

Glenn E. Stauffer, Jay J. Rotella, Robert A. Garrott, and William L. Kendall. Year. Environmental correlates of temporary emigration for female Weddell seals and consequences for recruitment. *Ecology* VOL:pp–pp.

APPENDIX A: Details of ORDMS modeling, and estimates for survival and within-season parameters.

Description of open robust design multi-state models

We used open robust design multi-state (ORDMS) models (Kendall and Bjorkland 2001, Kendall 2004) to investigate patterns of variation in survival rates, recruitment rates, and rates of temporary emigration (TE) of juvenile Weddell seals. ORDMS models are based on observations from multiple secondary (within-primary-season) sampling occasions over multiple primary occasions (typically years). These 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 at the beginning of year t . Survival and transition probabilities can be age-dependent or 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 , given it is available; 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. Note that ϕ defined this way is different from its usage in other capture-mark-recapture models such as the Cormack-Jolly-Seber model (Williams et al. 2002). Individuals are assumed to enter the population once and leave during a primary period, and the probability that an individual enters the study area and leaves again between secondary capture occasions is assumed to be zero (Kendall and Bjorkland 2001). In this study, secondary

occasions included intensive, study-area-wide surveys separated by 3 – 6 days, as well as the 2 – 3 days of less-intensive observation effort preceding and following each intensive survey.

Consequently, and also because most individuals were observed >1 time, we believe that violation of the above assumption likely was minimal.

Modeling transition probabilities

We defined 7 possible breeding state classifications (Fig. A1): 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 F (observable first-time mom). Temporary emigration was defined as any transition into any unobservable state (ψ^{P0U0} , ψ^{U0U0} , ψ^{P1U1} , ψ^{U1U1} , ψ^{P2U2} , ψ^{U2U2}) and recruitment as any transition into state F (ψ^{U0F} , ψ^{P1F} , ψ^{U1F} , ψ^{P2F} , ψ^{U2F}). We fixed to zero all transition probabilities that were either biologically impossible or not allowed because encounter histories were right-censored after recruitment (these are not represented by arrows in Fig. A1). Because the probabilities of all possible transitions for any given state logically must sum to 1, one transition rate for each state must be derived by subtraction (e.g., $\psi^{P2P2} + \psi^{P2U2} + \psi^{P2F} = 1$; thus if ψ^{P2U2} and ψ^{P2F} are estimated, $\psi^{P2P2} = 1 - (\psi^{P2U2} + \psi^{P2F})$ 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 originating in state F. Such censoring simplified the analysis by limiting the number of

possible state transitions to be estimated and was justified by the nearly certain detection of mothers within the Erebus Bay study area (Rotella *et al.* 2009, Stauffer *et al.* 2013a).

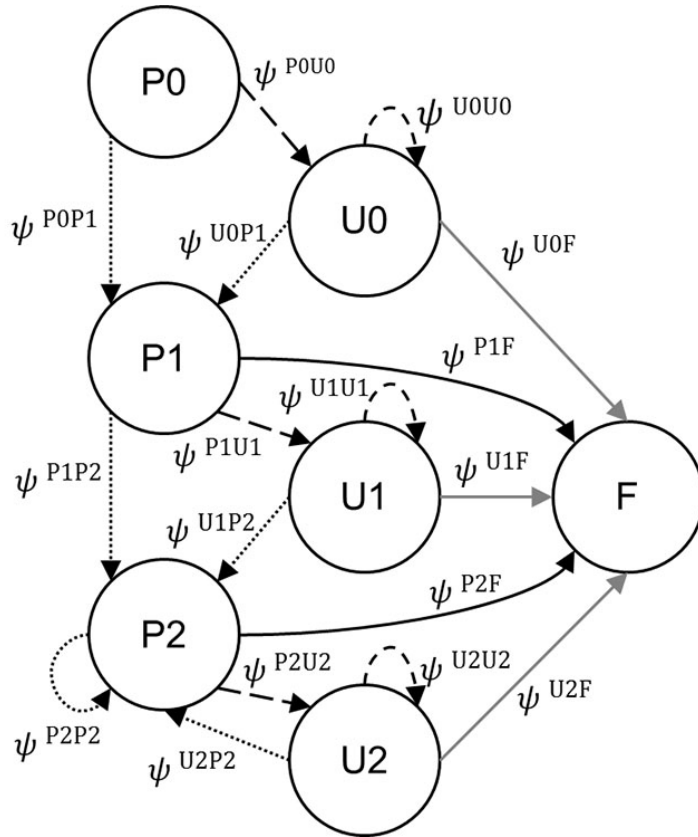


FIG. A1. Breeding state classifications and possible state transitions for a population of female Weddell seals in Erebus Bay, McMurdo Sound, Antarctica. States denote first-time breeders (F) and either observable (P) or unobservable (U) prebreeders that previously have attended Erebus Bay reproductive colonies 0, 1, or ≥ 2 times since they were pups (state P0). Solid lines and dashed lines represent, respectively, recruitment (gray is recruitment from an unobservable state) and temporary emigration. Dotted lines indicate transitions into observable prebreeding states that were not estimated in our models but can be derived by subtraction.

