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

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Abstract:	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 (Ursus maritimus). 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,

	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.

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

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Abstract

1. In species providing extended parental care, one or both parents care for altricial young over a period including more than one breeding season. We expect large parental investment and long-term dependency within family units to cause high variability in life trajectories among individuals with complex consequences at the population level. So far, models for estimating demographic parameters in free-ranging animal populations mostly ignore extended parental care, thereby limiting our understanding of its consequences on parents and offspring life histories.

2. 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 (*Ursus maritimus*).

3. Our model performed well in terms of bias and mean square error and in estimating demographic parameters in all simulated scenarios, 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, 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.

4. 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. This is of interest in terms of conservation because species providing extended parental care are often long-living mammals vulnerable or threatened with extinction.

Key-words: apex predator, arctic ecosystem, Bayesian modeling, capture-recapture, dependency among individuals, family structure, parental care, state uncertainty, timing at independence.

INTRODUCTION

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

the parent's reproductive success (Trivers 1972). Altricial mammals having offspring that need to learn complex skills to ensure survival beyond independence, such as hunting, orientation, or nest building, show extended parental care (hereafter EPC; Clutton-Brock 1991). It is defined as a prolonged period, i.e. lasting more than one breeding season, over which one or both parents care for one or several dependent young. This period typically lasts for several years and can extend until lifelong maternal care in primates (Van Noordwijk 2012). For the offspring, the quality and quantity of care received can have long-lasting effects on future survival (e.g. Pavard and Branger 2012), social status (e.g. Shenk and Scelza 2012) and reproduction (Royle et al. 2012). For the parent, investment in one offspring can compromise its own condition or survival and/or its ability to invest in other offspring (siblings or future offspring) (Williams 1966, Stearns 1992). It can indeed take several years during which a parent caring for its offspring will not be available to reproduce, sometimes not until the offspring have reached independence, e.g. on average 2.5 years for female polar bears (Ramsay and Stirling 1988), 3.5 to 6 years for female African elephants (Lee and Moss 1986), and 9.3 years for female Sumatran orangutans (Wich et al. 2004). The fitness costs of losing one offspring, in terms of lost investment and skipped breeding opportunities, are particularly high if death occurs near independence. We therefore expect EPC, through large parental investment and multiple-year dependency among individuals within family units, to cause high variability in life trajectories among individuals and family groups, in interbirth intervals depending on offspring's fate, and consequently on lifetime reproductive success for the caring parent (Clutton-Brock 1991).

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

failed breeding events (e.g., Lagrange et al. 2017) and include varying litter or clutch size (e.g., Doligez et al. 2002) and memory effects (Cole et al. 2014), to investigate the costs of reproduction on survival and future reproduction for species providing short-term parental care, i.e. when offspring reach independence before the next breeding season (e.g., Yoccoz et al. 2002). Indeed, most CR models rely on the assumption of independence among individual CR histories (Lebreton et al. 2009).

In the case of species providing EPC, one challenge stems from the multiple-year dependency among individual's life histories within parent-offspring units. Only few attempts have been made to tackle this issue when estimating demographic parameters, despite the fact that species providing EPC are often among long-living mammals vulnerable or threatened with extinction (e.g. polar bears, orangutans, elephants). Lunn et al. (2016) proposed to model CR histories of mother-offspring units (instead of individuals) to consider the multiple-year dependency of female breeding probability upon offspring survival status for polar bears in Hudson Bay. However, in this model, offspring survival after 9 months is assumed independent of mother survival. Lunn et al. (2016)'s model does therefore not handle multiple-year dependency of offspring survival upon mother survival status, typical of species providing EPC. In addition, because litter size is modeled separately, Lunn et al. (2016)'s model (also used in Regehr et al. (2018)) does not permit to explore potential trade-offs among offspring traits and parental phenotypic or demographic traits.

Another challenge involves dealing with uncertain timing at offspring independence, when the offspring departs the caring parent(s) and becomes independent. When studying free-ranging populations, this key life history event is rarely directly observed. When a mature individual is observed without dependent offspring, it is often impossible to know if its offspring have died or already departed its natal group. As a result, estimates of demographic rates and trade-offs can be underestimated. Based on the analysis of mother-offspring units CR

histories, Couet et al. (2019) provided estimates of dolphin reproductive parameters corrected for state uncertainty, but their model assumed a fixed age and timing at offspring independence. Lunn et al. (2016)'s model included variable age at independence, but variability in the timing at offspring independence was not fully dealt with. Demographic rates were corrected by the average annual probability that independence occurred prior to sampling for all offspring, and offspring survival was assumed independent of litter size (Regehr et al. 2018). In most species, timing at offspring independence is variable and could depend on the offspring phenotypic traits (e.g. body size in brown bears, Dahle and Swenson 2003), on parental traits (e.g. parent-offspring conflict in kestrels, Vergara et al. 2010), social and mating system (e.g. helping behavior in humans, Kramer 2005), or other environmental determinants (e.g. food supply, Eldegard and Sonerud 2010). To our knowledge, no model is available to tackle both the issues of multiple-year dependency among individuals and variable timing at offspring independence. Because of these methodological challenges, the population-level consequences of EPC remain to be understood, especially in free-ranging animal populations.

Here, we develop a CR model specifically for species providing EPC. It is designed to handle multiple-years statistical dependency (until offspring independence) among individual demographic parameters by modeling CR histories grouped within family units. The model accounts for uncertain timing at offspring independence. In addition, our model allows for variability in the number of offspring born and recruited at each breeding event, variable offspring survival depending on number of siblings, and includes the influence of past reproductive history on the caring parent's current status. Finally, estimates of survival rates, breeding probability and litter size probability are corrected for imperfect detection possibly depending upon family unit composition.

In what follows, we present the model, assess its performance using simulated data, and illustrate its use with a long-term dataset collected on the Svalbard polar bears. Female polar

bears rely solely on stored fat reserves during pregnancy and the first three months of lactation, before feeding and protecting litters of one to three young, usually during two more years (Ramsay and Stirling 1988). They can lose more than 40% of body mass while fasting (Atkinson and Ramsay 1995). In many areas, climate change and related sea ice decline impact female bear condition and capacity to provide care for their young, with an associated decline in reproductive output (Derocher et al. 2004; Stirling and Derocher, 2012, Laidre et al. 2020). More insights into the species demography, such as the consequences of long-duration parental care on mother and offspring life histories, could help our understanding of polar bear population responses to environmental perturbations and extinction risks in future decades (Hunter et al., 2010; Regehr et al., 2016).

METHODS

1. Capture-recapture model for species providing EPC

1.1 Principle

We develop a CR model in the multievent framework (Pradel 2005) that is also known as a hidden Markov modeling framework (Gimenez et al. 2012). The principle is to relate the field observations, called events, to the underlying demographic states of interest through the observation process. Uncertainty on state assignment due to variable timing at offspring independence is included in the observation process. In parallel, the state process describes the transition rates between states from one year to the next. The transition rates correspond here to the demographic parameters corrected for imperfect detection and state uncertainty. Below we describe the general procedure to specify the model by defining the states and state-to-state transition process, then the events and observation process. However, for simplicity, the events and states are chosen to match the polar bear life cycle (i.e. females are captured in spring, alone

or together with a litter of one or two dependent offspring; offspring gain independence in the year following their second birthday, and offspring cannot survive the loss of their mother before gaining independence). The resulting model assumptions and its applicability to other species are discussed below.

1.2 Specification of states and state process

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

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

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

	'4'	capture of a 5yo independent subadult female
	'5'	capture of a mother with one dependent cub of the year
	'6'	capture of a mother with two dependent cub of the year
	'7'	capture of a mother with one dependent yearling
	'8'	capture of a mother with two dependent yearlings
	'9'	capture of a mother with one dependent two-year old offspring
	'10'	capture of a mother with two dependent two-year old offspring
	'11'	capture of an adult female without dependent offspring
	'0'	non observation

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

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

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

	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 - φ_1
J3	0	φ_2	0	0	0	0	0	0	0	0	0	1 - φ_2
SA4	0	0	φ_3	0	0	0	0	0	0	0	0	1 - φ_3
SA5	0	0	0	φ_4	0	0	0	0	0	0	0	1 - φ_4
A01	0	0	0	0	φ_5	0	0	0	0	0	0	1 - φ
A02	0	0	0	0	0	φ_6	0	0	0	0	0	1 - φ_6
A11	0	0	0	0	0	0	φ_7	0	0	0	0	1 - φ_7
A12	0	0	0	0	0	0	0	φ_8	0	0	0	1 - φ_8
AS1	0	0	0	0	0	0	0	0	φ_9	0	0	1 - φ_9
AS2	0	0	0	0	0	0	0	0	0	φ_{10}	0	1 - φ_{10}
A	0	0	0	0	0	0	0	0	0	0	φ_{11}	1 - φ_{11}
D	0	0	0	0	0	0	0	0	0	0	0	1

(eq. 1)

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

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

	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- κ	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)

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

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

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

	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)

Parameter β is breeding probability conditioned upon mother and offspring's 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 at the beginning of the year).

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

	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)

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

Parameter 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 the loss a cub litter, γ_2 loss of a yearling litter, γ_3 for successful breeder, γ_4 for female without dependent offspring at the beginning of the year).

By modifying the constraints on parameters (i.e. setting them equal or different among states), the model can be used to investigate: i) the cost of reproduction on parent's survival (by comparing the φs in matrix Φ), ii) the influence of litter size on individual offspring survival (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} and l_{11} to l_{12}), iv) the influence of past reproductive history on breeding probability (by comparing the βs in matrix Ψ_2), and on litter size probability (by comparing the γs in matrix Ψ_3).

1.3 Specification of events and observation process

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

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

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

The E_1 matrix (eq. 5), relates the states S to the possible observations at the time of capture, O = {1,2,3,4,5,6,7,8,9,10,11,12} (same code as the events, see Table 1), through the 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	$1\text{-}\alpha_{i,d}$	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

(eq.5)

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

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

(eq.6)

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

1.4 Applicability to other species

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

To apply the model to other species, one should modify the number of events and states to match the species life cycle (depending on age at sexual maturity, number of care providers, maximum litter size, duration of parental care) but the number of matrices should remain the same. For example, modeling a hypothetical species similar to polar bears but in which both males and females care for offspring would increase the number of unique states from 24 to 42 (8 states for immature females and males, 21 states for dependent offspring cared for by both parents, just the mother in case of father loss, or just the father in case of mother loss). Such a model could be used to assess the influence of father versus mother loss on litter size, offspring survival and father and/or mother breeding probabilities. After defining the states and events, one should modify the shape of the relationship between departure probability and date of capture to match the species life cycle. In species like primates or wolves, departure from the family unit can occur throughout the year, at a more or less constant rate depending on the season, while it occurs only between February and May in polar bears due to environmental constraints. In addition, the influence of individual traits such as age or body weight, or environmental variables such as temperature, can be included in the model under the form of individual or temporal covariates (Pollock 2002). Other specificities related to data collection can be included in a similar way, such as trap effects (Pradel and Sanz-Aguilar 2012) or latent individual heterogeneity by using mixture of distributions or random effects (Gimenez et al. 2018). Guidance to fit the model in a Bayesian framework in program Jags for real and simulated data are provided in Appendices 1 and 2.

Simulation study

The simulation study was aimed at evaluating the performance of our model to estimate demographic parameters under various assumptions about the timing at offspring independence (constant versus seasonal departure rate) and various degrees of capture probability (low p=

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

We simulated data for a virtual long-lived mammal species mimicking the polar bear using the model described in box 1. We used $\varphi = 0.9$ for independent female bear survival (aged 2+ y.o.), $s_1 = l_{01} = 0.6$ for singleton cub survival, $s_2 = 0.55$ for twin litter' s cub survival (corresponding to twin litter survival $l_{02} = 0.7975$), $s_3 = 0.8$ for singleton yearling survival and $s_4 = 0.75$ for twin litter's yearling survival (corresponding to litter survival $l_{12} = 0.94$). Offspring survival rates were conditioned upon mother survival. If a mother dies, its dependent offspring had no chances of surviving. For breeding probabilities, we used $\beta_1 = 0.5$, $\beta_2 = 0.7$, $\beta_3 = 0.9$ and $\beta_4 = 0.8$. For litter size probabilities, we used $\gamma_1 = 0.4$, $\gamma_2 = 0.5$, $\gamma_3 = 0.6$ and $\gamma_4 = 0.7$. We set $\kappa = 0$ and assumed that females had their first litter at age 6 or older.

We assumed that captures occurred each year between mid-March to end of May (day of the year d=80 to d=130). For each capture event, date of capture was randomly sampled from the distribution of the polar bear data dates of capture (see Appendix 1). In the constant scenario, we assumed that two-year old bears reached independence at a constant departure rate (α) during the field season, independently of the date of capture. We chose an intermediate value of α = 0.5 (if independence occurred always after the field season, α = 0, versus always before the field season, α = 1). In the seasonal scenario, we assumed that departure rate varied with date of capture (d) following a logistic relationship (regression coefficients were estimated from the polar bear data, see Appendix 2). Most of the two-year old offspring were captured with their mother at the beginning of the field season, while departure probability increased logistically up to 80% at the end of the field season.

We simulated 100 CR datasets for each of the 4 scenarios (S1: low detection with constant departure, S2: low detection with seasonal departure, S3: high detection with constant departure, S4: high detection with seasonal departure). We simulated the data using program R. We fitted the model using program jags called from R (Plummer 2016). For each parameter and each dataset, we calculated absolute bias as $\hat{B} = \hat{\theta} - \theta$, and root mean squared error as $\widehat{RMSE} = \sqrt{(\hat{\theta} - \theta)^2}$, with θ the parameter used to simulate the data and $\hat{\theta}$ the mean value of the estimated parameter. Appendix 1 containing guidance, R code and files to simulate data and fit the model is available on GitHub at https://github.com/SCubaynes/Appendix1_extendedparentalcare.

Case study: Polar bears in Svalbard

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

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

Bears captured in Svalbard are shown to be a mixture of resident and pelagic bears (Mauritzen et al. 2002). To focus on the resident population, independent bears captured only once were not included in our analysis. We therefore analyzed N = 158 encounter histories of resident polar bear family units captured each spring after den emergence between doy 80 to 130 (mid-March to mid-May), from 1992 to 2019, in Svalbard. It corresponds to 81 capture events of juvenile and subadults, 231 cubs, 96 yearling, 23 dependent two-year old, and 444 captures of adult females. Polar bears were caught and individually marked as part of a long-term monitoring program on the ecology of polar bears in the Barents Sea region (Derocher 2005). All bears one year or older were immobilized by remote injection of a dart (Palmer Cap-Chur Equipment, Douglasville, GA, USA) with the drug Zoletil® (Virbac, Carros, France) (Stirling et al. 1989). The dart was fired from a small helicopter (Eurocopter 350 B2 or B3), usually from a distance of about 4 to 10 meters. Cubs of the year were immobilized by injection with a syringe. Cubs and yearlings were highly dependent on their mother; therefore, they remained in her vicinity and were captured together with their mother. A female captured alone was considered to have no dependent offspring alive. Death of the cubs could have occurred in the den or shortly after den emergence but before capture. Hereafter, estimated cub survival thus refers to survival after capture. Infant mortality occurring before capture will be assigned to a reduced litter size. Because only 3% of females were observed with 3 offspring, we analyzed jointly litters of twins with triplets.

We built the model described above with 12 states and 12 events to describe the life cycle (Table 1). Preliminary analyses suggested that mother survival did not vary according to state, we therefore constrained parameter φ to be equal among all states in matrix Φ. To avoid identifiability issues due to a relatively small sample size, we assumed breeding probability and litter size probability did not vary between successful breeders (states AS1 and AS2) and female without dependent offspring (state A) by setting $\beta_3 = \beta_4$ and $\gamma_3 = \gamma_4$. . We also assumed that litter size probability did not vary among failed breeders (loss of a cub versus a yearling litter), by setting $\gamma_1 = \gamma_2$. We could not assess formally the fit of our model because no test is yet available for multievent models. However, the multi-state version of our model (without uncertainty on timing at independence) fitted the data adequately. Adding a level of complexity should make the model even more adequate.

Using the conditional probabilities estimated in the model, we calculated the net probability for a female to raise none, Pr(X=0), one, Pr(X=1), or two offspring, Pr(X=2) to independence over a 3-year period (details are provided in Appendix 2).

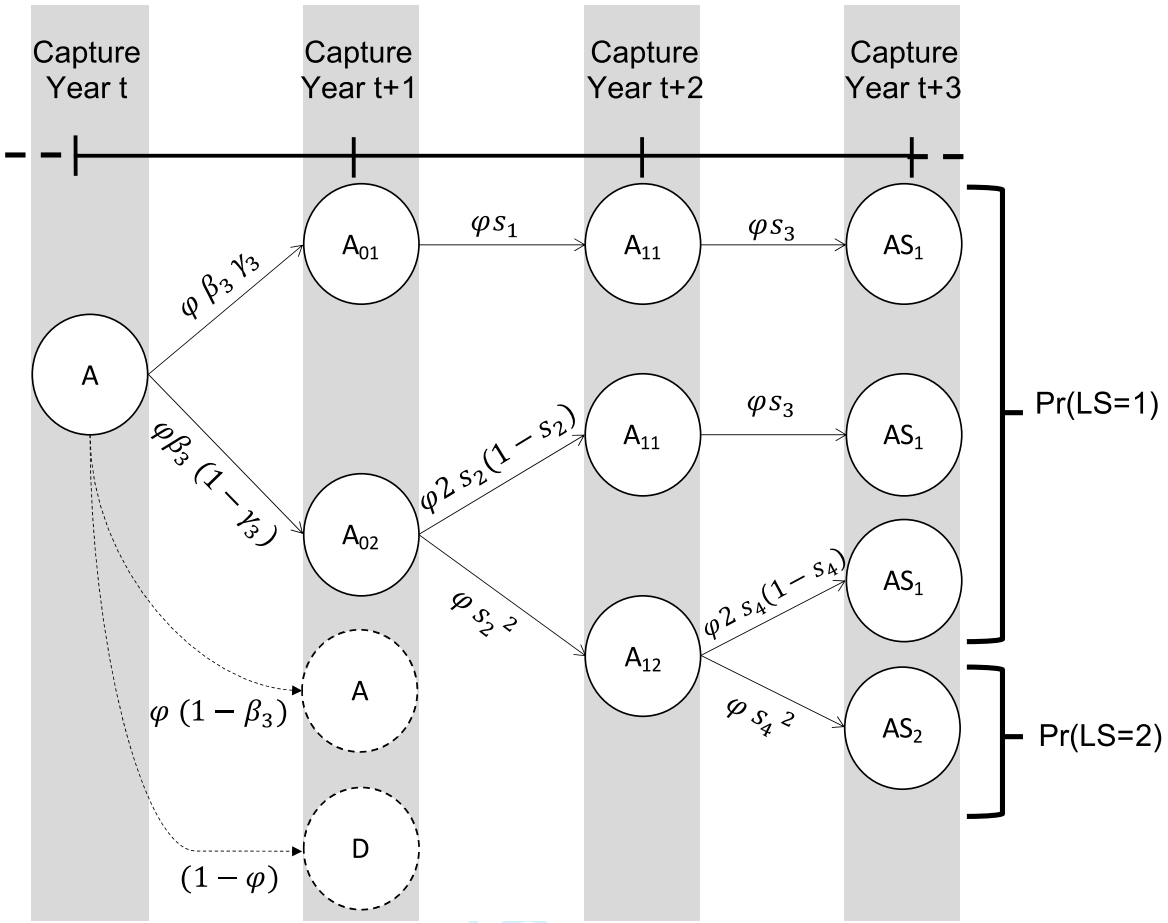

Figure 1: Life history events with associated probabilities of raising one (X=1) or two (X=2) offspring to independence over a 3 years period for a female polar bear alive and without dependent offspring at the beginning of the period (state A). State A01 represents a female with one dependent cub of 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.

