INLAND NORWAY
UNIVERSITY
OF APPLIED SCIENCES

FACULTY OF APPLIED ECOLOGY, AGRICULTURAL SCIENCES AND BIOTECHNOLOGY

**DEGITU ENDALE BORECHA**

PhD Thesis

# Population dynamics of grouse in the Nordic countries

**PhD In Applied Ecology**

**2018**

| | | |
|---|---|---|
| Samtykker til utlån hos høgskolebiblioteket | JA ☒ | NEI ☐ |
| Samtykker til tilgjengeliggjøring i digitalt arkiv Brage | JA ☒ | NEI ☐ |

# 1 Preface

This thesis is a product of many brilliant and warm-hearted people. People I happened to meet by chance but have opened up a whole new chapter in my life. It was Sunday when I first landed on the pristine Evenstad. There was not a soul on the road. While I was half carrying and half dragging my three bags on the road to campus, a white fancy car suddenly appeared from nowhere. The driver came out and greeted me with a warm smile. I returned the greeting with scepticism. He then asked me if I needed help. I said "no thanks". But the driver was persistent, you see. He offered me if he could at least drop off my suitcases in the campus. This time I said yes. He drove past me with two of my bags in his car. I took ages to arrive at the students' flat while pondering about the stranger I just met. After few minutes on the flat, the stranger showed up, again, this time with a couple of sandwiches and a soda on his hands. He said, without giving me a chance to speak, there is no shop or restaurant within 20 km radius of this area that opens until tomorrow 8:00. Then it hit me. This person is not an ordinary person. I asked him if he works here. He said yes. Then my mind started knitting info together. Then I asked "are you Harry?" Yes, he was. The person who sent a welcome email a week earlier to the newcomers students. So that was how I met the dean of college, Harry Peter Andreassen. We met by pure chance that Sunday, while he was heading to his office. It took me by surprise how helpful, friendly, cheerful, down to the earth, and positive he always is. His assistance did not stop there. He was always and always there when I needed one. I was even offered to join the school's grand tour to Chobe-Victoria fall only after month of my employment. Who else would take such a risk on the person like me? I thank you a million times, dear Harry! You are an inspiring great role model.

This all started and cultivated by one of the smartest people I know, Maria Hörnell-Willebrand. Maria, I would not be here if it was not for you. You have introduced me to the grouse world when you recruited me to your project during my master study. Most importantly, you have believed in me and encouraged me to pursue further. I am deeply in debt to you for that.

I would like to extend my heartfelt gratitude to my supervisors i.e. Ólafur Nielsen, and Tomas Willebrand as well as to our co-author Michael Schaub. Thank you for your time, adventure, and the rough journey. I thank you Michael for your unconditional help, and turning the paper around. Oli, kudos for letting me play with your priceless data. You were the reason I was also welcomed by your institution and your colleagues. Here I extend my genuine gratitude to the Icelandic Institute of Natural History, and all its staffs and the volunteers for their unrestrained hospitality during my stay at Reykjavik as well as during one of the bird trapping trip on Hrísey. You guys had even given me a ride to the Viking era's Iceland with your precious and exclusive yearly time travel machine Þorrablót. Those were the bizarrest food I ever tested, followed by, of course, Tomas' Surströmming. ☺ That being said, I feel deeply honoured for getting the chance to come closer to the soul of the Icelandic life. I thank you!

Ilse Storch is another special person that I would like to extend my heartfelt appreciation to. Ilse, I was taken aback when you showed a willing to host me at your department, Freiburg University. I must admit that I was petrified before I asked you, leave alone when the time was due for me to come. You turned my fear and scepticism into lifelong meaning experiences. You and your team know well how to make people at ease and feel welcomed. I have spent an amazing, and eventful time at your department. I thank you and your department for all the motivating scientific talks and social events.

I am grateful to the Inland Norway University of Applied Science community, especially to my colleagues at Evenstad. Barbara Zimmerman thank for prolonging my life in Evenstad in 2010; Kristin Gangås, Marcel Schrijvers-Gonlag, Karen Marie Mathiesen, Marieke Gonlag-Schrijvers, Olivier Devineau, Marius Hassve, Kaja Johnsen, Alina Evans, Madhu Chetri, Torfinn Jahren, Ole Andersen Bakmann, Ann-Kristin Grebstad, Rangnhild Østerhagen, Marianne Nygård, Øystein Vaagan, & David Sánchez, thank you for the small talks, for being inclusive and friends, and, most of all, for engaging me in different activities. I owe you a great deal, and was an honour working with you all!

Everyone needs friends. And if there is something I know I know that decent friends are extra hard to come by. I consider myself lucky to have decent and non-judgemental friends that were always there to hear my nonsense blabbing, and mentor me accordingly. It is you Solgunn Eidheim and Halfdan Karlsen Eidheim. I could not have done this without you. Thank you for being part of my life, the encouragements, and all the moral and practical helps.

# 2 Contents

# 3 Sammendrag

Populasjonsdynamikk bestemmes av både romslige og tidsmessige forandringer av antall individer. Disse dimensjonene er avhengig av hverandre. Innvandring, utvandring, og overlevelse er tre av de fire demografiske komponenter av populasjonsdynamikk (fødsel blir den fjerde). Individs utvandring, og innvandring (dvs. spredning) er de to grunnleggende romslige dimensjoner som handler om bevegelses av individer mellom populasjoner over landskap. Overlevelse er en av de to avgjørende tidsparameterer som dreier om individers overlevelse mellom tidsrom. Disse tre parameterer oppretter sammen en annen romslig parameter som heter vandring. Vandring eller migrasjon er ikke direkte knyttet til populasjonsdynamikk, men den har stor betydning for overlevelse av både individer og populasjoner. På en annen side er overlevelse av individer avhengig av både spredning, og vandring.

I dette prosjektet formålet vi å undersøke overlevelse, spredning, og vandring av både orrfugl *Tetrao tetrix* og fjellrype *Lagopus muta* populasjoner i Norden. Populasjoner av disse to fuglearter pleide å vise regelmessige antallsvinging, like som de fleste nordlige arters populasjoner. Allikevel er den svingingen ikke lenger like regelmessig og deres populasjonsbestandsstørrelse har også begynt å synke. Forfall av individers overlevelse hevdet som hoved årsak for de fenomenene. Vi studerte overtids overlevelse variasjon av unge og voksne aldre grupper, og unges overlevelser i den nedgangs- og oppgangs-perioden av bestandssvingingen av Islandsk fjellrype. Vi studerte både utvandring, innvandring, og vandring av fjellrype og orrfugl for å forklare: 1) kilde-sluk dynamikk; 2) tendens for hekkesteds- og fødselssted trofasthet (dvs. savn av spredning og vandring); og 3) bevegelses variasjoner mellom de to kjønn og aldre grupper, og dets sannsynlighet å føre til kjønn og aldre grupper segregasjon over landskap. Vi brukte fangst-ring-gjenfangst, observasjonstelling på leike, og radiomerke metoder å samle data på orrfugl populasjon (vi undersøkte bare orre). Vi studerte begge kjønn av fjellrype. Vi samlet dataen gjennom fangst-ring-gjenfangst-gjensyn, fangst-ring-gjenfunn, og jaktrapport på antall individer per kjønn.

Vi har funnet ut at voksne fjellrype overlevde mye bedre enn de unge gjennom studieperioden, spesielt etter 1961. Dessuten rekognosert vi at gjennomsnitteoverlevelsen av begge aldre grupper verken sinket eller økte stadig over studietidsperioden. Men den

årliggjennomsnittoverlevelsen av ungen var lavere i løpet av nedgangefasen enn oppgangefasen av bestandssvingingen.

Når det gjelder bevegelser, viste hann av både fjellrype og orrfugl bedre trofasthet til både hekke- og fødselsted enn hunner. Unge orre rekrutteres til den nærmeste leike til fødselstedet hans. De voksne orre røpet ingen tendens å migrere eller spre fra leike områdene sine over hele året. Hunn fjellrype spredde lengre avstander enn hanner. Vi observerte den spredningen bare i nordlige subpopulasjoner (dvs. Hrísey og Northeast) hvor bestandsstørrelse er de aller beste. Begge kjønn av fjellrype har vandret, men de ungehanner vandret kortere avstand enn voksne hanner, og resultatet av jaktdata-en viste at hannfjellrype var de fleste i nordlige områder mens hunner var vanlige i sørlige regioner. Vandrings lengden har blitt forklart på latitude og jakttilgang. Subpopulasjons som var åpne for jakt vandret lengre avstander enn den som var stengte for jakt. I tillegg migrerte de nordlige subpopulasjoner lengre lengde enn de sørlige subpopulasjoner. I motsetning til dette, vandret null individ til nordlige subpopulasjoner eller til den som var stengte for jakt.

Vi konkluderer at 1) en leike av orrfugl kan behandlet som avhengig orre populasjon spesiell om våren; I Island, 2) fjellrypes årliggjennomsnittoverlevelse har ikke sinket, og dette påpeker at individers overlevelse var ikke årsaken at bestandsstørrelse begynte å synker og svingingen er i gange å forsvinne; 3) det er kjønn og aldre grupper segregasjon om vinteren, og forskjellen mellom vandring lengde mellom de aldre gruppene og kjønnene er som står bak den atskillelsen; 4) fjellrypes populasjonsdynamikk er kontrollert om de ungindivider relativt til de voksenindivider; 5) de to nordlige fjellrype subpopulasjoner funger som kilde populasjoner mens de andre subpopulasjoner virker som sluk; og 6) på grunn av den segregasjonen, den ujevne bestandsstørrelsen over landskap i landet, antar vi at ungehannen er påvirket av jakt mer enn de andre grupper.

# 4 Abstract

Population dynamics is determined by both spatial and temporal changes of individual abundance. These two dimensions are highly assimilated. Survival, emigration, and immigration embody three of the four demographic components of population dynamics (birth being the fourth). Emigration and immigration of individuals (i.e. dispersal) are the basic spatial strands, and deal with the movement of individuals between populations. Survival is one of the two determinant temporal segments, and conveys the endurance chance of individuals and/or populations. These three parameters collectively generate another spatial segment called migration. Migration is not plainly connected to population dynamics but strongly compliment population as well as individual survival. Survival, in turn, is partly dependent on immigration, emigration, and migration.

In this project, we aimed to study survival, emigration, immigration, and migration of Swedish black grouse *Tetrao tetrix* and Icelandic rock ptarmigan *Lagopus muta* populations. The population of these species show periodic multiannual population cycles similar to the other populations in the Northern hemisphere. Nevertheless, nowadays, their cycles are collapsing; their abundances are decreasing, and decrease of their survival chance assumed to be the reason behind. Here we studied survival of rock ptarmigan population to elucidate temporal variation of juvenile and adult survival, and survival of juvenile during the increase and the decrease phases of the population cycle. We studied movements of both black grouse and rock ptarmigan to explain: 1) source- sink dynamics; 2) the tendency for site fidelity, and –tenacity (i.e. lack of dispersal and migration); and 3) and spatial variation in sex and/or age dependent movements, and possibility of sex and/or age segregation. We used ring-recapture, observation count on lek, and radio-telemetry methods to collect data on black grouse (only males studied). For rock ptarmigan, we studied both sexes, and collected the data using ring-recapture-resight, and ring-recovery, and harvest statistics.

We found that adult rock ptarmigan survived significantly better than juveniles over the study period, particularly after year 1961. But the average survival probability of either of the age groups’ neither decreased nor increased steadily over the study time. In the cycle phases, the survival of juvenile was lower during the decrease phase than the increase phase.

From the movement analyses, we learnt that males of both rock ptarmigan and black grouse have high natal site-fidelity, and site-tenacity than the females. Juvenile male black grouse recruited to leks near their natal site, and, particularly the adult males, stay put close to their breeding ground year round with no tendency of migration or dispersal. As for the rock ptarmigan, juvenile female rock ptarmigan dispersed longer distance than juvenile males. We detected dispersal only in northern sub-populations (i.e. Hrísey (an island) and Northeast), and relative to the sub-population that was open for hunting, the sub-population that was closed for hunting showed longer natal dispersal. When it comes to migration, both sexes had migrated but juvenile male migrated meaningfully shorter distance than adult males. The bag data, correspondingly, revealed that males dominated in the northern regions' harvest data whilst the females were more common in the southern. The migration distance were explained by latitude, and hunting pressure. Individuals from both the northern regions and from hunted sub-populations migrated longer distance than the southern and the sub-populations closed for hunting. On the contrary, no single individual migrated or dispersed toward the northern sub-populations.

We conclude that 1) a lek of black grouse may be treated as a standalone male population in Sweden; and in Iceland: 2) the average survival probability of the rock ptarmigan population did not decrease over time; pinpointing that survival was not the reason of the recent period's decrease of abundance, and population acyclicity; 3) rock ptarmigan populations show a sexual segregation, and, to some extent, age segregation in winter, and the differences of migration distance between the age and sex groups is the reason behind segregation; 4) rock ptarmigan population dynamics is controlled by the juveniles, which is consistent with previous observations; and 5) two of the northern sub-populations serve as source populations to the rest of the sub-populations.

# 5 List of Papers

This thesis is based on the following original publications, indicated in the text by their roman numerals, I-III below.

