

1 **Assessing the effect of predator control on an endangered**
2 **goose population subjected to predator-mediated food web**
3 **dynamics**

4 Filippo Marolla^{1*}, Tomas Aarvak², Ingar J. Øien², Jarad P. Mellard¹, John-André Henden¹,
5 Sandra Hamel¹, Audun Stien³, Torkild Tveraa³, Nigel G. Yoccoz¹, Rolf A. Ims¹

6
7 ¹*Department of Arctic and Marine Biology, UiT The Arctic University of Norway, Tromsø, 9037, Norway;*
8 ²*Norwegian Ornithological Society, BirdLife Norway, NO 7012, Trondheim, Norway;* ³*Norwegian Institute for*
9 *Nature Research (NINA), FRAM – High North Research Centre for Climate and the Environment, NO-9296*
10 *Tromsø, Norway*

11
12 *Correspondence author. E-mail: filippo.marolla@uit.no

13
14
15 Word count: title = 17; key words = 8; summary = 303; main text = 4458; author contributions statement = 44;
16 acknowledgements = 62; figure captions = 615; references = 1718; total = 7458

17 **Keywords:** management evaluation, red fox, tundra food web, Lesser White-fronted Goose, rodents, culling,
18 reindeer, carrion

19
20
21
22
23
24
25
26

27 **Abstract**

28 **1.** Assessing the effectiveness of conservation actions to halt population declines is challenging
29 when confounded by other factors. We assessed whether culling of red fox, a predator currently
30 increasing in the sub-Arctic, contributed to recent recovery of the critically endangered
31 Fennoscandian population of Lesser White-fronted Goose *Anser erythropus*, while controlling
32 for potentially confounding food web dynamics.

33 **2.** Using 19 years of data, 10 before and 9 after the implementation of annual red fox culling,
34 we estimated the effect of this action on annual performance of the goose population. We
35 corrected for the potentially confounding effects of cyclic rodent dynamics and semi-domestic
36 reindeer carrion abundance, both of which are expected to trigger predator functional and
37 numerical responses, as well as for annual variation in spring phenology.

38 **3.** Goose reproductive success fluctuated in synchrony with the rodent cycle and was negatively
39 related to abundant carrion. When accounting for these aspects of food web dynamics, there
40 was no evidence for an effect of red fox culling on reproductive success. There was, however,
41 a tendency for fox culling to increase adult survival.

42 **4.** Our analysis suggests that goose performance in their breeding area is influenced by
43 fluctuating offspring predation, mediated by mainly natural (rodents) and partly anthropogenic
44 (semi-domestic reindeer) dynamic components of the food web.

45 **5. *Synthesis and applications.*** The effect of a decade-long red fox culling on goose reproductive
46 success and survival is currently uncertain, despite predation driving reproductive success
47 through changes in rodent and reindeer carrion abundance. New management actions may
48 consist of regulation of reindeer herd sizes and/or removal of carcasses to reduce the subsidizing
49 effect of reindeer carrion on mesopredators. Getting robust evidence regarding the impact of
50 red fox culling on population recovery depends on continuing research to disentangle food web
51 dynamics and efficiency of management actions.

52 **Introduction**

53 Conservation programs for endangered populations often lack a strategy for evaluating their
54 effectiveness (Sutherland *et al.* 2004). Making such evaluations is challenging, especially when
55 the cause of the population decline is uncertain (Caughley 1994) and when populations have
56 become so small that proper experimental designs underpinning the evaluation of actions are
57 not feasible (Taylor *et al.* 2017). Therefore, management decisions and their evaluations are
58 often based on ecological intuition rather than scientific evidence (Sutherland *et al.* 2004).

59 Conservation actions are typically considered successful when the size of the target
60 population increases (Taylor *et al.* 2017). Population dynamics, however, is governed by biotic
61 and abiotic interactions. Therefore, attributing a population recovery to a given management
62 action requires considering potential confounding factors (Angerbjörn *et al.* 2013). Here, we
63 evaluated the effectiveness of a management action implemented to reverse the negative trend
64 of the critically endangered Fennoscandian population of Lesser White-fronted Goose *Anser*
65 *erythropus*.

66 This goose species is a long-distance migrant that breeds in sub-Arctic tundra and
67 overwinters in temperate Eurasia. Three distinct populations exist, of which the Fennoscandian
68 population is considered a single management unit (Ruokonen *et al.* 2004), despite the
69 occurrence of immigration of males from the neighbouring West-Russian population
70 (Ruokonen *et al.* 2010). The Fennoscandian population was breeding in large numbers in
71 northern Fennoscandia until 1920, but in the 1970s, small population sizes started to cause
72 concern (Norderhaug & Norderhaug 1982). In 2008, the population was estimated to be less
73 than 20 breeding pairs (Aarvak *et al.* 2009) and conservation actions were deemed necessary to
74 prevent it from extinction. Actions including habitat restoration, surveillance of stopover sites,
75 and attempts to reduce poaching have been implemented through two EU Life projects
76 (Vougioukalou, Kazantzidis & Aarvak 2017). The most prominent action is culling of red foxes

77 *Vulpes vulpes* in the goose breeding area. This action is motivated by two hypothesized impacts
78 of red fox predation: 1) that it is a key determinant of goose reproductive success (Aarvak, Øien
79 & Karvonen 2017), and 2) that it causes early reproductive failure and the subsequent choice
80 of an alternative moult migration route associated with reduced adult survival (Øien *et al.* 2009;
81 Fig. 1a). Both hypotheses are based on the long-term increase of red fox abundance in the Arctic
82 (Elmhagen *et al.* 2017), while the second posits on the potential risk of adult birds being
83 illegally shot at moulting and staging areas in Russia and, especially, north-western Kazakhstan
84 (Jones *et al.* 2008). There, hundreds of hunters may be unaware of species protection and
85 unknowingly illegally hunt Lesser White-fronted geese (Jones, Whytock & Bunnefeld 2017).
86 No estimates of hunting effects on survival rates are available. However, seven out of ten
87 transmitter-equipped failed breeders took the alternative route between 1995 and 2006, of
88 which two were later reported shot and three had the signal ceasing abruptly in the supposedly
89 risky areas (Lorentsen *et al.* 1999; Aarvak & Øien 2003; Øien *et al.* 2009). Additionally, four
90 ringed geese were recovered shot-to-death in those areas (Lorentsen *et al.* 1999). Although this
91 is not a strong evidence for a higher risk along this migratory route, these observations are
92 consistent with this hypothesis. The fact that this goose population was decreasing by 4.4%
93 annually before the onset of the red fox culling program and increased approximately by 15%
94 annually after (Aarvak, Øien & Karvonen 2017; Fig. 1b), may suggest a positive effect of this
95 management action. This interpretation, however, may be confounded by other dynamical
96 components of the sub-Arctic food web that have also changed in recent decades.

97 First, population cycles of small rodents are important drivers of tundra food web dynamics
98 (Ims & Fuglei 2005) exerting an indirect impact on bird breeding success through the alternative
99 prey mechanism (e.g. Ims *et al.* 2013; McKinnon, Berteaux & Bêty 2014). Numerical and
100 functional responses of fox populations to rodent cycles are key components of this mechanism,
101 which typically causes breeding success of many bird species (the alternative prey) to fluctuate

102 in synchrony with the rodent cycle. While long-term declines in rodent cycle amplitude may
103 have contributed to population declines in northern bird species (Kausrud *et al.* 2008; Elmhagen
104 *et al.* 2015), the fact that recent rodent peak densities in northern Fennoscandia have been
105 relatively high (Angerbjörn *et al.* 2013; Ims *et al.* 2017) could have had a positive effect.

