

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

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20 **Abstract**

- 21 1. Partial migration, where a portion of the population migrates between winter and
22 summer (breeding) areas and the rest remains year-round resident, is a common
23 phenomenon across several taxonomic groups. Several hypotheses have been put
24 forward to explain why some individuals migrate while others stay resident, as well as
25 the fitness consequences between the different strategies. Yet, 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 related to 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). Such seasonal migrations
50 can increase individual fitness (Alerstam et al., 2003; Somveille et al., 2015), as it allows the
51 birds to utilize highly productive habitats all year round. In contrast, other bird species do not
52 perform long-distance seasonal migrations, as they are adapted to remain at northern latitudes
53 throughout the entire year and survive the low-productive winters (Barta et al., 2006; Svorkmo-
54 Lundberg et al., 2006). However, species that display such behaviour may perform shorter
55 migrations between summer and winter areas in heterogeneous landscapes where availability
56 and/or quality of resources vary between seasons (Barraquand & Benhamou, 2008; Fedy et al.,
57 2012). Some overwintering populations are partially migratory (Chapman et al., 2011),
58 implying that a portion of the population migrates between summer and winter areas, whereas
59 the rest stay resident.

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

78 body size hypothesis, the dominance hypotheses (Gauthreaux, 1982) suggest that larger
79 individuals have a competitive advantage in environments with limited food resources
80 (Mysterud et al., 2011) or nesting sites (Gillis et al., 2008), which could trigger migration in
81 smaller individuals. The arrival time hypothesis (Ketterson & Nolan, 1976) suggests that
82 because of early occupancy of territories, and higher fitness of early arriving birds, individuals
83 arriving early at the breeding site have higher reproductive success. Hence, birds that are
84 staying in the territory year-round, are expected to have higher reproductive success. The body
85 size, dominance and arrival time hypotheses suggest that the decision to migrate or stay in the
86 area year-round is influenced by individual state, intraspecific interactions or environmental
87 conditions, and that the fitness reward from the two alternative strategies can differ. These
88 different hypothesis might play out differently in populations where residents and migrants
89 share a non-breeding habitat but breed allopatrically (i.e. *breeding partial migration*) and in
90 populations where residents and migrants share a breeding habitat but live allopatrically during
91 the non-breeding season (i.e. *non-breeding partial migration*) (Chapman et al. 2011). So far,
92 most research has focused on non-breeding partial migration, but breeding partial migration
93 has been studied in e.g. American dippers *Cinclus mexicanus* (Gillis et al. 2008).

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

110 partially migrating populations, and that the choice to migrate may be to make “the best of a
111 bad job” (Chapman et al. 2011).

112 Empirical studies on potential fitness consequences of partial migration have so far been
113 limited to passerines, although partial migration is a common phenomenon reported in multiple
114 bird orders, such as Galliformes (Cade & Hoffman, 1993; Chapman et al., 2011; Holte et al.,
115 2016; Grist et al., 2017) The willow ptarmigan *Lagopus lagopus* is a tetraonid bird with a
116 circumpolar distribution (Fuglei et al., 2020), which lives year-round in heterogeneous alpine
117 and arctic ecosystems. The male willow ptarmigan has been found to display polygamy, and
118 breeding success among males is therefore less often known (Tarasov, 2003). Several studies
119 have reported migratory behaviour in ptarmigan populations (Irving et al., 1967; Hoffman &
120 Braun, 1975; Gruys, 1993; Brøseth et al., 2005; Hörnell-Willebrand et al., 2014; Nilsen et al.,
121 2020a). From Sweden, Hörnell-Willebrand et al. (2014) reported considerable individual
122 variation in seasonal migration distances in willow ptarmigan, with some individuals
123 considered to be residents and others to be migrants. Empirical data from other Scandinavian
124 ptarmigan populations imply non-migratory behaviour (Pedersen et al., 2003), suggesting that
125 there are both inter- and intra-population differences in the propensity to migrate between
126 summer and winter areas in willow ptarmigan. Willow ptarmigan from some populations often
127 gather in distinct wintering areas (Weeden, 1964), which suggests these populations to be
128 breeding partially migratory (Chapman et al. 2011) due to some individuals migrating to
129 breeding areas during spring while others stay resident, either in the wintering or in the breeding
130 areas. Currently, the drivers and consequences of partial migration in willow ptarmigan is
131 poorly understood.

132 Here, we test a number of predictions from a pre-registered hypothesis (Nilsen et al., 2020b;
133 Arnekleiv et al., 2019) put forward to explain causes and consequences of partial migration
134 behaviour in female willow ptarmigan. We focused on females only because we did not have
135 access breeding success data from males in our study population. Assuming that migrants are
136 making the best of a bad job (Lundberg, 1987), and based on the hypotheses about state
137 dependent evolution of partial migration in birds outlined above, we predict that:

- 138 1) Female willow ptarmigan with a) large body size are more likely to remain resident
139 than females with smaller body size, and b) juveniles are more likely to be migrants
140 than adults.
- 141 2) Migration is not a fixed strategy in female willow ptarmigan.

142 3) Resident female willow ptarmigan have higher nesting success than migrants.

143 Following recommendations to preregister hypotheses and predictions when conducting
144 confirmatory (hypothesis testing) research (Nilsen et al., 2020b), the predictions were
145 preregistered at the Open Science Framework (OSF) prior to analysing data (Arnekleiv et al.,
146 2019).

