

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

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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; Reevermann 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). In general,
39 alpine populations should be expected to move upwards, whereas polar tundra species are
40 expected to conduct latitudinal movements (Lehikoinen et al., 2019). Among the few resident
41 birds in these habitats, the rock ptarmigan (*Lagopus muta*) has a wide, circumpolar
42 distribution across the northern tundra and high-mountain regions (Storch, 2007; Fuglei et al.,
43 2019). Rock ptarmigan as a species is expected to be strongly affected by climate change
44 (Booms et al., 2012; Reevermann et al., 2012; Hansen et al., 2013), and is therefore a suitable
45 model species for examining climate change effects on alpine wildlife populations. Globally
46 rock ptarmigan is considered as least concern (LC) in the international Red List of Species
47 (BirdLife_International, 2016), but locally there are concerns about declining populations. In
48 2015 the species was classified as near threatened (NT) in the Norwegian Red List of Species
49 (Henriksen and Hilmo, 2015).

50

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

64

65 In this case study, we provide insight into some key aspects of rock ptarmigan demography
66 and ecology in a study area in central Scandinavia (**Figure 1**), based on a small radio telemetry
67 project. Although our study is completely descriptive and does not intend to test any specific
68 hypothesis about rock ptarmigan ecology or demography, there are two specific aspects that
69 we focus on:

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

79

80

81 **2. Materials and Methods**

82 **2.1. Study area**

83 The current study was conducted in central Norway, in the municipality Lierne (central
84 location for our core study area: 64°25'N, 13°59'E), partly within the Lierne National Park
85 (**Figure 1**). The study area cover both the northern boreal, low- and mid-alpine ecoregions.
86 The lower parts is dominated by willow (*Salix* spp.) and scattered forests of mountain birch
87 (*Betula pubescens*), the mid areas sedges, grasses, patches of dwarf birch (*B. nana*) and
88 snowbed communities, while the highest parts lack continuous vegetation cover. Yearly
89 precipitation normal is equivalent to 675 millimeter per year, while the temperature normal
90 is –10°C for January and 12°C for July. Snowdepth at the study area is 1–3 m deep during
91 winter and snowcover persists from early October to late May. Based on field observations
92 and previous studies, important predator species on juvenile and adult rock ptarmigan in the
93 study area include gyrfalcon (*Falco rusticolus*) and golden eagle (*Aquila chrysaetos*), red
94 foxes (*Vulpes vulpes*), arctic foxes (*V. lagopus*) and to a limited extent wolverine (*Gulo gulo*).
95 Potential additional predators on eggs and chicks includes raven (*Corvus corax*) and hooded
96 crow (*C. cornix*).
97

98 **2.2. Field data collection**

99 Rock ptarmigan were captured at night in the winter in 2012 and 2013, with handheld
100 spotlights and long-handled dip nets from snowmobiles. Similar approach has been used in
101 previous studies on willow ptarmigan (*L. lagopus*) in Norway (Sandercock et al., 2011). At
102 capture, birds were aged as juveniles or adults and sexed, and morphometric measures
103 (weight (g) and wing length (mm)) were taken. We sexed and aged (juvenile: born the
104 proceeding summer, adult: all older birds) the birds based on plumage coloration, wing
105 length, and patterns of pigmentation of the three outermost primaries (Bergerud et al.,
106 1963). In total, we captured and radio collared 84 rock ptarmigan (n= 44 males, n=40
107 females, n=50 juveniles, n=34 adults) across the two seasons. Note that there was a marked
108 difference in the proportion of juveniles among captured birds in 2012 (78%) and 2013
109 (24%), corresponding well with a large difference in breeding success in 2011 (high) and
110 2012 (low) respectively (E. B. Nilsen, pers com, based on line transect data on willow
111 ptarmigan from the study area).
112

