

1 **Drivers and Consequences of Partial Migration in an Alpine Bird**
2 **Species**

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17 Number of tables: 7

18 Number of figures: 5

19 Word count: 8111

20 **Abstract**

- 21 1. Partial migration, where a portion of the population migrates between winter and
22 summer (breeding) areas and the rest remain year-round resident, is a common
23 phenomenon across several taxonomic groups. Yet, although several hypotheses have
24 been put forward to explain why some individuals migrate while others stay resident –
25 as well as the fitness consequences of the different strategies – the drivers and
26 consequences of the decision to migrate or not are poorly understood.
- 27 2. We used data from radio-tagged female (n=73) willow ptarmigan *Lagopus lagopus* in
28 an alpine study area in Central Norway to test if i) the decision to migrate was dependent
29 on individual state variables (age and body size), ii) individuals repeated migratory
30 behaviour between seasons, and iii) the choice of migratory strategy was related to
31 nesting performance.
- 32 3. Partially supporting our prediction that migratory strategy depends on individual state,
33 we found that juvenile birds with small body sizes were more likely to migrate whereas
34 large juveniles stayed resident. For adult females, we found no relationship between
35 migratory strategy and body weight. We found strong evidence for high individual
36 repeatability of migratory strategy between seasons. Migratory strategy did not explain
37 variation in nesting performance among individuals, suggesting no direct influence of
38 the chosen strategy on nesting success.
- 39 4. Our results indicate that partial migration in willow ptarmigan is determined by juvenile
40 body weight, and that migratory behaviour becomes a part of the individual life history
41 as a fixed strategy. Nesting success was not affected by migratory strategy in our study
42 population, but future studies should assess other traits to further test potential fitness
43 consequences.

44 **Keywords:** *Lagopus lagopus*; eco-evolution; climate change; alpine wildlife; migration

45

46 1 | Introduction

47 Migration between distinct breeding and wintering areas is a widespread behavioural trait in
48 many species across a wide range of taxa, and is generally assumed to be an adaptation to
49 seasonal variation in environmental conditions (Reid et al. 2018). Well known examples are
50 long-distance annual migrations carried out by many bird species on the northern hemisphere
51 between breeding grounds at northern latitudes and wintering grounds at southern latitudes
52 (Dingle & Drake, 2007; Åkesson et al., 2017). Such seasonal migrations can increase individual
53 fitness (Alerstam et al., 2003; Somveille et al., 2015), as it allows the birds to utilize highly
54 productive habitats all year round. In contrast, other bird species do not perform long-distance
55 seasonal migrations, as they are adapted to remain resident at northern latitudes throughout the
56 entire year and survive the low-productive winters (Barta et al., 2006; Svorkmo-Lundberg et
57 al., 2006). However, even such ‘resident’ species may perform shorter migrations between
58 summer and winter areas in heterogeneous landscapes where availability and/or quality of
59 resources vary between seasons (Barraquand & Benhamou, 2008; Fedy et al., 2012). Some
60 overwintering populations are partially migratory (Chapman et al., 2011), implying that a
61 portion of the population migrates between summer and winter areas, whereas the rest stay
62 resident.

63 Partial migration has received considerable attention in the literature in the last decade
64 (Chapman et al., 2011; Pulido, 2011; Cobben & van Noordwijk, 2017; Reid et al., 2018; Berg
65 et al., 2019; Hegemann et al., 2019), and several hypotheses have been put forward to explain
66 both within-species and within-population variation in migratory behaviour. Lundberg (1997;
67 1988) suggested that the evolution of partial migration could be explained by two alternative
68 hypotheses; it could either evolve i) as a frequency dependent evolutionary stable strategy
69 (ESS) with two phenotypic tactics – or genetic dimorphism with two coexisting morphs (i.e.
70 migrants and residents) – with equal fitness pay-offs, or ii) as a conditional strategy where
71 individual state variables and interactions with environmental factors determine the decision to
72 migrate or not at the individual level. Moreover, three well established hypotheses have been
73 put forward to explain the drivers behind partial migration based on individual traits (i.e.
74 conditional strategies; Chapman et al., 2011). These traits can be individual fixed state
75 variables such as age and sex, or plastic state variables such as body condition (Lundberg,
76 1988). The body size hypotheses (Ketterson & Nolan, 1976; Hegemann et al., 2015) suggest
77 that large individuals are more likely to stay resident due to higher ability to endure seasonal

78 fluctuations in food abundance and temperature/weather conditions, whereas smaller
79 individuals and juveniles are more likely to migrate to search for better habitats with more
80 stable environmental conditions. In contrast, the dominance hypotheses (Gauthreaux, 1982)
81 suggest that larger individuals have a competitive advantage in environments with limited food
82 resources (Mysterud et al., 2011) or nesting sites (Gillis et al., 2008), which could trigger
83 migration in smaller individuals. The arrival time hypothesis (Ketterson & Nolan, 1976)
84 suggests that because of early occupancy of territories, and higher fitness of early arriving
85 birds, individuals arriving early at the breeding site have higher reproductive success. Hence,
86 birds that are staying in the territory year-round, are expected to have higher reproductive
87 success. The body size, dominance and arrival time hypotheses suggest that the decision to
88 migrate or stay in the area year-round is influenced by individual state, intraspecific
89 interactions or environmental conditions, and that the fitness reward from the two alternative
90 strategies can differ.

91 The fitness consequences of being resident vs. migratory in a partially migratory population
92 are poorly understood (Chapman et al., 2011; Berg et al., 2019). Nevertheless, differences
93 between resident and migratory individuals in fitness parameters such as survival and
94 reproduction have been suggested in theoretical and reported from empirical studies.
95 Theoretical studies suggest that a conditional strategy can result in unequal fitness between
96 strategies in partially migratory populations (Lundberg, 1987; Lundberg, 1988; Chapman et
97 al., 2011; Kokko, 2011). Most empirical studies also report fitness to differ between migratory
98 strategies (Buchan et al., 2019). For instance, Gillis et al. (2008) found that migratory American
99 dippers *Cinclus mexicanus* in a partially migratory population had lower reproductive success
100 but higher survival rates compared to resident individuals. The higher survival rates did
101 however not offset the lower reproductivity. Adriaensen & Dhondt (1990) found both higher
102 survival and reproductive success in resident European robins *Erithacus rubecula* and
103 hypothesized that the differences could be attributed to a conditional strategy. In contrast,
104 Hegemann et al. (2015) found no differences in reproductive success between migrants and
105 residents in a skylark *Alauda arvensis* population, despite higher average body mass in resident
106 birds. Both theoretical and empirical studies generally suggest migration to be a losing strategy
107 within partially migrating populations, and that the choice to migrate may be to make “the best
108 of a bad job” (Chapman et al. 2011).

