Density-dependent demography and movements in a cyclic

brown lemming population

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Abstract

Theoretical modelling predicts that both direct and delayed density-dependence are key

factors to generate population cycles. Deciphering density-dependent processes that lead

to variable population growth characterizing different phases of the cycles remain

challenging. This is particularly the case for the period of prolonged low densities, which

is inherently data deficient. However, demographic analyses based on long-term capture-

mark-recapture datasets can help resolve this question. We relied on a 16-yr (2004-2019)

live-trapping program to analyse the summer demography and movements of a cyclic

brown lemming population in the Canadian Arctic. More specifically, we examined if

inversely density-dependent processes could explain why population growth can remain

low during the prolonged low phase. We found that the proportion of females in the

population was inversely density-dependent with a strong male-biased sex ratio at low

densities but not at high densities. However, survival of adult females was higher than

adult males, but both had lower survival at low densities than at high ones. Distances

moved by both adult males and females were density-dependent, and proportion of

females in reproductive condition was weakly density-dependent as it tended to increase

at low density. Individual body condition, measured as monthly change in body mass,

was not density-dependent. Overall, the strong male-biased sex ratio at very low densities

suggests a loss of reproductive potential due to the rarity of females and appears to be the

most susceptible demographic factor that could contribute to the prolonged low phase in

cyclic brown lemmings. What leads to this sex-bias in the first place is still unclear,

potentially owing to our trapping period limited to the summer, but we suggest that it

could be due to high predations rate on breeding females in winter.

Key words: Small mammals, rodents, food web, top-down regulation, tundra, trough

phase.

Introduction

Theory predicts that population cycles observed in herbivore populations are driven by

density-dependent processes that are either caused by extrinsic or intrinsic factors

(Stenseth, 1999). Among the different phases of population cycles, the most obscure and

enigmatic one remains the prolonged low abundance phase that can last for several years

after the decline in some species (Barraquand et al., 2017; Boonstra, Krebs, & Stenseth,

1998). From theoretical models, one can explain the low phase by delayed density-

dependent effects of factors such as predation or low food abundance (Bjornstad, Falck,

& Stenseth, 1995; Sheriff, Krebs, & Boonstra, 2009; Stenseth, 1999) and phase

dependent factors (Barraquand, Pinot, Yoccoz, & Bretagnolle, 2014), such as delayed

maturation. However, empirical evidence in support of changing density-dependence

across phases is still lacking especially because of the difficulty to study populations at

their lowest densities. Some support for the specialist predator hypothesis through a

delayed response was found to explain the low phase in cyclic lemmings and voles (Gilg,

Hanski, & Sittler, 2003; Norrdahl & Korpimäki, 2000), but others have rejected this

hypothesis (Graham & Lambin, 2002). Non-lethal effects such as reproduction

impairment that may last over several generations through maternal effects have gained

support, especially for snowshoe hare (*Lepus americanus*, Sheriff et al. 2009) and more

recently for meadow voles (*Microtus pennsylvanicus*; Edwards et al. 2021; but see

Boonstra and Boag 1992; Fauteux et al. 2018). The current lack of empirical evidence for

58 changes in demography and population structure in cyclic species at low vs high densities

59 is hampering our understanding of why these populations are susceptible to prolonged

60 low phases.

61   Detailed demographic analyses of populations in relation to densities are useful to

62 disentangle what factors are responsible for population growth in cyclic species (Aars &

63 Ims, 2002; Fauteux, Gauthier, & Berteaux, 2015; Hodges, Krebs, & Sinclair, 1999). By

64 identifying how survival, dispersal and reproduction are changing with density, we can

65 infer on the most plausible cause of slow growth at low density based on known

66 relationships between specific demographic traits and various extrinsic (e.g. predation)

67 and intrinsic factors (e.g. social interactions). Here, we address this question using a live-

68 trapping dataset collected on brown lemmings (*Lemmus trimucronatus*) in the Canadian

69 Arctic over 16 years (2004-2019), the longest capture-mark-recapture time series of

70 lemmings in the Arctic. In this population, brown lemmings show regular, high amplitude

71 cycles of abundance with a 3-4 yr periodicity (Gauthier et al., 2013). Our objectives were

72 to determine if summer demographic parameters or movement are density-dependent,

73 and if so, which one could contribute to slow population growth at low densities. In other

74 words, we were particularly interested in identifying inversely density-dependent

75 parameters during the summer period.

76   Based on past studies highlighting the importance of predation in causing the

77 decline phase of cyclic lemmings and northern voles (Fauteux, Gauthier, & Berteaux,

78 2016; Gilg et al., 2003; Norrdahl & Korpimäki, 1995; Wilson, Krebs, & Sinclair, 1999),

79 we hypothesized that the lack of population growth at low density could be caused by

80 both direct effects of generalist predators (e.g. Arctic fox, *Vulpes lagopus*) and the

81 delayed density-dependent response of mustelids (Ilkka Hanski, Hansson, & Henttonen,

82 1991). If this hypothesis is correct, we expected an inversely density-dependent survival

83 (i.e. lowest survival at low density) in lemmings caused by the delayed numerical and

84 functional response of mustelids (Gilg et al., 2006). Animal movement can be an

85 important factor affecting their vulnerability to predation. Adult males are known to be

86 more active and more mobile than females (Banks, Brooks, & Schnell, 1975), which can

87 lead to increased exposure to predation as seen in voles (Norrdahl & Korpimäki, 1998).

88 In addition, when densities reach extremely low levels (<0.1 lemming ha^{-1}), lemmings

89 may rarely encounter conspecifics within their usual home range (0.5-1.5 ha; Banks et al.

90 1975), which may force them to move or disperse over longer distances to find mates

91 (Andreassen & Ims, 2001; Ostfeld & Canham, 1995). Consequently, we expected that 1)

92 males should move more than females, 2) all lemmings should move more at low

93 densities, 3) males should have lower survival than females, especially at low densities,

94 and 4) this should lead to a female-biased sex-ratio at low density.

95   Aside from predation, other factors have been proposed to be responsible for the

96 low phase of cycles (e.g. lack of food following overgrazing at high density, maternal

97 effects, or parasites). These factors could also lead to lower survival at low densities than

98 at high ones, but one important difference with the predation hypothesis is that these

99 factors should also lead to less healthy animals (i.e. lower body condition or growth), and

100 possibly lower reproduction at low density. If one of these hypotheses was correct, we

101 thus expected that body mass gain lemmings and proportions of females in reproductive

102 condition during the summer should be lower at low than at high densities.

103

Material and Methods

Study area – Our study was conducted in the Qarlikturvik Valley on Bylot Island,

Nunavut, Canada (73º 08' N, 80º 00' W). Only two rodents are present: brown lemmings,

which are mostly found in wet and mesic tundra areas, and collared lemmings, which

(*Dicrostonyx groenlandicus*) are mostly found in the mesic habitat and drier hills. Both

species are cyclic (Gauthier et al., 2013), but brown lemmings have much larger

population fluctuations, increasing by up to 100-fold between low and high densities, and

is the most abundant of the two species. Maximum densities of brown lemmings may

reach up to ~15 ha^{-1} in peak years while collared lemmings may reach 1 ha^{-1}.

