

1 ***Survival and migration of rock ptarmigan in central Scandinavia***

2 **Erlend B. Nilsen^{1,#}, Pål F. Moa^{2,#}, Henrik Brøseth¹, Hans Chr. Pedersen¹, Bjørn R. Hagen²**

3
4 1: Norwegian Institute for Nature Research, NINA, Box 5685 Torgard, NO-7485, Trondheim,
5 Norway

6 2: Nord University, Faculty of Biosciences and Aquaculture, Steinkjer, Norway

7 # Both as shared first authors

8
9 **Correspondence:**

10 Erlend B. Nilsen

11 erlend.nilsen@nina.no

12
13 **Key words:** Alpine wildlife; population ecology; hunting mortality, Tetraonids; Survival

14
15 **Abstract**

16 In a world undergoing massive declines in the distribution and abundance of many wildlife
17 species, documenting basic ecological characteristics is often needed to be able to understand
18 and potentially mitigate current and future pressures. Species living in alpine areas might be
19 particularly vulnerable to climate change, in part because they are less likely to be able to
20 migrate to new suitable areas. Here we report from a two year case study of rock ptarmigan
21 (*Lagopus muta*) in central Scandinavia. Ptarmigan were captured in winter (n=84), and fitted
22 with radio collars. We estimated the natural survival from mid-winter to late summer to be
23 0.55 (SE: 0.07), with no distinct differences between juveniles and adults, sex, or between the
24 two years. Natural survival through late winter (February – April) was estimated at 0.77 (SE:
25 0.05), survival through breeding season May-July at 0.65 (SE: 0.08), and harvest mortality
26 through the February winter harvest at 9% (SE: 3%). Moreover, we documented large scale
27 movement from the wintering grounds before the breeding season in the spring. The longest
28 recorded movement was 79.5 km, and the mean distance from the capture site for birds still
29 in the sample in May-July was 20.3 (SD: 18) km. We discuss the implications of the results in
30 terms of ongoing climate change.

31
32
33 **Running title:** Rock ptarmigan demography in Scandinavia

34 **1. Introduction**

35 Species inhabiting alpine or polar habitats are expected to be particularly affected by ongoing
36 climate change (Post et al., 2009; Revertmann et al., 2012). This is partly because these areas
37 are likely to become much warmer in the future, but also because species inhabiting such
38 areas have less possibilities to find new locations to thrive (Sirami et al., 2017). Among the few
39 resident birds in these habitats, the rock ptarmigan (*Lagopus muta*) has a wide, circumpolar
40 distribution across the northern tundra and high-mountain regions (Storch, 2007). Rock
41 ptarmigan as a species are expected to be strongly affected by climate change (Booms et al.,
42 2012; Revertmann et al., 2012; Hansen et al., 2013), and are therefore a suitable model species
43 for examining climate change effects on alpine wildlife populations. Globally rock ptarmigan
44 is at present considered least concern in the international Red List of Species
45 (BirdLife_International, 2016), but locally there are concerns about declining populations. In
46 2015 the species was classified as near threatened (NT) in the Norwegian Red List of Species
47 (Henriksen and Hilmo, 2015).

48

49 Compared to other grouse species, the rock ptarmigan are among the least studied species in
50 terms of number of scientific publications (Moss et al., 2010). Rock ptarmigan ecology and
51 demography has earlier been studied in e.g. UK (e.g. Watson et al. 1998), North-America
52 (Wilson and Martin, 2008; 2010), Russia (e.g. Potapov and Potapov, 2012), Japan (e.g. Suzuki
53 et al., 2013), high-alpine areas in the Italian Alps, French Alps and Pyrenees (Scherini et al.,
54 2003; Novoa et al., 2008; Novoa et al., 2011), Iceland (e.g. Nielsen, 1999) and the archipelago
55 of Svalbard (e.g. Pedersen et al., 2012; Unander et al., 2016). However, from an important
56 part of their distribution across mainland Scandinavia, only aspects relating to population
57 genetics (e.g. Costanzi and Steifetten, 2019), habitat use (Pedersen et al., 2013) and
58 population dynamics based on harvest bag data (Kvasnes et al., 2010) has been studied.
59 Baseline demography and ecology, including spatial behavior, is largely unknown.