147

148 **2 | Methods**

149 **2.1 | Study area**

150 The study was conducted in Lierne municipality in the northeastern part of Trøndelag county,
151 Norway, with minor extensions of the study area into neighbouring municipalities Snåsa,
152 Røyrvik and Grong due to longer movements from the main study area by some individuals
153 (FIGURE 1). Ptarmigan were captured at two sites (Guslia and Lifjellet), which were located 20
154 km apart near Blåfjella-Skjækerfjella National Park (FIGURE 1). Both in winter and summer,
155 willow ptarmigan are distributed across the larger study area, and some birds overwinter also
156 in the breeding areas of the migratory birds from this study. Because we only captured during
157 winter at two specific capture areas, the birds that were resident at other sites in the larger study
158 area would not be available for capture in our study. The study area was situated in the low
159 alpine and north boreal bioclimatic zones (Moen, 1999); the low alpine zone was dominated
160 by *Salix spp.*, dwarf birch *Betula nana* and *Ericaceae spp.* interspersed with birch *Betula*
161 *pubescens*, whereas the north boreal zone was dominated by Norway spruce *Picea abies*, Scots
162 pine *Pinus sylvestris*, birch *Betula spp.*, *Ericaceae* dwarf shrubs and bryophytes.

163

164 **2.2 | Field data collection**

165 Willow ptarmigan were captured during February and March during winter 2015 - 2019. The
166 birds were spotted from snowmobiles during night-time and temporarily blinded with powerful
167 headlamps and caught with long-handled dip-nets (Brøseth et al., 2005; Sandercock et al.,
168 2011; Hörnell-Willebrand et al., 2014). Body weight (measured with Pesola LightLine 1000g
169 spring scale – rounded to nearest 5 g) and wing length (measured with Axminster Workshop
170 Hook Rule 300mm – carpal to tip of longest primary of flattened wing, measured to nearest
171 mm) were measured prior to instrumenting the birds with collars. Captured birds were

172 identified in the field as either female or male based on saturation of red in the eyebrow, where
173 males have more pronounced red colour than females (Pedersen & Karlsen, 2007). One feather
174 was collected for DNA-analyses to confirm sex, and the genetic marker Z-054 (Dawson et al.,
175 2015) was used to determine the sex of the bird. 85 % of sex assignments in the field were
176 correct (Israelsen et al. 2020). Captured birds were also classified into juvenile (captured during
177 the first winter following the year of birth) and adult (2nd year +) based on the amount of
178 pigments in primary feathers 8 and 9, where juveniles got more black pigments in 9 than in 8
179 (Bergerud et al., 1963). Each individual was marked with a steel ring with a unique
180 identification number. The majority of the birds were equipped with a VHF radio-tag (Holohil
181 - RI-2DM, 14,1 gram) on the 152 MHz frequency band. For all marked birds, the combined
182 weight of the leg ring and radio transmitter was < 3.5% of the body weight. Radio-transmitters
183 were programmed to send mortality-signals after recording no movement for more than 12
184 hours. In March 2018, five ptarmigan were captured and marked with GPS-transmitters (Milsar
185 - GsmRadioTag-S9, 12 gram). The transmitters sent position data over the GSM network every
186 forth hour.

187 Willow ptarmigan positions were for the most part collected once a month by manual tracking
188 on foot by triangulation, using handheld receivers (Followit – RX98) and antennas (Followit –
189 four-element Yagi-antenna); 2-5 bearings were used to determine best position and the distance
190 between each telemetry location varied from 0.3 – 1 kilometre. If only two bearings were
191 obtained, the cross-section was included when the terrain indicated that the observation was
192 trustworthy (e.g. when the cross-bearing pointed to a position in the end of a valley). Few
193 positions were collected in January and December, due to short daylength and challenging
194 weather conditions. To avoid loss of data due to long-distance movements, we conducted wider
195 aerial triangulation using a helicopter or fixed-winged airplane three times a year (May,
196 September and November) in the years 2016-2019. In 2015, we only conducted triangulation
197 from the air in October. Additional positions were either on-site direct observations from
198 captures or homing in on individuals.

199 Nesting success in spring was first assessed by homing in on radio-tagged females to check
200 whether they were nesting. Further, incubating females were flushed off the nest, eggs were
201 counted, and a wildlife camera (Reconyx HF2X Hyperfire 2 or Wingcam II TL) with
202 movement sensor was deployed 2-5 meters from each nest. The nests were revisited in July
203 after hatching to determine the fate of the nest by inspecting and counting the eggshells to see

204 whether and how many eggs were hatched or predated. In addition, pictures from the cameras
205 were examined.

206

207 **2.3 | Classification of migratory behaviour**

208 In order to examine migratory movements between seasons, we classified January – March as
209 winter and May – July as summer. Out of a total of n=101 captured female ptarmigan, only
210 females with data from at least one winter and the consecutive summer season were included
211 in the analysis (n=73) (TABLE 1). We collected 1-2 positions per individual in the winter and
212 1-5 positions per individual during summer. For each female in each season, migratory strategy
213 was determined by whether or not there was overlap between the winter home range and the
214 consecutive summer home range (FIGURE 2), and between the summer home range and the
215 consecutive winter home range.