106 Secondly, reindeer *Rangifer tarandus* are a key component of tundra food webs (Ims *et al.*
107 2007). Fennoscandian semi-domesticated reindeer are maintained at high population densities
108 and often subjected to high mortality rates (Tveraa *et al.* 2007). Reindeer carcasses constitute a
109 significant part of the winter diet of red foxes in the low phase of the rodent cycle (Killengreen
110 *et al.* 2011). The increase in red fox abundance has been partly attributed to increased
111 availability of reindeer carrion (Henden *et al.* 2014; Elmhagen *et al.* 2017; Ims *et al.* 2017),
112 resulting from increased herd sizes and changed winter climate (Tveraa *et al.* 2014). The
113 numerical response of the red fox to increased carrion availability is expected to have a negative
114 effect on other prey species (Henden, Ims & Yoccoz 2009), including the Lesser White-fronted
115 Goose (Lee *et al.* 2010).

116 A third important component is spring phenology. In the Arctic, spring onset typically
117 exhibits large variability between years (Tveraa *et al.* 2013), with a trend towards earlier springs
118 during the last decades in Fennoscandia (Karlsen *et al.* 2009). Spring phenology is expected to
119 affect reproductive success in birds (Visser, Holleman & Gienapp 2006), for example by
120 reducing nesting performance in geese in response to extensive snow cover at onset of breeding
121 (e.g. Reed, Gauthier & Giroux 2004; Madsen *et al.* 2007).

122 We evaluated whether red fox culling had the expected positive effect on Fennoscandian
123 Lesser White-fronted Goose reproductive success and avoidance by adult birds of the
124 alternative, supposedly riskier migration route, while accounting for rodent population
125 dynamics, amount of reindeer carrion, and spring phenology. We based our analysis on a 19-
126 year time series on goose demography that included 10 years before and 9 years after the onset

127 of the management action. We predicted goose breeding success, as well as the number of adults
128 not embarking on the alternative migration route, 1) to fluctuate in synchrony with the rodent
129 cycle due to the alternative prey mechanism, and 2) to respond negatively to increases in
130 reindeer carcasses, because these would enhance fox survival during the winter, leading to
131 higher spring fox abundance and thereby greater predation risk (Fig. 2; Supp. Info S1). We
132 predicted the association between goose population dynamics, rodent population dynamics, and
133 reindeer carrion abundance to be weaker after the implementation of the fox culling program,
134 since the mediation role of red fox would come undone if foxes are effectively removed. Finally,
135 we expected early snowmelt to improve access to nesting sites and thus increase goose-nesting
136 performance.

137

138 **Materials and methods**

139 *Monitoring of the goose population*

140 Approximately 90% of the Fennoscandian Lesser White-fronted Goose population breeds in
141 Finnmark County, Norway (69°N to 71°N, Fig. 1a, Aarvak *et al.* 2009). Geese typically arrive
142 at the staging site at the coastal Valdak Marshes, Stabbursnes (70°10'N 24°40'E) in mid-May,
143 and move to the core inland breeding area by Lake Iešjávri after a staging period of about one
144 week (Øien *et al.* 2009). Eggs hatch at the end of June, and successful pairs start moulting and
145 become flightless. In mid-August, adults and fledglings return to the staging area and stay there
146 for three weeks before embarking on the autumn migration. Breeding and staging sites are likely
147 to be exclusively utilized by Fennoscandian breeding pairs, because immigration of birds from
148 Russia is restricted to males and follows pair formation during the non-breeding season
149 (Ruokonen *et al.* 2010). Immigration is therefore unlikely to occur between the two staging
150 periods. We monitored the goose population annually at the staging site, in spring (since 1990)
151 and autumn (since 1994, Fig. 2a). In spring, we recorded the total number of individuals and

152 potential breeding pairs. We identified individuals based on unique patterns in the black belly
153 patch by means of telescopes and digital videos. In autumn, we recorded the total number of
154 adults, juveniles, broods and brood sizes. These counts provided a minimum number of birds
155 that is probably close to the number of birds that utilized the breeding area, under the
156 assumption that most birds also used the staging site. Because the belly patch pattern changes
157 slightly each year, individuals could not be identified across years. See Øien *et al.* (1996) and
158 Aarvak *et al.* (2009).

159

160 *Red fox culling*

161 Field inspectors from the Norwegian Environment Agency culled red foxes in February-
162 May during 2008-2016 in an area of 1242 km² encompassing the goose breeding grounds (Fig.
163 1a). Culling was aided by means of snowmobiles and snow conditions that allow detection of
164 fresh fox tracks, and finished when snow conditions made the search for fox tracks ineffective.
165 The number of foxes culled varied considerably between years (mean [range] = 101 [10, 360]),
166 owing to both variation in snow conditions and fox numerical response to rodent cycles (Fig.
167 S1). By means of a removal model fitted to the number of red foxes culled every year, we
168 estimated the reduction in fox population size due to culling as varying between 22% and 43%
169 among years (Supp. Info S2; Fig. S2).

170

171 *Dynamical and environmental components*

172 Data on small rodent population dynamics comes from a monitoring program conducted in
173 the coastal birch forest along the Porsanger Fiord, approximately 50 km from the goose
174 breeding area. The numerically dominant rodent species in the study region, the grey-sided vole
175 *Myodes rufocanus*, was live-trapped on eight 60×60 m grids each year in June and September
176 between 1998 and 2016. The rodent index was derived from capture-mark-recapture data as

177 described in Ehrlich, Yoccoz and Ims (2009). We used the average number of individuals per
178 trapping grid and year as a measure of rodent abundance (Fig. S3).

179 Data on reindeer carrion comes from the national database on livestock found dead by
180 reindeer herders (www.rovbase.no). As an index of carrion availability, we used the number of
181 reindeer carcasses found between 1998 and 2016 in the herding areas of Karasjok West and
182 Kautokeino East, which include the main goose breeding area (Fig. 1c). This index does not
183 result from a rigorous sampling design, as the search for dead reindeer is opportunistic. Thus,
184 carcass abundance is likely to be underestimated. However, the number of livestock found dead
185 strongly correlates with the number of animals claimed lost by reindeer herders ($r = 0.76$, 95%
186 CI [0.39, 0.92], $n = 14$), a metric used in previous studies (e.g. Tveraa *et al.* 2014), and with
187 the estimated minimum available carrion biomass ($r = 0.99$, 95% CI [0.98, 1.00], $n = 14$; see
188 Supp. Info S3).

189 We used Normalized Difference Vegetation Index (NDVI) remote sensing data from the
190 Global Inventory Modeling and Mapping Studies (GIMMS), with 8 km spatial and bimonthly
191 temporal resolution, to measure vegetation green-up in spring in the study area (Pettorelli 2013;
192 Fig. S4). We used this NDVI product as a measure of phenology because it is the only satellite
193 product available over the whole period of our study. GIMMS-based NDVI correlates well with
194 winter snow depth and spring temperature (Nielsen *et al.* 2012) and gives a spatially explicit
195 measure of spring conditions. See Supp. Info S4.