Competition between both species favors brown lemmings (Morris, Davidson, & Krebs,

2000). For those reasons, we focused our study only on brown lemmings. Their main

predators are Arctic foxes, ermines (*Mustela erminea*), snowy owls (*Bubo scandiacus*),

long-tailed jaegers (*Stercorarius longicaudus*), and rough-legged hawks (*Buteo lagopus*).

On Bylot Island, brown lemmings feed mainly on willows (*e.g. Salix arctica*), mosses

(*e.g. Aulacomnium* sp., *Polytrichum* sp.) and, to a lesser extent, grasses (*e.g. Alopecurus*

sp., *Arctagrostis* sp.; Soininen et al. 2015; Fauteux et al. 2017).

Lemming live-trapping – From 2004 to 2019, lemmings were live-trapped from June to

August in two 11-ha trapping grids, one located in wet tundra and the other in mesic

tundra (also called mesic grid 1). Each trapping grid consisted of 144 trapping stations

spaced out every 30-m according to a Cartesian plane (12 x 12) and each station had one

Longworth live-trap. Starting in 2007, a third trapping grid made of 96 trapping stations

(8 x 12) was added in the mesic tundra habitat (also called mesic grid 2). In 2013-2019,

127   this 9-ha grid was fenced and covered by a net made of fishing lines to prevent predators

128   from accessing the lemmings (hereafter the predator exclosure), creating specific

129   conditions for this grid in those years (Fauteux et al., 2016). Thus, we added a fourth

130   level to the trapping grid covariate in the analyses corresponding to years with a predator-

131   exclosure. Capture-mark-recapture schedules consisted of three primary periods (four in

132   the first four years) and up to 10 secondary periods (i.e. traps being visited every 12h) per

133   primary period each summer. All lemmings captured were identified, sexed, weighed,

134   aged, their reproductive condition noted and marked with a passive integrated

135   transponder or an ear-tag. More details on live-trapping schedules, baiting, and marking

136   lemmings can be found in Appendix S1. All field manipulations and animal care

137   precautions were approved by the Animal Welfare Committees of Université Laval and

138   the Canadian Museum of Nature, and by Parks Canada.

139

140   ***Densities and sex and age ratios*** – We estimated densities of adult and juvenile males

141   and females with spatially-explicit capture-recapture (SECR) models for each primary

142   period, grid, and year. In the models, we used a 100-m buffer that corresponds to 3-4

143   times the daily movement of lemmings and a half-normal detection function. For the high

144   abundance years, densities were estimated separately for each primary period (i.e.

145   monthly trapping session in June, July, and August) and trapping grid. For the low

146   abundance years, which typically have ≤5 individuals captured per primary period, we

147   combined datasets from all years for each trapping grid and assumed that the probability

148   of capture and the movement parameter (sigma) were constant over those years, but

149   different among trapping grids. This allowed us to estimate the population densities with

150   a constant but imperfect probability of detection during the low abundance years. To

151   further reduce the number of parameters, densities were derived from models that used

152   the conditional likelihood (Borchers & Efford, 2008).

153   We calculated the proportion of each sex and age category by bootstrapping

154   where each SECR model was repeated 200 times with different randomized datasets each

155   time. These datasets were obtained by resampling capture histories of the original

156   datasets with replacement while keeping the same sample size. The randomization

157   process was repeated for each primary period, grid, and year. The final proportions are

158   the mean proportions obtained across the 200 iterations of each dataset and the standard

159   errors were obtained from the standard deviation of the mean.

160

161   ***Distances moved*** – We calculated the maximum and average Euclidean distance moved

162   for each lemming based on the location of their initial capture and the location of

163   subsequent recaptures within trapping grids. These distances were calculated for each

164   individual, trapping grid, and year. When individuals were captured in more than one

165   primary period of the same year, captures were pooled. Trapping grids were separated by

166   >600 m and no lemming was ever captured in more than one trapping grid.

167

168   ***Reproduction*** –We analysed the reproductive condition of adult females only because the

169   condition of males was not noted systematically during all sampling years and because of

170   the importance of females to population dynamics in general. From 2009-2019, captured

171   females were classified as non-reproductive (no sign of past or current reproduction) or

172   reproductive (perforate vagina, lactating or showing enlarged nipples, or pregnant with an

173   enlarged abdomen and palpable foetuses).

174

175   ***Daily change in body mass*** –We measured the daily change in body mass (g) of

176   lemmings between consecutive periods from the difference between the body mass at the

177   primary trapping period $t+1$ and the body mass at the primary period t divided by 20 or

178   30 days, depending on the time between primary periods. Individuals recaptured but in

179   non-consecutive primary periods (e.g. captured in June, not captured in July, recaptured

180   in August), were ignored for this analysis. If an individual was captured more than once

181   within a primary period, we averaged its body mass. Because primary trapping periods

182   were separated by either 20 or 30 days with traps locked open without any bait added

183   during the interval, we assumed that trap-related effects on body mass were negligible.

184   Pregnant females were excluded from the analysis.

185

186   ***Statistical analyses*** – We modelled the influence of total population density on the

187   proportion of each age/sex group with a robust linear model where extreme values were

188   given a weight based on residuals with the *M*-estimator (Huber, 1981; Venables &

189   Ripley, 2002). The trapping grid was added as a covariate. To consider the errors of the

190   data points on both axes, we used a bootstrapping approach to obtain coefficients and

191   their 95% confidence intervals. We first generated 2 000 new datasets, each with the

192   same sample size as the original, by resampling with replacement paired X and Y values

193   in our datasets. To apply a normal distribution, observations were transformed on the

194   logit scale for proportions or log scale for densities prior to resampling. We applied the

195   robust linear model on each of the randomly generated datasets and estimated regression

9

196 coefficients as the mean from the 2000 models and their 95% confidence interval

197 boundaries as the 2.5% and 97.5% quantiles (i.e. 50th and 1950th predicted values in

198 ascending order). The package "*MASS*" in the software R was used to run the robust

199 linear models (Venables & Ripley, 2002). All the following analyses were run in the R

200 software as well, except for survival estimations.

201 We used the software E-Surge (Choquet, Rouan, & Pradel, 2009) to estimate

202 summer survival probabilities among primary periods. Overwinter survival could not be

203 estimated due to extremely low recapture rates between summers (<1%). We elaborated a

204 set of candidate models to test the effects of sex, age, trapping grid, year, and primary

205 period on survival. For this analysis and the following ones, the selected model was the

206 simplest (i.e. least number of parameters) among the most parsimonious models

207 (ΔAICc<2). We used unequal time intervals to consider that primary periods were

208 separated by 20 days from 2004 to 2007 and 30 days afterwards. We could not directly

209 test the relationship between monthly survival and SECR population density due to our

210 complex dataset and the definition of the design matrices in E-Surge. Instead, we

211 conducted an *a posteriori* analysis using a robust linear model relating survival

212 probabilities estimated between primary periods t and $t+1$ for each year, and sex- age

213 groups with densities at t.