216 Due to the limited amount of location data for each individual, we were not able to use the
217 more data-hungry approaches that have been developed targeting research on GPS tagged
218 individuals (Cagnacci *et al.* 2016). Thus, we opted to create a decision rule for classification
219 of migratory behaviour based on the available data and the assumption that all females shared
220 a common home range size in summer and winter, respectively. We used the following
221 approach:

222 First, we calculated an average winter home range size from positions of three of the GPS-
223 tagged ptarmigan during the winter 2018, all marked in March 2018. Individual home range
224 sizes were calculated as 95% Minimum Convex Polygons (MCP) using the function *mcp* in R
225 package *adehabitatHR* (Calenge, 2006). The average 95% MCP for the three GPS-tagged
226 ptarmigan was 4.08 km². Before calculating the individual 95% MCPs, we removed inaccurate
227 positions (due to GPS error) We defined a position as an outlier if the distance between two
228 consecutive position (i.e. time t and t-1, respectively) where more than two times the distance
229 between positions surrounding the focal position (i.e. distance between position taken at t-1
230 and t+1). Positions from the GPS-tagged ptarmigan were only used to estimate the average
231 ‘baseline’ winter home range size, and these birds were not included in further analyses. For
232 each of the VHF-tagged females included in the analyses, we assumed they had a circular
233 winter home range equal to the size calculated from the GPS data (4.08 km² (radius = 1140 m))
234 centred around the activity centre (determined by triangulation) of each female in each winter
235 season as a proxy for individual winter home range size and location.

236 Second, we estimated the size of the summer home ranges using data from VHF-tagged female
237 ptarmigan with ≥ 3 positions during the summer season (May - July). For each female, we drew
238 a polygon based on the positions, and calculated the area of the polygon. As a measure of a
239 'baseline' summer home range for further analysis, we used the median of all the individual
240 summer home range sizes (n=46). The baseline home range area was estimated to be 0.058
241 km², corresponding to a circular home range with radius=136 m. This size is in good agreement
242 with previous studies of ptarmigan summer home range sizes (Eason & Hannon, 2003). For
243 each of the females included in the analyses, we assumed a circular summer home range of
244 0.058 km² (radius = 136 m) centred around the activity centre (determined by triangulation and
245 nest location) of each female in each summer season, as a proxy for individual summer home
246 range. When calculating the activity centre, the activity centre for nesting hens (n=68) was
247 shifted towards the nest location, by assigning equal weights to the position of the nest and the
248 sum of all other positions. All spatial computations were done using R (R Core Team, 2019).

249 Females with overlapping winter/summer or summer/winter home ranges were classified as
250 residents, whereas females with no overlap were classified as migrants. Based on the 'baseline'
251 home range sizes, ptarmigan moving further than 1276 m (radius winter home range + radius
252 summer home range) were consequently classified as migrants and females moving less than
253 1276 m were classified as residents.

254

255 **2.4 | Statistical analysis**

256 To test our predictions about state dependent migration strategy, we used a generalized linear
257 mixed effects model (*glmmTMB* function in R package *glmmTMB*; Brooks et al., 2017), with
258 migratory strategy as a binary response variable and body weight, age and body weight \times age
259 interaction as fixed explanatory terms. Body weight is used as a measure of body size. Body
260 weight might however fluctuate as across short and long time intervals, and such intra-
261 individual variation might make body mass a less reliable measure of body size; we
262 acknowledge this limitation of the current study. For all models, the body weight variable was
263 standardized by extracting the mean and dividing by the standard deviation. Bird identity was
264 included as random effect to account for pseudoreplication caused by repeated observations of
265 individual birds. Because body mass was only recorded at capture, we also repeated the
266 analyses based on generalized linear models (GLM) using the approach above, but including
267 only the first season with data for each individual.

268 As an additional test of prediction 1, we also tested whether the distance migrated was
269 influenced by age and body weight by fitting linear mixed models (*glmmTMB* function in R
270 package *glmmTMB*) with log(movement distance) as response variable, and weight, age and
271 weight×age interaction as fixed explanatory terms. We used an identity link function, assuming
272 a Gaussian distribution of the residuals. Bird identity was included as random effect to account
273 for repeated observations of individual birds.

274 To assess if migration was a fixed strategy in female willow ptarmigan, we estimated the
275 repeatability R_M in a mixed effect model with log(movement distance) as response variable.
276 Only females with 2 or more observations of seasonal movement were included. We also
277 assessed models for repeatability in migratory status (binary response), but do not report those
278 due to convergence failure. Repeatability R_M was estimated as the proportion of the total
279 variance that was attributed to within group (bird identity) variation (Sokal & Rohlf, 1995):

$$280 \quad R_M = \frac{\sigma_{\alpha}^2}{\sigma_{\alpha}^2 + \sigma_{\epsilon}^2}$$

281 Agreement repeatability was estimated based on the intercept-only model (i.e. not accounting
282 for any fixed factors), whereas adjusted repeatability was estimated with age included as a fixed
283 effect term in the model (Nakagawa & Schielzeth, 2010). Repeatability was calculated using
284 the rptR package (Stoffel et al., 2017), and the 95% confidence interval for the repeatability
285 was estimated using parametric bootstrapping (n=1000).

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

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

299 **3 | Results**

300 **3.1 | Migration strategy in relation to age and body weight**

301 A total of 104 cases of seasonal movement behaviours (defined as both migratory or resident
302 behaviours) were included in this study (TABLE 2), of which 87 were winter area to summer
303 area movements and 17 were movements from the summer area to the winter area. Overall,
304 three times as many cases of migratory ($n = 78, 75\%$) than of resident ($n = 26, 25\%$) behaviours
305 were observed (TABLE 2). Mean and median movement distance – for both juvenile and adult
306 females – was substantially longer than the distance limit for being classified as migrant (1276
307 m; TABLE 3). Overall, 67% of the seasonal movement behaviours were shorter than 10 km,
308 25% were between 10 and 25 km, whereas only a few (8%) seasonal movement behaviours
309 were longer than 25 km (FIGURE 3). In general, observed seasonal movement behaviours
310 distances were longer for birds marked at Guslia compared to birds marked at Lifjellet (FIGURE
311 3). Mean and median differences in weight between juveniles and adults were small (TABLE
312 3). There was no evidence for a difference ($p=0.79$ – linear model) in elevation in the nest site
313 location between residents (mean elevation: 600 m.a.s. \pm 21) and migrants (593 m.a.s. \pm 26).

