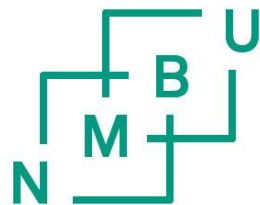Norwegian University
of Life Sciences

Drivers and Consequences of Partial Migration in an Alpine Bird Species

Øyvind Lorvik Arnekleiv

Masters of Science in General Ecology

Preface

This master thesis is in context with my Master of Science in Ecology at the Norwegian University of Life Sciences (NMBU). The thesis is a part of the project "The willow ptarmigan in a changing environment" conducted by Norwegian Institute for Nature Research (NINA) and Nord University and is financed by Norwegian Environment Agency. I would like to provide a huge thank you to my main supervisor Katrine Eldegard (Associate Professor, NMBU) for great feedback and guidance throughout the whole process of conducting this thesis. A huge thank you goes to my co-supervisor Erlend B. Nilsen (Senior Research Scientist, NINA) for great follow-up with all-time feedback, guidance and great discussions. I would also like to thank my second co-supervisor Lasse Frost Eriksen (PhD-student, NINA) for great feedback, discussions and time spent together in the field. Thanks to Markus Israelsen (Department engineer, NINA) for help with learning R, statistical advice and countless hours spent in the field. I would like to thank Signe Nybø (Research Director, NINA) for providing me a workplace at NINA in Trondheim and at last, thanks to everyone at NINA for great hospitality throughout my stay.

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Abstract

1. Partial migration, where parts of a population migrate between winter and summer (breeding) areas and the rest remain year-round resident, is a common phenomenon across several bird species. However, both drivers and consequences of the decision to migrate in partially migrating bird populations are poorly understood.

2. Several hypotheses have been put forward to explain why some individuals migrate whereas others stay resident, as well as the fitness consequence of a given strategy.

3. In this thesis, I used data from n=73 radio-tagged female willow ptarmigan *Lagopus lagopus* in an alpine study area in Central Norway to test key hypothesis about drivers and consequences of partial migration. Specifically, I tested i) to which extent the decision to migrate was dependent on individual state variables such as age and body-size, ii) if individuals repeat migratory behaviour between seasons, and iii) if the consequences of migratory strategy affect fitness in terms of nesting performance.

4. I found that juvenile birds with small body-sizes were more likely to migrate whereas large juveniles stayed resident. However, body-size did not explain migratory strategy in adult females. There was strong evidence for high individual repeatability of migratory strategy between seasons. However, migratory strategy did not explain variation in nesting performance between individuals.

5. These results suggest partial migration in willow ptarmigans to be determined by body size as juveniles, which becomes a part of the individual life history as a fixed strategy. Fitness seems not to be affected by migratory strategy, but survival as fitness parameter should be accounted for. This study provides data which enhances our knowledge of migratory behaviour in female willow ptarmigans and should be taken into consideration in further advancements in managing this species.

Keywords: Alpine bird, game bird, Lagopus lagopus, long-term monitoring, migratory strategy, partial migration, telemetry, tetraonid, willow ptarmigan.

Contents

Introduction

Migration between distinct breeding and wintering areas is an adaptation to seasonal environmental variation that is found in several species across a wide range of taxa. Well known examples are the annual long-distance migrations, carried out by many bird species (Dingle & Drake, 2007; Åkesson et al., 2017) that typically breed at northern latitudes and migrate south in the winter. 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 at all times of the year. In contrast, many other bird species do not perform long-distance seasonal migrations, and have instead adapted to stay at northern latitudes all year round 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 quality and availability of resources vary between seasons (Barraquand & Benhamou, 2008; Fedy et al., 2012). Some overwintering populations are partially migratory (Chapman et al., 2011), implying that only parts of the population migrate 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 within-species and within-population variation in migratory behaviour. Chapman et al. (2011) described three types of partial migration: 1) Populations with yearly variation in individual breeding participation where non-breeding individuals stay resident while breeders migrate; 2) Migrants and residents breed in the same place (sympatrically) but overwinter in different locations (allopatrically); and 3) Migrants and residents overwinter sympatrically but breed allopatrically, also referred to as "breeding partial migration". Lundberg (1997; 1988) suggested that the evolution of partial migration could be explained by two alternative hypotheses; it could 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.

Three well established hypotheses have been put forward to explain the drivers behind partial migration based on individual traits (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 high 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 at 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 partial migratory population are poorly understood (Chapman et al., 2011; Berg et al., 2019), but differences between resident and migratory individuals in fitness parameters such as survival and reproduction have been reported in both theoretical and empirical studies. Theoretical studies suggest a conditional strategy can yield unequal fitness between strategies in partial migratory populations (Lundberg, 1987; Lundberg, 1988; Chapman et al., 2011; Kokko, 2011). The majority of empirical studies do also report fitness to be unequal between migratory strategies (Buchan et al., 2019). Gillis et al. (2008) found that migratory American dippers *Cinclus mexicanus* in a partially migratory population had lower reproductive success and higher survival rates compared to resident individuals. The higher survival rates did however not offset the low reproductivity. Adriaensen & Dhondt (1990) found both higher survival and reproductive success in resident European robins *Erithacus rubecula* and hypothesized the differences to be caused by 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

suggest migration to be a losing strategy in partially migrating populations, and that the choice to migrate may be to make "the best of a bad job". However, empirical studies on the consequence of partial migration seems to be limited to passerines only, 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). This include tetraonid populations in the northern hemisphere (Hörnell-Willebrand et al., 2014), but there are no studies on the fitness consequence of alternative migration strategies in tetraonid populations.

