Modeling the demography of species providing extended parental care: A capture-recapture approach with a case study on Polar Bears (*Ursus maritimus)*

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Abstract

1. In species providing extended parental care, one or both parents care for altricial young over a period including more than one breeding season. We expect large parental investment and long-term dependency within family units to cause high variability in life trajectories among individuals with complex consequences at the population level. So far, models for estimating demographic parameters in free-ranging animal populations do not include extended parental care, thereby limiting our understanding of its consequences on parents and offspring life histories.

2. We developed a capture-recapture model for studying the demography of species providing extended parental care. Our model jointly handles statistical dependency among individual demographic parameters within family units until offspring independence, inter-individual variability in breeding frequency, variability in the number of offspring born and recruited at

each breeding event, the influence of past reproductive history on the caring parent status, while accounting for imperfect detection of family units. We present the model, assess its performances using simulated data, and illustrate its use with a long-term dataset collected on the Svalbard polar bears (*Ursus maritimus*).

3. Our model performed well, in terms of bias and mean square error, in estimating demographic parameters in all simulated scenarios. As expected, bias and rmse were higher in the scenario with low detectability. For the polar bear case study, we showed that mother age and outcome of the previous breeding event influenced breeding probability, litter size and offspring survival. Old females had a higher probability of raising at least one offspring to independence over a 3-year period, suggesting a higher reproductive success of more experienced females possibly due to an improvement of hunting skills with age.

4. Overall, our results show the importance of accounting for i) the statistical dependency within family units until offspring independence, and ii) past reproductive history of the caring parent. If ignored, estimates obtained for breeding probability, litter size, and survival can be biased. This is of interest in terms of conservation because species providing extended parental care are often long-living mammals vulnerable or threatened with extinction.

Key-words: apex predator, arctic ecosystem, Bayesian modeling, capture-recapture, dependency among individuals, family structure, multi-state models, parental care, sociality.

INTRODUCTION

Altricial mammals having offspring that need to learn complex skills to ensure survival beyond independence, such as hunting, orientation, or nest building, show extended or prolonged parental care (Clutton-Brock, 1991). In such species, one or both parents care for one or several young over a period including more than one breeding season. This can extend

until lifelong maternal care in primates (Van Noordwijk, 2012). Parental care includes any pre-natal and post-natal allocation, such as feeding and protecting the young, which benefits an individual offspring development and survival chances, thereby enhancing the parent's reproductive success (Trivers, 1972). For the offspring, the quality and quantity of care received can have long-lasting effects on future survival (e.g. Pavard & Branger, 2012), social status (e.g. Shenk & Scelza, 2012) and reproduction (Royle, Smiseth, & Kölliker, 2012). For the parent, investment in one young is at the cost of the parent's ability to invest in other offspring (siblings or future offspring) (Trivers, 1972). It can indeed take several years during which a parent caring for his young will not be available to reproduce, sometimes not until the offspring have reached independence, e.g. 2.5 years for female polar bears (Ramsay & Stirling, 1988), 3.5 to 6 years for female African elephants (Lee & Moss, 1986), and 9.3 years for female Sumatran orangutans (Wich et al., 2004). The fitness cost of losing one offspring, in terms of lost investment and skipped breeding opportunities, is therefore particularly high if death occurs near independence. We expect extended parental care, through large parental investment and long-term dependency within family units, to cause high variability in life trajectories among individuals and family groups, in interbirth intervals depending on offspring's fate, and consequently on lifetime reproductive success for the caring parent (Clutton-Brock, 1991). Because parental care can affect simultaneously several parental and offspring traits, its consequences at the population level are still poorly understood, especially in free-ranging animal populations.

Capture-recapture (CR) models allow studying species with complex demography in the wild, e.g. by considering 'breeder' and 'non-breeder' reproductive states to estimate breeding probabilities and status-specific demographic parameters while accounting for imperfect detectability (e.g., Lebreton, Nichols, Barker, Pradel, & Spendelow, 2009). One can distinguish between successful and failed breeding events (e.g., Lagrange et al., 2017) and

include varying litter or clutch size (e.g., Doligez et al., 2002) and memory effects (Cole et al., 2014), to investigate the costs of reproduction on survival and future reproduction for species providing short-term parental care, i.e. when offspring reach independence before the next breeding season (e.g., Yoccoz, Erikstad, Bustnes, Hanssen, & Tveraa, 2002). By including non-observable states (Lebreton et al., 2009), one can differentiate between pre-breeders, first-time breeders, experienced breeders, and adult non-breeders to estimate the probabilities of skipping one breeding opportunity (e.g., Cubaynes, Doherty, Schreiber, & Gimenez, 2011). Currently however, there is no CR approach for modelling the demography of species providing extended parental care. This is of particular interest in terms of conservation because species providing extended parental care are often among long-living mammals vulnerable or threatened with extinction (e.g. polar bears, orangutans, elephants).

Here, we develop a CR model for studying the demography of species providing extended parental care. Our model jointly handles statistical dependency among individual demographic parameters within family units until offspring independence, inter-individual variability in breeding frequency, variability in the number of offspring born and recruited at each breeding event, the influence of past reproductive history on the caring parent current status, and accounts for imperfect detection possibly depending upon family unit composition. In what follows, we present the model, assess its performances using simulated data, and illustrate its use with a long-term dataset collected on the Svalbard polar bears. Female polar bears rely only on stored fat reserves during pregnancy and the first three months of lactation, before feeding and protecting litters of one to three young, usually during two and a half more years (Ramsay & Stirling, 1988). They can lose more than 40% of body mass while fasting (Atkinson & Ramsay, 1995). In many areas, climate change and related sea ice decline impact female bear condition and capacity to provide care for their young, with an associated decline in reproductive output (Derocher, Lunn, & Stirling, 2004; Stirling & Derocher, 2012). More

insights into the species demography, such as the consequences of long-duration parental care on mother and offspring life histories, could help our understanding of polar bear population responses to environmental perturbations and extinction risks in future decades (Hunter et al., 2010; Regehr et al., 2016).

