1 **Modeling the demography of species providing extended parental care:**

2 **A capture-recapture approach with a case study on Polar Bears (*Ursus maritimus)***

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13

14 **Abstract**

15 1. In species providing extended parental care, one or both parents care for altricial young

16 over a period including more than one breeding season. We expect large parental investment

17 and long-term dependency within family units to cause high variability in life trajectories

18 among individuals with complex consequences at the population level. So far, models for

19 estimating demographic parameters in free-ranging animal populations do not include

20 extended parental care, thereby limiting our understanding of its consequences on parents and

21 offspring life histories.

22 2. We developed a capture-recapture model for studying the demography of species providing

23 extended parental care. Our model jointly handles statistical dependency among individual

24 demographic parameters within family units until offspring independence, inter-individual

25 variability in breeding frequency, variability in the number of offspring born and recruited at

26   each breeding event, the influence of past reproductive history on the caring parent status,

27   while accounting for imperfect detection of family units. We present the model, assess its

28   performances using simulated data, and illustrate its use with a long-term dataset collected on

29   the Svalbard polar bears (*Ursus maritimus*).

30   3. Our model performed well, in terms of bias and mean square error, in estimating

31   demographic parameters in all simulated scenarios. As expected, bias and rmse were higher in

32   the scenario with low detectability. For the polar bear case study, we showed that mother age

33   and outcome of the previous breeding event influenced breeding probability, litter size and

34   offspring survival. Old females had a higher probability of raising at least one offspring to

35   independence over a 3-year period, suggesting a higher reproductive success of more

36   experienced females possibly due to an improvement of hunting skills with age.

37   4. Overall, our results show the importance of accounting for i) the statistical dependency

38   within family units until offspring independence, and ii) past reproductive history of the

39   caring parent. If ignored, estimates obtained for breeding probability, litter size, and survival

40   can be biased. This is of interest in terms of conservation because species providing extended

41   parental care are often long-living mammals vulnerable or threatened with extinction.

42

43   **Key-words:** apex predator, arctic ecosystem, Bayesian modeling, capture-recapture,

44   dependency among individuals, family structure, multi-state models, parental care, sociality.

45

46   **INTRODUCTION**

47   Altricial mammals having offspring that need to learn complex skills to ensure survival

48   beyond independence, such as hunting, orientation, or nest building, show extended or

49   prolonged parental care (Clutton-Brock, 1991). In such species, one or both parents care for

50   one or several young over a period including more than one breeding season. This can extend

51   until lifelong maternal care in primates (Van Noordwijk, 2012). Parental care includes any

52   pre-natal and post-natal allocation, such as feeding and protecting the young, which benefits

53   an individual offspring development and survival chances, thereby enhancing the parent's

54   reproductive success (Trivers, 1972). For the offspring, the quality and quantity of care

55   received can have long-lasting effects on future survival (e.g. Pavard & Branger, 2012), social

56   status (e.g. Shenk & Scelza, 2012) and reproduction (Royle, Smiseth, & Kölliker, 2012). For

57   the parent, investment in one young is at the cost of the parent's ability to invest in other

58   offspring (siblings or future offspring) (Trivers, 1972). It can indeed take several years during

59   which a parent caring for his young will not be available to reproduce, sometimes not until the

60   offspring have reached independence, e.g. 2.5 years for female polar bears (Ramsay &

61   Stirling, 1988), 3.5 to 6 years for female African elephants (Lee & Moss, 1986), and 9.3 years

62   for female Sumatran orangutans (Wich et al., 2004). The fitness cost of losing one offspring,

63   in terms of lost investment and skipped breeding opportunities, is therefore particularly high if

64   death occurs near independence. We expect extended parental care, through large parental

65   investment and long-term dependency within family units, to cause high variability in life

66   trajectories among individuals and family groups, in interbirth intervals depending on

67   offspring's fate, and consequently on lifetime reproductive success for the caring parent

68   (Clutton-Brock, 1991). Because parental care can affect simultaneously several parental and

69   offspring traits, its consequences at the population level are still poorly understood, especially

70   in free-ranging animal populations.

71   Capture-recapture (CR) models allow studying species with complex demography in

72   the wild, e.g. by considering 'breeder' and 'non-breeder' reproductive states to estimate

73   breeding probabilities and status-specific demographic parameters while accounting for

74   imperfect detectability (e.g., Lebreton, Nichols, Barker, Pradel, & Spendelow, 2009). One can

75   distinguish between successful and failed breeding events (e.g., Lagrange et al., 2017) and

76   include varying litter or clutch size (e.g., Doligez et al., 2002) and memory effects (Cole et al.,

77   2014), to investigate the costs of reproduction on survival and future reproduction for species

78   providing short-term parental care, i.e. when offspring reach independence before the next

79   breeding season (e.g., Yoccoz, Erikstad, Bustnes, Hanssen, & Tveraa, 2002). By including

80   non-observable states (Lebreton et al., 2009), one can differentiate between pre-breeders,

81   first-time breeders, experienced breeders, and adult non-breeders to estimate the probabilities

82   of skipping one breeding opportunity (e.g., Cubaynes, Doherty, Schreiber, & Gimenez, 2011).