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 demonstrated that ptarmigans are migratory (Irving et al., 1967; Hoffman & Braun, 1975; Gruys, 1993; Brøseth et al., 2005; Hörnell-Willebrand et al., 2014; Nilsen et al., 2020b). Hörnell-Willebrand et al. (2014) reported large individual variation in seasonal migration distances in willow ptarmigans. Some individuals were considered to be residents and others to be migrants, suggesting that the population was partially migratory. However, empirical data suggests that several Norwegian willow ptarmigan populations stay resident year-round (Pedersen et al., 2003). Willow ptarmigan populations that show migratory tendencies often gather in distinct wintering areas (Weeden, 1964), which suggests these populations to be breeding partial migratory due to some individuals migrating to breeding areas during spring while others stay resident in the wintering area. Yet, the drivers and consequences of partial migration in willow ptarmigan is still poorly understood.

In this thesis, I tested a set of a-priori hypotheses about partial migration patterns in female willow ptarmigans. 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, I hypothesized that:

1) Female willow ptarmigans 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 ptarmigans.
3) Resident female willow ptarmigans have higher reproductive success than migrants.

Following recommendations to preregister hypotheses when conducting confirmatory (hypothesis testing) research (Nilsen et al., 2020a), the hypotheses in this thesis were preregistered on the Open Science Framework (OSF) prior to getting access to and analysing data (Arnekleiv et al., 2019).

Methods

Study area

The study was mainly conducted in Lierne municipality in the northeastern part of Trøndelag county, Norway. Extensions of the study area to neighbouring municipalities Snåsa, Røyrvik and Grong occurred due to long-migrating individuals (Figure 1). Ptarmigans 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*,* Ericaceae dwarf shrubs and bryophytes.
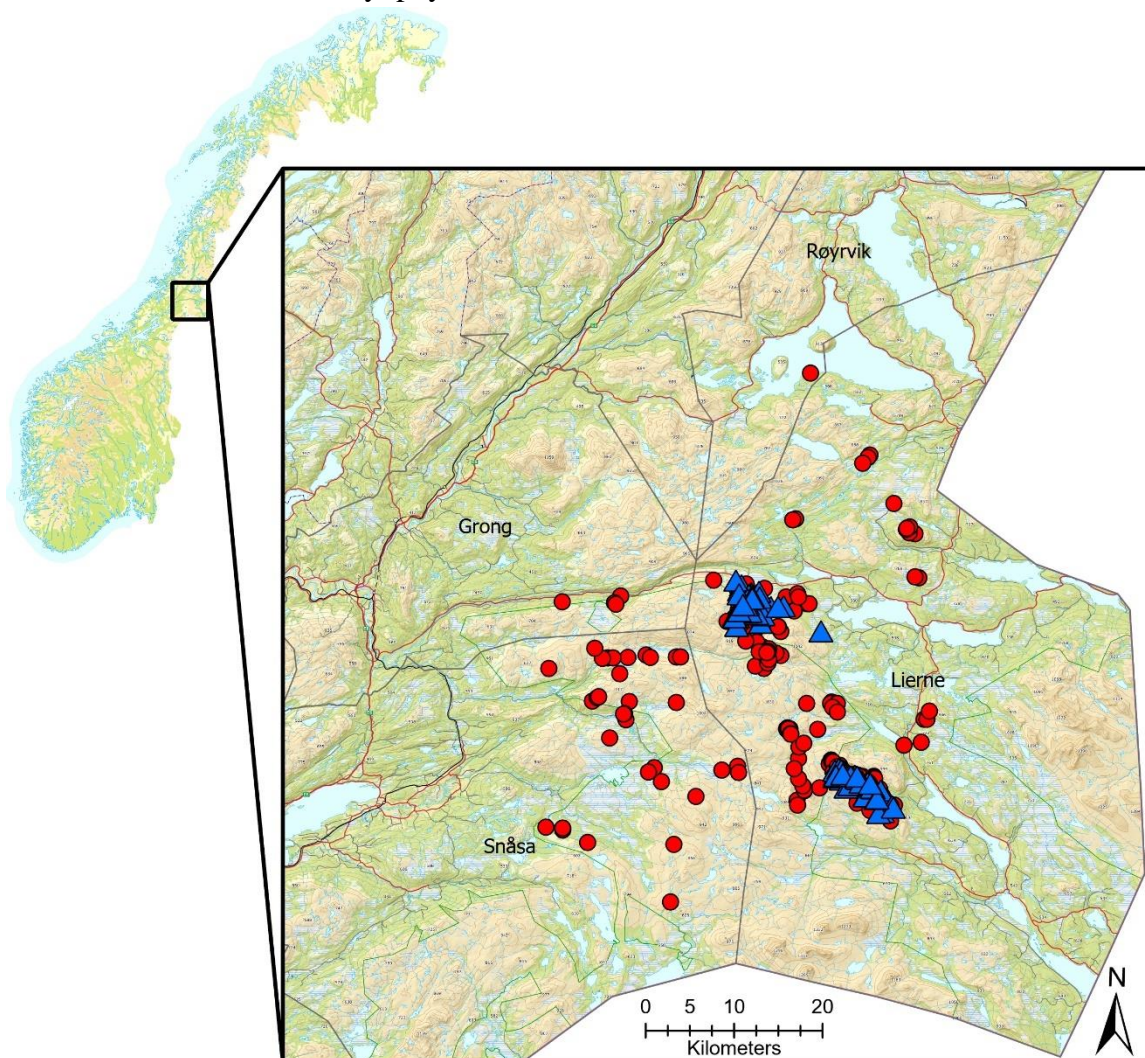

Figure 1: Triangulated positions (red circles) of all female willow ptarmigan during the study period in the winter (January – March) and summer (May – July) seasons. The blue triangles represent capture locations, where the upper cluster is Lifjellet capture site and the lower cluster is Guslia capture site.

Data collection

Willow ptarmigans were captured during February and March each winter in the period 2015 to 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 (Pesola LightLine 1000g spring scale – rounded to nearest 5 g) and wing length (Axminster Workshop Hook Rule 300mm – wrist 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 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 (year after hatching year) 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 banded 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. Radio-transmitters were programmed to send mortality-signals after recording no movement for more than 12 hours. In March 2018, five ptarmigans 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 ptarmigans 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. Occasionally, other tracking techniques were used to determine bird positions; taking cross bearings when tracking on foot, and tracking from plane or helicopter. Few positions were collected in January and December, due to short days and challenging weather conditions. The time lag between telemetry sessions varied from 15-120 minutes. Headphones were used in windy conditions to make it easier to determine the strongest signal and thus increase accuracy of the recorded bearings. Additional positions were either on-site direct observations from captures or homing in on individuals.

