Female Weddell seals show flexible strategies of colony attendance related to varying environmental conditions

Authors: Thierry Chambert, Jay J. Rotella, & Robert A. Garrott

Chambert, Thierry, Jay J. Rotella, and Robert A. Garrott. “Female Weddell Seals Show Flexible Strategies of Colony Attendance Related to Varying Environmental Conditions.” Ecology 96, no. 2 (February 2015): 479–488.
http://dx.doi.org/10.1890/14-0911.1

Ecology, 96(2), 2015, pp. 479–488

Female Weddell seals show flexible strategies of colony attendance related to varying environmental conditions

THIERRY CHAMBERT,[1,2,3,4] JAY J. ROTELLA,[1] AND ROBERT A. GARROTT[1]

[1]*Department of Ecology, Montana State University, Bozeman, Montana 59717 USA*
[2]*USGS Patuxent Wildlife Research Center, Laurel, Maryland 20708 USA*
[3]*Department of Ecosystem Science and Management, Penn State University, University Park, Pennsylvania 16802 USA*

Abstract. Many animal life cycles involve movements among different habitats to fulfill varying resource demands. There are inherent costs associated with such movements, and the decision to leave or stay at a given location ought to be motivated by the benefits associated with potential target habitats. Because movement patterns, especially those associated with reproduction, can have important implications for the success (survival, reproduction) of individual animals, and therefore a population's dynamics, it is important to identify and understand their sources of variation (environmental and individual). Here, using a mark–recapture, multistate modeling approach, we investigated a set of a priori hypotheses regarding sources and patterns of variation in breeding-colony attendance for Weddell seal (*Leptonychotes weddellii*) females on sabbatical from pup production. For such females, colony attendance might be motivated by predation avoidance and positive social interactions related to reproduction, but some costs, such as reduced foraging opportunities or aggressive interactions with conspecifics, might also exist. We expected these benefits and costs to vary with a female's condition and the environment. Results revealed that the probability of being absent from colonies was higher (1) in years when the extent of local sea ice was larger, (2) for the youngest and oldest individuals, and (3) for females with less reproductive experience. We also found substantial levels of residual individual heterogeneity in these rates. Based on our a priori predictions, we postulate that the decision to attend breeding colonies or not is directly influenced by an individual's physiological condition, as well as by the ice-covered distance to good foraging areas, availability of predator-free haul-out sites, and the level of negative interactions with conspecifics inside colonies. Our results support the idea that in iteroparous species, and colonial animals in particular, seasonal and temporary movements from/to reproductive sites represent flexible behavioral strategies that can play an important role in coping with environmental variability.

Key words: animal movement; colony attendance; Leptonychotes weddellii; *life history; mark–recapture; Ross Sea, Antarctica; sea-ice extent; seasonal migration; temporary emigration; unobservable state; Weddell seal.*

INTRODUCTION

Many animal species have a life cycle that involves movements among different habitats to access various resources (Swingland and Greenwood 1983, Alerstam et al. 2003). The need to occupy and exploit different habitats is usually directly linked to varying demands at different stages of an animal's life cycle (Begon et al. 2009), but it can also be aimed at decreasing exposure to predation and competition (e.g., Creel et al. 2005). The decision of whether a site should be left for another is the result of a trade-off between the benefits provided by the target habitat and the costs associated with no longer using the current area and moving to the new site (Alerstam et al. 2003, Bowler and Benton 2005). Some movements are obligate and therefore undertaken by all individuals of a population or a species, such as predictable seasonal movements (e.g., in migratory birds) and dispersal events related to life stage (e.g., in anurans, salmonids). On the other hand, migration and dispersal movements can, in some species, be optional and condition-dependent, such that movement patterns vary substantially over time and/or across individuals (Alerstam et al. 2003). For instance, spring migrations in pronghorn (*Antilocapra americana*) populations of the Greater Yellowstone area are undertaken by only a fraction of the population each year, and some individuals have a temporally variable migration strategy, choosing to migrate in only some years (White et al. 2007). Similarly, in colonial species, attendance rates at breeding-aggregation sites can vary widely among individuals and across years (Halley et al. 1995, Beauplet et al. 2005). The optimal balance of costs–benefits, and therefore the decision to occupy a particular site or habitat, generally depends on an individual's status and the conditions of the environment at the time the

---

Manuscript received 13 May 2014; accepted 3 July 2014. Corresponding Editor: J. P. Y. Arnould.

[4] E-mail: Thierry.chambert@gmail.com

decision is made (Alerstam and Lindström 1990). For instance, partial migrations of Tropical Kingbirds (*Tyrannus melancholicus*) in the Amazon basin have been shown to be influenced by the size, age, and dominance status of individual birds, as well as by local levels of food limitation (Jahn et al. 2010).

In seasonal environments, non-obligate movements are often linked to reproduction, which often occurs in a specific area, at a particular time of the year. An individual's decision to attend or remain outside the breeding area can be permanent or temporary. Permanent emigration from a breeding site (i.e., dispersal) can be motivated by poor local conditions, high intraspecific competition, or breeding failure (Clobert et al. 2001, 2004). Temporary movements from breeding areas can be linked to similar factors, but they are generally more specifically driven by temporal variation in environmental conditions (Halley et al. 1995, Frederiksen and Bregnballe 2000, Stauffer et al. 2013, 2014). In long-lived iteroparous species, years of absence from breeding colonies can be key times to recover from past bouts of reproduction and/or to store body reserves for future reproductive attempts. Understanding the sources and patterns of variation in such flexible movement is of primary interest because rates of attendance and temporary emigration from a breeding site can have important implications for the future reproductive success and fitness of individuals (Schjørring et al. 1999, Aubry et al. 2009), as well as for the spatial distribution of wild populations and species (Kéry et al. 2009).

Mark–recapture methods have been shown to be a reliable and informative approach for studying temporary emigration at the level of a population and over an extended time period (Kendall et al. 1997, Kendall and Nichols 2002). Although this approach does not provide precise spatial information on individual movements, as can be obtained with spatial tracking devices, it can provide accurate information regarding the presence or absence of known individuals in the specific area(s) where sampling occurs. In mark–recapture studies, where only a fraction of all potentially used sites are sampled, temporary emigration has a precise methodological definition corresponding to the nonavailability of an individual for detection (Kendall et al. 1997). In general, however, the temporary absence of an individual from the study area also corresponds to particular biological states of interest (i.e., condition-dependent behavioral or physiological states), such as skipped reproduction, alternative foraging strategy, or even dormancy (Kéry et al. 2005, Stauffer et al. 2013).