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

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

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

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

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.

RESULTS

Model performance evaluated on simulated datasets

Model performance was satisfying and comparable in all 4 simulated scenarios (S1 with low detection and constant departure, S2 with low detection and seasonal departure, S3 with high detection and constant departure and S4 with high detection and seasonal departure), with low average bias ($B_{S1} =$ - 0.000, $B_{S2} =$ - 0.004, $B_{S3} =$ - 0.004, $B_{S4} =$ - 0.003) and root-mean-square error ($rmse_{S1} =$ 0.042, $rmse_{S2} = 0.041$, $rmse_{S3} = 0.031$ and $rmse_{S4} = 0.031$) (see Appendix 1 for details).

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

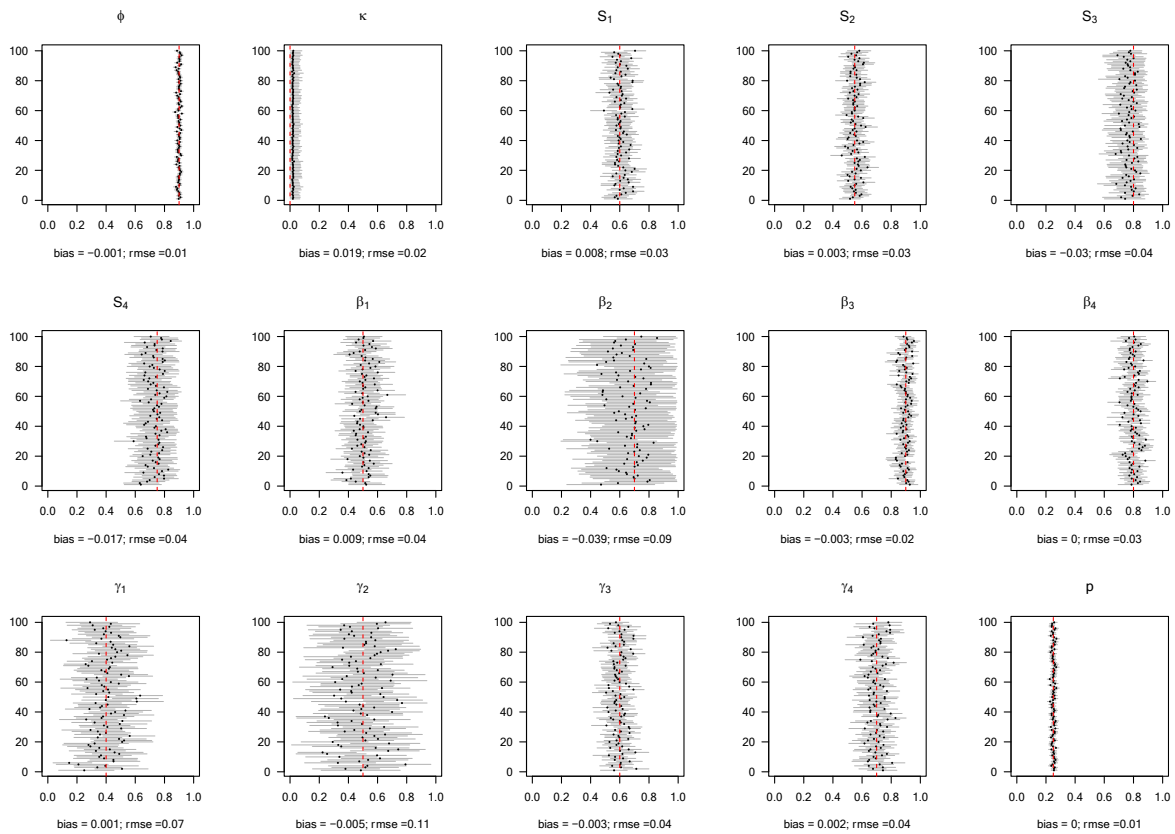

Figure 2. Performance of the model on simulated data with low detection with seasonal departure (scenario S2). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given by 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.

Case study: Polar bear demography

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

Table 2: Parameter estimates. Means are given with 95% credible intervals (CI). Dependent offspring (cub age <1 y.o., yearling 1 y.o.) survival and breeding probabilities are conditioned upon mother survival, litter size probability of producing a singleton is as well conditioned upon 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**	γ_1=γ_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

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

DISCUSSION

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

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

population growth rate. However, the biological relevance of our model is currently limited, because we ignored temporal and individual heterogeneity among females in the model. Survival rates for independent female bears (0.93) were close to an earlier study for the same population (0.96), based on telemetry data (Wiig 1998). Our results may overestimate dependent offspring survival because we focused on resident bears captured more than once. Wiig (1998) results indicated that females in Svalbard went into den on average every second year (while successful breeding means denning on a three-year interval), which seems coherent with our results (about 33% chances of successful reproduction over a three-year period).

Here, we proposed a general model structure that can be applied to other species providing EPC. The originalities of our approach lie in using family structure to define statistical units in our model, and the inclusion of variable timing at offspring independence. Using families instead of individuals allows for the inclusion of dependency among individuals over multiple-years and therefore the evaluation of trade-offs and correlations between offspring's and parents' life history parameters. Our model could be used, for example, to evaluate the population-level consequences of positive or negative correlation between parents' and offspring's traits (e.g. food sharing among group members Lee 2008; or parent-offspring conflict Kölliker et al. 2013). In the case of social species (e.g. primates, elephants, orcas, wolves), several adults often play a role in caring for offspring. In addition, females often give birth to new offspring while still caring for older offspring and, above a certain age, adolescent dependent offspring can survive despite the loss of their mother and gain independence at various ages. In such cases, the number of states to represent all possible family units' composition can rapidly increase, leading to potential computational challenges to deal with huge matrices. One solution is to use sparse matrices to store the data efficiently and optimize matrix calculations. Above this level of complexity, an alternative solution is to limit the number of states by simplifying the life cycle depending on the question of interest (e.g.

focusing on mother and maternal grand-mother considering only one litter, or focusing on mother caring alone for one or more litters). For polar bears specifically, future analyses will integrate in the model the effect of female age on survival and reproductive success (Atkinson and Ramsay 1995; Folio et al. 2019) and influence of climatic variables on body weight and demography (Derocher et al. 2004; Stirling and Derocher 2012) as individual and environmental covariates in a regression-like framework. Our model could then be used to provide population predictions of the demographic response of the Barents Sea polar bear population under climate change (Hunter et al., 2010; Regehr et al., 2016, 2018, Laidre et al. 2020).

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Data Accessibility Statement : Authors agree to archive the data used in this manuscript in a publicly accessible repository such as Dryad and Github upon acceptance of the manuscript (together with R scripts to run the model and the simulation study).

Authors' contributions: SC, OG, NY and RP conceived the ideas and designed methodology; JA, RAI and ØW collected the data; SC analysed the data; SC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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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

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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 occuring 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, apha constant=0.5), S2 (low detection alpha varies with date of capture), S3 (high detection, apha constant=0.5) or S4 (low detection alpha 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 = doy, pred.values=doypred,interval = TRUE,
            plot.points = FALSE,y.label = "departure probability")
```

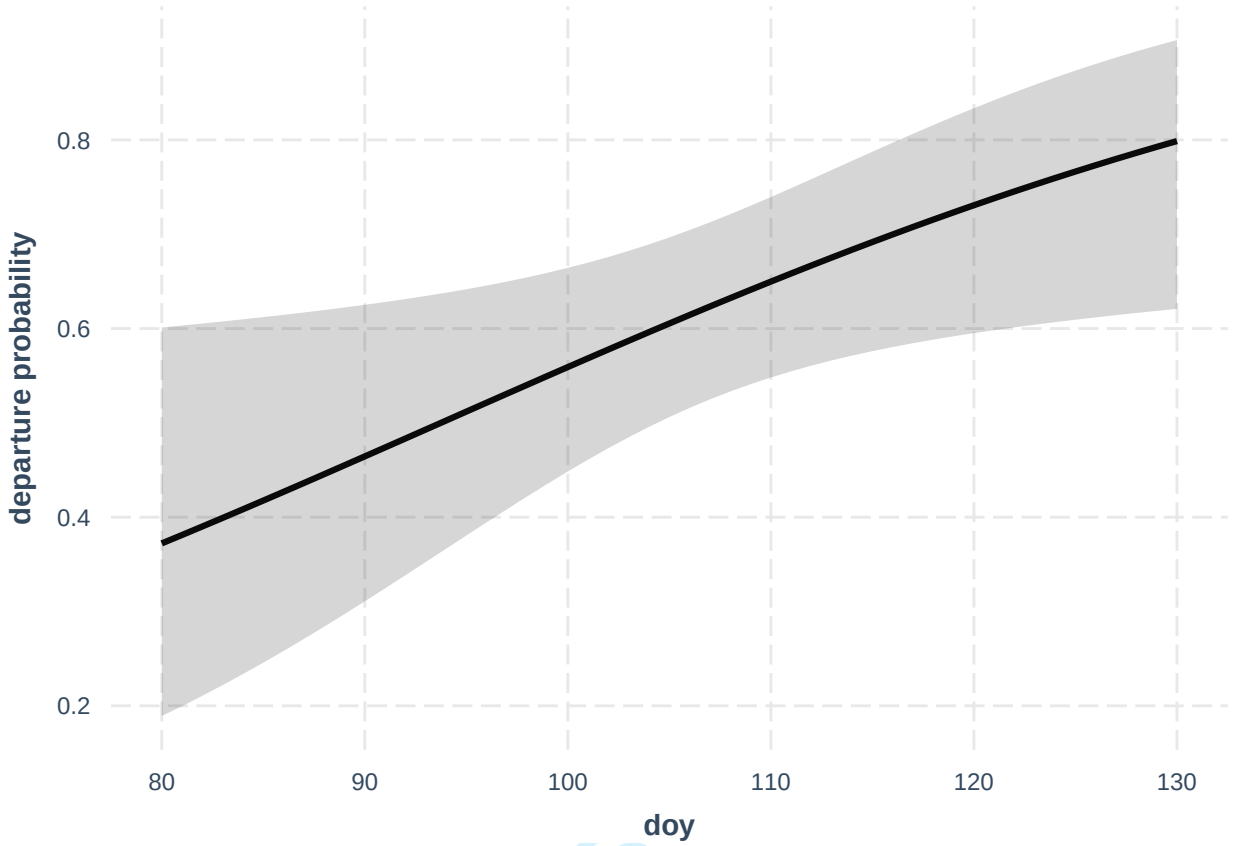


Figure S1. Departure probability of two-year old bears as a fuction of date of capture within the field season in day of the year (doy).

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
```

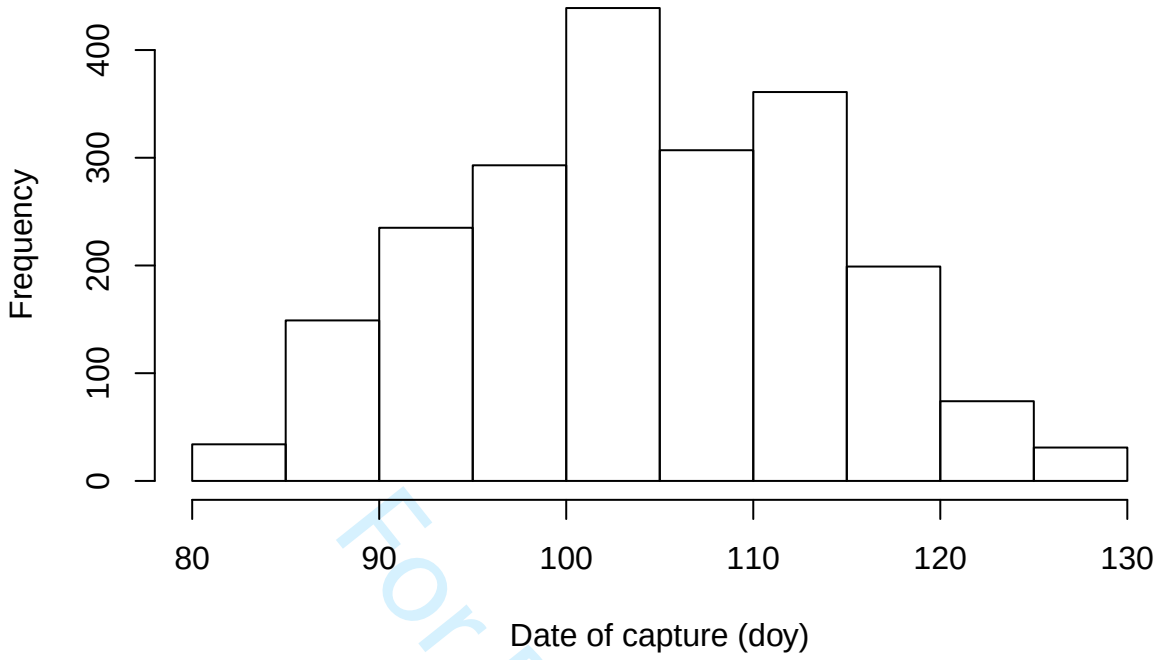


Figure S2. Histogram of te dates of capture of polar bears in Svalbard in day of the year (doy).

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])) #0.7975for 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 decribed in the methods section
```

```
    # J2  independent 2yo juvenile female
    # J3 independent 3yo juvenile female
    #SA4 independent 4yo subadult female
    #SA5 independent 5yo subadult female
    #A01 adult female caring for 1 dependent offspring of the year (age <1)
    #A02 adult female caring for 2 dependent offspring of the year (age <1)
    #A11 adult female caring for 1 dependent yearling (age 1)
    #A12 adult female caring for 2 dependent yearlings (age 1)
    #AS1 adult female successful breeder raising 1 offspring reaching independence
    #AS2  adult female successful breeder raising 2 offspring reaching independence
    #A adult female without dependent offspring
    # D dead state
n.states <- 11
all.states <- n.states + 1 # with dead state

## Define the events
# as defined in the methods section
    # non-observation code "0"
    # capture of a 2y female code "1"
    # capture of a 3y female code "2"
    # capture of a 4y female code "3"
    # capture of a 5y female code "4"
    # capture of an adult female with 1 offspring of the year (age <1) code "5"
    # capture of an adult female with 2 offspring of the year (age <1) code "6"
    # capture of an adult female with 1 yearling code "7"
    # capture of an adult female with 2 yearlings code "8"
    # capture of an adult female with 1 two-year old offspring code "9"
    # capture of an adult female with 2 two-year old offspring code "10"
    # capture of an adult female alone code "11"
n.events <- 11
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, PS11, PSI2, PSI3 involved in the state process:

```
### State transitions
# define PHI matrix gathering survival of independent juveniles, subadults and adults
temp1 <- diag(c(phi,phi,phi,phi,rep(phi,7)),nrow=all.states,ncol=n.states)
PHI <- cbind(temp1,c(1-phi,1-phi,1-phi,1-phi,rep(1-phi,7),1))

# Define PSI matrices gathering state-to-state transition probabilities, it includes:

# PSI1: litter survival, individual dependent offspring suvival and growth to next age:
PSI1 <- matrix(0,nrow=all.states,ncol=all.states + 1)
for(i in 1:3){PSI1[i,i] <- 1} # juvenile and subadults grow to next age
PSI1[4,12] <- 1 # 5a grow to sexually mature female without dependent offspring
PSI1[5,4] <- psi[1] ; PSI1[5,8] <- (1-psi[1]) #a0 offspring survives or dies
PSI1[6,4] <- psi[2] ; PSI1[6,5] <- psi[3] ; PSI1[6,8] <- psi[4]#1,both
#or any a0 offspring in a litter of 2 survive
PSI1[7,6] <- psi[5] ; PSI1[7,9] <- (1-psi[5])#a1 offspring in a litter
#of 1 survives or die
```

```
PSI1[8,6] <- psi[6] ; PSI1[8,7] <- psi[7] ;PSI1[8,9] <- psi[8]#1,both or any
#a1 offspring in a litter of 2 survive or die
for(i in 9:12){PSI1[i,i+1] <- 1} # for offspring reaching independence and females
#without dependent offspring

# PSI2: breeding probabilities:
PSI2 <- matrix(0,nrow=all.states+1,ncol=all.states+4)
for(i in 1:7){PSI2[i,i] <- 1} # here we assume that juveniles, subaduts and adults
#caring for dependent offspring are not available to breed
PSI2[8,8] <- beta[1];PSI2[8,9] <- 1-beta[1]
PSI2[9,10] <- beta[2];PSI2[9,11] <- 1-beta[2]
PSI2[10,12] <- beta[3];PSI2[10,13] <- 1-beta[3]
PSI2[11,12] <- beta[3];PSI2[11,13] <- 1-beta[3]
PSI2[12,14] <- beta[4];PSI2[12,15] <- 1-beta[4]
PSI2[13,16] <- 1 # dead state

# PSI3:litter size probabilities
#(Pr(singleton litter) = gamma, Pr(twin litter)= 1-gamma)
PSI3 <- matrix(0,nrow=all.states+4,ncol=all.states)
for(i in 1:3){PSI3[i,i+1] <- 1}
for(i in 4:7){PSI3[i,i+3] <- 1}
PSI3[8,5] <- gamma[1];PSI3[8,6] <- 1-gamma[1]
PSI3[9,11] <-1
PSI3[10,5] <- gamma[2];PSI3[10,6] <- 1-gamma[2]
PSI3[11,11] <-1
PSI3[12,5] <- gamma[3];PSI3[12,6] <- 1-gamma[3]
PSI3[13,11] <-1
PSI3[14,5] <- gamma[4];PSI3[14,6] <- 1-gamma[4]
PSI3[15,11] <-1
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:

```
# Define observation process
# step 1 : matrix E1
# it involves departure probability which is function of day of capture,
#it will be define below within the loop

# step 2 : matrix E2, involves capture probability
E2 <- matrix(0,nrow=all.states, ncol=all.events)
for(i in 1:all.states){E2[i,i] <- p} #detection probability
E2[,all.events] <- c(rep(1-p,4), rep(1-p,7),1)
```

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.