METHODS

Capture-recapture model for species providing extended parental care

The model is based on data on individual encounter histories that record the subsequent observations or non-observations of individuals in the field, with specific information on the state of each individual at each capture occasion. States can refer to various characteristics, such as breeding status, epidemiological status, or a site (Lebreton et al., 2009). We used four sets of parameters: 1) the proportion of individuals in each state at first capture, 2) state-specific survival probabilities from occasion t to $t+1$; 3) transition probabilities from one state at time t to another state at $t+1$ conditioned upon being alive at time $t+1$; and 4) state-specific individual recapture probabilities at occasion t (Lebreton et al., 2009).

The novelty of our model lies in that the encounter histories are defined for each family unit instead of each individual. Let us consider a study over K encounter occasions and N family units. The encounter history for family unit i is denoted $h_{ij} = (o_{i1}, \ldots, o_{ik})$ where o_{ik} records whether family unit i, at occasion k, is observed in state m ($o_{ik} = m$) or not ($o_{ik} = 0$). The states m correspond to the composition of family units observed in the field. Thus, the number and type of states will vary depending on the species considered, the duration and distribution of parental care between parents, and variability in the number of young produced. For example, let us consider a species in which a single parent care for a maximum of X young over Y years. The states will be defined as $m = (P_0 , \ldots, P_{x,y} ,\ldots , D)$ where P_0

stands for a family unit composed of a single parent, $P_{x,y}$ for a family unit composed of the caring parent of x offspring in their y^{th} year of life (with $1 \leq x \leq X$ and $1 \leq y \leq Y$) and D is the dead state.

Our model can be decomposed in several matrices gathering the probabilities of the initial states and four conditional sets of events representing the species life cycle: parent(s) survival (Φ, eq. 1), offspring survival and growth (S, eq. 2), breeding probabilities (A, eq. 3) and number of offspring produced per breeding event (B, eq. 4), and a matrix gathering the family unit's recapture probabilities (P, eq. 5). First, we define the vector $\Pi_{m-1} = (\pi_0, \dots, \pi_{x,y}, \dots, \pi_{X,Y})$ gathering the initial probabilities of each live state. A first matrix, $[\phi]_{m,m}$ gathers the state-specific survival probability for the caring parent from time t to $t + 1$. Then, the transition matrix gathering transition probabilities among states between each occasion t to $t+1$ is decomposed into three intermediate steps conditioning upon each other. The decomposition helps in estimating meaningful biological quantities corresponding to all possible events occurring between two capture occasions. We write $\Psi = S_{m,m_1} A_{m_1,m_2} B_{m_2,m}$. The first matrix, S_{m,m_1}, gathers the state-specific transition probabilities from states m to intermediary states m_1, which correspond to the offspring survival probabilities to the next age, depending on the caring parent survival, the young age, and number of siblings. Intermediate states of arrival are defined as $m_1 = (P_{0\to0}, P_{1,1\to1,2}, P_{1,1\to0} \dots, P_{x,y\to x,y+1}, P_{x,y\to x-1,y+1}, \dots, P_{X,Y-1\to X,Y})$, where, during the interval between occasions t and $t+1$, a non-breeder parent alive always remain non breeder ($0 \to 0$), and for a family unit composed of a caring parent with at least one young, each of the young can survive and grow to the next age ($x, y \to x, y + 1$), or die ($x, y \to x - 1, y + 1$). The second matrix, A_{m_1,m_2}, gathers the state-specific transition probabilities from intermediate states m_1 to intermediate states m_2, which correspond to the state-specific breeding probabilities. Intermediate states of arrival are defined as

$m_2 = (P'_{0\to0\to0}, P'_{0\to0\to r}, \dots, P'_{x,y\to x,y+1\to0}, P'_{x,y\to x,y+1\to r}, \dots, P'_{X,Y-1\to X,Y\to r})$, where during the interval between time *t* and *t+1*, a parent non-breeder at the beginning of the interval and still alive can breed ($0 \to 0 \to r$) or remain non-breeder ($0 \to 0 \to 0$), and a parent caring for at least one young still alive can breed again ($x, y \to x, y+1 \to r$) or not ($x, y \to x, y+1 \to 0$), and a parent that just lost one (or several) young of a certain age can breed ($x, y \to x-1, y+1 \to r$) or not ($x, y \to x, y+1 \to 0$). The third matrix, $B_{m_2,m}$, gathers the state-specific transition probabilities from intermediate states m_2 to departures states m , which correspond to the probability of producing a certain number of young depending on the previous steps. The probability will be set to 0 for non-breeders, and can differ for a breeder that was non breeder at the beginning of the interval ($0 \to 0 \to r \to x', y' = 1$), a parent that breeds while caring for other young ($x, y \to x, y+1 \to r \to x', y' = 1$), or a parent that breeds again while it has just lost its young of a certain age ($x, y \to 0 \to r \to x', y' = 1$). A fifth matrix, the so-called event matrix, $[P]_{m,2}$, gathers the detection probability of family units, where the state-specific probability of being observed ($p(_{Px,y})$) or not (1 - $p(_{Px,y})$) at occasion *t* can vary depending on the composition of the family unit.