In this study, we investigate several sources of variation in temporary emigration from breeding colonies in a philopatric population of Weddell seals, and the consequences for future reproduction. Each year, females from this population aggregate in colonies inside the Erebus Bay area (Ross Sea, Antarctica), where they give birth and rear their pup on consolidated sea ice (Stirling 1969*b*, Cameron and Siniff 2004). Aggregation in colonies occurs from October to late December, and pups are being born and weaned between mid-October and mid-December. Many females without pups also attend colonies during the pup-rearing season, and these are a mixture of pre-breeders and females known to be on sabbatical from pup production. Males also attend colonies and compete for underwater territories and mating opportunities (Siniff et al. 1977). Mating is thought to occur at the end of the lactating period, between late November and late December (Stirling 1969*b*). The rest of the year, after a phase of molting in January–February, seals spend most of their time foraging in a vast area extending from McMurdo Sound (i.e., close to breeding colonies) to the northern part of the Ross Sea (Testa 1994). Not all females haul out in Erebus Bay every year, and the level of attendance is also known to vary across years (Cameron and Siniff 2004, Cameron et al. 2007). In this population, which has been subject to an intensive mark–recapture monitoring program for several decades, the occasional absence of females from colonies during the breeding season represents a form of temporary emigration. Indeed, because the multiple annual population surveys are conducted in the entire Erebus Bay area during the breeding season, females that do not haul out in the study area one year are not available for detection. Besides having methodological implications for detection rates, this phenomenon is of primary ecological interest because it represents an individual-specific behavioral strategy, which is probably linked to the benefits and costs of moving to and attending breeding colonies during several weeks. Two previous studies have investigated the patterns of temporary emigration variation across years and ages in pre-breeder females and their consequences for recruitment (Stauffer et al. 2013, 2014). These studies found that, for pre-breeders, motivation to attend colonies varied annually and increased as seals grew older and larger, which suggests that temporary emigration is a condition-dependent strategy that varies among individuals. The results also provided evidence that a female's probability of recruiting to the pup-producing portion of the population was higher if she was present in the study area the year before, suggesting that colony attendance might have a social function for females, perhaps by favoring the synchronization of ovulation, the interaction with males, and/or the gathering of other types of social information. Temporary emigration has also been documented in recruited females on sabbatical from pup production (Cameron et al. 2007), but neither the pattern nor the sources of environmental and individual variation are well documented.

In the present study, temporary emigration is defined as the absence of an adult female from the ice surface of the Erebus Bay study area during the breeding period from mid-October to early December. Here, we assume that locally born females that do not attend Erebus Bay are not pupping in other colonies. This key assumption is supported by observations from annual visits conducted in the years 1997–2000 and 2004–2013 in seal-pupping aggregations located outside Erebus Bay (Cameron et al. 2007, Hadley et al. 2007*a*). During these extensive searches, a substantial number of seals born and tagged in Erebus Bay were found, but very few of those were found with a pup. The reasons why some non-pupping females attend Erebus Bay colonies during the breeding season is not well understood, but several hypotheses can be formulated. First, it could be a way to avoid predation, given that, at that time of the year, Erebus Bay colonies are typically inaccessible to predators (Testa 1994, Smith et al. 2007). Second, colony attendance might be motivated by social interactions with males and breeding females (Stauffer et al. 2013), which might help to synchronize ovulation and reproduction (Langvatn et al. 1996). On the other hand, breeding colonies are relatively distant from the main foraging sources, which are located in the middle and northern part of the Ross Sea (Smith et al. 2007), and foraging opportunities for seals that are hauled out in Erebus Bay are thought to be limited (e.g., Stauffer et al. 2014). Further, access to breathing and haul-out holes within colonies can be a source of aggressive interactions with other seals (Davis et al. 2013). Higher food availability and fewer aggressive interactions could therefore motivate certain nonbreeding females to stay away from colonies. We hypothesized that the relative balance between the costs and benefits of colony attendance depends on an individual's condition as well as the environment. We thus expected to observe substantial individual and temporal variability in probabilities of temporary emigration for females on sabbatical from reproduction. Specifically, we predicted that prime-age females, which are usually in better condition and thus can more easily cope with poorer environmental conditions than young and old females, would display a higher rate of colony attendance. Further, we expected that the effects of distance to foraging sites and avoidance of aggressive interaction on the motivation to stay outside colonies would be amplified during years when sea ice was locally more extensive, because movements from foraging areas to colonies would require more effort and would depend even more than usual on access to breathing holes. We thus predicted a negative relationship between the distance from colonies to the fast-ice edge and the probabilities of colony attendance and reproduction.

Material and Methods

Study population and data collection

The study area is located in Erebus Bay, in the southwestern part of the Ross Sea, Antarctica (77.62° to 77.87° S, 166.3° to 167.0° E). Each year, during the austral spring, breeding colonies are formed by reproducing and nonreproducing female Weddell seals in this study area. Each reproducing female births and nurses a single pup for ~5 weeks, and copulation with males happens at the end of this lactation period. This study population has been monitored through a mark–recapture program for more than four decades (Siniff et al. 1977). Since the 1970s, all Erebus Bay colonies have been visited every 3–5 days, each year, during the breeding season, to individually tag newborn pups as well as adults with no or missing tags. In addition, 5–8 population surveys have been conducted annually in the entire study area (see Cameron and Siniff 2004). Because all pups born in Erebus Bay have been systematically tagged since 1982, most adults in our study area are of known age. Currently, all locally born females and more than 90% of adults that regularly use the study area are marked. Females are known to be strongly philopatric (Cameron et al. 2007, Hadley et al. 2007*a*), and their probability of being detected at least once on the ice over the course of multiple within-season surveys is ~1.0 (Hadley et al. 2006, Stauffer et al. 2013), providing us with comprehensive encounter and reproductive histories for a large number of locally born, known-age female Weddell seals (Chambert et al. 2012, Rotella et al. 2012).

