

**An integrated population model for a long-lived ungulate:  
more efficient data use with Bayesian methods**

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Abstract:	We develop an integrated population model for a population of Svalbard reindeer ( <i>Rangifer tarandus platyrhynchus</i> ), and show how the model succeeds in extracting more information from the data and separating different sources of variability in population estimates. The model combines individual mark-recapture data with population counts and harvesting data within a Bayesian model framework, and accounts for observation error, environmental and demographic stochasticity and age structure. From this model we obtain estimates of population size, as well as age-specific survival and fecundity over time. The model provides estimates of age structure at a finer scale than that found in the census data, and enables us to estimate a survival parameter for which there is no information in the mark-recapture data. We use data from independent censuses of the same population to evaluate population estimates obtained from the model, and show that it is successful at correcting for different types of observation error. Our work demonstrates how integrated Bayesian population

	<p>modeling can be used to increase the amount of information extracted from collections of data. This includes estimating age structure from non-age-structured census data and combining it with estimates of age-specific life history parameters, while accounting for different sources of variability. This represents an important step towards increasing the predictive ability of population growth models for long-lived species.</p>

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## 18 **Abstract**

19 We develop an integrated population model for a population of Svalbard reindeer  
20 (*Rangifer tarandus platyrhynchus*), and show how the model succeeds in extracting  
21 more information from the data and separating different sources of variability in  
22 population estimates. The model combines individual mark-recapture data with  
23 population counts and harvesting data within a Bayesian model framework, and  
24 accounts for observation error, environmental and demographic stochasticity and  
25 age structure. From this model we obtain estimates of population size, as well as  
26 age-specific survival and fecundity over time. The model provides estimates of age  
27 structure at a finer scale than that found in the census data, and enables us to  
28 estimate a survival parameter for which there is no information in the  
29 mark-recapture data. We use data from independent censuses of the same  
30 population to evaluate population estimates obtained from the model, and show  
31 that it is successful at correcting for different types of observation error. Our work  
32 demonstrates how integrated Bayesian population modeling can be used to increase  
33 the amount of information extracted from collections of data. This includes  
34 estimating age structure from non-age-structured census data and combining it  
35 with estimates of age-specific life history parameters, while accounting for different  
36 sources of variability. This represents an important step towards increasing the  
37 predictive ability of population growth models for long-lived species.

## 38 **Introduction**

39 Understanding demographic processes and how they are influenced by the  
40 environment is a fundamental goal of ecological research. This task is becoming  
41 ever more important as environments are changing and many populations are in  
42 decline (Hirsch 2010). However, there are a number of challenges involved in  
43 analyzing the dynamics and demography of wild populations.

44 Biological systems are complex, and population dynamics are often  
45 influenced by a large number of factors, including interspecific interactions, life  
46 history traits, density effects, migration, and a multitude of environmental  
47 variables. In order to make meaningful predictions about how a population might  
48 respond to changed conditions one must understand how these different effects  
49 interact. This requires both good data and population models that capture the  
50 underlying processes (Buckland et al. 2007).

51 Disentangling the different processes is made harder by the fact that  
52 observational data are subject to measurement error (Clark and Bjørnstad 2004).  
53 Thus, observed fluctuations in population size and demographic rates reflect both  
54 true demographic variability and variation caused by observation error (e.g.  
55 Ahrestani et al. 2013). In addition, population dynamics are influenced by two  
56 types of stochasticity (Lande et al. 2003). Chance realizations of survival and  
57 reproduction create variation among individuals, known as demographic  
58 stochasticity (May 1973, Roughgarden 1975), whereas fluctuations in the  
59 environment lead to environmental stochasticity (May 1973, Leigh 1981). This  
60 causes the observed survival and fecundity to differ from expected rates. To make

61 matters more complicated, population structure can have a substantial influence on  
62 how populations respond to perturbations. Different types of individuals (e.g.  
63 individuals of different ages) often respond differently to factors such as density and  
64 climate, causing potentially large differences in population dynamics in populations  
65 of equal size, even when they are exposed to the same conditions (Coulson et al.  
66 2001).

67         Separating these different sources of variability in the data can be tricky.  
68 Hidden process models provide a useful way of dealing with the observation error  
69 (Newman et al. 2006) by using separate, but parallel and linked models of the  
70 underlying (unknown) population process and of our observations. Integrated  
71 population modeling (IPM) is a technique that has been developing rapidly over  
72 recent years and that allows one to combine different types of observations in a  
73 single model framework that utilizes hidden process models (Besbeas et al. 2002,  
74 Buckland et al. 2007, Schaub and Abadi 2011). In this way it is possible to account  
75 for different types of uncertainty in the data, and to exploit available data in a  
76 more efficient manner (Schaub and Abadi 2011). By combining population count  
77 data with different types of demographic data in a single model one can obtain  
78 more precise estimates of demographic parameters, and even estimate parameters  
79 that have not been measured directly (Besbeas et al. 2002, Tavecchia et al. 2009,  
80 Abadi et al. 2010).

81         In this paper we present an IPM for a population of wild Svalbard reindeer  
82 (*Rangifer tarandus platyrhynchus*) and demonstrate how the above issues can be  
83 dealt with to improve estimates of population size and demographic parameters.

84 This system has several characteristics that makes it particularly useful for  
85 overcoming some of the described challenges. Svalbard reindeer are fairly  
86 stationary, and show little fear of humans (Tyler and Øritsland 1989). They are  
87 found in small groups in areas with high visibility and no predators, making them  
88 easier to observe and count than many other large ungulates. Svalbard reindeer are  
89 long lived and are part of a simple community with no other competing herbivores  
90 (Hansen et al. 2013), but experience extreme fluctuations in weather and  
91 environmental conditions. This makes the system a suitable candidate for studying  
92 effects of climate and density on mammal life history and population processes.  
93 Previous studies of the system have demonstrated strong inter-annual variation in  
94 survival, fecundity and population growth rates (Aanes et al. 2000, Solberg et al.  
95 2001, Albon et al. 2002, Stien et al. 2002, Hansen et al. 2011), indicating that there  
96 are also substantial fluctuations in age structure. This means that age should be  
97 accounted for in future studies, but also provides an opportunity to examine how  
98 this variation in population structure influences population dynamics. In this paper  
99 we combine individual mark-recapture data with census data in a model that not  
100 only accounts for age effects, but also estimates population numbers at a finer scale  
101 of age structure than is directly represented in the census data. Estimates are then  
102 compared to count data from independent censuses in the same study area.

