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34

## Abstract

35

In nature, individual reproductive success is seldom independent from year to year, due to factors such as reproductive costs and individual heterogeneity.

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However, population projection models that incorporate temporal

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autocorrelations in individual reproduction can be difficult to parameterize,

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particularly when data are sparse. We therefore examine whether such

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models are necessary to avoid biased estimates of stochastic population

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growth and extinction risk, by comparing output from a matrix population

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model that incorporates reproductive autocorrelations to output from a

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standard age-structured matrix model that does not. We use a range of

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parameterizations, including a case study using moose data, treating

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probabilities of switching reproductive class as either fixed or fluctuating.

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Expected time to extinction from the two models is found to differ by only

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small amounts (under 10%) for most parameterizations, indicating that

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explicitly accounting for individual reproductive autocorrelations is in most

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cases not necessary to avoid bias in extinction estimates.

## 50 INTRODUCTION

51 The stochastic dynamics and structure of populations is determined by patterns of  
52 variation in fecundity and survival over the lifetime of individuals. Age-dependence  
53 is one important source of such patterns, and age-structured population models are  
54 therefore extensively used in studies of population dynamics (e.g. Caswell 2001).  
55 However, survival and reproduction are realized at the level of individuals, and  
56 individual demographic rates are not necessarily independent. This gives rise to  
57 correlations in individual demographic rates, potentially influencing population  
58 dynamics. For instance, trade-offs between reproduction and survival have been  
59 widely documented (Stearns 1989), and simulation studies have shown that these  
60 trade-offs can have major effects on population dynamics (Proaktor et al. 2008;  
61 Kuparinen et al. 2012). Similarly, trade-offs between current and future  
62 reproduction have frequently been documented (Stearns 1989; Roff 2002), but  
63 population effects of these trade-offs are more difficult to study using traditional  
64 population models, due to the temporal aspect of the correlation.

65         Correlations in individual reproductive success from one year (or time  
66 step) to the next (hereafter “reproductive autocorrelations”) are found in a wide  
67 range of taxa, including birds (Cam et al. 1998; Veran & Beissinger 2009),  
68 mammals (Boyd et al. 1995; Hamel et al. 2010), amphibians (Yurewicz et al. 2004),  
69 reptiles (Rivalan et al. 2005) and plants (Obeso 2002). Such autocorrelations can  
70 be produced by different underlying biological processes. If reproduction carries a  
71 cost in terms of energy use (Stearns 1992; Edward & Chapman 2011) we might  
72 expect negative reproductive autocorrelation if offspring production in one year

73 reduces the energy an individual has available for offspring production the next  
74 year, or if energy from non-breeding years can be saved up for future breeding (Roff  
75 2002; Yurewicz et al. 2004; Hamel et al. 2010). Individual heterogeneity in female  
76 quality is more likely to cause positive autocorrelation with some females  
77 consistently producing more offspring than others (Högstedt 1980; Weladji et al.  
78 2008). There are two main explanations for individual heterogeneity. There may be  
79 differences among individuals that are fixed from birth or shortly after (“fixed  
80 heterogeneity”; e.g., individuals with different probabilities of producing offspring),  
81 or differences may be the outcome of stochastic processes with identical underlying  
82 fitness traits (“dynamic heterogeneity”; e.g., individuals with the same underlying  
83 probability of producing offspring but with different realized offspring production)  
84 (Tuljapurkar et al. 2009; Cam et al. 2016). Although we generally assume one or  
85 the other in population models, it is likely that both types of heterogeneity are  
86 present in real populations (Steiner et al. 2010; Plard et al. 2015; Cam et al. 2016).

87         Previous studies have shown that temporal autocorrelation in the  
88 environment can affect the dynamics and expected time to extinction of  
89 populations (Petchey et al. 1997; Levine & Rees 2004; Ruokolainen et al. 2009).  
90 However, empirical studies suggest that long-term effects on population growth of  
91 vital rate autocorrelations caused by stochastic environments are small (Morris  
92 et al. 2011; Ferguson et al. 2016), and theoretical analyses indicate that the  
93 temporal scaling of environmental autocorrelation must be long to have real impact  
94 on long-term population growth rates (Engen et al. 2013). Environmental  
95 fluctuations affect vital rates of all individuals in a population simultaneously (but

196 not necessarily identically), and can therefore create autocorrelations in the total  
197 reproductive output of the population. The environmental variance,  $\sigma_e^2$ , captures  
198 this by measuring among-year variation in the expected individual contributions to  
199 the future population, caused by temporal fluctuations in the environment (Engen  
200 et al. 2009). In contrast, the within-individual reproductive autocorrelations we  
201 focus on here create (or are created by) differences among individuals, and can be  
202 more stable over time. These autocorrelations in individual reproductive histories  
203 can be expected to affect the demographic variance,  $\sigma_d^2$ , which measures the  
204 temporal mean of the within-year variance in individual contributions (calculated  
205 from the variance in individual contributions to the future population from within  
206 each class, as well as covariances between them, weighted by the stable stage  
207 structure; see Engen et al. (2009) and Appendix S1) (Kendall & Fox 2002;  
208 Vindenes et al. 2008). Both environmental and demographic stochasticity  
209 (measured by  $\sigma_e^2$  and  $\sigma_d^2$ ) act to decrease long-run stochastic population growth  
210 (Lande et al. 2003). It is therefore important to account for them when analyzing  
211 stochastic population dynamics and extinction risk.

212           In the presence of reproductive autocorrelations, age-structured projection  
213 matrices are no longer independent across time steps, potentially introducing biases  
214 in estimated stochastic population dynamics. Models that classify individuals by  
215 reproductive success or stage in addition to age can be used to project population  
216 dynamics in the presence of reproductive autocorrelations (Cam et al. 2002;  
217 Jenouvrier et al. 2005, 2015; Steiner et al. 2010; Waugh et al. 2015), but they  
218 require estimation of a large number of parameters, requiring high-quality

119 long-term data sets that are available for a limited number of populations. This  
120 raises the question of how much individual reproductive autocorrelations affect  
121 stochastic population dynamics, and how much bias is likely to be introduced into  
122 estimates of extinction dynamics if such autocorrelations are present without being  
123 accounted for in our models.