Modeling and estimation of temporary emigration

Analyses were based on mark–recapture data from females born and recruited inside Erebus Bay. We used a multistate modeling approach to estimate annual survival, reproduction, and temporary emigration probabilities. In any given year, a female could belong to one of the five following states: (1) first-time breeder, F; (2) experienced breeder, E; (3) skip-breeder attending breeding colonies, S; (4) unobservable skip-breeder, U, corresponding to a nonbreeder staying outside colonies that year (i.e., temporary emigrant); and (5) dead, D. Because the overall detection probability is 1.0 for females that haul out on the ice inside the study area, individuals in state F, E, and S a given year were systematically detected, making estimation of state transition probabilities straightforward and avoiding the need for a robust-design modeling approach. Females present in the study area, but not hauled out on the ice, can be temporarily unobservable for a single survey. However, because it is highly unlikely that a female would be in the water during all of the surveys conducted within a season, we can confidently assume that state U represent animals that remain outside the study area during the extent of the pup-rearing season. For the work presented here, the first encounter of an individual was a female's first reproductive event (state F). Subsequent encounters consisted of combinations of the three following possible observation events: observed in state E, observed in state S, or not observed (0), which could correspond to state U or D. Probabilities of reproduction and temporary emigration were defined as the probabilities of transition, conditional on survival, from any live state to states E or U, respectively. The probability of transition into state S was obtained as 1 minus the sum of the two latter probabilities. Annual survival was estimated as the probability of not transitioning into the dead state. In a given year, females in state U could in theory have been giving birth and nursing a pup outside Erebus Bay, but as stated in the *Introduction*, previous work has shown that locally born females are highly philopatric, such that reproductive events outside the study area are extremely rare (Cameron et al. 2007, Hadley et al. 2007*a*). We can thus be confident that virtually all temporary emigration events correspond to females skipping a year of reproduction.

The multistate model used for inferences included (1) a set of covariates that has been shown to influence survival and reproduction in our study population (Hadley et al. 2007*a*, *b*, Rotella et al. 2012, Chambert et al. 2013) and (2) a set of covariates aimed at testing our predictions regarding sources of variation in temporary emigration. Annual survival probability (ϕ) was modeled as a function of reproductive state (Hadley et al. 2007*a*), as follows:

$$\text{logit}(\phi_k) = \mu^{\phi} + \delta_k^{\phi}$$

where μ^{ϕ} represents the population average survival value and δ_k^{ϕ} corresponds to the effect of being in a given state *k*. To make δ_{U}^{ϕ} identifiable, we had to assume that δ_{U}^{ϕ} was equal to δ_k^{ϕ} for one of the observable states (Kendall and Nichols 2002). Here, we chose to set it equal to δ_{S}^{ϕ}, which represents the effect for the other nonbreeding state, i.e., a state with no costs of reproduction. Transition probabilities into states E ($\psi^{k\text{E}}$) and U ($\psi^{k\text{U}}$) were both modeled as functions of the following covariates: (1) a female's reproductive state *k* in year $t-1$ ($\delta_{k,t-1}$); (2) a female's current age $A_{i,t}$ in year *t* (quadratic trend, with first- and second-order parameters γ_1 and γ_2); (3) the current year *t* (random effect η_t); (4) a female's identity (individual random effect α_i); and (5) the distance from the study area to the sea-ice edge (DistEdge) a given year (linear slope β_{Dist}). The covariate structure used for these transition probabilities was as follows:

$$\text{logit}(\psi_{i,t}^{k\text{E}}) = \mu^{k\text{E}} + \delta_{k,\,t-1}^{k\text{E}} + \eta_t^{k\text{E}} + \alpha_i^{k\text{E}} + \gamma_1^{k\text{E}} A_{i,t} + \gamma_2^{k\text{E}} A_{i,t}^2 + \beta_{\text{Dist}}^{k\text{E}} \text{DistEdge}$$

$$\text{logit}(\psi_{i,t}^{k\text{U}}) = \mu^{k\text{U}} + \delta_{k,\,t-1}^{k\text{U}} + \eta_t^{k\text{U}} + \alpha_i^{k\text{U}} + \gamma_1^{k\text{U}} A_{i,t} + \gamma_2^{k\text{U}} A_{i,t}^2 + \beta_{\text{Dist}}^{k\text{U}} \text{DistEdge}$$

where $\mu^{k\text{E}}$ and $\mu^{k\text{U}}$ represent the theoretical mean values for probabilities of survival and for transitions to states E and U, respectively. The covariate DistEdge was used as a proxy of local sea-ice conditions, which are hypothesized to affect the motivation of seals to attend colonies. For each year, this covariate was measured as the linear distance, in nautical miles, of sea ice that an icebreaker ship had to work through to gain access to McMurdo Station, which is located at the southern limit of the study area. Transition-specific random effect parameters η_t and α_i were each assumed to follow a normal distribution, $N(0,\sigma_\eta)$ and $N(0,\sigma_\alpha)$, respectively. The multistate model was implemented under a Bayesian framework in program OpenBUGS (Lunn et al. 2009), using a Gibbs sampling algorithm and Monte Carlo Markov chain (MCMC) to approximate the posterior distribution of model parameters. We assigned flat prior distributions to all model parameters, as follows. A uniform U(0,10) prior was assigned to the standard deviation hyperparameters σ_η and σ_α, and a normal N(0,1000) prior was assigned to all other parameters. The goodness of fit of the model and its adequacy for making inferences about processes of interest were assessed with posterior predictive checks (Appendix). The results indicated that the model provided accurate predictions of all data features and derived quantities relevant to the questions of interest here. In the following section, parameter estimates are reported as the mean of the corresponding posterior distribution, along with the 2.5% and 97.5% limits of a 95% credible interval reported in brackets.

RESULTS

Encounter histories were available for 1098 known-age females that produced at least one pup during 1982–2012 and contained 7347 known-state observations:1098 observations in state F, 3972 in state E, 1602 in state S, and 675 known observations in state U (i.e., nonterminal 0's). The range of ages for recruited females in our data set was 4–30 years old. Distance to ice edge for years 1982–2012 ranged from 8 to 52 nautical miles, with a mean of 24.9 nautical miles (SD = 12.9 nautical miles; 1 nautical mile = 1.852 km).

As shown in previous studies (Rotella et al. 2012), recruited females had high annual survival rates (estimated average of 0.91, with 95% credible interval = [0.91, 0.92]) and an average probability of reproduction of about 0.71, with 95% CI (credible interval) = [0.65, 0.76] (Table 1). Each year, about 25% of recruited females, on average, did not produce a pup, but still hauled out in the study area during the pupping season (posterior mean = 0.25, 95% CI = [0.20, 0.30]), while only 4% appeared to have remained outside colonies (posterior mean = 0.04, 95% CI = [0.03, 0.07]; Table 1). Therefore, among females on sabbatical from reproduction, most (86%) did not temporarily emigrate, which confirms that females have strong motivations (e.g., predation avoidance, social interactions) to attend breeding colonies even in years when they do not produce a pup. However, a nontrivial portion (14%) of skip-breeder females remained outside colonies.

