VARIATION IN TEMPORARY EMIGRATION AND SURVIVAL RATES AND IMPLICATIONS FOR RECRUITMENT FOR FEMALE WEDDELL SEALS

by

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APPROVAL

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

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ABSTRACT

The life-history of many colonial-breeding species includes a period of absence from the natal colony followed by a period of attendance as prebreeders prior to first reproduction. During this prebreeder period, survival rates, and the probability of temporary emigration is variable, and patterns of attendance can have implications for future reproduction. We used 26 – 28 years of encounter data of female Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica to estimate variability in survival and temporary emigration rates and to evaluate implications for recruitment rates. Temporary emigration rates were nearly 1 at age 1, decreased until age 8, and increased slightly thereafter. Annual variation in temporary emigration rates was substantial, and rates were positively related to the distance from the fast-ice edge to Erebus Bay and to the population of adult females in the previous year. Recruitment rates varied annually, and were typically, but not always, positively related to the number of years (0, 1, 2+) that a prebreeder had previously attended reproductive colonies in Erebus Bay. Survival rates varied by birth-cohort and were positively related to the extent of current-year winter sea-ice in the Ross Sea. The influence of birth-cohort on survival rates was persistent for several years but did not last indefinitely. Survivorship from birth to age 6 was related to the specific sequence of sea-ice conditions experienced by each cohort, and cohort-specific rates varied from 0.13 (SE = 0.04) to 0.42 (SE = 0.06), and averaged 0.25 (SE = 0.02). Our results suggest that (1) the influences on survival of conditions experienced in early life, along with later influences, act as a filter that determines what proportion of a cohort of female Weddell seals reaches reproductive maturity, and (2) there are benefits and potential costs to prebreeders that are associated with attending reproductive colonies, and the decision to attend or not likely depends on the balance of consequent tradeoffs. Useful avenues for additional research include (1) inter-annual movements within and outside Erebus Bay, especially in relation to previous-year conditions, and (2) implications of prebreeder attendance patterns and age at first reproduction for reproductive success after recruitment.

CHAPTER 1

INTRODUCTION TO DISSERTATION

Introduction

In the life-history of many long-lived colonial-breeding species, young-of-the year leave the reproductive colony for one or more years, after which they might attend a reproductive colony for one or more years before producing young of their own. Eventual successful recruitment into the breeding population is contingent on surviving these first several crucial years, gaining physiological reproductive maturity, mating successfully, and successfully rearing young. Juvenile survival rates often are highly variable among years or cohorts. Annual environmental conditions can influence survival and recruitment probabilities (Barbraud *et al.* 2000; Hadley, Rotella, & Garrott 2007a), but conditions experienced in early life can also have short-term or persistent effects on survival or reproductive probabilities (Gaillard *et al.* 1997; Reid *et al.* 2003; Cam, Monnat, & Hines 2003; van de Pol *et al.* 2006).

Attendance of reproductive colonies by prebreeders is best-known in colonial seabirds, and numerous examples indicate that such attendance might facilitate the acquisition of information, experience, or skills necessary for successful mating and rearing of young. Association with reproductively active females might also facilitate onset or synchrony of estrus (McClintock 1978; Handelmann, Ravizza, & Ray 1980; Stern & McClintock 1998). However, attendance at reproductive colonies might entail costs for prebreeders related to limited foraging opportunities or intra-specific conflict at

breeding colonies (Furness & Birkhead 1984), and these costs may vary with environmental conditions or attributes of individuals. Thus, prebreeders that previously have attended a colony may subsequently skip a year prior to returning again or recruiting into the breeding population (Beauplet *et al.* 2005; Jenouvrier *et al.* 2008).

When sampling is focused on a breeding colony, it is useful to define one or more unobservable states to represent absence and one or more observable states, including a state to represent first-time reproduction, to represent presence at the breeding colony, and then to estimate transitions between states. In the ecological literature, transitions into an unobservable state are often termed temporary emigration (TE), and multistate capture-mark-recapture models can be used to estimate transition probabilities between observable and unobservable states – or the probability of remaining in the current state (e.g., Kendall, Nichols, & Hines 1997; Fujiwara & Caswell 2002; Kendall & Nichols 2002; Schaub *et al.* 2004; Converse *et al.* 2009). Evaluating variation in TE rates can provide insights about conditions when prebreeders are more or less likely to attend colonies and about implications of attendance for recruitment.

In this dissertation I use multistate capture-mark-recapture models to analyze encounter histories of individually marked female Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica. Recent work on this population indicated considerable variation in age at first reproduction (recruitment), annual variation in recruitment probability, and in the proportion of females from each cohort that eventually produces young (Hadley *et al.* 2006; Hadley, Rotella, & Garrott 2008; Garrott *et al.* 2012). Maternal parturition mass and pup weaning mass are related to annual

environmental conditions, presumably through the influence of environmental conditions on food resources (Proffitt *et al.* 2007a,b). Temporary emigration is known to occur in this population, and observed density-dependence in annual population growth rates possibly is related to density-dependence in TE rates (Hadley, Rotella, & Garrott 2007b; Rotella *et al.* 2009).

The objective of my dissertation was to gain further insight about sources of variation in TE and survival rates prior to recruitment, to evaluate evidence for persistent influences of early conditions on survival and recruitment rates, and to evaluate implications of TE for recruitment rates. In Chapter 2, I estimated age-specific TE and recruitment rates and evaluated support in the data for several possible sources of variation in these rates. I expected considerable variation over time and tested whether such variation was best explained by a current-year effect or a cohort-wide birth-year effect. I also expected that rates would be state-dependant, with greater TE rates and lower recruitment rates for prebreeders that did not attend Erebus Bay in the previous year.

The proportion of each female Weddell seal cohort that eventually recruits into the breeding population varies nearly four-fold and appears to be related to birth-year environmental conditions (Garrott *et al.* 2012). I suspected that most of the among-cohort variation is due to variation in early survival rates of prebreeders. In Chapter 3, I explored relationships between survival rates of prebreeders and potential birth-year and current-year influences. I included models where survival was related to birth-year influences, current-year influences, or both. I also evaluated a sub-set of models where the duration

of a birth-year influence was short-term, persistent, or intermediate. Lastly, I tested whether variation in recruitment rates was best explained by conditions in the current year or the birth year.

In Chapter 4, I evaluated potential causes of annual variation in age-specific TE rates and consequences of attendance patterns for age-specific recruitment rates. TE rates might be density-dependent or be related to access to breeding colony or available food resources in a given year, so my analysis included covariates representing each of these possibilities. If colony attendance facilitates the acquisition of useful information or skills, then age-specific recruitment rates might be greater for seals that attend a reproductive colony as a prebreeder more than once than for seals that attend only once or never. Colony attendance also might allow prebreeders to time estrus optimally to maximize probability of successful mating. I tested these hypotheses by modeling age-specific and state-specific recruitment rates, where state reflected whether seals had attended colonies as prebreeders 0, 1, or ≥2 years, and whether they had attended in the immediate previous year.

In Chapter 5, I briefly discuss my findings in Chapters 2-4 and suggest avenues for related research to provide further insights into the types of questions addressed in this dissertation. The research presented in Chapters 2-4 was a collaborative effort of several individuals, and each of these chapters either has been, or will be submitted as journal articles with several authors. Consequently, there is considerable overlap in some sections of each chapter (e.g., descriptions of the study area and data collection methods), and the text throughout these chapters is written in the first-person plural.

CHAPTER 2

VARIABILITY IN TEMPORARY EMIGRATION RATES OF FEMALE WEDDELL SEALS PRIOR TO FIRST REPRODUCTION

Abstract

In many species, temporary emigration (TE) is a phenomenon, often indicative of life-history characteristics such as dormancy, skipped reproduction, or partial migration, whereby certain individuals in a population are temporarily unobservable at a particular site. TE may be a flexible condition-dependent strategy that allows individuals to mitigate effects of adverse conditions. Consequently, TE rates ought to be highly variable, but sources of variation are poorly understood for most species. We used capture-mark-recapture data from known-aged female Weddell seals (*Leptonychotes weddellii*) tagged in Erebus Bay, Antarctica to investigate sources of variation in TE rates prior to reproduction and to evaluate possible implications for recruitment (first reproduction) into the breeding portion of the population. TE rates were near 1 the year after birth, decreased by age 8 to an average of 0.15 (sd = 0.16), and were similar thereafter. TE rates varied substantially from year-to-year and were lower for seals that attended reproductive colonies the previous year than for seals that did not attend. Recruitment rates were marginally greater for seals that did attend than for seals that did not attend colonies the previous year. For Weddell seals specifically, our results suggest that 1) motivation to attend colonies varied temporally, 2) as seals grew older they had increased motivation to attend even before reproductive maturity, and 3) seals appear to

follow variable attendance strategies. More broadly, our results support the idea of TE as a variable, condition-dependent strategy, and highlight the utility of TE models for providing population and life-history insights for diverse taxa.

Introduction

The analysis of long-term data with statistical capture-mark-recapture (CMR) models is useful for estimating, and testing hypotheses about demographic rates of wild populations (see reviews in Lebreton *et al.* 1992; Williams, Nichols, & Conroy 2002). For example, long-term CMR analysis has yielded insights about disease dynamics, reproductive costs, transition probabilities between different life-history stages and implications for various demographic rates of environmental conditions experienced at different life-history stages (e.g., Gaillard *et al.* 1997; Reid *et al.* 2003; Hadley *et al.* 2007b; Conn & Cooch 2009). One well-known assumption of CMR studies is that emigration from a study area is permanent; when such emigration occurs, estimates of apparent survival are the product of true survival rates and site-fidelity rates. However, in many species certain individuals may make non-permanent moves away from a site, and those moves may not follow the predictable and repeatable patterns of migratory moves. Such movement is called temporary emigration (TE) in the ecological literature (e.g., Spendelow & Nichols 1989; Kendall *et al.* 1997; Converse *et al.* 2009). If ignored, TE can, under certain, plausible conditions, bias estimates of survival, detection, or breeding probabilities, and modeling TE can sometimes cause parameter redundancy (Kendall & Nichols 2002; Kendall 2004; Schaub *et al.* 2004; Bailey, Converse, & Kendall 2010).

Even when explicitly modeled, non-random TE can sometimes bias survival estimates at the end of a time series, especially when both TE and survival are temporally variable (Langtimm 2009). Consequently, much recent literature has focused on technical aspects of modeling TE. However, from a CMR perspective, TE can be defined as a transition by individuals into any sort of behavior that causes them to be unobservable until they transition out of that behavior, and improved understanding of variation in such transitions ought to also provide important insights about life history, ecology, and population dynamics of diverse species.

A useful way to model TE is to define 1 or more unobservable states that encompass, but perhaps do not differentiate behaviors that cause individuals to be unobservable, and then to estimate transition probabilities into those states using multistate mark recapture (MSMR) models (Kendall & Bjorkland 2001; Kendall & Nichols 2002; Lebreton *et al.* 2009). The classification or interpretation of behaviors as TE depends on the study system, the perspective of the observer, and the temporal scale at which observations are made. Temporary emigration is sometimes implicitly acknowledged in ecological studies, but careful definition of, and explicit estimation of transitions into unobservable states is relatively rare. One example of TE is the absence from breeding areas of some immature individuals or adults skipping reproduction. Such behavior has been documented or explicitly modeled as TE in pinnipeds (e.g., Schwarz & Stobo 1997; Beauplet *et al.* 2005; Hadley *et al.* 2007b; de Bruyn *et al.* 2011), whales (e.g., Fujiwara & Caswell 2002; Bradford *et al.* 2006), colonial birds (e.g., Frederiksen & Bregnballe 2000; Converse *et al.* 2009), and pond-breeding amphibians (e.g., Bailey *et*

al. 2004; Muths *et al.* 2006). In rare cases it may be possible to observe individuals at all known populations centers, thus obviating the need to estimate or account for TE; such appears to be the case with Hawaiian monk seals (*Monachus schauinslandi*; Baker & Thompson 2007). Seasonal movements of individuals to breeding areas is analogous to migration (Dingle 1996), and TE by some individuals in some years is analogous to partial migration, (i.e., when there is a variable segment of the population that migrates; see White *et al.* 2007; Jahn *et al.* 2010). At shorter temporal scales, foraging trips away from colonies (Lunn, Boyd, & Croxall 1994) could be modeled as TE, provided transition periods are appropriately defined. Dispersal of young from a natal location to an adult breeding area or inter-annual dispersal of adults typically is permanent (Dobson & Jones 1985) and thus do not typically fit into a TE framework. However, inter-annual breeding dispersal between sub-populations of a metapopulation could be manifested as TE if observations are made at only one or a few sub-populations; in this case TE would not equate to reproductive skipping. Temporary emigration also need not entail absence from a location. In small mammal studies, underground torpor or temporary movement off a trapping grid constitutes TE (e.g., Kendall *et al.* 1997), and in plants, annual underground dormancy rates can be estimated by modeling TE (e.g., Kéry, Gregg, & Schaub 2005).

In many populations, individual decisions whether to move (or to become dormant) or not in a given year may depend on current environmental conditions or status of individuals, and many ecologists are interested in understanding such variation in, and consequences of such movement choices (Ims & Hjermann 2001; Hoover 2003; White *et al.* 2007; Holyoak *et al.* 2008; Jahn *et al.* 2010). Unfortunately, inferences that can be

made from CMR studies about movements away from a site generally are limited when animals are sampled from only that single study site (Nichols & Kaiser 1999). However, if absences are temporary and represent ecologically interesting phenomena such as skipped or delayed breeding (e.g., Clobert *et al.* 1994; Schwarz & Stobo 1997; Kendall & Bjorkland 2001; Lebreton *et al.* 2003), or dormancy (Kendall *et al.* 1997; Kéry *et al.* 2005), then estimates of TE can be useful and ecologically interesting, even when populations are sampled from only a single site.

For colonial breeding species, TE might be advantageous if it allows adults skipping reproduction or immature individuals to avoid potential costs to future survival resulting from lost foraging opportunities away from breeding areas, conflict with reproductive adults, or increased risk of predation (Testa et al. 1985; Crespin et al. 2006). However, many immature individuals or adults skipping reproduction sometimes do attend breeding sites, and such attendance can improve subsequent breeding success (Schjørring *et al.* 1999; Aubry *et al.* 2009b). For example, close association with reproductive adults may facilitate the gathering of information or social skills (Danchin *et al.* 2004) or may synchronize ovulation and reproduction (McClintock 1978; Langvatn *et al.* 2004). If a major motivation for TE is greater access to resources, then individuals in the poorest condition should have the greatest motivation to avoid possible costs associated with attending colonies. Also, TE rates might increase during years when environmental conditions are poor if such conditions results in decreased ability or unwillingness by individuals to risk costs to survival (Frederiksen & Bregnballe 2000). For long-lived species, selection ought to minimize variability in survival at the expense

of other demographic rates (Pfister 1998). Thus, temporary emigration might be an important and temporally variable demographic rate.

Temporary emigration from breeding sites might have either positive or negative ecological implications for individuals, but little is known for most taxa about sources of variation in this rate. A population of Weddell seals (*Leptonychotes weddellii*) breeding in Erebus Bay, Antarctica is well suited for investigating TE because 1) the population lives in a temporally variable and relatively pristine environment that currently is little affected by anthropogenic perturbation (Ainley 2002); 2) an intensive mark-recapture study of this population has been conducted over multiple decades (Siniff *et al.* 1977; Cameron & Siniff 2004; Hadley *et al.* 2006); 3) TE is known to occur for both immature and mature seals at rates that likely vary among years as well as with animal age and reproductive state (Testa & Siniff 1987; Hadley *et al.* 2007b); and 4) female seals born in Erebus Bay exhibit remarkable site-fidelity, and surviving females eventually return to Erebus Bay to give birth to their first pup (Hadley *et al.* 2006; Cameron *et al.* 2007). Thus we are confident that failure to observe seals in Erebus Bay only very rarely equates to reproduction elsewhere. We used 28 years (1980 – 2008) of data from this population to estimate rates of TE of female Weddell seals prior to first reproduction, to evaluate sources of variation, and to evaluate possible implications for age-specific rates of first reproduction (recruitment). Seals were unobservable when absent, or perhaps in rare instances when they were briefly present, but never hauled out during any of the repeated surveys that were conducted. To make ecological interpretations, we therefore considered two behaviors: (1) colony attendance, which entails prolonged presence at breeding sites

within a breeding season such that seals are readily detectable, and (2) TE, which represents complete absence from, or unobservable presence at the breeding colonies for at least one year between birth and first reproduction.

Methods

Study Area and Population

Erebus Bay is located in southeastern McMurdo Sound in the western Ross Sea, Antarctica (Figure 2.1). Tidal action of fast-ice against land and the movements of the Erebus Glacier Tongue pushing against the fast-ice result in perennial cracks that provide reliable access for seals to the surface of the fast-ice (Stirling 1969; Siniff *et al.* 1977). Seal pupping colonies form at 8–14 of these perennial cracks, and from late October to mid-November approximately 300–600 pups are born on the ice surface. Females usually give birth to a single pup (Gelatt *et al.* 2001), and mothers and pups remain in close association throughout the 30–45 day lactation period. Mothers rely primarily on stored body reserves for most of the lactation period (Eisert *et al.* 2005). Non-reproductive seals also routinely haul out in the study area and are also readily detected. Males defend underwater territories, and mating typically takes place near the end of the pupping season each year (Stirling 1969; Siniff *et al.* 1977).

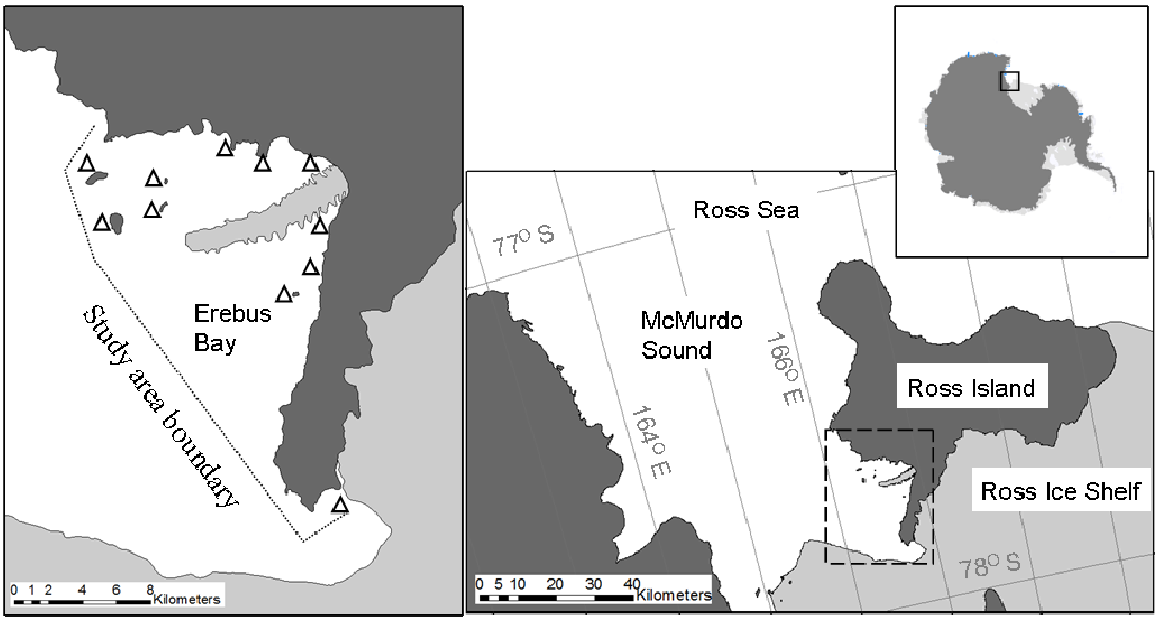

Figure 2.1. Erebus Bay study area, McMurdo Sound, Antarctica. Locations of the main pupping colonies are indicated by triangles.

Data Collection

Each year since 1969, Weddell seal pups in Erebus Bay were marked with 4 individually identifiable tags in the interdigital webbing of each hind flipper, and since 1979 nearly all pups born in Erebus Bay have been marked. Broken or missing tags on adults were subsequently replaced as necessary. Currently the majority of the female population is marked, and most marked seals are of known ages. From 1973 onward, 5–8 resighting surveys of the study population have been conducted annually (separated by 3–6 days) during early November through mid-December. Seals were highly approachable and tags usually could be read from within 0.5 m.

In this study, we used data from 5,450 female seals tagged as pups during 1980–2008, 1,300 of which were observed in at least one subsequent year, and 900 of which recruited into the study area's breeding population (mean age at 1st reproduction = 7.5,

SE = 0.05) by 2008. Two hundred thirty-three seals were not observed between the time they were born and when they first gave birth (mean age at 1st reproduction = 6.8, SE = 0.08), whereas 667 were observed at least 1 time during the same period (mean age at 1st reproduction = 7.7, SE = 0.06). For seals in the latter group, the mean age when they first were sighted after birth was 4.5 years (SE = 0.02) and the mean number of years observed as prebreeders was 2.1 (SE = 0.05). Most females attended colonies for ≤2 years prior to producing their first pup, and many attended zero years, but females clearly followed a variety of attendance strategies (Figure 2.2).

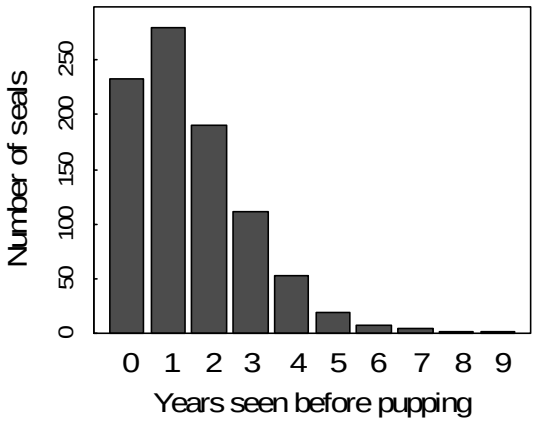

Figure 2.2. Number of years that known-age female Weddell seals were observed in Erebus Bay prior to being documented with their first pup. Given that seals were seen prior to recruitment, the mean number of years observed as prebreeders was 2.1 (SE = 0.05)

Predictions

We evaluated 3 possible sources of variation in TE and recruitment rates of female Weddell seals. We expected rates to vary with age, to vary depending on whether

or not a seal attended a reproductive colony in the previous year, and to vary temporally depending on annual conditions in either the current year or the year an animal was born.

We suspected that absence from breeding colonies early in life was partly motivated by limited food resources in Erebus Bay (Siniff *et al.* 1977; Testa *et al.* 1985) or by social conflict or competition between young seals and reproductive adults (Stirling 1969). Growth should be of primary importance to young seals, and given observed sighting patterns, we expected that TE rates would be very high for at least the first year or 2 of life. However, seals should have increasing motivation to attend the reproductive colonies as they approach reproductive size and maturity because pupping colonies are foci of mating activity where female seals might observe underwater territorial defense by breeding males and interactions of males and females (Siniff *et al.* 1977). Seals might also benefit from observing interactions of mothers with pups. Given that many seals are observed ≥1 time prior to recruitment, we expected that TE rates would decrease well before females reached reproductive maturity.

Based on resighting patterns and the known life history of Weddell seals (Stirling 1969; Hadley *et al.* 2006), we also expected that TE rates would be state-dependent (i.e., follow a first-order Markov process) for a given age such that seals absent in year t would be more likely to be absent again in year t+1 than seals that attended a colony in year t. Our hypothesis that attending colonies might facilitate beneficial information-gathering by seals also led to the prediction that recruitment rates in year t+1 should be greater for seals that attended breeding colonies in year t than for seals that did not attend. Alternatively, recruitment and TE rates might not be state-dependent (i.e., non-

Markovian) if the benefits of TE compensate for loss of benefits from attending colonies, or if colony attendance is relatively unimportant.

Given the assumption of reduced foraging opportunity or increased intra-specific conflict when seals attend colonies and given that this population of Weddell seals has been shown to buffer its demography from variability in survival (Rotella *et al.* 2012), we suspected that colony attendance might represent a trade-off of costs and benefits, the balance of which might vary with environmental conditions. We thus predicted that TE and recruitment rates would vary annually across all ages and cohorts. In contrast, we predicted that TE and recruitment rates would vary by birth cohort if environmental conditions experienced by pups exerted a greater influence on phenotype than did later environmental conditions. Annual environmental conditions can influence demographic rates such as dispersal (Dugger *et al.* 2010), recruitment (Crespin *et al.* 2006; Hadley *et al.* 2006), or breeding success (Nevoux & Barbraud 2006), but environmental conditions experienced in the first year of life may also affect phenotypic quality and demographic rates later in life (Lindström 1999; Forchhammer *et al.* 2001; Cam *et al.* 2003; Garrott *et al.* 2012). Such effects can be of either short or long duration. Birth-year effects may be temporary if compensatory growth can overcome early disadvantages (Bjorndal *et al.* 2003). We predicted that differences in recruitment or TE rates among cohorts would persist for only a few years if seals are able to overcome poor early life conditions.

Although our primary focus was on TE rates, we also evaluated several sources of variation in apparent survival (hereafter survival) probabilities. We predicted that survival would increase with age up to age 3 (Cameron & Siniff 2004; Hadley *et al.*

2006). Conditions at birth strongly influence early survival in several species of short-lived (Rödel, von Holst, & Kraus 2009) and long-lived animals (Gaillard *et al.* 1997; Forchhammer *et al.* 2001). We predicted a long-term cohort effect on survival if early conditions have greater influence on survival than more immediate conditions, and we also considered the possibility that cohort effects may only be temporary. In contrast, we predicted annual variation if current-year environmental conditions primarily influence survival. We did not have predictions about differences in survival rates depending on the TE status of seals, because generally such differences cannot be estimated (Kendall & Nichols 2002; Schaub *et al.* 2004) or testing for such differences is not possible (Bailey *et al.* 2010).

