Drivers and Consequences of Partial Migration in an Alpine Bird Species

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Number of tables: 7

Number of figures: 5

Word count: 8111

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

2.2 | Field data collection

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

Willow ptarmigan positions were for the most part collected once a month by manual tracking on foot by triangulation, using handheld receivers (Followit – RX98) and antennas (Followit – 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

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

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

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

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

2.4 | Statistical analysis

To test our predictions about state dependent migration strategy, we used a generalized linear mixed effects model (*glmmTMB* function in R package glmmTMB; Brooks et al., 2017), with migratory strategy as a binary response variable and body weight, age and body weight×age interaction as fixed explanatory terms. Body weight is used as a measure of body size. For all models, the body weight variable was standardized by extracting the mean and dividing by the standard deviation. Bird identity was included as random effect to account for pseudoreplication caused by repeated observations of individual birds.

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

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

$$R_M = \frac{\sigma_{\alpha}^{2}}{\sigma_{\alpha}^{2} + \sigma_{\varepsilon}^{2}}$$

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

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

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

3 | Results

3.1 | Migration strategy in relation to age and body weight

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

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

3.2 | Repeatability of migratory behaviour

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

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

3.3 | Nesting success

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

4 | Discussion

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

4.1 | Migration strategy in relation to age and body weight

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

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

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

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

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

4.2 | Repeatability of migration strategy

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

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

4.3 | Nesting success in relation to migration strategy

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

ACKNOWLEDGMENT

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

REFERENCES

Adriaensen, F. & Dhondt, A. (1990). Population Dynamics and Partial Migration of the European Robin (Erithacus rubecula) in Different habitats. Journal of Animal Ecology, 59(3), 1077-1090. DOI: 10.2307/5033

Alerstam, T., Hedenström, A. & Åkesson, S. (2003). Long-distance migration: evolution and determinants. Oikos, 103(2), 247-260. DOI: https://doi.org/10.1034/j.1600-0706.2003.12559.x

Arnekleiv, Ø. L., Nilsen, E. B., Eriksen, L. F., Moa, P. F. & Eldegard, K. (2019). Causes and consequences of partial migration in an alpine tetraonid species. OSF. DOI: https://doi.org/10.17605/OSF.IO/C9E8N

Barraquand, F. & Benhamou, S. (2008). Animal Movements in Heterogeneous Landscapes: Identifying Profitable Places and Homogeneous Movement Bouts. Ecology, 89(12), 3336-3348. DOI: https://doi.org/10.1890/08-0162.1

Barta, Z., Houston, A. I., McNamara, J. M., Welham, R. K., Hedenström, A., Weber, T. P. & Feró, O. (2006). Annual routines of non-migratory birds: optimal moult strategies. Oikos, 112(3), 580-593. DOI: https://doi.org/10.1111/j.0030-1299.2006.14240.x

Berg, J. E., Hebblewhite, M., St. Clair, C. C. & Merrill, E. H. (2019). Prevalence and Mechanisms of Partial Migration in Ungulates. Frontiers in Ecology and Evolution, 7(325). DOI: https://doi.org/10.3389/fevo.2019.00325

Bergerud, A. T., Peters, S. S. & McGrath, R. (1963). Determining Sex and Age of Willow Ptarmigan in Newfoundland. The Journal of Wildlife Management, 27(4), 700-711. DOI: 10.2307/3798486

Bolker, B. M., Brooks, M. E., Clark, C. J., Geange, S. W., Poulsen, J. R., Stevens, M. H. H. & White, J.-S. S. (2008). Generalized linear mixed models: a practiacal guide for ecology and evolution. Trends in Ecology and Evolution, 24, 127-135. DOI: 10.1016/j.tree.2008.10.008

Bonte, D., Van Dyck, H., Bullock, J. M., Coulon, A., Delgado, M., Gibbs, M., … Travis, J. M. J. (2011). Costs of dispersal. Biological Reviews, 87(2), 290-312. DOI: https://doi.org/10.1111/j.1469-185X.2011.00201.x

Brooks, M.E., Kristensen, K., van Benthem, K. J., Magnusson, A., Berg, C. W., Nielsen, A., Skaug, H. J., Maechler, M. & Bolker, B. (2017) glmmTMB Balancs Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modelling. The R Journal, 9(2), 378-400.