83   Currently however, there is no CR approach for modelling the demography of species

84   providing extended parental care. This is of particular interest in terms of conservation

85   because species providing extended parental care are often among long-living mammals

86   vulnerable or threatened with extinction (e.g. polar bears, orangutans, elephants).

87   Here, we develop a CR model for studying the demography of species providing

88   extended parental care. Our model jointly handles statistical dependency among individual

89   demographic parameters within family units until offspring independence, inter-individual

90   variability in breeding frequency, variability in the number of offspring born and recruited at

91   each breeding event, the influence of past reproductive history on the caring parent current

92   status, and accounts for imperfect detection possibly depending upon family unit composition.

93   In what follows, we present the model, assess its performances using simulated data, and

94   illustrate its use with a long-term dataset collected on the Svalbard polar bears. Female polar

95   bears rely only on stored fat reserves during pregnancy and the first three months of lactation,

96   before feeding and protecting litters of one to three young, usually during two and a half more

97   years (Ramsay & Stirling, 1988). They can lose more than 40% of body mass while fasting

98   (Atkinson & Ramsay, 1995). In many areas, climate change and related sea ice decline impact

99   female bear condition and capacity to provide care for their young, with an associated decline

100   in reproductive output (Derocher, Lunn, & Stirling, 2004; Stirling & Derocher, 2012). More

101   insights into the species demography, such as the consequences of long-duration parental care

102   on mother and offspring life histories, could help our understanding of polar bear population

103   responses to environmental perturbations and extinction risks in future decades (Hunter et al.,

104   2010; Regehr et al., 2016).

105

106   **METHODS**

107

108   *Capture-recapture model for species providing extended parental care*

109   The model is based on data on individual encounter histories that record the subsequent

110   observations or non-observations of individuals in the field, with specific information on the

111   state of each individual at each capture occasion. States can refer to various characteristics,

112   such as breeding status, epidemiological status, or a site (Lebreton et al., 2009). We used four

113   sets of parameters: 1) the proportion of individuals in each state at first capture, 2) state-

114   specific survival probabilities from occasion t to $t+1$; 3) transition probabilities from one state

115   at time t to another state at $t+1$ conditioned upon being alive at time $t+1$; and 4) state-specific

116   individual recapture probabilities at occasion t (Lebreton et al., 2009).

117   The novelty of our model lies in that the encounter histories are defined for each

118   family unit instead of each individual. Let us consider a study over K encounter occasions and

119   N family units. The encounter history for family unit i is denoted $h_{ij} = (o_{i1}, \ldots, o_{ik})$ where o_{ik}

120   records whether family unit i, at occasion k, is observed in state m ($o_{ik} = m$) or not ($o_{ik} = 0$).

121   The states m correspond to the composition of family units observed in the field. Thus, the

122   number and type of states will vary depending on the species considered, the duration and

123   distribution of parental care between parents, and variability in the number of young

124   produced. For example, let us consider a species in which a single parent care for a maximum

125   of X young over Y years. The states will be defined as $m = (P_0, \ldots, P_{x,y}, \ldots, D)$ where P_0

126   stands for a family unit composed of a single parent, $P_{x,y}$ for a family unit composed of the

127   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

128   the dead state.

129   Our model can be decomposed in several matrices gathering the probabilities of the

130   initial states and four conditional sets of events representing the species life cycle: parent(s)

131   survival (Φ, eq. 1), offspring survival and growth (S, eq. 2), breeding probabilities (A, eq. 3)

132   and number of offspring produced per breeding event (B, eq. 4), and a matrix gathering the

133   family unit's recapture probabilities (P, eq. 5). First, we define the vector $\Pi_{m-1} =$

134    $\left(\pi_0, \dots, \pi_{x,y}, \dots, \pi_{X,Y}\right)$ gathering the initial probabilities of each live state. A first matrix,

135    $[\phi]_{m,m}$ gathers the state-specific survival probability for the caring parent from time t to $t + 1$.

136   Then, the transition matrix gathering transition probabilities among states between each

137   occasion t to $t+1$ is decomposed into three intermediate steps conditioning upon each other.

138   The decomposition helps in estimating meaningful biological quantities corresponding to all

139   possible events occurring between two capture occasions. We write $\Psi = S_{m,m_1} A_{m_1,m_2} B_{m_2,m}$.

140   The first matrix, S_{m,m_1}, gathers the state-specific transition probabilities from states m to

141   intermediary states m_1, which correspond to the offspring survival probabilities to the next

142   age, depending on the caring parent survival, the young age, and number of siblings.