60

61 In this case study, we provide insight into some key aspects of rock ptarmigan demography
62 and ecology in a study area in central Scandinavia (**Figure 1**). The case study is based on 84
63 birds marked with VHF collars in 2012-2013, and followed until they were either recorded as
64 dead, or until we lost contact (i.e censored). Although our study is completely descriptive and
65 does not intend to test any specific hypothesis about rock ptarmigan ecology or demography,
66 there are two specific aspects that we focus on:

- 67 1) First, we use known fate models to estimate survival probabilities. We investigate to
68 which extent survival probability differs between years, age (juvenile vs adult) and sex
69 (females vs males). We estimate survival probabilities during a six month period from
70 February-July, as well as for late winter (settlement period) and in the breeding period.
71 We also report harvest mortality rates for the winter harvest season in February.
- 72 2) Second, we estimate movement rates away from the wintering grounds, using mean
73 displacement rates as our estimator of interest. The rationale for this was to identify
74 to which extent the birds captured at their wintering grounds were stationary or
75 moved to other areas in the breeding season.

76

77

78 **2. Materials and Methods**

79 **2.1. Study area**

80 The current study was conducted in central Norway, in the municipality Lierne (central
81 location for our core study area: 64°25'N, 13°59'E), partly within the Lierne National Park
82 (**Figure 1**). The study area cover both the northern boreal, low- and mid-alpine ecoregions.
83 Poor vegetation types dominate the area, but there are also features of richer types such as
84 intermediate marshes. The lower parts is dominated by willow (*Salix* spp.) and scattered
85 forests of mountain birch (*Betula pubescens*), the mid areas of sedges, grasses, patches of
86 dwarf birch (*B. nana*) and snowbed communities, while the highest parts lack continuous
87 vegetation cover. Yearly precipitation normal is equivalent to 675 millimeter per year, while
88 the temperature normal is -10°C for January and 12°C for July. Snowcover at the study area
89 is 1–3 m deep during winter and persists from early October to late May. The main predators
90 on juvenile and adult rock ptarmigan in the study area were gyrfalcon (*Falco rusticolus*) and
91 golden eagle (*Aquila chrysaetos*), with occasional observations of red foxes (*Vulpes vulpes*),
92 arctic foxes (*V. lagopus*) and wolverines (*Gulo gulo*). Potential additional predators on egg
93 and chicks includes raven (*Corvus corax*) and hooded crow (*C. cornix*).
94

95 **2.2. Field data collection**

96 Rock ptarmigan were captured at night in the winter of 2012-2013, with handheld spotlights
97 and long-handled dip nets from snowmobiles. Similar approach has been used in previous
98 studies on willow ptarmigan (*L. lagopus*) in Norway (Sandercock et al., 2011). At capture,
99 birds were aged as juveniles or adults and sexed, and morphometric measures (weight (g)
100 and wing length (mm)) were taken. We sexed and aged (juvenile: born the proceeding
101 summer, adults: all older birds) the birds based on plumage coloration, wing length, and
102 patterns of pigmentation of the outer primaries (Bergerud et al., 1963). In total, we captured
103 and radio collared 84 rock ptarmigan (n= 44 males, n=40 females, n=50 juveniles, n=34
104 adults) across the two seasons. Note that there was a marked difference in the proportion of
105 juveniles among captured birds in 2012 (78%) and 2013 (24%), corresponding well with a
106 large difference in breeding success in 2011 (high) and 2012 (low) respectively (E. B. Nilsen,
107 pers com based on line transect data on willow ptarmigan from the study area).
108

109 Each bird was marked with a uniquely numbered leg ring, and instrumented with a necklace
110 VHF-radio transmitter (Holohil, 12g) with a 24 months expected battery life. The collars had
111 mortality switches, so that we could detect when a bird was dead. Previous studies have
112 shown that necklace radios of this size have little to no effect on the demographic
113 parameters or movements of ptarmigan under natural conditions (see Sandercock et al.,
114 2011 and citations therein).
115

116 Radio collared birds were tracked from the ground or air at irregular intervals. When tracking
117 from ground (using ski or snowmobile during winter, and on foot during spring/summer), we
118 either conducted radio-triangulation at relatively close distances (from 50 m – to a few
119 hundred meters) to obtain precise positions, or obtained just one signal so we could
120 determine the state of the bird based on the mortality switch. When tracking from the air,
121 we used either a small winged aircraft or a small helicopter. Whenever we obtained a
122 mortality signal, we tried to locate the bird on the ground to determine the cause of death.
123 In addition, we were notified by small game hunters in the region when a marked bird was
124 shot (hunting is allowed from August/September-February in this part of Scandinavia).

125 Hunters cannot normally see the collars during a hunting situation, and there were no
126 particular restrictions for hunters regarding shooting marked birds. We believe that all or
127 most shot birds were reported, but do not have any independent data to back up this
128 statement.