Paper I:

Borecha, D. E., Willebrand, T., Nielsen, O. K., and Schaub, M. (2017). Age dependent survival estimates for Rock Ptarmigan *Lagopus muta* based on long-term ring-recapture-recovery data. *Manuscript.*

Paper II:

Borecha, D. E. and Nielsen, O. K. (2017). Males stay at home while females are touring: Migration and dispersal patterns of Icelandic rock ptarmigan *Lagopus muta*. *Manuscript.*

Paper III:

Borecha, D. E., Willebrand, T., and Nielsen, O. K. (2017). Lek site defines annual spatial use of male Black Grouse *Tetrao tetrix. Ornis Fennica* 94, 3, 150-160.

The original publications have been reproduced with the permission of the publishers.

# 1. Introduction

## 1.1.Population dynamics

Population dynamics is determined by both spatial and temporal changes of individual abundance (Taylor and Taylor 1977, Pulliam 1988, McPeek and Holt 1992, Hanski 1998). The spatial change deals with the movement of individuals between populations or locations (Roff 1975, Stacey and Taper 1992, Hanski et al. 1994), whereas the temporal change is defined by individuals' survival and birth over time (Elton 1953, den Boer 1981, Clutton-Brock et al. 1987, Gaillard et al. 2000). These two dimensions are highly integrated, and are subject to both environmental and demographic stochastic events (Krebs 1978, Ims 1995). Thus, it is not straightforward to examine these two dimensions separately (Krebs 1978).

Survival, emigration, and immigration embody three of the four demographic components of population dynamics (death being the last component). On a landscape level, populations are connected by emigration and immigration of individuals (i.e. dispersal) (Hansson 1991, Baguette and Van Dyck 2007), and by seasonal migration (Taylor 1986, Cheke and Tratalos 2007). Migration is not directly connected to population dynamics but it strongly compliments both the population as well as individual's survival, and is a product of immigration, emigration, and survival. Survival chance of the individuals is a determinant factor for endurance of the populations, and is partly dependent on these movements.

## 1.2. Aim of the study

The overall aim of this project was to study some aspects of both the spatial and temporal population dynamics of grouse in the Nordic countries focusing on survival, emigration, immigration, and migration. We studied movements to be able to explain: 1) the spatial variation between sub-populations, i.e. source- sink dynamics (Pulliam 1988); 2) the tendency for site fidelity and – tenacity (i.e. lack of dispersal and migration); and 3) and geographical differences in population demography. For instance, to determine whether sex – and/or age dependent movements explain age – and/or sex segregation in certain regions. We studied survival to elucidate temporal variation of population dynamics, which also may be sex – and/or age dependent.

We used two grouse species in the study: the black grouse *Tetrao tetrix* and the rock ptarmigan *Lagopus muta.* These populations show periodic multiannual population cycles, which is common to many populations in the northern hemisphere (Kendall et al. 1998).

To achieve the overall aim we conducted various population analyses that are divided into three papers. These papers are:

**Paper I** in which we evaluated whether or not the average annual survival probabilities of juvenile and adult rock ptarmigan have declined over 86 years' time in Iceland. We also estimated average juvenile survival probability during both the increase and decrease phases of the population cycle.

**Paper II** where we studied the Icelandic rock ptarmigan's (1) migration potential by estimating the different individual groups' movement distance between seasons, and the proportion of the sex distribution in various parts of the country during open season, and (2) both natal and breeding dispersal distances of different individual groups.

**Paper III** wherein we quantified lek site fidelity of black grouse males among neighbouring leks using data from 230 marked full-grown individuals, and 76 chicks in two areas in Sweden. The overall question of this paper was whether black grouse males at a lek site can be considered as a separate group, or if there is a significant exchange of males between lek sites.

Here, I first introduce the concepts of population cycles, dispersal, migration and survival. Later, I will use these concepts to explain variations in site fidelity and population structure (age – and sex composition). I will also include a discussion on habitat characteristics to describe spatial variations between sub-populations.

## 2. Concepts

### 2.1. Population cycles

The northern hemisphere, beyond the southern border of the taiga forest, is a unique location for some populations (Hanski et al. 1991). In this hemisphere, the population abundance of several species show regular population cycles with population peaks every few years (Elton and Nicholson 1942, Kendall et al. 1998, Turchin et al. 2003). The period between population peaks varies geographically, and normally follows a latitudinal gradient (Hansson and Henttonen 1985, Hanski et al. 1991, Bjørnstad et al. 1995; but see Henden et al. 2009). Despite numerous efforts, researchers have not yet cracked the causes of the population cycles and/or why they vary between locations (Krebs 1996, Moss and Watson 2001). The most mysterious regular population cycles are the ones for the small herbivores, primarily rodents (Microtinae) and hares (Leporidae) in Fennoscandia and North-America (Hagen 1952, Krebs and Myers 1974).

Rodents and hares are the primary consumers in the food chain and are food for many predators. Their predators' abundance coils with theirs. The predators, in turn, transpose the dynamic into their alternative preys' population by the time rodents and hares are drained (O'Donoghue et al. 1998, Krebs 2011). In addition to the predators (Krebs 1996), factors intrinsic to the populations e.g. physiological, genetic and/or behavioural (Andreassen et al. 2013), extrinsic or environmental factors such as weather, and or plant-mast are being considered as the driving forces for population cycles Nevertheless, a few findings advocate that both intrinsic and extrinsic factors play a complicated role in the population cycle system (Krebs 1996, Andreassen et al. 2013, Radchuk et al. 2016).

The majority of populations exhibiting population cycles show a temporal synchrony across large spatial scales (Kvasnes et al. 2010), and the population dynamics may even be synchronized across species (Krebs et al. 2002). The spatial synchrony between populations fades out with distance (Elton and Nicholson 1942, Ranta et al. 1995, Lindstrom et al. 1996).

Some researches show that demographic parameters, for instance, survival and/or breeding success vary with respect to the phases of the population cycle. Populations often show higher average survival and fertility rates during the increase phase than the decrease phase of the cycle (Chitty 1960, Boonstra et al. 1998, Sinclair et al. 2003). It is believed that these variations might depend on the age - and the sex composition of the population or it is age-dependent (Leslie and Ranson 1940, Krebs and Myers 1974, Sinclair et al. 2003). Andreassen et al. (2013) proposed that adults outnumber the young individuals during the crash phase. Nevertheless, there are many exceptions. For instance, mortality of 4-5 week old chicks of willow ptarmigan *Lagopus lagopus* in Russia does neither synchronize with the population cycle nor with any weather parameters (Andreev 1987).

Nowadays, the regular population cycles for the majority of populations are fading out/collapsing (Ims et al. 2008, Henden et al. 2009). This is also the case for the grouse populations' cycle, e.g. the ptarmigan populations, of both North-America and European countries (Williams et al. 2004, Ludwig et al. 2006). As for the origin of the cycle, the cause of the collapse is also a mystery (Brommer et al. 2010).

## 2.2.Dispersal

Dispersal consists of three interdependent stages: emigration from a home site, immigration and settlement onto a new home site, and the movement between these two home sites (Stenseth and Lidicker 1992, Ims and Yoccoz 1997). Dispersal mix populations via the exchange of individuals (Dingle and Drake 2007), and has proved to be the most crucial demographic parameter in spatially heterogeneous landscapes (Krebs et al. 1969, Wiens et al. 1993, Diffendorfer 1998).

Individuals disperse ultimately to avoid inbreeding (Pusey 1987) or resource competition (Liberg and Schantz 1985), and are driven by proximate factors such as population density and intraspecific competition (Howard 1960, Johnson and Gaines 1990, Ims and Andreassen 2000), and/or differential resource distribution in a heterogeneous landscape (Roff 1975, Johnson and Gaines 1990, Amarasekare 1998, Holt and Barfield 2001). Dispersal is unidirectional (Taylor 1986, Dingle 1996), and it can be categorized as pre- and post-breeding (Howard 1960, Dingle 1996). The pre-breeding dispersal, hereafter termed natal dispersal, is carried out by juveniles. Natal dispersal is common in most species, and conducted more frequently than post-breeding dispersal, which is conducted by the breeding segment of the population, and determined by experience (Howard 1960), e.g. the loss of a litter (Andreassen and Ims 2001).

In birds, the females are the natal dispersive sex, while in mammals males is the dispersing sex (Haartman 1949, Lack 1954, Greenwood 1980, Wolff and Plissner 1998). In birds, juvenile males tend to be philopatric, settle near their relatives and/or inherit their father's territory (Greenwood and Harvey 1982). Philopatry, hereafter called natal site-fidelity, is the settlement of an individual to its natal location for breeding (Pearce 2007). Individuals that secure a territory have higher fitness than those without, and this encourages natal site-fidelity (Kokko and Lundberg 2001). The drawback of this is that species with high site fidelity can be vulnerable to habitat fragmentation and loss (Warkentin and Hernandez 1996).

## 2.3.Migration

Migration is another movement related to dispersal (Dingle 1996, Semlitsch 2008). However, while dispersal is connected to life history traits, migration is connected to seasonal changes, and the variation of resources associated to it (Cox 1985, Taylor 1986, Dingle 1996, Semlitsch 2008). Similar to dispersal, migration could also be performed by individuals of any population regardless of geographic location (Lack 1954, Elgood et al. 1973, Jahn et al. 2004, Boyle 2008).

It is not always so that each and every individual in a population migrate as it is usually perceived. In a number of populations there is a partial and/or differential migration, where only a subset of the population migrates (i.e. partial migration), or a subset of the population migrates different distances or at separate time (i.e. differential migration) (Lack 1944, Cox 1985, Jahn et al. 2004). For bird species, migration is a regularly timed, mostly biannual (i.e. a roundtrip) movement conducted by a portion or all individuals in a population (Lack 1944, 1954, Taylor 1986, Dingle 1996, Dingle and Drake 2007).

Partial migration with specific segments of a population creates sex - and age segregation in winter populations. In grouse species, commonly males overwinter near their breeding ground while females and juveniles migrate (Tellería and Pérez-Tris 2004). There is no particular parameter that seems to describe the migration pattern, but individuals tend to migrate away from harsher weather condition (Cox 1985).

## 2.4.Survival

Those species that live longer than a year are adapted to cope with spatial and seasonal fluctuations or stochastic environmental variability (Pianka 1970). Migration and dispersal are individuals’ adaptations to these fluctuations for improving their fitness. For instance, a literature review shows that migrant individuals have higher survival chance than their sedentary conspecifics (Cox 1985), but migrants could compromise their chance of reproduction (Wheelwright and Mauck 1998).

Nature favours the fittest and the longest survivor over time (Pianka 1970, Gaillard and Yoccoz 2003). The dissimilarity of migration and dispersal patterns of males and females, for example, is a signal that their fitness is affected by different factors. These factors impose the two groups to take diverse strategies in order to optimise their survival chance. For instance, adult females prioritise survival over reproduction in ungulates (Gaillard and Yoccoz 2003). These give the adults stable survival over time relative to juveniles, which suffer more from stochastic variation than the adults (Gaillard et al. 1998, Gaillard and Yoccoz 2003). In birds, survival is age-dependent, in which juveniles universally have higher risk of mortality than adults (Martin 1995). This vulnerability of juveniles has distinctive negative consequence in the dynamics of their populations (Gaillard et al. 1998). The number of juveniles, joining a breeding population is modulated by both their natal dispersal capacity and their survival probability (Howard 1960, Pulliam 1988, Cooke and Francis 1993).

Animals living in wild populations die of both natural and anthropogenic causes. Legal hunting or harvest is one of the major human-induced causes of mortality for game species. Whether or not hunting is compensatory or additive to natural mortality, it is still equivocal (Servanty et al. 2010, Sandercock et al. 2011). But halting hunting has evidently helped to revive a few populations (Merkel 2010). In addition, the impact of hunting varies for sedentary and migratory species, as does the length of the hunting period (Sunde and Asferg 2014).

For relatively small-sized birds, survival is commonly estimated using ring-recapture-resight, ring-recovery, and/or radio-telemetry (Lebreton et al. 1993). Site fidelity could be used as a conservative estimate of survival and it could be implement through ring-recapture techniques (Lebreton et al. 1995). The drawback of this method, however, is that it underestimates the survival as it does not consider dispersal (Reed and Oring 1993, Hanski et al. 1994, Koenig et al. 1996, Lambrechts et al. 1999). This is because it is difficult to tell dispersed and deceased individuals apart (Catchpole et al. 1998). The same situation applies for ring-recovery to estimate migration or dispersal, in which the survival and the movements are inseparable due to difficulty of recovering the ring (Schwarz 1993). Combining ring-recapture-resight and ring-recovery methods are quite indispensable for they complement each other (Clobert and Lebreton 1991, Catchpole et al. 1998).

## 3. The study species

We studied two sexually dimorphic galliform species (sub-family Tetraoninae) namely black grouse and rock ptarmigan. The black grouse study was conducted in two locations of central Sweden, and we only studied the male population. The rock ptarmigan study comprised both sexes, and was conducted in the entire Iceland. Both species are popular game birds, they are herbivores, and were known to have cyclic population abundance in the Nordic countries (Linden 1988, Lindstrom et al. 1995, Nielsen and Pétursson 1995).

### 3.1.Rock ptarmigan

Rock ptarmigan is a tundra bird that dwells in the northern hemisphere all year around. The species play an unquestionable ecological role in the thin food chain of the region. In Iceland, they inhabit nearly the entire country, except perhaps the central highland desert. They prefer to breed on heathland (Nielsen 1993), nearby coastal areas where there is a good pasture (Nielsen 1995), and they have never been observed outside the country. In the northern regions of Iceland, i.e. on Hrísey, and in Northeast, rock ptarmigan prefers to inhabit areas below 400 m above sea level (masl) as this elevation ranges have better fodder (Gudmundsson 1960). The densities of the ptarmigan on Hrísey and in the Northeast region outnumbers the rest of the populations/regions (Gudmundsson 1960, Nielsen 1993), and have been studied for the longest period along with the population of the southeast region (Nielsen 1999b).