### 103 **The study species and data**

104 This study is based on data from a population of Svalbard reindeer, a wild  
105 sub-species of *Rangifer* that is endemic to Svalbard. Data were collected in the

106 Reindalen-Semmeldalen-Colesdalen valley system (approx. 78N, 16E) in central  
107 Spitsbergen, the largest island in the Svalbard archipelago (see Solberg et al. 2001,  
108 Stien et al. 2012, for a detailed description of the study area). In Svalbard, suitable  
109 vegetated reindeer habitat is mainly restricted to semi-isolated valleys and lowland  
110 plains separated by glaciers, mountains or fjords. Thus, in contrast to most other  
111 *Rangifer*, Svalbard reindeer do not migrate and are fairly stationary year-round,  
112 typically with overlapping seasonal ranges and annual home range sizes of a few  
113 km<sup>2</sup> (Tyler and Øritsland 1989). The reindeer occur alone or in small groups of up  
114 to about five animals. Females produce their first calf at two years of age or later,  
115 and calving is highly synchronous, with 90% of calves being born within the first  
116 ten days of June (Tyler 1987). Twinning has never been reported.

117 Previous studies have shown that female Svalbard reindeer can live to an  
118 age of at least 16 years (Tyler and Øritsland 1999). They are unlikely to be subject  
119 to strong interspecific competition for resources, being the only large herbivore in  
120 Svalbard, and they also experience no significant predation. Only a handful of  
121 observations exist of reindeer being killed by polar bears (*Ursus maritimus*;  
122 Derocher et al. 2000), and predation on newborn reindeer calves (by Arctic fox,  
123 *Vulpes lagopus*) has only been observed once (Prestrud 1992). However, each fall  
124 approximately 150-200 Svalbard reindeer are shot by local hunters (about 39% of  
125 these within the study area; Governor of Svalbard 2009).

126 In 1994, 23 female reindeer were caught and marked in late summer. Since  
127 then, between 10 and 90 new females (mainly calves) have been caught and marked  
128 in winter (around April) each year, and previously marked individuals have been



129 recaught (on average 60–70 animals recaught each winter, although numbers vary).  
130 The current study uses data from 1994-2012. In addition, summer censuses have  
131 been conducted in July-August each year since 1996, in which numbers of  
132 unmarked animals (identified as calves, yearling females, yearling males, adult  
133 females, or adult males) and the identity of observed marked individuals have been  
134 recorded, along with information about their reproductive status (with or without  
135 calf at heel).

136 Winter captures and summer censuses have been carried out in the main  
137 valleys Reindalen, Semmeldalen and Colesdalen as well as in smaller side valleys  
138 (hereafter referred to as the study or census area). High mountains, glaciers and  
139 the ocean keep the study area quite isolated from surrounding valleys and  
140 populations, and observations of marked individuals outside the defined study area  
141 are infrequent. From GPS-collars fitted on 38 adult females for the period  
142 2009-2012 (Meland 2014), only 9% of downloaded positions during the summer  
143 censuses were located outside the study area. During the winter capture field work  
144 the number was higher, with 27% outside, but a large proportion of these positions  
145 were close to the study area border (typically at a slightly higher elevation than the  
146 300 meters above sea level limit set for detection in summer). These excursions out  
147 of the study area are usually of a temporary nature, with the animals returning  
148 either in the same season or later. This demonstrates the high site fidelity of female  
149 Svalbard reindeer in this semi-isolated system, wherein they return to the same  
150 calving areas each summer (Hansen et al. 2010), and suggests that the exchange of  
151 individuals with surrounding populations is limited.

152 Summer censuses are conducted on foot by two or more observers, using  
153 binoculars and telescopes. The length of these censuses has varied from 5-12 days  
154 due to parallel studies performed in some years. Because of the study area's open  
155 landscape, animals are often spotted at long distances (up to several km),  
156 regardless of whether they are collared or not, and observers rarely fail to identify  
157 marked individuals. During the whole study period there were only 21 cases of  
158 unidentified marked females. Unmarked individuals are recorded as calves, male  
159 yearlings, female yearlings, male adults or female adults. In this study we only use  
160 data on females (except for calves, in which sex is not known; see section on  
161 Population Model). All observations of marked individuals during the census  
162 period are recorded, both within and outside the actual census. Observed calves  
163 are assigned to females by their behavior. Calves usually stay close to their  
164 mothers, so females with no unassigned calves nearby are recorded as not having a  
165 calf (after a period of observation). In this way, the reproductive status has been  
166 reliably determined for more than 90% of observed marked females. Repeated  
167 observations of females and calves during the summer season have shown that the  
168 misclassification rate of reproductive status using these methods is lower than 2%.

169 In addition to the mark-recapture data and summer census data we have  
170 used hunting statistics from the Governor of Svalbard (a total of 531 female  
171 reindeer hunted in the study area between 1994 and 2011) and information about  
172 285 females that were culled between 1994 and 2008 for the purpose of an  
173 experimental parasite study (Albon et al. 2002, Stien et al. 2002). These animals  
174 are hereafter referred to as "hunted" and "culled," respectively. Furthermore,

175 estimates from the IPM are compared with counts from independent census data  
176 (from transects walked through the study area; see Solberg et al. 2001). This  
177 independent census also recorded the number of reindeer carcasses. Carcasses of  
178 reindeer that died within the last year (typically the previous winter; Tyler 1987)  
179 are easily detected as white (fur) patches on the tundra and are quite  
180 distinguishable from older carcasses. Therefore, the number of carcasses found may  
181 serve as a proxy of winter mortality (Tyler 1987).

## 182 **The model**

183 In this integrated population model we combine individual mark-recapture data,  
184 census data and hunt/cull data in a common Bayesian model framework. A  
185 population process model is used to describe the changes in population size and  
186 structure over time. This is the underlying biological system that we are trying to  
187 understand. Observation models are used to link the different types of observed  
188 data to this latent process.

189 Individual mark-recapture data from winter and resighting data from  
190 summer are used to estimate natural (apparent) survival rates. Survival of hunted  
191 and culled individuals (up until death) is included in the estimation process, but  
192 their death is not since it does not represent natural mortality. The summer  
193 resighting data is also used to estimate fecundity based on observed reproductive  
194 status. In addition, census data on unmarked individuals help to inform these  
195 rates. We distinguish between the observation probability of marked individuals  
196 within the census period (assumed to be equal to that of unmarked individuals; see

197 model section 3 below) and the observation probability of marked individuals  
 198 outside the census period. Both types of observations are included in the  
 199 estimation of survival and fecundity rates (model section 2). An overview of  
 200 different types of data and where they enter the model is presented in Fig. 1, and a  
 201 list of the main parameters can be found in Table 1.