214 We analysed the maximum and average distance moved during the summer

215 between the first capture of individuals and their subsequent recaptures. When all

216 captures were at the same trap, a value of 0 was assigned to that individual. Due to the

217 many zeros inherent to such data, we used a negative binomial regression. A set of

218 candidate models was developed with additive and interactive effects of sex, age,

219 trapping grid, and annual population density (i.e. average of July and August densities).

220 We controlled for unequal number of recaptures between individuals with an offset (log-

221 transformed total number of captures). Model selection was conducted in the same way

222 as for the survival analysis.

223   For each adult female that was reproductive when captured, a value of 1 was

224 attributed, and a value of 0 when non-reproductive. We used a mixed-effects binomial

225 model with individuals as the random variable to consider the repeated measures taken on

226 them. The set of candidate models included additive effects of population density,

227 primary period, and trapping grid as fixed effects to control for when and where

228 lemmings were captured. The top model was selected using the same approach as for the

229 other analyses.

230   We tested whether change in body mass was density-dependent with linear

231 mixed-effects models where individuals were also used as the random variable. All

232 candidate models included the initial body mass of lemmings as a fixed variable to

233 consider the more rapid growth of young individuals compared to adults. The other fixed

234 variables included additive or interactive effects of sex, primary period, trapping grid and

235 population density to consider ontological, seasonal, spatial, and density-dependent

236 effects. Model selection was conducted in the same way as for the previous analyses. All

237 model coefficients and estimates are reported with their 95% confidence intervals in

238 brackets.

239

240 **Result**s

241 ***Sex and age ratio*** – Densities of brown lemmings on the different grids varied

242   throughout the years, going from local extirpation in 2013 to a maximum of 9 lemmings

243   ha^{-1} in 2014. Sample sizes are presented in the Appendix, Table S1. The proportion of

244   adult females in the population was positively related to population density (β = 0.060,

245   [0.027, 0.092]; Figure 1). In contrast, proportions of adult males (β = -0.025, [-0.069,

246   0.018]), juvenile males (β = -0.020, [-0.062, 0.012]) and juvenile females (β = 0.083,

247   [-0.013, 0.026]) did not vary significantly with density. At high densities, the

248   female:male ratio of adults was close to 1:1, but it was approximately 1:3 at low

249   densities. The age ratio was generally in favour of adults with, on average, 2.5 adults per

250   juvenile (Appendix S1, Figure S1).

251

252   ***Survival*** – The most parsimonious model from the survival analyses included full-time

253   effects (i.e. variations among each month and year), an interaction between lemming age-

254   sex groups and primary periods, and an additive effect of trapping grids (Appendix, Table

255   S2, Figure S2). Adult females had higher apparent monthly survival ($\hat{s}$ = 0.43, [0.40,

256   0.47]) than adult males ($\hat{s}$ = 0.32, [0.29, 0.35]), whereas the converse was found in

257   juveniles (females, $\hat{s}$ = 0.49, [0.46, 0.52]; males, $\hat{s}$ = 0.24, [0.20, 0.27]). Monthly survival

258   of adults were slightly lower in late ($\hat{s}$ = 0.31, [0.26, 0.36]) summer compared to early

259   summer ($\hat{s}$ = 0.40, [0.27, 0.55]), whereas the opposite was true for juveniles ($\hat{s}$ = 0.42,

260   [0.38, 0.46] vs $\hat{s}$ = 0.26, [0.09, 0.56]). Apparent monthly survival was highest in the

261   predator exclosure grid ($\hat{s}$ = 0.49, [0.46, 0.52]) and lowest in the wet grid ($\hat{s}$ = 0.29, [0.27,

262   0.32]). Capture probability was estimated at 0.92 ([0.85, 0.96]) overall and did not vary

263   according to age and sex or over time. The *a posteriori* analysis of the relationship

264   between apparent monthly survival and density shows that survival increased with

265 density in both adult females (β = 0.052, [0.005, 0.098]) and males (β = 0.037, [0.004,

266 0.068]; Figure 2). It is noteworthy that all lemmings captured in 2012 and 2018 (n = 17),

267 two years of very low density, were never recaptured between primary periods, leaving

268 those years to be the only ones with a survival probability of 0. Survival of juvenile

269 females (β = -0.027, [-0.123, 0.049]) and males (β = -0.006, [-0.038, 0.022]) were not

270 related to density.

271

272 *Movements within trapping grids* – The most parsimonious model of the analysis of

273 maximum distance moved included a negative effect of density (β = -0.076, [-0.112, -

274 0.040]) and an interaction between sex and age (β = -0.497, [-0.968, -0.039]; Figure 3;

275 Appendix S1, Table S3). Maximum distances moved by lemmings decreased from 78 ±

276 63 m (standard deviation) at very low density to 48 ± 49 m at high density. Maximum

277 distance moved was highest in adult males (66 ± 56 m), intermediate in adult females (41

278 ± 42 m) and lowest in juveniles (males: 25 ± 32 m, females: 22 ± 36 m). Similar results

279 were obtained with average distances (density: β = -0.068, [-0.105, -0.031]; interaction

280 between sex and age: β = -0.62, [-1.111, -0.152]).

281

282 *Reproductive conditions* – The most parsimonious model for the proportion of adult

283 females in reproductive condition analysis included the variables density, primary periods

284 and trapping grids (Appendix, Table S4). The proportion of adult females in reproductive

285 condition slightly decreased with density (β = -0.090, [-0.170, -0.004]; Figure 4;

286 Appendix, Table S5). Proportion of reproductive females in mid-July was higher than in

287 mid-June but not in mid-August. Finally, the proportion of reproductive females was

288 lower in the mesic trapping grid (0.67) than in the wet trapping grid (0.81) and was

289 highest in the predator exclosure (0.94).

290

291 ***Daily change in body mass*** – The most parsimonious model for change in body mass (g

292 d^{-1}) included an interaction ($\beta = 0.006$, 95% CI = [0.004:0.009]) between initial body

293 mass and primary period (June-July vs July-August), suggesting both ontological and

294 seasonal effects, but no relationship with population density (Figure 5; Appendix, Table

295 S6). Young (i.e. <30 g) lemmings gained less mass in late than in early summer, whereas

296 adults generally gained mass in early summer but lost mass in late summer, especially

297 among the largest lemmings. Change in body mass was similar between the wet tundra

298 and the predator exclosure trapping grids but lower in the two mesic grids.