129

130 At the onset of the study, we opted to follow the birds throughout their full annual cycle, as
131 has been done in previous studies on willow ptarmigan (Sandercock et al., 2011). However,
132 because of the high combined loss-rates (i.e. combination of censoring and mortality), and
133 the fact that the birds were spread across a huge area (**Figure 2**) during summer and
134 fall/early winter, we obtained relatively few locations in that period. We therefore here
135 restrict our analysis to the time between February 1st and July 31st each year. In the study
136 periods, we conducted 3 and 4 flights in the years 2012 and 2013, respectively. For each
137 individual, we had between zero and 16 relocations. Birds that were never relocated after
138 marking (n=2) were not included in the analysis.

139

140 All data used in this study is published and openly accessible through GBIF, located here:
141 <https://www.gbif.org/dataset/b848f1f3-3955-4725-8ad8-e711e4a9e0ac> (Nilsen et al., 2017). The
142 animal study was reviewed and approved by Norwegian Food Safety Authority (Application
143 ID 3960).

144

145 **2.3 Statistical analysis**

146 Based on the data described above, we examined the two aspects of rock ptarmigan ecology
147 and demography as outlined above. To examine survival during late winter, spring and
148 summer (February 1st – July 31st), we first determined the entry – and exit time for each bird
149 into the sample, at a monthly basis for each of the two years of the study period. Entry point
150 was determined as either i) the month of capture, or ii) February for birds that survived the
151 first year and entered into their second study year. Exit from the sample were again
152 determined on a monthly basis, and were coded as either mortality or censored. Censored
153 birds were either i) those that we lost contact with, or ii) those that survived until the end of
154 the annual study period. Because we did not have continuous follow-up times, we adjusted
155 our data to a monthly schedule. For birds of which mortality was recorded, exit was defined
156 to occur in the mid-point between the last live contact and the first mortality signal. For
157 birds that were censored because we lost contact, we censored the birds the first month
158 after the last detection. We used Kaplan-Meier models (Pollock et al., 1989; Murray, 2006)
159 to estimate survival probabilities, the non-parametric cumulative incidence function
160 (NPCIFE) to estimate cause-specific mortality (Heisey and Patterson, 2006), and cox-
161 proportional hazard models (Murray, 2006; Murray and Patterson, 2006) to test for
162 differences among years (2012 vs 2013), age (juveniles vs adults) and sex (males vs females).
163 We could not consider interactions between independent variables, because of relatively
164 low sample sizes. We used Akaike's Information Criterion (AIC) to guide the model selection
165 procedures (Burnham and Anderson, 2002). All analysis were conducted in program R
166 version 3.6.0 (R Development Core Team, 2019), and survival analysis were conducted using
167 add-on library survival (Therneau, 2010).

168

169 The R-code for performing the analysis reported here is available at Open Science
170 Framework through an add-on connection with GitHub (<https://osf.io/gcm3u/>).

171

172 3. Results

173 Out of 84 radio marked rock ptarmigans, 9 were shot by hunters in the study area, and 33
174 were recorded as dead due to other causes (mostly predation). The birds were marked in
175 February and March, and we estimated the harvest mortality during the four weeks of
176 February to be 0.09 (SE: 0.03).

177 Based on cox proportional hazard models, we did not find any signs that natural survival
178 differed between years, or between age- and sex categories (AIC for null model: 224.59; AIC
179 for model including year: 225.73; AIC for model including sex: 223.74; AIC for model
180 including age: 226.02). For all models, the proportional hazards assumption was met (year-
181 model: $\chi^2=0.5$, $p=0.48$; sex-model: $\chi^2=0.02$, $p=0.9$; age-model: $\chi^2=0.93$, $p=0.33$).
182 Based on the pooled sample, overall probability to survive from February 1st and through
183 July was estimated at 0.45 (SE: 0.07) (**Figure 2**), with natural survival (i.e. disregarding birds
184 that were shot by hunters during the harvest season) estimated at 0.55 (SE: 0.07). Survival
185 probability for late winter to start of the breeding season (February 1st - April 30th) was
186 estimated at 0.7 (SE: 0.05), with natural survival estimated at 0.77 (SE: 0.05). Survival
187 probability for the breeding season (May 1st -July 31st) was estimated at 0.65 (SE: 0.08).

