# Drivers and Consequences of Partial Migration in an Alpine Bird Species

**Øyvind Arnekleiv[1] | Katrine Eldegard[1] | Pål F. Moa[2] | Lasse F. Eriksen[2,3,4] | Erlend B. Nilsen[2,3,4]**

1: Faculty of Environmental Sciences and Natural Resource Management, Norwegian University of Life Sciences (NMBU), Ås, Norway

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

3: Department for Terrestrial Biodiversity, Norwegian Institute for Nature Research (NINA), Trondheim, Norway

4: Centre for Biodiversity Dynamics (CBD), Norwegian University of Science and Technology (NTNU), Trondheim, Norway


**Correspondence**

Erlend B. Nilsen

erlend.nilsen@nina.no

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**Abstract**

1. Partial migration, where a portion of the population migrates between winter and summer (breeding) areas and the rest remain year-round resident, is a common phenomenon across several taxonomic groups. Yet, although several hypotheses have been put forward to explain why some individuals migrate while others stay resident – as well as the fitness consequences of the different strategies – the drivers and consequences of the decision to migrate or not are poorly understood.

2. We used data from radio-tagged female (n=73) willow ptarmigan *Lagopus lagopus* in an alpine study area in Central Norway to test if i) the decision to migrate was dependent on individual state variables (age and body size), ii) individuals repeated migratory behaviour between seasons, and iii) the choice of migratory strategy was related to nesting performance.

3. Partially supporting our prediction that migratory strategy depends on individual state, we found that juvenile birds with small body sizes were more likely to migrate whereas large juveniles stayed resident. For adult females, we found no relationship between migratory strategy and body weight. We found strong evidence for high individual repeatability of migratory strategy between seasons. Migratory strategy did not explain variation in nesting performance among individuals, suggesting no direct influence of the chosen strategy on nesting success.

4. Our results indicate that partial migration in willow ptarmigan is determined by juvenile body weight, and that migratory behaviour becomes a part of the individual life history as a fixed strategy. Nesting success was not affected by migratory strategy in our study population, but future studies should assess other traits to further test potential fitness consequences.

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

# 1| Introduction

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

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

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

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

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

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

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

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

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

# 2 | Methods

## 2.1 | Study area

The study was conducted in Lierne municipality in the northeastern part of Trøndelag county, Norway, with minor extensions of the study area into neighbouring municipalities Snåsa, 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.

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### 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 ($2^{nd}$ 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 forth 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

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

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

### 2.3 | Classification of migratory behaviour

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

We calculated an average 'baseline' winter home range size from positions of three of the GPS-tagged ptarmigan during the winter 2018, all marked in March 2018. Individual home range sizes were calculated as 95% Minimum Convex Polygons (MCP) using the function *mcp* in R package adehabitatHR (Calenge, 2006). The average 95% MCP for the three GPS-tagged ptarmigan was 4.08 km$^2$. Before calculating the individual 95% MCPs, we removed inaccurate positions (due to GPS error) using the following algorithm:

*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  $4.08 \text{ km}^2$ (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 $\geq 3$ 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  $\text{km}^2$, 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  $0.058 \text{ km}^2$ (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     
$$R_M = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

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).

## 3 | Results

270

### 3.1 | Migration strategy in relation to age and body weight

271

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 × 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

### 3.2 | Repeatability of migratory behaviour

294

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

### 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

## 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 *Falcipennis*

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

### 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.

9

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 the 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    *brachyhynchos* 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

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

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

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

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

**DATA AVAILABILITY**

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

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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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**TABLE 2:** Distribution of cases of migratory and resident behaviour observed for 73 female willow 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 |

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 |

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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 | $AIC_c$ | $\Delta AIC_c$ | $AIC_c Wt$ | 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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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 | $\Delta AIC_c$ | $AIC_cWt$ | 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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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 | $AIC_c$ | $\Delta AIC_c$ | $AIC_c$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 |

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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 | $AIC_c$ | $\Delta AIC_c$ | $AIC_cWt$ | 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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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.

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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).