143   Intermediate   states   of   arrival   are   defined   as

144    $m_1 = (P_{0 \to 0}, P_{1,1 \to 1,2}, P_{1,1 \to 0} \dots, P_{x,y \to x,y+1}, P_{x,y \to x-1,y+1}, \dots, P_{X,Y-1 \to X,Y})$, where, during the

145   interval between occasions t and $t+1$, a non-breeder parent alive always remain non breeder

146    $(0 \to 0)$, and for a family unit composed of a caring parent with at least one young, each of

147   the young can survive and grow to the next age $(x, y \to x, y + 1)$, or die $(x, y \to x - 1, y +$

148   1). The second matrix, A_{m_1,m_2}, gathers the state-specific transition probabilities from

149   intermediate states m_1 to intermediate states m_2, which correspond to the state-specific

150   breeding   probabilities.   Intermediate   states   of   arrival   are   defined   as

151 $m_2 = (P'_{0 \to 0 \to 0}, P'_{0 \to 0 \to r}, \ldots, P'_{x,y \to x,y+1 \to 0}, P'_{x,y \to x,y+1 \to r}, \ldots, P'_{X,Y-1 \to X,Y \to r})$, where during

152 the interval between time t and $t+1$, a parent non-breeder at the beginning of the interval and

153 still alive can breed $(0 \to 0 \to r)$ or remain non-breeder $(0 \to 0 \to 0)$, and a parent caring for

154 at least one young still alive can breed again $(x, y \to x, y + 1 \to r)$ or not $(x, y \to x, y + 1 \to$

155 $0)$, and a parent that just lost one (or several) young of a certain age can breed $(x, y \to x -$

156 $1, y + 1 \to r)$ or not $(x, y \to x, y + 1 \to 0$). The third matrix, $B_{m_2,m}$, gathers the state-specific

157 transition probabilities from intermediate states m_2 to departures states m , which correspond

158 to the probability of producing a certain number of young depending on the previous steps.

159 The probability will be set to 0 for non-breeders, and can differ for a breeder that was non

160 breeder at the beginning of the interval $(0 \to 0 \to r \to x', y' = 1)$, a parent that breeds while

161 caring for other young $(x, y \to x, y + 1 \to r \to x', y' = 1)$, or a parent that breeds again while

162 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-

163 called event matrix, $[P]_{m,2}$, gathers the detection probability of family units, where the state-

164 specific probability of being observed $(p(P_{x,y}))$ or not $(1 - p(P_{x,y}))$ at occasion t can vary

165 depending on the composition of the family unit.

166 The structure of the model implies that the number of offspring produced per breeding

167 event is conditioned upon breeding decision. Breeding decision is conditioned upon the status

168 and number of dependent offspring already cared for by the parent, which itself is conditioned

169 upon parental survival. This particular formulation permits to investigate, among others, the

170 cost of reproduction on female survival (step 1), the influence of litter size on litter survival

171 (step 2), the influence of past reproductive history on both breeding probability (step 3), and

172 on litter size (step 4). The influence of individual traits such as age or body weight, or

173 environmental variables such as temperature, can be included in the model under the form of

174 individual or temporal covariates (Pollock, 2002). In addition, specificities related to data

175 collection can also be included in a similar way, such as trap effects (Pradel & Sanz-Aguilar,

176   2012) or latent individual heterogeneity by using mixture of distributions or random effects

177   (Gimenez, Cam, & Gaillard, 2018).

178

179   *Simulation study*

180   We evaluated the performance of our model using simulated data for a virtual long-lived

181   mammal species, mimicking the polar bear case study (see next section for details). We

182   considered that care of offspring was provided by the mother only, to one, two or three

183   offspring, for 3 years maximum. Parameters included mother survival, young survival,

184   breeding probabilities and litter size probabilities, as well as detection probability.

185   Specifically, we used $\phi_{mother} = 0.9$ for annual adult survival assumed independent of family

186   unit composition, $\phi_{cub} = 0.3$ for annual cub survival and $\phi_{yearling} = 0.5$ for annual yearling

187   survival, independently of litter size and conditioned upon mother survival. Breeding

188   probability was $\alpha_{alone} = 0.6$ for a female alive without dependent offspring, $\alpha_{cub\dagger} = 0.1$ for

189   a female alive that just lost her cub litter, $\alpha_{yearling\dagger} = 0.3$ for a female alive that just lost her

190   yearling litter, and $\alpha_{offspring} = 0$ for a female alive with dependent offspring alive. Litter

191   size probability of one cub for breeding females was i) $\Pr(LS = 1) = \beta_{alone} = 0.4$ and of

192   multiple cubs (2 or 3) was $\Pr(LS>1) = 0.6$, for a female previously without offspring, and ii)

193     $\Pr(LS = 1) = \beta_{offspring\dagger} = 0.5$ and of multiple cubs $\Pr(LS>1) = 0.5$ for a female that lost

194   offspring during the year.

195   We considered three scenarios with low ($p = 0.3$), medium ($p = 0.5$), and high ($p = $

196   0.8), detection of family units. We simulated 100 CR datasets for each detectability scenario

197   with 25 sampling occasions and 50 newly family units released at each occasion. We

198   simulated the data using program R. We fitted the model using maximum likelihood in

199   package TMB called from R (Kristensen, Nielsen, Berg, Skaug, & Bell, 2015). For each

200 parameter, we calculated the bias and root-mean-square error. The code used for carrying out

201 the simulations is provided in Appendix 1.