The structure of the model implies that the number of offspring produced per breeding event is conditioned upon breeding decision. Breeding decision is conditioned upon the status and number of dependent offspring already cared for by the parent, which itself is conditioned upon parental survival. This particular formulation permits to investigate, among others, the cost of reproduction on female survival (step 1), the influence of litter size on litter survival (step 2), the influence of past reproductive history on both breeding probability (step 3), and on litter size (step 4). The influence of individual traits such as age or body weight, or environmental variables such as temperature, can be included in the model under the form of individual or temporal covariates (Pollock, 2002). In addition, specificities related to data collection can also be included in a similar way, such as trap effects (Pradel & Sanz-Aguilar,

2012) or latent individual heterogeneity by using mixture of distributions or random effects (Gimenez, Cam, & Gaillard, 2018).

Simulation study

We evaluated the performance of our model using simulated data for a virtual long-lived mammal species, mimicking the polar bear case study (see next section for details). We considered that care of offspring was provided by the mother only, to one, two or three offspring, for 3 years maximum. Parameters included mother survival, young survival, breeding probabilities and litter size probabilities, as well as detection probability. Specifically, we used $\phi_{mother} = 0.9$ for annual adult survival assumed independent of family unit composition, ϕ_{cub}= 0.3 for annual cub survival and $\phi_{yearling} = 0.5$ for annual yearling survival, independently of litter size and conditioned upon mother survival. Breeding probability was $\alpha_{alone} = 0.6$ for a female alive without dependent offspring, $\alpha_{cub^{\dagger}} = 0.1$ for a female alive that just lost her cub litter, $\alpha_{yearling^{\dagger}} = 0.3$ for a female alive that just lost her yearling litter, and $\alpha_{offspring} = 0$ for a female alive with dependent offspring alive. Litter size probability of one cub for breeding females was i) $\Pr(LS = 1) = \beta_{alone} = 0.4$ and of multiple cubs (2 or 3) was Pr(LS>1) = 0.6, for a female previously without offspring, and ii) $\Pr(LS = 1) = \beta_{offspring^{\dagger}} = 0.5$ and of multiple cubs Pr(LS>1) = 0.5 for a female that lost offspring during the year.

We considered three scenarios with low (p = 0.3), medium (p = 0.5), and high (p = 0.8), detection of family units. We simulated 100 CR datasets for each detectability scenario with 25 sampling occasions and 50 newly family units released at each occasion. We simulated the data using program R. We fitted the model using maximum likelihood in package TMB called from R (Kristensen, Nielsen, Berg, Skaug, & Bell, 2015). For each

parameter, we calculated the bias and root-mean-square error. The code used for carrying out the simulations is provided in Appendix 1.

Case study: Polar bears in Svalbard

In Polar bears, care of offspring is provided by the mother only (Amstrup, 2003). Males were therefore discarded from our analysis. Adult female polar bears mate in spring (February to May, Amstrup, 2003), and in Svalbard usually have their first litter at the age of six years (Derocher, 2013). They have delayed implantation where the egg attaches to the uterus in autumn (Ramsay & Stirling, 1988). A litter with small cubs (ca 600 grams) is born around November to January, in a snow den that the mothers dig out in autumn, and where the family stay 4-5 months. The family usually emerges from the den in March-April, and stay close to the den while the cubs get accustomed to the new environment outside their home, for a few days up to 2-3 weeks (Hansson & Thomassen, 1983). Litter size in early spring vary from one to three, with two cubs being most common, three cubs in most areas being rare, and commonly around one out of three litters having one cub only (Amstrup, 2003). The weaning age of cubs varies between populations, and is approximatively 2.3 years in the Barents Sea. The cubs typically depart from the mother in their third spring (March-April), when the mother can mate again. Thus, the minimum reproductive interval for successful Barents Sea polar bears is 3 years. On the contrary, loss of a cub litter shortly after den emergence may mean the mother can produce new cubs in winter the same year (North, 1953).

We analyzed n = 496 encounter histories of polar bear family units monitored over 25 years, each spring, from 1992 to 2016, in Svalbard. Polar bears were caught and individually marked as part of a long-term monitoring program on the ecology of polar bears in the Barents Sea region. The captures occur each year shortly after den emergence (mid-March to late April; Andersen Derocher, Wiig, & Aars, 2012). All bears one year or older were

immobilized by remote injection of a dart (Palmer Cap-Chur Equipment, Douglasville, GA, USA) with the drug Zoletil® (Virbac, Carros, France) (Stirling, Spencer, & Andriashek, 1989). The dart was fired from a small helicopter (Eurocopter 350 B2 or B3), usually from a distance of about 4 to 10 meters. Cubs of the year were immobilized by injection with a syringe. Cubs and yearlings are captured together with their mother. Because they are highly dependent on her, they remain in her vicinity. A female captured alone has no dependent offspring alive, but could have lost her cubs in the den or shortly after den emergence but before capture. Hereafter, estimated cub survival thus refers to survival after capture. Infant mortality occurring before capture will be assigned to a reduced litter size. Because only 3% of females were observed with 3 offspring, we analyzed jointly litters of twins with triplets.

