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1 **Density- and age-dependent reproduction partially compensates culling efforts of invasive non-**

2 **native American mink**

3

4 Yolanda Melero[1,2] Ella Robinson[1] and Xavier Lambin[1]

5 (1) School of Biological Sciences, University of Aberdeen. Aberdeen AB24 2TZ, UK.

6 (2) CREAF (Center for Ecological Research and Forestry Applications), Autonomous University of

7 Barcelona, E-08193 Bellaterra, Spain

8

9 (1,2) Yolanda Melero: y.melero@abdn.ac.uk; Present address: y.melero@creaf.uab.es

10 (1) Ella Robinson: ella.robinson.10@aberdeen.ac.uk

11 (1) Xavier Lambin (corresponding author): x.lambin@abdn.ac.uk; phone: + 44(0)1224 273 259

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13

14   **Abstract**

15   Management strategies of wildlife species must pay due regard to density dependent changes in vital

16   rates. Knowledge of density dependent relationships is sparse for most species but such knowledge

17   ought to inform adaptive management. Using data from a large-scale, six years of control effort of the

18   invasive non-native American mink (*Neovison vison*) in Scotland, we analysed density dependent

19   changes in reproduction as revealed by placental scar counts in culled females. Control strongly

20   reduced mink density but it varied substantially over time and space, reflecting variation in when

21   control was initiated in each river section. We used hurdle statistical models to simultaneously relate

22   the probability of conception, litter size and female age to prevailing mink density in river sections

23   where the female was culled. Both the probability of conceiving a litter (average 0.81) and litter size

24   (average 5.52 pups) increased as the density of females, but not males, declined. In addition, there was

25   a senescent decline in both components of fecundity, which given culling of mink and subsequent

26   reinvasions, resulted in a younger population, adding further to density dependent compensation in

27   fecundity. There was no evidence of depensation, even at the lowest density. The predicted combined

28   impact of changes in density and age structure could lead to an increase in fecundity of up to 2.1 pups

29   per female occupying or reinvading the controlled area. Control strategies must be sufficiently

30   adaptable and robust in order to overcome this compensation and suppress densities of mink and other

31   invasive mammals.

32

33   **Keywords** Density dependence; compensation; senescence; fecundity; introduced species

34

Introduction

Density dependence demographic processes underpin the sustainable harvest of wildlife species. Indeed, a reduction in population density may lead to density dependent compensation (i.e. per capita growth rate increases as population density decreases). as a consequence of abundant per capita resource availability at low density. In some circumstances however, individuals living in low and sparsely populated areas may experience depensation or Allee effects (i.e. per capita growth rate decreases as the density decreases) which may reduce their fitness (Courchamp et al., 2008). Strong Allee effects may even give rise to inverse (or positive) density dependence, which in principle could result in a minimum threshold population size below which the population growth rate becomes negative and extinction is expected (Gregory & Courchamp 2010).

While changes in per-capita resource availability typically underpin patterns of density dependent variation in the population growth rate, the specific limiting resources driving the changes are rarely identified (Sinclair and Pech, 1996). In addition to inducing density dependent changes in vital rates, elevated mortality through harvesting may truncate age and size structures. This truncation typically leads to more young animals in harvested populations with a subsequent impact on vital rates that are not density dependent *per se* (e.g. Robinson et al. 2008).

Studies of animal populations occurring at low densities are notoriously difficult to perform and hence relatively scarce. As a result, much uncertainty remains on the relative contributions of compensatory and depensatory processes in shaping per capita growth rate in low-density populations for species with different social systems or reproductive physiologies. Indeed, evidence of depensation is controversial and largely restricted to failures of cooperative processes in social species across taxa (Gregory et al., 2010; Kramer et al., 2009). In this respect, control campaigns of nefarious introduced non-native species (INNS hereafter) designed to reduce the abundance of target species to very low values provide useful, quasi-experimental conditions to study density dependent processes.