202

203 *Case study: Polar bears in Svalbard*

204 In Polar bears, care of offspring is provided by the mother only (Amstrup, 2003). Males were

205 therefore discarded from our analysis. Adult female polar bears mate in spring (February to

206 May, Amstrup, 2003), and in Svalbard usually have their first litter at the age of six years

207 (Derocher, 2013). They have delayed implantation where the egg attaches to the uterus in

208 autumn (Ramsay & Stirling, 1988). A litter with small cubs (ca 600 grams) is born around

209 November to January, in a snow den that the mothers dig out in autumn, and where the family

210 stay 4-5 months. The family usually emerges from the den in March-April, and stay close to

211 the den while the cubs get accustomed to the new environment outside their home, for a few

212 days up to 2-3 weeks (Hansson & Thomassen, 1983). Litter size in early spring vary from one

213 to three, with two cubs being most common, three cubs in most areas being rare, and

214 commonly around one out of three litters having one cub only (Amstrup, 2003). The weaning

215 age of cubs varies between populations, and is approximatively 2.3 years in the Barents Sea.

216 The cubs typically depart from the mother in their third spring (March-April), when the

217 mother can mate again. Thus, the minimum reproductive interval for successful Barents Sea

218 polar bears is 3 years. On the contrary, loss of a cub litter shortly after den emergence may

219 mean the mother can produce new cubs in winter the same year (North, 1953).

220 We analyzed n = 496 encounter histories of polar bear family units monitored over 25

221 years, each spring, from 1992 to 2016, in Svalbard. Polar bears were caught and individually

222 marked as part of a long-term monitoring program on the ecology of polar bears in the

223 Barents Sea region. The captures occur each year shortly after den emergence (mid-March to

224 late April; Andersen Derocher, Wiig, & Aars, 2012). All bears one year or older were

225   immobilized by remote injection of a dart (Palmer Cap-Chur Equipment, Douglasville, GA,

226   USA) with the drug Zoletil® (Virbac, Carros, France) (Stirling, Spencer, & Andriashek,

227   1989). The dart was fired from a small helicopter (Eurocopter 350 B2 or B3), usually from a

228   distance of about 4 to 10 meters. Cubs of the year were immobilized by injection with a

229   syringe. Cubs and yearlings are captured together with their mother. Because they are highly

230   dependent on her, they remain in her vicinity. A female captured alone has no dependent

231   offspring alive, but could have lost her cubs in the den or shortly after den emergence but

232   before capture. Hereafter, estimated cub survival thus refers to survival after capture. Infant

233   mortality occurring before capture will be assigned to a reduced litter size. Because only 3%

234   of females were observed with 3 offspring, we analyzed jointly litters of twins with triplets.

235   Prior fitting models, we performed goodness-of-fit tests (Pradel, Wintrebert, & Gimenez,

236   2003) using the R package R2ucare (Gimenez, Lebreton, Choquet, & Pradel, 2018). The

237   overall test was not significant (df = 137, χ^2=67.402, p-value = 1), suggesting no major lack

238   of fit of the standard time-dependent multistate CR model to our data. Because bears captured

239   in Svalbard are shown to be a mixture of resident and pelagic bears (Mauritzen, Derocher, &

240   Wiig, 2011), we included hidden heterogeneity in the detection process. To do so, we

241   considered a mixture of two classes of individuals on recapture probability (Gimenez, Cam,

242   & Gaillard, 2018) to account for the lower probability for pelagic bears of being detected

243   every year. Last, previous studies have found senescence starts around age 15 in polar bears,

244   we therefore distinguished survival and reproductive parameters of 'prime-age' <15 y.o. and

245   'old' ≥15 y.o. (Derocher & Stirling, 1994).

246   We built the model with 8 states corresponding to the field observations of different

247   family units composition: $m = (F_o , F_c , F_{c+} , F_y , F_{y+} , F_t , F_{t+} , D)$ respectively standing for

248   female alone, female with one cub, female with multiple cubs, female with 1 yearling, female

249   with multiple yearlings, female with one two-year old, female with multiple two-year olds,

250 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

251 proportion of family units in each live state at first capture. The first step determines mother

252 survival depending on offspring number and age, with matrix $[\phi]_{m,m}$ defined as:

253

$$[\phi]_{m,m} = \begin{bmatrix} F_{o,j} & 0 & 0 & 0 & 0 & 0 & 0 & 1-F_{o,j} \\ 0 & F_{c,j} & 0 & 0 & 0 & 0 & 0 & 1-F_{c,j} \\ 0 & 0 & F_{c+,j} & 0 & 0 & 0 & 0 & 1-F_{c+,j} \\ 0 & 0 & 0 & F_{y,j} & 0 & 0 & 0 & 1-F_{y,j} \\ 0 & 0 & 0 & 0 & F_{y+,j} & 0 & 0 & 1-F_{y+,j} \\ 0 & 0 & 0 & 0 & 0 & F_{t,j} & 0 & 1-F_{t,j} \\ 0 & 0 & 0 & 0 & 0 & 0 & F_{t+,j} & 1-F_{t+,j} \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix},$$ (eq. 1)

254 where $_{i,j}$ is the annual survival probability of a mother of age j in state i at capture occasion t.

255 Preliminary analyses showed that mother survival did not vary according to composition of

256 the family unit. We therefore did not include variation among states and included only the

257 effect of age on mother survival, hereafter $_{1,j}$ with $j = 1$ for prime-age and $j = 2$ for old

258 females.

