

1 **Survival and cause-specific mortality of harvested willow**
2 **ptarmigan (*Lagopus lagopus*) in central Norway**

3 Markus Fjellstad Israelsen^{1,2}, Lasse F. Eriksen^{1,2,3}, Pål Fosslund Moa², Bjørn Roar Hagen² and
4 Erlend B. Nilsen^{1,3}

5 ¹*Terrestrial division, Norwegian Institute for Nature Research (NINA), Høgskoleringen 9, 7030*
6 *Trondheim, Norway;* ²*Faculty of Biosciences and Aquaculture, Nord University, Skolegata 22, 7713*
7 *Steinkjer, Norway;* and ³*Centre for Biodiversity Dynamics, Department of Biology, Norwegian*
8 *University of Science and Technology, Trondheim, Norway*

9 **Correspondence**

10 Erlend B. Nilsen, Department for Terrestrial Biodiversity, Norwegian Institute for Nature Research,
11 Høgskoleringen 9, 7030 Trondheim, Norway. Email: erlend.nilsen@nina.no

12

13 **Abstract**

14 Survival is a key demographic component that often vary as a result of human activities such
15 as recreational harvest. Detailed understanding of seasonal variation in mortality patterns and
16 the role of various risk factors is thus crucial for understanding the link between
17 environmental variation and wildlife population dynamics, and to design sustainable harvest
18 management systems. Here, we report from a detailed seasonal and cause-specific
19 decomposition of mortality risks in willow ptarmigan (*Lagopus lagopus*) in central Norway.
20 The analyses are based on radio collared (n=188) birds that were monitored across all
21 seasons, and we used time-to-event models for competing risks to estimate mortality patterns.
22 Overall, annual survival was estimated at 0.43 (SE: 0.04), with no distinct difference among
23 years (2015/16 to 2018/19) or between sexes. Analysis of mortality risk factors revealed that
24 on the annual basis, the risk of harvest mortality was lower than the risk of dying from natural
25 causes. However, during the autumn harvest season (Sept. – Nov.), survival was low and the
26 dominating cause of mortality was harvest. During winter (Dec. – Mar.) and spring seasons
27 (Apr. - May), survival was in general high and did not vary between males and females.
28 However, during the spring season juveniles (i.e. birds born last year) of both sexes had lower
29 survival than adults, potentially because they are more prone to predation. During the summer
30 season (June – Aug.) females experienced a higher hazard than males, underlining the greater
31 parental investment of females during egg production, incubation and chick rearing compared
32 to males. Our analyses provide unique insight into demographic and seasonal patterns in
33 willow ptarmigan mortality risks in a harvested population, and revealed a complex interplay
34 across seasons, risk factors and demographic classes. Such insight is valuable when designing
35 sustainable management plans in a world undergoing massive environmental perturbations.

36

37 **Key words:** demography, grouse, harvest, cause-specific mortality, survival

38

39

40 Introduction

41 Population dynamics is driven by temporal and spatial fluctuations in demographic rates, that
42 together determine the population growth rate λ (Sæther *et al.* 1999; Sæther & Bakke 2000).
43 Both survival and reproductive output contribute to the observed variation, and their general
44 contribution varies both in time and space (Sæther & Bakke 2000; Nilsen *et al.* 2009). In
45 addition, research focusing on the evolution of life history strategies have found that species
46 can be classified along a slow-fast continuum (Stearns 1983; Sæther & Bakke 2000; Bielby *et al.*
47 *et al.* 2007). Generally, fast living species have low survival and high reproductive output,
48 whereas slow living species have high survival rates and lower reproductive output (Sæther *et al.*
49 *et al.* 2013). Species on opposite ends of the continuum also differ in the way age-specific
50 survival contributes to the population growth rate (Sæther *et al.* 2013). The potential
51 contribution of adult survival is higher in slow living species (Sæther & Bakke 2000),
52 whereas the potential contribution of early life survival is higher in fast living species (Bielby
53 *et al.* 2007). Annual mortality patterns are often very different for species on different ends of
54 the continuum. Therefore, understanding the spatiotemporal variation in survival and cause-
55 specific mortality rates are imperative for understanding the population dynamics of wildlife
56 species (DelGiudice *et al.* 2002; Heisey & Patterson 2006; Murray 2006).

57 Previous studies have reported that demographic factors such as sex and age can significantly
58 affect the survival probability (Shackell *et al.* 1994; Caizergues & Ellison 1997; Beauplet *et al.*
59 *et al.* 2006) and mortality causes (Hannon, Gruys & Schieck 2003; Delgiudice *et al.* 2006;
60 Chilvers & MacKenzie 2010; Asmyhr, Willebrand & Hörnell-Willebrand 2012) of a range of
61 avian species. Moreover, in temporally variable environments mortality risk might vary
62 through time (Gauthier *et al.* 2001; Crespin *et al.* 2002), and the ability to deal with
63 unpredictable environmental conditions may vary between life stages (Delgiudice *et al.* 2006).
64 For instance, adult survival is often reported to be higher and less variable than juvenile
65 survival (Guillemain *et al.* 2013). Finally, in seasonal environments certain seasons within the
66 year may also place more stress on one sex than the other, such as the energy demanding
67 process of egg production (Nilsson & Råberg 2001) and incubation (Haftorn & Reinertsen
68 1985) for female birds or risky behavior undertaken by males in the mating season (Hannon,
69 Gruys & Schieck 2003).

70 In wild vertebrate populations, individuals are typically facing competing risks from a range
71 of different sources, and these sources might have different intensities in different times of the
72 year. In exploited populations, previous studies have demonstrated that harvest-related
73 mortality risks may be close to or even higher than natural mortality risks in parts of the year
74 (Rolland *et al.* 2010; Sandercock *et al.* 2011). Harvest mortality is often assumed to be
75 partially compensated through reduced natural mortality (Pedersen *et al.* 2004). However, this
76 may only be true at low harvest rates, where harvest mortality above certain levels may be
77 increasingly additive or even super-additive (Sandercock *et al.* 2011). Knowledge of such
78 thresholds and any compensatory mechanisms is thus essential information for sustainable
79 harvest management (Brøseth *et al.* 2005). For harvested wildlife populations, understanding
80 the interplay between harvest induced mortality and other natural mortality sources is
81 important in order to establish sustainable harvest strategies (Sandercock *et al.* 2011).

82 Willow ptarmigan (*Lagopus lagopus* L.) is a valued game species, and is hunted in many parts
83 of its distributional range (Storch 2007), including Scandinavia (Aanes *et al.* 2002; Asmyhr,

84 Willebrand & Hörnell-Willebrand 2012). After a strong decline in population numbers, the
85 willow ptarmigan was in 2015 classified as near threatened (NT) in the Norwegian Red List
86 for Species (Henriksen & Hilmo 2015), fueling a debate of harvest effects on population
87 development (Breisjøberget *et al.* 2018). This makes the Norwegian willow ptarmigan
88 population a highly relevant case study for a detailed examination of variation in mortality
89 patterns for a managed wildlife species. To this end, we used five years of telemetry data from
90 central Norway to characterize annual and seasonal mortality risks for different sex- and age
91 classes. In particular, we first (i) estimated annual survival rates for the different demographic
92 groups in the population. Second, (ii) we decomposed the annual cycle into distinct seasons
93 and assessed sex- and age- effects within seasons. Finally, (iii) we estimated the relative
94 natural and harvest induced risks using a competing risks formulation, and estimated seasonal
95 patterns in hazard rates. In sum, these analyses will provide an important description of how
96 different hazards shape the annual mortality patterns for different demographic groups in a
97 wildlife population.