## 202 1. Population model

203 The population model describes how the study population changes in size and  
 204 structure over time. Due to the nature of the available data, the population model  
 205 is a combination of stochastic and deterministic processes. Natural survival is  
 206 modeled as a binomial process with a mean survival rate,  $q_{a,t}$ , where  $a$  is age and  $t$   
 207 is year. However, each year a number of individuals are killed by humans, either  
 208 hunted or culled for scientific purposes. These numbers are treated as known, and  
 209 therefore have to be subtracted from the population in a deterministic manner.  
 210 Given the number of individuals of age  $a$  in year  $t$ , we therefore have (for yearlings  
 211 and adults,  $a > 0$ )

$$N_{a+1,t+1} \sim \text{Bin}(N_{a,t} - H_{a,t}, q_{a,t}), \quad (1)$$

212 where  $N_{a,t}$  is the number of females of age  $a$  in the population at time  $t$ , and  $H_{a,t}$  is  
 213 the number of females of age  $a$  that were killed by humans at time  $t$ . A year in the  
 214 model runs from August to August.

215 Female Svalbard reindeer do not produce more than a single calf per  
 216 season (Tyler 1987). Therefore, the number of calves present from females of age  $a$   
 217 at a given time step can be modeled as a binomial distribution,

$$C_{a,t} \sim \text{Bin}(N_{a,t}, f_{a,t}), \quad (2)$$

218 where  $f_{a,t}$  is the probability of a female of age  $a$  having a calf at heel at time  $t$ . For  
 219 simplicity, we will refer to the probability of having a calf at heel during the census  
 220 as fecundity, but it is important to note that early calf mortality affects this rate.  
 221 The total number of calves in the population is then  $N_{C,t} = \sum_a C_{a,t}$ , and the  
 222 number of female calves can be modeled as  $N_{0,t} \sim \text{Bin}(N_{C,t}, r)$ , where  $r$  is the calf  
 223 sex ratio. We have set  $r = 0.5$ , as we do not have sufficient data to estimate this  
 224 sex ratio accurately, nor any evidence that it is skewed.

225 The population at time  $t$ ,  $N_t$ , consists of two types of individuals; marked  
 226 ( $M_t$ ) and unmarked ( $U_t$ ), such that  $N_t = M_t + U_t$ . Information about  $M_t$  is  
 227 contained in the mark-recapture data, whereas information about  $U_t$  is found in the  
 228 census data. Because we assume that the whole population follows the same  
 229 growth model (Eq. 1 and Eq. 2 above) the two subpopulations have shared  
 230 parameters that can be jointly estimated from the two types of data, as described  
 231 in each of the model sections below. Note that individuals that are caught and  
 232 marked for the first time transition out of the unmarked subpopulation and into  
 233 the marked one. These transitions are known and can be entered directly into the  
 234 model without any stochasticity.

## 235 **2. Model for individual mark-recapture data**

236 The likelihood of the mark-recapture data is constructed based on a state-space  
 237 formulation of the Cormack-Jolly-Seber model (Lebreton et al. 1992, Gimenez et al.

238 2007, Royle 2008, Kéry and Schaub 2012). Thus, a state process governs whether  
 239 an individual is alive ( $z = 1$ ) or dead ( $z = 0$ ), and the total number of marked  
 240 animals in the population at time  $t$  is estimated as  $\sum z$  over all individuals (note  
 241 that subscripts for individual and time have been left off here for simplicity). The  
 242 probability of an individual being resighted at a given time step is then modeled as  
 243 the product of an observation probability,  $p_t$ , and the state  $z$  of that individual,  
 244 thus ensuring that dead individuals can never be resighted. Because females in our  
 245 population only produce single calves, we have also treated the presence or absence  
 246 of a calf as a female state. We are not interested in the probabilities of females  
 247 moving between these two states, and have therefore chosen not to use a multistate  
 248 model, but rather to add a second state process similar to the survival process.  
 249 Thus, the reproductive state of an individual is treated as the outcome of a  
 250 Bernoulli process with a probability consisting of the product of fecundity ( $f_{a,t}$ )  
 251 and the alive/dead state variable  $z$ .

252 Because our data is collected twice a year we estimate seasonal survival  
 253 (August to April, and April to August), instead of yearly survival. We have

$$\text{logit}(s_{a,i}) = \mu_{s,a} + \epsilon_{s,i} + \gamma_{s,a,i}, \quad (3)$$

254 where the subscript  $a$  signifies age (from yearling and up,  $a > 0$ ),  $i$  denotes time (in  
 255 seasonal periods), and  $\epsilon_{s,i} \sim N(0, \sigma_s^2)$ . The term  $\epsilon_{s,i}$  represents temporal  
 256 fluctuations that are shared across all age groups (e.g. common responses to  
 257 density and environmental effects). The term  $\gamma_{s,a,i} \sim N(0, \sigma_{s\gamma}^2)$  accounts for  
 258 differences among age groups in the temporal fluctuations. Then,  $q_{a,t}$  in Eq. 1 is

259 equal to  $s_{a,i} \times s_{a,i+1}$ , where  $i$  and  $i + 1$  are the two seasonal periods (August to  
260 April and April to August) of year  $t$ . Estimates of recapture probability in winter  
261 and observation probability within and outside the census period in summer are  
262 allowed to vary randomly from year to year.

263 Calves are born in June, but do not get marked until the following April.  
264 Thus, new individuals do not enter the mark-recapture data until they are about 10  
265 months old. This leaves a gap in the survival estimates. In the data used for this  
266 study we have no information about calves before the summer census, and therefore  
267 use the number of calves seen in summer as a measure of fecundity. We know from  
268 previous studies that the survival of calves from shortly after birth through their  
269 first summer is extremely high (close to one; Tyler 1987), but survival from a calf's  
270 first August until the next April is not known. However, because we are using an  
271 integrated population model that links all the different available data and  
272 processes, we still have the opportunity to estimate these "missing" survival rates  
273 (based on information such as the number of calves seen in August compared to the  
274 number of yearlings seen next August, combined with survival estimates for the  
275 period from when they are marked at 10 months old until the August census). We  
276 let (female) survival in this initial age step ( $s_{0,i}$ ) follow the same type of model as  
277 survival from August to April in older individuals (Eq. 3), with a calf-specific mean  
278 ( $\mu_{s,0}$ ), the same temporal residual as other ages ( $\epsilon_{s,i}$ ), and a calf-specific temporal  
279 residual term ( $\gamma_{s,0,i} \sim N(0, \sigma_{s\gamma,c}^2)$ ).