124         Here, we examine the effect of incorporating autocorrelations in individual  
125 reproductive rates when calculating population growth rates and expected time to  
126 extinction. We derive the demographic variance in a stochastic matrix population  
127 model that incorporates different types of autocorrelation in individual  
128 reproductive rates, and analyze different parameterizations of this model, with and  
129 without environmental fluctuations. Calculated growth rates and extinction times  
130 are compared to those obtained from a standard age-structured model without  
131 autocorrelations. Finally, we present a case study, parameterizing the model with  
132 estimates from a wild population of moose, *Alces alces*, that show positive  
133 reproductive autocorrelations.

## 134 MATERIAL AND METHODS

### 135 General model

136 Consider an age-structured population model with a stochastic projection matrix,  
137  $L$ , such that  $n_{\tau+1} = Ln_{\tau}$  describes the population vector at time  $\tau + 1$ , given the  
138 population vector at time  $\tau$ . The population vector is a column vector of the  
139 number of females in each of  $k$  age classes,  $n_{\tau} = (n_1, n_2, \dots, n_k)^T$ , where the



140 superscript T indicates a transposed vector. Each age class is further divided into  
141 classes based on number of offspring produced, such that  $n_i = n_{i,0}, n_{i,1}, \dots, n_{i,\alpha_i}$ ,  
142 where the second subscript indicates the number of offspring, and  $\alpha_i$  is the  
143 maximum number of offspring produced by a female of age  $i$ . As presented, this  
144 model is most useful for species with low  $\alpha_i$ -values (but see Appendix S2).

145 We assume individuals are counted after reproduction, so that the number  
146 of offspring produced by each individual is known. However, in contrast to ordinary  
147 postbreeding census models (Caswell 2001), this model does not have a class of  
148 newborns. Offspring that survive their first year enter the class of one-year-olds one  
149 time step after they are born. Up until that point they are included in the model  
150 through their mother only. Since females are classified according to number of  
151 offspring produced, the count of females in different classes also contains  
152 information about the number of newborn offspring in the population. The last age  
153 class is assumed to have 0 survival.

154 In the classical, age-structured case, all surviving individuals of age  $i$  enter  
155 the single class of  $(i + 1)$ -year-olds at the next time step. However, in our model  
156 there are  $\alpha_{i+1}$  possible classes for surviving  $i$ -year-olds to enter, depending on their  
157 offspring production at age  $i + 1$ . Thus, transitions are driven by the product of  
158 survival probability and the probability of producing  $m$  offspring at time  $\tau + 1$ .  
159 Both of these probabilities could depend on the number of offspring produced at  
160 time  $\tau$ . Let  $s_{i,j}$  (for  $i > 0$ ) be the survival probability from age  $i$  to  $i + 1$  of an  
161 individual that produced  $j$  offspring at age  $i$ , and let  $q_{i,mj}$  be the probability of  
162 such an individual producing  $m$  offspring at age  $i + 1$ , given survival. Note that the

163 comma in the subscripts separates age indices from reproductive class indices.  
 164 Then, an individual from age class  $i$  that produced  $j$  offspring has probabilities  
 165  $(s_{i,j}q_{i,0j}; s_{i,j}q_{i,1j}; \dots; s_{i,j}q_{i,\alpha_{i+1}j})$  of surviving and producing  $0, 1, \dots, \alpha_{i+1}$  offspring,  
 166 respectively, at age  $i + 1$ , as well as a probability  $1 - s_{i,j}$  of not surviving. The  
 167 mean projection matrix has the same general form as a standard Leslie matrix,  
 168 with fecundities  $b_1, \dots, b_k$  in the first row, and survival and transition into the next  
 169 age class,  $p_1, \dots, p_{k-1}$ , on the subdiagonal (Caswell 2001). However, instead of each  
 170 entry being a single number, as in the classical age-structured case, each entry now  
 171 consists of a submatrix of the form

$$p_i = \begin{bmatrix} s_{i,0}q_{i,00} & \dots & s_{i,\alpha_i}q_{i,0\alpha_i} \\ \vdots & \ddots & \vdots \\ s_{i,0}q_{i,\alpha_{i+1}0} & \dots & s_{i,\alpha_i}q_{i,\alpha_{i+1}\alpha_i} \end{bmatrix}, \quad (1)$$

172 where each possible combination of offspring production at age  $i$  and  $i + 1$  has an  
 173 entry, resulting in a projection matrix with  $\sum_{i=1}^k (\alpha_i + 1)$  rows and  $\sum_{i=1}^k (\alpha_i + 1)$   
 174 columns. The  $q_{i,mj}$  sum to one within each column. The exact form of the  
 175 submatrices depends on assumptions of the model (see Appendix S2).

176 If we can assume that one-year-olds do not reproduce, such that all  
 177 offspring enter the same class, the  $b_i$  entries are  $b_1 = 0$ , and  
 178  $b_i = (s_0 \cdot 0, s_0 \cdot 1, \dots, s_0 \cdot \alpha_i) = (0, s_0, \dots, s_0 \alpha_i)$  for  $i > 1$ , where  $s_0$  is the probability  
 179 of newborns being female and surviving to age one. Since the model only keeps  
 180 track of females, we have merged offspring survival and sex ratio into a single rate  
 181 to simplify notation. The number of offspring born is given directly by the class of

182 mothers  $(0, 1, \dots, \alpha_i)$  within each age. If one-year-olds do reproduce we must keep  
 183 track of both which class the mother is in, and which class the offspring end up in.  
 184 Then, each  $b_i$  can be written as

$$b_i = \begin{bmatrix} 0 & s_0 t_0 & \dots & s_0 \alpha_i t_0 \\ \vdots & \vdots & \ddots & \vdots \\ 0 & s_0 t_{\alpha_1} & \dots & s_0 \alpha_i t_{\alpha_1} \end{bmatrix}, \quad (2)$$

185 where  $t_k$  is the probability of a one-year-old producing  $k$  offspring. Some useful  
 186 expansions of this model are presented in Appendix S2. Derivation of the  
 187 demographic and environmental variances is presented in Appendix S1.