Data Analysis

We applied open robust design multistate (ORDMS; Kendall & Bjorkland 2001; Kendall 2006; Converse *et al.* 2009) models to encounter histories for 5,450 female seals born in Erebus Bay during 1980–2008. ORDMS models make use of multiple surveys per year to allow estimation of detection probabilities from within-season data, while properly accounting for staggered entry of seals into the study area (further modeling details in Appendix A). Because mothers with pups have a season-level detection rate of ~1.00 (Hadley *et al.* 2006; Rotella *et al.* 2009), we could reliably assign each seal 1 of 4 breeding state classifications each season: pup (N); prebreeder (P, seal attending the study area and never documented with a pup); unobservable (U, prebreeder not attending the study area); and breeder (B, recruit, or first-time mother with pup). Although we generally equated TE with absence from reproductive colonies, in some cases it might

have been possible for seals to briefly visit colonies but never haul long enough to be detected in one of our surveys. True absence and unobservable presence are indistinguishable from our data, but evidence from previous analysis suggests that prebreeders are highly detectable and that duration of attendance at colonies is usually long enough that seals are available for detection during ≥1 survey (Rotella *et al.* 2009). Temporary emigration was defined by transitions into U, including P to U ($\psi_{t,age}^{PU}$) as well as U back to U ($\psi_{t,age}^{UU}$), and recruitment as transitions into B ($\psi_{t,age}^{PB}$ or $\psi_{t,age}^{UB}$). Because the probabilities of all possible transitions for any given state logically must sum to 1, one transition rate for each state was derived by subtraction (see Appendix A for further details). Our choice of which transition rates to estimate directly was made so that our competing models focused on testing hypotheses about 2 types of transitions: into an unobservable state (TE) and into a breeding state (recruitment). Our goal was to investigate variation in vital rates of prebreeders, so we right-censored information for seals that recruited and only estimated rates for seals in states N, P, and U. Such censoring simplified the analysis by limiting the number of possible state transitions and was justified by the nearly certain detection of mothers.

We used a 2-step approach to model $S_{t,age}^{r}$ and $\psi_{t,age}^{rz}$, where for a given year or cohort, *t*, and state, *r*, $S_{t,age}^{r}$ is the probability of surviving and not permanently emigrating, and $\psi_{t,age}^{rz}$ is the probability, given survival, that an individual will make a transition into state *z*. We first modeled a suite of 3 a priori structures for temporal variation in $S_{t,age}^{r}$ with $\psi_{t,age}^{rz}$ modeled generally (age and time variation) and identified the

model with the lowest value for the bias-corrected Akaike's information criterion (AIC_c, Burnham & Anderson 2002). We then used this structure for $S^r_{t,age}$ in a second suite of models to evaluate competing hypotheses about $\psi^{rz}_{i,age}$. This approach efficiently identified the model with the lowest overall AIC_c value (Doherty, White, & Burnham 2010). The $S^r_{t,age}$ suite included 1 model that allowed $S^r_{t,age}$ to vary by year, where year effects were shared by all states and ages; this model evaluated the hypothesis that annual variation in environmental conditions influence all seals. Two competing models allowed $S^r_{t,age}$ to vary by cohort (either permanently or temporarily for 3 years after birth); these models evaluated the hypotheses that environmental conditions at birth influenced survival rates and that adult survival is less related to current environmental conditions. In each of the 3 structures for $S^r_{t,age}$ we allowed survival to vary by age, where age was modeled as a categorical variable with 3 nominal classes: 1, 2, and ≥3 (Hadley *et al.* 2006). Because hypotheses about state-dependent survival of females in an unobservable state cannot be differentiated on the basis of model selection (Bailey *et al.* 2010), we made the necessary assumption that $S^U_t = S^P_t$. Previous analysis suggests that biases in survival estimates because of non-random TE were minimal for this population of Weddell seals when TE was modeled as time-invariant (Hadley *et al.* 2007b). However when state-dependent TE and survival are both temporally variable, TE can cause negative bias in survival estimates at the end of a time-series (Langtimm 2009). Consequently, we avoided interpretation of survival estimates for the final 4 cohorts and focused primarily on possible ecological or biological reasons for state-dependent TE

rather than on technical implications of TE for survival estimates. Also, because not all parameters are identifiable in fully time-dependent models, in models with annual variation we set survival equal for the final 2 years and did not interpret survival for the final years. We adjusted all survival estimates for tag loss as described in Hadley *et al.* (2006).

To address hypotheses about temporal variation in transition probabilities, we allowed rates to vary either as a function of year or birth cohort. Cohort effects were either permanent or, for TE rates only, terminated 3 years after birth. We also considered whether transition rates were Markovian or not. In all models, we estimated ψ_t^{rU} for 10 nominal age classes (1, 2-3, 4, 5, 6, 7, 8, 9, 10, ≥11 years old) and ψ_t^{rB} for 7 nominal age classes (5, 6, 7, 8, 9, 10, ≥11 years old), and we evaluated 2 functional forms for age-related variation in transition rates. Age was treated as either a categorical variable that allowed transition rates for each age to vary independently from each other or used as a continuous variable in a quadratic model that allowed rates to increase for young age classes and to then level off or decrease for older age classes. We fixed $\psi_t^{PU} = 0$ for the first age-class because all seals in this age-class necessarily were pups and transition thus originated from state N. Also, we fixed $\psi_t^{rB} = 0$ for all seals aged <5 years because no seals in our dataset recruited prior to age 5. We constrained year effects to be shared across all ages and states (Hadley *et al.* 2006); we constrained cohort effects similarly. Age denotes a female's age at the end of an interval, i.e., $\psi_{t,age5}^{rz}$ is the probability that a 4-year-old seal in state *r* in year *t-1* will transition state *z* when she is 5 years old in year *t*.

Based on apparent patterns from previous within-year analyses (Rotella *et al.* 2009), we felt justified in modeling only 1 structure for within-year parameters, which, for a given year, *t*, secondary occasion *j*, and state, *r*, were: probability that an individual is a new arrival to the study area ($pent_{tj}^{r}$); probability of detection (p_{tj}^{r}); and probability of staying in the study area until secondary occasion $j + 1$, given entry *k* occasions prior (ϕ_{tjk}^{r}). We allowed $pent_{tj}^{r}$ to follow a state-dependent (states P, B and N pooled) linear trend for $j > 1$ (common for all seasons). Detection probability also was allowed to follow a year-constant and state-dependent (states N, P, and B) within-season linear trend. We allowed ϕ_{tjk}^{r} to vary only by state (N, P, and B). All within-season parameters were fixed to zero for state U.

We performed analyses in program MARK (White & Burnham 1999) through the RMark package (Laake *et al.* 2012) in program R (R Development Core Team 2012). Currently there is no general goodness-of-fit test for the type of ORDMS models we used in our analysis, and the median $\hat{c}$ procedure implemented into program MARK is not available for robust design data. In previous analyses of Weddell seal data from Erebus Bay with simpler models, Hadley et al. (2006) found only modest levels of overdispersion. Therefore we used AIC_c rather than quasi-likelihood AIC_c ($QAIC_c$) as our model selection criterion. However, to assess the possible influence on overdispersion on model selection results, we examined how model rankings changed as we increased $\hat{c}$ from 1.0 to 5.5, which is twice the highest level of overdispersion observed previously in these data (Hadley *et al.* 2007a).

Results

The best-supported model in the survival suite included a permanent cohort effect on $\hat{S}^{r}_{t,age}$ (Table 2.1). The top model retained its rank for all values of $\hat{c} \leq 5$. Based on this model, the majority of female seals were present on the first survey each year, and the probability of detection at least once during the season was >0.91 for prebreeders and >0.99 for pups and mothers (see Appendix A for further details). As predicted, $\hat{S}$ was greater for seals ≥2 years old ($\bar{\hat{S}}_{cohort} = 0.94$, $\overline{\widehat{SE}} = 0.01$) than it was for pups ($\bar{\hat{S}}_{cohort} = 0.63$, $\overline{\widehat{SE}} = 0.09$) or yearlings ($\bar{\hat{S}}_{cohort} = 0.55$, $\overline{\widehat{SE}} = 0.08$), for which 95% CIs overlapped broadly in each year (Figure 2.3). Survival rates dropped sharply for the final few cohorts, possibly reflecting some negative bias at the end of the time series (Langtimm 2009).

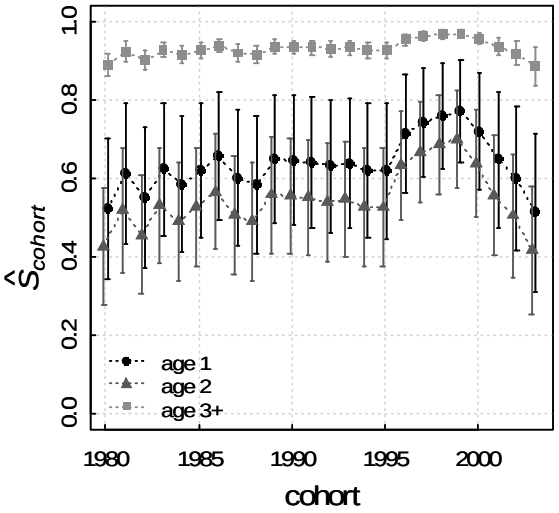

Figure 2.3. Apparent survival of pre-reproductive female Weddell seals in Erebus Bay, Antarctica for 3 age classes and 24 cohorts. Error bars represent 95% confidence intervals. Estimates are corrected for tag loss

Table 2.1. Model selection results for models representing hypotheses about variation in survival and transition probabilities for female Weddell seals in Erebus Bay, Antarctica. Only the top 3 models are shown for transition probability suite. Age structures are as follows: a3 = 3 nominal age classes (0, 1, 2+); a8 = 8 nominal age classes (0-4, 5, 6, 7, 8, 9, 10, 11+), and a11=11 nominal age classes (0, 1-2, 3, 4, 5, 6, 7, 8, 9, 10, 11+). A8 and A11 represent quadratic functional forms of the nominal age classes. AIC_c, ΔAIC_c, and w_i (weight of evidence for each model) values represent within-suite values. Coh represents a short-term cohort effect ending after 3 years. Markovian transitions are 1st order. See Table A.2 in Appendix A for complete model selection results.

Model	K	AICc	ΔAICc	w_i	Deviance
Survival-probabilities suite					
$S_{\text{a3+cohort}}$	108	74788.3	0.00	0.910	74571.7
$S_{\text{a3+year}}$	111	74793.5	5.21	0.067	74570.9
$S_{\text{a3+coh}}$	108	74795.6	7.32	0.023	74579.0
Transition-probabilities suite					
$\psi^{rB}{}_{\text{a8+year}}, \psi^{rU}{}_{\text{a11+year, Markovian}}$	108	74788.3	0.00	1.000	74571.7
$\psi^{rB}{}_{\text{A8+year}}, \psi^{rU}{}_{\text{A11+year, Markovian}}$	97	74833.9	45.57	0.000	74639.4
$\psi^{rB}{}_{\text{a8+cohort}}, \psi^{rU}{}_{\text{a11+year, Markovian}}$	108	74848.7	60.44	0.000	74632.1

Transition rates were very similar regardless of the parameterization of $\hat{S}^{r}_{t,age}$. Therefore, we used the top model in the survival-probabilities suite to further model $\psi^{rz}_{t,age}$. The best-supported model in the transition-probabilities suite received all the support from the data and included categorical age effects on $\psi^{rz}_{t,age}$, year effects that were shared among states and age classes, and state-dependant transitions (Table 2.1). The top model retained its rank for all values of $\hat{c} \leq 3.0$, and had >95% of the model weight for

values of $\hat{c} \leq 2.4$. Consequently, we present results from only the top model (See Appendix A, Table A.3).

Our top model supported our predictions of age- and state-dependency in annual TE rates (Figure 2.4). As expected, first-year TE rates were close to 1 ($\bar{\hat{\psi}}^{NU}_{t,age1} = 0.98$, $\overline{\widehat{SE}} = <0.01$, $sd\left[\hat{\psi}^{NU}_{t,age1}\right] = 0.021$), and estimates of TE rates decreased steadily with age. The average point estimates of TE rates were lowest at age 8 years ($\bar{\hat{\psi}}^{PU}_{t,age8} = 0.15$, $\overline{\widehat{SE}} = 0.02$, $sd\left[\hat{\psi}^{PU}_{t,age8}\right] = 0.16$), but estimates were similar across age classes for females >5 years old (Figure 2.4). As predicted, TE rates were higher for females that had been temporary emigrants in the previous year ($\hat{\beta}_{Markovian\ effect} = 1.4$, $\widehat{SE} = 0.10$, 95% CI = 1.2 to 1.6; e.g., $\overline{\hat{\psi}^{UU}_{t,age8} - \hat{\psi}^{PU}_{t,age8}} = 0.204$, $sd\left[\hat{\psi}^{UU}_{t,age8} - \hat{\psi}^{PU}_{t,age8}\right] = 0.084$). Temporary emigration rates also varied considerably from year-to-year, especially between 2000 and 2007. For example, $\hat{\psi}^{PU}_{t,age8}$ was 0.088 ($\widehat{SE} = 0.019$) in 2003, 0.766 ($\widehat{SE} = 0.046$) in 2004, and 0.049 ($\widehat{SE} = 0.014$) in 2007. Such variability is consistent with our hypothesis that highly variable environment conditions should influence motivation or ability of prebreeders to attend colonies.

Recruitment rates were also strongly age-dependent, varied by year, and depended on a female's TE status in the previous year (Figure 2.4). Recruitment rates were low at age 5 ($\bar{\hat{\psi}}^{PB}_{t,\,age5} = 0.06$, $\overline{\widehat{SE}} = 0.02$, $sd\left[\hat{\psi}^{PB}_{t,\,age5}\right] = 0.03$), increased gradually, and, depending on TE status in the previous year, peaked at either age 10 ($\bar{\hat{\psi}}^{PB}_{t,\,\text{age }10} = 0.52$, $\overline{\widehat{SE}} = 0.06$, *sd*

$\left[\hat{\psi}^{PB}_{t,\text{ age 10}}\right]$ = 0.18) or age 8 ($\bar{\hat{\psi}}^{UB}_{t,age8}$ = 0.35, $\overline{\widehat{SE}}$ = 0.05, $sd\left[\hat{\psi}^{UB}_{t,age8}\right]$ = 0.15). As expected in a highly variable environment, annual variation in recruitment rates was substantial, and year-to-year variation was especially pronounced between 2000 and 2007. For example, $\hat{\psi}^{PB}_{i,\text{ age 8}}$ was 0.66 ($\widehat{SE}$ = 0.06) in 2002, 0.09 ($\widehat{SE}$ = 0.03) in 2004, and 0.53 ($\widehat{SE}$ = 0.05) in 2007. As predicted, recruitment rates were greater for seals that were present the previous year (e.g., $\overline{\hat{\psi}^{PB}_{t,age8} - \hat{\psi}^{UB}_{t,age8}}$ = 0.13, $sd\left[\hat{\psi}^{PB}_{t,age8} - \hat{\psi}^{UB}_{t,age8}\right]$ = 0.05). However, 95% confidence intervals for the effect of TE on recruitment included zero ($\hat{\beta}_{Markovian\ effect}$ = -0.11, $\widehat{SE}$ = -0.11, 95% CI = -0.32 to 0.10).

Discussion

Using a 28-year time series of encounter histories of female Weddell seals, we were able to evaluate hypotheses and predictions about temporal variation and state-dependency in age-specific TE rates for a long-lived marine mammal. Our predictions about age-related and annual variability in TE and recruitment rates and about state dependent TE rates were supported by our results. Our data also provided some evidence that a female's recruitment rate was related to her TE status in the previous year. Observed variability in survival rates among cohorts likely account for observed differences in the proportion of each female Weddell seal birth cohort that eventually recruits into the pup-producing portion of the population (Garrott *et al.* 2012).

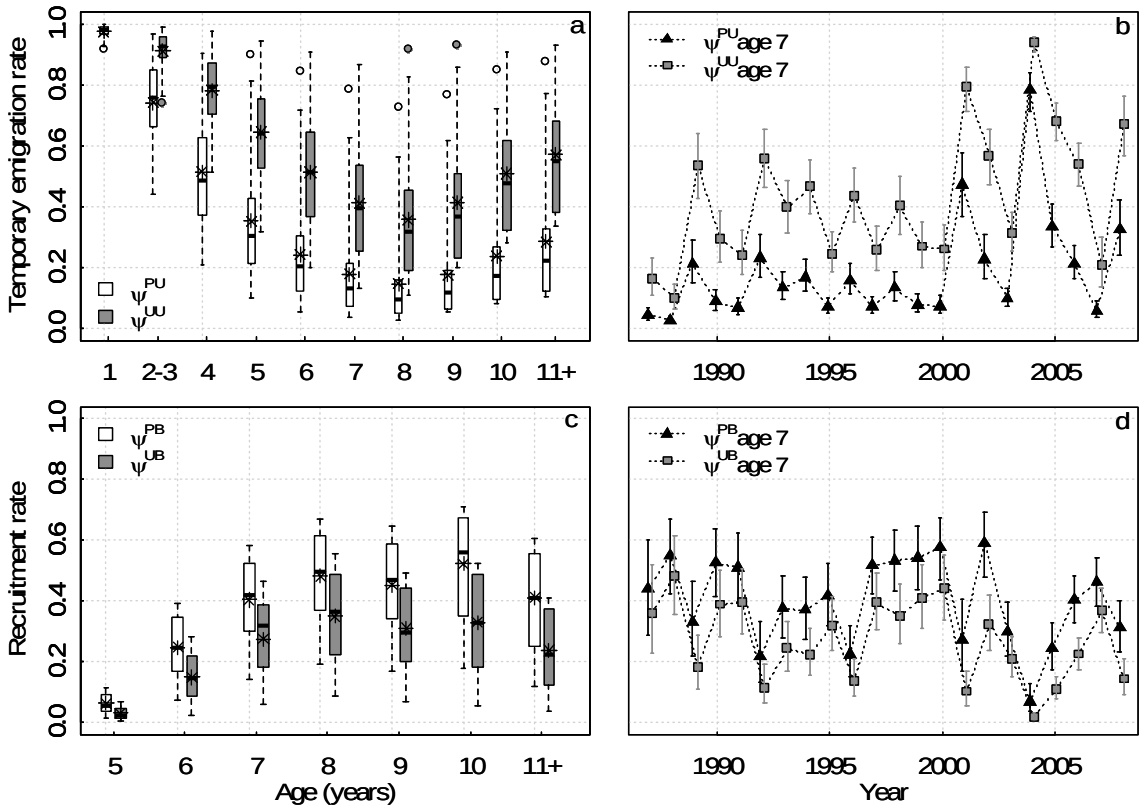

Figure 2.4. Temporary emigration rates (a, b) and recruitment rates (c, d) of pre-reproductive female Weddell seals in Erebus Bay, Antarctica. Estimates are generated from the best supported model (Markovian transitions, annual variation shared among ages; see Table 1), and are presented for seals that were observable in the study area the previous year ($\hat{\psi}_t^{PU}$, $\hat{\psi}_t^{PB}$) or were unobservable (temporary emigrants) the previous year ($\hat{\psi}_t^{UU}$, $\hat{\psi}_t^{UB}$). (a and c) Summary of age-specific temporary emigration (a) and recruitment (c) rates with medians (dark bars), means (stars), and whiskers bounding 2.5th and 97.5th percentiles of annual point estimates, and (b and d) Annual rates and 95% confidence intervals for temporary emigration (b) and recruitment (d) rates of age 7 seals showing the temporal patterns shared in the model for each age class.

When reviewing our survival estimates, it is important to remember that Markovian TE is known to sometimes cause negative biases in survival estimates at the end of time series, especially when survival rates are high and TE rates are variable (Langtimm 2009). Accordingly, we avoided making interpretations about or presenting

survival estimates for the final few cohorts. However, given that the lowest survival estimate is for the final cohort we do present (Figure 2.3), it is possible that a slight negative bias remains for the final year or 2 of the time series we present. It is unlikely that such biases propagate back to earlier years (Langtimm 2009).

As expected, temporary emigration rates were high for young animals, decreased substantially prior to the age where recruitment was possible, and once seals made the transition to an observable state they were less likely than temporary emigrants to be unobservable the following year (Figure 2.4). These results support the notion of a threshold body size or condition necessary for attending colonies (Laws 1956), and also provide some circumstantial evidence that, as they grow older, Weddell seals have motivation to attend colonies beyond that of immediate mating. One possible motivation might be to gather information that could improve subsequent reproductive success (Danchin *et al.* 2004). Current evidence of such benefits for prebreeders primarily comes from studies of colonial-breeding seabirds (Schjørring *et al.* 1999; Aubry *et al.* 2009b), but some reproductively mature birds (e.g., Doligez, Danchin, & Clobert 2002) and lekking mammals (e.g., Deutsch & Nefdt 1992) also might use information from conspecifics to assess quality of future nesting locations or to assess potential mates. Prebreeder Weddell seals may observe the interactions of mother-pup pairs during birth and lactation, and during the initial swimming bouts of pups. For example, mothers often help pups to haul out by reaming ice holes with their teeth. Inasmuch as the Weddell seal mating system is comparable to lekking (Stirling 1969; Siniff *et al.* 1977), prebreeders also might gain experience in assessing male quality when attending colonies in years

prior to recruitment. Lastly, most surviving female seals born in Erebus Bay eventually recruit at 1 of the reproductive colonies in Erebus Bay (Stirling 1969; Cameron & Siniff 2004; Hadley *et al.* 2006), and prospecting within Erebus Bay might help prebreeders evaluate the quality of specific colonies.

Predator avoidance might also provide motivation to attend colonies, which, in striking contrast to the situation for many colonial-breeding species, typically are safe locations inaccessible to important predators during the breeding season (Testa 1994). Thus, prebreeders in good condition may be able to forgo better foraging opportunities to attend colonies and avoid predation, and perhaps simultaneously acquire useful information. Necessary modeling assumptions precluded a test for differences in survival for seals that did or did not attend reproductive colonies. However, such a test also is irrelevant for the youngest age classes, which are most likely to have state-dependent survival rates, because they are almost entirely absent from Erebus Bay. Apparently, most young seals initially cannot afford to attend colonies regardless of any possible benefits from such attendance.

The state-dependent TE rates that we observed (Figure 2.4), along with the observation that many seals apparently recruited without first attending colonies (Figure 2.2), suggest that prolonged TE could be a strategy emphasizing improved body condition over potential benefits of information-gathering at reproductive colonies. Emigration behavior and foraging efficiency, especially in adverse conditions, can be influenced by phenotype and genotype (Ims & Hjermann 2001; McMahon & Matter 2006; Lescroël *et al.* 2010). Benefits of improved body condition from prolonged TE

could include earlier onset of reproduction than would otherwise be possible or the ability to produce larger pups, which are more likely to survive (McMahon, Burton, & Bester 2003; Proffitt, Garrott, & Rotella 2008b). It is possible that attendance strategies influence choices of recruitment locations, interactions with pups, or long-term reproductive trajectories. Accumulating data on parturition and weaning masses of first-time mothers and their pups should prove useful for evaluating possible trade-offs of alternative TE strategies followed by prebreeders. For at least one species (black-legged kittiwakes; *Rissa tridactyla*) an information-gathering strategy rather than a strategy of prolonged TE resulted in the greatest long-term reproductive success (Aubry *et al.* 2009b). Postulating benefits of TE rests on the reasonable assumptions that TE allows higher-quality foraging than is possible in the reproductive areas, and that such increased opportunity can translate into improved body condition. Validating these assumptions will require currently unavailable data on actual movements and body conditions of seals.

We observed considerable annual variation in recruitment and TE rates, which suggests that perhaps one or both types of demographic rates are influenced by variation in annual environmental conditions. In particular, our results indicate a period of increased TE rates and roughly correspondent decreases in recruitment rates after 2000 (Figure 2.4b, d), with a possible consequent increase in the average recruitment age (7.1, SE = 0.6 before 2004; 8.3, SE = 09 afterward). During this period, an unusually large iceberg that broke off the Ross Ice Shelf became grounded in the Ross Sea northeast of Ross Island and dramatically altered sea-ice dynamics in McMurdo Sound and beyond, and also directly or indirectly influenced primary productivity and population dynamics

of top-trophic species (Arrigo *et al.* 2002; Arrigo & van Dijken 2003; Kooyman *et al.* 2007; Remy *et al.* 2008). Recruitment rates of Weddell seals rebounded sharply and TE rates dropped after the iceberg broke up and moved away from McMurdo Sound in 2006 (Fig. 3). It remains to be seen whether the average recruitment age will decrease. Although the mechanisms by which the iceberg might have influenced Weddell seal demographic rates remain somewhat unclear, the timing of shifts in recruitment and TE rates that we observed suggests that shifts likely are related to changes in ice conditions resulting from the grounding of this large iceberg. Sea-ice dynamics possibly influence TE rates by directly influencing food availability, by shifting spatial distribution of the best foraging areas, or by altering access to Erebus Bay and other alternative breeding locations. Primary production in the southwest Ross Sea tends to be greatest in years with minimal summer sea ice-extent (Arrigo & van Dijken 2003), and although lags in the presumed trophic cascades relevant to Weddell seal foraging ecology are not well described, increased productivity eventually should drive increased foraging success for Weddell seals, which in turn could motivate greater colony attendance as growth or maintenance needs are met. In contrast, in years with extensive fast-ice, the prey-rich marginal ice zone (Brierley *et al.* 2002) is distant from Erebus Bay, and colony attendance would necessitate more time away from high-quality foraging areas.

Consistent with life-history theory (Pfister 1998), Weddell seal population growth rate is most sensitive to changes in adult survival, and adult survival rate has low temporal variability (Rotella *et al.* 2012). In a highly variable environment, the costs and benefits of attending colonies also should be variable, and we suggest that Weddell seal

populations and other species might vary their TE rates in accordance with environmental conditions to buffer the effects of environmental variability, perhaps including annual population density (Rotella *et al.* 2009), on survival. The Southern Ocean environment is highly variable, and reproductive effort or success consequently varies considerably for colonial pinnipeds and seabirds (e.g., Nevoux & Barbraud 2005; Forcada, Trathan, & Murphy 2008). Prebreeder elephant seals (*Mirounga leonina*), subantarctic fur seals (*Arctocephalus tropicalis*), and Antarctic fur seals (*A. gazella*) typically are absent from reproductive colonies for the first few years of life (Hindell 1991; Lunn *et al.* 1994; Beauplet *et al.* 2005), and TE rates for subantarctic fur seals vary among cohorts and are state-dependent (Beauplet *et al.* 2005, 2006). Lake et al. (2008) estimated highly variable rates of detection for Weddell seals in eastern Antarctica, which may partly reflect variability in TE rates. In the northern hemisphere, colonial-breeding phocids such as northern elephant seals (*M. angustirostris*) and grey seals (*Halichoerus grypus*) have juveniles and non-reproductive adults that typically, but not always, are absent from the reproductive colonies (Sydeman *et al.* 1991; Pomeroy *et al.* 1994). We suspect that TE rates in many of the above populations might be highly variable among years.