98

99 **Materials and methods**

100 **Study area**

101 The basis of our field study was two locations, Lifjellet (64°25' – 64°30'N, 13°11' – 13°24'E,
102 approx. 96km²) and Gusvatnet (64°15' – 64°18'N, 13°25' – 13°37'E, approx. 54km²)
103 respectively, in Lierne municipality in Central Norway, where all captures and marking of
104 birds occurred (Figure 1). Because some birds migrated relatively long distances (> 25km,
105 Arnekleiv 2020), our dataset also include several relocations in neighboring municipalities.
106 Radio tagged willow ptarmigan were triangulated inside the total study area, as the birds
107 dispersed or migrated out of the main areas. The capture sites for willow ptarmigan (see next
108 section) spanned elevations from 459 – 757m, and were located in the subalpine to alpine
109 bioclimatic zone. The subalpine bioclimatic zone was dominated by spruce (*Picea abies* L.)
110 interspersed with birch (*Betula pubescens*). Dwarf birch (*B. nana* L.) and willows (*Salix spp.*)
111 comprise most of the shrubbery scattered amongst forest patches. At lower elevations
112 bogs/marshes are covered by grasses and sedges and the forests by ericaceous plants, while
113 the vegetation at higher altitudes is dominated by dwarf birch heather, sedges and lichens. The
114 ground is typically snow-covered from October until May. Main predators on adult willow
115 ptarmigan observed in the study area include, gyrfalcons (*Falco rusticolus* L.), golden eagles
116 (*Aquila chrysaetos* L.) and red fox (*Vulpes Vulpes* L.). Red fox and golden eagles predate on
117 both nests (E. B. Nilsen, unpublished data) and adult willow ptarmigan (Munkebye *et al.*
118 2003; Nyström *et al.* 2006b), while gyrfalcons mostly prey upon yearling or adult willow
119 ptarmigan (Booms & Fuller 2003; Nyström *et al.* 2006a; Barichello & Mossop 2011). In
120 addition, arctic fox (*Vulpes lagopus* L.) and lynx (*Lynx lynx* L.) are present in the study area,
121 but probably does not represent major mortality risks for ptarmigan in the study area due to
122 low densities.

123

124 **Field methods**

125 During February and March 2015-2019, we captured a total of 188 willow ptarmigan at night
126 using snowmobiles and large hand nets with prolonged handles, as described in Nilsen *et al.*

127 (2020). To prevent birds from flying off before the field personnel were close enough to
128 capture them, a high-powered head lamp was used to dazzle the birds. After capture, we
129 placed the birds in an opaque bag to reduce stress. We aged the birds based on descriptions in
130 Bergerud, Peters and McGrath (1963) and Myrberget (1975), by examining the pigmentation
131 on the outer primaries and categorized them as either juvenile (< 1 year old) or adult (> 1 year
132 old). We assessed the sex of each bird in the field by visual inspection of morphological
133 characteristics and later confirmed the sex by DNA analyses using a feather sample collected
134 during capture. For 17 birds we did not obtain any biological samples or the DNA analysis
135 was unsuccessful, and could thus not confirm sex using DNA. Based on the birds where both
136 field-based and DNA-based sex determination was obtained (n=166), field-based
137 determination was correct in 85% (141/166) of the cases. We therefore opted to include birds
138 where sex was not verified using DNA analyses; we are aware that this induces a potential
139 bias. Before releasing the birds, they were fitted with a uniquely numbered leg ring (~ 2.4g)
140 and a Holohil RI-2BM or Holohil RI-2DM radio transmitter (~ 14.1g). The radio transmitters
141 had an expected battery lifetime of 24 months (RI-2BM) or 30 months (RI-2DM), and
142 included a mortality circuit that was activated if a bird had been immobile for 12 hours. For
143 all marked birds, the combined weight of the leg ring and radio transmitter were < 3.5% of the
144 body mass. From the total number of birds that we instrumented with VHF radio collars (n =
145 188), some birds (n = 6) were never relocated after release and were thus excluded from the
146 study. This left us with a total sample of n = 182 individual willow ptarmigan included in the
147 analyses. Of these birds, there were 53% females and 47% males. During the study period, we
148 recorded mortalities for 124 birds (i.e., 68% of all birds marked), whereas 58 birds (32%)
149 were censored either because we lost contact or because they were alive at the end of the
150 study period (Table 1). As previous studies did not find adverse effects of radio tags on
151 survival (Thirgood *et al.* 1995; Hannon, Gruys & Schieck 2003; Terhune *et al.* 2007), we
152 assumed the radio tags would not influence the survival of willow ptarmigan.

153

154 Following release of the radio tagged birds, they were triangulated from the ground at least
155 once a month for 10 months of the year (February – November) by qualified field personnel.
156 If a mortality signal was heard from the transmitter, we recovered it as soon as possible to
157 determine cause of death. A number of birds dispersed out of the main study areas and was
158 thus out of signal range for field personnel on the ground. To avoid loss of data, we conducted
159 aerial triangulation using a helicopter or airplane three times a year (May, September and
160 November) in the years 2016-2019. In 2015, we only conducted one triangulation from the air
161 in October.

162 The data used here is based on an ongoing field project, and the dataset is therefore
163 continuously updated as new data is registered. For analyses reported here we used data
164 collected between 16.02.2015 to 27.11.2019.

165

166 **Individual capture histories**

167 As a basis for our analysis of annual survival probabilities, we set 1 August to represent the
168 start of the biological year. This choice made it possible to directly compare our results with
169 those from previous studies in Scandinavia (Smith & Willebrand 1999; Sandercock *et al.*
170 2011). With the redefined year, the first time period of the study started 1 August 2014 and

171 ended on 31 July 2015, while the final time period (6 in total) started 1 August 2019 and ends
172 31 July 2020. Hereafter, “year” refers to the biological year from 1 August to 31 July.

173 In addition to the analysis of annual survival probabilities, we also assessed patterns of
174 survival in four distinct seasons. First, we defined the autumn season as 1 September to 30
175 November. This season is strongly affected by the annual recreational harvest season starting
176 10 September, and previous studies from Scandinavia have shown that harvest is a
177 dominating mortality factor in autumn (Smith & Willebrand 1999; Sandercock *et al.* 2011).
178 Most of the hunting effort usually takes place during the first weeks after the hunting season
179 has started (Smith & Willebrand 1999; Willebrand, Hörnell-Willebrand & Asmyhr 2011). In
180 our case, there were only two harvest-related mortalities outside the defined autumn season
181 (during the winter harvest season in February), these were included as mortalities in the
182 winter and full year analyses. Second, we defined the winter season as 1 December to 31
183 March. Winter survival of willow ptarmigan in Scandinavia have typically been found to be
184 high (Smith & Willebrand 1999; Sandercock *et al.* 2011). Finally, we defined the mating and
185 pre-brooding period as the spring season (1 April to 31 May), while the incubation and chick
186 rearing period was defined as the summer season (1 June to 31 August). The age of each bird
187 (juvenile vs adult) was estimated at capture in February/March and separated into two age
188 categories (< 1 year old and > 1 year old). In the further analyses, age was only included as a
189 predictor variable for the spring survival analysis, as the presence of juvenile willow
190 ptarmigan could only be known with certainty for the spring season. Given that juveniles were
191 approx. nine months old at capture, there were no marked juveniles present during the autumn
192 season for our study. Further, a comparison between the survival of “yearlings” and adults
193 could not be made due to the low number of yearlings still alive in the autumn and winter
194 months.

195 Based on the time schedules described above, we constructed capture histories for each bird
196 following a time-to-event modelling approach (Pollock *et al.* 1989). Birds that were alive at
197 the end of the year (31 July) or season (see above for definitions) were censored, and re-
198 entered in a new row in the dataset for the next year or season. All juvenile birds alive at the
199 end of the year were re-entered as adults at the start of the new year (1 August). Thus, each
200 observation in the dataset is one bird in one given year. For all years in total, we had 350
201 observations or ‘bird-years’. Naturally, with only one tagging session in February/March the
202 number of observations available for analyses decreased due to mortalities from winter ($n =$
203 251), spring ($n = 232$), summer ($n = 206$) to autumn ($n = 161$). In addition to the capture-
204 related variables (ring identification number, sex and age), five new variables were created:
205 time period, entry day, exit day, event (if the bird was alive = 0 or dead = 1) and cause of
206 death (harvest = 1 or natural = 2). Natural causes were defined as any non-harvest related
207 mortality. All unknown mortality causes were assumed to be natural (since harvested marked
208 ptarmigans were reported), but not identifiable to a single natural cause. We assumed that all
209 harvested birds were reported as harvested. Hunters were frequently reminded to report and
210 return radio tags and/or leg rings and since marked birds were not banned from harvest, this
211 should be a valid assumption. Nevertheless, some harvested birds may not have been reported
212 and could thus yield a slight underestimation of harvest mortality rates.