299

300 **Discussion**

301 As expected, we found that adult males had lower survival rate than adult females during

302 the summer and there was evidence for an inversely density-dependent survival rate in

303 adults, with a slightly lower survival at low density. Sex-ratio was strongly dependent on

304 density but, contrary to our initial prediction it was heavily biased in favor of males at

305 low density. This suggests a large reduction in the number of adult females in the

306 population compared to adult males at low densities. This shift in sex ratio is counter-

307 intuitive and our data did not allow us to pinpoint the precise demographic mechanism

308 that led to it. However, considering that females contribute more to population growth

309 than males, especially in polygynous, multivoltine species like small mammals (Erlinge,

310 Hasselquist, Svensson, Frodin, & Nilsson, 2000), this reveals a shortage of females in the

311   population. A rarity of females combined with the reduced survival of adults at low

312   population density (<1 lemming ha^{-1}) is likely to lead to a slow recruitment in the

313   population and could be an explanation for the prolonged low abundance phase. We now

314   explore potential explanations for the male-biased sex-ratio at low densities.

315

316   ***Trappability and mobility*** – We found that adult females moved over shorter distance

317   than males as reported in other studies on small rodents (Banks et al., 1975; Koivunen,

318   Korpimäki, & Hakkarainen, 1996). A higher mobility of males may potentially lead to

319   different detectability than females if not taken into account. However, capture

320   probabilities of lemmings estimated in the survival analysis was high (>0.90) and did not

321   differ between sex and age groups. Moreover, if low mobility reduces trappability, then

322   the increased movements at low density observed here for all lemmings should have led

323   to higher trappability of both males and females, not less. Thus, there is no evidence that

324   different trappability between sexes could explain the male-biased sex-ratio at low

325   density.

326

327   ***Sex-specific mortality and predation*** – The lower survival of adult males compared to

328   females may be explained by their higher mobility, which increase their vulnerability to

329   predation. During the summer, a large proportion of lemming mortality is due to

330   predation by avian predators (Therrien, Gauthier, Korpimäki, & Bêty, 2014). In western

331   Finland, studies on cyclic voles have shown that males were more often hunted by avian

332   predators, whereas females were more often hunted by weasels (Koivunen et al., 1996;

333   Norrdahl & Korpimäki, 1998). Although high avian predation could be the cause of the

low summer survival of male lemmings observed here, it cannot explain the reduced

adult survival at low density because many avian predators are absent during the low

lemming phase (Gilg et al., 2006; Therrien et al., 2014). Considering the delayed

response of mustelids to small mammal population outbreaks (Gilg et al., 2003; I.

Hanski, Turchin, Korpimaki, & Henttonen, 1993), their impact should be stronger late in

the cycle, namely at the beginning of the low phase, and could explain the latter result.

However, it is still unclear why the sex-ratio became highly male-biased at low densities

considering that females had higher summer survival. A possible explanation is that

females may be more susceptible to predation than males at other times of the year such

as in fall or winter when populations typically crash (Fauteux et al., 2015). Previous

studies found that large winter nests in which females raise their young had more signs of

predation by mammals (i.e. lemming bones, skin) than smaller nests with no reproduction

(Bilodeau, Gauthier, & Berteaux, 2013; Schmidt et al., 2021).

Food limitation, parasites, and intrinsic factors – It is more difficult to explain the

strong male-biased sex ratio that we observed by a high mortality or a reduced

reproductive rate due to starvation or infections. In the High Arctic, studies revealed that

lemmings have low to no impact on the vegetation they eat even during the peak

abundance phase (Bilodeau, Gauthier, Fauteux, & Berteaux, 2014), potentially because

their maximum densities (~15 ha^{-1}) never reach outbreak levels. In contrast, abundance

indices of lemmings in Fennoscandia, where some evidence of overgrazing was observed

after peak population years, can reach up to 30 lemmings per 100 trap-nights, which are

values much higher than maximum lemming abundance recorded at our study site (<5

357 lemmings per 100 trap-nights; Fauteux, Gauthier, Mazerolle, et al., 2018; Olofsson,

358 Tømmervik, & Callaghan, 2012; Ruffino et al., 2015). Moreover, both sexes did not gain

359 less body mass at low than at high density, suggesting that starvation and poor health was

360 not more prevalent in one situation than the other. Indeed, negative physiological effects

361 were mainly observed in small rodent populations that typically reach much higher

362 densities (e.g. lemmings up to 200 ha^{-1} in Alaska, Pitelka & Batzli, 2007; voles up to 400

363 ha^{-1} in semi-natural enclosures; Bian et al., 2015; Edwards et al., 2021). There could be

364 sex-specific effects of parasites mediated through endocrinal responses as observed with

365 ticks in voles (Hughes & Randolph, 2001), but there is no evidence that such effect can

366 have a significant impact on survival at the population level (Khokhlova, Serobyan,

367 Degen, & Krasnov, 2010; Steen, Taitt, & Krebs, 2002). Finally, intact brown lemming

368 carcasses were virtually never found on top of the snow in May and June, on the tundra

369 immediately after the snow melt, or in their winter nests, suggesting minimal mortalities

370 caused by health problems in winter.

371

372 ***Explaining the low phase*** – The most surprising result of our study is the presence of an

373 inversely density-dependent sex-ratio strongly in favour of males at low density in cyclic

374 brown lemmings. Given that lemmings are polygamous and multivoltine, the high

375 number of males and their increased movements at low density should help maintain a

376 high mating success and prevent an Allee effect due to a low fertilization rate of females

377 (Berec, Angulo, & Courchamp, 2007). A similar proportion of juveniles in the population

378 at all densities and a tendency for a higher proportion of females in reproductive

379 condition at low density further suggest that reduced fertilization of females is not

380   occurring at low density. We acknowledge that there may be other intrinsic factors at

381   play that we could not measure such as fewer and smaller litters at low densities

382   compared to high ones (e.g. Mihok & Boonstra, 1992), and such data may be increasingly

383   accessible with new technologies such as subnivean cameras (Kalhor et al., 2021).

384   Nonetheless, the low proportion of adult females in the population at very low density

385   must be a strong limiting factor for the reproductive potential of the population.

386   A high mortality rate of females outside the summer season could explain the

387   paradox observed in our results, namely a male biased sex-ratio at low density despite a

388   lower summer survival rate in males than in females. Females may be more vulnerable to

389   mammalian predators in winter due to the auditory and olfactory cues present around

390   their nests under the snow when nursing their young (Bilodeau et al., 2013; Duchesne,

391   Gauthier, & Berteaux, 2011). This could have a major impact on their population

392   dynamics considering that the winter season could last up to 9 months in the High Arctic.