109 Empirical studies on potential fitness consequences of partial migration have so far been
110 limited to passerines, although partial migration is a common phenomenon reported in multiple

111 bird families (Cade & Hoffman, 1993; Chapman et al., 2011; Holte et al., 2016; Grist et al.,
112 2017) The willow ptarmigan *Lagopus lagopus* is a tetraonid bird with a circumpolar
113 distribution (Fuglei et al., 2020), which lives year-round in heterogeneous alpine and arctic
114 ecosystems. Several studies have reported migratory behaviour in ptarmigan populations
115 (Irving et al., 1967; Hoffman & Braun, 1975; Gruys, 1993; Brøseth et al., 2005; Hörnell-
116 Willebrand et al., 2014; Nilsen et al., 2020a). From Sweden, Hörnell-Willebrand et al. (2014)
117 reported considerable individual variation in seasonal migration distances in willow ptarmigan,
118 with some individuals considered to be residents and others to be migrants. Empirical data from
119 other Scandinavian ptarmigan populations imply non-migratory behaviour (Pedersen et al.,
120 2003), suggesting that there are both inter- and intra-population differences in the propensity
121 to migrate between summer and winter areas in willow ptarmigan. Willow ptarmigan from
122 some populations often gather in distinct wintering areas (Weeden, 1964), which suggests these
123 populations to be breeding partially migratory (Chapman et al. 2011) due to some individuals
124 migrating to breeding areas during spring while others stay resident in the wintering area.
125 Currently, the drivers and consequences of partial migration in willow ptarmigan is poorly
126 understood.

127 Assuming that migrants are making the best of a bad job (Lundberg, 1987), and based on the
128 hypotheses about the evolution of partial migration in birds outlined above, we predict that:

- 129 1) Female willow ptarmigan with large body size are more likely to remain resident than
130 females with smaller body size, and juveniles are more likely to be migrants than adults.
- 131 2) Migration is not a fixed strategy in female willow ptarmigan.
- 132 3) Resident female willow ptarmigan have higher nesting success than migrants.

133 Following recommendations to preregister hypotheses and predictions when conducting
134 confirmatory (hypothesis testing) research (Nilsen et al., 2020b), the predictions were
135 preregistered at the Open Science Framework (OSF) prior to analysing data (Arnekleiv et al.,
136 2019).

137 **2 | Methods**

138 **2.1 | Study area**

139 The study was conducted in Lierne municipality in the northeastern part of Trøndelag county,
140 Norway, with minor extensions of the study area into neighbouring municipalities Snåsa,
141 Røyrvik and Grong due to long-distance movements from the main study area by some

142 individuals (FIGURE 1). Ptarmigan were captured at two sites (Guslia and Lifjellet), which were
143 located 20 km apart near Blåfjella-Skjækerfjella National Park (FIGURE 1). The study area was
144 situated in the low alpine and north boreal bioclimatic zones (Moen, 1999); the low alpine zone
145 was dominated by *Salix spp.*, dwarf birch *Betula nana* and *Ericaceae spp.* interspersed with
146 birch *Betula pubescens*, whereas the north boreal zone was dominated by Norway spruce *Picea*
147 *abies*, Scots pine *Pinus sylvestris*, birch *Betula spp.*, *Ericaceae* dwarf shrubs and bryophytes.

148

149 **2.2 | Field data collection**

150 Willow ptarmigan were captured during February and March during winter 2015 - 2019. The
151 birds were spotted from snowmobiles during night-time and paralyzed with powerful
152 headlamps and caught with long-handled dip-nets (Brøseth et al., 2005; Sandercock et al.,
153 2011; Hörnell-Willebrand et al., 2014). Body weight (measured with Pesola LightLine 1000g
154 spring scale – rounded to nearest 5 g) and wing length (measured with Axminster Workshop
155 Hook Rule 300mm – carpal to tip of longest primary of flattened wing, measured to nearest
156 mm) were measured prior to instrumenting the birds with collars. Captured birds were
157 identified in the field as either female or male based on saturation of red in the eyebrow, where
158 males have more pronounced red colour than females (Pedersen & Karlsen, 2007). One feather
159 was collected for DNA-analyses to confirm sex, and the genetic marker Z-054 (Dawson et al.,
160 2015) was used to determine the sex of the bird. Captured birds were also classified into
161 juvenile (captured during the first winter following the year of birth) and adult (2nd year +)
162 based on the amount of pigments in primary feathers 8 and 9, where juveniles got more black
163 pigments in 9 than in 8 (Bergerud et al., 1963). Each individual was marked with a steel ring
164 with a unique identification number. The majority of the birds were equipped with a VHF
165 radio-tag (Holohil - RI-2DM, 14,1 gram) on the 152 MHz frequency band. For all marked
166 birds, the combined weight of the leg ring and radio transmitter was < 3.5% of the body weight.
167 Radio-transmitters were programmed to send mortality-signals after recording no movement
168 for more than 12 hours. In March 2018, five ptarmigan were captured and marked with GPS-
169 transmitters (Milsar - GsmRadioTag-S9, 12 gram). The transmitters sent position data over the
170 GSM network every fourth hour.

171 Willow ptarmigan positions were for the most part collected once a month by manual tracking
172 on foot by triangulation, using handheld receivers (Followit – RX98) and antennas (Followit –
173 four-element Yagi-antenna); 2-5 bearings were used to determine best position and the distance

174 between each telemetry location varied from 0.3 – 1 kilometre. If only two bearings were
175 obtained, the cross-section was included when the terrain indicated that the observation was
176 trustworthy (e.g. when the cross-bearing pointed to a position in the end of a valley). Few
177 positions were collected in January and December, due to short daylength and challenging
178 weather conditions. To avoid loss of data due to long-distance movements, we conducted wider
179 aerial triangulation using a helicopter or fixed-winged airplane three times a year (May,
180 September and November) in the years 2016-2019. In 2015, we only conducted triangulation
181 from the air in October. Additional positions were either on-site direct observations from
182 captures or homing in on individuals.

183 Nesting success in spring was first assessed by homing in on radio-tagged females to check
184 whether they were nesting. Further, incubating females were flushed off the nest, eggs were
185 counted, and a wildlife camera (Reconyx HF2X Hyperfire 2 or Wingcam II TL) with
186 movement sensor was deployed 2-5 meters from each nest. The nests were revisited in July
187 after hatching to determine the fate of the nest by inspecting and counting the eggshells to see
188 whether and how many eggs were hatched or predated. In addition, pictures from the cameras
189 were examined.