Previously, the Icelandic ptarmigan population showed population cycles with 10-12 years periodicity (Nielsen and Pétursson 1995, Brynjarsdóttir et al. 2003), in which all the populations in the country were fluctuating nearly in synchrony (Nielsen 1996, Nielsen 1999b). But except the Hrísey and Northeast populations, the rest of the populations have been out of synchrony since the 1970s (Nielsen 1999b, Nielsen et al. 2004). In addition, after 1981 the amplitude of the cycle got shorter, and the population abundance started declining (Brynjarsdóttir et al. 2003, Magnússon et al. 2004). Since 2003 the cycle itself became less pronounced and irregular (Brynjarsdóttir et al. 2003, Nielsen 2011, Sturludóttir 2015). It is speculated that the population decline and the observed lack of cyclicity are due to increased mortality (Magnússon et al. 2004).

Unlike other northern countries, for example in North-America and Fennoscandia, where the ptarmigan populations also fluctuate regularly, there is neither a microtine rodent nor hares in Iceland (Gardarsson 1988, Nielsen 1999b). Hares and voles are normally part of the regular population cycle puzzle (Krebs and Myers 1974, Hörnfeldt 1978, Linden 1988, Ims and Fuglei 2005). Rock ptarmigan, instead of being an alternative prey, replace their position in the food chain as a primary prey. This makes the Icelandic rock ptarmigan one of a kind.

Iceland researchers and wildlife managers have carried out several experiments to understand the factors that regulate ptarmigan populations, and to find alternative management strategies. Along with the natural mortality that incurred mainly by predators, the Icelandic rock ptarmigan were harvested for generations. Up until the end of the Second World War, the harvest had strong international commercial function in the country (Nielsen and Pétursson 1995). Nationally, the bird has profound cultural, nutritional, and ecological significance. Nonetheless, the country was not regulating the hunting before 1994, when six hunting zones was introduced (Nielsen 1999b). Recently, an absolute ban on ptarmigan hunt was also implemented between 2003 and 2004, during which a noticeable increase in the population abundance was observed (Nielsen 2011). Before 2003, hunting was allowed in all parts of the country except on Hrísey, However, after 2003 and onwards, the southwest region is also closed for hunting, Since 2005 market hunting is prohibited and the number of hunting days (Nielsen et al. 2013), and hunting quotas has been greatly reduced. (http://www.ust.is/einstaklingar/frettir/frett/2013/09/25/Fyrirkomulag-rjupnaveida-2013-Hofsemi-i-fyrirrumi/). After the introduction of these regulations, on average, 60,000 individuals are being harvested between mid-Octobers to mid-Decembers, hereafter termed the open season, every year (http://www.ust.is/, Sturludóttir 2015).

The main predator of the ptarmigan in Iceland is the gyrfalcon *Falco rusticolus islandus*, which is specialized on ptarmigan (Nielsen and Cade 1990, Nielsen 1999a, 2011). Icelandic gyrfalcon populations are cyclic (12-14 years), non-migratory, and have higher density in northern Iceland than the rest of the country (Nielsen 1996, Nielsen 1999a, 2011). Gyrfalcons mainly prey on adult territorial male rock ptarmigan in spring (Wayre and Jolly 1958, Gardarsson 1988, Nielsen 1999a, 2011). The gyrfalcon was assumed as the main driver of the rock ptarmigan cycle in Iceland, but this assertion is still under scrutiny because the falcon abundance is stable while the rock ptarmigan is decreasing (Nielsen 1999a, Brynjarsdóttir et al. 2003, Nielsen 2011). Rock ptarmigan are also predated by generalist predators such as raven *Corvus corax* (Woodin and Route 1980, Nielsen 1996), arctic fox *Vulpes lagopus*, mink *Mustela vison*, and domestic cat *Felis catus*. The ptarmigan also host numerous pathogenic parasites (Skirnisson et al. 2012), and one endo-parasite seems to have a signature in the cycle (Stenkewitz et al. 2016).

In winter, the males and the females of Icelandic rock ptarmigan stay partially segregated (Gardarsson 1988). Males are territorial during mating period (late April–May) (Gardarsson 1988, Nielsen 1999b). The species can be portrayed as monogamous (Weeden 1964, Gardarsson 1988), but the male could be observed mating with more than one partner (Brodsky 1988, Holder and Montgomerie 1993). A few of the males may not get a chance to mate at all (Bart and Earnst 1999, Cotter 1999), and nearly none of them help raising the chicks (Gardarsson 1988). The females start breeding as yearlings, and they have high mating success (Cotter1999). The species is sexually dimorphic in Iceland with the male being the largest sex (Nielsen et al. 2013).

## 3.2.Black grouse

Black grouse dwell in diverse habitat types, ranging from treeless areas to forest areas (Storaas and Wegge 1987, Kurki et al. 2000, Storch 2007). In Fennoscandia, the species normally dwells in the boreal zone and prefers mires and birch sprinkled young spruce forest (Brittas et al. 1987, Storaas and Wegge 1987, Jönsson et al. 1991). The Fennoscandian black grouse show population cycles with 6-7 years periodicity (Linden 1988, Lindstrom et al. 1995). Even if the populations in the region have reasonably intact habitats and are genetically diverse (Höglund et al. 2003, Corrales and Hoglund 2012), their population abundance is decreasing, and their regular cycle is waning (Ludwig et al. 2006, Gregersen and Gregersen 2009, Jahren et al. 2016). Besides ageing of forests (Wegge and Rolstad 2011), types of the implemented silvicultural methods (Kurki et al. 2000), and changes of climate parameters such as temperature, seem to bring stress on the breeding success of the individuals and eventually causing the populations to decline (Ludwig et al. 2006).

Male black grouse commonly form leks; an arena where the males display together to attract females (Koivisto 1965, Kruijt and de Vos 1988). They display primarily in spring, but they do so also in autumn in less intensity (Rintamaki et al. 1999). The autumn lekking is more of confirming and updating their ownership of their territory, which has a crucial benefit for the spring breeding success (Rintamäki et al. 1999). Some observational reports also state that solitary display or so-called non-lekking behaviour could also happen (Höglund and Stohr 1997, Svobodova et al. 2011); which is probably due to lack of suitable habitat and disturbances (Höglund et al. 1997, Watson and Moss 2008). The solitary display could be aggravated due to their site fidelity (Zurell et al. 2012).

Adult male black grouse have a high level of lek fidelity (Alatalo et al. 1992). The juvenile males, on the other hand, are relatively less faithful to a lek (Caizergues and Ellison 2002, Warren and Baines 2002, Corrales and Hoglund 2012). The majority of the juveniles visit at least one more leks than their natal before they settle on one (Alatalo et al. 1992). However, they were not observed settling more than two km away from their natal site (Caizergues and Ellison 2002, Warren and Baines 2002). At large, juvenile male black grouse have a reduced overall chance of breeding success as compared to the adults (Wegge et al. 2003). Albeit their restricted reproduction fitness with this setting, they attend leks, and their attendance boost the success of the lek (Alatalo et al. 1992). The presence of juvenile males on leks dominated by adult males increases the mating success of the adults (Kokko and Lindström 1996). This could be the reason why they usually join leks that have small number of adult males (Alatalo et al. 1992) or overall smaller leks (Wegge et al. 2003). At the same time, their attendance increases their probability to meet their father on the same lek (Kokko and Lindström 1996).

# 4. Methods

## 4.1. Data and study area

To collect data on black grouse, we used three methods namely ring-recapture, observation count, and radio-telemetry. For rock ptarmigan, we used two types of data: (1) ring-recapture-resight and ring-recovery; and (2) hunting statistics (i.e. count of harvested males and females). The recaptured-resighted rock ptarmigan were purely unintentionally as there was no effort implemented to recapture-resight the individuals. Thus, the main study method was ring-recovery.

## 4.2. Ring-recapture-resight and ring-recovery and study area

A total of 8916 Icelandic rock ptarmigan (17% adults and 83% juveniles; 30% females, 31% males, and 39% unknown sex individuals) were tagged with a standard engraved aluminium leg ring by the Icelandic Institute of Natural History's bird-ringing program. The institution has started the ptarmigan ringing in 1927, and we used the data for the period 1927-2013. Iceland (65°N, 18°W) has an altitude that ranges up to 2100 masl; including the glacier height (**Figure 1**). The majority of mountains are located in the North-Northeast regions, where the elevation reaches 1300 masl. The bird ringing sites were distributed all-over the country. One of the study areas was an island, Hrísey, and was located on north (**Fig 1b; Paper II**). Most of the birds (82%) were ringed both on Hrísey and in the Northeast region; hereafter both collectively termed northern regions. The rest were ringed in the Southeast (12%), and Southwest (6%) parts of the country, hereafter both collectively termed southern regions.

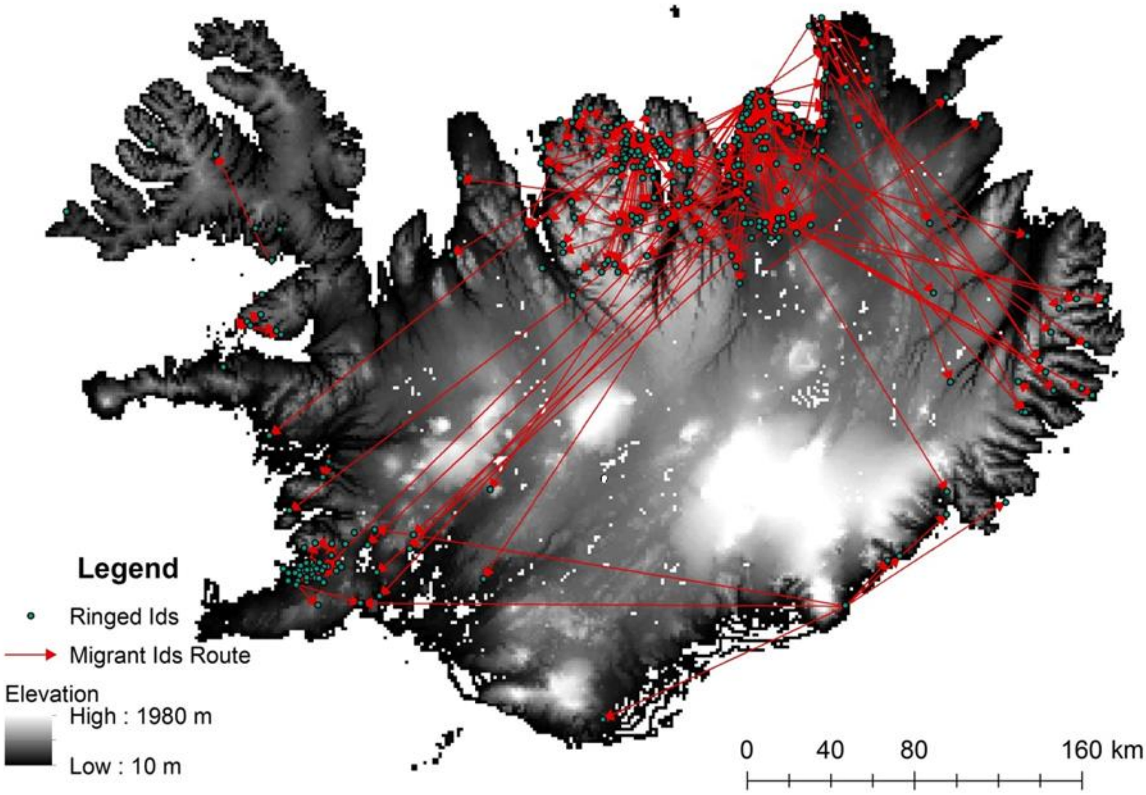


**Figure 1.** The topography of Iceland, and ringing-recovery locations, and movement direction and ringed rock ptarmigan (n = 8916) in Iceland between 1927 and 2013. The white-grey colours indicate both mountain and glacier. The northern region has higher elevation landscape (greyish) than the rest of the regions. But these norther mountain ranges are free of glacier. Hrísey, the island, is sandwiched between these mountains (**Paper 1**). The biggest glacier is located in southeast (white). The bird ringing and recovery locations were situated along the coastal areas.

The number of ptarmigan ringed per year varied due to variations in the ringing effort and the cyclic changes in the abundance of the ptarmigan population. The highest proportion of the birds was ringed in May–September with peak in September (**Figure 2**). Among the ringed birds, 1249 individuals have been recovered dead, and 271 birds were recaptured or resighted (7 individuals) at least once. In **Paper I**, we used ptarmigans ringed from July to September (6615 individuals) as the other ringing months had short exposure time for annual survival estimates (Table 1). In **Paper II,** we used all the recovered and recaptured-resighted individuals.

