



HAL
open science

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

Sarah Cubaynes, Jon Aars, Nigel Yoccoz, Roger Pradel, Oystein Wiig, Rolf A. Ims, Olivier O. Gimenez

► To cite this version:

Sarah Cubaynes, Jon Aars, Nigel Yoccoz, Roger Pradel, Oystein Wiig, et al.. Modeling the demography of species providing extended parental care: A capture-recapture approach with a case study on Polar Bears (*Ursus maritimus*). *Ecology and Evolution*, 2021, 10.1002/ece3.7296 . hal-03121578

HAL Id: hal-03121578

<https://hal.science/hal-03121578>

Submitted on 26 Jan 2021

HAL is a multi-disciplinary open access archive for the deposit and dissemination of scientific research documents, whether they are published or not. The documents may come from teaching and research institutions in France or abroad, or from public or private research centers.

L'archive ouverte pluridisciplinaire **HAL**, est destinée au dépôt et à la diffusion de documents scientifiques de niveau recherche, publiés ou non, émanant des établissements d'enseignement et de recherche français ou étrangers, des laboratoires publics ou privés.

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

Journal:	<i>Ecology and Evolution</i>
Manuscript ID	ECE-2020-11-01798.R1
Wiley - Manuscript type:	Original Research
Date Submitted by the Author:	n/a
Complete List of Authors:	CUBAYNES, SARAH; CEFE-CNRS Aars, Jon; Norwegian Polar Institute, FRAM Centre Yoccoz, Nigel; UiT Arctic University of Norway, Arctic and Marine Biology Pradel, Roger; CEFE-CNRS Wiig, Oystein; Natural History Museum, University of Oslo, Norway Ims, Rolf; University of Tromso, Institute of Biology Gimenez, Olivier; CNRS, CEFE
Category:	Population Ecology
Habitat:	Marine, Theoretical
Organism:	Vertebrate
Approach:	Statistical
Abstract:	<p>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 mostly ignore extended parental care, thereby limiting our understanding of its consequences on parents and offspring life histories. We designed a capture-recapture multi-event model for studying the demography of species providing extended parental care. It handles statistical multiple-year dependency among individual demographic parameters grouped within family units, variable litter size, and uncertainty on the timing at offspring independence. It allows for the evaluation of trade-offs among demographic parameters, the influence of past reproductive history on the caring parent's survival status, breeding probability and litter size probability, while accounting for imperfect detection of family units. We assess the model performance using simulated data, and illustrate its use with a long-term dataset collected on the Svalbard polar bears (<i>Ursus maritimus</i>).</p> <p>Our model performed well, both when offspring departure probability from the family unit occurred at a constant rate or varied during the field season depending on the date of capture. For the polar bear case study,</p>

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

	<p>we provide estimates of adult and dependent offspring survival rates, breeding probability and litter size probability. Results showed that the outcome of the previous reproduction influenced breeding probability. Overall, our results show the importance of accounting for i) the multiple-year statistical dependency within family units, ii) uncertainty on the timing at offspring independence, and iii) past reproductive history of the caring parent. If ignored, estimates obtained for breeding probability, litter size, and survival can be biased.</p>



1
2
3 1 **Modeling the demography of species providing extended parental care:**

4
5 2 **A capture-recapture multievent model with a case study on Polar Bears (*Ursus***
6
7 3 ***maritimus*)**

8
9
10 4
11
12 5 Sarah Cubaynes¹, Jon Aars², Nigel G. Yoccoz³, Roger Pradel¹, Øystein Wiig⁴, Rolf A Ims³
13
14 and Olivier Gimenez¹

15 6
16
17 7 ¹ CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Univ Paul Valéry

18
19 8 Montpellier 3, Montpellier, France

20
21 9 ² Norwegian Polar Institute, FRAM Centre, Tromsø, Norway

22
23 10 ³ UiT The Arctic University of Norway, Department of Arctic and Marine Biology, Tromsø,
24
25 Norway

26
27 11 ⁴Natural History Museum, University of Oslo, Norway

28
29 12
30
31 13
32
33 14 **Abstract**

34
35 15 1. In species providing extended parental care, one or both parents care for altricial young over
36
37 16 a period including more than one breeding season. We expect large parental investment and
38
39 17 long-term dependency within family units to cause high variability in life trajectories among
40
41 18 individuals with complex consequences at the population level. So far, models for estimating
42
43 19 demographic parameters in free-ranging animal populations mostly ignore extended parental
44
45 20 care, thereby limiting our understanding of its consequences on parents and offspring life
46
47 21 histories.

48
49
50 22 2. We designed a capture-recapture multi-event model for studying the demography of species
51
52 23 providing extended parental care. It handles statistical multiple-year dependency among
53
54 24 individual demographic parameters grouped within family units, variable litter size, and
55
56 25 uncertainty on the timing at offspring independence. It allows for the evaluation of trade-offs
57
58
59
60

1
2
3 26 among demographic parameters, the influence of past reproductive history on the caring
4
5 27 parent's survival status, breeding probability and litter size probability, while accounting for
6
7 28 imperfect detection of family units. We assess the model performance using simulated data,
8
9 29 and illustrate its use with a long-term dataset collected on the Svalbard polar bears (*Ursus*
10
11 *maritimus*).

12 30
13
14 31 3. Our model performed well in terms of bias and mean square error and in estimating
15
16 32 demographic parameters in all simulated scenarios, both when offspring departure probability
17
18 33 from the family unit occurred at a constant rate or varied during the field season depending on
19
20 34 the date of capture. For the polar bear case study, we provide estimates of adult and dependent
21
22 35 offspring survival rates, breeding probability and litter size probability. Results showed that the
23
24 36 outcome of the previous reproduction influenced breeding probability.

25
26 37 4. Overall, our results show the importance of accounting for i) the multiple-year statistical
27
28 38 dependency within family units, ii) uncertainty on the timing at offspring independence, and
29
30 39 iii) past reproductive history of the caring parent. If ignored, estimates obtained for breeding
31
32 40 probability, litter size, and survival can be biased. This is of interest in terms of conservation
33
34 41 because species providing extended parental care are often long-living mammals vulnerable or
35
36 42 threatened with extinction.

37
38 43
39
40 44 **Key-words:** apex predator, arctic ecosystem, Bayesian modeling, capture-recapture,
41
42 45 dependency among individuals, family structure, parental care, state uncertainty, timing at
43
44 46 independence.

45 47 46 48 **INTRODUCTION**

47
48 49 Parental care includes any pre-natal and post-natal allocation, such as feeding and protecting
49
50 50 the young, which benefits the offspring development and survival chances, thereby enhancing

1
2
3 51 the parent's reproductive success (Trivers 1972). Altricial mammals having offspring that need
4
5 52 to learn complex skills to ensure survival beyond independence, such as hunting, orientation,
6
7 53 or nest building, show extended parental care (hereafter EPC; Clutton-Brock 1991). It is defined
8
9 54 as a prolonged period, i.e. lasting more than one breeding season, over which one or both
10
11 55 parents care for one or several dependent young. This period typically lasts for several years
12
13 56 and can extend until lifelong maternal care in primates (Van Noordwijk 2012). For the
14
15 57 offspring, the quality and quantity of care received can have long-lasting effects on future
16
17 58 survival (e.g. Pavard and Branger 2012), social status (e.g. Shenk and Scelza 2012) and
18
19 59 reproduction (Royle et al. 2012). For the parent, investment in one offspring can compromise
20
21 60 its own condition or survival and/or its ability to invest in other offspring (siblings or future
22
23 61 offspring) (Williams 1966, Stearns 1992). It can indeed take several years during which a parent
24
25 62 caring for its offspring will not be available to reproduce, sometimes not until the offspring
26
27 63 have reached independence, e.g. on average 2.5 years for female polar bears (Ramsay and
28
29 64 Stirling 1988), 3.5 to 6 years for female African elephants (Lee and Moss 1986), and 9.3 years
30
31 65 for female Sumatran orangutans (Wich et al. 2004). The fitness costs of losing one offspring,
32
33 66 in terms of lost investment and skipped breeding opportunities, are particularly high if death
34
35 67 occurs near independence. We therefore expect EPC, through large parental investment and
36
37 68 multiple-year dependency among individuals within family units, to cause high variability in
38
39 69 life trajectories among individuals and family groups, in interbirth intervals depending on
40
41 70 offspring's fate, and consequently on lifetime reproductive success for the caring parent
42
43 71 (Clutton-Brock 1991).

51 72 Capture-recapture (CR) models allow studying species with complex demography in
52
53 73 the wild, e.g. by considering 'breeder' and 'non-breeder' reproductive states to estimate
54
55 74 breeding probabilities and status-specific demographic parameters while accounting for
56
57 75 imperfect detectability (e.g., Lebreton et al. 2009). One can distinguish between successful and
58
59
60

1
2
3 76 failed breeding events (e.g., Lagrange et al. 2017) and include varying litter or clutch size (e.g.,
4
5 77 Doligez et al. 2002) and memory effects (Cole et al. 2014), to investigate the costs of
6
7 78 reproduction on survival and future reproduction for species providing short-term parental care,
8
9
10 79 i.e. when offspring reach independence before the next breeding season (e.g., Yoccoz et al.
11
12 80 2002). Indeed, most CR models rely on the assumption of independence among individual CR
13
14 81 histories (Lebreton et al. 2009).

15
16
17 82 In the case of species providing EPC, one challenge stems from the multiple-year
18
19 83 dependency among individual's life histories within parent-offspring units. Only few attempts
20
21 84 have been made to tackle this issue when estimating demographic parameters, despite the fact
22
23 85 that species providing EPC are often among long-living mammals vulnerable or threatened with
24
25 86 extinction (e.g. polar bears, orangutans, elephants). Lunn et al. (2016) proposed to model CR
26
27 87 histories of mother-offspring units (instead of individuals) to consider the multiple-year
28
29 88 dependency of female breeding probability upon offspring survival status for polar bears in
30
31 89 Hudson Bay. However, in this model, offspring survival after 9 months is assumed independent
32
33 90 of mother survival. Lunn et al. (2016)'s model does therefore not handle multiple-year
34
35 91 dependency of offspring survival upon mother survival status, typical of species providing EPC.
36
37 92 In addition, because litter size is modeled separately, Lunn et al. (2016)'s model (also used in
38
39 93 Regehr et al. (2018)) does not permit to explore potential trade-offs among offspring traits and
40
41 94 parental phenotypic or demographic traits.

42
43
44
45
46 95 Another challenge involves dealing with uncertain timing at offspring independence,
47
48 96 when the offspring departs the caring parent(s) and becomes independent. When studying free-
49
50 97 ranging populations, this key life history event is rarely directly observed. When a mature
51
52 98 individual is observed without dependent offspring, it is often impossible to know if its
53
54 99 offspring have died or already departed its natal group. As a result, estimates of demographic
55
56 100 rates and trade-offs can be underestimated. Based on the analysis of mother-offspring units CR
57
58
59
60

1
2
3 101 histories, Couet et al. (2019) provided estimates of dolphin reproductive parameters corrected
4
5 102 for state uncertainty, but their model assumed a fixed age and timing at offspring independence.
6
7 103 Lunn et al. (2016)'s model included variable age at independence, but variability in the timing
8
9 104 at offspring independence was not fully dealt with. Demographic rates were corrected by the
10
11 105 average annual probability that independence occurred prior to sampling for all offspring, and
12
13 106 offspring survival was assumed independent of litter size (Regehr et al. 2018). In most species,
14
15 107 timing at offspring independence is variable and could depend on the offspring phenotypic traits
16
17 108 (e.g. body size in brown bears, Dahle and Swenson 2003), on parental traits (e.g. parent-
18
19 109 offspring conflict in kestrels, Vergara et al. 2010), social and mating system (e.g. helping
20
21 110 behavior in humans, Kramer 2005), or other environmental determinants (e.g. food supply,
22
23 111 Eldegard and Sonerud 2010). To our knowledge, no model is available to tackle both the issues
24
25 112 of multiple-year dependency among individuals and variable timing at offspring independence.
26
27 113 Because of these methodological challenges, the population-level consequences of EPC remain
28
29 114 to be understood, especially in free-ranging animal populations.
30
31
32
33
34

35 115 Here, we develop a CR model specifically for species providing EPC. It is designed to
36
37 116 handle multiple-years statistical dependency (until offspring independence) among individual
38
39 117 demographic parameters by modeling CR histories grouped within family units. The model
40
41 118 accounts for uncertain timing at offspring independence. In addition, our model allows for
42
43 119 variability in the number of offspring born and recruited at each breeding event, variable
44
45 120 offspring survival depending on number of siblings, and includes the influence of past
46
47 121 reproductive history on the caring parent's current status. Finally, estimates of survival rates,
48
49 122 breeding probability and litter size probability are corrected for imperfect detection possibly
50
51 123 depending upon family unit composition.
52
53
54

55
56 124 In what follows, we present the model, assess its performance using simulated data, and
57
58 125 illustrate its use with a long-term dataset collected on the Svalbard polar bears. Female polar
59
60

1
2
3 126 bears rely solely on stored fat reserves during pregnancy and the first three months of lactation,
4
5 127 before feeding and protecting litters of one to three young, usually during two more years
6
7 128 (Ramsay and Stirling 1988). They can lose more than 40% of body mass while fasting
8
9 129 (Atkinson and Ramsay 1995). In many areas, climate change and related sea ice decline impact
10
11 130 female bear condition and capacity to provide care for their young, with an associated decline
12
13 131 in reproductive output (Derocher et al. 2004; Stirling and Derocher, 2012, Laidre et al. 2020).
14
15 132 More insights into the species demography, such as the consequences of long-duration parental
16
17 133 care on mother and offspring life histories, could help our understanding of polar bear
18
19 134 population responses to environmental perturbations and extinction risks in future decades
20
21 135 (Hunter et al., 2010; Regehr et al., 2016).
22
23
24
25
26
27

28 137 **METHODS**

29 138 30 139 *1. Capture-recapture model for species providing EPC*

31 140 *1.1 Principle*

32
33 141 We develop a CR model in the multievent framework (Pradel 2005) that is also known as a
34
35 142 hidden Markov modeling framework (Gimenez et al. 2012). The principle is to relate the field
36
37 143 observations, called events, to the underlying demographic states of interest through the
38
39 144 observation process. Uncertainty on state assignment due to variable timing at offspring
40
41 145 independence is included in the observation process. In parallel, the state process describes the
42
43 146 transition rates between states from one year to the next. The transition rates correspond here
44
45 147 to the demographic parameters corrected for imperfect detection and state uncertainty. Below
46
47 148 we describe the general procedure to specify the model by defining the states and state-to-state
48
49 149 transition process, then the events and observation process. However, for simplicity, the events
50
51 150 and states are chosen to match the polar bear life cycle (i.e. females are captured in spring, alone
52
53
54
55
56
57
58
59
60

1
2
3 151 or together with a litter of one or two dependent offspring; offspring gain independence in the
4
5 152 year following their second birthday, and offspring cannot survive the loss of their mother
6
7 153 before gaining independence). The resulting model assumptions and its applicability to other
8
9 154 species are discussed below.
10
11
12
13

155

156 *1.2 Specification of states and state process*

157 One specificity of our model lies in the use of CR histories based on family groups instead of
18
19 158 individuals, which permits to include the multiple-year dependency among the caring parent
20
21 159 and dependent offspring's demographic rates and life history traits. Below, we describe the
22
23 160 specification of 24 unique states and 6 matrices needed to construct the model.
24
25

26 161 States correspond to the 'real' demographic states of the individuals composing the
27
28 162 family. We consider 12 states S , $S = \{J2, J3, SA4, SA5, A01, A02, A11, A12, AS1, AS2, A, D\}$, to
29
30 163 represent the polar bear life cycle (defined in Table 1). In addition, we specify 13 intermediary
31
32 164 states S' , $S' = \{J3, SA4, SA5, A11, A12, AS1, AS2, A0-, A1-, I/AS1, I/AS2, A, D\}$, and 16
33
34 165 intermediary states S'' , $S'' = \{J3, SA4, SA5, A11, A12, AS1, AS2, B/A0-, NB/A0-, B/A1-, NB/A1-,$
35
36
37 166 $B/AS, NB/AS, B/A, NB/A, D\}$, leading to a total of 24 unique states (defined in Table 1). The
38
39 167 specification of intermediary states is what permits to distinguish between failed and successful
40
41 168 breeders in the transition matrix to consider the influence of past reproductive history on
42
43 169 parameters (see below).
44
45
46
47
48

170

49 171 Table 1. Definition of the states and events used in the model to describe the polar bear life
50
51 172 cycle.
52
53

TYPE	CODE	DEFINITION
STATES	J2	2 y.o. independent juvenile female
	J3	3 y.o. independent juvenile female

60

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

SA4	4 y.o. independent subadult female
SA5	5 y.o. independent subadult female
A01	mother with one dependent cub of the year
A02	mother with two dependent cubs of the year
A11	mother with one dependent yearling
A12	mother with two dependent yearlings
AS1	successful female breeder with one two-year old offspring reaching independence
AS2	successful female breeder with two two-year old offspring reaching independence
A	adult female without dependent offspring
D	dead state
A0-	failed breeder, death of all offspring cubs of the year
A1-	failed breeder, death of all offspring yearlings
I/AS1	successful female breeder alone after departure of one independent offspring
I/AS2	successful female breeder alone after departure of two independent offspring
B/A0-	breeder following loss of a cub of the year litter
NB/A0-	non breeder following loss of a cub of the year litter
B/A1-	breeder following loss of a yearling litter
NB/A1-	non breeder following loss of a yearling litter
B/AS	breeder following successful reproduction
NB/AS	non breeder following successful reproduction
B/A	breeder given that previously without dependent offspring
NB/A	non breeder given that previously without dependent offspring
EVENTS	'1' capture of a 2yo independent female juvenile
	'2' capture of a 3yo independent female juvenile
	'3' capture of a 4yo independent subadult female

1		
2		
3		
4		
5		
6		
7		
8		
9		
10		
11		
12		
13		
14		
15		
16		
17		
18		
19		
20		
21		
22		
23		
24		
25		
26		
27		
28		
29		
30		
31		
32		
33		
34		
35		
36		
37		
38		
39		
40		
41		
42		
43		
44		
45		
46		
47		
48		
49		
50		
51		
52		
53		
54		
55		
56		
57		
58		
59		
60		

173

174 The model is conditioned upon first capture. The initial state vector, s_0 , gathers the
 175 proportions of family units in each state S at first capture, $s_0 = (\pi_1, \dots, \pi_{11}, 0)'$ (with $\pi_{12} = 0$
 176 for state D , because an individual must be alive at first capture).

177 The transition matrix, Ψ , describing all possible state-to-state transitions from spring
 178 one year (t) to spring the next year ($t+1$), is obtained as the matrix product of four matrices
 179 $\Psi = \Phi \cdot \Psi_1 \cdot \Psi_2 \cdot \Psi_3$. This decomposition is another particularity of our model which permits
 180 to estimate the relevant set of demographic parameters: independent juvenile, subadult and
 181 adult survival (matrix Φ), dependent offspring survival (matrix Ψ_1), breeding probabilities
 182 (matrix Ψ_2) and litter size probabilities (matrix Ψ_3), and potential trade-offs among them. This
 183 formulation of the transition matrix implies that litter size is conditioned upon breeding
 184 decision, itself conditioned upon offspring survival, itself conditioned upon survival of the
 185 caring parent to deal with the statistical dependency existing among individuals within family
 186 units.

187 The Φ matrix (eq. 1) describes transitions from each state S at time t (rows) to each state
 188 S after the occurrence of the survival process for independent individuals (columns):

189

	J2	J3	SA4	SA5	A01	A02	A11	A12	AS1	AS2	A	D
J2	φ_1	0	0	0	0	0	0	0	0	0	0	$1 - \varphi_1$
J3	0	φ_2	0	0	0	0	0	0	0	0	0	$1 - \varphi_2$
SA4	0	0	φ_3	0	0	0	0	0	0	0	0	$1 - \varphi_3$
SA5	0	0	0	φ_4	0	0	0	0	0	0	0	$1 - \varphi_4$
A01	0	0	0	0	φ_5	0	0	0	0	0	0	$1 - \varphi_5$
A02	0	0	0	0	0	φ_6	0	0	0	0	0	$1 - \varphi_6$
A11	0	0	0	0	0	0	φ_7	0	0	0	0	$1 - \varphi_7$
A12	0	0	0	0	0	0	0	φ_8	0	0	0	$1 - \varphi_8$
AS1	0	0	0	0	0	0	0	0	φ_9	0	0	$1 - \varphi_9$
AS2	0	0	0	0	0	0	0	0	0	φ_{10}	0	$1 - \varphi_{10}$
A	0	0	0	0	0	0	0	0	0	0	φ_{11}	$1 - \varphi_{11}$
D	0	0	0	0	0	0	0	0	0	0	0	1

(eq. 1)

190

191 In the Φ matrix, $\varphi_1, \dots, \varphi_{11}$ correspond to survival of immature independent (juveniles and
 192 subadults) and adult female bears.

193

194 The Ψ_1 matrix (eq.2) describes transitions from states S after the occurrence of the survival
 195 process for independent individuals (rows) to states S' after the occurrence of the offspring
 196 survival process (columns):

197

	J3	SA4	SA5	A11	A12	AS1	AS2	A0-	A1-	I/AS1	I/AS2	A	D
J2	1	0	0	0	0	0	0	0	0	0	0	0	0
J3	0	1	0	0	0	0	0	0	0	0	0	0	0
SA4	0	0	$1 - \kappa$	0	0	0	0	0	0	0	0	κ	0
SA5	0	0	0	0	0	0	0	0	0	0	0	1	0
A01	0	0	0	s_1	0	0	0	$1 - s_1$	0	0	0	0	0
A02	0	0	0	$2 \cdot s_2 \cdot (1 - s_2)$	s_2^2	0	0	$1 - s_2^2 - 2 \cdot s_2 \cdot (1 - s_2)$	0	0	0	0	0
A11	0	0	0	0	0	s_3	0	0	$1 - s_3$	0	0	0	0
A12	0	0	0	0	0	$2 \cdot s_4 \cdot (1 - s_4)$	s_4^2	0	$1 - s_4^2 - 2 \cdot s_4 \cdot (1 - s_4)$	0	0	0	0
AS1	0	0	0	0	0	0	0	0	0	1	0	0	0
AS2	0	0	0	0	0	0	0	0	0	0	1	0	0
A	0	0	0	0	0	0	0	0	0	0	0	1	0
D	0	0	0	0	0	0	0	0	0	0	0	0	1

(eq.2)

198

199 In the Ψ_1 matrix, κ is the probability of first reproduction at age 5, s is dependent offspring
 200 survival conditioned upon mother survival (s_1 for singleton cub, s_2 for singleton yearling; s_3
 201 for twin litter's individual cub, and s_4 for twin litter's individual yearling). Litter survival rates
 202 can be obtained from individual offspring survival rates (for singleton litters $l_{01} = s_1$ and $l_{11} =$

203 s_3 for cub and yearling respectively, and for twin litters $l_{02} = 1 - (1 - s_2^2 - 2 \cdot s_2 \cdot (1 - s_2))$
 204 and $l_{12} = 1 - (1 - s_4^2 - 2 \cdot s_4 \cdot (1 - s_4))$ for cubs and yearlings respectively).

205

206

207 The Ψ_2 matrix (eq.3) describes transitions from states S' after occurrence of the survival
 208 processes (rows) to states S'' depending on breeding decision (columns):

209

	J3	SA4	SA5	A11	A12	AS1	AS2	B/A0-	NB/A0-	B/A1-	NB/A1-	B/AS1	B/AS2	B/A	NB/A	D
J3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SA4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SA5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
A11	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
A12	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
A21	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
A22	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0 (eq.3)
A0-	0	0	0	0	0	0	0	β_1	$1 - \beta_1$	0	0	0	0	0	0	0
A1-	0	0	0	0	0	0	0	0	0	β_2	$1 - \beta_2$	0	0	0	0	0
I/AS1	0	0	0	0	0	0	0	0	0	0	0	β_3	$1 - \beta_3$	0	0	0
I/AS2	0	0	0	0	0	0	0	0	0	0	0	β_3	$1 - \beta_3$	0	0	0
A	0	0	0	0	0	0	0	0	0	0	0	0	0	β_4	$1 - \beta_4$	0
D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

210

211 Parameter β is breeding probability conditioned upon mother and offspring's survival status
 212 (β_1 following loss of a cub litter, β_2 loss of a yearling litter, β_3 for successful breeder, β_4 for
 213 female without dependent offspring at the beginning of the year).

214

215 The Ψ_3 matrix (eq. 4) describes transitions from states S'' after occurrence of the
 216 survival processes and breeding decision (rows) to states S at t+1 after determination of litter
 217 size for breeders (columns):

218

	J2	J3	SA4	SA5	A01	A02	A11	A12	AS1	AS2	A	D
J3	0	1	0	0	0	0	0	0	0	0	0	0
SA4	0	0	1	0	0	0	0	0	0	0	0	0
SA5	0	0	0	1	0	0	0	0	0	0	0	0
A11	0	0	0	0	0	0	1	0	0	0	0	0
A12	0	0	0	0	0	0	0	1	0	0	0	0
AS1	0	0	0	0	0	0	0	0	1	0	0	0
AS2	0	0	0	0	0	0	0	0	0	1	0	0 (eq.4)

219

220

B/A0-	0	0	0	0	γ_1	$1 - \gamma_1$	0	0	0	0	0	0
NB/A0-	0	0	0	0	0	0	0	0	0	0	1	0
B/A1-	0	0	0	0	γ_2	$1 - \gamma_2$	0	0	0	0	0	0
NB/A1-	0	0	0	0	0	0	0	0	0	0	1	0
B/AS1	0	0	0	0	γ_3	$1 - \gamma_3$	0	0	0	0	0	0
B/AS2	0	0	0	0	γ_3	$1 - \gamma_3$	0	0	0	0	1	0
B/A	0	0	0	0	γ_4	$1 - \gamma_4$	0	0	0	0	0	0
NB/A	0	0	0	0	0	0	0	0	0	0	1	0
D	0	0	0	0	0	0	0	0	0	0	0	1

219

220 Parameter γ is the probability of producing a singleton litter conditioned upon mother's and
 221 offspring's survival status and upon breeding decision (γ_1 following the loss a cub litter, γ_2 loss
 222 of a yearling litter, γ_3 for successful breeder, γ_4 for female without dependent offspring at the
 223 beginning of the year).

224

225 By modifying the constraints on parameters (i.e. setting them equal or different among
 226 states), the model can be used to investigate: i) the cost of reproduction on parent's survival (by
 227 comparing the ϕ s in matrix Φ), ii) the influence of litter size on individual offspring survival
 228 (by comparing s_1 to s_2 , and s_3 to s_4 in matrix Ψ_1) and on litter survival (by comparing l_{01} to l_{02}
 229 and l_{11} to l_{12}), iv) the influence of past reproductive history on breeding probability (by
 230 comparing the β s in matrix Ψ_2), and on litter size probability (by comparing the γ s in matrix Ψ_3
 231).

232

233 *1.3 Specification of events and observation process*

234 The events correspond to the observation or non-observation of family units in the field at each
 235 sampling occasion. Each event is coded depending on the number and age of the individuals
 236 composing the family. Here, we consider 12 possible events, $\Omega = \{1,2,3,4,5,6,7,8,9,10,11,12\}$
 237 to describe field observations for polar bears family groups (defined in Table 1).

238 In a multievent model, one specific event may relate to several possible states. Due to
 239 variable timing at offspring independence, a female successful breeder (state 'AS1' or 'AS2')

60

240 can be captured together with 1 or 2 two-year old dependent offspring (event ‘9’ or ‘10’) or
 241 without (event ‘11’) its two-year old offspring or not captured (event ‘12’) depending on i)
 242 whether the offspring has already departed from its mother at the time of capture and ii) on
 243 capture probability. To include uncertainty on state assignment due to variable timing at
 244 offspring independence, we decompose the observation process into two event matrices, E_1 and
 245 E_2 , modeling respectively departure probability (α) and capture probability (p).

246 The E_1 matrix (eq. 5), relates the states S to the possible observations at the time of
 247 capture, $O = \{1,2,3,4,5,6,7,8,9,10,11,12\}$ (same code as the events, see Table 1), through the
 248 departure probability, denoted α .

	‘1’	‘2’	‘3’	‘4’	‘5’	‘6’	‘7’	‘8’	‘9’	‘10’	‘11’	‘12’
J2	1	0	0	0	0	0	0	0	0	0	0	0
J3	0	1	0	0	0	0	0	0	0	0	0	0
SA4	0	0	1	0	0	0	0	0	0	0	0	0
SA5	0	0	0	1	0	0	0	0	0	0	0	0
A01	0	0	0	0	1	0	0	0	0	0	0	0
A02	0	0	0	0	0	1	0	0	0	0	0	0
A11	0	0	0	0	0	0	1	0	0	0	0	0
A12	0	0	0	0	0	0	0	1	0	0	0	0
AS1	0	0	0	0	0	0	0	0	$1-\alpha_{i,d}$	0	$\alpha_{i,d}$	0
AS2	0	0	0	0	0	0	0	0	$2 \cdot \alpha_{i,d} \cdot (1 - \alpha_{i,d})$	$1 - 2 \cdot \alpha_{i,d} \cdot (1 - \alpha_{i,d}) - \alpha_{i,d}^2$	$\alpha_{i,d}^2$	0
A	0	0	0	0	0	0	0	0	0	0	1	0
D	0	0	0	0	0	0	0	0	0	0	0	1

249
 250 Here, $\alpha_{i,d}$ is the departure probability of a two-year old individual offspring belonging to family
 251 unit i on its date of capture d. The relationship between date of capture and departure probability
 252 is species-specific and either assessed from prior knowledge on the species’ biology or field
 253 data (see Appendix 2). Here we assume that siblings’ timing at independence can, but does not
 254 have to, occur independently (if both offspring can only depart the family on the same date, the
 255 transition from state ‘AS2’ to event ‘9’ should be set to 0).

256 The second event matrix, E_2 , (eq. 6) relates all possible observations at the time of
 257 capture O to the events, Ω , actually observed in the field through the state-dependent capture
 258 probability, denoted p_s .

	1'	2'	3'	4'	5'	6'	7'	8'	9'	10'	11'	12'
1'	p_1	0	0	0	0	0	0	0	0	0	0	$1 - p_1$
2'	0	p_2	0	0	0	0	0	0	0	0	0	$1 - p_2$
3'	0	0	p_3	0	0	0	0	0	0	0	0	$1 - p_3$
4'	0	0	0	p_4	0	0	0	0	0	0	0	$1 - p_4$
5'	0	0	0	0	p_5	0	0	0	0	0	0	$1 - p_5$
6'	0	0	0	0	0	p_6	0	0	0	0	0	$1 - p_6$
7'	0	0	0	0	0	0	p_7	0	0	0	0	$1 - p_7$
8'	0	0	0	0	0	0	0	p_8	0	0	0	$1 - p_8$
9'	0	0	0	0	0	0	0	0	p_9	0	0	$1 - p_9$
10'	0	0	0	0	0	0	0	0	0	p_{10}	0	$1 - p_{10}$
11'	0	0	0	0	0	0	0	0	0	0	p_{11}	$1 - p_{11}$
12'	0	0	0	0	0	0	0	0	0	0	0	1

259
 260
 261 The composite event matrix, E , which relates the events to the states, is obtained as the
 262 matrix product of these two matrices $E = E_1 \cdot E_2$. Because the model is conditioned upon first
 263 capture, the initial event vector, e_0 , takes the value of 1 for all events (except of 0 for the event
 264 '12' corresponding to a non-observation).

266 1.4 Applicability to other species

267 The model described above matches the Svalbard polar bear life cycle. The model therefore
 268 assumes that care is provided by the mother only, to one or two offspring (we modelled triplets
 269 as twins because there were just 8 litters of triplets in the data), for a duration of two years
 270 maximum. Offspring under age 2 cannot survive if the mother dies. A mother caring for
 271 offspring cannot mate and produce a second litter. Independent males (that have already
 272 departed from the family unit) are not included in the model.

1
2
3 273 To apply the model to other species, one should modify the number of events and states
4
5 274 to match the species life cycle (depending on age at sexual maturity, number of care providers,
6
7 275 maximum litter size, duration of parental care) but the number of matrices should remain the
8
9 276 same. For example, modeling a hypothetical species similar to polar bears but in which both
10
11 277 males and females care for offspring would increase the number of unique states from 24 to 42
12
13 278 (8 states for immature females and males, 21 states for dependent offspring cared for by both
14
15 279 parents, just the mother in case of father loss, or just the father in case of mother loss). Such a
16
17 280 model could be used to assess the influence of father versus mother loss on litter size, offspring
18
19 281 survival and father and/or mother breeding probabilities. After defining the states and events,
20
21 282 one should modify the shape of the relationship between departure probability and date of
22
23 283 capture to match the species life cycle. In species like primates or wolves, departure from the
24
25 284 family unit can occur throughout the year, at a more or less constant rate depending on the
26
27 285 season, while it occurs only between February and May in polar bears due to environmental
28
29 286 constraints. In addition, the influence of individual traits such as age or body weight, or
30
31 287 environmental variables such as temperature, can be included in the model under the form of
32
33 288 individual or temporal covariates (Pollock 2002). Other specificities related to data collection
34
35 289 can be included in a similar way, such as trap effects (Pradel and Sanz-Aguilar 2012) or latent
36
37 290 individual heterogeneity by using mixture of distributions or random effects (Gimenez et al.
38
39 291 2018). Guidance to fit the model in a Bayesian framework in program Jags for real and
40
41 292 simulated data are provided in Appendices 1 and 2.
42
43
44
45
46
47
48
49

50
51 293
52 294 *Simulation study*

53
54 295 The simulation study was aimed at evaluating the performance of our model to estimate
55
56 296 demographic parameters under various assumptions about the timing at offspring independence
57
58 297 (constant versus seasonal departure rate) and various degrees of capture probability (low $p=$
59
60

1
2
3 298 0.25, high $p=0.7$), for a medium-size data set ($T=15$ sampling occasions, with $R=80$ newly
4
5 299 marked at each occasion in equal proportion among the 11 alive states).
6

7 300 We simulated data for a virtual long-lived mammal species mimicking the polar bear
8
9 301 using the model described in box 1. We used $\varphi = 0.9$ for independent female bear survival
10
11 302 (aged 2+ y.o.), $s_1 = l_{01} = 0.6$ for singleton cub survival, $s_2 = 0.55$ for twin litter's cub
12
13 303 survival (corresponding to twin litter survival $l_{02} = 0.7975$), $s_3 = 0.8$ for singleton yearling
14
15 304 survival and $s_4 = 0.75$ for twin litter's yearling survival (corresponding to litter survival l_{12}
16
17 305 $= 0.94$). Offspring survival rates were conditioned upon mother survival. If a mother dies, its
18
19 306 dependent offspring had no chances of surviving. For breeding probabilities, we used $\beta_1 = 0.5$
20
21 307 , $\beta_2 = 0.7$, $\beta_3 = 0.9$ and $\beta_4 = 0.8$. For litter size probabilities, we used $\gamma_1 = 0.4$, $\gamma_2 = 0.5$, γ_3
22
23 308 $= 0.6$ and $\gamma_4 = 0.7$. We set $\kappa = 0$ and assumed that females had their first litter at age 6 or
24
25 309 older.
26
27
28
29
30

31 310 We assumed that captures occurred each year between mid-March to end of May (day
32
33 311 of the year $d=80$ to $d=130$). For each capture event, date of capture was randomly sampled from
34
35 312 the distribution of the polar bear data dates of capture (see Appendix 1). In the constant scenario,
36
37 313 we assumed that two-year old bears reached independence at a constant departure rate (α)
38
39 314 during the field season, independently of the date of capture. We chose an intermediate value
40
41 315 of $\alpha = 0.5$ (if independence occurred always after the field season, $\alpha = 0$, versus always before
42
43 316 the field season, $\alpha = 1$). In the seasonal scenario, we assumed that departure rate varied with
44
45 317 date of capture (d) following a logistic relationship (regression coefficients were estimated from
46
47 318 the polar bear data, see Appendix 2). Most of the two-year old offspring were captured with
48
49 319 their mother at the beginning of the field season, while departure probability increased
50
51 320 logistically up to 80% at the end of the field season.
52
53
54
55
56
57
58
59
60

1
2
3 321 We simulated 100 CR datasets for each of the 4 scenarios (S1: low detection with constant
4
5 322 departure, S2: low detection with seasonal departure, S3: high detection with constant
6
7 323 departure, S4: high detection with seasonal departure). We simulated the data using program
8
9 324 R. We fitted the model using program jags called from R (Plummer 2016). For each
10
11 325 parameter and each dataset, we calculated absolute bias as $\hat{B} = \hat{\theta} - \theta$, and root mean squared
12
13 326 error as $RMSE = \sqrt{(\hat{\theta} - \theta)^2}$, with θ the parameter used to simulate the data and $\hat{\theta}$ the mean
14
15 327 value of the estimated parameter. Appendix 1 containing guidance, R code and files to
16
17 328 simulate data and fit the model is available on GitHub at
18
19 329 https://github.com/SCubaynes/Appendix1_extendedparentalcare.

330

331 *Case study: Polar bears in Svalbard*

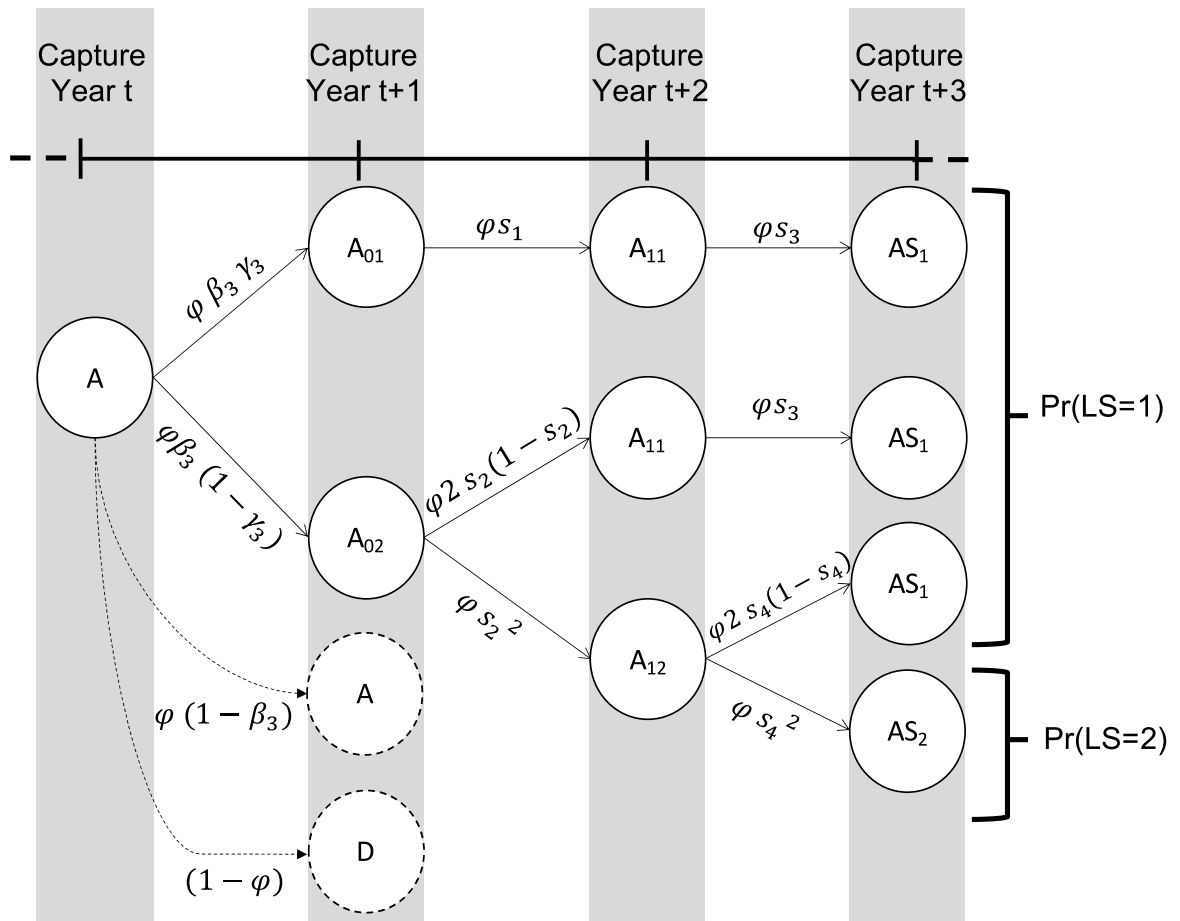
332 In polar bears, care of offspring is provided by the mother only (Amstrup, 2003). Males
333 were therefore discarded from our analysis. Adult female polar bears mate in spring (February
334 to May, Amstrup 2003), and in Svalbard usually have their first litter at the age of six years, but
335 some females can have their first litter at five years (Derocher 2013). They have delayed
336 implantation where the egg attaches to the uterus in autumn (Ramsay and Stirling 1988). A
337 litter with small cubs (ca 600 grams) is born around November to January, in a snow den that
338 the mothers dig out in autumn, and where the family stay 4-5 months. The family usually
339 emerges from the den in March-April, and stay close to the den while the cubs get accustomed
340 to the new environment outside their home, for a few days up to 2-3 weeks (Hansson and
341 Thomassen 1983). Litter size in early spring vary from one to three, with two cubs being most
342 common, three cubs in most areas being rare, and commonly around one out of three litters
343 having one cub only (Amstrup 2003). In Svalbard, polar bears become independent from their
344 mother shortly after their second birthday (average age at independence is 2.3). Two-year old
345 bears typically depart from the mother in spring (between mid-March to end of May), when the

1
2
3 346 mother can mate again. There is only one anecdotal record of a yearling alive without his
4
5 347 mother. Because the field season can last for several weeks, some two-year-old bears were
6
7 348 captured together with their mother and others were already independent at the time of capture.
8
9
10 349 The minimum reproductive interval for successful Barents Sea polar bears is 3 years. On the
11
12 350 contrary, loss of a cub litter shortly after den emergence may mean the mother can produce new
13
14 351 cubs in winter the same year (Ramsay and Stirling 1988).

15
16
17 352 Bears captured in Svalbard are shown to be a mixture of resident and pelagic bears
18
19 353 (Mauritzen et al. 2002). To focus on the resident population, independent bears captured only
20
21 354 once were not included in our analysis. We therefore analyzed $N = 158$ encounter histories of
22
23 355 resident polar bear family units captured each spring after den emergence between day 80 to
24
25 356 130 (mid-March to mid-May), from 1992 to 2019, in Svalbard. It corresponds to 81 capture
26
27 357 events of juvenile and subadults, 231 cubs, 96 yearling, 23 dependent two-year old, and 444
28
29 358 captures of adult females. Polar bears were caught and individually marked as part of a long-
30
31 359 term monitoring program on the ecology of polar bears in the Barents Sea region (Derocher
32
33 360 2005). All bears one year or older were immobilized by remote injection of a dart (Palmer Cap-
34
35 361 Chur Equipment, Douglasville, GA, USA) with the drug Zoletil® (Virbac, Carros, France)
36
37 362 (Stirling et al. 1989). The dart was fired from a small helicopter (Eurocopter 350 B2 or B3),
38
39 363 usually from a distance of about 4 to 10 meters. Cubs of the year were immobilized by injection
40
41 364 with a syringe. Cubs and yearlings were highly dependent on their mother; therefore, they
42
43 365 remained in her vicinity and were captured together with their mother. A female captured alone
44
45 366 was considered to have no dependent offspring alive. Death of the cubs could have occurred in
46
47 367 the den or shortly after den emergence but before capture. Hereafter, estimated cub survival
48
49 368 thus refers to survival after capture. Infant mortality occurring before capture will be assigned
50
51 369 to a reduced litter size. Because only 3% of females were observed with 3 offspring, we
52
53 370 analyzed jointly litters of twins with triplets.
54
55
56
57
58
59
60

1
2
3 371 We built the model described above with 12 states and 12 events to describe the life
4
5 372 cycle (Table 1). Preliminary analyses suggested that mother survival did not vary according to
6
7
8 373 state, we therefore constrained parameter φ to be equal among all states in matrix Φ . To avoid
9
10 374 identifiability issues due to a relatively small sample size, we assumed breeding probability
11
12 375 and litter size probability did not vary between successful breeders (states AS1 and AS2) and
13
14 376 female without dependent offspring (state A) by setting $\beta_3 = \beta_4$ and $\gamma_3 = \gamma_4$. We also
15
16
17 377 assumed that litter size probability did not vary among failed breeders (loss of a cub versus a
18
19 378 yearling litter), by setting $\gamma_1 = \gamma_2$. We could not assess formally the fit of our model because
20
21
22 379 no test is yet available for multievent models. However, the multi-state version of our model
23
24 380 (without uncertainty on timing at independence) fitted the data adequately. Adding a level of
25
26 381 complexity should make the model even more adequate.

27
28
29 382 Using the conditional probabilities estimated in the model, we calculated the net
30
31 383 probability for a female to raise none, $\Pr(X=0)$, one, $\Pr(X=1)$, or two offspring, $\Pr(X=2)$ to
32
33 384 independence over a 3-year period (details are provided in Appendix 2).
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



385

386 Figure 1: Life history events with associated probabilities of raising one ($X=1$) or two ($X=2$)
 387 offspring to independence over a 3 years period for a female polar bear alive and without
 388 dependent offspring at the beginning of the period (state A). State A01 represents a female with
 389 one dependent cub of the year, A02 with two dependent cubs of the year, A11 with one
 390 dependent yearling, A12 with two dependent yearlings, AS1 a successful female breeder with
 391 one two-year old offspring reaching independence and AS2 a successful female breeder with
 392 two two-year old offspring reaching independence. Parameter φ is adult survival, β_3 is breeding
 393 probability of a female without dependent offspring, γ_3 is the probability of a singleton litter,
 394 s_1 is cub and s_2 is yearling survival in a singleton litter, s_3 is cub and s_4 yearling survival in a
 395 twin litter.