280 The oldest female in our data set had an estimated age of 19 years at  
281 death, but nearly all females die before they turn 16. Based on visual inspection of

282 the age variation in the survival and fecundity estimates from a fully age-structured  
283 model, we pool the ages into six age classes; 0 years, 1, 2, 3-8, 9-11, and 12 and  
284 older; and estimate seasonal survivals within each.

285 For fecundity we use a similar model,

$$\text{logit}(f_{a,t}) = \mu_{f,a} + \epsilon_{f,t} + \gamma_{f,a,t}, \quad (4)$$

286 where  $a > 1$  because Svalbard reindeer never produce calves before two years of  
287 age. Here we again assume that  $\epsilon_{f,t} \sim N(0, \sigma_f^2)$  and  $\gamma_{f,a,t} \sim N(0, \sigma_{f\gamma}^2)$ . Note that  
288 time here is given in whole years, rather than seasons, since calves are produced  
289 only once a year. Fecundity (probability of giving birth to a calf, or more precisely  
290 having a calf (of either sex) in August) is estimated for age classes 2 years, 3, 4-9,  
291 10-12, and 13 and over. Thus, each fecundity estimate can be paired with a  
292 (annual) survival estimate during pregnancy (e.g. fecundity of 4-9-year-olds is  
293 linked to survival of 3-8-year-olds).

### 294 3. Model for census data

295 We assume that the observation probability of unmarked animals equals that of  
296 marked individuals within the census. We therefore use a binomial model to  
297 describe the relationship between our counts of unmarked animals and the true size



298 of the unmarked population each year,

$$\begin{aligned} U_{1,t}^c &\sim \text{Bin}(U_{1,t}, p_t), \\ U_{ad,t}^c &\sim \text{Bin}\left(\sum_{a>1} U_{a,t}, p_t\right), \end{aligned} \tag{5}$$

299 where  $U^c$  is the number of unmarked individuals of an age class (yearling, adult)  
 300 counted in year  $t$ ,  $U$  represents the total population of unmarked individuals  
 301 (modeled by Eq. 1), and  $p_t$  is the observation probability which is also estimated  
 302 from individual mark-recapture data within the census.

303 In summer, calves are not marked and therefore do not have an observation  
 304 probability estimated from the mark-recapture data. However, calf observations in  
 305 this system are not independent of adult observations, because calves stay close to  
 306 their mothers. We assume that if a calf is counted, so is its mother. We believe  
 307 that the converse is also true, but have chosen to let the model estimate the  
 308 observation probability of calves given that their mother was counted, to allow for  
 309 the possibility that calves are more difficult to spot in the field than adults. A more  
 310 detailed description of this can be found in the appendix.

## 311 **Model implementation**

312 About 80% of marked individuals were marked as calves and are therefore of known  
 313 age. Animals that were marked as adults and are later hunted, culled, or recovered  
 314 as carcasses have ages estimated from tooth eruption patterns or counts of tooth  
 315 cementum annuli (see Veiberg et al. 2007). Those individuals without an estimated

316 year of birth are reassigned as unmarked individuals for the purpose of the model  
317 (i.e. they are removed from the individual mark-recapture data and reassigned as  
318 unmarked in the census data). This leaves a total of 464 individuals in the  
319 mark-recapture data.

320         Some unmarked animals are recorded with unknown sex. We use the sex  
321 ratio in the rest of the (unmarked) census data each year to estimate how many of  
322 these were females. This is, however, the case for only a small proportion of  
323 individuals (0.01 of adults and 0.13 of yearlings).

324         Because the census periods go over multiple days, it is possible that the  
325 same individual could be counted several times. We have therefore calculated the  
326 average number of times each (observed) marked animal was seen during a given  
327 census (the average ranges from 1.03 to 1.46 in different years), and adjusted the  
328 counts of unmarked animals accordingly.

329         We use annual hunting statistics and the age estimates described above (as  
330 well as known ages of marked individuals, calves and yearlings), to estimate  
331 numbers and ages of hunted females during the study period. The hunting  
332 statistics from before the year 2000 do not contain information about location.  
333 From 2000 forward the statistics show that an average of 39% of the hunted  
334 individuals were shot in our study area, and that the proportion varied little from  
335 year to year. We have assumed that this proportion was the same for earlier years,  
336 as there have been no significant changes in the hunting regime. Hunted individuals  
337 without records of age and/or sex are assigned an age and sex by extrapolation of  
338 the estimated sex and age distributions among the rest of the hunted individuals.

339 In addition to the hunted individuals, 285 females (of these, 25 marked) were culled  
340 between 1994 and 2008 for scientific purposes (Albon et al. 2002). Fifteen of these  
341 were of unknown age and therefore had an age assigned to them based on the mean  
342 annual age distribution of culled individuals.

343 Posterior distributions were found from Markov Chain Monte Carlo  
344 techniques using OpenBUGS (Lunn et al. 2009) via the R2WinBUGS package  
345 (Sturtz et al. 2005) in R 3.0.1 (R Core Team 2013). Uninformative priors were used  
346 throughout the model (Unif(0, 1) for all probabilities/rates, or N(0, 0.001) if on  
347 logit scale; Unif(0, 10) for all  $\sigma^2$ , except  $\sigma_f^2$  and  $\sigma_{f\gamma}^2 \sim \text{Unif}(0, 7)$ ). Our results are  
348 based on 3 chains of 1600000 iterations, discarding the first 1300000 iterations as a  
349 burn in and retaining 3000 (i.e. every 100th) of the remaining values from each  
350 chain. With this approach convergence was reached for most of the nodes as  
351 indicated by Gelman and Rubin's diagnostics (Gelman and Rubin 1992). However,  
352 there were four years in which not all age classes had converged size estimates  
353 (2-year-olds in 1996, 3-8-year-olds in 1996, 2000 and 2002, 9-11-year-olds in 2002  
354 and 2005, and 12 years and older in 2005). Despite this, estimates of total  
355 population size reached convergence for all years.

## 356 Results

357 Annual survival estimates vary among age classes and exhibit strong temporal  
358 variation (Fig. 2a). The highest survival rates are found in the three age classes  
359 containing individuals aged one to eight years. Calves and individuals that are nine

360 years old or above (age classes 9–11 and 12+) have significantly lower mean  
361 survival and also exhibit higher temporal fluctuations in annual survival. Temporal  
362 fluctuations in survival follow similar patterns in all age classes, but there is also  
363 clear evidence of age-year interactions (Fig. 2a;  $\sigma_s^2 = 1.75$  (Credible interval  
364 (CI):1.23–2.46);  $\sigma_{s\gamma}^2 = 0.52$ , (CI:0.18–0.85)). In calves, survival from August to  
365 April is estimated to be high in most years (higher than 0.90 in 14 of the 18 years),  
366 but very low in some years, causing the corresponding variance component to be  
367 large (although with high uncertainty;  $\sigma_{s,c}^2 = 3.01$ , CI:0.54–8.67).