196

197 *Data analysis*

198 We used three measures of the annual goose performance. First, the proportion of breeding
199 pairs that were successful in year t , $b(t) = \frac{B_a(t)}{P_s(t)}$, where B_a is the number of breeding pairs that
200 had at least one fledgling counted during the autumn monitoring, and P_s is the number of
201 potential breeding pairs counted during the spring monitoring. Second, the average brood size,

202 $j(t) = \frac{F_a(t)}{P_s(t)}$, where F_a is the total number of fledglings counted during the autumn monitoring.
203 These two variables were highly correlated (r [95% CI] = 0.97 [0.93, 0.99], $n = 19$), but we
204 decided to analyse both as they reflect different aspects of the breeding success. Lastly, we
205 calculated the ratio of adult birds in the autumn (A_a) to adult birds in the spring (A_s), $a(t) =$
206 $\frac{A_a(t)}{A_s(t)}$. The ratio can exceed 1 because in some years more adult birds are counted during the
207 autumn monitoring than in the spring monitoring. This ratio is assumed to give an inverse
208 estimate of how common the use of the eastern and likely more risky migration route is among
209 adults, because adults that fly that route should have left before the autumn surveys were
210 conducted. The correlations between this ratio and the other two measures of annual
211 performance were 0.66 (95% CI [0.30, 0.86], $n = 19$) and 0.74 (95% CI [0.42, 0.89], $n = 19$),
212 respectively. To evaluate the different hypotheses regarding the impact of fox culling on the
213 performance of the goose population, we developed a suite of seven *a-priori* models that
214 included different combinations of confounding factors while avoiding overparameterization.
215 The seven models were fitted to each of the three measures of goose performance. We then
216 assessed the influence of each parameter by evaluating whether effect sizes were similar across
217 models. We did not use model selection criteria or model averaging methods because our aim
218 was to assess the consistency of parameters across different models, not to find the most
219 supported models or to provide an overall estimate. For sensible interpretation of effects, this
220 approach is preferred to other approaches such as model averaging, especially when interactions
221 among predictors are tested (Cade 2015). Rodent abundance, number of reindeer found dead,
222 rodent abundance the previous year, onset of spring, and the categorical variable “culling”
223 indicating absence or presence of red fox culling, were entered as predictor variables. Density-
224 dependence was not included, given the low goose population density in the breeding area.
225 Because we expected small rodent abundance to be a key driver of variation in breeding success,
226 this variable was present in all the models. We tested for an interaction between rodent

227 abundance and number of reindeer carcasses to evaluate whether red fox responses might reach
228 some degree of saturation during the rodent peak. We also tested for interactions between
229 culling and both rodent abundance and number of reindeer carcasses, because we expected the
230 effect of the latter two variables to become weaker after the onset of the fox culling program.
231 Similarly, we tested for an interaction between culling and rodent abundance the previous year,
232 because we expected any delayed effect of rodent abundances through predator numerical
233 responses to be dampened by fox culling.

234 We used generalized linear mixed models to model annual variation in the proportion of
235 breeding pairs that were successful, the average brood size, and the ratio of adults in autumn to
236 spring. We used a logit link function and assumed a binomial distribution to analyse the
237 proportion of breeding pairs that were successful. For both average brood size and ratio of adults
238 in autumn to spring, we used a log link function assuming a Poisson distribution, modelling F_a
239 as the response with $\log(P_s)$ as an offset for average brood size, and A_a as the response with
240 $\log(A_s)$ as the offset for the ratio of adults in autumn to spring. Because of overdispersion, we
241 used quasi-likelihood methods for all models (Ver Hoef & Boveng 2007). Model fit was
242 evaluated by residual diagnostics. To avoid systematic patterns in the residuals, we included a
243 random rodent cycle effect (five categories reflecting the five rodent cycles in our time series:
244 1998-2000, 2001-2004, 2005-2008, 2009-2012, 2013-2016; Fig. 3) in the models for proportion
245 of successful pairs and average brood size. We assessed multicollinearity with correlation plots
246 and Variance Inflation Factors, and excluded highly correlated variables from the same models.
247 We performed all statistical analyses with R 3.4.3 (R Core Team 2017). Estimates of effect
248 sizes and uncertainty of covariates on average brood size from the function `glmmPQL` in the
249 “MASS” package (Venables & Ripley 2002) were similar to those provided by the `glmmTMB`
250 function in the more recent “glmmTMB” package (Magnusson *et al.* 2017). We chose to use
251 `glmmPQL` because it allows fitting quasi-likelihood methods also with binomial distributed

252 data for mixed models, i.e. for analysis of $b(t)$. Parameter estimates of all fitted models are
253 provided in Supp. Info Tables S1-S3.

254

255 **Results**

256 The proportion of breeding pairs that were successful ranged between 0.04 (in 2000) and
257 1.00 (in 2010), while average brood size ranged between 0.08 (in 2000) and 3.18 (in 2010; Fig.
258 3). The ratio of adults in autumn to spring varied between 0.16 (in 2000) and 1.50 (in 2007;
259 Fig. S5). The average proportion of successful pairs and the average brood size in the 9 years
260 after the onset of fox culling was similar to the 10 years before, while the ratio of adults in
261 autumn to spring slightly increased (Table 1). The 19-year study included four full rodent cycles
262 with a period of 4-5 years between the peaks (Fig. 3). The two cycles after the onset of the fox
263 culling program tended to show somewhat higher peak densities than the cycles before (Fig. 3;
264 Table 1). Number of reindeer found dead was on average higher after the onset of the culling
265 program (Table 1) and ranged between 88 (in 2003) and 621 (in 2011; Fig. 1c).

266 Rodent abundance showed a positive effect on both the proportion of breeding pairs that
267 were successful (Fig. 4a; Table S1) and average brood size (Fig. 4c; Table S2). On average,
268 92% of breeding pairs were successful in years with rodent peaks (i.e. ~ 40 voles/grid), while
269 on average only 21% was successful in the rodent crash phase (i.e., ~ 5 voles/grid). Similarly,
270 fledgling success was on average 4.2 during a peak phase and 0.7 in the crash phase. In all
271 models that included a reindeer carrion effect (Tables S1-S2), an increase in the number of
272 reindeer found dead tended to show a negative effect on the measures of breeding success (Fig.
273 4b, d). Approximately 24% of breeding pairs were successful and 0.7 fledglings were produced
274 per breeding pair in years with high carrion abundance (i.e. ~ 600 reindeer found dead), whereas
275 approximately 61% of breeding pairs were successful and 1.9 fledglings were produced per
276 breeding pair in years with low carrion abundance (i.e. ~ 100 reindeer found dead). Estimated

277 effect sizes for carrion abundance were consistent among the models (Tables S1-S2). There was
278 no evidence for an effect of onset of spring, rodent abundance the previous year, or an
279 interaction between rodent and carcass numbers on the measures of breeding success (Tables
280 S1-S2). Most importantly, there was no evidence for the fox culling program and its interactions
281 with other predictors to affect measures of breeding success (Tables S1-S2).

282 With respect to the ratio of adults in autumn to spring, the models only suggested a weak
283 effect of small rodent abundance (Table S3). We did not find support for an effect of other
284 predictors and their interactions (confidence intervals widely overlapping 0), but point
285 estimates for the effect of carrion abundance were consistently negative in all the models (Table
286 S3). In addition, the model including rodent abundance, carrion abundance, and culling
287 suggested that culling could increase the ratio (Fig. 5), but the evidence is inconclusive because
288 of wide confidence intervals and considerable variation in effect size estimated from different
289 models.