188 Most of the birds captured and marked with radio collars left the area where they had been
189 captured before the breeding season started in the spring (**Figure 3**). Based on the maximum
190 displacement for birds still alive and in the sample ($n=36$), mean displacement distance was
191 estimated at 7.8 (SD: 12.2)km in April. In a pooled sample for May-July, the displacement for
192 birds still alive and in the sample ($n=25$) was estimated at 20.3 (SD: 18)km. We note that this
193 is probably an underestimation, because we are more likely to have lost contact with birds
194 that moved long distances. The maximum recorded movement from the capture site was
195 79.5 km. A total of 6 birds moved longer than 50 km, of which 4 were males and 2 were
196 females. For 16 birds, we detected movements longer than 25 km from the capture site,
197 including 7 males and 9 females.

198

199 4. Discussion

200 A main contribution of our study is to provide updated information about some central
201 aspect of rock ptarmigan biology within a central part of its distribution. Although our study
202 is purely exploratory in nature, we assessed some basic ecological aspects of a rock
203 ptarmigan population in Norway. We conclude that i) overwinter survival is relatively low
204 but with no marked differences between years, age classes or sexes, and ii) that there are
205 distinct movements between winter and summer areas, and that few birds remained
206 resident in the wintering area.

207 Survival is a key demographic rate, and variation in survival rates will influence both short-
208 and long term population growth rate (Caswell, 2001). In our study, overwinter (February –
209 July) natural survival was estimated at 55%. Assuming similar mortality risk for the remaining
210 part of the annual cycle (which might not be justified), annual survival can be extrapolated to
211 be around 30% (0.55×0.55). Compared to annual survival probabilities for rock ptarmigan in
212 Japan (estimated at 44-74% for birds of different ages: Suzuki et al. (2013)), France (61% and
213 70% in Haut Giffre and Canigou Massif, respectively: Novoa et al. (2011)) and Svalbard (40-
214 50% for males and females, respectively: Unander et al. (2016)) this is very low survival,
215 bearing in mind that we only estimated survival for a part of the year. At Island, rock

216 ptarmigan survival was shown to be highly variable, varying between 36-65% for adult birds
217 and constant at 19% for juveniles (Sturludottir et al., 2018). Because our study only lasted
218 two years, we are not able to estimate robustly any between year variation due to stochastic
219 environmental factors or variation in harvest pressure. Often, populations inhabiting alpine
220 areas (i.e. high altitudes) have higher survival and lower reproduction compared to
221 populations/species at lower elevations (Sandercock et al., 2005a; b). In our study area, this
222 model would predict that rock ptarmigan should have higher survival and lower reproductive
223 output than the willow ptarmigan inhabiting lower elevations. Our results from this short
224 term study is not consistent with a “high survival strategy” for rock ptarmigans in our study
225 area, but we can not conclude if this inconsistency arise due to the short term nature of the
226 field study, or represent a more general life history strategy for rock ptarmigan in
227 Scandinavian mountains.

228 Most birds that were captured during winter moved out of the wintering area before the
229 breeding season in the spring. Such movements have been discussed in the literature for
230 willow ptarmigan in central Scandinavia, with slightly different conclusions from different
231 study areas (Brøseth et al., 2005; Hornell-Willebrand et al., 2014). For rock ptarmigan we
232 have no comparable data from Scandinavia, but long distance movements have been
233 documented (Gardarsson and Bossert, 1997) with flights >300km. Examining the genetic
234 structure of rock ptarmigan in southern Scandinavia, Costanzi (Costanzi, 2019) reported low
235 genetic differentiation among rock ptarmigan in a large contiguous mountain habitat in
236 southern Norway, but with considerable differentiation between neighboring populations
237 separated by unsuitable rock ptarmigan habitat. Because climate change is likely to result in
238 reduced area occupancy and suitable habitat for rock ptarmigan in alpine areas (see e.g.
239 Revermann et al., 2012 for an example from the Swizz alps), a plausible prediction is that the
240 alpine islands that rock ptarmigan inhabit in the Scandinavian landscape will become both
241 smaller and more isolated in the future. Understanding their spatial behavior, including their
242 propensity to long scale dispersal, seasonal migration and the landscape effects on
243 movement behavior will be key when designing future conservation plans for rock ptarmigan
244 in Scandinavia.

245

246 **Acknowledgement**

247 We would like to thank the Norwegian Environment Agency for funding this study. Several
248 students helped us in the field, and Lierne Fjellstyre provided invaluable help with capture
249 and radio tracking of birds.