368 Fecundity is estimated to be quite low for 2-year-olds (0.12, CI:0.07–0.19,  
369 Fig. 2b) and to increase until prime age at 4–9 years when a mean proportion of  
370 0.62 (CI:0.58–0.65) of the individuals produce a calf each year. Fecundity decreases  
371 for older individuals, and those aged 13 years or above are shown to have  
372 significantly lower fecundity than prime-aged individuals (0.37, CI:0.24–0.51). Our  
373 estimates show large temporal fluctuations in fecundity. For example, only 12%  
374 (CI:8–16) of prime-aged females (4–9 years) produced a calf in 2008, while in 1999  
375 85% (CI:79–91) of the individuals in this age class contributed an offspring. These  
376 large fluctuations are seen in all age classes. Overall, the different age classes are  
377 shown to have responded similarly to time effects, with the variance in the  
378 interaction term between time and age in the fecundity model ( $\sigma_{f\gamma}^2 = 0.18$ ,  
379 CI:0.01–0.48) being substantially lower than the variance in the term accounting  
380 for time effects alone ( $\sigma_f^2 = 1.14$ , CI:0.80–1.65).

381 The estimated total number of female individuals in the population  
382 fluctuates between 792 (CI:715–891) and 1284 (CI:1206–1371) within the study

383 period with available census data (1996-2012, Fig. 3a). This is on average  
384 approximately two to three times the number of individuals observed in the annual  
385 censuses. The 95% credible intervals are narrow for all population estimates (Fig.  
386 3). The population is dominated by prime-aged individuals (3-8-year-olds). The  
387 calves are the second largest age class in most years, but some years are  
388 characterized by very low calf production causing large fluctuations in the  
389 proportion of calves (from 0.04 (CI:0.04–0.05) to 0.25 (CI:0.23–0.27)), and thus also  
390 in the total population size (Fig. 2b, 3b).

391 The estimated total population size correlates well with the original census  
392 counts to which the model has been fitted (including both marked and unmarked  
393 females observed within the census; Pearson correlation coefficient of 0.52  
394 (0.40–0.62), Fig. 3a). Compared to independent counts of the same population  
395 (covering roughly the same area but conducted along transects through the valleys)  
396 the correlation is slightly higher (0.59 (0.46–0.71), Fig. 3a). Comparing the  
397 estimated annual mortalities to the number of carcasses observed in the study area  
398 each year, we see that spikes in mortality are accompanied by a high incidence of  
399 observed carcasses, whereas years with lower mortality typically show so few  
400 carcass observations that direct comparisons of numbers become difficult (Fig. 4).

401 The recapture probability in winter is estimated to have fluctuated  
402 between 0.25 (CI:0.16-0.36) and 0.68 (CI:0.61-0.76), while the observation  
403 probability within the summer census period ranged between 0.21 (CI:0.18-0.25)  
404 and 0.63 (CI:0.56-0.72). At the beginning of the study period (1995-1999) marked  
405 individuals were also observed outside the census, due to parallel studies and

406 somewhat longer periods with observers present in the study area, but in later  
407 summers most observations were made within the census. The estimated  
408 observation probability of calves of observed females was 0.96 (CI:0.92–1.00),  
409 supporting our notion that if a mother is observed her calf is usually observed as  
410 well. This is also reflected in a close correspondence between the observed and  
411 estimated numbers of calves per female (Fig. 4c).

## 412 Discussion

413 Combining several different types of data in a common framework for analysis  
414 makes it possible to exploit available data in a more efficient manner than with  
415 separate analyses. Here, the integrated population model allows us to extract more  
416 information about each age class than would be possible by analyzing each data set  
417 separately. The joint framework allows information to flow between the different  
418 sections of the model through shared parameters. The data that contain the most  
419 information about a parameter will automatically be given greater weight in the  
420 analysis. In our model we see that the majority of information about survival and  
421 fecundity is found in the individual mark-recapture data. Analysis of this data on  
422 its own produces similar estimates of survival and fecundity as those obtained from  
423 the complete model (although with somewhat higher uncertainties). However, the  
424 IPM allows us to estimate survival for an age class for which we have no individual  
425 survival data (calf survival from August to April). This would not be possible  
426 without the joint model framework. The flow of information from the individual

427 mark-recapture data to the population estimates is high and allows us to obtain  
428 much more detailed population estimates than we would be able to get from the  
429 census data alone. The available census data for this population consists of counts  
430 of calves, yearlings and adults, and does not contain any information about the age  
431 structure within the adult population. By linking the individual mark-recapture  
432 data to this count data through the IPM we have obtained information about this  
433 age structure and how it varies. There are four years for which the model is unable  
434 to separate all age classes reliably (seen by a few estimates that do not converge).  
435 The estimates involved indicate that the model has trouble separating the two  
436 cohorts born in 1993 and 1994. This is not altogether surprising, given that  
437 relatively few individuals were caught in the first year of the study, and there was  
438 no census data, giving the model little information with which to separate the two  
439 cohorts that were calves and yearlings when the individual mark-recapture study  
440 started.

441 Differential variation in survival among age classes (Fig. 2a), combined  
442 with large fluctuations in fecundity (Fig. 2b), causes changes in the population age  
443 structure that persist over long time periods (Fig. 3b). If different age groups  
444 respond differently to environmental conditions, population density etc., these  
445 changes in age structure could potentially have an important influence on the way  
446 population size responds to different conditions (Coulson et al. 2001, Haridas and  
447 Tuljapurkar 2007, Sæther et al. 2013). In addition to accounting for age structure,  
448 our model incorporates variability among individuals in their realized fecundity and  
449 survival, and also allows the expected values of these rates to vary across time

450 steps. In this way, age structure, demographic stochasticity and environmental  
451 stochasticity are all incorporated, making it possible to analyze age structure  
452 effects on population growth, as well as separating out age and demographic  
453 stochasticity effects from those of density dependence and environmental  
454 stochasticity in studies of climate effects and population dynamics.

455         Using shared parameters to link different data sets in this way can cause  
456 problems if the same individuals are found both in the individual data and in the  
457 census data (Kéry and Schaub 2012). The likelihood of the complete model is  
458 formulated based on an assumption that the different data sets are independent,  
459 and a violation of this assumption can cause problems in certain cases (Abadi et al.  
460 2010, Besbeas et al. 2009). We have avoided this by only including unmarked  
461 individuals in the census data (model section 3), while the marked animals are used  
462 in the individual mark-recapture data (model section 2).