190

191 **2.3 | Classification of migratory behaviour**

192 In order to examine migratory movements between seasons, we classified January – March as
193 winter and May – July as summer. All female ptarmigan with location data for at least one
194 winter and the consecutive summer season were included in the analysis (n=73) (TABLE 1). We
195 collected 1-2 positions per individual in the winter and 1-5 positions per individual during
196 summer. For each female in each season, migratory strategy was determined by whether or not
197 there was overlap between the winter home range and the consecutive summer home range
198 (FIGURE 2), and between the summer home range and the consecutive winter home range.

199 We calculated an average ‘baseline’ winter home range size from positions of three of the GPS-
200 tagged ptarmigan during the winter 2018, all marked in March 2018. Individual home range
201 sizes were calculated as 95% Minimum Convex Polygons (MCP) using the function *mcp* in R
202 package *adehabitatHR* (Calenge, 2006). The average 95% MCP for the three GPS-tagged
203 ptarmigan was 4.08 km². Before calculating the individual 95% MCPs, we removed inaccurate
204 positions (due to GPS error) using the following algorithm:

205 *Outlier removal of pos(t) if*

206 $eucl.distance(pos(t)-pos(t-1)) > 2 * eucl.distance(pos(t+1)-pos(t-1))$, where t represent the
207 sequential time of observation.

208 Positions from the GPS-tagged ptarmigan were only used to estimate the average 'baseline'
209 winter home range size, and these birds were not included in further analyses. For each of the
210 VHF-tagged females included in the analyses, we assumed a circular winter home range of
211 4.08 km^2 (radius = 1140 m) centred around the activity centre (determined by triangulation) of
212 each female in each winter season as a proxy for individual winter home range size and
213 location.

214 To estimate the size of the summer home ranges, we used data from VHF-tagged female
215 ptarmigan with ≥ 3 positions during the summer season (May - July). For each female, we drew
216 a polygon based on the positions, and calculated the area of the polygon. As a measure of a
217 'baseline' summer home range for further analysis, we used the median of all the individual
218 summer home range sizes (n=46). The baseline home range area was estimated to be 0.058
219 km^2 , corresponding to a circular home range with radius=136 m. This size is in good agreement
220 with previous studies of ptarmigan summer home range sizes (Eason & Hannon, 2003). For
221 each of the females included in the analyses, we assumed a circular summer home range of
222 0.058 km^2 (radius = 136 m) centred around the activity centre (determined by triangulation and
223 nest location) of each female in each summer season, as a proxy for individual summer home
224 range. When calculating the activity centre, the activity centre for nesting hens (n=68) was
225 shifted towards the nest location, by assigning equal weights to the position of the nest and the
226 sum of all other positions. All spatial computations were done using R (R Core Team, 2019).

227 Females with overlapping winter/summer or summer/winter home ranges were classified as
228 residents, whereas females with no overlap were classified as migrants. Based on the 'baseline'
229 home range sizes, ptarmigan moving further than 1276 m (radius winter home range + radius
230 summer home range) were consequently classified as migrants and females moving less than
231 1276 m were classified as residents.

232

233 **2.4 | Statistical analysis**

234 To test our predictions about state dependent migration strategy, we used a generalized linear
235 mixed effects model (*glmmTMB* function in R package *glmmTMB*; Brooks et al., 2017), with
236 migratory strategy as a binary response variable and body weight, age and body weight×age
237 interaction as fixed explanatory terms. Body weight is used as a measure of body size. For all

238 models, the body weight variable was standardized by extracting the mean and dividing by the
239 standard deviation. Bird identity was included as random effect to account for
240 pseudoreplication caused by repeated observations of individual birds.

241 To test whether the distance migrated was influenced by age and body weight, we fitted a linear
242 mixed model (*glmmTMB* function in R package *glmmTMB*) with log(migratory distance) as
243 response variable, weight, age and weight×age interaction as fixed explanatory terms. We used
244 an identity link function, assuming a Gaussian distribution of the residuals. Bird identity was
245 included as random effect to account for repeated observations of individual birds.

246 To assess if migration was a fixed strategy in female willow ptarmigan, we estimated the
247 repeatability R_M in a mixed effect model with log(movement distance) as response variable.
248 Repeatability R_M was estimated as the proportion of the total variance that was attributed to
249 within group (bird identity) variation (Sokal & Rohlf, 1995):

$$250 \quad R_M = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\epsilon}^2}$$

251 Agreement repeatability was estimated based on the intercept-only model (i.e. not accounting
252 for any fixed factors), whereas adjusted repeatability was estimated with age included as a fixed
253 effect term in the model (Nakagawa & Schielzeth, 2010). Repeatability was calculated using
254 the rptR package (Stoffel et al., 2017), and the 95% confidence interval for the repeatability
255 was estimated using parametric bootstrapping (n=1000). A likelihood ratio test (LRT) was used
256 to test whether the repeatability was above 0.

257 To test whether nesting success was influenced by migratory strategy, we 1) fitted a generalized
258 linear mixed effects model (*glmmTMB* function in R package *glmmTMB*) with number of laid
259 eggs as response variable and migratory strategy, age, weight and year as explanatory variables,
260 and with bird identity as random effect. Because clutch size data is often underdispersed
261 (Kendall & Wittmann 2010), we used a Conway-Maxwell Poisson distribution, that includes
262 an additional parameter (ϕ) that accounts for violations of the mean-variance assumption in a
263 standard Poisson distribution. Then, 2) we fitted a generalized linear mixed effects model
264 (*glmmTMB* function in R package *glmmTMB*) with nest fate as binary response variable (i.e.
265 hatched chicks vs. predated or abandoned nest) and migratory strategy, age, weight and year
266 as explanatory variables and with bird identity as random effect.

267 All model selection was based on the Akaike's information criterion corrected for small sample
268 sizes (AICc) (see e.g. Bolker et al., 2008). The AICc encourages parsimony by adding a term
269 to penalise more complex (larger number of parameters) models (e.g. Bolker et al., 2008).