While eradication of INNS is the management objective on islands not subjected to immigration, reducing INNS to densities where their ecological impact on native communities becomes benign is widely practiced in "mainland areas" where ultimate eradication is a distant goal (Bomford and O'Brien, 1995; Simberloff et al., 2013). Thus many INNS mammalian carnivores are

63 controlled through sustained trapping rather than through one-off poisoning campaigns in areas where

64 the use of toxins is inappropriate (e.g. Bonesi & Palazón 2007). Management strategies involving

65 either large numbers of "citizen conservationists" (e.g. Bryce et al. 2011) or substantial injection of

66 resources (Ebbert and Byrd, 2011; Harding et al., 2001) have successfully reduced INNS to low

67 densities over large areas. In most cases, the species involved are territorial, solitary, highly mobile

68 and fecund mammals with relatively low survival (e.g. mongooses, feral cats *Felis catus* and

69 American mink *Neovison vison*). To date, consideration of the roles of compensatory and depensatory

70 processes as well as demographic stochasticity in INNS biology has been largely restricted to the

71 early establishment stage of invasive species spread (e.g. Sax et al., 2007). Yet the same processes

72 may also contribute to invasive species′ response to reduction in population density following control

73 programs, and as such, are of both fundamental and applied interest. However, empirical evidence of

74 compensatory and depensatory mechanisms in wildlife species is still scarce and mostly represented

75 by compensatory dispersal from the outer perimeter of controlled area (e.g. Englund 1970), or by

76 juvenile dispersers (e.g. Berry et al. 2013). Little is known about how changes in *in situ* reproduction

77 by individuals who either escaped control or immigrated might contribute to compensation or

78 depensation in the persisting low density population. Specifically, the relative contribution of

79 variation in per capita resource availability and mate finding to variation in the reproductive output is

80 scarcely known for most pest species.

81   Here we use data from a large-scale participatory INNS control effort, during which densities

82 of a small carnivore were reduced over a very large area, to determine whether compensatory and

83 depensatory processes affecting reproduction countered or facilitated control.

84

85 Study Species

86 The American mink (mink hereafter) is a widely distributed mammalian INNS and the focus of much

87 control effort worldwide (see Dunstone, 1993; Genovesi et al., 2012; Santulli et al., 2014). Mink is a

88 highly mobile, solitary, territorial species occupying linear territories arranged along waterways.

89 Mating takes place in March-April with males abandoning their territories and becoming nomadic in

90 search of mating opportunities during the rut (Dunstone, 1993). Female mink mate with, and can be

91 fertilised by, multiple males per mating season (superfecundation). They continue ovulating after

92 successfully mating (superfoetation) and have embryonic diapauses which synchronise embryonic

93 development (Dunstone, 1993; Thom et al., 2004). The combination of these characteristics results in

94 the production of a single annual litter of typically 4-5 offspring (up to 14), frequently of different

95 paternities (Yamaguchi et al., 2004). Kits are born in April-May and can fend for themselves by late

96 August. Juveniles leave the maternal territory and disperse from October when approximately 5

97 months old and seek a vacant territory in which they typically settle by the end of the year. Once

98 settled, mink do not abandon their territories except for males during mating. Juveniles mature

99 sexually when 8-10 months old (Dunstone, 1993; Melero and Palazón, 2011).

100   Based on knowledge of mink social system and reproductive physiology and the assumption

101 that food availability constrains body condition and fecundity, we predicted that female fecundity

102 would rise with decreasing mink density. We assumed that territory size would become less

103 constrained by the presence of conspecifics and that immigrants would be able to settle in the best

104 quality territories. We thus expected that females would be able to attain higher body condition and

105 hence conceive larger litters. We further envisaged that as mink density declined to very low values,

106 the number of mating events per oestrus would decline. Thus we predicted that the relationship

107 between litter size and mink density would be non-linear, with a decline below a threshold reflecting a

108 reduction in mating frequency and an increasing fraction of females failing to conceive at very low

109 male density.