113 Each bird was marked with a uniquely numbered leg ring, and equipped with a necklace
114 VHF-radio transmitter (Holohil Systems Ltd, 10/15g) with a 24 months expected battery life.
115 The collars had mortality switches, so that we could detect when a bird was dead. Previous
116 studies have shown that necklace radios of this size have little to no effect on the
117 demographic parameters or movements of ptarmigan under natural conditions (see
118 Sandercock et al., 2011 and citations therein).
119

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

128 shot (hunting is allowed from August/September-February in this part of Scandinavia).
129 Hunters cannot normally see the collars during a hunting situation, and there were no
130 particular restrictions for hunters regarding shooting marked birds. We believe that all or
131 most shot birds were reported, but do not have any independent data to back up this
132 statement.

133

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

143

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

148

149 **2.3 Statistical analysis**

150 Based on the data described above, we examined the two aspects of rock ptarmigan ecology
151 and demography as outlined above. To examine survival during late winter, spring and
152 summer (February 1st – July 31st), we first determined the entry – and exit time for each bird
153 into the sample, at a weekly basis for each of the two years of the study period. Entry point
154 was determined as either i) the week of capture, or ii) first week of February for birds that
155 survived the first year and entered into their second study year. Exit from the sample were
156 again determined on a monthly basis, and were coded as either mortality or censored.
157 Censored birds were either i) those that we lost contact with, or ii) those that survived until
158 the end of the annual study period. Because we did not have continuous follow-up times, we
159 adjusted our data to a monthly schedule. For birds of which mortality was recorded, exit was
160 defined to occur in the mid-point between the last live contact and the first mortality signal.
161 For birds that were censored because we lost contact, we censored the birds the first month
162 after the last detection. We used Kaplan-Meier models (Pollock et al., 1989; Murray, 2006)
163 to estimate survival probabilities, the non-parametric cumulative incidence function
164 (NPCIFE) to estimate cause-specific mortality (Heisey and Patterson, 2006), and cox-
165 proportional hazard models (Murray, 2006; Murray and Patterson, 2006) to test for
166 differences among years (2012 vs 2013), age (juveniles vs adults) and sex (males vs females).
167 We could not consider interactions between independent variables, because of relatively
168 low sample sizes. We used Akaike's Information Criterion corrected for small sample sizes
169 (AICc) to guide the model selection procedures (Burnham and Anderson, 2002). All analysis
170 were conducted in program R version 3.6.0 (R Development Core Team, 2019), and survival
171 analysis were conducted using add-on library survival (Therneau, 2015).

172

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

175

176 **3. Results**

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

181 Based on cox proportional hazard models, we did not find any clear evidence that survival
182 differed between years, or between age- and sex categories (**Table 1**). Moreover, we did not
183 detect any effects of weight (at capture) on the the mortality risk, whether we controlled for
184 potential confounding effects of age- and sex or not (**Table 1**). For all models, the
185 proportional hazards assumption was met (year-model: $\chi^2=0.5$, $p=0.48$; sex-model:
186 $\chi^2=0.02$, $p=0.9$; age-model: $\chi^2=0.93$, $p=0.33$; weight-model: $\chi^2=0.94$, $p=0.33$;
187 weight-sex model: global $p=0.58$; weight-age model: global $p=0.58$). Based on the pooled
188 sample, overall probability to survive from February 1st and through July was estimated at
189 0.45 (SE: 0.07) (**Figure 2**), with natural survival (i.e. disregarding birds that were shot by
190 hunters during the harvest season) estimated at 0.55 (SE: 0.07). Survival probability for late
191 winter to start of the breeding season (February 1st - April 30th) was estimated at 0.7 (SE:
192 0.05), with natural survival estimated at 0.77 (SE: 0.05). Survival probability for the breeding
193 season (May 1st -July 31st) was estimated at 0.65 (SE: 0.08).