Nesting success in spring were determined by homing in on radio-tagged females to check whether they were nesting. Incubating females were flushed off the nest, eggs were counted, and a wildlife camera (Reconyx HF2X Hyperfire 2 or Wingcam II TL) was deployed at each

nest to determine nest fate. 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 as well as examining pictures from the cameras.

Data preparation

In order to examine movements between seasons, a winter season (January – March) and a summer season (May – July) was defined. 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). In the winter season, 1-2 positions were collected per individual, whereas during the summer season 1-5 positions were collected.

Table 1: Number of radio-tagged female willow ptarmigans 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

I calculated an average 'baseline' winter home range size from positions of three of the GPS-tagged ptarmigans in March. Individual home range sizes were calculated as 95% Minimum Convex Polygons (using the function *mcp* in R package adehabitatHR, Calenge, 2006). The average 95% MCP for the three GPS-tagged females was 4,08 km^2. Before calculating the individual 95% MCPs, I used the following algorithm to detect and remove inaccurate data points in the GPS-data (i.e. due to GPS error); if the distance between point A and B was two times greater than the distance between point A and C, point B was discarded as an outlier. Positions from the GPS-tagged ptarmigans 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 confirmed to be alive during minimum one winter season, I 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.

To estimate the size of the summer home ranges, I used data from female ptarmigan with n≥3 positions during the summer season (May - July). For each female, I draw 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, I used the median of all the home range sizes (n=46). The baseline home range area was estimated at 0.058km², corresponding to a circular home range with radius=136 m, which is comparable to home range sizes reported from previous studies (Eason & Hannon, 2003). For each of the females confirmed to be active during minimum one summer season, I assumed a circular summer home range of 0.058km² (radius = 136m) 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, I skewed the activity centre for nesting hens (n=68) towards the nest location, by assigning equal weights to the position of the nest and the sum of all other positions. All spatial computing was done using R (R Core Team, 2019) and validated visually using QGIS (QGIS Development Team, 2019).
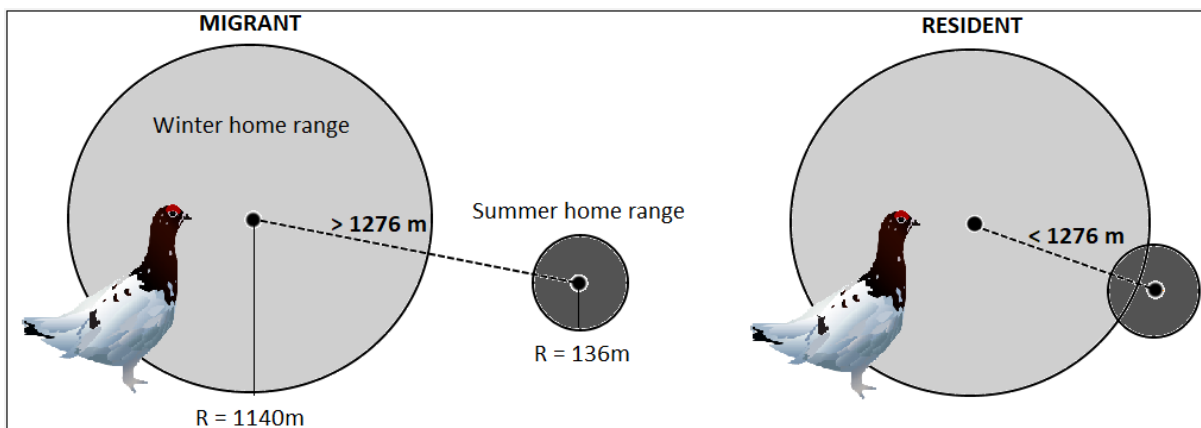

Figure 2: Female ptarmigans were classified as either migrants, if the distance between the centroids of winter and summer home ranges exceeded 1276 meters (no overlap), or residents, if the distance between the centroids of winter and summer home range was less than 1276 (overlap).

Based on the summer and winter home ranges described above, migratory strategy was determined by the overlap between the winter home range and the home range from the consecutive summer season (Figure 2), and between the summer home range and the home range from the consecutive winter season. Females with overlapping home ranges where classified as residents, whereas females with no overlap between summer and winter home ranges were classified as migrants. Based on the calculated home range sizes, ptarmigan moving further than 1276m (radius winter home range + radius summer home range) was thus classified as migrants and females moving less than 1276m, were classified as residents.

Statistical analysis

To test whether the decision to migrate was influenced by age and body weight, I used a generalized linear mixed model (glmer function in R package lme4; Bates et al., 2015) with migratory strategy as a binary response variable and body weight, age and body weight×age interaction as fixed explanatory terms. For all models, the body weight variable was standardized by centring the mean and dividing it in the standard deviation. Bird identity was included as random effect to account for repeated observations of individual birds. To test whether the distance migrated was influenced by age and body weight, I fitted a linear mixed model (lmer function in lme4) with migratory distance as response variable, weight, age and weight×age interaction as fixed explanatory terms. I 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 test if migration was a fixed strategy in female willow ptarmigans, I estimated the repeatability in a mixed effect model with movement distance as response variable. Repeatability *R* were measured of the variance within and among groups in the data (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), with 95% confidence intervals estimated based on parametric bootstrapping (n=1000). A likelihood ratio test (LRT) was used to test whether the repeatability was above 0.

To test whether reproductive success was influenced by migratory strategy, I 1) fitted a GLMM on the Poisson distribution 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. Then, 2) I fitted a GLMM with nest fate as binary response variable and migratory strategy, age, weight and year as explanatory variables and with bird identity as random effect. After fitting the full models, I used Akaike's information criterion (AIC) (see e.g. Bolker et al., 2008) to perform model selection. The AIC encourages parsimony by adding a term to penalise more complex (larger number of parameters) models (e.g. Bolker et al., 2008).

