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Appendix C from S. Jenouvrier et al., "Mating Behavior, Population Growth, and the Operational Sex Ratio: A Periodic Two-Sex Model Approach"

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Estimation of Survival and Return Probabilities

We used multistate capture-mark-recapture statistical models (CMR) to estimate the probabilities of survival s_x and of returning to the breeding site r_x. Multistate CMR models include three kinds of state-specific parameters (Lebreton et al. 1992, 2009; Lebreton and Pradel 2002; table C1). For emperor penguins the model contains two states and three groups (see table C2). Model selection starts by assessing the goodness of fit of a general model to the data, and this has been done previously (Jenouvrier et al. 2005*b*). Emperor penguins capture and marking occurred from 1968 to 1986, and recapture has occurred since 1968, with no data in 1990. For group 1, the data are sparse and the analysis was conducted over the period 1968–1981. For groups 2 and 3, the analysis was conducted over the period 1972–2000 (excluding 1990), because the first three captures were suppressed for adults to avoid heterogeneity in the data (see "Goodness of Fit," Jenouvrier et al. 2005*b*).

Complex multistate CMR models contain parameters that cannot be estimated, either due to a lack of data or because of structural redundancy (Giménez et al. 2004). In some cases, this can be solved by adding specific assumptions to the parameters (Fujiwara and Caswell 2002; Hunter and Caswell 2008).

The emperor penguin CMR model is built with the following assumptions. (i) Capture probabilities of state 1 are zero because it is an unobservable state. For state 2, they varied freely with time and are different between individuals marked as chick and those marked as adult. Adult capture probabilities are similar between males and females (Jenouvrier et al. 2005*b*), and they are set to 0 during the first 3 years (the first three captures were suppressed) and to a constant from 1990 to 2000 because the data are sparse. (ii) The newborn survival ($\phi_1^1(a_1) = s_0$) is disentangled from the survival of prebreeders older than 2 years ($\phi_1^1(a_{2^+}) = s_1 = s_3$) by including an effect of age (a). The survival of prebreeders was set to equal to adult survival for individuals marked as chick: $\phi_1^1(a_2^+) = \phi_1^2(.)$. (iii) The transition probabilities correspond to the probability of returning to the breeding site. For the individuals marked as chick, the adult observable state acts as the absorbing state, and $\psi_1^{2-2} = 1$.

The selection model procedure starts from an umbrella model where survival and returning probabilities differ according to sex and states and compares it to simpler models nested in the structure of the umbrella model. Two hypotheses were tested: (i) probabilities differ between individuals present or absent at the colony, and (ii) probabilities differ between sexes.

Model selection is based on the Akaike Information Criterion (Burnham and Anderson 2002). Analyses were conducted with software M-Surge (Choquet et al. 2004). This approach results in the selection of a model (table C3) with an effect of sex on adult survival probabilities and of state on transition probabilities. Therefore adult survival differs between sexes, and return probability differs between breeders that are present at the colony and nonbreeders that are absent from the colony (see tables 1–3 for estimates).

Table C1
Definition of probabilities for multistate capture-mark-recapture statistical models

Notation	Definition
p_t^j	Probability that an individual is captured at time t in state j, given that it is alive and present at time t
ϕ_t^i	Probability that an individual in state i at time t survives until time $t + 1$
ψ_t^{ji}	Probability that an individual in state i at time t is in state j at time $t + 1$, given that the individual has survived from time t to time $t + 1$

Table C2
Capture-mark-recapture model definition for the emperor penguin

State	Group
1. individuals absent from the colony (unobservable state)	1. individuals marked as chick
2. individuals present at the colony	2. females marked as adult 3. males marked as adult

Table C3
Capture-mark-recapture model selection

Questions and models	No. parameters	Deviance	AIC	Answer
Umbrella model	58	9,683.85	−6.38	
Return probabilities:				
Equal between NB and B?	54	9,746.80	−61.32	No
Equal between sex?	54	9,687.30	−1.83	Yes
Survival probabilities:				
Equal between NB and B?	50	9,693.47	.00	Yes
Equal between sex?	48	9,703.97	−6.49	No

Note. The umbrella model assumes that emperor penguins adult survival and return probabilities differ between sexes and states (breeders [B] present at the colony vs. nonbreeders [NB] absent from the colony). $\Delta\mathrm{AIC} = \mathrm{AIC}^* - \mathrm{AIC}_m$, where AIC^* is the AIC of the best model and AIC_m is the AIC of the model m. AIC = Akaike Information Criterion.

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