270 **3 | Results**

271 **3.1 | Migration strategy in relation to age and body weight**

272 A total of 104 cases of seasonal movements were included in this study (TABLE 2), of which
273 87 were winter area to summer area movements and 17 were movements from the summer area
274 to the winter area. Overall, three times as many cases of migratory ($n = 78$, 75%) than of
275 resident ($n = 26$, 25%) behaviours were observed (TABLE 2). Mean and median movement
276 distance – for both juvenile and adult females – was substantially longer than the distance limit
277 for being classified as migrant (1276 m; TABLE 3). Overall, 67% of the seasonal movements
278 were shorter than 10 km, 25% were between 10 and 25 km, whereas only a few (8%) seasonal
279 movements were longer than 25 km (FIGURE 3A). In general, observed seasonal movement
280 distances were longer for birds marked at Guslia compared to birds marked at Lifjellet (FIGURE
281 3B). Mean and median differences in weight between juveniles and adults were small (TABLE
282 3). In addition, weight distribution in residents differed between juveniles and adults (FIGURE
283 3C; 3D).

284 When modelling migratory strategy as a function of age and body weight, we found strongest
285 support for the full model including the weight \times age interaction (TABLE 4, Appendix A). The
286 full model received substantially more support than the second-ranked model (TABLE 4). For
287 juveniles, the probability of migrating decreased with body weight (FIGURE 4), and thus the
288 likelihood of remaining resident increased with weight, whereas for adults there was no
289 apparent influence of body weight on migration strategy. When modelling distance moved as
290 a function of age and weight, we found only very weak support for a difference between
291 juveniles and adults (TABLE 5, Appendix A), and the intercept only-model had lower AICc
292 than the model with age as explanatory variable.

293

294 **3.2 | Repeatability of migratory behaviour**

295 Repeatability of migratory behaviour within individuals was very high (FIGURE 5), and
296 repeatability within individuals increased each consecutive season. Agreement repeatability
297 (based on the intercept only model) for movement distance revealed very high repeatability (R

298 = 0.75, 95% CI = 0.57-0.87). Adjusted repeatability (when including age as fixed effect in the
299 model) was equally high (R = 0.76, 95% CI = 0.60 – 0.88).

300

301 **3.3 | Nesting success**

302 Modelling clutch size as a function of migratory strategy, age and weight, model selection
303 based on AICc suggested the intercept-only model to be most supported (TABLE 6, Appendix
304 A). Also when modelling nest fate as a function of migratory strategy, age and weight, model
305 selection suggested the intercept model to be most supported (TABLE 7, Appendix A), and no
306 other models gain substantial support.

307

308 **4 | Discussion**

309 We found that the willow ptarmigan population in the study area was partially migratory, with
310 a majority (75%) of the females carrying out seasonal migrations. Similar behaviour has been
311 reported from several other species of Galliformes, including spruce grouse *Falciennis*
312 *canadensis* (Herzog & Keppie, 1980) and blue grouse *Dendragapus obscurus* (Cade &
313 Hoffman, 1993). Partly in line with our first prediction, we found that body weight affected the
314 decision to migrate or to remain resident. This effect was only found among juvenile birds,
315 where individuals with high body weight had a higher probability of remaining in the winter
316 area. Among adult females, body weight did not appear to be an important driver for the choice
317 of migratory strategy. In contrast with our second prediction, we found that migration was a
318 fixed strategy once established, and individuals for which data on more than one seasonal
319 movement was available, showed a high degree of repeatability in migratory behaviour.
320 Finally, we found no support for our third prediction, as resident female willow ptarmigans had
321 similar nesting success to migrants.

322

323 **4.1 | Migration strategy in relation to age and body weight**

324 One key finding of our study was that juvenile willow ptarmigan with small body sizes had a
325 higher probability of migrating. Such a pattern is in line with i) the body size hypothesis, ii)
326 the dominance hypothesis, or iii) arrival time hypothesis (Chapman et al., 2011). Below, we
327 discuss the likely importance of each hypothesis for our results.

328 Migratory strategy being affected by body weight in juvenile birds is partly in line with the
329 body size hypothesis (Ketterson & Nolan, 1976), predicting that larger individuals are more
330 likely to stay resident in their wintering areas compared to smaller individuals. Similar results
331 have been reported by Hegemann et al. (2015) for skylarks *Alauda arvensis*, where migration
332 strategy is dependent on body size and immune function but not on age and sex. However, the
333 body size hypothesis posits that large body sizes will be advantageous to endure thermal
334 variations and variation in food availability in harsh winter climates. In willow ptarmigan,
335 winter survival is generally high and stable (Israelsen et al. 2020), and therefore it seems
336 unlikely that the body size hypothesis alone could explain why body weight affects migratory
337 strategy in juvenile willow ptarmigan.

338 More likely, individuals with high body weight have a competitive advantage to smaller
339 individuals, forcing smaller individuals to migrate as posited by the dominance hypothesis
340 (Gauthreaux, 1982). For the dominance hypothesis to work there must be an intraspecific
341 competition for limited resources such as food or nest sites (Newton, 1998; Matthysen, 2005).
342 Nesting sites close to the wintering grounds might be a limited resource (Gillis et al., 2008),
343 and large dominant individuals might occupy the best breeding territories forcing juvenile
344 ptarmigans to migrate in the search of a suitable breeding territory. This may be the case in the
345 wintering areas where ptarmigan density is high during the winter months, and smaller (less
346 dominant) individuals must migrate to find a suitable breeding territory in spring. Although
347 two previous studies on dispersing juvenile willow ptarmigans in Scandinavia found no
348 density-dependence in dispersal rates (Brøseth et al., 2005; Hörnell-Willebrand et al., 2014),
349 intraspecific competition driven by positive density-dependent factors might still be an
350 important driver of partial migration in our study population.

351 Finally, although several studies have found support for the arrival time hypothesis as a driver
352 of partial migration (Ketterson & Nolan, 1976; Fudickar et al., 2013; Lundblad & Conway,
353 2020), lack of data on when the females arrive in their breeding territory prevent us from
354 further tests of this hypothesis. However, willow ptarmigans to some extent adjust the start of
355 the breeding season to the timing of spring (Myrberget, 1986), hence, earlier spring leads to an
356 early start to the breeding season. In years with mild winters and early spring, resident
357 ptarmigans may have an advantage in occupying high quality territories prior to migrating
358 individuals.

359 Migratory strategy being affected by body weight in juveniles but not in adults is only partly
360 in line with the body size hypothesis and the dominance hypothesis. However, if migration in
361 juveniles is affected by density-dependent factors, such as limitations in available territories,
362 the dominance hypothesis may explain partial migration in juvenile ptarmigan.