290

291 **Discussion**

292 Using 19 years of data, we contrasted 9 years of conservation action (red fox control) against
293 10 years of non-action, on measures of annual performance of the Fennoscandian Lesser White-
294 fronted Goose population while accounting for food web components expected to affect
295 predation pressure. As expected, we found goose breeding success to fluctuate in synchrony
296 with the rodent cycle (i.e. apparent facilitation, Fig. 2b and c), and to decrease in years with
297 high abundance of reindeer carcasses (i.e. apparent competition, Fig. 2b and c). This suggests
298 that temporal variation in predation, mediated by major fluxes in the tundra food web, is likely
299 to be an important driver of goose population dynamics. While red foxes were expected to play
300 a pivotal role in these dynamics, we found no evidence for red fox culling to affect these food-
301 web interactions.

302 As is typical for most critically endangered populations, the targeted goose population is so
303 small and spatially restricted that using replicates and controls in a rigorous experimental
304 management design is not feasible. An equivalent red fox culling action performed in the
305 context of Arctic fox conservation in Fennoscandia (Angerbjörn *et al.* 2013) benefited from the
306 existence of several remaining populations, among which different actions could be allocated
307 to provide evidence of a positive effect of red fox culling. Here, despite a design based on a
308 single before-after comparison, the lack of evidence for a positive effect on goose breeding
309 success after nine years of intensive red fox control suggests that the management action has
310 not been effective in this respect. Both failing at emptying the area of foxes and/or
311 compensatory immigration (Newsome, Crowther & Dickman 2014; Lieury *et al.* 2015) after
312 the completion of the culling may explain this result. Alternatively, the biological impact of red
313 fox predation on goose dynamics may have been overrated, as the importance of other generalist
314 predators such as corvids and eagles (Henden *et al.* 2014) may have been overlooked. Also, the
315 possibility of a substitutable effect by other nest predators, such as mustelids (Parker 1984),
316 may disguise the effect of fox removal on goose dynamics. We found a tendency for the ratio
317 of adult geese in autumn to spring to be higher after the onset of the red fox control program.
318 This may suggest that fewer adults embarked on the likely riskier migration through western
319 Asia. Thus, the red fox culling may have affected goose behaviour in a way that made them
320 stay in the sub-Arctic for longer and then use the putatively safer migration route. Such a
321 positive effect of culling may have contributed to the recent increase in the goose population,
322 but the uncertainty in the model estimates makes it impossible to draw firm conclusions at this
323 point.

324 The role of rodent cycles as drivers of predation pressure on eggs and chicks has previously
325 been shown for many tundra-nesting birds (e.g. Ims *et al.* 2013; McKinnon, Berteaux & Bêty
326 2014) as well as other Arctic geese (e.g. Summers & Underhill 1987; Gauthier *et al.* 2004).

327 Nonetheless, the relationship between Lesser White-fronted Goose reproductive success and
328 the vole cycle appears to be exceptionally strong and temporally consistent (Fig. 3). Northern
329 rodent cycles show systematic changes over time (Henden, Ims & Yoccoz 2009) and appear to
330 be particularly sensitive to climatic change (Kausrud *et al.* 2008). Thus, the Fennoscandian
331 population may be negatively impacted if the rodent cycles become more irregular and
332 dampened due to increased climate warming (Nolet *et al.* 2013).

333 The negative relation between reindeer carrion abundance and goose breeding success
334 provides the first empirical support for the hypothesis that resource-driven (i.e. bottom-up)
335 mesopredator release (Killengreen *et al.* 2011) may negatively affect tundra-breeding birds
336 (Henden *et al.* 2014; Henden *et al.* 2017). In Finnmark, 56% of the carcass availability occurs
337 in the mid-late winter (i.e. February-May, Fig. S6), when body conditions of
338 mesopredators/scavengers are likely to be at their lowest. Hence, high carrion availability likely
339 enhances red fox survival during this critical period, increasing the probability of predation
340 during the bird's nesting season in June/July. Therefore, with respect to conservation of the
341 Lesser White-fronted Goose and tundra birds in general, changes in reindeer management
342 strategies should be considered.

343 Contrary to previous studies on bird breeding success (Reed, Gauthier & Giroux 2004;
344 Madsen *et al.* 2007), we found no direct effect of spring phenology on both measures of goose
345 reproductive success, although estimates were in the expected direction. The spatial resolution
346 of the GIMMS data may have been too coarse to catch the precise phenology of the relatively
347 small goose breeding area. However, using the higher-resolution MODIS NDVI data on a
348 shorter time period did not reveal any effect of spring phenology (Tables S4-S6). This suggests
349 that Arctic geese might be able to start nesting as soon as enough suitable nest sites have become
350 free of snow, even at a time when much of the tundra is still snow-covered (Madsen *et al.* 2007).

351 Alternatively, NDVI might have been a low-quality proxy compared with a more direct measure
352 of timing of snowmelt, which was not available for our study.

353

354 MANAGEMENT IMPLICATION

355 The Lesser White-fronted Goose case study has both general and specific implications.
356 Generally, it highlights challenges in assessments of management efforts applied to small
357 populations that are subjected to complex food web dynamics, especially when such dynamics
358 involves compensatory mechanisms (e.g. predator functional and numerical responses) or
359 transience (e.g. changing rodent cycle). This emphasizes the need for obtaining long-term data,
360 not only on the conservation target itself, but also on important drivers in the food web. Here,
361 we benefited from long time series on the dynamics of rodent and reindeer carrion, which could
362 be linked to the performance of the goose population, allowing us to conclude that the red fox
363 culling action has not improved goose reproductive success. To determine the cause of this lack
364 of effect, we would have required direct time series data on predator functional and numerical
365 responses, which are extremely hard to obtain.

366 Another important insight is that subtle changes, but still demographically influential
367 changes in performance, may be involved in the response of the target population to
368 management actions. As indicated by our analysis, it is possible that red fox culling has
369 increased the survival rate of adult geese by affecting their migratory behaviour. Nevertheless,
370 the high uncertainty in our estimates implies that more data are required to determine whether
371 nest predation rates truly influences adult survival. In addition, comprehensive demographic
372 analyses will be necessary to assess the influence of nest predation on the long-term growth rate
373 of this goose population.

374 Our study provided also the first empirical support for the hypothesis that high availability
375 of ungulate carrion exert a negative impact on ground-nesting tundra birds (Killengreen *et al.*

2011). The hypothesized mechanism involves mesopredator species that act also as facultative scavengers, which both expand into carrion-rich ecosystems and respond numerically to the surge in the carrion pool (Henden *et al.* 2014), thereby exerting a cascading impact on native species. Given the large extent of occurrence of semi-domesticated reindeer in the Eurasian tundra, and the acknowledged range expansion of boreal mesocarnivores like the red fox into the Arctic (Elmhagen *et al.* 2017), the implications of our study extend beyond the borders of Northern Fennoscandia. Furthermore, changes in climate and herding strategies are likely to affect patterns of reindeer mortality. Although earlier springs and longer growing seasons should benefit semi-domesticated reindeer (Tveraa *et al.* 2013), density-dependence and unfavourable snow condition (e.g. ice-crusting snow from more frequent thaw-freeze cycles) may lead to very high winter mortality, subsidizing the facultative scavenger community. Accordingly, we suggest that management strategies for both semi-domestic and wild populations of reindeer, as well as other boreal and Arctic ungulates, should account for the potential subsidizing effect of carrions. In the case of the endangered Lesser White-fronted Goose population, new management actions could aim at regulating herd size to reduce winter mortality or removing carcasses in the surroundings of the breeding area, although distant carcasses may still exert an impact by sustaining populations of highly mobile predators. Overall, it is important to continue both the population monitoring and the management assessment including new data, in order to better assess the importance of red fox culling in the population recovery.