110

111 **Material and methods**

112

113 The project

114 Carcasses of mink culled as part of the Cairngorm Water vole Conservation Project (2006-2009;

115 Bryce et al. 2011) and its successor the Scottish Mink Initiative (2009-present) were collected in an

116 area centred around the Cairngorms National Park (57º 0′N 3º3′W) in northern Scotland. The culling

117   area extended to 10,000km^2 by 2009 and gradually expanded to cover more than 20,000km^2 in 2013.

118   Both projects used mink rafts (details in Reynolds et al., 2010), which were deployed at regular

119   intervals along waterways and operated more or less continuously by volunteers, with support from

120   one to four project officers. A cage trap was placed on the raft only when a mink was detected and left

121   in place for a few days or until a mink was caught (38 % of detections resulted in capture in 2006-

122   2009; Beirne, 2011). The spatial coverage of the projects expanded over time but in a non-systematic

123   manner. This variation was largely a consequence of the temporal and spatial variation in project

124   funding (details in Bryce et al. 2011). The projects were funded through a succession of awards, each

125   of one to three years duration, and there were also some interim periods with minimal funding. This

126   led to variation in levels of staffing and hence variation in the level of mink detection effort by

127   volunteers, the intensity of mink raft coverage and in the collection of data. There was a marked

128   temporary decline in late 2009 in particular.

129

130   Mink sampling

131   Carcasses of culled mink were frozen upon collection from volunteers. Uteri were then extracted and

132   refrozen until subsequent examination. Embryos and placental scars in the uteri were counted to

133   estimate litter size. In mink, as in other mammals with a zonary endotheliochorial or discoid

134   hemochorial type of placenta (Burton et al., 1994), the uteri is left with one placental scar per

135   implanted embryo that heals within 10-11 months of parturition. The scars become visible and can be

136   counted when the uteri is stained following the protocol described by Fournier-Chambrillon et al.

137   (2010). A single observer (YM) counted the scars twice in quick succession and gave a subjective

138   confidence score to each count, as some scars were difficult to discern. Mink age was estimated in

139   two steps. First an X-ray image of canines was taken and individuals were classed as younger or older

140   than 10 months based on the appearance of dental pulp (Helldin, 1997). Those judged to be older than

141   10 months were further aged using tooth cementum analyses which was performed by Matson

142   Laboratory LLC (MT, USA). Throughout, kits were assumed to be born in May and females were

143   assumed to be able to conceive from 10 months old.

144

145   Derived variables

146   The expansion of the mink control projects and the collection of mink carcasses took place in a

147   heterogeneous physical landscape with overlaid heterogeneity both in the timing of comprehensive

148   mink control being first implemented and in the number of conspecifics known to persist when each

149   focal mink was caught (see Bryce et al. 2011). In order to reflect this heterogeneity, we divided the

150   project area into 21 river sections (average length of waterways: 153 km, SD = 26) with a consistent

151   control history. Each section was assigned a "year since first controlled". In order to estimate the

152   degree of saturation of mink territories (i.e. the relative mink density post control) in each river

153   section at a given time, we estimated the maximum number of territories per section. To do so, we

154   first buffered all capture locations of settled adult mink in all years by 2 km along rivers. Next, we

155   merged the buffers to describe areas which were ever settled by mink and divided the total occupied

156   length of waterway by 2 km territories assuming no-overlap (Birks and Linn, 1982; Dunstone and

157   Birks, 1987). Relative mink densities were then taken to be the ratio of the number of occupied

158   territories per year and section, relative to the maximum number of territories estimated under the

159   above assumptions (Fig 1a). Even though saturation of river section with territories was an empirical

160   cumulative measure, 15 of 21 sections had reached the maximum number of territories by the second

161   year of control, meaning that no new mink territories were discovered after the second year

162   (Appendix: Fig. 1).