213 Because the birds were not monitored in continuous time, the exit date (i.e., date for mortality
214 or censoring) had to be estimated in many cases. For birds that were alive at the end of the
215 study, exit day was set to the day that they were last confirmed to be alive. Birds that died due

216 to natural causes, had their exit day defined as the midpoint between the last day they were
217 heard alive and the first time the mortality signal from the transmitter was heard. For birds
218 that were shot by hunters, exit day was set according to the day the bird was shot, as reported
219 by the hunters. A few birds (n = 4) that were censored due to loss of contact (radio transmitter
220 failure or other), re-entered the study when they were reported as shot and their status was
221 changed to alive until the day they were shot.

222

223 **Survival analyses**

224 Survival rates were estimated using five years of radio telemetry data, collected between 2015
225 and 2019 in Lierne, Snåsa, Grong and Røyrvik municipalities. We applied Pollock *et al.*
226 (1989) staggered-entry modification of the Kaplan-Meier procedure (Kaplan & Meier 1958)
227 to estimate annual and seasonal survival rates on a daily basis in the statistical software R,
228 version 3.6.1 (R Core Team 2019), employing functions from the *survival* package (Therneau
229 2015). Other analyses and data handling were also conducted in R.

230 To examine variation in mortality risk due to sex, age and year, we used Cox proportional
231 hazards regression models fitted using the function *coxph* (Therneau 2015). To account for
232 non-independence caused by the fact that some individuals were represented by more than
233 one observation, individual ID (ring identification number) was included as a random
234 variable. The proportional hazards assumption of all cox regression models were assessed by
235 running model diagnostics with the *cox.zph* function (Therneau 2015). Annual cause-specific
236 mortality under the competing risks of natural and harvest mortality was estimated by
237 employing a nonparametric cumulative incidence function estimator (NPCIFE) described by
238 Heisey and Patterson (2006), using the code modified by Sandercock *et al.* (2011). The same
239 procedure was also used to estimate the cumulative risk of natural and harvest mortality
240 during autumn only. To test for any dependencies in harvest or natural mortality risk due to
241 sex, we used a stratified Cox proportional hazards analysis. We first stratified the data by
242 mortality cause (natural or harvest) and then ran two separate Cox proportional hazards
243 regressions, one for natural mortality risk and one for harvest mortality risk, testing for an
244 effect of sex in each model. Finally, we estimated separate continuous annual hazard
245 functions for both mortality causes combined, for harvest mortality only and natural mortality
246 only by employing Gu (2014) smoothing spline functions.

247 All survival analysis figures were created using package *ggplot2* (Wickham 2016), while the
248 map in Figure 1 was created with packages *leaflet* and *mapview* (Cheng, Karambelkar & Xie
249 2018; Appelhans *et al.* 2019).

250

251 **Results**

252 **Annual survival probabilities**

253 Annual survival probability of willow ptarmigan across all years was estimated to be $0.43 \pm$
254 0.04 SE (Figure 2a). For females and males, annual survival was estimated to be 0.40 ± 0.05
255 SE and 0.45 ± 0.05 SE respectively (Figure 2b). When stratified by sex, the proportional
256 hazards assumption was not met ($\chi^2 = 5.71$, $P = 0.02$), and we therefore did not use Cox

257 proportional regression to assess this difference statistically. We further examined if there was
258 any between-year variation in annual survival (Figure 2c), but no significant between-year
259 variation in annual survival was found (Wald test = 1.67, df = 3, P = 0.60). The assumption
260 about proportional hazards for the global model was met ($\chi^2 = 7.27$, P = 0.06). Therefore,
261 annual survival estimates remained relatively stable for all years.

262

263 **Seasonal survival rates**

264 In the second part of the analysis we created distinct datasets for the various seasons (as
265 defined in the methods), and estimated survival probabilities for each season separately. As
266 expected, autumn survival was low (0.67 ± 0.04 SE), and there were some indications that
267 males had higher mortality risk than females during this season (HR = 1.53, 95% CI = 0.90 –
268 2.60, z = 1.58, P = 0.11; Figure 3a). The assumption of proportional hazards was met when
269 stratified by sex ($\chi^2 = < 0.01$, P = 0.98). During the winter season, overall survival probability
270 was high (0.90 ± 0.03 SE), with no discernible difference in mortality risk between males and
271 females (HR = 0.65, 95% CI = 0.24 – 1.78, z = -0.84, P = 0.40). The assumption of
272 proportional hazards when stratified by sex was met ($\chi^2 = 2.28$, P = 0.13). Also during spring,
273 survival probabilities were high (0.90 ± 0.02 SE). The proportional hazards assumption was
274 met for sex ($\chi^2 = 0.07$, P = 0.79) and age ($\chi^2 = 0.08$, P = 0.78), for the spring survival data.
275 There were no difference in survival between males and females (HR = 1.10, 95% CI = 0.47 –
276 2.58, z = 0.23, P = 0.82) in spring, but juveniles (< 1 year old) had a substantially higher risk
277 of mortality than adult birds (HR = 2.35, 95% CI = 1.01 – 5.45, z = 1.98, P = 0.05; Figure 3b).
278 During the three month long summer season, survival probability was lower than both winter
279 and spring survival (0.82 ± 0.03 SE), and males had a substantially lower mortality risk than
280 females (HR = 0.33, 95% CI = 0.16 – 0.69, z = -2.93, P = < 0.01; Figure 3c). The summer
281 survival data for sex met the assumption of proportional hazards ($\chi^2 = 3.09$, P = 0.08). For all
282 seasonal analyses, year did not explain a significant amount of the variation in mortality risk
283 for any season and the proportional hazards assumption was met for all seasonal data (except
284 summer) used to test for effects of year (see Appendix 1).

285

286 **Temporal variation in cause-specific mortality risk**

287 In the third and final part of the analyses we investigated annual and seasonal cause-specific
288 mortality risk. Annually, there was a higher probability of mortality due to natural causes
289 (CIF = 0.33 ± 0.03 SE, 95% CI = 0.28 – 0.38) than being shot (CIF = 0.25 ± 0.04 SE, 95% CI
290 = 0.19 – 0.31) for willow ptarmigan in this study (Figure 4a). Unsurprisingly, this relationship
291 was reversed when we examined the autumn season only, with harvest mortality being
292 substantially higher (CIF = 0.24 ± 0.04 SE, 95% CI = 0.18 – 0.30) than the probability of
293 dying of natural causes (CIF = 0.09 ± 0.03 SE, 95% CI = 0.04 – 0.14; Figure 4b). We did not
294 find any clear difference in mortality risk between males and females for the risk of being
295 shot (HR = 1.51, 95% CI = 0.81 – 2.81, z = 1.28, P = 0.20) or dying of natural causes (HR =
296 1.60, 95% CI = 0.53 – 4.82, z = 0.83, P = 0.41).

297 Finally, we estimated smoothed instantaneous mortality risk for natural and harvest
298 mortalities combined (total), harvest mortalities only and natural mortality only (Figure 4c).
299 In general, the mortality risk was highest in September and October, coinciding with the first

300 few weeks of the hunting season (10 September to 28 February). During winter and early
301 spring mortality risk was very low, but increased slowly and gradually until mid-June,
302 yielding another peak in mortality risk. The risk of harvest mortality is mainly relevant in the
303 autumn, and the spring peak in mortality risk is driven exclusively by natural mortality
304 factors.

