate change and seal survival: evidence for environmentally-mediated changes in elephant seal, *Mirounga leonina*, pup survival. Proceedings of the Royal Society B 272:923-928.

Nichols, J.D., J. Bart, R.J. Limpert, W.J.L. Sladen, and J.E. Hines. 1992. Annual survival rates of adult and immature eastern population tundra swans. Journal of Wildlife Management 56:485-494.

Nichols, J.D., and W.L. Kendall. 1995. The use of multi-state capture-recapture models to address questions in evolutionary ecology. Journal of Applied Statistics 22:835-846.

Ollason, J.C., and G.M. Dunnet. 1988. Variation in breeding success in Fulmars. Pages 263-278 *in* T. H. Clutton-Brock, editor. Reproductive Success. University of Chicago Press, Chicago, Illinois, USA.

Pistorius, P.A., M.N. Bester, M.N. Lewis, F.E. Taylor, C. Campagna, and S.P. Kirkman. 2004. Adult female survival, population trend, and the implications of early primiparity in a capital breeder, the southern elephant seal (*Mirounga leonina*). Journal of Zoology – London 263:107-119.

Reid, W.V. 1987. The cost of reproduction in Glaucous-winged Gull. Oecologia 74: 458-467.

Reiter, J., and B.J. LeBoeuf. 1991. Life-history consequences of variation in age at primiparity in northern elephant seals. Behavioral Ecology and Sociobiology 28:153-160

Reznick, D. 1985. Costs of reproduction: an evaluation of the empirical evidence. Oikos 44:257-267.

Reznick, D. 1992. Measuring the costs of reproduction. Trend in Ecology and Evolution 7:42-45.

Roff, D.A. 1992. The evolution of life histories: theory and analysis. Chapman and Hall, New York, New York, USA.

Ross, R.M., and L.B. Quetin. 1991. Ecological physiology of larval euphausiids, *Euphausia superba* (Euphausiaceae). Memoirs of the Queensland Museum 31:321-333.

Sæther, B.-E., and H. Haagenrud. 1983. Life history of the moose (*Alces alces*): fecundity rates in relation to age and carcass weight. Journal of Mammalogy 64:226-232.

Sand, H. 1996. Life history patterns in female moose (*Alces alces*): the relationship between age, body size, fecundity, and environmental conditions. Oecologia 106:212-220.

Siniff, D.B., D.M. DeMaster, R.J. Hofman, and L.L. Eberhardt. 1977. An analysis of the dynamics of a Weddell seal population. Ecological Monographs 47:319-335.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, New York, New York, USA.

Stirling, I. 1969. Ecology of the Weddell seal in McMurdo Sound, Antarctica. Ecology 50:573-586.

Stirling, I. 1974. Movements of Weddell seals in McMurdo Sound, Antarctica. Australian Journal of Zoology 22:39-43.

Sydeman, W.J., H.R. Huber, S.D. Emslie, C.A. Ribic, and N. Nur. 1991. Age-specific weaning success in northern elephant seals in relation to previous breeding experience. Ecology 72:2204-2217.

Sydeman, W.J., and N. Nur. 1994. Life history strategies of female northern elephant seals. Pages 136-153 *in* R. J. LeBoeuf and R. M. Laws, editors. Elephant seals: population ecology, behavior, and physiology. University of California Press, Berkeley, California, USA.

Tavecchia, G., T. Coulson, B.J.T. Morgan, J.M. Pemberton, J.C. Pilkington, F.M.D. Gulland, and T.H. Clutton-Brock. 2005. Predictors of reproductive cost in female Soay sheep. Journal of Animal Ecology 74:201-213.

Testa, J.W. 1987. Long-term reproductive patterns and sighting bias in Weddell seals (*Leptonychotes weddellii*). Canadian Journal of Zoology 65:1091-1099.

Testa, J.W., and D.B. Siniff. 1987. Population dynamics of Weddell seals (*Leptonychotes weddellii*) in McMurdo Sound, Antarctica. Ecological Monographs 57:149-165.

Testa, J.W., S.E.B. Hill, and D.B. Siniff. 1989. Diving behavior and maternal investment in Weddell seals (*Leptonychotes weddellii*). Marine Mammal Science 5:399-405.

Viallefont, A., F. Cooke, and J.-D. Lebreton. 1995. Age-specific costs of first-time breeding. Auk 112:67-76.

Weimerskirch, H. 1990. The influence of age and experience on breeding performance of the Antarctic fulmar, *Fulmarus glacialoides*. Journal of Animal Ecology 59:867-875.