```
## Generate data
for(r in 1:nrepet){ # number of dataset generated

  marked <- matrix(0, ncol = all.states, nrow = n.occasions) # empty object to store
  #marked family units
```

```
  for(t in 1:n.occasions){
    marked[t,] <- rmultinom(1,R,prob=S0) # define states at first capture
  }
  # Below we use transition and event matrices wwtih 4-dimensions:
  # Dimension 1: state of departure
  # Dimension 2: state of arrival
  # Dimension 3: family unit
  # Dimension 4: time

  # 1. State process matrix
  totrel <- sum(marked)*(n.occasions-1)
  PSI.STATE <- array(NA, dim=c(all.states, all.states, totrel, n.occasions-1))

  for (i in 1:totrel){
    for (t in 1:(n.occasions-1)){
      PSI.STATE[,,i,t] <- PHI %*% PSI1 %*% PSI2 %*% PSI3 # transition matrix
      #is the matrix product of PHI PSI1 PSI2 and PSI3 defiend above
    } #t
  } #i

  # 2.Observation process matrix
  E <- array(NA, dim=c(all.states, all.events, totrel, n.occasions-1))

  # day of capture, sampled from polar bears capture dates
  daycapt <- matrix(sample(wcapt,size=(totrel*(n.occasions-1)),
                           replace=TRUE), nrow=totrel, ncol=n.occasions-1)

    for (i in 1:totrel){
    for (t in 1:(n.occasions-1)){

  # predict departure probability function of date of capture
  alpha <- predict(modeld,newdata=list(doy=daycapt[i,t]),type="response")

  # now define event matrix E1 using departure probability alpha
  E1 <- diag(1,nrow=all.states,ncol=all.events)
  E1[9,9    ]<- 1-alpha
  E1[9,10]<-    0
  E1[9,11]<-    alpha
  E1[10,9]<-    2*(1-alpha)*alpha
  E1[10,10]<-   1 - (2*(1-alpha)*alpha) - (alpha)^2
  E1[10,11]<-   (alpha)^2

      E[,,i,t] <- E1 %*% E2 # define E which is the matrix product of E1 and E2
    } #t
  } #i
}#r
```

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

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

```
  # Define a vector with the occasion of marking
  mark.occ <- matrix(0, ncol = dim(PSI.STATE)[1], nrow = sum(marked))
  g <- colSums(marked)
  for (s in 1:dim(PSI.STATE)[1]){
    if (g[s]==0) next  # To avoid error message if nothing to replace
    mark.occ[(cumsum(g[1:s])-g[s]+1)[s]:cumsum(g[1:s])[s],s] <-
      rep(1:n.occasions, marked[1:n.occasions,s])
  } #s
  for (i in 1:sum(marked)){
    for (s in 1:dim(PSI.STATE)[1]){
      if (mark.occ[i,s]==0) next
      first <- mark.occ[i,s]
      CH[i,first] <- s
      CH.TRUE[i,first] <- s
    } #s
    for (t in (first+1):n.occasions){
      # Multinomial trials for state transitions
      if (first==n.occasions) next
      state <- which(rmultinom(1, 1, PSI.STATE[CH.TRUE[i,t-1],,i,t-1])==1)
      CH.TRUE[i,t] <- state
      # Multinomial trials for observation process
      event <- which(rmultinom(1, 1, E[CH.TRUE[i,t],,i,t-1])==1)
      CH[i,t] <- event
      dayC[i,t] <- daycapt[i,t-1]
    } #t
  } #i
  # Replace the NA and the highest state number (dead) in the file by 0
  CH[is.na(CH)] <- 0
  CH[CH==dim(PSI.STATE)[1]] <- 0
  CH[CH==unobservable] <- 0
  id <- numeric(0)
  for (i in 1:dim(CH)[1]){
    z <- min(which(CH[i,]!=0))
    ifelse(z==dim(CH)[2], id <- c(id,i), id <- c(id))
  }
  return(list(CH=CH[-id,], CH.TRUE=CH.TRUE[-id,],dayC=dayC[-id,]))
  # CH: capture histories to be used
  # CH.TRUE: capture histories with perfect observation
  # dayC: date of capture
}
```

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

```
# Execute function
sim <- simul.ms(PSI.STATE, E, marked)
CH <- sim$CH  # family units CR histories
init <- sim$CH.TRUE # real state matrix used as initial values for jags model
daycapt <- sim$dayC # info on date of capture
# save files
write.table(CH,paste("simCH",r,"_p",p,"_T",n.occasions,".txt",
                     sep=""),row.names=F, col.names=F, sep =" ")
write.table(init,paste("siminit",r,"_p",p,"_T",n.occasions,".txt",
                       sep=""),row.names=F, col.names=F, sep =" ")
```

```
  write.table(daycapt,paste("simdaycapt",r,"_p",p,"_T",n.occasions,".txt",sep=""),
              row.names=F, col.names=F, sep =" ")
}
```

Fit the model to simulated data

First, load the required package:

```
# Load packages
library(jagsUI)
```

```
## Loading required package: lattice
```

```
##
## Attaching package: 'jagsUI'
```

```
## The following object is masked from 'package:utils':
##
##     View
```

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

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

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

filename <- c("glmdeparture_alphaconstant05.Rdata","glm_departure_date.Rdata",
              "glmdeparture_alphaconstant05.Rdata","glm_departure_date.Rdata")
fileS <- filename[S]
load(file=paste(fileS))

n.occasions =15 # number of sampling occasions
nrepet = 100 # number of simulated dataset (repetitions)
```

Sink the jags model :

```
# JAGS MODEL
sink("Multieventmodel_Fit_simul.txt")
cat("

model {
  # Probabilities of events given states and states given states

  # vector of initial states
  S0[1] <- prop[1] / (1 + sum(prop[1:10])) # prob. of being in initial state J2
  S0[2] <- prop[2] / (1 + sum(prop[1:10])) # prob. of being in initial state J3
  S0[3] <- prop[3] / (1 + sum(prop[1:10])) # prob. of being in initial state SA4
  S0[4] <- prop[4] / (1 + sum(prop[1:10])) # prob. of being in initial state SA5
  S0[5] <- prop[5] / (1 + sum(prop[1:10])) # prob. of being in initial state A01
```

```
S0[6] <- prop[6] / (1 + sum(prop[1:10])) # prob. of being in initial state A02
S0[7] <- prop[7] / (1 + sum(prop[1:10])) # prob. of being in initial state A11
S0[8] <- prop[8] / (1 + sum(prop[1:10])) # prob. of being in initial state A12
S0[9] <- prop[9] / (1 + sum(prop[1:10])) # prob. of being in initial state AS1
S0[10] <- prop[10] / (1 + sum(prop[1:10])) # prob. of being in initial state AS2
S0[11] <- 1 / (1 + sum(prop[1:10])) # prob. of being in initial state A-
S0[12] <- 0 # prob. of being in initial state dead

# State process: define probabilities of S(t+1) given S(t)
# define PHI matrix gathering survival of independent juveniles, subadults and adults
PHI   [   1   ,   1   ]<- phi
PHI   [   1   ,   2   ]<- 0
PHI   [   1   ,   3   ]<- 0
PHI   [   1   ,   4   ]<- 0
PHI   [   1   ,   5   ]<- 0
PHI   [   1   ,   6   ]<- 0
PHI   [   1   ,   7   ]<- 0
PHI   [   1   ,   8   ]<- 0
PHI   [   1   ,   9   ]<- 0
PHI   [   1   ,   10  ]<- 0
PHI   [   1   ,   11  ]<- 0
PHI   [   1   ,   12  ]<- 1-phi

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

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

PHI   [   4   ,   1   ]<- 0
PHI   [   4   ,   2   ]<- 0
PHI   [   4   ,   3   ]<- 0
PHI   [   4   ,   4   ]<- phi
```

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

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

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

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

PHI   [   8   ,   1   ]<- 0
PHI   [   8   ,   2   ]<- 0
PHI   [   8   ,   3   ]<- 0
PHI   [   8   ,   4   ]<- 0
PHI   [   8   ,   5   ]<- 0
```

```
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
```

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

# Define PSI matrices gathering state-to-state transition probabilities, it includes:
# PSI1: offspring survival and growth to next age, proba of sexual maturation:
PSI1  [   1   ,   1   ]<- 1
PSI1  [   1   ,   2   ]<- 0
PSI1  [   1   ,   3   ]<- 0
PSI1  [   1   ,   4   ]<- 0
PSI1  [   1   ,   5   ]<- 0
PSI1  [   1   ,   6   ]<- 0
PSI1  [   1   ,   7   ]<- 0
PSI1  [   1   ,   8   ]<- 0
PSI1  [   1   ,   9   ]<- 0
PSI1  [   1   ,   10  ]<- 0
PSI1  [   1   ,   11  ]<- 0
PSI1  [   1   ,   12  ]<- 0
PSI1  [   1   ,   13  ]<- 0

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

PSI1  [   3   ,   1   ]<- 0
PSI1  [   3   ,   2   ]<- 0
PSI1  [   3   ,   3   ]<- 1-kappa # first repro at age 6
PSI1  [   3   ,   4   ]<- 0
PSI1  [   3   ,   5   ]<- 0
PSI1  [   3   ,   6   ]<- 0
PSI1  [   3   ,   7   ]<- 0
PSI1  [   3   ,   8   ]<- 0
PSI1  [   3   ,   9   ]<- 0
PSI1  [   3   ,   10  ]<- 0
PSI1  [   3   ,   11  ]<- 0
PSI1  [   3   ,   12  ]<- kappa # first repro at age 5
PSI1  [   3   ,   13  ]<- 0

PSI1  [   4   ,   1   ]<- 0
PSI1  [   4   ,   2   ]<- 0
```

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

PSI1 [ 5 , 1 ]<- 0
PSI1 [ 5 , 2 ]<- 0
PSI1 [ 5 , 3 ]<- 0
PSI1 [ 5 , 4 ]<- s[1] # litter of 1, cub's survival
PSI1 [ 5 , 5 ]<- 0
PSI1 [ 5 , 6 ]<- 0
PSI1 [ 5 , 7 ]<- 0
PSI1 [ 5 , 8 ]<- 1-s[1] #litter of 1, cub's death
PSI1 [ 5 , 9 ]<- 0
PSI1 [ 5 , 10 ]<- 0
PSI1 [ 5 , 11 ]<- 0
PSI1 [ 5 , 12 ]<- 0
PSI1 [ 5 , 13 ]<- 0

PSI1 [ 6 , 1 ]<- 0
PSI1 [ 6 , 2 ]<- 0
PSI1 [ 6 , 3 ]<- 0
PSI1 [ 6 , 4 ]<- 2*s[2]*(1-s[2]) # litter of 2, 1 cub survives
PSI1 [ 6 , 5 ]<- s[2]^2 # litter of 2, both cubs survive
PSI1 [ 6 , 6 ]<- 0
PSI1 [ 6 , 7 ]<- 0
PSI1 [ 6 , 8 ]<- (1- s[2]^2 -2*s[2]*(1-s[2])) #litter of 2, both cubs die
PSI1 [ 6 , 9 ]<- 0
PSI1 [ 6 , 10 ]<- 0
PSI1 [ 6 , 11 ]<- 0
PSI1 [ 6 , 12 ]<- 0
PSI1 [ 6 , 13 ]<- 0

PSI1 [ 7 , 1 ]<- 0
PSI1 [ 7 , 2 ]<- 0
PSI1 [ 7 , 3 ]<- 0
PSI1 [ 7 , 4 ]<- 0
PSI1 [ 7 , 5 ]<- 0
PSI1 [ 7 , 6 ]<- s[3] # litter of 1, yearling's survival
PSI1 [ 7 , 7 ]<- 0
PSI1 [ 7 , 8 ]<- 0
PSI1 [ 7 , 9 ]<- (1-s[3] ) # litter of 1, yearling's death
PSI1 [ 7 , 10 ]<- 0
PSI1 [ 7 , 11 ]<- 0
PSI1 [ 7 , 12 ]<- 0
PSI1 [ 7 , 13 ]<- 0
```

```
PSI1 [ 8 , 1 ]<- 0
PSI1 [ 8 , 2 ]<- 0
PSI1 [ 8 , 3 ]<- 0
PSI1 [ 8 , 4 ]<- 0
PSI1 [ 8 , 5 ]<- 0
PSI1 [ 8 , 6 ]<- 2*s[4]*(1-s[4]) # litter of 2, 1 yearling survives
PSI1 [ 8 , 7 ]<- s[4]^2 # litter of 2, both yearlings survive
PSI1 [ 8 , 8 ]<- 0
PSI1 [ 8 , 9 ]<- (1- s[4]^2 -2*s[4]*(1-s[4])) #litter of 2, both yearlings die
PSI1 [ 8 , 10 ]<- 0
PSI1 [ 8 , 11 ]<- 0
PSI1 [ 8 , 12 ]<- 0
PSI1 [ 8 , 13 ]<- 0

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

PSI1 [ 10 , 1 ]<- 0
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
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
```

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

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

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

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

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[4]
PSI2 [ 12 , 15 ]<- 1-beta[4]
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
PSI3 [ 1 , 2 ]<- 1
PSI3 [ 1 , 3 ]<- 0
PSI3 [ 1 , 4 ]<- 0
PSI3 [ 1 , 5 ]<- 0
PSI3 [ 1 , 6 ]<- 0
PSI3 [ 1 , 7 ]<- 0
PSI3 [ 1 , 8 ]<- 0
PSI3 [ 1 , 9 ]<- 0
PSI3 [ 1 , 10 ]<- 0
PSI3 [ 1 , 11 ]<- 0
PSI3 [ 1 , 12 ]<- 0

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

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

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

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

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

PSI3 [ 11 , 1 ]<- 0
PSI3 [ 11 , 2 ]<- 0
```

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

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

PSI3 [ 13 , 1 ]<- 0
PSI3 [ 13 , 2 ]<- 0
PSI3 [ 13 , 3 ]<- 0
PSI3 [ 13 , 4 ]<- 0
PSI3 [ 13 , 5 ]<- 0
PSI3 [ 13 , 6 ]<- 0
PSI3 [ 13 , 7 ]<- 0
PSI3 [ 13 , 8 ]<- 0
PSI3 [ 13 , 9 ]<- 0
PSI3 [ 13 , 10 ]<- 0
PSI3 [ 13 , 11 ]<- 1
PSI3 [ 13 , 12 ]<- 0

PSI3 [ 14 , 1 ]<- 0
PSI3 [ 14 , 2 ]<- 0
PSI3 [ 14 , 3 ]<- 0
PSI3 [ 14 , 4 ]<- 0
PSI3 [ 14 , 5 ]<- gamma[4]
PSI3 [ 14 , 6 ]<- 1-gamma[4]
PSI3 [ 14 , 7 ]<- 0
PSI3 [ 14 , 8 ]<- 0
PSI3 [ 14 , 9 ]<- 0
PSI3 [ 14 , 10 ]<- 0
PSI3 [ 14 , 11 ]<- 0
PSI3 [ 14 , 12 ]<- 0

PSI3 [ 15 , 1 ]<- 0
PSI3 [ 15 , 2 ]<- 0
PSI3 [ 15 , 3 ]<- 0
```

```
PSI3  [   15  ,   4   ]<- 0
PSI3  [   15  ,   5   ]<- 0
PSI3  [   15  ,   6   ]<- 0
PSI3  [   15  ,   7   ]<- 0
PSI3  [   15  ,   8   ]<- 0
PSI3  [   15  ,   9   ]<- 0
PSI3  [   15  ,   10  ]<- 0
PSI3  [   15  ,   11  ]<- 1
PSI3  [   15  ,   12  ]<- 0

PSI3  [   16  ,   1   ]<- 0
PSI3  [   16  ,   2   ]<- 0
PSI3  [   16  ,   3   ]<- 0
PSI3  [   16  ,   4   ]<- 0
PSI3  [   16  ,   5   ]<- 0
PSI3  [   16  ,   6   ]<- 0
PSI3  [   16  ,   7   ]<- 0
PSI3  [   16  ,   8   ]<- 0
PSI3  [   16  ,   9   ]<- 0
PSI3  [   16  ,   10  ]<- 0
PSI3  [   16  ,   11  ]<- 0
PSI3  [   16  ,   12  ]<- 1

# Matrix product for state-to-state transitions S
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]


## Observation process: Define probabilities of E(t) given S(t).

#for initial capture, conditional on first capture
E0    [   1   ,   1   ]<- 0
E0    [   1   ,   2   ]<- 1
E0    [   1   ,   3   ]<- 0
E0    [   1   ,   4   ]<- 0
E0    [   1   ,   5   ]<- 0
E0    [   1   ,   6   ]<- 0
E0    [   1   ,   7   ]<- 0
E0    [   1   ,   8   ]<- 0
E0    [   1   ,   9   ]<- 0
E0    [   1   ,   10  ]<- 0
E0    [   1   ,   11  ]<- 0
E0    [   1   ,   12  ]<- 0

E0    [   2   ,   1   ]<- 0
E0    [   2   ,   2   ]<- 0
E0    [   2   ,   3   ]<- 1
E0    [   2   ,   4   ]<- 0
E0    [   2   ,   5   ]<- 0
E0    [   2   ,   6   ]<- 0
E0    [   2   ,   7   ]<- 0
E0    [   2   ,   8   ]<- 0
E0    [   2   ,   9   ]<- 0
E0    [   2   ,   10  ]<- 0
```

```
E0    [   2   ,   11  ]<- 0
E0    [   2   ,   12  ]<- 0

E0    [   3   ,   1   ]<- 0
E0    [   3   ,   2   ]<- 0
E0    [   3   ,   3   ]<- 0
E0    [   3   ,   4   ]<- 1
E0    [   3   ,   5   ]<- 0
E0    [   3   ,   6   ]<- 0
E0    [   3   ,   7   ]<- 0
E0    [   3   ,   8   ]<- 0
E0    [   3   ,   9   ]<- 0
E0    [   3   ,   10  ]<- 0
E0    [   3   ,   11  ]<- 0
E0    [   3   ,   12  ]<- 0

E0    [   4   ,   1   ]<- 0
E0    [   4   ,   2   ]<- 0
E0    [   4   ,   3   ]<- 0
E0    [   4   ,   4   ]<- 0
E0    [   4   ,   5   ]<- 1
E0    [   4   ,   6   ]<- 0
E0    [   4   ,   7   ]<- 0
E0    [   4   ,   8   ]<- 0
E0    [   4   ,   9   ]<- 0
E0    [   4   ,   10  ]<- 0
E0    [   4   ,   11  ]<- 0
E0    [   4   ,   12  ]<- 0

E0    [   5   ,   1   ]<- 0
E0    [   5   ,   2   ]<- 0
E0    [   5   ,   3   ]<- 0
E0    [   5   ,   4   ]<- 0
E0    [   5   ,   5   ]<- 0
E0    [   5   ,   6   ]<- 1
E0    [   5   ,   7   ]<- 0
E0    [   5   ,   8   ]<- 0
E0    [   5   ,   9   ]<- 0
E0    [   5   ,   10  ]<- 0
E0    [   5   ,   11  ]<- 0
E0    [   5   ,   12  ]<- 0

E0    [   6   ,   1   ]<- 0
E0    [   6   ,   2   ]<- 0
E0    [   6   ,   3   ]<- 0
E0    [   6   ,   4   ]<- 0
E0    [   6   ,   5   ]<- 0
E0    [   6   ,   6   ]<- 0
E0    [   6   ,   7   ]<- 1
E0    [   6   ,   8   ]<- 0
E0    [   6   ,   9   ]<- 0
E0    [   6   ,   10  ]<- 0
E0    [   6   ,   11  ]<- 0
```