Our results revealed interesting sources of individual and annual variation in colony attendance by females on sabbatical from pup production, supporting our predictions that absence from colonies would be higher for younger and older individuals and when sea ice was

TABLE 1. Posterior summaries of estimated model parameters for temporary emigration and reproduction, as well as annual survival, in Weddell seals (*Leptonychotes weddellii*) in the Ross Sea, Antarctica.

Parameter or state	Temporary emigration	Reproduction	Survival probability
A) Principal transition parameters			
Average value (μ)	0.04 [0.03, 0.07]	0.71 [0.65, 0.76]	
DistEdge effect (β_{Dist})	0.04 [0.01, 0.07]	−0.02 [−0.07, 0.02]	
Age effect (γ_1)	0.11 [0.03, 0.20]	−0.11 [−0.18, −0.05]	
Age effect (γ_2)	0.12 [0.05, 0.21]	−0.14 [−0.20, −0.08]	
Individual SD (σ_α)	0.06 [0.03, 0.09]	0.13 [0.11, 0.15]	
Scaled value of σ_α	0.28 [0.17, 0.43]	0.28 [0.23, 0.34]	
Annual SD (σ_η)	0.03 [0.02, 0.05]	0.10 [0.07, 0.14]	
Scaled value of σ_η	0.14 [0.08, 0.23]	0.21 [0.14, 0.32]	
B) State-specific transition			
From state F	0.08 [0.04, 0.13]	0.57 [0.49, 0.65]	
From state E	0.04 [0.02, 0.06]	0.70 [0.65, 0.75]	
From state S	0.02 [0.01, 0.03]	0.78 [0.73, 0.83]	
From state U	0.06 [0.03, 0.10]	0.75 [0.68, 0.81]	
C) Annual survival			
Average value			0.91 [0.91, 0.92]
State E			0.89 [0.88, 0.90]
State F			0.92 [0.90, 0.94]
State S & U			0.93 [0.91, 0.94]

Notes: For ease of interpretation, all parameter values are transformed back on the original scale of a probability (i.e., [0, 1]). The values in brackets correspond to the 2.5% and 97.5% limits of a 95% posterior distribution credible interval. (A) Posterior summaries of the principal parameters associated to probabilities of transition in state U (temporary emigration) and state E (reproduction) with corresponding Greek symbols in parentheses (see *Methods*). Note that the two parameters of the age effect correspond to the first- (γ_1) and second-order (γ_2) parameters of the quadratic trend. (B) Posterior summaries of state-specific transition parameters, i.e., transition probabilities to state U and E, given that a female was in a given state at time $t - 1$. (C) Posterior summaries of the average and state-specific annual survival probabilities.

more extensive between colonies and feeding grounds to the north. First, we found clear evidence of a positive relationship between the distance to sea-ice edge and temporary emigration rates (mean $\beta^{kU}_{\text{Dist}} = 0.04$; 95% CI = [0.01, 0.07]; Table 1). As predicted, females were less likely to attend colonies when there was more sea ice locally, and the rate of temporary emigration doubled (from 0.04 to 0.08) when the distance to sea-ice edge increased from its mean to ~1 SD above its average value (Fig. 1). Regarding the sources of individual variation, we found that the probability of temporary emigration was also influenced by the age, the previous reproductive state, and the identity of an individual. There was a clear curvilinear relationship between age and temporary emigration probability (Table 1, Fig. 2): the youngest and oldest females were more likely to stay outside the study area when not rearing a pup. Moreover, first-time breeders and females in the unobservable state were the two groups most likely to temporarily emigrate the following year. Finally, the magnitude of residual individual variation, after accounting for age and reproductive states, appeared to be relatively large: its value was indeed about twice as large as that of residual annual variation (Table 1) and at least as large as the amount of individual variation in reproductive rates (Table 1), which has itself been shown to be important (Chambert et al. 2013). This is a clear indication that some females are inherently more likely to stay outside the study area than others, after their age and previous reproductive status are accounted for. To summarize, evidence from the data supported our prediction that temporary emigration rates would (1) be higher when local sea-ice extent was larger and (2) differ among individuals, with females in poorer condition (young and old females, first-time breeders) being more likely to remain outside the breeding area during the reproductive season than others.

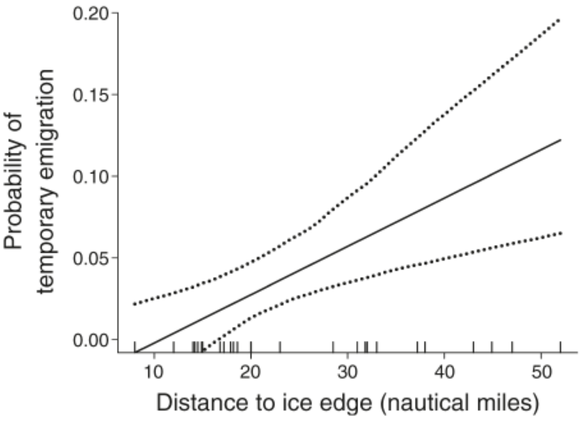

FIG. 1. Estimated relationship between probability of temporary emigration of Weddell seals (*Leptonychotes weddellii*) and distance to sea-ice edge in the study area in Erebus Bay, southwestern Ross Sea, Antarctica. The black solid line represents the average trend, while black dotted lines correspond to the 95% credible interval, all obtained through posterior distribution sampling. The rug on the *x*-axis represents the actual data for the "distance to ice edge" covariate (for conversion to SI units, 1 nautical mile = 1.852 km).

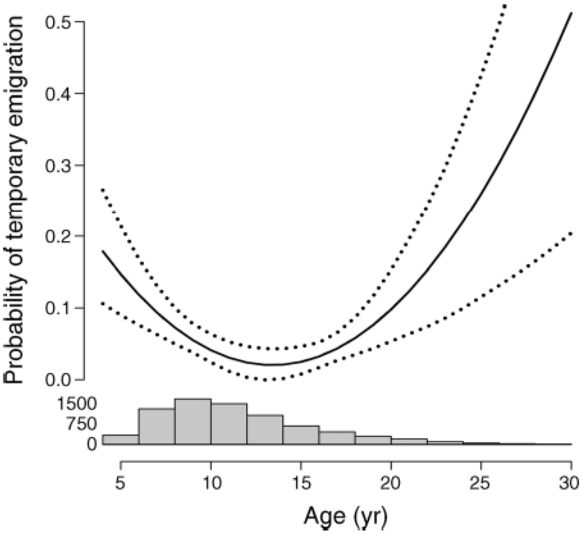

FIG. 2. Estimated relationship between the probability of temporary Weddell seal emigration and the age of a female seal. The black solid line represents the average trend; black dotted lines correspond to the 95% credible interval. These curves were obtained through posterior distribution sampling. The gray histogram under the curve represents the distribution of data available for each age, from the sample of 1098 females available. Note that each female can contribute to more than one age category.