White, G.C., and K.P. Burnham. 1999. Program MARK: Survival estimation from populations of marked animals. Bird Study 46 (Supplement):120-138.

Williams, B.K., J.D. Nichols, and M.J. Conroy. 2002. Analysis and Management of Animal Populations. Academic Press, San Diego, California, USA.

Williams, G.C. 1966. Natural selection, the costs of reproduction, and a refinement of Lack's principle. American Naturalist 100:687-690.

Wooller, R.D., J.S. Bradley, I.J. Skira, and D.L. Serventy. 1990. Reproductive success of short-tailed shearwaters *Puffinus tenuirostris* in relation to their age and breeding experience. Journal of Animal Ecology 59:161-170.

Wooller, R.D., and J.C. Coulson. 1977. Factors affecting the age of first breeding in the Kittiwake, *Rissa tridactyla*. Ibis 119:339-349.

CHAPTER FIVE.

CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

Summary

The efforts of numerous researchers have combined to create an increasingly detailed picture of the Antarctic marine ecosystem and its many facets. Broad-reaching studies have revealed interesting linkages between upper trophic predators (such as sea birds and seals), mid-level species (including fish and krill), and oceanographic processes (including annual and seasonal sea-ice dynamics and global-scale phenomena such as the Southern Oscillation and El Niño). In this dissertation, we have attempted to build from these studies and fill in gaps in our knowledge for one upper trophic organism, the Weddell seal. As a result, we have gained insight into 1) the extent of within-population variation in important life-history characteristics and 2) the sources of this variation and potential linkages with environmental variables.

In Chapter 2, we found that mean age at first reproduction in this southerly-located study population (7.62 years of age, SD = 1.71) was greater than age at first reproduction for a Weddell seal population at a more northerly and typical latitude for breeding Weddell seals (mean = 4-5 years of age). This difference suggests that age at first reproduction may be influenced by whether a population inhabits the core or periphery of its range. Age at first reproduction varied from four to 14, suggesting that substantial individual heterogeneity exists among females in this population. We provided evidence that the probability of breeding for the first time varied by age and year, and the amount of annual variation varied with age (average variance ratio for age-specific rates = 4.3%). Our results affirmed the predictions of life-history theory that age at first reproduction in long-lived mammals will be sensitive to environmental variation. In terms of life-history evolution, this variability suggests that Weddell seals display flexibility in age at first reproduction in order to maximize reproductive output under varying environmental conditions.

In Chapter 3, analyses of multi-state mark-resight models with three states (prebreeders, breeders, and nonbreeders) supported our prediction that maternal age was related to variation in probabilities of both survival and recruitment of young. Survival rate for prebreeders (averaged across age classes) was maximized for offspring of age-14 mothers ($\hat{\phi}_P = 0.70$ [$\hat{SE} = 0.08$]), whereas seals born to younger or older mothers had lower survival probabilities ($\hat{\phi}_P = 0.64$ [$\hat{SE} = 0.09$] for seals born to age-6 or age-22 mothers). In contrast to this (and contrary to our prediction), we found that recruitment probability for pups born to young mothers was higher than the rate for other pups. For example, probability of recruitment at age 7 was an average of 43% lower for seals born to age-14 mothers than for seals born to age-6 mothers. We hypothesize that such a result occurred because (1) the females that breed at the youngest ages tend to be of higher quality than females with more delayed primiparity and (2) reproductive capabilities are heritable. Given the lower survival rate for offspring of young mothers described above, the finding of higher recruitment probabilities suggests the influence of countervailing selection, a scenario in which favored genotypes for reproductive success are generally those that are selected against as juveniles, resulting in high recruitment probabilities for individuals that had low juvenile survival rates. Additionally, we found evidence from exploratory models that a pup's eventual recruitment probability was positively related to the number of previous pups produced by the mother (coefficient for effect of maternal experience = 0.35; $S\hat{E}$ = 0.16), but only for mothers $\leq$10 years of age. Recruitment probabilities also varied by location of birth but not for the reason we had hypothesized, as the observed pattern was not related to spatial variation in maternal age distribution. As predicted, we found evidence that oceanographic conditions affected annual recruitment rates. Specifically, recruitment probability tended to be lower in the year after a winter of minimal sea-ice extent and two years after a year of high sea surface temperatures. We hypothesize that cascading effects of oceanographic conditions on marine primary productivity and food availability for newly mature or newly pregnant female Weddell seals are responsible for these results but more information is needed regarding linkages between oceanographic variables and Weddell seal demography. Our study found strong evidence that both maternal characteristics and environmental factors affect probability of survival to age of maturity and probability of recruitment, thus advancing our understanding of the recruitment process. This study also revealed the influence of individual-level variation in quality among Weddell seals in Erebus Bay, and we therefore recommend that future studies incorporate individual variation into models of population vital rates.