Brøseth, H., Tufto, J., Pedersen, H. C., Steen, H. & Kastdalen, L. (2005). Dispersal patterns in a harvested willow ptarmigan population. Journal of Applied Ecology, 42(3), 453-459. https://doi.org/10.1111/j.1365-2664.2005.01031.x

Buchan, C., Gilroy, J. J., Catry, I. & Franco, A. M. A. (2019). Fitness consequences of different migratory strategies in partially migratory populations: A multi-taxa meta-analysis. Journal of Animal Ecology, 89(3), 678-690. DOI: https://doi.org/10.1111/1365-2656.13155

Cade, B. S. & Hoffman, R. W. (1993). Differential Migration of Blue Grouse in Colorado. The Auk, 110(1), 70-77.

Calenge, C. (2006). The package “adehabitat” for the R software: A tool for the analysis of space and habitat use by animals. Ecological Modelling, 197(3-4), 516-519. DOI: 10.1016/j.ecolmodel.2006.03.017

Chambon, R., Gélinaud, G., Paillisson, J.-M., Lemesle, J.-C., Ysnel, F. & Dugravot, S. (2019). The first winter influences lifetime wintering decisions in a partially migrant bird. Animal Behaviour, 149, 23-32. DOI: https://doi.org/10.1016/j.anbehav.2018.12.018

Chapman, B. B., Brönmark, C., Nilsson, J.-Å. & Hansson, L.-H. (2011). The ecology and evolution of partial migration. Oikos, 120(12), 1764-1775. DOI: https://doi.org/10.1111/j.1600-0706.2011.20131.x

Cobben, M. M. P. & van Noordwijk, A. J. (2017). Consequences of the genetic threshold model for observing partial migration under climate change scenarios. Ecology and Evolution, 7(20), 8379-8387. DOI: https://doi.org/10.1002/ece3.3357

Dale, C. A., Nocera, J. J., Franks, S. E., Kyser, T. K. & Ratcliffe, L. M. (2019). Correlates of alternative migratory strategies in western bluebirds. Journal of Avian Biology, 50(4). DOI: 10.1111/jav.02 031

Daniels, S. J. & Walters, J. R. (2000). Between-year breeding dispersal in Red-cockaded woodpeckers: Multiple causes and estimated cost. Ecology, 81(9), 2473-2484. DOI: https://doi.org/10.1890/0012-9658(2000)081[2473:BYBDIR]2.0.CO;2

Dawson, D., Bird, S., Horsburgh, G. & Ball, A. (2015). Autosomal and Z-linked microsatellite markers enhanced for cross-species utility and assessed in a range of birds, including species of conservation concern. - Conservation Genet Resour, 7, 881-886.

Dingle, H. & Drake, V. A. (2007). What is Migration. BioScience, 57(2), 113-121. DOI: https://doi.org/10.1641/B570206

Eason, P. K. & Hannon, S. J. (2003). Effect of pairing status on use of space by territorial willow ptarmigans (Lagopus lagopus): bachelor males choose life on the edge. The Auk, 120(2), 497 – 504.

Fedy, B. C., Aldridge, C. L., Doherty, K. E., O'Donnell, M., Beck, J. L., Bedrosian, B., … Walker, B. L. (2012). Interseasonal Movements of Greater Sage-Grouse, Migratory Behavior, and an Assessment of the Core Regions Concept in Wyoming. Journal of Wildlife Management, 76(5), 1062-1071. DOI: 10.1002/jwmg.337

Fudickar, A. M., Schmidt, A., Hau, M., Quetting, M. & Partecke, J. (2013). Female-biased obligate strategies in a partially migratory population. Journal of Animal Ecology, 82(4), 863-871. DOI: https://doi.org/10.1111/1365-2656.12052

Fuglei, E., Henden, J.-A., Callahan, C. T., Gilg, O., Hansen, J., Ims, R. A., … Martin, K. (2020). Circumpolar status of Arctic ptarmigan: Population dynamics and trends. Ambio, 49, 749-761. DOI: https://doi.org/10.1007/s13280-019-01191-0

Gauthreaux, S. A. (1982). The ecology and evolution of avian migration systems. – In: Farner D. S et al. (Eds.), Avian biology. Academic Press, pp. 93-186.