Prior fitting models, we performed goodness-of-fit tests (Pradel, Wintrebert, & Gimenez, 2003) using the R package R2ucare (Gimenez, Lebreton, Choquet, & Pradel, 2018). The overall test was not significant (df = 137, χ^2=67.402, p-value = 1), suggesting no major lack of fit of the standard time-dependent multistate CR model to our data. Because bears captured in Svalbard are shown to be a mixture of resident and pelagic bears (Mauritzen, Derocher, & Wiig, 2011), we included hidden heterogeneity in the detection process. To do so, we considered a mixture of two classes of individuals on recapture probability (Gimenez, Cam, & Gaillard, 2018) to account for the lower probability for pelagic bears of being detected every year. Last, previous studies have found senescence starts around age 15 in polar bears, we therefore distinguished survival and reproductive parameters of ‘prime-age’ <15 y.o. and ‘old’ ≥15 y.o. (Derocher & Stirling, 1994).

We built the model with 8 states corresponding to the field observations of different family units composition: m = (F_o , F_c , F_{c+} , F_y , F_{y+} , F_t , F_{t+} , D) respectively standing for female alone, female with one cub, female with multiple cubs, female with 1 yearling, female with multiple yearlings, female with one two-year old, female with multiple two-year olds,

and dead female. The vector of initial states, $\Pi_0 = (\pi_1, \pi_2, \pi_3, \pi_4, \pi_5, \pi_6, \pi_7, 0)$ gathers the proportion of family units in each live state at first capture. The first step determines mother survival depending on offspring number and age, with matrix $[\phi]_{m,m}$ defined as:

$$[\phi]_{m,m} = \begin{bmatrix} \mathrm{Fo,j} & 0 & 0 & 0 & 0 & 0 & 0 & 1 - \mathrm{Fo,j} \\ 0 & Fc,j & 0 & 0 & 0 & 0 & 0 & 1 - Fc,j \\ 0 & 0 & Fc+,j & 0 & 0 & 0 & 0 & 1 - Fc+,j \\ 0 & 0 & 0 & Fy,j & 0 & 0 & 0 & 1 - Fy,j \\ 0 & 0 & 0 & 0 & Fy+,j & 0 & 0 & 1 - Fy+,j \\ 0 & 0 & 0 & 0 & 0 & Ft,j & 0 & 1 - Ft,j \\ 0 & 0 & 0 & 0 & 0 & 0 & Ft+,j & 1 - Ft+,j \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \qquad \text{(eq. 1)}$$

where $_{i,j}$ is the annual survival probability of a mother of age *j* in state *i* at capture occasion *t*. Preliminary analyses showed that mother survival did not vary according to composition of the family unit. We therefore did not include variation among states and included only the effect of age on mother survival, hereafter $_{1,j}$ with j = 1 for prime-age and j = 2 for old females.

The second step determines young survival and growth conditioned upon mother survival during time interval *t* to *t* + 1. Intermediary states are defined such as m_1 = (F_o , F_{c-} , F_{y-} , F_y , F_{y+} , F_t , F_{t+} , D) respectively standing for surviving female alone, surviving female losing all cubs, surviving female losing all yearlings, surviving female with one surviving cub growing into a yearling, surviving female with multiple surviving cubs growing into multiple yearlings, surviving female with one surviving yearling growing into one two-year old, surviving female with multiple surviving yearlings growing into multiple two-year olds, and dead females. The second matrix, $[S]_{m,m_1}$ gathering young survival probabilities depending on age and on sibling's number is defined as:

$$[S]_{m,m_1} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 1 - \phi_{2,j} & 0 & \phi_{2,j} & 0 & 0 & 0 & 0 \\ 0 & 1 - S_{11,j} - S_{2,j} & 0 & S_{1,j} & S_{2,j} & 0 & 0 & 0 \\ 0 & 0 & 1 - \phi_{3,j} & 0 & 0 & \phi_{3,j} & 0 & 0 \\ 0 & 0 & 1 - S_{3,j} - S_{4,j} & 0 & 0 & S_{3,j} & S_{4,j} & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \qquad \text{(eq. 2)}$$

where, for litters of singletons, $\phi_{2,j}$ is cub survival, and $\phi_{3,j}$ is yearling survival for a surviving mother of age *j* during time interval *t* to *t+1*. For litters of multiple offspring, S_{ij} is the probability that only one cub, $S_{1,j}$, resp. one yearling, $S_{3,j}$, or all cubs, $S_{2,j}$, resp. all yearling, $S_{4,j}$, survive conditioned upon mother survival for a mother of age *j*.

The third step determines breeding probability conditioned upon mother survival, age and young survival and growth during time interval *t* to *t* + 1. Intermediary states are defined such as m_2 = (F_0 , $F_{0\to r}$, $F_{f\to r}$, F_y , F_{y+} , F_t , F_{t+} , D) respectively standing for surviving female alone remaining non-breeder, surviving female alone becoming breeder, surviving female that lost her offspring becoming breeder, surviving female with one surviving cub growing into a yearling remaining non-breeder, surviving female with multiple surviving cubs growing into several yearlings remaining non-breeder, surviving female with one surviving yearling growing into one two-year old remaining non-breeder, surviving female with multiple surviving yearlings growing into several two-year old remaining non-breeder, and dead females. The third matrix, $[A]_{m_1,m_2}$ gathering breeding probabilities depending on the previous steps is defined as:

$$[A]_{m_1,m_2} = \begin{bmatrix} 1-\alpha_{1,j} & \alpha_{1,j} & 0 & 0 & 0 & 0 & 0 & 0 \\ 1-\alpha_{2,j} & 0 & \alpha_{2,j} & 0 & 0 & 0 & 0 & 0 \\ 1-\alpha_{3,j} & 0 & \alpha_{3,j} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \qquad \text{(eq. 3)}$$

where $\alpha_{i,j}$ is the breeding probability of a surviving female of age *j* alone (α_1), that lost cubs (α_2), and that lost yearlings (α_3).