463         Our survival estimates show that after their first year of life, female  
464 Svalbard reindeer in the study population generally have a very high survival until  
465 they are about nine years of age (Fig. 2a). This corresponds well with survival  
466 estimates found in a different Svalbard reindeer population by comparing carcass  
467 counts to live counts the previous year (Tyler and Øritsland 1999). However, we  
468 also find quite high survival in the remaining age groups in most years, but with  
469 dramatic decreases in some years. In particular, 1995-1996, 2001-2002 and  
470 2007-2008 were characterized by low survival (and low fecundity and population  
471 growth rates). These drops in vital rates coincide with years of high animal density  
472 combined with icy conditions due to rain-on-snow events, and low population sizes



473 in the following years were also found in a neighboring study population in  
474 Adventdalen (Hansen et al. 2013). The environment therefore seems to have a  
475 strong effect on the survival of the youngest and oldest female reindeer, suggesting  
476 that changes in age structure would modify the response of the population growth  
477 rate to environmental fluctuations. The model presented here makes it possible to  
478 quantify these age-specific environmental effects by separating them from other  
479 factors influencing survival, such as population density (Tyler and Øritsland 1999,  
480 Solberg et al. 2001, Ahrestani et al. 2013). In the current analysis we have not  
481 separated out effects of density on survival and fecundity, but incorporating such  
482 effects more explicitly is a natural next step.

483         The survival probabilities estimated in this model represent apparent  
484 survival, because mortality cannot be separated from permanent emigration out of  
485 the study area. This is common in CJS models (Kéry and Schaub 2012). However,  
486 as described previously, results from a study of GPS-collared females indicate that  
487 permanent emigration is low in this population, at least among adult females, in  
488 which case the estimated survival rates should be close to the true rates in the  
489 study population. Temporary movement in and out of the study area does take  
490 place, so the "true" study area is larger than the area in which data have been  
491 collected. However, exchange of individuals with surrounding populations seems  
492 to be limited, so this does not represent a major problem.

493         The fecundity estimates follow the same annual pattern as survival rates  
494 and correspond well to previous fecundity estimates based on observations of  
495 marked females aged 3 years and above (Stien et al. 2012), showing the same

496 dramatic fluctuations among years and the same basic patterns (Fig. 2b). However,  
497 using the model presented here we have been able to investigate how fecundity  
498 varies among the different age classes (Fig. 2b). Although two-year-olds show  
499 significantly lower fecundity than older individuals, all ages show similar  
500 fluctuations in fecundity from year to year. Thus, none of the age classes are  
501 protected from the extreme drops in offspring production that are seen periodically  
502 throughout the study period (Fig. 2b). Nevertheless, accounting for age-specific  
503 fecundity (along with age structure) could improve the ability of future studies to  
504 predict trends in population growth and how they might be affected by e.g. climate  
505 change. In addition, the extreme drops in fecundity are shown to coincide with  
506 years with lowered survival in some age groups, in particular calves and old  
507 individuals. This means that each of these bad years has a strong negative effect on  
508 two consecutive cohorts (calves and unborn offspring), and thus substantial  
509 influences on future age structure in the population.

510         The strong covariation in fecundity and survival rates in Svalbard reindeer  
511 has also been indicated in previous studies based on live calf:female counts and  
512 carcass counts in summer (Tyler and Øritsland 1999, Solberg et al. 2001). Through  
513 comparison with our independent estimates of survival and population size, we  
514 have shown here that such carcass data can, when compared to population size  
515 estimates the previous year, provide valuable information on extreme drops in  
516 overall survival rates in the population as a whole. Thus, such data can function as  
517 an indicator of population performance, particularly in years with high mortality.  
518 However, carcass data do not (neither alone nor combined with only population

519 counts) provide detailed information on age-specific survival in this population.

520         Our population estimates correlate quite well with the original census data  
521 that went into the model. However, we have also compared our population  
522 estimates to independent counts of the same population. These counts were carried  
523 out along transects with a focus on keeping the search effort and length of census  
524 period as stable as possible from year to year. Having an independent data set of  
525 this kind gives us a unique opportunity to evaluate the population estimates  
526 obtained from the IPM. We see that the population estimates from the IPM  
527 correlate more closely with this independent count data than with the census data  
528 that were included in the model. This indicates that the model has been successful  
529 at correcting for the variation in observation probability in the input census data,  
530 demonstrating the strength of this modeling approach in dealing with observation  
531 error.

532         Using the census data as direct population estimates would indicate  
533 population changes that are inconsistent with the breeding biology of this species.  
534 For example, the census data show a 68% increase in the number of females from  
535 2002 to 2003. This is unlikely in a population without twinning, unless the calf sex  
536 ratio were extremely female biased or a substantial immigration event occurred.  
537 Looking more closely at the data, the number of adult females counted increased by  
538 130 individuals in 2003, despite only 5 female yearlings being counted in 2002. The  
539 integrated population model has successfully weeded out these inconsistencies from  
540 the population estimates. The increase in the estimated number of females from  
541 2002 to 2003 in the model is a much more realistic 22%.

542 Svalbard reindeer are considered easier to observe and count than many  
543 other ungulates (Tyler and Øritsland 1999). Despite this, population estimates  
544 found from the IPM are about two to three times higher than the number of  
545 individuals registered in annual censuses. Thus, our study clearly demonstrates the  
546 importance of using models that account for observation error, rather than relying  
547 directly on count data for obtaining population estimates.

548 In conclusion, using a Bayesian IPM framework has enabled us to combine  
549 individual mark-recapture data, census data and harvesting data in a way that  
550 greatly increases the amount of information provided by the model. In particular,  
551 being able to estimate age structure from non-age-structured census data and to  
552 combine this with estimates of age-specific life history parameters, while accounting  
553 for different sources of variability, is an important step for increasing the predictive  
554 ability of population growth models for long-lived species.

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Table 1: Model parameters and notation

<b>Subscripts/indices:</b>
$a$ – age
$t$ – year
$i$ – season
<b>Variables:</b>
$N$ – total population size
$M$ – number of marked individuals
$U$ – number of unmarked individuals
$C$ – number of calves
$H$ – number of harvested individuals
<b>Parameters:</b>
$q$ – yearly survival
$s$ – seasonal survival
$f$ – fecundity
$r$ – calf sex ratio (proportion females)
$p$ – observation probability
$\mu$ – mean (survival or fecundity) on logit scale
$\epsilon$ – shared temporal residual
$\gamma$ – age-specific temporal residual
$\sigma^2$ – temporal variances

684 **Figure captions**

685 Figure 1. Overview of the different types of data and where they enter the model.  
686 The figure does not show all possible routes of information flow (e.g. counts of  
687 unmarked animals within the census period inform estimation of survival and  
688 fecundity), but is rather meant as a tool for understanding how the model is built  
689 up around the available data sources and where in this paper the different sections  
690 are described. Boxes with dashed outlines represent animals that are not observed.  
691 Blue backgrounds represent unmarked animals, while red backgrounds show  
692 marked individuals. Parameters are in boxes with rounded edges, while square  
693 boxes indicate data. Age is a special case because it enters the model as data, but  
694 is obtained from a combination of other data sources. S1, S2 and S3 indicate model  
695 sections in the text. U, M and N signify the unmarked, marked and total  
696 population, respectively.