305

306 **Discussion**

307 **Survival**

308 In our study area we estimated annual survival to be 0.43 ± 0.04 SE, with no discernible
309 distinction between years. This annual survival probability is comparable to previous studies
310 from other localities in Norway (Figure 5; Sandercock *et al.* 2011) and North America
311 (Martin, Hannon & Rockwell 1989; Sandercock, Martin & Hannon 2005). Annual survival in
312 our study area was lower than the estimates by Sandercock *et al.* (2011) for annual survival in
313 non-harvested areas (0.54, 95% CI = 0.38 – 0.70) and areas with experimental treatments of
314 15% harvest (0.47, 95% CI = 0.35 – 0.59), as well as the estimate in Smith and Willebrand
315 (1999) for non-harvested areas (0.53, 95% CI = 0.40 – 0.67). However, the survival
316 probability found in our study area was higher than those reported under 30% experimental
317 harvest in central Norway (Sandercock *et al.* 2011; 0.30, 95% CI = 0.20 – 0.40) and under
318 harvest in central Sweden (Smith & Willebrand 1999; 0.28, 95% CI = 0.18 – 0.38, Figure 5).
319 During our study period (2015/16 to 2019/20) local management reported an average harvest
320 rate of 18% (Tord Åberg, pers. comm., 25.06.2020), based on estimated population size and
321 total bag size, in our study region in Lierne municipality. Taken together, these studies
322 indicate that higher harvest rates yield lower annual survival of willow ptarmigan, which
323 further demonstrate that harvest mortalities are at least partially additive to natural mortalities.
324 This gives some insight into the importance of harvest intensity on annual survival for willow
325 ptarmigan in Scandinavia. We did not find any clear difference in annual survival between
326 males and females. This might be the result of counteracting seasonal effects, as suggested by
327 (Hannon, Gruys & Schieck 2003); in general we found that males tended towards lower
328 survival (although not statistically significant) than females in autumn, while females had
329 substantially lower survival than males during summer.

330

331 In winter and spring, survival was generally high, and there were no clear signs of sex
332 differences in survival. However, juvenile birds had much lower survival in spring than adult
333 birds. Willow ptarmigan vigorously defend their established territories from any intruders,
334 including juveniles (Pedersen, Steen & Andersen 1983; Rørvik, Pedersen & Steen 1998;
335 Eason & Hannon 2003). We expect that inexperienced yearlings trying to acquire a territory
336 may be less alert to predators during this time, and may therefore suffer greater mortality risk
337 than adults. This difference might arise due to differential predation pressure, and Barichello
338 and Mossop (2011) suggested that gyrfalcon exerts higher predation pressure on young
339 ptarmigan compared to adults. Such a preference would indicate that juveniles are easier prey
340 than adult birds and could explain the lower survival of juveniles in spring found in this study.
341 Inexperience may also affect the foraging ability of young birds during winter-spring,
342 resulting in poor spring body condition (Wiebe & Martin 1998).

343 We also found a distinct difference in survival between males and females during summer,
344 with female willow ptarmigan having markedly lower survival compared to males. Hannon,
345 Gruys and Schieck (2003) suggest that female willow ptarmigan are more prone to predation
346 in the breeding season than males as a result of their great parental investment. This
347 investment includes the process of egg laying and incubation, as well as any clutch defense
348 behavior towards predators (Martin & Horn 1993). Both male and female willow ptarmigan
349 defend the nest from predators, although males for the most part indirectly defend the nest by
350 defending their female partner (Martin 1984; Martin & Horn 1993). The higher survival of
351 males during summer suggest that they do not invest as much in the nest and are therefore in
352 better condition than females during this time, allowing them to more effectively avoid
353 predation.

354 There was no significant distinction in autumn survival between male and female willow
355 ptarmigan, but our results did provide some indications that females have higher survival
356 during autumn. Because our sample size in autumn is lower than in the other seasons resulting
357 from mortalities between winter tagging and autumn, the power to detect any trend is also
358 lower in autumn compared to the other seasons.

359

360 **Cause-specific mortality risk**

361 In our study, we found that natural mortality risk varied throughout the year, revealing a
362 minor peak in late September and a major peak in mid-June. Sandercock *et al.* (2011) found a
363 very similar pattern, although they reported an autumn peak that was more distinct and a
364 summer peak that occurred somewhat earlier than mid-May. In our study, the summer peak in
365 natural mortality risk (Figure 4c) coincided with late incubation or hatching stage, a period
366 which has previously been associated with high mortality risk (Winder *et al.* 2014; Winder *et al.*
367 *et al.* 2016). The reason for this heterogeneity between the studies is of yet unknown.
368 Differences in climate between the two locations could explain the observed distinctions, with
369 the Lierne study area being located both further north and further inland than Meråker-Selbu,
370 which may cause the breeding dates of willow ptarmigan and/or predators to differ between
371 the two areas. The distance and distinct climates between Lierne and Meråker-Selbu means
372 that there could also be spatial differences in the predator communities of the two areas as
373 well, yielding differing mortality risk patterns. Moreover, our data was collected
374 approximately 20 years later than the data analyzed by Sandercock *et al.* (2011), which means
375 that temporal changes to the predator community is also a potential explanation for the
376 observed differences.

377 As expected, the vast majority of harvest mortalities occurred during the first weeks of the
378 autumn hunting season, and the annual patterns in harvest mortality risk were mostly driven
379 by these weeks. We found our estimated harvest mortality risk (0.24 ± 0.04 SE) to be identical
380 to the estimate of hunting mortality in autumn in central Sweden (Smith & Willebrand 1999).
381 It is important to note that the core areas in our study (Gusvatnet and Lifjellet) are easily
382 accessible, and areas close to infrastructure are often associated with higher hunting effort
383 compared to more remote locations (Brøseth & Pedersen 2000; Breisjøberget *et al.* 2018).

384 We found no significant autumnal difference between the sexes for either natural mortality
385 risk or harvest mortality risk. Asmyhr, Willebrand and Hörnell-Willebrand (2012) were also

386 unable to find an effect of sex on harvest risk in a harvested area in central Sweden.
387 Interestingly, Sandercock *et al.* (2011) showed that females were more at risk of harvest
388 mortality under experimental harvest. In their experiment hunters mostly used pointing dogs
389 during the hunt (Sandercock *et al.* 2011), while our study area had a mix of hunters with and
390 without dogs (Nils Vidar Bratlandsmo, pers. comm., 08.04.2020). Male and female willow
391 ptarmigan are to different degrees following the brood during the autumn hunting season, and
392 this may affect the susceptibility for being shot (Bunnefeld *et al.* 2009). We speculate whether
393 this grouping behavior may have different effects on harvest with or without dogs. As using a
394 hunting dog usually gives the hunter more time to prepare before firing in each situation, it is
395 likely that hunters may have time to shoot more individuals from large coveys of ptarmigan
396 than if hunting without a dog. Since females are more prone to grouping, this might imply that
397 more females may be shot when hunting with dogs than without, which would give a possible
398 reason for the observed differences between our study and Sandercock *et al.* (2011).

399

400 **Harvest management**

401 In our study area the willow ptarmigan harvest mortality risk was substantially higher than
402 what is generally considered to be compensatory (Sandercock *et al.* 2011). Moreover, there
403 seem to be a clear connection between harvest rate and willow ptarmigan survival, where
404 willow ptarmigan in non-harvested areas have higher survival (Figure 5). It is therefore
405 important to implement harvest strategies that can reduce risks of overharvest. Threshold
406 harvest strategies have often been proposed as a way to counterbalance risk of harvest,
407 especially when the exploited population occur at low densities (Eriksen, Moa & Nilsen
408 2018), as it only permits harvest above a certain population threshold (Lande, Sæther &
409 Engen 1997). Although, it does imply no harvest in the years where the population size is
410 below this threshold (Lande, Sæther & Engen 1997).

411

412 **Conclusion**

413 The temporal resolution of this study allowed us to accurately estimate willow ptarmigan
414 annual and seasonal survival, as well as cause-specific mortality risks. We concluded that
415 seasonal patterns in mortality might differ between demographic groups, and that these
416 differences might not be visible when analyzed at a coarser temporal resolution. Such patterns
417 might be important when seeking to understand the evolution of life histories in fluctuating
418 environments. Our results also provide insights into the relative importance of harvest and
419 natural mortality for overall survival probability. Although natural mortality risk outweighed
420 the estimated harvest mortality risk on an annual basis, harvest still constituted a relatively
421 large percentage of mortalities observed. Comparison with non-hunted populations support
422 the view that such harvest mortality is at least partially additive. By identifying demographic
423 differences in mortality risk throughout the year, our results are applicable for highlighting
424 areas where conservationists or small game area managers should focus their efforts.