396

397 We considered adult females without dependent offspring at the beginning of the time period,
 398 so that we have:

$$399 \Pr(X=1) = \varphi^3 \cdot \beta_3 \cdot [\gamma_3 \cdot s_1 \cdot s_3 + (1 - \gamma_3) \cdot (2 s_2(1 - s_2) \cdot s_3 + s_2^2 \cdot 2 s_4(1 - s_4))],$$

$$400 \Pr(X=2) = \varphi^3 \cdot \beta_3 \cdot (1 - \gamma_3) \cdot s_2^2 \cdot s_4^2,$$

1
2
3 401 $\Pr(X = 0) = 1 - \Pr(X = 1) - \Pr(X = 2)$.
4
5

6 402 Appendix 2 containing guidance, R code, data files to fit the model to the polar bear data, and
7
8 403 additional results is available on GitHub at
9
10 404 https://github.com/SCubaynes/Appendix2_extendedparentalcare.
11
12
13

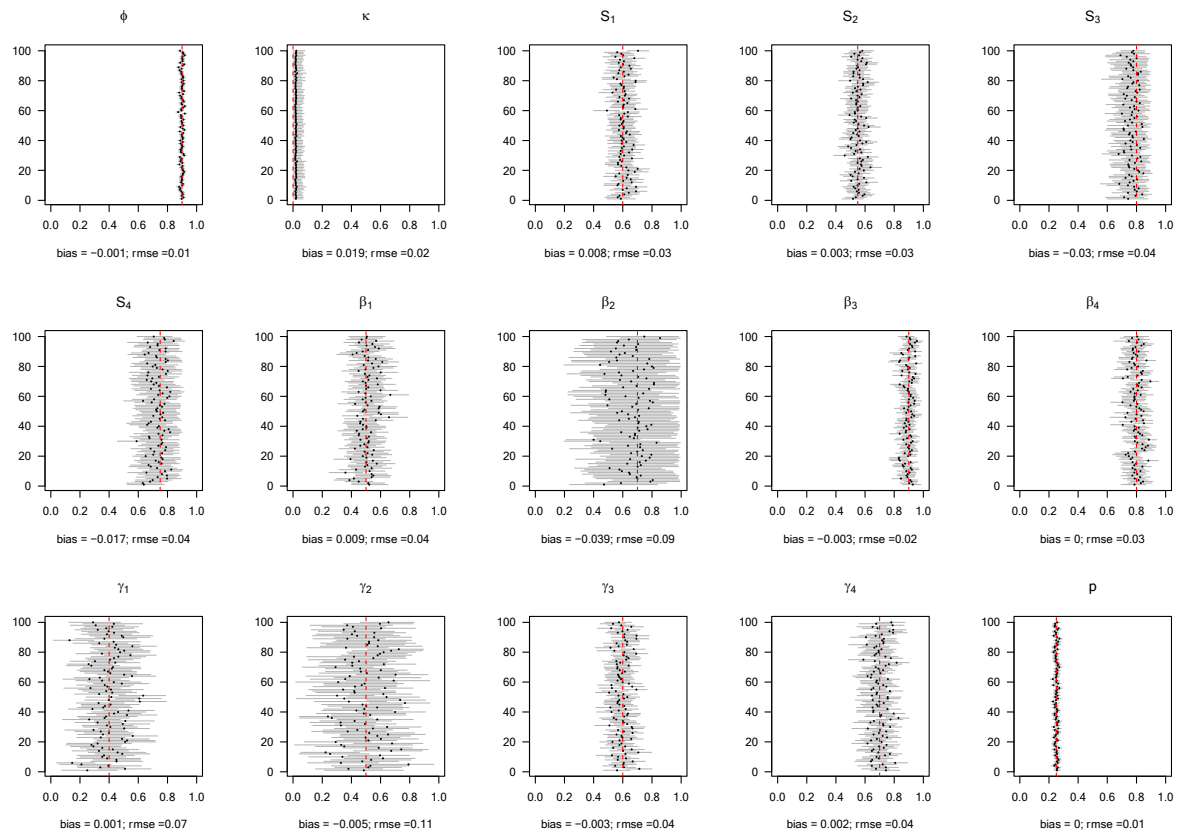
14
15 405

16 406 **RESULTS**

17 407 *Model performance evaluated on simulated datasets*

18
19 408 Model performance was satisfying and comparable in all 4 simulated scenarios (S1 with low
20
21 409 detection and constant departure, S2 with low detection and seasonal departure, S3 with high
22
23 410 detection and constant departure and S4 with high detection and seasonal departure), with low
24
25 411 average bias ($B_{S1} = -0.000$, $B_{S2} = -0.004$, $B_{S3} = -0.004$, $B_{S4} = -0.003$) and root-mean-
26
27 412 square error ($rmse_{S1} = 0.042$, $rmse_{S2} = 0.041$, $rmse_{S3} = 0.031$ and $rmse_{S4} = 0.031$) (see
28
29 413 Appendix 1 for details).
30
31
32
33
34

35 414 For most parameters, bias was very low, $B < 0.02$, except for parameters β_2 in scenarios
36
37 415 S2, S3 and S4 ($-0.04 < B < -0.03$) and s_3 in scenario S2 ($B = -0.03$), $rmse < 0.05$, except for
38
39 416 parameters β_2 , γ_1 and γ_2 ($0.05 < rmse < 0.07$). For these three parameters, precision was lower
40
41 417 in the two scenarios with low detection (see Appendix 1). Estimates obtained for the scenario
42
43 418 mimicking the polar bear study case (S2: low detection and seasonal departure) are provided in
44
45 419 Figure 2.
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



420

421 Figure 2. Performance of the model on simulated data with low detection with seasonal
 422 departure (scenario S2). For each of the 100 simulated data sets, we displayed the mean (circle)
 423 and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of
 424 the parameter is given by the vertical dashed red line. The estimated absolute bias and root-
 425 mean-square error are provided in the legend of the X-axis for each parameter. Regarding
 426 notations, ϕ stands for juvenile, subadult and adult survival, κ is the probability of first
 427 reproduction at age 5, s is dependent offspring survival conditioned upon mother survival (s_1
 428 and s_2 for singleton cub resp. yearling; s_3 and s_4 for twin litter's cub resp. yearling), β is
 429 breeding probability conditioned upon mother and offspring survival status (β_1 following loss
 430 of a cub litter, β_2 loss of a yearling litter, β_3 for successful breeder, β_4 for female without
 431 dependent offspring), γ is the probability of producing a singleton litter conditioned upon
 432 mother's and offspring's survival status and upon breeding decision (γ_1 following loss of a cub
 433 litter, γ_2 loss of a yearling litter, γ_3 for successful breeder, γ_4 for female without dependent
 434 offspring), p is detection probability.

435

436 *Case study: Polar bear demography*

60

437 Departure probability was about 40% at the end of March and reached 80% at mid-May
 438 (Appendix 2). About half of the two-year old bears had departed their mother at the time of
 439 capture. Estimates of demographic parameters are provided in Table 2 (more results are
 440 provided in Appendix 2). Independent female (aged 2+) survival was high (0.93). Individual
 441 offspring survival rates, conditioned upon mother survival, did not vary significantly with litter
 442 size for cubs or yearlings. Average yearling survival was lower for singleton (0.67) than for
 443 litters of twin (0.80), although the 95% credible intervals did overlap. Concerning litter survival
 444 conditioned upon mother survival, it was higher for twin compared to singleton, for both cubs'
 445 and yearlings' litters. A small proportion of females, about 12%, started to reproduce (i.e.
 446 produced a litter that survived at least until the first spring) at 5 y.o. Outcome of the previous
 447 reproduction influenced breeding probability. Breeding probability following the loss of a cub
 448 litter during the year (after capture) was low, about 10%, while it was about 50-60% for female'
 449 successful breeders or without dependent offspring at the beginning of the year or after the loss
 450 of a yearling litter. Detection probability was relatively low, about 0.25 (0.22 - 0.27). At first
 451 capture, 37% were independent juvenile or subadult females, 18% were adult females alone,
 452 28% were adult females with one or two cubs, 12% with one or two yearlings and 5% with two-
 453 year old bears.

454
 455 Table 2: Parameter estimates. Means are given with 95% credible intervals (CI). Dependent
 456 offspring (cub age <1 y.o., yearling 1 y.o.) survival and breeding probabilities are conditioned
 457 upon mother survival, litter size probability of producing a singleton is as well conditioned upon
 458 breeding decision.

Parameter	Notation	Mean	Standard error	95% CI
Survival of female juveniles (2yo,3yo) subadults (4yo, 5yo) and adults (5+ yo)	φ	0.93	0.01	0.92 – 0.95
Cub survival (<1yo)				

- singleton (=litter survival)	$s_1 = l_{01}$	0.54	0.10	0.34 - 0.72
- litter of 2 (averaged individual survival)	s_2	0.51	0.05	0.41 - 0.62
Yearling survival (1yo)				
- Singleton (=litter survival)	$s_3 = l_{11}$	0.67	0.11	0.46 - 0.87
- litter of 2 (averaged individual survival)	s_4	0.80	0.09	0.59 - 0.93
Litter survival for twin litters				
- cubs	l_{02}	0.76	0.05	0.65 - 0.85
- yearlings	l_{12}	0.95	0.04	0.83 - 0.99
Probability of first reproduction at 5 yo (mate at 4yo)				
Breeding probability				
- following loss of a cub litter	β_1	0.09	0.06	0.01 - 0.23
- following loss of a yearling litter	β_2	0.58	0.21	0.19 - 0.96
- of successful female breeders or previously without dependent offspring	$\beta_3 = \beta_4$	0.52	0.04	0.43 - 0.61
Probability of singleton litter				
- following loss of a cub or yearling litter	$\gamma_1 = \gamma_2$	0.35	0.17	0.07 - 0.71
- of successful females breeders or previously without dependent offspring	$\gamma_3 = \gamma_4$	0.40	0.05	0.30 - 0.44
Capture probability				
	p	0.25	0.01	0.22 - 0.27

459

460 Over a 3 years period, the probability to successfully raise one offspring to independence
 461 for a female polar bear, alive and without dependent offspring at the beginning of the period,
 462 was on average 0.29 (0.20-0.38) and 0.04 (0.02-0.07) to raise two offspring to independence.
 463 The probability of failed breeding (no offspring successfully reached independence) over this
 464 period was high, about 0.67 (0.57-0.76). Note that this calculation includes breeding
 465 probability, and therefore does not reflect offspring survival until independence (see Method
 466 section).

467

60

468 **DISCUSSION**

469 Overall, our model performed well in estimating all demographic parameters in all the
470 simulated scenarios. A multievent approach is a promising tool to deal with uncertainty on the
471 timing at offspring independence both when departure probability was constant or varied within
472 the field season. Estimates obtained for adult and offspring survival, probability of sexual
473 maturation, breeding probability (except after the loss of a yearling litter), litter size
474 probabilities and detection probability were unbiased in most simulated scenarios. Precision
475 was satisfying in most cases, but it was lower for breeding probability after the loss of a yearling
476 litter and for litter size probabilities of failed breeders, especially in scenarios with low detection
477 (Appendix 1). These specific parameters should therefore be interpreted with caution for the
478 study case. In our simulations, T=15 sampling occasions appeared sufficient to obtain satisfying
479 estimates for most parameters. In the polar bear data, there were few recaptures of females on
480 subsequent years due to relatively low detection rate. As a result, preliminary analyses
481 suggested a potential confusion between these parameters. We dealt with this issue by including
482 a biologically realistic constraint on prior distributions, stating that cub survival was lower than
483 that of yearling survival (Amstrup and Durner, 1995) which was enough to ensure parameter
484 estimability. Inference in a Bayesian framework is useful in this regard, because it allows for
485 the inclusion of prior information when available (McCarthy and Masters 2005) to improve the
486 estimation of model parameters.

487 For polar bears, we showed that outcome of the previous breeding event influenced
488 breeding probability. Reduced offspring survival one year, for example due to poor
489 environmental conditions (Derocher et al. 2004), might therefore increase intervals between
490 successful reproduction through reduced breeding probability the next year (Wiig 1998). This
491 means that by ignoring multiple-year dependency among mother and offspring, classical
492 models can underestimate reproductive intervals, therefore risking to overestimate the

1
2
3 493 population growth rate. However, the biological relevance of our model is currently limited,
4
5 494 because we ignored temporal and individual heterogeneity among females in the model.
6
7
8 495 Survival rates for independent female bears (0.93) were close to an earlier study for the same
9
10 496 population (0.96), based on telemetry data (Wiig 1998). Our results may overestimate
11
12 497 dependent offspring survival because we focused on resident bears captured more than once.
13
14 498 Wiig (1998) results indicated that females in Svalbard went into den on average every second
15
16 499 year (while successful breeding means denning on a three-year interval), which seems coherent
17
18
19 500 with our results (about 33% chances of successful reproduction over a three-year period).

22
23 501 Here, we proposed a general model structure that can be applied to other species
24
25 502 providing EPC. The originalities of our approach lie in using family structure to define
26
27 503 statistical units in our model, and the inclusion of variable timing at offspring independence.
28
29 504 Using families instead of individuals allows for the inclusion of dependency among individuals
30
31
32 505 over multiple-years and therefore the evaluation of trade-offs and correlations between
33
34 506 offspring's and parents' life history parameters. Our model could be used, for example, to
35
36 507 evaluate the population-level consequences of positive or negative correlation between parents'
37
38 508 and offspring's traits (e.g. food sharing among group members Lee 2008; or parent-offspring
39
40 509 conflict Kölliker et al. 2013). In the case of social species (e.g. primates, elephants, orcas,
41
42 510 wolves), several adults often play a role in caring for offspring. In addition, females often give
43
44 511 birth to new offspring while still caring for older offspring and, above a certain age, adolescent
45
46 512 dependent offspring can survive despite the loss of their mother and gain independence at
47
48 513 various ages. In such cases, the number of states to represent all possible family units'
49
50 514 composition can rapidly increase, leading to potential computational challenges to deal with
51
52 515 huge matrices. One solution is to use sparse matrices to store the data efficiently and optimize
53
54 516 matrix calculations. Above this level of complexity, an alternative solution is to limit the
55
56 517 number of states by simplifying the life cycle depending on the question of interest (e.g.
57
58
59
60

1
2
3 518 focusing on mother and maternal grand-mother considering only one litter, or focusing on
4
5 519 mother caring alone for one or more litters). For polar bears specifically, future analyses will
6
7 520 integrate in the model the effect of female age on survival and reproductive success (Atkinson
8
9 521 and Ramsay 1995; Folio et al. 2019) and influence of climatic variables on body weight and
10
11 522 demography (Derocher et al. 2004; Stirling and Derocher 2012) as individual and
12
13 523 environmental covariates in a regression-like framework. Our model could then be used to
14
15 524 provide population predictions of the demographic response of the Barents Sea polar bear
16
17 525 population under climate change (Hunter et al., 2010; Regehr et al., 2016, 2018, Laidre et al.
18
19 526 2020).

20
21
22
23
24
25 527 Acknowledgements : This study was supported by World Wildlife Fund. We thank Magnus
26
27 528 Andersen for his participation in fieldwork, and Thor Larsen for initiating the monitoring. SC
28
29 529 is supported by a grant from the Agence Nationale de la Recherche (ANR-18-CE02-0011,
30
31 530 MathKinD).

32
33
34
35 531 Data Accessibility Statement : Authors agree to archive the data used in this manuscript in a
36
37 532 publicly accessible repository such as Dryad and Github upon acceptance of the manuscript
38
39 533 (together with R scripts to run the model and the simulation study).

40
41
42
43 534 Authors' contributions: SC, OG, NY and RP conceived the ideas and designed methodology;
44
45 535 JA, RAI and ØW collected the data; SC analysed the data; SC led the writing of the manuscript.

46
47 536 All authors contributed critically to the drafts and gave final approval for publication.

48
49
50
51 537
52
53
54
55
56
57
58
59
60

1
2
3 538 **Bibliography**
4
5

6 539 Amstrup, S. C., & DeMaster, D. P. (2003). Polar bear, *Ursus maritimus*. *Wild mammals of*
7
8
9 540 *North America: biology, management, and conservation*, 2, 587-610.

10
11 541 Amstrup, S. C., & Durner, G. M. (1995). Survival rates of radio-collared female polar bears
12
13
14 542 and their dependent young. *Canadian Journal of Zoology*, 73, 1312–1322.
15
16 543 doi:10.1139/z95-155

17
18
19 544 Atkinson, S. N., & Ramsay, M. A. (1995). The Effects of Prolonged Fasting of the Body
20
21 545 Composition and Reproductive Success of Female Polar Bears (*Ursus maritimus*).
22
23 546 *Functional Ecology*, 9(4), 559. doi:10.2307/2390145

24
25
26 547 Clutton-Brock, T. H. (1991). *The evolution of parental care*. Princeton: Princeton University
27
28 548 Press.

29
30
31 549 Cole, D. J., Morgan, B. J. T., McCrea, R. S., Pradel, R., Gimenez, O., & Choquet, R. (2014).
32
33 550 Does your species have memory? Analyzing capture-recapture data with memory models.
34
35 551 *Ecology and Evolution*, 4(11), 2124-2133.

36
37
38 552 Couet, P., Gally, F., Canonne, C., & Besnard, A. (2019). Joint estimation of survival and
39
40 553 breeding probability in female dolphins and calves with uncertainty in state assignment.
41
42 554 *Ecology and evolution*, 9(23), 13043-13055.

43
44
45 555 Dahle, B., & Swenson, J. E. (2003). Factors influencing length of maternal care in brown bears
46
47 556 (*Ursus arctos*) and its effect on offspring. *Behavioral Ecology and Sociobiology*, 54(4),
48
49 557 352-358.

50
51
52
53 558 Derocher A., & Stirling, I. (1994). Age-specific reproductive performance of female polar bears
54
55 559 (*Ursus maritimus*). *Journal of Zoology*, 234(4), 527–536.

56
57
58 560 Derocher, A. ., Lunn, N. ., & Stirling, I. (2004). Polar bears in a warming climate. (*Ursus*
59
60

- 1
2
3 561 maritimus). *Integrative and Comparative Biology*, 44(2), 163–176.
4
5
6 562 Derocher, A.E., 2005. Population ecology of polar bears at Svalbard, Norway. *Population*
7
8 563 Ecology, 47(3), pp.267-275.
9
10
11 564 Derocher, A. (2013). Polar bears: a complete guide to their biology and behavior. *Choice*
12
13 565 *Reviews Online*, 49(12), 49-6887-49–6887. doi:10.5860/choice.49-6887
14
15
16 566 Doligez, B., Clobert, J., Pettifor, R. A., Rowcliffe, M., Gustafsson, L., Perrins, C. M., &
17
18 567 McCleery, R. H. (2002). Costs of reproduction: Assessing responses to brood size
19
20 568 manipulation on life-history and behavioural traits using multi-state capture-recapture
21
22 569 models. *Journal of Applied Statistics*, 29(1–4), 407–423.
23
24
25 570 Eldegard, K., & Sonerud, G. A. (2010). Experimental increase in food supply influences the
26
27 571 outcome of within-family conflicts in Tengmalm’s owl. *Behavioral Ecology and*
28
29 572 *Sociobiology*, 64(5), 815-826.
30
31
32
33 573 Folio, D.M., Aars, J., Gimenez, O., Derocher, A.E., Wiig, Ø. and Cubaynes, S., (2019). How
34
35 574 many cubs can a mum nurse? Maternal age and size influence litter size in polar bears.
36
37 575 *Biology letters*, 15(5), p.20190070.
38
39
40 576 Gimenez, O., Lebreton, J.-D., Gaillard, J.-M., Choquet, R. and R. Pradel (2012). Estimating
41
42 577 demographic parameters using hidden process dynamic models. *Theoretical Population*
43
44 578 *Biology* 82, 307-316.
45
46
47 579 Gimenez, O., Cam, E., & Gaillard, J.-M. (2018). Individual heterogeneity and capture-recapture
48
49 580 models: what, why and how? *Oikos*, 127(5), 664–686.
50
51
52 581 Hansson, R., & Thomassen, J. (1983). Behavior of polar bears with cubs in the denning area.
53
54 582 *Bears: Their Biology and Management*, 246–254.
55
56
57 583 Hunter, C. M., Caswell, H., Runge, M. C., Regehr, E. V., Amstrup, S. C., & Stirling, I. (2010).
58
59 584 Climate change threatens polar bear populations: a stochastic demographic analysis.

1
2
3 585 *Ecology*, 91(10), 2883–2897.

4
5
6 586 Kölliker, M., Kilner, R. M., & Hinde, C. A. (2013). Parent–offspring conflict. In *The Evolution*
7
8 587 *of Parental Care*.

9
10
11 588 Kramer, K. L. (2005). Children's help and the pace of reproduction: cooperative breeding in
12
13 589 humans. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and*
14
15 590 *Reviews*, 14(6), 224–237.

16
17
18 591 Lagrange, P., Gimenez, O., Doligez, B., Pradel, R., Garant, D., Pelletier, F., & Bélisle, M.
19
20 592 (2017). Assessment of individual and conspecific reproductive success as determinants of
21
22 593 breeding dispersal of female tree swallows: A capture-recapture approach. *Ecology and*
23
24 594 *Evolution*, 7(18), 7334–7346.

25
26
27
28 595 Laidre, K. L., Atkinson, S., Regehr, E. V., Stern, H. L., Born, E. W., Wiig, Ø., ... & Dyck, M.
29
30 596 (2020). Interrelated ecological impacts of climate change on an apex predator. *Ecological*
31
32 597 *Applications*, e02071.

33
34
35 598 Lebreton, J. D., Nichols, J. D., Barker, R. J., Pradel, R., & Spendelov, J. A. (2009). Chapter 3
36
37 599 Modeling Individual Animal Histories with Multistate Capture-Recapture Models.
38
39 600 *Advances in Ecological Research*.

40
41
42 601 Lee, P. C., & Moss, C. J. (1986). Early maternal investment in male and female African elephant
43
44 602 calves. *Behavioral Ecology and Sociobiology*, 18(5), 353–361.

45
46
47 603 Lee, R. (2008). Sociality, selection, and survival: Simulated evolution of mortality with
48
49 604 intergenerational transfers and food sharing. *Proceedings of the National Academy of*
50
51 605 *Sciences*.

52
53
54 606 Lunn, N.J., Servanty, S., Regehr, E.V., Converse, S.J., Richardson, E. and Stirling, I. (2016).
55
56 607 Demography of an apex predator at the edge of its range: impacts of changing sea ice on
57
58 608 polar bears in Hudson Bay. *Ecological Applications*, 26(5), pp.1302–1320. Mauritzen, M.,

- 1
2
3 609 Derocher, A. E., & Wiig, Ø. (2011). Space-use strategies of female polar bears in a
4
5 610 dynamic sea ice habitat. *Canadian Journal of Zoology*, 79(9), 1704–1713.
6
7
8 611 Mauritzen, M., Derocher, A.E., Wiig, Ø., Belikov, S.E., Boltunov, A.N., Hansen, E. and Garner,
9
10 612 G.W., (2002). Using satellite telemetry to define spatial population structure in polar bears
11
12 613 in the Norwegian and western Russian Arctic. *Journal of Applied Ecology*, 39(1), pp.79-
13
14 614 90.
15
16
17 615 McCarthy, M. A., & Masters, P. (2005). Profiting from prior information in Bayesian analyses
18
19 616 of ecological data. *Journal of Applied Ecology*, 42(6), 1012–1019.
20
21
22 617 Pavard, S., & Branger, F. (2012). Effect of maternal and grandmaternal care on population
23
24 618 dynamics and human life-history evolution: A matrix projection model. *Theoretical*
25
26 619 *Population Biology*.
27
28
29 620 Plummer, M., Stukalov, A., Denwood, M. and Plummer, M.M., (2016). Package ‘rjags’.
30
31 621 Vienna, Austria.
32
33
34 622 Pollock, K. H. (2002). The use of auxiliary variables in capture-recapture modelling: An
35
36 623 overview. *Journal of Applied Statistics*, 29(1–4), 85–102.
37
38
39 624 Pradel, R. (2005) Multievent: An extension of multistate capture–recapture models to uncertain
40
41 625 states ». *Biometrics* 61: 442-447
42
43
44 626 Pradel, R., & Sanz-Aguilar, A. (2012). Modeling Trap-Awareness and Related Phenomena in
45
46 627 Capture-Recapture Studies. *PLoS ONE*, 7(3), e32666.
47
48
49 628 Ramsay, M. A., & Stirling, I. (1988). Reproductive biology and ecology of female polar bears
50
51 629 in western Hudson Bay. *Naturaliste Canadien*, 109(4), 941–946.
52
53
54 630 Regehr, E. V., Laidre, K. L., Resit Akcakaya, H., Amstrup, S. C., Atwood, T. C., Lunn, N. J.,
55
56 631 ... Wiig, Ø. (2016). Conservation status of polar bears (*Ursus maritimus*) in relation to
57
58 632 projected sea-ice declines. *Biology Letters*, 12(12).
59
60

- 1
2
3 633 Regehr, E.V., Hostetter, N.J., Wilson, R.R., Rode, K.D., Martin, M.S. and Converse, S.J.,
4
5 634 (2018). Integrated population modeling provides the first empirical estimates of vital rates
6
7 635 and abundance for polar bears in the Chukchi Sea. *Scientific reports*, 8(1), pp.1-12.
9
10 636 Royle, N., Smiseth, P., & Kölliker, M. (2012). The evolution of parental care.
11
12
13 637 Shenk, M. K., & Scelza, B. A. (2012). Paternal investment and status-related child outcomes:
14
15 638 Timing of father's death affects offspring success. *Journal of Biosocial Science*.
16
17
18 639 Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press.
19
20
21 640 Stirling, I., & Derocher, A. E. (2012). Effects of climate warming on polar bears: a review of
22
23 641 the evidence. *Global Change Biology*, 18(9), 2694–2706.
24
25
26 642 Stirling, I., Spencer, C., & Andriashek, D. (1989). Immobilization of polar bears (*Ursus*
27
28 643 maritimus) with Telazol in the Canadian Arctic. *Journal of Wildlife Diseases*, 25(2), 159–
29
30 644 168.
31
32
33 645 Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. G. Campbell,
34
35 646 editor. *Sexual selection and the descent of man, 1871-1971*. Aldine, Chicago
36
37
38 647 Van Noordwijk, M. A. (2012). From Maternal Investment to Lifetime Maternal Care. In
39
40 648 *Evolution of Primate Societies* (pp. 321–342).
41
42
43 649 Vergara, P., Fargallo, J. A., & Martínez-Padilla, J. (2010). Reaching independence: food
44
45 650 supply, parent quality, and offspring phenotypic characters in kestrels. *Behavioral*
46
47 651 *ecology*, 21(3), 507-512.
48
49
50 652 Wich, S., Utami-Atmoko, S., Setia, T. M., Rijksen, H. D., Schürmann, C., Van Hooff, J. A. R.
51
52 653 A. ., & van Schaik, C. P. (2004). Life history of wild Sumatran orangutans (*Pongo abelii*).
53
54 654 *Journal of Human Evolution*, 47(6), 385–398.
55
56
57
58 655 Wiig, Ø. (1998). Survival and Reproductive Rates for Polar Bears at Svalbard. *Ursus*, 10, 25–
59
60 656 32.

1
2
3 657 Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's
4
5 658 principle. *American Naturalist*. 100, 687–690
6
7

8 659 Yoccoz, N. G., Erikstad, K. E., Bustnes, J. O., Hanssen, S. A., & Tveraa, T. (2002). Costs of
9
10 660 reproduction in common eiders (*Somateria mollissima*): An assessment of relationships
11
12 661 between reproductive effort and future survival and reproduction based on observational
13
14 662 and experimental studies. *Journal of Applied Statistics*, 29(1–4), 57–64.
15
16
17

18 663
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Review Only

Appendix 1: Guidance and code to simulate multi-event data based on family units CR histories, with variable litter size and variable timing at offspring independence, and fit the model to the simulated data

Sarah Cubaynes

6/22/2020

All files associated with Appendix 1 are available on GitHub [here](#).

Simulate multi-event data based on family units CR histories

We assume a post-breeding census, with captures occurring in spring (after den exit, cubs are about 4 months old). The year goes from 1st of April year t to 1st of April $t+1$.

Load useful package :

```
library(jtools)
```

First, set the general parameters used to simulate the data:

```
n.occasions <- 15 # duration of the study
R <- 50 # number of newly family units captured per occasion
nrepet = 100 # number of simulated data set (repetitions)
```

Second, define scenario: S1 (low detection, α constant=0.5), S2 (low detection α varies with date of capture), S3 (high detection, α constant=0.5) or S4 (low detection α varies with date of capture):

```
S <- 2 # set to 1 for S1, 2 for S2, 3 for S3 or 4 for S4
```

```
capture <- c(0.25,0.25,0.5,0.5) # capture probability
p <- capture[S]
```

Load the model to infer departure status of two-year old bears at the time of capture (still with family unit or already departed from family unit) . For scenarios S1 and S3, departure probability is constant throughout the field season. For scenarios S2 and S4, we used the regression coefficients estimated from the polar bear data, see Appendix 2.

```
filename <- c("glmdeparture_alphaconstant05.Rdata", "glm_departure_date.Rdata",
             "glmdeparture_alphaconstant05.Rdata", "glm_departure_date.Rdata")
```

```
fileS <- filename[S]
load(file=paste(fileS))
```

```
# plot departure rate with date of capture
```

```
doypred<-80:130 # day of the year, match the timing of the polar bear field season (spring)
effect_plot(modeld, pred = doypred, pred.values=doypred,interval = TRUE,
            plot.points = FALSE,y.label = "departure probability")
```

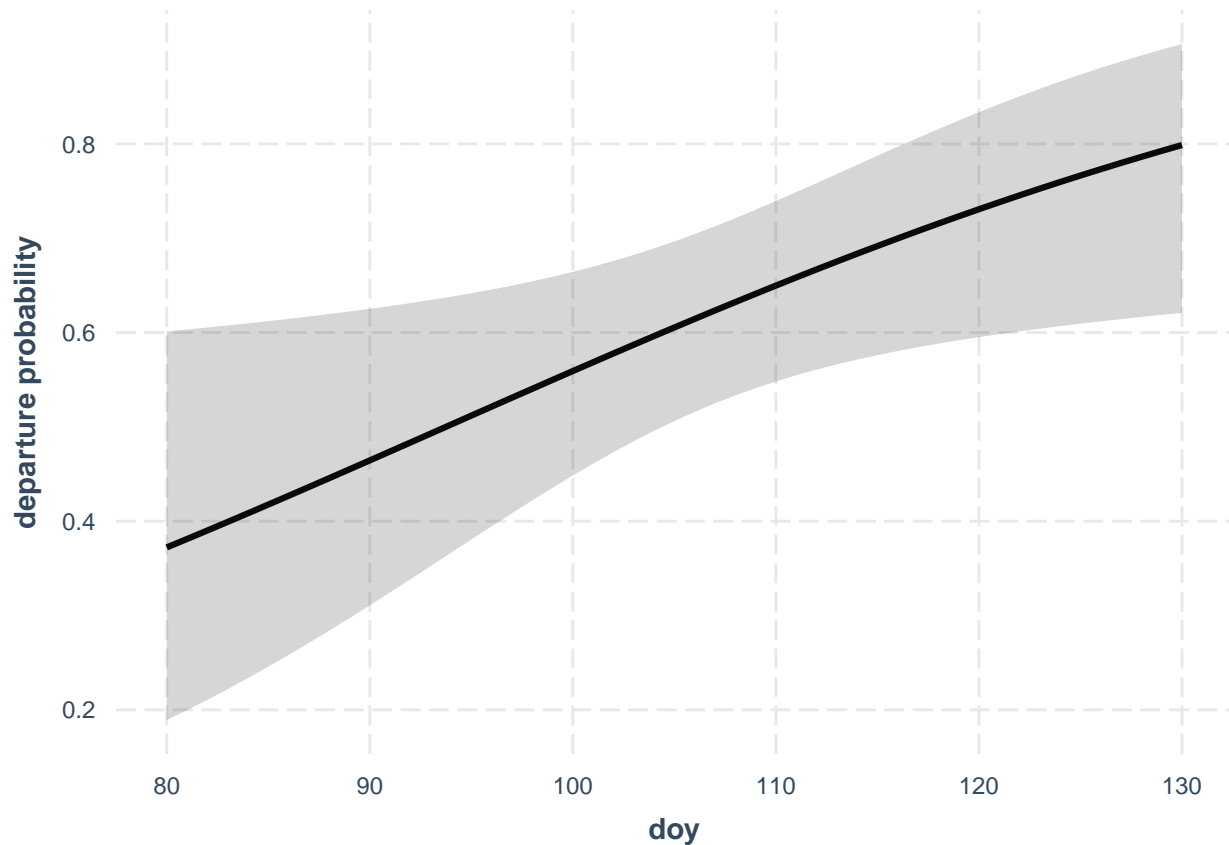
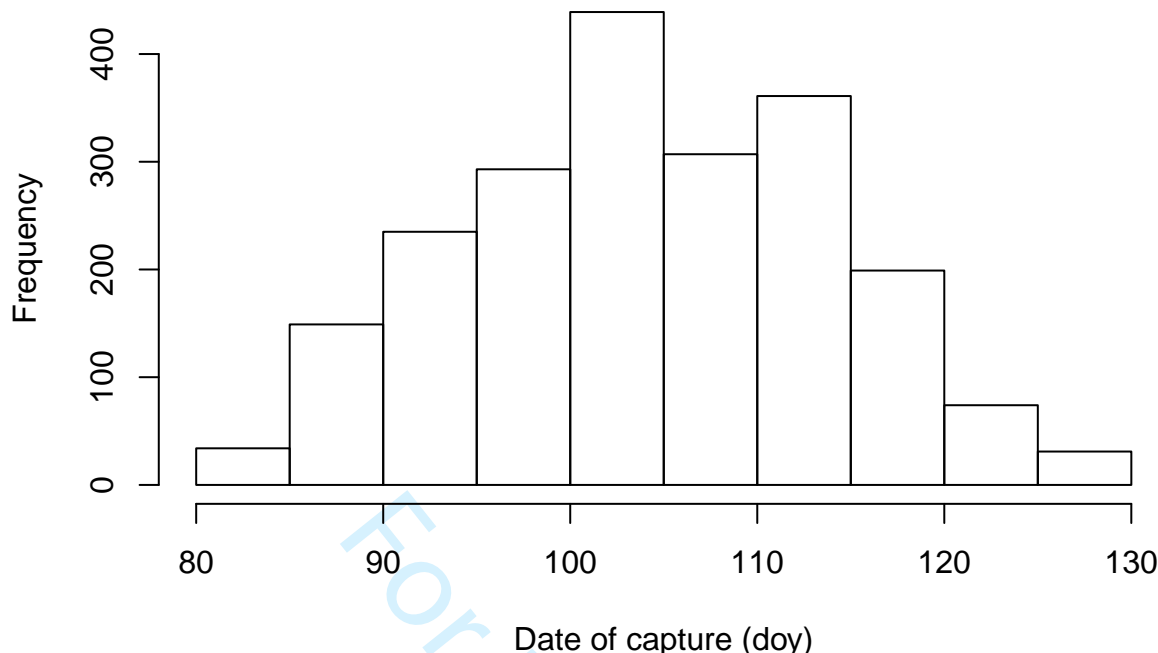


Figure S1. Departure probability of two-year old bears as a function of date of capture within the field season in day of the year (doy).

Dates of capture used in the simulations below are randomly sampled from the distribution of capture dates (in day of the year) from the polar bear data:

```
load(file="dateofcapturePB.Rdata") # load data on winter date of capture
hist(wcapt,main="",xlab="Date of capture (doy)") # plot dates of capture
```



Figure

S2. Histogram of the dates of capture of polar bears in Svalbard in day of the year (doy).

Define the demographic parameters used to simulate the data. Here we simulate a virtual long-lived species mimicking the polar bear:

```

phi <- 0.9 # survival of independent juvenile, subadult and adult (phi6+) females.
s <- c(0.6,0.55,0.8,0.75) # dependent offspring survival (conditional upon mother
#survival) by increasing age and litter size (in this order: s1,s2,s3,s4)
# we can calculate litter survival rates from individual offspring survival :
#Litter survival (lxy, x offspring age, y litter size):
l01 = s[1]
l02 = 1 - (1-s[2]^2-2*s[2]*(1-s[2])) #0.7975 for twin litter of cubs
l11= s[3]
l12= 1 - (1-s[4]^2-2*s[4]*(1-s[4]))#0.94 for twin litter of yearlings
# Probability that :
#- only one a0 offspring in a litter of 2 survives= 2*s[2]*(1-s[2]),
#- both survive :s[2]^2
# Probability that
#-only one a1 offspring in a litter of 2 survives= 2*s[2]*(1-s[2]),
#- both offspring survive:s[2]^2
# Which gives us the transition probabilities for litter size of 1 and 2 offspring,
#that one, both, or any offspring survive:
psi <- c(s[1],2*s[2]*(1-s[2]),s[2]^2,
(1- s[2]^2 -2*s[2]*(1-s[2])), s[3],2*s[4]*(1-s[4]),s[4]^2,
1- 2*s[4]*(1-s[4]) - s[4]^2)
# 0.6, 0.495,0.3025, 0.2025, 0.8, 0.375, 0.5625, 0.0625
beta <- c(0.5,0.7,0.9,0.8) # breeding probabilities
#(in the following order beta1,beta2,beta3,beta4)
gamma <- c(0.4,0.5,0.6,0.7) # probability of litter size of 2
#(in the following order gamma1,gamma2,gamma3,gamma4)

```

Define the states and the events used in the model:

```

## Define the states (12 states = 11 alive+ 1dead) describe family unit composition
# as described in the methods section

```

```

1
2
3
4 # J2 independent 2yo juvenile female
5 # J3 independent 3yo juvenile female
6 #SA4 independent 4yo subadult female
7 #SA5 independent 5yo subadult female
8 #A01 adult female caring for 1 dependent offspring of the year (age <1)
9 #A02 adult female caring for 2 dependent offspring of the year (age <1)
10 #A11 adult female caring for 1 dependent yearling (age 1)
11 #A12 adult female caring for 2 dependent yearlings (age 1)
12 #AS1 adult female successful breeder raising 1 offspring reaching independence
13 #AS2 adult female successful breeder raising 2 offspring reaching independence
14 #A adult female without dependent offspring
15 # D dead state
16 n.states <- 11
17 all.states <- n.states + 1 # with dead state
18
19 ## Define the events
20 # as defined in the methods section
21 # non-observation code "0"
22 # capture of a 2y female code "1"
23 # capture of a 3y female code "2"
24 # capture of a 4y female code "3"
25 # capture of a 5y female code "4"
26 # capture of an adult female with 1 offspring of the year (age <1) code "5"
27 # capture of an adult female with 2 offspring of the year (age <1) code "6"
28 # capture of an adult female with 1 yearling code "7"
29 # capture of an adult female with 2 yearlings code "8"
30 # capture of an adult female with 1 two-year old offspring code "9"
31 # capture of an adult female with 2 two-year old offspring code "10"
32 # capture of an adult female alone code "11"
33 n.events <- 11
34 all.events <- n.events + 1 #with not seen

```

Define the initial state vector, gathering the proportion of individual in each state at first capture:

```
S0 <- c(rep(1/n.states,n.states),0)#initial state vector S0
```

Here we considered equal proportions in the eleven alive states.