259 The second step determines young survival and growth conditioned upon mother survival

260 during time interval t to $t + 1$. Intermediary states are defined such as $m_1 = $ (F_o , F_{c-} , F_{y-} , F_y ,

261 F_{y+} , F_t , F_{t+} , D) respectively standing for surviving female alone, surviving female losing all

262 cubs, surviving female losing all yearlings, surviving female with one surviving cub growing

263 into a yearling, surviving female with multiple surviving cubs growing into multiple

264 yearlings, surviving female with one surviving yearling growing into one two-year old,

265 surviving female with multiple surviving yearlings growing into multiple two-year olds, and

266 dead females. The second matrix, $[S]_{m,m_1}$ gathering young survival probabilities depending

267 on age and on sibling's number is defined as:

268

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

269

270 where, for litters of singletons, $\phi_{2,j}$ is cub survival, and $\phi_{3,j}$ is yearling survival for a

271 surviving mother of age j during time interval t to $t+1$. For litters of multiple offspring, S_{ij} is

272 the probability that only one cub, $S_{1,j}$, resp. one yearling, $S_{3,j}$, or all cubs, $S_{2,j}$, resp. all

273 yearling, $S_{4,j}$, survive conditioned upon mother survival for a mother of age j.

274 The third step determines breeding probability conditioned upon mother survival, age

275 and young survival and growth during time interval t to $t + 1$. Intermediary states are defined

276 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

277 female alone remaining non-breeder, surviving female alone becoming breeder, surviving

278 female that lost her offspring becoming breeder, surviving female with one surviving cub

279 growing into a yearling remaining non-breeder, surviving female with multiple surviving cubs

280 growing into several yearlings remaining non-breeder, surviving female with one surviving

281 yearling growing into one two-year old remaining non-breeder, surviving female with

282 multiple surviving yearlings growing into several two-year old remaining non-breeder, and

283 dead females. The third matrix, $[A]_{m_1,m_2}$ gathering breeding probabilities depending on the

284 previous steps is defined as:

285
$$[A]_{m_1,m_2} = \begin{bmatrix} 1 - \alpha_{1,j} & \alpha_{1,j} & 0 & 0 & 0 & 0 & 0 & 0 \\ 1 - \alpha_{2,j} & 0 & \alpha_{2,j} & 0 & 0 & 0 & 0 & 0 \\ 1 - \alpha_{3,j} & 0 & \alpha_{3,j} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix},$$
 (eq. 3)

286

287 where $\alpha_{i,j}$ is the breeding probability of a surviving female of age j alone (α_1), that lost cubs

288 (α_2), and that lost yearlings (α_3).

289   The fourth step determines litter size probabilities for reproductions occurring during

290   the time interval t to $t+1$ depending on the previous steps, with matrix $[B]_{m_2,m}$ being defined

291   as:

292
$$[B]_{m_2,m} = \begin{bmatrix} 1 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & \beta_{1,j} & 1-\beta_{1,j} & 0 & 0 & 0 & 0 & 0 \\ 0 & \beta_{2,j} & 1-\beta_{2,j} & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 1 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 1 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 1 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 1 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix},$$
(eq. 4)

293

294   where $\beta_{i,j}$ (resp. $1-\beta_{i,j}$) is the probability of producing a single cub per litter (resp. a litter of

295   twins) for females of age j that were alone, $\beta_{1,j}$, or have lost offspring, $\beta_{2,j}$, during the time

296   interval t to $t+1$.

297   The fifth step relates the states to field observations $e = (F_o, F_c, F_{c+}, F_y, F_{y+}, F_t, F_{t+},$

298   0), '0' meaning non-detected. The observation matrix that gathers the family unit's

299   probability of detection at occasion t is defined as:

300
$$[P]_{m,e} = \begin{bmatrix} p_i & 0 & 0 & 0 & 0 & 0 & 0 & 1-p_i \\ 0 & p_i & 0 & 0 & 0 & 0 & 0 & 1-p_i \\ 0 & 0 & p_i & 0 & 0 & 0 & 0 & 1-p_i \\ 0 & 0 & 0 & p_i & 0 & 0 & 0 & 1-p_i \\ 0 & 0 & 0 & 0 & p_i & 0 & 0 & 1-p_i \\ 0 & 0 & 0 & 0 & 0 & p_i & 0 & 1-p_i \\ 0 & 0 & 0 & 0 & 0 & 0 & p_i & 1-p_i \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 1 \end{bmatrix},$$
(eq. 5)

301

302   where, p_i, respectively $1-p_i$, is the probability of being detected, respectively not detected, for

303   family unit composition belonging to sub-population i. Each family unit has a probability

304     $\rho_{resident}$ (resp. $1-\rho_{resident} = \rho_{pelagic}$) of belonging to one or the other mixture component.

305   We provide the code with guidance to fit the model in a Bayesian framework in program Jags

306   called from R in Appendix 2.