## 188 **Model analysis**

189 We used our model to calculate  $\sigma_d^2$  for several systems with autocorrelations in  
 190 reproductive success, and compared these quantities to  $\sigma_d^2$  calculated from a  
 191 standard age-structured model (Leslie matrix) of the same systems (equation 4 in  
 192 Engen et al. 2009). The survival and fecundity parameters for the Leslie matrix  
 193 were calculated from the parameters for each subclass in the more complicated  
 194 reproductive autocorrelation model by weighting them by the stable stage structure  
 195 (found from the right eigenvector of the mean projection matrix; Caswell 2001).  
 196 We calculated the distribution of expected time to extinction using the equation

$$P(T_{ext} \leq \tau) = \exp \left[ -\frac{2N_0 \ln(\lambda)}{\sigma_d^2 (1 - e^{-\ln(\lambda)\tau})} \right], \quad (3)$$

197 where  $T_{ext}$  is time to extinction,  $\tau$  is time, and  $N_0$  is the population size at time 0  
 198 (Cox & Miller 1970; Engen et al. 2005b). This equation utilizes the fact that a  
 199 diffusion approximation with just three parameters (the expected growth rate and  
 200 the demographic and environmental variances) gives accurate estimates of the  
 201 distribution of population size over time in age-structured populations (Engen  
 202 et al. 2005b). We confirmed that this also holds for the model with reproductive  
 203 autocorrelations by comparing simulated population trajectories with diffusion  
 204 approximations (Appendix S3). The estimated distributions from equation 3  
 205 matched time to extinction found from simulations of the full system (Appendix  
 206 S3). In systems with environmental stochasticity, expected time to extinction was  
 207 found by simulation. We selected systems to cover a range from extreme levels of  
 208 reproductive autocorrelation to moderate levels that we expect to be common in  
 209 natural populations, focusing on systems with relatively long-lived individuals  
 210 where lifetime reproductive success is gained through several reproductive events.

211 We tested the sensitivity of our results to the choice of survival parameters  
 212 by calculating the maximum deviation in mean expected time to extinction  
 213 ( $\max(\Delta\bar{T}_{ext})$ ; i.e. how much the expected time to extinction deviated from that of  
 214 the Leslie model in the most extreme case of each model) when  $s_0$  and then  $s_i$  were  
 215 varied one at a time. Here,  $\Delta\bar{T}_{ext} = (\bar{T}_{ext,Les} - \bar{T}_{ext,Rac})/\bar{T}_{ext,Les}$ , where  $\bar{T}_{ext,Les}$  and  
 216  $\bar{T}_{ext,Rac}$  are the calculated mean expected time to extinction in the plain  
 217 age-structured model (*Les*) and the model with reproductive autocorrelations  
 218 (*Rac*), respectively. The number of age classes in the model was adjusted such that  
 219 the proportion of individuals expected to reach the last age class (after which they

220 all die) was just under 0.05.

221       **System 1, Switching or staying:** In our first system females produced 0  
222 or 1 offspring, and the probability of switching reproductive status,  $w$ , was the  
223 same for all ages and in both directions (i.e., the probability of transitioning from  
224 breeder to nonbreeder equaled the probability of transitioning from nonbreeder to  
225 breeder; Appendix S4). Survival was set relatively high ( $s_0 = 0.25$ ,  $s_i = 0.85$ ), and  
226 results were found for a range of  $w$ , from 0.0001 to 0.9999. Here,  $w = 0.5$  describes  
227 a system without reproductive autocorrelations,  $w < 0.5$  gives positive  
228 autocorrelations (at any time step individuals are more likely to stay in the same  
229 reproductive class than to switch), and  $w > 0.5$  gives negative autocorrelations  
230 (probability of switching reproductive status is greater than probability of not  
231 switching). All remaining individuals were assumed to die at age 11. We added  
232 environmental stochasticity by letting the probability of breeding at age 1,  $t_1$ , vary  
233 over time according to a symmetric beta distribution with mean 0.5 and different  
234 variances. This gives a hump-shaped distribution centered on 0.5 (see Fig. S5.1 in  
235 Appendix S5). As the variance increases, the distribution eventually becomes  
236 uniform (flat) between 0 and 1.

237       **System 2, Individual heterogeneity:** In our second system, females  
238 could produce 0 or 1 offspring at age one, and 0, 1 or 2 offspring at older ages. The  
239 probability of staying in the same breeding class from one time step to the next,  $h$ ,  
240 varied from 0.49 to 0.96, while the probability of going from nonbreeder (0  
241 offspring) to highly successful (2 offspring) or back was very low (0.02). This  
242 created varying degrees of heterogeneity among individuals (see Appendix S4 for

243 full transition matrix). We adjusted  $t_1$  to hold  $\lambda$  constant as  $h$  varied. This was not  
244 necessary in the first system due to symmetry in the transition probabilities. We  
245 calculated the demographic variance and expected time to extinction given the  
246 different values of  $h$ , and then calculated a new time to extinction when  $h$  was  
247 allowed to vary stochastically through time according to a symmetric beta  
248 distribution with mean 0.725.

249 **System 3, Gradual increase in reproductive success:** Finally, we  
250 analyzed a system where individuals were likely to improve their breeding situation  
251 over time, such that highly successful breeders were likely to remain successful,  
252 females with a single offspring were likely to produce one or two offspring at the  
253 next time step, and nonbreeders were likely to either remain as nonbreeders or  
254 produce one offspring. We expect this to be a common situation in long-lived  
255 species. The probability of transitioning to a more successful state increased as  $h$   
256 was varied from 0.49 to 0.96 (Appendix S4).  $\lambda$  was again held constant by  
257 adjusting  $t_1$ .

258 All calculations were performed in R 3.3.2 (R Core Team 2016). R code for  
259 setting up and analyzing matrix models with reproductive autocorrelations is  
260 provided in Appendix S6.

## 261 **RESULTS**

262 In systems without reproductive autocorrelations our model gave the same  
263 demographic variance,  $\sigma_d^2$ , as an age-structured Leslie model (Fig. 1a), but as

264 reproductive autocorrelations became stronger (positive or negative) the  
265 demographic variance deviated from that found from a Leslie matrix (Fig. 1a, 2a).  
266 Positive autocorrelations increased the demographic variance (Fig. 1a, 2a) and  
267 shortened the expected time to extinction (Fig. 1b, 2b), whereas negative  
268 autocorrelations decreased the demographic variance (Fig. 1a) and hence increased  
269 expected time to extinction (Fig. 1b). However, these deviations were small in all  
270 but the most extreme cases. In the “Switching or staying” system, the calculated  
271  $\sigma_d^2$  ranged from 0.69 when the probability of switching reproductive status  
272  $w = 0.0001$  to 0.32 when  $w = 0.9999$  (Fig. 1a), causing the mean expected time to  
273 extinction of a population starting at 100 females to range from 47.3 to 57.2 (Fig.  
274 1b). The equivalent Leslie matrix model gave  $\sigma_d^2 = 0.35$  and mean time to  
275 extinction 56.0. Thus, in the most extreme case ( $w = 0.0001$ ), the mean expected  
276 time to extinction was reduced by 15.5% compared to that calculated from the  
277 Leslie matrix model, but in most cases the deviation was much lower (4.5% when  
278  $w = 0.2$ ). Adjusting the size of the initial population caused only minor changes in  
279 these results (for example, the 15.5% became 12.7% at  $N_0 = 50$  and 17.8% at  
280  $N_0 = 300$ ). The “Individual heterogeneity” and “Gradual increase in reproductive  
281 success” systems showed only minor deviations in all cases (Fig. 2a,b, maximum  
282 deviation 8.0%; Fig. 3a,b, maximum deviation 2.3%).