Now construct the transition matrices PHI, PSI1, PSI2, PSI3 involved in the state process:

```

41 ### State transitions
42 # define PHI matrix gathering survival of independent juveniles, subadults and adults
43 temp1 <- diag(c(phi,phi,phi,phi,rep(phi,7)),nrow=all.states,ncol=n.states)
44 PHI <- cbind(temp1,c(1-phi,1-phi,1-phi,1-phi,rep(1-phi,7),1))
45
46 # Define PSI matrices gathering state-to-state transition probabilities, it includes:
47
48 # PSI1: litter survival, individual dependent offspring survival and growth to next age:
49 PSI1 <- matrix(0,nrow=all.states,ncol=all.states + 1)
50 for(i in 1:3){PSI1[i,i] <- 1} # juvenile and subadults grow to next age
51 PSI1[4,12] <- 1 # 5a grow to sexually mature female without dependent offspring
52 PSI1[5,4] <- psi[1] ; PSI1[5,8] <- (1-psi[1]) #a0 offspring survives or dies
53 PSI1[6,4] <- psi[2] ; PSI1[6,5] <- psi[3] ; PSI1[6,8] <- psi[4] #1,both
54 #or any a0 offspring in a litter of 2 survive
55 PSI1[7,6] <- psi[5] ; PSI1[7,9] <- (1-psi[5])#a1 offspring in a litter
56 #of 1 survives or die
57
58
59
60

```



```

1
2
3
4 PSI1[8,6] <- psi[6] ; PSI1[8,7] <- psi[7] ;PSI1[8,9] <- psi[8] #1,both or any
5 #a1 offspring in a litter of 2 survive or die
6 for(i in 9:12){PSI1[i,i+1] <- 1} # for offspring reaching independence and females
7 #without dependent offspring
8
9 # PSI2: breeding probabilities:
10 PSI2 <- matrix(0,nrow=all.states+1,ncol=all.states+4)
11 for(i in 1:7){PSI2[i,i] <- 1} # here we assume that juveniles, subadults and adults
12 #caring for dependent offspring are not available to breed
13 PSI2[8,8] <- beta[1];PSI2[8,9] <- 1-beta[1]
14 PSI2[9,10] <- beta[2];PSI2[9,11] <- 1-beta[2]
15 PSI2[10,12] <- beta[3];PSI2[10,13] <- 1-beta[3]
16 PSI2[11,12] <- beta[3];PSI2[11,13] <- 1-beta[3]
17 PSI2[12,14] <- beta[4];PSI2[12,15] <- 1-beta[4]
18 PSI2[13,16] <- 1 # dead state
19
20 # PSI3:litter size probabilities
21 # (Pr(singleton litter) = gamma, Pr(twin litter)= 1-gamma)
22 PSI3 <- matrix(0,nrow=all.states+4,ncol=all.states)
23 for(i in 1:3){PSI3[i,i+1] <- 1}
24 for(i in 4:7){PSI3[i,i+3] <- 1}
25 PSI3[8,5] <- gamma[1];PSI3[8,6] <- 1-gamma[1]
26 PSI3[9,11] <-1
27 PSI3[10,5] <- gamma[2];PSI3[10,6] <- 1-gamma[2]
28 PSI3[11,11] <-1
29 PSI3[12,5] <- gamma[3];PSI3[12,6] <- 1-gamma[3]
30 PSI3[13,11] <-1
31 PSI3[14,5] <- gamma[4];PSI3[14,6] <- 1-gamma[4]
32 PSI3[15,11] <-1
33 PSI3[16,12] <-1

```

We can now define the part of the observation process (matrix $E2$ modeling capture probability, matrix $E1$ will be defined later) which does not depend on capture date:

```

34
35
36 # Define observation process
37 # step 1 : matrix E1
38 # it involves departure probability which is function of day of capture,
39 #it will be define below within the loop
40
41 # step 2 : matrix E2, involves capture probability
42 E2 <- matrix(0,nrow=all.states, ncol=all.events)
43 for(i in 1:all.states){E2[i,i] <- p} #detection probability
44 E2[,all.events] <- c(rep(1-p,4), rep(1-p,7),1)
45
46

```

Below, we generate the data using multinomial trials for each sampling occasion, for each family unit. This script is based on the script from Chapter 7 in Kery and Schaub (2011) to simulate multistate CMR data. To deal with variable timing at offspring independence, the probabilities within matrix $E1$ used in the observation process depend on date of capture. Matrix $E1$ is therefore defined within the loop for each individual at each sampling occasion depending on its date of capture.

```

47
48 ## Generate data
49 for(r in 1:nrepet){ # number of dataset generated
50
51   marked <- matrix(0, ncol = all.states, nrow = n.occasions) # empty object to store
52   #marked family units
53
54
55
56
57
58
59
60

```

```

1
2
3
4 for(t in 1:n.occasions){
5   marked[t,] <- rmultinom(1,R,prob=S0) # define states at first capture
6 }
7 # Below we use transition and event matrices wwith 4-dimensions:
8 # Dimension 1: state of departure
9 # Dimension 2: state of arrival
10 # Dimension 3: family unit
11 # Dimension 4: time
12
13 # 1. State process matrix
14 totrel <- sum(marked)*(n.occasions-1)
15 PSI.STATE <- array(NA, dim=c(all.states, all.states, totrel, n.occasions-1))
16
17 for (i in 1:totrel){
18   for (t in 1:(n.occasions-1)){
19     PSI.STATE[, ,i,t] <- PHI %*% PSI1 %*% PSI2 %*% PSI3 # transition matrix
20     #is the matrix product of PHI PSI1 PSI2 and PSI3 defiend above
21   } #t
22 } #i
23
24 # 2.Observation process matrix
25 E <- array(NA, dim=c(all.states, all.events, totrel, n.occasions-1))
26
27 # day of capture, sampled from polar bears capture dates
28 daycapt <- matrix(sample(wcapt,size=(totrel*(n.occasions-1))),
29                   replace=TRUE), nrow=totrel, ncol=n.occasions-1)
30
31 for (i in 1:totrel){
32   for (t in 1:(n.occasions-1)){
33
34     # predict departure probability function of date of capture
35     alpha <- predict(modeld,newdata=list(doy=daycapt[i,t]),type="response")
36
37     # now define event matrix E1 using departure probability alpha
38     E1 <- diag(1,nrow=all.states,ncol=all.events)
39     E1[9,9] <- 1-alpha
40     E1[9,10] <- 0
41     E1[9,11] <- alpha
42     E1[10,9] <- 2*(1-alpha)*alpha
43     E1[10,10] <- 1 - (2*(1-alpha)*alpha) - (alpha)^2
44     E1[10,11] <- (alpha)^2
45
46     E[, ,i,t] <- E1 %*% E2 # define E which is the matrix product of E1 and E2
47   } #t
48 } #i
49 }#r

```

Make a function to simulate the data using the state and event matrices we just defined:

```

51 # Define function to simulate multistate capture-recapture data
52 simul.ms <- function(PSI.STATE, E, marked, unobservable = NA){
53   # Unobservable: number of state that is unobservable
54   n.occasions <- dim(PSI.STATE)[4] + 1
55   CH <- CH.TRUE <- dayC <- matrix(NA, ncol = n.occasions, nrow = sum(marked))
56
57
58
59
60

```

```

1
2
3
4   # Define a vector with the occasion of marking
5   mark.occ <- matrix(0, ncol = dim(P.SI.STATE)[1], nrow = sum(marked))
6   g <- colSums(marked)
7   for (s in 1:dim(P.SI.STATE)[1]){
8     if (g[s]==0) next # To avoid error message if nothing to replace
9     mark.occ[(cumsum(g[1:s])-g[s]+1)[s]:cumsum(g[1:s])[s],s] <-
10      rep(1:n.occasions, marked[1:n.occasions,s])
11  } #s
12  for (i in 1:sum(marked)){
13    for (s in 1:dim(P.SI.STATE)[1]){
14      if (mark.occ[i,s]==0) next
15      first <- mark.occ[i,s]
16      CH[i,first] <- s
17      CH.TRUE[i,first] <- s
18    } #s
19    for (t in (first+1):n.occasions){
20      # Multinomial trials for state transitions
21      if (first==n.occasions) next
22      state <- which(rmultinom(1, 1, P.SI.STATE[CH.TRUE[i,t-1],,i,t-1])==1)
23      CH.TRUE[i,t] <- state
24      # Multinomial trials for observation process
25      event <- which(rmultinom(1, 1, E[CH.TRUE[i,t],,i,t-1])==1)
26      CH[i,t] <- event
27      dayC[i,t] <- daycapt[i,t-1]
28    } #t
29  } #i
30  # Replace the NA and the highest state number (dead) in the file by 0
31  CH[is.na(CH)] <- 0
32  CH[CH==dim(P.SI.STATE)[1]] <- 0
33  CH[CH==unobservable] <- 0
34  id <- numeric(0)
35  for (i in 1:dim(CH)[1]){
36    z <- min(which(CH[i,]!=0))
37    ifelse(z==dim(CH)[2], id <- c(id,i), id <- c(id))
38  }
39  return(list(CH=CH[-id,], CH.TRUE=CH.TRUE[-id,],dayC=dayC[-id,]))
40  # CH: capture histories to be used
41  # CH.TRUE: capture histories with perfect observation
42  # dayC: date of capture
43  }

```

Generate the data using the function above, and save the family units CR histories, underlying states and dates of captures:

```

44
45
46  # Execute function
47  sim <- simul.ms(P.SI.STATE, E, marked)
48  CH <- sim$CH # family units CR histories
49  init <- sim$CH.TRUE # real state matrix used as initial values for jags model
50  daycapt <- sim$dayC # info on date of capture
51  # save files
52  write.table(CH,paste("simCH",r,"_p",p,"_T",n.occasions,".txt",
53                    sep=""),row.names=F, col.names=F, sep = " ")
54  write.table(init,paste("siminit",r,"_p",p,"_T",n.occasions,".txt",
55                    sep=""),row.names=F, col.names=F, sep = " ")
56
57
58
59
60

```

```

1
2
3
4 write.table(daycapt,paste("simdaycapt",r,"_p",p,"_T",n.occasions,".txt",sep=""),
5         row.names=F, col.names=F, sep = " ")
6
7
8
9

```

Fit the model to simulated data

First, load the required package:

```

11
12 # Load packages
13 library(jagsUI)
14
15 ## Loading required package: lattice
16 ##
17 ## Attaching package: 'jagsUI'
18 ## The following object is masked from 'package:utils':
19 ##
20 ##      View
21

```

Choose working directory name corresponding to scenario S1, S2, S3 or S4 (to read the corresponding data):

```

22
23 rep <- c("S1_p025alphaconstant", "S2p025alphadate", "S3p05alphaconstant", "S4p05alphadate")
24 repname <- rep[1] ## 1 for S1, 2 for S2, 3 for S3, 4 for S4
25

```

Define capture probability and model to infer departure probability used to simulate the data in the corresponding scenario: S1 (low detection, alpha constant=0.5), S2 (low detection alpha varies with date of capture), S3 (high detection, alpha constant=0.5) or S4 (low detection alpha varies with date of capture):

```

26
27 S <- 2 # set to 1 for S1, 2 for S2, 3 for S3 or 4 for S4
28
29
30
31 capture <- c(0.25,0.25,0.5,0.5) # capture probability
32 p <- capture[S]
33
34
35 filename <- c("glmdeparture_alphaconstant05.Rdata", "glm_departure_date.Rdata",
36             "glmdeparture_alphaconstant05.Rdata", "glm_departure_date.Rdata")
37 fileS <- filename[S]
38 load(file=paste(fileS))
39
40 n.occasions =15 # number of sampling occasions
41 nrepet = 100 # number of simulated dataset (repetitions)
42

```

Sink the jags model :

```

43
44 # JAGS MODEL
45 sink("Multieventmodel_Fit_simul.txt")
46 cat("
47
48 model {
49   # Probabilities of events given states and states given states
50
51   # vector of initial states
52   SO[1] <- prop[1] / (1 + sum(prop[1:10])) # prob. of being in initial state J2
53   SO[2] <- prop[2] / (1 + sum(prop[1:10])) # prob. of being in initial state J3
54   SO[3] <- prop[3] / (1 + sum(prop[1:10])) # prob. of being in initial state SA4
55   SO[4] <- prop[4] / (1 + sum(prop[1:10])) # prob. of being in initial state SA5
56   SO[5] <- prop[5] / (1 + sum(prop[1:10])) # prob. of being in initial state A01
57
58
59
60

```

```

1
2
3
4 S0[6] <- prop[6] / (1 + sum(prop[1:10])) # prob. of being in initial state A02
5 S0[7] <- prop[7] / (1 + sum(prop[1:10])) # prob. of being in initial state A11
6 S0[8] <- prop[8] / (1 + sum(prop[1:10])) # prob. of being in initial state A12
7 S0[9] <- prop[9] / (1 + sum(prop[1:10])) # prob. of being in initial state AS1
8 S0[10] <- prop[10] / (1 + sum(prop[1:10])) # prob. of being in initial state AS2
9 S0[11] <- 1 / (1 + sum(prop[1:10])) # prob. of being in initial state A-
10 S0[12] <- 0 # prob. of being in initial state dead
11
12 # State process: define probabilities of S(t+1) given S(t)
13 # define PHI matrix gathering survival of independent juveniles, subadults and adults
14 PHI [ 1 , 1 ]<- phi
15 PHI [ 1 , 2 ]<- 0
16 PHI [ 1 , 3 ]<- 0
17 PHI [ 1 , 4 ]<- 0
18 PHI [ 1 , 5 ]<- 0
19 PHI [ 1 , 6 ]<- 0
20 PHI [ 1 , 7 ]<- 0
21 PHI [ 1 , 8 ]<- 0
22 PHI [ 1 , 9 ]<- 0
23 PHI [ 1 , 10 ]<- 0
24 PHI [ 1 , 11 ]<- 0
25 PHI [ 1 , 12 ]<- 1-phi
26
27 PHI [ 2 , 1 ]<- 0
28 PHI [ 2 , 2 ]<- phi
29 PHI [ 2 , 3 ]<- 0
30 PHI [ 2 , 4 ]<- 0
31 PHI [ 2 , 5 ]<- 0
32 PHI [ 2 , 6 ]<- 0
33 PHI [ 2 , 7 ]<- 0
34 PHI [ 2 , 8 ]<- 0
35 PHI [ 2 , 9 ]<- 0
36 PHI [ 2 , 10 ]<- 0
37 PHI [ 2 , 11 ]<- 0
38 PHI [ 2 , 12 ]<- 1-phi
39
40 PHI [ 3 , 1 ]<- 0
41 PHI [ 3 , 2 ]<- 0
42 PHI [ 3 , 3 ]<- phi
43 PHI [ 3 , 4 ]<- 0
44 PHI [ 3 , 5 ]<- 0
45 PHI [ 3 , 6 ]<- 0
46 PHI [ 3 , 7 ]<- 0
47 PHI [ 3 , 8 ]<- 0
48 PHI [ 3 , 9 ]<- 0
49 PHI [ 3 , 10 ]<- 0
50 PHI [ 3 , 11 ]<- 0
51 PHI [ 3 , 12 ]<- 1-phi
52
53 PHI [ 4 , 1 ]<- 0
54 PHI [ 4 , 2 ]<- 0
55 PHI [ 4 , 3 ]<- 0
56 PHI [ 4 , 4 ]<- phi
57
58
59
60

```

```

1
2
3
4 PHI [ 4 , 5 ]<- 0
5 PHI [ 4 , 6 ]<- 0
6 PHI [ 4 , 7 ]<- 0
7 PHI [ 4 , 8 ]<- 0
8 PHI [ 4 , 9 ]<- 0
9 PHI [ 4 , 10 ]<- 0
10 PHI [ 4 , 11 ]<- 0
11 PHI [ 4 , 12 ]<- 1 - phi
12
13 PHI [ 5 , 1 ]<- 0
14 PHI [ 5 , 2 ]<- 0
15 PHI [ 5 , 3 ]<- 0
16 PHI [ 5 , 4 ]<- 0
17 PHI [ 5 , 5 ]<- phi
18 PHI [ 5 , 6 ]<- 0
19 PHI [ 5 , 7 ]<- 0
20 PHI [ 5 , 8 ]<- 0
21 PHI [ 5 , 9 ]<- 0
22 PHI [ 5 , 10 ]<- 0
23 PHI [ 5 , 11 ]<- 0
24 PHI [ 5 , 12 ]<- 1 - phi
25
26 PHI [ 6 , 1 ]<- 0
27 PHI [ 6 , 2 ]<- 0
28 PHI [ 6 , 3 ]<- 0
29 PHI [ 6 , 4 ]<- 0
30 PHI [ 6 , 5 ]<- 0
31 PHI [ 6 , 6 ]<- phi
32 PHI [ 6 , 7 ]<- 0
33 PHI [ 6 , 8 ]<- 0
34 PHI [ 6 , 9 ]<- 0
35 PHI [ 6 , 10 ]<- 0
36 PHI [ 6 , 11 ]<- 0
37 PHI [ 6 , 12 ]<- 1 - phi
38
39 PHI [ 7 , 1 ]<- 0
40 PHI [ 7 , 2 ]<- 0
41 PHI [ 7 , 3 ]<- 0
42 PHI [ 7 , 4 ]<- 0
43 PHI [ 7 , 5 ]<- 0
44 PHI [ 7 , 6 ]<- 0
45 PHI [ 7 , 7 ]<- phi
46 PHI [ 7 , 8 ]<- 0
47 PHI [ 7 , 9 ]<- 0
48 PHI [ 7 , 10 ]<- 0
49 PHI [ 7 , 11 ]<- 0
50 PHI [ 7 , 12 ]<- 1-phi
51
52 PHI [ 8 , 1 ]<- 0
53 PHI [ 8 , 2 ]<- 0
54 PHI [ 8 , 3 ]<- 0
55 PHI [ 8 , 4 ]<- 0
56 PHI [ 8 , 5 ]<- 0
57
58
59
60

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```
PHI [ 8 , 6 ]<- 0
PHI [ 8 , 7 ]<- 0
PHI [ 8 , 8 ]<- phi
PHI [ 8 , 9 ]<- 0
PHI [ 8 , 10 ]<- 0
PHI [ 8 , 11 ]<- 0
PHI [ 8 , 12 ]<- 1-phi

PHI [ 9 , 1 ]<- 0
PHI [ 9 , 2 ]<- 0
PHI [ 9 , 3 ]<- 0
PHI [ 9 , 4 ]<- 0
PHI [ 9 , 5 ]<- 0
PHI [ 9 , 6 ]<- 0
PHI [ 9 , 7 ]<- 0
PHI [ 9 , 8 ]<- 0
PHI [ 9 , 9 ]<- phi
PHI [ 9 , 10 ]<- 0
PHI [ 9 , 11 ]<- 0
PHI [ 9 , 12 ]<- 1-phi

PHI [ 10 , 1 ]<- 0
PHI [ 10 , 2 ]<- 0
PHI [ 10 , 3 ]<- 0
PHI [ 10 , 4 ]<- 0
PHI [ 10 , 5 ]<- 0
PHI [ 10 , 6 ]<- 0
PHI [ 10 , 7 ]<- 0
PHI [ 10 , 8 ]<- 0
PHI [ 10 , 9 ]<- 0
PHI [ 10 , 10 ]<- phi
PHI [ 10 , 11 ]<- 0
PHI [ 10 , 12 ]<- 1-phi

PHI [ 11 , 1 ]<- 0
PHI [ 11 , 2 ]<- 0
PHI [ 11 , 3 ]<- 0
PHI [ 11 , 4 ]<- 0
PHI [ 11 , 5 ]<- 0
PHI [ 11 , 6 ]<- 0
PHI [ 11 , 7 ]<- 0
PHI [ 11 , 8 ]<- 0
PHI [ 11 , 9 ]<- 0
PHI [ 11 , 10 ]<- 0
PHI [ 11 , 11 ]<- phi
PHI [ 11 , 12 ]<- 1-phi

PHI [ 12 , 1 ]<- 0
PHI [ 12 , 2 ]<- 0
PHI [ 12 , 3 ]<- 0
PHI [ 12 , 4 ]<- 0
PHI [ 12 , 5 ]<- 0
PHI [ 12 , 6 ]<- 0
```

```

1
2
3
4 PHI [ 12 , 7 ]<- 0
5 PHI [ 12 , 8 ]<- 0
6 PHI [ 12 , 9 ]<- 0
7 PHI [ 12 , 10 ]<- 0
8 PHI [ 12 , 11 ]<- 0
9 PHI [ 12 , 12 ]<- 1
10
11 # Define PSI matrices gathering state-to-state transition probabilities, it includes:
12 # PSI1: offspring survival and growth to next age, proba of sexual maturation:
13 PSI1 [ 1 , 1 ]<- 1
14 PSI1 [ 1 , 2 ]<- 0
15 PSI1 [ 1 , 3 ]<- 0
16 PSI1 [ 1 , 4 ]<- 0
17 PSI1 [ 1 , 5 ]<- 0
18 PSI1 [ 1 , 6 ]<- 0
19 PSI1 [ 1 , 7 ]<- 0
20 PSI1 [ 1 , 8 ]<- 0
21 PSI1 [ 1 , 9 ]<- 0
22 PSI1 [ 1 , 10 ]<- 0
23 PSI1 [ 1 , 11 ]<- 0
24 PSI1 [ 1 , 12 ]<- 0
25 PSI1 [ 1 , 13 ]<- 0
26
27 PSI1 [ 2 , 1 ]<- 0
28 PSI1 [ 2 , 2 ]<- 1
29 PSI1 [ 2 , 3 ]<- 0
30 PSI1 [ 2 , 4 ]<- 0
31 PSI1 [ 2 , 5 ]<- 0
32 PSI1 [ 2 , 6 ]<- 0
33 PSI1 [ 2 , 7 ]<- 0
34 PSI1 [ 2 , 8 ]<- 0
35 PSI1 [ 2 , 9 ]<- 0
36 PSI1 [ 2 , 10 ]<- 0
37 PSI1 [ 2 , 11 ]<- 0
38 PSI1 [ 2 , 12 ]<- 0
39 PSI1 [ 2 , 13 ]<- 0
40
41 PSI1 [ 3 , 1 ]<- 0
42 PSI1 [ 3 , 2 ]<- 0
43 PSI1 [ 3 , 3 ]<- 1-kappa # first repro at age 6
44 PSI1 [ 3 , 4 ]<- 0
45 PSI1 [ 3 , 5 ]<- 0
46 PSI1 [ 3 , 6 ]<- 0
47 PSI1 [ 3 , 7 ]<- 0
48 PSI1 [ 3 , 8 ]<- 0
49 PSI1 [ 3 , 9 ]<- 0
50 PSI1 [ 3 , 10 ]<- 0
51 PSI1 [ 3 , 11 ]<- 0
52 PSI1 [ 3 , 12 ]<- kappa # first repro at age 5
53 PSI1 [ 3 , 13 ]<- 0
54
55 PSI1 [ 4 , 1 ]<- 0
56 PSI1 [ 4 , 2 ]<- 0
57
58
59
60

```



```

1
2
3
4 PSI1 [ 4 , 3 ]<- 0
5 PSI1 [ 4 , 4 ]<- 0
6 PSI1 [ 4 , 5 ]<- 0
7 PSI1 [ 4 , 6 ]<- 0
8 PSI1 [ 4 , 7 ]<- 0
9 PSI1 [ 4 , 8 ]<- 0
10 PSI1 [ 4 , 9 ]<- 0
11 PSI1 [ 4 , 10 ]<- 0
12 PSI1 [ 4 , 11 ]<- 0
13 PSI1 [ 4 , 12 ]<- 1
14 PSI1 [ 4 , 13 ]<- 0
15
16 PSI1 [ 5 , 1 ]<- 0
17 PSI1 [ 5 , 2 ]<- 0
18 PSI1 [ 5 , 3 ]<- 0
19 PSI1 [ 5 , 4 ]<- s[1] # litter of 1, cub's survival
20 PSI1 [ 5 , 5 ]<- 0
21 PSI1 [ 5 , 6 ]<- 0
22 PSI1 [ 5 , 7 ]<- 0
23 PSI1 [ 5 , 8 ]<- 1-s[1] #litter of 1, cub's death
24 PSI1 [ 5 , 9 ]<- 0
25 PSI1 [ 5 , 10 ]<- 0
26 PSI1 [ 5 , 11 ]<- 0
27 PSI1 [ 5 , 12 ]<- 0
28 PSI1 [ 5 , 13 ]<- 0
29
30 PSI1 [ 6 , 1 ]<- 0
31 PSI1 [ 6 , 2 ]<- 0
32 PSI1 [ 6 , 3 ]<- 0
33 PSI1 [ 6 , 4 ]<- 2*s[2]*(1-s[2]) # litter of 2, 1 cub survives
34 PSI1 [ 6 , 5 ]<- s[2]^2 # litter of 2, both cubs survive
35 PSI1 [ 6 , 6 ]<- 0
36 PSI1 [ 6 , 7 ]<- 0
37 PSI1 [ 6 , 8 ]<- (1- s[2]^2 -2*s[2]*(1-s[2])) #litter of 2, both cubs die
38 PSI1 [ 6 , 9 ]<- 0
39 PSI1 [ 6 , 10 ]<- 0
40 PSI1 [ 6 , 11 ]<- 0
41 PSI1 [ 6 , 12 ]<- 0
42 PSI1 [ 6 , 13 ]<- 0
43
44 PSI1 [ 7 , 1 ]<- 0
45 PSI1 [ 7 , 2 ]<- 0
46 PSI1 [ 7 , 3 ]<- 0
47 PSI1 [ 7 , 4 ]<- 0
48 PSI1 [ 7 , 5 ]<- 0
49 PSI1 [ 7 , 6 ]<- s[3] # litter of 1, yearling's survival
50 PSI1 [ 7 , 7 ]<- 0
51 PSI1 [ 7 , 8 ]<- 0
52 PSI1 [ 7 , 9 ]<- (1-s[3] ) # litter of 1, yearling's death
53 PSI1 [ 7 , 10 ]<- 0
54 PSI1 [ 7 , 11 ]<- 0
55 PSI1 [ 7 , 12 ]<- 0
56 PSI1 [ 7 , 13 ]<- 0
57
58
59
60

```

```

1
2
3
4   PSI1 [ 8 , 1 ]<- 0
5   PSI1 [ 8 , 2 ]<- 0
6   PSI1 [ 8 , 3 ]<- 0
7   PSI1 [ 8 , 4 ]<- 0
8   PSI1 [ 8 , 5 ]<- 0
9   PSI1 [ 8 , 6 ]<- 2*s[4]*(1-s[4]) # litter of 2, 1 yearling survives
10  PSI1 [ 8 , 7 ]<- s[4]^2 # litter of 2, both yearlings survive
11  PSI1 [ 8 , 8 ]<- 0
12  PSI1 [ 8 , 9 ]<- (1- s[4]^2 -2*s[4]*(1-s[4])) #litter of 2, both yearlings die
13  PSI1 [ 8 , 10 ]<- 0
14  PSI1 [ 8 , 11 ]<- 0
15  PSI1 [ 8 , 12 ]<- 0
16  PSI1 [ 8 , 13 ]<- 0
17
18  PSI1 [ 9 , 1 ]<- 0
19  PSI1 [ 9 , 2 ]<- 0
20  PSI1 [ 9 , 3 ]<- 0
21  PSI1 [ 9 , 4 ]<- 0
22  PSI1 [ 9 , 5 ]<- 0
23  PSI1 [ 9 , 6 ]<- 0
24  PSI1 [ 9 , 7 ]<- 0
25  PSI1 [ 9 , 8 ]<- 0
26  PSI1 [ 9 , 9 ]<- 0
27  PSI1 [ 9 , 10 ]<- 1
28  PSI1 [ 9 , 11 ]<- 0
29  PSI1 [ 9 , 12 ]<- 0
30  PSI1 [ 9 , 13 ]<- 0
31
32  PSI1 [ 10 , 1 ]<- 0
33  PSI1 [ 10 , 2 ]<- 0
34  PSI1 [ 10 , 3 ]<- 0
35  PSI1 [ 10 , 4 ]<- 0
36  PSI1 [ 10 , 5 ]<- 0
37  PSI1 [ 10 , 6 ]<- 0
38  PSI1 [ 10 , 7 ]<- 0
39  PSI1 [ 10 , 8 ]<- 0
40  PSI1 [ 10 , 9 ]<- 0
41  PSI1 [ 10 , 10 ]<- 0
42  PSI1 [ 10 , 11 ]<- 1
43  PSI1 [ 10 , 12 ]<- 0
44  PSI1 [ 10 , 13 ]<- 0
45
46  PSI1 [ 11 , 1 ]<- 0
47  PSI1 [ 11 , 2 ]<- 0
48  PSI1 [ 11 , 3 ]<- 0
49  PSI1 [ 11 , 4 ]<- 0
50  PSI1 [ 11 , 5 ]<- 0
51  PSI1 [ 11 , 6 ]<- 0
52  PSI1 [ 11 , 7 ]<- 0
53  PSI1 [ 11 , 8 ]<- 0
54  PSI1 [ 11 , 9 ]<- 0
55  PSI1 [ 11 , 10 ]<- 0
56  PSI1 [ 11 , 11 ]<- 0

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```
PSI1 [ 11 , 12 ]<- 1
PSI1 [ 11 , 13 ]<- 0

PSI1 [ 12 , 1 ]<- 0
PSI1 [ 12 , 2 ]<- 0
PSI1 [ 12 , 3 ]<- 0
PSI1 [ 12 , 4 ]<- 0
PSI1 [ 12 , 5 ]<- 0
PSI1 [ 12 , 6 ]<- 0
PSI1 [ 12 , 7 ]<- 0
PSI1 [ 12 , 8 ]<- 0
PSI1 [ 12 , 9 ]<- 0
PSI1 [ 12 , 10 ]<- 0
PSI1 [ 12 , 11 ]<- 0
PSI1 [ 12 , 12 ]<- 0
PSI1 [ 12 , 13 ]<- 1
```

```
# PSI2: breeding probabilities:
```

```
PSI2 [ 1 , 1 ]<- 1
PSI2 [ 1 , 2 ]<- 0
PSI2 [ 1 , 3 ]<- 0
PSI2 [ 1 , 4 ]<- 0
PSI2 [ 1 , 5 ]<- 0
PSI2 [ 1 , 6 ]<- 0
PSI2 [ 1 , 7 ]<- 0
PSI2 [ 1 , 8 ]<- 0
PSI2 [ 1 , 9 ]<- 0
PSI2 [ 1 , 10 ]<- 0
PSI2 [ 1 , 11 ]<- 0
PSI2 [ 1 , 12 ]<- 0
PSI2 [ 1 , 13 ]<- 0
PSI2 [ 1 , 14 ]<- 0
PSI2 [ 1 , 15 ]<- 0
PSI2 [ 1 , 16 ]<- 0

PSI2 [ 2 , 1 ]<- 0
PSI2 [ 2 , 2 ]<- 1
PSI2 [ 2 , 3 ]<- 0
PSI2 [ 2 , 4 ]<- 0
PSI2 [ 2 , 5 ]<- 0
PSI2 [ 2 , 6 ]<- 0
PSI2 [ 2 , 7 ]<- 0
PSI2 [ 2 , 8 ]<- 0
PSI2 [ 2 , 9 ]<- 0
PSI2 [ 2 , 10 ]<- 0
PSI2 [ 2 , 11 ]<- 0
PSI2 [ 2 , 12 ]<- 0
PSI2 [ 2 , 13 ]<- 0
PSI2 [ 2 , 14 ]<- 0
PSI2 [ 2 , 15 ]<- 0
PSI2 [ 2 , 16 ]<- 0

PSI2 [ 3 , 1 ]<- 0
```

```
1
2
3
4 PSI2 [ 3 , 2 ]<- 0
5 PSI2 [ 3 , 3 ]<- 1
6 PSI2 [ 3 , 4 ]<- 0
7 PSI2 [ 3 , 5 ]<- 0
8 PSI2 [ 3 , 6 ]<- 0
9 PSI2 [ 3 , 7 ]<- 0
10 PSI2 [ 3 , 8 ]<- 0
11 PSI2 [ 3 , 9 ]<- 0
12 PSI2 [ 3 , 10 ]<- 0
13 PSI2 [ 3 , 11 ]<- 0
14 PSI2 [ 3 , 12 ]<- 0
15 PSI2 [ 3 , 13 ]<- 0
16 PSI2 [ 3 , 14 ]<- 0
17 PSI2 [ 3 , 15 ]<- 0
18 PSI2 [ 3 , 16 ]<- 0
19
20 PSI2 [ 4 , 1 ]<- 0
21 PSI2 [ 4 , 2 ]<- 0
22 PSI2 [ 4 , 3 ]<- 0
23 PSI2 [ 4 , 4 ]<- 1
24 PSI2 [ 4 , 5 ]<- 0
25 PSI2 [ 4 , 6 ]<- 0
26 PSI2 [ 4 , 7 ]<- 0
27 PSI2 [ 4 , 8 ]<- 0
28 PSI2 [ 4 , 9 ]<- 0
29 PSI2 [ 4 , 10 ]<- 0
30 PSI2 [ 4 , 11 ]<- 0
31 PSI2 [ 4 , 12 ]<- 0
32 PSI2 [ 4 , 13 ]<- 0
33 PSI2 [ 4 , 14 ]<- 0
34 PSI2 [ 4 , 15 ]<- 0
35 PSI2 [ 4 , 16 ]<- 0
36
37 PSI2 [ 5 , 1 ]<- 0
38 PSI2 [ 5 , 2 ]<- 0
39 PSI2 [ 5 , 3 ]<- 0
40 PSI2 [ 5 , 4 ]<- 0
41 PSI2 [ 5 , 5 ]<- 1
42 PSI2 [ 5 , 6 ]<- 0
43 PSI2 [ 5 , 7 ]<- 0
44 PSI2 [ 5 , 8 ]<- 0
45 PSI2 [ 5 , 9 ]<- 0
46 PSI2 [ 5 , 10 ]<- 0
47 PSI2 [ 5 , 11 ]<- 0
48 PSI2 [ 5 , 12 ]<- 0
49 PSI2 [ 5 , 13 ]<- 0
50 PSI2 [ 5 , 14 ]<- 0
51 PSI2 [ 5 , 15 ]<- 0
52 PSI2 [ 5 , 16 ]<- 0
53
54 PSI2 [ 6 , 1 ]<- 0
55 PSI2 [ 6 , 2 ]<- 0
56 PSI2 [ 6 , 3 ]<- 0
57
58
59
60
```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```
PSI2 [ 6 , 4 ]<- 0
PSI2 [ 6 , 5 ]<- 0
PSI2 [ 6 , 6 ]<- 1
PSI2 [ 6 , 7 ]<- 0
PSI2 [ 6 , 8 ]<- 0
PSI2 [ 6 , 9 ]<- 0
PSI2 [ 6 , 10 ]<- 0
PSI2 [ 6 , 11 ]<- 0
PSI2 [ 6 , 12 ]<- 0
PSI2 [ 6 , 13 ]<- 0
PSI2 [ 6 , 14 ]<- 0
PSI2 [ 6 , 15 ]<- 0
PSI2 [ 6 , 16 ]<- 0

PSI2 [ 7 , 1 ]<- 0
PSI2 [ 7 , 2 ]<- 0
PSI2 [ 7 , 3 ]<- 0
PSI2 [ 7 , 4 ]<- 0
PSI2 [ 7 , 5 ]<- 0
PSI2 [ 7 , 6 ]<- 0
PSI2 [ 7 , 7 ]<- 1
PSI2 [ 7 , 8 ]<- 0
PSI2 [ 7 , 9 ]<- 0
PSI2 [ 7 , 10 ]<- 0
PSI2 [ 7 , 11 ]<- 0
PSI2 [ 7 , 12 ]<- 0
PSI2 [ 7 , 13 ]<- 0
PSI2 [ 7 , 14 ]<- 0
PSI2 [ 7 , 15 ]<- 0
PSI2 [ 7 , 16 ]<- 0

PSI2 [ 8 , 1 ]<- 0
PSI2 [ 8 , 2 ]<- 0
PSI2 [ 8 , 3 ]<- 0
PSI2 [ 8 , 4 ]<- 0
PSI2 [ 8 , 5 ]<- 0
PSI2 [ 8 , 6 ]<- 0
PSI2 [ 8 , 7 ]<- 0
PSI2 [ 8 , 8 ]<- beta[1]
PSI2 [ 8 , 9 ]<- 1-beta[1]
PSI2 [ 8 , 10 ]<- 0
PSI2 [ 8 , 11 ]<- 0
PSI2 [ 8 , 12 ]<- 0
PSI2 [ 8 , 13 ]<- 0
PSI2 [ 8 , 14 ]<- 0
PSI2 [ 8 , 15 ]<- 0
PSI2 [ 8 , 16 ]<- 0

PSI2 [ 9 , 1 ]<- 0
PSI2 [ 9 , 2 ]<- 0
PSI2 [ 9 , 3 ]<- 0
PSI2 [ 9 , 4 ]<- 0
PSI2 [ 9 , 5 ]<- 0
```

```
1
2
3
4 PSI2 [ 9 , 6 ]<- 0
5 PSI2 [ 9 , 7 ]<- 0
6 PSI2 [ 9 , 8 ]<- 0
7 PSI2 [ 9 , 9 ]<- 0
8 PSI2 [ 9 , 10 ]<- beta[2]
9 PSI2 [ 9 , 11 ]<- 1-beta[2]
10 PSI2 [ 9 , 12 ]<- 0
11 PSI2 [ 9 , 13 ]<- 0
12 PSI2 [ 9 , 14 ]<- 0
13 PSI2 [ 9 , 15 ]<- 0
14 PSI2 [ 9 , 16 ]<- 0
15
16 PSI2 [ 10 , 1 ]<- 0
17 PSI2 [ 10 , 2 ]<- 0
18 PSI2 [ 10 , 3 ]<- 0
19 PSI2 [ 10 , 4 ]<- 0
20 PSI2 [ 10 , 5 ]<- 0
21 PSI2 [ 10 , 6 ]<- 0
22 PSI2 [ 10 , 7 ]<- 0
23 PSI2 [ 10 , 8 ]<- 0
24 PSI2 [ 10 , 9 ]<- 0
25 PSI2 [ 10 , 10 ]<- 0
26 PSI2 [ 10 , 11 ]<- 0
27 PSI2 [ 10 , 12 ]<- beta[3]
28 PSI2 [ 10 , 13 ]<- 1-beta[3]
29 PSI2 [ 10 , 14 ]<- 0
30 PSI2 [ 10 , 15 ]<- 0
31 PSI2 [ 10 , 16 ]<- 0
32
33 PSI2 [ 11 , 1 ]<- 0
34 PSI2 [ 11 , 2 ]<- 0
35 PSI2 [ 11 , 3 ]<- 0
36 PSI2 [ 11 , 4 ]<- 0
37 PSI2 [ 11 , 5 ]<- 0
38 PSI2 [ 11 , 6 ]<- 0
39 PSI2 [ 11 , 7 ]<- 0
40 PSI2 [ 11 , 8 ]<- 0
41 PSI2 [ 11 , 9 ]<- 0
42 PSI2 [ 11 , 10 ]<- 0
43 PSI2 [ 11 , 11 ]<- 0
44 PSI2 [ 11 , 12 ]<- beta[3]
45 PSI2 [ 11 , 13 ]<- 1-beta[3]
46 PSI2 [ 11 , 14 ]<- 0
47 PSI2 [ 11 , 15 ]<- 0
48 PSI2 [ 11 , 16 ]<- 0
49
50 PSI2 [ 12 , 1 ]<- 0
51 PSI2 [ 12 , 2 ]<- 0
52 PSI2 [ 12 , 3 ]<- 0
53 PSI2 [ 12 , 4 ]<- 0
54 PSI2 [ 12 , 5 ]<- 0
55 PSI2 [ 12 , 6 ]<- 0
56 PSI2 [ 12 , 7 ]<- 0
57
58
59
60
```

```

1
2
3
4 PSI2 [ 12 , 8 ]<- 0
5 PSI2 [ 12 , 9 ]<- 0
6 PSI2 [ 12 , 10 ]<- 0
7 PSI2 [ 12 , 11 ]<- 0
8 PSI2 [ 12 , 12 ]<- 0
9 PSI2 [ 12 , 13 ]<- 0
10 PSI2 [ 12 , 14 ]<- beta[4]
11 PSI2 [ 12 , 15 ]<- 1-beta[4]
12 PSI2 [ 12 , 16 ]<- 0
13
14 PSI2 [ 13 , 1 ]<- 0
15 PSI2 [ 13 , 2 ]<- 0
16 PSI2 [ 13 , 3 ]<- 0
17 PSI2 [ 13 , 4 ]<- 0
18 PSI2 [ 13 , 5 ]<- 0
19 PSI2 [ 13 , 6 ]<- 0
20 PSI2 [ 13 , 7 ]<- 0
21 PSI2 [ 13 , 8 ]<- 0
22 PSI2 [ 13 , 9 ]<- 0
23 PSI2 [ 13 , 10 ]<- 0
24 PSI2 [ 13 , 11 ]<- 0
25 PSI2 [ 13 , 12 ]<- 0
26 PSI2 [ 13 , 13 ]<- 0
27 PSI2 [ 13 , 14 ]<- 0
28 PSI2 [ 13 , 15 ]<- 0
29 PSI2 [ 13 , 16 ]<- 1
30
31 # PSI3:litter size probabilities
32 PSI3 [ 1 , 1 ]<- 0
33 PSI3 [ 1 , 2 ]<- 1
34 PSI3 [ 1 , 3 ]<- 0
35 PSI3 [ 1 , 4 ]<- 0
36 PSI3 [ 1 , 5 ]<- 0
37 PSI3 [ 1 , 6 ]<- 0
38 PSI3 [ 1 , 7 ]<- 0
39 PSI3 [ 1 , 8 ]<- 0
40 PSI3 [ 1 , 9 ]<- 0
41 PSI3 [ 1 , 10 ]<- 0
42 PSI3 [ 1 , 11 ]<- 0
43 PSI3 [ 1 , 12 ]<- 0
44
45 PSI3 [ 2 , 1 ]<- 0
46 PSI3 [ 2 , 2 ]<- 0
47 PSI3 [ 2 , 3 ]<- 1
48 PSI3 [ 2 , 4 ]<- 0
49 PSI3 [ 2 , 5 ]<- 0
50 PSI3 [ 2 , 6 ]<- 0
51 PSI3 [ 2 , 7 ]<- 0
52 PSI3 [ 2 , 8 ]<- 0
53 PSI3 [ 2 , 9 ]<- 0
54 PSI3 [ 2 , 10 ]<- 0
55 PSI3 [ 2 , 11 ]<- 0
56 PSI3 [ 2 , 12 ]<- 0
57
58
59
60

```

```
1
2
3
4 PSI3 [ 3 , 1 ]<- 0
5 PSI3 [ 3 , 2 ]<- 0
6 PSI3 [ 3 , 3 ]<- 0
7 PSI3 [ 3 , 4 ]<- 1
8 PSI3 [ 3 , 5 ]<- 0
9 PSI3 [ 3 , 6 ]<- 0
10 PSI3 [ 3 , 7 ]<- 0
11 PSI3 [ 3 , 8 ]<- 0
12 PSI3 [ 3 , 9 ]<- 0
13 PSI3 [ 3 , 10 ]<- 0
14 PSI3 [ 3 , 11 ]<- 0
15 PSI3 [ 3 , 12 ]<- 0
16
17 PSI3 [ 4 , 1 ]<- 0
18 PSI3 [ 4 , 2 ]<- 0
19 PSI3 [ 4 , 3 ]<- 0
20 PSI3 [ 4 , 4 ]<- 0
21 PSI3 [ 4 , 5 ]<- 0
22 PSI3 [ 4 , 6 ]<- 0
23 PSI3 [ 4 , 7 ]<- 1
24 PSI3 [ 4 , 8 ]<- 0
25 PSI3 [ 4 , 9 ]<- 0
26 PSI3 [ 4 , 10 ]<- 0
27 PSI3 [ 4 , 11 ]<- 0
28 PSI3 [ 4 , 12 ]<- 0
29
30 PSI3 [ 5 , 1 ]<- 0
31 PSI3 [ 5 , 2 ]<- 0
32 PSI3 [ 5 , 3 ]<- 0
33 PSI3 [ 5 , 4 ]<- 0
34 PSI3 [ 5 , 5 ]<- 0
35 PSI3 [ 5 , 6 ]<- 0
36 PSI3 [ 5 , 7 ]<- 0
37 PSI3 [ 5 , 8 ]<- 1
38 PSI3 [ 5 , 9 ]<- 0
39 PSI3 [ 5 , 10 ]<- 0
40 PSI3 [ 5 , 11 ]<- 0
41 PSI3 [ 5 , 12 ]<- 0
42
43 PSI3 [ 6 , 1 ]<- 0
44 PSI3 [ 6 , 2 ]<- 0
45 PSI3 [ 6 , 3 ]<- 0
46 PSI3 [ 6 , 4 ]<- 0
47 PSI3 [ 6 , 5 ]<- 0
48 PSI3 [ 6 , 6 ]<- 0
49 PSI3 [ 6 , 7 ]<- 0
50 PSI3 [ 6 , 8 ]<- 0
51 PSI3 [ 6 , 9 ]<- 1
52 PSI3 [ 6 , 10 ]<- 0
53 PSI3 [ 6 , 11 ]<- 0
54 PSI3 [ 6 , 12 ]<- 0
55
56 PSI3 [ 7 , 1 ]<- 0
57
58
59
60
```



```

1
2
3
4 PSI3 [ 7 , 2 ]<- 0
5 PSI3 [ 7 , 3 ]<- 0
6 PSI3 [ 7 , 4 ]<- 0
7 PSI3 [ 7 , 5 ]<- 0
8 PSI3 [ 7 , 6 ]<- 0
9 PSI3 [ 7 , 7 ]<- 0
10 PSI3 [ 7 , 8 ]<- 0
11 PSI3 [ 7 , 9 ]<- 0
12 PSI3 [ 7 , 10 ]<- 1
13 PSI3 [ 7 , 11 ]<- 0
14 PSI3 [ 7 , 12 ]<- 0
15
16 PSI3 [ 8 , 1 ]<- 0
17 PSI3 [ 8 , 2 ]<- 0
18 PSI3 [ 8 , 3 ]<- 0
19 PSI3 [ 8 , 4 ]<- 0
20 PSI3 [ 8 , 5 ]<- gamma[1]
21 PSI3 [ 8 , 6 ]<- 1-gamma[1]
22 PSI3 [ 8 , 7 ]<- 0
23 PSI3 [ 8 , 8 ]<- 0
24 PSI3 [ 8 , 9 ]<- 0
25 PSI3 [ 8 , 10 ]<- 0
26 PSI3 [ 8 , 11 ]<- 0
27 PSI3 [ 8 , 12 ]<- 0
28
29 PSI3 [ 9 , 1 ]<- 0
30 PSI3 [ 9 , 2 ]<- 0
31 PSI3 [ 9 , 3 ]<- 0
32 PSI3 [ 9 , 4 ]<- 0
33 PSI3 [ 9 , 5 ]<- 0
34 PSI3 [ 9 , 6 ]<- 0
35 PSI3 [ 9 , 7 ]<- 0
36 PSI3 [ 9 , 8 ]<- 0
37 PSI3 [ 9 , 9 ]<- 0
38 PSI3 [ 9 , 10 ]<- 0
39 PSI3 [ 9 , 11 ]<- 1
40 PSI3 [ 9 , 12 ]<- 0
41
42 PSI3 [ 10 , 1 ]<- 0
43 PSI3 [ 10 , 2 ]<- 0
44 PSI3 [ 10 , 3 ]<- 0
45 PSI3 [ 10 , 4 ]<- 0
46 PSI3 [ 10 , 5 ]<- gamma[2]
47 PSI3 [ 10 , 6 ]<- 1-gamma[2]
48 PSI3 [ 10 , 7 ]<- 0
49 PSI3 [ 10 , 8 ]<- 0
50 PSI3 [ 10 , 9 ]<- 0
51 PSI3 [ 10 , 10 ]<- 0
52 PSI3 [ 10 , 11 ]<- 0
53 PSI3 [ 10 , 12 ]<- 0
54
55 PSI3 [ 11 , 1 ]<- 0
56 PSI3 [ 11 , 2 ]<- 0
57
58
59
60

```

```

1
2
3
4 PSI3 [ 11 , 3 ]<- 0
5 PSI3 [ 11 , 4 ]<- 0
6 PSI3 [ 11 , 5 ]<- 0
7 PSI3 [ 11 , 6 ]<- 0
8 PSI3 [ 11 , 7 ]<- 0
9 PSI3 [ 11 , 8 ]<- 0
10 PSI3 [ 11 , 9 ]<- 0
11 PSI3 [ 11 , 10 ]<- 0
12 PSI3 [ 11 , 11 ]<- 1
13 PSI3 [ 11 , 12 ]<- 0
14
15 PSI3 [ 12 , 1 ]<- 0
16 PSI3 [ 12 , 2 ]<- 0
17 PSI3 [ 12 , 3 ]<- 0
18 PSI3 [ 12 , 4 ]<- 0
19 PSI3 [ 12 , 5 ]<- gamma[3]
20 PSI3 [ 12 , 6 ]<- 1-gamma[3]
21 PSI3 [ 12 , 7 ]<- 0
22 PSI3 [ 12 , 8 ]<- 0
23 PSI3 [ 12 , 9 ]<- 0
24 PSI3 [ 12 , 10 ]<- 0
25 PSI3 [ 12 , 11 ]<- 0
26 PSI3 [ 12 , 12 ]<- 0
27
28 PSI3 [ 13 , 1 ]<- 0
29 PSI3 [ 13 , 2 ]<- 0
30 PSI3 [ 13 , 3 ]<- 0
31 PSI3 [ 13 , 4 ]<- 0
32 PSI3 [ 13 , 5 ]<- 0
33 PSI3 [ 13 , 6 ]<- 0
34 PSI3 [ 13 , 7 ]<- 0
35 PSI3 [ 13 , 8 ]<- 0
36 PSI3 [ 13 , 9 ]<- 0
37 PSI3 [ 13 , 10 ]<- 0
38 PSI3 [ 13 , 11 ]<- 1
39 PSI3 [ 13 , 12 ]<- 0
40
41 PSI3 [ 14 , 1 ]<- 0
42 PSI3 [ 14 , 2 ]<- 0
43 PSI3 [ 14 , 3 ]<- 0
44 PSI3 [ 14 , 4 ]<- 0
45 PSI3 [ 14 , 5 ]<- gamma[4]
46 PSI3 [ 14 , 6 ]<- 1-gamma[4]
47 PSI3 [ 14 , 7 ]<- 0
48 PSI3 [ 14 , 8 ]<- 0
49 PSI3 [ 14 , 9 ]<- 0
50 PSI3 [ 14 , 10 ]<- 0
51 PSI3 [ 14 , 11 ]<- 0
52 PSI3 [ 14 , 12 ]<- 0
53
54 PSI3 [ 15 , 1 ]<- 0
55 PSI3 [ 15 , 2 ]<- 0
56 PSI3 [ 15 , 3 ]<- 0
57
58
59
60

```