Gillis, E. A., Green, D. J., Middleton, H. A. & Morrissey, C. A. (2008). Life history correlates of alternative migratory strategies in American dippers. Ecology, 89(6), 1687-1695. DOI: https://doi.org/10.1890/07-1122.1

Greenwood, P. J. & Harvey, P. H. (1982). The natal and breeding dispersal in birds. Annual Review of Ecology and Systematics, 13, 1-21.

Grist, H., Daunt, F., Wanless, S., Burthe, S. J., Newell, M. A., Harris, M. P. & Reid, J. M. (2017). Reproductive performance of resident and migrant males, females and pairs in a partially migratory bird. Journal of Animal Ecology, 86(5), 1010-1021. DOI: https://doi.org/10.1111/1365-2656.12691

Gruys, R. C. (1993). Autumn and Winter Movements and Sexual Segregation of Willow Ptarmigan. Artic, 48(3): 228-239.

Hebblewhite, M. & Merrill, E. H. (2007). Multiscale wolf predation for elk: does migration reduce risk? Oecologia, 152, 377-387. DOI: 10.1007/s00442-007-0661-y

Hegemann, A., Fudickar, A. M. & Nilsson, J.-Å. (2019). A physiological perspective on the ecology and evolution of partial migration. Journal of Ornithology, 160(3), 893-905. DOI: https://doi.org/10.1007/s10336-019-01648-9

Hegemann, A., Marra, P. P. & Tieleman, B. I. (2015). Causes and Consequences of Partial Migration in a Passerine Bird. The American Naturalist, 186(4), 531-546. DOI: https://doi.org/10.1086/682667

Heino, M., Metz, J. A. J. & Kaitala, V. (1998). The enigma of frequency-dependent selection. Trends in Ecology and Evolution, 13(9), 367-370. DOI: https://doi.org/10.1016/S0169-5347(98)01380-9

Herzog, P. W. & Keppie, D. M. (1980). Migration in a local population of spruce grouse. The Condor, 82(4), 366-372.

Hoffman, R. & Braun, C. E. (1975). Migration of a Wintering Population of White-Tailed Ptarmigan in Colorado. The Journal of Wildlife Management, 39(3), 784-490. DOI: 10.2307/3800388

Holte, D., Köppen, U. & Schmitz-Ornés, A. (2016). Partial Migration in a Central European Raptor Species: An Analysis of Ring Re-Encounter Data of Common Kestrels Falco Tinnunculus. Acta Ornithologica, 51(1), 39-54. DOI: https://doi.org/10.3161/00016454AO2016.51.1.004

Hörnell-Willebrand, M., Willebrand, T. & Smith, A. A. (2014). Seasonal movements and dispersal patterns: Implications for recruitment and management of willow ptarmigan (Lagopus lagopus). The Journal of Wildlife Management, 78(2), 194-201. DOI: https://doi.org/10.1002/jwmg.650

Irving, L., West, G. C., Peyton, L. J. & Paneak, S. (1967). Migration of Willow Ptarmigan in Artic Alaska. Artic, 20, 77-85.

Israelsen, M.F., Eriksen, L. F., Moa, P. F., Hagen, B. R. & Nilsen, E. B. (2020). Survival and cause-specific mortality of harvested willow ptarmigan (*Lagopus lagopus)* in central Noreway. Ecology and Evolution, 10(20), 11144-11154. https://doi.org/10.1002/ece3.6754

Kendall, B., E & Wittmann, M. (2010) A Stochastic Model for Annual Reproductive Success. The American Naturalist, 175, 461-468. DOI: 10.1086/650724

Ketterson, E. D. & Nolan Jr., V. (1976). Geographic variation and its climate correlates in the sex ratio of eastern-wintering dark-eyed juncos (junco hyemalis hyemalis). Ecology, 57(4), 679-693. DOI: 10.2307/1936182

Kokko, H. (2011). Directions in modelling partial migration: how adaptation can cause a population decline and why the rules of territory acquisition matter. Oikos, 120(12), 1826-1837. DOI: https://doi.org/10.1111/j.1600-0706.2011.19438.x

Lundberg, P. (1987). Partial Bird Migration and Evolutionarily Stable Strategies. Journal of Theoretical Biology, 125, 351-360.