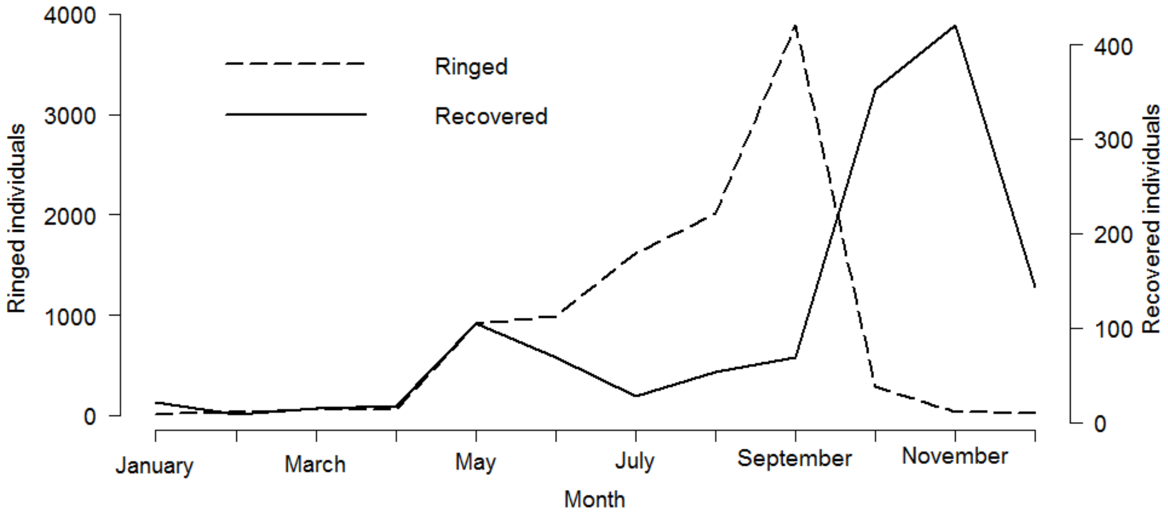


**Figure 2**. The number of ringed and recovered Iceland rock ptarmigan over the study period (1927-2013) summarized per months.

All the capture-recapture practices took place in daylight. Birds were spotted by walking within the habitat. Over the years, the birds were captured-recaptured by a combination of various trapping methods that included snaring, fishing nets, drop netting, mist netting, and driving birds into corrals (Nielsen 1995a). A captured or recaptured bird was immediately put in a blind, weighted, ringed, and released.

We grouped all the ringed individuals as juveniles (< 1 year old) or adults (> 1 year old). Rock ptarmigan ringed before year 1967 were aged based on plumage, body size, and growth of primaries, whereas those ringed after 1967 were aged based on the pigmentation of their primary feathers (Weeden and Watson 1967). As ptarmigan chicks hatch at the end of June in Iceland (Gardarsson 1988), we defined 1st July as the beginning of the bird´s calendar year.

## 4.3.Bag statistics and study area

Data from the harvested rock ptarmigan was collected by visiting hunters or game dealers. The bag statistics included 49 832 aged and sexed harvested rock ptarmigan based on collected wings during 1964-2002 in 9 different regions of Iceland (**Paper II**).

## 4.4.Ring-recapture, radio-tracking, lek observation, and study area

Male black grouse's lek fidelity was studied between 1984 and 1992 in two sites in central Sweden (**Fig 1, Paper III**). Site 1 (Boda) had six leks in a 32 km$^2$ area and situated in Gävleborg County (approx. 61° N, 15° E). The second site (Länstersjön) was located in Västernorrland County (approx. 62° N, 14° E), and had only two leks that were 1.10 km apart in a 19 km$^2$ area. These two sites were 200 km apart. Both sites located in boreal zone, and consisted of intensively managed pine *Pinus sylvestris* and *P. contorta*, and Norway spruce *Picea abies* forests.

In total, 230 full-grown (juvenile and adult) male black grouse (66% juveniles) were captured and leg ringed, and 76 black grouse that were less than three weeks old chicks (both sexes) were captured and wing tagged. The captured individuals were aged according to the form and pigmentation of their primary feathers (Helminen 1963), and two age groups were recognized i.e. juveniles (≤ 18 months), and adults (> 18 months). Among leg ringed full-grown individuals, 113 males were radio-tagged with 15-17 gram radio collars, which had a minimum battery lifetime of 10 months. All the radio tracking positions were recorded by triangulation every other week during daylight throughout a year. In addition, the numbers of lek-attending males were systematically counted from a well-camouflaged hiding spot in late winter–spring. In autumn, lekking activities were recorded from 16th September to 1st October (**Paper III**).

Two different methods were used to capture-recapture the individuals over the study period. During the spring lekking period, males were captured on leks using drop-traps covered with soft net (Willebrand, 1988, Willebrand 1992). Outside the lekking period, males were captured in snow-burrows, and these males captured aided by locating radio-collared males that were previously captured on a lek. The captures were performed every year during the study period with the recaptures occurring when we carried out these captures.

## 4.5.Analysis

### 4.5.1. Survival probability analysis

We estimated age-dependent average annual survival, recovery, recapture, and site fidelity probabilities for rock ptarmigan populations during: 1) Three time periods. The three periods were subsets of the 86 (1927-2013) study years, and the motive behind the subgrouping was changes in the characteristics of the population cycle and abundance. The first period (1927-1960) was characterized by large amplitude population cycles. During the second period (1961-1980), the population abundance showed a peak with low amplitude in 1966, and no visible cycle in the 1970s. The third period (1981-2013) was characterised by a general decrease in population abundance and shortening of the cycle period. 2) Increase and decrease phases of the population cycle. For this, we could only use ringing data for years 1950-2013 when reliable census data of population abundance were also available. We used a multistate model with a Bayesian framework (Kéry and Schaub 2012) that combined both ring-recapture-resight and dead recovery data (**Paper I**).

### 4.5.2. Migration, dispersal, and sex distribution analyses

For both migration and dispersal (**paper II**), we assessed the movement of rock ptarmigan between years rather than within years. We calculated the linear distance between the ringing, and the recapture-resight and/or recovery locations. We grouped the ringing locations into five regions, namely (1) Southwest, (2) Hrísey, (3) Northeast, (4) Southeast, and (5) West (**Fig.2, Paper II**). We considered these ringing regions as sub-populations of the whole country's population, and as the individuals breeding site in all the analyses and interpretations.

For natal dispersal, we considered juveniles ringed between July-September (i.e. their first summer-autumn), and recaptured-resighted, and/or recovered dead between April–August the following year. For breeding dispersal, we set individuals that were ringed in April–September when they were ≥ 10 months old and recaptured-resighted, and/or recovered dead in April-August in subsequent years. All ptarmigan that were ringed between April–September and recovered in October-March were used in the migration analysis.

We used generalized linear models to analyse the effect of individuals' age, sex, ringing locations, and their interactions on the migration distance using Gamma distribution. We considered the age only for the individuals recovered within their first winter after ringing since juveniles turn adult after the first winter. We presented median and range (minimum and maximum) for the natal dispersal and breeding dispersals because the majority of the individuals had zero km dispersal distance. In order to determine sexual distribution (sex composition) of the harvested birds in different regions, we compared the proportion of males in the bag data in each of the nine regions.

### 4.5.3. Site fidelity analysis

For **Paper III**, we calculated the shortest distance of all radio locations to all lek sites. For each individual, we used the proportion of spring relocations when closest to its capture lek as a measure of site fidelity. We considered that an individual had changed leks when it was recaptured at a lek other than that of first capture, and/or if it showed weak site tenacity i.e., when ≥ 50% of the spring relocations were nearer to another lek than that of its first capture. We compared the maximum number of males observed in each lek to assess lek attendance before- and during the mating periods. We fitted generalized linear mixed models to determine the effect of age and period on the average distance of each individual's relocation to its captured lek. In addition, we calculated 95% kernel home ranges to evaluate the different leks' home range and overlap.

# 5. Results and discussions

## 5.1 Dispersal, migration, and site fidelity

Males of both rock ptarmigan and black grouse have higher natal site-fidelity, and site tenacity than females (**Paper I, II** & **III**). Seven out of the 76 ringed black grouse chicks were recaptured on the lek closest to their natal area after a year (**Paper III)**. Even if the natal and breeding dispersals of rock ptarmigan did not depict any clear pattern, the juvenile rock ptarmigan males conducted shorter natal distance movements than females, portraying a tendency of natal site-fidelity also among male rock ptarmigan (**Paper II)**.

Site tenacity was age dependent for both species. As soon as they started breeding, adult male black grouse showed high site tenacity rates (**Fig. 2, Paper III).** Contrary to black grouse, adult male rock ptarmigan showed less site tenacity than juvenile males (**Table 2** & **Fig. 2, Paper II**; **Fig. 3**, **Paper I**).

The rock ptarmigan results could be biased due to methodical limitations. Unless birds were killed and recovered, there is no chance to know the whereabouts of individuals between the ringing and the recovery sites when using ring-recovery method. It is also difficult to differentiate dispersal from migratory behaviour. Moreover, the mortality rate of juveniles during open season is so high that they perhaps did not get a chance to disperse at all (**Paper II**). However, the wintering grounds are not the breeding sites for the migratory individuals, and dispersed individuals also tend to be migrants; i.e. visiting their natal site (Stenseth and Lidicker 1992, Ims and Yoccoz 1997).

The natal site-fidelity feature among black grouse juvenile males results in that juvenile males aggregate around lekking arenas located near their natal site. Nevertheless, a few of them do explore their chances at other nearby leks before they commit to one specific lek (**Fig. 1b, Paper III**). This was confirmed by both our recaptures and radio-telemetry relocations. This inter-lek movement probably takes place during the peak mating period, when juveniles display less to avoid hostility with aggressive adult males (Koivisto 1965, Wegge and Larsen 1987, Alatalo et al. 1992). It seems that this was the reason why juveniles ended up having a wider home range size than the adults in spring (**Paper III**).

None of the black grouse males migrated during winter. In fact, they stayed near the lek area all year-round and the overlap of home ranges between males from different leks was small. Given there is a high chance of natal site-fidelity and high lek-site tenacity among the adult males, the chances for the juveniles displaying on their father's lek is high (Kokko and Lindström 1996). This may be because parents are less aggressive towards their progeny, and relatives are less hostile to each other to increase their indirect fitness (Hamilton 1963, Watson et al. 1994).

Unlike black grouse males, rock ptarmigan migrate, and this is not limited to Icelandic rock ptarmigan (Fuglei et al. 2017). However, neither all individuals nor all sub-populations migrate in Iceland (**Figure 3)**. A few individuals of both sexes over-winter on their breeding ground. Males generally migrate shorter than females, and the northern sub-populations migrate longer than the southern ones (**Figure 2, Fig 3, Table 4; Paper II**). Unlike dispersal, migration distance increased with age for males, in which adults did migrate longer average distances than juveniles.

Both our natal site-fidelity and site tenacity results are consistent with previous studies for bird species (Greenwood 1980, Wolff and Plissner 1998, Hörnell-Willebrand et al. 2014). Males' site fidelity and - tenacity are a survival strategy and are investment strategies in reproduction (Myers 1981, Nolan et al. 1999). This applies both for lekking and non-lekking grouse species, in which the adult males stick to their first breeding site (Bergerud and Gratson 1988).

Male's site tenacity has been assumed to be due to breeding ground scarcity, especially in the northern hemisphere where the breeding period is short, and requires a lifetime investment for mating success (Myers 1981, Ketterson and Nolan 1982, 1983). Male grouse are territorial, and the chance of managing the mating relies partly on the quality of their territory (Bergerud and Gratson 1988, Bart and Earnst 1999, Pedersen et al. 2007). Hence, for males staying on or nearby breeding ground boosts their chance of securing territory (**Paper III**). For non-lekking species like the rock ptarmigan, wintering near the breeding ground may be an alternative means to arrive on the breeding ground as soon as spring period arrives. Prior arrival on breeding ground pays off in this instance since first arrival is always a winner (Smith 1974). Smith (1974) also noted that the loser is the one that arrives later, and this individual settle on less favourable location. A nine year study conducted on savannah sparrows *Passerculus sandwichensis* showed that natal fidelity males had better reproduction as compared to the less philopatric individuals (Wheelwright and Mauck 1998). Hence, increased reproductive success could compensate for decreases survival rates when over-wintering close to breeding ranges where the weather can turn into less suitable (Wheelwright and Mauck 1998).

## 5.2 Spatial and hunting pressure differences in migrations

How far an individual rock ptarmigan migrates to the winter ground is also determined by how far north the individual's breeding range is located (**Fig 3, Table A3**; **Paper II**). Latitude was not a factor for the black grouse study as both study sites were located on the same parallels. Rock ptarmigan from Hrísey and Northeast conducted longer migration distance than individuals from the other sub-populations. Essentially, individuals from the Northeast migrated significantly longer than the birds from Hrísey; regardless of sex and age of the individuals (**Fig 3, Paper II**). No single individual migrated toward the northern sub-populations; neither did any bird migrate to Hrísey. These two regions are located approximately at the same latitude. But Hrísey is an island and hunting is forbidden, whereas the Northeast sub-population is part of the mainland and it is open for hunting similar to the other regions.

The observed migration distance difference between the Hrísey and the Northeast individuals is most likely explained by the difference of hunting pressure between them. This is because hunting disturbance is known to shape individuals' location choice and distribution (Frid and M. Dill 2001, Tolon et al. 2009). Similarly, several grouse species respond to hunting and other human disturbances by shifting to better secured sites (Storch 2013).

Behaviourally, rock ptarmigan are less shy to people on Hrísey than individuals in other part of the country. Hrísey rock ptarmigan behave almost like domestic chicken i.e. landing on roofs and feeding on gardens of the local houses. This is evidently an adaptation to the long term absence of hunting, and evidence that there is no immigration to the island. Japanese rock ptarmigan, which nearly have never been hunted, have the closest behaviour to the Hrísey sub-population (Nakamura 2010).

The reason behind the migration pattern differences between the northern and southern regions could be because of weather, predator community, and/or habitat quality differences among the locations. These differences are correlated with latitude. Weather parameters such as snow depth and/or temperature at the locations may also explain the ptarmigan movement. It is warmer and lesser snow in the southern Iceland, particularly in the Southwest (http://en.vedur.is/). Snow depth and ptarmigan migration has been shown to be correlated in other grouse populations, wherein ptarmigan migrate from their breeding site due to deep snow (Bergerud and Gratson 1988, Gruys 1993).