Results

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, whereas 17 were summer area to winter area movements. Overall, three times as many cases of migratory (n = 78, 75%) than of resident (n = 26, 25%) behaviours were observed (Table 2). Of the 73 individuals included in the analyses, one seasonal movement was recorded for 59 birds and more than one seasonal movement were recorded for 14 birds.

Table 2: Distribution of cases of migratory and resident behaviour observed for 73 female willow ptarmigans 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	

Mean and median movement distance – for both juvenile and adult females – was substantially longer than the distance limit for being classified as migrant (1276m; Table 3). Overall, 67% of the seasonal movements were shorter than 10 km, 25% was between 10 and 25 km, whereas only a few (8%) seasonal movements were longer than 25km (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). Only one resident juvenile female willow ptarmigan weighed less than the median/mean weight, whereas 54% of the migrating juveniles weighed less than the median/mean weight (Figure 3C). For adults, there was no clear pattern in the distribution of seasonal migration behaviours in relation to body weight (Figure 3D).

Table 3: Distance moved and weight of juvenile and adult female willow ptarmigans. N distance is the total number of movement distances observed, whereas N weight is the number of individuals weighed.

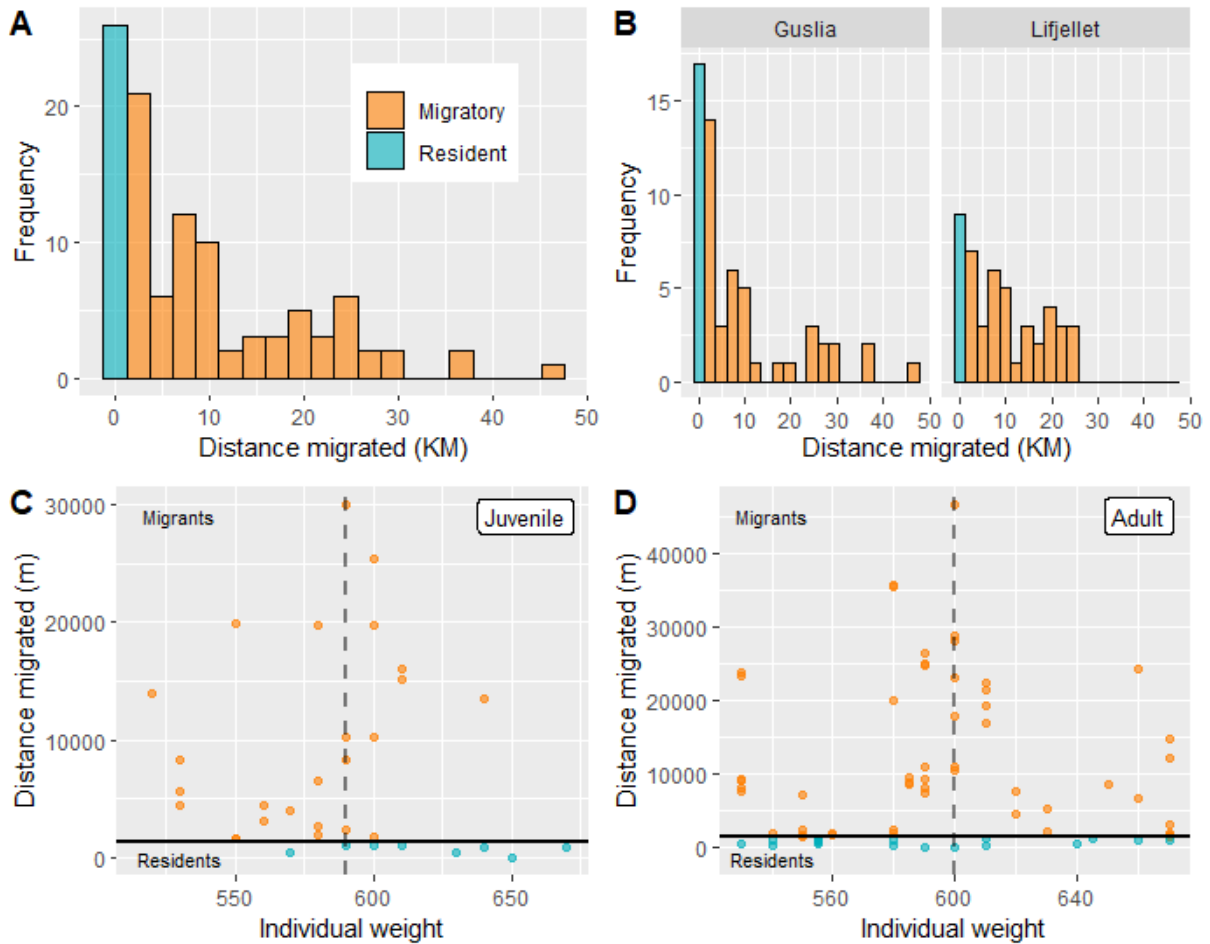|	Age	Min.	Mean	Median	Max.	N
Distance (km)	Juv	0.0	7.8	4.5	30	33
	Ad	0.0	9.6	7.0	46.5	71
Weight (g)	Juv	520	590	590	670	33
	Ad	530	600	600	670	40

Figure 3: **Panel A:** Distribution of all observed seasonal migration distances for female willow ptarmigans. Blue bar represents resident individuals, orange bars represents migrants. See figure 2 for definition of resident and migratory individuals. **Panel B:** Differences in distance migrated between the two capture sites within the study area. **Panel 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 (1276m). **Panel D:** Same as panel C, but for adult birds.

When modelling migratory strategy as a function of age and body weight, I found strongest support for the full model including the main effects age and weight and the weight × age interaction (Table 4, Appendix B). 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 strong influence of body weight on migration strategy.