363

364 **4.2 | Repeatability of migration strategy**

365 Once established, migratory behaviour seems to be a relatively fixed trait in our study
366 population, and the repeatability in migration strategy within individuals was very high. Our
367 findings are in line with several studies on breeding partial migratory populations, which have
368 found migratory strategy to be fixed within individuals (Gillis et al., 2008; Chambon et al.,
369 2019). For example, in a breeding partial migratory population of American crow *Corvus*
370 *brachyrynchos* in USA, Townsend et al. (2018) found that migratory strategy was fixed within
371 individuals, the proportion of migrants was 78% and with high breeding-site fidelity.
372 Interestingly, bird populations that breed sympatrically but winter allopatrically seem to have
373 a higher degree of non-fixed migration behaviour (Hegemann et al., 2015; Dale et al., 2019;
374 Lundblad & Conway, 2020).

375 A potential benefit of a fixed migratory strategy may be less exposure to unfamiliar habitat,
376 and higher mortality rates that are associated by switching breeding sites between years (often
377 referred to as breeding dispersal) has been reported (Greenwood & Harvey, 1982; Daniels &
378 Walters, 2000; Bonte et al., 2011). Returning to the same breeding territory may also be
379 beneficial due to familiarity with food resources and shelter from predators, which in turn leads
380 to a more efficient use of resources (Greenwood & Harvey, 1982). This effect may be enhanced
381 in individuals remaining resident all year, and according to Buchan et al. (2019) most studies
382 on the consequence of partial migration reported higher mortality in migrants than in resident
383 individuals. The high repeatability in migratory strategy within willow ptarmigans may be
384 caused by resistance against moving to unfamiliar breeding wintering sites.

385

386 **4.3 | Nesting success in relation to migration strategy**

387 In contrast to our third prediction, we did not find any statistical support for higher nesting
388 success (measured as clutch size or nest fate) of resident birds. Our prediction was based on
389 the “best of a bad job” hypothesis (Lundberg, 1987), positing that migration is a losing strategy
390 that should lead to reduced fitness. Based on a multi-taxa assessment, Buchan et al. 2019

391 reported that although most studies reported fitness differences between resident and migratory
392 (73% of the studied populations reported higher fitness of residents, 22% reported higher
393 fitness of migrants, and 5% reported equal fitness), fitness differences were most often caused
394 by differences in survival. They argue the reason for this finding can be that anthropogenic
395 changes reduce the survival of migratory individuals. Our finding that migratory behaviour
396 seems to be relatively fixed once established appears to be in line with with the finding that
397 fitness does not differ between the strategies in our study population. However, our results
398 show some tendency that resident female first-time breeders have higher nesting success than
399 migratory first-time breeders (Table 7 & Appendix B), but low statistical power preclude
400 further assessment of this in our study. In addition, there may be differences in survival between
401 residents and migrants, in which needs to be further investigated.

402 For fitness to be equal between the two migratory strategies, theoretical studies suggest that
403 higher survival in migrants must offset the increased nesting success in residents (Lundberg,
404 1987; Chapman et al., 2011). Predator release (Hebblewhite & Merrill, 2007; Skov et al., 2010),
405 escape from harsh climatic conditions and better forage are pointed at as important factors
406 enhancing survival in migrants. Our results show a high proportion of the willow ptarmigan
407 population to be migrants with little variation between years. If migratory strategy is
408 genetically determined, the fitness balancing between strategies may be frequency-dependent
409 where the fitness pay-off by one genotype increases or decreases with the genotype's frequency
410 in the population (Lundberg, 1987; Heino et al., 1998). Negative frequency-dependent
411 selection rewards the strategy with lowest frequency in the population i.e. selection is density-
412 dependent. The population may reach an equilibrium in an evolutionary stable state between
413 migrants and residents where both strategies (genetic morphs) yield the same fitness. The
414 frequencies of migrants and residents may stabilize at any ratio, and the small between-year
415 changes in the migrants:residents ratio in this willow ptarmigan population may indicate that
416 it is in equilibrium. This may explain why we did not find any differences in fitness reward
417 between the two strategies. If this is indeed the case, migrants are not making “the best of a
418 bad job” where migration is the losing strategy in both survival and reproduction, and
419 contradicts the findings of most empirical studies (Chapman et al., 2011; Buchan et al., 2019).

420 To conclude, we found that willow ptarmigans in central Norway were partially migratory,
421 making them well suited for studies of the evolution of partial migration. The probability of
422 remaining resident in the wintering area increased with increased body weight in juveniles, but
423 not in adults. We found partly support for the dominance hypothesis for explaining partial

424 migration, but cannot exclude the arrival time hypothesis as a potential driver of the observed
425 pattern. The migratory strategy displayed as juveniles appeared to be fixed throughout the
426 individuals' lifetime. We found no difference in average nesting success between migratory
427 strategies, which indicates that both strategies yield equal fitness unless there are differences
428 in survival between the strategies.

429

430 **ACKNOWLEDGMENT**

431 We want to thank our field personnel for all effort through vast amounts of monitoring
432 sessions, as well as local hunting area managers (in particular Fjellstyra i Lierne led by Nils
433 Vidar Bratlandsmo) and mountain rangers for access to the area and invaluable assistance in
434 the field. We also thank Bjørn Roar Hagen and Markus F. Israelsen for important
435 contributions to field work and data management. We are grateful to the Norwegian
436 Environment Agency for funding this study (grant number 17010522 and 19047014).

437

438 **DATA AVAILABILITY**

439 During the review process, data and R-code is available through an open GitHub repository
440 (https://github.com/ErlendNilsen/WillowPtarmigan_PartialMigration). Upon acceptance, data
441 and code will be archived in a public repository according to best practice open science
442 standards.

443

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- 644
- 645

646 **TABLE 1:** Number of radio-tagged female willow ptarmigan captured in the capture sites Guslia and
 647 Lifjellet, total number of female individuals included in the analysis and the number of monitored nests.

Year	Guslia	Lifjellet	N	N included in analyses	N Nests
2015	14	6	20	14	10
2016	10	10	20	16	16
2017	8	12	20	15	10
2018	4	13	17	10	13
2019	11	13	24	18	19
Total	47	54	101	73	68

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649

650 **TABLE 2:** Distribution of cases of migratory and resident behaviour observed for 73 female willow
651 ptarmigan during the five-year study period.

Year	Residents	Migrants	Total	% Migrants
2015	6	8	14	57
2016	5	18	23	78
2017	5	19	24	79
2018	4	16	20	80
2019	6	17	23	74
Total	26	78	104	75

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653

654 **TABLE 3:** Distance moved and weight of juvenile and adult female willow ptarmigan. N distance is the
 655 total number of movement distances observed, whereas N weight is the number of individuals weighed.