The fourth step determines litter size probabilities for reproductions occurring during the time interval *t* to *t+1* depending on the previous steps, with matrix $[B]_{m_2,m}$ being defined as:

$$[B]_{m_2,m} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \beta_{1,j} & 1-\beta_{1,j} & 0 & 0 & 0 & 0 & 0 \\ 0 & \beta_{2,j} & 1-\beta_{2,j} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \qquad \text{(eq. 4)}$$

where $\beta_{i,j}$ (resp. $1-\beta_{i,j}$) is the probability of producing a single cub per litter (resp. a litter of twins) for females of age *j* that were alone, $\beta_{1,j}$, or have lost offspring, $\beta_{2,j}$, during the time interval *t* to *t* + 1.

The fifth step relates the states to field observations e = (F_o , F_c , F_{c+} , F_y , F_{y+} , F_t , F_{t+} , 0), '0' meaning non-detected. The observation matrix that gathers the family unit's probability of detection at occasion *t* is defined as:

$$[P]_{m,e} = \begin{bmatrix} p_i & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_i \\ 0 & p_i & 0 & 0 & 0 & 0 & 0 & 1-p_i \\ 0 & 0 & p_i & 0 & 0 & 0 & 0 & 1-p_i \\ 0 & 0 & 0 & p_i & 0 & 0 & 0 & 1-p_i \\ 0 & 0 & 0 & 0 & p_i & 0 & 0 & 1-p_i \\ 0 & 0 & 0 & 0 & 0 & p_i & 0 & 1-p_i \\ 0 & 0 & 0 & 0 & 0 & 0 & p_i & 1-p_i \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix}, \qquad \text{(eq. 5)}$$

where, p_i, respectively 1- p_i, is the probability of being detected, respectively not detected, for family unit composition belonging to sub-population *i*. Each family unit has a probability $\rho_{resident}$ (resp. $1-\rho_{resident} = \rho_{pelagic}$) of belonging to one or the other mixture component. We provide the code with guidance to fit the model in a Bayesian framework in program Jags called from R in Appendix 2.

Using the conditional probabilities estimated in the model, we calculated the net probability for a female of age *j* to raise none, Pr(X=0), one, Pr(X=1), or two young, Pr(X=2) close to independence (age 2) over a 3-year period (Figure 1).

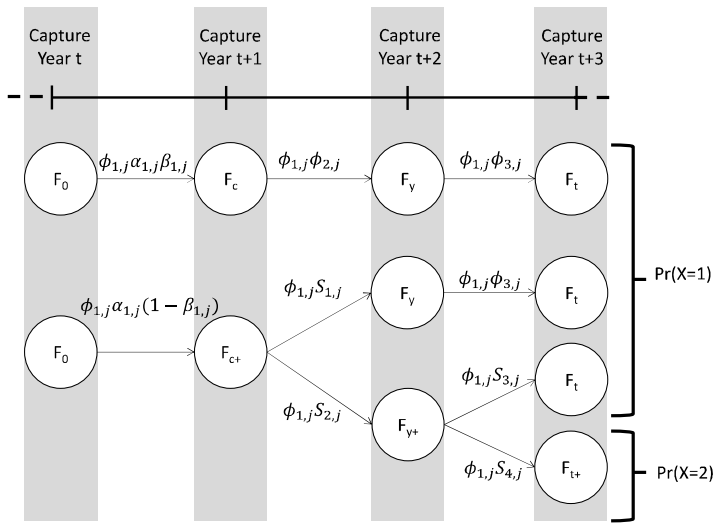

Figure 1: Life history events with associated probabilities of raising at least one young near independence (to age 2) over a 3 years period. For a female polar bear of age *j*, *j* = 1 for 'prime-age' and *j* = 2 for 'old', alive and without dependent young at the beginning of the period, $\phi_{1,j}$ is adult survival, $\alpha_{1,j}$ is breeding probability, $\beta_{1,j}$ is litter size probability of one, Pr(LS=1), $\phi_{2,j}$ and $\phi_{3,j}$ resp. cub and yearling survival in a singleton litter. In a litter of multiple young $S_{1,j}$, resp. $S_{2,j}$, is the probability that only one cub survives, resp. all cubs in the litter survive and $S_{3,j}$, resp. $S_{4,j}$, is the probability that only one yearling survives, resp. all yearlings in the litter survive.