393   Interestingly, the reduced survival of lemmings at low densities contrasts with the high

394   survival of cyclic snowshoe hares during the low phase (Hodges et al., 1999). A negative

395   consequence of maintaining high survival during this stressful phase is a partial

396   suppression of reproduction (Sheriff et al., 2009). The case of brown lemmings is

397   different in this regard because even when stressed by predators, their reproductive

398   activity remains high (Fauteux, Gauthier, Berteaux, et al., 2018). However, the presence

399   of ermines, a specialised predator known to show a delayed response to fluctuations in

400   small mammal density (Gilg et al., 2003) and efficient in hunting small mammals in

401   winter under the snow (Bilodeau et al., 2013) may be a key factor in the case of

402   lemmings.

403   The prolonged low phase of cyclic populations remains the most difficult part of

404   the cycle to explain but comparison of our results to other studies suggests that factors

405   involved may differ between species. Although our study is limited to the summer period,

406   it provides empirical evidence that change in population structure, and especially in sex

407   ratio, throughout the population cycles are important parameters to consider and can

408   provide useful clues to uncover factors driving the population dynamics. In the case of

409   arctic small mammals, we suggest that sex-specific winter predation may be a key factor,

410   and should the focus of future studies despite the challenge associated with winter field

411   work in the High Arctic. In addition to subnivean cameras, genetic analyses of lemming

412   body remains found in winter nests such as paws, pieces of skin, guts or skulls could be

413   useful approaches.

414

424

425   **Declarations:**

432 **Conflicts of interest/Competing interests:** The authors declare no conflict of interest.

433 **Ethics approval:** All manipulations conducted on lemmings were evaluated and

434 approved by the Animal Welfare committees of Université Laval and the Canadian

435 Museum of Nature, and Parks Canada.

436 **Consent to participate**: No humans involved in the study.

437 **Consent for publication**: No humans involved in the study.

438 **Data accessibility:** All data are currently available in open access on the NordicanaD

439 website.

440 Reference of the dataset: Gauthier, G. 2020. Lemming monitoring on Bylot Island,

441 Nunavut, Canada, v. 1.3 (1994-2019). Nordicana D22, doi: 10.5885/45400AW-

442 9891BD76704C4CE2.

443 **Code availability:** All codes will be communicated on request.

444 **Authors' contributions**

445 DF collected data, conducted the analyses and wrote the first draft of the manuscript; GG

446 collected data and contributed significantly to the revision of the text.

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617

Figure legends

Figure 1. Proportion of adult females (a; ≥28 g), adult males (b; ≥30 g), juvenile males (c) and juvenile females (d) in the population in relation with total population density (i.e. sum of density of each lemming group) at Bylot Island, 2004-2019. Solid lines represent the robust regression estimated by bootstrapping and dotted lines represent the 95% confidence intervals (absence of lines indicate non-significance). Black circles: wet meadow trapping grid 1; white circles: mesic trapping grid 1; black triangles: mesic trapping grid 2; white triangles: predator exclosure trapping grid.
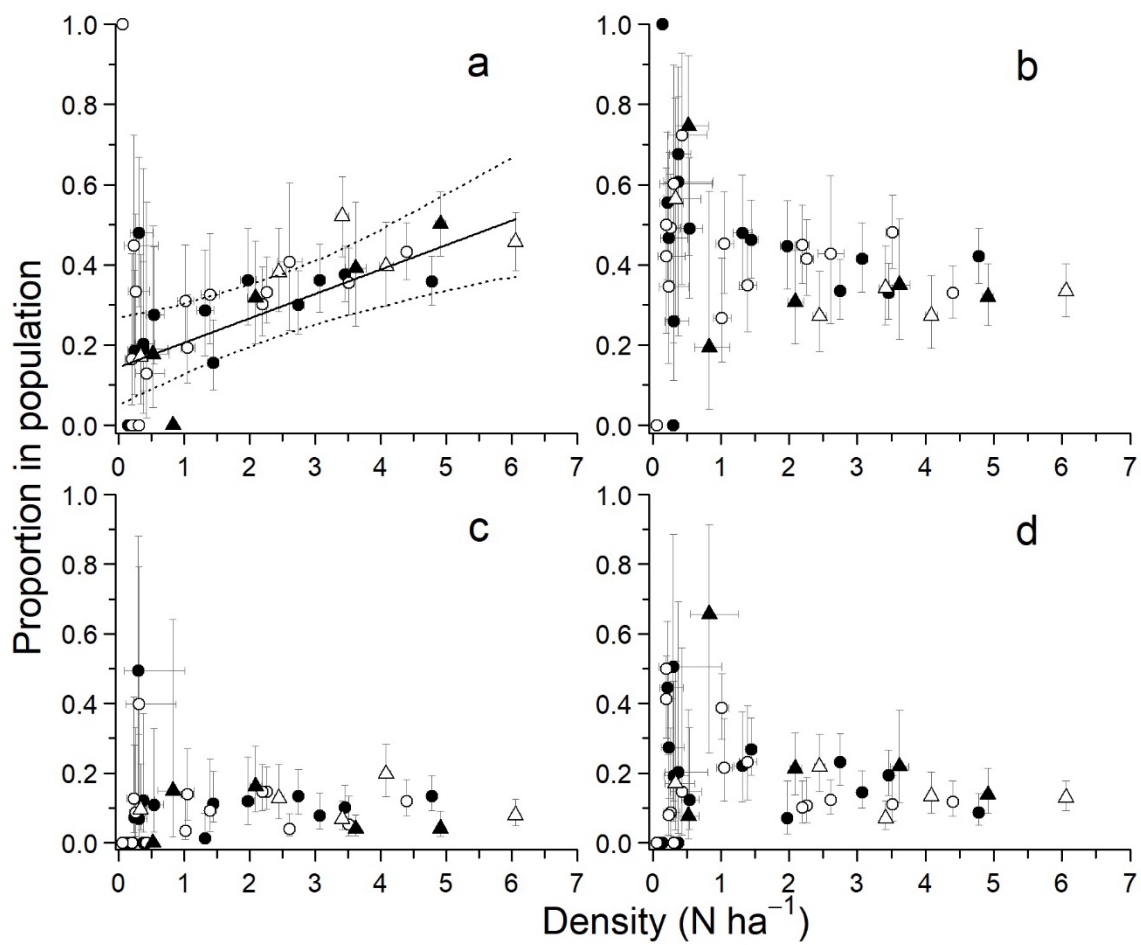
Figure 2. Monthly summer survival probabilities of adult female (a), adult male (b), juvenile female (c) and juvenile male (d) brown lemmings in relation to population density at Bylot Island, 2004-2019. Solid lines represent significant relationship from the robust regressions and dotted lines represent the 95% confidence intervals (absence of lines indicate non-significance). Black circles: wet meadow trapping grid 1; white circles: mesic trapping grid 1; black triangles: mesic trapping grid 2; white triangles: predator exclosure trapping grid. Grey lines are the 95% confidence intervals on both axes for each observation.

Figure 3. Maximum distance (m) between the initial capture and any recapture of brown lemmings during the same summer in relation with annual population density at Bylot Island, 2004-2019. For better visualisation of the raw data, empty grey circles represent maximum movements of each individual and filled grey squares are the averaged

640   movements for each year. The solid black line represents the negative binomial

641   regression and dotted lines represent the 95% confidence intervals.