```

1
2
3
4 PSI3 [ 15 , 4 ]<- 0
5 PSI3 [ 15 , 5 ]<- 0
6 PSI3 [ 15 , 6 ]<- 0
7 PSI3 [ 15 , 7 ]<- 0
8 PSI3 [ 15 , 8 ]<- 0
9 PSI3 [ 15 , 9 ]<- 0
10 PSI3 [ 15 , 10 ]<- 0
11 PSI3 [ 15 , 11 ]<- 1
12 PSI3 [ 15 , 12 ]<- 0
13
14 PSI3 [ 16 , 1 ]<- 0
15 PSI3 [ 16 , 2 ]<- 0
16 PSI3 [ 16 , 3 ]<- 0
17 PSI3 [ 16 , 4 ]<- 0
18 PSI3 [ 16 , 5 ]<- 0
19 PSI3 [ 16 , 6 ]<- 0
20 PSI3 [ 16 , 7 ]<- 0
21 PSI3 [ 16 , 8 ]<- 0
22 PSI3 [ 16 , 9 ]<- 0
23 PSI3 [ 16 , 10 ]<- 0
24 PSI3 [ 16 , 11 ]<- 0
25 PSI3 [ 16 , 12 ]<- 1
26
27 # Matrix product for state-to-state transitions S
28 S[1:12,1:12] <- PHI[1:12,1:12] %*% PSI1[1:12,1:13] %*% PSI2[1:13,1:16] %*% PSI3[1:16,1:12]
29
30 ## Observation process: Define probabilities of E(t) given S(t).
31
32 #for initial capture, conditional on first capture
33 EO [ 1 , 1 ]<- 0
34 EO [ 1 , 2 ]<- 1
35 EO [ 1 , 3 ]<- 0
36 EO [ 1 , 4 ]<- 0
37 EO [ 1 , 5 ]<- 0
38 EO [ 1 , 6 ]<- 0
39 EO [ 1 , 7 ]<- 0
40 EO [ 1 , 8 ]<- 0
41 EO [ 1 , 9 ]<- 0
42 EO [ 1 , 10 ]<- 0
43 EO [ 1 , 11 ]<- 0
44 EO [ 1 , 12 ]<- 0
45
46 EO [ 2 , 1 ]<- 0
47 EO [ 2 , 2 ]<- 0
48 EO [ 2 , 3 ]<- 1
49 EO [ 2 , 4 ]<- 0
50 EO [ 2 , 5 ]<- 0
51 EO [ 2 , 6 ]<- 0
52 EO [ 2 , 7 ]<- 0
53 EO [ 2 , 8 ]<- 0
54 EO [ 2 , 9 ]<- 0
55 EO [ 2 , 10 ]<- 0
56
57
58
59
60

```

```
1
2
3
4 EO [ 2 , 11 ]<- 0
5 EO [ 2 , 12 ]<- 0
6
7 EO [ 3 , 1 ]<- 0
8 EO [ 3 , 2 ]<- 0
9 EO [ 3 , 3 ]<- 0
10 EO [ 3 , 4 ]<- 1
11 EO [ 3 , 5 ]<- 0
12 EO [ 3 , 6 ]<- 0
13 EO [ 3 , 7 ]<- 0
14 EO [ 3 , 8 ]<- 0
15 EO [ 3 , 9 ]<- 0
16 EO [ 3 , 10 ]<- 0
17 EO [ 3 , 11 ]<- 0
18 EO [ 3 , 12 ]<- 0
19
20 EO [ 4 , 1 ]<- 0
21 EO [ 4 , 2 ]<- 0
22 EO [ 4 , 3 ]<- 0
23 EO [ 4 , 4 ]<- 0
24 EO [ 4 , 5 ]<- 1
25 EO [ 4 , 6 ]<- 0
26 EO [ 4 , 7 ]<- 0
27 EO [ 4 , 8 ]<- 0
28 EO [ 4 , 9 ]<- 0
29 EO [ 4 , 10 ]<- 0
30 EO [ 4 , 11 ]<- 0
31 EO [ 4 , 12 ]<- 0
32
33 EO [ 5 , 1 ]<- 0
34 EO [ 5 , 2 ]<- 0
35 EO [ 5 , 3 ]<- 0
36 EO [ 5 , 4 ]<- 0
37 EO [ 5 , 5 ]<- 0
38 EO [ 5 , 6 ]<- 1
39 EO [ 5 , 7 ]<- 0
40 EO [ 5 , 8 ]<- 0
41 EO [ 5 , 9 ]<- 0
42 EO [ 5 , 10 ]<- 0
43 EO [ 5 , 11 ]<- 0
44 EO [ 5 , 12 ]<- 0
45
46 EO [ 6 , 1 ]<- 0
47 EO [ 6 , 2 ]<- 0
48 EO [ 6 , 3 ]<- 0
49 EO [ 6 , 4 ]<- 0
50 EO [ 6 , 5 ]<- 0
51 EO [ 6 , 6 ]<- 0
52 EO [ 6 , 7 ]<- 1
53 EO [ 6 , 8 ]<- 0
54 EO [ 6 , 9 ]<- 0
55 EO [ 6 , 10 ]<- 0
56 EO [ 6 , 11 ]<- 0
57
58
59
60
```

```
1
2
3
4   EO   [ 6 , 12 ]<- 0
5
6   EO   [ 7 , 1 ]<- 0
7   EO   [ 7 , 2 ]<- 0
8   EO   [ 7 , 3 ]<- 0
9   EO   [ 7 , 4 ]<- 0
10  EO   [ 7 , 5 ]<- 0
11  EO   [ 7 , 6 ]<- 0
12  EO   [ 7 , 7 ]<- 0
13  EO   [ 7 , 8 ]<- 1
14  EO   [ 7 , 9 ]<- 0
15  EO   [ 7 , 10 ]<- 0
16  EO   [ 7 , 11 ]<- 0
17  EO   [ 7 , 12 ]<- 0
18
19  EO   [ 8 , 1 ]<- 0
20  EO   [ 8 , 2 ]<- 0
21  EO   [ 8 , 3 ]<- 0
22  EO   [ 8 , 4 ]<- 0
23  EO   [ 8 , 5 ]<- 0
24  EO   [ 8 , 6 ]<- 0
25  EO   [ 8 , 7 ]<- 0
26  EO   [ 8 , 8 ]<- 0
27  EO   [ 8 , 9 ]<- 1
28  EO   [ 8 , 10 ]<- 0
29  EO   [ 8 , 11 ]<- 0
30  EO   [ 8 , 12 ]<- 0
31
32  EO   [ 9 , 1 ]<- 0
33  EO   [ 9 , 2 ]<- 0
34  EO   [ 9 , 3 ]<- 0
35  EO   [ 9 , 4 ]<- 0
36  EO   [ 9 , 5 ]<- 0
37  EO   [ 9 , 6 ]<- 0
38  EO   [ 9 , 7 ]<- 0
39  EO   [ 9 , 8 ]<- 0
40  EO   [ 9 , 9 ]<- 0
41  EO   [ 9 , 10 ]<- 1
42  EO   [ 9 , 11 ]<- 0
43  EO   [ 9 , 12 ]<- 0
44
45  EO   [ 10 , 1 ]<- 0
46  EO   [ 10 , 2 ]<- 0
47  EO   [ 10 , 3 ]<- 0
48  EO   [ 10 , 4 ]<- 0
49  EO   [ 10 , 5 ]<- 0
50  EO   [ 10 , 6 ]<- 0
51  EO   [ 10 , 7 ]<- 0
52  EO   [ 10 , 8 ]<- 0
53  EO   [ 10 , 9 ]<- 0
54  EO   [ 10 , 10 ]<- 0
55  EO   [ 10 , 11 ]<- 1
56  EO   [ 10 , 12 ]<- 0
57
58
59
60
```

```

1
2
3
4 EO [ 11 , 1 ]<- 0
5 EO [ 11 , 2 ]<- 0
6 EO [ 11 , 3 ]<- 0
7 EO [ 11 , 4 ]<- 0
8 EO [ 11 , 5 ]<- 0
9 EO [ 11 , 6 ]<- 0
10 EO [ 11 , 7 ]<- 0
11 EO [ 11 , 8 ]<- 0
12 EO [ 11 , 9 ]<- 0
13 EO [ 11 , 10 ]<- 0
14 EO [ 11 , 11 ]<- 0
15 EO [ 11 , 12 ]<- 1
16
17 EO [ 12 , 1 ]<- 1
18 EO [ 12 , 2 ]<- 0
19 EO [ 12 , 3 ]<- 0
20 EO [ 12 , 4 ]<- 0
21 EO [ 12 , 5 ]<- 0
22 EO [ 12 , 6 ]<- 0
23 EO [ 12 , 7 ]<- 0
24 EO [ 12 , 8 ]<- 0
25 EO [ 12 , 9 ]<- 0
26 EO [ 12 , 10 ]<- 0
27 EO [ 12 , 11 ]<- 0
28 EO [ 12 , 12 ]<- 0
29
30 # departure probability of a2 offspring
31 for(i in 1:N){
32   for(t in 1:(Years-1)){
33     E1 [ 1 , 1 ,i,t]<- 1
34     E1 [ 1 , 2 ,i,t]<- 0
35     E1 [ 1 , 3 ,i,t]<- 0
36     E1 [ 1 , 4 ,i,t]<- 0
37     E1 [ 1 , 5 ,i,t]<- 0
38     E1 [ 1 , 6 ,i,t]<- 0
39     E1 [ 1 , 7 ,i,t]<- 0
40     E1 [ 1 , 8 ,i,t]<- 0
41     E1 [ 1 , 9 ,i,t]<- 0
42     E1 [ 1 , 10,i,t]<- 0
43     E1 [ 1 , 11,i,t]<- 0
44     E1 [ 1 , 12,i,t]<- 0
45
46     E1 [ 2 , 1 ,i,t]<- 0
47     E1 [ 2 , 2 ,i,t]<- 1
48     E1 [ 2 , 3 ,i,t]<- 0
49     E1 [ 2 , 4 ,i,t]<- 0
50     E1 [ 2 , 5 ,i,t]<- 0
51     E1 [ 2 , 6 ,i,t]<- 0
52     E1 [ 2 , 7 ,i,t]<- 0
53     E1 [ 2 , 8 ,i,t]<- 0
54     E1 [ 2 , 9 ,i,t]<- 0
55     E1 [ 2 , 10,i,t]<- 0
56     E1 [ 2 , 11,i,t]<- 0
57
58
59
60

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```

E1 [ 2 , 12,i,t]<- 0

E1 [ 3 , 1 ,i,t]<- 0
E1 [ 3 , 2 ,i,t]<- 0
E1 [ 3 , 3 ,i,t]<- 1
E1 [ 3 , 4 ,i,t]<- 0
E1 [ 3 , 5 ,i,t]<- 0
E1 [ 3 , 6 ,i,t]<- 0
E1 [ 3 , 7 ,i,t]<- 0
E1 [ 3 , 8 ,i,t]<- 0
E1 [ 3 , 9 ,i,t]<- 0
E1 [ 3 , 10,i,t]<- 0
E1 [ 3 , 11,i,t]<- 0
E1 [ 3 , 12,i,t]<- 0

E1 [ 4 , 1 ,i,t]<- 0
E1 [ 4 , 2 ,i,t]<- 0
E1 [ 4 , 3 ,i,t]<- 0
E1 [ 4 , 4 ,i,t]<- 1
E1 [ 4 , 5 ,i,t]<- 0
E1 [ 4 , 6 ,i,t]<- 0
E1 [ 4 , 7 ,i,t]<- 0
E1 [ 4 , 8 ,i,t]<- 0
E1 [ 4 , 9 ,i,t]<- 0
E1 [ 4 , 10,i,t]<- 0
E1 [ 4 , 11,i,t]<- 0
E1 [ 4 , 12,i,t]<- 0

E1 [ 5 , 1,i,t]<- 0
E1 [ 5 , 2,i,t]<- 0
E1 [ 5 , 3,i,t]<- 0
E1 [ 5 , 4,i,t]<- 0
E1 [ 5 , 5,i,t]<- 1
E1 [ 5 , 6,i,t]<- 0
E1 [ 5 , 7,i,t]<- 0
E1 [ 5 , 8,i,t]<- 0
E1 [ 5 , 9,i,t]<- 0
E1 [ 5 , 10,i,t]<- 0
E1 [ 5 , 11,i,t]<- 0
E1 [ 5 , 12,i,t]<- 0

E1 [ 6 , 1 ,i,t]<- 0
E1 [ 6 , 2 ,i,t]<- 0
E1 [ 6 , 3 ,i,t]<- 0
E1 [ 6 , 4 ,i,t]<- 0
E1 [ 6 , 5 ,i,t]<- 0
E1 [ 6 , 6 ,i,t]<- 1
E1 [ 6 , 7 ,i,t]<- 0
E1 [ 6 , 8 ,i,t]<- 0
E1 [ 6 , 9 ,i,t]<- 0
E1 [ 6 , 10,i,t]<- 0
E1 [ 6 , 11,i,t]<- 0
E1 [ 6 , 12,i,t]<- 0

```

```

1
2
3
4     E1     [ 7 , 1 ,i,t]<- 0
5     E1     [ 7 , 2 ,i,t]<- 0
6     E1     [ 7 , 3 ,i,t]<- 0
7     E1     [ 7 , 4 ,i,t]<- 0
8     E1     [ 7 , 5 ,i,t]<- 0
9     E1     [ 7 , 6 ,i,t]<- 0
10    E1     [ 7 , 7 ,i,t]<- 1
11    E1     [ 7 , 8 ,i,t]<- 0
12    E1     [ 7 , 9 ,i,t]<- 0
13    E1     [ 7 , 10,i,t]<- 0
14    E1     [ 7 , 11,i,t]<- 0
15    E1     [ 7 , 12,i,t]<- 0
16
17    E1     [ 8 , 1 ,i,t]<- 0
18    E1     [ 8 , 2 ,i,t]<- 0
19    E1     [ 8 , 3 ,i,t]<- 0
20    E1     [ 8 , 4 ,i,t]<- 0
21    E1     [ 8 , 5 ,i,t]<- 0
22    E1     [ 8 , 6 ,i,t]<- 0
23    E1     [ 8 , 7 ,i,t]<- 0
24    E1     [ 8 , 8 ,i,t]<- 1
25    E1     [ 8 , 9 ,i,t]<- 0
26    E1     [ 8 , 10,i,t]<- 0
27    E1     [ 8 , 11,i,t]<- 0
28    E1     [ 8 , 12,i,t]<- 0
29
30    E1     [ 9 , 1 ,i,t]<- 0
31    E1     [ 9 , 2 ,i,t]<- 0
32    E1     [ 9 , 3 ,i,t]<- 0
33    E1     [ 9 , 4 ,i,t]<- 0
34    E1     [ 9 , 5 ,i,t]<- 0
35    E1     [ 9 , 6 ,i,t]<- 0
36    E1     [ 9 , 7 ,i,t]<- 0
37    E1     [ 9 , 8 ,i,t]<- 0
38    E1     [ 9 , 9 ,i,t]<- 1-alpha[i,t+1]
39    E1     [ 9 , 10,i,t]<- 0
40    E1     [ 9 , 11,i,t]<- alpha[i,t+1]
41    E1     [ 9 , 12,i,t]<- 0
42
43    E1     [ 10 , 1,i,t]<- 0
44    E1     [ 10 , 2,i,t]<- 0
45    E1     [ 10 , 3,i,t]<- 0
46    E1     [ 10 , 4,i,t]<- 0
47    E1     [ 10 , 5,i,t]<- 0
48    E1     [ 10 , 6,i,t]<- 0
49    E1     [ 10 , 7,i,t]<- 0
50    E1     [ 10 , 8,i,t]<- 0
51    E1     [ 10 , 9,i,t]<- 2*(1-alpha[i,t+1])*alpha[i,t+1]
52    E1     [ 10 , 10,i,t]<- 1 - (2*(1-alpha[i,t+1])*alpha[i,t+1]) - (alpha[i,t+1])^2
53    E1     [ 10 , 11,i,t]<- (alpha[i,t+1])^2
54    E1     [ 10 , 12,i,t]<- 0
55
56    E1     [ 11 , 1 ,i,t]<- 0
57
58
59
60

```


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```

E1 [ 11 , 2 ,i,t]<- 0
E1 [ 11 , 3 ,i,t]<- 0
E1 [ 11 , 4 ,i,t]<- 0
E1 [ 11 , 5 ,i,t]<- 0
E1 [ 11 , 6 ,i,t]<- 0
E1 [ 11 , 7 ,i,t]<- 0
E1 [ 11 , 8 ,i,t]<- 0
E1 [ 11 , 9 ,i,t]<- 0
E1 [ 11 , 10,i,t]<- 0
E1 [ 11 , 11,i,t]<- 1
E1 [ 11 , 12,i,t]<- 0

E1 [ 12 , 1 ,i,t]<- 0
E1 [ 12 , 2 ,i,t]<- 0
E1 [ 12 , 3 ,i,t]<- 0
E1 [ 12 , 4 ,i,t]<- 0
E1 [ 12 , 5 ,i,t]<- 0
E1 [ 12 , 6 ,i,t]<- 0
E1 [ 12 , 7 ,i,t]<- 0
E1 [ 12 , 8 ,i,t]<- 0
E1 [ 12 , 9 ,i,t]<- 0
E1 [ 12 , 10,i,t]<- 0
E1 [ 12 , 11,i,t]<- 0
E1 [ 12 , 12,i,t]<- 1

# for recapture probability
E2 [ 1 , 1 ,i,t]<- 1 -p
E2 [ 1 , 2 ,i,t]<- p
E2 [ 1 , 3 ,i,t]<- 0
E2 [ 1 , 4 ,i,t]<- 0
E2 [ 1 , 5 ,i,t]<- 0
E2 [ 1 , 6 ,i,t]<- 0
E2 [ 1 , 7 ,i,t]<- 0
E2 [ 1 , 8 ,i,t]<- 0
E2 [ 1 , 9 ,i,t]<- 0
E2 [ 1 , 10,i,t]<- 0
E2 [ 1 , 11,i,t]<- 0
E2 [ 1 , 12,i,t]<- 0

E2 [ 2 , 1 ,i,t]<- 1 -p
E2 [ 2 , 2 ,i,t]<- 0
E2 [ 2 , 3 ,i,t]<- p
E2 [ 2 , 4 ,i,t]<- 0
E2 [ 2 , 5 ,i,t]<- 0
E2 [ 2 , 6 ,i,t]<- 0
E2 [ 2 , 7 ,i,t]<- 0
E2 [ 2 , 8 ,i,t]<- 0
E2 [ 2 , 9 ,i,t]<- 0
E2 [ 2 , 10,i,t]<- 0
E2 [ 2 , 11,i,t]<- 0
E2 [ 2 , 12,i,t]<- 0

E2 [ 3 , 1 ,i,t]<- 1 -p

```

```

1
2
3
4 E2 [ 3 , 2 ,i,t]<- 0
5 E2 [ 3 , 3 ,i,t]<- 0
6 E2 [ 3 , 4 ,i,t]<- p
7 E2 [ 3 , 5 ,i,t]<- 0
8 E2 [ 3 , 6 ,i,t]<- 0
9 E2 [ 3 , 7 ,i,t]<- 0
10 E2 [ 3 , 8 ,i,t]<- 0
11 E2 [ 3 , 9 ,i,t]<- 0
12 E2 [ 3 , 10,i,t]<- 0
13 E2 [ 3 , 11,i,t]<- 0
14 E2 [ 3 , 12,i,t]<- 0
15
16 E2 [ 4 , 1 ,i,t]<- 1 -p
17 E2 [ 4 , 2 ,i,t]<- 0
18 E2 [ 4 , 3 ,i,t]<- 0
19 E2 [ 4 , 4 ,i,t]<- 0
20 E2 [ 4 , 5 ,i,t]<- p
21 E2 [ 4 , 6 ,i,t]<- 0
22 E2 [ 4 , 7 ,i,t]<- 0
23 E2 [ 4 , 8 ,i,t]<- 0
24 E2 [ 4 , 9 ,i,t]<- 0
25 E2 [ 4 , 10,i,t]<- 0
26 E2 [ 4 , 11,i,t]<- 0
27 E2 [ 4 , 12,i,t]<- 0
28
29 E2 [ 5 , 1,i,t]<- 1 -p
30 E2 [ 5 , 2,i,t]<- 0
31 E2 [ 5 , 3,i,t]<- 0
32 E2 [ 5 , 4,i,t]<- 0
33 E2 [ 5 , 5,i,t]<- 0
34 E2 [ 5 , 6,i,t]<- p
35 E2 [ 5 , 7,i,t]<- 0
36 E2 [ 5 , 8,i,t]<- 0
37 E2 [ 5 , 9,i,t]<- 0
38 E2 [ 5 , 10,i,t]<- 0
39 E2 [ 5 , 11,i,t]<- 0
40 E2 [ 5 , 12,i,t]<- 0
41
42 E2 [ 6 , 1 ,i,t]<- 1 -p
43 E2 [ 6 , 2 ,i,t]<- 0
44 E2 [ 6 , 3 ,i,t]<- 0
45 E2 [ 6 , 4 ,i,t]<- 0
46 E2 [ 6 , 5 ,i,t]<- 0
47 E2 [ 6 , 6 ,i,t]<- 0
48 E2 [ 6 , 7 ,i,t]<- p
49 E2 [ 6 , 8 ,i,t]<- 0
50 E2 [ 6 , 9 ,i,t]<- 0
51 E2 [ 6 , 10,i,t]<- 0
52 E2 [ 6 , 11,i,t]<- 0
53 E2 [ 6 , 12,i,t]<- 0
54
55 E2 [ 7 , 1 ,i,t]<- 1 -p
56 E2 [ 7 , 2 ,i,t]<- 0
57
58
59
60

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```

E2 [ 7 , 3 ,i,t]<- 0
E2 [ 7 , 4 ,i,t]<- 0
E2 [ 7 , 5 ,i,t]<- 0
E2 [ 7 , 6 ,i,t]<- 0
E2 [ 7 , 7 ,i,t]<- 0
E2 [ 7 , 8 ,i,t]<- p
E2 [ 7 , 9 ,i,t]<- 0
E2 [ 7 , 10,i,t]<- 0
E2 [ 7 , 11,i,t]<- 0
E2 [ 7 , 12,i,t]<- 0

E2 [ 8 , 1 ,i,t]<- 1 -p
E2 [ 8 , 2 ,i,t]<- 0
E2 [ 8 , 3 ,i,t]<- 0
E2 [ 8 , 4 ,i,t]<- 0
E2 [ 8 , 5 ,i,t]<- 0
E2 [ 8 , 6 ,i,t]<- 0
E2 [ 8 , 7 ,i,t]<- 0
E2 [ 8 , 8 ,i,t]<- 0
E2 [ 8 , 9 ,i,t]<- p
E2 [ 8 , 10,i,t]<- 0
E2 [ 8 , 11,i,t]<- 0
E2 [ 8 , 12,i,t]<- 0

E2 [ 9 , 1 ,i,t]<- 1-p
E2 [ 9 , 2 ,i,t]<- 0
E2 [ 9 , 3 ,i,t]<- 0
E2 [ 9 , 4 ,i,t]<- 0
E2 [ 9 , 5 ,i,t]<- 0
E2 [ 9 , 6 ,i,t]<- 0
E2 [ 9 , 7 ,i,t]<- 0
E2 [ 9 , 8 ,i,t]<- 0
E2 [ 9 , 9 ,i,t]<- 0
E2 [ 9 , 10,i,t]<- p
E2 [ 9 , 11,i,t]<- 0
E2 [ 9 , 12,i,t]<- 0

E2 [ 10 , 1,i,t]<- 1-p
E2 [ 10 , 2,i,t]<- 0
E2 [ 10 , 3,i,t]<- 0
E2 [ 10 , 4,i,t]<- 0
E2 [ 10 , 5,i,t]<- 0
E2 [ 10 , 6,i,t]<- 0
E2 [ 10 , 7,i,t]<- 0
E2 [ 10 , 8,i,t]<- 0
E2 [ 10 , 9,i,t]<- 0
E2 [ 10 , 10,i,t]<- 0
E2 [ 10 , 11,i,t]<- p
E2 [ 10 , 12,i,t]<- 0

E2 [ 11 , 1 ,i,t]<- 1 - p
E2 [ 11 , 2 ,i,t]<- 0
E2 [ 11 , 3 ,i,t]<- 0

```

```

1
2
3
4     E2     [ 11 , 4 ,i,t]<- 0
5     E2     [ 11 , 5 ,i,t]<- 0
6     E2     [ 11 , 6 ,i,t]<- 0
7     E2     [ 11 , 7 ,i,t]<- 0
8     E2     [ 11 , 8 ,i,t]<- 0
9     E2     [ 11 , 9 ,i,t]<- 0
10    E2     [ 11 , 10,i,t]<- 0
11    E2     [ 11 , 11,i,t]<- 0
12    E2     [ 11 , 12,i,t]<- p
13
14    E2     [ 12 , 1 ,i,t]<- 1
15    E2     [ 12 , 2 ,i,t]<- 0
16    E2     [ 12 , 3 ,i,t]<- 0
17    E2     [ 12 , 4 ,i,t]<- 0
18    E2     [ 12 , 5 ,i,t]<- 0
19    E2     [ 12 , 6 ,i,t]<- 0
20    E2     [ 12 , 7 ,i,t]<- 0
21    E2     [ 12 , 8 ,i,t]<- 0
22    E2     [ 12 , 9 ,i,t]<- 0
23    E2     [ 12 , 10,i,t]<- 0
24    E2     [ 12 , 11,i,t]<- 0
25    E2     [ 12 , 12,i,t]<- 0
26
27    # Matrix product for offspring independence and recapture
28    E[1:12,1:12,i,t] <- E1[1:12,1:12,i,t] %*% E2[1:12,1:12,i,t]
29  }
30 }
31
32 ## LIKELIHOOD
33
34 for (i in 1:N) # for each individual
35 {
36   # The estimated probabilities of initial states S0 are the proportions in each state
37   #at first capture occasion
38   alive[i,First[i]] ~ dcat(S0[1:12])
39   mydata[i,First[i]] ~ dcat(E0[alive[i,First[i]],1:12])
40
41   for (j in (First[i]+1):Years)
42   {
43     ## STATE EQUATIONS ##
44     # draw S(t) given S(t-1)
45     alive[i,j] ~ dcat(S[alive[i,j-1],1:12])
46
47     ## OBSERVATION EQUATIONS ##
48     # draw events E(t) given states S(t)
49
50     mydata[i,j] ~ dcat(E[alive[i,j],1:12,i,j-1])
51
52   }
53 }
54
55
56
57
58
59
60

```

```

1
2
3
4  ## PRIORS
5  # capture probability
6  p ~ dunif(0,1)
7
8  # juveniles, subadults and adult survival
9  phi ~ dunif(0,1)
10
11 # initial states
12 for (i in 1:10){ log(prop[i]) <- theta[i]
13   theta[i] ~ dnorm(0,1)}
14
15 # offspring survival
16 # litter survival n=2 offspring
17 102 <- 1 -(1- s[2]^2 -2*s[2]*(1-s[2]))
18 112 <- 1- (1- s[4]^2 -2*s[4]*(1-s[4]))
19 # individual offspring survival
20 for(i in 1:2){s[i]~ dunif(0,1)}
21   # Set constraints
22   for(u in 1:2){ X[u] ~ dunif(0,1)} # with X ~ U[0,1] then (a + ( b - a ) * X)
23   #so that s[1] < s[3] < phi[1] for litter of 1
24   s[3] <- s[1] + (phi[1] - s[1]) * X[1]
25   # and s[2] < s[4] < phi[1] for litters of 2
26   s[4] <- s[2] + (phi[1] - s[2]) * X[2]
27
28 # Breeding probability
29 kappa ~ dunif(0,1)
30 for(i in 1:4){beta[i]~ dunif(0,1)}
31
32 # Litter size probability
33 for(i in 1:4){gamma[i]~ dunif(0,1)}
34
35 } # end model
36
37   ",fill=TRUE)
38 sink()
39 #####
40 #####

```

We used non-informative priors on the model parameters, with uniform distribution between 0 and 1 for probabilities, and normal distribution with mean 0 and variance of 1 for regression coefficients. To help estimation of the parameters in the model, we introduced the constraint that survival of cubs (age <1) was lower than that of yearling survival (aged 1). We used one chain with 10 000 iterations and 4000 burnin.

Load the data (family unit CR histories, initial state matrix, date of captures) and fit the model :

```

47 RES <- list()
48
49 for(r in 1:100){
50
51 nameCH <- paste(repname, "/simCH", r, "_p", p, "_T", n.occasions, ".txt", sep="")
52 # load capture histories
53 data <- read.table(paste(nameCH), sep=" ", header=FALSE)
54 # initial values for state matrix
55 nameINIT <- paste(repname, "/siminit", r, "_p", p, "_T", n.occasions, ".txt", sep="")
56 initmat <- read.table(paste(nameINIT), sep="")
57
58
59
60

```

```

1
2
3
4 # date of capture
5 nameDAY <- paste(repname, "/simdaycapt", r, "_p", p, "_T", n.occasions, ".txt", sep="")
6 daycapt <- read.table(paste(nameDAY), sep="")
7
8 data <- data.matrix(data)
9 alive1 <- data.matrix(initmat)
10 head(data)
11 N <- dim(data)[1]
12 Years <- dim(data)[2]
13
14 # Compute vector with occasion of first capture
15 get.first <- function(x) min(which(x!=0))
16 First <- apply(data, 1, get.first)
17
18 # Predict departure probability function of date of capture
19 alpha = matrix(0,nrow=N,ncol=Years)
20   for(i in 1:N){
21     for(j in (First[i]+1):Years){
22       alpha[i,j] <- predict(modeld,newdata=list(doy=daycapt[i,j]),type="response")
23     }
24   }
25
26 # Bundle data for jags
27 mydatax <- list(N=N,First=First,Years=Years,mydata=data.matrix(data+1)
28               ,alpha=data.matrix(alpha))
29
30 # Initial values
31 init1 <- list(theta=rnorm(10, mean = 0, sd = 1), alive=alive1) #
32 inits <- list(init1)
33
34 # Parameters monitored
35 params <- c("phi","kappa","s","l02","l12","beta","gamma","p","S0")
36
37 # Call JAGS from R to fit the model
38 out <- jags(data=mydatax,inits=inits, parameters.to.save=params,
39            model.file = 'Multieventmodel_Fit_simul.txt',n.chains=1,
40            n.iter=10000,n.burnin=4000)
41
42 RES[[r]] <- out # store results
43 print(paste(r))
44 }
45 save(RES,file=paste('RES',n.occasions,'p',p,'.RData',sep="")) # save results
46
47
48
49

```

Post process simulation results

Load and plot the results:

```

51 # load results of the simulations
52 capture <- c(0.25,0.25,0.5,0.5)
53 filenames <- c("S1RESp0.25alpha05.RData","S2RESp0.25alphaDate.RData",
54              "S3RESp0.5alpha05.RData","S4RESp0.5alphaDate.RData")
55
56 EST <- CI1 <- CI2 <- simres <- biasall <- rMSEall <- list()
57
58
59
60

```

```

1
2
3
4 for(S in 1:4){
5   p = capture[S]
6
7   load(paste(filenamees[S]))
8
9   # parameters used to simulate the data in same order
10  # phi, kappa, s1,s2,s3,s4,beta1,beta2,beta3,beta4,gamma1,gamma2,gamma3,gamma4,p
11  theta <- c(0.9,0,0.6,0.55,0.8,0.75,0.5,0.7,0.9,0.8,0.4,0.5,0.6,0.7,as.numeric(paste(p)))
12  nparam <- length(theta)
13  nrepet <- length(RES)
14
15  # Calculate summary of posterior distribution estimated for all parameters
16  # (mean, and 95% credible interval) and calculate bias and root mean-square-errors :
17  est <- ci1 <- ci2 <- BIAS <- pBIAS <- rMSE <- matrix(NA,nrow=length(RES),ncol=nparam)
18  for(i in 1:nrepet){
19    #get estimates
20    est[i,] <- unlist(RES[[i]]$mean[c(1,2,3,6,7,8)])
21    ci1[i,] <- unlist(RES[[i]]$q2.5[c(1,2,3,6,7,8)])
22    ci2[i,] <- unlist(RES[[i]]$q97.5[c(1,2,3,6,7,8)])
23    # absolute bias, and root mean square error
24    BIAS[i,] <- (est[i,] - theta)
25    rMSE[i,] <- sqrt( (est[i,] - theta)^2 )
26  }#nrepet
27
28  # Plot the results
29  # pdf(width=9,height=6,pointsize=4,file="test.pdf",paper="a4r")
30  par(mfrow=c(3,5))
31  xlabs <- c(expression(phi),expression(kappa),expression(S[1]),expression(S[2]),
32            expression(S[3]),expression(S[4]),
33            expression(beta[1]),expression(beta[2]),
34            expression(beta[3]),expression(beta[4]),
35            expression(gamma[1]),expression(gamma[2]),
36            expression(gamma[3]),expression(gamma[4]),
37            expression(p))
38
39  for(j in 1:nparam){
40    plot(est[,j], 1:nrepet, ylab='',xlim=c(0,1),las=TRUE,cex=1,type="n",
41         main=xlabs[j],xlab=paste("bias = ",round(mean(BIAS[,j]),3),
42                                "; rmse =",round(mean(rMSE[,j]),2), sep=""))
43    segments(ci1[,j], 1:100,ci2[,j], 1:nrepet,col="grey70",lwd=0.5)
44    points(est[,j], 1:nrepet,col="black",cex=0.4,pch=16,)
45    abline(v=theta[j], lty=2, col='red')
46  }
47  # dev.off()
48
49  #store results
50  EST[[S]] <- est
51  CI1[[S]] <- ci1
52  CI2[[S]] <- ci2
53  simres[[S]] <- RES
54  biasall[[S]] <- BIAS
55  rMSEall[[S]] <- rMSE
56
57
58
59
60

```

} #S

For Review Only

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

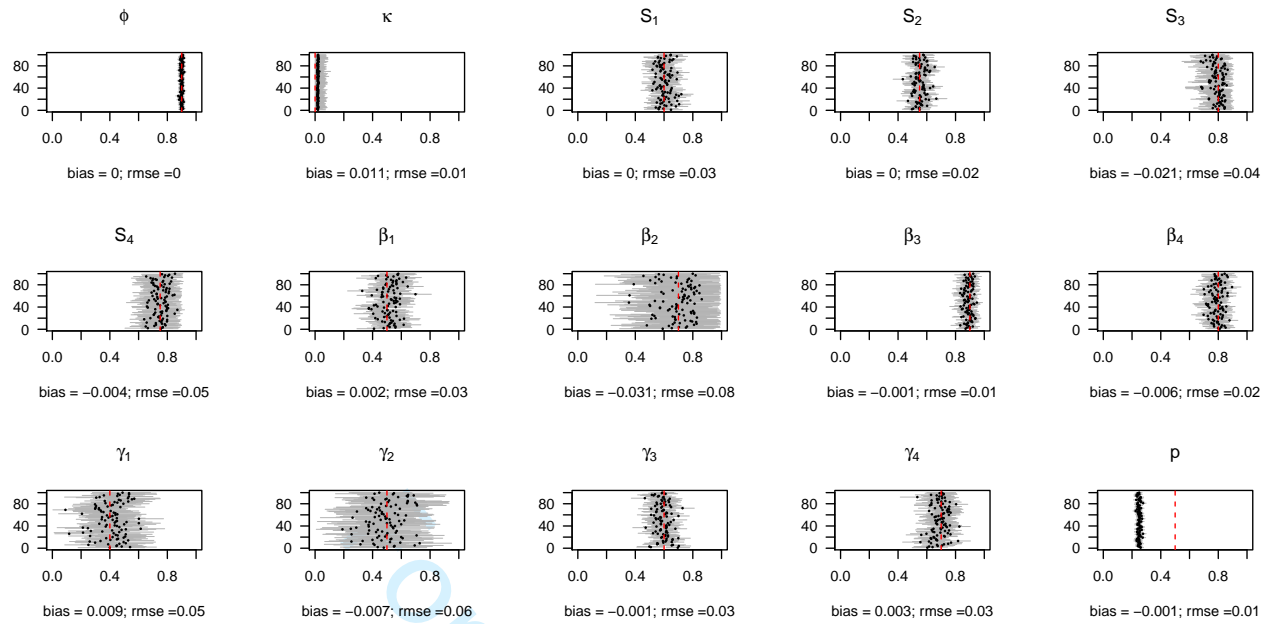


Figure S3. Performance of the model on simulated data with low detection with constant departure (scenario S1). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given 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.

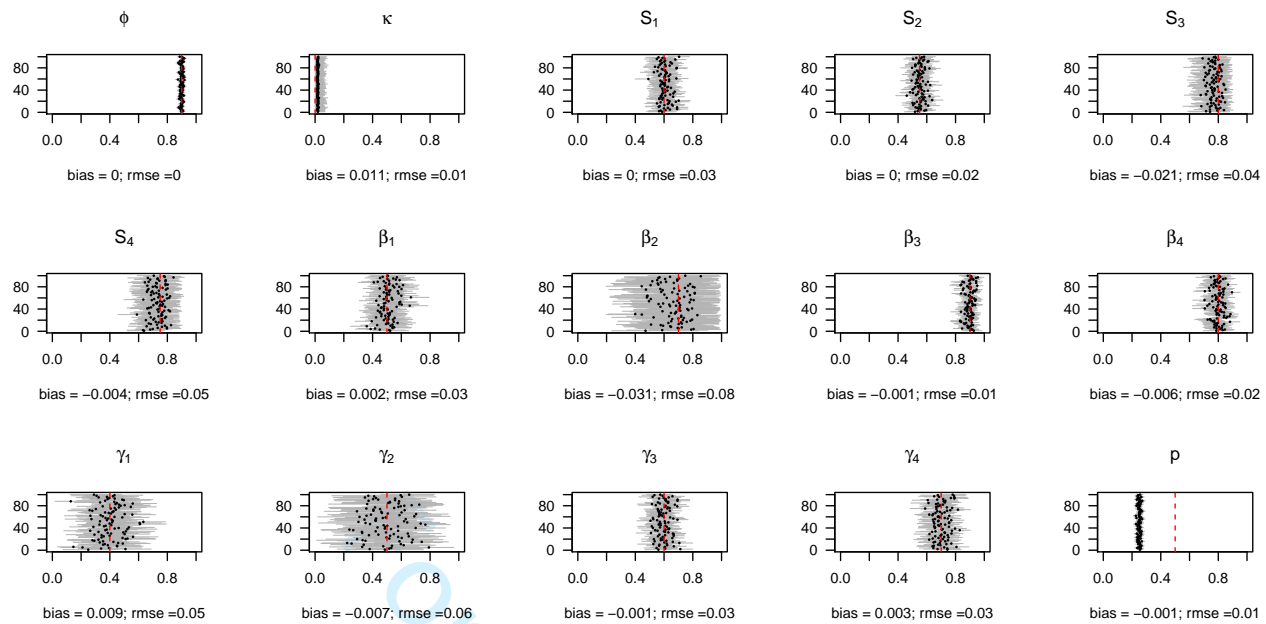


Figure S4. Performance of the model on simulated data with low detection with departure varying with date of capture (scenario S2). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the 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.

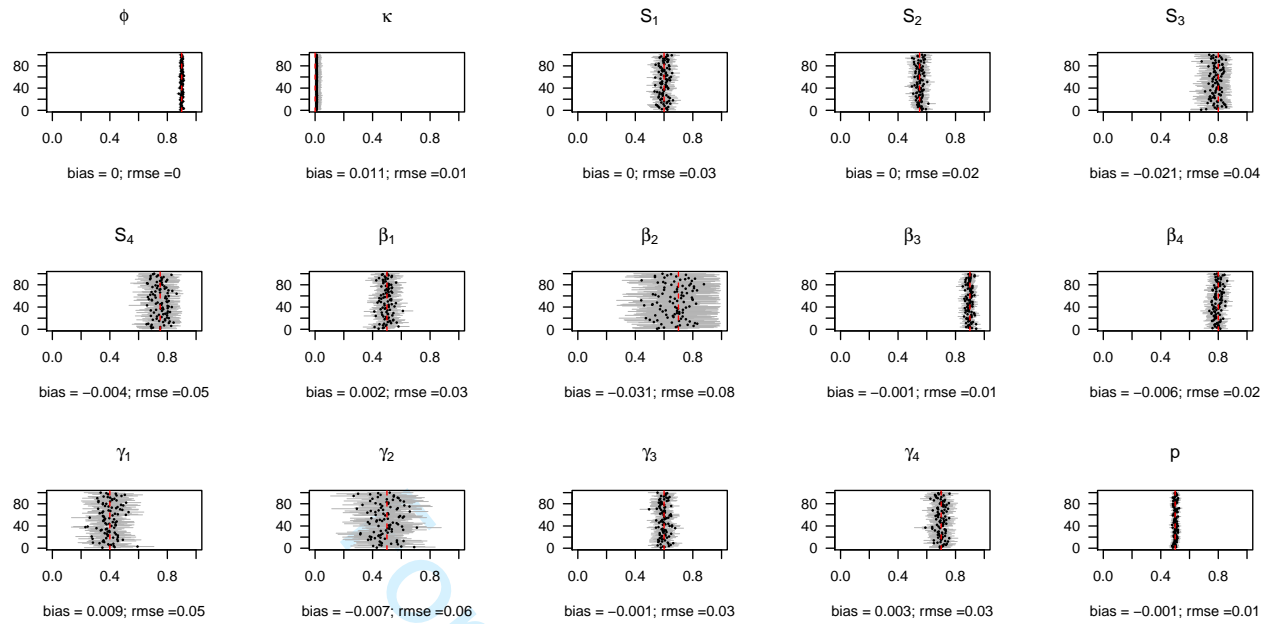


Figure S5. Performance of the model on simulated data with high detection with constant departure (scenario S3). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given 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.

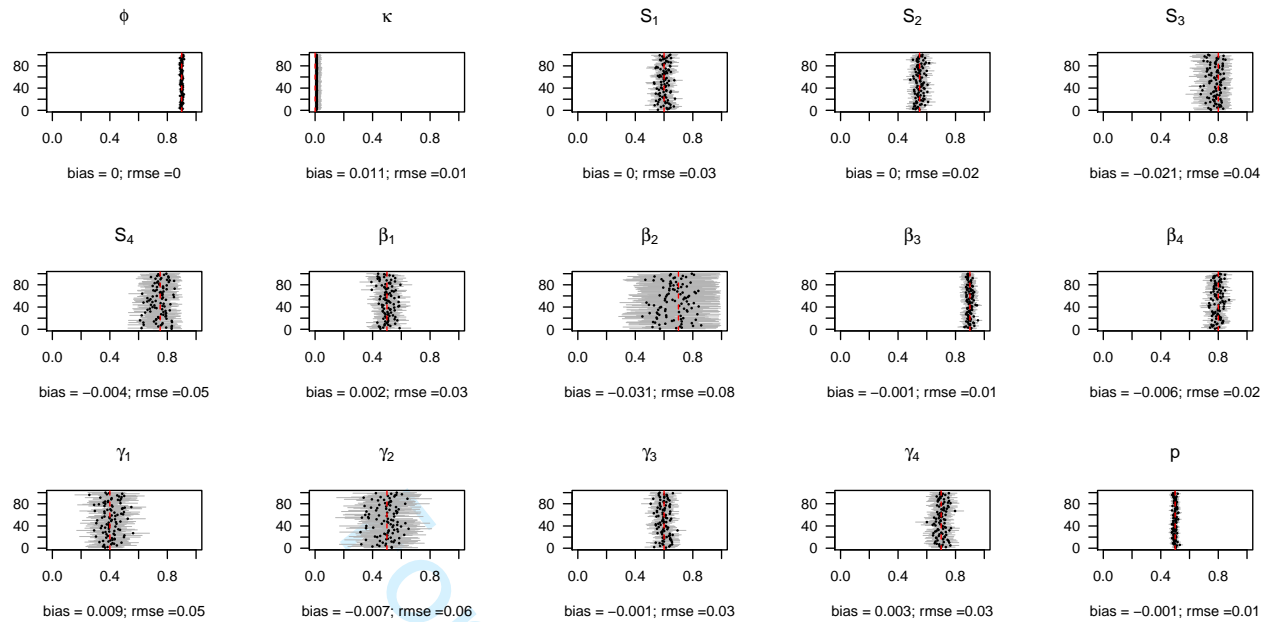


Figure S6. Performance of the model on simulated data with high detection with departure varying with date of capture (scenario S4). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the 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.

Make tables with values of bias and rsme for each parameter for all scenarios:

```
# average bias
mean(c(biasall[[1]],biasall[[2]],biasall[[3]],biasall[[4]]))

## [1] -0.002881172

# average rmse
mean(c(rMSEall[[1]],rMSEall[[2]],rMSEall[[3]],rMSEall[[4]]))

## [1] 0.03638131

tabB <- rbind( round(apply(biasall[[1]],2,mean),2), round(apply(biasall[[2]],2,mean),2),
              round(apply(biasall[[3]],2,mean),2), round(apply(biasall[[4]],2,mean),2) )

tabR <- rbind( round(apply(rMSEall[[1]],2,mean),2), round(apply(rMSEall[[2]],2,mean),2),
              round(apply(rMSEall[[3]],2,mean),2), round(apply(rMSEall[[4]],2,mean),2) )

parnames <- c(expression(phi),expression(kappa),expression(S[1]),expression(S[2]),
              expression(S[3]),expression(S[4]),
              expression(beta[1]),expression(beta[2]),expression(beta[3]),
              expression(beta[4]),expression(gamma[1]),expression(gamma[2]),expression(gamma[3]),
              expression(gamma[4]), expression(p))
colnames(tabB) <- colnames(tabR) <- parnames
rownames(tabB) <- rownames(tabR) <- c("S1","S2","S3","S4")

tabB

##      phi kappa S[1] S[2] S[3] S[4] beta[1] beta[2] beta[3] beta[4] gamma[1]
## S1   0  0.02 0.00   0 -0.01 0.00   0.02  -0.01  -0.01  -0.01   0.01
## S2   0  0.02 0.01   0 -0.03 -0.02   0.01  -0.04   0.00   0.00   0.00
```

```

1
2
3   ## S3  0  0.01 0.00  0 -0.01  0.00  0.00 -0.03  0.00  0.00  0.00
4   ## S4  0  0.01 0.00  0 -0.02  0.00  0.00 -0.03  0.00 -0.01  0.01
5   ##      gamma[2] gamma[3] gamma[4] p
6   ## S1  -0.01  -0.01  -0.01  0
7   ## S2   0.00   0.00   0.00  0
8   ## S3  -0.01   0.00   0.00  0
9   ## S4  -0.01   0.00   0.00  0
10
11  tabR
12
13  ##      phi kappa S[1] S[2] S[3] S[4] beta[1] beta[2] beta[3] beta[4] gamma[1]
14  ## S1  0.01  0.02  0.04  0.03  0.04  0.04  0.05  0.09  0.02  0.03  0.08
15  ## S2  0.01  0.02  0.03  0.03  0.04  0.04  0.04  0.09  0.02  0.03  0.07
16  ## S3  0.00  0.01  0.02  0.02  0.03  0.04  0.03  0.08  0.02  0.02  0.05
17  ## S4  0.00  0.01  0.03  0.02  0.04  0.05  0.03  0.08  0.01  0.02  0.05
18  ##      gamma[2] gamma[3] gamma[4] p
19  ## S1   0.09   0.04   0.04  0.01
20  ## S2   0.11   0.04   0.04  0.01
21  ## S3   0.07   0.02   0.02  0.01
22  ## S4   0.06   0.03   0.03  0.01
23  #write.csv(tabB,file = "RES_biasperparam.csv")
24  #write.csv(tabR,file = "RES_rmseperparam.csv")

```

Bibliography

Kéry, M., & Schaub, M. (2011). Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.