Studies that explicitly estimate TE rates and provide ecological interpretations are uncommon in the ecological literature, but we believe that an understanding of variability in TE rates could provide life-history insights for diverse taxa, especially in cases where actual movement of individuals in a population cannot be followed. For example, partial migration is a common and often conditional phenomenon in many species, especially fish, birds, and mammals (e.g., White *et al.* 2007; Brodersen *et al.* 2008; Boyle 2008),

and can be manifested as TE if individuals are not observable in certain periods. Similarly, individuals skipping reproduction in certain years often, but not always are unobservable (Frederiksen & Bregnballe 2000; Rivalan *et al.* 2005; Muths *et al.* 2006; Converse *et al.* 2009), and TE models can be used to evaluate hypotheses about reproductive costs (Kendall *et al.* 1997; Hadley *et al.* 2007b; Converse *et al.* 2009). Temporary emigration models also can provide interesting insights about environmental and individual influences on patterns of torpor in small mammals (e.g., Kendall *et al.* 1997) or dormancy in herbaceous perennial plants (e.g., Kéry *et al.* 2005). Lastly, information about TE allows a fuller understanding of change in population size than is possible with estimates of only survival and reproduction. Based on our work and other examples cited here, we regard estimation of TE rates not as a nuisance but as an opportunity to gain useful insights about ecological and demographic processes of populations.

CHAPTER 3

INFLUENCE OF BIRTH-YEAR AND CURRENT-YEAR CONDITIONS ON SURVIVAL RATES OF FEMALE WEDDELL SEALS PRIOR TO FIRST REPRODUCTION

Abstract

In long-lived species, juvenile survival typically is lower and more variable than adult survival. Variation in juvenile survival rates can be related to birth- or current-year influences, and the duration of birth-year conditions can be short-term (survival filter), persistent (spoon effects), or intermediate. We used data from known-aged prebreeder female Weddell seals (*Leptonychotes weddellii*) tagged in Erebus Bay, Antarctica to evaluate the importance of birth- and current-year influences on survival and recruitment rates and the duration of birth-year influences on survival rates. Our results provide evidence that both birth- and current-year conditions acted in combination to influence survival. Survival rates differed for each cohort, but also were positively related to current-year winter sea-ice conditions ($\hat{\beta}_{ySIEw}$ = 0.19, SE = 0.09). Our estimate of the duration of a birth-cohort effect on survival was 6 years, indicating multi-year (intermediate) survival filters rather than short-term filters or permanent spoon effects. Survivorship from birth to age 6, considering the specific sequence of sea-ice conditions experienced by each cohort varied from 0.13 (SE = 0.04) to 0.42 (SE = 0.06), and averaged 0.25 (SE = 0.02). Recruitment rates varied annually, but a relationship with birth-year was not supported. Although for many species the influences of birth- or

current-year conditions on survival are well-studied, we suggest that modeling survival rates as a function of birth- and current-year influences simultaneously could lead to better understanding of survival patterns for other long-lived species, and improved stochastic models to project their population dynamics.

Introduction

Population growth rates of long-lived species often are most sensitive to changes in adult survival rates, but variability in juvenile survival rates may be responsible for much of the actual variation in population growth rates (Gaillard, Festa-Bianchet, & Yoccoz 1998). This is because in long-lived species, evolution of life-history strategies that minimize or buffer variability in adult survival are expected (Pfister 1998; Gaillard *et al.* 2000). In contrast, juvenile survival rates often are highly variable, perhaps in part because juveniles typically are less developed and less experienced than adults and are thus more vulnerable to mortality risks, especially during harsh conditions (McMahon, Burton, & Bester 2000; Forcada *et al.* 2008; Bonenfant *et al.* 2009).

Variability in juvenile survival rates can arise in diverse ways. Attributes of individuals or environmental conditions experienced around the time of birth or hatching can have either short-term or persistent influence on survival rates. When conditions experienced by young during development influence early survival, but have no further influences on fitness, they can be viewed as filters that simply allow fewer or more individuals to survive to maturity (e.g., Gaillard *et al.* 1997; Drummond, Rodríguez, & Oro 2011). Early conditions can also have persistent fitness consequences for diverse

taxa (Lindström 1999; Monaghan 2008), and such "spoon" effects (Grafen 1988) have been shown for various fitness components, including survival. The duration of birth-year influences could also be intermediate in duration, i.e., multi-year survival filters that blur the distinction between short-term filters and spoon effects.

Birth-year influences such as attributes of mothers, rearing environment, or birth location can introduce within- or among-cohort variation in survival rates (Gaillard *et al.* 1997; Reid *et al.* 2003; van de Pol *et al.* 2006; Hadley *et al.* 2007a; Rödel *et al.* 2009). Maternal attributes such as age and mass at parturition have been linked to short-term and persistent intra-cohort variation in survival rates, onset of breeding, and/or lifetime reproductive success (LRS; Hadley *et al.* 2007a; Rödel & von Holst 2009). Influences of maternal attributes might be especially important during harsh conditions when mothers mitigate their own mortality risk by passing survival costs on to their offspring (Martin & Festa-Bianchet 2010). McMahon and Burton (2005) observed variation in first-year survival of southern elephant seals (*Mirounga leonina*) related to weaning mass and birth-year environmental conditions. In subantarctic fur seals (*Arctocephalus tropicalis*), first-year survival, but not subsequent survival rates were related to pup growth rate during lactation and environmental conditions in the 6 months after weaning (Beauplet *et al.* 2005). Subordinate nestling blue-footed boobies (*Sula nebouxii*) had elevated stress hormone levels and suffered greater prefledging mortality than did singletons or dominant nestlings, but no differences were detected among the groups in subsequent rates of survival or reproduction (Drummond *et al.* 2011). In contrast, hatching order of kittiwakes (*Rissa tridactyla*) was related to long-term intra-clutch differences in survival

and recruitment probabilities (Cam *et al.* 2003). Similarly, oystercatchers (*Haematopus ostralegus*) raised in high-quality habitat had greater juvenile and adult prebreeder survival, were more likely to also settle in high-quality habitat as breeders, and had greater LRS than did individuals raised in low-quality habitat (van de Pol *et al.* 2006).

Short- or long-term effects can be related to individual attributes as in the above examples. They can also be related to environmental conditions experienced early in life and so be shared by entire birth cohorts. Food availability during development can influence growth rates of all individuals in a cohort (Larsson *et al.* 1998; Madsen & Shine 2000), but fitness consequences are not necessarily consistent across species or even among populations of the same species. In roe deer (*Capreolus capreolus*), birth-year environmental variation resulted in long-term differences among cohorts in survival rates and breeding abilities in one population whereas in another differences among cohorts were manifested only as a short-term filter influencing how many members of each cohort survived the first year or two of life (Gaillard *et al.* 1997). In red-billed choughs (*Pyrrhocorax pyrrhocorax*), both filter (survival early in life) and spoon effects (reproductive success later in life) were related to environmental conditions experienced during fledging (Reid *et al.* 2003).

Conditions experienced at birth can impact survival during subsequent years, but conditions throughout life can also exert influence, particularly for slow-maturing species experiencing substantial annual variation in environmental conditions. It might therefore be important to consider birth-year and subsequent current-year influences on variability in juvenile survival. Current-year environmental conditions might influence survival of

all extant cohorts similarly, but inter-cohort variation can persist because of conditions experienced during the birth year. Regardless of subsequent environmental conditions, the "filter hypothesis" predicts that age-specific survival rates will differ among cohorts at young ages but then be similar later in life, whereas the spoon hypothesis predicts persistent differences in age-specific survival rates. Even if conditions experienced at birth have little influence beyond the birth year, different cohorts could still have different survivorship to older ages simply because they experience different series of environmental conditions; however, annual survival rates for older age classes might be similar because all older animals are influenced by the same current-year conditions.

To address questions about the importance and persistence of birth-year influences and of current-year conditions on survival in long-lived species requires long-term data from populations in variable environments. We used 27 years of data collected from a population of Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica to evaluate the following: (1 & 2) the magnitude and duration of inter-cohort variation in survival rates, (3) potential associations between birth-year environmental covariates and inter-cohort variation in survival either early in life, later in life, or both, (4) potential associations between current-year covariates and variation in subsequent annual survival shared by surviving members of all cohorts; and (5) relative support for inter-cohort or inter-annual variation in recruitment rates. We restricted analysis to data from females prior to first reproduction (i.e., prebreeders) as this allowed us to focus our attention on survival during the life-history period when ~80% of females typically disappear from a cohort (Garrott *et al.* 2012). This population of seals lives in a polar environment with

substantial annual variation in ice conditions; maternal effects on survival and subsequent reproduction (Hastings & Testa 1998; Hadley *et al.* 2007a; Proffitt, Rotella, & Garrott 2010) as well as differences in survival among cohorts (Cameron & Siniff 2004) have previously been documented. Further, the proportion of each female cohort that eventually produces a pup varies fourfold, which likely results from either short-term filter effects or longer-term spoon effects of early conditions on survival (Garrott *et al.* 2012), or effects that are intermediate in duration.

Methods

Study Area and Population

Erebus Bay is located in McMurdo Sound in the southwestern Ross Sea, Antarctica, where sea-ice condition are highly variable (e.g., summer sea-ice extent in the Ross Sea varies five-fold from year-to year). In Erebus Bay, tidal action and glacial pressures create and maintain 8–14 sea-ice cracks in the same areas each year, and reproductive colonies of seals form each austral spring around these cracks. Weddell seals typically give birth to a single pup on the sea-ice surface during late-October to mid-November following a gestation period of approximately 9 months. Mothers and pups remain on the ice surface nearly continually for about a week post-parturition, after which they swim for brief periods each day. Lactation lasts 5–6 weeks, is supported primarily from resources that mothers accumulated during the previous summer and winter (Wheatley *et al.* 2007), and is terminated abruptly when mothers abandon pups. Many other seals are present in the colonies for ≥1 year prior to reproductive maturity

(prebreeders) or in years where they skip reproduction (skip-breeders). Most seals in the colonies spend a considerable portion of each day on the surface of the ice and consequently are highly detectable and approachable (Thomas & DeMaster 1983; Rotella *et al.* 2009).

Food resources for seals probably are limited in Erebus Bay (Testa *et al.* 1985), and adults and pups are believed to move out into food-rich foraging areas in the Southwest Ross Sea following the pupping season (Smith 1965; Burns, Castellini, & Testa 1999). Females born in Erebus Bay typically are not observed for ≥1 year following birth, but surviving females are highly philopatric and most prebreeders return to Erebus Bay for ≥1 year prior to recruiting into the reproductive population (Hadley *et al.* 2006). The mean age of recruitment is 7.6 years, and females typically produce one pup every 1.5–2.2 years thereafter (Hadley *et al.* 2006, 2007b).

Data Collection

Each year since 1969, Weddell seal pups born in Erebus Bay were marked with individually identifiable and paired plastic livestock tags attached to the interdigital webbing of each hind flipper. The proportion of pups tagged each year varied in the early years of the study, but since 1982, virtually all pups born in the study area have been tagged. Subsequently, broken or missing tags were replaced as necessary. Resighting surveys of the study population were conducted every 3–6 days (5–8 surveys/year) during early November through mid-December of each year. Our dataset included observations from 5459 female seals born between 1980 and 2007, 862 (16%) of which went on to produce a pup by 2007.

Covariates of Survival

The environmental covariates of prebreeder survival that we considered were (1) winter sea-ice extent (SIEw) for the Ross Sea sector measured just prior to the pupping season in September of year *t* , (2) summer sea ice-extent (SIEs) measured in February of year *t*+1 shortly after the end of the pupping season in year *t*, (3) Southern Oscillation Index (SOIw) averaged for the winter (July – September) prior to pupping in year *t*, (4) Southern Oscillation Index (SOIs) averaged for the summer (December – February) following the pupping of year *t*, and (5) Antarctic Dipole (ADP) averaged for the summer (December – February) following the pupping of year *t*. Microbial ice communities constitute a substantial portion an annual primary productivity in the Ross Sea (Arrigo & Thomas 2004), and winter sea-ice is important in the life cycle of krill (Loeb *et al.* 1997). Increased krill abundance may benefit Antarctic silverfish (*Pleurogramma antarcticum*), a primary food source for Weddell seals (Burns *et al.* 1998). Additionally, Weddell seals are better able to exploit resources under ice than are other Antarctic predators, and extensive winter sea-ice may reduce competition for prey. Therefore, we reasoned that Weddell seal mothers could build body reserves best in years with extensive winter sea-ice, and we predicted a positive relationship between birth-year SIEw and survival of prebreeders. Similarly, we predicted that current-year SIEw would be positively related to survival. In contrast, extensive summer sea-ice reduces the amount of open water available for phytoplankton blooms in the Ross Sea and apparently reduces foraging success of female Weddell seals during the summer and is negatively related to subsequent pup weaning mass (Proffitt *et al.* 2007a,b). However, extensive summer sea-

ice might also provide protection from predation for young seals. Therefore, we predicted that survival rates for prebreeders would be negatively related to birth-year SIEs, but positively related to current-year SIEs. Although sea-ice extent probably is an important factor in Weddell seal biology, large-scale, integrative indices may capture more environmental variation and thus better explain variation in vital rates than do local covariates (Stenseth *et al.* 2003). The Southern Oscillation Index (SOI) and the ADP are two such measures available for the Ross Sea. SOI is a climatic index based on sea-surface pressure differences in the Southern Ocean and commonly used as a measure of El Niño/Southern Oscillation (ENSO) strength. SOI is positively correlated with sea-ice extent in the Ross Sea (Kwok & Comiso 2002), and positive SOI phases have been linked to increases in seal pup weaning mass, population size, and reproductive rates (Testa *et al.* 1991; Proffitt *et al.* 2007a; Rotella *et al.* 2009). Therefore, we predicted increased survival for cohorts produced following positive SOI phases in either the winter or summer of the birth year or current year. The ADP is a climate mode reflecting high-latitude characteristics of ENSO forcing (Yuan 2004). For Erebus Bay seals, the ADP the summer following birth is positively related to eventual recruitment into the reproductive population (Garrott *et al.* 2012), and so we predicted that survival would be positively related to ADP during the summer months following birth. We recognize that population responses to environmental conditions may involve nonlinearities and time lags, but as a logical starting point we chose to restrict our analyses to linear and direct environmental effects. We used standardized values (mean = 0, sd = 1) of each of the environmental covariates in all analyses. SIE data were obtained from <ftp://sidads.colorado.edu/pub/

DATASETS/nsidc0192_seaice_trends_climo/ice-extent/nasateam/> and SOI data from <www.bom.gov.au/climate/current/soihtm1.shtml>. Covariate values varied substantially among years (Figure 3.1) and pair-wise correlations among covariates ranged from -0.16 to 0.42.

Besides environmental covariates, we also considered birth-year and current-year cohort size as covariates that might explain variation among prebreeder survival rates, where cohort-size is the count of pups born in Erebus Bay. It is likely that many environmental factors influence the ability of female Weddell seals to produce a pup in any given year, and pupping rates and cohort size should be greatest when overall environmental conditions are favorable for pup production. In Weddell seals, birth-year cohort size is positively related to the probability that a female seal will eventually recruit into the reproductive population (Garrott *et al.* 2012). Therefore, we viewed cohort size as an integrated index of overall environmental favorability, and we predicted that cohort size in either the birth year or the current year would be positively related to survival of prebreeders. Because the population of seals available to produce pups is finite, we expected that incremental increases in cohort size would diminish as environmental conditions improved. Therefore, we use the natural log of cohort size in our analyses rather than actual cohort size.

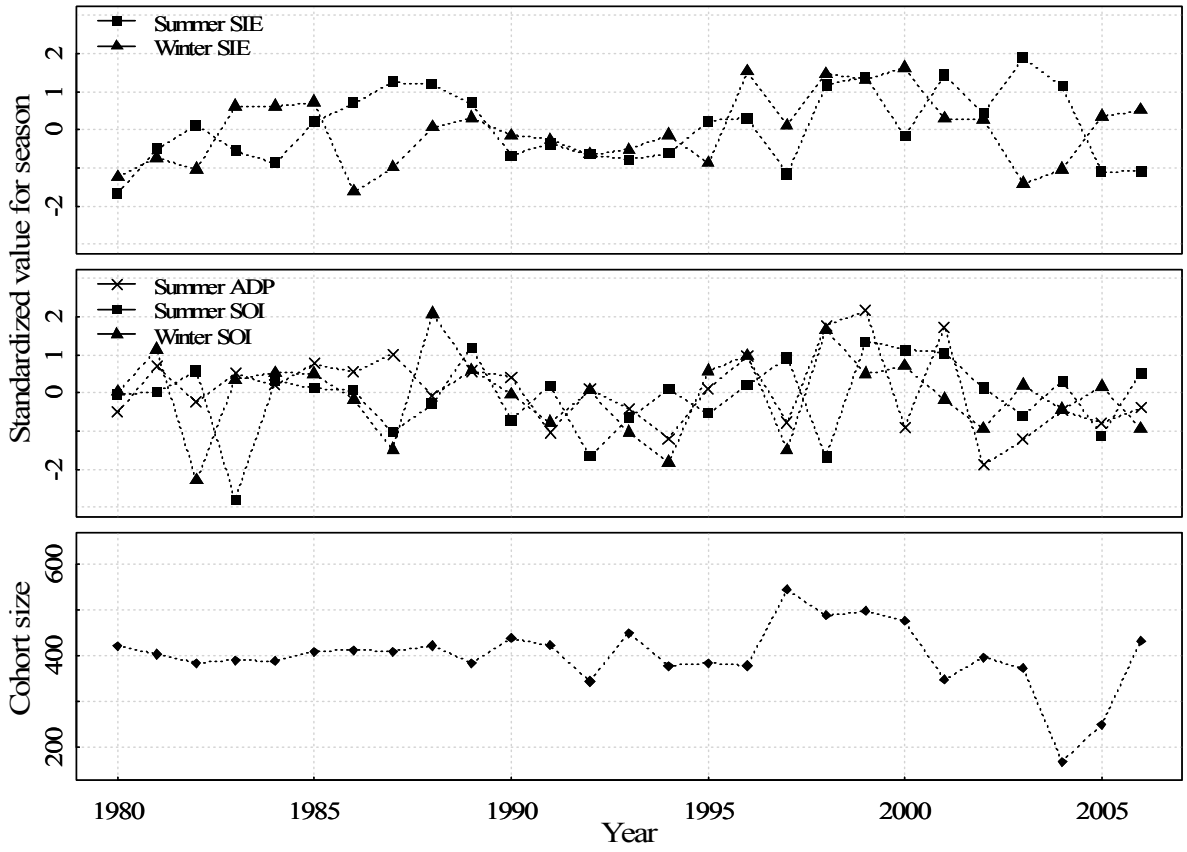

Figure 3.1. Covariate considered in models estimating survival rates of Weddell seals prior to first reproduction. Environmental covariate values are expressed as standardized values (mean = 0, sd =1), and cohort size was log-transformed (natural log) prior to modeling. Environmental covariates are Sea-ice extent (SIE), Southern Oscillation Index (SOI), and Antarctic Dipole (ADP).

Data analysis

We used multistate capture-mark-recapture models (e.g., Brownie *et al.* 1993; Nichols & Kendall 1995) to evaluate influences of environmental conditions on survival rates of female Weddell seals prior to first reproduction. Mothers with pups in this population are highly approachable and reliably detected each breeding season (Hadley *et al.* 2006; Rotella *et al.* 2009). Consequently, we could readily determine when females produced pups and could therefore reliably assign each seal into either a prebreeder (P,

present in the study area and never documented with a pup) or breeder (B, mother with pup) state each year it was observed. The transition from P to B between year *t* and year *t*+1 defined recruitment, and multistate models allow estimation of this recruitment probability each year. For the hypotheses evaluated here, we were interested primarily in survival rates prior to recruitment and so did not include encounters of females after they recruited into the breeding population. In conducting our modeling, we used age classes for prebreeders previously shown to be appropriate for this population (Hadley *et al.* 2006). Accordingly, survival was modeled for 3 age classes: age 1 = survival from birth to age 1 year, age 2 = survival from age 2 to age 3, and age 3+ = subsequent annual survival and detection probabilities were modeled for 4 age classes: ages 1, 2, 3–6, and greater than 6 years old. Recruitment probabilities were modeled for 8 age classes: ages 4, 5, 6, 7, 8, 9, 10, and 11+ years old. For example, recruitment at age 7 denoted the probability of making a transition from state P at age 6 to state B at age 7 years old. We used a 2-step model-selection process, first identifying an appropriate parameterization for survival probabilities, then modifying the top survival model to evaluate 2 different structures for recruitment (Doherty *et al.* 2010).

We considered 3 types of survival models a priori: models that included only influences of birth-year covariates, models that included only influences of current-year covariates, and models that combined influences of both the birth-year and the current year. We also evaluated models without environmental covariates that instead allowed survival to differ for each cohort (cohort effect) or each year. All covariates were modeled so as to influence log-odds of survival in a linear fashion. To avoid

overparameterization of combined models, we allowed only one current-year covariate or a year effect and one birth-year covariate or a cohort effect in each model, and we considered all possible combinations of such models. To evaluate duration of birth-year influences, we considered combined models that allowed birth-year effects to persist indefinitely or to last only for the first 2 years of life, when survival rates are substantially lower than later in life (Hadley *et al.* 2006). For example, when effects were persistent, the log-odds of survival differed for each cohort by a constant amount. When effects were short-term, the difference in log-odds lasted for only the first 2 age classes. We recognized that influences of birth-year conditions might be intermediate in duration, so after a priori analyses were completed, we also explored several models where the duration of birth-year influences was allowed to vary from 2-8 years. All exploratory models were modifications of the top-ranked a priori model. Previous analyses indicated that an appropriate model structure for detection and recruitment probabilities allowed variation among age classes and differences among years shared by each age class (Hadley *et al.* 2006), so we used this structure throughout when evaluating survival models. Once we identified our best survival model, we evaluated one additional model where recruitment rates were allowed to differ by cohort rather than year.

We performed analyses in program MARK (White & Burnham 1999) through the RMark package (Laake *et. al* 2012) in program R (R Development Core Team 2012). To evaluate goodness-of-fit, we used the median $\hat{c}$ procedure implemented in program MARK to estimate an overdispersion parameter, *c*, for our most general model. This model did not include cohort size or any environmental covariates and instead allowed

survival to differ by cohort and year. We subsequently used $\hat{c}$ to inflate the variances of our estimates and to calculate a bias-corrected and quasi-likelihood form of Akaike's information criterion ($QAIC_c$; Burnham & Anderson 2002), which we then used to rank models.

When individuals are typically absent for the first few years of life, their unavailability for capture can result in negative bias in survival rates for younger age classes near the end of the time series. In general, if data are collected from additional years when surviving, but previously unobservable individuals become available for capture, the bias disappears (Langtimm 2009). Because of this potential for negative bias, we avoided making inferences for cohorts born in the final 4 years of our time series, i.e., cohorts born in 2003-2006.

Results

We estimated overdispersion as 1.56 and accordingly used $QAIC_c$ to rank models and $\hat{c}$ = 1.56 to inflate variances of estimates. Detection probabilities were highly variable among years and very low for young seals ($\hat{\bar{p}}_{age1}$ = 0.03, SD = 0.02), but increased substantially for older seals ($\hat{\bar{p}}_{age7}$ = 0.54, SD = 0.20). These estimates largely reflect temporary emigration, as true detection rates for this population is nearly 1 (Chapter 2). Model selection results provided clear evidence of temporal variation in survival rates; models that allowed survival to vary by age but not over time received no support (Table 3.1). Models that combined birth-year and current-year influences were better-supported than models that included only birth-year or only current-year

influences, and models that predicted survival as a function of named birth-year environmental covariates or cohort size were not as well supported as models that simply allowed unique survival rates for each cohort (cohort effect). A persistent cohort effect was supported over a short-term cohort effect, but exploratory analysis indicated that the duration of birth-year influences on juvenile survival was intermediate. A model that allowed age-specific recruitment probabilities to vary by current-year was better-supported than a model that allowed variation to vary by birth cohort. Thus, the data provided no evidence for spoon effects on recruitment probability, but do indicate multi-year survival filters or non-permanent spoon effects on survival. However, we were not able to link such effects to any specific environmental covariates.

The best-supported a priori model included a persistent categorical cohort effect and, as expected, a positive influence of current-year SIEw ($\hat{\beta}_{ycohsize}$ = 0.19, SE = 0.09). The second ranked model ($\Delta QAIC_c$ = 1.14) was similar to the top-ranked model except that it included a short-term rather than persistent cohort effect. Three other models within 2 $QAIC_c$ units (Table 3.1) included persistent cohort effects and positive influences of either current-year ADP ($\hat{\beta}_{yADP}$ = 0.16, SE = 0.09), current-year cohort size ($\hat{\beta}_{ycohsize}$ = 0.30, SE = 0.41), or current-year SOIw ($\hat{\beta}_{ySOIw}$ = 0.15, SE = 0.09). In each of these 3 models, the sign of the relationship of the current-year covariate with juvenile survival was in the predicted direction, but 95% CIs for the estimated coefficient relating the covariate to survival overlapped zero. The best-supported model that did not include a categorical cohort effect ($\Delta QAIC_c$ = 2.78; Table 3.1) contained a persistent influence of

birth-year cohort size that, as predicted, was positive ($\hat{\beta}_{cohsize}$ = 0.40, SE = 0.23) as well as a positive influence of current-year SIEw ($\hat{\beta}_{ySIEw}$ = 0.32, SE = 0.05). Besides a model that included only a persistent cohort effect, the best-supported models among those that included only birth-year or current-year influences always included a positive influence of winter sea-ice extent (Table B.1 in Appendix B).