163   Relative mink densities were calculated per year for (a) adult conspecifics of both sexes as a

164   measure of competition for territories; (b) adult females as a measure of intersexual competition for

165   territories and mating opportunities; (c) adult males reflecting competition for territories after the rut;

166   and (d) mating males as a measure of mating opportunities. Mating males were all the potential

167   mating partners present during the mating season of year t. They were defined as adult males captured

168   from the beginning of March to the end of the calendar year (year t hereafter) and the individual male

169   mink captured from January to the end of February the next year (year t+1) if >21 months old (Fig

170   1b).

171 To quantify the mating opportunities that females experienced, while taking into account the mobility

172 of males during the rut, we calculated an index of connectivity between all relevant adult males and

173 each focal oestrus female. The connectivity index S^{mm} was the sum of the number of mating males

174 weighed by a negative exponential function of the Euclidean distance (in m) between the focal

175 females i and the location of capture of each male d_{ij}. Keeping in mind that the capture location of

176 males may not reflect their location at the time of mating, S^{mm} should only be considered as an index

177 of the number of mating opportunities. S^{mm} was expressed as: $S_i^{mm} = \sum e^{(-d_{ij}/d')}$ where S^{mm}

178 increases with the number of adult male mink in a female's neighbourhood, and decreases with the

179 distance following a negative exponential function shaped by the parameter d' (also expressed as $\alpha =$

180 $1/d'$). The parameter d' should reflect the mobility and mate finding ability of mink and was estimated

181 from the data using profile likelihood. The global models (see statistical analysis below), with

182 probability of conception and litter size as response variables, were iteratively fitted to the data using

183 values of S^{mm} estimated for a range of values of d' (1000–40000). The most likely value of d' was

184 taken as that which yielded the model with the highest log-likelihood. When d' is large, connectivity

185 becomes the total number of males un-weighted by distance (d_{ij}). All covariates, including

186 connectivity, were standardized by subtracting the mean and dividing by two standard deviations.

187 Because the best models did not include connectivity between females and males (see section 3.2), the

188 relative density of mating males was not calculated by section but rather per year over the entire

189 project area, as the ratio of mating males' territories relative to the maximum number of territories that

190 could have been accommodated in that year.

191

192 Hypotheses testing and statistical analyses

193 When testing our predictions on density dependence in mink fecundity, we modelled pregnancy status

194 (whether the female had conceived a litter or not) and litter size (the number of placental scars) in

195 relation to four measures of mink density (a-d, testing first for co-linearity), including the connectivity

196 index to mating males. To investigate the influence of the control history of each river section on

197 pregnancy rate and litter size, we also tested the time (in years) elapsed from "year since first

198   controlled". In all models, we also considered female age (in months) at conception (setting April as

199   the month of conception), and the month of capture to account for possible changes in the

200   detectability of placental scars after parturition.

201   In all analyses, we first sought evidence of non-linear relationships between mink fecundity and

202   indices of mink density or the month of capture, using generalised additive mixed models (GAMM),

203   with year as a random variable. Wherever smoothing terms were non-significant, we used hurdle

204   models, also called mixture models, because the zeros are modelled as arising from two different

205   processes: the binomial process (of conceiving) and the count process (of the number of embryos

206   implanted) fitted as a truncated Poisson distribution (Zuur et al 2009). Confidence in the measurement

207   of placental scars based on two counts was included in all relevant models by weighing each

208   observation according to:

209    $W_i = (1 - (LS_{i1} - LS_{i2})/5)xR_{i1}/100$, where the weight ($W$) of each count of litter size i is a

210   function of the difference between the two counts (*i1* and *i2*) divided by five to avoid zeros and

211   multiplying by the confidence score R_{i1} scaled 0-1. For each analysis, a global model was defined

212   containing all mentioned covariates and model selection was conducted by sequentially dropping

213   terms based on AIC (Table 1 in Supplementary material). Only additive effects were considered.

214   Model averaging and estimates weighting across the most likely models (ΔAIC < 1) were used to

215   incorporate model uncertainty in the parameter estimates using the R package MuMIn (Bartoń, 2014).

216   Analyses were carried out in R using packages gamm4, pscl and nlme (Jackman, 2012; Pinheiro et al ,

217   2014; Wood, 2014).