Guidance to fit the model to the polar bear data, R code, and additional results.

Sarah Cubaynes

6/23/2020

We fitted our model to the Polar bear data in a Bayesian framework using Markov Chain Monte Carlo (MCMC) simulation implemented in program JAGS (Hornik et al. 2003) called from R using package jagsUI (Kellner 2015). We ran two MCMC in parallel with different initial values, we used 20,000 iterations with an initial burn-in of 9,000 iterations, thinning every 5 iterations, to reach convergence to a stationary distribution, assessed by visual inspection of trace plots for each model parameter to ensure adequate mixing and by using the Gelman and Rubin diagnostic ($R\text{-hat} < 1.02$). We used non-informative priors on the model parameters, with uniform distribution between 0 and 1 for probabilities, and normal distribution with mean 0 and variance of 1 for regression coefficients. To help estimation of the parameters in the model, we introduced the constraint that survival of cubs was lower than that of yearling survival (Amstrup and Durner, 1995). The constraint was enough to reach convergence with satisfactory posterior distribution for each of the estimated parameters (see Figure below).

Below we provide the code to prepare the data, run the model and analyse the results. All files associated with Appendix 2, including the polar bear data files, are available on GitHub [here](#).

Prepare data and run jags model

Load data and useful packages :

```
load(file = "CRlocalbears_revision2MEE.Rdata") # family units CR histories
data <- data.matrix(CRlb)

load(file = "daylocalbears_revision2MEE.Rdata") # capture date in day of the yaer
daycapt <- daylb
load(file="initstatelocalbears_revision2MEE.Rdata")#matrix of initial states

alive1 <- data.matrix(initmatlb)

load(file = "dataweaning_revision2MEE.Rdata") # all two-year old bear captures

library(jagsUI) # to run jags model

## Loading required package: lattice
##
## Attaching package: 'jagsUI'
## The following object is masked from 'package:utils':
##
## View
```

```
library(jtools) # to make predict plot from glm
```

Define useful quantities:

```
N <- dim(data)[1] # number of family units
Years <- dim(data)[2] #number of sampling occasions
```

```
# Compute vector with occasion of first capture
get.first <- function(x) min(which(x!=0))
First <- apply(data, 1, get.first)
```

We use the ratio of two-year old bears captured alone versus still together with their mother (include all bears, not only resident females) to estimate the shape of the relationship between offspring departure probability and date within the field season:

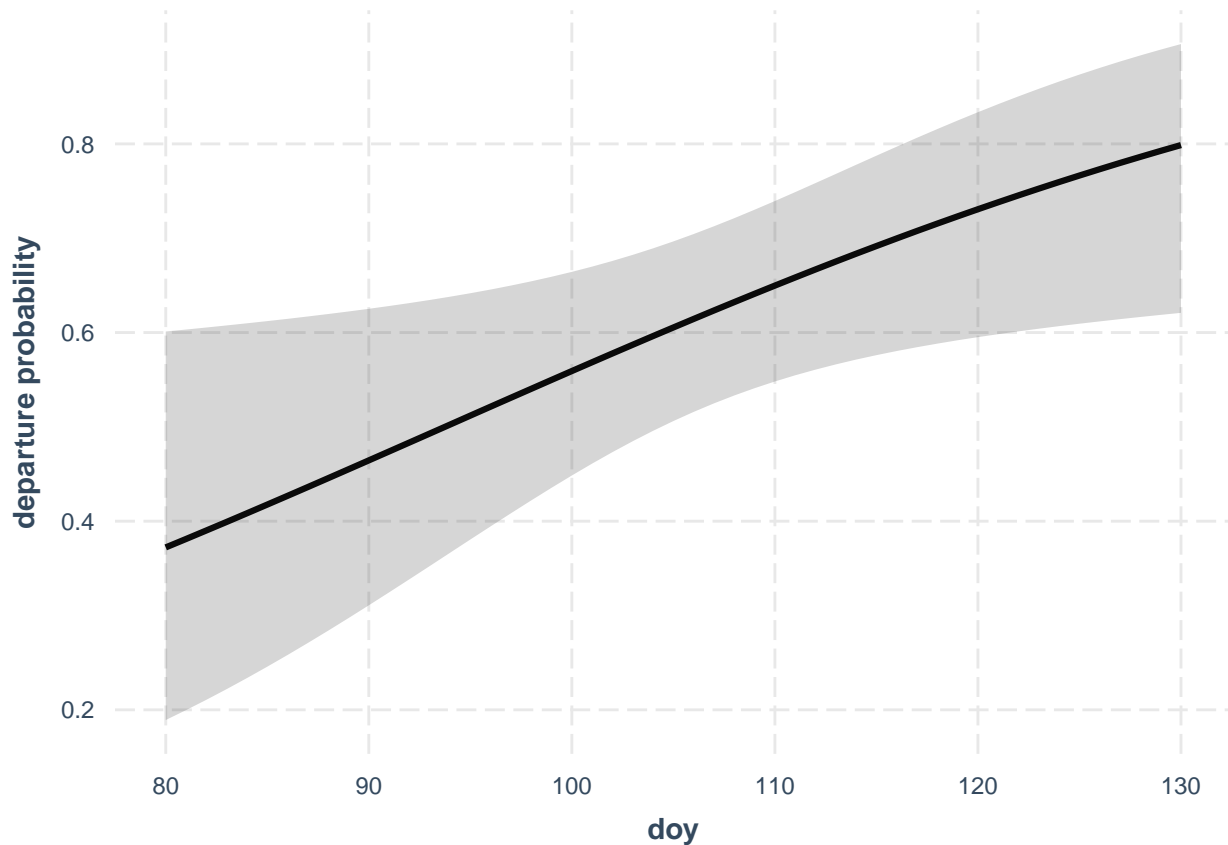
```
nty <- dim(dataweaning)[[1]] # number of two-year old bears captured
status <- dataweaning$status #status of two-year old bears at the time of capture :
#1 alone (already departed from family unit),
#0 still together with mother (not yet departed from family unit)
doy <- dataweaning$daysinseason # date of capture

# glm of departure probability as a function of date of capture
modeld<-glm(status~doy,family="binomial")
summary(modeld)
```

```
##
## Call:
## glm(formula = status ~ doym, family = "binomial")
##
## Deviance Residuals:
##      Min       1Q   Median       3Q      Max
## -1.7056  -1.2304   0.7665   0.9143   1.3215
##
## Coefficients:
##              Estimate Std. Error z value Pr(>|z|)
## (Intercept) -3.56486    1.75383  -2.033  0.0421 *
## doym         0.03803    0.01646   2.310  0.0209 *
## ---
## Signif. codes:  0 '***' 0.001 '**' 0.01 '*' 0.05 '.' 0.1 ' ' 1
##
## (Dispersion parameter for binomial family taken to be 1)
##
##      Null deviance: 154.11  on 119  degrees of freedom
## Residual deviance: 137.99  on 118  degrees of freedom
## AIC: 141.99
##
## Number of Fisher Scoring iterations: 6
```

Plot predicted departure probability of two-year old bears as a function of date in day of the year (doy):

```
effect_plot(modeld, pred = doym, pred.values=80:130,interval = TRUE,
            plot.points = FALSE,y.label = "departure probability")
```



Departure probability increased throughout the field season. It was about 40% at the end of March and reached 80% at mid-May.

Predict departure probability from date of capture for resident family units (departure probability will be used in matrix E2 of the observation process to relate state to events for family units in states AS1 or AS2):

```
# Predict departure probability function of date of capture
daycapt <- daylb # dates of capture

# if not captured, replace with 80 (in date of capture) to avoid NAs
daycapt <- replace(daycapt,is.na(daycapt),80)

# create empty object to store predicted departure probability
alpha = matrix(0,nrow=N,ncol=Years)
# predict departure probability based on date of capture using modeld
for(i in 1:N){
  for(j in (First[i]):Years){
    alpha[i,j] <- predict(modeld,newdata=list(doy=daycapt[i,j]),type="response")
  }
}
```

Create a list containing the data to run the jags model:

```
# Bundle data for jags
mydatax <- list(N=N,First=First,Years=Years,mydata=data.matrix(data+1),alpha=data.matrix(alpha))
```

Generate initial values for each of the two chains:

```
set.seed(42)
# Initial values
```



```

1
2
3
4 init1 <- list(theta=rnorm(10, mean = 0, sd = 1),alive=alive1)
5 init2 <- list(theta=rnorm(10, mean = 0, sd = 1),alive=alive1)
6 inits <- list(init1,init2)

```

Create a list with names of the parameters to monitor:

```

7
8 # Parameters monitored
9 params <- c("phi","s","l02","l12","kappa","beta","gamma","p","prop")

```

Load the script of the jags model :

```

10
11
12 # JAGS MODEL
13 sink("Multieventmodel_FitresidentBeardata.txt")
14 cat("
15
16
17 model {
18   # Probabilities of events given states and states given states
19
20   # vector of initial states
21   S0[1] <- prop[1] / (1 + sum(prop[1:10])) # prob. of being in initial state J2
22   S0[2] <- prop[2] / (1 + sum(prop[1:10])) # prob. of being in initial state J3
23   S0[3] <- prop[3] / (1 + sum(prop[1:10])) # prob. of being in initial state SA4
24   S0[4] <- prop[4] / (1 + sum(prop[1:10])) # prob. of being in initial state SA5
25   S0[5] <- prop[5] / (1 + sum(prop[1:10])) # prob. of being in initial state A01
26   S0[6] <- prop[6] / (1 + sum(prop[1:10])) # prob. of being in initial state A02
27   S0[7] <- prop[7] / (1 + sum(prop[1:10])) # prob. of being in initial state A11
28   S0[8] <- prop[8] / (1 + sum(prop[1:10])) # prob. of being in initial state A12
29   S0[9] <- prop[9] / (1 + sum(prop[1:10])) # prob. of being in initial state AS1
30   S0[10] <- prop[10] / (1 + sum(prop[1:10])) # prob. of being in initial state AS2
31   S0[11] <- 1 / (1 + sum(prop[1:10])) # prob. of being in initial state A-
32   S0[12] <- 0 # prob. of being in initial state dead
33
34   # State process: define probabilities of S(t+1) given S(t)
35   # define PHI matrix gathering survival of independent juveniles, subadults and adults
36   PHI [ 1 , 1 ]<- phi[1]
37   PHI [ 1 , 2 ]<- 0
38   PHI [ 1 , 3 ]<- 0
39   PHI [ 1 , 4 ]<- 0
40   PHI [ 1 , 5 ]<- 0
41   PHI [ 1 , 6 ]<- 0
42   PHI [ 1 , 7 ]<- 0
43   PHI [ 1 , 8 ]<- 0
44   PHI [ 1 , 9 ]<- 0
45   PHI [ 1 , 10 ]<- 0
46   PHI [ 1 , 11 ]<- 0
47   PHI [ 1 , 12 ]<- 1-phi[1]
48
49   PHI [ 2 , 1 ]<- 0
50   PHI [ 2 , 2 ]<- phi[1]
51   PHI [ 2 , 3 ]<- 0
52   PHI [ 2 , 4 ]<- 0
53   PHI [ 2 , 5 ]<- 0
54   PHI [ 2 , 6 ]<- 0
55   PHI [ 2 , 7 ]<- 0
56   PHI [ 2 , 8 ]<- 0

```

```

1
2
3
4 PHI [ 2 , 9 ]<- 0
5 PHI [ 2 , 10 ]<- 0
6 PHI [ 2 , 11 ]<- 0
7 PHI [ 2 , 12 ]<- 1-phi[1]
8
9 PHI [ 3 , 1 ]<- 0
10 PHI [ 3 , 2 ]<- 0
11 PHI [ 3 , 3 ]<- phi[1]
12 PHI [ 3 , 4 ]<- 0
13 PHI [ 3 , 5 ]<- 0
14 PHI [ 3 , 6 ]<- 0
15 PHI [ 3 , 7 ]<- 0
16 PHI [ 3 , 8 ]<- 0
17 PHI [ 3 , 9 ]<- 0
18 PHI [ 3 , 10 ]<- 0
19 PHI [ 3 , 11 ]<- 0
20 PHI [ 3 , 12 ]<- 1-phi[1]
21
22 PHI [ 4 , 1 ]<- 0
23 PHI [ 4 , 2 ]<- 0
24 PHI [ 4 , 3 ]<- 0
25 PHI [ 4 , 4 ]<- phi[1]
26 PHI [ 4 , 5 ]<- 0
27 PHI [ 4 , 6 ]<- 0
28 PHI [ 4 , 7 ]<- 0
29 PHI [ 4 , 8 ]<- 0
30 PHI [ 4 , 9 ]<- 0
31 PHI [ 4 , 10 ]<- 0
32 PHI [ 4 , 11 ]<- 0
33 PHI [ 4 , 12 ]<- 1 - phi[1]
34
35 PHI [ 5 , 1 ]<- 0
36 PHI [ 5 , 2 ]<- 0
37 PHI [ 5 , 3 ]<- 0
38 PHI [ 5 , 4 ]<- 0
39 PHI [ 5 , 5 ]<- phi[1]
40 PHI [ 5 , 6 ]<- 0
41 PHI [ 5 , 7 ]<- 0
42 PHI [ 5 , 8 ]<- 0
43 PHI [ 5 , 9 ]<- 0
44 PHI [ 5 , 10 ]<- 0
45 PHI [ 5 , 11 ]<- 0
46 PHI [ 5 , 12 ]<- 1 - phi[1]
47
48 PHI [ 6 , 1 ]<- 0
49 PHI [ 6 , 2 ]<- 0
50 PHI [ 6 , 3 ]<- 0
51 PHI [ 6 , 4 ]<- 0
52 PHI [ 6 , 5 ]<- 0
53 PHI [ 6 , 6 ]<- phi[1]
54 PHI [ 6 , 7 ]<- 0
55 PHI [ 6 , 8 ]<- 0
56 PHI [ 6 , 9 ]<- 0

```

```
1
2
3
4 PHI [ 6 , 10 ]<- 0
5 PHI [ 6 , 11 ]<- 0
6 PHI [ 6 , 12 ]<- 1 - phi[1]
7
8 PHI [ 7 , 1 ]<- 0
9 PHI [ 7 , 2 ]<- 0
10 PHI [ 7 , 3 ]<- 0
11 PHI [ 7 , 4 ]<- 0
12 PHI [ 7 , 5 ]<- 0
13 PHI [ 7 , 6 ]<- 0
14 PHI [ 7 , 7 ]<- phi[1]
15 PHI [ 7 , 8 ]<- 0
16 PHI [ 7 , 9 ]<- 0
17 PHI [ 7 , 10 ]<- 0
18 PHI [ 7 , 11 ]<- 0
19 PHI [ 7 , 12 ]<- 1-phi[1]
20
21 PHI [ 8 , 1 ]<- 0
22 PHI [ 8 , 2 ]<- 0
23 PHI [ 8 , 3 ]<- 0
24 PHI [ 8 , 4 ]<- 0
25 PHI [ 8 , 5 ]<- 0
26 PHI [ 8 , 6 ]<- 0
27 PHI [ 8 , 7 ]<- 0
28 PHI [ 8 , 8 ]<- phi[1]
29 PHI [ 8 , 9 ]<- 0
30 PHI [ 8 , 10 ]<- 0
31 PHI [ 8 , 11 ]<- 0
32 PHI [ 8 , 12 ]<- 1-phi[1]
33
34 PHI [ 9 , 1 ]<- 0
35 PHI [ 9 , 2 ]<- 0
36 PHI [ 9 , 3 ]<- 0
37 PHI [ 9 , 4 ]<- 0
38 PHI [ 9 , 5 ]<- 0
39 PHI [ 9 , 6 ]<- 0
40 PHI [ 9 , 7 ]<- 0
41 PHI [ 9 , 8 ]<- 0
42 PHI [ 9 , 9 ]<- phi[1]
43 PHI [ 9 , 10 ]<- 0
44 PHI [ 9 , 11 ]<- 0
45 PHI [ 9 , 12 ]<- 1-phi[1]
46
47 PHI [ 10 , 1 ]<- 0
48 PHI [ 10 , 2 ]<- 0
49 PHI [ 10 , 3 ]<- 0
50 PHI [ 10 , 4 ]<- 0
51 PHI [ 10 , 5 ]<- 0
52 PHI [ 10 , 6 ]<- 0
53 PHI [ 10 , 7 ]<- 0
54 PHI [ 10 , 8 ]<- 0
55 PHI [ 10 , 9 ]<- 0
56 PHI [ 10 , 10 ]<- phi[1]
57
58
59
60
```

```

1
2
3
4 PHI [ 10 , 11 ]<- 0
5 PHI [ 10 , 12 ]<- 1-phi[1]
6
7 PHI [ 11 , 1 ]<- 0
8 PHI [ 11 , 2 ]<- 0
9 PHI [ 11 , 3 ]<- 0
10 PHI [ 11 , 4 ]<- 0
11 PHI [ 11 , 5 ]<- 0
12 PHI [ 11 , 6 ]<- 0
13 PHI [ 11 , 7 ]<- 0
14 PHI [ 11 , 8 ]<- 0
15 PHI [ 11 , 9 ]<- 0
16 PHI [ 11 , 10 ]<- 0
17 PHI [ 11 , 11 ]<- phi[1]
18 PHI [ 11 , 12 ]<- 1-phi[1]
19
20 PHI [ 12 , 1 ]<- 0
21 PHI [ 12 , 2 ]<- 0
22 PHI [ 12 , 3 ]<- 0
23 PHI [ 12 , 4 ]<- 0
24 PHI [ 12 , 5 ]<- 0
25 PHI [ 12 , 6 ]<- 0
26 PHI [ 12 , 7 ]<- 0
27 PHI [ 12 , 8 ]<- 0
28 PHI [ 12 , 9 ]<- 0
29 PHI [ 12 , 10 ]<- 0
30 PHI [ 12 , 11 ]<- 0
31 PHI [ 12 , 12 ]<- 1
32
33 # Define PSI matrices gathering state-to-state transition probabilities, it includes:
34 # PSI1: offspring survival and growth to next age, proba of sexual maturation:
35 PSI1 [ 1 , 1 ]<- 1
36 PSI1 [ 1 , 2 ]<- 0
37 PSI1 [ 1 , 3 ]<- 0
38 PSI1 [ 1 , 4 ]<- 0
39 PSI1 [ 1 , 5 ]<- 0
40 PSI1 [ 1 , 6 ]<- 0
41 PSI1 [ 1 , 7 ]<- 0
42 PSI1 [ 1 , 8 ]<- 0
43 PSI1 [ 1 , 9 ]<- 0
44 PSI1 [ 1 , 10 ]<- 0
45 PSI1 [ 1 , 11 ]<- 0
46 PSI1 [ 1 , 12 ]<- 0
47 PSI1 [ 1 , 13 ]<- 0
48
49 PSI1 [ 2 , 1 ]<- 0
50 PSI1 [ 2 , 2 ]<- 1
51 PSI1 [ 2 , 3 ]<- 0
52 PSI1 [ 2 , 4 ]<- 0
53 PSI1 [ 2 , 5 ]<- 0
54 PSI1 [ 2 , 6 ]<- 0
55 PSI1 [ 2 , 7 ]<- 0
56 PSI1 [ 2 , 8 ]<- 0
57
58
59
60

```

```

1
2
3
4 PSI1 [ 2 , 9 ]<- 0
5 PSI1 [ 2 , 10 ]<- 0
6 PSI1 [ 2 , 11 ]<- 0
7 PSI1 [ 2 , 12 ]<- 0
8 PSI1 [ 2 , 13 ]<- 0
9
10 PSI1 [ 3 , 1 ]<- 0
11 PSI1 [ 3 , 2 ]<- 0
12 PSI1 [ 3 , 3 ]<- 1-kappa#1 #
13 PSI1 [ 3 , 4 ]<- 0
14 PSI1 [ 3 , 5 ]<- 0
15 PSI1 [ 3 , 6 ]<- 0
16 PSI1 [ 3 , 7 ]<- 0
17 PSI1 [ 3 , 8 ]<- 0
18 PSI1 [ 3 , 9 ]<- 0
19 PSI1 [ 3 , 10 ]<- 0
20 PSI1 [ 3 , 11 ]<- 0
21 PSI1 [ 3 , 12 ]<- kappa #0
22 PSI1 [ 3 , 13 ]<- 0
23
24 PSI1 [ 4 , 1 ]<- 0
25 PSI1 [ 4 , 2 ]<- 0
26 PSI1 [ 4 , 3 ]<- 0
27 PSI1 [ 4 , 4 ]<- 0
28 PSI1 [ 4 , 5 ]<- 0
29 PSI1 [ 4 , 6 ]<- 0
30 PSI1 [ 4 , 7 ]<- 0
31 PSI1 [ 4 , 8 ]<- 0
32 PSI1 [ 4 , 9 ]<- 0
33 PSI1 [ 4 , 10 ]<- 0
34 PSI1 [ 4 , 11 ]<- 0
35 PSI1 [ 4 , 12 ]<- 1
36 PSI1 [ 4 , 13 ]<- 0
37
38 PSI1 [ 5 , 1 ]<- 0
39 PSI1 [ 5 , 2 ]<- 0
40 PSI1 [ 5 , 3 ]<- 0
41 PSI1 [ 5 , 4 ]<- s[1] # litter of 1, cub survives
42 PSI1 [ 5 , 5 ]<- 0
43 PSI1 [ 5 , 6 ]<- 0
44 PSI1 [ 5 , 7 ]<- 0
45 PSI1 [ 5 , 8 ]<- 1-s[1] #litter of 1, cub dies
46 PSI1 [ 5 , 9 ]<- 0
47 PSI1 [ 5 , 10 ]<- 0
48 PSI1 [ 5 , 11 ]<- 0
49 PSI1 [ 5 , 12 ]<- 0
50 PSI1 [ 5 , 13 ]<- 0
51
52 PSI1 [ 6 , 1 ]<- 0
53 PSI1 [ 6 , 2 ]<- 0
54 PSI1 [ 6 , 3 ]<- 0
55 PSI1 [ 6 , 4 ]<- 2*s[2]*(1-s[2]) # litter of 2, 1 cub survives
56 PSI1 [ 6 , 5 ]<- s[2]^2 # litter of 2, both cubs survive
57
58
59
60

```

```

1
2
3
4 PSI1 [ 6 , 6 ]<- 0
5 PSI1 [ 6 , 7 ]<- 0
6 PSI1 [ 6 , 8 ]<- (1- s[2]^2 -2*s[2]*(1-s[2])) #litter of 2, both cubs die
7
8 PSI1 [ 6 , 9 ]<- 0
9 PSI1 [ 6 , 10 ]<- 0
10 PSI1 [ 6 , 11 ]<- 0
11 PSI1 [ 6 , 12 ]<- 0
12 PSI1 [ 6 , 13 ]<- 0
13
14 PSI1 [ 7 , 1 ]<- 0
15 PSI1 [ 7 , 2 ]<- 0
16 PSI1 [ 7 , 3 ]<- 0
17 PSI1 [ 7 , 4 ]<- 0
18 PSI1 [ 7 , 5 ]<- 0
19 PSI1 [ 7 , 6 ]<- s[3] # litter of 1, yearling survives
20 PSI1 [ 7 , 7 ]<- 0
21 PSI1 [ 7 , 8 ]<- 0
22 PSI1 [ 7 , 9 ]<- (1-s[3] ) # litter of 1, yearling dies
23 PSI1 [ 7 , 10 ]<- 0
24 PSI1 [ 7 , 11 ]<- 0
25 PSI1 [ 7 , 12 ]<- 0
26 PSI1 [ 7 , 13 ]<- 0
27
28 PSI1 [ 8 , 1 ]<- 0
29 PSI1 [ 8 , 2 ]<- 0
30 PSI1 [ 8 , 3 ]<- 0
31 PSI1 [ 8 , 4 ]<- 0
32 PSI1 [ 8 , 5 ]<- 0
33 PSI1 [ 8 , 6 ]<- 2*s[4]*(1-s[4]) # litter of 2, 1 yearling survives
34 PSI1 [ 8 , 7 ]<- s[4]^2 # litter of 2, both yearlings survive
35 PSI1 [ 8 , 8 ]<- 0
36 PSI1 [ 8 , 9 ]<- (1- s[4]^2 -2*s[4]*(1-s[4])) #litter of 2, both yearlings die
37 PSI1 [ 8 , 10 ]<- 0
38 PSI1 [ 8 , 11 ]<- 0
39 PSI1 [ 8 , 12 ]<- 0
40 PSI1 [ 8 , 13 ]<- 0
41
42 PSI1 [ 9 , 1 ]<- 0
43 PSI1 [ 9 , 2 ]<- 0
44 PSI1 [ 9 , 3 ]<- 0
45 PSI1 [ 9 , 4 ]<- 0
46 PSI1 [ 9 , 5 ]<- 0
47 PSI1 [ 9 , 6 ]<- 0
48 PSI1 [ 9 , 7 ]<- 0
49 PSI1 [ 9 , 8 ]<- 0
50 PSI1 [ 9 , 9 ]<- 0
51 PSI1 [ 9 , 10 ]<- 1
52 PSI1 [ 9 , 11 ]<- 0
53 PSI1 [ 9 , 12 ]<- 0
54 PSI1 [ 9 , 13 ]<- 0
55
56 PSI1 [ 10 , 1 ]<- 0
57
58
59
60

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```
PSI1 [ 10 , 2 ]<- 0  
PSI1 [ 10 , 3 ]<- 0  
PSI1 [ 10 , 4 ]<- 0  
PSI1 [ 10 , 5 ]<- 0  
PSI1 [ 10 , 6 ]<- 0  
PSI1 [ 10 , 7 ]<- 0  
PSI1 [ 10 , 8 ]<- 0  
PSI1 [ 10 , 9 ]<- 0  
PSI1 [ 10 , 10 ]<- 0  
PSI1 [ 10 , 11 ]<- 1  
PSI1 [ 10 , 12 ]<- 0  
PSI1 [ 10 , 13 ]<- 0
```

```
PSI1 [ 11 , 1 ]<- 0  
PSI1 [ 11 , 2 ]<- 0  
PSI1 [ 11 , 3 ]<- 0  
PSI1 [ 11 , 4 ]<- 0  
PSI1 [ 11 , 5 ]<- 0  
PSI1 [ 11 , 6 ]<- 0  
PSI1 [ 11 , 7 ]<- 0  
PSI1 [ 11 , 8 ]<- 0  
PSI1 [ 11 , 9 ]<- 0  
PSI1 [ 11 , 10 ]<- 0  
PSI1 [ 11 , 11 ]<- 0  
PSI1 [ 11 , 12 ]<- 1  
PSI1 [ 11 , 13 ]<- 0
```

```
PSI1 [ 12 , 1 ]<- 0  
PSI1 [ 12 , 2 ]<- 0  
PSI1 [ 12 , 3 ]<- 0  
PSI1 [ 12 , 4 ]<- 0  
PSI1 [ 12 , 5 ]<- 0  
PSI1 [ 12 , 6 ]<- 0  
PSI1 [ 12 , 7 ]<- 0  
PSI1 [ 12 , 8 ]<- 0  
PSI1 [ 12 , 9 ]<- 0  
PSI1 [ 12 , 10 ]<- 0  
PSI1 [ 12 , 11 ]<- 0  
PSI1 [ 12 , 12 ]<- 0  
PSI1 [ 12 , 13 ]<- 1
```

```
# PSI2: breeding probabilities:
```

```
PSI2 [ 1 , 1 ]<- 1  
PSI2 [ 1 , 2 ]<- 0  
PSI2 [ 1 , 3 ]<- 0  
PSI2 [ 1 , 4 ]<- 0  
PSI2 [ 1 , 5 ]<- 0  
PSI2 [ 1 , 6 ]<- 0  
PSI2 [ 1 , 7 ]<- 0  
PSI2 [ 1 , 8 ]<- 0  
PSI2 [ 1 , 9 ]<- 0  
PSI2 [ 1 , 10 ]<- 0  
PSI2 [ 1 , 11 ]<- 0
```

```
1
2
3
4 PSI2 [ 1 , 12 ]<- 0
5 PSI2 [ 1 , 13 ]<- 0
6 PSI2 [ 1 , 14 ]<- 0
7 PSI2 [ 1 , 15 ]<- 0
8 PSI2 [ 1 , 16 ]<- 0
9
10 PSI2 [ 2 , 1 ]<- 0
11 PSI2 [ 2 , 2 ]<- 1
12 PSI2 [ 2 , 3 ]<- 0
13 PSI2 [ 2 , 4 ]<- 0
14 PSI2 [ 2 , 5 ]<- 0
15 PSI2 [ 2 , 6 ]<- 0
16 PSI2 [ 2 , 7 ]<- 0
17 PSI2 [ 2 , 8 ]<- 0
18 PSI2 [ 2 , 9 ]<- 0
19 PSI2 [ 2 , 10 ]<- 0
20 PSI2 [ 2 , 11 ]<- 0
21 PSI2 [ 2 , 12 ]<- 0
22 PSI2 [ 2 , 13 ]<- 0
23 PSI2 [ 2 , 14 ]<- 0
24 PSI2 [ 2 , 15 ]<- 0
25 PSI2 [ 2 , 16 ]<- 0
26
27 PSI2 [ 3 , 1 ]<- 0
28 PSI2 [ 3 , 2 ]<- 0
29 PSI2 [ 3 , 3 ]<- 1
30 PSI2 [ 3 , 4 ]<- 0
31 PSI2 [ 3 , 5 ]<- 0
32 PSI2 [ 3 , 6 ]<- 0
33 PSI2 [ 3 , 7 ]<- 0
34 PSI2 [ 3 , 8 ]<- 0
35 PSI2 [ 3 , 9 ]<- 0
36 PSI2 [ 3 , 10 ]<- 0
37 PSI2 [ 3 , 11 ]<- 0
38 PSI2 [ 3 , 12 ]<- 0
39 PSI2 [ 3 , 13 ]<- 0
40 PSI2 [ 3 , 14 ]<- 0
41 PSI2 [ 3 , 15 ]<- 0
42 PSI2 [ 3 , 16 ]<- 0
43
44 PSI2 [ 4 , 1 ]<- 0
45 PSI2 [ 4 , 2 ]<- 0
46 PSI2 [ 4 , 3 ]<- 0
47 PSI2 [ 4 , 4 ]<- 1
48 PSI2 [ 4 , 5 ]<- 0
49 PSI2 [ 4 , 6 ]<- 0
50 PSI2 [ 4 , 7 ]<- 0
51 PSI2 [ 4 , 8 ]<- 0
52 PSI2 [ 4 , 9 ]<- 0
53 PSI2 [ 4 , 10 ]<- 0
54 PSI2 [ 4 , 11 ]<- 0
55 PSI2 [ 4 , 12 ]<- 0
56 PSI2 [ 4 , 13 ]<- 0
57
58
59
60
```


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```
PSI2 [ 4 , 14 ]<- 0
PSI2 [ 4 , 15 ]<- 0
PSI2 [ 4 , 16 ]<- 0

PSI2 [ 5 , 1 ]<- 0
PSI2 [ 5 , 2 ]<- 0
PSI2 [ 5 , 3 ]<- 0
PSI2 [ 5 , 4 ]<- 0
PSI2 [ 5 , 5 ]<- 1
PSI2 [ 5 , 6 ]<- 0
PSI2 [ 5 , 7 ]<- 0
PSI2 [ 5 , 8 ]<- 0
PSI2 [ 5 , 9 ]<- 0
PSI2 [ 5 , 10 ]<- 0
PSI2 [ 5 , 11 ]<- 0
PSI2 [ 5 , 12 ]<- 0
PSI2 [ 5 , 13 ]<- 0
PSI2 [ 5 , 14 ]<- 0
PSI2 [ 5 , 15 ]<- 0
PSI2 [ 5 , 16 ]<- 0

PSI2 [ 6 , 1 ]<- 0
PSI2 [ 6 , 2 ]<- 0
PSI2 [ 6 , 3 ]<- 0
PSI2 [ 6 , 4 ]<- 0
PSI2 [ 6 , 5 ]<- 0
PSI2 [ 6 , 6 ]<- 1
PSI2 [ 6 , 7 ]<- 0
PSI2 [ 6 , 8 ]<- 0
PSI2 [ 6 , 9 ]<- 0
PSI2 [ 6 , 10 ]<- 0
PSI2 [ 6 , 11 ]<- 0
PSI2 [ 6 , 12 ]<- 0
PSI2 [ 6 , 13 ]<- 0
PSI2 [ 6 , 14 ]<- 0
PSI2 [ 6 , 15 ]<- 0
PSI2 [ 6 , 16 ]<- 0

PSI2 [ 7 , 1 ]<- 0
PSI2 [ 7 , 2 ]<- 0
PSI2 [ 7 , 3 ]<- 0
PSI2 [ 7 , 4 ]<- 0
PSI2 [ 7 , 5 ]<- 0
PSI2 [ 7 , 6 ]<- 0
PSI2 [ 7 , 7 ]<- 1
PSI2 [ 7 , 8 ]<- 0
PSI2 [ 7 , 9 ]<- 0
PSI2 [ 7 , 10 ]<- 0
PSI2 [ 7 , 11 ]<- 0
PSI2 [ 7 , 12 ]<- 0
PSI2 [ 7 , 13 ]<- 0
PSI2 [ 7 , 14 ]<- 0
PSI2 [ 7 , 15 ]<- 0
```

```

1
2
3
4   PSI2 [ 7 , 16 ]<- 0
5
6   PSI2 [ 8 , 1 ]<- 0
7   PSI2 [ 8 , 2 ]<- 0
8   PSI2 [ 8 , 3 ]<- 0
9   PSI2 [ 8 , 4 ]<- 0
10  PSI2 [ 8 , 5 ]<- 0
11  PSI2 [ 8 , 6 ]<- 0
12  PSI2 [ 8 , 7 ]<- 0
13  PSI2 [ 8 , 8 ]<- beta[1]
14  PSI2 [ 8 , 9 ]<- 1-beta[1]
15  PSI2 [ 8 , 10 ]<- 0
16  PSI2 [ 8 , 11 ]<- 0
17  PSI2 [ 8 , 12 ]<- 0
18  PSI2 [ 8 , 13 ]<- 0
19  PSI2 [ 8 , 14 ]<- 0
20  PSI2 [ 8 , 15 ]<- 0
21  PSI2 [ 8 , 16 ]<- 0
22
23  PSI2 [ 9 , 1 ]<- 0
24  PSI2 [ 9 , 2 ]<- 0
25  PSI2 [ 9 , 3 ]<- 0
26  PSI2 [ 9 , 4 ]<- 0
27  PSI2 [ 9 , 5 ]<- 0
28  PSI2 [ 9 , 6 ]<- 0
29  PSI2 [ 9 , 7 ]<- 0
30  PSI2 [ 9 , 8 ]<- 0
31  PSI2 [ 9 , 9 ]<- 0
32  PSI2 [ 9 , 10 ]<- beta[2]
33  PSI2 [ 9 , 11 ]<- 1-beta[2]
34  PSI2 [ 9 , 12 ]<- 0
35  PSI2 [ 9 , 13 ]<- 0
36  PSI2 [ 9 , 14 ]<- 0
37  PSI2 [ 9 , 15 ]<- 0
38  PSI2 [ 9 , 16 ]<- 0
39
40  PSI2 [ 10 , 1 ]<- 0
41  PSI2 [ 10 , 2 ]<- 0
42  PSI2 [ 10 , 3 ]<- 0
43  PSI2 [ 10 , 4 ]<- 0
44  PSI2 [ 10 , 5 ]<- 0
45  PSI2 [ 10 , 6 ]<- 0
46  PSI2 [ 10 , 7 ]<- 0
47  PSI2 [ 10 , 8 ]<- 0
48  PSI2 [ 10 , 9 ]<- 0
49  PSI2 [ 10 , 10 ]<- 0
50  PSI2 [ 10 , 11 ]<- 0
51  PSI2 [ 10 , 12 ]<- beta[3]
52  PSI2 [ 10 , 13 ]<- 1-beta[3]
53  PSI2 [ 10 , 14 ]<- 0
54  PSI2 [ 10 , 15 ]<- 0
55  PSI2 [ 10 , 16 ]<- 0
56
57
58
59
60

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```

PSI2 [ 11 , 1 ]<- 0
PSI2 [ 11 , 2 ]<- 0
PSI2 [ 11 , 3 ]<- 0
PSI2 [ 11 , 4 ]<- 0
PSI2 [ 11 , 5 ]<- 0
PSI2 [ 11 , 6 ]<- 0
PSI2 [ 11 , 7 ]<- 0
PSI2 [ 11 , 8 ]<- 0
PSI2 [ 11 , 9 ]<- 0
PSI2 [ 11 , 10 ]<- 0
PSI2 [ 11 , 11 ]<- 0
PSI2 [ 11 , 12 ]<- beta[3]
PSI2 [ 11 , 13 ]<- 1-beta[3]
PSI2 [ 11 , 14 ]<- 0
PSI2 [ 11 , 15 ]<- 0
PSI2 [ 11 , 16 ]<- 0

PSI2 [ 12 , 1 ]<- 0
PSI2 [ 12 , 2 ]<- 0
PSI2 [ 12 , 3 ]<- 0
PSI2 [ 12 , 4 ]<- 0
PSI2 [ 12 , 5 ]<- 0
PSI2 [ 12 , 6 ]<- 0
PSI2 [ 12 , 7 ]<- 0
PSI2 [ 12 , 8 ]<- 0
PSI2 [ 12 , 9 ]<- 0
PSI2 [ 12 , 10 ]<- 0
PSI2 [ 12 , 11 ]<- 0
PSI2 [ 12 , 12 ]<- 0
PSI2 [ 12 , 13 ]<- 0
PSI2 [ 12 , 14 ]<- beta[3]
PSI2 [ 12 , 15 ]<- 1-beta[3]
PSI2 [ 12 , 16 ]<- 0

PSI2 [ 13 , 1 ]<- 0
PSI2 [ 13 , 2 ]<- 0
PSI2 [ 13 , 3 ]<- 0
PSI2 [ 13 , 4 ]<- 0
PSI2 [ 13 , 5 ]<- 0
PSI2 [ 13 , 6 ]<- 0
PSI2 [ 13 , 7 ]<- 0
PSI2 [ 13 , 8 ]<- 0
PSI2 [ 13 , 9 ]<- 0
PSI2 [ 13 , 10 ]<- 0
PSI2 [ 13 , 11 ]<- 0
PSI2 [ 13 , 12 ]<- 0
PSI2 [ 13 , 13 ]<- 0
PSI2 [ 13 , 14 ]<- 0
PSI2 [ 13 , 15 ]<- 0
PSI2 [ 13 , 16 ]<- 1

# PSI3:litter size probabilities
PSI3 [ 1 , 1 ]<- 0

```

```
1
2
3
4 PSI3 [ 1 , 2 ]<- 1
5 PSI3 [ 1 , 3 ]<- 0
6 PSI3 [ 1 , 4 ]<- 0
7 PSI3 [ 1 , 5 ]<- 0
8 PSI3 [ 1 , 6 ]<- 0
9 PSI3 [ 1 , 7 ]<- 0
10 PSI3 [ 1 , 8 ]<- 0
11 PSI3 [ 1 , 9 ]<- 0
12 PSI3 [ 1 , 10 ]<- 0
13 PSI3 [ 1 , 11 ]<- 0
14 PSI3 [ 1 , 12 ]<- 0
15
16 PSI3 [ 2 , 1 ]<- 0
17 PSI3 [ 2 , 2 ]<- 0
18 PSI3 [ 2 , 3 ]<- 1
19 PSI3 [ 2 , 4 ]<- 0
20 PSI3 [ 2 , 5 ]<- 0
21 PSI3 [ 2 , 6 ]<- 0
22 PSI3 [ 2 , 7 ]<- 0
23 PSI3 [ 2 , 8 ]<- 0
24 PSI3 [ 2 , 9 ]<- 0
25 PSI3 [ 2 , 10 ]<- 0
26 PSI3 [ 2 , 11 ]<- 0
27 PSI3 [ 2 , 12 ]<- 0
28
29 PSI3 [ 3 , 1 ]<- 0
30 PSI3 [ 3 , 2 ]<- 0
31 PSI3 [ 3 , 3 ]<- 0
32 PSI3 [ 3 , 4 ]<- 1
33 PSI3 [ 3 , 5 ]<- 0
34 PSI3 [ 3 , 6 ]<- 0
35 PSI3 [ 3 , 7 ]<- 0
36 PSI3 [ 3 , 8 ]<- 0
37 PSI3 [ 3 , 9 ]<- 0
38 PSI3 [ 3 , 10 ]<- 0
39 PSI3 [ 3 , 11 ]<- 0
40 PSI3 [ 3 , 12 ]<- 0
41
42 PSI3 [ 4 , 1 ]<- 0
43 PSI3 [ 4 , 2 ]<- 0
44 PSI3 [ 4 , 3 ]<- 0
45 PSI3 [ 4 , 4 ]<- 0
46 PSI3 [ 4 , 5 ]<- 0
47 PSI3 [ 4 , 6 ]<- 0
48 PSI3 [ 4 , 7 ]<- 1
49 PSI3 [ 4 , 8 ]<- 0
50 PSI3 [ 4 , 9 ]<- 0
51 PSI3 [ 4 , 10 ]<- 0
52 PSI3 [ 4 , 11 ]<- 0
53 PSI3 [ 4 , 12 ]<- 0
54
55 PSI3 [ 5 , 1 ]<- 0
56 PSI3 [ 5 , 2 ]<- 0
57
58
59
60
```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```

PSI3 [ 5 , 3 ]<- 0
PSI3 [ 5 , 4 ]<- 0
PSI3 [ 5 , 5 ]<- 0
PSI3 [ 5 , 6 ]<- 0
PSI3 [ 5 , 7 ]<- 0
PSI3 [ 5 , 8 ]<- 1
PSI3 [ 5 , 9 ]<- 0
PSI3 [ 5 , 10 ]<- 0
PSI3 [ 5 , 11 ]<- 0
PSI3 [ 5 , 12 ]<- 0

PSI3 [ 6 , 1 ]<- 0
PSI3 [ 6 , 2 ]<- 0
PSI3 [ 6 , 3 ]<- 0
PSI3 [ 6 , 4 ]<- 0
PSI3 [ 6 , 5 ]<- 0
PSI3 [ 6 , 6 ]<- 0
PSI3 [ 6 , 7 ]<- 0
PSI3 [ 6 , 8 ]<- 0
PSI3 [ 6 , 9 ]<- 1
PSI3 [ 6 , 10 ]<- 0
PSI3 [ 6 , 11 ]<- 0
PSI3 [ 6 , 12 ]<- 0

PSI3 [ 7 , 1 ]<- 0
PSI3 [ 7 , 2 ]<- 0
PSI3 [ 7 , 3 ]<- 0
PSI3 [ 7 , 4 ]<- 0
PSI3 [ 7 , 5 ]<- 0
PSI3 [ 7 , 6 ]<- 0
PSI3 [ 7 , 7 ]<- 0
PSI3 [ 7 , 8 ]<- 0
PSI3 [ 7 , 9 ]<- 0
PSI3 [ 7 , 10 ]<- 1
PSI3 [ 7 , 11 ]<- 0
PSI3 [ 7 , 12 ]<- 0

PSI3 [ 8 , 1 ]<- 0
PSI3 [ 8 , 2 ]<- 0
PSI3 [ 8 , 3 ]<- 0
PSI3 [ 8 , 4 ]<- 0
PSI3 [ 8 , 5 ]<- gamma[1]
PSI3 [ 8 , 6 ]<- 1-gamma[1]
PSI3 [ 8 , 7 ]<- 0
PSI3 [ 8 , 8 ]<- 0
PSI3 [ 8 , 9 ]<- 0
PSI3 [ 8 , 10 ]<- 0
PSI3 [ 8 , 11 ]<- 0
PSI3 [ 8 , 12 ]<- 0

PSI3 [ 9 , 1 ]<- 0
PSI3 [ 9 , 2 ]<- 0
PSI3 [ 9 , 3 ]<- 0