307   Using the conditional probabilities estimated in the model, we calculated the net

308   probability for a female of age j to raise none, $\Pr(X=0)$, one, $\Pr(X=1)$, or two young, $\Pr(X=2)$

309   close to independence (age 2) over a 3-year period (Figure 1).
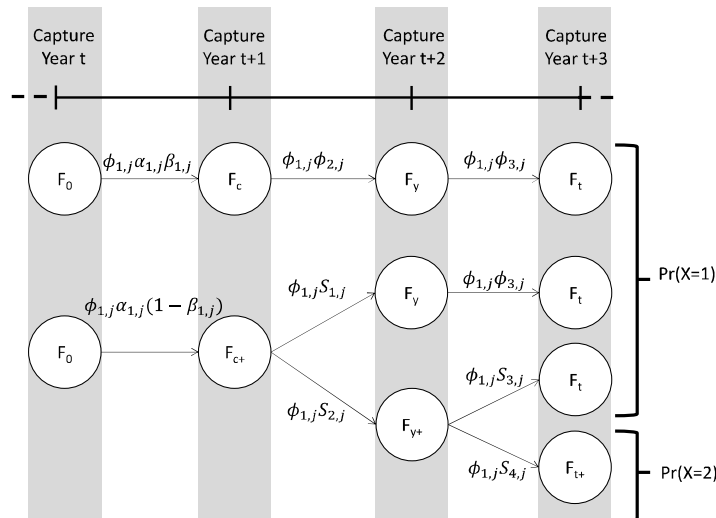
310

311   Figure 1: Life history events with associated probabilities of raising at least one young near

312   independence (to age 2) over a 3 years period. For a female polar bear of age j, $j = 1$ for

313   'prime-age' and $j = 2$ for 'old', alive and without dependent young at the beginning of the

314   period, $\phi_{1,j}$ is adult survival, $\alpha_{1,j}$ is breeding probability, $\beta_{1,j}$ is litter size probability of one,

315    $\Pr(LS=1)$, $\phi_{2,j}$ and $\phi_{3,j}$ resp. cub and yearling survival in a singleton litter. In a litter of

316   multiple young $S_{1,j}$, resp. $S_{2,j}$, is the probability that only one cub survives, resp. all cubs in

317   the litter survive and $S_{3,j}$, resp. $S_{4,j}$, is the probability that only one yearling survives, resp. all

318   yearlings in the litter survive.

319

320   We considered mature females that were without dependent offspring at the beginning of the

321   time period, so that we have for females of age j:

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

323    $\Pr(X = 2 \,|j) = \left(\phi_{1,j}\right)^3 \cdot \alpha_{1,j} \cdot \left(1 - \beta_{1,j}\right) \cdot S_{2,j} \cdot S_{4,j}$,
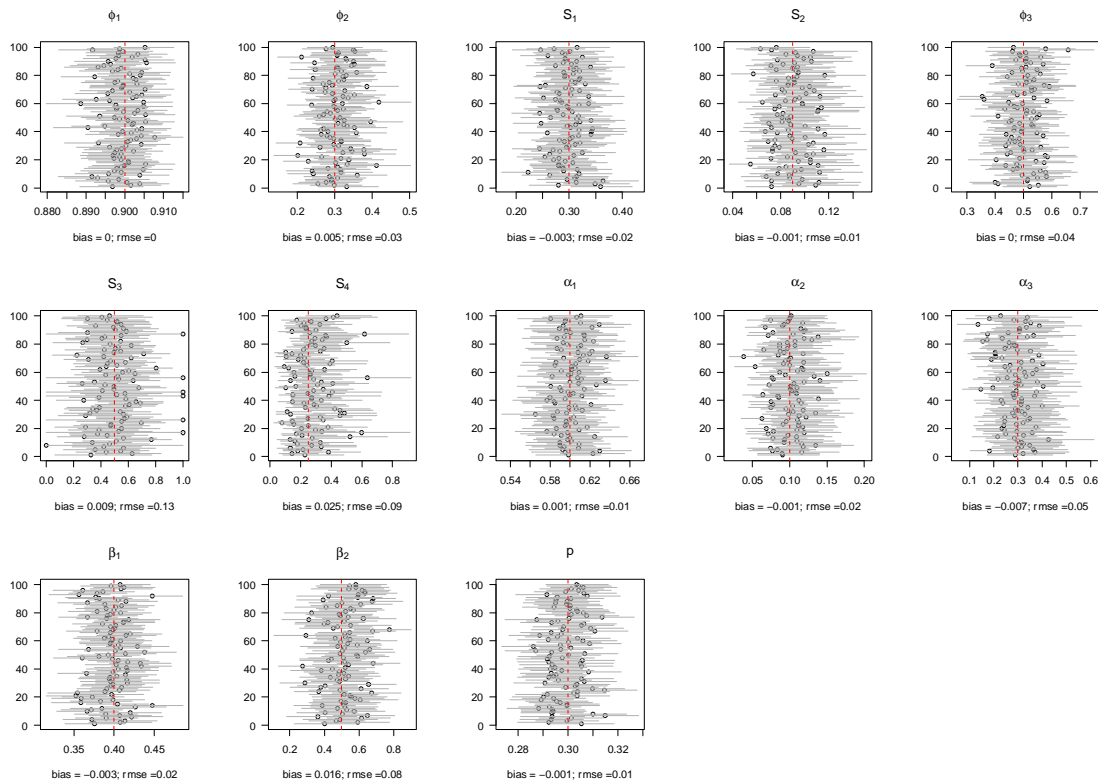
324    $Pr(X = 0|j) = 1 - \Pr(X = 1) - \Pr(X = 2)$.