Our findings relating probability of reproduction to past states, age, and environmental conditions were a mixture of results that corroborated past results, contradicted some of our predictions, and provided novel insights. First, the estimated effect of age and the magnitude of annual and individual variation (Table 1) were identical to those found in a previous study (Chambert et al. 2013). For this reason, they are not further developed here. Second, contrary to our predictions, we found very weak support for a relationship between distance to sea-ice edge and probability of reproduction $\beta^{kE}_{\mathrm{Dist}} = -0.02$; 95% CI = [−0.07, 0.02]). This result, which is in contrast to what was found for probability of temporary emigration, further suggests that extensive sea ice does not inhibit movement, because females producing a pup are able to access colonies as usual. Finally, the estimated reproduction probability for females that were in state U in the preceding year was similar to that for females that were in state S, much higher than the estimated rate for females that were first-time breeders the year before, and slightly higher than that for females that were in state E (Table 1). This result confirms the existence of a cost of current-year reproduction to next year's chance of reproduction (Chambert et al. 2013).

DISCUSSION

This study investigated patterns of individual and environmental variation in colony attendance and their consequences for future reproduction in adult female Weddell seals on sabbatical from pup production. We used comprehensive, long-term data from a philopatric population breeding in Erebus Bay, Antarctica. We found that, each year, most non-pupping females (~86%) were present in colonies, revealing the existence of strong motivations, not related to giving birth, for attending the breeding grounds. We hypothesize that such motivations are linked to predator avoidance and reproductive social interactions. In the pack ice and other areas close to open water, adult Weddell seals are exposed to predation from orcas (*Orcinus orca*; Pitman and Durban 2012). Thanks to its reliable fast ice that usually lasts the entire spring season, Erebus Bay probably represents the safest haul-out shelter for Weddell seals in the Ross Sea (Testa 1994). Avoidance of predators can be an important motivation for such seasonal movements (e.g., Brodersen et al. 2008) and, in our case, this hypothesis is further supported by the negative relationship observed between colony attendance and distance to sea-ice edge, which probably reflects sea-ice conditions in the southwestern Ross Sea region. When regional sea-ice extent is low, southerly located Erebus Bay becomes one of the only places free of predators, which would explain the observed increase in attendance rates. Such a mechanism is also evidenced by the fact that years of higher attendance of locally born seals also tend to be years when more immigrants are observed in the study area (Chambert et al. 2012). On the other hand, when sea ice is extensive, there is less pressure to travel so far from foraging locations to find refuge, because predator-safe locations are also available farther north. Similar adaptations of habitat use to current predation risk level, in balance with other requirements, have been shown for many species (Lima and Dill 1990) in terrestrial (Abramsky et al. 1996), freshwater (Brodersen et al. 2008), and marine environments (Heithaus and Dill 2002). Regarding social motivations for attending colonies when not giving birth, we think that male choice and mating play a primary role. Weddell seals are polygynous and have a mating system similar to lekking, in which males defend underwater territories inside breeding colonies (Siniff et al. 1977). The evolution of such reproductive systems in the animal kingdom is generally associated with assessment of male quality by females (Balmford 1991), and it is likely that, by attending colonies, females enhance their chances of mating with the males of higher quality. Besides mating, prolonged attendance on breeding grounds of non-lactating females could also be linked to social facilitation of estrus synchronization. This mechanism has been suggested previously for young females not yet recruited to the pup-producing portion of the population (i.e., pre-breeders; Stauffer et al. 2014). Social facilitation of ovulation synchronization occurs in some ungulates (Iason and Guinness 1985); in combination with delayed embryo implantation, it can be a critical factor for species living in seasonal environments, where there usually is a strong selective pressure for the timing of birth dates to coincide with a period of favorable conditions (Lack 1968). Such selective pressure is certainly very strong in polar regions, and birth synchrony is known to occur in Weddell seals (Proffitt et al. 2010) and other Antarctic pinnipeds (Boness and Bowen 1996). For these species, social facilitation of estrus synchronization can thus be an important motivation for aggregating in colonies during the breeding season, even when not giving birth to a pup. This hypothesis could be further assessed by investigating potential differences in the synchronization of parturition dates, in year $t+1$, between females that were temporarily emigrated the previous year and those that were not.

The probability of reproduction for females that did not attend colonies in the previous year was similar to that for skip-breeders that attended colonies, indicating that temporary emigrants do not suffer the reproductive cost displayed by breeding females. This result further supports our assumption that locally born females usually do not give birth outside Erebus Bay. This result also indicates that temporary emigration does not reduce the chances of mating with a male or a female's ability to produce a pup in the following season. Females that temporarily emigrated from Erebus Bay in a given pupping season might be inseminated by males from a different area. For instance, in southern elephant seals (*Mirounga leonina*), it has been suggested that skip-breeding and colony avoidance could be an active female strategy to mate with males outside established harems (de Bruyn et al. 2011). Alternatively, these females might still be bred inside Erebus Bay after arriving later in the pupping season when most pups have weaned and our population surveys have already ended. From this result, we might also wonder whether there is any benefit from not attending colonies, such as easier access to food resources, given that there is no direct apparent advantage in terms of reproductive rates. In fact, such benefits might exist, but also be counterbalanced by the fact that females remaining outside colonies are in poorer condition. This idea is supported by our findings about individual and environmental effects (as we will discuss). In combination with the observation that most non-lactating females still chose to attend colonies every year, this result supports our hypothesis that, for this species, temporary emigration is not an optimal strategy for females in good condition, but instead, a condition-dependent strategy primarily displayed by seals that cannot afford to attend colonies. It has been shown that temporary emigration is the primary factor explaining interannual variation in local colony size for this population (Chambert et al. 2012), but the long-term demographic consequences of multiple occurrences of temporary emigration should be further assessed.