642

643   **Figure 4.** Proportion of adult females in reproductive condition (i.e. with perforate

644   vagina, lactating, or pregnant) per trapping grid, primary period, and year in relation with

645   the total population density at Bylot Island, 2009-2019. The solid line represents the

646   predicted values from the binomial model and the dotted lines are the 95% confidence

647   intervals. Black circles: wet meadow trapping grid 1; white squares: mesic trapping grid

648   1; black triangles: mesic trapping grid 2; white triangles: predator exclosure trapping

649   grid. Size of points represent sample size with the smallest being 1 to the largest being

650   54.

651

652   **Figure 5.** Predicted (slopes) and observed (circles) daily gain in body mass of lemmings

653   in relation with initial body mass for early summer (June-July; filled circles, solid line)

654   and late summer (July-August; open circles, dashed line) at Bylot Island, 2004-2019.

655   Predictions and their 95% confidence intervals (dotted lines) are based on the most

656   parsimonious and simplest linear mixed-effects model. The horizontal grey dashed line is

657   presented for visual guidance only.
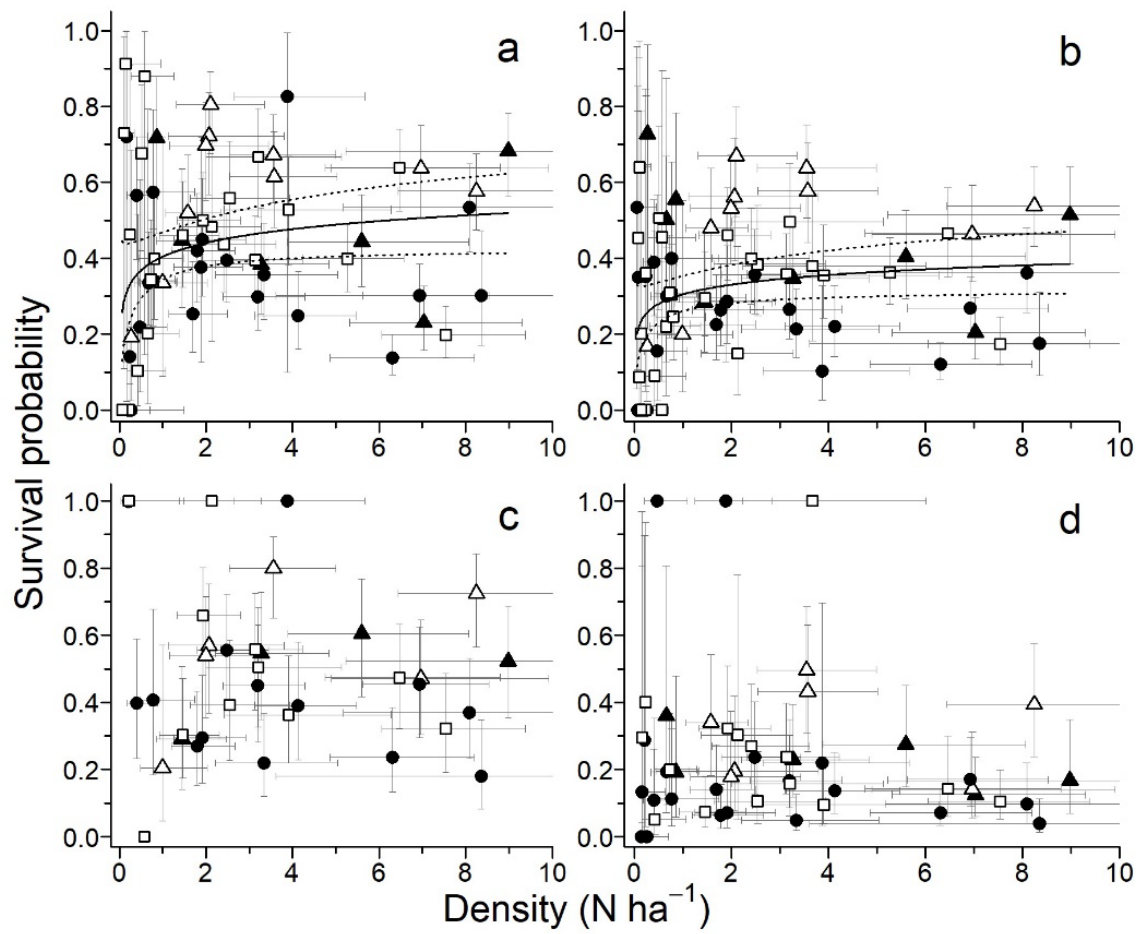
659

660   **Figure 1.**
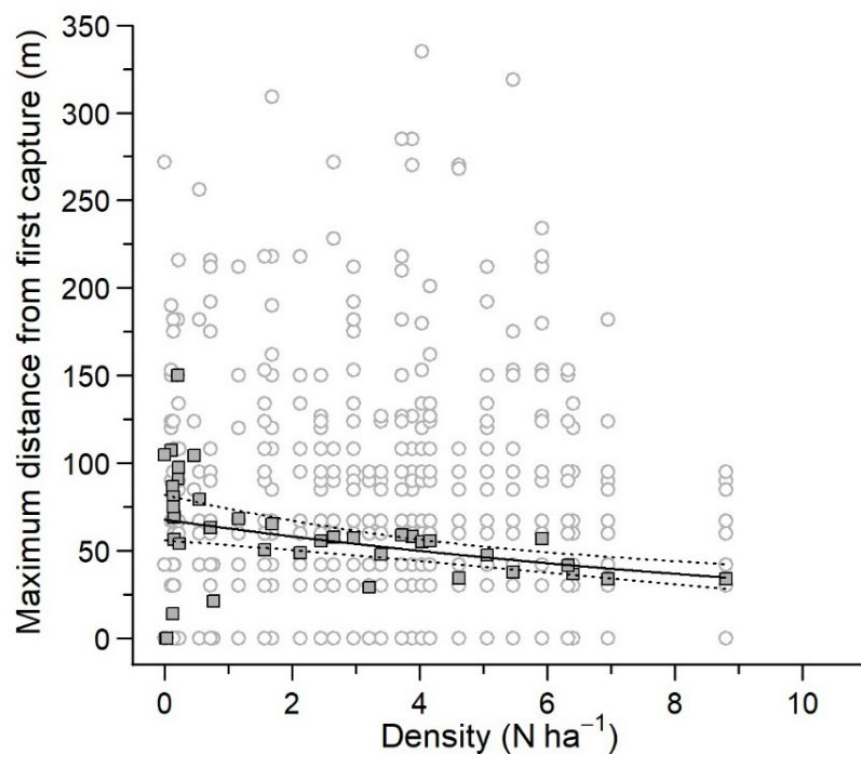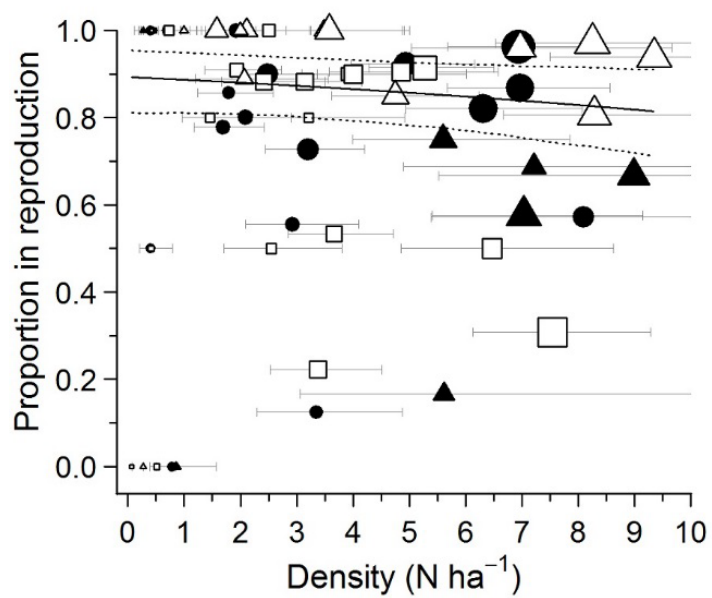
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Figure 2.