```

```

1
2
3
4 PSI3 [ 9 , 4 ]<- 0
5 PSI3 [ 9 , 5 ]<- 0
6 PSI3 [ 9 , 6 ]<- 0
7 PSI3 [ 9 , 7 ]<- 0
8 PSI3 [ 9 , 8 ]<- 0
9 PSI3 [ 9 , 9 ]<- 0
10 PSI3 [ 9 , 10 ]<- 0
11 PSI3 [ 9 , 11 ]<- 1
12 PSI3 [ 9 , 12 ]<- 0
13
14 PSI3 [ 10 , 1 ]<- 0
15 PSI3 [ 10 , 2 ]<- 0
16 PSI3 [ 10 , 3 ]<- 0
17 PSI3 [ 10 , 4 ]<- 0
18 PSI3 [ 10 , 5 ]<- gamma[1]
19 PSI3 [ 10 , 6 ]<- 1-gamma[1]
20 PSI3 [ 10 , 7 ]<- 0
21 PSI3 [ 10 , 8 ]<- 0
22 PSI3 [ 10 , 9 ]<- 0
23 PSI3 [ 10 , 10 ]<- 0
24 PSI3 [ 10 , 11 ]<- 0
25 PSI3 [ 10 , 12 ]<- 0
26
27 PSI3 [ 11 , 1 ]<- 0
28 PSI3 [ 11 , 2 ]<- 0
29 PSI3 [ 11 , 3 ]<- 0
30 PSI3 [ 11 , 4 ]<- 0
31 PSI3 [ 11 , 5 ]<- 0
32 PSI3 [ 11 , 6 ]<- 0
33 PSI3 [ 11 , 7 ]<- 0
34 PSI3 [ 11 , 8 ]<- 0
35 PSI3 [ 11 , 9 ]<- 0
36 PSI3 [ 11 , 10 ]<- 0
37 PSI3 [ 11 , 11 ]<- 1
38 PSI3 [ 11 , 12 ]<- 0
39
40 PSI3 [ 12 , 1 ]<- 0
41 PSI3 [ 12 , 2 ]<- 0
42 PSI3 [ 12 , 3 ]<- 0
43 PSI3 [ 12 , 4 ]<- 0
44 PSI3 [ 12 , 5 ]<- gamma[2]
45 PSI3 [ 12 , 6 ]<- 1-gamma[2]
46 PSI3 [ 12 , 7 ]<- 0
47 PSI3 [ 12 , 8 ]<- 0
48 PSI3 [ 12 , 9 ]<- 0
49 PSI3 [ 12 , 10 ]<- 0
50 PSI3 [ 12 , 11 ]<- 0
51 PSI3 [ 12 , 12 ]<- 0
52
53 PSI3 [ 13 , 1 ]<- 0
54 PSI3 [ 13 , 2 ]<- 0
55 PSI3 [ 13 , 3 ]<- 0
56 PSI3 [ 13 , 4 ]<- 0
57
58
59
60

```

```

1
2
3
4 PSI3 [ 13 , 5 ]<- 0
5 PSI3 [ 13 , 6 ]<- 0
6 PSI3 [ 13 , 7 ]<- 0
7 PSI3 [ 13 , 8 ]<- 0
8 PSI3 [ 13 , 9 ]<- 0
9 PSI3 [ 13 , 10 ]<- 0
10 PSI3 [ 13 , 11 ]<- 1
11 PSI3 [ 13 , 12 ]<- 0
12
13 PSI3 [ 14 , 1 ]<- 0
14 PSI3 [ 14 , 2 ]<- 0
15 PSI3 [ 14 , 3 ]<- 0
16 PSI3 [ 14 , 4 ]<- 0
17 PSI3 [ 14 , 5 ]<- gamma[2]
18 PSI3 [ 14 , 6 ]<- 1-gamma[2]
19 PSI3 [ 14 , 7 ]<- 0
20 PSI3 [ 14 , 8 ]<- 0
21 PSI3 [ 14 , 9 ]<- 0
22 PSI3 [ 14 , 10 ]<- 0
23 PSI3 [ 14 , 11 ]<- 0
24 PSI3 [ 14 , 12 ]<- 0
25
26 PSI3 [ 15 , 1 ]<- 0
27 PSI3 [ 15 , 2 ]<- 0
28 PSI3 [ 15 , 3 ]<- 0
29 PSI3 [ 15 , 4 ]<- 0
30 PSI3 [ 15 , 5 ]<- 0
31 PSI3 [ 15 , 6 ]<- 0
32 PSI3 [ 15 , 7 ]<- 0
33 PSI3 [ 15 , 8 ]<- 0
34 PSI3 [ 15 , 9 ]<- 0
35 PSI3 [ 15 , 10 ]<- 0
36 PSI3 [ 15 , 11 ]<- 1
37 PSI3 [ 15 , 12 ]<- 0
38
39 PSI3 [ 16 , 1 ]<- 0
40 PSI3 [ 16 , 2 ]<- 0
41 PSI3 [ 16 , 3 ]<- 0
42 PSI3 [ 16 , 4 ]<- 0
43 PSI3 [ 16 , 5 ]<- 0
44 PSI3 [ 16 , 6 ]<- 0
45 PSI3 [ 16 , 7 ]<- 0
46 PSI3 [ 16 , 8 ]<- 0
47 PSI3 [ 16 , 9 ]<- 0
48 PSI3 [ 16 , 10 ]<- 0
49 PSI3 [ 16 , 11 ]<- 0
50 PSI3 [ 16 , 12 ]<- 1
51
52 # Matrix product for state-to-state transitions S
53 S[1:12,1:12] <- PHI[1:12,1:12] %*% PSI1[1:12,1:13] %*% PSI2[1:13,1:16] %*% PSI3[1:16,1:12]
54
55 ## Observation process: Define probabilities of E(t) given S(t).
56
57
58
59
60

```

```
1  
2  
3  
4 #for initial capture, conditional on first capture
```

```
5 EO [ 1 , 1 ]<- 0
```

```
6 EO [ 1 , 2 ]<- 1
```

```
7 EO [ 1 , 3 ]<- 0
```

```
8 EO [ 1 , 4 ]<- 0
```

```
9 EO [ 1 , 5 ]<- 0
```

```
10 EO [ 1 , 6 ]<- 0
```

```
11 EO [ 1 , 7 ]<- 0
```

```
12 EO [ 1 , 8 ]<- 0
```

```
13 EO [ 1 , 9 ]<- 0
```

```
14 EO [ 1 , 10 ]<- 0
```

```
15 EO [ 1 , 11 ]<- 0
```

```
16 EO [ 1 , 12 ]<- 0
```

```
17  
18 EO [ 2 , 1 ]<- 0
```

```
19 EO [ 2 , 2 ]<- 0
```

```
20 EO [ 2 , 3 ]<- 1
```

```
21 EO [ 2 , 4 ]<- 0
```

```
22 EO [ 2 , 5 ]<- 0
```

```
23 EO [ 2 , 6 ]<- 0
```

```
24 EO [ 2 , 7 ]<- 0
```

```
25 EO [ 2 , 8 ]<- 0
```

```
26 EO [ 2 , 9 ]<- 0
```

```
27 EO [ 2 , 10 ]<- 0
```

```
28 EO [ 2 , 11 ]<- 0
```

```
29 EO [ 2 , 12 ]<- 0
```

```
30  
31 EO [ 3 , 1 ]<- 0
```

```
32 EO [ 3 , 2 ]<- 0
```

```
33 EO [ 3 , 3 ]<- 0
```

```
34 EO [ 3 , 4 ]<- 1
```

```
35 EO [ 3 , 5 ]<- 0
```

```
36 EO [ 3 , 6 ]<- 0
```

```
37 EO [ 3 , 7 ]<- 0
```

```
38 EO [ 3 , 8 ]<- 0
```

```
39 EO [ 3 , 9 ]<- 0
```

```
40 EO [ 3 , 10 ]<- 0
```

```
41 EO [ 3 , 11 ]<- 0
```

```
42 EO [ 3 , 12 ]<- 0
```

```
43  
44 EO [ 4 , 1 ]<- 0
```

```
45 EO [ 4 , 2 ]<- 0
```

```
46 EO [ 4 , 3 ]<- 0
```

```
47 EO [ 4 , 4 ]<- 0
```

```
48 EO [ 4 , 5 ]<- 1
```

```
49 EO [ 4 , 6 ]<- 0
```

```
50 EO [ 4 , 7 ]<- 0
```

```
51 EO [ 4 , 8 ]<- 0
```

```
52 EO [ 4 , 9 ]<- 0
```

```
53 EO [ 4 , 10 ]<- 0
```

```
54 EO [ 4 , 11 ]<- 0
```

```
55 EO [ 4 , 12 ]<- 0
```


1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```
EO [ 5 , 1 ]<- 0
EO [ 5 , 2 ]<- 0
EO [ 5 , 3 ]<- 0
EO [ 5 , 4 ]<- 0
EO [ 5 , 5 ]<- 0
EO [ 5 , 6 ]<- 1
EO [ 5 , 7 ]<- 0
EO [ 5 , 8 ]<- 0
EO [ 5 , 9 ]<- 0
EO [ 5 , 10 ]<- 0
EO [ 5 , 11 ]<- 0
EO [ 5 , 12 ]<- 0

EO [ 6 , 1 ]<- 0
EO [ 6 , 2 ]<- 0
EO [ 6 , 3 ]<- 0
EO [ 6 , 4 ]<- 0
EO [ 6 , 5 ]<- 0
EO [ 6 , 6 ]<- 0
EO [ 6 , 7 ]<- 1
EO [ 6 , 8 ]<- 0
EO [ 6 , 9 ]<- 0
EO [ 6 , 10 ]<- 0
EO [ 6 , 11 ]<- 0
EO [ 6 , 12 ]<- 0

EO [ 7 , 1 ]<- 0
EO [ 7 , 2 ]<- 0
EO [ 7 , 3 ]<- 0
EO [ 7 , 4 ]<- 0
EO [ 7 , 5 ]<- 0
EO [ 7 , 6 ]<- 0
EO [ 7 , 7 ]<- 0
EO [ 7 , 8 ]<- 1
EO [ 7 , 9 ]<- 0
EO [ 7 , 10 ]<- 0
EO [ 7 , 11 ]<- 0
EO [ 7 , 12 ]<- 0

EO [ 8 , 1 ]<- 0
EO [ 8 , 2 ]<- 0
EO [ 8 , 3 ]<- 0
EO [ 8 , 4 ]<- 0
EO [ 8 , 5 ]<- 0
EO [ 8 , 6 ]<- 0
EO [ 8 , 7 ]<- 0
EO [ 8 , 8 ]<- 0
EO [ 8 , 9 ]<- 1
EO [ 8 , 10 ]<- 0
EO [ 8 , 11 ]<- 0
EO [ 8 , 12 ]<- 0

EO [ 9 , 1 ]<- 0
```

```

1
2
3
4 EO [ 9 , 2 ]<- 0
5 EO [ 9 , 3 ]<- 0
6 EO [ 9 , 4 ]<- 0
7 EO [ 9 , 5 ]<- 0
8 EO [ 9 , 6 ]<- 0
9 EO [ 9 , 7 ]<- 0
10 EO [ 9 , 8 ]<- 0
11 EO [ 9 , 9 ]<- 0
12 EO [ 9 , 10 ]<- 1
13 EO [ 9 , 11 ]<- 0
14 EO [ 9 , 12 ]<- 0
15
16 EO [ 10 , 1 ]<- 0
17 EO [ 10 , 2 ]<- 0
18 EO [ 10 , 3 ]<- 0
19 EO [ 10 , 4 ]<- 0
20 EO [ 10 , 5 ]<- 0
21 EO [ 10 , 6 ]<- 0
22 EO [ 10 , 7 ]<- 0
23 EO [ 10 , 8 ]<- 0
24 EO [ 10 , 9 ]<- 0
25 EO [ 10 , 10 ]<- 0
26 EO [ 10 , 11 ]<- 1
27 EO [ 10 , 12 ]<- 0
28
29 EO [ 11 , 1 ]<- 0
30 EO [ 11 , 2 ]<- 0
31 EO [ 11 , 3 ]<- 0
32 EO [ 11 , 4 ]<- 0
33 EO [ 11 , 5 ]<- 0
34 EO [ 11 , 6 ]<- 0
35 EO [ 11 , 7 ]<- 0
36 EO [ 11 , 8 ]<- 0
37 EO [ 11 , 9 ]<- 0
38 EO [ 11 , 10 ]<- 0
39 EO [ 11 , 11 ]<- 0
40 EO [ 11 , 12 ]<- 1
41
42 EO [ 12 , 1 ]<- 1
43 EO [ 12 , 2 ]<- 0
44 EO [ 12 , 3 ]<- 0
45 EO [ 12 , 4 ]<- 0
46 EO [ 12 , 5 ]<- 0
47 EO [ 12 , 6 ]<- 0
48 EO [ 12 , 7 ]<- 0
49 EO [ 12 , 8 ]<- 0
50 EO [ 12 , 9 ]<- 0
51 EO [ 12 , 10 ]<- 0
52 EO [ 12 , 11 ]<- 0
53 EO [ 12 , 12 ]<- 0
54
55 # departure probability of a2 offspring
56 for(i in 1:N){
57
58
59
60

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```

for(t in 1:(Years-1)){
  E1 [ 1 , 1 ,i,t]<- 1
  E1 [ 1 , 2 ,i,t]<- 0
  E1 [ 1 , 3 ,i,t]<- 0
  E1 [ 1 , 4 ,i,t]<- 0
  E1 [ 1 , 5 ,i,t]<- 0
  E1 [ 1 , 6 ,i,t]<- 0
  E1 [ 1 , 7 ,i,t]<- 0
  E1 [ 1 , 8 ,i,t]<- 0
  E1 [ 1 , 9 ,i,t]<- 0
  E1 [ 1 , 10,i,t]<- 0
  E1 [ 1 , 11,i,t]<- 0
  E1 [ 1 , 12,i,t]<- 0

  E1 [ 2 , 1 ,i,t]<- 0
  E1 [ 2 , 2 ,i,t]<- 1
  E1 [ 2 , 3 ,i,t]<- 0
  E1 [ 2 , 4 ,i,t]<- 0
  E1 [ 2 , 5 ,i,t]<- 0
  E1 [ 2 , 6 ,i,t]<- 0
  E1 [ 2 , 7 ,i,t]<- 0
  E1 [ 2 , 8 ,i,t]<- 0
  E1 [ 2 , 9 ,i,t]<- 0
  E1 [ 2 , 10,i,t]<- 0
  E1 [ 2 , 11,i,t]<- 0
  E1 [ 2 , 12,i,t]<- 0

  E1 [ 3 , 1 ,i,t]<- 0
  E1 [ 3 , 2 ,i,t]<- 0
  E1 [ 3 , 3 ,i,t]<- 1
  E1 [ 3 , 4 ,i,t]<- 0
  E1 [ 3 , 5 ,i,t]<- 0
  E1 [ 3 , 6 ,i,t]<- 0
  E1 [ 3 , 7 ,i,t]<- 0
  E1 [ 3 , 8 ,i,t]<- 0
  E1 [ 3 , 9 ,i,t]<- 0
  E1 [ 3 , 10,i,t]<- 0
  E1 [ 3 , 11,i,t]<- 0
  E1 [ 3 , 12,i,t]<- 0

  E1 [ 4 , 1 ,i,t]<- 0
  E1 [ 4 , 2 ,i,t]<- 0
  E1 [ 4 , 3 ,i,t]<- 0
  E1 [ 4 , 4 ,i,t]<- 1
  E1 [ 4 , 5 ,i,t]<- 0
  E1 [ 4 , 6 ,i,t]<- 0
  E1 [ 4 , 7 ,i,t]<- 0
  E1 [ 4 , 8 ,i,t]<- 0
  E1 [ 4 , 9 ,i,t]<- 0
  E1 [ 4 , 10,i,t]<- 0
  E1 [ 4 , 11,i,t]<- 0
  E1 [ 4 , 12,i,t]<- 0

```

```

1
2
3
4 E1 [ 5 , 1,i,t]<- 0
5 E1 [ 5 , 2,i,t]<- 0
6 E1 [ 5 , 3,i,t]<- 0
7 E1 [ 5 , 4,i,t]<- 0
8 E1 [ 5 , 5,i,t]<- 1
9 E1 [ 5 , 6,i,t]<- 0
10 E1 [ 5 , 7,i,t]<- 0
11 E1 [ 5 , 8,i,t]<- 0
12 E1 [ 5 , 9,i,t]<- 0
13 E1 [ 5 , 10,i,t]<- 0
14 E1 [ 5 , 11,i,t]<- 0
15 E1 [ 5 , 12,i,t]<- 0
16
17 E1 [ 6 , 1 ,i,t]<- 0
18 E1 [ 6 , 2 ,i,t]<- 0
19 E1 [ 6 , 3 ,i,t]<- 0
20 E1 [ 6 , 4 ,i,t]<- 0
21 E1 [ 6 , 5 ,i,t]<- 0
22 E1 [ 6 , 6 ,i,t]<- 1
23 E1 [ 6 , 7 ,i,t]<- 0
24 E1 [ 6 , 8 ,i,t]<- 0
25 E1 [ 6 , 9 ,i,t]<- 0
26 E1 [ 6 , 10,i,t]<- 0
27 E1 [ 6 , 11,i,t]<- 0
28 E1 [ 6 , 12,i,t]<- 0
29
30 E1 [ 7 , 1 ,i,t]<- 0
31 E1 [ 7 , 2 ,i,t]<- 0
32 E1 [ 7 , 3 ,i,t]<- 0
33 E1 [ 7 , 4 ,i,t]<- 0
34 E1 [ 7 , 5 ,i,t]<- 0
35 E1 [ 7 , 6 ,i,t]<- 0
36 E1 [ 7 , 7 ,i,t]<- 1
37 E1 [ 7 , 8 ,i,t]<- 0
38 E1 [ 7 , 9 ,i,t]<- 0
39 E1 [ 7 , 10,i,t]<- 0
40 E1 [ 7 , 11,i,t]<- 0
41 E1 [ 7 , 12,i,t]<- 0
42
43 E1 [ 8 , 1 ,i,t]<- 0
44 E1 [ 8 , 2 ,i,t]<- 0
45 E1 [ 8 , 3 ,i,t]<- 0
46 E1 [ 8 , 4 ,i,t]<- 0
47 E1 [ 8 , 5 ,i,t]<- 0
48 E1 [ 8 , 6 ,i,t]<- 0
49 E1 [ 8 , 7 ,i,t]<- 0
50 E1 [ 8 , 8 ,i,t]<- 1
51 E1 [ 8 , 9 ,i,t]<- 0
52 E1 [ 8 , 10,i,t]<- 0
53 E1 [ 8 , 11,i,t]<- 0
54 E1 [ 8 , 12,i,t]<- 0
55
56 E1 [ 9 , 1 ,i,t]<- 0
57
58
59
60

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```

E1 [ 9 , 2 ,i,t]<- 0
E1 [ 9 , 3 ,i,t]<- 0
E1 [ 9 , 4 ,i,t]<- 0
E1 [ 9 , 5 ,i,t]<- 0
E1 [ 9 , 6 ,i,t]<- 0
E1 [ 9 , 7 ,i,t]<- 0
E1 [ 9 , 8 ,i,t]<- 0
E1 [ 9 , 9 ,i,t]<- 1-alpha[i,t+1]
E1 [ 9 , 10,i,t]<- 0
E1 [ 9 , 11,i,t]<- alpha[i,t+1]
E1 [ 9 , 12,i,t]<- 0

E1 [ 10 , 1,i,t]<- 0
E1 [ 10 , 2,i,t]<- 0
E1 [ 10 , 3,i,t]<- 0
E1 [ 10 , 4,i,t]<- 0
E1 [ 10 , 5,i,t]<- 0
E1 [ 10 , 6,i,t]<- 0
E1 [ 10 , 7,i,t]<- 0
E1 [ 10 , 8,i,t]<- 0
E1 [ 10 , 9,i,t]<- 2*(1-alpha[i,t+1])*alpha[i,t+1]
E1 [ 10 , 10,i,t]<- 1 - (2*(1-alpha[i,t+1])*alpha[i,t+1]) - (alpha[i,t+1])^2
E1 [ 10 , 11,i,t]<- (alpha[i,t+1])^2
E1 [ 10 , 12,i,t]<- 0

E1 [ 11 , 1 ,i,t]<- 0
E1 [ 11 , 2 ,i,t]<- 0
E1 [ 11 , 3 ,i,t]<- 0
E1 [ 11 , 4 ,i,t]<- 0
E1 [ 11 , 5 ,i,t]<- 0
E1 [ 11 , 6 ,i,t]<- 0
E1 [ 11 , 7 ,i,t]<- 0
E1 [ 11 , 8 ,i,t]<- 0
E1 [ 11 , 9 ,i,t]<- 0
E1 [ 11 , 10,i,t]<- 0
E1 [ 11 , 11,i,t]<- 1
E1 [ 11 , 12,i,t]<- 0

E1 [ 12 , 1 ,i,t]<- 0
E1 [ 12 , 2 ,i,t]<- 0
E1 [ 12 , 3 ,i,t]<- 0
E1 [ 12 , 4 ,i,t]<- 0
E1 [ 12 , 5 ,i,t]<- 0
E1 [ 12 , 6 ,i,t]<- 0
E1 [ 12 , 7 ,i,t]<- 0
E1 [ 12 , 8 ,i,t]<- 0
E1 [ 12 , 9 ,i,t]<- 0
E1 [ 12 , 10,i,t]<- 0
E1 [ 12 , 11,i,t]<- 0
E1 [ 12 , 12,i,t]<- 1

# for recapture probability
E2 [ 1 , 1 ,i,t]<- 1 -p

```

```

1
2
3
4 E2 [ 1 , 2 ,i,t]<- p
5 E2 [ 1 , 3 ,i,t]<- 0
6 E2 [ 1 , 4 ,i,t]<- 0
7 E2 [ 1 , 5 ,i,t]<- 0
8 E2 [ 1 , 6 ,i,t]<- 0
9 E2 [ 1 , 7 ,i,t]<- 0
10 E2 [ 1 , 8 ,i,t]<- 0
11 E2 [ 1 , 9 ,i,t]<- 0
12 E2 [ 1 , 10,i,t]<- 0
13 E2 [ 1 , 11,i,t]<- 0
14 E2 [ 1 , 12,i,t]<- 0
15
16 E2 [ 2 , 1 ,i,t]<- 1 -p
17 E2 [ 2 , 2 ,i,t]<- 0
18 E2 [ 2 , 3 ,i,t]<- p
19 E2 [ 2 , 4 ,i,t]<- 0
20 E2 [ 2 , 5 ,i,t]<- 0
21 E2 [ 2 , 6 ,i,t]<- 0
22 E2 [ 2 , 7 ,i,t]<- 0
23 E2 [ 2 , 8 ,i,t]<- 0
24 E2 [ 2 , 9 ,i,t]<- 0
25 E2 [ 2 , 10,i,t]<- 0
26 E2 [ 2 , 11,i,t]<- 0
27 E2 [ 2 , 12,i,t]<- 0
28
29 E2 [ 3 , 1 ,i,t]<- 1 -p
30 E2 [ 3 , 2 ,i,t]<- 0
31 E2 [ 3 , 3 ,i,t]<- 0
32 E2 [ 3 , 4 ,i,t]<- p
33 E2 [ 3 , 5 ,i,t]<- 0
34 E2 [ 3 , 6 ,i,t]<- 0
35 E2 [ 3 , 7 ,i,t]<- 0
36 E2 [ 3 , 8 ,i,t]<- 0
37 E2 [ 3 , 9 ,i,t]<- 0
38 E2 [ 3 , 10,i,t]<- 0
39 E2 [ 3 , 11,i,t]<- 0
40 E2 [ 3 , 12,i,t]<- 0
41
42 E2 [ 4 , 1 ,i,t]<- 1 -p
43 E2 [ 4 , 2 ,i,t]<- 0
44 E2 [ 4 , 3 ,i,t]<- 0
45 E2 [ 4 , 4 ,i,t]<- 0
46 E2 [ 4 , 5 ,i,t]<- p
47 E2 [ 4 , 6 ,i,t]<- 0
48 E2 [ 4 , 7 ,i,t]<- 0
49 E2 [ 4 , 8 ,i,t]<- 0
50 E2 [ 4 , 9 ,i,t]<- 0
51 E2 [ 4 , 10,i,t]<- 0
52 E2 [ 4 , 11,i,t]<- 0
53 E2 [ 4 , 12,i,t]<- 0
54
55 E2 [ 5 , 1,i,t]<- 1 -p
56 E2 [ 5 , 2,i,t]<- 0
57
58
59
60

```

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

```

E2 [ 5 , 3,i,t]<- 0
E2 [ 5 , 4,i,t]<- 0
E2 [ 5 , 5,i,t]<- 0
E2 [ 5 , 6,i,t]<- p
E2 [ 5 , 7,i,t]<- 0
E2 [ 5 , 8,i,t]<- 0
E2 [ 5 , 9,i,t]<- 0
E2 [ 5 , 10,i,t]<- 0
E2 [ 5 , 11,i,t]<- 0
E2 [ 5 , 12,i,t]<- 0

E2 [ 6 , 1 ,i,t]<- 1 -p
E2 [ 6 , 2 ,i,t]<- 0
E2 [ 6 , 3 ,i,t]<- 0
E2 [ 6 , 4 ,i,t]<- 0
E2 [ 6 , 5 ,i,t]<- 0
E2 [ 6 , 6 ,i,t]<- 0
E2 [ 6 , 7 ,i,t]<- p
E2 [ 6 , 8 ,i,t]<- 0
E2 [ 6 , 9 ,i,t]<- 0
E2 [ 6 , 10,i,t]<- 0
E2 [ 6 , 11,i,t]<- 0
E2 [ 6 , 12,i,t]<- 0

E2 [ 7 , 1 ,i,t]<- 1 -p
E2 [ 7 , 2 ,i,t]<- 0
E2 [ 7 , 3 ,i,t]<- 0
E2 [ 7 , 4 ,i,t]<- 0
E2 [ 7 , 5 ,i,t]<- 0
E2 [ 7 , 6 ,i,t]<- 0
E2 [ 7 , 7 ,i,t]<- 0
E2 [ 7 , 8 ,i,t]<- p
E2 [ 7 , 9 ,i,t]<- 0
E2 [ 7 , 10,i,t]<- 0
E2 [ 7 , 11,i,t]<- 0
E2 [ 7 , 12,i,t]<- 0

E2 [ 8 , 1 ,i,t]<- 1 -p
E2 [ 8 , 2 ,i,t]<- 0
E2 [ 8 , 3 ,i,t]<- 0
E2 [ 8 , 4 ,i,t]<- 0
E2 [ 8 , 5 ,i,t]<- 0
E2 [ 8 , 6 ,i,t]<- 0
E2 [ 8 , 7 ,i,t]<- 0
E2 [ 8 , 8 ,i,t]<- 0
E2 [ 8 , 9 ,i,t]<- p
E2 [ 8 , 10,i,t]<- 0
E2 [ 8 , 11,i,t]<- 0
E2 [ 8 , 12,i,t]<- 0

E2 [ 9 , 1 ,i,t]<- 1-p
E2 [ 9 , 2 ,i,t]<- 0
E2 [ 9 , 3 ,i,t]<- 0

```

```

1
2
3
4 E2 [ 9 , 4 ,i,t]<- 0
5 E2 [ 9 , 5 ,i,t]<- 0
6 E2 [ 9 , 6 ,i,t]<- 0
7 E2 [ 9 , 7 ,i,t]<- 0
8 E2 [ 9 , 8 ,i,t]<- 0
9 E2 [ 9 , 9 ,i,t]<- 0
10 E2 [ 9 , 10,i,t]<- p
11 E2 [ 9 , 11,i,t]<- 0
12 E2 [ 9 , 12,i,t]<- 0
13
14 E2 [ 10 , 1,i,t]<- 1-p
15 E2 [ 10 , 2,i,t]<- 0
16 E2 [ 10 , 3,i,t]<- 0
17 E2 [ 10 , 4,i,t]<- 0
18 E2 [ 10 , 5,i,t]<- 0
19 E2 [ 10 , 6,i,t]<- 0
20 E2 [ 10 , 7,i,t]<- 0
21 E2 [ 10 , 8,i,t]<- 0
22 E2 [ 10 , 9,i,t]<- 0
23 E2 [ 10 , 10,i,t]<- 0
24 E2 [ 10 , 11,i,t]<- p
25 E2 [ 10 , 12,i,t]<- 0
26
27 E2 [ 11 , 1 ,i,t]<- 1 - p
28 E2 [ 11 , 2 ,i,t]<- 0
29 E2 [ 11 , 3 ,i,t]<- 0
30 E2 [ 11 , 4 ,i,t]<- 0
31 E2 [ 11 , 5 ,i,t]<- 0
32 E2 [ 11 , 6 ,i,t]<- 0
33 E2 [ 11 , 7 ,i,t]<- 0
34 E2 [ 11 , 8 ,i,t]<- 0
35 E2 [ 11 , 9 ,i,t]<- 0
36 E2 [ 11 , 10,i,t]<- 0
37 E2 [ 11 , 11,i,t]<- 0
38 E2 [ 11 , 12,i,t]<- p
39
40 E2 [ 12 , 1 ,i,t]<- 1
41 E2 [ 12 , 2 ,i,t]<- 0
42 E2 [ 12 , 3 ,i,t]<- 0
43 E2 [ 12 , 4 ,i,t]<- 0
44 E2 [ 12 , 5 ,i,t]<- 0
45 E2 [ 12 , 6 ,i,t]<- 0
46 E2 [ 12 , 7 ,i,t]<- 0
47 E2 [ 12 , 8 ,i,t]<- 0
48 E2 [ 12 , 9 ,i,t]<- 0
49 E2 [ 12 , 10,i,t]<- 0
50 E2 [ 12 , 11,i,t]<- 0
51 E2 [ 12 , 12,i,t]<- 0
52
53 # Matrix product for offspring independence and recapture
54 E[1:12,1:12,i,t] <- E1[1:12,1:12,i,t] %*% E2[1:12,1:12,i,t]
55 }
56 }
57
58
59
60

```



```

1
2
3
4  ## LIKELIHOOD
5
6  for (i in 1:N) # for each individual
7  {
8    # The estimated probabilities of initial states S0 are the proportions in each state at first capture
9    alive[i,First[i]] ~ dcat(S0[1:12])
10   mydata[i,First[i]] ~ dcat(E0[alive[i,First[i]],1:12])
11
12   for (j in (First[i]+1):Years)
13   {
14
15     ## STATE EQUATIONS ##
16     # draw S(t) given S(t-1)
17     alive[i,j] ~ dcat(S[alive[i,j-1],1:12])
18
19     ## OBSERVATION EQUATIONS ##
20     # draw events E(t) given states S(t)
21
22     mydata[i,j] ~ dcat(E[alive[i,j],1:12,i,j-1])
23
24   }
25 }
26
27
28 ## PRIORS
29 # capture probability
30 p ~ dunif(0,1)
31
32 # juveniles, subadults and adult survival
33 #for(i in 1:2){phi[i] ~ dunif(0,1)}
34 phi[1] ~ dunif(0,1)
35
36 # initial states
37 for (i in 1:10){ log(prop[i]) <- theta[i]
38 theta[i] ~ dnorm(0,1)}
39
40 # offspring survival
41 # litter survival n=2 offspring
42 102 <- 1 - (1 - s[2]^2 - 2*s[2]*(1-s[2]))
43 112 <- 1 - (1 - s[4]^2 - 2*s[4]*(1-s[4]))
44 # individual offspring survival
45 #for(i in 1:4){s[i] ~ dunif(0,1)}
46
47 for(i in 1:2){s[i] ~ dunif(0,1)}
48 # Set constraints
49 for(u in 1:2){ X[u] ~ dunif(0,1)} # with X ~ U[0,1] then (a + (b - a) * X)
50 #so that s[1] < s[3] < phi[1] for litter of 1
51 s[3] <- s[1] + (phi[1] - s[1]) * X[1]
52 # and s[2] < s[4] < phi[1] for litters of 2
53 s[4] <- s[2] + (phi[1] - s[2]) * X[2]
54
55 # Breeding probability
56 kappa ~ dunif(0,1)
57
58
59
60

```

```

1  for(i in 1:3){beta[i]~ dunif(0,1)}
2
3
4  # Litter size probability
5  for(i in 1:2){gamma[i]~ dunif(0,1)}
6
7
8 } # end model
9
10
11 ")

```

This model differs from the model used for the simulations in just a few points. It assumes breeding probability and litter size probability does not vary between successful breeders (states AS1 and AS2) and female without dependent offspring (state A) by setting $\beta_3 = \beta_4$ (in the code beta[3]) and $\gamma_3 = \gamma_4$ (in the code gamma[2]). It also assumes that litter size probability is the same among failed breeders (loss of cub versus yearling litter), by setting $\gamma_1 = \gamma_2$ (in the code gamma[1]).

Run the jags model and save the results:

```

19 # Call JAGS from R
20 out <- jags(data=mydataax, inits=inits, parameters.to.save=params,
21            model.file = 'Multieventmodel_FitresidentBeardata.txt', n.chains=2, n.iter=20000, n.burnin=9000)
22
23 save(out, file='noage_lb_phip.RData')
24
25

```

Analyse the results

Load useful packages:

```

30 library(jagsUI)
31 library(MCMCvis)

```

Load model results and print a summary :

```

34 load(file='Fit_beardata.RData')
35 MCMCsummary(out, round=2)

```

##	mean	sd	2.5%	50%	97.5%	Rhat	n.eff
## phi	0.93	0.01	0.92	0.93	0.95	1.00	2027
## s[1]	0.54	0.10	0.34	0.54	0.72	1.00	4400
## s[2]	0.51	0.05	0.41	0.51	0.62	1.00	4400
## s[3]	0.67	0.11	0.46	0.68	0.87	1.00	1458
## s[4]	0.80	0.09	0.59	0.82	0.93	1.01	422
## 102	0.76	0.05	0.65	0.76	0.85	1.00	4400
## 112	0.95	0.04	0.83	0.97	0.99	1.01	331
## kappa	0.12	0.08	0.02	0.11	0.30	1.00	4400
## beta[1]	0.09	0.06	0.01	0.07	0.23	1.00	2978
## beta[2]	0.58	0.21	0.19	0.57	0.96	1.00	4400
## beta[3]	0.52	0.04	0.43	0.52	0.61	1.00	1763
## gamma[1]	0.35	0.17	0.07	0.34	0.71	1.00	2652
## gamma[2]	0.40	0.05	0.30	0.40	0.51	1.00	4400
## p	0.25	0.01	0.22	0.25	0.27	1.01	182
## prop[1]	0.56	0.16	0.30	0.54	0.92	1.00	4400
## prop[2]	0.46	0.14	0.24	0.44	0.79	1.00	4400
## prop[3]	0.66	0.18	0.37	0.63	1.08	1.00	4400
## prop[4]	0.42	0.14	0.21	0.40	0.74	1.00	4400
## prop[5]	0.80	0.21	0.45	0.77	1.28	1.00	4400

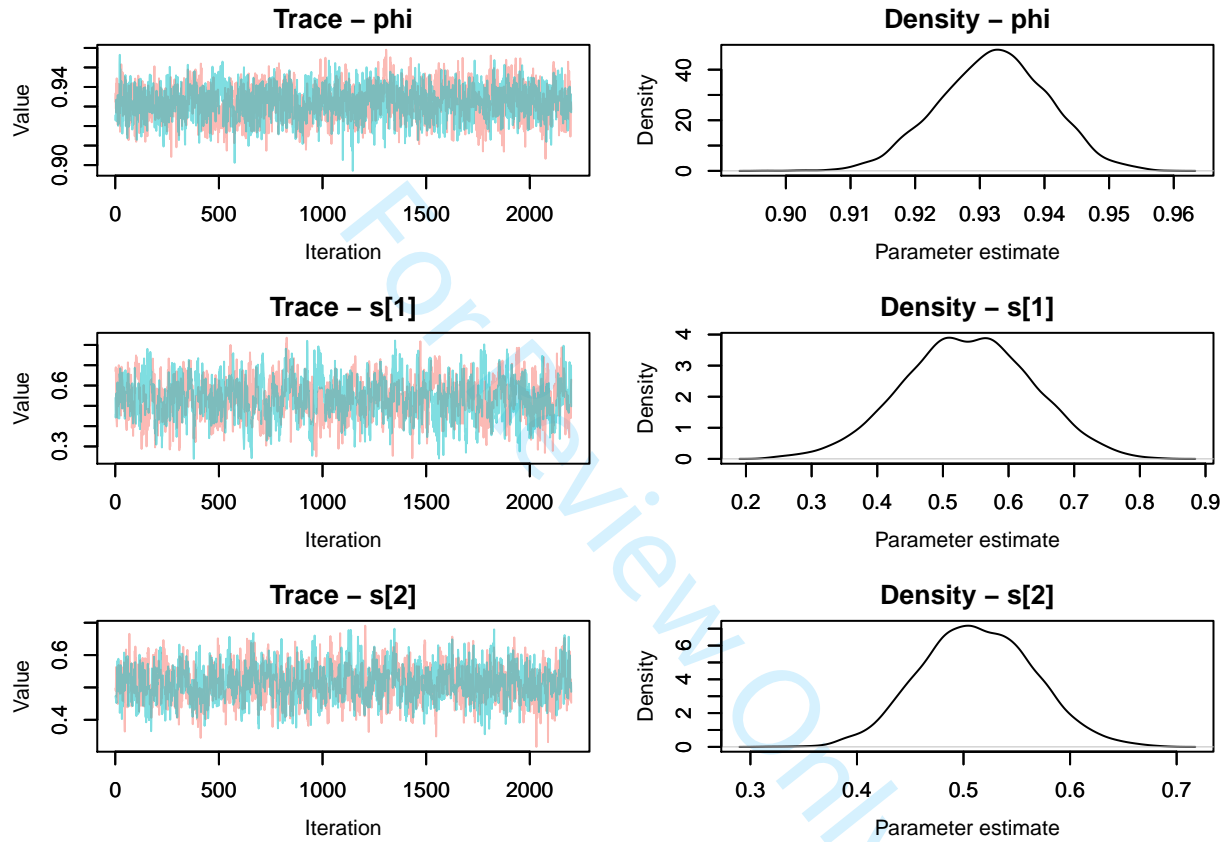
```

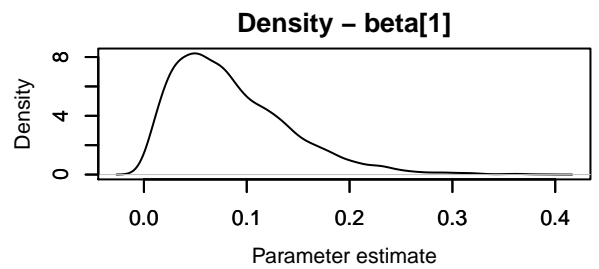
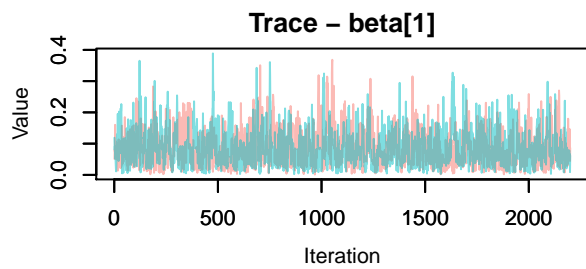
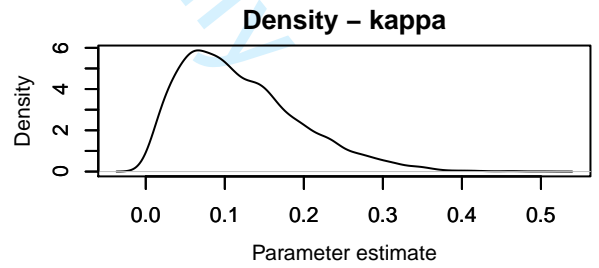
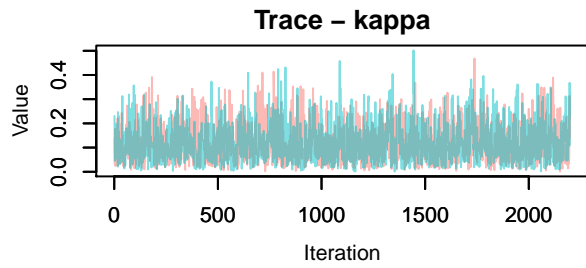
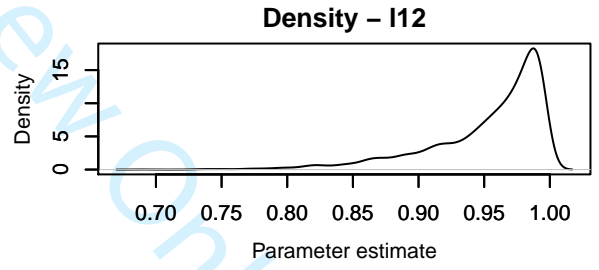
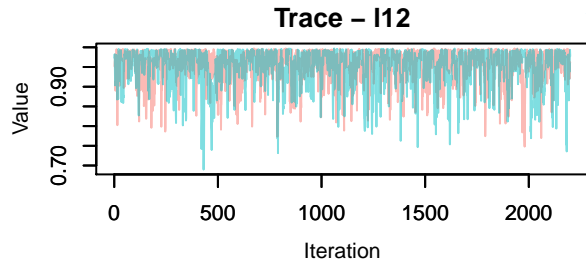
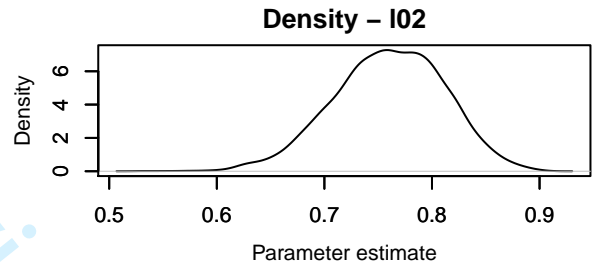
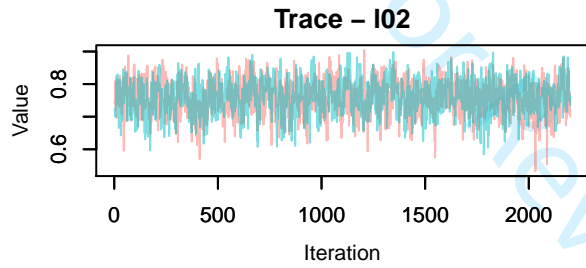
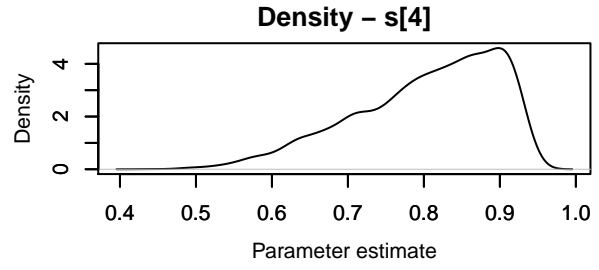
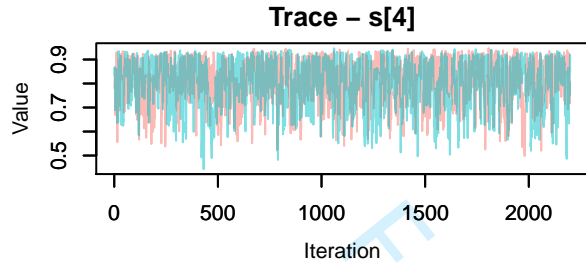
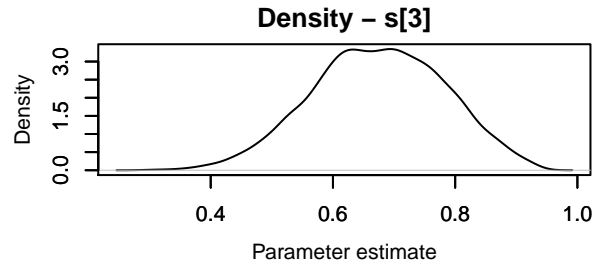
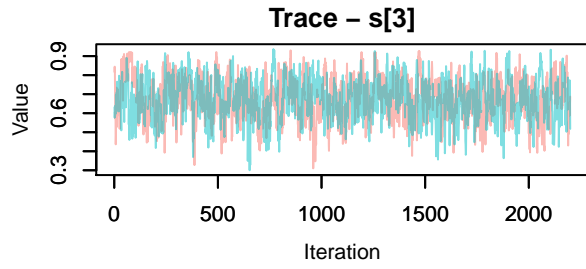
1
2
3  ## prop[6]      0.76  0.20   0.43   0.74   1.22  1.00  4400
4  ## prop[7]      0.46  0.15   0.24   0.44   0.80  1.00  4400
5  ## prop[8]      0.20  0.08   0.08   0.19   0.40  1.00  4400
6  ## prop[9]      0.20  0.08   0.08   0.19   0.40  1.00  4400
7  ## prop[10]     0.09  0.05   0.02   0.08   0.22  1.00  4400
8  ## deviance 1611.02 25.81 1563.30 1609.45 1664.85 1.02   133
9