314 When modelling migratory strategy as a function of age and body weight, we found strongest
315 support for the full model including the weight \times age interaction (TABLE 4, Appendix A). This
316 is in partial support of our prediction 1. A similar result was found when including only the
317 first year of data and only spring movements for each individual female ptarmigan (Appendix
318 A). The full model received substantially more support than the second-ranked model (TABLE
319 4). For juveniles, the probability of migrating decreased with body weight (FIGURE 4), and thus
320 the likelihood of remaining resident increased with weight, whereas for adults there was no
321 apparent influence of body weight on migration strategy. When modelling distance moved as
322 a function of age and weight, we found no or very weak support for a difference between
323 juveniles and adults (TABLE 5, Appendix A), and the intercept only-model had lowest AICc.
324 Similar inference was made when including only first year of data and only spring movements
325 for each individual (Appendix A).

326

327 **3.2 | Repeatability of migratory behaviour**

328 Repeatability of migratory behaviour within individuals was very high (FIGURE 5), and
329 repeatability within individuals increased each consecutive season. Among those individuals
330 that changed migratory status, some were originally migratory whereas others were originally

331 resident. Agreement repeatability (based on the intercept only model) for movement distance
332 revealed very high repeatability ($R = 0.69$, 95% CI = 0.36-0.85). Repeatability was equally
333 high after controlling for potential age effects (ie. adjusted repeatability) in movement distance
334 ($R = 0.71$, 95% CI = 0.40 – 0.87).

335

336 **3.3 | Nesting success**

337 In contrast to our third prediction, we did not find evidence that clutch size (TABLE 6, Appendix
338 A) or nest fate (TABLE 7, Appendix A) varied as function of migratory strategy, age and weight.
339 For both dependent variables, the ranking of models was identical (clutch size) or similar (nest
340 fate) when using only first year of data for each individual (Appendix A).

341

342 **4 | Discussion**

343 We found that the willow ptarmigan population in the study area was partially migratory, with
344 a majority (75%) of the observed migratory behaviours being defined as seasonal migrations.
345 Similar behaviour has been reported from several other species of Galliformes, including
346 spruce grouse *Falci pennis canadensis* (Herzog & Keppie, 1980) and blue grouse *Dendragapus*
347 *obscurus* (Cade & Hoffman, 1993). Partly in line with our first prediction, we found that body
348 weight related to the decision to migrate or to remain resident. This effect was only found
349 among juvenile birds, where individuals with high body weight had a higher probability of
350 remaining in the winter area. Among adult females, body weight did not appear to be an
351 important driver for the choice of migratory strategy. In contrast with our second prediction,
352 we found that migration was a fixed strategy once established, and individuals for which data
353 on more than one seasonal movement behaviours was available, showed a high degree of
354 repeatability in migratory behaviour. Finally, we found no support for our third prediction, as
355 resident female willow ptarmigans had similar nesting success to migrants.

356

357 **4.1 | Migration strategy in relation to age and body weight**

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

362 Migratory strategy being affected by body weight in juvenile birds is partly in line with the
363 body size hypothesis (Ketterson & Nolan, 1976), predicting that larger individuals are more
364 likely to stay resident in their wintering areas compared to smaller individuals in a non-
365 breeding partial migration system. Similar results have been reported by Hegemann et al.
366 (2015) for skylarks *Alauda arvensis*, where migration strategy is dependent on body size and
367 immune function but not on age and sex. However, the body size hypothesis posits that large
368 body sizes will be advantageous to endure thermal variations and variation in food availability
369 in harsh winter climates. In willow ptarmigan, winter survival is generally high and stable
370 (Israelsen et al. 2020), and therefore it seems unlikely that the body size hypothesis alone could
371 explain why body weight affects migratory strategy in juvenile willow ptarmigan.

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

385 Finally, although several studies have found support for the arrival time hypothesis as a driver
386 of partial migration (Ketterson & Nolan, 1976; Fudickar et al., 2013; Lundblad & Conway,
387 2020), lack of data on when the females arrive in their breeding territory prevent us from
388 further tests of this hypothesis. However, willow ptarmigans to some extent adjust the start of
389 the breeding season to the timing of spring (Myrberget, 1986), hence, earlier spring leads to an
390 early start to the breeding season. In years with mild winters and early spring, resident
391 ptarmigans may have an advantage in occupying high quality territories prior to migrating
392 individuals.

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

397

398 **4.2 | Repeatability of migration strategy**

399 Once established, migratory behaviour seems to be a relatively fixed trait in our study
400 population, and the repeatability in migration strategy within individuals was very high. Our
401 findings are in line with several studies on breeding partial migratory populations, which have
402 found migratory strategy to be fixed within individuals (Gillis et al., 2008; Chambon et al.,
403 2019). For example, in a breeding partial migratory population of American crow *Corvus*
404 *brachyrynchos* in USA, Townsend et al. (2018) found that migratory strategy was fixed within
405 individuals, the proportion of migrants was 78% and with high breeding-site fidelity.
406 Interestingly, bird populations that breed sympatrically but winter allopatrically seem to have
407 a higher degree of non-fixed migration behaviour (Hegemann et al., 2015; Dale et al., 2019;
408 Lundblad & Conway, 2020).