## 5.3 Population structure

Our rock ptarmigan bag data revealed a difference in male and female distribution among regions in winter in Iceland, where the males dominated in the northern areas and females were more common in the southern hunting regions (**Fig. 4** & **Table A1, Paper II**). Moreover, the sex - and/or age biased migration indirectly indicates that individuals aggregate based on sex - and/or age groups in winter (**Paper II, III**). Thus, the rock ptarmigan sub-populations show a sexual segregation and to some extent an age segregation in winter. This could be explained by the habitat quality differences and food quality sensitivity between sexes. Food is a critical factor for survival in winter (Johnsen et al. 2017). Migration is one of the coping mechanisms of this challenge. Gardarsson (1988) have documented that female rock ptarmigan prefer higher quality food in all seasons than males and thus tend to track better habitats whereas the males stay put on their breeding ground regardless of food quality change.

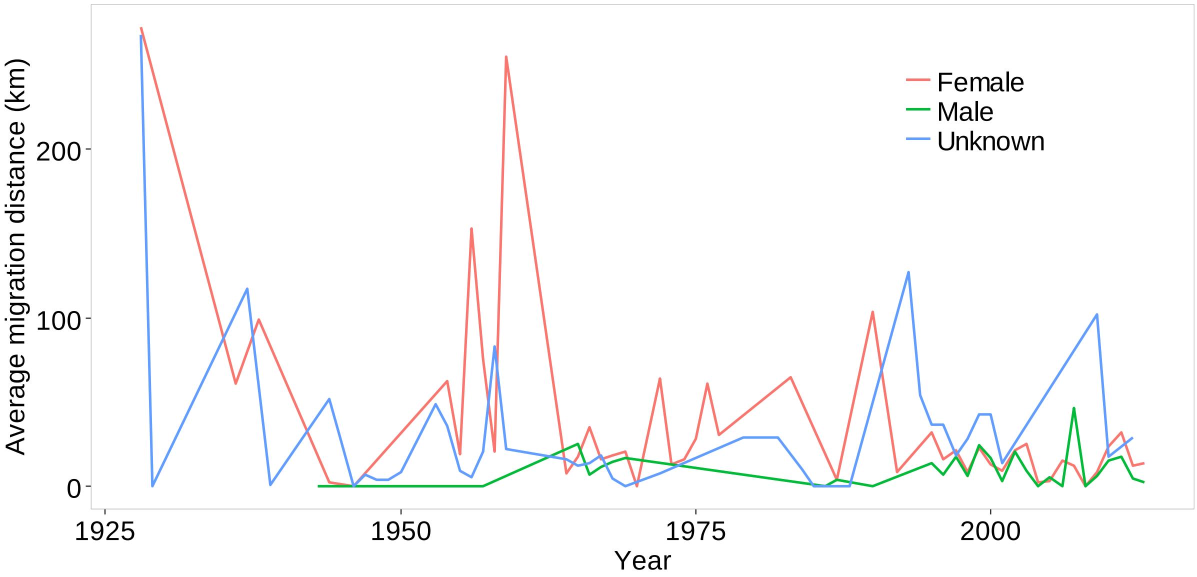


**Figure 3**. Average migration distance of the three groups' of rock ptarmigan individuals over the study year i.e. 1927-2013, Iceland. The unknown sex individuals' were chicks ringed between the end of July and the beginning of August, when they were 3-5 weeks old.

## 5.4 Population dynamics and cycle (I & II)

Adult rock ptarmigan survived significantly better than juveniles in all the three periods studied, particularly after year 1961 (**Fig. 2, Paper I**). The estimates show the highest survival among adults and the lowest among juveniles between 1961 and 1980. During the period that followed i.e. 1981-2013, the juvenile and adult survival differences were slightly narrowed. Yet, the adults' survival probability was better during this latter period than the oldest period's i.e. 1927-1960 when the rock ptarmigan population was assumed cycling and the abundance was better. The juveniles' survival, however, was moderately lower. In line with these three periods' estimates, the juvenile survival was lower during the decrease phase than the increase phase (**Table 4, Paper I**).

We entirely agree with Magnússon et al. (2004) and Nielsen (1999b) that the recruitment of the juvenile is what brings a difference in the population dynamics. But we do not agree with

Magnússon et al. (2004) that the causes of mortality and degree of vulnerability of both juvenile and adult are the same, and adult survival is more crucial than juvenile's for the population cyclicity to materialise or continue. If population abundance decreases, it is a direct signal that either the individuals' reproduction success or their survival probability or both are decreased. Unlike snowshoe hares (Sinclair et al. 2003), the average fecundity of the Hrísey and the Northeast ptarmigan sub-populations appear to be the same in both phases of the cycle (Nielsen 1999b). But, in closer look, the average chick numbers/brood sizes in late summer tend to fluctuate in synchrony with the territorial males index in spring (Nielsen 1999b; Nielsen et al. 2004; unpublished data). Plus the reproduction success the two age groups of all the populations are not deeply examined yet. A recent study reveals that reproduction success is different between locations, in which the Northeast hens are more successful and productive than the Southwest ones (Snæþórsson 2012).

A model on the rock ptarmigan population has shown that the mortality of adults and juveniles has increased since 1981, and has speculated that the decrease of adult survival was the reason for the decline of population abundance and the acyclicity of the population (Magnússon et al. 2004). Our survival estimates do not confirm these results as survival have not decreased over time.

The sources of departure between the results of Magnússon et al. (2004) and ours could be manifold, but we argue that the main reasons are type of data, and the following assumptions of the modelling. Firstly, the data Magnússon et al. (2004) used was exclusively sampled from the northern sub-populations. The time frame of the study was also limited to 1981-2004. Also our data were biased toward the better populated regions i.e. most of the ringing took place in northern localities. Nevertheless, the chance of recovering the rings or dead birds, in our case, was open for the entire country and it lasted for 86 years. The northern sub-populations have a distinctive migration, dispersal, density, and habitat attribute compared to the other sub-populations (**Paper I, II**). Consequently, those sub-populations and their dynamics do not represent the whole country's population.

Secondly, unlike Magnusson et al. (2004), our survival estimates are relative to the other previous periods rather than inter-annual variations, which could have been caused by either stochastic variabilities or the cyclic effect itself (Kéry and Schaub 2012).

Thirdly, Magnusson et al. (2004) has used all available data that ranged from territorial male counts in spring, to age ratio in summer and spring. All these data are based on equal age and sex ratio, and site fidelity assumptions. Except for the summer data, the spring age ratio was based on observed gyrfalcon and raven kills. Even if we have no strong ground to say that the age - and sex ratio was biased (but see Nielsen 1999b and Gardarsson 1988), using territorial males as a measure of population abundance might misrepresent the population, and there is no justification that the kills of gyrfalcon and raven are age-neutral. Although the males are more bound to their natal site, and are the dominant sex in the north during winter (**Paper II**), rock ptarmigan are not strictly monogamous (Holder and Montgomerie 1993, Bart and Earnst 1999). That is also observed in Iceland (Nielsen, O.K. personal communication, Gardarsson 1988). Further, the census plots have been kept constant for a long period. Therefore, the decrease of individual abundance or territorial male numbers could simply be an indication of habitat suitability shift or land-use change, where the males forced to establish other breeding ground. Because of these, we think it is the female rather than the males that limit population size or portray the population status.

As our migration results have shown, the juvenile males overwinter nearby their natal sites as compared to the juvenile females in Iceland (**paper II**). In addition, the proportion of juvenile rock ptarmigan in a given population is circa 3-4 times higher than that of the adults' in a given time nearly regardless of the population cycle phase (Gardarsson 1988, Nielsen 1999b). Juveniles are also dominant in hunting bag. For instance, in situations where both females and males were proportionally equal, juveniles account for > 70% of the country bag data (Nielsen 1999b, Nielsen et al. 2004). A study on willow ptarmigan in Norway has shown that juveniles are, in general, more susceptible to hunting than adults as long as they occur in groups (Asmyhr et al. 2012). Another study that has used ring-recovery method on the same species has also found that the majority of juveniles that were recovered were shot, and males outnumbered females (Myrberget 1975); indicating that juveniles, particularly male juveniles are vulnerable to hunting. In Iceland, hunting and arctic fox depredation (Gardarsson 1988, Hersteinsson and Macdonald 1996, Ellgutter 2017) are the two known main ptarmigan mortality causes that occur nearly exclusively during winter until March; after which the gyrfalcons take the lead (Nielsen 1993, 1996). But as we have no data on the hunters' effort per region, we do not know to how much extent the particular age and sex groups are influenced by hunters due to their differential migration.

Age ratio of the summer-spring population census indicates that the juveniles are exposed to higher mortality during the decrease phase than the increase phases (Nielsen 1999b). Our population cycle phases' survival probabilities (**Paper I**) are proportionally consistent with this apparent survival estimates. The number of juveniles also tend to be lower than adults in the decline phase than the increase phase (Nielsen 1999b), which is in agreement with the Scottish rock ptarmigan (Watson et al. 1998), and vole populations (Andreassen et al. 2013). It is well documented that Icelandic gyrfalcon population abundances fluctuate with the rock ptarmigan population with 0-4 years' lag, and both species are more densely populated in northern regions than the rest of the regions (Nielsen 1999a, Brynjarsdóttir et al. 2003, Nielsen 2011). According to Nielsen (1999a), the falcon's pressure is more pronounced during the peak phase than low phase (Nielsen 1999a).

We speculate that the hunting pressure was constant regardless of the phases. Since hunting regulation was in place, the hunters might have harvested equally regardless of the abundance fluctuation. If so, this could have put proportionally constant mortality upon the birds during both cycle phases, given the hunting efforts and hunter number stayed constant. Moreover, generalist predators, raven in this instance (Nielsen 1999a), might have played a dampening effect on the ptarmigan population cycle. Ravens dwell all over Iceland (Harðardottir and Nielsen 1999), and individuals from both southern and eastern part of country are registered dispersing > 70 km (Skarphedinsson et al. 1990). During the increase phase of ptarmigan, individuals from these dispersive sub-populations have a potential to redistribute themselves to the northern region where there are abundant ptarmigan and bring down the ptarmigan density. However, this dampening effect might be milder in recent years, as ravens are being persecuted in high intensity (Harðardottir and Nielsen 1999).

## 6. Conclusions and further perspectives

Our results illustrate that male black grouse have limited dispersal, and null migration tendency. These pinpoint that a lek could be treated as a standalone male population and neither dispersal nor migration of males play role in population abundance synchrony.

Counting the displaying males in spring in early morning on arena before peak mating week could give a reasonable number of males since the juveniles tend to stay away from lek during peak mating period. Our rock ptarmigan findings emphasises that population dynamics is controlled by the juveniles, which is consistent with previous observations (Gardarsson 1988; Nielsen 1999b). Given the average migration distance between males and females, segregation of males and females, and juveniles and adults in winter, and unequal population density distribution throughout the country at a given time, we think that juvenile rock ptarmigan males might be more exposed to hunting than the other group of individuals in Iceland.

The Icelandic rock ptarmigan population abundance is declining, and at the same time the cycle is vanishing and becoming asynchronous between regions. However, our survival estimates do not support that the average survival of the species has decreased in recent years as compared to their previous periods. Hence, the claim that adult survival probability can be used an indicator of the population cyclicity is not supported in this study. However, migration distance (or misinterpreted dispersal) of the species has generally decreased through the study period (Figure 3); a factor which we could not model due to inadequate data per regions. The reason behind diminishing of migration/dispersal distance could be the increasing average temperature in the country (http://en.vedur.is/climatology/data/), and/or the decrease of the population abundance itself. Populations cease to synchronize as soon as they decrease in abundance (Paradis et al. 1998, 1999).

Taking the following points into account, we conclude that the two northern Icelandic rock ptarmigan sub-populations serve as source populations to the rest of the country. This is because 1) the Northeast sub-population has better chick production and better hen survival during summer than the Southwest (Snæþórsson 2012). 2) Both the Northeast and Hrísey have proportional high rock ptarmigan abundances than the rest of the country (Gudmundsson 1960, Gardarsson 1988, Nielsen 1996). 3) We observed both natal and breeding dispersals in these two sub-populations, i.e. a high degree of emigration. Density dependent dispersal is a common phenomenon in birds, and the majority of the dispersal is positive density dependent (Matthysen 2005).

The collapse of a periodic population cycle, whether it is temporary or long-lasting, is global; cropping up in regions where the pattern was once common in many populations. However, the particular cause of the cycles' collapse is still unknown. This is not surprising given that what triggers the cycle itself is not clearly known yet (Ims et al. 2008). It is speculated that the fading of Fennoscandian rodent population cycle is influenced by climate change (Ims et al. 2008, Cornulier et al. 2013) even if the climate change does not seem to provide full explanation yet (Brommer et al. 2010). Rodents do not play any part in the Icelandic rock ptarmigan population cycle as the ptarmigan stands nearly alone at the bottom of the thin food chain in the country. If the change in climate has significance in the population cycle, it is possible that it challenges the Icelandic rock ptarmigan population too. This is because it has been observed that rock ptarmigan chicks are highly fragile to abnormal weather condition (Gardarsson 1988, Nielsen 2004) and the species react strongly to climate changes (Kozma et al. 2016). As far as we know, no one in Iceland has investigated ptarmigan's fodder chemical change (plant-mast) in relation to rock ptarmigan population cycle. Besides, a few researches demonstrated that the perceived population cycle crashes, for example of rodents and foxes, are not new as it is being claimed. An analysis on fox bag statistics has shown that the collapse of population cycle has had happened before and the cycle's pattern along the latitudinal gradients was not stationary (Henden et al. 2009). If an answer to the cause of population cycles or the collapse of population cycle could be found, it is easier to detect it in Iceland than other locations since the country has the simplest ecosystem we can monitor and an extensive high standard data that have been collected for many years.