In some models, we estimated TE rates with a different Markovian (dependent on prior state) structure than the structure for recruitment. For example a design matrix might specify full state-dependency in recruitment estimates ψ^{U0F} , ψ^{P1F} , ψ^{U1F} , ψ^{P2F} , ψ^{U2F} , and only partial state-dependency in TE estimates, $\psi^{P1U1} = \psi^{P2U2}$ 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 is induced in back-transformed real parameter TE estimates (i.e., $\psi^{U0U0} \neq \psi^{P1U1} \neq \psi^{U1U1} \neq \psi^{P2U2} \neq \psi^{U2U2}$). To see why this is the case, consider a simple contrived example with the beta parameters β_0 = intercept for all transitions, β_1 = common offset for ψ^{P1U1} and ψ^{P2U2} , β_2 = offset for ψ^{P1F} , and β_3 = offset for ψ^{P2F} (i.e., TE, but not recruitment, are constrained to be equal for states P1 and P2). Use of mlogit links to back-transform to real parameter TE estimates yields $\psi^{P1U1} = \frac{e^{\beta_0 + \beta_1}}{1 + e^{\beta_0 + \beta_1} + e^{\beta_0 + \beta_2}}$ and $\psi^{P2U2} = \frac{e^{\beta_0 + \beta_1}}{1 + e^{\beta_0 + \beta_1} + e^{\beta_0 + \beta_3}}$. The denominators in the 2 back-transformations are different because of state specificity in recruitment rates. Consequently, differences are induced in the real parameter estimates for TE despite the fact that the design matrix rows are identical for these two parameters. This issue of induced state-dependency can be avoided if logit rather than mlogit link functions are used to specify transition parameters, but mlogit links often are necessary for parameter estimates to converge to the MLE. We used mlogit links and simply recognized that for some models, slight state-dependent differences in real parameter TE estimates are an artifact of analogous state-dependency in parameter estimates for recruitment.

Modeling survival probabilities

Based on strong model support from previous analyses, we considered a single structure for survival and for each of the within-season parameters (Hadley et al. 2006, Stauffer et al. 2013b). We estimated survival $S_{SIE,age}^c$ as a function of age class ($age = 1, 2, 3+$, for consistency with notation used for transition rates, age denotes age at the end of the survival interval) and current-year winter SIE (standardized and centered) in year $t-1$, with an additional transient effect of birth-cohort ($c = 1983 - 2009$). As in previous analyses, we expected survival rate would be positively related to SIE (Stauffer et al. 2013b). 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. 2007). However, TE can cause substantial negative bias in survival estimates at the end of a time-series when survival and state-dependent TE rates are both temporally variable (Langtimm 2009). Consequently, we do not present survival estimates for the final 4 cohorts of our time series (2006 – 2009) or transition probabilities for the final year.

Modeling within-year probabilities

We modeled within-season parameters based on overall patterns observed in previous analyses of individual years (Rotella et al. 2009). In those analyses we found that the model performing best varied by year, but point estimates were similar across years, with uniformly high point estimates for p_{tj}^r and ϕ_{tjk}^r , and estimate $pent_{tj}^r$ generally low and decreasing for breeders but increasing slightly for prebreeders (i.e., most individuals present at the first survey period each year). We therefore allowed $pent_{tj}^r$ to follow a state-dependent (states P1 and P2

pooled, P0 and F pooled) linear trend for $j > 1$ (trend common for all seasons). Breeders and pups were pooled because in most cases pups were present the first time we encountered breeders during a season. For the first encounter occasion each year, we derived $pent_{t_0}^r = 1 - \sum_{j=2}^{max} pent_{t_j}^r$. Detection probability p_{tj}^r also was allowed to follow a year-constant and state-dependent linear trend (states P0 = P1 = P2, and F). We allowed ϕ_{tjk}^r to vary only by state (P0 = P1 = P2, and F). All within-season parameters were fixed to zero for all unobservable states. The probability that an individual would be detected at least once in a primary occasion (p_t^{r*}) can be derived from the secondary occasion-specific parameters (Kendall and Bjorkland 2001). For example, for a year with 3 secondary occasions:

$$p_t^{r*} = pent_{t_1}^r [p_{t_1}^r + (1 - p_{t_1}^r) \phi_{t_{10}}^r p_{t_2}^r + (1 - p_{t_1}^r) \phi_{t_{10}}^r (1 - p_{t_2}^r) \phi_{t_{21}}^r p_{t_3}^r] \\ + pent_{t_2}^r [p_{t_2}^r + (1 - p_{t_2}^r) \phi_{t_{20}}^r p_{t_3}^r] \\ + pent_{t_3}^r p_{t_3}^r$$

Goodness of fit

We performed analyses in program MARK (White and Burnham 1999) through the RMark package (Laake 2013) in program R (R Development Core Team 2012). Currently there is no general goodness-of-fit (GOF) 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. It may be possible to conduct GOF testing for ORDMS models by combining GOF tests for individual years and a GOF test (e.g., median \hat{c}) for pooled data across years, this approach is ad-hoc and unproven. Instead, we assessed the potential influence of overdispersion on model-selection results by examining how model rankings based on QAIC_c changed as we increased \hat{c} . As expected, point estimated did not change much, but uncertainty in estimates increased with increasing \hat{c} . However, model rankings were robust to increases in \hat{c} values (Table B1). Therefore, although we acknowledge that

modest amounts of overdispersion would reduce the precision of our estimates, we are confident that our conclusions would be minimally influenced.

Multiple imputation of missing covariate data

Images from which to derive a value for the DIST covariate were missing for the years 1983, 1985, 1987, 1990, 1991, 1993, 1997, and 1999. For initial model selection, we replaced missing values with the mean of non-missing values. We then used multiple imputation methods (Schafer 1999) to make inferences based on the top-ranked covariate model (model 9, see Table B1). We used the R package norm (Schafer 2012) to impute values for missing DIST data based on correlations with the annual sea-ice concentration in McMurdo Sound and the distance from the ice edge to McMurdo Station traveled by a resupply vessel each year. The norm package assumes a multivariate normal distribution and uses an MCMC data augmentation algorithm (Tanner and Wong 1987) to impute missing values, which can be interpreted as random draws from a posterior distribution of possible values. Multiple imputation accounts for missing value uncertainty through the generation and analysis of m independent datasets followed by inference based on a combination of these analyses (Schafer 1999). Rubin (1987) showed that $m = 3-5$ usually is sufficient to account for most of the missing value uncertainty. We therefore generated 5 imputed datasets and analyzed each dataset in program MARK (White and Burnham 1999), using our top-ranked model structure. With $m = 5$, we calculated beta estimates $\hat{\theta}_m$ based on the recommendations by Rubin (1987) where $\hat{\theta}_m = \frac{1}{m} \sum_{i=1}^m \hat{\theta}_i$ and $var(\hat{\theta}_m) = \bar{V} + \left(1 + \frac{1}{m}\right) B$, and where $\bar{V} = \frac{1}{m} \sum_{i=1}^m var(\hat{\theta}_i)$ represents the within-imputation variance and $B = \left(\frac{1}{m-1}\right) \sum_{i=1}^m [\hat{\theta}_m - \hat{\theta}_i]$ represents the between-imputation variance. We also used the R package RMark (Laake 2013) to calculate model-averaged estimates for real parameters from analysis of the 5 imputed datasets, based on a reasonable range of covariate values. We used these values for

comparison with estimates from baseline models with either unstructured or no annual variation in TE rates.

Results for survival and within-year modeling

Cohort-specific survival estimates (Fig. A2) for cohorts born in 1983 – 2005 were greater for seals ≥ 2 years ($\hat{S}_{SIE,age3+}^c = 0.92$, $\widehat{SE} = 0.01$) than for pups ($\hat{S}_{SIE,age1}^c = 0.72$, $\widehat{SE} = 0.12$) and yearlings ($\hat{S}_{SIE,age2}^c = 0.50$, $\widehat{SE} = 0.09$), for which 95% CIs of point estimates overlapped broadly. We found evidence that current-year sea-ice extent was positively associated with survival ($\hat{\beta}_{SIE} = 0.15$, $\widehat{SE} = 0.08$; Fig. A2b).