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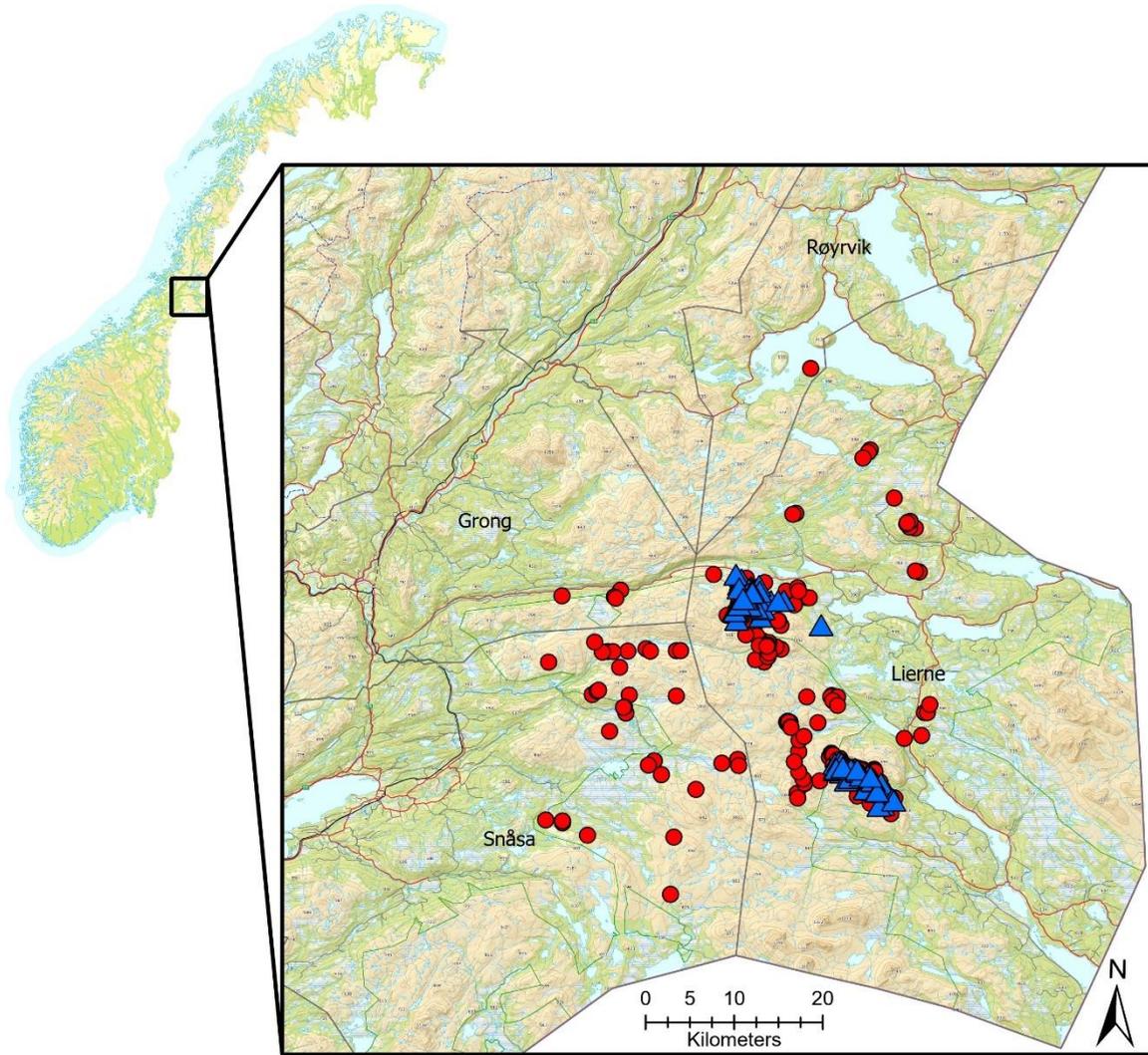
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705 **FIGURE 4:** Estimated relationship (solid line) between body weight (g) and migratory strategy in adult
706 and juvenile female willow ptarmigan. The shaded polygons show a 95% confidence interval.