283         The deviations in mean time to extinction ( $\Delta\bar{T}_{ext}$ ) showed little sensitivity  
284 to specific parameter choices. When survival was particularly high, “Switching or  
285 staying” systems with extremely low probability of switching reproductive status  
286 ( $w = 0.0001$ ) reached deviations of 18% (Fig. 1b,c;  $s_0 = 0.322$  and  $s_i = 0.85$  gave

287  $\max(\Delta\bar{T}_{ext})= 0.181$ ;  $s_0 = 0.25$  and  $s_i = 0.888$  gave  $\max(\Delta\bar{T}_{ext})= 0.175$ ). In these  
288 cases,  $\lambda$  was close to 1 (0.988 and 0.987). Increasing  $w$  to 0.2 brought  $\max(\Delta\bar{T}_{ext})$   
289 in these cases down to 0.069 and 0.057. Deviations in the other two systems never  
290 exceeded 12.8% ("Individual heterogeneity") and 2.4% ("Gradual increase in  
291 reproductive success") (Fig. 2b,c 3b,c).

292           Introducing environmental stochasticity in the probability of one-year-olds  
293 producing offspring (i.e. letting the  $t$ -values vary over time) showed only small  
294 increases in the environmental variance ( $\sigma_e^2 = 0.011$  when  $w = 0.0001$  and  $t_1$  varied  
295 according to a uniform distribution between 0 and 1. Other values were smaller; see  
296 Fig. S5.2a in Appendix S5), and negligible change in expected time to extinction  
297 (Fig. S5.2b in Appendix S5). Letting the probability of remaining in the same  
298 breeding class from one time step to the next fluctuate stochastically within the  
299 range 0.49-0.96 also had no measurable effects on time to extinction (Fig. S5.2d in  
300 Appendix S5), as would be expected given the weak influence of  $h$  on the  
301 demographic variance (Fig. 2a).

## 302 **Moose Case Study**

303 We applied our model to data from a population of moose (*Alces alces*) on the  
304 island of Vega off the coast of northern Norway. Females in this population can  
305 give birth to up to two calves per year from the time they are two years old.  
306 Estimates of transition probabilities between different breeding states (0, 1 or 2  
307 calves) in this population show that the probability of twinning increases with the



308 number of offspring produced at the previous time step, making it an example of  
309 the "Gradual increase in reproductive success" type of system (System 3 above)  
310 (Table 1). Transition and survival estimates were obtained from multistate models  
311 run in E-SURGE (Appendix S7, Choquet et al. 2009). Mortality in the system  
312 comes mainly from hunting. It has previously been shown that environmental  
313 stochasticity has little effect on the dynamics of this population (Sæther et al.  
314 2007). Environmental effects were therefore ignored. More details of the multistate  
315 models can be found in Appendix S7.

316           In order to isolate the effect of reproductive autocorrelations on the  
317 demographic variance, we first parameterized the model assuming no covariation  
318 between survival and fecundity. In other words, survival was estimated for each age  
319 class, but was assumed not to differ among breeding states within an age class  
320 (Appendix S7). We parameterized the model with these estimates, calculated the  
321 demographic variance, and then compared this to the demographic variance  
322 calculated from the model parameterized with the same survival estimates but  
323 simple age-specific fecundity rates (Appendix S7). Using estimated parameters  
324 directly in the model without incorporating uncertainty gave estimates of  $\sigma_d^2 = 0.33$   
325 when accounting for reproductive autocorrelations and  $\sigma_d^2 = 0.29$  from the standard  
326 age-structured model. Such high estimates of  $\sigma_d^2$  are quite common in long-lived  
327 species with positive growth rates (Sæther et al. 2013). Next, we incorporated  
328 uncertainty in the parameter estimates by repeating the analysis, drawing 10000  
329 values from the distributions for each parameter and performing the calculations  
330 for each of the 10000 sets of parameters. The resulting distributions of  $\sigma_d^2$  showed

331 only a very slight difference between the two models (Fig. 4a).

332           Finally, we investigated the effect of incorporating covariance in survival  
333 and fecundity. In the model with reproductive autocorrelations this meant allowing  
334 survival estimates to differ among the different breeding states (Appendix S7). In  
335 the standard age-structured models this was accounted for by adding a covariance  
336 term in the expression for  $\sigma_d^2$  (Engen et al. 2009). The moose show positive  
337 covariance between survival and fecundity because hunters prefer to shoot  
338 individuals without calves (Appendix S7, Sæther & Haagenrud 1983). Adding this  
339 covariance to the model increased estimates of  $\sigma_d^2$  (Fig. 4b). The increase was  
340 greatest in the standard age-structured model which treats this type of variation as  
341 random variation among average individuals, whereas the model with demographic  
342 autocorrelations treats this as systematic structured differences among breeding  
343 states (Fox & Kendall 2002; Lee et al. 2017).

## 344 **DISCUSSION**

345 Demographic and environmental stochasticity both have negative effects on  
346 population growth rates (Lande et al. 2003), necessitating population models that  
347 accurately incorporate stochastic effects, in particular when predicting expected  
348 impacts of environmental changes on the population size of threatened or  
349 endangered species (Doak et al. 2005; Engen et al. 2005b; Morris et al. 2008;  
350 Jenouvrier 2013). However, as models become more complex the number of  
351 parameters that must be estimated increases, causing challenges when applying the

352 models to sparse population data. We have therefore examined how much the use  
353 of standard age-structured models that do not account for autocorrelations in  
354 individual reproductive success biases estimates of expected time to extinction  
355 when used on populations where such autocorrelations are present. Our results  
356 show that such biases can be assumed to be small in all but the most extreme cases.