396

Authors' contribution: all authors contributed to conceive the ideas and collect the data; F.M., J.P.M., N.G.Y. and A.S. analysed the data; F.M. and R.I. led the writing of the manuscript. All authors contributed critically to the drafts and gave final approval for publication.

400

401 **Acknowledgements**

402 This study was supported by the RCN funded project SUSTAIN and the terrestrial flagship of
403 FRAM – High North Research Centre for Climate and the Environment. The goose monitoring
404 has been financed by the Norwegian Environment Agency. We thank Rebecca Cavicchia for
405 valuable help with the graphics of Figs. 1 & 2. None of the authors has conflict of interest to
406 declare.

407

408 **Data accessibility:** Data available via the Dryad Digital Repository.

409

410 **Figure legends**

411 **Fig. 1.** (a) Map showing the study area and the migration routes of the Fennoscandian Lesser
412 White-fronted Goose. In the autumn, successful breeders and fledglings migrate over Europe
413 to the wintering sites in Greece (black arrows). Breeders failing at an early stage and non-
414 breeders tend to migrate to moulting tundra areas in western Russia, from the Kanin to the
415 Taymyr Peninsula (Aarvak & Øien 2003). From there, the autumn migration route takes them
416 through Central Asia with Kazakhstan as a major staging ground, before turning west to the
417 same wintering areas in Greece as the successful breeders (grey arrows). Due to hunting, geese
418 may experience high mortality on this route. (b) Annual goose population size counted during
419 the spring monitoring. The vertical dotted line indicates the onset of the red fox culling program.
420 (c) Annual number of reindeer found dead in the study area.

421

422 **Fig. 2.** (a) Diagram showing the annual cycle of the Fennoscandian Lesser White-fronted Goose
423 population, food web dynamics, monitoring, and predator control. Darkest bars mean higher
424 availability and accessibility of the prey item for red foxes. In the study area, rodents show 3-5
425 years population cycles. (b) Conceptual model depicting *a-priori* interactions between the main

426 species. Full arrows show predation by the main predator, the red fox, on the different prey
427 items. Dashed arrows depict expected indirect predator-mediated relationships. Thicker arrows
428 mean preference for that prey when it is abundant. (c) Model-based predictions (see Supp. Info
429 S1) showing the effect of alternative resource supplies (small rodents and reindeer carcasses)
430 on predation pressure exerted by red foxes on goose offspring (eggs and chicks). The model
431 predicts that small rodents should show apparent facilitation to geese, while reindeer carrions
432 should show apparent competition with geese.

433

434 **Fig. 3.** Time series of measures of Lesser White-fronted Goose (LWfG) breeding success
435 (proportion of breeding pairs that were successful and average brood size) and rodent
436 abundance (average catches per grid). Note that the scale on the two y-axes is different. The
437 vertical green line indicates the onset of the red fox culling program.

438

439 **Fig. 4.** Effect of small rodent abundance and reindeer carcass abundance on the proportion of
440 Lesser White-fronted Goose breeding pairs that were successful (a, b) and average brood size
441 (c, d). Full line indicates model prediction (based on model 2 in Tables S1 and S2, respectively),
442 dashed lines indicate 95% confidence interval, dots are partial residuals. Slope (β) estimates
443 [95% CI] on the logit (a and b) and the log scale (c and d) are provided on top of each panel.
444 Predictors are here rescaled (rodents/10, carcasses/100). Note that the scale on the y-axes differs
445 between (c) and (d).

446

447 **Fig. 5.** Effect of red fox culling on the ratio of adult geese counted in the autumn to the spring.
448 This measure is assumed to reflect the portion of the Lesser White-fronted geese that takes the
449 alternative, likely riskier migration route through western Russia. Nine years of fox culling
450 (2008-2016) are compared to 10 years without management actions (1998-2007). Predicted

451 values, standard errors (thick black lines), and 95% confidence intervals (whiskers) are based
452 on model 5 in Table S3. Note that the ratio of adults in the fall to adults in the spring can be
453 higher than 1 (see Material and methods).

454

455 **Table 1.** Mean, minimum, and maximum values of the different variables before and after the
456 onset of the culling program. Rodent abundance is expressed as average voles captured per
457 trapping grid. Note that the ratio of adults counted in the autumn to spring can be higher than 1
458 (see Material and methods). Onset of spring represented vegetation green-up, with higher values
459 representing greener vegetation and thus earlier spring.

460

461

462

463

464

465

466

467

468

469

470

471

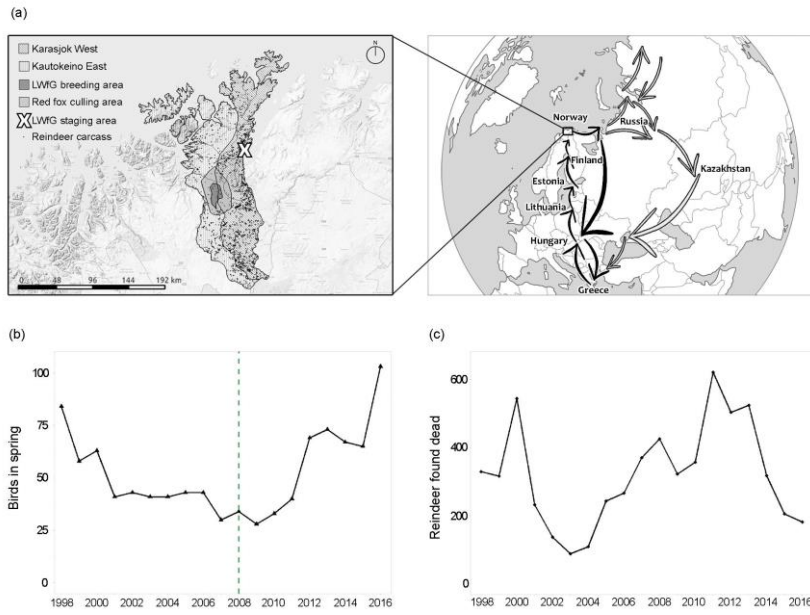
472

473

474

475

476 **Figures**



477

478 **Fig. 1.**

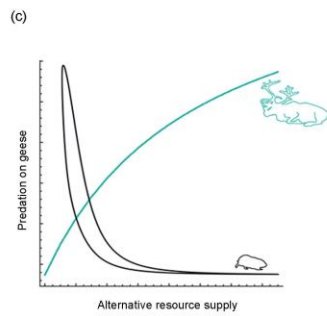
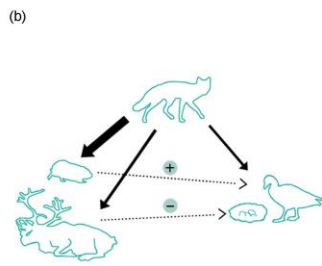
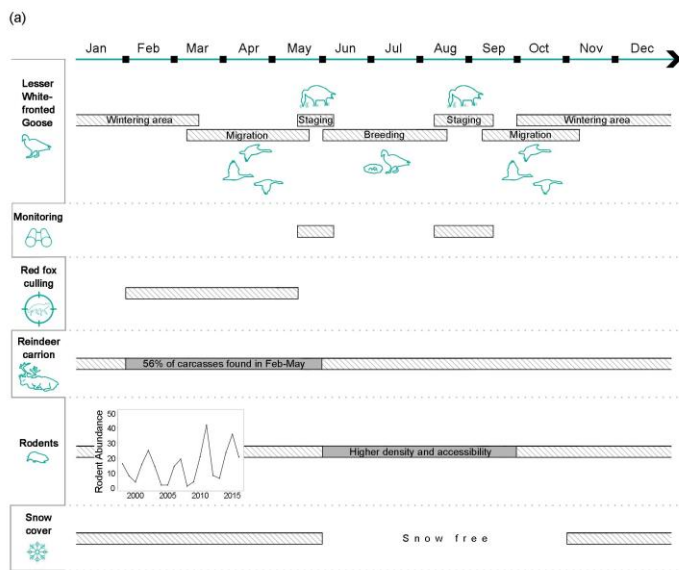
479