250

251 **Reference**

- 252 Caswell, H. (2001) *Matrix population Models: Construction, analysis and interpretation*, 2 edn.
253 Sinauer Associates Inc., Massachusetts.
- 254 Bergerud, A.T., Peters, S.S., and McGrath, R. (1963). Determining sex and age of willow ptarmigan in
255 Newfoundland. *Journal of Wildlife Management* 27, 700-711.
- 256 BirdLife_International (2016). *Lagopus muta (errata version published in 2017)*. *The IUCN Red List of*
257 *Threatened Species 2016* [Online]. [Accessed].
- 258 Booms, T.L., Lindgren, M., and Huettmann, F. (2012). "Linking Alaska's predicted Climate, Gyrfalcon,
259 and Ptarmigan distribution in space and time: A unique 200-year perspective," in *Gyrfalcons*
260 *and Ptarmigans in a Changing World, Volume 1.*, eds. R.T. Watson, T.J. Cade, M.R. Fuller, G.
261 Hunt & E. Potapov. (Boise, Idaho: The Peregrin Fund).
- 262 Brøseth, H., Tufto, J., Pedersen, H.C., Steen, H., and Kastdalen, L. (2005). Dispersal patterns in a
263 harvested willow ptarmigan population. *Journal of Applied Ecology* 42(3), 453-459. doi:
264 10.1111/j.1365-2664.2005.01031.x.
- 265 Burnham, K.P., and Anderson, D.R. (2002). *Model selection and multimodel inference: a practical*
266 *information-theoretic approach*. New York: Springer-Verlag.
- 267 Caswell, H. (2001). *Matrix population Models: Construction, analysis and interpretation*.
268 Massachusetts: Sinauer Associates Inc.
- 269 Costanzi, J.-M. (2019). *Habitat isolation in an alpine landscape: effects on population genetics and*
270 *adult sex ratios in the rock ptarmigan Lagopus muta*. PhD, University of South-Eastern
271 Norway.
- 272 Costanzi, J.-M., and Steifetten, Ø. (2019). Island biogeography theory explains the genetic diversity of
273 a fragmented rock ptarmigan (*Lagopus muta*) population. 9(7), 3837-3849. doi:
274 10.1002/ece3.5007.
- 275 Gardarsson, A., and Bossert, A. (1997). *Ptarmigan*. London, UK: Poyser.
- 276 Hansen, B.B., Grotan, V., Aanes, R., Saether, B.E., Stien, A., Fuglei, E., et al. (2013). Climate Events
277 Synchronize the Dynamics of a Resident Vertebrate Community in the High Arctic. *Science*
278 339(6117), 313-315. doi: 10.1126/science.1226766.
- 279 Heisey, D.M., and Patterson, B.R. (2006). A review of methods to estimate cause-specific mortality in
280 presence of competing risks. *Journal of Wildlife Management* 70(6), 1544-1555.
- 281 Henriksen, S., and Hilmo, O. (2015). "Norsk rødliste for arter 2015". (Artsdatabanken, Norge).
- 282 Hornell-Willebrand, M., Willebrand, T., and Smith, A.A. (2014). Seasonal Movements and Dispersal
283 Patterns: Implications for Recruitment and Management of Willow Ptarmigan (*Lagopus*
284 *lagopus*). *Journal of Wildlife Management* 78(2), 194-201. doi: 10.1002/jwmg.650.
- 285 Kvasnes, M.A.J., Storaas, T., Pedersen, H.C., Bjork, S., and Nilsen, E.B. (2010). Spatial dynamics of
286 Norwegian tetraonid populations. *Ecological Research* 25(2), 367-374. doi: 10.1007/s11284-
287 009-0665-7.
- 288 Moss, R., Storch, I., and Muller, M. (2010). Trends in grouse research. *Wildlife Biology* 16(1), 1-11.
289 doi: Doi 10.2981/09-055.
- 290 Murray, D.L. (2006). On improving telemetry-based survival estimation. *Journal of Wildlife*
291 *Management* 70(6), 1530-1543.
- 292 Murray, D.L., and Patterson, B.R. (2006). Wildlife survival estimation: Recent advances and future
293 directions. *Journal of Wildlife Management* 70(6), 1499-1503.
- 294 Nielsen, O.K. (1999). Gyrfalcon predation on ptarmigan: numerical and functional responses. *Journal*
295 *of Animal Ecology* 68(5), 1034-1050. doi: DOI 10.1046/j.1365-2656.1999.00351.x.
- 296 Nilsen, E.B., Pedersen, H.C., Brøseth, H., and Moa, P.F. (2017). " Rock ptarmigan (*Lagopus muta*) radio
297 telemetry in Lierne, Norway. v1.2." GBIF, <https://doi.org/10.15468/o4zcd3>.
- 298 Novoa, C., Besnard, A., Brenot, J.F., and Ellison, L.N. (2008). Effect of weather on the reproductive
299 rate of Rock Ptarmigan *Lagopus muta* in the eastern Pyrenees. *Ibis* 150(2), 270-278.
- 300 Novoa, C., Desmet, J.-F., Brenot, J.-F., Muffat-Joly, B., Arvin-Bérod, M.A., and Tran, B. (2011).
301 "Demographic traits of two alpine populations of rock ptarmigan," in *Ecology, conservation*

302 *and management of grouse*, eds. B.K. Sandercock, K. Martin & G. Segelbacher. University of
303 California Press), 267-280.