357         In extreme cases, we found that reproductive autocorrelations could  
358 shorten the expected time to extinction by nearly 20% (Fig. 1c,d). However, this  
359 required that females have an extremely low probability of switching reproductive  
360 status between years, and that they be long-lived. In real populations, we would  
361 expect probabilities of switching reproductive status to be less extreme and less  
362 consistent over time and age. In a more realistic scenario, expected time to  
363 extinction was reduced by just over 2% (Fig. 3b). Overall, most of the systems we  
364 studied showed decreases in expected time to extinction that were well under 10%  
365 (Fig. 2b,c 3b,c). Given the uncertainty that is typically present in estimates of  
366 stochastic population dynamics and extinction risk from population data, such  
367 small differences in the theoretical time to extinction are in most cases unlikely to  
368 merit the use of these more complex models. This conclusion is supported by our  
369 case study on moose, where differences in  $\sigma_d^2$  were less pronounced after accounting  
370 for uncertainty in the parameter estimates (Fig. 4a). The differences in  $\sigma_d^2$   
371 estimated for the moose case study using mean parameter estimates without  
372 accounting for uncertainty were of the magnitude predicted by our theoretical  
373 results (Fig. 3a).

374         For simplicity, our theoretical results focus on systems in which adults have

375 constant (expected) vital rates, independent of age. However, probabilities of  
376 breeding are known to depend on age in many species (e.g., Sedingler et al. 2001;  
377 Beauplet et al. 2006; Arroyo et al. 2007). Our model is constructed to accomodate  
378 this, and can be used to quantify the effect of reproductive autocorrelations in  
379 systems with more complicated structure (see e.g the moose case study). However,  
380 in general we expect even smaller differences in the demographic variance when  
381 breeding probabilities vary with age, compared to the systems studied here. For  
382 example, if the switching probability in Fig. 1 were 0.0001 for some ages, but  
383 higher for others, the demographic variance would be lower than shown, causing  
384 less change in the expected time to extinction.

385         Our results indicate that reproductive autocorrelations must be very strong  
386 to have any measurable effect on long-term population growth. This is consistent  
387 with empirical findings and theoretical results on related questions. For example, in  
388 the California spotted owl (*Strix occidentalis occidentalis*) it has been shown that  
389 negative reproductive autocorrelation caused by costly breeding has the potential  
390 to create biennial cycles in population-level reproductive output in the presence of  
391 environmental variation (Stoelting et al. 2015), but lasting cycles only occurred  
392 when the autocorrelation was very strong. Morris et al. (2011) found that effects of  
393 vital rate autocorrelations caused by stochastic environments on long-term fitness  
394 in seven primate species were extremely weak, and theoretical analyses have shown  
395 that long-term population growth rates are only affected by environmental  
396 autocorrelations when the temporal scaling is long (Engen et al. 2013). In addition,  
397 it has been shown that the realized correlation between the reproductive stages of

398 an individual over time is quite low in many species (Tuljapurkar et al. 2009).  
399 Thus, our results give a good indication that using models that do not incorporate  
400 reproductive autocorrelations should give reasonable estimates of demographic  
401 variance and expected time to extinction in most populations.

402         Models that classify individuals by reproductive success or stage in  
403 addition to age, such as the one used here, require estimation of a large number of  
404 parameters. Obtaining accurate estimates of all these parameters is challenging,  
405 particularly in small, endangered populations, causing high uncertainty in results.  
406 Thus, it may be good news that simple age-structured models seem to give good  
407 estimates of expected time to extinction in the face of reproductive  
408 autocorrelations. However, it is essential to note that these results were based on  
409 accurate estimates of mean fecundity for each age class in the model. Only the  
410 autocorrelations were ignored. In the wild, breeders and nonbreeders often have  
411 different detection probabilities (Katzner et al. 2011). Failing to account for this, or  
412 estimating fecundity based on a non-random subset of the population (e.g., only  
413 breeders), introduces much more serious biases than those examined here (Lee  
414 et al. 2017). Models that classify individuals by reproductive success therefore have  
415 an important role in analyzing the dynamics of certain types of populations.

416         In the wild, environmental conditions have been shown to affect breeding  
417 probabilities of both first-time breeders (e.g., Reed et al. 2003) and adults (e.g.,  
418 Cubaynes et al. 2011), as well as survival rates (e.g., Cayuela et al. 2014). One  
419 might therefore expect the strength of reproductive autocorrelations to vary from  
420 year to year, for example if differences among individuals were more pronounced in

421 years with poor (or conversely, with good) environmental conditions (Pfister &  
422 Wang 2005; Hamel et al. 2009b; Pesendorfer et al. 2016). We analyzed a system  
423 where the probability of staying in the same breeding class from one time step to  
424 the next varied stochastically from year to year, causing the reproductive  
425 autocorrelations to vary in strength over time. We found that this caused the  
426 effects of the reproductive autocorrelations to be so weak that estimates of  
427 expected time to extinction were practically identical in the models with and  
428 without such environmental fluctuations (Fig. S5.2d in Appendix S5). It has  
429 previously been shown that the deterministic population growth rate tends to be  
430 less sensitive to changes in breeding probabilities than to changes in survival,  
431 particularly in long-lived species (Lee et al. 2017). Then we would also expect  
432 fluctuations in breeding probabilities to have less effect on population growth and  
433 extinction, thus weakening the selection pressures that may lead to demographic  
434 buffering (Pfister 1998; Gaillard et al. 2000).

435         Survival rates that differ among reproductive classes give rise to covariance  
436 between survival and reproduction (Lee et al. 2017). This covariance can be  
437 directly accounted for when estimating the demographic variance from a standard  
438 age-structured model (Engen et al. 2009; Lee et al. 2017). However, structured  
439 variation of this type can actually decrease the demographic variance compared to  
440 that found in homogeneous populations (“variance reduction effect”, Fox & Kendall  
441 2002; Lee et al. 2017). Thus, increases in estimates of  $\sigma_d^2$  caused by this covariance,  
442 such as that seen in figure 4b do not necessarily reflect increases in the random  
443 variation among individuals. Negative covariance between survival and

444 reproduction can allow populations to persist in a wider range of environmental  
445 conditions, through demographic compensation (Doak et al. 2005; Villellas et al.  
446 2015).