480

481

482

483



484

485 **Fig. 2.**

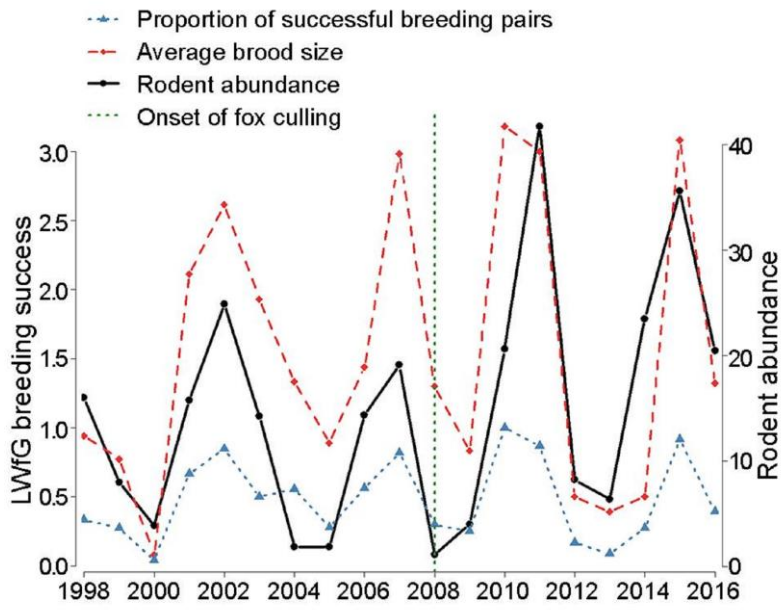
486

487

488

489

490



491

492 **Fig. 3.**

493

494

495

496

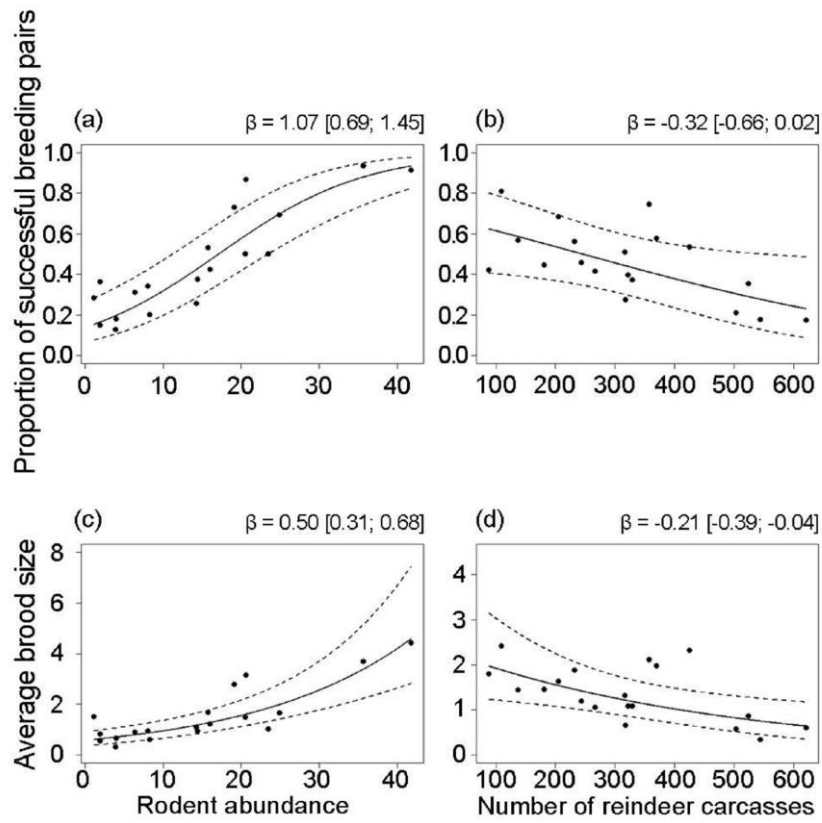
497

498

499

500

501



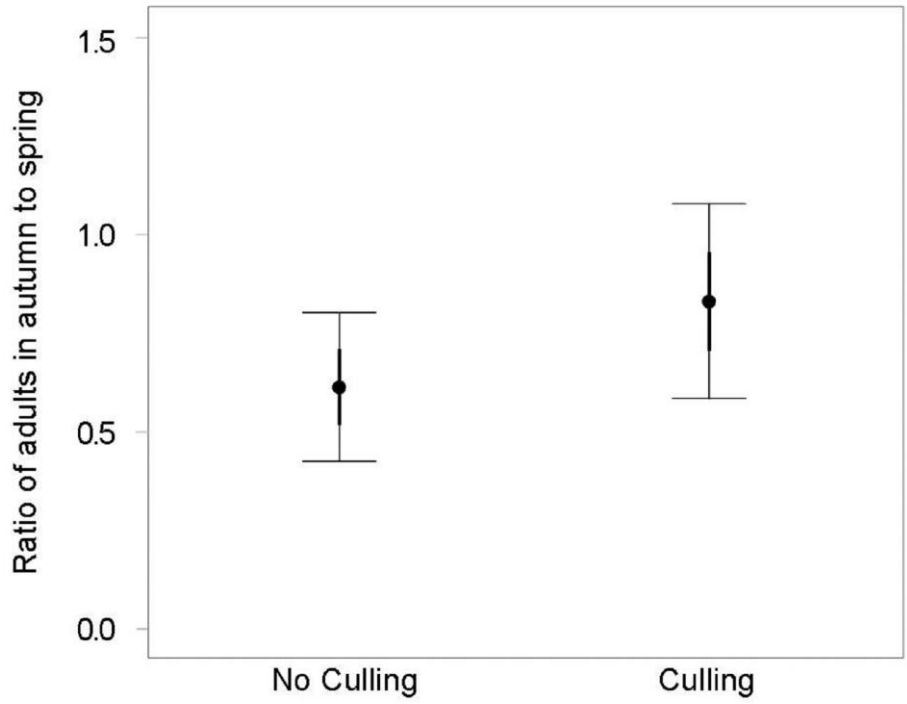
502

503 **Fig. 4.**

504

505

506



507

508 **Fig. 5.**

509

510

511

512

513

514

515

516

517

518

519

520

521

522 **Table 1.**

523

Variable	Before (n=10 years)	After (n=9 years)
Proportion successful pairs	0.49 (0.04 - 0.85)	0.47 (0.09 - 1.00)
Fledglings per pair	1.51 (0.08 - 3.00)	1.57 (0.39 - 3.18)
Ratio adults autumn to spring	0.71 (0.16 - 1.50)	0.89 (0.50 - 1.40)
Rodent abundance	12.00 (1.88 - 24.88)	17.97 (1.13 - 41.75)
Number of carcasses	263 (88 - 544)	384 (181 - 621)
Onset of spring	0.43 (0.28 - 0.61)	0.42 (0.30 - 0.56)