Results from Chapter 4 strongly supported the presence of reproductive costs to survival (mean annual survival probability was 0.91 for breeders versus 0.94 for nonbreeders), a notable difference for a long-lived organism. This result demonstrates that investment in reproduction does result in a cost to survival for Weddell seals, contrary to the fixed-strategy hypothesis. Reproductive costs to fecundity were also present for first-time breeders (mean probability of breeding the next year was 0.20 lower for first-time breeders than for experienced breeders and nonbreeders), thus supporting our prediction of the influence of breeding experience. Age at first reproduction was not a strong predictor of reproductive costs, which agreed with our hypothesis. However, a moderately supported model suggested that females that delayed breeding until later in life experienced the highest reproductive costs to fecundity, possibly due to their inferiority relative to other individuals in the population. In contrast, early breeders experienced no cost to fecundity and in fact were more likely to breed in consecutive years than to skip years, suggesting the presence of important heterogeneity in individual quality. We detected substantial annual variation in survival and breeding probabilities, and there was some evidence of a correlation between sea-ice extent (SIE) and costs to fecundity. Experienced breeders with a pup were more likely to breed the year following a year of high SIE than seals without a pup. However, a model with annual variation unrelated to any of our climate or sea-ice covariates performed best, indicating that further study will be needed to determine the appropriate mechanism or combination of mechanisms underlying this annual variation.

Directions for Future Research

Throughout the chapters of this dissertation, the presence of important heterogeneity in individual quality of seals has been suggested by our findings. Investigations into life-history traits of pinnipeds have made it clear that individual quality often plays a substantial role in other populations (Boyd 1996, Harwood et al. 2000, Boltnev and York 2001, Bradshaw et al. 2003) and we propose that incorporating individual quality into population models for Weddell seals is an important next step in this research program. Although individual quality can be a vague concept, and little is known about the underlying physiological mechanisms (but see Service 2000 regarding genetic versus environmental sources of heterogeneity, and Haussmann et al. 2005), individual quality has been incorporated into life-history studies in various ways. Indicators of individual quality can be categorized into various types: physiological indices (weight, body condition, basal metabolic rate (BMR)), behavioral indices (timing of nesting), reproductive-performance indices (offspring production, reproductive longevity), or fitness indices. Each of these approaches has inherent strengths and weaknesses, as well as varying degrees of feasibility or applicability to the Weddell seal dataset.

Fitness is a function of survival and fecundity rates, and at the individual level these rates are latent features, describing the most likely outcomes for an individual. Chance events and natural variation are likely to result in different values of realized fitness for genetically identical individuals with common values of latent fitness. Link et al. (2002) point out that these latent rates are the most relevant to fitness and provide an approach for estimating individual latent fitness that relies on Bayesian techniques for estimating latent survival and fecundity rates, because they are not directly observable. The Bayesian technique, also used by Cam et al. (2002), uses models with individual random effects permitting variation and covariation in fitness components among individuals.

Of all the possible methods, the use of random effects to model individual latent fitness appears to be the most sensible way to incorporate individual variation into models of survival and breeding probability, but one limitation is that it does not provide insight into the mechanism underlying the individual variation (e.g., differences in body weight). However, the motivation for this type of modeling is the realization that, for many wildlife populations, we may be able to observe certain important traits that vary among individuals, but we will never be able to account for all possible sources of variation. Thus, random effects modeling may be the most realistic way to incorporate variation in individual quality into life-history studies, and represents an important direction for future research on life-history strategies of Weddell seals in Erebus Bay.

Another important direction for future research will be the incorporation of individual mass data into studies of life-history traits. In addition to potentially explaining some of the variation in individual quality (as mentioned above), mass is an important variable to measure because it can be used as a surrogate measure of annual variation in food resources and may be used to understand linkages between oceanographic processes and vital rates of the study population (Ireland et al. 2006). A research initiative is currently underway that will increase the number of known-age females in the Erebus Bay population for which we also will have body mass measurements. Possessing knowledge of age, reproductive history, and repeated annual measurements of body mass will allow researchers to evaluate increasingly detailed predictions about effects of climate and sea-ice covariates on mass, and resulting implications for seal vital rates and life history strategies.

Literature Cited

Boltnev, A.I. and A.E. York. 2001. Maternal investment in northern fur seals (*Callorhinus ursinus*): interrelationships among mothers' age, size, parturition date, offspring size and sex ratios. Journal of Zoology-London 254:219-228.