We recommend that chick production variability per age and region, overwinter survival of juveniles, and hunters' effort should be examined further. Let alone ptarmigan, obtaining data on any bird species is awfully tedious and expensive. Perhaps combining the ringing with satellite tracking, which is already tested in Norwegian and Swedish ptarmigan, would greatly profit the study especially during winter relocation. In addition, in our data, there were reasonable numbers of unidentified-sex individuals. These individuals conducted incompatible migration patterns than the known-sex individuals. Genetic analysis could come handy in these circumstances and we recommend applying the method whenever possible in the future study. Furthermore, anticipate the possibility of biased sex and age distribution whenever using the hunting statistics and population census for any future analysis or management issues since it might conceal an essential fact and mislead the management. If territorial, and killed males are to be used as a population index, and if juvenile males are shot more often, as we assume, then the reason for the observed population decline might also be embedded in between these factors.

## 7. Reference

Alatalo, R. V., J. Hoglund, A. Lundberg, and W. J. Sutherland. 1992. Evolution of black grouse leks - Female preferences benefit males in larger leks. Behavioral Ecology **3**:53-59.

Amarasekare, P. 1998. Interactions between local dynamics and dispersal: Insights from single species models. Theoretical Population Biology **53**:44-59.

Andreassen, H. P., P. Glorvigen, A. Rémy, and R. A. Ims. 2013. New views on how population-intrinsic and community-extrinsic processes interact during the vole population cycles. Oikos **122**:507-515.

Andreassen, H. P., and R. A. Ims. 2001. Dispersal in patchy vole populations: Role of patch configuration, density dependence, and demography. Ecology **82**:2911-2926.

Andreev, A. 1987. The years of observations on the willow grouse of lower Kolyma.*in* 4th International grouse symposium. World Pheasant Association, Lam, West Germany.

Asmyhr, L., T. Willebrand, and M. Hörnell-Willebrand. 2012. Successful adult willow grouse are exposed to increased harvest risk. Journal of Wildlife Management **76**:940-943.

Baguette, M., and H. Van Dyck. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. Landscape Ecology **22**:1117-1129.

Bart, J., and S. L. Earnst. 1999. Relative importance of male and territory quality in pairing success of male rock ptarmigan (Lagopus mutus). Behavioral Ecology and Sociobiology **45**:355-359.

Bergerud, A. T., and M. W. Gratson. 1988. Survival and breeding strategies of grouse. Pages 473-577 *in* A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis.

Bjørnstad, O. N., W. Falck, and N. C. Stenseth. 1995. A geographic gradient in small rodent density fluctuations: A statistical modelling approach. Proceedings of the Royal Society of London. Series B: Biological Sciences **262**:127-133.

Boonstra, R., C. J. Krebs, and N. C. Stenseth. 1998. Population cycles in small mammals: The problem of explaining the low phase. Ecology **79**:1479-1488.

Boyle, W. A. 2008. Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. Journal of Animal Ecology **77**:1122-1128.

Brittas, R., V. marcstrom, and E. Engren. 1987. Habitat use by Swedish black grouse during summer.*in* 4th International grouse symposium. World Pheasant Association, Lam, West Grmany.

Brodsky, L. M. 1988. Mating tactics of male rock ptarmigan *Lagopus mutus*: A conditional mating strategy. Animal Behaviour **36**:335-342.

Brommer, J. E., H. Pietiainen, K. Ahola, P. Karell, T. Karstinen, and H. Kolunen. 2010. The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. Global Change Biology **16**:577-586.

Brynjarsdóttir, J., S. H. Lund, K. G. Magnússon, and Ó. K. Nielsen. 2003. Analysis of time series for rock ptarmigan and gyrfalcon populations in north-east Iceland. University of Iceland, Reykjavík.

Caizergues, A., and L. N. Ellison. 2002. Natal dispersal and its consequences in black grouse *Tetrao tetrix*. Ibis **144**:478-487.

Catchpole, E. A., S. N. Freeman, B. J. T. Morgan, and M. P. Harris. 1998. Integrated recovery/recapture data analysis. Biometrics **54**:33-46.

Cheke, R. A., and J. A. Tratalos. 2007. Migration, patchiness, and population processes illustrated by two migrant pests. Bioscience **57**:145-154.

Chitty, D. 1960. Population processes in the vole and their relevance to general theory. Canadian Journal of Zoology **38**:99-113.

Clobert, J., and J. D. Lebreton. 1991. Estimation of demographic parameters in bird population. Pages xvi, 683 *in* C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Bird population studies: Relevance to conservation and management. Oxford University Press, Oxford, New York, Tokyo.

Clutton-Brock, T. H., M. Major, S. D. Albon, and F. E. Guinness. 1987. Early development and population dynamics in red deer. I. Density-dependent effects on juvenile survival. Journal of Animal Ecology **56**:53-67.

Cooke, F., and C. M. Francis. 1993. Challenges in the analysis of recruitment and spatial organization of population. Pages 295-308 *in* J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhäuser Verlag, Basel, Boston, Berlin.

Cornulier, T., N. G. Yoccoz, V. Bretagnolle, J. E. Brommer, A. Butet, F. Ecke, D. A. Elston, E. Framstad, H. Henttonen, B. Hornfeldt, O. Huitu, C. Imholt, R. A. Ims, J. Jacob, B. Jedrzejewska, A. Millon, S. J. Petty, H. Pietiainen, E. Tkadlec, K. Zub, and X. Lambin. 2013. Europe-wide dampening of population cycles in keystone herbivores. Science **340**:63-66.

Corrales, C., and J. Hoglund. 2012. Maintenance of gene flow by female-biased dispersal of black grouse *Tetrao tetrix* in northern Sweden. Journal of Ornithology **153**:1127-1139.

Cotter, R. C. 1999. The reproductive biology of rock ptarmigan *Lagopus mutus* in the central Canadian Arctic. Arctic **52**:23-32.

Cox, G. W. 1985. The evolution of avian migration systems between temperate and tropical regions of the new world. The American Naturalist **126**:451-474.

den Boer, P. J. 1981. On the survival of populations in a heterogeneous and variable environment. Oecologia **50**:39-53.

Diffendorfer, J. E. 1998. Testing models of source-sink dynamics and balanced dispersal. Oikos **81**:417-433.

Dingle, H. 1996. Migration: The biology of life on the move Oxford University Press, ProQuest Ebook Central.

Dingle, H., and V. A. Drake. 2007. What is migration? Bioscience **57**:113-121.

Elgood, J. H., C. H. Fry, and R. J. Dowsett. 1973. African migrants in Nigeria. Ibis **115**:375-409.

Ellgutter, J. A. C. 2017. An analysis of dietary variation in Icelandic arctic fox *Vulpes lagopus* over a period of 30 years using stable isotopes. Norges Arktiske Universitet, Tromsø.

Elton, C. 1953. The ecology of animals. Forth edition. Methuen & Co. Ltd, London.

Elton, C., and M. Nicholson. 1942. Fluctuations in numbers of the muskrat *Ondatra zibethica* in Canada. Journal of Animal Ecology **11**:pp. 96-126.

Frid, A., and L. M. Dill. 2001. Human-caused disturbance stimuli as a form of predation risk. 6 **1**.

Fuglei, E., M. A. Blanchet, S. Unander, R. A. Ims, and A. O. Pedersen. 2017. Hidden in the darkness of the Polar night: A first glimpse into winter migration of the Svalbard rock ptarmigan. Wildlife Biology:1-8.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: Variable recruitment with constant adult survival. Trends in Ecology & Evolution **13**:58-63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics **31**:367-393.

Gaillard, J.-M., and N. G. Yoccoz. 2003. Temporal variation in survival of mammals: A case of environmental canalization? Ecology **84**:3294-3306.

Gardarsson, A. 1988. Cyclic population changes and some related events in rock ptarmigan in Iceland. Pages 300-329 *in* A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press and Fitzhenry & Whiteside Limited, Minneapolis and Markham.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour **28**:1140-1162.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics **13**:1-21.

Gregersen, F., and H. Gregersen. 2009. Ongoing population decline and range contraction in Norwegian forest grouse. Ornis Norvegica **32**:179-189.

Gruys, R. C. 1993. Autumn and winter movements and sexual segregation of willow ptarmigan. Arctic **46**:228-239.

Gudmundsson, F. 1960. Some reflections on ptarmigan cycles in Iceland. Pages 259-265 *in* Proceedings of the XII International Ornithological Congress, Helsinki.

Haartman, L. v. 1949. Der trauerfliegenschnäpper i. Ortstreue und rassenbildung. Acta zoologica Fennica **56**:1-107, In Germany.

Hagen, Y. 1952. Rovfuglene og viltpleien. Gyldendal Norsk Forlag, Oslo, In Norwegian.

Hamilton, W. D. 1963. The evolution of altruistic behavior. The American Naturalist **97**:354-356.

Hanski, I. 1998. Metapopulation dynamics. Nature **396**:41-49.

Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology **60**:353-367.

Hanski, I., M. Kuussaari, and M. Nieminen. 1994. Metapopulation structure and migration in the butterfly *Melitaea cinxia*. Ecology **75**:747-762.

Hansson, L. 1991. Dispersal and connectivity in metapopulations. Biological Journal of the Linnean Society **42**:89-103.

Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents: The importance of latitude and snow cover. Oecologia **67**:394-402.

Harðardottir, M., and Ó. K. Nielsen. 1999. the status of the raven populatin in Þinceyjarsýslur, north-east Iceland. Náttúrufræðingurinn **68**:147-154, In Icelandic with English summary.

Helminen, M. 1963. Composition of the Finnish populations of capercaillie *Tetrao urogallus*, and black grouse *Lyrurus tetrix* in the autumns of 1952-1961, as revealed by a study of wings. Helsinki.

Henden, J.-A., R. A. Ims, and N. G. Yoccoz. 2009. Nonstationary spatio-temporal small rodent dynamics: Evidence from long-term Norwegian fox bounty data. Journal of Animal Ecology **78**:636-645.

Hersteinsson, P., and D. W. Macdonald. 1996. Diet of arctic foxes *Alopex lagopus* in Iceland. Journal of Zoology **240**:457-474.

Holder, K., and R. Montgomerie. 1993. Red colour bands do not improve the mating success of male rock ptarmigan. Ornis Scandinavica **24**:53-58.

Holt, R. D., and M. Barfield. 2001. On the relationship between the ideal free distribution and the evolution of dispersal. Page 85:96 *in* J. Clobert, E. Danchin, A. A. dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. The American Midland Naturalist **63**:152-161.

Höglund, J., D. Baines, J. K. Larsson, and G. Segelbacher. 2003. Population fragmentation and genetic variability in European Black Grouse - a progress report. SYLVIA **39**:17-23.

Höglund, J., T. Johansson, and C. Pelabon. 1997. Behaviourally mediated sexual selection: Characteristics of successful male black grouse. Animal Behaviour **54**:255-264.

Höglund, J., and S. Stohr. 1997. A non-lekking population of black grouse Tetrao tetrix. Journal of Avian Biology **28**:184-187.

Hörnell-Willebrand, M., T. Willebrand, and A. A. Smith. 2014. Seasonal movements and dispersal patterns: Implications for recruitment and management of willow ptarmigan *Lagopus lagopus*. Journal of Wildlife Management **78**:194-201.

Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls, and Tularemia in Northern Sweden. Oecologia **32**:141-152.

Ims, R. A. 1995. Movement patterns related to spatial structures. Pages 85-109 *in* L. Hansson, L. Fahrig, and G. Merriam, editors. Mosaic Landscapes and Ecological Processes, Dordrecht.

Ims, R. A., and H. P. Andreassen. 2000. Spatial synchronization of vole population dynamics by predatory birds. Nature **408**:194-196.

Ims, R. A., and E. Fuglei. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. Bioscience **55**:311-322.

Ims, R. A., J.-A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. Trends in Ecology and Evolution **23**:79-86.

Ims, R. A., and N. G. Yoccoz. 1997. Studying transfer processes in metapopulations: Emigration, migration, and colonization. Pages 247-265 *in* I. Hanski and M. E. Gilpin, editors. Metapopulation Biology. Academic Press, San Diego.

Jahn, A. E., D. J. Levey, and K. G. Smith. 2004. Reflections across hemispheres: A system-wide approach to new world bird migration. The Auk **121**:1005-1013.

Jahren, T., T. Storaas, T. Willebrand, P. F. Moa, and B. R. Hagen. 2016. Declining reproductive output in capercaillie and black grouse-16 countries and 80 years. Animal Biology **66**:363-400.

Johnsen, K., R. Boonstra, S. Boutin, O. Devineau, C. J. Krebs, and H. P. Andreassen. 2017. Surviving winter: Food, but not habitat structure, prevents crashes in cyclic vole populations. Ecology and Evolution **7**:115-124.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal - Theoretical-models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics **21**:449-480.

Jönsson, K. I., P. K. Angelstam, and E. S. Jon. 1991. Patterns of life-history and habitat in Palaearctic and nearctic forest grouse. Ornis Scandinavica **22**:275-281.