425

426 **Acknowledgements**

427 We want to thank our field personnel for all effort through vast amounts of monitoring
428 sessions, as well as local hunting area managers (in particular Fjellstyra i Lierne led by Nils
429 Vidar Bratlandsmo) and mountain rangers for access to the area and invaluable assistance in
430 the field. The project was funded by the Norwegian Environment Agency (Funding reference
431 number: 17010522 and 19047014).

432

433 **Conflict of interest**

434 None declared.

435

436 **Author contributions**

437 M. F. Israelsen conducted the data analysis, supervised by E. B. Nilsen. E.B. Nilsen conveyed
438 the main research question. All authors contributed to the data acquisition, data interpretation
439 and preparation of the manuscript. All authors approved the submitted version of the
440 manuscript.

441

442 **Data availability statement**

443 Temporary location of raw data used in the analyses:

444 [https://github.com/markusfisra/WillowPtarmiganSurvival---
445 Review/blob/master/rawdataAnalysis.csv](https://github.com/markusfisra/WillowPtarmiganSurvival---Review/blob/master/rawdataAnalysis.csv)

446 Temporary location of scripts developed to conduct analyses and produce figure illustrations:

447 [https://github.com/markusfisra/WillowPtarmiganSurvival---
448 Review/blob/master/Willow%20ptarmigan%20survival%20-%20Review%20edit%2007.07.20.Rmd](https://github.com/markusfisra/WillowPtarmiganSurvival---Review/blob/master/Willow%20ptarmigan%20survival%20-%20Review%20edit%2007.07.20.Rmd)

449 Upon acceptance, both data and analysis scripts will be archived in a stable repository with a
450 citable DOI.

451

452 **References**

- 453 Aanes, S., Engen, S., Sæther, B.-E., Willebrand, T. & Marcström, V. (2002) Sustainable harvesting
454 strategies of willow ptarmigan in a fluctuating environment. *Ecological applications*, **12**, 281-
455 290.
- 456 Appelhans, T., Detsch, F., Reudenbach, C. & Woellauer, S. (2019) mapview: Interactive Viewing of
457 Spatial Data in R. R package version 2.7.0.
- 458 Arnekleiv, Ø.L. (2020) Drivers and consequences of partial migration in an alpine bird species. MSc
459 Thesis, Norwegian University of Life Sciences.
- 460 Asmyhr, L., Willebrand, T. & Hörnell-Willebrand, M. (2012) Successful adult willow grouse are
461 exposed to increased harvest risk. *Journal of Wildlife Management*, **76**, 940-943.
- 462 Barichello, N. & Mossop, D. (2011) The overwhelming influence of ptarmigan abundance on gyrfalcon
463 reproductive success in the central Yukon, Canada. *Gyrfalcons and ptarmigan in a changing
464 world, Volume I* (eds R.T. Watson, T.J. Cade, M. Fuller, G. Hunt & E. Potapov), pp. 307-322.
465 The Peregrine Fund, Boise, Idaho, USA.

466 Beuplet, G., Barbraud, C., Dabin, W., Küssener, C. & Guinet, C. (2006) Age-specific survival and
467 reproductive performances in fur seals: evidence of senescence and individual quality. *Oikos*,
468 **112**, 430-441.

469 Bergerud, A.T., Peters, S.S. & McGrath, R. (1963) Determining sex and age of willow ptarmigan in
470 Newfoundland. *Journal of Wildlife Management*, **27**, 700-711.

471 Bielby, J., Mace, G.M., Bininda-Emonds, O.R., Cardillo, M., Gittleman, J.L., Jones, K.E., Orme, C.D.L. &
472 Purvis, A. (2007) The fast-slow continuum in mammalian life history: an empirical
473 reevaluation. *The American Naturalist*, **169**, 748-757.

474 Booms, T.L. & Fuller, M.R. (2003) Gyrfalcon diet in central west Greenland during the nesting period.
475 *The Condor*, **105**, 528-537.

476 Breisjøberget, J.I., Odden, M., Storaas, T., Nilsen, E.B. & Kvasnes, M.A. (2018) Harvesting a red-listed
477 species: determinant factors for willow ptarmigan harvest rates, bag sizes, and hunting
478 efforts in Norway. *European journal of wildlife research*, **64**, 54 (2018).

479 Brøseth, H. & Pedersen, H.C. (2000) Hunting effort and game vulnerability studies on a small scale: a
480 new technique combining radio-telemetry, GPS and GIS. *Journal of Applied Ecology*, **37**, 182-
481 190.

482 Brøseth, H., Tufto, J., Pedersen, H.C., Steen, H. & Kastdalen, L. (2005) Dispersal patterns in a
483 harvested willow ptarmigan population. *Journal of Applied Ecology*, **42**, 453-459.

484 Bunnefeld, N., Baines, D., Newborn, D. & Milner-Gulland, E.J. (2009) Factors affecting unintentional
485 harvesting selectivity in a monomorphic species. *Journal of Animal Ecology*, **78**, 485-492.

486 Caizergues, A. & Ellison, L.N. (1997) Survival of black grouse *Tetrao tetrix* in the French Alps. *Wildlife*
487 *Biology*, **3**, 177-187.

488 Cheng, J., Karambelkar, B. & Xie, Y. (2018) leaflet: Create Interactive Web Maps with the JavaScript
489 'Leaflet' Library. R package version 2.0.2.

490 Chilvers, B.L. & MacKenzie, D.I. (2010) Age- and sex-specific survival estimates incorporating tag loss
491 for New Zealand sea lions, *Phocarcos hookeri*. *Journal of Mammalogy*, **91**, 758-767.

492 Crespin, L., Verhagen, R., Stenseth, N.C., Yoccoz, N.G., Prévot-Julliard, A.C. & Lebreton, J.D. (2002)
493 Survival in fluctuating bank vole populations: seasonal and yearly variations. *Oikos*, **98**, 467-
494 479.

495 Delgiudice, G.D., Fieberg, J., Riggs, M.R., Powell, M.C. & Pan, W. (2006) A long-term age-specific
496 survival analysis of female white-tailed deer. *Journal of Wildlife Management*, **70**, 1556-1568.

497 DelGiudice, G.D., Riggs, M.R., Joly, P. & Pan, W. (2002) Winter severity, survival, and cause-specific
498 mortality of female white-tailed deer in north-central Minnesota. *Journal of Wildlife*
499 *Management*, 698-717.

500 Eason, P.K. & Hannon, S.J. (2003) Effect of pairing status on use of space by territorial willow
501 ptarmigan (*Lagopus lagopus*): bachelor males choose life on the edge. *The Auk*, **120**, 497-
502 504.

503 Eriksen, L.F., Moa, P.F. & Nilsen, E.B. (2018) Quantifying risk of overharvest when implementation is
504 uncertain. *Journal of Applied Ecology*, **55**, 482-493.

505 Gauthier, G., Pradel, R., Menu, S. & Lebreton, J.-D. (2001) Seasonal survival of greater snow geese
506 and effect of hunting under dependence in sighting probability. *Ecology*, **82**, 3105-3119.

507 Gu, C. (2014) Smoothing Spline ANOVA Models: R Package *gss*. *Journal of Statistical Software*, **58**, 1-
508 25.

509 Guillemain, M., Fox, A.D., Pöysä, H., Väänänen, V.-M., Christensen, T.K., Triplet, P., Schricke, V. &
510 Korner-Nievergelt, F. (2013) Autumn survival inferred from wing age ratios: Wigeon juvenile
511 survival half that of adults at best? *Journal of Ornithology*, **154**, 351-358.

512 Haftorn, S. & Reinertsen, R.E. (1985) The effect of temperature and clutch size on the energetic cost
513 of incubation in a free-living blue tit (*Parus caeruleus*). *The Auk*, **102**, 470-478.

514 Hannon, S.J., Gruys, R.C. & Schieck, J.O. (2003) Differential seasonal mortality of the sexes in willow
515 ptarmigan *Lagopus lagopus* in northern British Columbia, Canada. *Wildlife Biology*, **9**, 317-
516 327.

517 Heisey, D.M. & Patterson, B.R. (2006) A review of methods to estimate cause-specific mortality in
518 presence of competing risks. *Journal of Wildlife Management*, **70**, 1544-1555.