We considered mature females that were without dependent offspring at the beginning of the time period, so that we have for females of age *j*:

$$\Pr(\mathrm{X} = 1\,|j) = \left(\phi_{1,j}\right)^3 \cdot \alpha_{1,j} \cdot \left[\beta_{1,j} \cdot \phi_{2,j} \cdot \phi_{3,j} + \left(1 - \beta_{1,j}\right) \cdot (S_{1,j} \cdot \phi_{3,j} + S_{2,j} \cdot S_{3,j})\right] ,$$

$$\Pr(\mathrm{X} = 2\,|j) = \left(\phi_{1,j}\right)^3 \cdot \alpha_{1,j} \cdot \left(1 - \beta_{1,j}\right) \cdot S_{2,j} \cdot S_{4,j} \quad ,$$

$$Pr(X = 0|j) = 1 - \Pr(X = 1) - \Pr\,(X = 2)\ .$$

RESULTS

Model performance evaluated on simulated datasets

Model performance was satisfying in all simulated scenarios, with average bias $B = 0.0014$ and root-mean-square error $rmse = 0.027$. As expected, bias and rmse were higher in the scenario with low detectability (Figure 2; results for medium and high detectability are provided in Appendix 3). For most parameters, bias was very low, B < 0.01, except for S_4, the probability that both twins in a litter survive from their second year of life, B = 0.025.

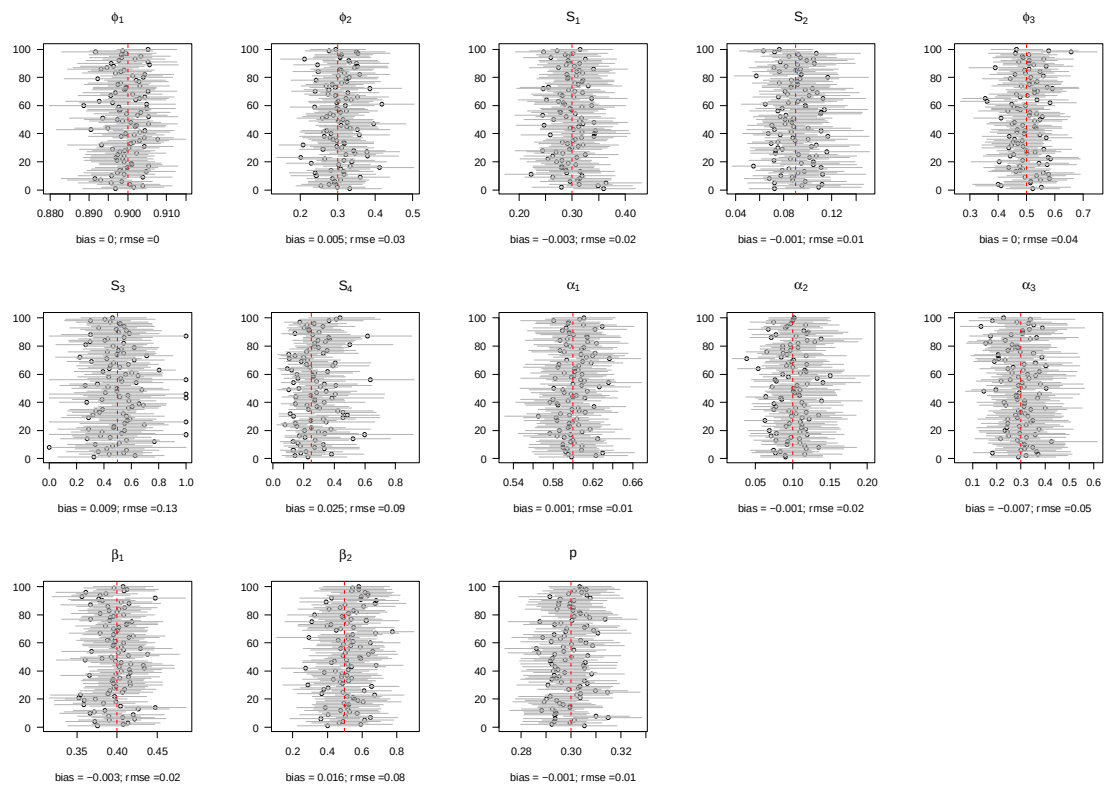

Figure 2. Performance of the model on simulated data with low detectability. For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given by the vertical dashed red line. The estimated absolute bias and root-mean-square error are provided in the legend of the X-axis for each parameter. Regarding notations, ϕ_1 is adult survival, ϕ_2 and ϕ_3 resp. cub and yearling survival in a singleton litter. In a litter of multiple young S_1 , resp. S_2, is the probability that only one cub survives, resp. all cubs in the litter survive and

S_3, resp. S_4, is the probability that only one yearling survives, resp. all yearlings in the litter survive. Then, α_1, resp. α_2, resp. α_3, is the breeding probability of a female previously alone, resp. that have lost a cub litter, resp. that lost a yearling litter during the year, and β_1, resp. β_2, is litter size probability of one, Pr(LS=1), for females previously non breeder, resp. failed breeder that lost a litter during the year, p is the family unit's detection probability.

Case study: Polar bear demography

Posterior distributions are given for all estimated parameters (Appendix 2). Annual female survival was high and lower for old females (Table 1 and Figure 3). Cubs and yearling survival rates, conditioned upon mother survival, were lower for singleton than for litters of twin for young mothers but were higher and did not depend on litter size for old mothers (Table 1 and Figure 3). Outcome of the previous reproduction influenced breeding probability for young and old females (Figure 3). Breeding probability was <15% for females that lost a cub litter during the year, about 20-30% for females that lost a yearling litter and increased to 50-65% for females that were alone at the beginning of the year (Table 1). Old females had a higher probability than young females of breeding when alone, but about the same if they had lost a litter at the beginning of the year. For breeding females that had lost a litter at the beginning of the year, the probability of producing a single cub was higher for older than younger females, while there was no difference in litter size probability between young and old females that did not fail at previous reproduction (Table 1 and Figure 3).