194 Most of the birds captured and marked with radio collars left the area where they had been
195 captured before the breeding season started in the spring (**Figure 3**). Based on the maximum
196 displacement for birds still alive and in the sample ($n=36$), mean displacement distance was
197 estimated at 7.8 (SD: 12.2)km in April. In a pooled sample for May-July, the displacement for
198 birds still alive and in the sample ($n=25$) was estimated at 20.3 (SD: 18)km. We note that this
199 is probably an underestimation, because we are more likely to have lost contact with birds
200 that moved long distances. The maximum recorded movement from the capture site was
201 79.5 km. A total of 6 birds moved longer than 50 km, of which 4 were males and 2 were
202 females. For 16 birds, we detected movements longer than 25 km from the capture site,
203 including 7 males and 9 females.

204

205 **4. Discussion**

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

213 Survival is a key demographic rate, and variation in survival rates will influence both short-
214 and long term population growth rate (Caswell, 2001). In our study, overwinter (February –
215 July) natural survival was estimated at 55%. Compared to annual survival probabilities for
216 rock ptarmigan in Japan (estimated at 44-74% for birds of different ages: Suzuki et al.
217 (2013)), France (61% and 70% in Haut Giffre and Canigou Massif, respectively: Novoa et al.

218 (2011)) and Svalbard (40-50% for males and females, respectively: Unander et al. (2016)) this
219 is very low survival, bearing in mind that we only estimated survival for a part of the year. At
220 Island, rock ptarmigan survival was shown to be highly variable, varying between 36-65% for
221 adult birds and constant at 19% for juveniles (Sturludottir et al., 2018). Because our study
222 only lasted two years, we are not able to estimate robustly any between year variation due
223 to stochastic environmental factors or variation in harvest pressure. In addition, recent
224 studies of rock ptarmigan throughout their range has shown that cyclic dynamics is a
225 common feature (Fuglei et al., 2019), suggesting that also demographic rates are likely to
226 fluctuate temporarily. Often, populations inhabiting alpine areas (i.e. high altitudes) have
227 higher survival and lower reproduction compared to populations/species at lower elevations
228 (Sandercock et al., 2005a; b). In our study area, this model would predict that rock
229 ptarmigan should have higher survival and lower reproductive output than the willow
230 ptarmigan inhabiting lower elevations. Our results from this short term study is not
231 consistent with a “high survival strategy” for rock ptarmigans in our study area, but we can
232 not conclude if this inconsistency arise due to the short term nature of the field study, or
233 represent a more general life history strategy for rock ptarmigan in Scandinavian mountains.
234 It is however important to note that part of the winter mortality reported in our case study
235 was caused by harvest, which is previously shown to be at least partially additive to other
236 mortality sources (Sandercock et al., 2011).

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

254

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259

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376

377 **Tables**

378 **Table 1** Results from cox-proportional hazard models used to test for differences in survival
 379 between sex- and age-classes, as well as between years. K is the number of parameters in
 380 the model. A total of n=84 birds were included in the analysis.

Mod.names	K	AICc	ΔAICc	AICcWt	Cum.Wt
<i>S(sex)</i>	1	223.79	0.00	0.30	0.30
<i>Intercept only</i>	0	224.59	0.80	0.20	0.51
<i>S(weight + sex)</i>	2	224.90	1.11	0.17	0.68
<i>S(year)</i>	1	225.78	1.99	0.11	0.79
<i>S(age)</i>	1	226.06	2.27	0.10	0.89
<i>S(weight)</i>	1	226.62	2.83	0.07	0.97
<i>S(weight + age)</i>	2	228.13	4.34	0.03	1.00