Lundberg, P. (1988). The evolution of partial migration in birds. Trends in Ecology & Evolution, 3(7), 172-175.

Lundblad, C. G. & Conway, C. J. (2020). Testing four hypotheses to explain partial migration: balancing reproductive benefits with limits to fasting endurance. Behavioral Ecology and Sociobiology, 74(26). DOI: https://doi.org/10.1007/s00265-019-2796-3

Matthysen, E. (2005). Density-dependent dispersal in birds and mammals. Ecography, 28(3), 403-416. DOI: https://doi.org/10.1111/j.0906-7590.2005.04073.x

Moen, A. (1999). National Atlas of Norway Vegetation. Norwegian Mapping Authority. Hønefoss. 200pp.

Myrberget, S. (1986). Annual variation in timing of egg-laying in a population of Willow Grouse Lagopus lagopus. Fauna norvegica, Serie C, 9, 1-6.

Mysterud, A., Loe, L. E., Zimmerman, B., Bischof, R., Veiberg, V. & Meisingset, E. (2011). Partial migration in expanding red deer populations at northern latitudes – a role for density dependence? Oikos, 120(12), 1817-1825. DOI: https://doi.org/10.1111/j.1600-0706.2011.19439.x

Nakagawa, S. & Schielzeth, H. (2010). Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biological Reviwes, 85(4), 935-956. DOI: 10.1111/j.1469-185X.2010.00141.x

Newton, I. (1998). Population limitation in birds. Academic Press. Boston. 578pp.

Nilsen, E. B., Moa, P. F., Brøseth, H., Pedersen, H. C. & Hagen, B. R. (2020a). Survival and Migration of Rock Ptarmigan in Central Scandinavia. Frontiers in Ecology and Evolution, 8(34). DOI: 10.3389/fevo.2020.00034

Nilsen, E. B., Bowler, D. E. & Linnell, J. D. C. (2020b). Exploratory and confirmatory research in the open science era. Journal of Applied Ecology, 00, 1-6. DOI: https://doi.org/10.1111/1365-2664.13571

Pedersen, H. C. & Karlsen, D. H. (2007). Alt om rypa – biologi, jakt, forvaltning. Tun forlag. Oslo. 259 pp.

Pedersen, H. C., Steen, H., Kastdalen, L., Brøseth, H., Ims, R. A., Svendsen, W. & Yoccoz, N. G. (2003). Weak compensation of harvest despite strong density-dependent growth in willow ptarmigan. Proceedings of the Royal Society of London, 271(1537), 381-385. DOI: https://doi.org/10.1098/rspb.2003.2599

Pulido, F. (2011). Evolutionary genetics of partial migration threshold model of migration revisited. Oikos, 120(12), 1776-1783. DOI: https://doi.org/10.1111/j.1600-0706.2011.19844.x

R Core Team. (2019). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. URL https://www.R-project.org/

Reid, J. M., Travis, J. M. J., Daunt, F., Burthe, S. J., Wanless, S. & Dytham, C. (2018). Population and evolutionary dynamics in spatially structured seasonally varying environments. Biological Reviews, 93(3), 1578-1603. DOI: https://doi.org/10.1111/brv.12409

Sandercock, B. K., Nilsen, E. B., Brøseth, H. & Pedersen, H. C. (2011). Is hunting mortality additive or compensatory to natural mortality? Effects of experimental harvest on the survival and cause-specific mortality of willow ptarmigan. Journal of Animal Ecology, 80(1), 244-258. DOI: https://doi.org/10.1111/j.1365-2656.2010.01769.x

Skov, C., Baktoft, H., Brodersen, J., Brönmark, C., Chapman, B. B., Hansson, L.-A. & Nilsson, P. A. (2011). Sizing up your enemy: individual predation vulnerability predicts migratory probability. Proceedings of the Royal Society B, 278, 1414-1418. DOI: https://doi.org/10.1098/rspb.2010.2035

Sokal, R. R. & Rohlf, F. J. (1995). Biometry: The principles and practice of statistics in biological research, 3rd edition. W.H. Freeman and Company, New York.