218

219   **Results**

220

221   A total of 979 mink were captured of which 387 were female, 452 were male and 140 were of

222   unrecorded sex. Amongst females, 238 were > 10 months old, hence potentially reproductive. Only

223   seven females were culled when pregnant. The repeated placental scar counts were identical for 97%

224   of instances. Overall, 81% of the females conceived, with an average litter size of 5.52 (SD = 2.89;

225   Fig. 2a, b). There were four instances of litters of one pup, in different river sections and years. One

226 11 months old female at parturition had an apparent litter size of 12 (based on placental scars) in the

227 first year of control of a river section. Female age at conception varied between years from 11 to 59

228 months (~5 years) old with an average of 16.76 months (SD = 10.86) (Fig. 2c, d). The proportion of

229 females judged to have conceived declined with the calendar month of capture, from all females in

230 January to 81% in December. A similar pattern was evident for the estimated litter size which varied

231 from six to three pups (Table 1, Appendix: Fig. 2 and 3). These patterns persisted when 22 litters from

232 females culled in January-March with above average size were excluded from the analyses.

233

234 *Population relative density and female age*

235 The relative density of conspecifics per section varied widely between river sections and fluctuated

236 over time. There was a consistent decline in density when time since control was instigated, with a

237 project-wide reduction of 80% after six years of control. Relative density decreased to less than 20%

238 of the estimated maximum in six sections, and to 50% in eight other sections during the first year of

239 control. Relative mink density in the remaining seven sections increased in the first but decreased in

240 the second year of control (Fig. 3a, b). Overall, 57% of culled females inhabited river sections with

241 relative densities lower than 20 and 6.7 % females at relative densities lower than 10 and 5% of the

242 local maximum respectively.

243 None of our indices of relative density were significantly or strongly correlated to each other

244 (all p-values >0.1), with the relative density of conspecifics and females having the highest Pearson

245 correlation $r_p = 0.23$.

246 Culling lead to an increasingly young population, with the percentage of females older than

247 two years declining from an average of 38% in the first two years of control to 23% in the fifth year

248 and 0% in the sixth when all culled females were yearlings (Fig. 3b).

249

250 *Modelling mink fecundity: density dependence and senescence*

251 Our prediction of density dependence was supported by the best models of fecundity. The part of the

252 hurdle model relating to the probability that a female conceived included negative relationships with

253 the relative density of females, as well as with female age at conception and month of capture. The

254 litter size part of the model also included the above covariates, as well as relative densities of males

255 and mating males (Appendix: Table 1). Our prediction of a non-linear effect of density on fecundity

256 was not supported since no smoothing terms were deemed to be significant for any of the GAMM

257 models, providing no evidence for non-linearity in the influence of any of the density indices

258 indicative of depensation. The best models relating conception probability and litter size in relation to

259 mating males did not include connectivity between females and males (max d' Δloglikelihood= 0.15;

260 Appendix: Table 1 and Fig. 4). Throughout, model selection was unaffected by weighing observation

261 according to repeatability (w).

262 Probability of conception decreased monotonically with an increase in the relative density of

263 females and the age of the focal female. Using all other covariates within their real range of values,

264 the hurdle model predicted conception probabilities ranging from 0.92 (95% CI 0.86-0.96) at the

265 minimum recorded relative densities of females (<2%) to 0.82 (0.51-0.93) at the maximum relative

266 densities (84%). Predicted probability of conception declined in relation to female age from 0.86

267 (0.73-0.94) in yearling females (n=127) to 0.55 (0.23-0.85) in the oldest females in the fifth breeding

268 year (59 months old, n=2) (Table 1 and Fig. 4a, b). The effects of both covariates on the probability of

269 conception were equivalent in strength (coefficients of standardised covariates: -0.369 and -0.351

270 respectively, Table 1).