Estimates of first-year survival rates from the top-ranked model ranged from 0.45 (SE = 0.10) for a weak cohort (1980) in a hypothetical year with unfavorable (minimal extent) winter sea-ice conditions to 0.76 (SE = 0.07) for a good cohort (1999) in a year with favorable (maximal extent) winter sea-ice conditions (Figure 3.2a). Although the top model allowed age-specific survival rates to vary by cohort with no constraints on the pattern of variation, cohort-specific estimates of age-specific rates of survival were actually quite similar for most actual cohorts with only 2 of 23 1st-year survival estimates < 0.54 and four > 0.69 (Figure 3.2b).

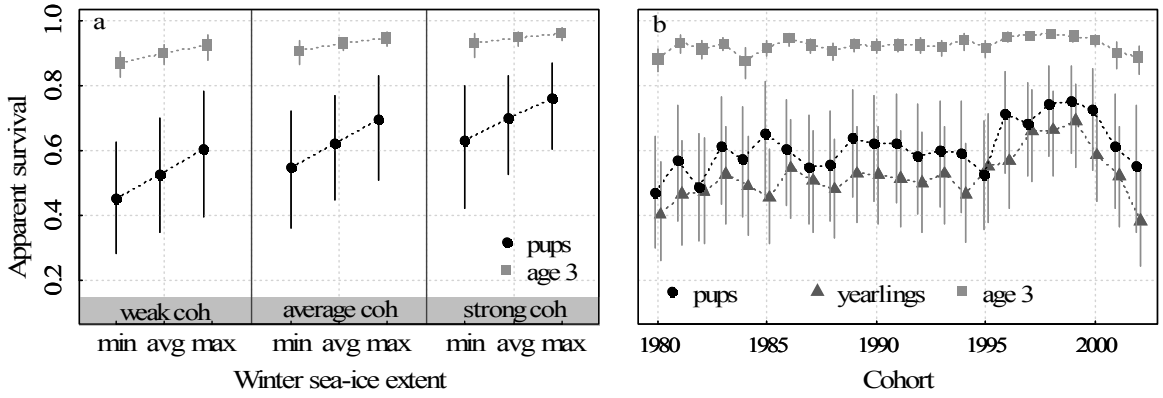

Figure 3.2. Predicted survival (a) for "weak", "average", and "strong" cohorts when SIE is minimal, average, or maximal, and estimated survival (b) from best-supported a priori model for 1st, 2nd, and 3rd-year survival. Error bars indicate 95% confidence intervals.

Table 3.1. Multistate model selection results representing structures of variation in survival (S_t) rates for female Weddell seals in Erebus Bay, Antarctica. Results are shown for all models that had $\Delta QAIC_c < 4$, and a model with no temporal variation. In all models, detection probabilities were modeled for 4 nominal age classes (1, 2, 3-6, ≥7 years old) and with time variation shared among all age classes. Similarly, in all models recruitment probabilities (transitions from a non-reproductive to a reproductive state) were modeled with annual variation shared among 8 nominal age classes (0-4, 5, 6, 7, 8, 9, 10, 11+ years). In all models, survival was modeled for 3 nominal age classes (0, 1, ≥2). K represents number of parameters in the model, Δ_i represents $\Delta QAIC_c$, QDev represents model deviance and w_i represents model weight.

Model[1]	K	$QAIC_c$	Δ_i	w_i	QDev
(136) cohort+ySIEw	88	12424.4	0.00	0.181	3364.2
(142) coh+ySIEw	88	12425.5	1.14	0.103	3365.3
(133) cohort+yADP	88	12425.9	1.47	0.087	3365.6
(132) cohort+ycohsize	88	12425.9	1.52	0.085	3365.7
(137) cohort+ySOIw	88	12426.1	1.66	0.079	3365.8
(66) cohort	87	12426.6	2.15	0.062	3368.3
(143) coh+ySOIw	88	12426.8	2.36	0.056	3366.5
(180) cohsize+ySIEw	64	12427.2	2.78	0.045	3415.9
(140) coh+ySIEw	88	12427.5	3.07	0.039	3367.2
(141) coh+ySOIw	88	12427.8	3.36	0.034	3367.5
(139) coh+yADP	88	12428.0	3.64	0.029	3367.8
(138) coh+ycohsize	88	12428.2	3.77	0.028	3367.9
(135) cohort+ySOIs	88	12428.3	3.93	0.025	3368.1
(135) no temporal variation	62	12499.4	75.0	0.000	3492.2

1. Categorical covariates are: cohort = permanent effect of birth year; coh = temporary effect of birth year; Current-year covariates are: ySIEw = effect of current-year winter sea-ice extent (SIE); yADP = effect of summer Antarctic Dipole; ySOIs = effect of summer Southern Oscillation Index (SOI); ySOIw = effect of winter SOI; ycohsize = effect of cohort size. Birth-year covariates are denoted similarly, but without preceding y, e.g., cohsize = effect of birth-year cohort size.

The data provided strong support for models in which birth- and current-year conditions are both related to juvenile survival rates and reasonable support for models

that included a persistent rather than a short-term influence of birth-year conditions. In exploratory analysis, we modified our top model to evaluate whether birth-year effects on survival might be of some intermediate duration. The best-supported exploratory model indicated that the duration for the influence of birth-year on survival rates was 6 years (Table 3.2), and this model had substantially more support than a model that allowed the influence of birth year to persist for only 2 years ($\Delta QAIC_c = 8.8$) or indefinitely ($\Delta QAIC_c = 7.7$). The second-best-supported model ($\Delta QAIC_c = 4.0$) allowed the influence of birth year to persist for 8 years.

We multiplied together age-specific survival rates from our top model and used the delta method (see Powell 2007) to estimate survivorship trajectories and associated uncertainties from birth to age 6 for: (1) hypothetical "strong" and "weak" cohorts that subsequently experienced consecutive years of either favorable or unfavorable sea-ice conditions; and (2) actual cohorts that experienced actual sea-ice condition. Both initial differences between cohorts and subsequent sea-ice conditions influenced survivorship trajectories (Figure 3.3). However, initial differences between cohorts appeared to have a greater influence on 6-year survivorship outcomes than did subsequent conditions, as indicated by the fact that most trajectories change little in relation to others (i.e., trajectories rarely cross; Figure 3.3d). The proportion of each actual cohort that was estimated to survive to age 6 varied from a low of 0.13 (SE = 0.04) to a high of 0.42 (SE = 0.06) and averaged 0.25 (SE = 0.02).

Table 3.2. Comparison of models where (1) duration of a birth-year influence on survival of female Weddell seals prior to first reproduction was allowed to vary from 2 years to >8 years, and (2) age-specific recruitment probabilities were modeled as a function of age and birth-year or age and current-year. In all models, survival was modeled for 3 nominal age classes (0, 1, ≥2 years old), and recruitment was modeled for 8 nominal age classes (0-4, 5, 6, 7, 8, 9, 10, 11+ years). K represents number of parameters in the model, Δ_i represents $\Delta QAIC_c$, QDev represents model deviance and w_i represents model weight.

Model	K	$QAIC_c$	Δ_i	w_i	QDev
Duration of birth-year influence					
6 years	88	12439.3	0.00	0.831	3379.1
8 years	88	12443.3	3.96	0.114	3383.0
4 years	88	12446.2	6.85	0.027	3385.9
more than 8 years	88	12447.0	7.67	0.018	3386.7
2 years	88	12448.1	8.81	0.010	3387.9
Source of variation in recruitment probability					
Current year	88	12447.0	0.00	1.000	3386.7
Birth year	88	12591.2	144.16	0.000	3530.9

We compared our best a priori survival model, which estimated age-specific recruitment probabilities as a function of the current-year, with an analogous model that instead estimated recruitment probabilities as a function of the birth-year. The model with inter-annual variation in recruitment probabilities (our best a priori model) was far better supported ($\Delta QAICc = 144.2$) than the model with inter-cohort variation in recruitment probabilities (Table 3.2). Age-specific recruitment probability was greatest for prebreeders of age 7 years and was highly variable among years; the average estimate for recruitment probability for this age class was 0.43 (SE = 04), but estimates varied from a low of 0.07 (SE = 0.03) to a high of 0.66 (SE = 0.07).

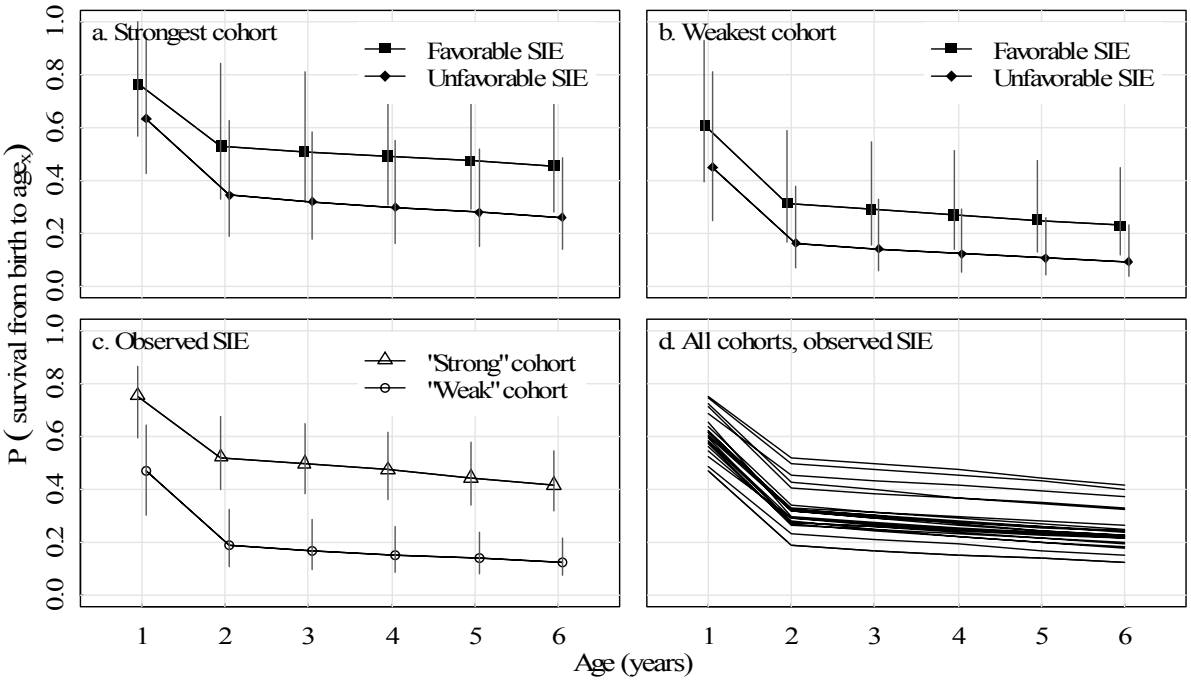

Figure 3.3. Predicted survivorship trajectories comparing (a) a "strong" cohort and (b) a "weak" cohort that each subsequently experienced consecutive years with either favorable or unfavorable winter sea-ice extent (SIE); and survivorship trajectories based on actual estimated survival rates for (c) a "strong" and "weak" cohort, and (d) all cohorts born during 1980 through 2003. Predictions were generated using survival estimates from our best-supported a priori model (Table 1) which allowed different estimates for each cohort, and a positive influence of current-year winter SIE. Error bars represent 95% confidence intervals.

Discussion

We evaluated birth-year and current-year influences on survival and recruitment rates of female prebreeder Weddell seals. Here we highlight 3 main results from our analysis. First, survival rates prior to first reproduction were influenced by (1) birth-year conditions that were unique to each cohort, but were not identified by any of our measured covariates; and (2) current-year conditions experienced by surviving members of all extant cohorts and best modeled using the extent of winter sea-ice. Second, the

influence of birth-year conditions on subsequent survival persisted for 6–8 years (about the length of the prebreeder period for a typical female) but did not appear to be permanent. Third, age-specific recruitment probabilities were influenced primarily by current-year conditions experienced by surviving members of all extant cohorts rather than by persistent influences of conditions experienced by pups or moms during or prior to the birth year. Thus, the influence of birth-year conditions on survival of Weddell seals does not appear to be a short-term survival filter such as those documented for other Southern Ocean pinnipeds (e.g., McMahon *et al.* 2000; Hall, McConnell, & Barker 2001; McMahon & Burton 2005; Beauplet *et al.* 2005). However, there also is little evidence that seals are endowed with life-long spoons resulting from environmental conditions experienced at birth. We view the influence of birth-year conditions as a multi-year filter or a shorter-term spoon effect generating inter-cohort variation in the proportion of individuals that eventually go on to produce young. Our results thus strongly support the suggestion by Garrott et al. (2012) that differences in survival rates among cohorts over the first several years of life, rather than difference in eventual age-specific recruitment rates, primarily determine what proportion of females in each cohort eventually produces pups. Although the duration of survival filters clearly was greater than 2 years, most of the variation in survivorship curves for different cohorts did occur in the first year or two of life, and most, though not all trajectories, did not change position relative to other trajectories (i.e., trajectories rarely crossed; Figure 3d).

Possible spoon effects resulting from maternal or individual attributions or natal location have been documented in Weddell seals and other species (e.g., Reid *et al.* 2003;

Cam *et al.* 2003; van de Pol *et al.* 2006; Hadley *et al.* 2007a; Proffitt *et al.* 2008b; Hadley *et al.* 2008; Rödel *et al.* 2009), and persistent differences in survival and reproduction among cohorts also have been documented (e.g., Gaillard *et al.* 1997; Reid *et al.* 2003). We cannot dismiss the possibility that, given recruitment, subsequent reproductive output by Weddell seals could be related to birth-year conditions experienced by all members of a cohort. However, we suggest that the eventual fitness of each cohort might be affected more by persistent influences of birth-year conditions on survival than by persistent influences of birth-year conditions on reproductive success.

We propose 2 plausible hypotheses to explain why annual survival rates for prebreeders from different birth cohorts might be similar beyond 6 to 8 years of age (about the average age of reproductive maturity; Hadley *et al.* 2006). First, once seals reach a certain threshold body size or condition, past inequalities might no longer matter, or might be evident only in senescence (Metcalfe & Monaghan 2001). Second, mortality might filter out the "frailest" members of each cohort (Cam, Link, Cooch, Monnat, & Danchin 2002), and tend to leave as survivors more of the higher-quality individuals that are less affected by unfavorable environmental conditions. The observations that age-specific recruitment probabilities do not vary among cohorts also is consistent with such a frailty hypothesis. Heterogeneous frailty has not yet been investigated in this population, but variation in reproductive quality among individuals has been proposed (Proffitt, Garrott, & Rotella 2008a; Hadley *et al.* 2008) and will be the subject of future investigations.

Our results suggest that current-year conditions and birth-year conditions both influenced survival. Although several environmental covariates were included in well-supported models, winter sea-ice extent was the best-supported covariate. Extensive winter ice is positively associated with krill abundances (Loeb *et al.* 1997), but current understanding of trophic connections between fish-eating seals and krill is limited. Based on the idea that the Ross Sea ecosystem is structured from the top down (Ainley, Ballard, & Dugger 2006), Garrott et al. (2012) suggested that Weddell seals, given their ability to dive deep and forage below extensive areas of ice, might face less competition from other top predators for food resources in years with extensive winter sea-ice extent. Evidence from several avian species of fish predators does indicate that species that need open-water areas for foraging suffer in years with extensive sea ice (Barbraud *et al.* 2000; Wilson *et al.* 2001; Jenouvrier, Barbraud, & Weimerskirch 2006). However, data are limited regarding other potential competitors such as cetaceans, other seal species, or Antarctic toothfish (*Dissostichus mawsoni*), which is also a potential prey item for Weddell seals (Ainley & Siniff 2009).

Population ecologists commonly use stochastic models to project population dynamics. We suggest that in some cases, especially when environmental covariates are used to predict survival, it might be important to account for persistent influences of birth-year conditions on survival as well as current-year conditions experienced by cohorts. Although we found evidence that birth-year influences on survival for prebreeders did not persist past 6–8 years of age, it is possible that conditions experienced near the time of birth might influence later reproductive performance or

patterns of survival (e.g., Metcalfe & Monaghan 2001; Reid *et al.* 2003). Birth-year conditions experienced by cohorts (or individuals) also might influence what set of future conditions is optimal for a given cohort of individual. For example, an individual born in harsh conditions might be better adapted for future poor conditions, relative to other individuals. In contrast, such an individual might be burdened with a "lead spoon" that exacerbates negative effects of poor conditions in the future (Monaghan 2008). By gaining better knowledge of environmental influences on Ross Sea productivity, and of the nature, timing, and strength of trophic links between primary producers and Weddell seals, we should be better positioned to predict influences of possible future environmental conditions on Weddell seal population dynamics. Furthermore, improved understanding of the roles of birth-year and subsequent environmental conditions in demography of other long-lived species ought to be useful for developing predictive models of population dynamics, especially in the face of projected changes in climate patterns.

CHAPTER 4

ENVIRONMENTAL CORRELATES OF TEMPORARY EMIGRATION AND CONSEQUENCES FOR RECRUITMENT OF FEMALE WEDDELL SEALS

Abstract

In colonial breeding species, prebreeders often emigrate temporarily from natal reproductive colonies then subsequently attend colonies for one or more years before producing young. Decisions about temporary emigration (TE) determine attendance patterns, and can influence subsequent probability of recruitment. Using open robust-design multistate models and 27 years of encounter data for prebreeding female Weddell seals (*Leptonychotes weddellii*), we evaluated competing models representing (1) hypotheses about the relationships of age-specific TE rates to environmental covariates or population size of adults seals the previous year, and (2) hypotheses about consequences of prior colony attendance for subsequent recruitment probability. TE rates were density-dependant ($\hat{\beta}_{BPOP} = 0.76,\ \widehat{SE} = 0.16$), increased when the fast-ice edge was distant from the breeding colonies ($\hat{\beta}_{DIST} = 0.81,\ \widehat{SE} = 0.04$), and were strongly age- and state-dependant, decreasing from nearly 1 at age 1 to an average of 0.15 ($sd = 0.16$) at age 8 for seals that had attended a colony in the previous year (0.40, $sd = 0.21$ for females that did not attend in the previous year). Recruitment rates also were age-and state-dependant. Seals that attended colonies for the first time in the previous year were more likely to recruit in the current year (e.g., mean rate at age 10 = 0.45, $sd = 0.15$) than seals that

never attended (e.g., mean rate at age 10 = 0.32, *sd* = 0.15), and seals that attended the previous year and at least 1 additional year had the greatest recruitment rates (e.g., mean rate at age 10 = 0.56, *sd* = 0.17), whereas rates were lower for seals that attended at least twice, but not in the year prior to recruitment (e.g., mean rate at age 10 = 0.32, *sd* = 0.15). Our observation of density-dependence and environmental influences on TE rates suggest annually shifting balances of potential tradeoffs between benefits and potential costs of colony attendance. Our results also provide some support for the hypotheses that colony attendance by prebreeders might facilitate acquisition of beneficial information or skills, or optimize timing of estrus in prebreeders with consequent increased probability of recruitment. Evaluation of subsequent reproductive success should provide additional insight about potential long-term implications of colony attendance by prebreeders.

Introduction

In long-lived colonial-breeding species, it is common for juveniles to be absent from breeding colonies for one or more years post-birth or hatching and to then subsequently attend colonies for one or more years prior to recruiting into the breeding population (e.g., Weimerskirch & Jouventin 1987; Cadiou, Monnat, & Danchin 1994; Beauplet *et al.* 2005; Crespin *et al.* 2006; Jenouvrier *et al.* 2008). When sampling occurs only at breeding sites, individuals that are alive, but absent from breeding colonies are unobservable and can be considered to have temporarily emigrated from colonies (Fujiwara & Caswell 2002). In some species (e.g., Halley, Harris, & Wanless 1995; Dittmann & Becker 2003), most prebreeders emigrate for about the same number of

years, nearly all surviving prebreeders return to their natal colony for the first time at a consistent age, or most individuals spend about the same number of years attending colonies as prebreeders. In other species, the number of years absent from breeding colonies or the number of years prebreeders attend colonies prior to recruitment varies considerably depending on characteristics of the individual or the environment (e.g., Weimerskirch & Jouventin 1987; Beauplet *et al.* 2005; Jenouvrier *et al.* 2008). Understanding the causes and consequences of variation in rates of temporary emigration (TE) or attendance (opposite of TE) is of considerable ecological interest, given that these patterns can influence age of recruitment and future reproductive success (Cam *et al.* 2002; Dittmann, Ezard, & Becker 2007; Aubry, Cam, & Monnat 2009a).

In several colonial-breeding species where TE of juveniles has been explicitly investigated, population-level TE rates vary considerably with age and among years (Chapter 2; Beauplet *et al.* 2005; Crespin *et al.* 2006; Jenouvrier *et al.* 2008). TE rates typically declined with increasing age, probably because older individuals have increased ability or motivation to attend colonies. Older individuals might be better able to navigate to colonies (Dittmann & Becker 2003) or might suffer fewer potential costs of attendance related to limited foraging opportunities or intra-specific conflict at breeding colonies (Furness & Birkhead 1984). Variation in food supply or foraging opportunities driven by environmental conditions can influence growth rates or body condition of individuals (Madsen & Shine 2000). Thus, environmental variability should generate annual variation in TE rates as individuals are less likely to attend colonies when conditions are unfavorable (Frederiksen & Bregnballe 2000; Jenouvrier *et al.* 2008). TE rates might also

be density-dependent (Rotella *et al.* 2009). Despite the prevalence of TE in the life-history of most colonial-breeding species, rigorous estimation of TE rates, especially as a function of environmental and population- or individual-level covariates remains rare in population studies.

One possible motivation for attendance of reproductive colonies by prebreeders is the opportunity to prospect for information or acquire reproductive skills by observing conspecifics. Possible prospecting behavior and consequent benefits have been investigated most often in avian species, especially colonial sea-birds (see review in Reed *et al.* 1999). Prebreeders that attend colonies for one or more years are more likely to recruit and breed successfully than individuals attending colonies for the first time (Halley *et al.* 1995; Dittmann *et al.* 2007). The age of recruitment and the extent to which prebreeders 'practice' breeding behavior has also been associated with subsequent breeding success (Cam *et al.* 2002; Aubry *et al.* 2009a). Prospecting kittiwakes (*Rissa tridactyla*) sometimes "squat" on active nests temporarily unoccupied by the nest owners, and this behavior appears to facilitate future mate pairing or acquisition of nearby nest-sites (Cadiou *et al.* 1994; Cam *et al.* 2002). Wandering albatross (*Diomedea exulans*) spend 2–8 years interacting with conspecifics at reproductive colonies prior to recruitment, and frequently pair up with a reproductive partner >1 year prior to mating (Pickering 1989). Prospecting might thus inform decisions about where or even how to recruit, especially when prebreeders participate in behavior typically associated with reproduction. That is, attendance of reproductive colonies by prebreeders and observation of conspecifics might facilitate social learning (see review in Galef Jr & Laland 2005)

and acquisition of certain social skills necessary for successful recruitment (Becker & Bradley 2007).

Some pinnipeds species also have a life-history of prolonged absence of prebreeders followed by ≥1 years of colony attendance prior to recruitment (e.g., Beauplet *et al.* 2005; Hadley *et al.* 2007b), but the implications of attendance for subsequent recruitment or breeding success are not as well-documented as for colonial seabirds. Prebreeders might benefit from observing pup births, interactions between mothers and pups during lactation or when pups first begin to swim, or by observation of mating interactions and potential mate quality. Mate choice by females has been shown for Antarctic fur seals (*Arctocephalus gazella*; Hoffman *et al.* 2007), and is a common feature of lekking species (see review in Balmford 1991). Sexual selection also has been proposed as one explanation for the evolution of coloniality (see review in Danchin & Wagner 1997).

Unlike birds, pinnipeds have long gestation periods such that individuals producing young in a given year must mate in the previous year (Atkinson 1997). Reproductive colonies are foci of mating activity, and thus another possible motivation for colony attendance by female prebreeders might be to initiate or synchronize estrus cycles by close association with reproductive adult females. Such synchronization occurs in several mammalian taxa, including humans (McClintock 1978; Handelmann *et al.* 1980; Stern & McClintock 1998). Although some seals likely mate while at sea (Gemmell *et al.* 2001; de Bruyn *et al.* 2011), attendance of reproductive colonies might increase the probability that first-time estrus is optimally timed.

Here we used 27 years (1983–2010) of capture-mark-recapture data for female prebreeders from a population of Weddell seals (*Leptonychotes weddellii*) breeding in Erebus Bay, Antarctica to investigate (1) causes of variability in age-specific TE rates in prebreeders and (2) possible motivations of attendance patterns and consequences for recruitment rates. This population is well suited for such investigation because Erebus Bay and surrounding marine regions are relatively pristine and experience considerable temporal variation in environmental conditions, multiple decades of encounter data are available for this seal population, individuals seals are easily approached, reproductive status is readily determined and thus recruitment can be reliably identified, and TE and recruitment rates are highly variable (Chapter 2; Hadley *et al.* 2006). We evaluated support for (1) the hypothesis that age-specific probability of TE is related to variability in the environment, local population size, or both; and (2) the non-exclusive hypotheses that attendance by prebreeders is motivated by opportunities to gather information, acquire skills, or facilitate timing or onset of estrus.

Methods

Study area and population

Erebus Bay is an embayment in Ross Island in southeastern McMurdo Sound. McMurdo Sound is located in the western Ross Sea, Antarctica, bounded to the east by Ross Island, and to the West by the Antarctic continent. Seal pupping colonies form each austral spring at 8–14 locations in Erebus Bay where tidal action and glacial pressures on fast-ice result in perennial sea-ice cracks that provide reliable access for seals to the

surface of the fast ice (Stirling 1969; Siniff *et al.* 1977). Approximately 300–600 pups are born on the surface of the fast-ice each year, with most births occurring between late October and mid November. Females give birth to a single pup after a gestation period of about 9 months, and then primarily use stored reserves to sustain a lactation lasting about 30–45 days. Mothers and pups remain in close association throughout the lactation period, and late in the lactation period mothers probably interact substantially with pups swimming under the ice. Lactation is terminated abruptly when mothers abandon pups and either move to a different part of the colony or leave the colony entirely. Many females that either have never produced a pup or currently are skipping reproduction also routinely haul out on the sea-ice surface. Males defend mating territories under the ice, where mating takes place under the ice near the end of the pupping season (Siniff *et al.* 1977).