304 Pedersen, A.O., Bardsen, B.J., Yoccoz, N.G., Lecomte, N., and Fuglei, E. (2012). Monitoring Svalbard
305 rock ptarmigan: Distance sampling and occupancy modeling. *Journal of Wildlife Management*
306 76(2), 308-316. doi: 10.1002/jwmg.276.

307 Pedersen, Å., Blanchet, M.-A., Hörnell-Willebrand, M., Jepsen, J., Biuw, M., and Fuglei, E. (2013). Rock
308 Ptarmigan (*Lagopus muta*) breeding habitat use in northern Sweden. *Journal of Ornithology*,
309 1-15. doi: 10.1007/s10336-013-1001-0.

310 Pollock, K.H., Winterstein, S.R., Bunck, C.M., and Curtis, P.D. (1989). SURVIVAL ANALYSIS IN
311 TELEMETRY STUDIES - THE STAGGERED ENTRY DESIGN. *Journal of Wildlife Management*
312 53(1), 7-15.

313 Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., et al.
314 (2009). Ecological Dynamics Across the Arctic Associated with Recent Climate Change.
315 *Science* 325(5946), 1355-1358. doi: 10.1126/science.1173113.

316 Potapov, R., and Potapov, E. (2012). *Willow and Rock Ptarmigan monitoring in Russia: An historic*
317 *overview*. Peregrine Fund.

318 R Development Core Team (2019). R: A language and environment for statistical computing.

319 Revermann, R., Schmid, H., Zbinden, N., Spaar, R., and Schröder, B. (2012). Habitat at the mountain
320 tops: how long can Rock Ptarmigan (*Lagopus muta helvetica*) survive rapid climate change in
321 the Swiss Alps? A multi-scale approach. *Journal of Ornithology*. doi: 10.1007/s10336-012-
322 0819-1.

323 Sandercock, B.K., Martin, K., and Hannon, S.J. (2005a). Demographic consequences of age-structure
324 in extreme environments: population models for arctic and alpine ptarmigan. *Oecologia*
325 146(1), 13-24. doi: DOI 10.1007/s00442-005-0174-5.

326 Sandercock, B.K., Martin, K., and Hannon, S.J. (2005b). Life history strategies in extreme
327 environments: Comparative demography of Arctic and alpine Ptarmigan. *Ecology* 86(8),
328 2176-2186.

329 Sandercock, B.K., Nilsen, E.B., Broseth, H., and Pedersen, H.C. (2011). Is hunting mortality additive or
330 compensatory to natural mortality? Effects of experimental harvest on the survival and
331 cause-specific mortality of willow ptarmigan. *J Anim Ecol* 80(1), 244-258. doi: 10.1111/j.1365-
332 2656.2010.01769.x.

333 Scherini, G.C., Tosj, G., and Wauters, L.A. (2003). Social behaviour, reproductive biology and breeding
334 success of alpine Rock Ptarmigan *Lagopus mutus helveticus* in northern Italy. *Ardea* 91, 11-
335 23.

336 Sirami, C., Caplat, P., Popy, S., Clamens, A., Arlettaz, R., Jiguet, F., et al. (2017). Impacts of global
337 change on species distributions: obstacles and solutions to integrate climate and land use.
338 26(4), 385-394. doi: 10.1111/geb.12555.

339 Storch, I. (2007). *Grouse: Status Survey and Conservation Action Plan 2006-2010*. IUCN, Gland and
340 Cambridge, and the World Pheasant Association, Reading.

341 Sturludottir, E., Nielsen, O.K., and Stefansson, G. (2018). Evaluation of Ptarmigan Management with a
342 Population Reconstruction Model. *Journal of Wildlife Management* 82(5), 958-965. doi:
343 10.1002/jwmg.21458.

344 Suzuki, A., Kobayashi, A., Nakamura, H., and Takasu, F. (2013). Population viability analysis of the
345 Japanese rock ptarmigan *Lagopus muta japonica* in Japan. *Wildlife Biology* 19(4), 339-346.
346 doi: 10.2981/13-021.