271 Litter size also declined with increasing relative density of females and with female age.

272 Predicted litter size declined from 5.6 pups (interval confidence 4.5-6.4) at the minimum recorded

273 densities to 3.8 pups (2.9-4.8) at maximum densities, while within the female age at parturition litter

274 size declined from 4.9 (4.8-5) in yearlings to 3.1 (2-4.8) pups in the eldest females (Fig. 4c, d).

275 Despite being part of the best model selected based on AIC scores, the impact of relative density of

276 males and of mating males on litter size had an effect size close to zero, with a litter size of 4.9 pups

277 seemingly invariant with male densities. Thus despite being selected in the best models (Fig. 5),

278   model parameters (either weighted or not) offer no evidence to support the notion that the potential

279   for multiple mating leads to higher litter size.

280

281   *Compensation in fecundity and mink control efforts*

282   Both population density and the average female age declined over the course of the management

283   project (Fig. 2d and Fig. 3c, d), and both influenced mink fecundity through the conception rate and

284   litter size components of fecundity. To illustrate the maximum model-predicted magnitude of their

285   combined impact, we selected two of the 21 project sections, which had constant coverage since the

286   start of the project and current low densities (Fig. 3). We used the observed range of their local values

287   for female density and age while holding all other covariates at their median value. Litter size was

288   predicted to have increased by 1.5 fold, from 3.67 (95% CI 2.42-5.26) pups in the first year of control

289   to 5.49 (95% CI 4.56-6.61; Fig. 2b) after six years of control. The probability of conception was

290   predicted to have increased from 0.78 (95% CI 0.79-0.93) to 0.91 (95% CI 0.83-0.96). When

291   considering the range of density and female age observed in all river sections, the model predicted a

292   combined increase of 2.1 pups per litter (95% CI 1.0-3.3). No such pattern is evident in the raw mink

293   fecundity data (Fig. 2b) owing to the fluctuations of asynchrony between river sections with different

294   control histories in their relative female density and age (Fig. 3d).

295

296   **Discussion**

297   We found evidence of a density dependent response in both conception rates and female fecundity to

298   the culling-induced decline of an invasive American mink population, with a negative relationship

299   between fecundity and relative density of females but not with the other indices of density we

300   evaluated. We found no evidence of depensation. In addition, we found evidence of reproductive

301   senescence, with a decrease in both the probability of conceiving and litter size with age. Mink culling

302   lead to a younger, more fecund mink population which ought to have contributed to an overall

303   compensation effect over the course of the management project.

304

Density dependence in mink fecundity

306   Sustained mink culling over multiple river catchments led to a substantial reduction in the relative

307   density of females with increasing number of years of control. The compensatory increases in the

308   proportion of females conceiving and in litter sizes must have partly counteracted control efforts.

309   Clearly the overall compensatory response was insufficient to negate the effects of culling since

310   density declined continuously within the years of control. Compensation effects are commonly

311   observed in the wild as a consequence of relaxation of competition at low density (e.g. Boyce et al.,

312   1999; Fryxell et al., 1999, 2001). We derived a pragmatic estimate of mink relative density by

313   comparing the number of settled mink in a given year with the potential number that could have

314   settled by combining information on the likely location of breeding territories over several years. On

315   that basis, mink densities in eight out of 21 river sections were never saturated, as in these areas the

316   maximum density in any year never reached the inferred maximum number of potential territories,

317   which were inferred from the capture locations of females (Fig. 3). This could indicate that female

318   mink were caught in, and possibly occupied, sub-optimal habitats in some years, denoting scope for

319   compensation.

320

321   While keeping in mind the caveats inherent to a non-experimental study like this one, the statistical

322   influence of female density on fecundity points towards female-biased intersexual competition for

323   territories occurring in American mink. While most females do conceive each year, the increase in

324   both conception rate and litter size suggest females attain better physiological condition at low

325   density. If conception and litter size were constrained by nutritional status, preferential settlement of

326   females in the best, most productive territories, might have contributed to the pattern we observed.