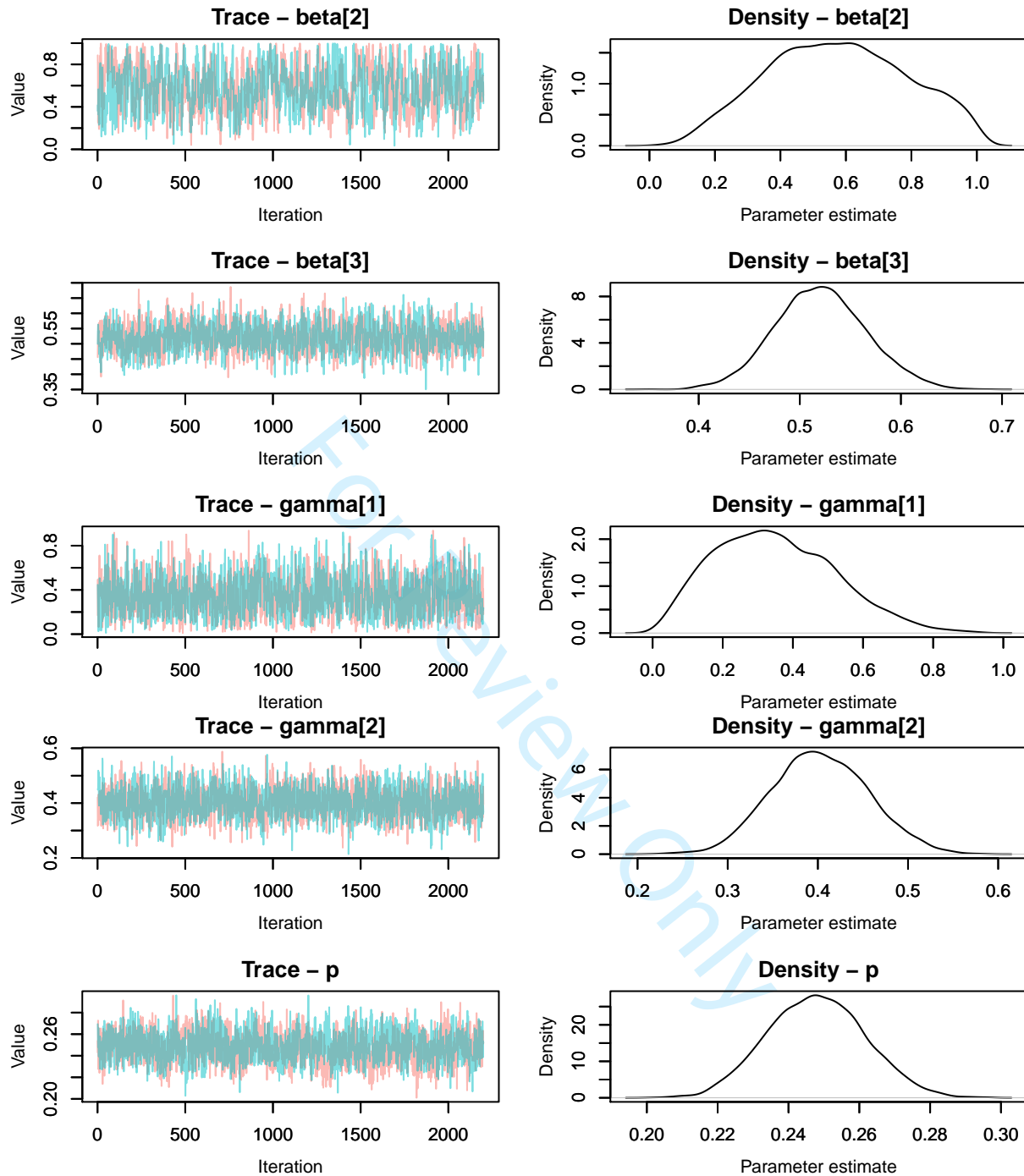
```

Check mixing of the chains and posterior distributions:

```
MCMCtrace(out, params = c('phi', 's', 'l02', 'l12', 'kappa', 'beta', 'gamma', 'p'), pdf=FALSE)
```







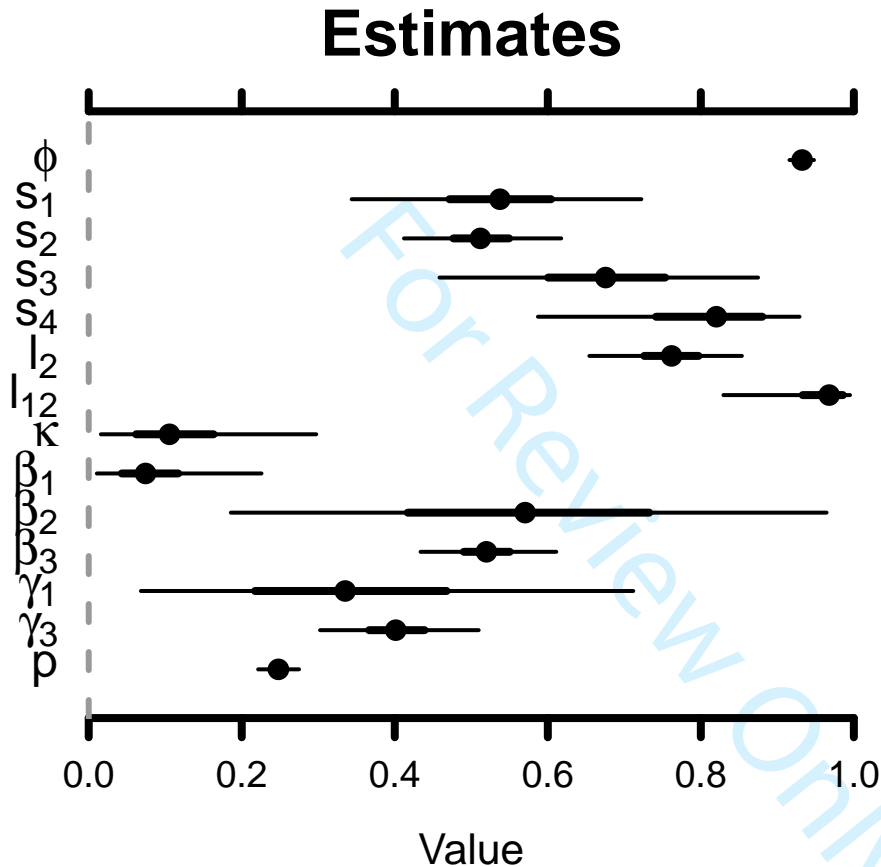
Plot a summary of the posterior distribution for each model parameter:

```
MCMCplot(out,
  params = c('phi', 's', 'l02', 'l12', 'kappa', 'beta', 'gamma', 'p'),
  xlim = c(0, 1),
  xlab = 'Value',
  main = 'Estimates',
  labels = c(expression(phi), expression(s[1]), expression(s[2]), expression(s[3]),
    expression(s[4]), expression(l[02]), expression(l[12]), expression(kappa),
    expression(beta[1]), expression(beta[2]), expression(beta[3])),
```

```

expression(gamma[1]),expression(gamma[3]),expression(p)),
col = 'black',
sz_labels = 1.5,
sz_med = 1.5,
sz_thick = 4,
sz_thin = 2,
sz_ax = 4,
sz_main_txt = 2)

```



Dots represent posterior medians, thick lines represent 50 percent credible intervals while thin lines represent 95 percent credible intervals.

Calculate the probabilities of successfully raising 1 or 2 or 0 offspring to independence over a three-year period for an adult female without dependent offspring at the start of the period:

```

prx1 <- (out$sims.list$phi)^3 * out$sims.list$beta[,3] *
(
  out$sims.list$gamma[,2] * out$sims.list$s[,1] * out$sims.list$s[,3]
+
  (1- out$sims.list$gamma[,2]) *
  (2 * out$sims.list$s[,2] * (1-out$sims.list$s[,2]) * out$sims.list$s[,3]
+ (out$sims.list$s[,2])^2 + 2 * out$sims.list$s[,4] * (1 -out$sims.list$s[,4])
)
)

prx2 <- (out$sims.list$phi)^3 * out$sims.list$beta[,3] *
(1- out$sims.list$gamma[,2]) * (out$sims.list$s[,2])^2 * (out$sims.list$s[,4])^2

```

```
prx0 <- 1 -prx1 -prx2
```

Make a table with the median value and 95% credible interval for the probabilities of successfully raising 1 or 2 or 0 offspring to independence over a three-year period for an adult female without dependent offspring at the start of the period:

```
# Summary of results
tabres <- matrix(NA,3,3)
tabres[1,]<-quantile(prx0,probs=c(0.025,0.5,0.975))
tabres[2,]<-quantile(prx1,probs=c(0.025,0.5,0.975))
tabres[3,]<-quantile(prx2,probs=c(0.025,0.5,0.975))
rownames(tabres)=c("Pr(X=0)", "Pr(X=1)", "Pr(X=2)")
colnames(tabres)=c("Q 2.5%", "Median", "Q 97.5%")
round(tabres,2)
```