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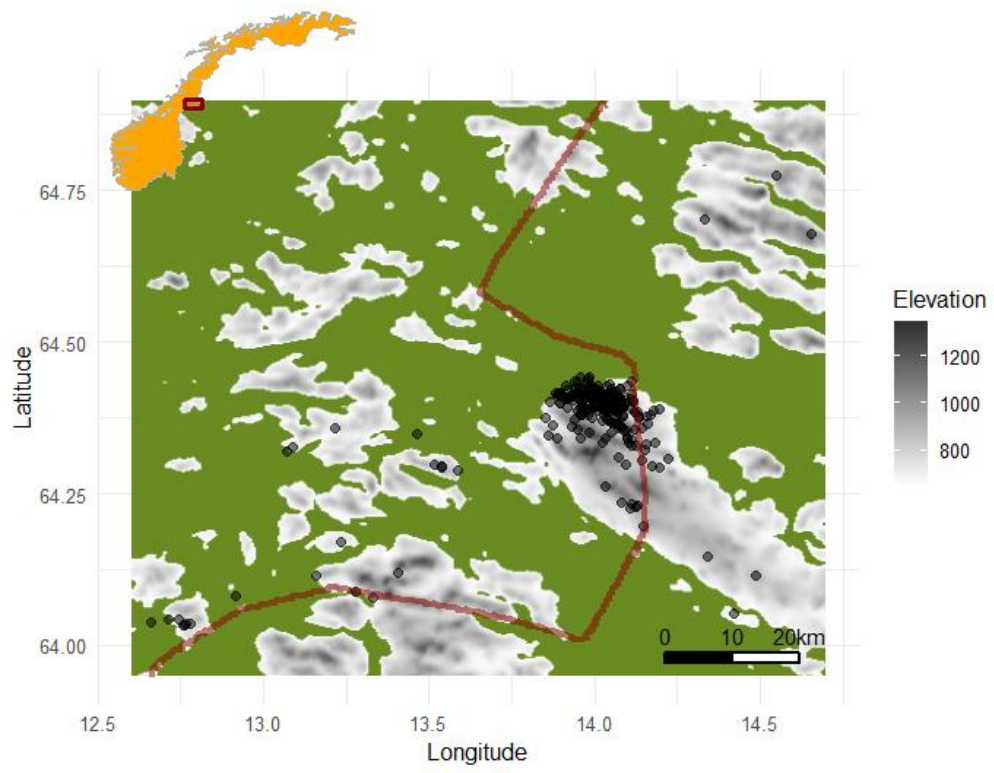
382 **Figure Legends**

383 **Figure 1:** Map of the study area. Inset map: Norway marked in orange, and study area
384 marked with a red rectangle. In the main map, areas below 650 m.a.s.l. is marked in green,
385 and areas above 650 (corresponding roughly to habitats used by rock ptarmigan) is grey
386 shaded by elevation. The border between Norway (west) and Sweden (east) is marked with a
387 red line. captures and relocations of rock ptarmigan is marked with black dots.

388 **Figure 2:** Kaplan-Meyer survival curve for a sample of rock ptarmigans radio collared in
389 Central Norway in 2012-2013. The time on the x-axis is shifted so that week 1 represent the
390 first week in February each year, whereas week 31 is the last week in July. Lower table
391 depicts the number at risk (i.e. time-specific sample sizes) throughout the study period.

392 **Figure 3:** Linear displacement from the capture site plotted against week. Each line represent
393 the trajectory for one individual bird (n=82 birds, for which we had at least two positions),
394 and red crosses indicates death events.