327

328   We postulated that features of female mink reproductive physiology might give rise to a positive

329   relationship between the number of males a female mated with and litter size. Despite a substantial

330   fraction of the culled females originating from river sections with severely depleted male mink, our

331   measures of the availability of males in spring provided no strong evidence of mating limitation or of

332 any impact on litter size. Indeed, the relative density of females was the most important predictor of

333 litter size and, together with age, was one of the two most important predictors of the probability of

334 conception. We expected that mink, being solitary animals, would have experienced a reduction in the

335 probability of conception because of inefficient mate finding at the lowest densities. However,

336 assuming that the proxy for density of mating males we used reflects mating opportunities, mate

337 availability only had a marginal effect on litter size and none on the probability of conception. We

338 considered separately the densities of females and conspecifics of either sex. Only female relative

339 density contributed to explaining variation in mink reproduction. On that basis, we find no evidence

340 for inter-sexual competition for territories such that the evidence is more consistent with the notion of

341 female territoriality.

342

343 The combined effect of age and female density reduction led to a predicted compensatory increase in

344 mink fecundity of up to 2.1 additional pups per surviving or immigrating female. Keeping all other

345 traits constant and using a simple two stage, female-only matrix model with adult and yearling

346 survival set at 0.5 % (Melero, 2007), the resulting increase in overall fecundity would increase the

347 annual population multiplication rate from 1.19 to 1.39, a difference of 26%. We know of no reliable

348 estimates of population growth rate for American mink, but our simple model approximations are in

349 line with estimates for similar sized mustelids such as the American marten (*Martes americana*), feral

350 ferret (*Mustela putorius*) and black footed ferret (*Mustela nigripes*), which can range between 1.3-

351 1.35 (Barlow and Norbury, 2001; Fryxell et al., 1999; Grenier et al., 2007). While this illustrates the

352 potency of an increase in fecundity for a short-lived species like mink, it is of course possible that

353 other traits such as post weaning juvenile survival could also be density-dependent and that the overall

354 compensation to culling might be greater still.

355

356 *Senescence in mink fecundity*

357 In addition to density dependence, mink fecundity was affected by senescence, with the youngest

358 breeding females having the largest litters and a higher pregnancy rate, resulting in higher fecundity.

14

359

360 Reproductive senescence has been detected in ungulates (e.g. McElligott et al., 2002; Jolles, 2007)

361 and rodents (reviewed in Nussey et al., 2013) but evidence is scarce for carnivores, being restricted to

362 long-lived species such as badgers (Dugdale et al., 2011), lions (Packer et al., 1988) and bears

363 (Schwartz et al., 2003). In a short-lived species with young age at primiparity such as mink,

364 senescence is expected to occur earlier than in long-lived ones (Bradley and Safran, 2014) but little

365 evidence is available. Litter size was reported to be independent of age in fur-farmed mink over the

366 first three years of age (Koivula et al., 2010). Thus to the best of our knowledge, this is the first time

367 that senescence in fecundity is detected in free ranging mink, and to our knowledge, in a short-lived

368 carnivore.

369

370 *Consequences and applications*

371 Despite a predicted increase in mink fecundity due to density dependence and changes in age structure

372 combined with senescence, the current management regime that entails ongoing mink detection

373 followed by trapping has succeeded in controlling invasive mink density over a large area. The model

374 prediction of an increase in fecundity was evident amongst females that re-invaded those river

375 sections in which mink control has been sustained over multiple years, with severely depressed

376 density. No such increase was discernible over the whole project area because the project expanded in

377 an asynchronous manner, with trapping in river sections beginning in different years. Our analyses

378 stress the importance of precluding recolonisation of low density areas by juveniles born in adjacent

379 areas and of early detection of immigrants before they express their potentially high fecundity.