At first capture, 52% of adult females were alone, 11% with one cub, 22% with two cubs, 8% with one yearling, 3% with multiple yearlings and 2% with one or multiple two-year old bears. About 15% (0.10 – 0.23) of family units belonged to the high detectability group, with an annual detection rate of 0.42 (0.33 – 0.51), while 85% (0.77 – 0.90) of family units had a low annual detection probability of 0.04 (0.02 – 0.06).

Table 1: Parameter estimates. Means are given with 95% credible intervals (CI). Offspring survival and breeding probabilities are conditioned upon mother survival, litter size probability of one Pr(LS=1) is as well conditioned upon breeding probability.

Parameter	**Female <15 y.o.**	**Mean with 95% CI**	**Female 15+ y.o.**	**Mean with 95% CI**
Mother survival	ϕ_{11}	0.90 (0.85 – 0.95)	ϕ_{12}	0.86 (0.82 – 0.90)
Offspring survival				
cub (single litter)	ϕ_{21}	0.36 (0.15 – 0.59)	ϕ_{22}	0.51 (0.31 - 0.71)
yearling (single litter)	ϕ_{31}	0.44 (0.22 - 0.68)	ϕ_{32}	0.60 (0.40 - 0.81)
only one cub (litter of 2)	S_{11}	0.36 (0.18 – 0.55)	S_{12}	0.19 (0.06 – 0.38)
both cubs (litter of 2)	S_{21}	0.22 (0.11 – 0.37)	S_{22}	0.43 (0.24 – 0.65)
all cubs die (litter of 2)	$1 - S_{11} - S_{21}$	0.42 (0.25 – 0.60)	$1 - S_{12} - S_{22}$	0.38 (0.19 – 0.58)
only one yearling (litter of n>1)	S_{31}	0.34 (0.08 – 0.70)	S_{32}	0.22 (0.05 – 0.49)
both yearling (litter of n>1)	S_{41}	0.39 (0.11 – 0.74)	S_{42}	0.23 (0.06 – 0.49)
all yearling die (litter of n>1)	$1 - S_{31} - S_{41}$	0.27 (0.08 – 0.54)	$1 - S_{32} - S_{42}$	0.55 (0.29 – 0.78)
Breeding probability				
female alone	α_{11}	0.51 (0.38 - 0.64)	α_{12}	0.64 (0.50 – 0.78)
failed breeder (lost cubs)	α_{21}	0.15 (0.02 – 0.38)	α_{22}	0.09 (0 – 0.13)
failed breeder (lost yearling)	α_{31}	0.31 (0.06 – 0.41)	α_{32}	0.19 (0.03 – 0.25)
Litter size probability				
previously alone	β_{11}	0.39 (0.22 – 0.57)	β_{12}	0.46 (0.31 – 0.61)
failed breeder	β_{21}	0.23 (0.01 – 0.65)	β_{22}	0.67 (0.23 – 0.99)

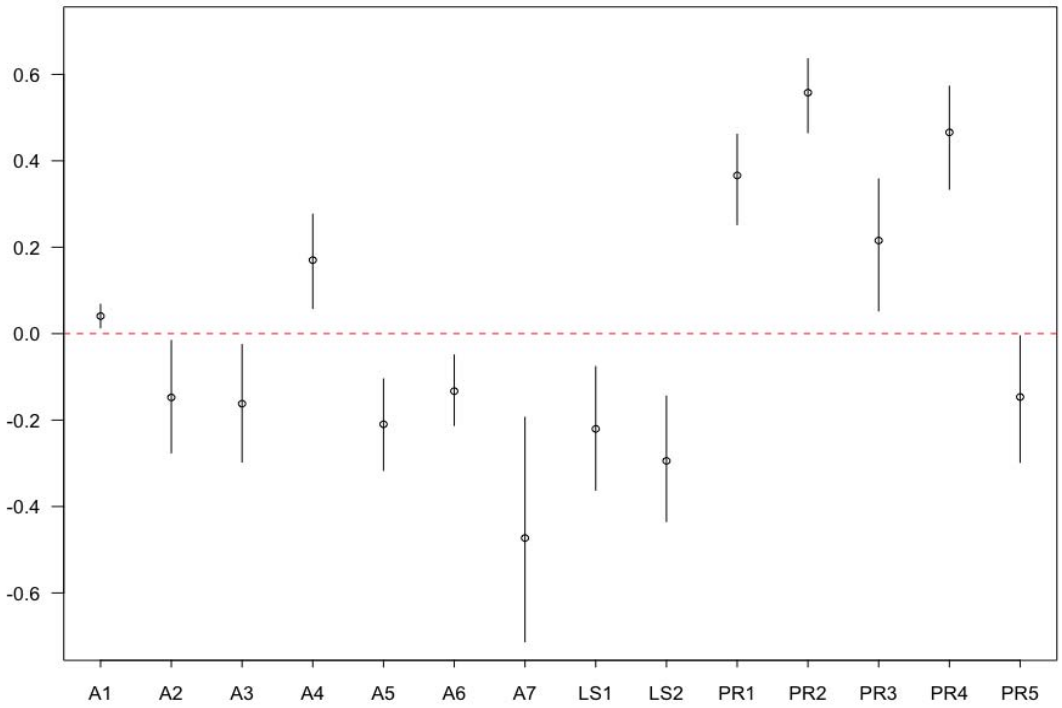

Figure 3. Effects of maternal age (A), litter size (LS) and outcome of the previous reproduction (PR) on adult and young survival, breeding probability and litter size. Median (dot) with 80% credible interval (segment) are displayed for significant effects only. Mother age effects (young female minus old female coefficient) on adult survival (A1), single litter cub survival (A2), single litter yearling survival (A3), on the probability that one (A4) or all (A5) cubs survive in a multiple litter, on breeding probability for females alone (A6), and on the probability of litter size of 1 for failed breeders (A7). Effects of litter size (single litter minus multiple litter coefficient) on cub litter survival for young mothers (LS1) and on yearling litter survival for young mothers (LS2). Effects of previous reproduction on breeding probability for young mothers (PR1, PR3 and PR5) and for old mothers (PR2 and PR4); the coefficient is either the difference between breeding probability of a female alone vs one that lost a cub litter (PR1 and PR2) or that lost a yearling litter (PR3 and PR4) or that lost a cub litter vs a yearling litter (PR5).