```
E0    [   6   ,   12  ]<- 0

E0    [   7   ,   1   ]<- 0
E0    [   7   ,   2   ]<- 0
E0    [   7   ,   3   ]<- 0
E0    [   7   ,   4   ]<- 0
E0    [   7   ,   5   ]<- 0
E0    [   7   ,   6   ]<- 0
E0    [   7   ,   7   ]<- 0
E0    [   7   ,   8   ]<- 1
E0    [   7   ,   9   ]<- 0
E0    [   7   ,   10  ]<- 0
E0    [   7   ,   11  ]<- 0
E0    [   7   ,   12  ]<- 0

E0    [   8   ,   1   ]<- 0
E0    [   8   ,   2   ]<- 0
E0    [   8   ,   3   ]<- 0
E0    [   8   ,   4   ]<- 0
E0    [   8   ,   5   ]<- 0
E0    [   8   ,   6   ]<- 0
E0    [   8   ,   7   ]<- 0
E0    [   8   ,   8   ]<- 0
E0    [   8   ,   9   ]<- 1
E0    [   8   ,   10  ]<- 0
E0    [   8   ,   11  ]<- 0
E0    [   8   ,   12  ]<- 0

E0    [   9   ,   1   ]<- 0
E0    [   9   ,   2   ]<- 0
E0    [   9   ,   3   ]<- 0
E0    [   9   ,   4   ]<- 0
E0    [   9   ,   5   ]<- 0
E0    [   9   ,   6   ]<- 0
E0    [   9   ,   7   ]<- 0
E0    [   9   ,   8   ]<- 0
E0    [   9   ,   9   ]<- 0
E0    [   9   ,   10  ]<- 1
E0    [   9   ,   11  ]<- 0
E0    [   9   ,   12  ]<- 0

E0    [   10  ,   1   ]<- 0
E0    [   10  ,   2   ]<- 0
E0    [   10  ,   3   ]<- 0
E0    [   10  ,   4   ]<- 0
E0    [   10  ,   5   ]<- 0
E0    [   10  ,   6   ]<- 0
E0    [   10  ,   7   ]<- 0
E0    [   10  ,   8   ]<- 0
E0    [   10  ,   9   ]<- 0
E0    [   10  ,   10  ]<- 0
E0    [   10  ,   11  ]<- 1
E0    [   10  ,   12  ]<- 0
```

```
E0    [   11  ,   1   ]<- 0
E0    [   11  ,   2   ]<- 0
E0    [   11  ,   3   ]<- 0
E0    [   11  ,   4   ]<- 0
E0    [   11  ,   5   ]<- 0
E0    [   11  ,   6   ]<- 0
E0    [   11  ,   7   ]<- 0
E0    [   11  ,   8   ]<- 0
E0    [   11  ,   9   ]<- 0
E0    [   11  ,   10  ]<- 0
E0    [   11  ,   11  ]<- 0
E0    [   11  ,   12  ]<- 1

E0    [   12  ,   1   ]<- 1
E0    [   12  ,   2   ]<- 0
E0    [   12  ,   3   ]<- 0
E0    [   12  ,   4   ]<- 0
E0    [   12  ,   5   ]<- 0
E0    [   12  ,   6   ]<- 0
E0    [   12  ,   7   ]<- 0
E0    [   12  ,   8   ]<- 0
E0    [   12  ,   9   ]<- 0
E0    [   12  ,   10  ]<- 0
E0    [   12  ,   11  ]<- 0
E0    [   12  ,   12  ]<- 0

# departure probability of a2 offspring
for(i in 1:N){
  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

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
```

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

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

      E1    [   9   ,   1   ,i,t]<- 0
      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
      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
```

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

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

      E2    [   5   ,   1,i,t]<-    1 -p
      E2    [   5   ,   2,i,t]<-    0
      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
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
```

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

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

    # Matrix product for offspring independence and recapture
    E[1:12,1:12,i,t] <- E1[1:12,1:12,i,t] %*% E2[1:12,1:12,i,t]
  }
}

## LIKELIHOOD

for (i in 1:N)  # for each individual
{
  # The estimated probabilities of initial states S0 are the proportions in each state
  #at first capture occasion
  alive[i,First[i]] ~ dcat(S0[1:12])
  mydata[i,First[i]] ~ dcat(E0[alive[i,First[i]],1:12])

  for (j in (First[i]+1):Years)
  {

    ## STATE EQUATIONS ##
    # draw S(t) given S(t-1)
    alive[i,j] ~ dcat(S[alive[i,j-1],1:12])

    ## OBSERVATION EQUATIONS ##
    # draw events E(t) given states S(t)

    mydata[i,j] ~ dcat(E[alive[i,j],1:12,i,j-1])

  }
}
```

```
  ## PRIORS
  # capture probability
  p ~ dunif(0,1)

  # juveniles, subadults and adult survival
  phi ~ dunif(0,1)

  # initial states
  for (i in 1:10){ log(prop[i]) <- theta[i]
  theta[i] ~ dnorm(0,1)}

  # offspring survival
  # litter survival n=2 offspring
  l02 <- 1 -(1- s[2]^2 -2*s[2]*(1-s[2]))
  l12 <- 1- (1- s[4]^2 -2*s[4]*(1-s[4]))
  # indiviual offspring survival
  for(i in 1:2){s[i]~ dunif(0,1)}
    # Set constraints
    for(u in 1:2){  X[u] ~ dunif(0,1)} # with X ~ U[0,1] then  (a + ( b - a ) * X)
    #so that s[1] < s[3] <phi[1] for litter of 1
    s[3] <- s[1] + (phi[1] - s[1]) * X[1]
    # and s[2] < s[4] < phi[1] for litters of 2
    s[4] <- s[2] + (phi[1] - s[2]) * X[2]

  # Breeding probability
  kappa ~ dunif(0,1)
  for(i in 1:4){beta[i]~ dunif(0,1)}

  # Litter size probability
  for(i in 1:4){gamma[i]~ dunif(0,1)}

} # end model

    ",fill=TRUE)
sink()
#######
#######
```

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 :

```
RES <- list()

for(r in 1:100){

nameCH <- paste(repname,"/simCH",r,"_p",p,"_T",n.occasions,".txt",sep="")
# load capture histories
data <- read.table(paste(nameCH),sep=" ",header=FALSE)
# initial values for state matrix
nameINIT <- paste(repname,"/siminit",r,"_p",p,"_T",n.occasions,".txt",sep="")
initmat <- read.table(paste(nameINIT),sep="")
```

```
# date of capture
nameDAY <- paste(repname,"/simdaycapt",r,"_p",p,"_T",n.occasions,".txt",sep="")
daycapt <- read.table(paste(nameDAY),sep="")

data <- data.matrix(data)
alive1 <- data.matrix(initmat)
head(data)
N <- dim(data)[1]
Years <- dim(data)[2]

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

# Predict departure probability function of date of capture
alpha = matrix(0,nrow=N,ncol=Years)
  for(i in 1:N){
    for(j in (First[i]+1):Years){
    alpha[i,j] <- predict(modeld,newdata=list(doy=daycapt[i,j]),type="response")
  }
}

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

# Initial values
init1 <- list(theta=rnorm(10, mean = 0, sd = 1), alive=alive1) #
inits <- list(init1)

# Parameters monitored
params <- c("phi","kappa","s","l02","l12","beta","gamma","p","S0")

# Call JAGS from R to fit the model
out <- jags(data=mydatax,inits=inits, parameters.to.save=params,
            model.file = 'Multieventmodel_Fit_simul.txt',n.chains=1,
            n.iter=10000,n.burnin=4000)

RES[[r]] <- out # store results
print(paste(r))
}
save(RES,file=paste('RES',n.occasions,'p',p,'.RData',sep="")) # save results
```

Post process simulation results

Load and plot the results:

```
# load results of the simulations
capture <- c(0.25,0.25,0.5,0.5)
filenames <- c("S1RESp0.25alpha05.RData","S2RESp0.25alphaDate.RData",
               "S3RESp0.5alpha05.RData","S4RESp0.5alphaDate.RData")

EST <- CI1 <- CI2 <- simres <- biasall <- rMSEall <- list()
```

```
for(S in 1:4){
  p = capture[S]

load(paste(filenames[S]))

# parameters used to simulate the data in same order
# phi, kappa, s1,s2,s3,s4,beta1,beta2,beta3,beta4,gamma1,gamma2,gamma3,gamma4,p
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)))
nparam <- length(theta)
nrepet <- length(RES)

# Calculate summary of posterior distribution estimated for all parameters
#(mean, and 95% credible interval) and calculate bias and root mean-square-errors :
  est <- ci1 <- ci2 <- BIAS <- pBIAS <- rMSE <- matrix(NA,nrow=length(RES),ncol=nparam)
  for(i in 1:nrepet){
    #get estimates
    est[i,] <- unlist(RES[[i]]$mean[c(1,2,3,6,7,8)])
    ci1[i,] <- unlist(RES[[i]]$q2.5[c(1,2,3,6,7,8)])
    ci2[i,] <- unlist(RES[[i]]$q97.5[c(1,2,3,6,7,8)])
    # absolute bias, and root mean square error
    BIAS[i,] <- (est[i,] - theta)
    rMSE[i,] <- sqrt( (est[i,] - theta)^2 )
  }#nrepet

# Plot the results
#    pdf(width=9,height=6,pointsize=4,file="test.pdf",paper="a4r")
    par(mfrow=c(3,5))
    xlabs <- 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))

    for(j in 1:nparam){
      plot(est[,j], 1:nrepet, ylab='',xlim=c(0,1),las=TRUE,cex=1,type="n",
           main=xlabs[j],xlab=paste("bias = ",round(mean(BIAS[,j]),3),
                                    "; rmse =",round(mean(rMSE[,j]),2), sep=""))
      segments(ci1[,j], 1:100,ci2[,j], 1:nrepet,col="grey70",lwd=0.5)
   points(est[,j], 1:nrepet,col="black",cex=0.4,pch=16,)
   abline(v=theta[j], lty=2, col='red')
   }
#    dev.off()

  #store results
  EST[[S]] <- est
  CI1[[S]] <- ci1
  CI2[[S]] <- ci2
  simres[[S]] <- RES
  biasall[[S]] <- BIAS
  rMSEall[[S]] <- rMSE
```

```
} #S
```

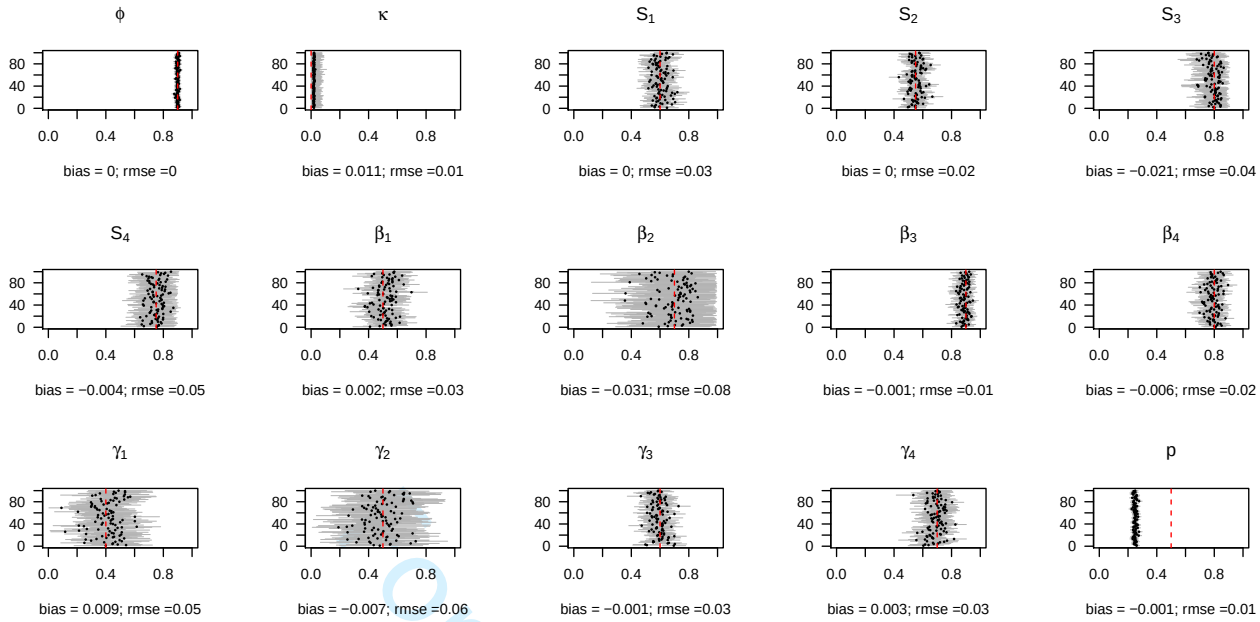


Figure S3. Performance of the model on simulated data with low detection with constant departure (scenario S1). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given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

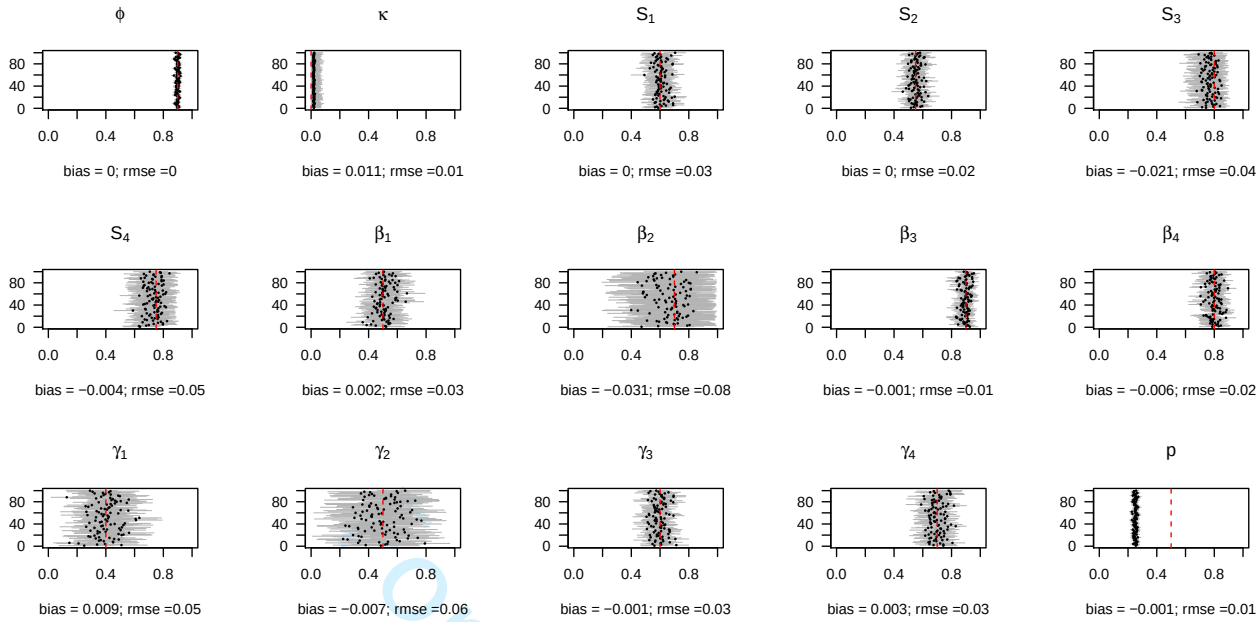


Figure S4. Performance of the model on simulated data with low detection with departure varying with date of capture (scenario S2). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the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

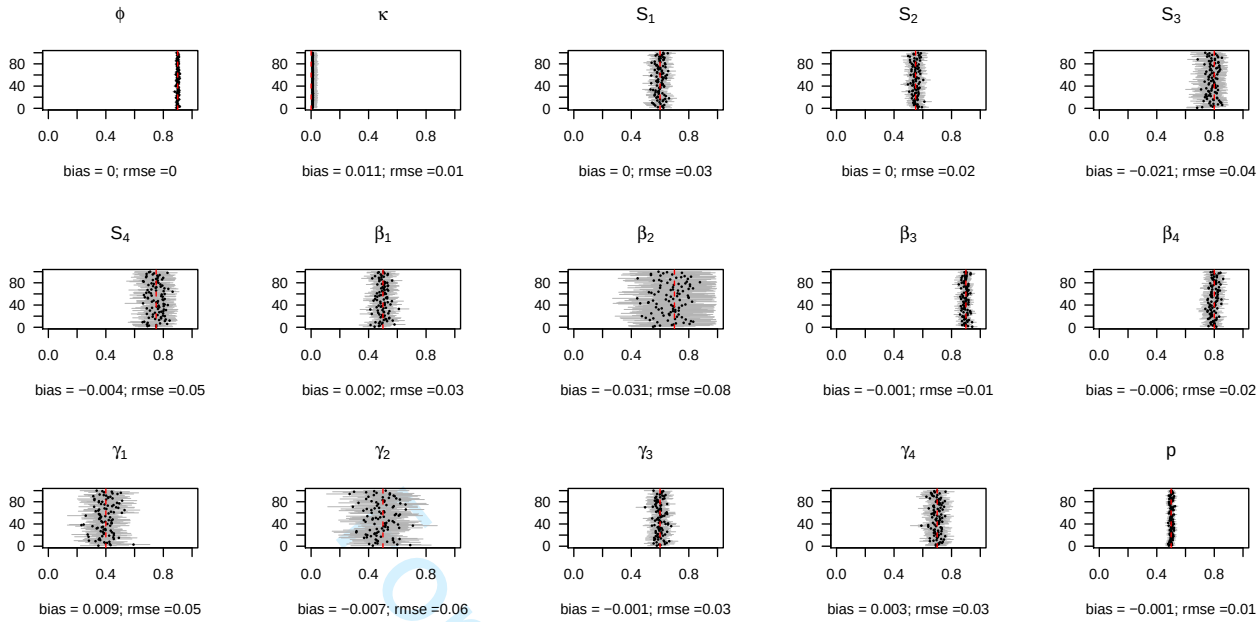


Figure S5. Performance of the model on simulated data with high detection with constant departure (scenario S3). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given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