Boyd, I.L. 1996. Individual variation in the duration of pregnancy and birth date in Antarctic fur seals: the role of environment, age, and sex of fetus. Journal of Mammalogy 77:124-133.

Bradshaw, C.J.A., R.J. Barker, R.G. Harcourt, and L.S. Davis. 2003. Estimating survival and capture probability of fur seal pups using multistate mark-recapture models. Journal of Mammalogy 84:65-80.

Cam, E., W.A. Link, E.G. Cooch, J.-Y. Monnat, and E. Danchin. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. American Naturalist 159:97-105.

Harwood, L.A., T.G. Smith, and H. Melling. 2000. Variation in reproduction and body condition of the ringed seal (*Phoca hispida*) in western Prince Albert Sound, NT, Canada, as assessed through a harvest-based sampling program. Arctic 53:422-431.

Haussmann, M.F., D.W. Winkler, and C.M. Vleck. 2005. Longer telomeres associated with higher survival in birds. Biology Letters 1:212-214.

Ireland, D.S., R.A. Garrott, J.J. Rotella, and J. Banfield. 2006. Development and application of a mass-estimation method for Weddell seals. Marine Mammal Science 22, *In press.*

Link, W.A., E.G. Cooch, and E. Cam. 2002. Model-based estimation of individual fitness. Journal of Applied Statistics 29:207-224.

Service, P.M. 2000. Heterogeneity in individual mortality risk and its importance for evolutionary studies of senescence. American Naturalist 156:1-13.

APPENDICES

APPENDIX A

REPRODUCTIVE COST MODELS – MODELING SURVIVAL PROBABILITIES FIRST

Models representing hypotheses about reproductive costs for female Weddell seals in Erebus Bay, Antarctica. Model parameters are state-dependent survival (ϕ^r), sighting (p^r), and transition or breeding (ψ^{rs}) probabilities where r and s are breeding states at times t and t+1. Covariates are indicated with model subscripts and include ***a*** (age; modeled with linear trend or quadratic effect), ***be*** (breeding experience; modeled by constraining survival and breeding probabilities following first breeding to differ from all subsequent breeding events), ***g*** (group; determined by age at first reproduction: 4-5, 6-8, or 9-14), and ***t*** (year; representing annual variation). Annual environmental covariates included ENSO (El-Niño Southern Oscillation score), SST (sea-surface temperature), and SIE (sea-ice extent). Results from model selection are included: k (number of parameters), Dev (model deviance), QAIC$_c$, Δ_i (difference in QAIC$_c$ value between the top model and each subsequent model i), w_i ("weight of evidence" in favor of each model i). Sighting probability (p^r) was always modeled first. Thereafter, model selection was conducted sequentially, fitting ϕ^r first, followed by ψ^{rs}. Results from fitting p^r first, followed by ψ^{rs}, and then ϕ^r are presented in Appendix B.

Model	*k*	Dev	QAIC$_c$	w_i	Δ_i	Within-suite Δ_i
Modeling sighting probabilities						
$\phi^r_{g*,t*}, p^r, \psi^{rs}_{g*,t*}$	**94**	**2598.34**	**2792.29**	**0.00**	**91.54**	**0.00**
$\phi^r_{g*,t*}, p^r_a, \psi^{rs}_{g*,t*}$	95	2597.97	2794.04	0.00	93.29	1.75
$\phi^r_{g*,t*}, p^r_{a+a^2}, \psi^{rs}_{g*,t*}$	96	2598.34	2796.55	0.00	95.80	4.26
$\phi^r_{g*,t*}, p^r_t, \psi^{rs}_{g*,t*}$	114	2560.12	2796.90	0.00	96.16	4.62
$\phi^r_{g*,t*}, p^r_{a+t+(a*t)}, \psi^{rs}_{g*,t*}$	135	2549.14	2831.54	0.00	130.79	39.25
Modeling survival probabilities						
$\phi^r_t, p^r, \psi^{rs}_{g*,t*}$	**70**	**2608.57**	**2751.84**	**0.00**	**51.10**	**0.00**
$\phi^r_{be,t}, p^r, \psi^{rs}_{g*,t*}$	71	2608.50	2753.87	0.00	53.13	2.03
$\phi^r_{g,t}, p^r, \psi^{rs}_{g*,t*}$	72	2607.89	2755.36	0.00	54.62	3.52
$\phi^r_{g,be,t}, p^r, \psi^{rs}_{g*,t*}$	73	2607.75	2757.32	0.00	56.58	5.48
$\phi^r_{g*,t}, p^r, \psi^{rs}_{g*,t*}$	74	2607.30	2758.97	0.00	58.22	7.12
$\phi^r_{a,SST}, p^r, \psi^{rs}_{g*,t*}$	52	2654.87	2760.68	0.00	59.93	8.83
$\phi^r_{g*,be,t}, p^r, \psi^{rs}_{g*,t*}$	75	2607.14	2760.91	0.00	60.17	9.07
$\phi^r_a, p^r, \psi^{rs}_{g*,t*}$	51	2659.93	2764.67	0.00	62.93	11.83
$\phi^r_{a*}, p^r, \psi^{rs}_{g*,t*}$	52	2657.87	2763.68	0.00	62.94	11.84
$\phi^r, p^r, \psi^{rs}_{g*,t*}$	50	2662.66	2764.34	0.00	63.59	12.49
$\phi^r_{a,ENSO}, p^r, \psi^{rs}_{g*,t*}$	52	2658.84	2764.65	0.00	63.90	12.80
$\phi^r_{a,a^2}, p^r, \psi^{rs}_{g*,t*}$	52	2659.06	2764.87	0.00	64.13	13.03