Somveille, M., Rodrigues, A. S. L. & Manica, A. (2015). Why do birds migrate? A macroecological perspective. Global Ecology and Biogeography, 24(6), 664-674. DOI: https://doi.org/10.1111/geb.12298

Stoffel, M. A., Nakagawa, S. & Schielzeth, H. (2017). rptR: repeatability estimation and variance decomposition by generalized linear mixed-effects models. Methods in Ecology and Evolution, 8, 1639-1644. DOI: 10.1111/2041-210X.12797

Svorkmo-Lundberg, T., Bakken, V., Helberg, M., Mork, K., Røer, J. E. & Sæbø, S. (2006). Norsk VinterfuglAtlas. Fuglenes utbredelse, bestandsstørrelse og økologi vinterstid. Norsk ornitologisk forening. Klæbu.

Townsend, A. K., Frett. B, McGarvey, A. & Taff, C. C. (2018). Where do winter crows go? Characterizing partial migration of American Crows with satellite telemetry, stable isotopes, and molecular markers. The Auk.,135(4), 964-974. DOI: 10.1642/AUK-18-23.1

Weeden, R. B. (1964). Spatial Separation of Sexes in Rock and Willow Ptarmigan in Winter. The Auk, 81(4), 534-541.

Åkesson, S., Ilieva, M., Karagicheva, J., Rakhimberdiev, E., Tomotani, B. & Helm, B. (2017). Timing avian long-distance migration: form internal clock mechanisms to global flights. Philosophical Transactions of the Royal Society B: Biological Science, 372(1734), 20160252. DOI: http://dx.doi.org/10.1098/rstb.2016.0252

TABLE 1: Number of radio-tagged female willow ptarmigan captured in the capture sites Guslia and 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

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

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

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

Response	Model	K	AIC_c	ΔAIC_c	AIC_cWt	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

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

Response	Model	K	AICc	ΔAIC_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 ×Age	6	393.58	2.65	0.12	0.92
	Weight + Age	5	394.28	3.35	0.08	1.00

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

Response	Model	K	AIC_c	$\Delta\mathrm{AIC}_c$	$\mathrm{AIC}_c\mathrm{Wt}$	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

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

Response	Model	K	AIC_c	ΔAIC_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