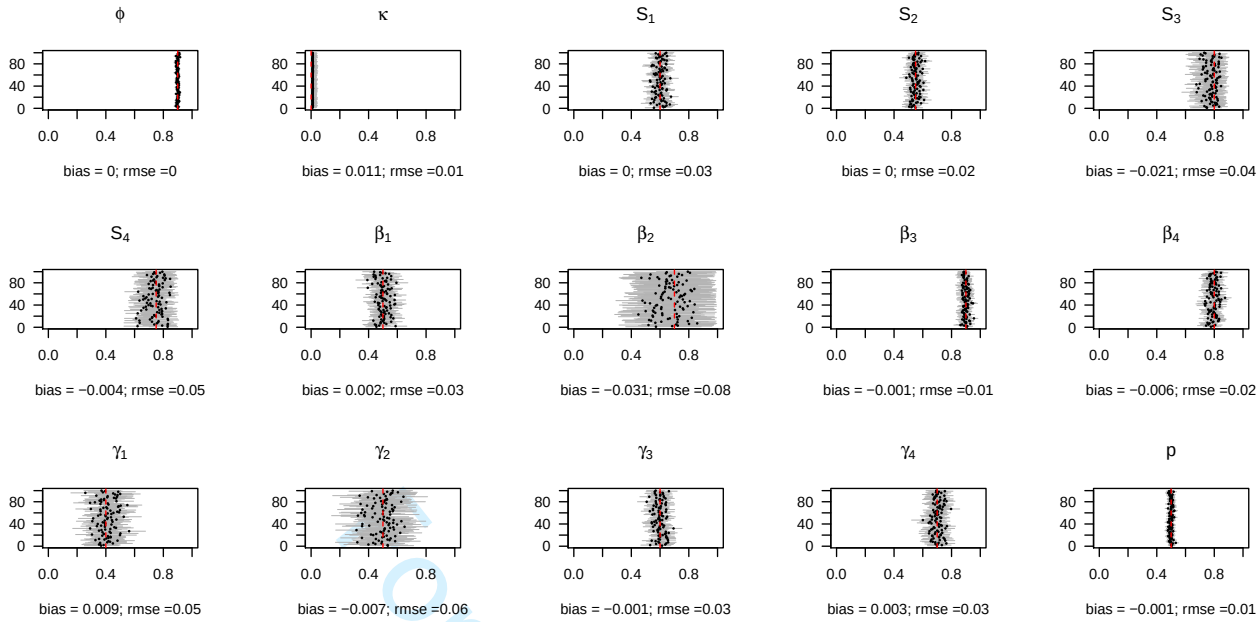


Figure S6. Performance of the model on simulated data with high detection with departure varying with date of capture (scenario S4). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the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

```
## S3   0  0.01 0.00    0 -0.01  0.00    0.00   -0.03    0.00    0.00     0.00
## S4   0  0.01 0.00    0 -0.02  0.00    0.00   -0.03    0.00   -0.01     0.01
##    gamma[2] gamma[3] gamma[4] p
## S1    -0.01    -0.01    -0.01 0
## S2     0.00     0.00     0.00 0
## S3    -0.01     0.00     0.00 0
## S4    -0.01     0.00     0.00 0
```

```
tabR
```

```
##     phi kappa S[1] S[2] S[3] S[4] beta[1] beta[2] beta[3] beta[4] gamma[1]
## S1 0.01  0.02 0.04 0.03 0.04 0.04    0.05    0.09    0.02    0.03     0.08
## S2 0.01  0.02 0.03 0.03 0.04 0.04    0.04    0.09    0.02    0.03     0.07
## S3 0.00  0.01 0.02 0.02 0.03 0.04    0.03    0.08    0.02    0.02     0.05
## S4 0.00  0.01 0.03 0.02 0.04 0.05    0.03    0.08    0.01    0.02     0.05
##    gamma[2] gamma[3] gamma[4]    p
## S1     0.09     0.04     0.04 0.01
## S2     0.11     0.04     0.04 0.01
## S3     0.07     0.02     0.02 0.01
## S4     0.06     0.03     0.03 0.01
```

```
#write.csv(tabB,file = "RES_biasperparam.csv")
#write.csv(tabR,file = "RES_rmseperparam.csv")
```

Bibliogrpahy

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-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:

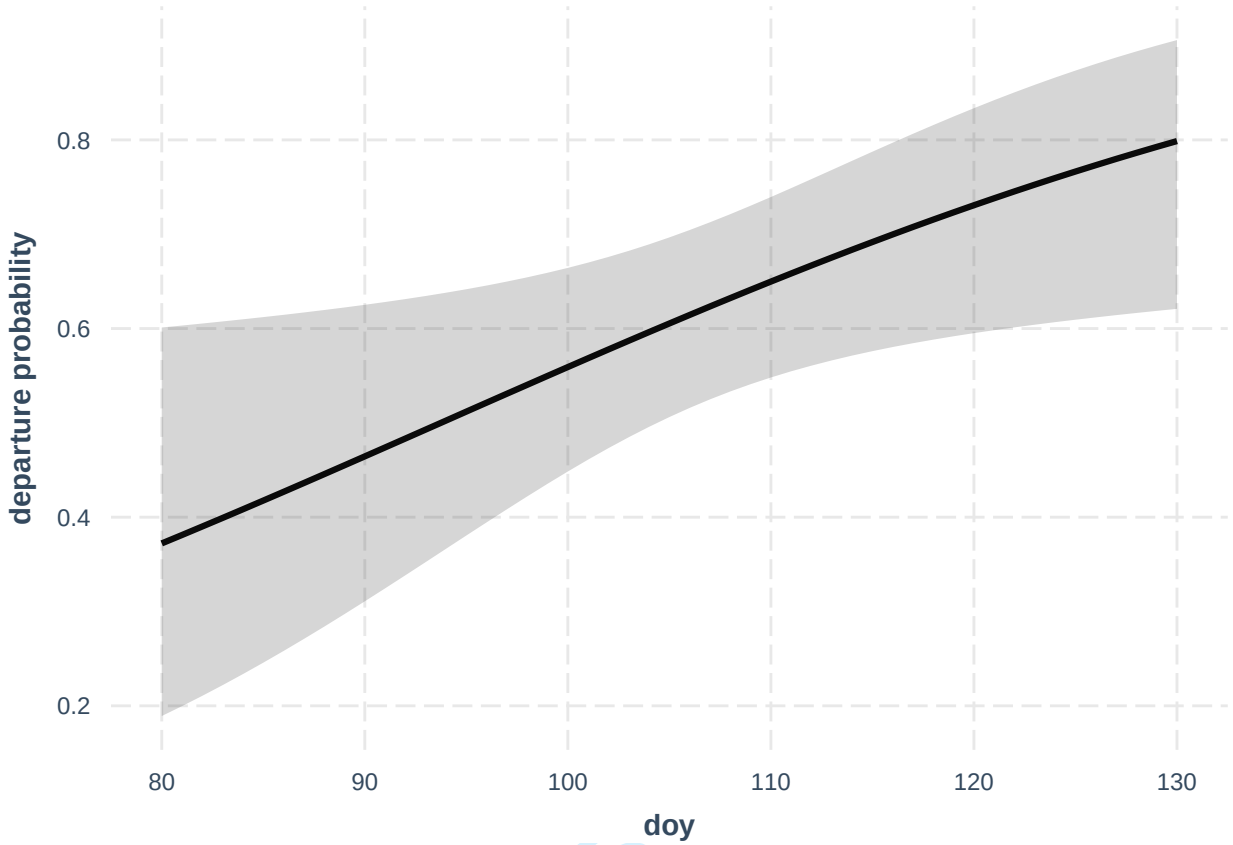
```
nty <- dim(dataweaning)[[1]] # number of two-year old bears captured
status <- dataweaning$status #status of two-year old bears at the time of capture :
#1 alone (already departed from family unit),
#0 still together with mother (not yet departed from family unit)
doy <- dataweaning$daysinseason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

```
init1 <- list(theta=rnorm(10, mean = 0, sd = 1),alive=alive1)
init2 <- list(theta=rnorm(10, mean = 0, sd = 1),alive=alive1)
inits <- list(init1,init2)
```

Create a list with names of the parameters to monitor:

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

Load the script of the jags model :

```
# JAGS MODEL
sink("Multieventmodel_FitresidentBeardata.txt")
cat("

model {
  # Probabilities of events given states and states given states

  # vector of initial states
  S0[1] <- prop[1] / (1 + sum(prop[1:10])) # prob. of being in initial state J2
  S0[2] <- prop[2] / (1 + sum(prop[1:10])) # prob. of being in initial state J3
  S0[3] <- prop[3] / (1 + sum(prop[1:10])) # prob. of being in initial state SA4
  S0[4] <- prop[4] / (1 + sum(prop[1:10])) # prob. of being in initial state SA5
  S0[5] <- prop[5] / (1 + sum(prop[1:10])) # prob. of being in initial state A01
  S0[6] <- prop[6] / (1 + sum(prop[1:10])) # prob. of being in initial state A02
  S0[7] <- prop[7] / (1 + sum(prop[1:10])) # prob. of being in initial state A11
  S0[8] <- prop[8] / (1 + sum(prop[1:10])) # prob. of being in initial state A12
  S0[9] <- prop[9] / (1 + sum(prop[1:10])) # prob. of being in initial state AS1
  S0[10] <- prop[10] / (1 + sum(prop[1:10])) # prob. of being in initial state AS2
  S0[11] <- 1 / (1 + sum(prop[1:10])) # prob. of being in initial state A-
  S0[12] <- 0 # prob. of being in initial state dead

  # State process: define probabilities of S(t+1) given S(t)
  # define PHI matrix gathering survival of independent juveniles, subadults and adults
  PHI   [   1   ,   1   ]<- phi[1]
  PHI   [   1   ,   2   ]<- 0
  PHI   [   1   ,   3   ]<- 0
  PHI   [   1   ,   4   ]<- 0
  PHI   [   1   ,   5   ]<- 0
  PHI   [   1   ,   6   ]<- 0
  PHI   [   1   ,   7   ]<- 0
  PHI   [   1   ,   8   ]<- 0
  PHI   [   1   ,   9   ]<- 0
  PHI   [   1   ,   10  ]<- 0
  PHI   [   1   ,   11  ]<- 0
  PHI   [   1   ,   12  ]<- 1-phi[1]

  PHI   [   2   ,   1   ]<- 0
  PHI   [   2   ,   2   ]<- phi[1]
  PHI   [   2   ,   3   ]<- 0
  PHI   [   2   ,   4   ]<- 0
  PHI   [   2   ,   5   ]<- 0
  PHI   [   2   ,   6   ]<- 0
  PHI   [   2   ,   7   ]<- 0
  PHI   [   2   ,   8   ]<- 0
```

```
PHI   [   2   ,   9   ]<- 0
PHI   [   2   ,   10  ]<- 0
PHI   [   2   ,   11  ]<- 0
PHI   [   2   ,   12  ]<- 1-phi[1]

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

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

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

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

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

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

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

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[1]
PHI   [   9   ,   10  ]<- 0
PHI   [   9   ,   11  ]<- 0
PHI   [   9   ,   12  ]<- 1-phi[1]

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[1]
```

```
PHI  [  10  ,  11  ]<- 0
PHI  [  10  ,  12  ]<- 1-phi[1]

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[1]
PHI  [  11  ,  12  ]<- 1-phi[1]

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

# Define PSI matrices gathering state-to-state transition probabilities, it includes:
# PSI1: offspring survival and growth to next age, proba of sexual maturation:
PSI1 [  1   ,  1   ]<- 1
PSI1 [  1   ,  2   ]<- 0
PSI1 [  1   ,  3   ]<- 0
PSI1 [  1   ,  4   ]<- 0
PSI1 [  1   ,  5   ]<- 0
PSI1 [  1   ,  6   ]<- 0
PSI1 [  1   ,  7   ]<- 0
PSI1 [  1   ,  8   ]<- 0
PSI1 [  1   ,  9   ]<- 0
PSI1 [  1   ,  10  ]<- 0
PSI1 [  1   ,  11  ]<- 0
PSI1 [  1   ,  12  ]<- 0
PSI1 [  1   ,  13  ]<- 0

PSI1 [  2   ,  1   ]<- 0
PSI1 [  2   ,  2   ]<- 1
PSI1 [  2   ,  3   ]<- 0
PSI1 [  2   ,  4   ]<- 0
PSI1 [  2   ,  5   ]<- 0
PSI1 [  2   ,  6   ]<- 0
PSI1 [  2   ,  7   ]<- 0
PSI1 [  2   ,  8   ]<- 0
```

```
PSI1 [ 2 , 9 ]<- 0
PSI1 [ 2 , 10 ]<- 0
PSI1 [ 2 , 11 ]<- 0
PSI1 [ 2 , 12 ]<- 0
PSI1 [ 2 , 13 ]<- 0

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

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

PSI1 [ 5 , 1 ]<- 0
PSI1 [ 5 , 2 ]<- 0
PSI1 [ 5 , 3 ]<- 0
PSI1 [ 5 , 4 ]<- s[1] # litter of 1, cub survives
PSI1 [ 5 , 5 ]<- 0
PSI1 [ 5 , 6 ]<- 0
PSI1 [ 5 , 7 ]<- 0
PSI1 [ 5 , 8 ]<- 1-s[1] #litter of 1, cub dies
PSI1 [ 5 , 9 ]<- 0
PSI1 [ 5 , 10 ]<- 0
PSI1 [ 5 , 11 ]<- 0
PSI1 [ 5 , 12 ]<- 0
PSI1 [ 5 , 13 ]<- 0

PSI1 [ 6 , 1 ]<- 0
PSI1 [ 6 , 2 ]<- 0
PSI1 [ 6 , 3 ]<- 0
PSI1 [ 6 , 4 ]<- 2*s[2]*(1-s[2]) # litter of 2, 1 cub survives
PSI1 [ 6 , 5 ]<- s[2]^2 # litter of 2, both cubs survive
```

```
PSI1 [ 6 , 6 ]<- 0
PSI1 [ 6 , 7 ]<- 0
PSI1 [ 6 , 8 ]<- (1- s[2]^2 -2*s[2]*(1-s[2])) #litter of 2, both cubs die

PSI1 [ 6 , 9 ]<- 0
PSI1 [ 6 , 10 ]<- 0
PSI1 [ 6 , 11 ]<- 0
PSI1 [ 6 , 12 ]<- 0
PSI1 [ 6 , 13 ]<- 0

PSI1 [ 7 , 1 ]<- 0
PSI1 [ 7 , 2 ]<- 0
PSI1 [ 7 , 3 ]<- 0
PSI1 [ 7 , 4 ]<- 0
PSI1 [ 7 , 5 ]<- 0
PSI1 [ 7 , 6 ]<- s[3] # litter of 1, yearling survives
PSI1 [ 7 , 7 ]<- 0
PSI1 [ 7 , 8 ]<- 0
PSI1 [ 7 , 9 ]<- (1-s[3] ) # litter of 1, yearling dies
PSI1 [ 7 , 10 ]<- 0
PSI1 [ 7 , 11 ]<- 0
PSI1 [ 7 , 12 ]<- 0
PSI1 [ 7 , 13 ]<- 0

PSI1 [ 8 , 1 ]<- 0
PSI1 [ 8 , 2 ]<- 0
PSI1 [ 8 , 3 ]<- 0
PSI1 [ 8 , 4 ]<- 0
PSI1 [ 8 , 5 ]<- 0
PSI1 [ 8 , 6 ]<- 2*s[4]*(1-s[4]) # litter of 2, 1 yearling survives
PSI1 [ 8 , 7 ]<- s[4]^2 # litter of 2, both yearlings survive
PSI1 [ 8 , 8 ]<- 0
PSI1 [ 8 , 9 ]<- (1- s[4]^2 -2*s[4]*(1-s[4])) #litter of 2, both yearlings die
PSI1 [ 8 , 10 ]<- 0
PSI1 [ 8 , 11 ]<- 0
PSI1 [ 8 , 12 ]<- 0
PSI1 [ 8 , 13 ]<- 0

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

PSI1 [ 10 , 1 ]<- 0
```

```
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
```

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

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

```
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
```

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

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

```
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
```

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

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

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

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

PSI3 [ 5 , 1 ]<- 0
PSI3 [ 5 , 2 ]<- 0
```

```
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
```

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

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

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

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

PSI3 [ 13 , 1 ]<- 0
PSI3 [ 13 , 2 ]<- 0
PSI3 [ 13 , 3 ]<- 0
PSI3 [ 13 , 4 ]<- 0
```

```
PSI3 [ 13 , 5 ]<- 0
PSI3 [ 13 , 6 ]<- 0
PSI3 [ 13 , 7 ]<- 0
PSI3 [ 13 , 8 ]<- 0
PSI3 [ 13 , 9 ]<- 0
PSI3 [ 13 , 10 ]<- 0
PSI3 [ 13 , 11 ]<- 1
PSI3 [ 13 , 12 ]<- 0

PSI3 [ 14 , 1 ]<- 0
PSI3 [ 14 , 2 ]<- 0
PSI3 [ 14 , 3 ]<- 0
PSI3 [ 14 , 4 ]<- 0
PSI3 [ 14 , 5 ]<- gamma[2]
PSI3 [ 14 , 6 ]<- 1-gamma[2]
PSI3 [ 14 , 7 ]<- 0
PSI3 [ 14 , 8 ]<- 0
PSI3 [ 14 , 9 ]<- 0
PSI3 [ 14 , 10 ]<- 0
PSI3 [ 14 , 11 ]<- 0
PSI3 [ 14 , 12 ]<- 0

PSI3 [ 15 , 1 ]<- 0
PSI3 [ 15 , 2 ]<- 0
PSI3 [ 15 , 3 ]<- 0
PSI3 [ 15 , 4 ]<- 0
PSI3 [ 15 , 5 ]<- 0
PSI3 [ 15 , 6 ]<- 0
PSI3 [ 15 , 7 ]<- 0
PSI3 [ 15 , 8 ]<- 0
PSI3 [ 15 , 9 ]<- 0
PSI3 [ 15 , 10 ]<- 0
PSI3 [ 15 , 11 ]<- 1
PSI3 [ 15 , 12 ]<- 0

PSI3 [ 16 , 1 ]<- 0
PSI3 [ 16 , 2 ]<- 0
PSI3 [ 16 , 3 ]<- 0
PSI3 [ 16 , 4 ]<- 0
PSI3 [ 16 , 5 ]<- 0
PSI3 [ 16 , 6 ]<- 0
PSI3 [ 16 , 7 ]<- 0
PSI3 [ 16 , 8 ]<- 0
PSI3 [ 16 , 9 ]<- 0
PSI3 [ 16 , 10 ]<- 0
PSI3 [ 16 , 11 ]<- 0
PSI3 [ 16 , 12 ]<- 1

# Matrix product for state-to-state transitions S
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]


## Observation process: Define probabilities of E(t) given S(t).
```

```
#for initial capture, conditional on first capture
E0    [   1   ,   1   ]<- 0
E0    [   1   ,   2   ]<- 1
E0    [   1   ,   3   ]<- 0
E0    [   1   ,   4   ]<- 0
E0    [   1   ,   5   ]<- 0
E0    [   1   ,   6   ]<- 0
E0    [   1   ,   7   ]<- 0
E0    [   1   ,   8   ]<- 0
E0    [   1   ,   9   ]<- 0
E0    [   1   ,   10  ]<- 0
E0    [   1   ,   11  ]<- 0
E0    [   1   ,   12  ]<- 0

E0    [   2   ,   1   ]<- 0
E0    [   2   ,   2   ]<- 0
E0    [   2   ,   3   ]<- 1
E0    [   2   ,   4   ]<- 0
E0    [   2   ,   5   ]<- 0
E0    [   2   ,   6   ]<- 0
E0    [   2   ,   7   ]<- 0
E0    [   2   ,   8   ]<- 0
E0    [   2   ,   9   ]<- 0
E0    [   2   ,   10  ]<- 0
E0    [   2   ,   11  ]<- 0
E0    [   2   ,   12  ]<- 0

E0    [   3   ,   1   ]<- 0
E0    [   3   ,   2   ]<- 0
E0    [   3   ,   3   ]<- 0
E0    [   3   ,   4   ]<- 1
E0    [   3   ,   5   ]<- 0
E0    [   3   ,   6   ]<- 0
E0    [   3   ,   7   ]<- 0
E0    [   3   ,   8   ]<- 0
E0    [   3   ,   9   ]<- 0
E0    [   3   ,   10  ]<- 0
E0    [   3   ,   11  ]<- 0
E0    [   3   ,   12  ]<- 0