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664 **Figure 3.**

665

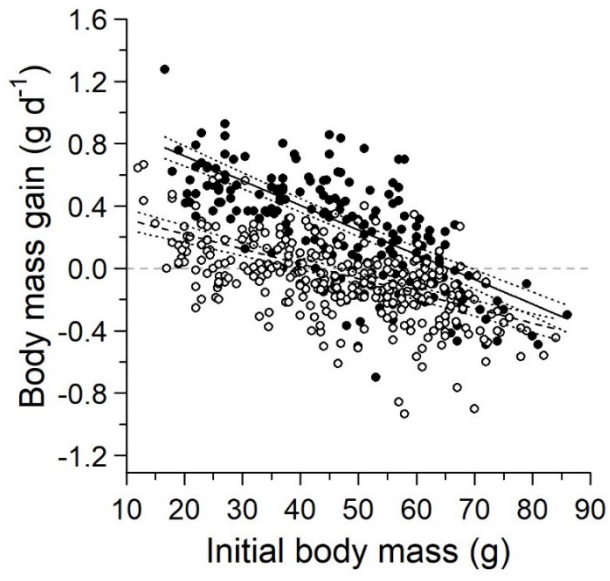666 **Figure 4.**

667

Figure 5.

669

670 **Appendix. Details on the live-trapping protocol, sample sizes,**

671 **and tables and figures presenting additional results.**

672

673 *Details of the live-trapping protocol*

674 We used four primary periods (i.e. mid June, early July, late July, and mid August) and

675 up to ten secondary periods (i.e. visits of traps every 12 h) in 2004-2007. In 2008, we

676 reduced the number of primary periods to three (i.e. mid-June, mid-July, mid-August)

677 and the secondary periods to six. Within primary periods our live-trapping design,

678 secondary periods consisted of visiting traps every 12 h for three to five consecutive days

679 depending on the year. For the first primary period, traps were set in the grids for ~24 h

680 in the locked-open mode (i.e. lemmings could enter without activating the trap). Then,

681 traps were activated with a piece of apple (2004-2015) or with both a piece of apple and a

682 small grape-sized ball of peanut butter mixed with oat and flour (2016-2019). Each

683 lemming trapped was identified to species, sex, weighed, and marked with a PIT-tag or

684 an ear-tag. Ear-tags were used to reduce costs but were employed only during the last

685 primary period of 2016-2019 to avoid false mortalities or emigration due to loss of tags.

686 Inter-annual recaptures are extremely rare due to most lemmings living less than a year

687 (Fauteux et al. 2018b). Recaptured lemmings were once again weighed, their

688 reproductive condition was noted, and the tag number was noted. We assigned

689 individuals to age classes (juveniles or adults) based on their body mass, with adult

690 female lemmings being ≥ 28 g and adult males being ≥ 30 g (Fauteux et al. 2015). Traps

691 were then left continuously in the locked-open mode between primary periods. Number

692 of individual lemmings trapped over the years are presented in Table S1.

36

693   **Table S1.** Number of individual brown lemmings captured per year for each sex and age

694   group. Lemmings from all primary periods and trapping grids have been pooled to

695   simplify the table.

Year	Adult females	Adult males	Juvenile females	Juvenile males
2004	19	47	11	28
2005	13	8	2	3
2006	5	5	1	13
2007	2	10	2	8
2008	56	60	25	57
2009	4	7	2	3
2010	83	114	19	49
2011	169	142	38	61
2012	1	9	4	1
2013*	0	0	0	0
2014	181	186	47	62
2015	98	101	57	62
2016	48	66	26	22
2017	3	12	5	4
2018	1	1	0	0
2019	43	53	19	40

696   *No brown lemming was captured in 2013 even if the exact same trapping protocol as the
697   other years was applied.

698

699　**Table S2**. Model selection for the survival analysis of brown lemmings on Bylot Island

700　conducted with E-SURGE. The most parsimonious model and the next two best models

701　are presented.

φ	K	Deviance	ΔAICc
year.*t*+AgeSex.*t*+grid	**51**	**1951.02**	**0.00**
year+AgeSex.*t*+grid	36	1987.87	5.92
AgeSex.*t*+grid	23	2025.02	16.51

702　year: annual variation; *t*: monthly variation (between primary periods within year);

703　AgeSex: categorical variable with four values (adult females, adult males, juvenile

704　females, juvenile males); grid: categorical variable with four values (wet tundra grid,

705　mesic tundra grid 1, mesic tundra grid 2, predator exclosure).

706   **Table S3.** Ranking of negative binomial models for the analysis on maximum and

707   average distances between the initial capture and recaptures based on the second order

708   Akaike's information criterion. The model selected for the results presented in the

709   manuscript is in bold. Models shown are those with a ΔAICc<4 and the following one.

710   All models included an offset based on the log-transformed number of recaptures. For

711   each model, the number of parameter (*K*), the log-likelihood (*LL*) and the dispersion

712   parameter for negative binomial models (θ) are also shown.

Movements	Model	*K*	Log-likelihood	ΔAICc	θ
Maximum distance	**density+sex*age**	**6**	**-5773.70**	**0.00**	**0.467**
	density*age+sex	6	-5774.79	2.19	0.467
	density+sex+age	5	-5775.97	2.51	0.466
	density*sex*age	9	-5772.68	4.05	0.468
Average distance	**density+sex*age**	**6**	**-5453.47**	**0.00**	**0.441**
	density*sex*age	9	-5452.19	3.53	0.442
	density+sex*age+grid	9	-5452.22	3.58	0.442
	density*age+sex	6	-5455.60	4.27	0.444

713

714   **Table S4.** Ranking of logistic mixed-effects models testing the relationship between the

715   proportions of adult females in reproductive condition (i.e. perforate vagina, lactating or

716   pregnant) and population density. All models with a ΔAICc <4 and the following one are

717   listed. The selected model is in bold.