Kendall, B. E., J. Prendergast, and O. N. Bjørnstad. 1998. Trophic interactions and population growth rates describing patterns and identifying mechanisms. Ecology Letters **1**:160-164.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: A hierarchical perspective. Elsevier Inc., Amsterdam.

Ketterson, E. D., and V. Nolan. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the dark-eyed junco, as determined from demographic analyses of winter populations. The Auk **99**:243-259.

Ketterson, E. D., and V. Nolan. 1983. The evolution of differential bird migration. Pages 357-402 *in* R. F. Johnston, editor. Current Ornithology. Springer US, Boston, MA.

Koenig, W. D., D. VanVuren, and P. N. Hooge. 1996. Detectability, philopatry, and the distribution of dispersal distances in vertebrates. Trends in Ecology & Evolution **11**:514-517.

Koivisto, I. 1965. Behavior of the black grouse, *Lyrurus tetrix* (L) during the spring display. Finnish Game Research, Helsinki.

Kokko, H., and J. Lindström. 1996. Kin selection and the evolution of leks: Whose success do young males maximize? Proceedings of the Royal Society of London Series B-Biological Sciences **263**:919-923.

Kokko, H., and P. Lundberg. 2001. Dispersal, migration, and offspring retention in saturated habitats. The American Naturalist **157**:188-202.

Kozma, R., P. Melsted, K. P. Magnússon, and J. Höglund. 2016. Looking into the past – The reaction of three grouse species to climate change over the last million years using whole genome sequences. Molecular Ecology **25**:570-580.

Krebs, C. J. 1978. A review of the Chitty Hypothesis of population regulation. Canadian Journal of Zoology **56**:2463-2480.

Krebs, C. J. 1996. Population cycles revisited. Journal of Mammalogy **77**:8-24.

Krebs, C. J. 2011. Of lemmings and snowshoe hares: The ecology of Northern Canada. Proceedings of the Royal Society B-Biological Sciences **278**:481-489.

Krebs, C. J., B. L. Keller, and R. H. Tamarin. 1969. Microtus population biology: Demographic changes in fluctuating populations of M. Ochrogaster and M. Pennsylvanicus in Southern indiana. Ecology **50**:587-607.

Krebs, C. J., A. J. Kenney, S. Gilbert, K. Danell, A. Angerbjorn, S. Erlinge, R. G. Bromley, C. Shank, and S. Carriere. 2002. Synchrony in lemming and vole populations in the Canadian Arctic. Canadian Journal of Zoology-Revue Canadienne De Zoologie **80**:1323-1333.

Krebs, C. J., and J. H. Myers. 1974. Population cycles in small mammals. Advances in Ecological Research **8**:267-399.

Kruijt, J. P., and G. J. de Vos. 1988. Individual variation in reproductive success in male black grouse *Tetrao tetrix* L. .*in* T. H. Clutton-Brock, editor. Reproductive Success. The University of Chicago Press, Chicago and London.

Kurki, S., A. Nikula, P. Helle, and H. Linden. 2000. Landscape fragmentation and forest composition effects on grouse breeding success in boreal forests. Ecology **81**:1985-1997.

Kvasnes, M. A. J., T. Storaas, H. C. Pedersen, S. Bjork, and E. B. Nilsen. 2010. Spatial dynamics of Norwegian tetraonid populations. Ecological Research **25**:367-374.

Lack, D. 1944. The problem of partial migration. British Birds **37**:122-130.

Lack, D. 1954. The natural regulation of animal numbers. First edition. Oxford Clarenden Press, Oxford.

Lambrechts, M. M., J. Blondel, A. Caizergues, P. C. Dias, R. Pradel, and D. W. Thomas. 1999. Will estimates of lifetime recruitment of breeding offspring on small-scale study plots help us to quantify processes underlying adaptation? Oikos **86**:147-151.

Lebreton, J. D., B. J. T. Morgan, R. Pradel, and S. N. Freeman. 1995. A simultaneous survival rate analysis of dead recovery and live recapture data. Biometrics **51**:1418-1428.

Lebreton, J. D., R. Pradel, and J. Clobert. 1993. The statistical-analysis of survival in animal populations. Trends in Ecology & Evolution **8**:91-95.

Leslie, P. H., and R. M. Ranson. 1940. The mortality, fertility and rate of natural increase of the vole *Microtus agrestis* as observed in the laboratory. Journal of Animal Ecology **9**:27-52.

Liberg, O., and T. v. Schantz. 1985. Sex-biased philopatry and dispersal in birds and mammals: The Oedipus hypothesis. The American Naturalist **126**:129-135.

Linden, H. 1988. Latitudinal gradients in predator-prey interactions, cyclicity and synchronism in voles and small game populations in Finland. Oikos **52**:341-349.

Lindstrom, J., E. Ranta, V. Kaitala, and H. Linden. 1995. The clockwork of Finnish tetraonid population dynamics. Oikos **74**:185-194.

Lindstrom, J., E. Ranta, and H. Linden. 1996. Large-scale synchrony in the dynamics of capercaillie, black grouse and hazel grouse populations in Finland. Oikos **76**:221-227.

Ludwig, G. X., R. V. Alatalo, P. Helle, H. Linden, J. Lindstrom, and H. Siitari. 2006. Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. Proceedings of the Royal Society B-Biological Sciences **273**:2009-2016.

Magnússon, K. G., J. Brynjarsdóttir, and Ó. K. Nielsen. 2004. Population cycles in rock ptarmigan *Lagopus muta*: modelling and parameter estimation. Science Institute, Reykjavík.

Martin, K. 1995. Patterns and mechanisms for age-dependent reproduction and survival in birds. American Zoologist **35**:340-348.

Matthysen, E. 2005. Density-dependent dispersal in birds and mammals. Ecography **28**:403-416.

McPeek, M. A., and R. D. Holt. 1992. The evolution of dispersal in spatially and temporally varying environments. The American Naturalist **140**:1010-1027.

Merkel, F. R. 2010. Evidence of recent population recovery in common eiders breeding in western Greenland. Journal of Wildlife Management **74**:1869-1874.

Moss, R., and A. Watson. 2001. Population cycles in birds of the grouse family (Tetraonidae). Advances in Ecological Research **32**:53-111.

Myers, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Canadian Journal of Zoology **59**:1527-1534.

Myrberget, S. 1975. Age distribution, motality and migration of willow grouse *Lagopus lagopu*s on Senja, North Norway. Astarte **8**:29-35.

Nakamura, H. 2010. Why Japanese rock ptarmigan never fear humans. Grouse News **40**:32-35.

Nielsen, O. K. 1993. Initiation of territoriality among Icelandic rock ptarmigan in spring. Náttúrufræðingurinn **63**:29-37, In Icelandic with English summary.

Nielsen, O. K. 1995. Rock ptarmigan density and heathland vegetation in suður'þlngeyjarsýsla, NE-Iceland. Náttúrufræðingurinn **65**:81-102, In Icelandic with English summary.

Nielsen, O. K. 1996. Rock ptarmigan censuses in northeast Iceland 1981 to 1994. Náttúrufræðingurinn **65**:137–151, In Icelandic with English summary.

Nielsen, Ó. K. 1999a. Gyrfalcon predation on ptarmigan: numerical and functional responses. Journal of Animal Ecology **68**:1034-1050.

Nielsen, Ó. K. 1999b. Vöktun rjúpnastofnsins. Nattúrufræðistofnunar Island, Reykjavik, In Icelandic with English summary.

Nielsen, Ó. K. 2011. Gyrfalcon population and reproduction in relation to rock ptarmigan numbers in Iceland. Pages 21-48 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E.

Potapov, editors. Gyrfalcons and Ptarmigan in a Changing World. The Peregrine Fund, Boise, Idaho.

Nielsen, Ó. K., J. Brynjarsdóttir, and K. G. Magnússon. 2004. Vöktun rjúpnastofnsins 1999-2003 Nattúrufræðistofnunar Island, Reykjavik, In Icelandic with English summary.

Nielsen, Ó. K., and T. J. Cade. 1990. Seasonal changes in food habits of gyrfalcons in NE-Iceland. Ornis Scandinavica **21**:202-211.

Nielsen, Ó. K., N. d. Pelsmaeker, and G. A. Guðmundsson. 2013. Rock ptarmigan *Lagopus muta* health studies in northeast Iceland 2012: Morphology and body reserves. Náttúrufræðistofnun íslands, Garðabær.

Nielsen, Ó. K., and G. Pétursson. 1995. Population fluctuations of gyrfalcon and rock ptarmigan: Analysis of export figures from Iceland. Wildlife Biology **1**:65-71.

Nolan, V., C. F. Thompson, E. D. Ketterson, and SpringerLink. 1999. Current Ornithology. Springer.

O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology **79**:1193-1208.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1998. Patterns of natal and breeding dispersal in birds. Journal of Animal Ecology **67**:518-536.

Paradis, E., S. R. Baillie, W. J. Sutherland, and R. D. Gregory. 1999. Dispersal and spatial scale affect synchrony in spatial population dynamics. Ecology Letters **2**:114-120.

Pedersen, Å. Ø., J. U. Jepsen, N. G. Yoccoz, and E. Fuglei. 2007. Ecological correlates of the distribution of territorial Svalbard rock ptarmigan (Lagopus muta hyperborea). Canadian Journal of Zoology **85**:122-132.

Pianka, E. R. 1970. On r- and K-Selection. The American Naturalist **104**:592-597.

Pulliam, H. R. 1988. Sources, sinks, and population regulation. American Naturalist **132**:652-661.

Pusey, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology & Evolution **2**:295-299.

Radchuk, V., R. A. Ims, and H. P. Andreassen. 2016. From individuals to population cycles: The role of extrinsic and intrinsic factors in rodent populations. Ecology **97**:720-732.

Ranta, E., V. Kaitala, J. Lindstrom, and H. Linden. 1995. Synchrony in population-dynamics. Proceedings of the Royal Society B-Biological Sciences **262**:113-118.

Reed, J. M., and L. W. Oring. 1993. Philopatry, site fidelity, dispersal, and survival of spotted sandpipers. The Auk **110**:541-551.

Rintamaki, P. T., E. Karvonen, R. V. Alatalo, and A. Lundberg. 1999. Why do black grouse males perform on lek sites outside the breeding season? Journal of Avian Biology **30**:359-366.

Roff, D. A. 1975. Population stability and the evolution of dispersal in a heterogeneous environment. Oecologia **19**:217-237.

Sandercock, B. K., E. B. Nilsen, H. Brøseth, and H. C. Pedersen. 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**:244-258.

Schwarz, C. J. 1993. Estimating migration rates using tag-recovery data. Pages 255-264 *in* J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhäuser Verlag, Basel, Boston, Berlin.

Semlitsch, R. D. 2008. Differentiating migration and dispersal processes for pond-breeding amphibians. The Journal of Wildlife Management **72**:260-267.

Servanty, S., R. Choquet, É. Baubet, S. Brandt, J.-M. Gaillard, M. Schaub, C. Toïgo, J.-D. Lebreton, M. Buoro, and O. Gimenez. 2010. Assessing whether mortality is additive using marked animals: a Bayesian state–space modeling approach. Ecology **91**:1916-1923.

Sinclair, A. R. E., D. Chitty, C. I. Stefan, and C. J. Krebs. 2003. Mammal population cycles: Evidence for intrinsic differences during snowshoe hare cycles. Canadian Journal of Zoology-Revue Canadienne De Zoologie **81**:216-220.

Skarphedinsson, K. H., O. K. Nielsen, S. Th6risson, S. Thorstensen, and S. A. Temple. 1990. Breeding biology, movements, and persecution of ravens in Iceland. Acta Naturalia Islandica **33**:1-45.

Skirnisson, K., S. T. Thorarinsdottir, and Ó. K. Nielsen. 2012. The parasite fauna of rock ptarmigan *Lagopus muta* in iceland: Prevalence, intensity, and distribution within the host population. Comparative Parasitology **79**:44-55.

Smith, J. M. 1974. The theory of games and the evolution of animal conflicts. Journal of Theoretical Biology **47**:209-221.

Snæþórsson, A. Ö. 2012. Reproductive success and survival of hen rock ptarmigan *Lagopus muta* during summer. University of Iceland, Reykjavik.

Stacey, P. B., and M. Taper. 1992. Environmental variation and the persistence of small populations. Ecological Applications **2**:18-29.

Stenkewitz, U., O. K. Nielsen, K. Skirnisson, and G. Stefansson. 2016. Host-parasite interactions and population dynamics of rock ptarmigan. Plos One **11**:1-19.

Stenseth, N. C., and W. Z. Lidicker. 1992. Animal dispersal: Small mammals as a model. Chapman and Hall, London.

Storaas, T., and P. Wegge. 1987. Nesting habitats and nest predation in sympatric populations of capercaillie and black grouse. The Journal of Wildlife Management **51**:167-172.

Storch, I. 2007. Grouse: Status survey and conservation action plan 2006-2010 IUCN, Gland, Switzerland and Fordingbridge, UK.

Storch, I. 2013. Human disturbance of grouse - Why and when? Wildlife Biology **19**:390-403.

Sturludóttir, E. 2015. Statistical analysis of trends in data from ecological monitoring. Univeristy of Iceland, Reykjavik.

Sunde, P., and T. Asferg. 2014. How does harvest size vary with hunting season length? Wildlife Biology **20**:176-184.

Svobodova, J., G. Segelbacher, and J. Hoglund. 2011. Genetic variation in Black Grouse populations with different lekking systems in the Czech Republic. Journal of Ornithology **152**:37-44.