325

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

342   S_3, resp. S_4, is the probability that only one yearling survives, resp. all yearlings in the litter

343   survive. Then, α_1, resp. α_2, resp. α_3, is the breeding probability of a female previously alone,

344   resp. that have lost a cub litter, resp. that lost a yearling litter during the year, and β_1, resp. β_2,

345   is litter size probability of one, Pr(LS=1), for females previously non breeder, resp. failed

346   breeder that lost a litter during the year, p is the family unit's detection probability.

347

348   *Case study: Polar bear demography*

349   Posterior distributions are given for all estimated parameters (Appendix 2). Annual female

350   survival was high and lower for old females (Table 1 and Figure 3). Cubs and yearling

351   survival rates, conditioned upon mother survival, were lower for singleton than for litters of

352   twin for young mothers but were higher and did not depend on litter size for old mothers

353   (Table 1 and Figure 3). Outcome of the previous reproduction influenced breeding probability

354   for young and old females (Figure 3). Breeding probability was <15% for females that lost a

355   cub litter during the year, about 20-30% for females that lost a yearling litter and increased to

356   50-65% for females that were alone at the beginning of the year (Table 1). Old females had a

357   higher probability than young females of breeding when alone, but about the same if they had

358   lost a litter at the beginning of the year. For breeding females that had lost a litter at the

359   beginning of the year, the probability of producing a single cub was higher for older than

360   younger females, while there was no difference in litter size probability between young and

361   old females that did not fail at previous reproduction (Table 1 and Figure 3).

362   At first capture, 52% of adult females were alone, 11% with one cub, 22% with two

363   cubs, 8% with one yearling, 3% with multiple yearlings and 2% with one or multiple two-year

364   old bears. About 15% (0.10 – 0.23) of family units belonged to the high detectability group,

365   with an annual detection rate of 0.42 (0.33 – 0.51), while 85% (0.77 – 0.90) of family units

366   had a low annual detection probability of 0.04 (0.02 – 0.06).

367

368

369   Table 1: Parameter estimates. Means are given with 95% credible intervals (CI). Offspring

370   survival and breeding probabilities are conditioned upon mother survival, litter size

371   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)

372

373
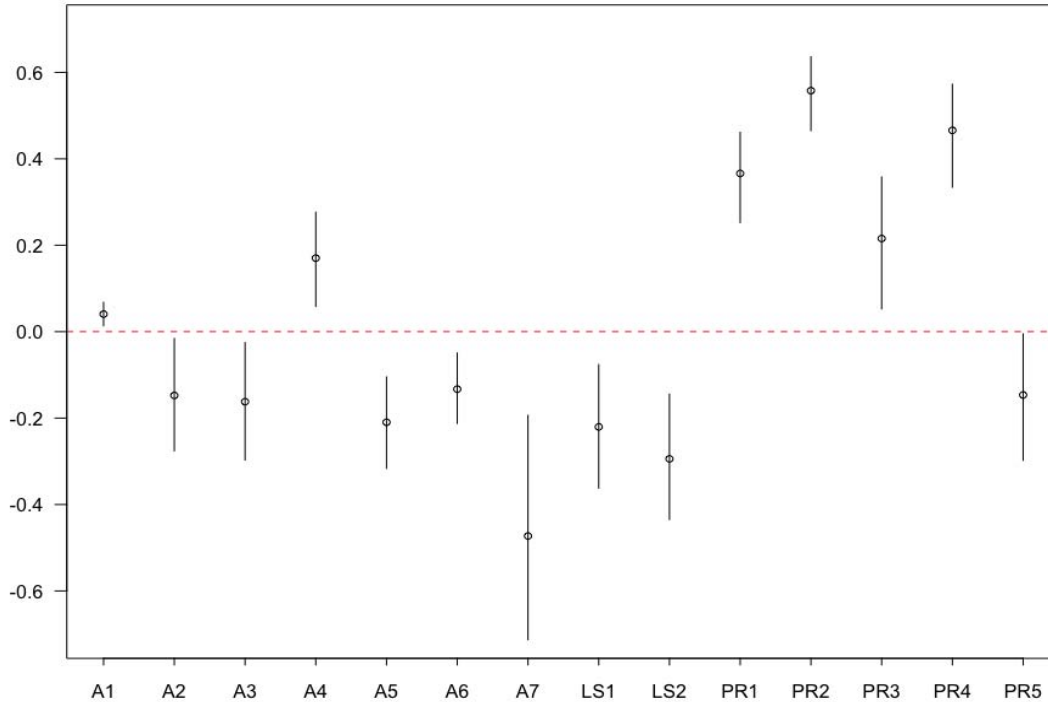
374
375 Figure 3. Effects of maternal age (A), litter size (LS) and outcome of the previous

376 reproduction (PR) on adult and young survival, breeding probability and litter size. Median

377 (dot) with 80% credible interval (segment) are displayed for significant effects only. Mother

378 age effects (young female minus old female coefficient) on adult survival (A1), single litter

379 cub survival (A2), single litter yearling survival (A3), on the probability that one (A4) or all

380 (A5) cubs survive in a multiple litter, on breeding probability for females alone (A6), and on

381 the probability of litter size of 1 for failed breeders (A7). Effects of litter size (single litter

382 minus multiple litter coefficient) on cub litter survival for young mothers (LS1) and on

383 yearling litter survival for young mothers (LS2). Effects of previous reproduction on breeding

384 probability for young mothers (PR1, PR3 and PR5) and for old mothers (PR2 and PR4); the

385 coefficient is either the difference between breeding probability of a female alone vs one that

386 lost a cub litter (PR1 and PR2) or that lost a yearling litter (PR3 and PR4) or that lost a cub

387 litter vs a yearling litter (PR5).