Appendix A cont.

Model	*k*	Dev	QAIC$_c$	w_i	Δ_i	Within-suite Δ_i
$\phi^r_{a,be}, p^r, \psi^{rs}_{g*,t*}$	52	2659.10	2764.91	0.00	64.16	13.06
$\phi^r_{a,SIE}, p^r, \psi^{rs}_{g*,t*}$	52	2659.79	2765.59	0.00	64.85	13.75
$\phi^r_{be}, p^r, \psi^{rs}_{g*,t*}$	51	2662.66	2766.40	0.00	65.66	14.56
$\phi^r_{g,a}, p^r, \psi^{rs}_{g*,t*}$	53	2659.45	2767.33	0.00	66.58	15.48
$\phi^r_{g}, p^r, \psi^{rs}_{g*,t*}$	52	2661.79	2767.60	0.00	66.85	15.75
$\phi^r_{g,a,be}, p^r, \psi^{rs}_{g*,t*}$	54	2658.72	2768.68	0.00	67.93	16.83
$\phi^r_{g,be}, p^r, \psi^{rs}_{g*,t*}$	53	2661.78	2769.66	0.00	68.92	17.82
$\phi^r_{g*,a}, p^r, \psi^{rs}_{g*,t*}$	55	2659.08	2771.10	0.00	70.36	19.26
$\phi^r_{g*}, p^r, \psi^{rs}_{g*,t*}$	54	2661.42	2771.37	0.00	70.63	19.53
$\phi^r_{g*,a,be}, p^r, \psi^{rs}_{g*,t*}$	56	2658.30	2772.40	0.00	71.65	20.55
$\phi^r_{g*,be}, p^r, \psi^{rs}_{g*,t*}$	55	2661.42	2773.44	0.00	72.70	21.6
$\phi^r_{a,t,a*t}, p^r, \psi^{rs}_{g*,t*}$	91	2596.64	2784.21	0.00	83.46	32.36
$\phi^r_{t*}, p^r, \psi^{rs}_{g*,t*}$	90	2599.36	2784.81	0.00	84.07	32.97
$\phi^r_{be,t*}, p^r, \psi^{rs}_{g*,t*}$	91	2599.34	2786.91	0.00	86.16	35.06
$\phi^r_{g,t*}, p^r, \psi^{rs}_{g*,t*}$	92	2598.78	2788.47	0.00	87.73	36.63
$\phi^r_{g,be,t*}, p^r, \psi^{rs}_{g*,t*}$	93	2598.65	2790.47	0.00	89.72	38.62
$\phi^r_{g*,be,t*}, p^r, \psi^{rs}_{g*,t*}$	95	2598.19	2794.26	0.00	93.52	42.42
$\phi^r_{a,a^2,t}, p^r, \psi^{rs}_{g*,t*}$	72	2750.23	2897.70	0.00	196.96	145.86
Modeling breeding probabilities						
$\phi^r_{t}, p^r, \psi^{rs}_{be,t}$	**47**	**2605.27**	**2700.75**	**0.67**	**0.00**	**0.00**
$\phi^r_{t}, p^r, \psi^{rs}_{g,be,t}$	49	2603.15	2702.76	0.24	2.01	2.01
$\phi^r_{t}, p^r, \psi^{rs}_{g*,be,t}$	51	2602.21	2705.95	0.05	5.21	5.21
$\phi^r_{t}, p^r, \psi^{rs}_{be,SIE*}$	29	2649.00	2707.57	0.02	6.83	6.83
$\phi^r_{t}, p^r, \psi^{rs}_{be,SIE}$	28	2653.96	2710.49	0.01	9.74	9.74
$\phi^r_{t}, p^r, \psi^{rs}_{be,ENSO*}$	29	2652.88	2711.45	0.01	10.70	10.70
$\phi^r_{t}, p^r, \psi^{rs}_{a,be}$	28	2655.17	2711.70	0.00	10.95	10.95
$\phi^r_{t}, p^r, \psi^{rs}_{be}$	27	2657.58	2712.07	0.00	11.33	11.33
$\phi^r_{t}, p^r, \psi^{rs}_{be,SST}$	28	2656.36	2712.89	0.00	12.15	12.15
$\phi^r_{t}, p^r, \psi^{rs}_{be,ENSO}$	28	2657.54	2714.07	0.00	13.32	13.32