	Age	Min.	Mean	Median	Max.	N
Distance (km)	Juv	0.0	7.8	4.5	30	33
	Ad	0.0	9.6	7.0	46.5	71
Weight (g)	Juv	520	590	590	670	33
	Ad	530	600	600	670	40

656

657

658 **TABLE 4:** Candidate models and model statistics for modelling migration strategy as a function of age
659 (juvenile or adult) and body weight for female willow ptarmigan. Results from generalized linear mixed
660 models (GLMMs) with binary response ($Y = 1 =$ migrated, $Y = 0 =$ remained resident) and logit link
661 function, assuming binomial error distribution. Individual identity was included as random effect to
662 account for repeated observations of the same birds.

Response	Model	K	AIC _c	ΔAIC _c	AIC _c Wt	CumWt
Migratory strategy	Weight + Age + Weight × Age	5	91.77	0.00	0.81	0.81
	Intercept	2	96.23	4.47	0.09	0.90
	Weight	3	97.58	5.81	0.04	0.94
	Age	3	98.05	6.28	0.04	0.98
	Weight + Age	4	99.00	7.24	0.02	1.00

663

664

665 **TABLE 5:** Candidate models and model statistics for modelling movement distance as a function of age
 666 (juvenile or adult) and body weight for female willow ptarmigan. Results from linear mixed models
 667 (LMMs) with continuous response assuming Gaussian error distribution. Individual identity was
 668 included as random effect to account for repeated observations of the same birds.

Response	Model	K	AICc	ΔAIC_c	AICcWt	CumWt
Distance	Intercept	3	390.93	0.00	0.43	0.43
	Age	4	392.49	1.56	0.20	0.63
	Weight	4	392.77	1.84	0.17	0.80
	Weight + Age + Weight \times Age	6	393.58	2.65	0.12	0.92
	Weight + Age	5	394.28	3.35	0.08	1.00

669

670

671 **TABLE 6:** Candidate models and model statistics for modelling number of laid eggs as a function of
 672 migratory strategy, age (juvenile or adult) and body weight for female willow ptarmigan. Results from
 673 generalized linear mixed models (GLMMs) with count response and log link function, assuming
 674 generalized Poisson error distribution (see methods). Individual identity was included as random effect
 675 to account for repeated observations of the same birds.

Response	Model	K	AIC _c	ΔAIC _c	AIC _c Wt	Cum Wt
N eggs	Intercept	3	239.2	0.00	0.33	0.33
	Age	4	240.18	0.96	0.20	0.53
	Weight	4	240.98	1.76	0.14	0.67
	Migratory strategy	4	241.36	2.14	0.11	0.78
	Age + Weight	5	242.26	3.04	0.07	0.86
	Age + Migratory strategy	5	242.32	3.10	0.07	0.93
	Migratory strategy + Weight	5	243.03	3.81	0.05	0.97
	Migratory strategy + Age + Weight	6	244.35	5.13	0.03	1.00

676

677

678 **TABLE 7:** Candidate models and model statistics for modelling nest fate as a function of migratory
 679 strategy, age (juvenile or adult) and body weight for female willow ptarmigan. Results from generalized
 680 linear mixed models (GLMMs) with binary response ($Y = 1 =$ hatched, $Y = 0 =$ abandoned/predated)
 681 and logit link function, assuming binomial error distribution. Individual identity was included as
 682 random effect to account for repeated observations of the same birds.

Response	Model	K	AIC _c	ΔAIC _c	AIC _c Wt	Cum Wt
Nest fate	Intercept	2	88.78	0.00	0.42	0.42
	Age	3	90.95	2.17	0.14	0.57
	Migratory strategy	3	90.98	2.20	0.14	0.71
	Weight	3	90.99	2.21	0.14	0.85
	Age + Migratory strategy	4	93.23	4.45	0.05	0.90
	Age + Weight	4	93.24	4.46	0.05	0.94
	Migratory strategy + Weight	4	93.27	4.49	0.04	0.99
	Migratory strategy + Age + Weight	5	95.60	6.82	0.01	1.00

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687 **FIGURE CAPTIONS**

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689 **FIGURE 1:** Triangulated positions (red circles) of all female willow ptarmigan during the study period
690 in the winter (January – March) and summer (May – July) seasons. The blue triangles represent capture
691 locations; the northern cluster is Lifjellet capture site and the southern cluster is Guslia capture site.
692 Map to the left shows the location of the study area in Central Norway.

693

694 **FIGURE 2:** Female ptarmigan were classified as either migrants, if the distance between the activity
695 centre of winter and summer home ranges exceeded 1276 meters (i.e. no overlap), or residents, if the
696 distance between the centroids of winter and summer home range was less than 1276 (i.e. overlap).

697

698 **FIGURE 3:** A) Distribution of all observed seasonal migration distances for female willow ptarmigan.
699 Blue bar represents resident individuals, orange bars represents migrants. See Figure 2 for definition of
700 resident and migratory individuals. B) Differences between the two capture sites in distance migrated.
701 C) Distances migrated plotted against body weights of individual juvenile birds. Dashed vertical line
702 represents mean and median weight and solid horizontal line marks the threshold movement distance
703 separating residents and migrants (1276 m). D) Same as C, but for adult birds.