380

381 Our analyses also uncovered a noticeable project area-wide increase in mink density in 2010,

382 coinciding with the decline of staff and vigilance in late 2009. Fortunately a key feature of the mink

383 management protocol implemented in this project, i.e. the fact that mink trapping effort is not constant

384 but adjusted locally in response to the detection of mink footprints on mink detection rafts, overcame

385 (i) this temporary setback and (ii) the model-predicted increase in fecundity at low mink density. Thus

386 there is a need to continue intensive detection and response to trapping in the event of any localised

387 mink reinvasion to counteract the density dependent increase in mink fecundity that putatively could

388 lead to the production of large litters of young, potentially dispersive mink by surviving breeding

389 females. While the management regime instigated by the management projects caters for this

390 eventuality (Bryce et al 2011), maintaining vigilance by volunteers operating mink rafts when mink

391 are scarce is an ongoing challenge.

392

393 Author contributions

394 Y.M and X.L. designed the study. Y.M. and E.R. carried out the laboratory uteri staining procedures.

395 Y.M. analysed the data and with X.L. wrote the manuscript.

396

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559

560   **Table 1** Weighted parameter estimates of the influence of standardised covariates with their

561   associated standard errors for variables included in the best hurdle models for the Probability of

562   conception and the Litter size at parturition in relation to the relative density of females (D_f), males

563   (D_m) and mating males (D_{mm}), the female age at conception in months (Age) and the month of capture

564   (Mcapt).

	Parameters	Estimate	SE	Z
Probability of conception ~	Intercept	3.607	1.005	3.586
	D_f	-0.369	0.237	-1.568
	Age	-0.351	0.205	-1.726
	Mcapt	-1.551	1.046	-1.482
Litter Size~	Intercept	1.982	0.131	14.807
	D_f	-0.067	0.103	-1.181
	D_m	-0.011	0.037	-0.801
	D_{mm}	-0.006	0.042	-0.212
	Age	-0.028	0.048	-0.543
	Mcapt	-0.263	0.159	-1.41

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570   **Fig. 1** (a) Illustrative example of maximum number of mink territories; symbols represent capture

571   locations per years, circles are 2 km buffers and the colour code represents territories in different

572   years. In the example dark grey is 2007, grey 2008 and light grey 2009. (b) Illustrative example for

573   the definition of mating males, M1, M2 and M3 represent adult males captured in May 2009 (M2) and

574   February 2010 (M1 and M3). M1 and M2 were considered "mating males" of female F1 because they

575   were adult and still alive during rut 2009. M2 was not a potential mating male of F1 since it was born

576   after the rut 2009

577

578   **Fig. 2** Violin plot for the litter size of females that conceived (n = 205) and age at parturition of all

579   sampled females (n = 238 > 10 months old) in relation to the year and the number of years of control.

580   Grey shapes show the density distribution of the y-axis covariate, grey circles stand for the median,

581   black bars for the quartiles Q1 and Q3, straight black lines for the minimum and maximum values and

582   black areas in (a) and (b) shows the density distribution of non-mated females.

583

584   **Fig. 3** Relative density of mink per (a) year and (b) years of control and relative density of females

585   per (c) year and (d) years of control. Solid black lines describe the project-wide relative density. Thin

586   lines show relative densities per river section with black dots denoting the year of first control for

587   each section, illustrating the gradual expansion of the project. Red and green lines notes the selected

588   project sections with constant coverage since the start of the project and currently low densities to

589   illustrate the maximum, model-predicted, magnitude of their combined impact.

590

591   **Fig. 4** Observed (dot) and hurdle model derived predictions (lines) probability of conception in

592   relation to (a) the relative density of females; (b) female age at conception; and litter size of females

593   that conceived in relation to (c) the relative density of females, (d) female age at conception.

594   Parameters were estimated using weighted estimates of the three top best models. Continuous line

595   relates to the estimated fit setting all the other covariates as constant at their median value; dashed

596   lines denote the 95% confidence intervals.

597

598 **Fig. 5** Observed (dot) and model predictions of the litter size of conceived females in relation to (a)

599 the relative density of males and (b) the relative density of mating males. Parameters were estimated

600 using weighted estimates of the three best models. Continuous line relates to the estimate fit setting all

601 the other covariates as constant at their median value dashed lines relate to the 95 % confidence

602 intervals.

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