347 Therneau, T. (2010). Survival: Survival analysis, including penalised likelihood.

348 Unander, S., Pedersen, A.O., Soininen, E.M., Descamps, S., Hornell-Willebrand, M., and Fuglei, E.
349 (2016). Populations on the limits: survival of Svalbard rock ptarmigan. *Journal of Ornithology*
350 157(2), 407-418. doi: 10.1007/s10336-015-1282-6.

351 Wilson, S., and Martin, K. (2008). Breeding habitat selection of sympatric White-tailed, Rock and
352 Willow Ptarmigan in the southern Yukon Territory, Canada. *Journal of Ornithology* 149(4),
353 629-637. doi: 10.1007/s10336-008-0308-8.

354 Wilson, S., and Martin, K. (2010). Variable reproductive effort for two ptarmigan species in response
355 to spring weather in a northern alpine ecosystem. *Journal of Avian Biology* 41(3), 319-326.
356 doi: 10.1111/j.1600-048X.2009.04945.x.

357

358

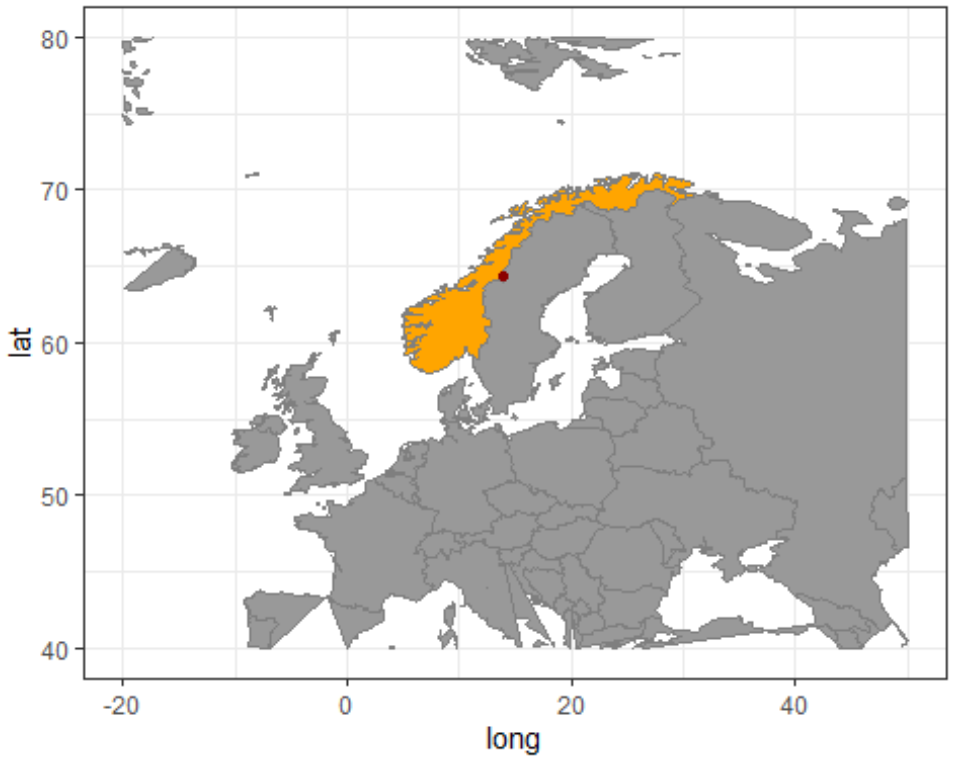
359 **Figure Legends**

360 *Figure 1:* Map of the study area, with Norway marked in orange and the study area marked
361 with a red circle.

362 *Figure 2:* Kaplan-Meyer survival curve for a sample of rock ptarmigans radio collared in
363 Central Norway in 2012-2013. The time on the x-axis is shifted so that week 1 represent the
364 first week in February each year, whereas week 31 is the last week in July. Lower table
365 depicts the number at risk throughout the study period.

366 *Figure 3:* Linear displacement from the capture site plotted against week since February 1st.
367 Each line represent the trajectory for one individual bird, and red crosses indicates death
368 events.