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 ptarmigans during the five-year study. Results from a generalized linear mixed model (GLMM) 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.

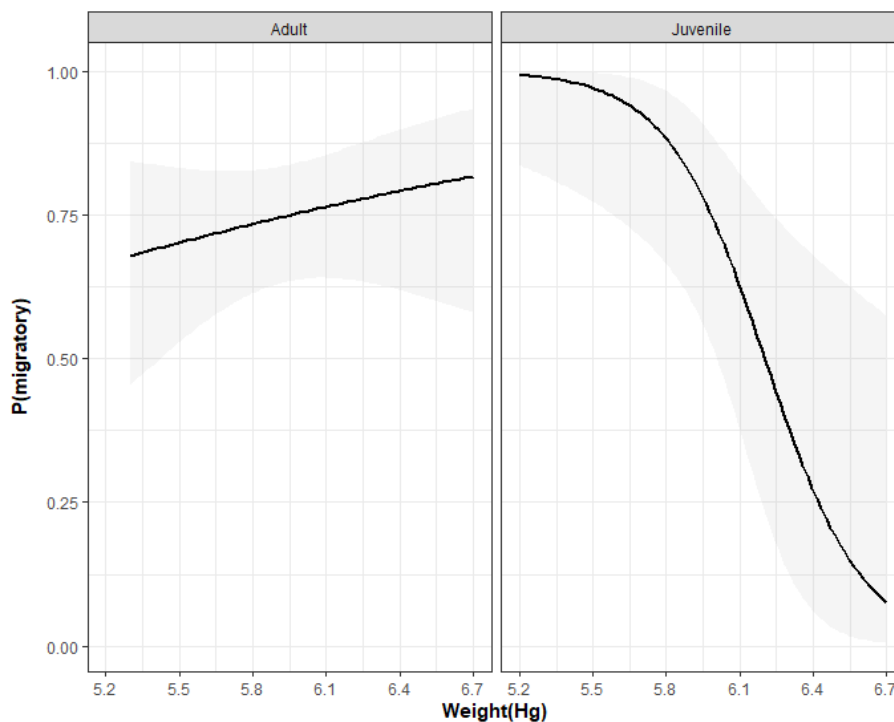| Response	Model	K	AIC_c	ΔAIC_c	AIC_cWt	CumWt
Migratory strategy	Weight + Age + Weight ×Age	5	105.15	0.00	0.79	0.79
	Weight	3	109.72	4.57	0.08	0.87
	Intercept	2	109.82	4.66	0.08	0.94
	Weight + Age	3	111.81	6.65	0.03	0.97
	Age	3	111.91	6.76	0.03	1.00

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

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 ptarmigans during the five-year study. Results from a linear mixed model (LMM) 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	Age	4	738.95	0.00	0.45	0.45
	Intercept	3	740.16	1.21	0.25	0.70
	Weight + Age	5	740.99	2.05	0.16	0.86
	Weight	4	742.27	3.32	0.09	0.94
	Weight + Age + Weight ×Age	6	743.12	4.17	0.06	1.00

When modelling distance moved as a function of age and weight, I found some support for a difference between juveniles and adults (Table 5, Figure 5, Appendix B), but the intercept model was competitive with the model with age as the only explanatory variable. Age was an important variable with a total AICc weight of 0.61 in the three most supported models.

Repeatability of migratory behaviour

Repeatability of migratory behaviour within individuals was very high (Figure 6), and repeatability within individuals increased each consecutive season. Agreement repeatability (based on the intercept only model) for movement distance revealed very high repeatability (R = 0.83, 95%CI = 0.70-0.90, p < 0.0001). Adjusted repeatability (when including age, a fixed effect in the model) was equally high (R = 0.84, 95%CI = 0.729 – 0.919, p < 0.0001).

Reproductive success

A total of 68 nesting events was observed during the study period, 57 included data on number of eggs and 59 included information about nest fate. Of the 59 nests that included data for nest fate, 20 were residents and 39 migrants. There were 15 failed and 15 successful nesting attempts in Lifjellet and 12 failed and 17 successful nesting attempts in Guslia. For 2nd year birds (marked as juveniles in winter) nesting success of residents were 10% higher than for migrants (Table 6). For adults, there was no difference in nesting success between residents and migrants.
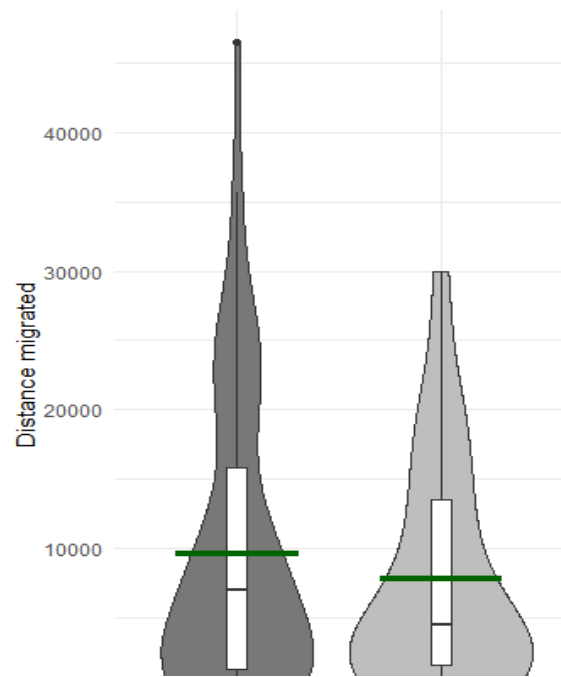