Appendix A cont.

Model	*k*	Dev	QAIC$_c$	w_i	Δ_i	Within-suite Δ_i
$\phi_t^r, p^r, \psi_{g,be}^{rs}$	29	2655.70	2714.27	0.00	13.52	13.52
$\phi_t^r, p^r, \psi_{g,be,a}^{rs}$	30	2654.00	2714.61	0.00	13.86	13.86
$\phi_t^r, p^r, \psi_{be,SST*}^{rs}$	29	2656.27	2714.84	0.00	14.09	14.09
$\phi_t^r, p^r, \psi_{g*,be}^{rs}$	31	2654.71	2717.36	0.00	16.61	16.61
$\phi_t^r, p^r, \psi_{g*,be,a}^{rs}$	32	2653.07	2717.76	0.00	17.01	17.01
$\phi_t^r, p^r, \psi_{a,a^2,t}^{rs}$	48	2620.97	2718.51	0.00	17.77	17.77
$\phi_t^r, p^r, \psi_{t}^{rs}$	46	2630.23	2723.64	0.00	22.90	22.90
$\phi_t^r, p^r, \psi_{g,t}^{rs}$	48	2627.20	2724.75	0.00	24.00	24.00
$\phi_t^r, p^r, \psi_{a,a^2}^{rs}$	28	2670.02	2726.55	0.00	25.81	25.81
$\phi_t^r, p^r, \psi_{be,t*}^{rs}$	67	2590.00	2727.01	0.00	26.26	26.26
$\phi_t^r, p^r, \psi_{a*}^{rs}$	28	2670.61	2727.14	0.00	26.39	26.39
$\phi_t^r, p^r, \psi_{g*,t}^{rs}$	50	2625.90	2727.58	0.00	26.83	26.83
$\phi_t^r, p^r, \psi_{g,be,t*}^{rs}$	69	2588.18	2729.37	0.00	28.63	28.63
$\phi_t^r, p^r, \psi_{t*}^{rs}$	56	2615.58	2729.68	0.00	28.94	28.94
$\phi_t^r, p^r, \psi_{g*,be,t*}^{rs}$	71	2586.38	2731.75	0.00	31.01	31.01
$\phi_t^r, p^r, \psi_{a,SIE}^{rs}$	28	2675.60	2732.13	0.00	31.38	31.38
ϕ_t^r, p^r, ψ^{rs}	26	2680.42	2732.88	0.00	32.13	32.13
$\phi_t^r, p^r, \psi_{a}^{rs}$	27	2679.82	2734.32	0.00	33.57	33.57
$\phi_t^r, p^r, \psi_{g}^{rs}$	28	2678.58	2735.11	0.00	34.37	34.37
$\phi_t^r, p^r, \psi_{g,a}^{rs}$	29	2677.20	2735.77	0.00	35.02	35.02
$\phi_t^r, p^r, \psi_{a,SST}^{rs}$	28	2679.27	2735.80	0.00	35.05	35.05
$\phi_t^r, p^r, \psi_{a,ENSO}^{rs}$	28	2679.51	2736.04	0.00	35.30	35.30
$\phi_t^r, p^r, \psi_{g*}^{rs}$	30	2676.23	2736.84	0.00	36.10	36.10
$\phi_t^r, p^r, \psi_{g*,a}^{rs}$	31	2675.16	2737.80	0.00	37.06	37.06
$\phi_t^r, p^r, \psi_{g,t*}^{rs}$	68	2611.07	2750.17	0.00	49.43	49.43
$\phi_t^r, p^r, \psi_{a,t,a*t}^{rs}$	67	2615.60	2752.60	0.00	51.86	51.86

* indicates an interaction between designated variable and breeding state.