Our findings on individual variation support the idea that temporary emigration is mainly displayed by individuals in suboptimal condition. Indeed, the rate of occurrence of this behavior is highest for (1) young and first-time mothers, which tend to be smaller and carry fewer body reserves (Proffitt et al. 2007), and (2) older females, which are usually in poorer body condition due to physiological senescence (Hindle et al. 2009). This pattern is probably driven by the necessity for such females to remain closer to good foraging areas. When food resources around breeding grounds are very limited, as is probably the case in Erebus Bay, it is common for animals in poor body condition or for subdominant individuals to be forced to temporarily leave the area. These two principles are, respectively, the foundation of the body size hypothesis and the dominance hypothesis of partial migration (Ketterson and Nolan 1983). Such mechanisms have been described mainly in birds (e.g., Jahn et al. 2010), but similar processes probably exist for colonial pinnipeds. For female Weddell seals with insufficient body fat reserves, it might indeed be challenging to spend several weeks in colonies with no or limited food resources. Furthermore, this challenge is probably amplified by strong intraspecific competition inside colonies and the potential for these very limited resources to be quickly depleted by dominant or higher-quality individuals (Testa et al. 1985). These two factors could motivate females in poorer condition to remain away from colonies, even if some other cost (e.g., exposure to predation) is involved. This "poorer condition" hypothesis could be further evaluated by a comparison of the timing of molting between females that attended colonies and those that did not. Indeed, if females that were temporarily emigrated in a given year spent more time foraging and less time hauled out, they would be expected to molt later and at a slower pace than females in better conditions.

Alternatively, higher temporary emigration rates of young and old females could be directly due to limitations in their ability to navigate under extensive sea ice to access breeding colonies. This hypothesis is also in accordance with the positive correlation found between probability of temporary emigration and the extent of ice between ice-free water and breeding colonies. Although Weddell seals are good divers and well adapted to living under consolidated sea ice (Stirling 1969*b*), their diving abilities are restricted by physiological and morphological constraints when young (Kooyman 1966, Burns et al. 1999), and by muscular senescence when old (Hindle et al. 2009). Moreover, the ability of young and old individuals to make their own breathing holes, and thus navigate under sea ice, might be hampered by the condition of the internal structure of their teeth (dentine), which is still developing in younger seals and can be worn out after many years of use in older seals (Stirling 1969*a*). In years when local sea ice is particularly extensive, there might be a real cost for old and young individuals to commit to the long swim required to access colonies. These mechanisms could act in parallel or synergy with the hypothesized influence of sea-ice extent on predation avoidance discussed previously. The investigation of interactions between annual sea-ice extent and individual age, which was not feasible here because of data and computational time constraints, would provide interesting insights to further address and disentangle these hypotheses. Furthermore, when traveling under extensive sea ice, Weddell seals depend heavily on breathing holes, where the chance of being exposed to aggressive interactions with conspecifics is high (Davis et al. 2013). Such intraspecific conflicts could thus further hamper the access of weaker competitors to colonies. These types of intraspecific conflicts are expected to be amplified at higher population density, as shown in other pinniped species (Fernández-Juricic and Cassini 2007) and some terrestrial mammals (Long et al. 2008). For this population of Weddell seals, an influence of population density on temporary emigration has been suggested for pre-breeders (Stauffer et al. 2014), but the underlying mechanisms remain unknown.

Besides the influence of age and reproductive status on temporary emigration rates, we also found a substantial amount of residual heterogeneity, captured here as random effects. The investigation of individual heterogeneity in reproductive and survival rates in wild populations is a topic of growing interest to ecologists (Tuljapurkar et al. 2009, Cam et al. 2012, Chambert et al. 2013), and ours is the first study to investigate this aspect for temporary emigration. The strong pattern of heterogeneity that we found could reflect different behavioral strategies, but also intrinsic individual differences in physiology or physical condition (Ogonowski and Conway 2009), dominance ranking (Jahn et al. 2010), personality traits (Dall et al. 2004), or other types of genetic or phenotypic "quality" (Lailvaux and Kasumovic 2011) that might translate into individual differences in competitive, diving, or foraging abilities. For instance, some females might be consistently less efficient at acquiring food and building body reserves, and might therefore be constrained more regularly to remain outside colonies to lengthen their period of foraging. Some females might also be inherently less aggressive, making them weaker competitors for access to breathing holes and local food sources.

Overall, our results confirm that temporary emigration patterns in adult female Weddell seals that are on sabbatical from pup production are affected by both individual and environmental conditions, similarly to what was found for pre-breeder Weddell seals (Stauffer et al. 2014). An individual's decision to attend colonies or not during the pupping season is likely to result from trade-offs between different costs and benefits associated with predation risk, social interactions, food access, and physiological and environmental constraints. Although colony attendance seems to be the logical choice for most females, temporary emigration probably represents a behavioral mechanism that helps individuals in suboptimal condition buffer survival against environmental challenges. Maximizing the chance of survival to the next reproductive season is indeed the most important component of fitness in this long-lived species (Rotella et al. 2012). Similar condition-dependent strategies of movements and habitat choices have been shown in many vertebrates (Clobert et al. 2009), including colonial birds (Cristol et al. 1999), cyprinid fishes (Brodersen et al. 2008), and several pinnipeds (gray seals *Halichoerus grypus*, Austin et al. [2004]; northern elephant seals *Mirounga angustirostris*, Stewart [1997]). Temporary and non-obligate animal movements have been attracting interest in the ecological literature for some time (Ketterson and Nolan 1983) and they are still being intensively investigated to help understand a variety of fundamental ecological and evolutionary processes (Cristol et al. 1999, Boyle 2008). Additionally, a better understanding of the mechanisms determining animal movements and habitat use could also prove to be important to efficient science-based conservation programs (Moore et al. 1995, Harrington et al. 2002). The rapid development of telemetry tracking devices, in combination with the improvements of analytical methods for both monitoring and telemetry data, should facilitate major advances in our understanding of this important topic in ecology.

ACKNOWLEDGMENTS

We thank the many individuals who have supervised and worked on the Erebus Bay Weddell seal population project since the 1960s, and particularly Donald B. Siniff, who started the long-term mark–recapture program on this population. The project was supported by the National Science Foundation, Division of Polar Programs (grant no ANT-1141326 to J. J. Rotella, R. A. Garrott, and D. B. Siniff) and prior NSF grants to R. A. Garrott, J. J. Rotella, D. B. Siniff, and J. W. Testa. Logistical support for fieldwork in Antarctica was provided by Lockheed Martin, Raytheon Polar Services Company, Antarctic Support Associates, the U.S. Navy and Air Force, and Petroleum Helicopters Incorporated. Animal captures and handling protocols were approved by Montana State University's Animal Care and Use Committee (Protocol #2011-38) and conducted under permits from the Marine Mammal Protection Act (permit No. 17236) and Antarctic Conservation Act (permit ACA 2013-007).