Figure 5: Relationship between age and migratory distance (m) in female willow ptarmigans. Violin width = frequency in migration distance and green lines = mean migration distance.
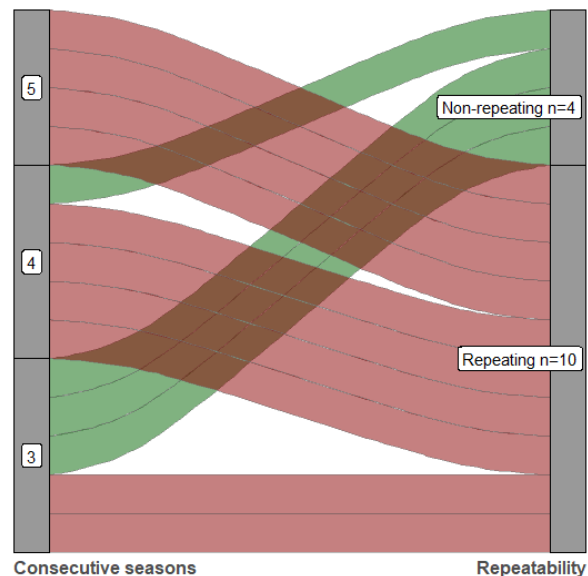

Figure 6: Repeatability of decision to migrate or remain resident between individuals. Red bands = individuals with 100% repeating migration strategy between consecutive seasons. Green bands = individuals that changed migration strategy.

Table 6: Nesting success and weight for different age groups (first time nesting i.e. 2nd year and second time nesting or more i.e. 3rd year+) and migratory strategies of female willow ptarmigans.

	Age	Mean n eggs/nest	Hatched nests (%)	Mean weight (g)
Residents	2nd year	9.4	57.1	615
	3rd year+	9.5	53.9	594
Migrants	2nd year	9.2	47.0	565
	3rd year+	10.1	59.0	594

Modelling number of eggs laid as a function of migratory strategy, age and weight, model selection suggested the intercept model to be most supported (Table 7, Appendix A & B). The models with age, weight and migratory strategy, respectively, as single explanatory variables, were the only models with >0.10 AICc weight whereas I found little or no support for the more complex models.

Table 7: 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 ptarmigans during the five-year study. Results from a generalized linear mixed model (GLMM) with count response and log link function, assuming Poisson 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
N eggs	Intercept	2	259.11	0.00	0.38	0.38
	Age	3	260.84	1.73	0.16	0.54
	Weight	3	261.04	1.93	0.15	0.69
	Migratory strategy	3	261.26	2.14	0.13	0.82
	Age + Weight	4	262.96	3.85	0.06	0.88
	Age + Migratory strategy	4	263.03	3.92	0.05	0.93
	Migratory strategy + Weight	4	263.18	4.07	0.05	0.98
	Migratory strategy + Age + Weight	5	265.17	6.06	0.02	1.00

When modelling nest fate as a function of migratory strategy, age and weight, model selection suggested the intercept model to be most supported (Table 8, Appendix A & B), the second most supported model was not competing with the intercept model.

Table 8: 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 ptarmigans during the five-year study. Results from a generalized linear mixed model (GLMM) with binary response (Y = 1 = hatched, Y = 0 = abounded/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	$AIC_c Wt$	Cum Wt
Nest fate	Intercept	2	77.89	0.00	0.41	0.41
	Age	3	79.90	2.01	0.15	0.56
	Migratory strategy	3	80.02	2.14	0.14	0.70
	Weight	3	80.04	2.16	0.14	0.84
	Age + Migratory strategy	4	82.10	4.21	0.05	0.89
	Age + Weight	4	82.16	4.27	0.05	0.94
	Migratory strategy + Weight	4	82.22	4.33	0.05	0.98
	Migratory strategy +Age + Weight	5	84.40	6.52	0.02	1.00

Discussion

I found that the willow ptarmigan population in my study area was partially migratory, with a majority (75%) of the females carrying out seasonal migration. Similar behaviour has been reported from several other species of Galliformes, e.g. spruce grouse *Falcipennis canadensis* (Herzog & Keppie, 1980) and blue grouse *Dendragapus obscurus* (Cade & Hoffman, 1993). Tian et al. (2018) emphasized the lack of research on long-term monitoring and life history information in many Galliformes species in which reduces the success of conservation, here I present the first study to quantify explicitly partial migration in ptarmigan. Partly in line with my first hypothesis, I found that body size (weight) affected the decision to migrate or to remain resident, but this effect was only found among juvenile birds. Juveniles with large body size had a higher probability of remaining in the winter area, whereas body size did not appear to be an important driver for the choice of migratory strategy in adult females. In contrast with my second hypothesis, I found that migration was a fixed strategy, and individuals for which data on more than one seasonal movement was available showed a high degree of repeatability in migratory behaviour. Finally, I found no support for my third hypothesis, i.e. that resident female willow ptarmigans have higher reproductive success than migrants.

Migration strategy in relation to age and body weight

One key finding of my study was that juvenile willow ptarmigan with small body sizes had a higher probability of migrating. As discussed in the introduction, such a pattern can potentially be explained by i) the body size hypothesis, ii) the dominance hypothesis, or iii) arrival time hypothesis. The possible drivers of partial migration presented above (Chapman et al., 2011) are well known hypotheses of which both the body size and dominance hypotheses include body size as a predictor of migratory strategy. Also, partial migration may be driven by other ecological mechanisms such as dispersal.

As found in this study, migratory strategy being affected by body size, 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) on a partial migratory skylark population, where migration strategy was dependent on body size and immune function but not on age and sex. Hence, they suggested that migratory strategy is determined by plastic state variables rather than fixed state variables. The body size hypothesis predicts that large body sizes can be advantageous in order to endure thermal variations and variation in food availability in harsh

winter climates. Willow ptarmigans in this study population gathers in distinct winter areas which holds traits that enhances survival, e.g. food abundance and benign winter conditions. Therefore, I think it is unlikely that the body size hypothesis explain why body size affects migratory strategy in juvenile willow ptarmigans.