519 Henriksen, S. & Hilmo, O. (2015) Norwegian red list of species 2015. (eds S. Henriksen & O. Hilmo).
520 Norwegian Biodiversity Information Centre, Norway.

521 Kaplan, E.L. & Meier, P. (1958) Nonparametric estimation from incomplete observations. *Journal of*
522 *the American statistical association*, **53**, 457-481.

523 Lande, R., Sæther, B.-E. & Engen, S. (1997) Threshold harvesting for sustainability of fluctuating
524 resources. *Ecology*, **78**, 1341-1350.

525 Martin, K. (1984) Reproductive defence priorities of male willow ptarmigan (*Lagopus lagopus*):
526 enhancing mate survival or extending paternity options? *Behavioral Ecology and*
527 *Sociobiology*, **16**, 57-63.

528 Martin, K., Hannon, S. & Rockwell, R. (1989) Clutch size variation and patterns of attrition in fecundity
529 of Willow Ptarmigan. *Ecology*, **70**, 1788-1799.

530 Martin, K. & Horn, A.G. (1993) Clutch defense by male and female willow ptarmigan *Lagopus*
531 *lagopus*. *Ornis Scandinavica*, 261-266.

532 Munkebye, E., Pedersen, H.C., Steen, J.B. & Brøseth, H. (2003) Predation of eggs and incubating
533 females in willow ptarmigan *Lagopus l. lagopus*. *Fauna norvegica*, **23**, 1-8.

534 Murray, D.L. (2006) On improving telemetry-based survival estimation. *Journal of Wildlife*
535 *Management*, **70**, 1530-1543.

536 Myrberget, S. (1975) Aldersbestemmelse av ryper. *Naturen*, **3**, 99-103.

537 Nilsen, E.B., Gaillard, J.M., Andersen, R., Odden, J., Delorme, D., Van Laere, G. & Linnell, J.D. (2009) A
538 slow life in hell or a fast life in heaven: demographic analyses of contrasting roe deer
539 populations. *Journal of Animal Ecology*, **78**, 585-594.

540 Nilsen, E.B., Moa, P.F., Brøseth, H., Pedersen, H.C. & Hagen, B.R. (2020) Survival and Migration of
541 Rock Ptarmigan in Central Scandinavia. *Frontiers in Ecology and Evolution*, **8:34**.

542 Nilsson, J.-Å. & Råberg, L. (2001) The resting metabolic cost of egg laying and nestling feeding in great
543 tits. *Oecologia*, **128**, 187-192.

544 Nyström, J., Dalén, L., Hellström, P., Ekenstedt, J., Angleby, H. & Angerbjörn, A. (2006a) Effect of local
545 prey availability on gyrfalcon diet: DNA analysis on ptarmigan remains at nest sites. *Journal of*
546 *Zoology*, **269**, 57-64.

547 Nyström, J., Ekenstedt, J., Angerbjörn, A., Thulin, L., Hellström, P. & Dalén, L. (2006b) Golden Eagles
548 on the Swedish mountain tundra-diet and breeding success in relation to prey fluctuations.
549 *Ornis Fennica*, **83**, 145-152.

550 Pedersen, H.C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R., Svendsen, W. & Yoccoz, N. (2004) Weak
551 compensation of harvest despite strong density-dependent growth in willow ptarmigan.
552 *Proceedings of the Royal Society of London. Series B: Biological Sciences*, **271**, 381-385.

553 Pedersen, H.C., Steen, J.B. & Andersen, R. (1983) Social organization and territorial behaviour in a
554 willow ptarmigan population. *Ornis Scandinavica*, **14**, 263-272.

555 Pollock, K.H., Winterstein, S.R., Bunck, C.M. & Curtis, P.D. (1989) Survival analysis in telemetry
556 studies: the staggered entry design. *Journal of Wildlife Management*, **53**, 7-15.

557 R Core Team (2019) R: A language and environment for statistical computing. R Foundation for
558 Statistical Computing, Vienna, Austria.

559 Rolland, V., Hostetler, J.A., Hines, T.C., Percival, H.F. & Oli, M.K. (2010) Impact of harvest on survival
560 of a heavily hunted game bird population. *Wildlife Research*, **37**, 392-400.

561 Rørvik, K.-A., Pedersen, H.C. & Steen, J.B. (1998) Dispersal in willow ptarmigan *Lagopus lagopus* -
562 who is dispersing and why? *Wildlife Biology*, **4**, 91-96.

563 Sandercock, B.K., Martin, K. & Hannon, S.J. (2005) Life history strategies in extreme environments:
564 comparative demography of arctic and alpine ptarmigan. *Ecology*, **86**, 2176-2186.

565 Sandercock, B.K., Nilsen, E.B., Brøseth, H. & Pedersen, H.C. (2011) Is hunting mortality additive or
566 compensatory to natural mortality? Effects of experimental harvest on the survival and
567 cause-specific mortality of willow ptarmigan. *Journal of Animal Ecology*, **80**, 244-258.

- 568 Shackell, N.L., Shelton, P.A., Hoenig, J.M. & Carscadden, J.E. (1994) Age- and sex-specific survival of
 569 northern Grand Bank capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic*
 570 *Sciences*, **51**, 642-649.
- 571 Smith, A. & Willebrand, T. (1999) Mortality causes and survival rates of hunted and unhunted willow
 572 grouse. *Journal of Wildlife Management*, **63**, 722-730.
- 573 Stearns, S.C. (1983) The influence of size and phylogeny on patterns of covariation among life-history
 574 traits in the mammals. *Oikos*, **41**, 173-187.
- 575 Storch, I. (2007) *Grouse: Status Survey and Conservation Action Plan 2006-2010*. Gland, Switzerland:
 576 IUCN and Fordingbridge, UK: World Pheasant Association.
- 577 Sæther, B.-E. & Bakke, Ø. (2000) Avian life history variation and contribution of demographic traits to
 578 the population growth rate. *Ecology*, **81**, 642-653.
- 579 Sæther, B.-E., Coulson, T., Grøtan, V., Engen, S., Altwegg, R., Armitage, K.B., Barbraud, C., Becker,
 580 P.H., Blumstein, D.T. & Dobson, F.S. (2013) How life history influences population dynamics in
 581 fluctuating environments. *The American Naturalist*, **182**, 743-759.
- 582 Sæther, B.-E., Ringsby, T.H., Bakke, Ø. & Solberg, E.J. (1999) Spatial and temporal variation in
 583 demography of a house sparrow metapopulation. *Journal of Animal Ecology*, **68**, 628-637.
- 584 Terhune, T.M., Sisson, D.C., Grand, J.B. & Stribling, H.L. (2007) Factors influencing survival of
 585 radiotagged and banded northern bobwhites in Georgia. *The Journal of Wildlife*
 586 *Management*, **71**, 1288-1297.
- 587 Therneau, T. (2015) A Package for Survival Analysis in S. version 2.38.
- 588 Thirgood, S.J., Redpath, S.M., Hudson, P.J., Hurley, M.M. & Aebischer, N.J. (1995) Effects of necklace
 589 radio transmitters on survival and breeding success of red grouse *Lagopus lagopus scoticus*.
 590 *Wildlife Biology*, **1**, 121-126.
- 591 Wickham, H. (2016) *ggplot2: Elegant Graphics for Data Analysis*. Springer-Verlag, New York.
- 592 Wiebe, K.L. & Martin, K. (1998) Age-specific patterns of reproduction in White-tailed and Willow
 593 Ptarmigan *Lagopus leucurus* and *L. lagopus*. *Ibis*, **140**, 14-24.
- 594 Willebrand, T., Hörnell-Willebrand, M. & Asmyhr, L. (2011) Willow grouse bag size is more sensitive
 595 to variation in hunter effort than to variation in willow grouse density. *Oikos*, **120**, 1667-
 596 1673.
- 597 Winder, V.L., Herse, M.R., Hunt, L.M., Gregory, A.J., McNew, L.B. & Sandercock, B.K. (2016) Patterns
 598 of nest attendance by female Greater Prairie-Chickens (*Tympanuchus cupido*) in northcentral
 599 Kansas. *Journal of Ornithology*, **157**, 733-745.
- 600 Winder, V.L., McNew, L.B., Gregory, A.J., Hunt, L.M., Wisely, S.M. & Sandercock, B.K. (2014) Effects of
 601 wind energy development on survival of female greater prairie-chickens. *Journal of Applied*
 602 *Ecology*, **51**, 395-405.