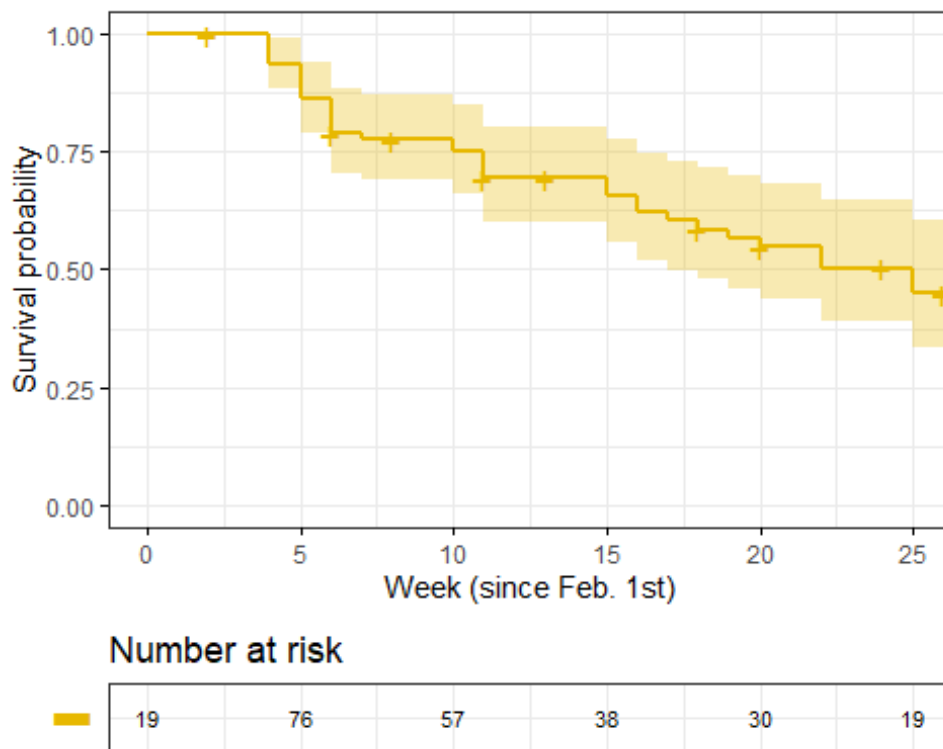
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397 **FIGURE 1**

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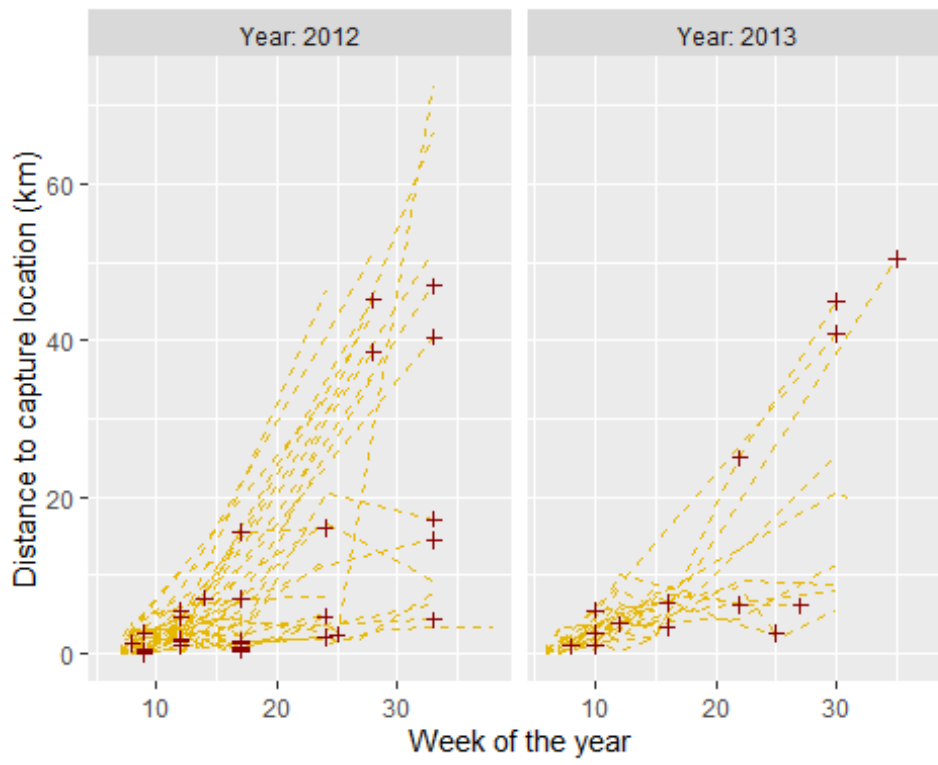


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400 **FIGURE 2**

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404 **FIGURE 3**

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