Migratory strategy being affected by body size may be better explained by the dominance hypothesis (Gauthreaux, 1982) which predicts individuals with large body sizes to have a competitive advantage to smaller individuals, forcing smaller individuals to migrate. For the dominance hypothesis to work there must be an intraspecific competition for limited resources, and the frequency of migrants may be positive density-dependent and can vary with environmental factors (Newton, 1998; Matthysen, 2005). Often, food is regarded a limited resource in harsh winter conditions with a continuous snow cover, but due to ptarmigans gathering in food rich areas during winter this seems rather unlikely. Another limited resource may be nesting sites (Gillis et al., 2008), where large dominant individuals 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 territory in spring. However, two previous studies on dispersing juvenile willow ptarmigan report natal dispersal distance not to be density-dependent (Brøseth et al., 2005; Hörnell-Willebrand et al., 2014). Due to the high number of adults and juveniles with small body sizes migrating out of the wintering areas prior to spring, one still cannot exclude intraspecific competition driven by positive density-dependent factors as a driver of partial migration in this ptarmigan population.

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). There was not sufficient data in my study to investigate whether this hypothesis could be a potential explanation for partial migration in the studied ptarmigan population. 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 warm weather and early spring, resident ptarmigans may have an advantage in occupying high quality territories prior to migrating individuals.

I found that body size did only affect migratory strategy in juveniles, whereas adults followed the same migration strategy as previous years. Therefore, I cannot exclude factors determining

natal dispersal as a possible drivers behind partial migration in willow ptarmigans. Natal dispersal is defined as an individual's movement from its birth site to a breeding site (Howard ,1960), where avoidance of inbreeding depression and intraspecific competition are pointed as important drivers for this mechanism (Liu & Zhang, 2008 and references within). Dispersal in willow ptarmigans is normally sex biased with females dispersing further than males (Warren & Baines, 2007; Hörnell-Willebrand et al., 2014; but see Brøseth et al., 2005). This strategy is associated with avoiding inbreeding depression (Lebigre et al., 2008) and a combination with intraspecific competition in the wintering areas may explain why smaller individuals have a higher chance of dispersing/migrating.

Migratory strategy being affected by body size 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 work as a driver of partial migration in juvenile ptarmigans. In order to fully test the arrival time hypothesis, more frequent collection of ptarmigan positions is necessary to get a detailed picture of arrival time at the nesting sites – utilizing ptarmigans with GPS-transmitters may increase data amount and will improve position accuracy. Natal dispersal in order to prevent inbreeding depression and competitive escape may be a better explanation for the observed pattern, mainly because body size did not affect the adult female's migratory strategy and migratory behaviour becomes fixed once established within an individual.

Repeatability of migration strategy

In contrast to the pattern found for young birds, with an increased propensity to migrate for smaller birds, no such pattern was observed among adults. Moreover, the repeatability in migration strategy within individuals was very high. This suggest that once established in the first year, migratory behaviour is a rather fixed strategy. My 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., 2018). 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 77,8% and with high breeding-site fidelity. Opposite of willow ptarmigans, 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).

An explanation for this fixed behaviour may be the avoidance of several fitness reducing factors such as a higher mortality rates that are associated by switching breeding sites between years (often referred to as breeding dispersal) (Greenwood & Harvey, 1982; Daniels & Walters, 2000; Bonte et al., 2011). Returning to the same territory may also be beneficial due to familiarity to 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) the majority of studies on the consequence of partial migration reported higher mortality in migrants than in resident individuals. However, a study on Ruffed grouse *Bonasa umbellus* from Wisconsin found no increase in mortality rates due to dispersal (Small et al., 1993). They did not study the effect of breeding dispersal on reproductive success. The high repeatability in migratory strategy within willow ptarmigans may be driven by not wanting to change neither breeding sites and wintering sites due to familiarities. However, there is a possibility that breeding dispersal might also be common in the population whereas individuals breaking the observed fixed pattern have an increased mortality and are thus less represented in the data.

Nesting success in relation to migration strategy

In contrast to my hypothesis, I did not find any statistical support for higher reproductive success (measured as clutch size or nest fate) of resident birds. This is however partly in line with a recent multi-taxa meta-analysis carried out by Buchan et al. (2019), reporting that fitness differences between resident and migratory individuals is more evident for survival compared to reproductive success. Specifically, they reported that 73% of the studied populations reported higher fitness of residents, 22% reported higher fitness of migrants, and 5% reported equal fitness. They argue the reason of this skewed distribution can be that anthropogenic changes reduce the survival of migratory individuals. My findings suggest migratory strategy to be fixed within willow ptarmigans and fits with the result of migratory strategy not affecting nesting success, so that both strategies yield equal fitness. However, my results show some tendency that resident female first-time breeders have higher reproductive success than migratory first-time breeders, but more data is needed to confirm this statistically. At the same time, the percentage of previous studies reporting equal fitness is low (5%; Buchan et al., 2019).

For fitness to be equal between the two migratory strategies, theoretical studies suggest higher survival in migrants will offset the increased reproductive 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. My results show a high proportion of the willow ptarmigan population to be migrants with little variations 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 reward the strategy with lowest frequency in the population i.e. density-dependent factors. 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 changes in the ratio between migratory strategies in this willow ptarmigan population may indicate that there is an equilibrium. This may be an explanation of why I did not find any differences in fitness reward between the two strategies. In this 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 in the majority of empirical studies (Chapman et al., 2011; Buchan et al., 2019).

Anthropogenic change

Population sizes in montane bird species are declining in Fennoscandia, and anthropogenic pressures such as climate and land-use change is pointed at as the main drivers for this decline (Lehikoinen et al., 2014; Lehikoinen et al., 2019). Climate change increases the frequency of extreme weather (Meehl et al., 2000) and willow ptarmigans can be vulnerable for extreme weather events during winter due to mild periods or extreme winds may develop a crust on the snow surface or icing – which may make vegetation inaccessible as food because it is covered with ice (Hansen et al., 2013). Increased competition for food resources can increase the proportion of migrants in the population which may increase mortality according to Buchan et al. (2019), they argue that the increased mortality in migrants can be due to anthropogenic change. Powerlines and fences are estimated to kill thousands of ptarmigans in Norway every year (Bevanger, 1995; Bevanger & Brøseth, 2000), and an increased pressure on development of wind farms in ptarmigan habitats may also increase both mortality and habitat loss. Willow ptarmigan is classified as Near threatened on the national red list of endangered species (Kålås et al., 2015) and is a nationally important game bird (Breisjøberget et al., 2018). My results prove that many individuals migrate far distances between seasons and emphasize that managers must take migration into consideration e.g. when determining quotas for the hunting seasons. Not accounting for migrants when determining hunting quotas might result in an overexploitation of the ptarmigan population (Eichholz et al. unpublished data).