388

389   Results obtained for the net probability of successfully raising 0, 1 or 2 young to their

390   second birthday for females over a 3-year period showed that old females had a higher

391   probability of raising at least one offspring. For all females, the probability of raising two

392   young to their second birthday, was very low (Table 2). Note that this calculation includes

393   breeding probability, and therefore does not reflect offspring survival until weaning (see

394   Method section).

395

396   Table 2: Probability of raising none, Pr(X=0), one, Pr(X=1), or two young, Pr(X=2) close to

397   independence (age 2) over a 3-year period for females younger than 15 y.o. and at least 15 y.o

398   that were alive and without dependent young at the beginning of the period. Medians with

399   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)

400

401

402   **DISCUSSION**

403   Overall, our model performed well on both simulated and real data. Estimates obtained for

404   mother and young survival rates within family units, probability of breeding and of litter

405   sizes, and detection probability were unbiased in most simulated scenarios. Bias and root-

406   mean square errors were the highest for twin yearling litter survival when family units'

407   detection rate was low. We believe bias on these specific parameters is due to parameters of

408   the transition matrices being conditioned upon each other. Because of this, having enough

409   yearling and two-year old litter of twin in the data to estimate twin yearling litter survival

410   requires high enough adult and cub survival, breeding probability and litter size probability of

411   two, as well as detection probability and number of individuals. Prior to fitting our model, one

412   should ensure via simulations (see Appendix 1) that sample size and detection probability is

413   high enough for its applicability. Inference in a Bayesian framework is useful in this regard,

414   because it allows to include prior information when available (McCarthy & Masters, 2005) to

415   help estimation of the model parameters. In the polar bear data, there were few recaptures of

416   females on subsequent years due to relatively low detection rate. As a result, preliminary

417   analyses suggested a potential confusion between these parameters. We dealt with this issue

418   by including a biologically realistic constraint on prior distributions, stating that cub survival

419   was lower than that of yearling (Amstrup & Durner, 1995) which was enough to ensure

420   parameter estimability.

421   For polar bears, we showed that mother age and outcome of the previous breeding

422   event influenced breeding probability, litter size and offspring survival. Reduced offspring

423   survival one year, for example due to poor environmental conditions (Derocher, Lunn, &

424   Stirling, 2004), might therefore increase intervals between successful reproduction through

425   reduced breeding probability and litter size the next year. This means that by ignoring long-

426   term dependency among mother and offspring life histories, classical models can

427   underestimate reproductive intervals, therefore risking to overestimate the population growth

428   rate. Adult survival and offspring survival to weaning were lower than previously estimated in

429   Svalbard (Wiig 1998). Our model likely underestimated yearling survival because two-year-

430   old bears frequently have already departed from their mother in Spring during the recaptures.

431   This could explain the low probability of successfully raising at least one offspring to two-

432   year-old over a 3-year period (Table 2). We also found that old females had a higher

433   probability of raising at least one offspring close to independence over a 3-year period. It

434   suggested a higher reproductive success of more experienced females possibly due to an

435   improvement of hunting skills with age (Folio et al., in press; Atkinson & Ramsay, 1995).

436   However, the biological relevance of our model is currently limited, because we ignored

437   temporal and individual heterogeneity among females in the model. Future analyses will

438   integrate in the model density-dependent processes and influence of climatic variables on

439   body weight and demography (Derocher et al., 2004; Stirling & Derocher, 2012) as individual

440   and environmental covariates in a regression-like framework. Date of capture will also be

441   included as a covariate on detection to model the probability of two-year olds still being with

442   the mother in spring.

443   Here, we proposed a general model structure that can be applied to other species

444   providing extended parental care, e.g. primates or elephants. The originality of our approach

445   lies in using family structure to define statistical units in our model. It allows to include

446   dependency among individuals and therefore evaluate correlations between offspring and

447   parents' life history parameters. By modifying the matrices to include a higher number of

448   family unit structures (eq. 1 to eq. 5), one can easily include biparental care, and/or grand-

449   parental care for species like wolves or humans, variable duration of parental care, number of

450   young, and breeding and litter size probabilities for breeding parents caring for older offspring

451   (Clutton-Brock et al. 1991). Such extensions of our model could be used, for example, to

452   evaluate the population-level consequences of positive or negative correlation between

453   parents and offspring traits (e.g. food sharing among group members Lee, 2008; or parent-

454   offspring conflict Kölliker, Kilner, & Hinde, 2013). For polar bears specifically, our model

455   could be used to extend the population model proposed by Hunter et al. (2010) to include

456   variability in litter size and breeding frequency depending on the fate of the mothers' past

457   breeding event. This approach would permit to reassess extinction risks and predictions of the

458   demographic response of polar bear populations under climate change (Hunter et al., 2010;

459   Regehr et al., 2016).

460

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