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

419

420 **4.3 | Nesting success in relation to migration strategy**

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

425 reported that although most studies reported fitness differences between resident and migratory
426 (73% of the studied populations reported higher fitness of residents, 22% reported higher
427 fitness of migrants, and 5% reported equal fitness), fitness differences were most often caused
428 by differences in survival. They argue the reason for this finding can be that anthropogenic
429 changes reduce the survival of migratory individuals. Our finding that migratory behaviour
430 seems to be relatively fixed once established appears to be in line with the finding that fitness
431 does not differ between the strategies in our study population. However, our results show some
432 tendency that resident female first-time breeders have higher nesting success than migratory
433 first-time breeders (Table 7 & Appendix B), but low statistical power preclude further
434 assessment of this in our study. In addition, there may be differences in survival between
435 residents and migrants, and we suggest further investigations to be carried out in order to get a
436 better understanding of the consequences of partial migration in the willow ptarmigan.

437 For fitness to be equal between the two migratory strategies, theoretical studies suggest that
438 higher survival in migrants must offset the increased nesting success in residents (Lundberg,
439 1987; Chapman et al., 2011). Reduced risk of predation (Hebblewhite & Merrill, 2007; Skov
440 et al., 2010), escape from harsh climatic conditions and better forage are pointed at as important
441 factors enhancing survival in migrants. Our results show a high proportion of the willow
442 ptarmigan population to be migrants with little variation between years. If migratory strategy
443 is genetically determined, the fitness balancing between strategies may be frequency-
444 dependent where the fitness pay-off by one genotype increases or decreases with the genotype's
445 frequency in the population (Lundberg, 1987; Heino et al., 1998). Negative frequency-
446 dependent selection rewards the strategy with lowest frequency in the population i.e. selection
447 is density-dependent. The population may reach an equilibrium in an evolutionary stable state
448 between migrants and residents where both strategies (genetic morphs) yield the same fitness.
449 The frequencies of migrants and residents may stabilize at any ratio, and the small between-
450 year changes in the migrants:residents ratio in this willow ptarmigan population may indicate
451 that it is in equilibrium. This may explain why we did not find any differences in fitness reward
452 between the two strategies. If this is indeed the case, migrants are not making "the best of a
453 bad job" where migration is the losing strategy in both survival and reproduction, and
454 contradicts the findings of most empirical studies (Chapman et al., 2011; Buchan et al., 2019).

455 To conclude, we found that willow ptarmigans in central Norway were partially migratory,
456 making them well suited for studies of the evolution of partial migration. The probability of
457 remaining resident in the wintering area increased with increased body weight in juveniles, but

458 not in adults. We found partly support for the dominance hypothesis for explaining partial
459 migration, but cannot exclude the arrival time hypothesis as a potential driver of the observed
460 pattern. The migratory strategy displayed as juveniles appeared to be fixed throughout the
461 individuals' lifetime. We found no difference in average nesting success between migratory
462 strategies, which indicates that both strategies yield equal fitness unless there are differences
463 in survival between the strategies.

464

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473

474 **DATA AVAILABILITY**

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

479

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682

683

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

Year	Guslia	Lifjellet	N marked	N birds included in analyses	N nests included in analyses
2015	14	6	20	14	10
2016	10	10	20	16	14
2017	8	12	20	15	7
2018	4	13	17	10	13
2019	11	13	24	18	18
Total	47	54	101	73	62

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687

688 **TABLE 2:** Distribution of cases of migratory and resident behaviour (winter to consecutive summer and
689 summer to consecutive winter) observed for 73 female willow ptarmigan during the five-year study
690 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

691

692

693 **TABLE 3:** Distance moved and weight of juvenile and adult female willow ptarmigan. N distance is the
 694 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

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696

697 **TABLE 4:** Candidate models and model statistics for modelling migration strategy as a function of age
 698 (juvenile or adult) and body weight for female willow ptarmigan. Results from generalized linear mixed
 699 models (GLMMs) with binary response ($Y = 1 =$ migrated, $Y = 0 =$ remained resident) and logit link
 700 function, assuming binomial error distribution. Individual identity was included as random effect to
 701 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

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704 **TABLE 5:** Candidate models and model statistics for modelling movement distance as a function of age
 705 (juvenile or adult) and body weight for female willow ptarmigan. Results from linear mixed models
 706 (LMMs) with continuous response assuming Gaussian error distribution. Individual identity was
 707 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

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710 **TABLE 6:** Candidate models and model statistics for modelling number of laid eggs as a function of
 711 migratory strategy, age (juvenile or adult) and body weight for female willow ptarmigan. Results from
 712 generalized linear mixed models (GLMMs) with count response and log link function, assuming
 713 generalized Poisson error distribution (see methods). Individual identity was included as random effect
 714 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	239.22	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

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717 **TABLE 7:** Candidate models and model statistics for modelling nest fate as a function of migratory
 718 strategy, age (juvenile or adult) and body weight for female willow ptarmigan. Results from generalized
 719 linear mixed models (GLMMs) with binary response ($Y = 1 =$ hatched, $Y = 0 =$ abandoned/predated)
 720 and logit link function, assuming binomial error distribution. Individual identity was included as
 721 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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726 **FIGURE CAPTIONS**

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

732

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

736

737 **FIGURE 3:** A) Distribution of all observed seasonal migration distances for female willow ptarmigan.
738 Purple bar represents resident individuals, orange bars represents migrants. See Figure 2 for definition
739 of resident and migratory individuals. B) Migratory distance plotted for each capture site C) Distances
740 migrated plotted against body weights of individual juvenile birds. Dashed vertical line represents mean
741 and median weight and solid horizontal line marks the threshold movement distance separating
742 residents and migrants (1276 m). D) Same as C, but for adult birds. Purple dots represent migratory
743 behaviour whereas orange dots represent residents.