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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 =
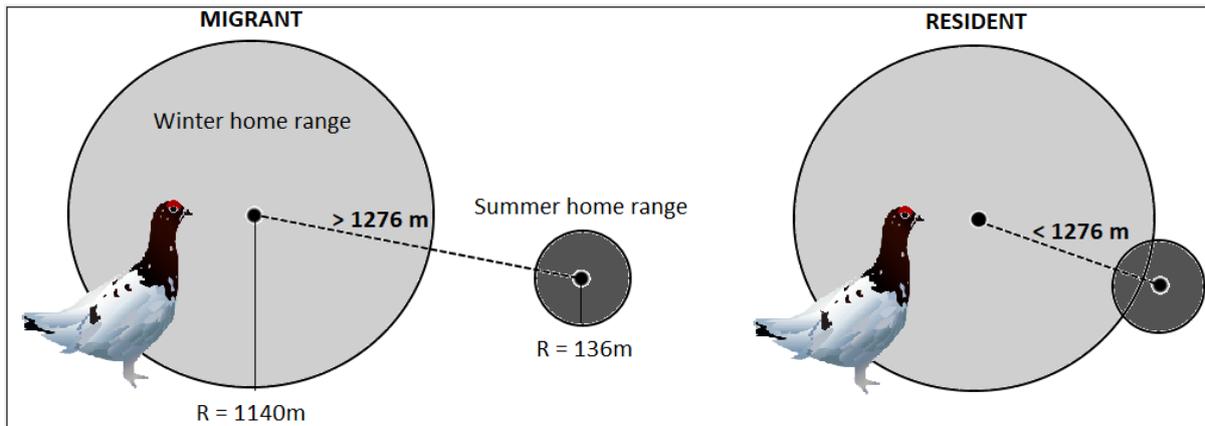710 individuals that changed migration strategy.
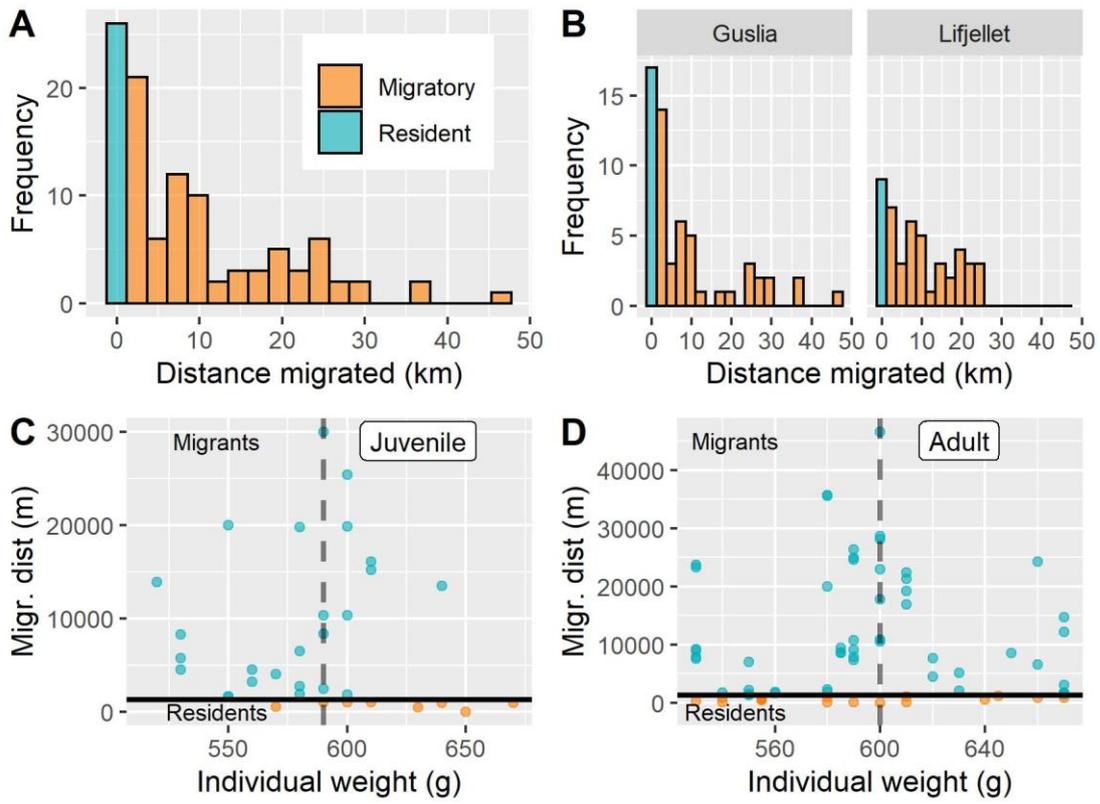
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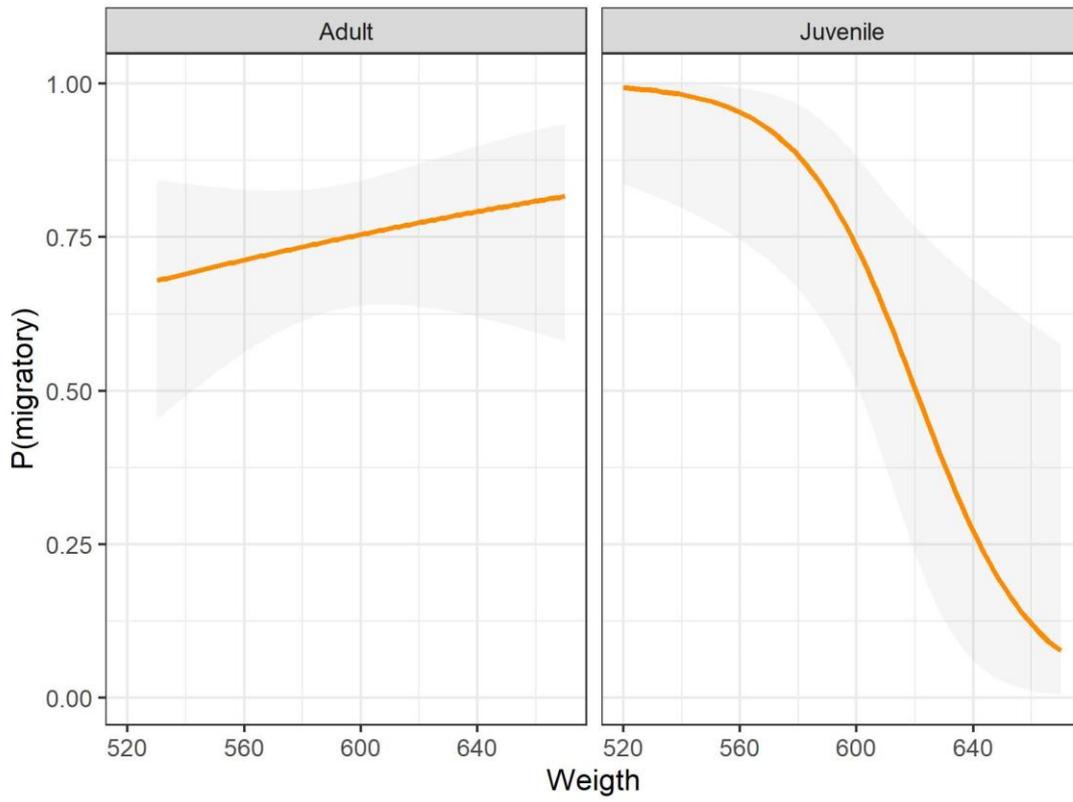714    **FIGURE 1**