E0    [   4   ,   1   ]<- 0
E0    [   4   ,   2   ]<- 0
E0    [   4   ,   3   ]<- 0
E0    [   4   ,   4   ]<- 0
E0    [   4   ,   5   ]<- 1
E0    [   4   ,   6   ]<- 0
E0    [   4   ,   7   ]<- 0
E0    [   4   ,   8   ]<- 0
E0    [   4   ,   9   ]<- 0
E0    [   4   ,   10  ]<- 0
E0    [   4   ,   11  ]<- 0
E0    [   4   ,   12  ]<- 0
```

```
E0    [   5   ,   1   ]<- 0
E0    [   5   ,   2   ]<- 0
E0    [   5   ,   3   ]<- 0
E0    [   5   ,   4   ]<- 0
E0    [   5   ,   5   ]<- 0
E0    [   5   ,   6   ]<- 1
E0    [   5   ,   7   ]<- 0
E0    [   5   ,   8   ]<- 0
E0    [   5   ,   9   ]<- 0
E0    [   5   ,   10  ]<- 0
E0    [   5   ,   11  ]<- 0
E0    [   5   ,   12  ]<- 0

E0    [   6   ,   1   ]<- 0
E0    [   6   ,   2   ]<- 0
E0    [   6   ,   3   ]<- 0
E0    [   6   ,   4   ]<- 0
E0    [   6   ,   5   ]<- 0
E0    [   6   ,   6   ]<- 0
E0    [   6   ,   7   ]<- 1
E0    [   6   ,   8   ]<- 0
E0    [   6   ,   9   ]<- 0
E0    [   6   ,   10  ]<- 0
E0    [   6   ,   11  ]<- 0
E0    [   6   ,   12  ]<- 0

E0    [   7   ,   1   ]<- 0
E0    [   7   ,   2   ]<- 0
E0    [   7   ,   3   ]<- 0
E0    [   7   ,   4   ]<- 0
E0    [   7   ,   5   ]<- 0
E0    [   7   ,   6   ]<- 0
E0    [   7   ,   7   ]<- 0
E0    [   7   ,   8   ]<- 1
E0    [   7   ,   9   ]<- 0
E0    [   7   ,   10  ]<- 0
E0    [   7   ,   11  ]<- 0
E0    [   7   ,   12  ]<- 0

E0    [   8   ,   1   ]<- 0
E0    [   8   ,   2   ]<- 0
E0    [   8   ,   3   ]<- 0
E0    [   8   ,   4   ]<- 0
E0    [   8   ,   5   ]<- 0
E0    [   8   ,   6   ]<- 0
E0    [   8   ,   7   ]<- 0
E0    [   8   ,   8   ]<- 0
E0    [   8   ,   9   ]<- 1
E0    [   8   ,   10  ]<- 0
E0    [   8   ,   11  ]<- 0
E0    [   8   ,   12  ]<- 0

E0    [   9   ,   1   ]<- 0
```

```
E0    [   9   ,   2   ]<- 0
E0    [   9   ,   3   ]<- 0
E0    [   9   ,   4   ]<- 0
E0    [   9   ,   5   ]<- 0
E0    [   9   ,   6   ]<- 0
E0    [   9   ,   7   ]<- 0
E0    [   9   ,   8   ]<- 0
E0    [   9   ,   9   ]<- 0
E0    [   9   ,   10  ]<- 1
E0    [   9   ,   11  ]<- 0
E0    [   9   ,   12  ]<- 0

E0    [   10  ,   1   ]<- 0
E0    [   10  ,   2   ]<- 0
E0    [   10  ,   3   ]<- 0
E0    [   10  ,   4   ]<- 0
E0    [   10  ,   5   ]<- 0
E0    [   10  ,   6   ]<- 0
E0    [   10  ,   7   ]<- 0
E0    [   10  ,   8   ]<- 0
E0    [   10  ,   9   ]<- 0
E0    [   10  ,   10  ]<- 0
E0    [   10  ,   11  ]<- 1
E0    [   10  ,   12  ]<- 0

E0    [   11  ,   1   ]<- 0
E0    [   11  ,   2   ]<- 0
E0    [   11  ,   3   ]<- 0
E0    [   11  ,   4   ]<- 0
E0    [   11  ,   5   ]<- 0
E0    [   11  ,   6   ]<- 0
E0    [   11  ,   7   ]<- 0
E0    [   11  ,   8   ]<- 0
E0    [   11  ,   9   ]<- 0
E0    [   11  ,   10  ]<- 0
E0    [   11  ,   11  ]<- 0
E0    [   11  ,   12  ]<- 1

E0    [   12  ,   1   ]<- 1
E0    [   12  ,   2   ]<- 0
E0    [   12  ,   3   ]<- 0
E0    [   12  ,   4   ]<- 0
E0    [   12  ,   5   ]<- 0
E0    [   12  ,   6   ]<- 0
E0    [   12  ,   7   ]<- 0
E0    [   12  ,   8   ]<- 0
E0    [   12  ,   9   ]<- 0
E0    [   12  ,   10  ]<- 0
E0    [   12  ,   11  ]<- 0
E0    [   12  ,   12  ]<- 0

# departure probability of a2 offspring
for(i in 1:N){
```

```
  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
```

```
      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

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

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

      E1    [   9   ,   1   ,i,t]<- 0
```

```
      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
```

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

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

E2    [   5   ,   1,i,t]<-    1 -p
E2    [   5   ,   2,i,t]<-    0
```

```
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
```

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

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

    # Matrix product for offspring independence and recapture
    E[1:12,1:12,i,t] <- E1[1:12,1:12,i,t] %*% E2[1:12,1:12,i,t]
  }
}
```

```
## LIKELIHOOD

for (i in 1:N)  # for each individual
{
  # The estimated probabilities of initial states S0 are the proportions in each state at first captu
  alive[i,First[i]] ~ dcat(S0[1:12])
  mydata[i,First[i]] ~ dcat(E0[alive[i,First[i]],1:12])

  for (j in (First[i]+1):Years)
  {

    ## STATE EQUATIONS ##
    # draw S(t) given S(t-1)
    alive[i,j] ~ dcat(S[alive[i,j-1],1:12])

    ## OBSERVATION EQUATIONS ##
    # draw events E(t) given states S(t)

    mydata[i,j] ~ dcat(E[alive[i,j],1:12,i,j-1])

  }
}


## PRIORS
# capture probability
p ~ dunif(0,1)

# juveniles, subadults and adult survival
#for(i in 1:2){phi[i] ~ dunif(0,1)}
phi[1] ~ dunif(0,1)

# initial states
for (i in 1:10){ log(prop[i]) <- theta[i]
theta[i] ~ dnorm(0,1)}

# offspring survival
# litter survival n=2 offspring
l02 <- 1 -(1- s[2]^2 -2*s[2]*(1-s[2]))
l12 <- 1- (1- s[4]^2 -2*s[4]*(1-s[4]))
# indiviual offspring survival
#for(i in 1:4){s[i]~ dunif(0,1)}

for(i in 1:2){s[i]~ dunif(0,1)}
  # Set constraints
  for(u in 1:2){  X[u] ~ dunif(0,1)} # with X ~ U[0,1] then  (a + ( b - a ) * X)
  #so that s[1] < s[3] <phi[1] for litter of 1
  s[3] <- s[1] + (phi[1] - s[1]) * X[1]
  # and s[2] < s[4] < phi[1] for litters of 2
  s[4] <- s[2] + (phi[1] - s[2]) * X[2]

# Breeding probability
kappa ~ dunif(0,1)
```

```
  for(i in 1:3){beta[i]~ dunif(0,1)}

  # Litter size probability
  for(i in 1:2){gamma[i]~ dunif(0,1)}

} # end model

 ")
```

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:

```
# Call JAGS from R
out <- jags(data=mydatax,inits=inits, parameters.to.save=params,
            model.file = 'Multieventmodel_FitresidentBeardata.txt',n.chains=2,n.iter=20000,n.burnin=900

save(out,file='noage_lb_phip.RData')
```

Analyse the results

Load useful packages:

```
library(jagsUI)
library(MCMCvis)
```

Load model results and print a summary :

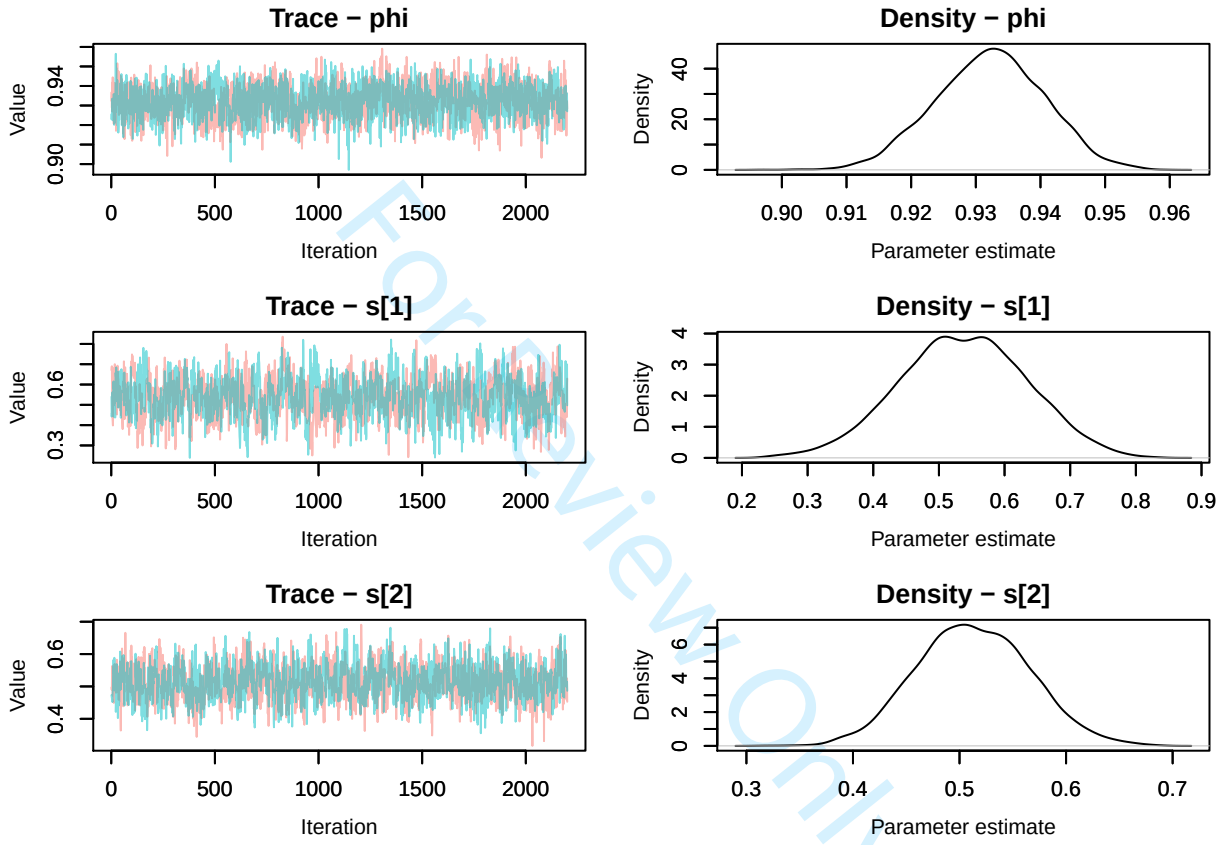
```
load(file='Fit_beardata.RData')
MCMCsummary(out,round=2)
```

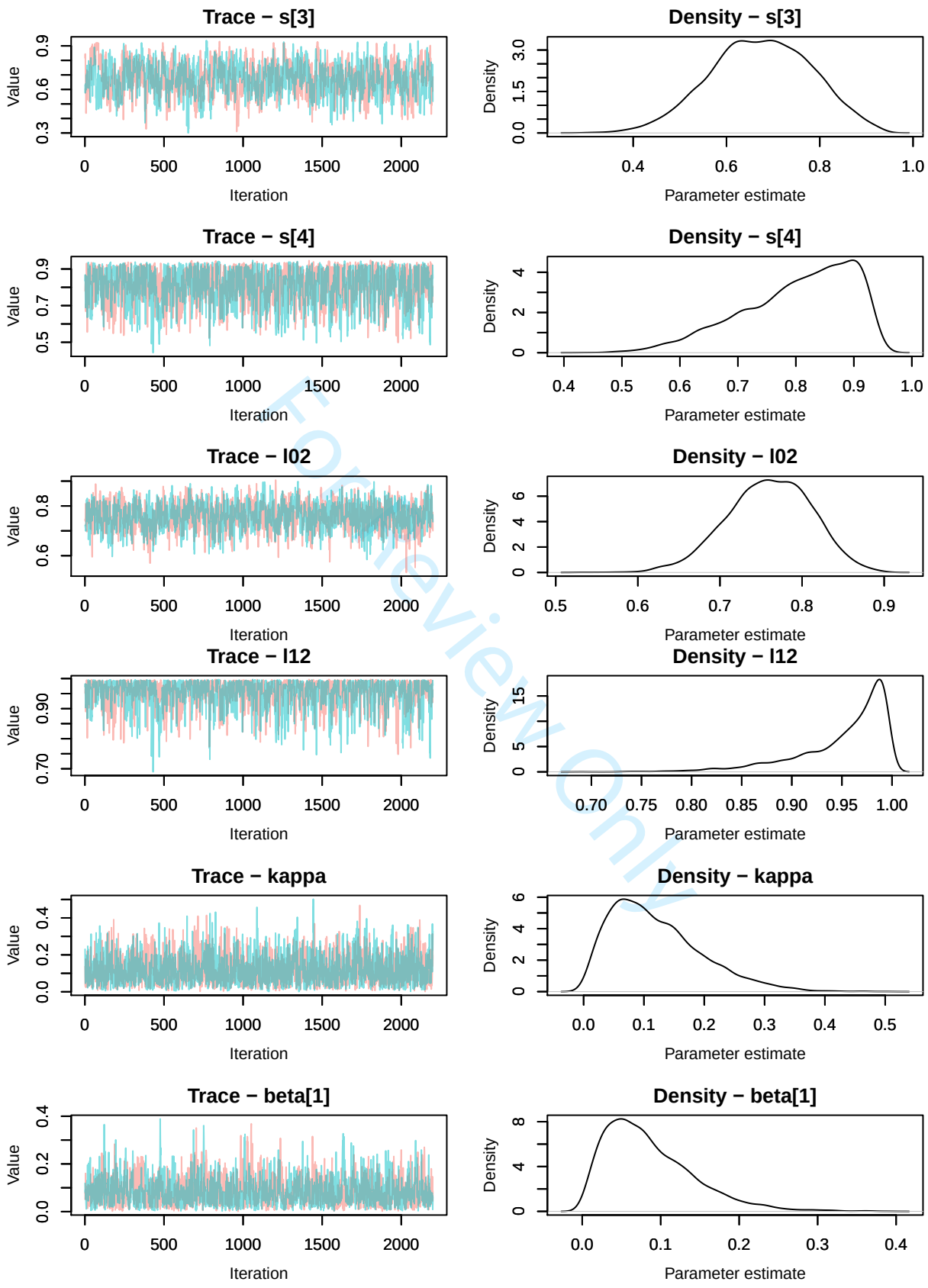
```
##             mean   sd  2.5%   50% 97.5% Rhat n.eff
## phi         0.93 0.01  0.92  0.93  0.95 1.00  2027
## s[1]        0.54 0.10  0.34  0.54  0.72 1.00  4400
## s[2]        0.51 0.05  0.41  0.51  0.62 1.00  4400
## s[3]        0.67 0.11  0.46  0.68  0.87 1.00  1458
## s[4]        0.80 0.09  0.59  0.82  0.93 1.01   422
## l02         0.76 0.05  0.65  0.76  0.85 1.00  4400
## l12         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
```

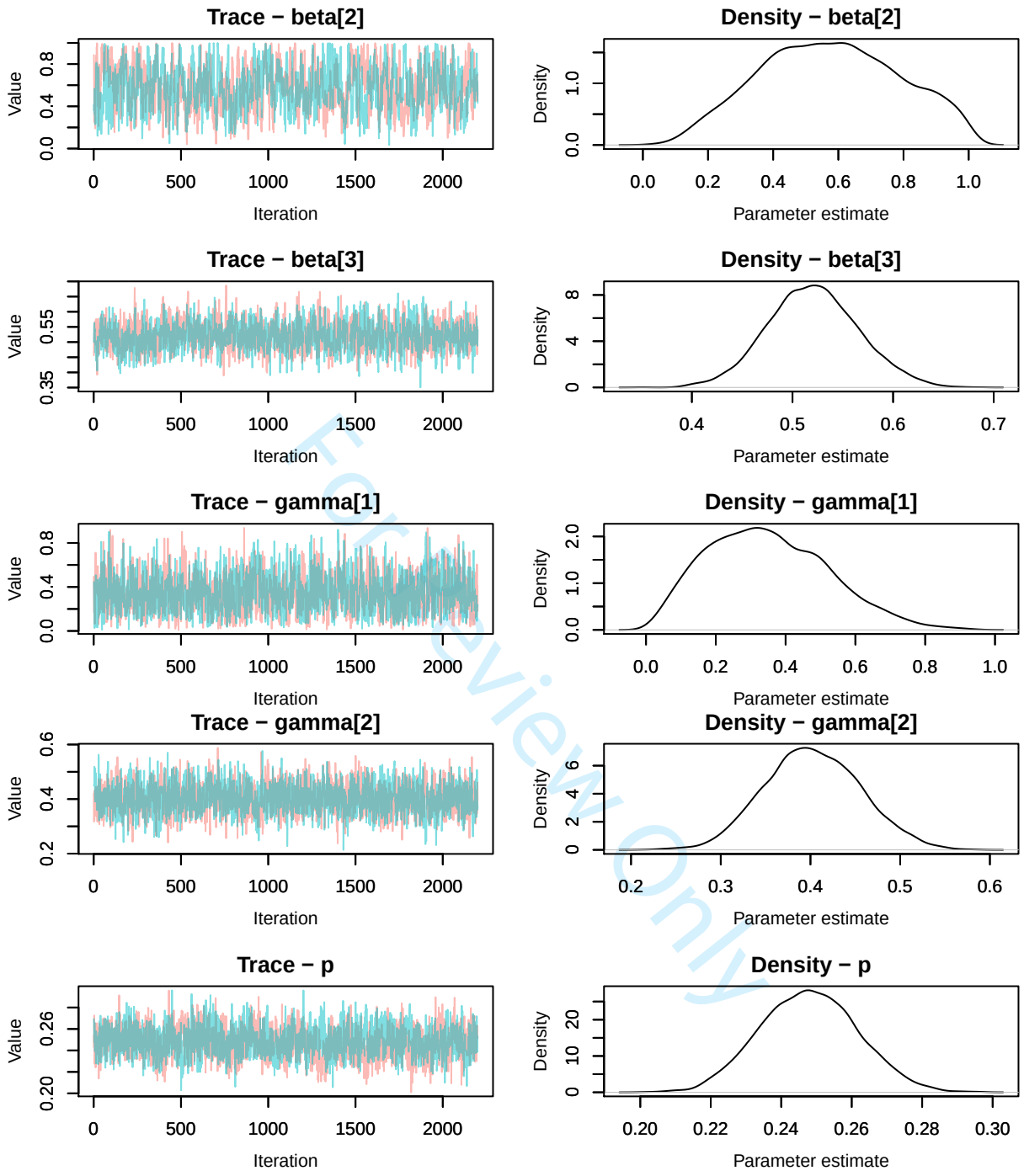
```
## prop[6]     0.76  0.20    0.43    0.74    1.22 1.00  4400
## prop[7]     0.46  0.15    0.24    0.44    0.80 1.00  4400
## prop[8]     0.20  0.08    0.08    0.19    0.40 1.00  4400
## prop[9]     0.20  0.08    0.08    0.19    0.40 1.00  4400
## prop[10]    0.09  0.05    0.02    0.08    0.22 1.00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