APPENDIX B

REPRODUCTIVE COST MODELS – MODELING BREEDING PROBABILITIES FIRST

Model selection results for alternate order of sequential modeling in which best fit is determined first for ψ^{rs} and then for ϕ^{r}. See Appendix A for description.

Model	***k***	**Dev**	**QAIC$_c$**	$\boldsymbol{w_i}$	$\boldsymbol{\Delta_i}$	**Within-suite** $\boldsymbol{\Delta_i}$
Modeling breeding probabilities						
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{be,t}$	**71**	**2598.21**	**2743.59**	**0.00**	**42.84**	0
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g,be,t}$	73	2596.03	2745.61	0.00	44.86	2.02
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g*,be,t}$	75	2592.28	2746.05	0.00	45.30	2.46
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{a,be}$	52	2644.49	2750.30	0.00	49.55	6.71
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{be}$	51	2646.90	2750.64	0.00	49.90	7.06
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g,be}$	53	2645.02	2752.90	0.00	52.15	9.31
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g,a,be}$	54	2643.33	2753.28	0.00	52.53	9.69
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g*,be}$	55	2643.90	2755.92	0.00	55.18	12.34
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g*,a,be}$	56	2642.26	2756.36	0.00	55.62	12.78
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{a,a^2,t}$	72	2611.12	2758.59	0.00	57.85	15.01
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{t}$	70	2620.38	2763.66	0.00	62.91	20.07
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g,t}$	72	2617.36	2764.84	0.00	64.09	21.25
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{a,a^2}$	52	2659.30	2765.11	0.00	64.36	21.52
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g*,t}$	74	2615.80	2767.47	0.00	66.73	23.89
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{be,t*}$	91	2580.25	2767.82	0.00	67.07	24.23
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g,be,t*}$	93	2578.44	2770.26	0.00	69.51	26.67
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{a,SIE}$	52	2665.31	2771.12	0.00	70.37	27.53
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}$	50	2670.05	2771.72	0.00	70.98	28.14
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g*,be,t*}$	95	2576.29	2772.37	0.00	71.62	28.78
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{a}$	51	2669.38	2773.12	0.00	72.38	29.54
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g}$	52	2668.14	2773.95	0.00	73.21	30.37
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g,a}$	53	2666.60	2774.48	0.00	73.74	30.90
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{a,SST}$	52	2668.71	2774.52	0.00	73.78	30.94
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{a,ENSO}$	52	2669.18	2774.99	0.00	74.24	31.40
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{a*}$	52	2669.38	2775.19	0.00	74.44	31.60
$\phi^{r}_{g*,t*}, p^{r}, \psi^{rs}_{g*}$	54	2665.77	2775.73	0.00	74.98	32.14