Conclusion

I found that willow ptarmigans in central Norway were partially migratory, with a majority of migrants. The probability of remaining resident in the wintering area increased with increased body weight in juveniles, but not in adults. I found partly support for the dominance hypothesis for explaining partial migration, but cannot exclude the arrival time hypothesis or dispersal as other potential drivers. The migratory strategy displayed as juveniles appeared to be fixed throughout the individual's lifetime, and this likely explains why body weight did not affect migratory strategy in adults. I found no difference in average reproductive success between migratory strategies, which could indicate that both strategies yield equal fitness. However, survival should be included as fitness parameter to better understand the fitness consequence between strategies. Climate change might worsen wintering conditions and increase the proportion of migrants and land-use change may increase mortality in migrants through fences, power lines and wind turbines. Managers should take migration into consideration when making harvest management plans in order to prevent overexploitation.

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Appendix

Appendix A

Tabel A1: Extended candidate models and model statistics for explanation of nesting success (number of eggs) for female willow ptarmigans during the five-year study (year is included).

Response	Model	K	AIC$_c$	ΔAIC$_c$	AIC$_c$Wt	CumWt
N eggs	Intercept	2	259.11	0.00	0.39	0.39
	Age	3	260.84	1.73	0.17	0.56
	Weight	3	261.04	1.93	0.15	0.71
	Migratory strategy	3	261.26	2.14	0.13	0.84
	Age + Weight	4	262.96	3.85	0.06	0.90
	Age + Migratory strategy	4	263.03	3.92	0.06	0.95
	Migratory strategy + Age + Weight	5	265.17	6.06	0.02	0.97
	Year	6	266.20	7.09	0.01	0.98
	Weight + Year	7	267.83	8.71	0.01	0.99
	Age + Year	7	268.02	8.91	0.00	0.99
	Migratory strategy + Year	7	268.81	9.69	0.00	1.00
	Year + Age + Weight	8	269.88	10.77	0.00	1.00
	Migratory strategy + Year + Weight	8	270.47	11.36	0.00	1.00
	Migratory strategy + Age + Year	8	270.73	11.62	0.00	1.00
	Migratory s strategy + Age + Weight + Year	9	272.62	13.51	0.00	1.00

Table A2: Extended candidate models and model statistics for explanation of nesting success (nest fate) for female willow ptarmigans during the five-year study (year is included).

Response	Model	K	AIC$_c$	ΔAIC$_c$	AIC$_c$Wt	CumWt
Nest fate	Intercept	2	77.89	0.00	0.39	0.39
	Age	3	79.90	2.01	0.14	0.53
	Migratory strategy	3	80.02	2.14	0.13	0.67
	Weight	3	80.04	2.16	0.13	0.80
	Age + Migratory strategy	4	82.10	4.21	0.05	0.85
	Age + Weight	4	82.16	4.27	0.05	0.90
	Year	6	82.93	5.05	0.03	0.93
	Migratory strategy + Age + Weight + Year	5	83.79	5.91	0.02	0.95
	Migratory strategy +Age + Weight	5	84.40	6.52	0.02	0.96
	Migratory strategy + Year	7	85.10	7.21	0.01	0.97
	Age + Year	7	85.29	7.40	0.01	0.98
	Year + Weight	7	85.50	7.61	0.01	0.99
	Migratory strategy + Age + year	8	87.60	9.71	0.00	0.99
	Migratory strategy + year + Weight	8	87.76	9.88	0.00	1.00
	Year + Age + Weight	8	87.97	10.08	0.00	1.00

Appendix B

Parameter estimates for the two best models from each analysis.

Table B1: Two best model when modelling migration strategy as a function of age (juvenile or adult) and body weight. Results from a generalized linear mixed model (GLMM) 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.

Model 1: Migratory strategy ~ Weight * Age	Estimate	Std.Error
Intercept	2.470	± 1.308
Weight	0.081	± 0.724
Age(juv)	0.505	± 1.389
Weight*Age(juv)	-4.769	± 2.908
Model 2: Migratory strategy ~ Weight		
Intercept	2.354	± 1.019
Weight	-0.836	± 0.670

Tabel B2: Two best model when modelling distance moved as a function of age (juvenile or adult) and body weight. Results from a linear mixed model (LMM) with continuous response assuming Gaussian error distribution. Individual identity was included as random effect to account for repeated observations of the same birds.

Model 1: Distance ~ Age	Estimate	Std.Error
Intercept	10.312	± 1.322
Age(juv)	-3.036	± 1.613
Model 2: Distance ~ Intercept		
Intercept	9.103	± 1.156

Table B3: Two best model when modelling number of eggs laid as a function of age (juvenile or adult), body weight and migratory strategy. Results from a generalized linear mixed model (GLMM) with count response and log link function, assuming Poisson error distribution. Individual identity was included as random effect to account for repeated observations of the same birds.

Model 1: Number of eggs ~ Intercept	Estimate	Std.Error
Intercept	2.263	± 0.042
Model 2: Number of eggs ~ Age		
Intercept	2.287	± 0.054
Age	-0.061	± 0.087

Table B4: Two best model when modelling number fate as a function of age (juvenile or adult), body weight and migratory strategy. Results from a generalized linear mixed model (GLMM) with binary response (Y = 1 = hatched, Y = 0 = abounded/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.

Model 1: Nest fate ~ Intercept	Estimate	Std.Error
Intercept	1.311	± 1.956
Model 2: Nest fate ~ Age		
Intercept	1.972	± 2.405
Age	-1.583	± 3.502