LITERATURE CITED

Abramsky, Z., E. Strauss, A. Subach, A. Riechman, and B. P. Kotler. 1996. The effect of barn owls (*Tyto alba*) on the activity and microhabitat selection of *Gerbillus allenbyi* and *G. pyramidum*. Oecologia 105:313–319.

Alerstam, T., A. Hedenström, and S. Åkesson. 2003. Long-distance migration: evolution and determinants. Oikos 103: 247–260.

Alerstam, T., and Å. Lindström. 1990. Optimal bird migration: the relative importance of time, energy, and safety. Pages 331–351 *in* E. Gwinner, editor. Bird migration: physiology and ecophysiology. Springer, Berlin, Germany.

Aubry, L. M., D. N. Koons, J.-Y. Monnat, and E. Cam. 2009. Consequences of recruitment decisions and heterogeneity on age-specific breeding success in a long-lived seabird. Ecology 90:2491–2502.

Austin, D., W. D. Bowen, and J. I. McMillan. 2004. Intraspecific variation in movement patterns: modeling individual behaviour in a large marine predator. Oikos 105: 15–30.

Balmford, A. 1991. Mate choice on leks. Trends in Ecology and Evolution 6:87–92.

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

Begon, M., C. R. Townsend, and J. L. Harper. 2009. Ecology: from individuals to ecosystems. John Wiley, New York, New York, USA.

Boness, D. J., and W. D. Bowen. 1996. The evolution of maternal care in pinnipeds. BioScience 46:645–654.

Bowler, D. E., and T. G. Benton. 2005. Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. Biological Reviews 80: 205–225.

Boyle, W. A. 2008. Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. Journal of Animal Ecology 77:1122–1128.

Brodersen, J., P. A. Nilsson, L.-A. Hansson, C. Skov, and C. Brönmark. 2008. Condition-dependent individual decision-making determines cyprinid partial migration. Ecology 89: 1195–1200.

Burns, J. M., M. A. Castellini, and J. W. Testa. 1999. Movements and diving behavior of weaned Weddell seal (*Leptonychotes weddellii*) pups. Polar Biology 21:23–36.

Cam, E., et al. 2012. Looking for a needle in a haystack: inference about individual fitness components in a heterogeneous population. Oikos 122:739–753.

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

Cameron, M. F., D. B. Siniff, K. M. Proffitt, and R. A. Garrott. 2007. Site fidelity of Weddell seals: the effects of sex and age. Antarctic Science 19:149–155.

Chambert, T., J. J. Rotella, and R. A. Garrott. 2012. Environmental extremes versus ecological extremes: Impact of a massive iceberg on the population dynamics of a high-level Antarctic marine predator. Proceedings of the Royal Society B 279:4532–4541.

Chambert, T., J. J. Rotella, M. D. Higgs, and R. A. Garrott. 2013. Individual heterogeneity in reproductive rates and cost of reproduction in a long-lived vertebrate. Ecology and Evolution 3:2047–2060.

Clobert, J., E. Danchin, A. A. Dhondt, and J. D. Nichols. 2001. Dispersal. Oxford University Press, New York, New York, USA.

Clobert, J., R. A. Ims, and F. Rousset. 2004. Causes, mechanisms and consequences of dispersal. Pages 307–335 *in* I. Hanski and O. E. Gaggiotti, editors. Ecology, genetics and evolution of metapopulations. Elsevier, Burlington, Massachusetts, USA.

Clobert, J., J.-F. Le Galliard, J. Cote, S. Meylan, and M. Massot. 2009. Informed dispersal, heterogeneity in animal dispersal syndromes and the dynamics of spatially structured populations. Ecology Letters 12:197–209.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

Cristol, D. A., M. B. Baker, and C. Carbone. 1999. Differential migration revisited. Current Ornithology 15:33–88.

Dall, S. R. X., A. I. Houston, and J. M. McNamara. 2004. The behavioural ecology of personality: consistent individual differences from an adaptive perspective. Ecology Letters 7: 734–739.

Davis, R. W., L. A. Fuiman, K. M. Madden, and T. M. Williams. 2013. Classification and behavior of free-ranging Weddell seal dives based on three-dimensional movements and video-recorded observations. Deep Sea Research Part II: Topical Studies in Oceanography 88–89:65–77.

de Bruyn, P. J. N., C. A. Tosh, M. N. Bester, E. Z. Cameron, T. McIntyre, and I. S. Wilkinson. 2011. Sex at sea: alternative mating system in an extremely polygynous mammal. Animal Behaviour 82:445–451.

Fernández-Juricic, E., and M. Cassini. 2007. Intra-sexual female agonistic behaviour of the South American sea lion (*Otaria flavescens*) in two colonies with different breeding substrates. Acta Ethologica 10:23–28.

Frederiksen, M., and T. Bregnballe. 2000. Diagnosing a decline in return rate of 1-year-old cormorants: mortality, emigration or delayed return? Journal of Animal Ecology 69:753–761.

Hadley, G. L., J. J. Rotella, and R. A. Garrott. 2007*a*. Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. Journal of Animal Ecology 76:448–458.

Hadley, G. L., J. J. Rotella, and R. A. Garrott. 2007*b*. Influence of maternal characteristics and oceanographic conditions on survival and recruitment probabilities of Weddell seals. Oikos 116:601–613.

Hadley, G. L., J. J. Rotella, R. A. Garrott, and J. D. Nichols. 2006. Variation in probability of first reproduction of Weddell seals. Journal of Animal Ecology 75:1058–1070.

Halley, D. J., M. P. Harris, and S. Wanless. 1995. Colony attendance patterns and recruitment in immature Common Murres (*Uria aalge*). Auk 112:947–957.

Harrington, B. A., S. C. Brown, J. Corven, and J. Bart. 2002. Collaborative approaches to the evolution of migration and the development of science-based conservation in shorebirds. Auk 119:914–921.

Heithaus, M. R., and L. M. Dill. 2002. Food availability and tiger shark predation risk influence bottlenose dolphin habitat use. Ecology 83:480–491.