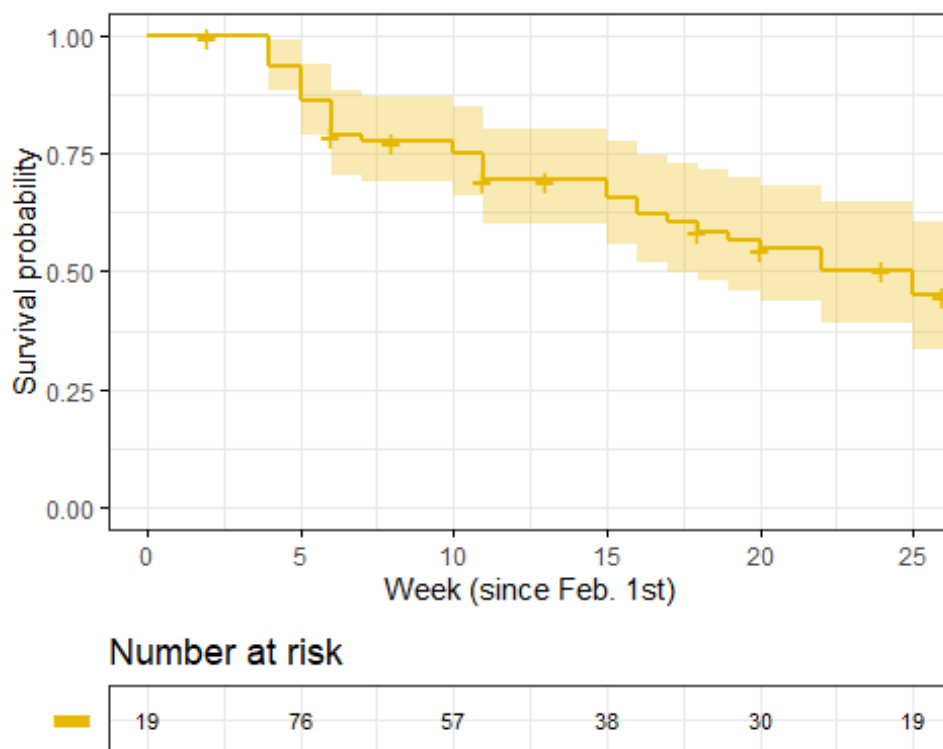
369



370

371 **FIGURE 1**

372

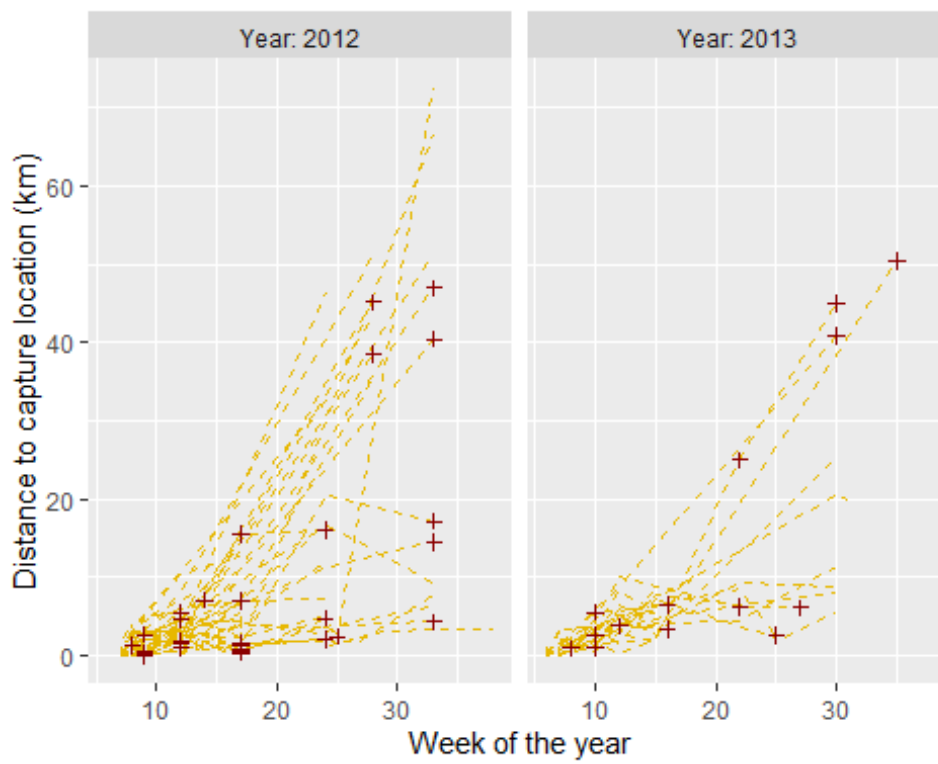


373

374 **FIGURE 2**

375

376



377

378 **FIGURE 3**

379

380