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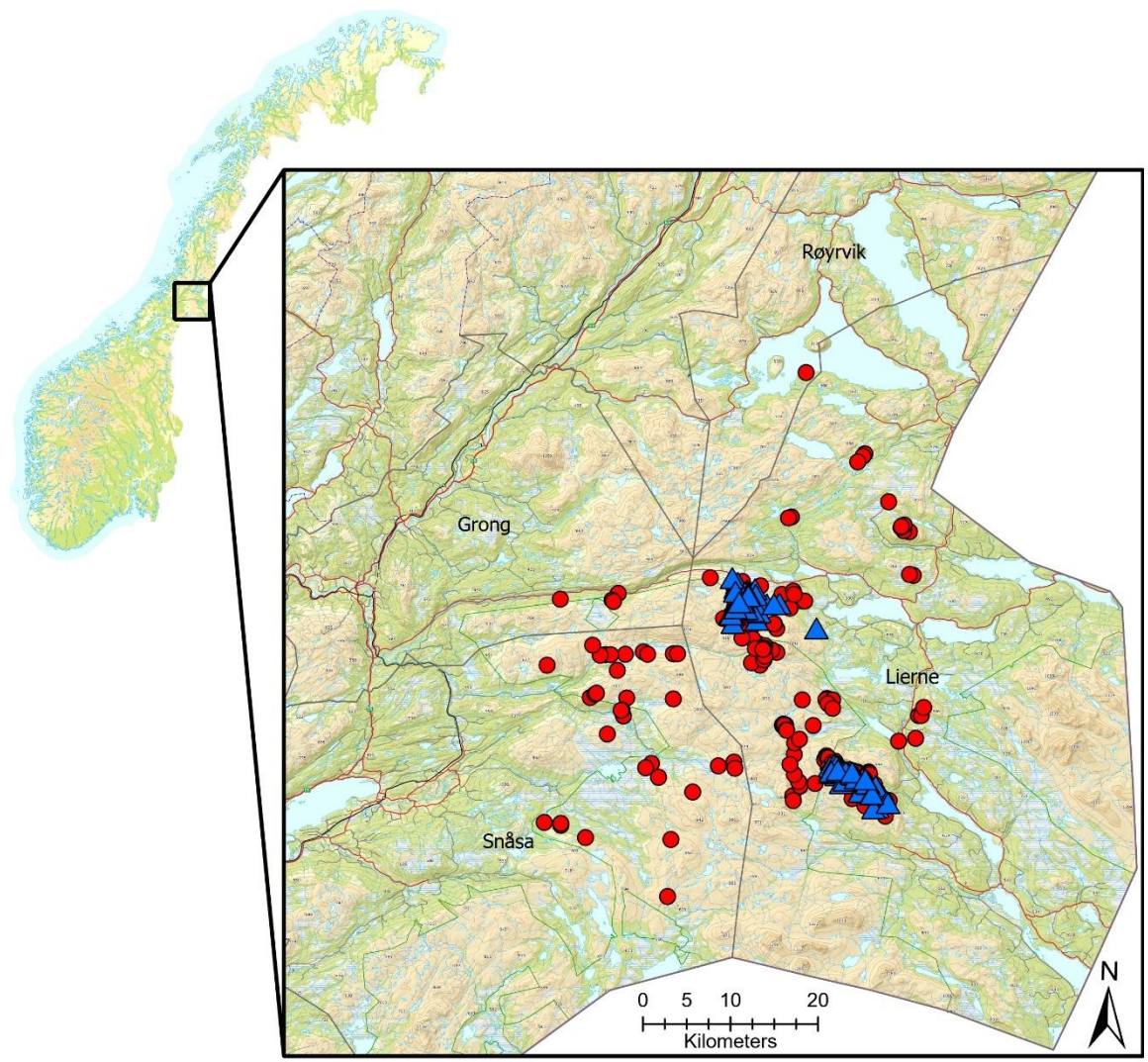
745 **FIGURE 4:** Estimated relationship (solid line) between body weight (g) and migratory strategy in adult
746 and juvenile female willow ptarmigan. The shaded ribbons represent 95% confidence interval.

747

748 **FIGURE 5:** Repeatability of decision to migrate or remain resident between individuals. Purple bands
749 = individuals with 100% repeating migration strategy between consecutive seasons. Orange bands =
750 individuals that changed migration strategy. Each band represents one individual.