FIG. A2. Estimated survival probabilities (a) from our baseline year model (model 21, Table S1) for 1st, 2nd, and 3rd-year of life, and predicted survival probabilities (b) for “weak”, “average”, and “strong” cohorts when current-year winter sea-ice extent in the Ross Sea is minimal, average, or maximal. Error bars indicate 95% confidence intervals.

Based on estimates from our baseline year model the majority of female seals were present at the first survey each year ($\widehat{pent}_{t1}^{P0 \text{ and } F} = 0.83$, $\widehat{SE} = 0.01$; $\widehat{pent}_{t1}^{P1 \text{ and } P2} = 0.63$, $\widehat{SE} = 0.03$). For pups and

breeders, estimated \widehat{pent}_{tj}^r decreased rapidly during the primary period (Fig. A3) from 0.11 ($\widehat{SE} < 0.01$) to <0.01 ($\widehat{SE} < 0.01$), whereas rates for prebreeders were essentially constant throughout the season ($\widehat{pent}^{P1 \text{ and } P2} = 0.06$, $\widehat{SE} = 0.01$). After entering the study area each year, seals in each state were likely to remain until the next secondary occasion ($\hat{\phi}^{P0} = 0.98$, $\widehat{SE} < 0.01$; $\hat{\phi}^{P1 \text{ and } P2} = 0.94$, $\widehat{SE} < 0.01$; $\hat{\phi}^F = 0.98$, $\widehat{SE} < 0.01$). For pups and breeders, \hat{p}_{tj}^r was high early in the season and decreased throughout the season, whereas for prebreeders, \hat{p}_{tj}^r increased throughout the season (Fig. A3). We detected nearly all seals that entered the study area (Table A1).

FIG. A3. For an example year with 8 secondary occasions, (a) secondary survey-specific entry probabilities, and (b) detection probabilities. Note differing y-scales. 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 A1. Probability of detection of female Weddell seals during ≥ 1 secondary occasions within a primary period (\hat{p}_t^{r*}) for primary periods with 5–8 secondary periods.

| | 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 |

LITERATURE CITED

- Bailey, L. L., S. J. Converse, and W. L. Kendall. 2010. Bias, precision, and parameter redundancy in complex multistate models with unobservable states. *Ecology* 91:1598–1604.
- Hadley, G. L., J. J. Rotella, and R. A. Garrott. 2007. Evaluation of reproductive costs for Weddell seals in Erebus Bay, Antarctica. *Journal of Animal Ecology* 76:448–458.
- 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.
- Kendall, W. L. 2004. Coping with unobservable and mis-classified states in capture-recapture studies. *Animal Biodiversity and Conservation* 27:97–107.
- Kendall, W. L., and R. Bjorkland. 2001. Using open robust design models to estimate temporary emigration from capture-recapture data. *Biometrics* 57:1113–1122.

Laake, J. L. 2013. RMark: An R interface for analysis of capture-recapture data with MARK.

AFSC Processed Rep 2013-01, 25p. Alaska Fisheries Science Service, NOAA, National Marine Fisheries Service, Seattle, Washington, USA.

Langtimm, C. A. 2009. Non-random temporary emigration and the robust design: conditions for bias at the end of a time series. Modeling demographic parameters in marked populations. 3:745–761.

R Development Core Team. 2012. R: A language and environment for statistical computing. R foundation for statistical computing. Vienna, Austria. ISBN 3-900051-07-0. URL <http://www.R-project.org>.

Rotella, J. J., W. A. Link, J. D. Nichols, G. L. Hadley, R. A. Garrott, and K. M. Proffitt. 2009. An evaluation of density-dependent and density-independent influences on population growth rates in Weddell seals. Ecology 90:975–984.

Rubin, D. B. 1987. Multiple Imputation for Nonresponse in Surveys. John Wiley & Sons.

Schafer, J. L. 1999. Multiple imputation: a primer. Statistical Methods in Medical Research 8:3–15.

Schafer, J. L. 2012. norm: Analysis of multivariate normal datasets with missing values. R package version 1.0-9.4 ported by A. A. Novo.

Stauffer, G. E., J. J. Rotella, and R. A. Garrott. 2013a. 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, and R. A. Garrott. 2013b. Birth-year and current-year influences on survival and recruitment rates of female Weddell seals. Population Ecology 55:405–415.

- Tanner, M. A., and W. H. Wong. 1987. The calculation of posterior distributions by data augmentation. *Journal of the American Statistical Association* 82:528–540.
- White, G. C., and K. P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* 46 (Suppl):120–138.
- Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations; modeling, estimation, and decision making. Academic, San Diego, California, USA.