```
##           Q 2.5% Median Q 97.5%
## Pr(X=0)   0.57   0.67   0.76
## Pr(X=1)   0.20   0.29   0.38
## Pr(X=2)   0.02   0.04   0.07
```

References

- Amstrup, S. C., & Durner, G. M. (1995). Survival rates of radio-collared female polar bears and their dependent young. *Canadian Journal of Zoology*, 73, 1312–1322. doi:10.1139/z95-155
- Hornik, K., Leisch, F., & Zeileis, A. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. In *Proceedings of DSC (Vol. 2, No. 1)*.
- Kellner, K. (2015). jagsUI: a wrapper around rjags to streamline JAGS analyses. R package version, 1(1).

1
2
3 1 **Modeling the demography of species providing extended parental care:**

4
5 2 **A capture-recapture multievent model with a case study on Polar Bears (*Ursus***
6
7 3 ***maritimus*)**

8
9
10 4
11
12 5 Sarah Cubaynes¹, Jon Aars², Nigel G. Yoccoz³, Roger Pradel¹, Øystein Wiig⁴, Rolf A Ims³
13
14 and Olivier Gimenez¹

15 6
16
17 7 ¹ CEFE, Univ Montpellier, CNRS, EPHE-PSL University, IRD, Univ Paul Valéry

18
19 8 Montpellier 3, Montpellier, France

20
21 9 ² Norwegian Polar Institute, FRAM Centre, Tromsø, Norway

22
23 10 ³ UiT The Arctic University of Norway, Department of Arctic and Marine Biology, Tromsø,
24
25 Norway

26
27 11 ⁴Natural History Museum, University of Oslo, Norway

28
29 12
30
31 13
32
33 14 **Abstract**

34
35 15 1. In species providing extended parental care, one or both parents care for altricial young over
36
37 16 a period including more than one breeding season. We expect large parental investment and
38
39 17 long-term dependency within family units to cause high variability in life trajectories among
40
41 18 individuals with complex consequences at the population level. So far, models for estimating
42
43 19 demographic parameters in free-ranging animal populations mostly ignore extended parental
44
45 20 care, thereby limiting our understanding of its consequences on parents and offspring life
46
47 21 histories.

48
49
50
51 22 2. We designed a capture-recapture multi-event model for studying the demography of species
52
53 23 providing extended parental care. It handles statistical multiple-year dependency among
54
55 24 individual demographic parameters grouped within family units, variable litter size, and
56
57 25 uncertainty on the timing at offspring independence. It allows ~~for theto evaluate~~ evaluation of

1
2
3 26 trade-offs among demographic parameters, the influence of past reproductive history on the
4
5 27 caring parent's survival status, breeding probability and litter size probability, while accounting
6
7
8 28 for imperfect detection of family units. We assess the model performances using simulated data,
9
10 29 and illustrate its use with a long-term dataset collected on the Svalbard polar bears (*Ursus*
11
12 30 *maritimus*).

13
14 31 3. Our model performed well in terms of bias and mean square error and in estimating
15
16 32 demographic parameters in all simulated scenarios, both when offspring departure probability
17
18 33 from the family unit occurred at a constant rate or varied during the field season depending on
19
20 34 the date of capture. For the polar bear case study, we provide estimates of adult and dependent
21
22 35 offspring survival rates, breeding probability and litter size probability. Results showed that the
23
24 36 outcome of the previous reproduction influenced breeding probability.
25
26
27

28 37 4. Overall, our results show the importance of accounting for i) the multiple-year statistical
29
30 38 dependency within family units, ii) uncertainty on the timing at offspring independence, and
31
32 39 iii) past reproductive history of the caring parent. If ignored, estimates obtained for breeding
33
34 40 probability, litter size, and survival can be biased. This is of interest in terms of conservation
35
36 41 because species providing extended parental care are often long-living mammals vulnerable or
37
38 42 threatened with extinction.
39
40
41

42 43
43
44 44 **Key-words:** apex predator, arctic ecosystem, Bayesian modeling, capture-recapture,
45
46 45 dependency among individuals, family structure, parental care, state uncertainty, timing at
47
48 46 independence.
49
50

51 47 52 53 48 **INTRODUCTION**

54
55
56 49 Parental care includes any pre-natal and post-natal allocation, such as feeding and protecting
57
58 50 the young, which benefits the offspring development and survival chances, thereby enhancing
59
60

1
2
3 51 the parent's reproductive success (Trivers 1972). Altricial mammals having offspring that need
4
5 52 to learn complex skills to ensure survival beyond independence, such as hunting, orientation,
6
7 53 or nest building, show extended parental care (hereafter EPC; Clutton-Brock 1991). It is defined
8
9 54 as a prolonged period, i.e. lasting more than one breeding season, over which one or both
10
11 55 parents care for one or several dependent young. This period typically lasts for several years
12
13 56 and can extend until lifelong maternal care in primates (Van Noordwijk 2012). For the
14
15 57 offspring, the quality and quantity of care received can have long-lasting effects on future
16
17 58 survival (e.g. Pavard and Branger 2012), social status (e.g. Shenk and Scelza 2012) and
18
19 59 reproduction (Royle et al. 2012). For the parent, investment in one offspring can compromise
20
21 60 its own condition or survival and/or its ability to invest in other offspring (siblings or future
22
23 61 offspring) (Williams 1966, Stearns 1992). It can indeed take several years during which a parent
24
25 62 caring for its offspring will not be available to reproduce, sometimes not until the offspring
26
27 63 have reached independence, e.g. on average 2.5 years for female polar bears (Ramsay and
28
29 64 Stirling 1988), 3.5 to 6 years for female African elephants (Lee and Moss 1986), and 9.3 years
30
31 65 for female Sumatran orangutans (Wich et al. 2004). The fitness costs of losing one offspring,
32
33 66 in terms of lost investment and skipped breeding opportunities, are particularly high if death
34
35 67 occurs near independence. We therefore expect EPC, through large parental investment and
36
37 68 multiple-year dependency among individuals within family units, to cause high variability in
38
39 69 life trajectories among individuals and family groups, in interbirth intervals depending on
40
41 70 offspring's fate, and consequently on lifetime reproductive success for the caring parent
42
43 71 (Clutton-Brock 1991).

51 72 Capture-recapture (CR) models allow studying species with complex demography in
52
53 73 the wild, e.g. by considering 'breeder' and 'non-breeder' reproductive states to estimate
54
55 74 breeding probabilities and status-specific demographic parameters while accounting for
56
57 75 imperfect detectability (e.g., Lebreton et al. 2009). One can distinguish between successful and
58
59
60

1
2
3 76 failed breeding events (e.g., Lagrange et al. 2017) and include varying litter or clutch size (e.g.,
4
5 77 Doligez et al. 2002) and memory effects (Cole et al. 2014), to investigate the costs of
6
7 78 reproduction on survival and future reproduction for species providing short-term parental care,
8
9
10 79 i.e. when offspring reach independence before the next breeding season (e.g., Yoccoz et al.
11
12 80 2002). Indeed, most CR models rely on the assumption of independence among individual CR
13
14 81 histories (Lebreton et al. 2009).

15
16
17 82 In the case of species providing EPC, one challenge stems from the multiple-year
18
19 83 dependency among individual's life histories within parent-offspring units. Only few attempts
20
21 84 have been made to tackle this issue when estimating demographic parameters, despite the fact
22
23 85 that species providing EPC are often among long-living mammals vulnerable or threatened with
24
25 86 extinction (e.g. polar bears, orangutans, elephants). Lunn et al. (2016) ~~and Couet et al. (2019)~~
26
27 87 proposed to model CR histories of ~~family-mother-offspring~~ units (instead of individuals) ~~which~~
28
29 88 ~~permits~~ to consider the multiple-year dependency ~~of offspring survival upon mother survival~~
30
31 89 ~~status and~~ of female breeding probability upon offspring survival status for polar bears in
32
33 90 Hudson Bay. ~~—However, in this model, offspring survival after 9 months is assumed~~
34
35 91 independent of mother survival. Lunn et al. (2016)'s model does therefore not handle multiple-
36
37 92 year dependency of offspring survival upon mother survival status, typical of ~~of~~ species
38
39 93 providing EPC. In addition, because litter size is modeled separately, Lunn et al. (2016)'s model
40
41 94 (also used in Regehr et al. (2018)) does not permit to explore potential trade-offs among
42
43 95 offspring traits and parental phenotypic or demographic traits. ~~Couet et al. (2019) provided~~
44
45 96 ~~estimates of dolphin reproductive parameters corrected for state uncertainty but their model~~
46
47 97 ~~assumed a fixed age and timing at offspring independence.~~

48
49
50
51
52
53 98 Another challenge involves dealing with uncertain timing at offspring independence,
54
55 99 when the offspring departs the caring parent(s) and becomes independent. When studying free-
56
57 100 ranging populations, this key life history event is rarely directly observed. When a mature
58
59
60

1
2
3 101 individual is observed without dependent offspring, it is often impossible to know if its
4
5 102 offspring have died or already departed its natal group. As a result, estimates of demographic
6
7 103 rates and trade-offs can be underestimated. Based on the analysis of mother-offspring units CR
8
9 104 histories, Couet et al. (2019) provided estimates of dolphin reproductive parameters corrected
10
11 105 for state uncertainty, but their model assumed a fixed age and timing at offspring independence.
12
13 106 Lunn et al. (2016)'s model ~~for polar bears in Hudson Bay (later used in Regehr et al. (2018))~~
14
15 107 included variable age at independence, but variability in the timing at offspring independence
16
17 108 was not fully dealt with. Demographic rates were corrected by the average annual probability
18
19 109 that independence occurred prior to sampling for all offspring, and offspring survival was
20
21 110 assumed independent of litter size (Regehr et al. 2018). In most species, timing at offspring
22
23 111 independence is variable and could depend on the offspring phenotypic traits (e.g. body size in
24
25 112 brown bears, Dahle and Swenson 2003), on parental traits (e.g. parent-offspring conflict in
26
27 113 kestrels, Vergara et al. 2010), social and mating system (e.g. helping behavior in humans,
28
29 114 Kramer 2005), or other environmental determinants (e.g. food supply, Eldegard and Sonerud
30
31 115 2010). To our knowledge, no model is available to tackle both the issues of multiple-year
32
33 116 dependency among individuals and variable timing at offspring independence. Because of these
34
35 117 methodological challenges, the population-level consequences of EPC remain to be understood,
36
37 118 especially in free-ranging animal populations.

38
39
40 119 Here, we develop a CR model specifically for species providing EPC. It is designed to
41
42 120 handle multiple-years statistical dependency (until offspring independence) among individual
43
44 121 demographic parameters by modeling CR histories grouped within family units. The model
45
46 122 accounts for uncertain timing at offspring independence. In addition, our model allows for
47
48 123 variability in the number of offspring born and recruited at each breeding event, variable
49
50 124 offspring survival depending on number of siblings, and includes the influence of past
51
52 125 reproductive history on the caring parent's current status. Finally, estimates of survival rates,
53
54
55
56
57
58
59
60

1
2
3 126 breeding probability and litter size probability are corrected for imperfect detection possibly
4
5 127 depending upon family unit composition.
6

7
8 128 In what follows, we present the model, assess its performances using simulated data,
9
10 129 and illustrate its use with a long-term dataset collected on the Svalbard polar bears. Female
11
12 130 polar bears rely solely on stored fat reserves during pregnancy and the first three months of
13
14 131 lactation, before feeding and protecting litters of one to three young, usually during two more
15
16 132 years (Ramsay and Stirling 1988). They can lose more than 40% of body mass while fasting
17
18 133 (Atkinson and Ramsay 1995). In many areas, climate change and related sea ice decline impact
19
20 134 female bear condition and capacity to provide care for their young, with an associated decline
21
22 135 in reproductive output (Derocher et al. 2004; Stirling and Derocher, 2012, Laidre et al. 2020).
23
24 136 More insights into the species demography, such as the consequences of long-duration parental
25
26 137 care on mother and offspring life histories, could help our understanding of polar bear
27
28 138 population responses to environmental perturbations and extinction risks in future decades
29
30 139 (Hunter et al., 2010; Regehr et al., 2016).
31
32
33
34

35 140

37 141 **METHODS**

38 142

42 143 *1. Capture-recapture model for species providing EPC*

44 144 *1.1 Principle*

46 145 We develop a CR model in the multievent framework (Pradel 2005) that is also known as a
47
48 146 hidden Markov modeling framework (Gimenez et al. 2012). The principle is to relate the field
49
50 147 observations, called events, to the underlying demographic states of interest through the
51
52 148 observation process. Uncertainty on state assignment due to variable timing at offspring
53
54 149 independence is included in the observation process. In parallel, the state process describes the
55
56 150 transition rates between states from one year to the next. The transition rates correspond here
57
58
59
60

1
2
3 151 to the demographic parameters corrected for imperfect detection and state uncertainty. Below
4
5 152 we describe the general procedure to specify the model by defining the states and state-to-state
6
7 153 transition process, then the events and observation process. However, for simplicity, the events
8
9
10 154 and states are chosen to match the polar bear life cycle (i.e. females are captured in sSpring,
11
12 155 alone or together with a litter of one or two dependent offspring; offspring gain independence
13
14 156 in the year following their second birthday, and offspring cannot survive the loss of their mother
15
16 157 before gaining independence). The resulting model assumptions and its applicability to other
17
18
19 158 species are discussed below.

159

160 *1.2 Specification of states and state process*

161 One specificity of our model lies in the use of CR histories based on family groups instead of
162 individuals, which permits to include the multiple-year dependency among the caring parent
163 and dependent offspring's demographic rates and life history traits. Below, we describe the
164 specification of 24 unique states and 6 matrices needed to construct the model.

165 States correspond to the 'real' demographic states of the individuals composing the
166 family. We consider 12 states S , $S = \{J2, J3, SA4, SA5, A01, A02, A11, A12, AS1, AS2, A, D\}$, to
167 represent the polar bear life cycle (defined in Table 1). In addition, we specify 13 intermediary
168 states S' , $S' = \{J3, SA4, SA5, A11, A12, AS1, AS2, A0-, A1-, I/AS1, I/AS2, A, D\}$, and 16
169 intermediary states S'' , $S'' = \{J3, SA4, SA5, A11, A12, AS1, AS2, B/A0-, NB/A0-, B/A1-, NB/A1-,$
170 $B/AS, NB/AS, B/A, NB/A, D\}$, leading to a total of 24 unique states (defined in Table 1). The
171 specification of intermediary states is what permits to distinguish between failed and successful
172 breeders in the transition matrix to consider the influence of past reproductive history on
173 parameters (see below).

174

175

176

177

178

179

180

181

182

183

184

175 Table 1. Definition of the states and events used in the model to describe the polar bear life
 176 cycle.

TYPE	CODE	DEFINITION
STATES	J2	2 y.o. independent juvenile female
	J3	3 y.o. independent juvenile female
	SA4	4 y.o. independent subadult female
	SA5	5 y.o. independent subadult female
	A01	mother with two <u>one</u> dependent offspring <u>cub of the year</u> <1yo
	A02	mother with one <u>two</u> dependent offspring <u>cubs of the year</u> <1yo
	A11	mother with one dependent offspring <u>yearling</u> 1yo
	A12	mother with two dependent offspring <u>yearlings</u> 1yo
	AS1	successful female breeder with one <u>two-year old</u> offspring reaching independence
	AS2	successful female breeder with two <u>two-year old</u> offspring reaching independence
	A	adult female without dependent offspring
	D	dead state
	A0-	failed breeder, death of all offspring <u>cubs of the year</u> aged <1yo
	A1-	failed breeder, death of all offspring <u>yearlings</u> aged 1yo
	I/AS1	successful female breeder alone after departure of one independent offspring
	I/AS2	successful female breeder alone after departure of two independent offspring
	B/A0-	breeder following loss of a <u>cub of the year</u> litter of <1yo offspring
	NB/A0-	non breeder following loss of a <u>cub of the year</u> litter of <1yo offspring
	B/A1-	breeder following loss of a <u>yearling</u> litter of 1yo offspring
	NB/A1-	non breeder following loss of a <u>yearling</u> litter of 1yo offspring
B/AS	breeder following successful reproduction	
NB/AS	non breeder following successful reproduction	

	B/A	breeder given that previously without dependent offspring
	NB/A	non breeder given that previously without dependent offspring
EVENTS	'1'	capture of a 2yo independent female juvenile
	'2'	capture of a 3yo independent female juvenile
	'3'	capture of a 4yo independent subadult female
	'4'	capture of a 5yo independent subadult female
	'5'	capture of a mother with one dependent <u>offspring-cub</u> of the year
	'6'	capture of a mother with two dependent <u>offspring-cub</u> of the year
	'7'	capture of a mother with one dependent <u>offspring aged 1yoyearling</u>
	'8'	capture of a mother with two dependent <u>offspring aged 1yoyearlings</u>
	'9'	capture of a mother with one dependent <u>offspring aged 2yotwo-year old offspring</u>
	'10'	capture of a mother with two dependent <u>two-year old offspringoffspring aged 2yo</u>
	'11'	capture of an adult female without dependent offspring
	'0'	non observation

177

178 The model is conditioned upon first capture. The initial state vector, s_0 , gathers the
 179 proportions of family units in each state S at first capture, $s_0 = (\pi_1, \dots, \pi_{11}, 0)'$ (with $\pi_{12} = 0$
 180 for state D , because an individual must be alive at first capture).

181 The transition matrix, Ψ , describing all possible state-to-state transitions from spring
 182 one year (t) to spring the next year ($t+1$), is obtained as the matrix product of four matrices
 183 $\Psi = \Phi \cdot \Psi_1 \cdot \Psi_2 \cdot \Psi_3$. This decomposition is another particularity of our model which permits
 184 to estimate the relevant set of demographic parameters: independent juvenile, subadult and
 185 adult survival (matrix Φ), dependent offspring survival (matrix Ψ_1), breeding probabilities
 186 (matrix Ψ_2) and litter size probabilities (matrix Ψ_3), and potential trade-offs among them. This
 187 formulation of the transition matrix implies that litter size is conditioned upon breeding

188 decision, itself conditioned upon offspring survival, itself conditioned upon survival of the
 189 caring parent to deal with the statistical dependency existing among individuals within family
 190 units.

191 The Φ matrix (eq. 1) describes transitions from each state S at time t (rows) to each state
 192 S after the occurrence of the survival process for independent individuals (columns):

193

	J2	J3	SA4	SA5	A01	A02	A11	A12	AS1	AS2	A	D
J2	$\varphi\phi_1$	0	0	0	0	0	0	0	0	0	0	$1 - \varphi\phi_1$
J3	0	$\varphi\phi_2$	0	0	0	0	0	0	0	0	0	$1 - \varphi\phi_2$
SA4	0	0	$\varphi\phi_3$	0	0	0	0	0	0	0	0	$1 - \varphi\phi_3$
SA5	0	0	0	$\varphi\phi_4$	0	0	0	0	0	0	0	$1 - \varphi\phi_4$
A01	0	0	0	0	$\varphi\phi_5$	0	0	0	0	0	0	$1 - \varphi\phi_5$
A02	0	0	0	0	0	$\varphi\phi_6$	0	0	0	0	0	$1 - \varphi\phi_6$
A11	0	0	0	0	0	0	$\varphi\phi_7$	0	0	0	0	$1 - \varphi\phi_7$
A12	0	0	0	0	0	0	0	$\varphi\phi_8$	0	0	0	$1 - \varphi\phi_8$
AS1	0	0	0	0	0	0	0	0	$\varphi\phi_9$	0	0	$1 - \varphi\phi_9$
AS2	0	0	0	0	0	0	0	0	0	$\varphi\phi_{10}$	0	$1 - \varphi\phi_{10}$
A	0	0	0	0	0	0	0	0	0	0	$\varphi\phi_{11}$	$1 - \varphi\phi_{11}$
D	0	0	0	0	0	0	0	0	0	0	0	1

(eq. 1)

194
 195 In the Φ matrix, $\varphi\phi_1, \dots, \varphi\phi_{11}$ correspond to survival of immature independent (juveniles and
 196 subadults) and adult female bears.

197
 198 The Ψ_1 matrix (eq.2) describes transitions from states S after the occurrence of the survival
 199 process for independent individuals (rows) to states S' after the occurrence of the offspring
 200 survival process (columns):

201

	J3	SA4	SA5	A11	A12	AS1	AS2	A0-	A1-	I/AS1	I/AS2	A	D
J2	1	0	0	0	0	0	0	0	0	0	0	0	0
J3	0	1	0	0	0	0	0	0	0	0	0	0	0
SA4	0	0	$\frac{1-\kappa}{\kappa}$	0	0	0	0	0	0	0	0	κ	0
SA5	0	0	0	0	0	0	0	0	0	0	0	1	0
A01	0	0	0	s_1	0	0	0	$1 - s_1$	0	0	0	0	0
A02	0	0	0	$2 \cdot s_2 \cdot (1 - s_2)$	s_2^2	0	0	$1 - s_2^2 - 2 \cdot s_2 \cdot (1 - s_2)$	0	0	0	0	0
A11	0	0	0	0	0	s_3	0	0	$1 - s_3$	0	0	0	0
A12	0	0	0	0	0	$2 \cdot s_4 \cdot (1 - s_4)$	s_4^2	0	$1 - s_4^2 - 2 \cdot s_4 \cdot (1 - s_4)$	0	0	0	0
AS1	0	0	0	0	0	0	0	0	0	1	0	0	0
AS2	0	0	0	0	0	0	0	0	0	0	1	0	0

(eq.2)

A	0	0	0	0	0	0	0	0	0	0	0	0	1	0
D	0	0	0	0	0	0	0	0	0	0	0	0	0	1

202

203 In the Ψ_1 matrix, κ is the probability of first reproduction at age 5, s is dependent offspring
 204 survival conditioned upon mother survival (s_1 ~~for singleton cub, and s_2 for singleton cub resp.~~
 205 ~~for singleton~~ yearling; s_3 ~~for twin litter's individual cub, and s_4 for twin litter's or twin litter's~~
 206 ~~cub individual resp.~~ yearling). Litter survival rates can be obtained from individual offspring
 207 survival rates (for singleton litters $l_{01} = s_1$ and $l_{11} = s_3$ for cub ~~resp. and~~ yearling respectively,
 208 and for twin litters $l_{02} = 1 - (1 - s_2^2 - 2 \cdot s_2 \cdot (1 - s_2))$ and $l_{12} = 1 - (1 - s_4^2 - 2 \cdot s_4 \cdot$
 209 $(1 - s_4))$ for cubs ~~resp. and~~ yearlings respectively).

210

211

212 The Ψ_2 matrix (eq.3) describes transitions from states S' after occurrence of the survival
 213 processes (rows) to states S'' depending on breeding decision (columns):

214

	J3	SA4	SA5	A11	A12	AS1	AS2	B/A0-	NB/A0-	B/A1-	NB/A1-	B/AS1	B/AS2	B/A	NB/A	D
J3	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SA4	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0	0
SA5	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0	0
A11	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0	0
A12	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0	0
A21	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0	0
A22	0	0	0	0	0	0	1	0	0	0	0	0	0	0	0	0
A0-	0	0	0	0	0	0	0	β_1	$1 - \beta_1$	0	0	0	0	0	0	0
A1-	0	0	0	0	0	0	0	0	0	β_2	$1 - \beta_2$	0	0	0	0	0
I/AS1	0	0	0	0	0	0	0	0	0	0	0	β_3	$1 - \beta_3$	0	0	0
I/AS2	0	0	0	0	0	0	0	0	0	0	0	β_3	$1 - \beta_3$	0	0	0
A	0	0	0	0	0	0	0	0	0	0	0	0	0	β_4	$1 - \beta_4$	0
D	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	1

(eq.3)

215

216 Parameter β is breeding probability conditioned upon mother and offspring's survival status
 217 (β_1 ~~following loss of a cub litter, and β_2 following the loss a cub litter resp.~~ loss of a yearling
 218 litter ~~for failed female breeders~~, β_3 for successful breeder, β_4 for female without dependent
 219 offspring at the beginning of the year).

220

221 The Ψ_3 matrix (eq. 4) describes transitions from states S'' after occurrence of the
 222 survival processes and breeding decision (rows) to states S at $t+1$ after determination of litter
 223 size for breeders (columns):

224

	J2	J3	SA4	SA5	A01	A02	A11	A12	AS1	AS2	A	D
J3	0	1	0	0	0	0	0	0	0	0	0	0
SA4	0	0	1	0	0	0	0	0	0	0	0	0
SA5	0	0	0	1	0	0	0	0	0	0	0	0
A11	0	0	0	0	0	0	1	0	0	0	0	0
A12	0	0	0	0	0	0	0	1	0	0	0	0
AS1	0	0	0	0	0	0	0	0	1	0	0	0
AS2	0	0	0	0	0	0	0	0	0	1	0	0
B/A0-	0	0	0	0	γ_1	$1 - \gamma_1$	0	0	0	0	0	0
NB/A0-	0	0	0	0	0	0	0	0	0	0	1	0
B/A1-	0	0	0	0	γ_2	$1 - \gamma_2$	0	0	0	0	0	0
NB/A1-	0	0	0	0	0	0	0	0	0	0	1	0
B/AS1	0	0	0	0	γ_3	$1 - \gamma_3$	0	0	0	0	0	0
B/AS2	0	0	0	0	γ_3	$1 - \gamma_3$	0	0	0	0	1	0
B/A	0	0	0	0	γ_4	$1 - \gamma_4$	0	0	0	0	0	0
NB/A	0	0	0	0	0	0	0	0	0	0	1	0
D	0	0	0	0	0	0	0	0	0	0	0	1

(eq.4)

225

226 Parameter γ is the probability of producing a singleton litter conditioned upon mother's and
 227 offspring's survival status and upon breeding decision (γ_1 following the loss a cub litter, and γ_2
 228 following the loss a cub litter resp. loss of a yearling litter, γ_3 for successful breeder, γ_4 for
 229 female without dependent offspring at the beginning of the year).

230

231 By modifying the constraints on parameters (i.e. setting them equal or different among
 232 states), the model can be used to investigate: i) the cost of reproduction on parent's survival (by
 233 comparing the ϕ 's in matrix Φ), ii) the influence of litter size on individual offspring survival
 234 (by comparing s_1 to s_2 , and s_3 to s_4 in matrix Ψ_1) and on litter survival (by comparing l_{01} to l_{02}
 235 and l_{11} to l_{12}), iv) the influence of past reproductive history on breeding probability (by
 236 comparing the β 's among them in matrix Ψ_2), and on litter size probability (by comparing the
 237 γ 's among them in matrix Ψ_3).

238

239 *1.3 Specification of events and observation process*

240 The events correspond to the observation or non-observation of family units in the field at each
 241 sampling occasion. Each event is coded depending on the number and age of the individuals
 242 composing the family. Here, we consider 12 possible events, $\Omega = \{1,2,3,4,5,6,7,8,9,10,11,12\}$
 243 to describe field observations for polar bears family groups (defined in Table 1).

244 In a multievent model, one specific event may relate to several possible states. Due to
 245 variable timing at offspring independence, a female successful breeder (state ‘AS1’ or ‘AS2’)
 246 can be captured together with 1 or 2 two-year old dependent offspring (event ‘9’ or ‘10’) or
 247 without (event ‘11’) its two-year old offspring or not captured (event ‘12’) depending on i)
 248 whether the offspring has already departed from its mother at the time of capture and ii) on
 249 capture probability. To include uncertainty on state assignment due to variable timing at
 250 offspring independence, we decompose the observation process into two event matrices, E_1 and
 251 E_2 , modeling respectively departure probability (α) and capture probability (p).

252 The E_1 matrix (eq. 5), relates the states S to the possible observations at the time of
 253 capture, $O = \{1,2,3,4,5,6,7,8,9,10,11,12\}$ (same code as the events, see Table 1), through the
 254 departure probability, denoted α .

	'1'	'2'	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'11'	'12'	
J2	1	0	0	0	0	0	0	0	0	0	0	0	(eq.5)
J3	0	1	0	0	0	0	0	0	0	0	0	0	
SA4	0	0	1	0	0	0	0	0	0	0	0	0	
SA5	0	0	0	1	0	0	0	0	0	0	0	0	
A0 ₁	0	0	0	0	1	0	0	0	0	0	0	0	
A0 ₂	0	0	0	0	0	1	0	0	0	0	0	0	
A1 ₁	0	0	0	0	0	0	1	0	0	0	0	0	
A1 ₂	0	0	0	0	0	0	0	1	0	0	0	0	
AS1	0	0	0	0	0	0	0	0	$1-\alpha_{i,d}$	0	$\alpha_{i,d}$	0	

AS2	0	0	0	0	0	0	0	0	0	$2 \cdot \alpha_{i,d} \cdot (1 - \alpha_{i,d})$	$1 - 2 \cdot \alpha_{i,d} \cdot (1 - \alpha_{i,d}) - \alpha_{i,d}^2$	$\alpha_{i,d}^2$	0
A	0	0	0	0	0	0	0	0	0	0	0	1	0
D	0	0	0	0	0	0	0	0	0	0	0	0	1

255

256 Here, $\alpha_{i,jd}$ is the departure probability of a two-year old individual offspring belonging to
 257 family unit i on its date of capture d . The relationship between date of capture and departure
 258 probability is species-specific and either be-assessed from prior knowledge on the species'
 259 biology or field data (see Appendix 2). Here we assume that siblings' timing at independence
 260 can, but does not have to, occur independently (if both offspring can only depart the family on
 261 the same date, the transition from state 'AS2' to event '9' should be set to 0).

262 The second event matrix, E_2 , (eq. 6) relates all possible observations at the time of
 263 capture O to the events, Ω , actually observed in the field through the state-dependent capture
 264 probability, denoted p_s .

	1'	2'	3'	4'	5'	6'	7'	8'	9'	10'	11'	Ω_{12}'
1'	p_1	0	0	0	0	0	0	0	0	0	0	$1 - p_1$
2'	0	p_2	0	0	0	0	0	0	0	0	0	$1 - p_2$
3'	0	0	p_3	0	0	0	0	0	0	0	0	$1 - p_3$
4'	0	0	0	p_4	0	0	0	0	0	0	0	$1 - p_4$
5'	0	0	0	0	p_5	0	0	0	0	0	0	$1 - p_5$
6'	0	0	0	0	0	p_6	0	0	0	0	0	$1 - p_6$
7'	0	0	0	0	0	0	p_7	0	0	0	0	$1 - p_7$
8'	0	0	0	0	0	0	0	p_8	0	0	0	$1 - p_8$
9'	0	0	0	0	0	0	0	0	p_9	0	0	$1 - p_9$
10'	0	0	0	0	0	0	0	0	0	p_{10}	0	$1 - p_{10}$
11'	0	0	0	0	0	0	0	0	0	0	p_{11}	$1 - p_{11}$
Ω_{12}'	0	0	0	0	0	0	0	0	0	0	0	1

265

266

267 The composite event matrix, E , which relates the events to the states, is obtained as the
 268 matrix product of these two matrices $E = E_1 \cdot E_2$. Because the model is conditioned upon first
 269 capture, the initial event vector, e_0 , takes the value of 1 for all events (except of 0 for the event
 270 '12' corresponding to a non-observation).

271

272 *1.4 Applicability to other species*

273 The model described above matches the Svalbard polar bear life cycle. The model therefore
274 assumes that care is provided by the mother only, to one or two offspring (we modelled triplets
275 as twins because there were just 8 litters of triplets in the data~~ignored triplets present at a low~~
276 probability in polar bears), for a duration of two years maximum. Offspring under age 2 cannot
277 survive if the mother dies. A mother caring for offspring cannot mate and produce a second
278 litter. Independent males (that have already departed from the family unit) are not included in
279 the model.

280 To apply the model to other species, one should modify the number of events and states
281 to match the species life cycle (depending on age at sexual maturity, number of care providers,
282 maximum litter size, duration of parental care) but the number of matrices should remain the
283 same and the shape of the relationship between departure probability and date of capture to
284 match the species life cycle. For example, modeling a hypothetical species similar to polar bears
285 but in which both males and females care for offspring would increase the number of unique
286 states from 24 to 42 (8 states for immature females and males, 21 states for dependent offspring
287 cared for by both parents, just the mother in case of father loss, or just the father in case of
288 mother loss). Such a model could be used to assess the influence of father versus mother loss
289 on litter size, offspring survival and father and/or mother breeding probabilities. ~~In~~ After
290 defining the states and events, one should modify the shape of the relationship between
291 departure probability and date of capture to match the species life cycle. In species-species like
292 primates or wolves, departure from the family unit can occur throughout the year, at a more or
293 less constant rate depending on the season, while it occurs only between February and May in
294 polar bears due to environmental constraints. In addition, The general model structure, types of
295 parameters involved and steps of model definition should remain similar. ~~The~~ influence of

1
2
3 296 individual traits such as age or body weight, or environmental variables such as temperature,
4
5 297 can be included in the model under the form of individual or temporal covariates (Pollock
6
7
8 298 2002). ~~In addition,~~ Other specificities related to data collection can ~~also~~ be included in a similar
9
10 299 way, such as trap effects (Pradel and Sanz-Aguilar 2012) or latent individual heterogeneity by
11
12 300 using mixture of distributions or random effects (Gimenez et al. 2018). Guidance to fit the
13
14 301 model in a Bayesian framework in program Jags for real and simulated data are provided in
15
16
17 302 Appendices 1 and 2.
18

19 303

20
21 304 *Simulation study*

22
23
24 305 The simulation study was aimed at evaluating the performance of our model to estimate
25
26 306 demographic parameters under various assumptions about the timing at offspring independence
27
28 307 (constant versus seasonal departure rate) and various degrees of capture probability (low $p=$
29
30 308 0.25, high $p=0.7$), for a medium-size data set ($T=15$ sampling occasions, with $R=80$ newly
31
32
33 309 marked at each occasion in equal proportion among the 11 alive states).

34
35 310 We simulated data for a virtual long-lived mammal species mimicking the polar bear
36
37 311 using the model described in box 1. We used $\varphi = 0.9$ for independent female bear survival
38
39 312 (aged 2+ y.o.), $s_1 = l_{01} = 0.6$ for singleton cub survival, $s_2 = 0.55$ for twin litter's cub
40
41 313 survival (corresponding to twin litter survival $l_{02} = 0.7975$), $s_3 = 0.8$ for singleton yearling
42
43 314 survival and $s_4 = 0.75$ for twin litter's yearling survival (corresponding to litter survival l_{12}
44
45 315 = 0.94). Offspring survival rates were conditioned upon mother survival. If a mother dies, its
46
47 316 dependent offspring had no chances of surviving. For breeding probabilities, we used $\beta_1 = 0.5$
48
49 317 , $\beta_2 = 0.7$, $\beta_3 = 0.9$ and $\beta_4 = 0.8$. For litter size probabilities, we used $\gamma_1 = 0.4$, $\gamma_2 = 0.5$,
50
51 318 ~~$\gamma_3 = 0.6$~~ and $\gamma_4 = 0.7$. We set $\kappa = 0$ and assumed that females had their first litter at age 6 or
52
53
54
55 319 older.
56
57
58
59
60

1
2
3 320 We assumed that captures occurred each year between mid-March to end of May (day
4
5 321 of the year $d=80$ to $d=130$). For each capture event, date of capture was randomly sampled from
6
7 322 the distribution of the polar bear data dates of capture (see Appendix 1). In the constant scenario,
8
9 323 we assumed that two-year old bears reached independence at a constant departure rate (α)
10
11 324 during the field season, independently of the date of capture. We chose an intermediate value
12
13 325 of $\alpha = 0.5$ (if independence occurred always after the field season, $\alpha = 0$, versus always before
14
15 326 the field season, $\alpha = 1$). In the seasonal scenario, we assumed that departure rate varied with
16
17 327 date of capture (d) following a logistic relationship (regression coefficients were estimated from
18
19 328 the polar bear data, see Appendix 2). Most of the two-year old offspring were captured with
20
21 329 their mother at the beginning of the field season, while departure probability increased
22
23 330 logistically up to 80% at the end of the field season.

24
25
26
27
28
29 331 We simulated 100 CR datasets for each of the 4 scenarios (S1: low detection with constant
30
31 332 departure, S2: low detection with seasonal departure, S3: high detection with constant
32
33 333 departure, S4: high detection with seasonal departure). We simulated the data using program
34
35
36 334 R. We fitted the model using program jags called from R (Plummer 2016). For each
37
38 335 parameter and each dataset, we calculated absolute bias as $\hat{B} = \hat{\theta} - \theta$, and root mean squared
39
40 336 error as $RMSE = \sqrt{(\hat{\theta} - \theta)^2}$, with θ the parameter used to simulate the data and $\hat{\theta}$ the mean
41
42 337 value of the estimated parameter. Appendix 1 containing guidance, R code and files to
43
44 338 simulate data and fit the model is available on GitHub at
45
46 339 https://github.com/SCubaynes/Appendix1_extendedparentalcare.

47
48
49
50
51
52 340

53 54 341 *Case study: Polar bears in Svalbard*

55
56 342 In polar bears, care of offspring is provided by the mother only (Amstrup, 2003). Males
57
58 343 were therefore discarded from our analysis. Adult female polar bears mate in spring (February
59
60

1
2
3 344 to May, Amstrup 2003), and in Svalbard usually have their first litter at the age of six years, but
4
5 345 some females can have their first litter at five years (Derocher 2013). They have delayed
6
7 346 implantation where the egg attaches to the uterus in autumn (Ramsay and Stirling 1988). A
8
9
10 347 litter with small cubs (ca 600 grams) is born around November to January, in a snow den that
11
12 348 the mothers dig out in autumn, and where the family stay 4-5 months. The family usually
13
14 349 emerges from the den in March-April, and stay close to the den while the cubs get accustomed
15
16 350 to the new environment outside their home, for a few days up to 2-3 weeks (Hansson and
17
18
19 351 Thomassen 1983). Litter size in early spring vary from one to three, with two cubs being most
20
21 352 common, three cubs in most areas being rare, and commonly around one out of three litters
22
23 353 having one cub only (Amstrup 2003). In Svalbard, polar bears become independent from their
24
25 354 mother shortly after their second birthday (average age at independence is 2.3). Two-year old
26
27
28 355 bears typically depart from the mother in spring (between mid-March to end of May), when the
29
30 356 mother can mate again. There is only one anecdotal record of a yearling alive without his
31
32 357 mother. Because the field season can last for several weeks, some two-year-old bears were
33
34 358 captured together with their mother and others were already independent at the time of capture.
35
36
37 359 The minimum reproductive interval for successful Barents Sea polar bears is 3 years. On the
38
39 360 contrary, loss of a cub litter shortly after den emergence may mean the mother can produce new
40
41 361 cubs in winter the same year (Ramsay and Stirling 1988).

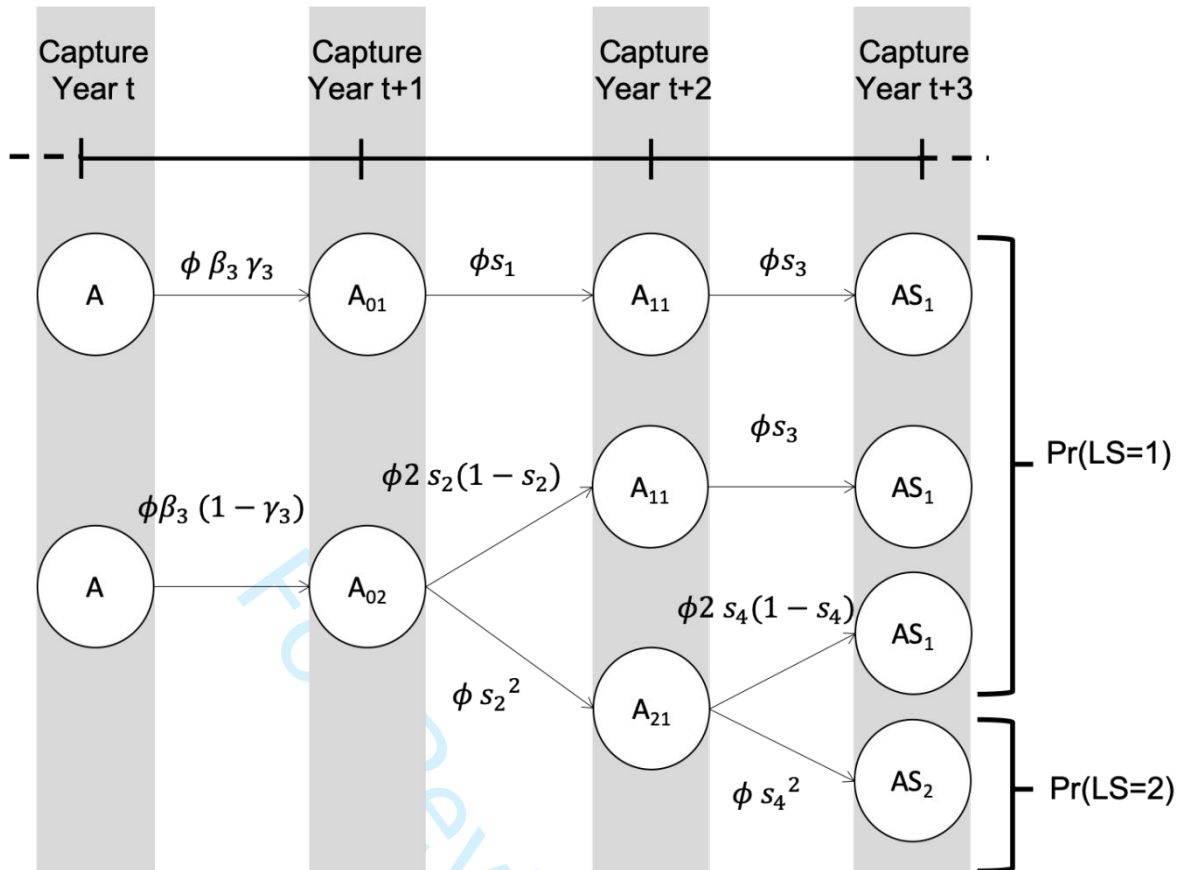
42
43
44 362 Bears captured in Svalbard are shown to be a mixture of resident and pelagic bears
45
46 363 (Mauritzen et al. 2002). To focus on the resident population, independent bears captured only
47
48 364 once were not included in our analysis. We therefore analyzed N = 158 encounter histories of
49
50 365 resident polar bear family units captured each spring after den emergence between day 80 to
51
52 366 130 (mid-March to mid-May), from 1992 to 2019, in Svalbard. It corresponds to 81 capture
53
54 367 events of juvenile and subadults, 231 cubs, 96 yearling, 23 dependent two-year old, and 444
55
56 368 captures of adult females. Polar bears were caught and individually marked as part of a long-

1
2
3 369 term monitoring program on the ecology of polar bears in the Barents Sea region (Derocher
4
5 370 2005). All bears one year or older were immobilized by remote injection of a dart (Palmer Cap-
6
7 371 Chur Equipment, Douglasville, GA, USA) with the drug Zoletil® (Virbac, Carros, France)
8
9 372 (Stirling et al. 1989). The dart was fired from a small helicopter (Eurocopter 350 B2 or B3),
10
11 373 usually from a distance of about 4 to 10 meters. Cubs of the year were immobilized by injection
12
13 374 with a syringe. Cubs and yearlings were highly dependent on their mother; therefore, they
14
15 375 remained in her vicinity and were captured together with their mother. A female captured alone
16
17 376 was considered to have no dependent offspring alive. Death of the cubs could have occurred in
18
19 377 the den or shortly after den emergence but before capture. Hereafter, estimated cub survival
20
21 378 thus refers to survival after capture. Infant mortality occurring before capture will be assigned
22
23 379 to a reduced litter size. Because only 3% of females were observed with 3 offspring, we
24
25 380 analyzed jointly litters of twins with triplets.

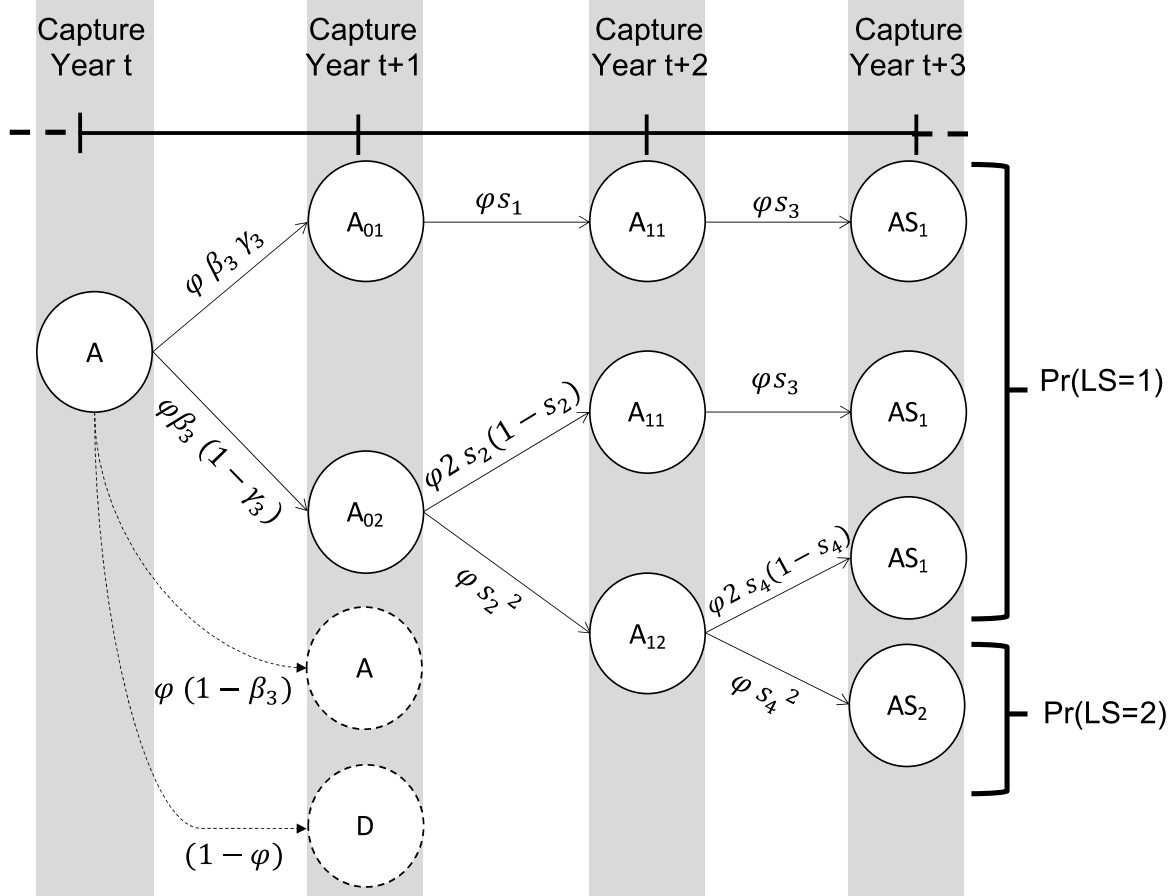
30 381 We built the model described above with 12 states and 12 events to describe the life
31
32 382 cycle (Table 1). Preliminary analyses suggested that mother survival did not vary according to
33
34 383 state, we therefore constrained parameter $\varphi\phi$ to be equal among all states in matrix Φ . To
35
36 384 avoid identifiability issues due to a relatively small sample size, we assumed breeding
37
38 385 probability and litter size probability did not vary between successful breeders (states AS1
39
40 386 and AS2) and female without dependent offspring (state A) by setting $\beta_3 = \beta_4$ and $\gamma_3 = \gamma_4$.
41
42
43
44 387 We also assumed that litter size probability did not vary among failed breeders (loss of a cub
45
46 388 versus a yearling litter), by setting $\gamma_1 = \gamma_2$. We could not assess formally the fit of our model
47
48 389 because no test is yet available for multievent models. However, the multi-state version of our
49
50 390 model (without uncertainty on timing at independence) fitted the data adequately. Adding a
51
52 391 level of complexity should make the model even more adequate.
53
54
55
56
57
58
59
60

1
2
3 392 Using the conditional probabilities estimated in the model, we calculated the net
4
5 393 probability for a female to raise none, $\Pr(X=0)$, one, $\Pr(X=1)$, or two offspring, $\Pr(X=2)$ to
6
7 394 independence over a 3-year period (details are provided in Appendix 2).
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Review Only



395



396

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

Figure 1: Life history events with associated probabilities of raising one ($X=1$) or two ($X=2$) offspring to independence over a 3 years period for a female polar bear alive and without dependent offspring at the beginning of the period (state A). State A01 represents a female with one dependent cub of the year, A02 with two dependent cubs of the year, A11 with one dependent yearling, A12 with two dependent yearlings, AS1 a successful female breeder with one two-year old offspring reaching independence and AS2 a successful female breeder with two two-year old offspring reaching independence. Parameter ϕ is adult survival, β_3 is breeding probability of a female without dependent offspring, γ_3 is the probability of a singleton litter, s_1 ~~is cub and~~ s_2 ~~is resp. cub and~~ yearling survival in a singleton litter, s_3 ~~is cub~~ and s_4 ~~resp. cub and~~ yearling survival in a twin litter).

We considered adult females without dependent offspring at the beginning of the time period, so that we have:

$$\Pr(X = 1) = \phi^3 \cdot \beta_3 \cdot [\gamma_3 \cdot s_1 \cdot s_3 + (1 - \gamma_3) \cdot (2 s_2(1 - s_2) \cdot s_3 + s_2^2 \cdot 2 s_4(1 - s_4))],$$

$$\Pr(X = 2) = \phi^3 \cdot \beta_3 \cdot (1 - \gamma_3) \cdot s_2^2 \cdot s_4^2,$$

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

Appendix 2 containing guidance, R code, data files to fit the model to the polar bear data, and additional results is available on GitHub at https://github.com/SCubaynes/Appendix2_extendedparentalcare.

416

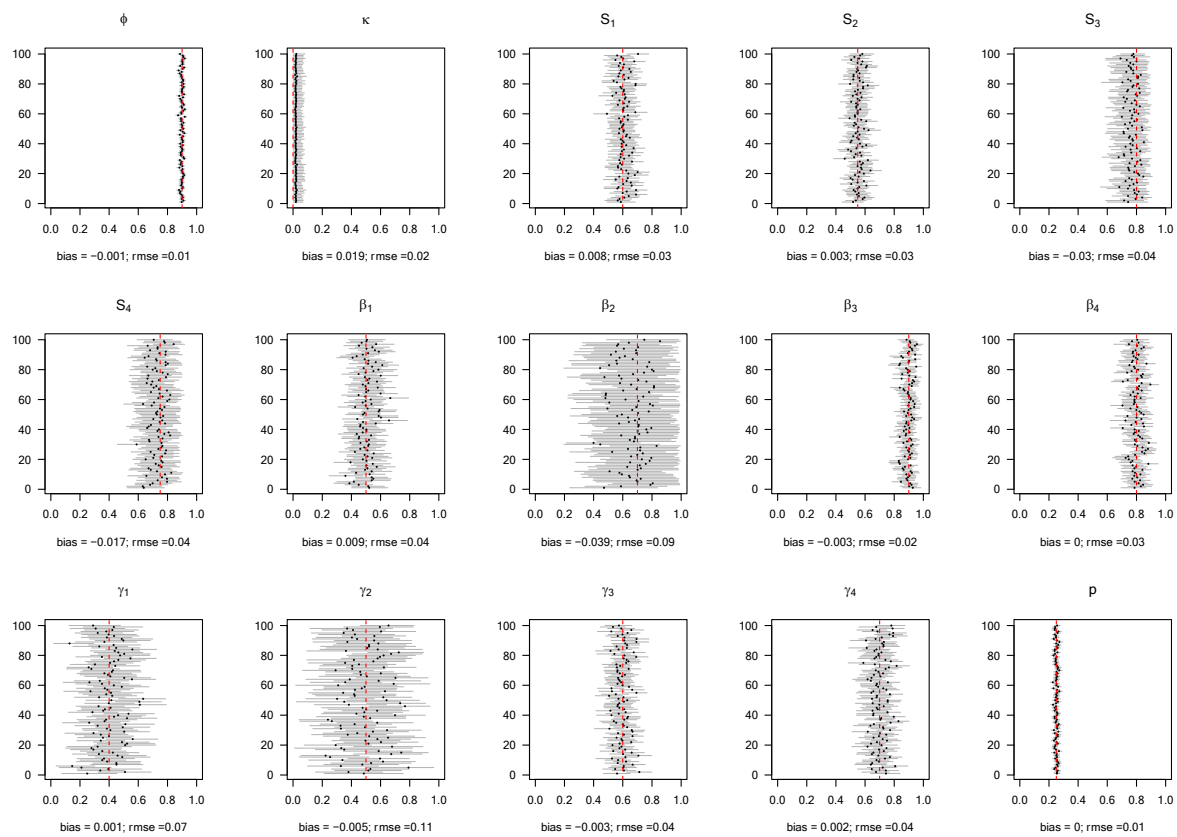
417 RESULTS

418 *Model performance evaluated on simulated datasets*

419 Model performance was satisfying and comparable in all 4 simulated scenarios (S1 with low
420 detection and constant departure, S2 with low detection and seasonal departure, S3 with high
421 detection and constant departure and S4 with high detection and seasonal departure), with low
422 average bias ($B_{S1} = -0.000$, $B_{S2} = -0.004$, $B_{S3} = -0.004$, $B_{S4} = -0.003$) and root-mean-

423 square error ($rmse_{S1} = 0.042$, $rmse_{S2} = 0.041$, $rmse_{S3} = 0.031$ and $rmse_{S4} = 0.031$) (see
 424 Appendix 1 for details).

425 For most parameters, bias was very low, $B < 0.02$, except for parameters β_2 in scenarios
 426 S2, S3 and S4 ($-0.04 < B < -0.03$) and s_3 in scenario S2 ($B = -0.03$), $rmse < 0.05$, except for
 427 parameters β_2 , γ_1 and γ_2 ($0.05 < rmse < 0.07$). For these three parameters, precision was lower
 428 in the two scenarios with low detection (see Appendix 1). Estimates obtained for the scenario
 429 mimicking the polar bear study case (S2: low detection and seasonal departure) are provided in
 430 Figure 2.



431
 432 Figure 2. Performance of the model on simulated data with low detection with seasonal
 433 departure (scenario S2). For each of the 100 simulated data sets, we displayed the mean (circle)
 434 and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of
 435 the parameter is given by the vertical dashed red line. The estimated absolute bias and root-
 436 mean-square error are provided in the legend of the X-axis for each parameter. Regarding
 437 notations, ϕ stands for juvenile, subadult and adult survival, κ is the probability of first

1
2
3 438 reproduction at age 5, s is dependent offspring survival conditioned upon mother survival (s_1
4 and s_2 for singleton cub resp. yearling; s_3 and s_4 for twin litter's cub resp. yearling), β is
5 439 breeding probability conditioned upon mother and offspring survival status (β_1 following loss
6 of a cub litter, and β_2 after loss a cub litter resp. loss of a yearling litter, β_3 for successful breeder,
7 440 β_4 for female without dependent offspring), γ is the probability of producing a singleton litter
8 441 conditioned upon mother's and offspring's survival status and upon breeding decision (γ_1
9 442 following loss of a cub litter, and γ_2 after loss a cub litter resp. loss of a yearling litter, γ_3 for
10 443 successful breeder, γ_4 for female without dependent offspring), p is detection probability.
11
12
13
14
15
16
17
18
19

20 447 *Case study: Polar bear demography*

21
22 448 Departure probability was about 40% at the end of March and reached 80% at mid-May
23
24 449 (Appendix 2). About half of the two-year old bears had departed their mother at the time of
25
26 450 capture. Estimates of demographic parameters are provided in Table 2 (more results are
27
28 451 provided in Appendix 2). Independent female (aged 2+) survival was high (0.93). Individual
29
30 452 offspring survival rates, conditioned upon mother survival, did not vary significantly with litter
31
32 453 size for cubs or yearlings. Average yearling survival was lower for singleton (0.67) than for
33
34 454 litters of twin (0.80), although the 95% credible intervals did overlap. Concerning litter survival
35
36 455 conditioned upon mother survival, it was higher for twin compared to singleton, for both cubs'
37
38 456 and yearlings' litters. A small proportion of females, about 12%, started to reproduce (i.e.
39
40 457 produced a litter that survived at least until the first spring) at 5 y.o. Outcome of the previous
41
42 458 reproduction influenced breeding probability. Breeding probability following the loss of a cub
43
44 459 litter during the year (after capture) was low, about 10%, while it was about 50-60% for female'
45
46 460 successful breeders or without dependent offspring at the beginning of the year or after the loss
47
48 461 of a yearling litter. Detection probability was relatively low, about 0.25 (0.22 - 0.27). At first
49
50 462 capture, 37% were independent juvenile or subadult females, 18% were adult females alone,
51
52 463 28% were adult females with one or two cubs, 12% with one or two yearlings and 5% with two-
53
54 464 year old bears.
55
56
57
58
59
60

465

466 Table 2: Parameter estimates. Means are given with 95% credible intervals (CI). Dependent
 467 offspring (cub age <1 y.o., yearling 1 y.o.) survival and breeding probabilities are conditioned
 468 upon mother survival, litter size probability of producing a singleton is as well conditioned upon
 469 breeding decision.

Parameter	Notation	Mean	Standard error	95% CI
Survival of female juveniles (2yo,3yo) subadults (4yo, 5yo) and adults (5+ yo)	φ	0.93	0.01	0.92 – 0.95
Cub survival (<1yo)				
- singleton (=litter survival)	$s_1 = l_{01}$	0.54	0.10	0.34 - 0.72
- litter of 2 (averaged individual survival)	s_2	0.51	0.05	0.41 - 0.62
Yearling survival (1yo)				
- Singleton (=litter survival)	$s_3 = l_{11}$	0.67	0.11	0.46 - 0.87
- litter of 2 (averaged individual survival)	s_4	0.80	0.09	0.59 - 0.93
Litter survival for twin litters				
- cubs	l_{02}	0.76	0.05	0.65 - 0.85
- yearlings	l_{12}	0.95	0.04	0.83 - 0.99
Probability of first reproduction at 5 yo (mate at 4yo)	κ	0.12	0.08	0.02 - 0.30
Breeding probability				
- following loss of a cub litter	β_1	0.09	0.06	0.01 - 0.23
- following loss of a yearling litter	β_2	0.58	0.21	0.19 - 0.96
- of successful female breeders or previously without dependent offspring	$\beta_3 = \beta_4$	0.52	0.04	0.43 - 0.61
Probability of singleton litter				
- following loss of a cub or yearling litter	$\gamma_1 = \gamma_2$	0.35	0.17	0.07 - 0.71
- of successful females breeders or previously without dependent offspring	$\gamma_3 = \gamma_4$	0.40	0.05	0.30 - 0.44
Capture probability	p	0.25	0.01	0.22 - 0.27

470

60

1
2
3 471 Over a 3 years period, the probability to successfully raise one offspring to independence
4
5 472 for a female polar bear, alive and without dependent offspring at the beginning of the period,
6
7 473 was on average 0.29 (0.20-0.38) and 0.04 (0.02-0.07) to raise two offspring to independence.
8
9 474 The probability of failed breeding (no offspring successfully reached independence) over this
10
11 475 period was high, about 0.67 (0.57-0.76). Note that this calculation includes breeding
12
13 476 probability, and therefore does not reflect offspring survival until independence (see Method
14
15 477 section).
16
17
18
19
20

478

479 **DISCUSSION**

21
22
23 480 Overall, our model performed well in estimating all demographic parameters in all the
24
25 481 simulated scenarios. A multievent approach is a promising tool to deal with uncertainty on the
26
27 482 timing at offspring independence both when departure probability was constant or varied within
28
29 483 the field season. Estimates obtained for adult and offspring survival, probability of sexual
30
31 484 maturation, breeding probability (except after the loss of a yearling litter), litter size
32
33 485 probabilities and detection probability were unbiased in most simulated scenarios. Precision
34
35 486 was satisfying in most cases, but it was lower for breeding probability after the loss of a yearling
36
37 487 litter and for litter size probabilities of failed breeders, especially in scenarios with low detection
38
39 488 (Appendix 1). These specific parameters should therefore be interpreted with caution for the
40
41 489 study case. In our simulations, T=15 sampling occasions appeared sufficient to obtain satisfying
42
43 490 estimates for most parameters. In the polar bear data, there were few recaptures of females on
44
45 491 subsequent years due to relatively low detection rate. As a result, preliminary analyses
46
47 492 suggested a potential confusion between these parameters. We dealt with this issue by including
48
49 493 a biologically realistic constraint on prior distributions, stating that cub survival was lower than
50
51 494 that of yearling survival (Amstrup and Durner, 1995) which was enough to ensure parameter
52
53 495 estimability. Inference in a Bayesian framework is useful in this regard, because it allows ~~to~~for
54
55
56
57
58
59
60

1
2
3 496 ~~the include-inclusion of~~ prior information when available (McCarthy and Masters 2005) to
4
5 497 improve the estimation of model parameters.
6

7
8 498 For polar bears, we showed that outcome of the previous breeding event influenced
9
10 499 breeding probability. Reduced offspring survival one year, for example due to poor
11
12 500 environmental conditions (Derocher et al. 2004), might therefore increase intervals between
13
14 501 successful reproduction through reduced breeding probability the next year (Wiig 1998). This
15
16 502 means that by ignoring multiple-year dependency among mother and offspring, classical
17
18 503 models can underestimate reproductive intervals, therefore risking to overestimate the
19
20 504 population growth rate. However, the biological relevance of our model is currently limited,
21
22 505 because we ignored temporal and individual heterogeneity among females in the model.
23
24 506 Survival rates for independent female bears (0.93) were close to an earlier study for the same
25
26 507 population (0.96), based on telemetry data (Wiig 1998). Our results may overestimate
27
28 508 dependent offspring survival because we focused on resident bears captured more than once.
29
30 509 Wiig (1998) results indicated that females in Svalbard went into den on average every second
31
32 510 year (while successful breeding means denning on a three-year interval), which seems coherent
33
34 511 with our results (about 33% chances of successful reproduction over a three-year period).
35
36
37
38
39
40

41 512 Here, we proposed a general model structure that can be applied to other species
42
43 513 providing EPC. The originalities of our approach lie in using family structure to define
44
45 514 statistical units in our model, and the inclusion of variable timing at offspring independence. ~~It~~
46
47 515 ~~allows~~ Using families instead of individuals allows for the inclusion of ~~to include~~ dependency
48
49 516 among individuals over multiple-years and therefore the evaluate-evaluation of trade-offs and
50
51 517 correlations ~~correlations~~ between offspring's and parents' life history parameters. Our model
52
53 518 could be ~~applied to other species providing EPC, such as wolves, showing variable litter size~~
54
55 519 ~~and age at offspring independence. However, applying our model to species like elephants,~~
56
57 520 ~~killer whales or humans would require including an additional 'post-reproductive' stage and~~
58
59
60

1
2
3 521 ~~estimate the age at menopause. Such extensions of our model could be~~ used, for example, to
4
5 522 evaluate the population-level consequences of positive or negative correlation between parents'
6
7 523 and offspring's traits (e.g. food sharing among group members Lee 2008; or parent-offspring
8
9 524 conflict Kölliker et al. 2013). In the case of social species (e.g. primates, elephants, orcas,
10
11 525 wolves), several adults often play a role in caring for offspring. In addition, females often give
12
13 526 birth to new offspring while still caring for older offspring and, above a certain age, adolescent
14
15 527 dependent offspring can survive despite the loss of their mother and gain independence at
16
17 528 various ages. In such cases, the number of states to represent all possible family units'
18
19 529 composition can rapidly increase, leading to potential computational challenges to deal with
20
21 530 huge matrices. One solution is to use sparse matrices ~~tools in matlab which seem to work well~~
22
23 531 up to XX states to store the data efficiently and optimize matrix calculations. Above this level
24
25 532 of complexity, an alternative solution is to limit the number of states by simplifying the life
26
27 533 cycle depending on the question of interest (e.g. focusing on mother and maternal grand-mother
28
29 534 considering only one litter, or focusing on mother caring alone for one or more litters). For polar
30
31 535 bears specifically, future analyses will integrate in the model the effect of female age on survival
32
33 536 and reproductive success (Atkinson and Ramsay 1995; Folio et al. 2019) and influence of
34
35 537 climatic variables on body weight and demography (Derocher et al. 2004; Stirling and Derocher
36
37 538 2012) as individual and environmental covariates in a regression-like framework. Our model
38
39 539 could then be used to provide population predictions of the demographic response of the Barents
40
41 540 Sea polar bear population under climate change (Hunter et al., 2010; Regehr et al., 2016, 2018,
42
43 541 Laidre et al. 2020).

52
53 542 Acknowledgements : This study was supported by World Wildlife Fund. We thank Magnus
54
55 543 Andersen for his participation in fieldwork, and Thor Larsen for initiating the monitoring. SC
56
57 544 is supported by a grant from the Agence Nationale de la Recherche (ANR-18-CE02-0011,
58
59 545 MathKinD).
60

1
2
3 546
4
5

6
7 547 Data Accessibility Statement : Authors agree to archive the data used in this manuscript in a
8
9 548 publicly accessible repository such as Dryad and Github upon acceptance of the manuscript
10
11 549 (together with R scripts to run the model and the simulation study).
12
13

14 550 Authors' contributions: SC, OG, NY and RP conceived the ideas and designed methodology;

15
16
17 551 JA, RAI and ØW collected the data; SC analysed the data; SC led the writing of the manuscript.
18

19 552 All authors contributed critically to the drafts and gave final approval for publication.
20
21

22
23 553
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Review Only

1
2
3 554 **Bibliography**
4
5

6 555 Amstrup, S. C., & DeMaster, D. P. (2003). Polar bear, *Ursus maritimus*. *Wild mammals of*
7
8
9 556 *North America: biology, management, and conservation*, 2, 587-610.

10
11 557 Amstrup, S. C., & Durner, G. M. (1995). Survival rates of radio-collared female polar bears
12
13 and their dependent young. *Canadian Journal of Zoology*, 73, 1312–1322.
14
15
16 559 doi:10.1139/z95-155

17
18
19 560 Atkinson, S. N., & Ramsay, M. A. (1995). The Effects of Prolonged Fasting of the Body
20
21 561 Composition and Reproductive Success of Female Polar Bears (*Ursus maritimus*).
22
23 562 *Functional Ecology*, 9(4), 559. doi:10.2307/2390145

24
25
26 563 Clutton-Brock, T. H. (1991). The evolution of parental care. Princeton: Princeton University
27
28 564 Press.

29
30
31 565 Cole, D. J., Morgan, B. J. T., McCrea, R. S., Pradel, R., Gimenez, O., & Choquet, R. (2014).
32
33 566 Does your species have memory? Analyzing capture-recapture data with memory models.
34
35 567 *Ecology and Evolution*, 4(11), 2124-2133.

36
37
38 568 Couet, P., Gally, F., Canonne, C., & Besnard, A. (2019). Joint estimation of survival and
39
40 569 breeding probability in female dolphins and calves with uncertainty in state assignment.
41
42 570 *Ecology and evolution*, 9(23), 13043-13055.

43
44
45
46 571 Dahle, B., & Swenson, J. E. (2003). Factors influencing length of maternal care in brown bears
47
48 572 (*Ursus arctos*) and its effect on offspring. *Behavioral Ecology and Sociobiology*, 54(4),
49
50 573 352-358.

51
52
53 574 Derocher A., & Stirling, I. (1994). Age-specific reproductive performance of female polar bears
54
55 575 (*Ursus maritimus*). *Journal of Zoology*, 234(4), 527–536.

56
57
58 576 Derocher, A. ., Lunn, N. ., & Stirling, I. (2004). Polar bears in a warming climate. (*Ursus*
59
60

- 1
2
3 577 maritimus). *Integrative and Comparative Biology*, 44(2), 163–176.
4
5
6 578 Derocher, A.E., 2005. Population ecology of polar bears at Svalbard, Norway. *Population*
7
8 579 *Ecology*, 47(3), pp.267-275.
9
10
11 580 Derocher, A. (2013). Polar bears: a complete guide to their biology and behavior. *Choice*
12
13 581 *Reviews Online*, 49(12), 49-6887-49–6887. doi:10.5860/choice.49-6887
14
15
16 582 Doligez, B., Clobert, J., Pettifor, R. A., Rowcliffe, M., Gustafsson, L., Perrins, C. M., &
17
18 583 McCleery, R. H. (2002). Costs of reproduction: Assessing responses to brood size
19
20 584 manipulation on life-history and behavioural traits using multi-state capture-recapture
21
22 585 models. *Journal of Applied Statistics*, 29(1–4), 407–423.
23
24
25 586 Eldegard, K., & Sonerud, G. A. (2010). Experimental increase in food supply influences the
26
27 587 outcome of within-family conflicts in Tengmalm’s owl. *Behavioral Ecology and*
28
29 588 *Sociobiology*, 64(5), 815-826.
30
31
32
33 589 Folio, D.M., Aars, J., Gimenez, O., Derocher, A.E., Wiig, Ø. and Cubaynes, S., (2019). How
34
35 590 many cubs can a mum nurse? Maternal age and size influence litter size in polar bears.
36
37 591 *Biology letters*, 15(5), p.20190070.
38
39
40 592 Gimenez, O., Lebreton, J.-D., Gaillard, J.-M., Choquet, R. and R. Pradel (2012). Estimating
41
42 593 demographic parameters using hidden process dynamic models. *Theoretical Population*
43
44 594 *Biology* 82, 307-316.
45
46
47 595 Gimenez, O., Cam, E., & Gaillard, J.-M. (2018). Individual heterogeneity and capture-recapture
48
49 596 models: what, why and how? *Oikos*, 127(5), 664–686.
50
51
52 597 Hansson, R., & Thomassen, J. (1983). Behavior of polar bears with cubs in the denning area.
53
54 598 *Bears: Their Biology and Management*, 246–254.
55
56
57 599 Hunter, C. M., Caswell, H., Runge, M. C., Regehr, E. V., Amstrup, S. C., & Stirling, I. (2010).
58
59 600 Climate change threatens polar bear populations: a stochastic demographic analysis.

1
2
3 601 *Ecology*, 91(10), 2883–2897.
4

5
6 602 Kölliker, M., Kilner, R. M., & Hinde, C. A. (2013). Parent–offspring conflict. In *The Evolution*
7
8 603 *of Parental Care*.

9
10 604 Kramer, K. L. (2005). Children's help and the pace of reproduction: cooperative breeding in
11
12 605 humans. *Evolutionary Anthropology: Issues, News, and Reviews: Issues, News, and*
13
14 606 *Reviews*, 14(6), 224–237.

15
16
17
18 607 Lagrange, P., Gimenez, O., Doligez, B., Pradel, R., Garant, D., Pelletier, F., & Bélisle, M.
19
20 608 (2017). Assessment of individual and conspecific reproductive success as determinants of
21
22 609 breeding dispersal of female tree swallows: A capture-recapture approach. *Ecology and*
23
24 610 *Evolution*, 7(18), 7334–7346.

25
26
27
28 611 Laidre, K. L., Atkinson, S., Regehr, E. V., Stern, H. L., Born, E. W., Wiig, Ø., ... & Dyck, M.
29
30 612 (2020). Interrelated ecological impacts of climate change on an apex predator. *Ecological*
31
32 613 *Applications*, e02071.

33
34
35 614 Lebreton, J. D., Nichols, J. D., Barker, R. J., Pradel, R., & Spendelov, J. A. (2009). Chapter 3
36
37 615 Modeling Individual Animal Histories with Multistate Capture-Recapture Models.
38
39 616 *Advances in Ecological Research*.

40
41
42 617 Lee, P. C., & Moss, C. J. (1986). Early maternal investment in male and female African elephant
43
44 618 calves. *Behavioral Ecology and Sociobiology*, 18(5), 353–361.

45
46
47 619 Lee, R. (2008). Sociality, selection, and survival: Simulated evolution of mortality with
48
49 620 intergenerational transfers and food sharing. *Proceedings of the National Academy of*
50
51 621 *Sciences*.

52
53
54 622 Lunn, N.J., Servanty, S., Regehr, E.V., Converse, S.J., Richardson, E. and Stirling, I. (2016).
55
56 623 Demography of an apex predator at the edge of its range: impacts of changing sea ice on
57
58 624 polar bears in Hudson Bay. *Ecological Applications*, 26(5), pp.1302–1320. Mauritzen, M.,

- 1
2
3 625 Derocher, A. E., & Wiig, Ø. (2011). Space-use strategies of female polar bears in a
4
5 626 dynamic sea ice habitat. *Canadian Journal of Zoology*, 79(9), 1704–1713.
6
7
8 627 Mauritzen, M., Derocher, A.E., Wiig, Ø., Belikov, S.E., Boltunov, A.N., Hansen, E. and Garner,
9
10 628 G.W., (2002). Using satellite telemetry to define spatial population structure in polar bears
11
12 629 in the Norwegian and western Russian Arctic. *Journal of Applied Ecology*, 39(1), pp.79-
13
14 630 90.
15
16
17 631 McCarthy, M. A., & Masters, P. (2005). Profiting from prior information in Bayesian analyses
18
19 632 of ecological data. *Journal of Applied Ecology*, 42(6), 1012–1019.
20
21
22 633 Pavard, S., & Branger, F. (2012). Effect of maternal and grandmaternal care on population
23
24 634 dynamics and human life-history evolution: A matrix projection model. *Theoretical*
25
26 635 *Population Biology*.
27
28
29 636 Plummer, M., Stukalov, A., Denwood, M. and Plummer, M.M., (2016). Package ‘rjags’.
30
31 637 Vienna, Austria.
32
33
34 638 Pollock, K. H. (2002). The use of auxiliary variables in capture-recapture modelling: An
35
36 639 overview. *Journal of Applied Statistics*, 29(1–4), 85–102.
37
38
39 640 Pradel, R. (2005) Multievent: An extension of multistate capture–recapture models to uncertain
40
41 641 states ». *Biometrics* 61: 442-447
42
43
44 642 Pradel, R., & Sanz-Aguilar, A. (2012). Modeling Trap-Awareness and Related Phenomena in
45
46 643 Capture-Recapture Studies. *PLoS ONE*, 7(3), e32666.
47
48
49 644 Ramsay, M. A., & Stirling, I. (1988). Reproductive biology and ecology of female polar bears
50
51 645 in western Hudson Bay. *Naturaliste Canadien*, 109(4), 941–946.
52
53
54 646 Regehr, E. V., Laidre, K. L., Resit Akcakaya, H., Amstrup, S. C., Atwood, T. C., Lunn, N. J.,
55
56 647 ... Wiig, Ø. (2016). Conservation status of polar bears (*Ursus maritimus*) in relation to
57
58 648 projected sea-ice declines. *Biology Letters*, 12(12).

- 1
2
3 649 Regehr, E.V., Hostetter, N.J., Wilson, R.R., Rode, K.D., Martin, M.S. and Converse, S.J.,
4
5 650 (2018). Integrated population modeling provides the first empirical estimates of vital rates
6
7 651 and abundance for polar bears in the Chukchi Sea. *Scientific reports*, 8(1), pp.1-12.
9
10 652 Royle, N., Smiseth, P., & Kölliker, M. (2012). The evolution of parental care.
11
12
13 653 Shenk, M. K., & Scelza, B. A. (2012). Paternal investment and status-related child outcomes:
14
15 654 Timing of father's death affects offspring success. *Journal of Biosocial Science*.
16
17
18 655 Stearns, S.C. 1992. *The Evolution of Life Histories*. Oxford University Press.
19
20
21 656 Stirling, I., & Derocher, A. E. (2012). Effects of climate warming on polar bears: a review of
22
23 657 the evidence. *Global Change Biology*, 18(9), 2694–2706.
24
25
26 658 Stirling, I., Spencer, C., & Andriashek, D. (1989). Immobilization of polar bears (*Ursus*
27
28 659 *maritimus*) with Telazol in the Canadian Arctic. *Journal of Wildlife Diseases*, 25(2), 159–
29
30 660 168.
31
32
33 661 Trivers, R. L. 1972. Parental investment and sexual selection. Pages 136-179 in B. G. Campbell,
34
35 662 editor. *Sexual selection and the descent of man, 1871-1971*. Aldine, Chicago
36
37
38 663 Van Noordwijk, M. A. (2012). From Maternal Investment to Lifetime Maternal Care. In
39
40 664 *Evolution of Primate Societies* (pp. 321–342).
41
42
43 665 Vergara, P., Fargallo, J. A., & Martínez-Padilla, J. (2010). Reaching independence: food
44
45 666 supply, parent quality, and offspring phenotypic characters in kestrels. *Behavioral*
46
47 667 *ecology*, 21(3), 507-512.
48
49
50 668 Wich, S., Utami-Atmoko, S., Setia, T. M., Rijksen, H. D., Schürmann, C., Van Hooff, J. A. R.
51
52 669 A. ., & van Schaik, C. P. (2004). Life history of wild Sumatran orangutans (*Pongo abelii*).
53
54 670 *Journal of Human Evolution*, 47(6), 385–398.
55
56
57
58 671 Wiig, Ø. (1998). Survival and Reproductive Rates for Polar Bears at Svalbard. *Ursus*, 10, 25–
59
60 672 32.

1
2
3 673 Williams, G.C. (1966) Natural selection, the costs of reproduction, and a refinement of Lack's
4
5 674 principle. *American Naturalist*. 100, 687–690
6
7

8 675 Yoccoz, N. G., Erikstad, K. E., Bustnes, J. O., Hanssen, S. A., & Tveraa, T. (2002). Costs of
9
10 676 reproduction in common eiders (*Somateria mollissima*): An assessment of relationships
11
12 677 between reproductive effort and future survival and reproduction based on observational
13
14
15 678 and experimental studies. *Journal of Applied Statistics*, 29(1–4), 57–64.
16
17

18 679
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60

For Review Only

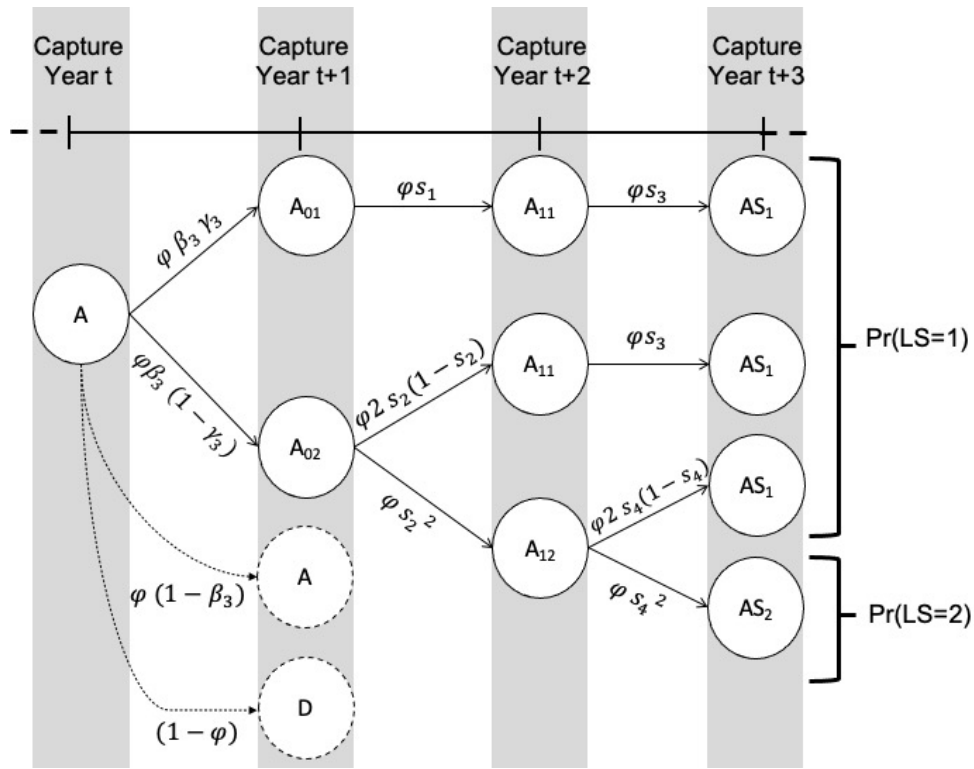


Figure 1: Life history events with associated probabilities of raising one ($X=1$) or two ($X=2$) offspring to independence over a 3 years period for a female polar bear alive and without dependent offspring at the beginning of the period (state A). State A01 represents a female with one dependent cub of the year, A02 with two dependent cubs of the year, A11 with one dependent yearling, A12 with two dependent yearlings, AS1 a successful female breeder with one two-year old offspring reaching independence and AS2 a successful female breeder with two two-year old offspring reaching independence. Parameter φ is adult survival, β_3 is breeding probability of a female without dependent offspring, γ_3 is the probability of a singleton litter, s_1 is cub and s_2 is yearling survival in a singleton litter, s_3 is cub and s_4 yearling survival in a twin litter.

250x190mm (72 x 72 DPI)

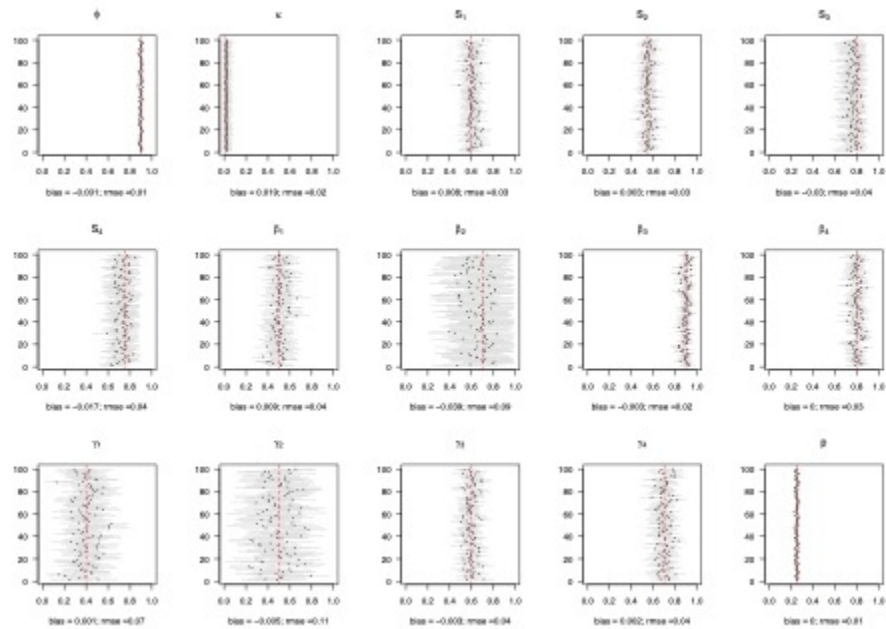


Figure 2. Performance of the model on simulated data with low detection with seasonal departure (scenario S2). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given by 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 stands for juvenile, subadult and adult survival, κ is the probability of first reproduction at age 5, s is dependent offspring survival conditioned upon mother survival (s_1 and s_2 for singleton cub resp. yearling; s_3 and s_4 for twin litter's cub resp. yearling), β is breeding probability conditioned upon mother and offspring survival status (β_1 following loss of a cub litter, β_2 loss of a yearling litter, β_3 for successful breeder, β_4 for female without dependent offspring), γ is the probability of producing a singleton litter conditioned upon mother's and offspring's survival status and upon breeding decision (γ_1 following loss of a cub litter, γ_2 loss of a yearling litter, γ_3 for successful breeder, γ_4 for female without dependent offspring), p is detection probability.

160x113mm (72 x 72 DPI)

1
2
3
4
5
6
7
8
9
10
11
12
13
14
15
16
17
18
19
20
21
22
23
24
25
26
27
28
29
30
31
32
33
34
35
36
37
38
39
40
41
42
43
44
45
46
47
48
49
50
51
52
53
54
55
56
57
58
59
60



Bear picture for graphical abstract or cover