FIGURE CAPTIONS

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

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

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

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

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

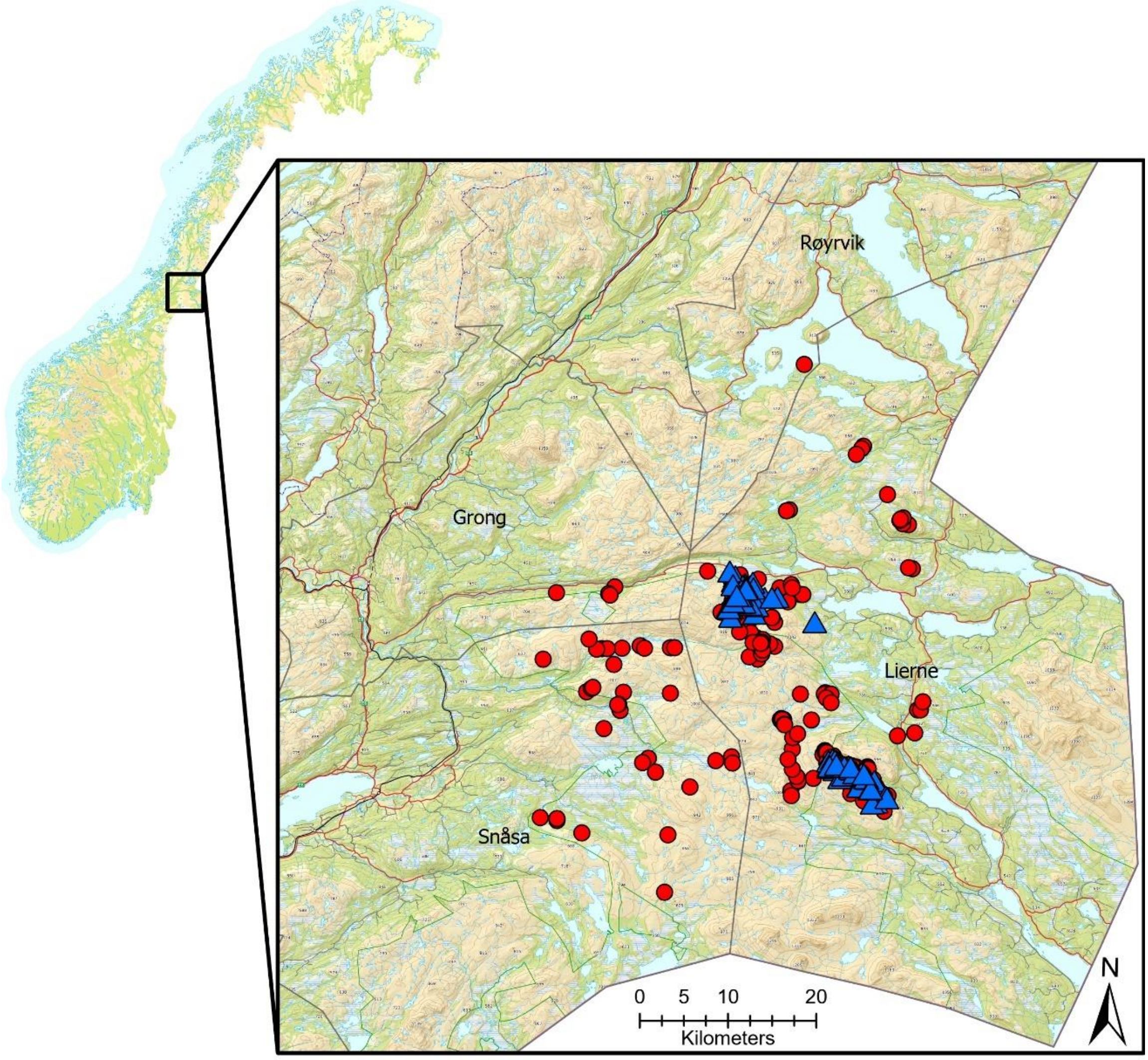


FIGURE 1

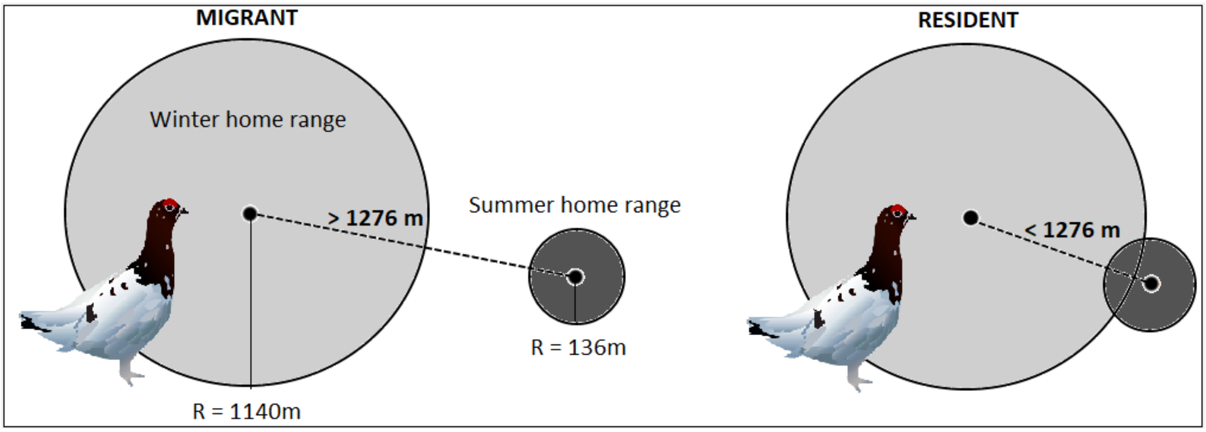
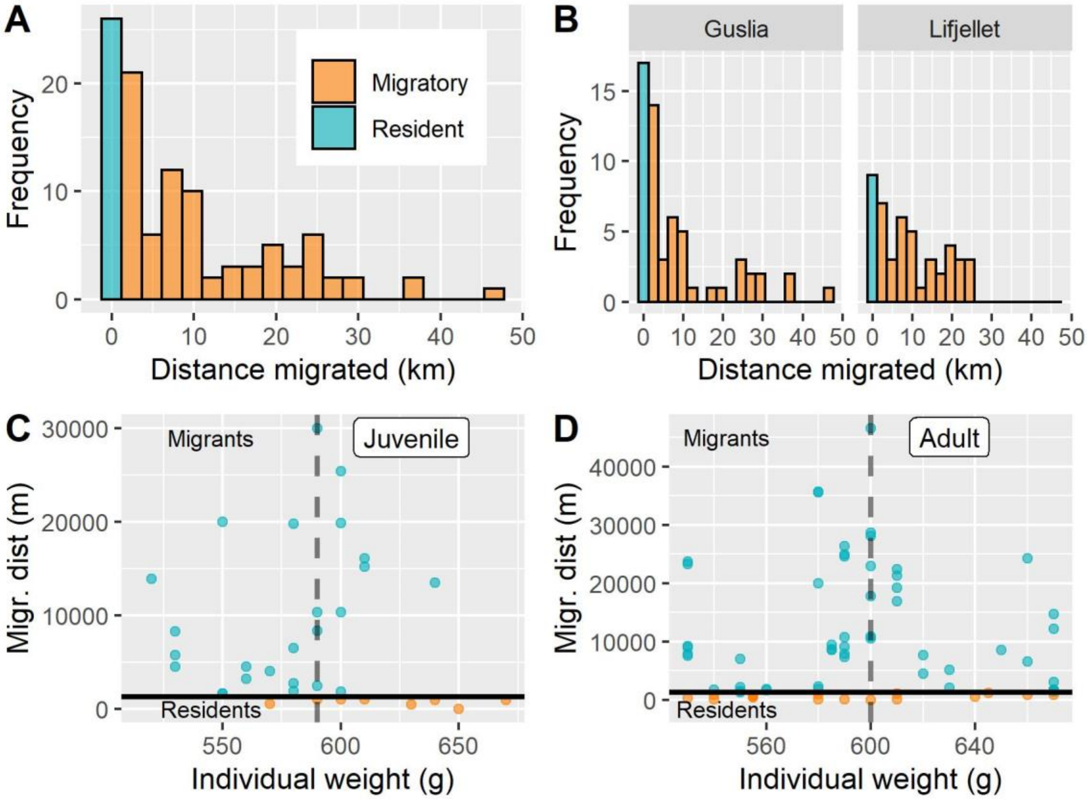

MIGRANT
Winter home range
> 1276 m
Summer home range
R = 136m
R = 1140m
RESIDENT
< 1276 m