Food resources for seals probably are limited in Erebus Bay (Testa *et al.* 1985), and adults and pups are believed to move out into food-rich foraging areas in the Southwest Ross Sea following the pupping season (Smith 1965; Burns *et al.* 1999; Stewart *et al.* 2000). Females born in Erebus Bay typically emigrate temporarily for ≥1 year following birth. Older females are highly philopatric to natal colonies and most prebreeders return to Erebus Bay for ≥1 year prior to recruiting into the reproductive population (Hadley *et al.* 2006; Cameron *et al.* 2007). The mean age of recruitment is 7.6 years, and females typically produce a pup every 1.5–2.2 years thereafter (Hadley *et al.* 2006, 2007b).

Data Collection

In this study, we used data from 5,550 female Weddell seals tagged as pups in Erebus Bay during 1983–2010. During these years, nearly all pups born in Erebus Bay were uniquely marked with 4 identical, numbered tags in the interdigital webbing of each hind flipper; broken or missing tags on adults were subsequently replaced as necessary. Currently the majority of the females in Erebus Bay are marked, and, because most were tagged as pups, are of known age. Resighting surveys of the study population were conducted every 3–6 days (5–8 surveys/year) during early November through mid-December. Seals were easily approached and tags usually were read from within 1 m.

Covariates of Temporary Emigration

We considered the following covariates of TE: (1) winter sea-ice extent (SIE) for the Ross Sea sector measured just prior to the pupping season in September of year *t*; (2) Southern Oscillation Index (SOI) averaged for the winter (July – September) prior to pupping in year *t*; (3) sea-ice concentration (SIC) averaged over eight 25-km grid cells in and around McMurdo Sound for November of year *t*; (4) shortest distance (DIST) from the edge of the fast-ice to Cape Evans, the northern border of the Erebus Bay study area, during the breeding season of year *t*; and (5) the size of the breeding population of females (BPOP) in year *t*–1. The first 2 covariates relate to food availability and the idea that in years with favorable conditions, females should be in better condition and more likely to forego foraging opportunities and attend reproductive colonies. Microbial ice communities constitute a substantial portion an annual primary productivity in the Ross Sea (Arrigo & Thomas 2004), and winter sea-ice is important in the life cycle of krill

(Loeb *et al.* 1997). Increased krill abundance may benefit Antarctic silverfish (*Pleurogramma antarcticum*), a primary food source for Weddell seals (Burns *et al.* 1998). Additionally, Weddell seals, given their excellent diving abilities (Castellini, Kooyman, & Ponganis 1992), probably are better able to exploit resources under extensive ice sheets than are other Antarctic predators, and extensive winter sea-ice may reduce competition for prey. Therefore, we predicted a negative relationship between SIE and TE. Large-scale, integrative indices may capture more environmental variation and thus better explain variation in vital rates than do local covariates (Stenseth *et al.* 2003). The SOI is a climatic index based on sea-surface pressure differences in the Southern Ocean and commonly used as a measure of El Niño/Southern Oscillation (ENSO) strength. SOI is positively correlated with sea-ice extent in the Ross Sea (Kwok & Comiso 2002), and positive SOI phases have been linked to increases in seal pup weaning mass, population size, and reproductive rates (Testa *et al.* 1991; Proffitt *et al.* 2007a; Rotella *et al.* 2009). Therefore, we also predicted decreased TE rates during positive SOI phases. SIC and DIST probably modify access to reproductive colonies by determining the distance seals have to swim under fast-ice or under highly concentrated pack ice to reach Erebus Bay. Thus we predicted a positive relationship between TE and DIST or SIC. Given the suggestion by Rotella et al. (2009) that TE rates of Weddell seals might be density-dependent, we predicted a positive relationship between TE and BPOP in the previous year.

We used standardized values (mean = 0, sd = 1) of each of the environmental covariates in all analyses. SIE and SIC data were obtained from

<ftp://sidads.colorado.edu/pub/ DATASETS/> and SOI data from <www.bom.gov.au/climate/current/soihtm1.shtml>. DIST was measured from geo-referenced satellite images dated as close as possible to 01 Nov; images were not available for all years, so missing values were assigned the mean value (zero, for standardized values). Population sizes were estimated annually following Rotella et al. (2009), and because estimates were very precise, we used point estimates and ignored uncertainty. We log-transformed population size prior to analysis.

Data Analysis

We used open robust design multistate (ORDMS; Kendall 2006; Converse *et al.* 2009) models to estimated demographic rates of Weddell seals. ORDMS models make use of multiple surveys per year, thus allowing estimation of detection probabilities from within-season data, while properly accounting for staggered entry of seals into the study area (full modeling details in Supplement). ORDMS models provide estimates for 5 types of parameters that account for within-season processes and between-season demographics (Table 4.1). We defined 7 possible breeding-state classifications (Figure 4.1): P0 (pup); U0 (unobservable prebreeder, never previously observed in Erebus Bay subsequent to birth); P1 (first-time observable prebreeder); U1 (unobservable prebreeder, previously observed once); P2 (observable prebreeder, previously observed ≥1 time); U2 (unobservable prebreeder, previously observed ≥2 times); and B (observable first-time mother). TE was defined as a transition into any of the unobservable states (e.g., $\psi_{t,age5}^{\mathrm{P1U1}}$ denotes a transition in year *t* by a seal in age class 5 from state P1 into the unobservable state U1), and recruitment as a transition into state B (e.g., $\psi_{t,age5}^{\mathrm{P1B}}$ denotes recruitment

from state P1 in year *t* by a seal in age class 5). Because the probabilities of all possible transitions for any given state logically must sum to 1, one transition rate for each state was derived by subtraction (see Appendix C for further details). Our choice of which transition rates to estimate directly was made so that our competing models focused on testing hypotheses about TE and recruitment. Our goal was to investigate possible sources of variation in transition rates of prebreeders, so we right-censored information for seals after they recruited. Such censoring simplified the analysis by limiting the number of possible state transitions and was justified by the near-perfect detection of mothers (Hadley *et al.* 2006). Although we equated TE with absence from reproductive colonies, it might have been possible for seals to briefly visit colonies but never haul out long enough to be detected in any of our surveys. However, evidence from previous analysis suggests that prebreeders are highly detectable and that duration of attendance at colonies is usually long enough that seals are available for detection on ≥1 survey (Rotella *et al.* 2009).

Based on the age structures found to be appropriate for prebreeder females in Erebus Bay (Chapter 2; Hadley *et al.* 2006), we estimated TE for 11 nominal age classes (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, ≥11 years old) and recruitment for 8 nominal age classes (4, 5, 6, 7, 8, 9, 10, ≥11 years old). Age, as specified here, denotes a female's age class at the end of an interval, i.e., $\psi^{rz}_{t,age5}$ is the probability that a 4-year-old seal in state *r* in year *t-1* will transition to state *z* when she is 5 years old in year *t*. We fixed to zero all transitions that were impossible based on our state structure. For example, $\psi^{P0z}_{t,age2} = 0$ because all seals in state P0 necessarily were pups and could not be in age class 2 at the end of the

next interval. Also, we fixed $\psi^{rB}_{t,age<4} = 0$ because no seals in our dataset recruited prior to age 4, and we fixed to zero any transitions out of B, because we censored encounter histories after seals recruited.

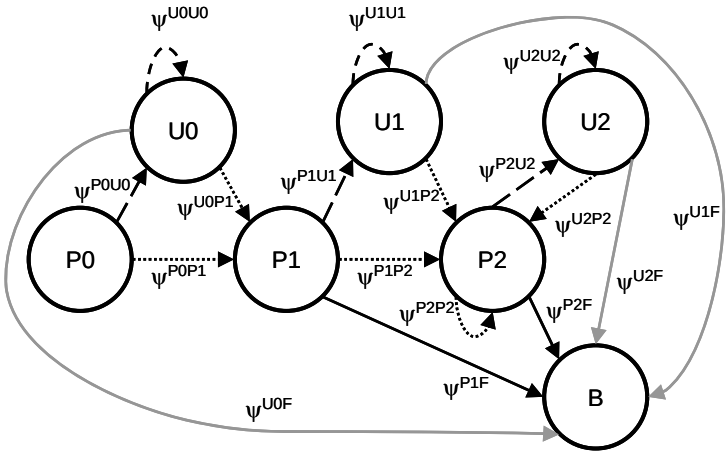

Figure 4.1. Breeding state classifications and possible transitions between states for a population of female Weddell seals in Erebus Bay, McMurdo Sound, Antarctica. States denote either observable (P) or unobservable (U) prebreeders that have attended Erebus Bay reproductive colonies 0, 1, or ≥2 times since they were pups (state P0), or first-time breeders (B). Solid lines and dashed lines represent, respectively, recruitment and temporary emigration. Dotted lines represent transitions into observable prebreeding states that were not estimated in our models but can be derived by subtraction.

To evaluate which covariates best explained TE rates, we constructed 17 models that estimated age-specific TE as a function of covariates. Our model list included all possible combinations of covariates with the constraint that we did not allow SIE and SOI in the same model and we did not allow SIC and DIST in the same model. We imposed these constraints based on pairwise correlations >0.4 for these pairs and the a priori hypothesis of similar effects of these covariates. In each of these models we allowed state-dependency in TE and recruitment rates based on whether or not females attended a

reproductive colony in year *t*–1. We also allowed time variation in recruitment rates, but constrained year effects to be shared across all ages and states (Hadley *et al.* 2006). Based on known life-histories of Weddell seals and previous observation, we expected that seals absent in year *t*–1 would be most likely to again be absent (have a greater TE rate) in year *t* (Chapter 2; Stirling 1969). We compared out best covariate model with a model that allowed different TE rates for each year and another model that specified equal TE rates for all years. However, because we allowed time variation in recruitment rates in the latter model, parameter-specific link functions for state transition parameters induced some minimal annual variation in TE rates (see Appendix C for details).

Table 4.1. Five types of parameters estimated in ORDMS models. Various constraints can be imposed on each of these parameters.

Parameter	Interpretation of notation
$\psi^{rz}_{t,age}$	probability that an individual of age class *age*-1 in state *r* in year *t-1* will transition to state *z* in year *t* at age class *age*, given survival to year *t*
$S^{c}_{SIE,age}$	annual apparent survival rate for individuals of age class *age* in cohort *c*, given current-year winter sea-ice extent
$pent^{r}_{tj}$	probability that an individual in state *r* is a new arrival to the study area in survey period *j* of year *t*
p^{r}_{tj}	probability that an individual in state *r* is detected in survey period *j* of year *t*, given that the individual is present in the study area
ϕ^{r}_{tjk}	probability that an individual in state *r* remains in the in the study area until survey period *j*+1 of year *t*, given entry *k* survey periods prior

To evaluate hypotheses about motivations for attendance by prebreeders and consequences for recruitment, we constructed 4 models with different state-dependent structures for recruitment rates. The first structure modeled age-specific recruitment as

equal for all states; this model represents the hypothesis that attendance patterns have little consequence for subsequent recruitment. The second structure modeled differences in age-specific recruitment rates in year *t* based on whether seals attended a reproductive colony in year *t*–1, but ignored attendance in years prior to *t*–1; this model represented the hypothesis that motivation to attend colonies is related to facilitation of optimal timing of estrus in prebreeders, and the prediction is that recruitment probability is positively related to attendance in the previous year. The third structure modeled differences in age-specific recruitment rates based on whether seals had attended a reproductive colony fewer than 2 or at least 2 years, but ignored information on when any attendance occurred; this model represented the hypothesis that attendance is motivated by opportunities to acquire information or skills, and the prediction is that more years of attendance is related to increased recruitment probability. The fourth structure modeled a different age-specific recruitment rate for each state, i.e., rates were allowed to differ based on attendance in year *t*–1 and total number of years of attendance; this model represented the possibility that attendance might allow acquisition of information as well as synchronization of estrus. In each of these models annual variation was unstructured (not a function of environmental covariates), and patterns differed for recruitment and TE rates, but patterns were shared across ages.

Based on results from previous analyses (Chapter 3; Hadley *et al.* 2006; Cameron & Siniff 2004), we used a single model structure to estimate age-specific survival rate of prebreeders. We estimated survival, $S^{c}_{SIE,age}$, as a function of age class (*age*), birth-cohort (*c*), and current-year winter SIE in year *t*–1, and we expected that survival rate was

positively related to SIE. Because hypotheses about state-dependent survival of females in an unobservable state cannot be evaluated on the basis of model selection (Bailey *et al.* 2010), we assumed equal survival for prebreeders in all states. Previous analysis suggests that biases in survival estimates because of non-random TE were minimal for this population of Weddell seals when TE was modeled as time-invariant (Hadley *et al.* 2007b). However when survival and state-dependent TE are both temporally variable, TE can cause substantial negative bias in survival estimates at the end of a time-series (Langtimm 2009). Consequently, we avoided interpretation of survival estimates for the final 4 cohorts of our time series.

Based on results from previous within-year analyses (Rotella *et al.* 2009), we felt justified in modeling a single structure for each of the within-year parameters (Table 4.1). We allowed $pent_{tj}^{r}$ to follow a state-dependent (states P1 and P2 pooled, P0 and B pooled) linear trend for j >1 (common for all seasons). For the first encounter occasion each year, we derived $pent_{t1}^{r} = 1 - \sum_{j>1} pent_{tj}^{r}$. Detection probability, p_{tj}^{r}, also was allowed to follow a year-constant and state-dependent (states P0, P1 and P2 pooled, and B) linear trend. We allowed ϕ_{tjk}^{r} to vary only by state (states P0, P1 and P2 pooled, and B). All within-season parameters were fixed to zero for all unobservable states.

We performed analyses in program MARK (White & Burnham 1999) through the RMark package (Laake *et al.* 2012) in program R (R Development Core Team 2012). Currently there is no general goodness-of-fit test for the type of ORDMS models we used in our analysis, and the median $\hat{c}$ procedure implemented into program MARK is not available for robust design data. In previous analyses of Weddell seal data from Erebus

Bay with simpler models, Hadley et al. (2006) found modest levels of overdispersion. Therefore we used AIC_c rather than quasi-likelihood AIC_c ($QAIC_c$) as our model selection criterion. However, to assess the possible influence on overdispersion on model selection results, we examined how model rankings changed as we increased $\hat{c}$ from 1.0 to 5.5, which is twice the highest level of overdispersion observed previously in these data (Hadley *et al.* 2007a).

Results

Of the 5,550 female seals in our dataset, 1,333 were observed as prebreeders during our survey periods in ≥1 year subsequent to tagging and prior to recruitment, and 942 recruited into the study area's breeding population (mean age at 1st reproduction = 7.7, SE = 0.05) by 2010. Between the year when they were born and the year when they gave birth to their first pup, 246 females were never observed in the breeding colonies as prebreeders (mean age at 1st reproduction = 7.0, SE = 0.10), 278 were observed as prebreeders in 1 year (mean age at 1st reproduction = 7.5, SE= 0.09), and 418 were observed as prebreeders in >1 year (mean age at 1st reproduction = 8.3, SE = 0.08). For seals that were observed as prebreeders in the colonies, the mean age at first observation was 4.6 years (SE = 0.06) and the mean number of years of prebreeders attendance was 2.1 (SE = 0.05).

The majority of females seals were present at the first survey period each year, and the probability of detection at least once during each season was >0.92 for prebreeders and >0.99 for pups and mothers (see Appendix C for further details). Cohort-

specific survival estimates for cohorts born in1983–2005 were greater for seals ≥2 years ($\bar{\hat{S}}_{cohort}$ = 0.93, $\overline{\widehat{SE}}$ = 0.01) than for pups ($\bar{\hat{S}}_{cohort}$ = 0.73, $\overline{\widehat{SE}}$ = 0.12) and yearlings ($\bar{\hat{S}}_{cohort}$ = 0.50, $\overline{\widehat{SE}}$ = 0.09), for which 95% CIs overlapped broadly (Figure 4.2a). As predicted, current-year sea-ice extent was positively associated with survival, although the 95% CI slightly overlapped zero ($\hat{\beta}_{\mathrm{SIE}}$ = 0.15, $\widehat{SE}$ = 0.08; Figure 4.2b).

As expected, TE rates were strongly age- and state-dependent, and, consistent with the hypothesis that highly variable environmental conditions should influence motivation or ability of prebreeders to attend colonies, year-to-year variability in TE rates was substantial, particularly after 2000 (Figure 4.3a, c). Our best-supported model evaluating possible sources of annual variation in TE rates (Table 4.2) supported the hypothesis that TE rates were density-dependant and related to distance to the fast-ice edge. As predicted, TE rates increased when current-year distance to fast-ice edge was great ($\hat{\beta}_{DIST}$ = 0.81, $\widehat{SE}$ = 0.04) and when the previous-year population of adult seals was large ($\hat{\beta}_{BPOP}$ = 0.76, $\widehat{SE}$ = 0.16). The distance from Erebus Bay to open water varied annually from <10 km to >80 km, and the population size of adults varied annually from <400 to >700 (Figure 3d). For a 5-year-old seal the predicted probability of TE was 0.39 ($\widehat{SE}$ = 0.03) in a year when the distance to the fast-ice edge was minimal and the previous year's adult population was small, but increased to 0.92 ($\widehat{SE}$ = 0.009) in a year when the distance to the fast-ice edge was maximal and the previous year's adult population was large (Figure 4.3b). Real parameter estimates of TE rates from our best-supported model were similar in most, but not all years, to those from the model that allowed year effects

in TE rates (Figure 3c). Our 2nd- and 3rd-best-supported models also included BPOP and DIST, and estimated coefficients and annual TE estimated were similar to those from the top model. The 2nd- best model also included SIE ($\hat{\beta}_{SIE} = 0.04$, $\widehat{SE} = 0.03$), and 3rd-best model also included SOI ($\hat{\beta}_{SOI} = 0.005$, $\widehat{SE} = 0.04$). Thus, although these latter 2 models were reasonably well-supported (Table 4.2), and pairwise correlations between BPOP, DIST, and SIE or SOI were relatively small (<|0.3|), SIE and SOI did not appear to provide much information for estimating TE rates when included in a model that also included BPOP and DIST.

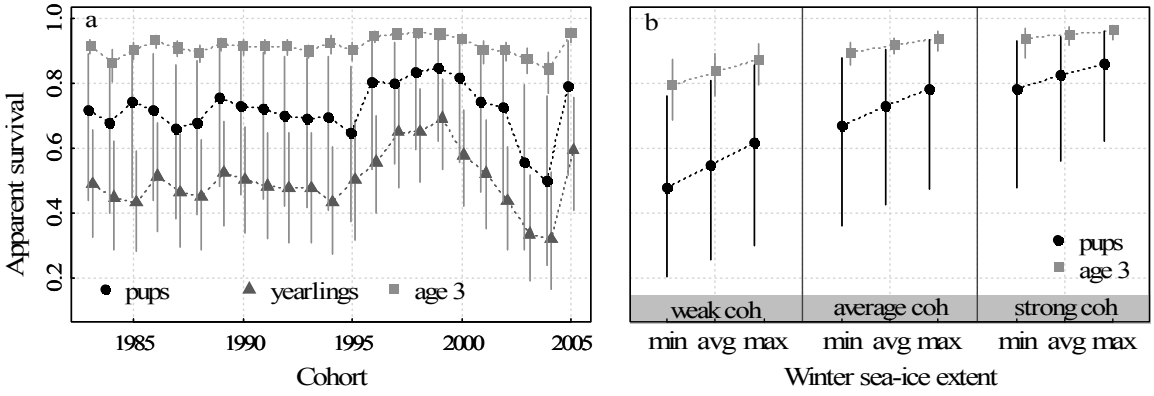

Figure 4.2. Estimated survival rates (a) from our best-supported model for 1st, 2nd, and 3rd-year of life, and predicted survival rates (b) for "weak", "average", and "strong" cohorts when current-year winter sea-ice extent in the Ross Sea is minimal, average, or maximal. Cohort "strength" was based on estimated survival rates (a) of cohorts relative to other cohorts. Error bars indicate 95% confidence intervals.

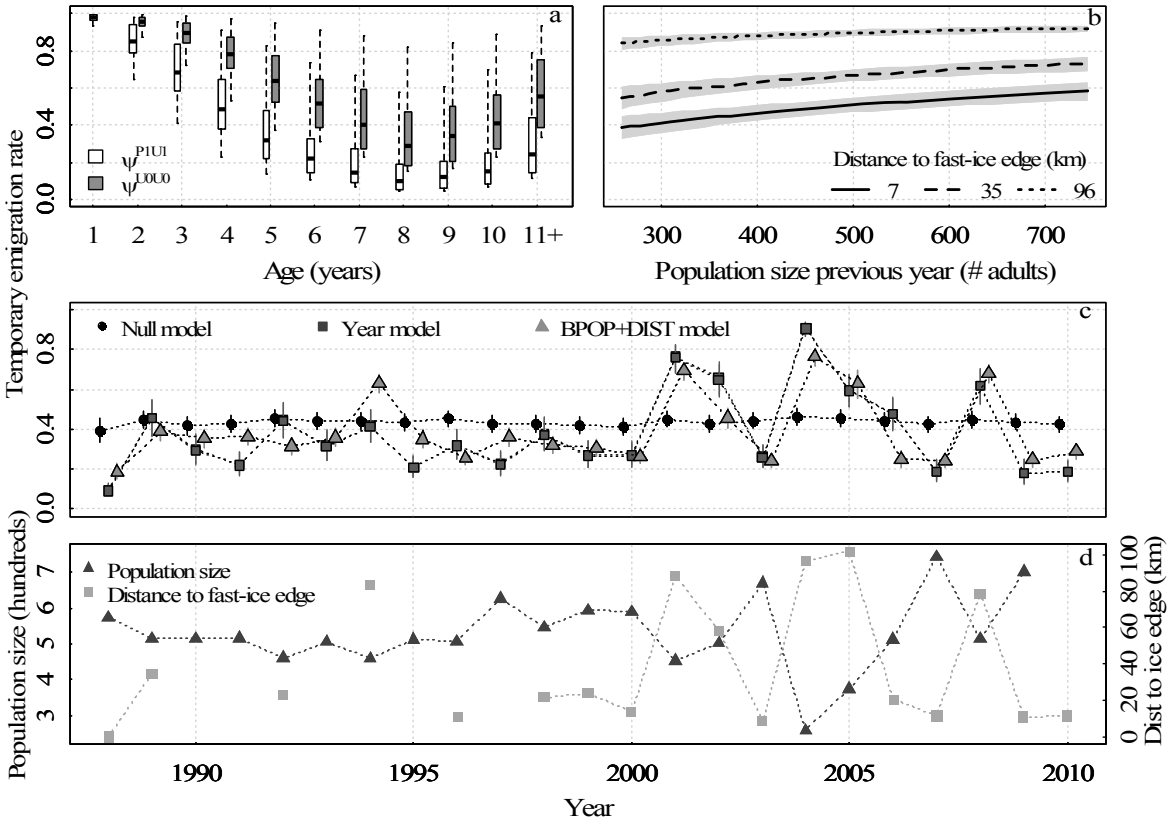

Figure 4.3. Annual covariate values and temporary emigration (TE) rates of pre-reproductive female Weddell seals in Erebus Bay, Antarctica. (a) Summary of annual TE rates estimated from model 21 (unstructured annual variation, see Table 4.2), with medians (dark bars), interquartile range (boxes), and whiskers bounding 2.5th and 97.5th percentiles of annual point estimates. (b) For seals at age 5, predicted temporary emigration (TE) rates and 95% CIs when distance to the fast-ice edge is "close", "intermediate" or "far", over a range of population sizes. Estimates were generated based on the best-supported covariate model (model 9, see Table 4.2). (c) For seals at age 5, comparison of annual TE rates (point estimates and 95% CIs) estimated from null model, year model, and best covariate model. Estimates from the 2nd- and 3rd-best-supported covariate models were very similar to those from the best-supported model. The null model had some annual variation in TE rates induced by annual variation in recruitment rates (see Appendix C for details). (d) Annual population size in Erebus Bay and distance to fast-ice.

Table 4.2. Model selection results for models representing hypotheses about variation in transition probabilities for female Weddell seals in Erebus Bay, Antarctica. Only the top 3 covariate models are shown for TE model suite. All models included annual variation and 9 nominal age classes (1-3, 4, 5, 6, 7, 8, 9, 10, 11+) for recruitment (ψ^{rB}) and 11 nominal age classes (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11+) for temporary emigration (TE; ψ^{rU}). The Markovian structure for TE specified different rates depending on colony attendance the previous year, whereas the Markovian structure for recruitment specified dependent on either: colony attendance (*a*), number of years of previous attendance experience at time of recruitment (*e*), both (*ae*), or neither (*non-Markovian*). Covariate values for TE are distance from Erebus Bay to the edge of the fast-ice (DIST), population size of adult females seals in the previous year (BPOP), winter sea-ice extent (SIE), and Southern Oscillation Index (SOI). See Appendix C, Table C.2 for complete table of model selection results.