524

525

526

527

528

529

530

531

532

533

534

535

536

537

538

539

540 References

- 541 Aarvak, T., Leinonen, A., Øien, I.J. & Tolvanen, P. (2009) Population size estimation of the
542 Fennoscandian Lesser White-fronted Goose based on individual recognition and colour
543 ringing. *Final report of the EU LIFE-Nature project 2005–2009*, pp. 71-75.
- 544 Aarvak, T. & Øien, I.J. (2003) Moulting and autumn migration of non-breeding Fennoscandian Lesser
545 White-fronted Geese *Anser erythropus* mapped by satellite telemetry. *Bird Conservation
546 International*, **13**, 213–226.
- 547 Aarvak, T., Øien, I.J. & Karvonen, R. (2017) Development and key drivers of the Fennoscandian Lesser
548 White-fronted Goose population monitored in Finnish Lapland and Finnmark, Norway. Pp. 29-
549 36 in: Vougioukalou, M., Kazantzidis, S. & Aarvak, T. (Eds.) *Safeguarding the Lesser White-
550 fronted Goose Fennoscandian population at key staging and wintering sites within the
551 European flyway*. Special publication. LIFE+10 NAT/GR/000638 Project, HOS/BirdLife Greece,
552 HAOD/Forest Research Institute, NOF/BirdLife Norway report no. 2017-2.
- 553 Angerbjörn, A., Eide, N.E., Dalen, L., Elmhagen, B., Hellström, P., Ims, R.A., Killengreen, S., Landa, A.,
554 Meijer, T., Mela, M., Niemimaa, J., Norén, K., Tannerfeldt, M., Yoccoz, N.G. & Henttonen, H.
555 (2013) Carnivore conservation in practice: replicated management actions on a large spatial
556 scale. *Journal of Applied Ecology*, **50**, 59-67.
- 557 Cade, B.S. (2015) Model averaging and muddled multimodel inferences. *Ecology*, **96**, 2370-2382.
- 558 Caughley, G. (1994) Directions in Conservation Biology. *Journal of Animal Ecology*, **63**, 215-244.
- 559 Ehrich, D., Yoccoz, N.G. & Ims, R.A. (2009) Multi-annual density fluctuations and habitat size enhance
560 genetic variability in two northern voles. *Oikos*, **118**, 1441-1452.
- 561 Elmhagen, B., Berteaux, D., Burgess, R.M., Ehrich, D., Gallant, D., Henttonen, H., Ims, R.A., Killengreen,
562 S.T., Niemimaa, J., Norén, K., Ollila, T., Rodnikova, A., Sokolov, A.A., Sokolova, N.A., Stickney,
563 A.A. & Angerbjörn, A. (2017) Homage to Hersteinsson and Macdonald: climate warming and
564 resource subsidies cause red fox range expansion and Arctic fox decline. *Polar Research*, **36**.
- 565 Elmhagen, B., Kindberg, J., Hellström, P. & Angerbjörn, A. (2015) A boreal invasion in response to
566 climate change? Range shifts and community effects in the borderland between forest and
567 tundra. *Ambio*, **44**, 39-50.
- 568 Gauthier, G., Bêty, J., Giroux, J.F. & Rochefort, L. (2004) Trophic interactions in a high arctic snow goose
569 colony. *Integrative and Comparative Biology*, **44**, 119-129.
- 570 Henden, J.A., Ims, R.A., Fuglei, E. & Pedersen, Å.Ø. (2017) Changed Arctic-alpine food web interactions
571 under rapid climate warming: implication for ptarmigan research. *Wildlife Biology*.
- 572 Henden, J.A., Ims, R.A. & Yoccoz, N.G. (2009) Nonstationary spatio-temporal small rodent dynamics:
573 evidence from long-term Norwegian fox bounty data. *Journal of Animal Ecology*, **78**, 636-645.
- 574 Henden, J.A., Stien, A., Bårdsen, B.J., Yoccoz, N.G. & Ims, R.A. (2014) Community-wide mesocarnivore
575 response to partial ungulate migration. *Journal of Applied Ecology*, **51**, 1525-1533.
- 576 Ims, R.A. & Fuglei, E. (2005) Trophic interaction cycles in tundra ecosystems and the impact of climate
577 change. *Bioscience*, **55**, 311-322.
- 578 Ims, R.A., Henden, J.A., Thingnes, A.V. & Killengreen, S.T. (2013) Indirect food web interactions
579 mediated by predator-rodent dynamics: relative roles of lemmings and voles. *Biology Letters*,
580 **9**.
- 581 Ims, R.A., Killengreen, S.T., Ehrich, D., Flagstad, Ø., Hamel, S., Henden, J.A., Jensvoll, I. & Yoccoz, N.G.
582 (2017) Ecosystem drivers of an Arctic fox population at the western fringe of the Eurasian
583 Arctic. *Polar Research*, **36**.
- 584 Ims, R.A., Yoccoz, N.G., Bråthen, K.A., Fauchald, P., Tveraa, T. & Hausner, V. (2007) Can reindeer
585 overabundance cause a trophic cascade? *Ecosystems*, **10**, 607-622.
- 586 Jones, I.L., Whytock, R.C. & Bunnefeld, N. (2017) Assessing motivations for the illegal killing of Lesser
587 White-fronted Geese at key sites in Kazakhstan. AEWA Lesser White-fronted Goose
588 International Working Group Report Series No. 6, Bonn, Germany.