Check mixing of the chains and posterior distributions:

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



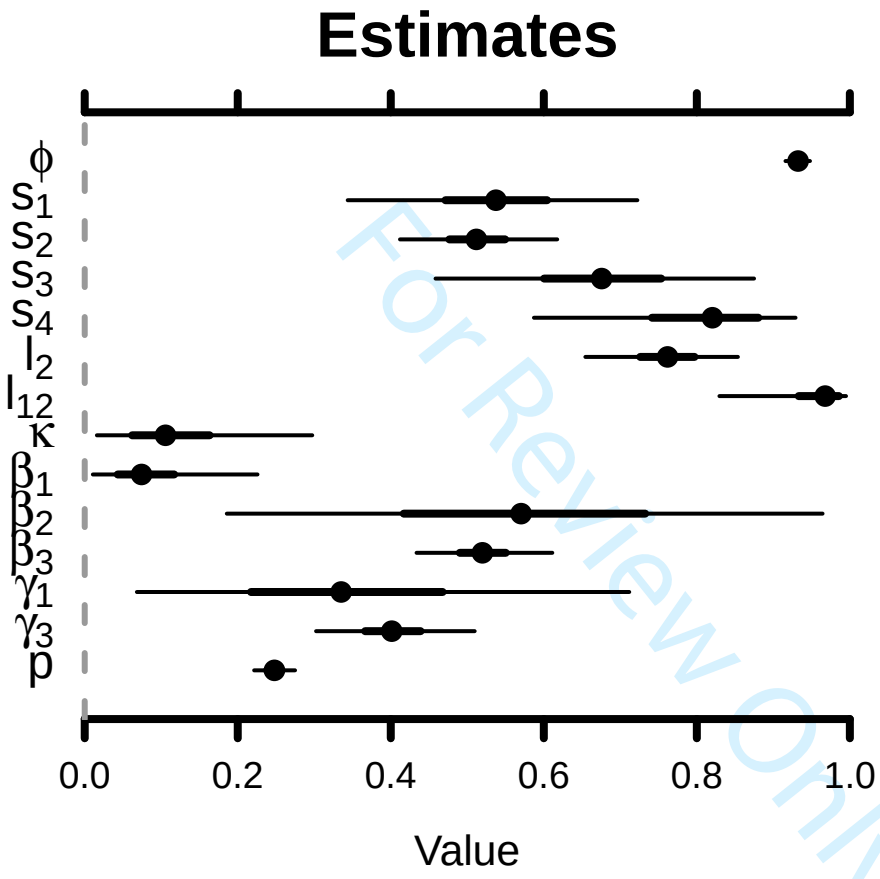




Plot a summary of the posterior distribution for each model parameter:

```
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

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

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Abstract

1. In species providing extended parental care, one or both parents care for altricial young over a period including more than one breeding season. We expect large parental investment and long-term dependency within family units to cause high variability in life trajectories among individuals with complex consequences at the population level. So far, models for estimating demographic parameters in free-ranging animal populations mostly ignore extended parental care, thereby limiting our understanding of its consequences on parents and offspring life histories.

2. 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~~to evaluate~~ 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 performances using simulated data, and illustrate its use with a long-term dataset collected on the Svalbard polar bears (*Ursus maritimus*).

3. Our model performed well in terms of bias and mean square error and in estimating demographic parameters in all simulated scenarios, 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, 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.

4. 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. This is of interest in terms of conservation because species providing extended parental care are often long-living mammals vulnerable or threatened with extinction.

Key-words: apex predator, arctic ecosystem, Bayesian modeling, capture-recapture, dependency among individuals, family structure, parental care, state uncertainty, timing at independence.

INTRODUCTION

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

the parent's reproductive success (Trivers 1972). Altricial mammals having offspring that need to learn complex skills to ensure survival beyond independence, such as hunting, orientation, or nest building, show extended parental care (hereafter EPC; Clutton-Brock 1991). It is defined as a prolonged period, i.e. lasting more than one breeding season, over which one or both parents care for one or several dependent young. This period typically lasts for several years and can extend until lifelong maternal care in primates (Van Noordwijk 2012). For the offspring, the quality and quantity of care received can have long-lasting effects on future survival (e.g. Pavard and Branger 2012), social status (e.g. Shenk and Scelza 2012) and reproduction (Royle et al. 2012). For the parent, investment in one offspring can compromise its own condition or survival and/or its ability to invest in other offspring (siblings or future offspring) (Williams 1966, Stearns 1992). It can indeed take several years during which a parent caring for its offspring will not be available to reproduce, sometimes not until the offspring have reached independence, e.g. on average 2.5 years for female polar bears (Ramsay and Stirling 1988), 3.5 to 6 years for female African elephants (Lee and Moss 1986), and 9.3 years for female Sumatran orangutans (Wich et al. 2004). The fitness costs of losing one offspring, in terms of lost investment and skipped breeding opportunities, are particularly high if death occurs near independence. We therefore expect EPC, through large parental investment and multiple-year dependency among individuals within family units, to cause high variability in life trajectories among individuals and family groups, in interbirth intervals depending on offspring's fate, and consequently on lifetime reproductive success for the caring parent (Clutton-Brock 1991).

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

failed breeding events (e.g., Lagrange et al. 2017) and include varying litter or clutch size (e.g., Doligez et al. 2002) and memory effects (Cole et al. 2014), to investigate the costs of reproduction on survival and future reproduction for species providing short-term parental care, i.e. when offspring reach independence before the next breeding season (e.g., Yoccoz et al. 2002). Indeed, most CR models rely on the assumption of independence among individual CR histories (Lebreton et al. 2009).

In the case of species providing EPC, one challenge stems from the multiple-year dependency among individual's life histories within parent-offspring units. Only few attempts have been made to tackle this issue when estimating demographic parameters, despite the fact that species providing EPC are often among long-living mammals vulnerable or threatened with extinction (e.g. polar bears, orangutans, elephants). Lunn et al. (2016) ~~and Couet et al. (2019)~~ proposed to model CR histories of ~~family~~ mother-offspring units (instead of individuals) ~~which permits~~ to consider the multiple-year dependency ~~of offspring survival upon mother survival status and~~ of female breeding probability upon offspring survival status for polar bears in Hudson Bay. ~~.—~~However, in this model, offspring survival after 9 months is assumed independent of mother survival. Lunn et al. (2016)'s model does therefore not handle multiple-year dependency of offspring survival upon mother survival status, typical of~~in~~ species providing EPC. In addition, because litter size is modeled separately, Lunn et al. (2016)'s model (also used in Regehr et al. (2018)) does not permit to explore potential trade-offs among offspring traits and parental phenotypic or demographic traits.~~Couet et al. (2019) provided estimates of dolphin reproductive parameters corrected for state uncertainty but their model assumed a fixed age and timing at offspring independence.~~

Another challenge involves dealing with uncertain timing at offspring independence, when the offspring departs the caring parent(s) and becomes independent. When studying free-ranging populations, this key life history event is rarely directly observed. When a mature

individual is observed without dependent offspring, it is often impossible to know if its offspring have died or already departed its natal group. As a result, estimates of demographic rates and trade-offs can be underestimated. Based on the analysis of mother-offspring units CR histories, Couet et al. (2019) provided estimates of dolphin reproductive parameters corrected for state uncertainty, but their model assumed a fixed age and timing at offspring independence. Lunn et al. (2016)'s model ~~for polar bears in Hudson Bay (later used in Regehr et al. (2018))~~ included variable age at independence, but variability in the timing at offspring independence was not fully dealt with. Demographic rates were corrected by the average annual probability that independence occurred prior to sampling for all offspring, and offspring survival was assumed independent of litter size (Regehr et al. 2018). In most species, timing at offspring independence is variable and could depend on the offspring phenotypic traits (e.g. body size in brown bears, Dahle and Swenson 2003), on parental traits (e.g. parent-offspring conflict in kestrels, Vergara et al. 2010), social and mating system (e.g. helping behavior in humans, Kramer 2005), or other environmental determinants (e.g. food supply, Eldegard and Sonerud 2010). To our knowledge, no model is available to tackle both the issues of multiple-year dependency among individuals and variable timing at offspring independence. Because of these methodological challenges, the population-level consequences of EPC remain to be understood, especially in free-ranging animal populations.

Here, we develop a CR model specifically for species providing EPC. It is designed to handle multiple-years statistical dependency (until offspring independence) among individual demographic parameters by modeling CR histories grouped within family units. The model accounts for uncertain timing at offspring independence. In addition, our model allows for variability in the number of offspring born and recruited at each breeding event, variable offspring survival depending on number of siblings, and includes the influence of past reproductive history on the caring parent's current status. Finally, estimates of survival rates,

breeding probability and litter size probability are corrected for imperfect detection possibly depending upon family unit composition.

In what follows, we present the model, assess its performances using simulated data, and illustrate its use with a long-term dataset collected on the Svalbard polar bears. Female polar bears rely solely on stored fat reserves during pregnancy and the first three months of lactation, before feeding and protecting litters of one to three young, usually during two more years (Ramsay and Stirling 1988). They can lose more than 40% of body mass while fasting (Atkinson and Ramsay 1995). In many areas, climate change and related sea ice decline impact female bear condition and capacity to provide care for their young, with an associated decline in reproductive output (Derocher et al. 2004; Stirling and Derocher, 2012, Laidre et al. 2020). More insights into the species demography, such as the consequences of long-duration parental care on mother and offspring life histories, could help our understanding of polar bear population responses to environmental perturbations and extinction risks in future decades (Hunter et al., 2010; Regehr et al., 2016).

METHODS

1. Capture-recapture model for species providing EPC

1.1 Principle

We develop a CR model in the multievent framework (Pradel 2005) that is also known as a hidden Markov modeling framework (Gimenez et al. 2012). The principle is to relate the field observations, called events, to the underlying demographic states of interest through the observation process. Uncertainty on state assignment due to variable timing at offspring independence is included in the observation process. In parallel, the state process describes the transition rates between states from one year to the next. The transition rates correspond here

to the demographic parameters corrected for imperfect detection and state uncertainty. Below we describe the general procedure to specify the model by defining the states and state-to-state transition process, then the events and observation process. However, for simplicity, the events and states are chosen to match the polar bear life cycle (i.e. females are captured in sSpring, alone or together with a litter of one or two dependent offspring; offspring gain independence in the year following their second birthday, and offspring cannot survive the loss of their mother before gaining independence). The resulting model assumptions and its applicability to other species are discussed below.

1.2 Specification of states and state process

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

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

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~~ one dependent ~~offspring~~ cub of the year~~<1yo~~
	A02	mother with ~~one~~ two dependent ~~offspring~~ cubs of the year ~~<1yo~~
	A11	mother with one dependent ~~offspring~~ yearling ~~1yo~~
	A12	mother with two dependent ~~offspring~~ yearlings ~~1yo~~
	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 ~~aged <1yo~~
	A1-	failed breeder, death of all offspring yearlings~~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 cub of the year litter ~~of <1yo offspring~~
	NB/A0-	non breeder following loss of a cub of the year litter ~~of <1yo offspring~~
	B/A1-	breeder following loss of a yearling litter ~~of 1yo offspring~~
	NB/A1-	non breeder following loss of a yearling 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 ~~offspring~~ cub of the year
	'6'	capture of a mother with two dependent ~~offspring~~ cub of the year
	'7'	capture of a mother with one dependent ~~offspring aged 1yo~~yearling
	'8'	capture of a mother with two dependent ~~offspring aged 1yo~~yearlings
	'9'	capture of a mother with one dependent ~~offspring aged 2yo~~two-year old offspring
	'10'	capture of a mother with two dependent two-year old offspring~~offspring aged 2yo~~
	'11'	capture of an adult female without dependent offspring
	'0'	non observation

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

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

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

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

	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	$\phi\varphi_{10}$	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)

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

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

	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-κ	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

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

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

	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)

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

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

	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)

Parameter 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 the loss a cub litter, ~~and~~ γ_2 ~~following the loss a cub litter resp.~~ loss of a yearling litter, γ_3 for successful breeder, γ_4 for female without dependent offspring at the beginning of the year).

By modifying the constraints on parameters (i.e. setting them equal or different among states), the model can be used to investigate: i) the cost of reproduction on parent's survival (by comparing the ~~$\varphi\phi$~~ 's in matrix Φ), ii) the influence of litter size on individual offspring survival (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} and l_{11} to l_{12}), iv) the influence of past reproductive history on breeding probability (by comparing the β ~~'~~s ~~among them~~ in matrix Ψ_2), and on litter size probability (by comparing the γ ~~'~~s ~~among them~~ in matrix Ψ_3).

1.3 Specification of events and observation process

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

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

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

	'1'	'2'	'3'	'4'	'5'	'6'	'7'	'8'	'9'	'10'	'11'	'~~0~~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	(eq.5)
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-$\alpha_{i,d}$~~a~~	0	$\alpha_{i,d}$~~a~~	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

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

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

	1'	2'	3'	4'	5'	6'	7'	8'	9'	10'	11'	~~0~~'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}	$1-p_{11}$
~~0~~'12'	0	0	0	0	0	0	0	0	0	0	0	1

(eq.6)

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

1.4 Applicability to other species

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

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

individual traits such as age or body weight, or environmental variables such as temperature, can be included in the model under the form of individual or temporal covariates (Pollock 2002). ~~In addition,~~Other specificities related to data collection can ~~also~~ be included in a similar way, such as trap effects (Pradel and Sanz-Aguilar 2012) or latent individual heterogeneity by using mixture of distributions or random effects (Gimenez et al. 2018). Guidance to fit the model in a Bayesian framework in program Jags for real and simulated data are provided in Appendices 1 and 2.

Simulation study