Model	K	Log-likelihood	ΔAICc
D+period+grid	**8**	**-439.49**	**0.00**
period+grid	7	-441.57	2.13
D+grid	6	-444.55	6.05

718

719 **Table S5**. Model coefficients (β) and 95% confidence intervals (CI) for the analysis of

720 the relationship between the proportion of reproductive adult females and population

721 density for each lemming group. Significant relationships are in bold.

Covariate	β	95% CI
D	**-0.087**	**[-0.170, -0.004]**
periodPP2	**0.690**	**[0.243, 1.154]**
periodPP3	0.282	[-0.190, 0.760]
grid LG2	**-0.820**	**[-1.275, -0.401]**
grid LX1	**-0.952**	**[-1.572, -0.396]**
grid Exclosure	**1.448**	**[0.832, 2.130]**

722

723 **Table S6.** Ranking of models testing the relationship between daily change in body mass

724 and ontogenical, seasonal, and density-dependent factors based on the Akaike's

725 information criterion. All models with a ΔAICc <4 and the following one are listed. The

726 selected model is in bold.

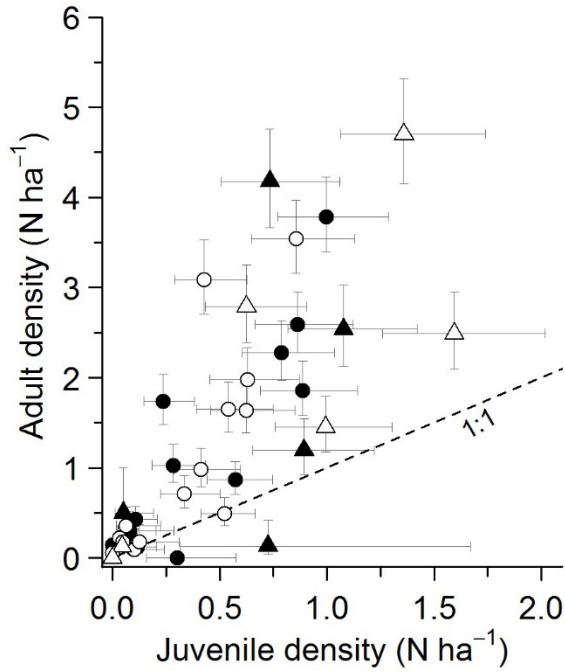| Model	K	Log-likelihood	ΔAICc
initial mass*sex*period+grid	13	72.87	0.00
initial mass*period+grid	**9**	**68.25**	**0.86**
initial mass*sex+initial mass*period+grid	11	68.36	4.83

727

Figure S1. Age-ratio (adult females, ≥28 g; adult males ≥30 g) on Bylot Island, 2004-2019.

Black circles: wet meadow trapping grid 1; white circles: mesic trapping grid 1; black triangles:

mesic trapping grid 2; white triangles: predator exclosure trapping grid. The dashed line is a

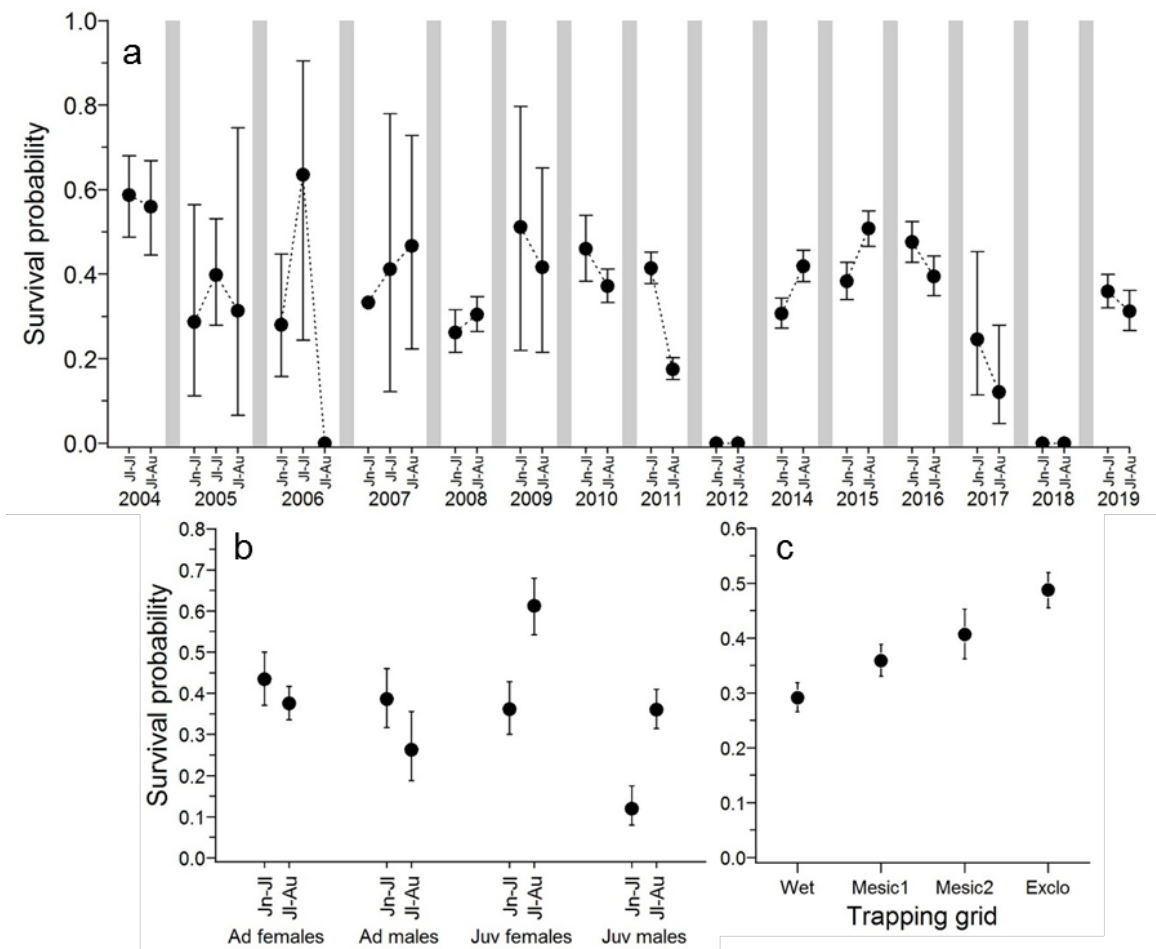visual guideline and represents a 1:1 ratio.

733

Figure S2.

735