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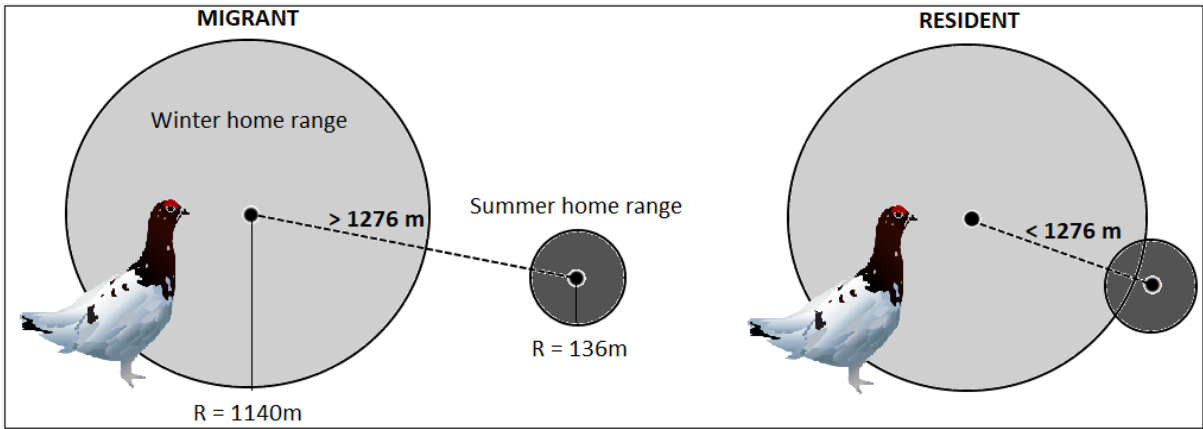
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754 **FIGURE 1**

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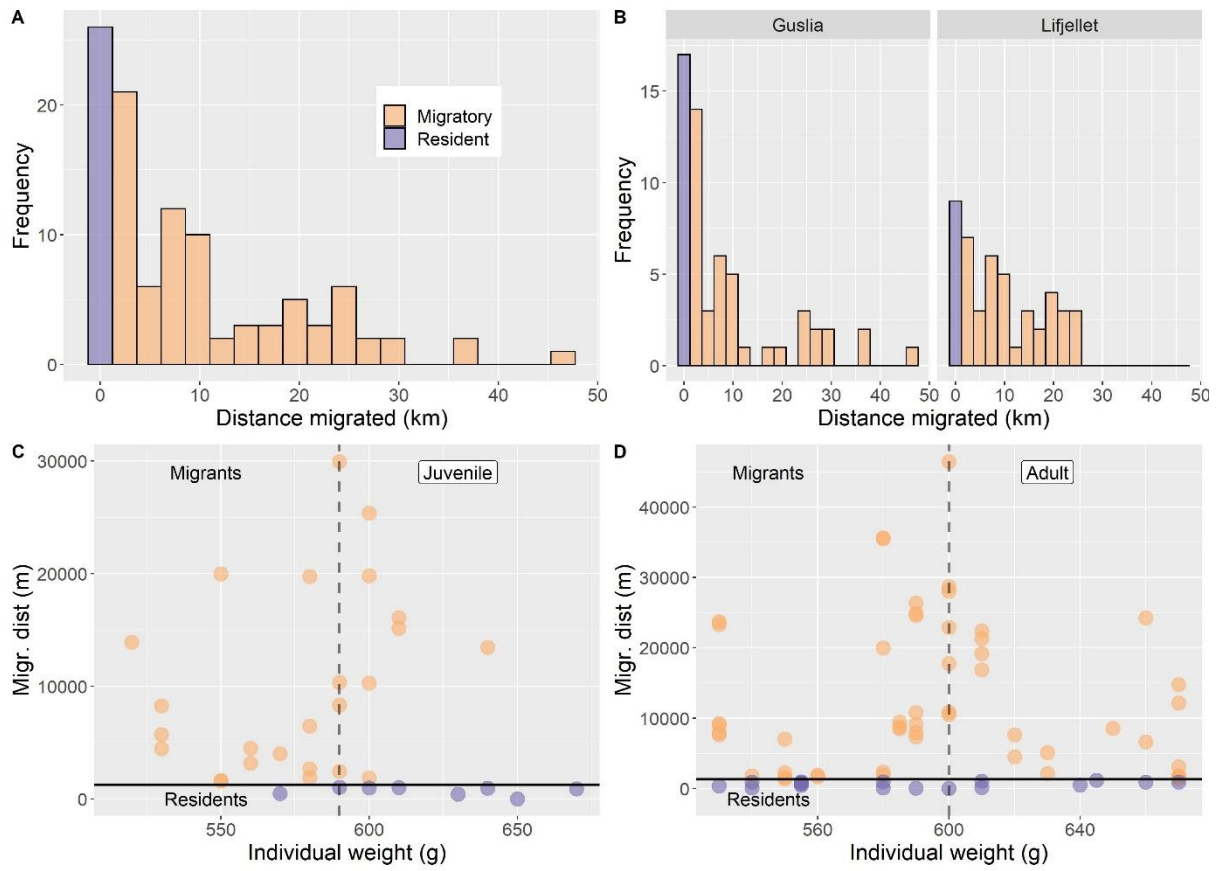
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757 **FIGURE 2**