FIGURE 2

713



714

715 **FIGURE 3**

716

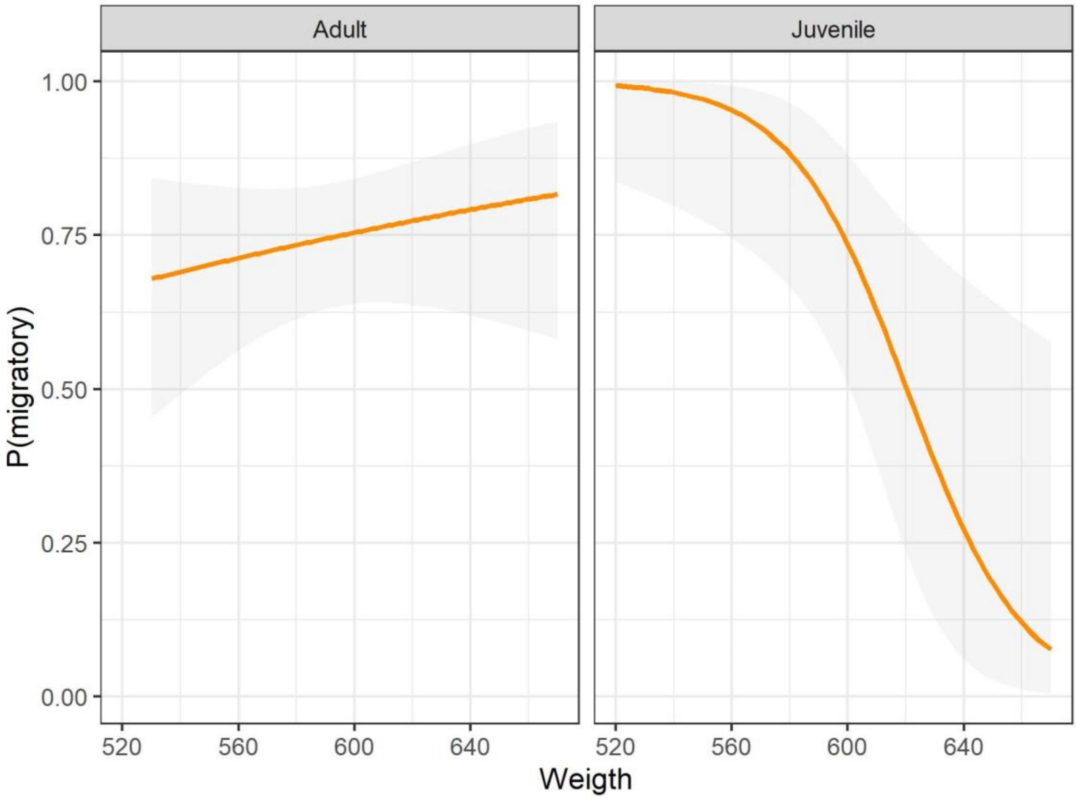

Adult
Juvenile
1.00
0.75
0.50
0.25
0.00
P(migratory)
520
560
600
640
520
560
600
640
Weigth

FIGURE 4

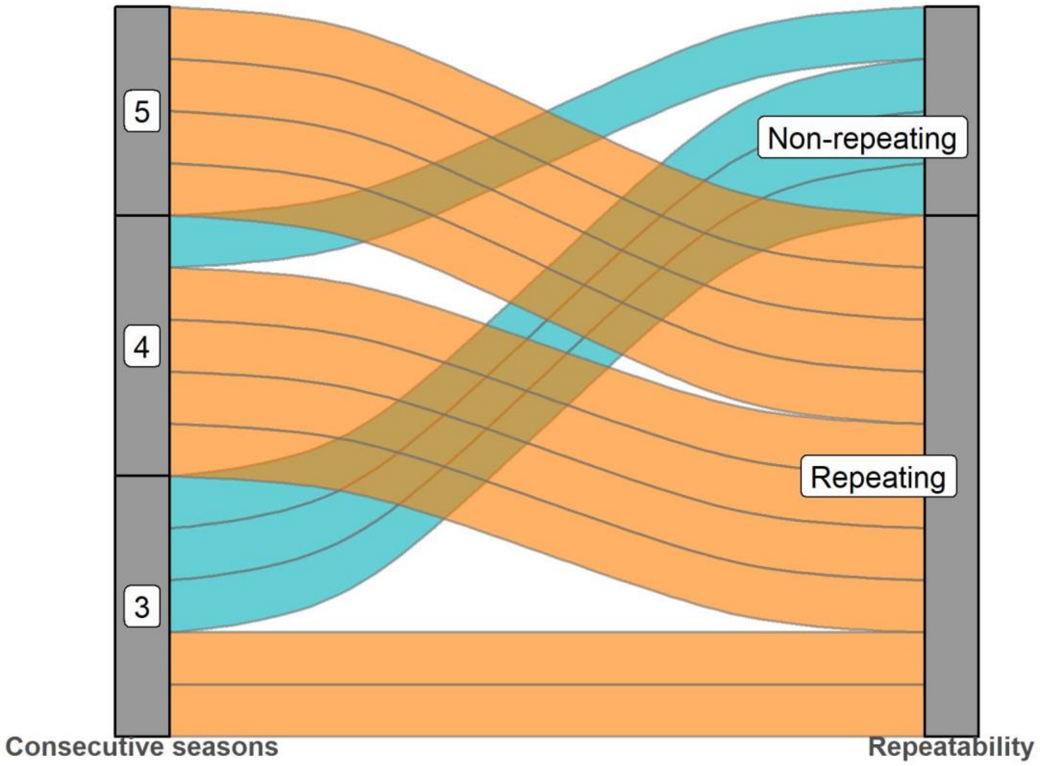

5
4
3
Non-repeating
Repeating
Consecutive seasons
Repeatability

FIGURE 5