Hindle, A. G., M. Horning, J.-A. E. Mellish, and J. M. Lawler. 2009. Diving into old age: muscular senescence in a large-bodied, long-lived mammal, the Weddell seal (*Leptonychotes weddellii*). Journal of Experimental Biology 212:790–796.

Iason, G. R., and F. E. Guinness. 1985. Synchrony of oestrus and conception in red deer (*Cervus elaphus* L.). Animal Behaviour 33:1169–1174.

Jahn, A. E., D. J. Levey, J. A. Hostetle, and A. M. Mamani. 2010. Determinants of partial bird migration in the Amazon Basin. Journal of Animal Ecology 79:983–992.

Kendall, W. L., and J. D. Nichols. 2002. Estimating state-transition probabilities for unobservable states using capture–recapture/resighting data. Ecology 83:3276–3284.

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

Kéry, M., K. B. Gregg, and M. Schaub. 2005. Demographic estimation methods for plants with unobservable life-states. Oikos 108:307–320.

Kéry, M., J. A. Royle, M. Plattner, and R. M. Dorazio. 2009. Species richness and occupancy estimation in communities subject to temporary emigration. Ecology 90:1279–1290.

Ketterson, E. D., and V. J. Nolan. 1983. The evolution of differential bird migration. Current Ornithology 1:357–402.

Kooyman, G. L. 1966. Maximum diving capacities of the Weddell seal, *Leptonychotes weddellii*. Science 151:1553–1554.

Lack, D. L. 1968. Ecological adaptations for breeding in birds. Clarendon Press, Oxford, UK.

Lailvaux, S. P., and M. M. Kasumovic. 2011. Defining individual quality over lifetimes and selective contexts. Proceedings of the Royal Society B 278:321–328.

Langvatn, R., S. D. Albon, T. Burkey, and T. H. Clutton-Brock. 1996. Climate, plant phenology and variation in age of first reproduction in a temperate herbivore. Journal of Animal Ecology 65:653–670.

Lima, S. L., and L. M. Dill. 1990. Behavioral decisions made under the risk of predation: a review and prospectus. Canadian Journal of Zoology 68:619–640.

Long, E. S., D. R. Diefenbach, C. S. Rosenberry, and B. D. Wallingford. 2008. Multiple proximate and ultimate causes of natal dispersal in white-tailed deer. Behavioral Ecology 19: 1235–1242.

Lunn, D., D. Spiegelhalter, A. Thomas, and N. Best. 2009. The BUGS project: Evolution, critique and future directions. Statistics in Medicine 28:3049–3067.

Moore, F. R., S. A. J. Gauthreaux, P. Kerlinger, and T. R. Simons. 1995. Habitat requirements during migration: important link in conservation. Pages 121–144 *in* T. Martin and D. Finch, editors. Ecology and management of neotropical migratory birds, a synthesis and review of critical issues. Oxford University Press, New York, New York, USA.

Ogonowski, M., and C. Conway. 2009. Migratory decisions in birds: extent of genetic versus environmental control. Oecologia 161:199–207.

Pitman, R. L., and J. W. Durban. 2012. Cooperative hunting behavior, prey selectivity and prey handling by pack ice killer whales (*Orcinus orca*), type B, in Antarctic Peninsula waters. Marine Mammal Science 28:16–36.

Proffitt, K. M., R. A. Garrott, J. J. Rotella, and K. E. Wheatley. 2007. Environmental and senescent related variations in Weddell seal body mass: implications for age-specific reproductive performance. Oikos 116:1683–1690.

Proffitt, K. M., J. J. Rotella, and R. A. Garrott. 2010. Effects of pup age, maternal age, and birth date on pre-weaning survival rates of Weddell seals in Erebus Bay, Antarctica. Oikos 119:1255–1264.

Rotella, J. J., W. A. Link, T. Chambert, G. E. Stauffer, and R. A. Garrott. 2012. Evaluating the demographic buffering hypothesis with vital rates estimated for Weddell seals from 30 years of mark–recapture data. Journal of Animal Ecology 81:162–173.

Schjørring, S., J. Gregersen, and T. Bregnballe. 1999. Prospecting enhances breeding success of first-time breeders in the great cormorant, *Phalacrocorax carbosinensis*. Animal Behaviour 57:647–654.

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

Smith, W. O., D. G. Ainley, and R. Cattaneo-Vietti. 2007. Trophic interactions within the Ross Sea continental shelf ecosystem. Philosophical Transactions of the Royal Society B 362:95–111.

Stauffer, G. E., J. J. Rotella, and R. A. Garrott. 2013. Variability in temporary emigration rates of individually marked female Weddell seals prior to first reproduction. Oecologia 172:129–140.

Stauffer, G. E., J. J. Rotella, R. A. Garrott, and W. L. Kendall. 2014. Environmental correlates of temporary emigration for female Weddell seals and consequences for recruitment. Ecology, *in press*.

Stewart, B. S. 1997. Ontogeny of differential migration and sexual segregation in northern elephant seals. Journal of Mammalogy 78:1101–1116.

Stirling, I. 1969*a*. Tooth wear as a mortality factor in the Weddell seal, *Leptonychotes weddellii*. Journal of Mammalogy 559–565.

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

Swingland, I. R., and P. J. Greenwood. 1983. The ecology of animal movement. Clarendon Press, Oxford, UK.

Testa, J. W. 1994. Over-winter movements and diving behavior of female Weddell seals (*Leptonychotes weddellii*) in the southwestern Ross Sea, Antarctica. Canadian Journal of Zoology 72:1700–1710.

Testa, J. W., D. B. Siniff, M. J. Ross, and J. D. Winter. 1985. Weddell seal–Antarctic cod interactions in McMurdo Sound. Pages 561–565 *in* W. R. Siegfried, P. R. Condy, and R. M. Laws, editors. Antarctic nutrient cycles and food webs. Proceedings of the 4th SCAR Symposium on Antarctic Biology. Springer, New York, New York, USA.

Tuljapurkar, S., U. K. Steiner, and S. H. Orzack. 2009. Dynamic heterogeneity in life histories. Ecology Letters 12: 93–106.

White, P. J., T. L. Davis, K. K. Barnowe-Meyer, R. L. Crabtree, and R. A. Garrott. 2007. Partial migration and philopatry of Yellowstone pronghorn. Biological Conservation 135:502–510.

SUPPLEMENTAL MATERIAL

Ecological Archives

The Appendix is available online: http://dx.doi.org/10.1890/14-0911.1.sm