Model	K	AICc	ΔAICc	w_i	Deviance
TE model suite					
(model 9) $\psi^{rB}_{(a)}, \psi^{rU}_{(BPOP + DIST)}$	87	74019.5	0.000	0.472	73845.2
(model 17) $\psi^{rB}_{(a)}, \psi^{rU}_{(BPOP + DIST +SIE)}$	88	74020.1	0.587	0.352	73843.7
(model 15) $\psi^{rB}_{(a)}, \psi^{rU}_{(BPOP + DIST +SOI)}$	88	74021.5	1.985	0.175	73845.1
Recruitment model suite					
(model 22) $\psi^{rB}_{(ae)}, \psi^{rU}_{(year)}$	113	73685.1	0.000	0.976	73458.4
(model 20) $\psi^{rB}_{(e)}, \psi^{rU}_{(year)}$	110	73692.7	7.580	0.022	73472.1
(model 21) $\psi^{rB}_{(a)}, \psi^{rU}_{(year)}$	110	73699.0	13.935	0.001	73478.4
(model 19) $\psi^{rB}_{(non\text{-}Markovian)}, \psi^{rU}_{(year)}$	109	73699.6	14.492	0.001	73481.0

Based on a time-dependent model (Model 21, Table 4.2), first-year TE rates were nearly 1 ($\bar{\hat{\psi}}^{P0U0}_{t,age1}$=0.98, $\widehat{\overline{SE}}$ = <0.01, $sd\left[\hat{\psi}^{P0U0}_{t,age1}\right]$=0.019); subsequently, TE rates decreased up to age class 8 ($\bar{\hat{\psi}}^{P1U1}_{t,age8}$=0.15, $\widehat{\overline{SE}}$ = 0.02, $sd\left[\hat{\psi}^{P1U1}_{t,age8}\right]$=0.16), then gradually increased up through the oldest age class ($\bar{\hat{\psi}}^{P1U1}_{t,age11+}$=0.29, $\widehat{\overline{SE}}$ = 0.05, $sd\left[\hat{\psi}^{P1U1}_{t,age11+}\right]$=0.22; Figure 4.3a). As expected, seals that attended a reproductive colony in year *t*–1 had lower TE rates

than seals that did not attend ($\hat{\beta}_{attend} = -1.35,\ \widehat{SE} = 0.10$, 95% CI = –1.54 to –1.15; e.g., $\overline{\hat{\psi}^{U2U2}_{t,age8} - \hat{\psi}^{P2U2}_{t,age8}} = 0.21,\ \overline{\widehat{SE}} = 0.024$).

Among the models evaluating consequences of prebreeder experience for recruitment (Table 4.2), our best-supported model allowed different age-specific recruitment rates for each prebreeder state and indicated strong age- and time-dependence (Figure 4.4). There was mixed support for the hypothesis that previous colony attendance by prebreeders increased age-specific recruitment rates. As predicted, seals that attended colonies in year *t*–1 and also had attended at least once previously were more likely to recruit in year *t* than seals of the same age attending for the first time in year *t*–1 (e.g., $\overline{\hat{\psi}^{P2F}_{t,age8} - \hat{\psi}^{P1F}_{t,age8}} = 0.11,\ \overline{\widehat{SE}} = 0.033$). Given that detection rates of prebreeders were slightly less than 1, this difference may be negatively biased, but any such bias must necessarily be very slight. Previous colony experience was less important for seals that did not attend breeding colonies in year *t*–1 (i.e., that recruited from an unobservable state). Seals that attended colonies in 1 previous year were slightly more likely to recruit than seals that had no previous colony experience (e.g., $\overline{\hat{\psi}^{U1F}_{t,age8} - \hat{\psi}^{U0F}_{t,age8}} = 0.08,\ \overline{\widehat{SE}} = 0.03$), but additional years of colony experience did not increase age-specific recruitment rates, and might even have decreased rates slightly (e.g., $\overline{\hat{\psi}^{U1F}_{t,age8} - \hat{\psi}^{U2F}_{t,age8}} = 0.08,\ \overline{\widehat{SE}} = 0.05$). Support was also mixed for the hypothesis that colony attendance is related to initiation of estrus in prebreeders, as consequences for recruitment of attendance in year *t*–1 depended on previous attendance history. Seals that attended for the first time in year *t*–1 and seals that attended in 1 previous year (but not in year *t*–1) had nearly identical

age-specific recruitment rates (e.g., $\overline{\hat{\psi}^{\mathrm{P1F}}_{t,age8} - \hat{\psi}^{\mathrm{U1F}}_{t,age8}} < 0.01$, $\overline{\widehat{SE}} = 0.038$). In contrast, seals that attended in year t–1 and also in ≥1 previous year were more likely to recruit in year t than seals that did not attend in year t–1 but did attend in ≥2 previous years (e.g., $\overline{\hat{\psi}^{\mathrm{P2F}}_{t,age8} - \hat{\psi}^{\mathrm{U2F}}_{t,age8}} = 0.19$, $\overline{\widehat{SE}} = 0.047$). Average recruitment rates were <0.01 for seals in age class 4, remained low (<0.1) for seals in age class 5, then gradually increased to a peak at age class 10 (e.g., $\bar{\hat{\psi}}^{\mathrm{P2F}}_{t,age10} = 0.56, \overline{\widehat{SE}} = 0.06, sd\left[\hat{\psi}^{\mathrm{P2F}}_{t,age10}\right] = 0.17$), than declined slightly in the oldest age class (e.g., $\bar{\hat{\psi}}^{\mathrm{P2F}}_{t,age11+} = 0.41, \overline{\widehat{SE}} = 0.06, sd\left[\hat{\psi}^{\mathrm{P2F}}_{t,age11+}\right] = 0.16$; Figure 4a). Recruitment rates were variable among years, and tended to be low when TE rates were high (Figure 4b).

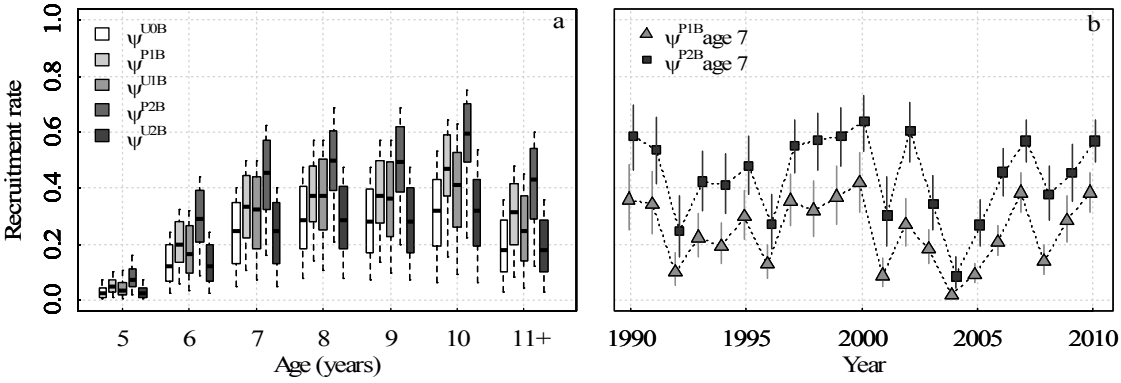

Figure 4.4. Age-specific recruitment rates of female Weddell seals in Erebus Bay, Antarctica, estimated from the best-supported model evaluating state-dependancy in recruitment rates (model 22, see Table 2). Presented are: a) summary of rates with median (dark bars), interquartile range (boxes), and whiskers bounding 2.5th and 97.5th percentiles of annual point estimates; and b) , annual rates and 95% confidence intervals for age 7 showing the temporal patterns shared by all ages and states in the model.

Discussion

In this study, we fit multistate capture-mark-recapture models to 27 years of encounter data for Weddell seals to evaluate possible causes of annual variation in age-specific TE rates and implications of colony attendance (the opposite of TE) for age-specific recruitment rates. Temporary emigration rates varied considerably from year-to-year, and our results provide support for previous suggestions that such variation is related to colony access, population size, or body condition (Chapter 2; Rotella *et al.* 2009). Our results also provide mixed support for the hypotheses that attending colonies for ≥1 year as prebreeders allows seals to time estrus optimally or to acquire skills or information, possibly including information about potential mates, which increase subsequent age-specific recruitment probabilities.

The distance from Erebus Bay to open water varied annually from <10 km to >80 km (Figure 3d), and as expected, distance to the edge of the fast-ice was strongly and positively related to TE rates. In years when fast-ice is extensive, it likely is difficult for younger or smaller seals to swim or even navigate to Erebus Bay. Diving behavior of young seals is subject to physiological or morphological constraints, and older and heavier Weddell seals have better diving abilities than younger and lighter seals (Kooyman 1966; Burns, Schreer, & Castellini 1997; Burns 1999). Thus, a long swim under extensive fast-ice might restrict access to Erebus Bay for prebreeders in poor physiological condition. Extensive fast-ice might also pose navigation difficulties for young seals. Anecdotal evidence from common terns (*Sterna hiruno*) suggests that

preebreeders might need to learn to navigate to their natal site (Dittmann & Becker 2003).

Underlying reasons for density-dependence in TE rates are not known. Positive density-dependence in dispersal rates has been shown for numerous species, sometimes associated with resource depletion and consequent resource need motivating movement (e.g., McMahon & Tash 1988; Clutton-Brock *et al.* 2002; see review in Matthysen 2005). Weddell seals occupy Erebus Bay seasonally, and most mature attending females are not foraging extensively during this time (but see Wheatley *et al.* 2007). Therefore, it is doubtful that food depletion in Erebus Bay from increased local populations in one year accounts for carry-over effects (*sensu* Harrison *et al.* 2011) such as increased TE rates in the following year. Large local populations in Erebus Bay might reflect a large regional population, with consequent increased competition for resources in major foraging areas. Increased competition might influence seal condition and subsequent motivation to attend or not attend Erebus Bay. Assessing regional population size, at least at major haul-out areas, might be possible using satellite images (LaRue *et al.* 2011), but assessing resource availability likely will remain a major challenge in the near future.

Large local populations of adults in breeding colonies might increase the level of social conflict between adults and prebreeders, thus discouraging attendance (increasing motivation for TE) by prebreeders the following year. Overt competition between females for space or access to breathing holes has not been described, but Stirling (1969) reported that during the breeding season, seals maintain greater distances from their nearest neighbors than after pups are weaned. Crowding of seals does appear to increase

levels of conflict between individuals (Siniff *et al.* 1977). Also, until late in the pupping season when most pups are weaned, prebreeders are found mostly in the periphery of the reproductive colonies, possibly because of aggression from breeding adults (Stirling 1969; Siniff *et al.* 1977). Intra-sexual aggression has also been documented in several other pinniped species (e.g., McCann 1982; Harcourt 1992; Fernández-Juricic & Cassini 2007), and in some ungulates appears to motivate natal dispersal (e.g., Long *et al.* 2008). Proposing that intra-sexual conflict in one year motivates TE the next year assumes either physiological costs to prebreeders that decrease ability to attend or psychological influences that decrease motivation to attend. One possibility is that high population densities in Erebus Bay motivate recruitment elsewhere, which could be manifested in our analysis as increased TE rates if seals subsequently return to Erebus Bay (otherwise, recruitment elsewhere could represent permanent emigration). Bradshaw *et al.* (2000) suggested a similar 'spill-over' effect in an expanding population of New Zealand fur seals (*Arctocephalus forsteri*). Most female Weddell seals born in Erebus Bay are believed to be philopatric (Cameron & Siniff 2004; Hadley *et al.* 2006), but recruitment outside Erebus Bay has been anecdotally observed. As observational data accumulate from outside Erebus Bay, it may be possible to better address the question of density-dependent natal dispersal from Erebus Bay.

It is possible that the density-dependence we observed in TE rates is apparent rather than real. Distance to fast-ice edge is inversely correlated to current-year population size, and years with maximal fast-ice tend to be followed by years with less ice, corresponding to decreased TE rates. However, dropping adult population size from

our top model greatly increased AIC_c, which suggests that population size as well as distance influences TE rates. Behavioral studies of intraspecific interactions or analysis of inter-annual movements between colonies as a function of population size for those seals that did attend Erebus Bay might provide additional insights about density-dependent movement in Weddell seals.

Our results provided mixed support for both the hypothesis that colony attendance by prebreeders might facilitate the acquisition of information and skills and the hypothesis that attendance might facilitate optimal timing of estrus in prebreeders. In support of the information hypothesis, age-specific recruitment rates were greater for seals that attended reproductive colonies once than for seals that never attended a colony as prebreeders, and recruitment rates increase further for seals that attended colonies ≥2 times, provided they attended in year t–1. Weddell seals have a breeding system similar to lekking, where males defend underwater territories focused on cracks in the ice (Siniff *et al.* 1977). In such a system, prebreeders that attend Erebus Bay might benefit from observing mating behavior of mature seals, either gaining experience in evaluating potential mates or simply copying the behavior of other females (Dugatkin & Godin 1993; Valone 2007). However, in contrast to our prediction, age-specific recruitment rates of seals that previously attended Erebus Bay in ≥2 year (but not in year t–1) were slightly lower that for seals that either attended once or at least twice, including in year t–1. This latter observation, that recruitment rates were greater for seals that attended at least twice, including in year t–1, than for seals that attended at least twice, but not in t–1 is consistent with the hypothesis that seals attending colonies are more likely to enter

estrus and successfully mate than are seals that don't attend. There is evidence for selective pressure for synchronized birth dates in Weddell seals and other pinnipeds (Boness, Bowen, & Iverson 1995; Proffitt *et al.* 2010), which might be facilitated by synchronized estrus. However, the observation of nearly equal recruitment rates for seals that attended reproductive colonies once before producing a pup, regardless of when that attendance took place, makes it difficult to draw firm conclusions about the importance of attendance for facilitating timing of estrus. Timing of mating and parturition can be uncoupled by embryonic diapause, which might be largely responsible for synchrony in parturition dates in pinnipeds species (Boyd 1991). The termination of diapause is not well-understood in pinnipeds, but is thought to involve sex hormones and photoperiod, as well as a critical body condition threshold (see reviews in Boyd 1991; Boyd, Lockyer, & Marsh 1999; Renfree & Shaw 2000; Pomeroy 2011). An alternative explanation for the observed differences in recruitment rates for seals that attended at least twice, either including or not included attendance in year t–1, is that there could be a segment of the population that is unlikely to ever recruit (Hadley *et al.* 2006). That is, a female attends twice but still does not recruit may be increasingly unlikely to ever recruit. This idea is consistent with all the observed state-dependant differences in recruitment rates, and is somewhat supported by the slight increases in TE rates and decreases in recruitment rates for the oldest age class, and the fact that the mean number of years seals attended prior to recruitment was 2.1 years.

That temporary emigration rates should be density-dependent is not intuitively obvious because reproductive colonies are aggregations that attract prebreeders, and

colony attendance can improve future reproductive success (e.g., Halley *et al.* 1995; Cam *et al.* 2002; Dittmann *et al.* 2007; Aubry *et al.* 2009a). The fact that that we found evidence for density-dependence in TE rates and for benefits of colony attendance supports the hypothesis that prebreeders might need to balance tradeoffs between costs and benefits of attending colonies. Such balances likely depend on annual environmental conditions, population size, and characteristics of individuals, and might strongly influence the age at which individual seals recruit. Evidence from kittiwakes (*Rissa tridactyla*) suggest that prebreeding behavior and experience can influence short-term and long-term reproductive success, and that recruitment at intermediate ages is optimal (Cam *et al.* 2002; Aubry *et al.* 2009b). An intermediate recruitment age also is optimal for future reproductive success of northern elephant seals (*Mirounga angustirostrus*; Reiter & Boeuf 1991). For Weddell seals, it has been suggested that the highest-quality individuals recruit at the youngest ages, but there also is evidence that offspring survival is lowest for young mothers (Hadley *et al.* 2007a). In this paper we only investigated the implications of TE patterns for age-specific recruitment rates, but we expect that investigation of reproductive performance of Weddell seals post-recruitment should lead to further insights and provide a fuller understanding of the role of colony attendance by prebreeeders in the life-history of Weddell seals.

CHAPTER 5

CONCLUSIONS AND DIRECTIONS FOR FURTHER RESEARCH

Summary

For many long-lived species with delayed reproduction, events that occur during the period from birth or hatching until recruitment into the breeding portion of the population have important implications for when, or even if, that recruitment takes place. These processes are well-studied in colonial seabirds, but less understood in pinnipeds. In this dissertation I evaluated variation in several demographic rates of female Weddell seals (*Leptonychotes weddellii*) in Erebus Bay, Antarctica from birth to recruitment. Specifically, I estimated the extent of variation in rates of age-specific temporary emigration (TE) from the Erebus Bay reproductive colonies, evaluated sources of variation in TE and survival rates and implications of TE for age-specific recruitment rates, and evaluated evidence for influences on survival and recruitment rates of environmental conditions experienced during the year of a pup's birth or each subsequent year.

In Chapter 2, I found that, as expected, TE rates were highly age-dependent. Nearly all females were absent at age one; TE rates subsequently decreased until age 8, and then increased slightly for the oldest age classes. As expected, recruitment rates also were strongly age-dependent, but TE rate decreased with age more quickly than recruitment rates increased. Recruitment rates were low at age 5, and peaked at age 10. These results support the notion of a threshold body size or condition necessary for

attending colonies, and also provide some circumstantial evidence that, as they grow older, Weddell seals have motivation to attend colonies beyond that of immediate mating. Most females attended reproductive colonies in Erebus Bay for >1 year prior to producing their first pup. TE rates were greater, and recruitment rates marginally lower, for seals absent from Erebus Bay during the previous year than they were for seals that attended reproductive colonies in the previous year. There was considerable annual variation in TE rates, which suggests that motivation to attend colonies might depend on annual environmental conditions. If there are costs (e.g., reduced foraging opportunities) as well as benefits (e.g., acquisition of information or skills) associated with colony attendance by prebreeders, then annual variation in TE rates might reflect shifts in balances of such tradeoffs.

In Chapter 3, I found that survival rates varied among cohorts, and I suggested that this variation is likely responsible for the considerable variation in the proportion of each female Weddell seal birth cohort that eventually recruits into the pup-producing portion of the population (Garrott *et al.* 2012). In Chapter 3, I therefore evaluated relationships between survival and various environmental and population-level covariates that were measured both for the year of birth for each cohort and for subsequent years. My results provide evidence that both birth- and current-year conditions acted in combination to influence survival. Survival rates differed for each cohort (i.e., each cohort had its own intercept in the model), but also were positively related to maximum extent of current-year winter sea-ice in the Ross Sea. The duration of a birth-cohort effect on survival was estimated to be 6 years, indicating a multi-year (intermediate) survival

filter that determined what proportion of each cohort reached reproductive age. Estimated cohort-specific survivorship from birth to age 6, based on the specific sequence of sea-ice conditions experienced by each cohort was similar for most cohorts (mean = 0.25, SE = 0.02), but a few cohorts had rates that deviated substantially from this mean. Recruitment rates varied annually, but a relationship with birth-year was not supported. These results thus support the hypothesis that persistent birth-year influences on survival, rather than recruitment rate for surviving females largely determine what proportion of each cohort will eventually produce young.

In Chapter 4, I explored correlates of TE rates, and implications of attendance patterns for age-specific recruitment. I found that TE rates were positively related to the distance from Erebus Bay to the fast-ice edge in a given year and to the population size of adult females in Erebus Bay in the previous year. In all but a few years, estimates from this model closely matched those from a model that simply allowed a different rate for each year. Seals must swim under the fast-ice to reach Erebus Bay, and when this distance is great, it likely increases costs of colony attendance for prebreeders. The reason for density-dependence in TE rates is not clear, but likely results from intra-specific conflict between prebreeders and adults. Recruitment rates varied annually, and typically, but not always, were positively related to the number of years (0, 1, 2+) a prebreeder had attended reproductive colonies in Erebus Bay. These results provide support for the hypothesis, proposed in Chapter 2, that there are benefits and possible costs to prebreeders that are associated with attending reproductive colonies, and decisions to attend or not likely depend on the balances of consequent tradeoffs each

year. As with many colonial seabirds, colony attendance by prebreeders might allow the acquisition of information or social skills that help facilitate the transition from prebreeders to breeder. It is also possible that attendance of reproductive colonies allows prebreeders to optimally time estrus to increase to probability of subsequent successful mating, but patterns of state-dependency in recruitment probabilities only partially supported this hypothesis.

Directions for Further Research

Throughout this dissertation I discuss the possibility that colony attendance by prebreeders in Erebus Bay entails both costs and benefits based in part by results from studies of colonial seabirds, which have found that colony attendance and the extent to which prebreeders 'practice' breeding behavior prior to actual breeding were related to increases in subsequent recruitment probability and breeding success (e.g., Cam *et al.* 2002; Dittmann *et al.* 2007). I have explored only the possible benefit of increased recruitment rates, but suggest that further insights might be gained by evaluating relationships between colony attendance by prebreeders and various measures of reproductive success after recruitment. Such measures could include annual breeding probability for females or survival rates of their offspring. For example, attending colonies might help prebreeders identify optimal timing for pupping. Pups born late in the season have the greatest pre-weaning survival (Proffitt *et al.* 2010) but also the least mass at weaning (Mannas 2011), and thus they might have greater mortality rates after weaning (Proffitt *et al.* 2008b).

Colony attendance by prebreeders might impose a cost to annual survival if reduced resource availability or conflict with adults has physiological costs. With my methods, I could not test for differences in survival rates between observable and unobservable states (Bailey *et al.* 2010). One possible but expensive and logistically challenging solution might be to fit a sample of seals with tracking devices so that movement in and out of the observable states could be directly monitored (Kendall 2004). However, because it is unlikely that mortality could be determined (i.e., when a seals dies the tracking device would vanish), information about survival in the unobservable state could not be directly obtained.

Tracking devices, however, could provide useful information about movements of prebreeders, and could allow differentiation of seals that truly were absent from reproductive colonies from seals that were present but never hauled out. Tracking devices also could provide valuable information about movements of prebreeders when they are absent from Erebus Bay (e.g., are they attending reproductive aggregations elsewhere?). Location information might help to clarify motivations for TE. For example, if many seals that are not observed at any of the reproductive colonies in Erebus Bay can be tracked in the Ross Sea, where food resources presumably are greatest, motivation for TE could possibly be more confidently linked to the need for resource acquisition. The ecological implications of TE ore poorly understood for most species, but my results suggest that temporary emigration potentially plays a substantial role in population dynamics and individual life-histories. Information about actual locations of individuals

when they are absent from a study area, although difficult to obtain, should lead to a fuller understanding of the ecological and population implication of TE.

APPENDICES

APPENDIX A

DETAILS OF OPEN ROBUST DESIGN MULTISTATE MODELING AND RESULTS OF WITHIN-YEAR MODELING FOR CHAPTER 1

Description of Open Robust Design MultiState Models

We used open robust-design multistate (ORDMS) models (Kendall & Bjorkland 2001; Kendall 2006; Converse *et al.* 2009) to investigate patterns of variation in survival rates, recruitment rates, and rates of temporary emigration (TE) of juvenile Weddell seals. Because the robust design uses information from multiple secondary capture occasions within each primary occasion (Pollock 1982), it is possible to separate estimation of detection probability from estimation of availability for detection (Kendall *et al.* 1997). This distinction between detection probability and availability provides information useful for estimating TE rates (Kendall & Nichols 1995; Kendall *et al.* 1997; Kendall & Nichols 2002). Estimation of TE rates is accomplished by defining and estimating a transition into an unobservable state (Fujiwara & Caswell 2002; Kendall & Nichols 2002; Schaub *et al.* 2004). The methods of Kendall *et al*. (1997) allowed state-dependent transitions but assumed demographic and geographic closure within primary periods, which is untenable in some cases. Schwarz and Stobo (1997) relaxed the closure assumption, allowing staggered entry and exit within a primary period, but did not allow state-dependant transitions. Kendall and Bjorkland (2001) combined the methods of Kendall *et al*. (1997) and Schwarz and Stobo (1997) to allow geographic openness within, and state-dependent transitions between, primary periods. ORDMS models are a generalization of Kendall and Bjorkland's (2001) approach that allow transitions between multiple states. The specific form of ORDMS models employed here used a modification of the open model of Schwarz and Arnason (1996) to model within-primary-period

dynamics and the multistate framework of Brownie *et al*. (1993) for between-primary-period dynamics.

ORDMS models provide estimates for five types of parameters. Apparent survival (S_t^r), hereafter survival, is the probability of surviving and not permanently emigrating from primary occasion t to $t+1$ for state r; ψ_t^{rz} is the probability, given survival, that an individual will make a transition between period t and $t+1$ from state r to state z. For a given primary period, t: $pent_{tj}^r$ is the probability that an individual in state r is a new arrival to the study area in secondary occasion j; p_{tj}^r is the probability of detection for individuals in state r during secondary occasion j; and ϕ_{tjk}^r is probability that individuals of state r will stay in the study area between secondary occasions j and $j+1$, given that they entered k secondary occasions prior. Individuals are allowed to enter the population once and leave during a primary period, and the probability that an individual enters the study area and leaves again prior to the first secondary capture occasion is assumed to be zero (Kendall & Bjorkland 2001).

Further Analysis Details

In the absence of reasonable a priori expectations, considering all possible combinations for even a few structures of $pent_{tj}^r$, p_{tj}^r, and ϕ_{tjk}^r would generate an intractably large model set. Instead, we used competing Schwarz-Arnason models to evaluate within-year dynamics for each year (Rotella et al. 2009). In preliminary analyses we found that the model that performed best varied by year, but point estimates were

similar across years. Estimates for p_{tj}^{r} and ϕ_{tjk}^{r} were uniformly high, and $pent_{tj}^{r}$ generally was low and decreasing for breeders but increasing slightly for prebreeders. We thus felt justified in modeling only one structure for $pent_{tj}^{r}$, p_{tj}^{r}, and ϕ_{tjk}^{r}. For $pent_{tj}^{r}$ we pooled breeders and pups because in most cases pups were present the first time we encountered breeders during a season. We allowed $pent_{tj}^{r}$ to vary by state (P, B and N pooled; fixed to zero for state U) and to follow a common state-dependent linear trend for j >1 within all primary periods. The probability of entry at j = 1, $pent_{t1}^{r}$, was calculated as $1-\sum_{j>1} pent_{tj}^{r}$.