603

604

605

606 **Table 1.** Number of radio tagged birds and mortalities for each calendar year of the study.
 607 Also shown is the total number of birds used in the analysis and the number of these that died
 608 or survived until the end of the study.

| Year | 2015 | 2016 | 2017 | 2018 | 2019 | Total | Total in analysis | Prop. Mort. | Prop. Surv. |
|---------------------|------|------|------|------|------|-------|-------------------|-------------|-------------|
| Tagged birds | 32 | 38 | 40 | 38 | 40 | 188 | 182 | (124 / 182) | (58 / 182) |
| Mortalities | 19 | 21 | 34 | 30 | 20 | 124 | 124 | 0.68 | 0.32 |

609
 610
 611
 612
 613
 614
 615
 616
 617
 618
 619
 620
 621
 622
 623
 624
 625
 626
 627
 628
 629
 630
 631
 632
 633
 634
 635
 636
 637

638 **Figure captions**

639 **Figure 1.** Study area (outlined box) showing all marking locations (red triangles) and
640 telemetry positions (blue dots) of the marked birds. The northern cluster of red triangles
641 represent the Lifjellet location and the southern cluster Gusvatnet.

642

643 **Figure 2.** (a) Survival of willow ptarmigan 1 August – 31 July (vertical lines represents
644 censoring events). (b) Annual survival for each sex and (c) annual survival for complete
645 willow ptarmigan years.

646

647 **Figure 3.** Seasonal survival in (a) autumn for males and females, (b) spring for juvenile and
648 adults and (c) summer for males and females. Vertical lines represent censoring events. Note
649 that the probabilities on the y-axis ranges from 0.5 to 1.

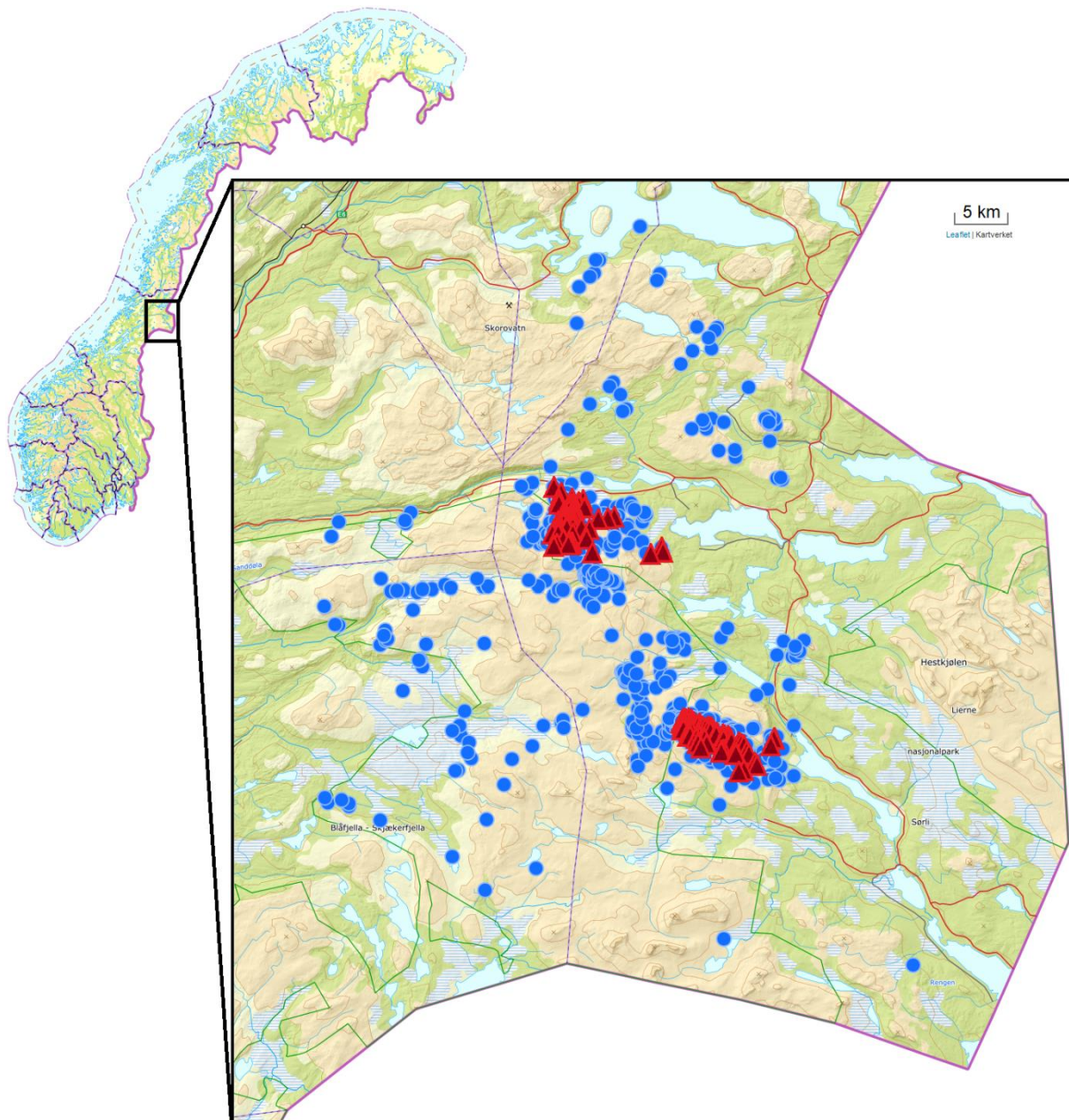
650

651 **Figure 4.** (a) Annual mortality probability due to natural causes and harvest. (b) Autumn
652 mortality probability due to natural causes and harvest. Note that the range of probabilities on
653 the y-axis goes from 0 to 0.40 for (a) and (b). (c) Smoothed instantaneous hazard function
654 showing daily hazard risk for total, harvest and natural mortality.

655

656 **Figure 5.** Annual survival estimates for this study (Lierne 2015-2019, harvested area, in
657 orange) in comparison to what was found in Sandercock *et al.* (2011; Meråker-Selbu in
658 central Norway, non-harvested area, 15% and 30% harvest rate) and Smith and Willebrand
659 (1999; central Sweden harvested area and central Sweden non-harvested area).