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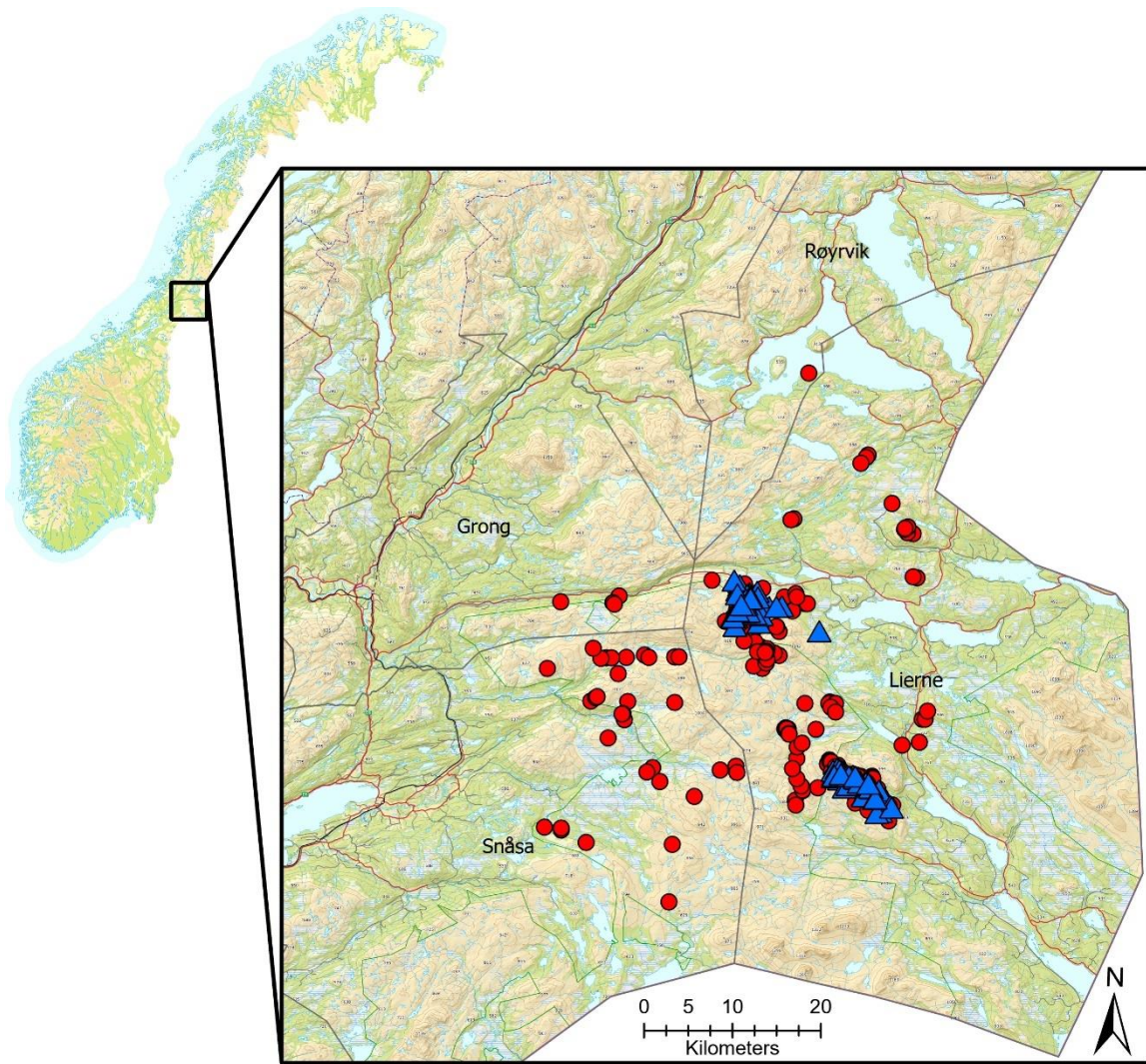
705 **FIGURE 4:** Estimated relationship (solid line) between body weight (g) and migratory strategy in adult
706 and juvenile female willow ptarmigan. The shaded polygons show a 95% confidence interval.

707

708 **FIGURE 5:** Repeatability of decision to migrate or remain resident between individuals. Orange bands
709 = individuals with 100% repeating migration strategy between consecutive seasons. Green bands =
710 individuals that changed migration strategy.

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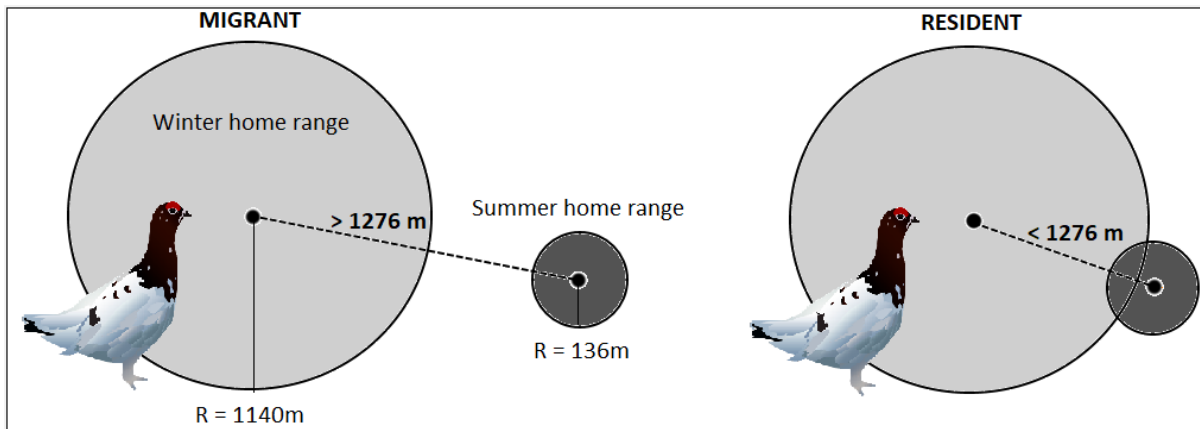
712



714 **FIGURE 1**

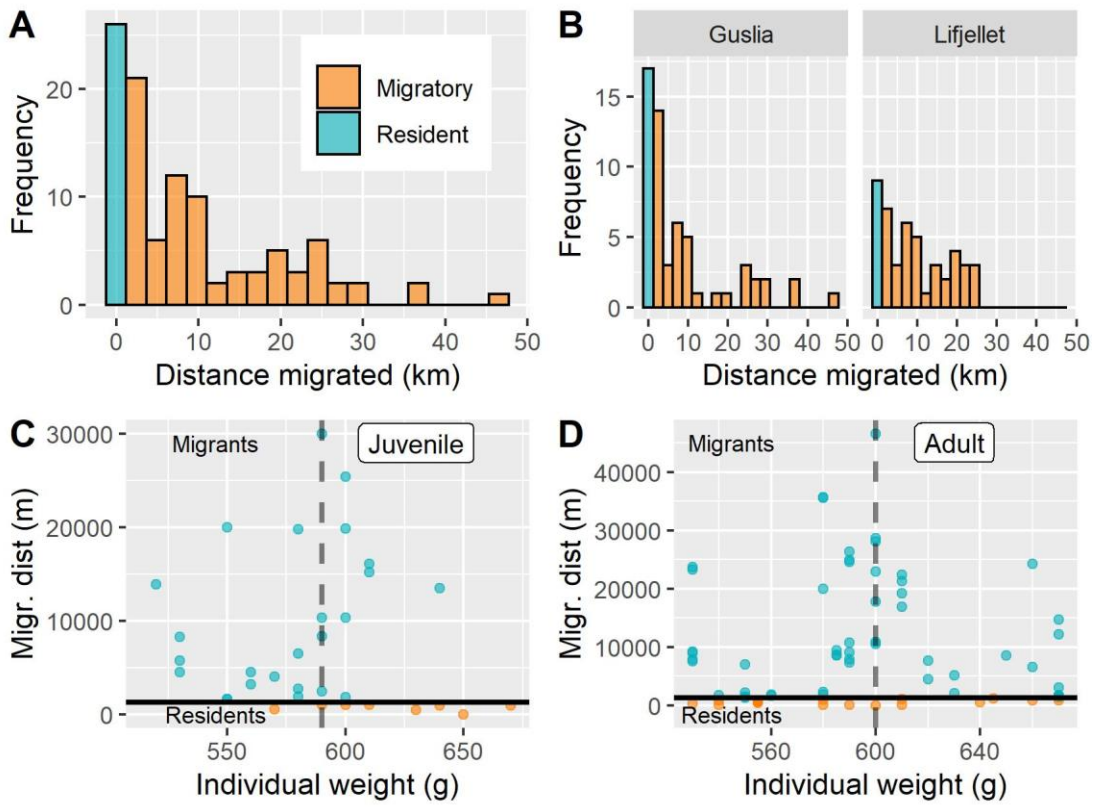
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717 **FIGURE 2**