Detection probability also was fixed to zero for the unobservable state and otherwise allowed to vary by state (N, P, and B) following a state-dependent linear trend that was constant for all years. We allowed ϕ_{tjk}^{r} to vary only by state (N, P, and B). The probability that an individual will be detected at least once in a primary occasion (p_{t}^{*r}) can be derived from the secondary occasion-specific parameters. For example, for a year with 3 secondary occasions:

$$\begin{aligned} p_{t}^{*r} = pent_{t1}^{r}\Big[p_{t1}^{r} + \left(1-p_{t1}^{r}\right)\phi_{t10}^{r}p_{t2}^{r} + \left(1-p_{t1}^{r}\right)\phi_{t10}^{r}p_{t2}^{r}\left(1-p_{t2}^{r}\right)\phi_{t21}^{r}p_{t3}^{r}\Big] \\ + pent_{t2}^{r}\Big[p_{t2}^{r} + \left(1-p_{t2}^{r}\right)\phi_{t20}^{r}p_{t3}^{r}\Big] \\ + pent_{t3}^{r}p_{t3}^{r}. \end{aligned}$$

In our ORDMS models we fixed to zero transition probabilities that were either biologically impossible (ψ_{t}^{NN}, ψ_{t}^{NB}, ψ_{t}^{PN}, ψ_{t}^{BN}, ψ_{t}^{UN}, ψ_{t}^{BP}) or not allowed because encounter histories were right-censored after recruitment (ψ_{t}^{BB}, ψ_{t}^{BU}).We estimated five types of transition probabilities (ψ_{t}^{NU}, ψ_{t}^{PU}, ψ_{t}^{PB}, ψ_{t}^{UU}, ψ_{t}^{UB}) directly in our models. The

remaining three transitions (ψ_t^{NP}, ψ_t^{PP}, ψ_t^{UP}) were derived by subtraction based on the fact that all rates for transition originating in any state must sum to 1 (e.g., $\psi_t^{\mathrm{PN}} + \psi_t^{PP} + \psi_t^{PU} + \psi_t^{PB} = 1$, where $\psi_i^{\mathrm{PN}} = 0$). Our choice of which transition rates to estimate directly was made so that our competing models focused on testing hypotheses about two types of transitions: into a breeding state (recruitment) and into an unobservable state (TE).

Tag loss is known to occur at a low rate in our study (Cameron 2001). Thus, S_i^r represents a product of the underlying survival rate and the probability that both tags are retained (Nichols *et al.* 1992). We therefore adjusted our estimates of survival as $\hat{S}^r_{adjusted,i} = \hat{S}_i^r / \hat{\theta}_i^r$, based on the formula presented by Arnason and Mills (1981) where $\hat{\theta}_i^r$ are cohort-specific tag-retention rates previously estimated for this population by Cameron (2001).

Results from Within-year Modeling

Each year, the majority of female seals were present on the first survey ($\widehat{\overline{pent}}_{t1}^{N\ and\ B}$ = 0.72, $\widehat{SE}$ = 0.02; $\widehat{\overline{pent}}_{i1}^{P}$ = 0.64, $\widehat{SE}$ = 0.03). For pups and breeders, $\widehat{pent}_{ij}^{r}$ decreased rapidly during the primary period (Fig A1) from 0.16 ($\widehat{SE}$ = 0.01) to <0.01 ($\widehat{SE}$ = <0.01), whereas $\widehat{pent}_{tj}^{P}$ increased slightly throughout the season ($\widehat{pent}_{t2}^{P}$ = 0.05, $\widehat{SE}$ = 0.01; $\widehat{pent}_{t8}^{P}$ = 0.07, $\widehat{SE}$ = 0.01). After entering the study area each year, seals in each state were likely to remain ($\hat{\phi}_{\cdot}^{N}$ = 0.99, $\widehat{SE}$ = <0.01; $\hat{\phi}_{\cdot}^{P}$ = 0.94, $\widehat{SE}$ = <0.01; $\hat{\phi}_{\cdot}^{B}$ = 0.98, $\widehat{SE}$ = <0.01). For

pups and breeders, $\hat{p}_{tj}^{r}$ was high early in the season and decreased linearly throughout the season, whereas for prebreeders, $\hat{p}_{tj}^{r}$ increased linearly throughout the season (Figure A.1). We detected ≥91% of all seals that entered the study area (Table A.1).

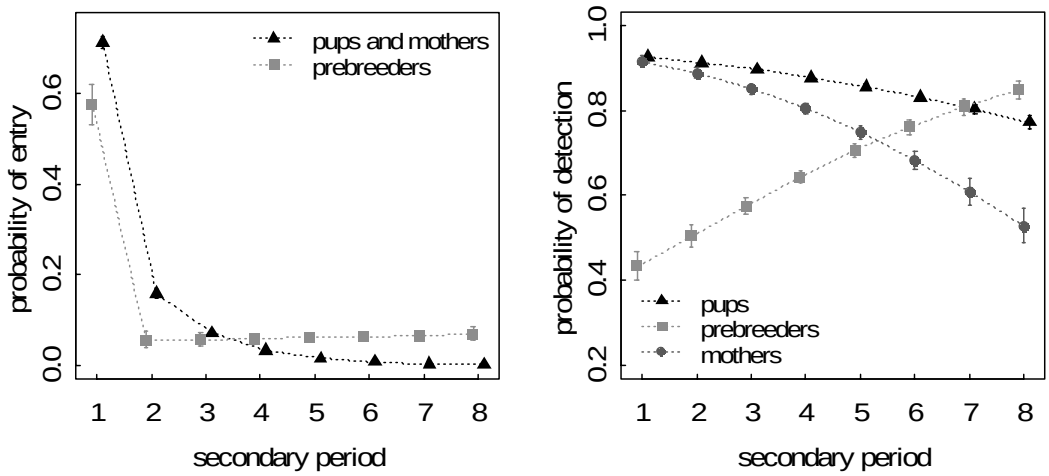

Figure A.1. Secondary survey-specific probability that a seal will be new to the study area (left) and will be detected (right). Example of a year with 8 secondary occasions. The first entry probability is derived as 1 minus the sum of the rest of the probabilities and represents the probability of presence at the beginning of the primary survey period. Error bars represent 95% confidence intervals.

Table A.1. Probability of detection of female Weddell seals during ≥1 secondary occasions with a primary period ($\hat{p}_{t}^{r}$ *) for a primary period with 5–8 secondary periods. Most primary occasions had ≥6 secondary occasions.

	5 secondary occasions		6 secondary occasions		7 secondary occasions		8 secondary occasions	
	$\hat{p}_{t}^{r}$ *	$\widehat{SE}$	$\hat{p}_{t}^{r}$ *	$\widehat{SE}$	$\hat{p}_{t}^{r}$ *	$\widehat{SE}$	$\hat{p}_{t}^{r}$ *	$\widehat{SE}$
pups	>0.99	<0.01	>0.99	<0.01	>0.99	<0.01	>0.99	<0.01
prebreeders	0.91	<0.01	0.92	<0.01	0.93	<0.01	0.94	<0.01
breeders	>0.99	<0.01	>0.99	<0.01	>0.99	<0.01	>0.99	<0.01

Table A.2. Model selection table for open robust design multistate models representing structures of variation in survival (S_t^r), temporary emigration (ψ_t^{rU}), and recruitment (ψ_t^{rB}) probabilities for female Weddell seals in Erebus Bay, Antarctica. Survival was modeled first, with state-dependant and categorical age effects on ψ_t^{rs}, and year effects on ψ_t^{rs} that were shared among states and age classes in all models. The top model in the survival-probabilities suite was used in all models in the transition-probabilities suite. In all models, $pent_{tj}^r$ was modeled with a linear trend for pups and recruits, and a separate trend for prebreeders; p_{tj}^r was modeled with different linear trends for all three states; ϕ_{tjk}^r was modeled as a separate constant parameter for all three states. Age structures are as follows: a3 = 3 nominal age classes (0, 1, 2+); a8 = 8 nominal age classes (0–4, 5, 6, 7, 8, 9, 10, 11+), and a11=11 nominal age classes (0, 1–2, 3, 4, 5, 6, 7, 8, 9, 10, 11+). A8 and A11 represent quadratic functional forms of the nominal age classes. AIC_c, ΔAIC_c, and w_i (weight of evidence for each model) values represent within-suite values. Coh represents a short-term cohort effect ending after 3 years. Markovian transitions are 1st order.

Model	K	AICc	ΔAICc	w_i	Deviance
Survival-probabilities suite					
$S_{\text{a3+cohort}}$	108	74788.29	0.00	0.910	74571.68
$S_{\text{a3+year}}$	111	74793.51	5.21	0.067	74570.86
$S_{\text{a3+coh}}$	108	74795.62	7.32	0.023	74579.00
Transition-probabilities suite					
ψ^{rB} a8+year, ψ^{rU} a11+year, Markovian	**108**	**74788.29**	**0.00**	**1.000**	**74571.68**
ψ^{rB} A8+year, ψ^{rU} A11+year, Markovian	97	74833.86	45.57	0.000	74639.37
ψ^{rB} a8+cohort, ψ^{rU} a11+year, Markovian	108	74848.73	60.44	0.000	74632.12
ψ^{rB} A8+cohort, ψ^{rU} A11+year, Markovian	97	74895.58	107.29	0.000	74701.09
ψ^{rB} a8+year, ψ^{rU} A11+year	106	75020.59	232.30	0.000	74808.00
ψ^{rB} A8+year, ψ^{rU} A11+year	95	75031.66	243.37	0.000	74841.19
ψ^{rB} a8+cohort, ψ^{rU} a11+year	106	75082.76	294.46	0.000	74870.16
ψ^{rB} A8+cohort, ψ^{rU} A11+year	95	75094.76	306.47	0.000	74904.29
ψ^{rB} a8+year, ψ^{rU} a11+cohort, Markovian	108	75479.21	690.92	0.000	75262.59
ψ^{rB} A8+year, ψ^{rU} A11+cohort, Markovian	97	75512.70	724.41	0.000	75318.21
ψ^{rB} a8+year, ψ^{rU} a11+coh, Markovian	108	75608.54	820.25	0.000	75391.93
ψ^{rB} A8+year, ψ^{rU} A11+coh, Markovian	97	75654.47	866.18	0.000	75459.98
ψ^{rB} a8+year, ψ^{rU} a11+cohort	106	75656.94	868.65	0.000	75444.35
ψ^{rB} A8+year, ψ^{rU} A11+cohort	95	75668.21	879.91	0.000	75477.73
ψ^{rB} a8+cohort, ψ^{rU} a11+cohort, Markovian	108	75682.34	894.05	0.000	75465.73
ψ^{rB} A8+cohort, ψ^{rU} A11+cohort, Markovian	97	75716.92	928.62	0.000	75522.42
ψ^{rB} a8+cohort, ψ^{rU} a11+coh, Markovian	108	75817.45	1029.15	0.000	75600.83
ψ^{rB} a8+year, ψ^{rU} a11+coh	106	75837.03	1048.73	0.000	75624.43

Table A.3. Estimates of beta parameters used to estimate demographic rates for female Weddell seals in Erebus Bay Antarctica. Estimates are generated from the best supported model (Markovian transitions, annual variation shared among ages; see Table S2), and are presented for seals that were observable in the study area the previous year ($\hat{\psi}_t^{PB}$) or were unobservable (temporary emigrants) the previous year ($\hat{\psi}_t^{UB}$). Confidence limits are for a 95% interval.

Role in model	Estimate	SE	lcl	ucl
Logit ($S_{cohort,\ age}$)				
Age >2; 1993 cohort	2.460	0.126	2.214	2.706
Pup offset; 1993 cohort	-1.892	0.364	-2.605	-1.179
Yearling offset; 1993 cohort	-2.292	0.305	-2.890	-1.694
1980 offset	-0.477	0.152	-0.774	-0.179
1981 offset	-0.112	0.182	-0.470	0.245
1982 offset	-0.363	0.150	-0.658	-0.069
1983 offset	-0.068	0.143	-0.349	0.213
1984 offset	-0.225	0.146	-0.512	0.062
1985 offset	-0.083	0.146	-0.368	0.203
1986 offset	0.075	0.146	-0.212	0.362
1987 offset	-0.157	0.146	-0.444	0.130
1988 offset	-0.226	0.148	-0.516	0.064
1989 offset	0.044	0.148	-0.246	0.334
1990 offset	0.029	0.145	-0.255	0.313
1991 offset	0.014	0.146	-0.271	0.299
1992 offset	-0.034	0.156	-0.339	0.272
1994 offset	-0.081	0.151	-0.376	0.215
1995 offset	-0.086	0.152	-0.383	0.212
1996 offset	0.349	0.149	0.056	0.642
1997 offset	0.493	0.139	0.221	0.765
1998 offset	0.581	0.145	0.298	0.865
1999 offset	0.646	0.148	0.356	0.936
2000 offset	0.370	0.147	0.083	0.658

Table A.3. continued.

Role in model	Estimate	SE	lcl	ucl
2000 offset	0.370	0.147	0.083	0.658
2001 offset	0.038	0.173	-0.302	0.377
2002 offset	-0.167	0.188	-0.536	0.202
2003 offset	-0.517	0.227	-0.962	-0.073
Mlogit ($pent^{r}_{.j}$)				
Prebreeders	-2.372	0.209	-2.782	-1.962
Offset for pups and mothers	0.864	0.213	0.447	1.282
Time trend for prebreeders	0.038	0.046	-0.052	0.128
Time trend for pups and mothers	-0.799	0.026	-0.849	-0.749
logit($p^{r}_{.j}$)				
Mothers	2.398	0.083	2.235	2.560
Offset for pups	0.128	0.095	-0.059	0.315
Offset for prebreeders	-2.670	0.110	-2.885	-2.456
Time trend for breeders	-0.326	0.021	-0.368	-0.285
Time trend for pups	0.140	0.024	0.093	0.187
Time trend for prebreeders	0.613	0.029	0.556	0.670
logit($\phi^{r}_{.}$)				
Mothers	4.125	0.184	3.764	4.487
Offset for pups	0.223	0.198	-0.165	0.611
Offset for prebreeders	-1.433	0.195	-1.816	-1.051
Mlogit($\psi^{rz}_{year,age}$)				
$P_{age\ 5} \rightarrow B$; 1993	-1.730	0.276	-2.271	-1.188
Offset for $U_{age\ 5} \rightarrow B$; 1993	-0.113	0.108	-0.324	0.099
$r \rightarrow B$; Offset for age 6	1.519	0.182	1.162	1.876
$r \rightarrow B$; Offset for age 7	2.211	0.184	1.850	2.572
$r \rightarrow B$; Offset for age 8	2.515	0.197	2.129	2.902
$r \rightarrow B$; Offset for age 9	2.472	0.226	2.028	2.916

Table A.3. continued.

Role in model	Estimate	SE	lcl	ucl
r→*B*; Offset for age 10	3.057	0.289	2.491	3.623
r→*B*; Offset for age >10	2.577	0.295	1.999	3.155
r→*B*; Offset for 1984	-0.026	1.064	-2.112	2.059
r→*B*; Offset for 1985	-0.338	0.591	-1.497	0.821
r→*B*; Offset for 1986	0.053	0.393	-0.719	0.824
r→*B*; Offset for 1987	0.474	0.329	-0.170	1.119
r→*B*; Offset for 1988	-0.104	0.360	-0.810	0.601
r→*B*; Offset for 1989	0.524	0.315	-0.093	1.141
r→*B*; Offset for 1990	0.411	0.309	-0.194	1.017
r→*B*; Offset for 1991	-0.713	0.373	-1.445	0.018
r→*B*; Offset for 1992	-0.052	0.305	-0.651	0.546
r→*B*; Offset for 1994	0.014	0.293	-0.560	0.588
r→*B*; Offset for 1995	-0.793	0.324	-1.428	-0.157
r→*B*; Offset for 1996	0.449	0.284	-0.107	1.005
r→*B*; Offset for 1997	0.686	0.303	0.091	1.280
r→*B*; Offset for 1998	0.569	0.299	-0.017	1.155
r→*B*; Offset for 1999	0.718	0.302	0.126	1.309
r→*B*; Offset for 2000	0.291	0.394	-0.481	1.063
r→*B*; Offset for 2001	1.395	0.330	0.748	2.042
r→*B*; Offset for 2002	-0.483	0.295	-1.062	0.096
r→*B*; Offset for 2003	-0.513	0.433	-1.361	0.335
r→*B*; Offset for 2004	-0.325	0.301	-0.916	0.266
r→*B*; Offset for 2005	0.262	0.267	-0.261	0.785
r→*B*; Offset for 2006	0.177	0.259	-0.331	0.685
r→*B*; Offset for 2007	0.067	0.300	-0.520	0.654
$P_{age\ 6}$ →U; 1993	-0.095	0.190	-0.468	0.278
Offset for $U_{age\ 6}$ →U; 1993	1.408	0.104	1.204	1.613
r→U; Offset for age 1	5.457	0.219	5.029	5.886

Table A.3. continued.

Role in model	Estimate	SE	lcl	ucl
r→U; Offset for age 2-3	2.683	0.117	2.454	2.911
r→U; Offset for age 4	1.476	0.116	1.249	1.702
r→U; Offset for age 5	0.338	0.112	0.119	0.557
r→U; Offset for age 7	-0.216	0.133	-0.477	0.044
r→U; Offset for age 8	-0.417	0.163	-0.736	-0.098
r→U; Offset for age 9	-0.229	0.213	-0.647	0.190
r→U; Offset for age 10	0.602	0.299	0.016	1.188
r→U; Offset for age >10	0.572	0.298	-0.013	1.156
r→U; Offset for 1980	0.281	1.029	-1.736	2.297
r→U; Offset for 1981	-0.036	0.621	-1.252	1.181
r→U; Offset for 1982	-1.649	0.301	-2.238	-1.059
r→U; Offset for 1983	-1.316	0.275	-1.855	-0.777
r→U; Offset for 1984	0.252	0.312	-0.361	0.864
r→U; Offset for 1985	-0.125	0.269	-0.653	0.403
r→U; Offset for 1986	-1.475	0.224	-1.914	-1.036
r→U; Offset for 1987	-1.841	0.225	-2.283	-1.399
r→U; Offset for 1988	0.233	0.243	-0.242	0.708
r→U; Offset for 1989	-0.474	0.229	-0.923	-0.025
r→U; Offset for 1990	-0.810	0.223	-1.246	-0.373
r→U; Offset for 1991	0.140	0.231	-0.313	0.592
r→U; Offset for 1992	-0.299	0.226	-0.742	0.144
r→U; Offset for 1994	-0.972	0.214	-1.391	-0.552
r→U; Offset for 1995	-0.375	0.223	-0.812	0.063
r→U; Offset for 1996	-0.711	0.223	-1.148	-0.274
r→U; Offset for 1997	0.086	0.234	-0.372	0.544
r→U; Offset for 1998	-0.593	0.219	-1.023	-0.164
r→U; Offset for 1999	-0.553	0.217	-0.978	-0.128
r→U; Offset for 2000	1.626	0.258	1.120	2.133

Table A.3. continued.

Role in model	Estimate	SE	lcl	ucl
r→U; Offset for 2001	1.228	0.246	0.746	1.710
r→U; Offset for 2002	-0.816	0.195	-1.199	-0.433
r→U; Offset for 2003	2.689	0.266	2.168	3.209
r→U; Offset for 2004	0.774	0.211	0.360	1.187
r→U; Offset for 2005	0.409	0.214	-0.011	0.829
r→U; Offset for 2006	-1.130	0.297	-1.712	-0.548
r→U; Offset for 2007	0.894	0.278	0.348	1.439

APPENDIX B

BETA ESTIMATES FOR TOP-RANKED A PRIORI MODEL

Table B.1. Estimates of beta parameters used to estimate demographic rates for female Weddell seals in Erebus Bay Antarctica. Estimates are generated from the best-supported a priori model (survival differs by age, birth cohort, and current-year winter sea-ice extent; recruitment and detection differ by age and year). Confidence limits are for a 95% interval.

Role in model	Estimate	SE	lcl	ucl
Logit ($S_{cohort, age}$)				
Intercept: Age >2; 1993 cohort	2.617	0.152	2.318	2.916
Pup offset; 1993 cohort	-2.110	0.353	-2.802	-1.418
Yearling offset; 1993 cohort	-2.474	0.313	-3.087	-1.860
1980 cohort offset	-0.389	0.202	-0.785	0.008
1981 cohort offset	-0.076	0.230	-0.526	0.375
1982 cohort offset	-0.363	0.190	-0.736	0.009
1983 cohort offset	-0.155	0.184	-0.516	0.206
1984 cohort offset	-0.319	0.186	-0.684	0.045
1985 cohort offset	-0.007	0.193	-0.385	0.371
1986 cohort offset	0.238	0.202	-0.158	0.634
1987 cohort offset	-0.127	0.187	-0.493	0.239
1988 cohort offset	-0.282	0.187	-0.647	0.084
1989 cohort offset	0.002	0.182	-0.354	0.359
1990 cohort offset	0.014	0.182	-0.343	0.371
1991 cohort offset	0.038	0.185	-0.324	0.400
1992 cohort offset	-0.036	0.198	-0.424	0.353
1994 cohort offset	-0.106	0.193	-0.484	0.273
1995 cohort offset	-0.235	0.197	-0.621	0.151
1996 cohort offset	0.106	0.199	-0.284	0.496
1997 cohort offset	0.240	0.185	-0.123	0.603
1998 cohort offset	0.283	0.202	-0.114	0.679
1999 cohort offset	0.350	0.206	-0.054	0.754
2000 cohort offset	0.147	0.191	-0.227	0.521
2001 cohort offset	-0.103	0.220	-0.535	0.328

Table B.1. continued.

Role in model	Estimate	SE	lcl	ucl
2002 cohort offset	-0.342	0.234	-0.800	0.116
2003 cohort offset	-0.910	0.281	-1.462	-0.359
2004 cohort offset	-1.197	0.422	-2.024	-0.370
2005 cohort offset	-1.302	0.632	-2.541	-0.062
Current-year winter sea ice effect	0.194	0.094	0.010	0.377
logit($p^r_{.j}$)				
Intercept: Ages 3-6; 1993 cohort	-0.877	0.168	-1.206	-0.548
Offset for age 2; 1993 cohort	-2.796	0.208	-3.203	-2.389
Offset for age 3; 1993 cohort	-1.985	0.145	-2.269	-1.702
Offset for ages ≥7; 1993 cohort	1.119	0.107	0.908	1.329
1981 offset	-0.184	0.924	-1.996	1.628
1982 offset	0.318	0.611	-0.878	1.515
1983 offset	1.225	0.342	0.555	1.896
1984 offset	0.624	0.309	0.018	1.230
1985 offset	-0.284	0.316	-0.904	0.337
1986 offset	-0.439	0.289	-1.005	0.126
1987 offset	0.752	0.242	0.276	1.227
1988 offset	1.314	0.237	0.849	1.779
1989 offset	-0.036	0.246	-0.518	0.446
1990 offset	0.103	0.242	-0.371	0.577
1991 offset	0.472	0.234	0.013	0.931
1992 offset	-0.249	0.240	-0.719	0.222
1994 offset	-0.248	0.236	-0.710	0.215
1995 offset	0.598	0.226	0.155	1.040
1996 offset	0.233	0.230	-0.218	0.683
1997 offset	0.497	0.233	0.040	0.953
1998 offset	-0.029	0.244	-0.507	0.449

Table B.1. continued.

Role in model	Estimate	SE	lcl	ucl
1999 offset	0.177	0.233	-0.279	0.634
2000 offset	-0.018	0.226	-0.461	0.425
2001 offset	-1.638	0.279	-2.185	-1.091
2002 offset	-1.668	0.274	-2.204	-1.131
2003 offset	0.237	0.208	-0.172	0.645
2004 offset	-2.303	0.299	-2.890	-1.716
2005 offset	-1.071	0.234	-1.529	-0.613
2006 offset	-0.473	0.238	-0.939	-0.006
2007 offset	1.495	0.446	0.622	2.369
Mlogit($\psi^{PB}_{year,age}$)				
Intercept: $P_{age\ 7} \rightarrow$B; 1993	-0.873	0.275	-1.411	-0.334
Offset for age 5; 1993	-2.661	0.224	-3.100	-2.222
Offset for age 6; 1993	-0.817	0.147	-1.105	-0.528
Offset for age 8; 1993	0.413	0.161	0.097	0.729
Offset for age 9; 1993	0.362	0.204	-0.038	0.761
Offset for age 10; 1993	0.430	0.278	-0.116	0.975
Offset for age >10; 1993	0.106	0.295	-0.473	0.685
Offset for 1984	0.170	1.313	-2.403	2.742
Offset for 1985	-0.248	0.720	-1.658	1.163
Offset for 1986	0.511	0.485	-0.439	1.462
Offset for 1987	1.123	0.405	0.329	1.918
Offset for 1988	0.139	0.426	-0.697	0.974
Offset for 1989	0.679	0.378	-0.062	1.420
Offset for 1990	0.698	0.372	-0.031	1.427
Offset for 1991	-0.721	0.449	-1.602	0.160
Offset for 1992	0.194	0.361	-0.513	0.902
Offset for 1994	0.322	0.351	-0.366	1.009

Table B.1. continued.

Role in model	Estimate	SE	lcl	ucl
Offset for 1995	-0.479	0.388	-1.241	0.282
Offset for 1996	0.747	0.340	0.081	1.414
Offset for 1997	0.781	0.357	0.081	1.481
Offset for 1998	0.860	0.358	0.157	1.562
Offset for 1999	0.936	0.364	0.222	1.650
Offset for 2000	-0.658	0.443	-1.526	0.209
Offset for 2001	0.247	0.350	-0.440	0.934
Offset for 2002	-0.367	0.352	-1.057	0.323
Offset for 2003	-2.145	0.483	-3.092	-1.199
Offset for 2004	-1.049	0.342	-1.719	-0.379
Offset for 2005	-0.041	0.305	-0.640	0.557
Offset for 2006	0.714	0.316	0.096	1.333

APPENDIX C

DETAILS OF OPEN ROBUST DESIGN MULTISTATE MODELING AND RESULTS OF WITHIN-YEAR MODELING FOR CHAPTER 3

Description of Open Robust Design Multistate Models

We used open robust design multistate (ORDMS) models (Kendall & Bjorkland 2001; Kendall 2006; Converse *et al.* 2009) to investigate patterns of variation in survival rates, recruitment rates, and rates of temporary emigration (TE) of juvenile Weddell seals. Because the robust design uses information from multiple secondary capture occasions within each primary occasion (Pollock 1982), it is possible to separate estimation of detection probability from estimation of availability for detection (Kendall *et al.* 1997). This distinction between detection probability and availability provides information useful for estimating TE rates (Kendall & Nichols 1995; Kendall *et al.* 1997; Kendall & Nichols 2002). Estimation of TE rates is accomplished by defining and estimating a transition into an unobservable state (Fujiwara & Caswell 2002; Kendall & Nichols 2002; Schaub *et al.* 2004). The methods of Kendall *et al*. (1997) allowed state-dependent transitions but assumed demographic and geographic closure within primary periods, which is untenable in some cases. Schwarz and Stobo (1997) relaxed the closure assumption, allowing staggered entry and exit within a primary period, but did not allow state-dependant transitions. Kendall and Bjorkland (2001) combined the methods of Kendall *et al*. (1997) and Schwarz and Stobo (1997) to allow geographic openness within, and state-dependent transitions between, primary periods. ORDMS models are a generalization of Kendall and Bjorkland's (2001) approach that allow transitions between multiple states. The specific form of ORDMS models employed here used a modification of the open model of Schwarz and Arnason (1996) to model within-primary-period

dynamics and the multistate framework of Brownie *et al*. (1993) for between-primary-period dynamics.