Results obtained for the net probability of successfully raising 0, 1 or 2 young to their second birthday for females over a 3-year period showed that old females had a higher probability of raising at least one offspring. For all females, the probability of raising two young to their second birthday, was very low (Table 2). Note that this calculation includes breeding probability, and therefore does not reflect offspring survival until weaning (see Method section).

Table 2: Probability of raising none, Pr(X=0), one, Pr(X=1), or two young, Pr(X=2) close to independence (age 2) over a 3-year period for females younger than 15 y.o. and at least 15 y.o that were alive and without dependent young at the beginning of the period. Medians with 95% credible intervals are provided.

	Pr(X=0)	Pr(X=1)	Pr(X=2)
female < 15y.o.	0.91 (0.85 – 0.95)	0.07 (0.04 – 0.13)	0.02 (0 – 0.04)
female ≥ 15 y.o.	0.88 (0.82 – 0.92)	0.10 (0.06 – 0.16)	0.02 (0.01 -0.05)

DISCUSSION

Overall, our model performed well on both simulated and real data. Estimates obtained for mother and young survival rates within family units, probability of breeding and of litter sizes, and detection probability were unbiased in most simulated scenarios. Bias and root-mean square errors were the highest for twin yearling litter survival when family units' detection rate was low. We believe bias on these specific parameters is due to parameters of the transition matrices being conditioned upon each other. Because of this, having enough yearling and two-year old litter of twin in the data to estimate twin yearling litter survival requires high enough adult and cub survival, breeding probability and litter size probability of

two, as well as detection probability and number of individuals. Prior to fitting our model, one should ensure via simulations (see Appendix 1) that sample size and detection probability is high enough for its applicability. Inference in a Bayesian framework is useful in this regard, because it allows to include prior information when available (McCarthy & Masters, 2005) to help estimation of the model parameters. In the polar bear data, there were few recaptures of females on subsequent years due to relatively low detection rate. As a result, preliminary analyses suggested a potential confusion between these parameters. We dealt with this issue by including a biologically realistic constraint on prior distributions, stating that cub survival was lower than that of yearling (Amstrup & Durner, 1995) which was enough to ensure parameter estimability.

For polar bears, we showed that mother age and outcome of the previous breeding event influenced breeding probability, litter size and offspring survival. Reduced offspring survival one year, for example due to poor environmental conditions (Derocher, Lunn, & Stirling, 2004), might therefore increase intervals between successful reproduction through reduced breeding probability and litter size the next year. This means that by ignoring long-term dependency among mother and offspring life histories, classical models can underestimate reproductive intervals, therefore risking to overestimate the population growth rate. Adult survival and offspring survival to weaning were lower than previously estimated in Svalbard (Wiig 1998). Our model likely underestimated yearling survival because two-year-old bears frequently have already departed from their mother in Spring during the recaptures. This could explain the low probability of successfully raising at least one offspring to two-year-old over a 3-year period (Table 2). We also found that old females had a higher probability of raising at least one offspring close to independence over a 3-year period. It suggested a higher reproductive success of more experienced females possibly due to an improvement of hunting skills with age (Folio et al., in press; Atkinson & Ramsay, 1995).

However, the biological relevance of our model is currently limited, because we ignored temporal and individual heterogeneity among females in the model. Future analyses will integrate in the model density-dependent processes and influence of climatic variables on body weight and demography (Derocher et al., 2004; Stirling & Derocher, 2012) as individual and environmental covariates in a regression-like framework. Date of capture will also be included as a covariate on detection to model the probability of two-year olds still being with the mother in spring.

Here, we proposed a general model structure that can be applied to other species providing extended parental care, e.g. primates or elephants. The originality of our approach lies in using family structure to define statistical units in our model. It allows to include dependency among individuals and therefore evaluate correlations between offspring and parents' life history parameters. By modifying the matrices to include a higher number of family unit structures (eq. 1 to eq. 5), one can easily include biparental care, and/or grand-parental care for species like wolves or humans, variable duration of parental care, number of young, and breeding and litter size probabilities for breeding parents caring for older offspring (Clutton-Brock et al. 1991). Such extensions of our model could be used, for example, to evaluate the population-level consequences of positive or negative correlation between parents and offspring traits (e.g. food sharing among group members Lee, 2008; or parent-offspring conflict Kölliker, Kilner, & Hinde, 2013). For polar bears specifically, our model could be used to extend the population model proposed by Hunter et al. (2010) to include variability in litter size and breeding frequency depending on the fate of the mothers' past breeding event. This approach would permit to reassess extinction risks and predictions of the demographic response of polar bear populations under climate change (Hunter et al., 2010; Regehr et al., 2016).

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