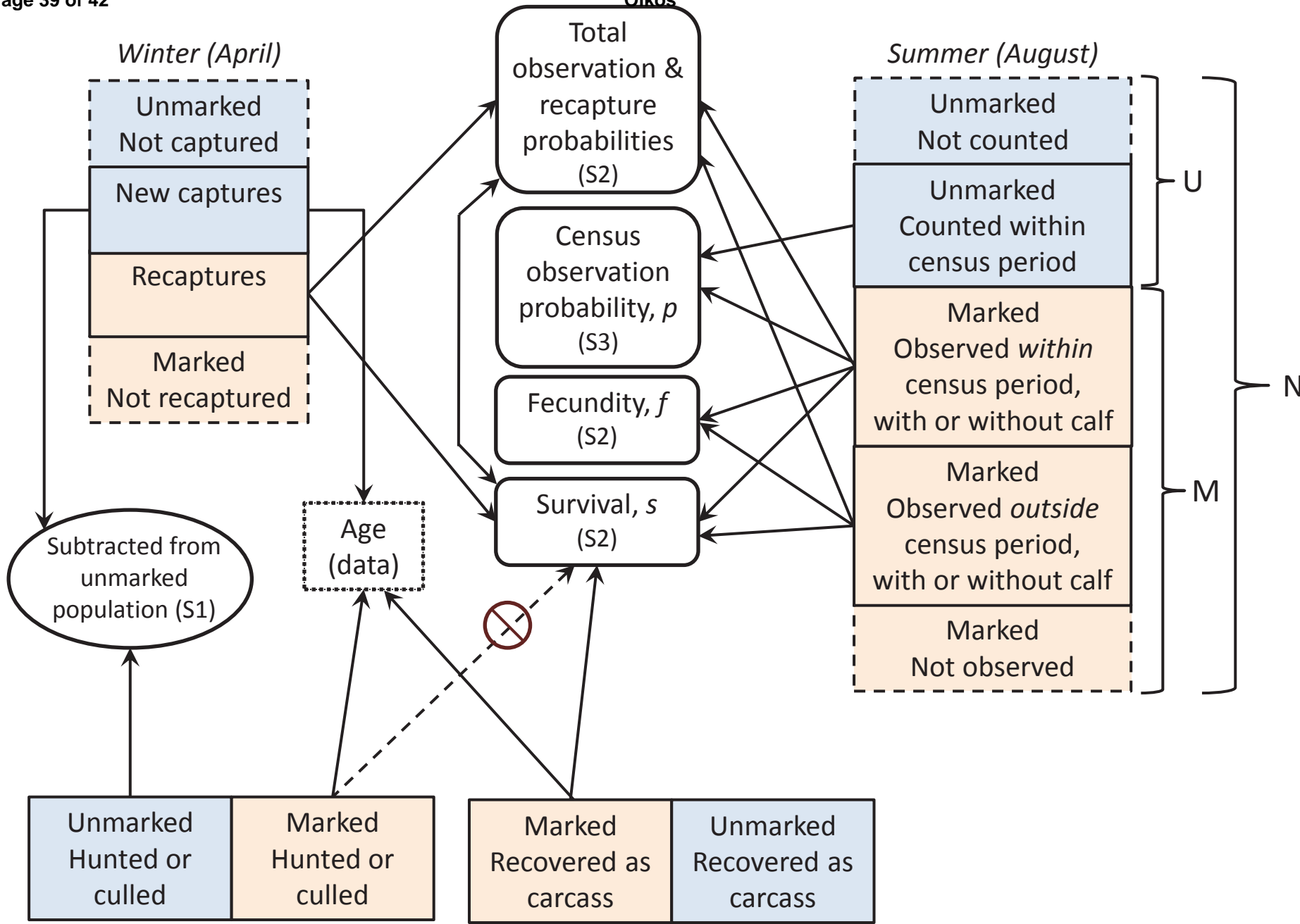
697 Figure 2. (A) Estimated annual survival from each year to the next ( $q_{a,t}$ ) and (B)  
698 estimated fecundity ( $f_{a,t}$ ) of different female age classes in Svalbard reindeer  
699 population. Parameter estimates are represented by the means of posterior  
700 distributions (lines) with associated 95% credible intervals (points at upper and  
701 lower limits) showing the uncertainty in the estimates.

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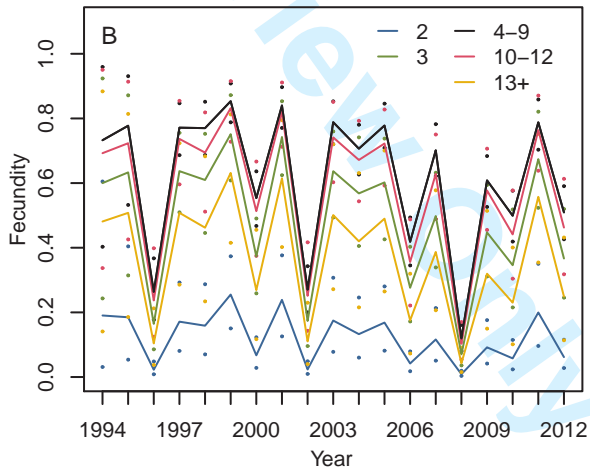
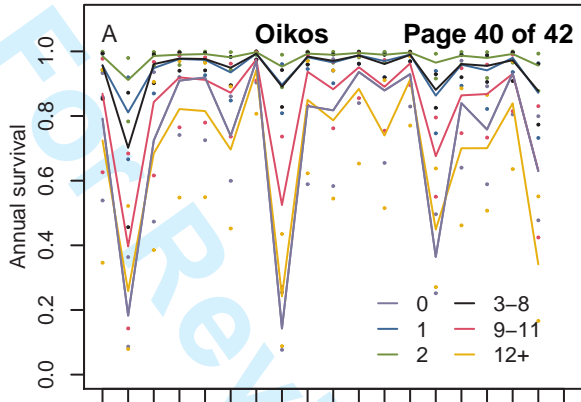
702 Figure 3. Estimated size of female segment of Svalbard reindeer population. (A)  
703 Estimated total population size (black line), annual census of the total population  
704 to which the IPM is fitted (grey solid line), and independent census data of the  
705 population (grey dashed line). From 2008 the two census data sets were not  
706 independent (dotted line). (B) Estimated size of each age class (solid lines).  
707 Estimates are represented by the means of posterior distributions (solid lines). The  
708 uncertainty of the estimates is shown by the 95% credible interval (points).