660

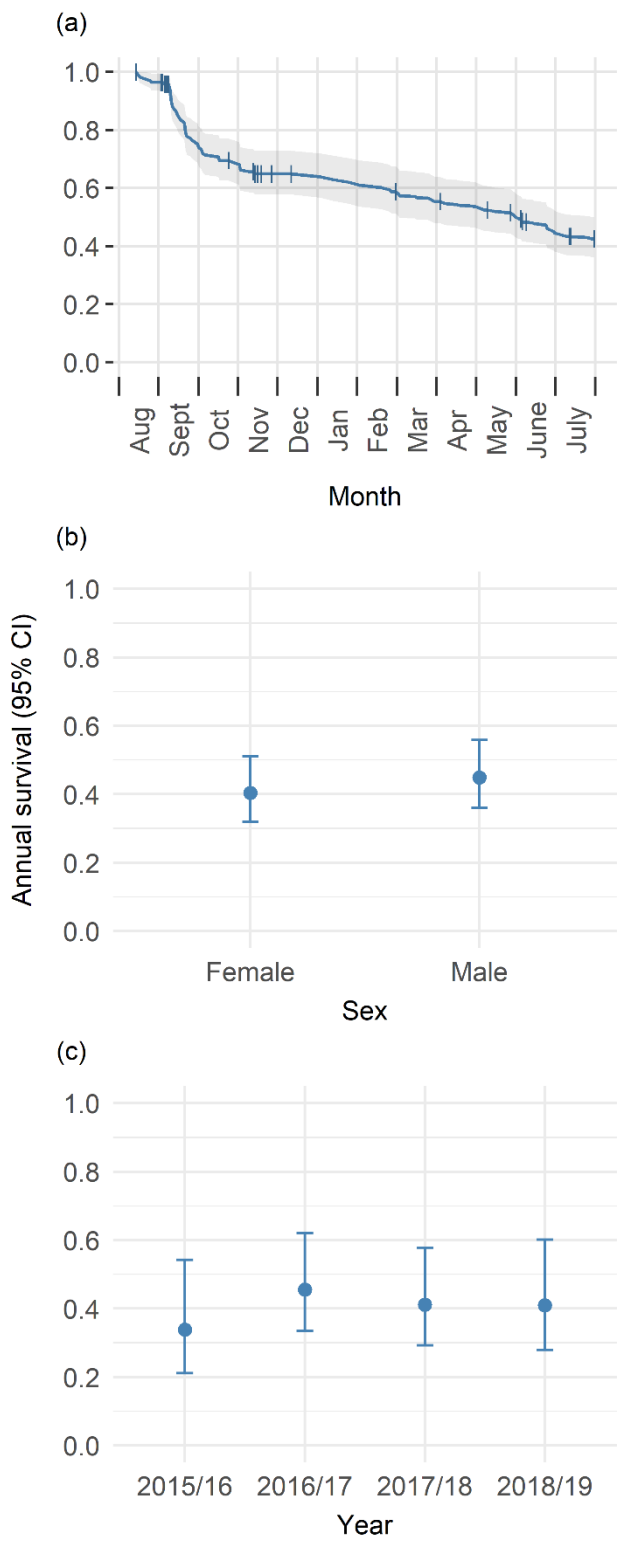


662

663 **Figure 1**

664

665



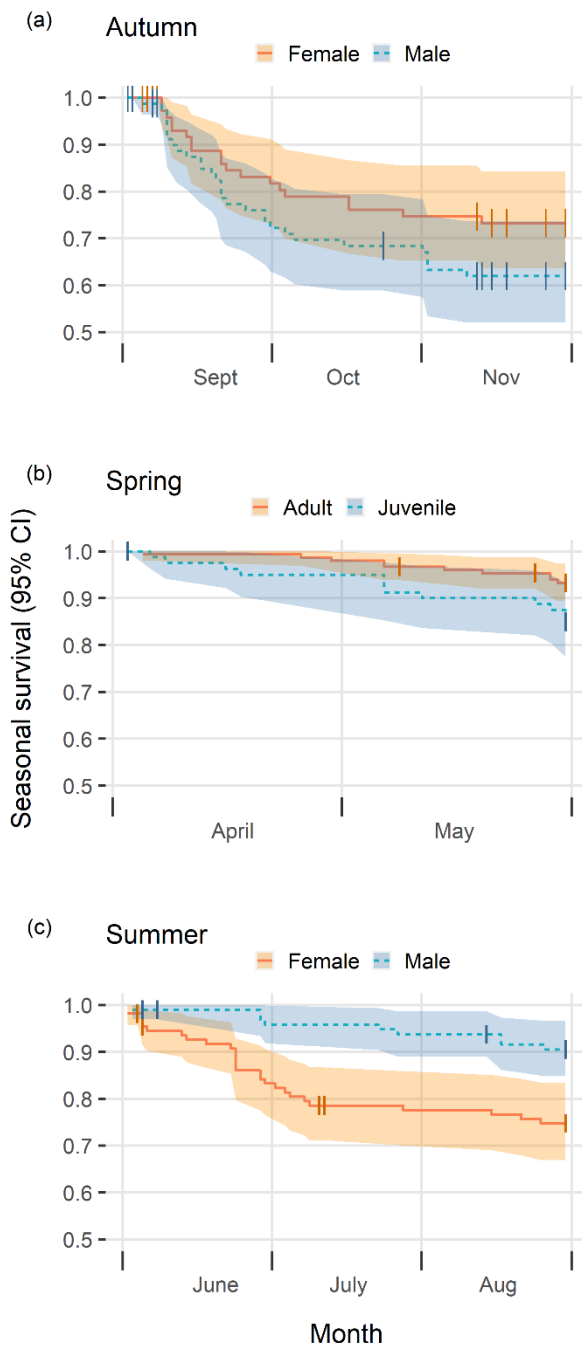
666

667

668 **Figure 2**

669

670



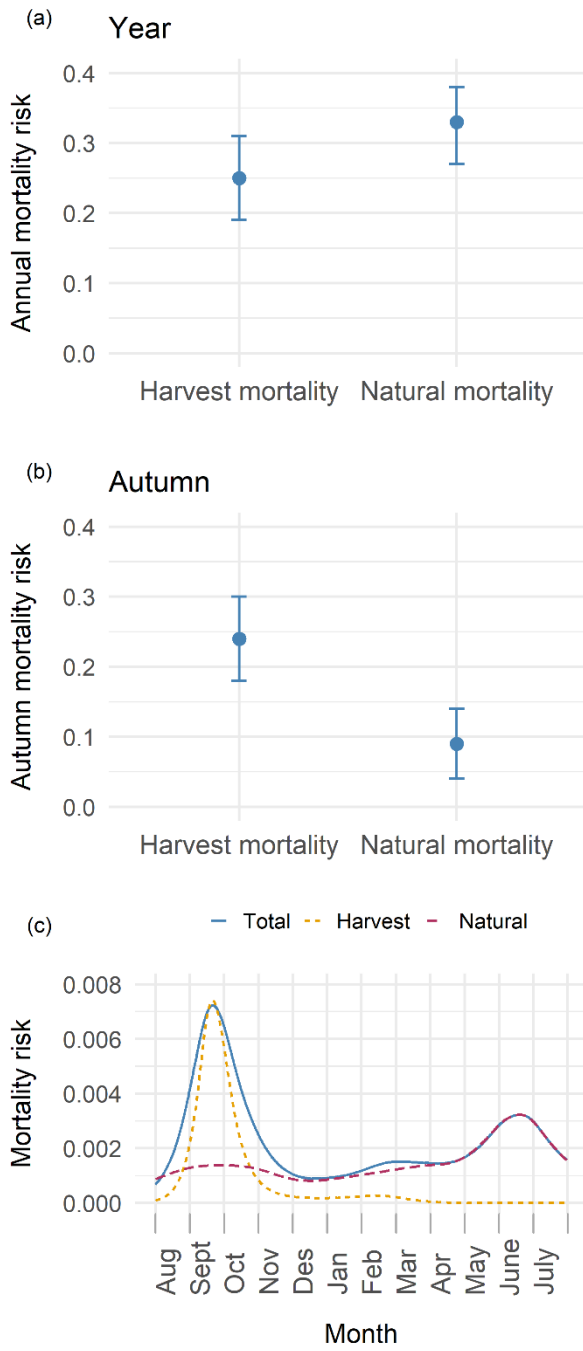
671

672

673 **Figure 3**

674

675



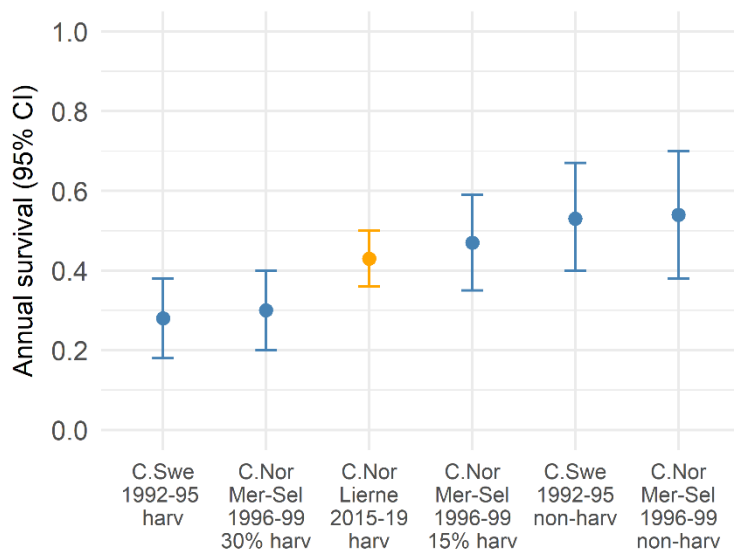
676

677

678 **Figure 4**

679

680



681

682

683 **Figure 5**