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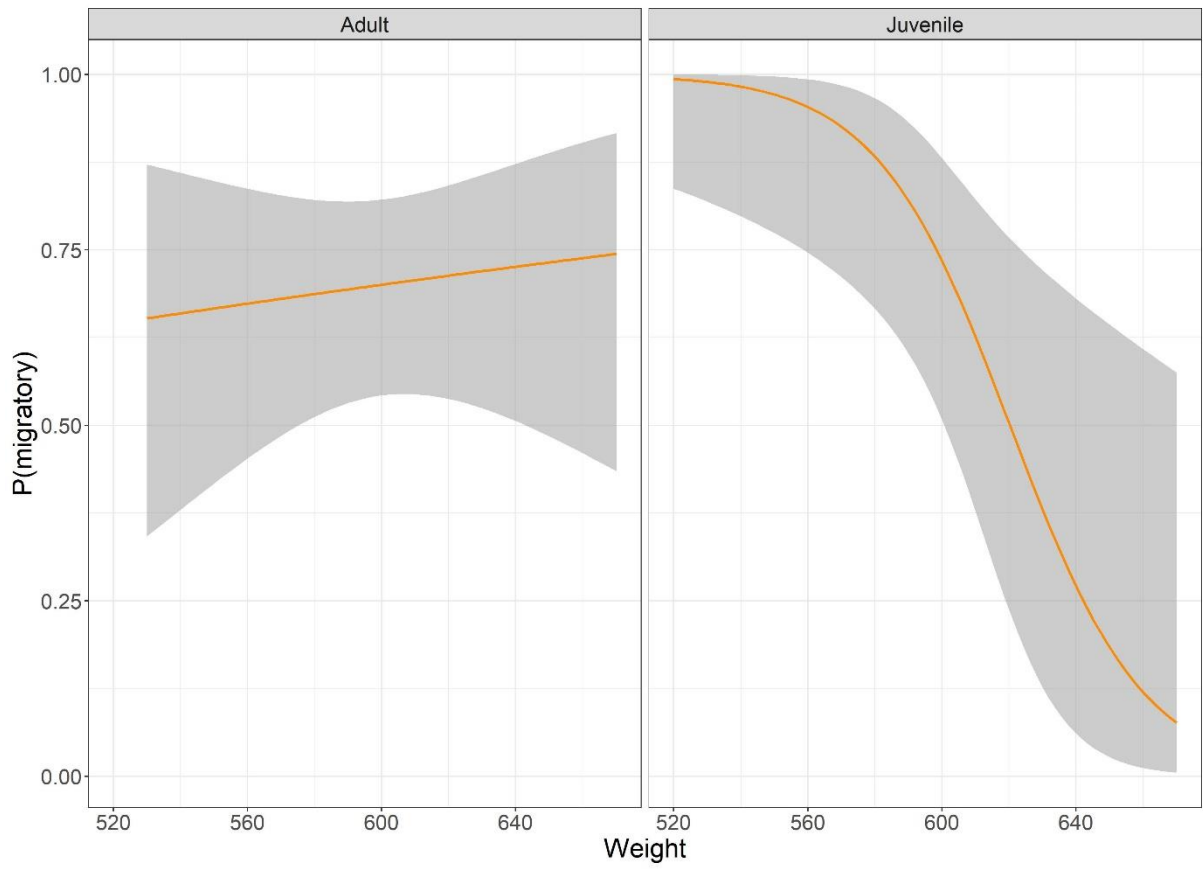


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761 **FIGURE 3**

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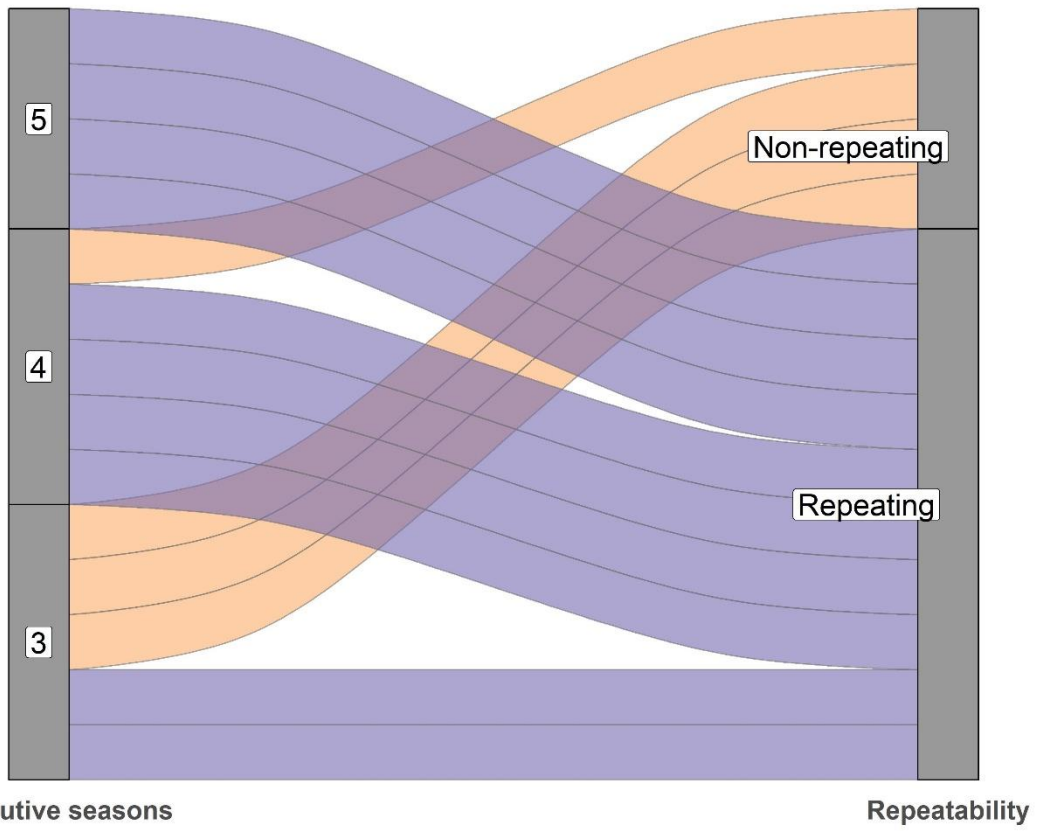


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765 **FIGURE 4**

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Consecutive seasons

Repeatability

769 **FIGURE 5**

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