709 Figure 4. Predicted relationships between estimates and independent observations  
710 of female mortality and number of calves per adult female (black solid lines) with  
711 95% credible intervals (black dotted lines). (A) Estimated number of dead calves  
712 from IPM vs. observed carcasses of calves. Intercept = 20.66 (10.63-32.98), slope =  
713 3.40 (2.78–3.99),  $R^2 = 0.85$  (0.72–0.95),  $n = 16$ . (B) Estimated number of dead  
714 adults from IPM vs. observed carcasses of adults. Intercept = 28.13 (18.30, 38.70),  
715 slope = 4.39 (3.30–5.56),  $R^2 = 0.76$  (0.59–0.89),  $n = 16$ . Parameter estimates are  
716 displayed by points (means of posterior distributions) with associated 95% credible  
717 intervals (vertical bars) showing the uncertainty of the estimates. The grey solid  
718 lines show the 1:1 relationships. Only female individuals are included. (C)  
719 Estimated number of calves per adult female vs. observed number of calves per  
720 adult female. Intercept = 0.08 (0.05–0.11), slope = 0.81 (0.74–0.86),  $R^2 = 0.96$   
721 (0.93–0.98),  $n = 12$ .

Oikos







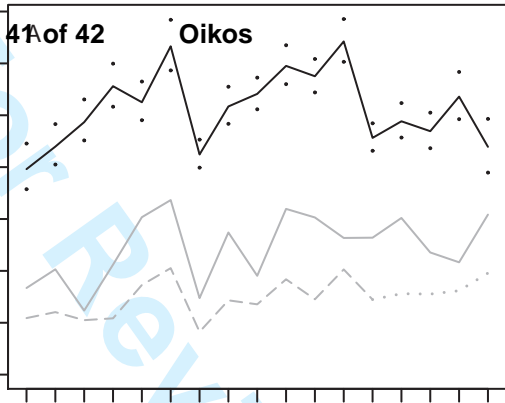
Number of individuals

1200

800

400

0



B

Number of individuals

600

400

200

0

0

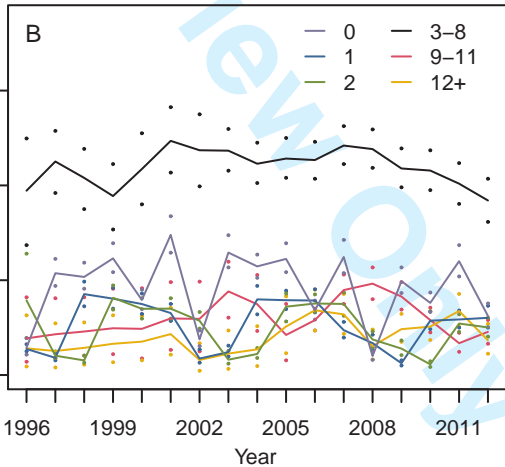
1

2

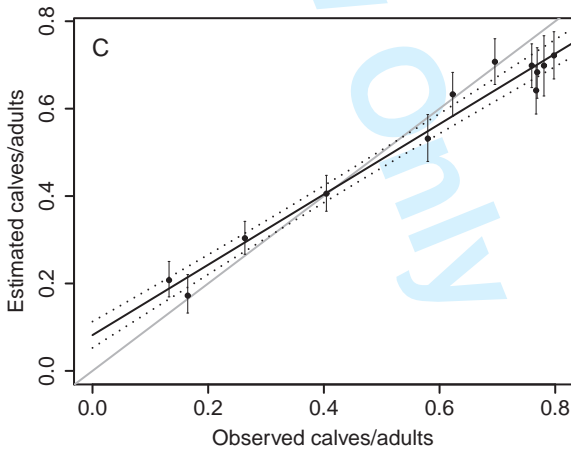
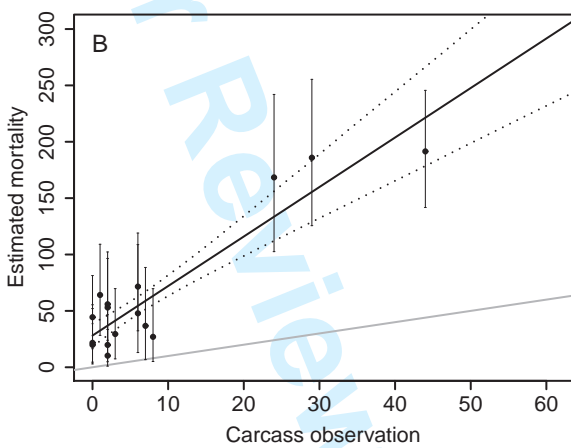
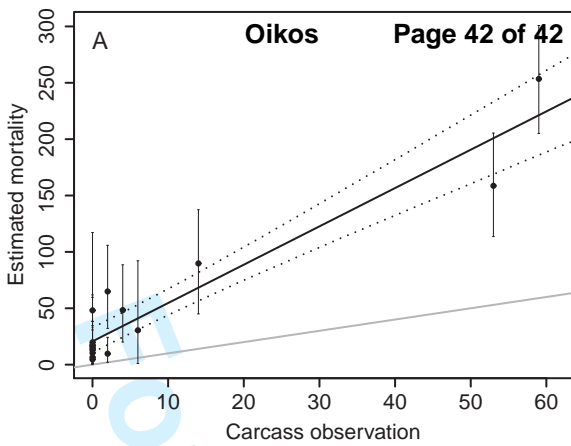
3-8

9-11

12+



Year



## Appendix: Observation probability of calves

We let the model estimate the observation probability of calves given that their mothers are observed. Observed females are of two types; marked and unmarked. The number of observed marked females that have calves is already estimated in the model as part of the reproductive state process, but the number of calves among observed unmarked females is unknown. We therefore use the ratio of the estimated number of calves produced by unmarked females (observed or unobserved) and the estimated number of unmarked females present in the population as the probability (in a binomial process) that an observed unmarked female is a mother. Adding these two estimates of calf numbers (among marked and unmarked females) gives an estimate of the total number of calves whose mothers are observed. The number of calves in our census data is then modeled as a binomial process in which these calves have a certain probability of being seen. We assume that this observation probability is the same across years.