The simulation study was aimed at evaluating the performance of our model to estimate demographic parameters under various assumptions about the timing at offspring independence (constant versus seasonal departure rate) and various degrees of capture probability (low p= 0.25, high p=0.7), for a medium-size data set (T= 15 sampling occasions, with R=80 newly marked at each occasion in equal proportion among the 11 alive states).

We simulated data for a virtual long-lived mammal species mimicking the polar bear using the model described in box 1. We used $\varphi = 0.9$ for independent female bear survival (aged 2+ y.o.), $s_1 = l_{01} = 0.6$ for singleton cub survival, $s_2 = 0.55$ for twin litter' s cub survival (corresponding to twin litter survival $l_{02} = 0.7975$), $s_3 = 0.8$ for singleton yearling survival and $s_4 = 0.75$ for twin litter's yearling survival (corresponding to litter survival $l_{12} = 0.94$). Offspring survival rates were conditioned upon mother survival. If a mother dies, its dependent offspring had no chances of surviving. For breeding probabilities, we used $\beta_1 = 0.5$, $\beta_2 = 0.7$, $\beta_3 = 0.9$ and $\beta_4 = 0.8$. For litter size probabilities, we used $\gamma_1 = 0.4$, $\gamma_2 = 0.5$, ~~γ~~$\gamma_3 = 0.6$ and $\gamma_4 = 0.7$. We set $\kappa = 0$ and assumed that females had their first litter at age 6 or older.

We assumed that captures occurred each year between mid-March to end of May (day of the year d=80 to d=130). For each capture event, date of capture was randomly sampled from the distribution of the polar bear data dates of capture (see Appendix 1). In the constant scenario, we assumed that two-year old bears reached independence at a constant departure rate (α) during the field season, independently of the date of capture. We chose an intermediate value of $\alpha = 0.5$ (if independence occurred always after the field season, $\alpha = 0$, versus always before the field season, $\alpha = 1$). In the seasonal scenario, we assumed that departure rate varied with date of capture (d) following a logistic relationship (regression coefficients were estimated from the polar bear data, see Appendix 2). Most of the two-year old offspring were captured with their mother at the beginning of the field season, while departure probability increased logistically up to 80% at the end of the field season.

We simulated 100 CR datasets for each of the 4 scenarios (S1: low detection with constant departure, S2: low detection with seasonal departure, S3: high detection with constant departure, S4: high detection with seasonal departure). We simulated the data using program R. We fitted the model using program jags called from R (Plummer 2016). For each parameter and each dataset, we calculated absolute bias as $\hat{B} = \hat{\theta} - \theta$, and root mean squared error as $\widehat{RMSE} = \sqrt{(\hat{\theta} - \theta)^2}$, with θ the parameter used to simulate the data and $\hat{\theta}$ the mean value of the estimated parameter. Appendix 1 containing guidance, R code and files to simulate data and fit the model is available on GitHub at https://github.com/SCubaynes/Appendix1_extendedparentalcare.

Case study: Polar bears in Svalbard

In polar bears, care of offspring is provided by the mother only (Amstrup, 2003). Males were therefore discarded from our analysis. Adult female polar bears mate in spring (February

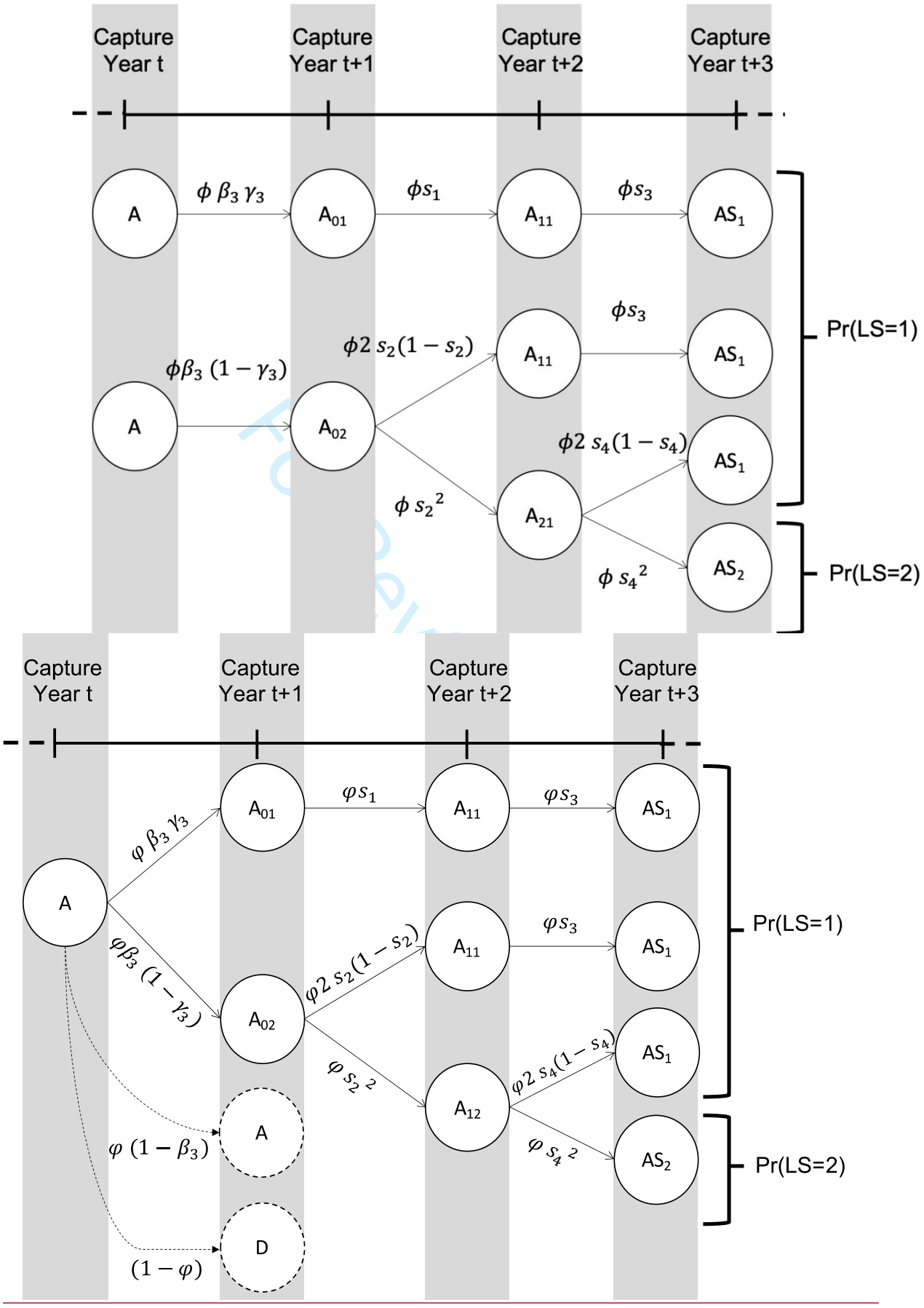
to May, Amstrup 2003), and in Svalbard usually have their first litter at the age of six years, but some females can have their first litter at five years (Derocher 2013). They have delayed implantation where the egg attaches to the uterus in autumn (Ramsay and Stirling 1988). A litter with small cubs (ca 600 grams) is born around November to January, in a snow den that the mothers dig out in autumn, and where the family stay 4-5 months. The family usually emerges from the den in March-April, and stay close to the den while the cubs get accustomed to the new environment outside their home, for a few days up to 2-3 weeks (Hansson and Thomassen 1983). Litter size in early spring vary from one to three, with two cubs being most common, three cubs in most areas being rare, and commonly around one out of three litters having one cub only (Amstrup 2003). In Svalbard, polar bears become independent from their mother shortly after their second birthday (average age at independence is 2.3). Two-year old bears typically depart from the mother in spring (between mid-March to end of May), when the mother can mate again. There is only one anecdotal~~ic~~ record of a yearling alive without his mother. Because the field season can last for several weeks, some two-year-old bears were captured together with their mother and others were already independent at the time of capture. The minimum reproductive interval for successful Barents Sea polar bears is 3 years. On the contrary, loss of a cub litter shortly after den emergence may mean the mother can produce new cubs in winter the same year (Ramsay and Stirling 1988).

Bears captured in Svalbard are shown to be a mixture of resident and pelagic bears (Mauritzen et al. 2002). To focus on the resident population, independent bears captured only once were not included in our analysis. We therefore analyzed N = 158 encounter histories of resident polar bear family units captured each spring after den emergence between doy 80 to 130 (mid-March to mid-May), from 1992 to 2019, in Svalbard. It corresponds to 81 capture events of juvenile and subadults, 231 cubs, 96 yearling, 23 dependent two-year old, and 444 captures of adult females. Polar bears were caught and individually marked as part of a long-

term monitoring program on the ecology of polar bears in the Barents Sea region (Derocher 2005). All bears one year or older were immobilized by remote injection of a dart (Palmer Cap-Chur Equipment, Douglasville, GA, USA) with the drug Zoletil® (Virbac, Carros, France) (Stirling et al. 1989). The dart was fired from a small helicopter (Eurocopter 350 B2 or B3), usually from a distance of about 4 to 10 meters. Cubs of the year were immobilized by injection with a syringe. Cubs and yearlings were highly dependent on their mother; therefore, they remained in her vicinity and were captured together with their mother. A female captured alone was considered to have no dependent offspring alive. Death of the cubs could have occurred in the den or shortly after den emergence but before capture. Hereafter, estimated cub survival thus refers to survival after capture. Infant mortality occurring before capture will be assigned to a reduced litter size. Because only 3% of females were observed with 3 offspring, we analyzed jointly litters of twins with triplets.

We built the model described above with 12 states and 12 events to describe the life cycle (Table 1). Preliminary analyses suggested that mother survival did not vary according to state, we therefore constrained parameter $\varphi\phi$ to be equal among all states in matrix Φ. To avoid identifiability issues due to a relatively small sample size, we assumed breeding probability and litter size probability did not vary between successful breeders (states AS1 and AS2) and female without dependent offspring (state A) by setting $\beta_3 = \beta_4$ and $\gamma_3 = \gamma_4$. . We also assumed that litter size probability did not vary among failed breeders (loss of a cub versus a yearling litter), by setting $\gamma_1 = \gamma_2$. We could not assess formally the fit of our model because no test is yet available for multievent models. However, the multi-state version of our model (without uncertainty on timing at independence) fitted the data adequately. Adding a level of complexity should make the model even more adequate.

Using the conditional probabilities estimated in the model, we calculated the net probability for a female to raise none, Pr(X=0), one, Pr(X=1), or two offspring, Pr(X=2) to independence over a 3-year period (details are provided in Appendix 2).


Capture Year t
Capture Year t+1
Capture Year t+2
Capture Year t+3
A
$\phi\ \beta_3\ \gamma_3$
A_{01}
ϕs_1
A_{11}
ϕs_3
AS_1
Pr(LS=1)
$\phi\beta_3\ (1-\gamma_3)$
A_{02}
$\phi 2\ s_2(1-s_2)$
ϕs_3
$\phi 2\ s_4(1-s_4)$
$\phi\ {s_2}^2$
A_{21}
AS_2
$\phi\ {s_4}^2$
Pr(LS=2)
Capture Year t
Capture Year t+1
Capture Year t+2
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A
$\varphi\ \beta_3\ \gamma_3$
A_{01}
φs_1
A_{11}
φs_3
AS_1
Pr(LS=1)
$\varphi\beta_3\ (1-\gamma_3)$
A_{02}
$\varphi 2\ s_2(1-s_2)$
φs_3
$\varphi\ {s_2}^2$
A_{12}
$\varphi 2\ s_4(1-s_4)$
AS_2
$\varphi\ {s_4}^2$
Pr(LS=2)
A
$\varphi\ (1-\beta_3)$
D
$(1-\varphi)$

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 ~~($\varphi\phi$~~ 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~~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:

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

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

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

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.

RESULTS

Model performance evaluated on simulated datasets

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

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

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

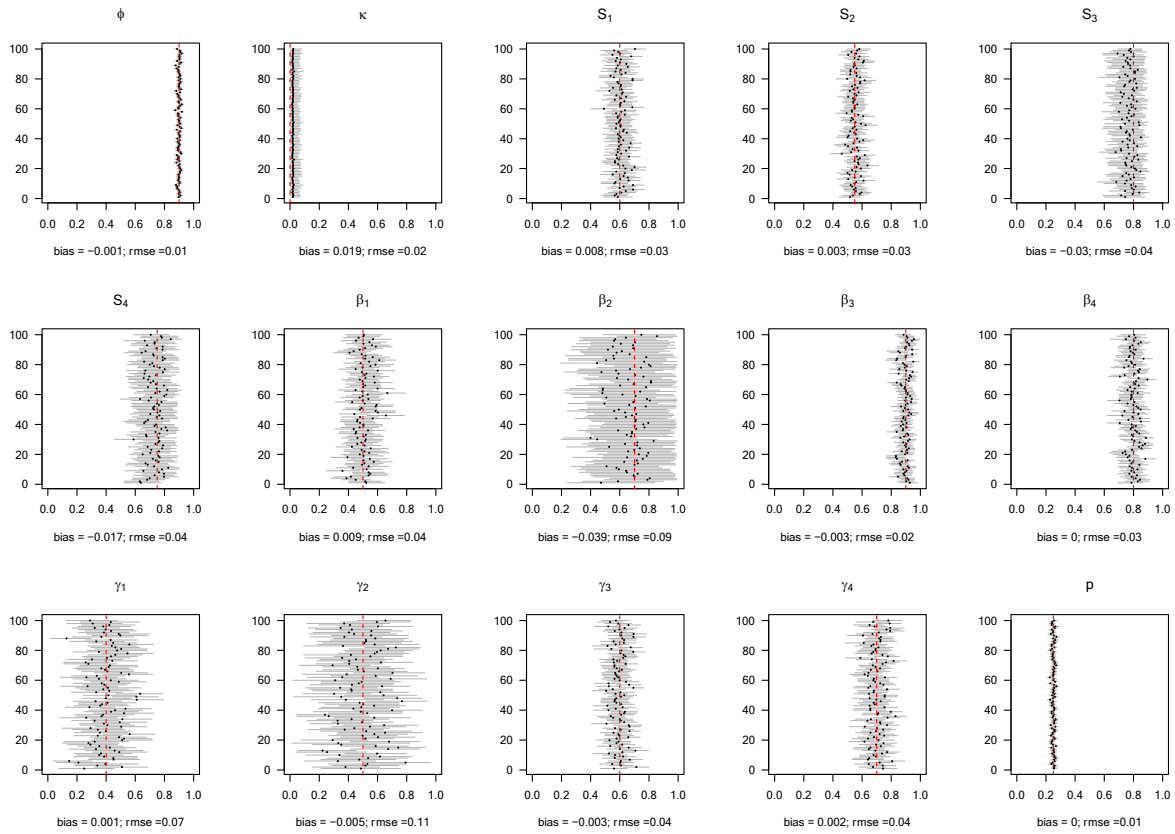

Figure 2. Performance of the model on simulated data with low detection with seasonal departure (scenario S2). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given by 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, ~~and~~ β_2 ~~after loss a cub litter resp.~~ 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, ~~and~~ γ_2 ~~after loss a cub litter resp.~~ loss of a yearling litter, γ_3 for successful breeder, γ_4 for female without dependent offspring), p is detection probability.

Case study: Polar bear demography

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

Table 2: Parameter estimates. Means are given with 95% credible intervals (CI). Dependent offspring (cub age <1 y.o., yearling 1 y.o.) survival and breeding probabilities are conditioned upon mother survival, litter size probability of producing a singleton is as well conditioned upon 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**	γ_1=γ_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

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

DISCUSSION

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

the ~~include~~ inclusion of prior information when available (McCarthy and Masters 2005) to improve the estimation of model parameters.

For polar bears, we showed that outcome of the previous breeding event influenced breeding probability. Reduced offspring survival one year, for example due to poor environmental conditions (Derocher et al. 2004), might therefore increase intervals between successful reproduction through reduced breeding probability the next year (Wiig 1998). This means that by ignoring multiple-year dependency among mother and offspring, classical models can underestimate reproductive intervals, therefore risking to overestimate the population growth rate. However, the biological relevance of our model is currently limited, because we ignored temporal and individual heterogeneity among females in the model. Survival rates for independent female bears (0.93) were close to an earlier study for the same population (0.96), based on telemetry data (Wiig 1998). Our results may overestimate dependent offspring survival because we focused on resident bears captured more than once. Wiig (1998) results indicated that females in Svalbard went into den on average every second year (while successful breeding means denning on a three-year interval), which seems coherent with our results (about 33% chances of successful reproduction over a three-year period).

Here, we proposed a general model structure that can be applied to other species providing EPC. The originalities of our approach lie in using family structure to define statistical units in our model, and the inclusion of variable timing at offspring independence. ~~It~~ ~~allows~~Using families instead of individuals allows for the inclusion of ~~to include~~ dependency among individuals over multiple-years and therefore the ~~evaluate~~ evaluation of trade-offs and correlations ~~correlations~~ between offspring's and parents' life history parameters. Our model could be ~~applied to other species providing EPC, such as wolves, showing variable litter size and age at offspring independence. However, applying our model to species like elephants, killer whales or humans would require including an additional 'post-reproductive' stage and~~

~~estimate the age at menopause. Such extensions of our model could be~~ used, for example, to evaluate the population-level consequences of positive or negative correlation between parents' and offspring's traits (e.g. food sharing among group members Lee 2008; or parent-offspring conflict Kölliker et al. 2013). In the case of social species (e.g. primates, elephants, orcas, wolves), several adults often play a role in caring for offspring. In addition, females often give birth to new offspring while still caring for older offspring and, above a certain age, adolescent dependent offspring can survive despite the loss of their mother and gain independence at various ages. In such cases, the number of states to represent all possible family units' composition can rapidly increase, leading to potential computational challenges to deal with huge matrices. One solution is to use sparse matrices ~~tools in matlab which seem to work well up to XX states~~ to store the data efficiently and optimize matrix calculations. Above this level of complexity, an alternative solution is to limit the number of states by simplifying the life cycle depending on the question of interest (e.g. focusing on mother and maternal grand-mother considering only one litter, or focusing on mother caring alone for one or more litters). For polar bears specifically, future analyses will integrate in the model the effect of female age on survival and reproductive success (Atkinson and Ramsay 1995; Folio et al. 2019) and influence of climatic variables on body weight and demography (Derocher et al. 2004; Stirling and Derocher 2012) as individual and environmental covariates in a regression-like framework. Our model could then be used to provide population predictions of the demographic response of the Barents Sea polar bear population under climate change (Hunter et al., 2010; Regehr et al., 2016, 2018, Laidre et al. 2020).

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Data Accessibility Statement : Authors agree to archive the data used in this manuscript in a publicly accessible repository such as Dryad and Github upon acceptance of the manuscript (together with R scripts to run the model and the simulation study).

Authors' contributions: SC, OG, NY and RP conceived the ideas and designed methodology; JA, RAI and ØW collected the data; SC analysed the data; SC led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

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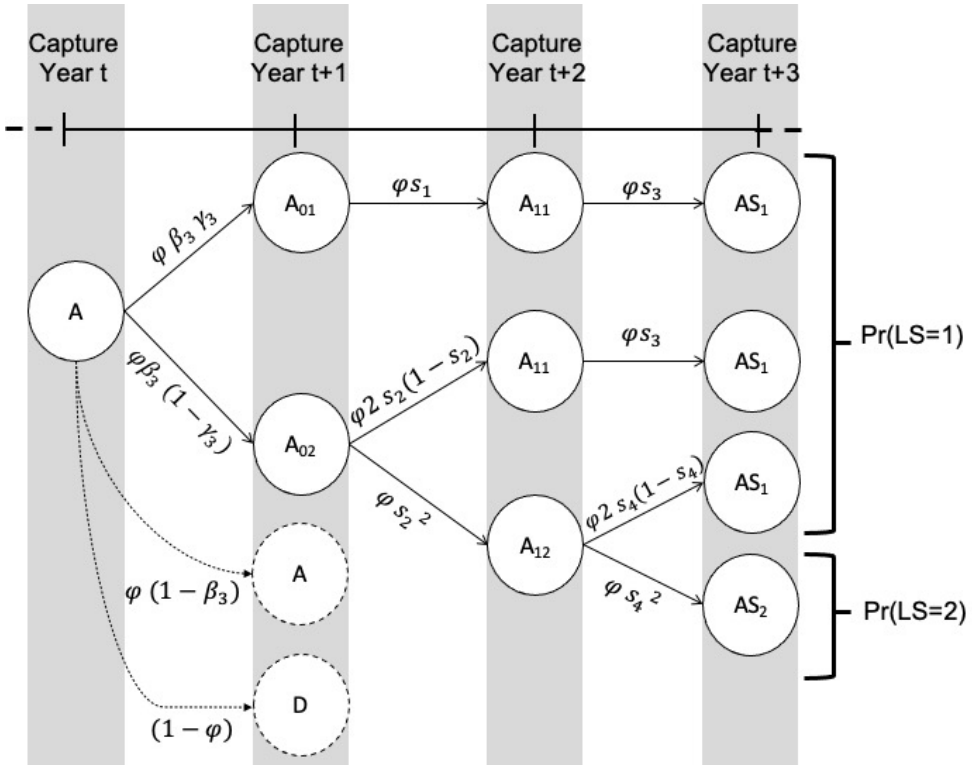

Figure 1: Life history events with associated probabilities of raising one (X=1) or two (X=2) offspring to independence over a 3 years period for a female polar bear alive and without dependent offspring at the beginning of the period (state A). State A01 represents a female with one dependent cub of 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.

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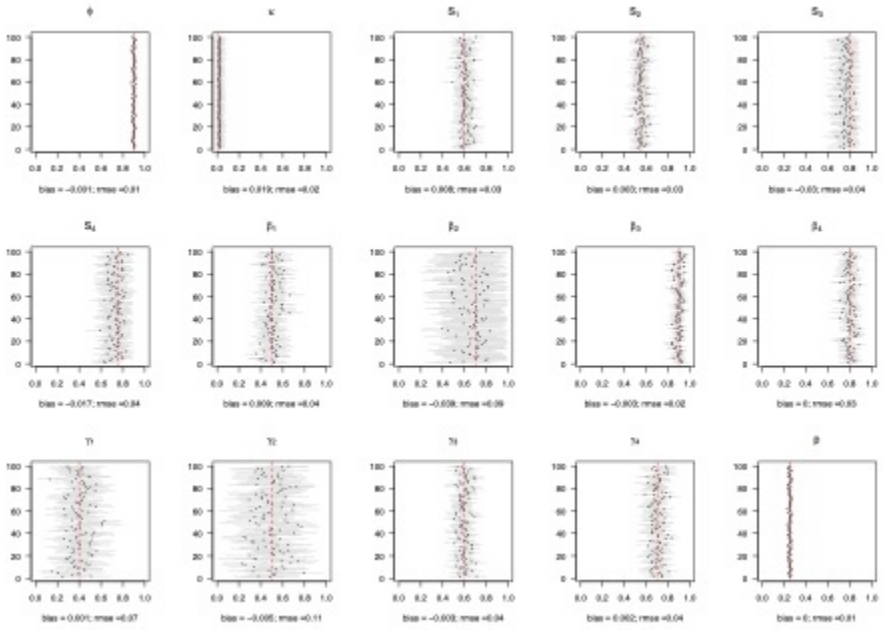

Figure 2. Performance of the model on simulated data with low detection with seasonal departure (scenario S2). For each of the 100 simulated data sets, we displayed the mean (circle) and the 95% confidence interval (horizontal solid line) of the parameter. The actual value of the parameter is given by 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.

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