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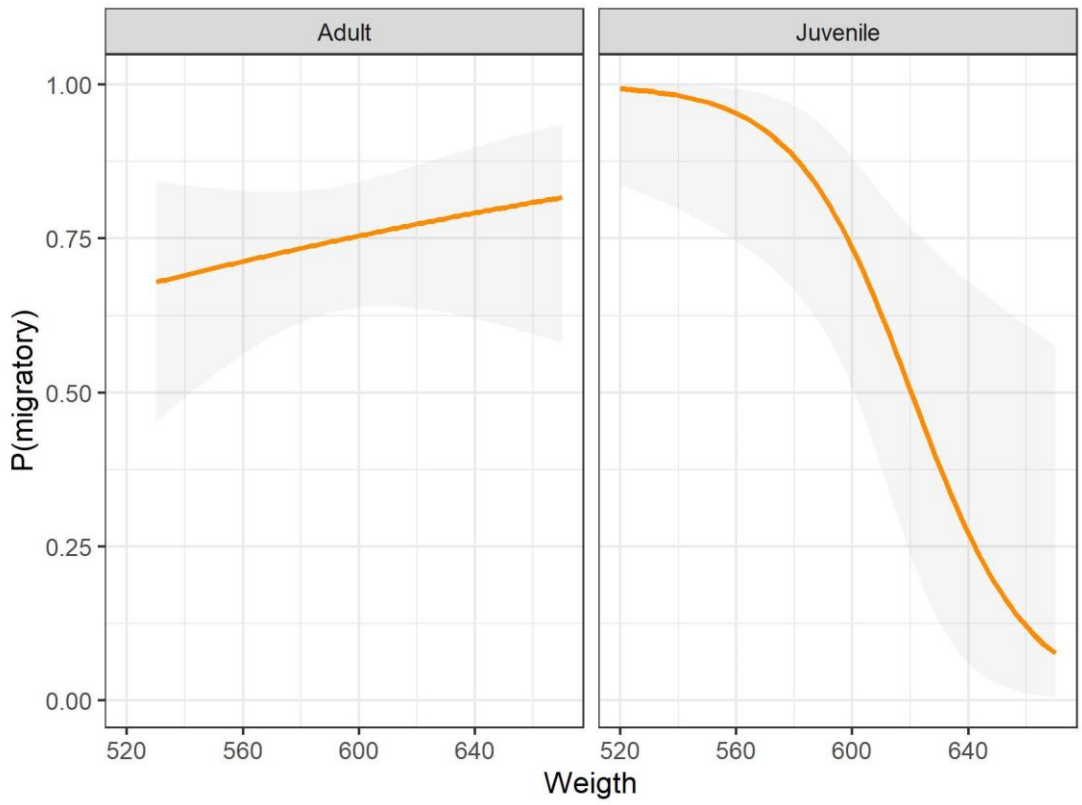


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721 **FIGURE 3**

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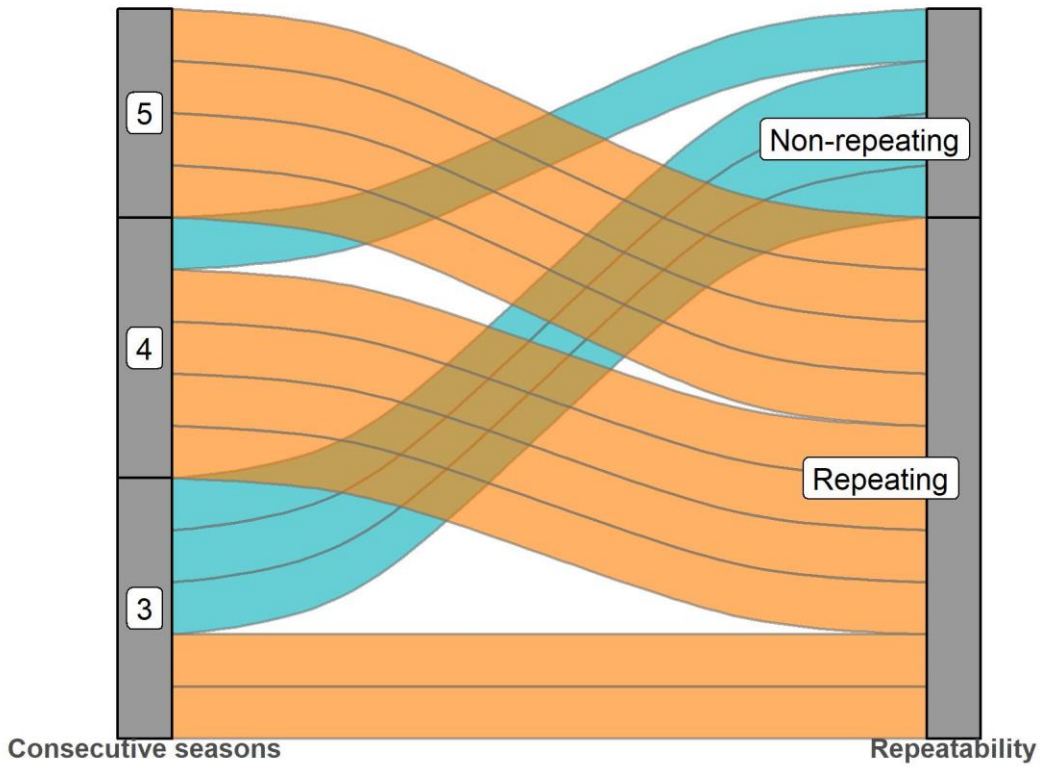


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725 **FIGURE 4**

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729 **FIGURE 5**

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