ORDMS models provide estimates for five types of parameters. Apparent survival (S^r), hereafter survival, is the probability for state *r* of surviving and not permanently emigrating; ψ_t^{rz} is the probability, given survival, that an individual will make a transition between state *r* to state *z*. Survival and transition probabilities can be age-dependent and vary by year or birth cohort. For a given primary period, *t*: $pent_{tj}^r$ is the probability that an individual in state *r* is a new arrival to the study area in secondary occasion j; p_{tj}^r is the probability of detection for individuals in state *r* during secondary occasion j; and ϕ_{tjk}^r is probability that individuals of state *r* will stay in the study area between secondary occasions j and $j + 1$, given that they entered *k* secondary occasions prior. Individuals are allowed to enter the population once and leave during a primary period, and the probability that an individual enters the study area and leaves again prior to the first secondary capture occasion is assumed to be zero (Kendall & Bjorkland 2001).

Further analysis details

We defined 7 possible breeding state classifications (see Figure 4.1): P0 (pup); U0 (unobservable prebreeder, never previously observed in Erebus Bay subsequent to birth); P1 (first-time observable prebreeder); U1 (unobservable prebreeder, previously observed once); P2 (observable prebreeder, previously observed ≥1 time); U2 (unobservable

prebreeder, previously observed ≥1 time); and B (observable first-time mom). Temporary emigration was defined as any transition into any unobservable state (i.e., $\psi^{P0U0}, \psi^{U0U0}, \psi^{P1U1}, \psi^{U1U1}, \psi^{P2U2}, \psi^{U2U2}$), and recruitment as any transition into B (i.e., $\psi^{U0B}, \psi^{P1B}, \psi^{U1B}, \psi^{P2B}, \psi^{U2B}$). We fixed to zero all transition probabilities that were either biologically impossible (all transitions to a previous state, except that ψ^{P2U2} and ψ^{U2P2} were allowed) or not allowed because encounter histories were right-censored after recruitment (ψ^{BB}). Because the probabilities of all possible transitions for any given state logically must sum to 1, one transition rate for each state was derived by subtraction (e.g., $\psi^{P1P0} + \psi^{P1U0} + \psi^{P1U1} + \psi^{P1P2} = 1$, where $\psi^{P1P0} = \psi^{P1U0} = 0$; thus if ψ^{P1U1} is estimated, $\psi^{P1P2} = 1 - \psi^{P1U1}$ for a given age and time period). Our choice of which transition rates to estimate directly was made so that our competing models focused on testing hypotheses about 2 types of transitions: into an unobservable state (TE) and into a breeding state (recruitment). Our goal was to investigate variation in vital rates of prebreeders, so we right-censored information for seals that recruited and did not estimate rates for seals in state B. Such censoring simplified the analysis by limiting the number of possible state transitions and was justified by the nearly certain detection of mothers (Rotella *et al.* 2012).

In some models, we estimated TE rates with a different Markovian structure than the structure for recruitment. For example a design matrix might specify state specific recruitment estimates $\psi^{U0B}, \psi^{P1B}, \psi^{U1B}, \psi^{P2B}$, and ψ^{U2B}, and partially state-specific TE estimates $\psi^{NU0} = \psi^{P1U1} = \psi^{P2U2}$, and $\psi^{U0U0} = \psi^{U1U1} = \psi^{U2U2}$ (i.e., TE rates are only

different depending on whether seals did or did not attend the study area the previous year; we used this Markovian structure for TE in all our models). However, because we used multinomial logit (mlogit) link functions to estimate beta parameters, full state dependency was induced in back-transformed real parameter TE estimates (i.e., $\psi^{\mathrm{P0U0}} \neq \psi^{\mathrm{P1U1}} \neq \psi^{\mathrm{P2U2}} \neq \psi^{\mathrm{U0U0}} \neq \psi^{\mathrm{U1U1}} \neq \psi^{\mathrm{U2U2}}$). To see why this is so, consider a simple contrived example where the beta parameters β_0 is an intercept, β_1 is an offset for ψ^{P1U1} and ψ^{P2U2} , β_2 is an offset for ψ^{P1B} , and β_3 is an offset for ψ^{P2B} . Back-transformed real TE estimates thus are $\psi^{\mathrm{P1U1}} = \frac{e^{\beta_0+\beta_1}}{1+e^{\beta_0+\beta_1}+e^{\beta_0+\beta_2}}$ and $\psi^{\mathrm{P2U2}} = \frac{e^{\beta_0+\beta_1}}{1+e^{\beta_0+\beta_1}+e^{\beta_0+\beta_3}}$. Because the denominators in the 2 link functions are different, differences are induced in the real parameter estimates despite the fact that the design matrix rows are identical for these two parameters. One solution is to use logit rather than mlogit link functions for transition parameters, but mlogit links often are necessary for parameter estimates to converge to the MLE. Thus we chose to use mlogit links and to recognize that for some models, state-dependent differences in TE estimates are an artifact of analogous state-dependency in estimates of recruitment rates.

Based on previous analyses, we considered a single structure for each of the within-season parameters. In the absence of reasonable a priori expectations, considering all possible combinations for even a few structures of $pent_{tj}^{r}$, p_{tj}^{r} , and ϕ_{tjk}^{r} would generate an intractably large model set. Instead, we used competing Schwarz-Arnason models to evaluate within-year dynamics for each year (Rotella et al. 2009). In preliminary analyses we found that the model that performed best varied by year, but point estimates were

similar across years. Estimates for p_{tj}^{r} and ϕ_{tjk}^{r} were uniformly high, and $pent_{tj}^{r}$ generally was low and decreasing for breeders but increasing slightly for prebreeders. We thus felt justified in modeling only one structure for $pent_{tj}^{r}$, p_{tj}^{r}, and ϕ_{tjk}^{r}. For $pent_{tj}^{r}$ we pooled breeders and pups because in most cases pups were present the first time we encountered breeders during a season; we also pooled both observable prebreeders state. We allowed $pent_{tj}^{r}$ to vary by state (states P1 and P2 pooled, P0 and B pooled; fixed to zero for states U0, U1, and U2) and to follow a common state-dependent linear trend for j >1 within all primary periods. The probability of entry at j = 1, $pent_{tj}^{r}$, was calculated as $1-\sum_{j>1} pent_{tj}^{r}$. Detection probability also was fixed to zero for unobservable states and otherwise allowed to vary by state (states P0, P1 and P2 pooled, and B) following a state-dependent linear trend that was constant for all years. We allowed ϕ_{tjk}^{r} to vary only by state (states N, P1 and P2 pooled, and B). The probability that an individual will be detected at least once in a primary occasion (p_{t}^{*r}) can be derived from the secondary occasion-specific parameters. For example, for a year with 3 secondary occasions:

$$\begin{aligned} p_{t}^{*r} = {} & pent_{t1}^{r}\left[p_{t1}^{r} + \left(1-p_{t1}^{r}\right)\phi_{t10}^{r}p_{i2}^{r} + \left(1-p_{t1}^{r}\right)\phi_{t10}^{r}p_{i2}^{r}\left(1-p_{t2}^{r}\right)\phi_{t21}^{r}p_{t3}^{r}\right] \\ & + pent_{t2}^{r}\left[p_{t2}^{r} + \left(1-p_{t2}^{r}\right)\phi_{t20}^{r}p_{t3}^{r}\right] \\ & + pent_{t3}^{r}p_{t3}^{r}. \end{aligned}$$

Tag loss is known to occur at a very low rate in our study (Cameron 2001). Thus, S_{t}^{r} represents a product of the underlying survival rate and the probability that both tags are retained (Nichols *et al.* 1992). We therefore adjusted our estimates of survival as

$\hat{S}^r_{adjusted,t} = \hat{S}^r_t / \hat{\theta}^r_t$, based on the formula presented by Arnason and Mills (1981) where $\hat{\theta}^r_t$ are cohort-specific tag-retention rates previously estimated for this population by Cameron (2001). The degree of adjustment was slight.

Results from Within-Year Modeling

Based on estimates from our best-supported model (Table C.2), the majority of female seals were present on the first survey each year ($\overline{\widehat{pent}}^{\text{P0 and B}}_{t1}$ = 0.83, $\widehat{SE}$ = 0.01; $\overline{\widehat{pent}}^{\text{P1and P2}}_{t1}$ = 0.63, $\widehat{SE}$ = 0.03). For pups and breeders, $\widehat{pent}^{r}_{tj}$ decreased rapidly during the primary period (Figure A.1) from 0.11 ($\widehat{SE}$ = <0.01) to <0.01 ($\widehat{SE}$ = <0.01), whereas $\widehat{pent}^{\text{P1 and P2}}_{tj}$ was essentially constant throughout the season ($\widehat{pent}^{\text{P1and P2}}_{i2}$ = 0.06, $\widehat{SE}$ = 0.01). After entering the study area each year, seals in each state were likely to remain ($\hat{\phi}^{\text{P0}}_{\cdot}$ = 0.98, $\widehat{SE}$ = <0.01; $\hat{\phi}^{\text{P1and P2}}_{\cdot}$ = 0.94, $\widehat{SE}$ = <0.01; $\hat{\phi}^{\text{B}}_{\cdot}$ = 0.98, $\widehat{SE}$ = <0.01). For pups and breeders, $\hat{p}^r_{tj}$ was high early in the season and decreased throughout the season, whereas for prebreeders, $\hat{p}^r_{tj}$ increased throughout the season (Figure C.1). We detected ≥92% of all seals that entered the study area (Table C.1).

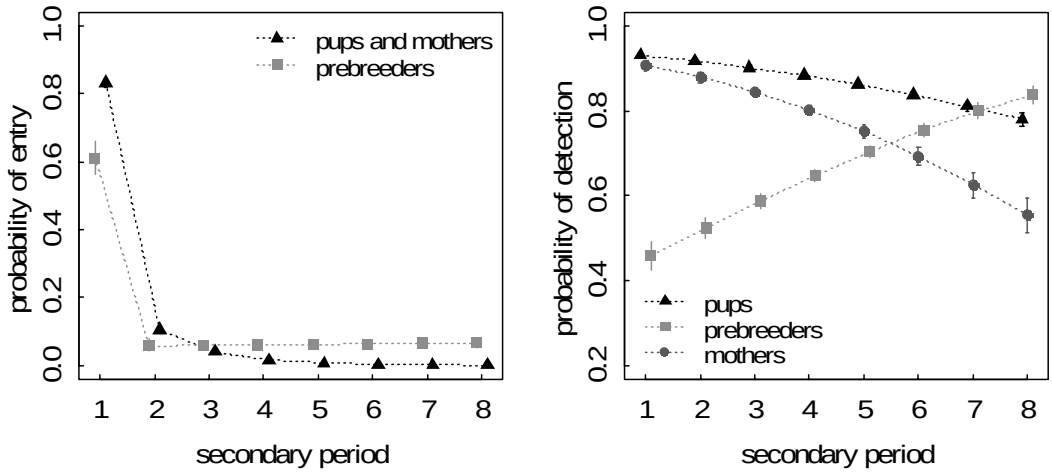

Figure C.1. Secondary survey-specific probability that a seal will be new to the study area (left) and will be detected (right). Example of a year with 8 secondary occasions. The first entry probability is derived as 1 minus the sum of the rest of the probabilities and represents the probability of presence at the beginning of the primary survey period. Error bars represent 95% confidence intervals.

Table C.1. Probability of detection of female Weddell seals during ≥1 secondary occasions with a primary period ($\hat{p}_t^r$ *) for a primary period with 5–8 secondary periods. Most primary periods had ≥6 secondary occasions.

	5 secondary occasions		6 secondary occasions		7 secondary occasions		8 secondary occasions	
	$\hat{p}_t^r$ *	$\widehat{SE}$	$\hat{p}_t^r$ *	$\widehat{SE}$	$\hat{p}_t^r$ *	$\widehat{SE}$	$\hat{p}_t^r$ *	$\widehat{SE}$
pups	>0.99	<0.01	>0.99	<0.01	>0.99	<0.01	>0.99	<0.01
prebreeders	0.92	<0.01	0.93	<0.01	0.94	<0.01	0.95	<0.01
breeders	>0.99	<0.01	>0.99	<0.01	>0.99	<0.01	>0.99	<0.01

Table C.2. Complete model selection results for models representing hypotheses about variation in transition probabilities for female Weddell seals in Erebus Bay, Antarctica. All models included annual variation and 9 nominal age classes (1–3, 4, 5, 6, 7, 8, 9, 10, 11+) for recruitment (ψ^{rB}) and 11 nominal age classes (1, 2, 3, 4, 5, 6, 7, 8, 9, 10, 11+) for temporary emigration (TE; ψ^{rU}). The Markovian structure for TE specified different rates depending on colony attendance the previous year, whereas the Markovian structure for recruitment specified dependent on either: colony attendance (*a*); number of years of previous attendance experience at time of recruitment (*e*); both (*ae*); or neither (*non-Markovian*). Covariate values for TE are distance from Erebus Bay to the edge of the fast-ice (DIST), population size of adult females seals in the previous year (BPOP), winter sea-ice extent (SIE), winter Southern Oscillation Index (SOI), and sea-ice concentration in and around McMurdo Sound (SIC).

Model	K	AICc	ΔAICc	w_i	Deviance
TE model suite					
(model 9) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP + DIST)}$	87	74019.53	0.000	0.472	73845.15
(model 17) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP + DIST +SIE)}$	88	74020.11	0.587	0.352	73843.72
(model 15) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP + DIST +SOI)}$	88	74021.51	1.985	0.175	73845.12
(model 5) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(DIST)}$	86	74039.97	20.445	0.000	73867.6
(model 13) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(DIST +SIE)}$	87	74040.35	20.827	0.000	73865.97
(model 11) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(DIST +SOI)}$	87	74040.59	21.063	0.000	73866.21
(model 14) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP + SIC +SOI)}$	88	74218.07	198.548	0.000	74041.68
(model 10) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(SIC +SOI)}$	87	74241.39	221.869	0.000	74067.01
(model 16) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP + SIC +SIE)}$	88	74260.68	241.157	0.000	74084.29
(model 12) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(SIC +SIE)}$	87	74272.86	253.331	0.000	74098.48
(model 7) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP + SIC)}$	87	74279.52	259.993	0.000	74105.14
(model 2) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(SIC)}$	86	74291.52	271.993	0.000	74119.15
(model 6) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP + SOI)}$	87	74545.31	525.780	0.000	74370.93
(model 1) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(SOI)}$	86	74548.83	529.305	0.000	74376.46
(model 4) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(SIE)}$	86	74548.83	529.305	0.000	74376.46
(model 8) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP +SIE)}$	87	74561.65	542.125	0.000	74387.27
(model 3) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(BPOP)}$	86	74579.35	559.822	0.000	74406.98
(model 18) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(constant)}$	85	74579.50	559.979	0.000	74409.14
Recruitment model suite					
(model 22) $\psi^{rB}_{(ae)}$, $\psi^{rU}_{(year)}$	113	73685.08	0.000	0.976	73458.43
(model 20) $\psi^{rB}_{(e)}$, $\psi^{rU}_{(year)}$	110	73692.66	7.580	0.022	73472.05
(model 21) $\psi^{rB}_{(a)}$, $\psi^{rU}_{(year)}$	110	73699.01	13.935	0.001	73478.40
(model 19) $\psi^{rB}_{(non\text{-}Markovian)}$, $\psi^{rU}_{(year)}$	109	73699.57	14.492	0.001	73480.97

Table C.3. Estimates of beta parameters from the best-supported model used to estimate state-dependent recruitment rates for female Weddell seals in Erebus Bay Antarctica (Model 22, Table C.2). Confidence limits are for a 95% interval.

Role in model	Estimate	SE	lcl	ucl
Logit ($S_{cohort,\ age}$)				
Age >2; 1993 cohort	2.377	0.081	2.218	2.536
Pup offset; 1993 cohort	-1.435	0.601	-2.612	-0.257
Yearling offset; 1993 cohort	-2.418	0.358	-3.120	-1.716
1983 offset	-0.065	0.141	-0.341	0.211
1984 offset	-0.244	0.142	-0.523	0.034
1985 offset	0.055	0.163	-0.264	0.374
1986 offset	0.282	0.167	-0.045	0.609
1987 offset	-0.082	0.146	-0.368	0.205
1988 offset	-0.171	0.144	-0.454	0.112
1989 offset	0.190	0.145	-0.094	0.475
1990 offset	0.129	0.143	-0.150	0.409
1991 offset	0.108	0.147	-0.180	0.395
1992 offset	0.061	0.157	-0.248	0.369
1994 offset	-0.058	0.154	-0.361	0.245
1995 offset	-0.148	0.167	-0.475	0.179
1996 offset	0.286	0.173	-0.054	0.626
1997 offset	0.468	0.162	0.151	0.785
1998 offset	0.498	0.177	0.150	0.845
1999 offset	0.631	0.175	0.287	0.974
2000 offset	0.346	0.150	0.052	0.639
2001 offset	0.120	0.155	-0.183	0.423
2002 offset	0.046	0.161	-0.270	0.363
2003 offset	-0.452	0.169	-0.783	-0.121
2004 offset	-0.741	0.237	-1.206	-0.275
2005 offset	0.376	0.242	-0.099	0.850

Table C.3. continued.

Role in model	Estimate	SE	lcl	ucl
2006 offset	-0.365	0.257	-0.869	0.138
2007 offset	-0.639	0.306	-1.238	-0.040
2008 offset	-0.776	0.547	-1.848	0.297
2009 offset	-3.160	1.219	-5.550	-0.771
Offset for SIE influence	0.147	0.081	-0.011	0.306
Mlogit($\psi^{rz}_{year,age}$)				
$P2_{age\ 7} \rightarrow$B; 1994	0.026	0.240	-0.445	0.497
Offset for $U0_{age\ 7} \rightarrow$B; 1994	-0.441	0.127	-0.690	-0.193
Offset for $U1_{age\ 7} \rightarrow$B; 1994	-0.055	0.149	-0.346	0.237
Offset for $U2_{age\ 7} \rightarrow$B; 1994	-0.438	0.220	-0.869	-0.007
Offset for $P1_{age\ 7} \rightarrow$B; 1994	-0.500	0.144	-0.783	-0.217
$r \rightarrow B$; Offset for age 4	-5.624	1.010	-7.604	-3.645
$r \rightarrow B$; Offset for age 5	-2.185	0.195	-2.566	-1.803
$r \rightarrow B$; Offset for age 6	-0.676	0.133	-0.937	-0.416
$r \rightarrow B$; Offset for age 8	0.125	0.140	-0.149	0.399
$r \rightarrow B$; Offset for age 9	0.172	0.172	-0.166	0.509
$r \rightarrow B$; Offset for age 10	0.701	0.232	0.246	1.155
$r \rightarrow B$; Offset for age >10	0.052	0.238	-0.414	0.517
$r \rightarrow B$; Offset for 1988	0.693	0.513	-0.312	1.698
$r \rightarrow B$; Offset for 1989	-0.160	0.458	-1.058	0.737
$r \rightarrow B$; Offset for 1990	0.580	0.333	-0.071	1.232
$r \rightarrow B$; Offset for 1991	0.299	0.320	-0.329	0.926
$r \rightarrow B$; Offset for 1992	-0.734	0.375	-1.468	0.001
$r \rightarrow B$; Offset for 1993	-0.076	0.305	-0.674	0.522
$r \rightarrow B$; Offset for 1995	0.053	0.293	-0.521	0.627
$r \rightarrow B$; Offset for 1996	-0.761	0.326	-1.400	-0.121
$r \rightarrow B$; Offset for 1997	0.363	0.284	-0.194	0.920

Table C.3. continued.

Role in model	Estimate	SE	lcl	ucl
$r \rightarrow B$; Offset for 1998	0.597	0.304	0.001	1.192
$r \rightarrow B$; Offset for 1999	0.551	0.301	-0.040	1.141
$r \rightarrow B$; Offset for 2000	0.774	0.303	0.180	1.368
$r \rightarrow B$; Offset for 2001	0.289	0.394	-0.484	1.061
$r \rightarrow B$; Offset for 2002	1.327	0.328	0.683	1.970
$r \rightarrow B$; Offset for 2003	-0.472	0.296	-1.052	0.109
$r \rightarrow B$; Offset for 2004	-0.433	0.434	-1.284	0.419
$r \rightarrow B$; Offset for 2005	-0.364	0.302	-0.955	0.227
$r \rightarrow B$; Offset for 2006	0.278	0.267	-0.245	0.801
$r \rightarrow B$; Offset for 2007	0.395	0.251	-0.097	0.888
$r \rightarrow B$; Offset for 2008	0.200	0.302	-0.393	0.792
$r \rightarrow B$; Offset for 2009	-0.079	0.290	-0.648	0.490
Offset for $r \rightarrow U_{\text{age 6}}$; 1994	0.668	0.266	0.146	1.189
Offset for $P_{\text{age 6}} \rightarrow U$; 1994	-1.337	0.098	-1.530	-1.144
$r \rightarrow$ U; Offset for age 1	4.922	0.235	4.462	5.383
$r \rightarrow$ U; Offset for age 3	2.840	0.152	2.542	3.138
$r \rightarrow$ U; Offset for age 3	1.879	0.125	1.635	2.123
$r \rightarrow$ U; Offset for age 4	1.052	0.112	0.833	1.271
$r \rightarrow$ U; Offset for age 5	0.385	0.109	0.172	0.597
$r \rightarrow$ U; Offset for age 7	-0.130	0.128	-0.381	0.121
$r \rightarrow$ U; Offset for age 8	-0.572	0.156	-0.878	-0.266
$r \rightarrow$ U; Offset for age 9	-0.435	0.206	-0.839	-0.032
$r \rightarrow$ U; Offset for age 10	0.224	0.280	-0.325	0.773
$r \rightarrow$ U; Offset for age >10	0.363	0.268	-0.162	0.887
$r \rightarrow$ U; Offset for 1984	-0.945	0.498	-1.921	0.032
$r \rightarrow$ U; Offset for 1985	1.451	1.020	-0.549	3.450
$r \rightarrow$ U; Offset for 1986	0.570	0.486	-0.382	1.522
$r \rightarrow$ U; Offset for 1987	-1.367	0.233	-1.824	-0.911

Table C.3. continued.

Role in model	Estimate	SE	lcl	ucl
$r \rightarrow$U; Offset for 1988	-1.906	0.221	-2.338	-1.474
$r \rightarrow$U; Offset for 1989	0.152	0.241	-0.321	0.624
$r \rightarrow$U; Offset for 1990	-0.461	0.224	-0.900	-0.023
$r \rightarrow$U; Offset for 1991	-0.896	0.213	-1.315	-0.478
$r \rightarrow$U; Offset for 1992	0.080	0.223	-0.357	0.516
$r \rightarrow$U; Offset for 1994	-0.435	0.215	-0.856	-0.013
$r \rightarrow$U; Offset for 1995	-0.997	0.205	-1.399	-0.596
$r \rightarrow$U; Offset for 1996	-0.458	0.215	-0.879	-0.037
$r \rightarrow$U; Offset for 1997	-0.866	0.214	-1.285	-0.447
$r \rightarrow$U; Offset for 1998	-0.125	0.224	-0.565	0.315
$r \rightarrow$U; Offset for 1999	-0.599	0.214	-1.018	-0.180
$r \rightarrow$U; Offset for 2000	-0.572	0.208	-0.979	-0.165
$r \rightarrow$U; Offset for 2001	1.538	0.250	1.048	2.027
$r \rightarrow$U; Offset for 2002	1.186	0.238	0.720	1.652
$r \rightarrow$U; Offset for 2003	-0.740	0.189	-1.109	-0.370
$r \rightarrow$U; Offset for 2004	2.593	0.259	2.084	3.101
$r \rightarrow$U; Offset for 2005	0.714	0.204	0.315	1.113
$r \rightarrow$U; Offset for 2006	0.281	0.203	-0.116	0.679
$r \rightarrow$U; Offset for 2007	-1.102	0.213	-1.520	-0.685
$r \rightarrow$U; Offset for 2008	0.839	0.240	0.369	1.310
$r \rightarrow$U; Offset for 2009	-1.184	0.242	-1.659	-0.709
Mlogit ($pent^{r}_{.j}$)				
Prebreeders	-2.303	0.193	-2.680	-1.925
Offset for pups and mothers	0.223	0.200	-0.169	0.614
Time trend for prebreeders	0.024	0.043	-0.061	0.108
Time trend for pups and mothers	-0.970	0.039	-1.047	-0.893
logit($\phi^{r}_{.}$)				

Table C.3. continued.

Role in model	Estimate	SE	lcl	ucl
Mothers	4.077	0.168	3.747	4.407
Offset for pups	0.056	0.179	-0.295	0.406
Offset for prebreeders	-1.310	0.180	-1.663	-0.957
logit($p^r_{.j}$)				
Mothers	2.288	0.079	2.134	2.443
Offset for pups	0.313	0.090	0.136	0.490
Offset for prebreeders	-2.455	0.104	-2.659	-2.252
Time trend for breeders	-0.296	0.020	-0.336	-0.256
Time trend for pups	0.105	0.023	0.059	0.151
Time trend for prebreeders	0.555	0.028	0.501	0.609

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