Appendix B cont

Model	***k***	**Dev**	**QAIC$_c$**	w_i	Δ_i	**Within-suite Δ_i**
$\phi^r_{g*,t*}, p^r, \psi^{rs}_{g*,a}$	55	2664.59	2776.61	0.00	75.86	33.02
$\phi^r_{g*,t*}, p^r, \psi^{rs}_{t*}$	90	2603.78	2789.23	0.00	88.48	45.64
$\phi^r_{g*,t*}, p^r, \psi^{rs}_{g,t*}$	92	2601.10	2790.79	0.00	90.04	47.20
$\phi^r_{g*,t*}, p^r, \psi^{rs}_{a,t,a*t}$	91	2617.59	2805.16	0.00	104.41	61.57
Modeling survival probabilities						
$\phi^r_{t}, p^r, \psi^{rs}_{be,t}$	**47**	**2605.27**	**2700.75**	**0.59**	**0.00**	**0.00**
$\phi^r_{be,t}, p^r, \psi^{rs}_{be,t}$	48	2605.23	2702.77	0.21	2.02	2.02
$\phi^r_{g,t}, p^r, \psi^{rs}_{be,t}$	49	2604.53	2704.14	0.11	3.39	3.39
$\phi^r_{g,be,t}, p^r, \psi^{rs}_{be,t}$	50	2604.51	2706.18	0.04	5.43	5.43
$\phi^r_{g*,t}, p^r, \psi^{rs}_{be,t}$	51	2604.16	2707.90	0.02	7.15	7.15
$\phi^r_{a,SST}, p^r, \psi^{rs}_{be,t}$	29	2650.40	2708.97	0.01	8.22	8.22
$\phi^r_{SST}, p^r, \psi^{rs}_{be,t}$	28	2652.57	2709.10	0.01	8.36	8.36
$\phi^r_{g*,be,t}, p^r, \psi^{rs}_{be,t}$	52	2604.13	2709.94	0.01	9.19	9.19
$\phi^r_{SST*}, p^r, \psi^{rs}_{be,t}$	29	2652.57	2711.14	0.00	10.39	10.39
$\phi^r_{a}, p^r, \psi^{rs}_{be,t}$	28	2655.50	2712.03	0.00	11.28	11.28
$\phi^r_{a*}, p^r, \psi^{rs}_{be,t}$	29	2654.18	2712.75	0.00	12.01	12.01
$\phi^r_{a,ENSO}, p^r, \psi^{rs}_{be,t}$	29	2654.42	2712.98	0.00	12.24	12.24
$\phi^r, p^r, \psi^{rs}_{be,t}$	27	2658.56	2713.06	0.00	12.31	12.31
$\phi^r_{a,a^2}, p^r, \psi^{rs}_{be,t}$	29	2654.82	2713.39	0.00	12.64	12.64
$\phi^r_{a,be}, p^r, \psi^{rs}_{be,t}$	29	2655.08	2713.65	0.00	12.90	12.90
$\phi^r_{ENSO}, p^r, \psi^{rs}_{be,t}$	28	2657.27	2713.80	0.00	13.05	13.05
$\phi^r_{a,SIE}, p^r, \psi^{rs}_{be,t}$	29	2655.36	2713.93	0.00	13.18	13.18
$\phi^r_{SIE}, p^r, \psi^{rs}_{be,t}$	28	2658.15	2714.68	0.00	13.93	13.93
$\phi^r_{be}, p^r, \psi^{rs}_{be,t}$	28	2658.47	2715.00	0.00	14.25	14.25
$\phi^r_{g,a}, p^r, \psi^{rs}_{be,t}$	30	2654.98	2715.58	0.00	14.84	14.84
$\phi^r_{ENSO*}, p^r, \psi^{rs}_{be,t}$	29	2657.23	2715.80	0.00	15.05	15.05
$\phi^r_{g}, p^r, \psi^{rs}_{be,t}$	29	2657.61	2716.18	0.00	15.43	15.43
$\phi^r_{SIE*}, p^r, \psi^{rs}_{be,t}$	29	2658.14	2716.71	0.00	15.96	15.96

Appendix B cont.

Model	*k*	Dev	QAIC$_c$	w_i	Δ_i	Within-suite Δ_i
$\phi^{r}_{g,a,be}, p^{r}, \psi^{rs}_{be,t}$	31	2654.65	2717.29	0.00	16.55	16.55
$\phi^{r}_{g,be}, p^{r}, \psi^{rs}_{be,t}$	30	2657.49	2718.09	0.00	17.35	17.35
$\phi^{r}_{g*,a}, p^{r}, \psi^{rs}_{be,t}$	32	2654.80	2719.49	0.00	18.74	18.74
$\phi^{r}_{g*}, p^{r}, \psi^{rs}_{be,t}$	31	2657.43	2720.08	0.00	19.33	19.33
$\phi^{r}_{g*,a,be}, p^{r}, \psi^{rs}_{be,t}$	33	2654.44	2721.17	0.00	20.42	20.42
$\phi^{r}_{g*,be}, p^{r}, \psi^{rs}_{be,t}$	32	2657.32	2722.01	0.00	21.26	21.26
$\phi^{r}_{a,t,a*t}, p^{r}, \psi^{rs}_{be,t}$	68	2593.44	2732.54	0.00	31.79	31.79
$\phi^{r}_{t*}, p^{r}, \psi^{rs}_{be,t}$	67	2599.11	2736.11	0.00	35.37	35.37
$\phi^{r}_{g,t*}, p^{r}, \psi^{rs}_{be,t}$	69	2595.74	2736.93	0.00	36.18	36.18
$\phi^{r}_{be,t*}, p^{r}, \psi^{rs}_{be,t}$	68	2599.08	2738.18	0.00	37.43	37.43
$\phi^{r}_{g,be,t*}, p^{r}, \psi^{rs}_{be,t}$	70	2595.72	2739.00	0.00	38.26	38.26
$\phi^{r}_{g*,be,t*}, p^{r}, \psi^{rs}_{be,t}$	72	2595.48	2742.96	0.00	42.21	42.21
$\phi^{r}_{a,a^2,t}, p^{r}, \psi^{rs}_{be,t}$	49	2670.50	2770.11	0.00	69.36	69.36

* indicates an interaction between designated variable and breeding state.