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717 **FIGURE 2**

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**FIGURE 3**

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725 **FIGURE 4**

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Consecutive seasons                    Repeatability
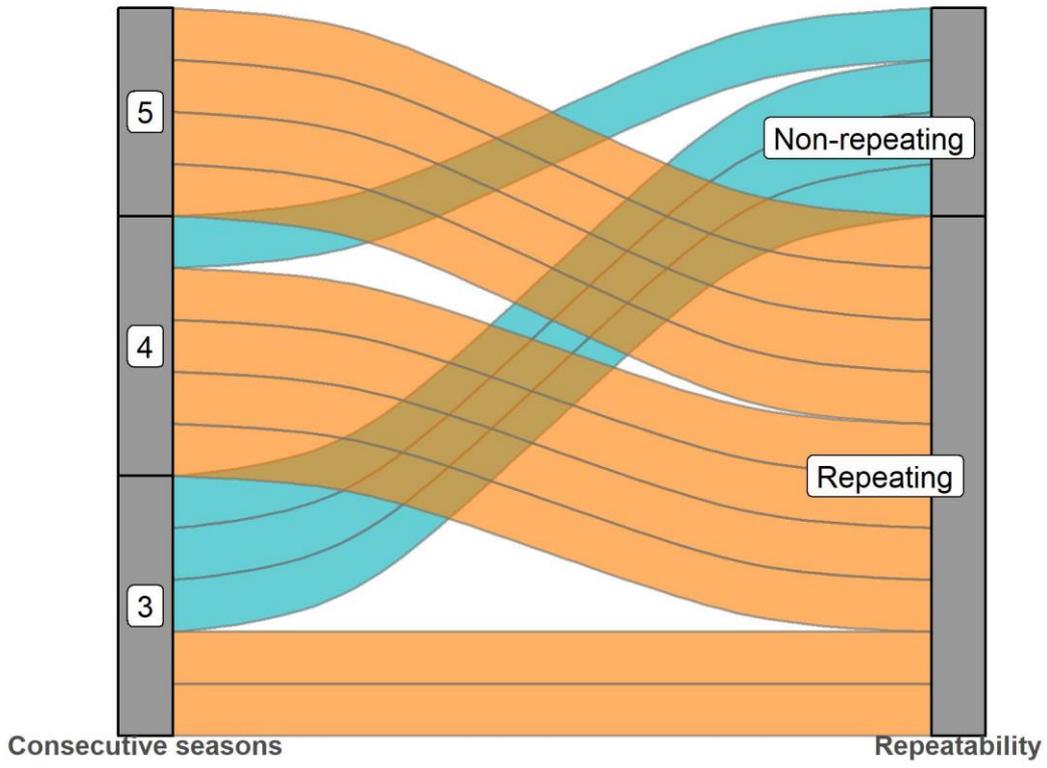
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**FIGURE 5**

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