447         In our model, heterogeneity in individual life history trajectories is driven  
448 by stochastic transition processes between reproductive classes (dynamic  
449 heterogeneity; Tuljapurkar et al. 2009; Cam et al. 2016). When reproductive costs  
450 and individual heterogeneity are both present in a population, positive and  
451 negative autocorrelations could cancel each other out, masking the underlying  
452 processes (Beauplet et al. 2006; Hamel et al. 2009a). Although population  
453 dynamics depend only on the realized autocorrelations, this creates a challenge for  
454 understanding the individual processes (Hamel et al. 2009a). Thus, results from our  
455 model cannot be used to infer for example an absence of reproductive costs directly.  
456 It is also important to note that our results focus on differences in the demographic  
457 variance calculated from models that either do or do not account for reproductive  
458 autocorrelations. Reproductive autocorrelations can also affect the deterministic  
459 growth rate of populations by affecting the proportion of breeders in the  
460 population. This would be reflected in fecundity estimates and should therefore not  
461 cause additional deviations between estimates from the two types of model. In our  
462 analyses, the deterministic growth rate was held constant as we varied the strength  
463 of reproductive autocorrelations in order to isolate the changes in the demographic  
464 variance. Thus, our results do not imply that reproductive autocorrelations have  
465 negligible effects on population growth itself.

466         As shown by Engen et al. (2005a) and Lee et al. (2011), the method we

467 used for deriving the demographic variance can also be used to study effective  
468 population size. This requires including males in the model, and can be  
469 accomplished following the logic of Lee et al. (2011), defining male reproduction by  
470 number of mates. Number of offspring produced is treated as a property of the  
471 females, and number of offspring per male is determined by his mates. The  
472 demographic variance and generation time calculated from the two-sex model can  
473 then be used to quantify genetic drift in the population (Engen et al. 2005a), and  
474 thus to predict loss of genetic diversity. In general, small populations with low  
475 demographic stochasticity are expected to lose genetic diversity at a lower rate  
476 than small populations with high demographic stochasticity (Engen et al. 2005a).  
477 In addition, Shpak (2007) showed that in finite populations selection tends to favor  
478 genotypes that decrease demographic stochasticity. This might suggest that  
479 positive reproductive autocorrelations could give a selective disadvantage in some  
480 cases, but the effect would be weak.

481         In conclusion, although positive autocorrelations in individual reproduction  
482 were shown to increase the demographic variance such that population models that  
483 did not account for these autocorrelations overestimated the expected time to  
484 extinction, the effects were found to be small. Environmental fluctuations in  
485 transition rates between different breeding states were found to have negligible  
486 effects on expected time to extinction. Thus, our results indicate that ignoring  
487 reproductive autocorrelations in population models is unlikely to cause any serious  
488 bias in estimates of population growth and expected time to extinction, except in  
489 extreme cases.



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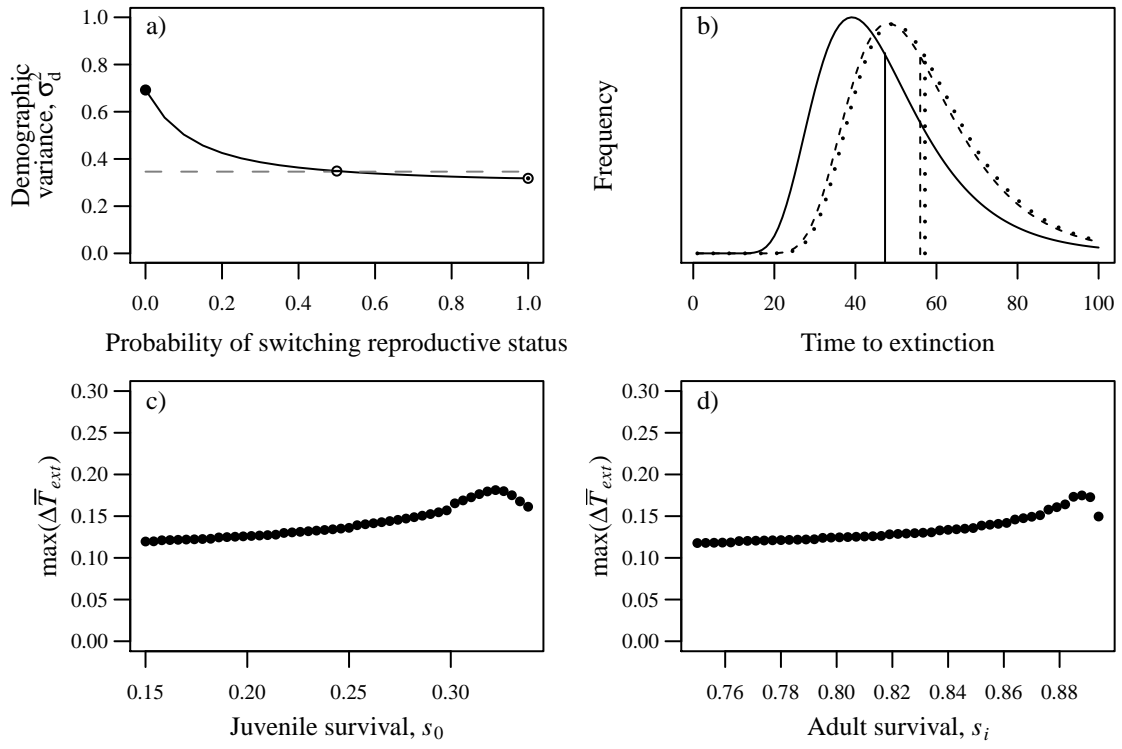


Figure 1:

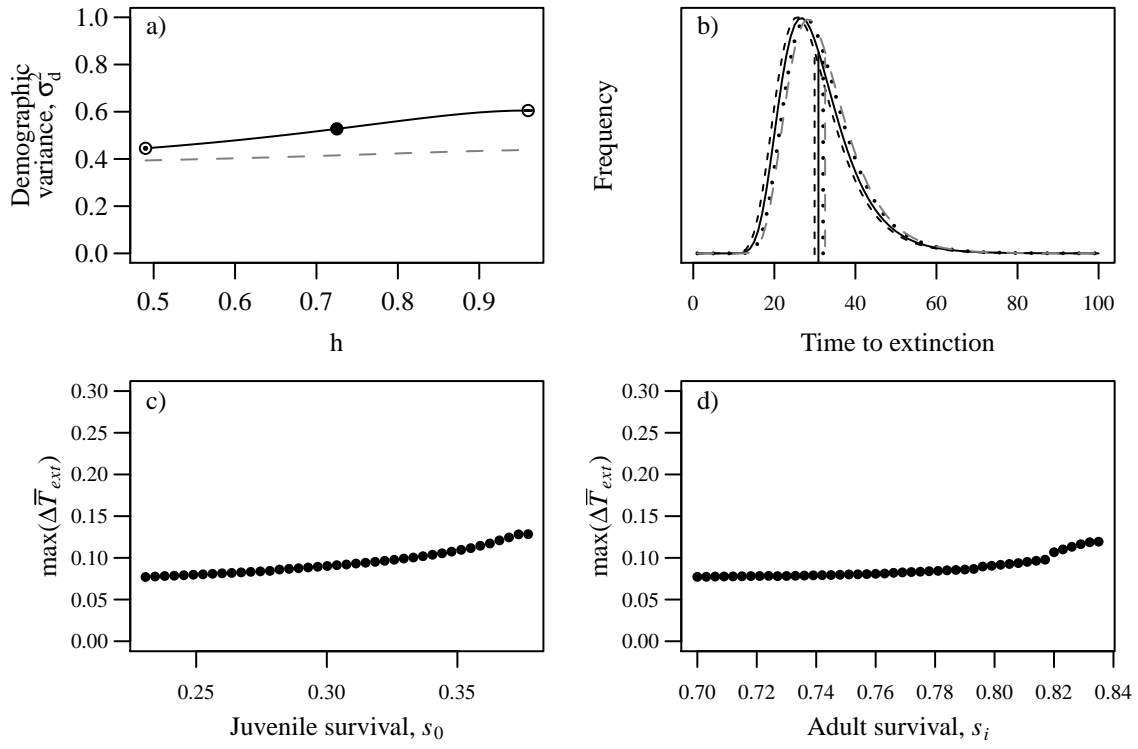


Figure 2:

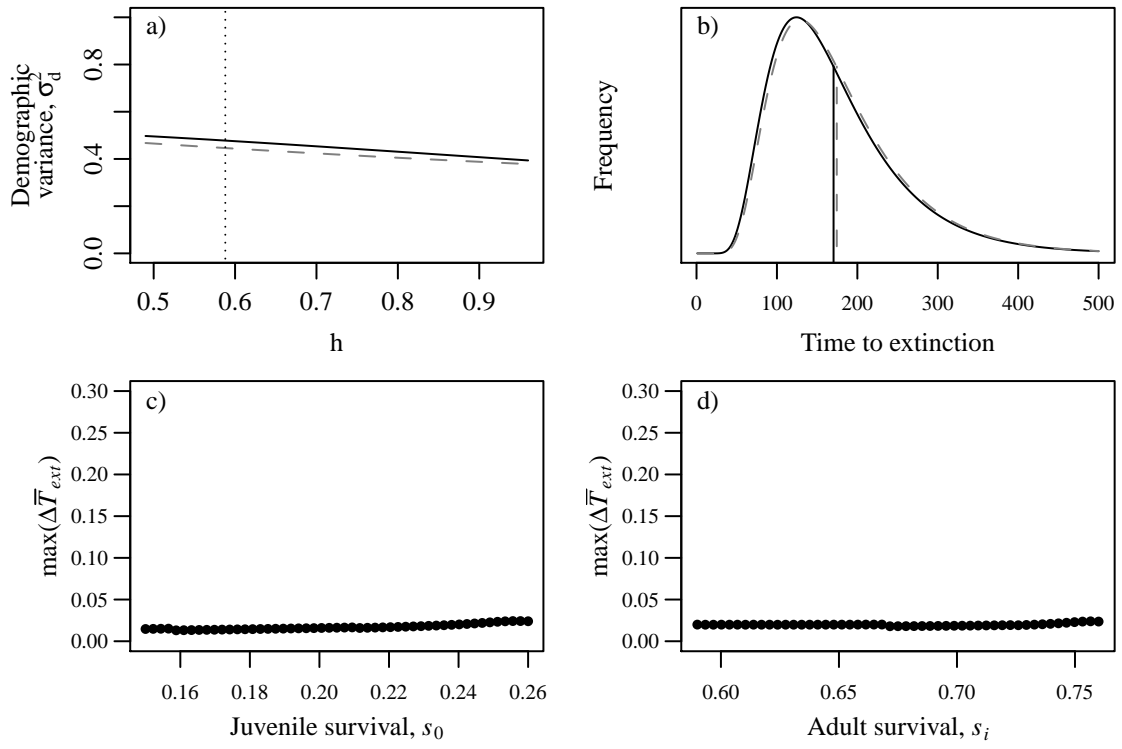


Figure 3:

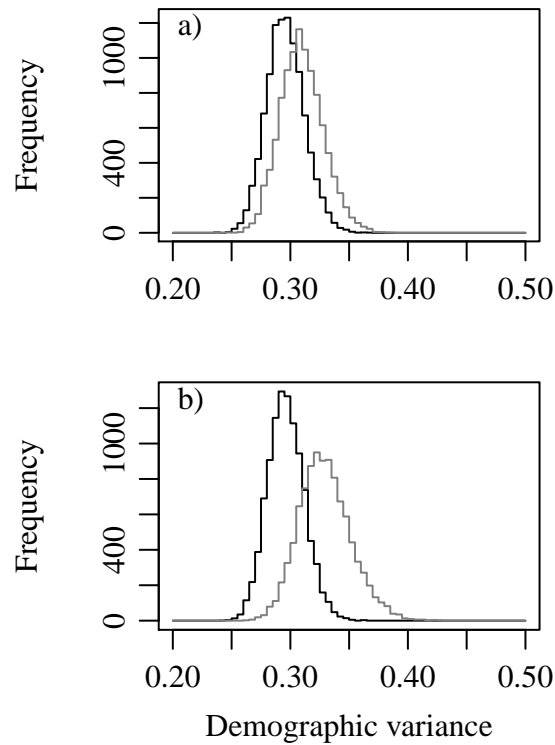


Figure 4:

654 **Figure 1:** Model output for System 1 (“Switching or staying”) with 11 age classes,  
655 0 or 1 offspring produced per female at each time step ( $\alpha = 1$ ), adult survival,  
656  $s_i = 0.85$ , offspring survival and probability of being female,  $s_0 = 0.25$ , and  
657 probability of breeding at age 1,  $t_1 = 0.5$ . a) Demographic variance estimates from  
658 our model with reproductive autocorrelations (solid line) compared to those from a  
659 standard age structured model (grey dashed line). The probability of switching  
660 reproductive status,  $w$ , is varied from 0.0001 to 0.9999. Points at  $w = 0.0001$ , 0.5  
661 and 0.9999 are marked by dots with fill corresponding to line types shown in panel  
662 b. b) Distribution of time to extinction, starting with 100 females, when

663  $w = 0.0001$  (solid line), 0.5 (dashed line; equal to the Leslie model) and 0.9999  
 664 (dotted line) (i.e, points on panel a).  $\lambda = 0.927$ . c) Maximum deviation in mean  
 665 expected time to extinction ( $\max(\Delta\bar{T}_{ext})$ , found at  $w = 0.0001$ ) when  $s_0$  is varied  
 666 from 0.15 to 0.35 and the number of age classes is adjusted from 8 to 13 to ensure  
 667 that the proportion of individuals expected to reach the last age class stays just  
 668 under 0.05.  $\lambda$  varies from 0.789 to 0.998. d) Maximum deviation in mean expected  
 669 time to extinction ( $\max(\Delta\bar{T}_{ext})$ , found at  $w = 0.0001$ ) when  $s_i$  is varied from 0.75  
 670 to 0.90 and the number of age classes is adjusted from 7 to 16 to ensure that the  
 671 proportion of individuals expected to reach the last age class stays just under 0.05.  
 672  $\lambda$  varies from 0.780 to 0.997.

673 **Figure 2:** Model output for System 2 (“Individual heterogeneity”) with 7 age  
 674 classes, 0 or 1 offspring produced per female at age 1, and 0, 1 or 2 offspring  
 675 thereafter ( $\alpha_1 = 1, \alpha_{2-7} = 2$ ), adult survival,  $s_i = 0.75$ , offspring survival and  
 676 probability of being female,  $s_0 = 0.25$ , and probability of breeding at age 1,  $t_1$   
 677 adjusted to keep  $\lambda$  constant ( $t_1$  varied from 0.262 to 0.696,  $\lambda = 0.868$ ). a)  
 678 Demographic variance estimates from our model with reproductive autocorrelations  
 679 (solid line) compared to those from a standard age structured model (dashed grey  
 680 line). The probability of staying in the same breeding class,  $h$ , was varied from 0.49  
 681 to 0.96. Points at  $h = 0.49, 0.725$  and 0.96 are marked by dots with fill  
 682 corresponding to line types shown in panel b. b) Distribution of time to extinction,  
 683 starting with 100 females, when  $h = 0.49$  (dotted line),  $h = 0.725$  (solid line) and  
 684  $h = 0.96$  (dashed line). The long-dashed grey line shows time to extinction

685 calculated from a standard age structured model without reproductive  
686 autocorrelations. c) Maximum deviation in mean expected time to extinction  
687 ( $\max(\Delta\bar{T}_{ext})$ , found at  $h = 0.96$ ) when  $s_0$  is varied from 0.23 to 0.38 and the  
688 number of age classes is adjusted from 7 to 9 to ensure that the proportion of  
689 individuals expected to reach the last age class stays just under 0.05.  $\lambda$  varies from  
690 0.850 to 0.999. d) Maximum deviation in mean expected time to extinction  
691 ( $\max(\Delta\bar{T}_{ext})$ , found at  $h = 0.96$ ) when  $s_i$  is varied from 0.70 to 0.835 and the  
692 number of age classes is adjusted from 6 to 10 to ensure that the proportion of  
693 individuals expected to reach the last age class stays just under 0.05.  $\lambda$  varies from  
694 0.798 to 0.992.

695 **Figure 3:** Model output for System 3 (“Gradual increase in reproductive success”)  
696 with 7 age classes, 0 or 1 offspring produced per female at age 1, and 0, 1 or 2  
697 offspring thereafter ( $\alpha_1 = 1, \alpha_{2-7} = 2$ ), adult survival,  $s_i = 0.75$ , offspring survival  
698 and probability of being female,  $s_0 = 0.25$ , and probability of breeding at age 1,  $t_1$   
699 adjusted to keep  $\lambda$  constant ( $t_1$  varied from 0.890 to 0.137,  $\lambda = 0.986$ ). a)  
700 Demographic variance estimates from our model with reproductive autocorrelations  
701 (solid line) compared to those from a standard age structured model (dashed line).  
702  $h$ , which here controls the probability of transitioning to a more successful state  
703 (see Appendix S4 for more details), was varied from 0.49 to 0.96. b) Distribution of  
704 time to extinction, starting with 100 females, when  $h = 0.588$  (dotted line on panel  
705 a). The long-dashed grey line shows time to extinction calculated from a standard  
706 age structured model without reproductive autocorrelations. c) Maximum

707 deviation in mean expected time to extinction ( $\max(\Delta\bar{T}_{ext})$ , found at  $h = 0.588$ )  
708 when  $s_0$  is varied from 0.15 to 0.26 and the number of age classes is adjusted from 5  
709 to 7 to ensure that the proportion of individuals expected to reach the last age  
710 class stays just under 0.05.  $\lambda$  varies from 0.788 to 0.996. d) Maximum deviation in  
711 mean expected time to extinction ( $\max(\Delta\bar{T}_{ext})$ , found at  $h = 0.588$ ) when  $s_i$  is  
712 varied from 0.59 to 0.76 and the number of age classes is adjusted from 5 to 7 to  
713 ensure that the proportion of individuals expected to reach the last age class stays  
714 just under 0.05.  $\lambda$  varies from 0.787 to 0.995.

715 **Figure 4:** Outlines of barplots showing distribution of estimated values of  $\sigma_d^2$  from  
716 10000 parameter draws for the moose population. Black lines (leftmost peak) are  
717 estimated from a model with reproductive autocorrelations. Grey lines (rightmost  
718 peak) are estimated from a standard age-structured model without accounting for  
719 reproductive autocorrelations a) Model without covariance between survival and  
720 fecundity. b) Model with positive covariance between survival and fecundity.