- 589 Jones, T., Martin, K., Barov, B. & Szabolcs, N. (2008) International Single Species Action Plan for the
590 Conservation of the Western Palearctic Population of the Lesser White-fronted Goose *Anser*
591 *erythropus*. AEWA Technical Series No.36. Bonn, Germany.
- 592 Karlsen, S.R., Høgda, K.A., Wielgolaski, F.E., Tolvanen, A., Tømmervik, H., Poikolainen, J. & Kubin, E.
593 (2009) Growing-season trends in Fennoscandia 1982-2006, determined from satellite and
594 phenology data. *Climate Research*, **39**, 275-286.
- 595 Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A.M.,
596 Mysterud, I., Solhøy, T. & Stenseth, N.C. (2008) Linking climate change to lemming cycles.
597 *Nature*, **456**, 93-U93.
- 598 Killengreen, S.T., Lecomte, N., Ehrich, D., Schott, T., Yoccoz, N.G. & Ims, R.A. (2011) The importance of
599 marine vs. human-induced subsidies in the maintenance of an expanding mesocarnivore in the
600 arctic tundra. *Journal of Animal Ecology*, **80**, 1049-1060.
- 601 Lee, R., Cranswick, P.A., Hilton, G.M. & Jarrett, N.S. (2010) Feasibility study for a re-
602 introduction/supplementation programme for the Lesser White-fronted Goose *Anser*
603 *erythropus* in Norway. WWT Report to the Directorate for Nature Management, Norway.
- 604 Lieury, N., Ruelle, S., Devillard, S., Albaret, M., Drouyer, F., Baudoux, B. & Millon, A. (2015)
605 Compensatory Immigration Challenges Predator Control: An Experimental Evidence-Based
606 Approach Improves Management. *Journal of Wildlife Management*, **79**, 425-434.
- 607 Lorentsen, S.H., Øien, I.J., Aarvak, T., Markkola, J., von Essen, L., Farago, S., Morozov, V., Syroechkovsky
608 Jr., E. & Tolvanen, P. (1999) Lesser White-fronted Goose *Anser erythropus*. Pp. 144-161 in:
609 Madsen, J., Cracknell, G. & Fox, A.D. (Eds.) *Goose populations of the Western Palearctic. A*
610 *review of status and distribution*. - Wetlands International, Wageningen, The Netherlands.
611 National Environment Research Institute, Rønde, Denmark. 344 pp.
- 612 Madsen, J., Tamstorf, M., Klaassen, M., Eide, N., Glahder, C., Rigét, F., Nyegaard, H. & Cottaar, F. (2007)
613 Effects of snow cover on the timing and success of reproduction in high-Arctic pink-footed
614 geese *Anser brachyrhynchus*. *Polar Biology*, **30**, 1363-1372.
- 615 Magnusson, A., Skaug, H.J., Nielsen, A., Berg, C.V., Kristensen, K., Maechler, M., van Bentham, K.J.,
616 Bolker, B.M. & Brooks, M.E. (2017) glmmTMB: Generalized Linear Mixed Models using
617 Template Model Builder. R package version 0.1.3.
- 618 McKinnon, L., Berteaux, D. & Bêty, J. (2014) Predator-mediated interactions between lemmings and
619 shorebirds: A test of the alternative prey hypothesis. *Auk*, **131**, 619-628.
- 620 Newsome, T.M., Crowther, M.S. & Dickman, C.R. (2014) Rapid recolonisation by the European red fox:
621 how effective are uncoordinated and isolated control programs? *European Journal of Wildlife*
622 *Research*, **60**, 749-757.
- 623 Nielsen, A., Yoccoz, N.G., Steinheim, G., Storvik, G.O., Rekdal, Y., Angeloff, M., Pettorelli, N., Holand, O.
624 & Mysterud, A. (2012) Are responses of herbivores to environmental variability spatially
625 consistent in alpine ecosystems? *Global Change Biology*, **18**, 3050-3062.
- 626 Nolet, B.A., Bauer, S., Feige, N., Kokorev, Y.I., Popov, I.Y. & Ebbinge, B.S. (2013) Faltering lemming cycles
627 reduce productivity and population size of a migratory Arctic goose species. *Journal of Animal*
628 *Ecology*, **82**, 804-813.
- 629 Norderhaug, A. & Norderhaug, M. (1982) *Anser erythropus* in Fennoscandia. *Aquila*, **89**, 93-101.
- 630 Øien, I.J., Aarvak, T., Ekker, M. & Tolvanen, P. (2009) Mapping of migration routes of the Fennoscandian
631 Lesser White-fronted Goose breeding population with profound implications for conservation
632 priorities. Pp. 12-18 in: Tolvanen, P., Øien, I.J. & Ruokolainen, K. (Eds.). Conservation of Lesser
633 White-fronted Goose on the European migration route. Final report of the EU LIFE-Nature
634 project 2005–2009. WWF Finland Report 27 & NOF/BirdLife Norway report no. 2009-1.
- 635 Øien, I.J., Aarvak, T., Lorentsen, S.H. & Bangjord, G. (1996) Use of individual differences in belly patches
636 in population monitoring of Lesser White-fronted Goose *Anser erythropus* at a staging ground.
637 *Fauna norv. Ser. C, Cinclus* **19**, 69-76.
- 638 Parker, H. (1984) Effect of Corvid Removal on Reproduction of Willow Ptarmigan and Black Grouse.
639 *Journal of Wildlife Management*, **48**, 1197-1205.
- 640 Pettorelli, N. (2013) *The Normalized Difference Vegetation Index*. Oxford University Press, Oxford.

641 R Core Team (2017) R: A language and environment for statistical computing. R Foundation for
642 Statistical Computing, Vienna, Austria.

643 Reed, E.T., Gauthier, G. & Giroux, J.F. (2004) Effects of spring conditions on breeding propensity of
644 Greater Snow Goose females. *Animal Biodiversity and Conservation*, **27.1**, 35–46.

645 Ruokonen, M., Aarvak, T., Chesser, R.K., Lundqvist, A.C. & Merila, J. (2010) Temporal increase in mtDNA
646 diversity in a declining population. *Molecular Ecology*, **19**, 2408-2417.

647 Ruokonen, M., Kvist, L., Aarvak, T., Markkola, J., Morozov, V.V., Øien, I.J., Syroechkovsky, E.E.,
648 Tolvanen, P. & Lumme, J. (2004) Population genetic structure and conservation of the lesser
649 white-fronted goose *Anser erythropus*. *Conservation Genetics*, **5**, 501-512.

650 Summers, R.W. & Underhill, L.G. (1987) Factors Related to Breeding Production of Brent Geese *Branta*
651 *Bernicla Bernicla* and Waders (Charadrii) on the Taimyr Peninsula. *Bird Study*, **34**, 161-171.

652 Sutherland, W.J., Pullin, A.S., Dolman, P.M. & Knight, T.M. (2004) The need for evidence-based
653 conservation. *Trends in Ecology & Evolution*, **19**, 305-308.

654 Taylor, G., Canessa, S., Clarke, R.H., Ingwersen, D., Armstrong, D.P., Seddon, P.J. & Ewen, J.G. (2017) Is
655 Reintroduction Biology an Effective Applied Science? *Trends in Ecology & Evolution*, **32**, 873-
656 880.

657 Tveraa, T., Fauchald, P., Yoccoz, N.G., Ims, R.A., Aanes, R. & Høgda, K.A. (2007) What regulate and limit
658 reindeer populations in Norway? *Oikos*, **116**, 706-715.

659 Tveraa, T., Stien, A., Bårdsen, B.J. & Fauchald, P. (2013) Population Densities, Vegetation Green-Up,
660 and Plant Productivity: Impacts on Reproductive Success and Juvenile Body Mass in Reindeer.
661 *Plos One*, **8**.

662 Tveraa, T., Stien, A., Brøseth, H. & Yoccoz, N.G. (2014) The role of predation and food limitation on
663 claims for compensation, reindeer demography and population dynamics. *Journal of Applied*
664 *Ecology*, **51**, 1264-1272.

665 Venables, W.N. & Ripley, B.D. (2002) Modern Applied Statistics with S. Springer, New York.

666 Ver Hoef, J.M. & Boveng, P.L. (2007) Quasi-poisson vs. negative binomial regression: How should we
667 model overdispersed count data? *Ecology*, **88**, 2766-2772.

668 Visser, M.E., Holleman, L.J.M. & Gienapp, P. (2006) Shifts in caterpillar biomass phenology due to
669 climate change and its impact on the breeding biology of an insectivorous bird. *Oecologia*, **147**,
670 164-172.

671 Vougioukalou, M., Kazantzidis, S. & Aarvak, T. (2017) Safeguarding the Lesser White-fronted Goose
672 Fennoscandian population at key staging and wintering sites within the European flyway.
673 Special publication. LIFE+10 NAT/GR/000638 Project, HOS/BirdLife Greece, HAOD/Forest
674 Research Institute, NOF/BirdLife Norway report no. 2017-2.

675