Taylor, L. R. 1986. Synoptic dynamics, migration and the rothamsted insect survey: Presidential address to the British Ecological Society, December 1984. Journal of Animal Ecology **55**:1-38.

Taylor, L. R., and R. A. Taylor. 1977. Aggregation, migration and population mechanics. Nature **265**:415-421.

Tellería, J. L., and J. Pérez-Tris. 2004. Consequences of the settlement of migrant european robins *Erithacus rubecula* in wintering habitats occupied by conspecific residents. Ibis **146**:258-268.

Tolon, V., S. Dray, A. Loison, A. Zeileis, C. Fischer, and E. Baubet. 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Canadian Journal of Zoology **87**:1129-1137.

Turchin, P., S. N. Wood, S. P. Ellner, B. E. Kendall, W. W. Murdoch, A. Fischlin, J. Casas, E. McCauley, and C. J. Briggs. 2003. Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. Ecology **84**:1207-1214.

Warkentin, I. G., and D. Hernandez. 1996. The conservation implications of site fidelity: A case study involving nearctic-neotropical migrant songbirds wintering in a Costa Rican mangrove. Biological Conservation **77**:143-150.

Warren, P. K., and D. Baines. 2002. Dispersal, survival and causes of mortality in black grouse *Tetrao tetrix* in northern England. Wildlife Biology **8**:91-97.

Watson, A., and R. Moss. 2008. Grouse: The natural history of British and Irish species. Collins, Hong Kong.

Watson, A., R. Moss, R. Parr, M. D. Mountford, and P. Rothery. 1994. Kin landownership, differential aggression between kin and non-kin, and population fluctuations in red grouse. Journal of Animal Ecology **63**:39-50.

Watson, A., R. Moss, and S. Rae. 1998. Population dynamics of Scottish Rock Ptarmigan cycles. Ecology **79**:1174-1192.

Wayre, P., and G. F. Jolly. 1958. Notes on the breeding of the Iceland gyrfalcon. British Birds **LI**:258-290.

Weeden, R. B. 1964. Spatial separation of sexes in rock and willow ptarmigan in winter. The Auk **81**:534-541.

Weeden, R. B., and A. Watson. 1967. Determining the age of rock ptarmigan in Alaska and Scotland. Journal of Wildlife Management **31**:825-826.

Wegge, P., T. Kvalsgard, O. Hjeljord, and A. V. Sivkov. 2003. Spring spacing behaviour of capercaillie *Tetrao urogallus* males does not limit numbers at leks. Wildlife Biology **9**:283-289.

Wegge, P., and B. B. Larsen. 1987. Spacing of adult and subadult male common capercaillie during the breeding season. Auk **104**:481-490.

Wegge, P., and J. Rolstad. 2011. Clearcutting forestry and Eurasian boreal forest grouse: Long-term monitoring of sympatric capercaillie *Tetrao urogallus* and black grouse *T. tetrix* reveals unexpected effects on their population performances. Forest Ecology and Management **261**:1520-1529.

Wheelwright, N. T., and R. A. Mauck. 1998. Philopatry, natal dispersal, and inbreeding avoidance in an island population of Savannah Sparrows. Ecology **79**:755-767.

Wiens, J. A., N. C. Stenseth, B. Vanhorne, and R. A. Ims. 1993. Ecological mechanisms and landscape ecology. Oikos **66**:369-380.

Williams, C. K., A. R. Ives, R. D. Applegate, and J. Ripa. 2004. The collapse of cycles in the dynamics of North American grouse populations. Ecology Letters **7**:1135-1142.

Wolff, J. O., and J. H. Plissner. 1998. Sex biases in avian natal dispersal: An extension of the mammalian model. Oikos **83**:327-330.

Woodin, N., and S. Route. 1980. Observations on gyrfalcon *Falco rusticolus* breeding near Lake Myvatn, Iceland, 1967. Journal of Raptor Research **14**:97-124.

Zurell, D., V. Grimm, E. Rossmanith, N. Zbinden, N. E. Zimmermann, and B. Schroder. 2012. Uncertainty in predictions of range dynamics: black grouse climbing the Swiss Alps. Ecography **35**:590-603.

# Paper I

Title: Age dependent survival estimates for rock ptarmigan *Lagopus muta* based on long-term ring-recapture-recovery data

DEGITU E. BORECHA, Inland Norway University of applied sciences, Faculty of Applied Ecology and Agricultural Sciences, Evenstad, N-2480 Koppang, Norway

TOMAS WILLEBRAND, Inland Norway University of applied sciences, Faculty of Applied Ecology and Agricultural Sciences, Evenstad, N-2480 Koppang, Norway

OLAFUR K. NIELSEN, The Icelandic Institute of Natural History, Urriðaholtsstræti 6–8, 212 Garðabær, Iceland

MICHAEL SCHAUB, Swiss Ornithological Institute, Seerose 1, 6204 Sempach, Switzerland

# Abstract

The rock ptarmigan is a popular game bird in Iceland that formerly experienced 10–12 years periodic population cycles. Recently, the population cycle is fading and the ptarmigan abundance is decreasing. Decreased survival probabilities have been hypothesized to be the proximate reason for both the abundance decline and the fading population cycle. In this paper, we estimated the age-dependent annual survival probabilities of the Icelandic rock ptarmigan population using 86 years of ring-recapture-resight and recovery histories from 6615 individuals. We divided the data into three periods based on the historical development of the rock ptarmigan population in the country. In addition, we evaluated the species survival during the decrease and increase phases of the population cycle. During the 3 periods, the average annual survival ± se varied between 0.12 ± 0.03 and 0.30 ± 0.06 for juveniles, and between 0.39 ± 0.05 and 0.58 ± 0.0.05 for adults. Survival was highest for adults in 1961-1980, the period before the population started crashing, and in the earliest period of 1927-

1960 for juveniles. The recent 1981-2013 period was the second best period for both juvenile and adult survivals. The average survival probabilities of the two age classes were significantly different for the last two periods. The juvenile survival and recovery probabilities were higher during the increase phase than during the decrease phase of the population cycle. Our results show that neither the adult nor the juvenile average annual survival has decreased or increased consistently over the years, and give no clue for the population abundance decrease and the collapse of the population cycle.

Key words: Bayesian analysis, capture-recapture, grouse, population cycle, survival probability

## Introduction

Periodic population fluctuations are a common phenomenon of many northern animal populations (Elton and Nicholson 1942, Kendall et al. 1998), including grouse (subfamily tetraonidae) (Kendall et al. 1998, Moss and Watson 2001). Trophic interactions such as predator-prey (Krebs 1996, Cortez and Weitz 2014), host-parasite (Hudson et al. 1998, Holmstad et al. 2005, Stenkewitz et al. 2016), and plant-herbivore (Laine and Henttonen 1983, Selås 1997, Liu et al. 2012) have been proposed as possible drivers of those cycles. In the boreal forest of North America, grouse populations show parallel population fluctuations to the 10 years cycles of snowshoe hares *Lepus americanus* (Boutin et al. 1995, Williams et al. 2004). This is likely because grouse serve as alternative prey for the lynx *Lynx canadensis* and other predators (O'Donoghue et al. 1998, Krebs 2011). Similar predator-prey links occur in Fennoscandia with predators of rodents and grouse creating a 3-7 years grouse population cycle (Hagen 1952, Hörnfeldt 1978, Angelstam et al. 1985, Lindstrom 1994). Starting in the late 1980s, however, several of these grouse population cycles have been collapsing both in North America (Williams et al. 2004) and in Fennoscandia (Lindstrom 1994, Hanski and

Henttonen 1996, Ims et al. 2008). Besides the cycle collapse, the abundance of Fennoscandian grouse populations such as black grouse *Tetrao tetrix* (Ludwig et al. 2006), capercaillie *T. urogallus* (Sirkia et al. 2010), willow ptarmigan *Lagopus lagopus* (Henden et al. 2011, Lehikoinen et al. 2014), and rock ptarmigan *L. muta* (Lehikoinen et al. 2014) have declined in many areas. Climate change has been described as a possible cause for the collapse of Fennoscandian populations (Ims et al. 2008, Cornulier et al. 2013). Nonetheless, the change in climate also failed to provide a full explanation, for instance for vole populations (Brommer et al. 2010).

In Iceland, the rock ptarmigan population has previously shown 10-12 years cyclic fluctuations in abundance, more or less in synchrony over the whole island (Gudmundsson 1960, Nielsen and Pétursson 1995). The gyrfalcon *Falco rusticolus* is the main predator of rock ptarmigan in the country and, together with host-parasite interactions, it is thought to be one of the most likely forces driving the rock ptarmigan cycles (Nielsen 1999a, 2011b, Stenkewitz et al. 2016). After several studies and seasonal censuses, it became obvious that the species population dynamics' is driven by their autumn-winter survival (Gardarsson 1988, Magnússon et al. 2004, Nielsen 2011b). Similar to other grouse populations in North America and Fennoscandia, the Iceland rock ptarmigan population cycle has weakened and the abundance has generally declined during the last half-century. The peaks of the population cycle have become lower (Brynjarsdóttir et al. 2003, Magnússon et al. 2004), and the cycle period has gotten shorter (Sturludóttir 2015). Decreased survival rates of mainly adults, but also juveniles, have been shown as the main demographic cause of this decline (Magnússon et al. 2004, Nielsen 2011b).

There is no reliable annual survival estimate of both juvenile and adult rock ptarmigan available for any of its range (Storch 2007). For juveniles, it is only the summer and/or spring survival that is commonly available (Watson and Moss 2008, Novoa et al. 2011, Kobayashi and Nakamura 2013). Most of the available adult survival estimates are based on return rates of ringed individuals to the capture areas (Gardarsson 1988, Watson and Moss 2008), and on counts or changes in age ratios from autumn to spring (Magnússon et al. 2004). In such data, unfortunately permanent emigration and mortality are confounded (Lebreton et al. 1992, Catchpole et al. 1998), and one can only estimate apparent survival, which is biased negatively as compared to true survival. The magnitude of bias depends on the species' site fidelity i.e. dispersal behaviour and the size of the study area (Schwarz 1993, Schaub and Royle 2014). A joint analysis of capture-recapture and dead recovery data overcomes these difficulties and allows the estimation of true survival, and of site fidelity (Clobert and Lebreton 1991, Burnham 1993, Lebreton et al. 1995). The application of a Bayesian framework is particularly well-suited to analyse joint data to estimate age dependent survivals (Kéry and Schaub 2012).

In this paper, we evaluate whether or not the average annual survival probabilities of juvenile and adult rock ptarmigan have declined over time in Iceland. We also estimate age-specific survival probability in both the increase and decrease phase of the population cycle. We jointly analyse ring-recovery and ring-recapture-resight data that have been collected during the last 86 years across Iceland. We expect to see a lower survival probability from 1981 onwards since it is the period when the ptarmigan population started to decline. We also expect to see a lower survival probability in the decrease phase of the population cycle than in the increase phase.

# Methods

## Study area

The ring-recapture-resight and dead recovery rock ptarmigan data were obtained from the Icelandic Institute of Natural History bird-ringing program, which started in 1921 (Petersen and Gudmundsson 1998). We used data for the period 1927-2013 (86 years). The ptarmigan ringing was conducted across the whole island, but preferentially in areas with higher ptarmigan density, and with reasonable accessibility (Fig. 1). Most of the birds were ringed in the north and northeast (82%). The rest were ringed in the southeast (12%), and southwest (6%) parts of the country.

All the capture-recapture activities took place in daylight. The birds were spotted during intensive systematic or after a wait in a hide in the habitat. They were captured with various trapping methods including snaring, drop netting, mist netting, and driving birds into corrals (Nielsen 1995a). The hand-held nets were normally laid over resting or feeding birds. Capture activity was generally restricted to May–September with a peak in September. A captured bird was immediately put in a blind, weighed, ringed, aged, and released. We distinguished two age classes: juveniles (< 1 year old) and adults (> 1 year). Individuals ringed before year 1967 were aged based on plumage, body size, and size of primary growth, whereas individuals ringed after 1967 were aged using the pigmentation of primary feathers (Weeden and Watson 1967).

## Data structure

A total of 8916 rock ptarmigan (17% adults & 83% juveniles), were ringed with a standard engraved aluminium leg ring. Among these, 1249 individuals (14%) were recovered and 271 birds (3%) were recaptured or resighted (7 individuals) at least once. The annual number of newly ringed individuals varied due to variable ringing effort and changes in the population abundance (Fig. 2). No ptarmigan ringing was conducted in years 1929-1931, 1939-1940 and 1961, and in 14 years no recoveries were obtained (1929-1932, 1939-1942, 1948, 1959-1962, 1978, 1988). The main reason behind the absence of ringing in many of these years was the absence of volunteers. The bird ringers were all volunteers at least until 1963. Hunting was not allowed between 1930-1932, and 1940-1942, explaining why there was no recovery in these years. There is no known explanation why no recovery was obtained in the other years.

## Data analysis

Capture-recapture models require instantaneous captures. Hence, we restricted our analyses to ptarmigan captured from July-September, but included all dead recoveries of these individuals regardless of when they occurred. We excluded birds of unknown age, as well as recoveries with inaccurate dates or obtained due to radio tracking. As ptarmigan chicks hatch at the end of June in Iceland (Gardarsson 1988), we defined July 1st as the beginning of the bird´s calendar year.

We included ringing data collected until the end of 2012, and recovery data until June 30th, 2013. We treated all ringing and recovery sites as one population. We ended up with data for 6615 individuals (10% adults, 90% juveniles), which corresponds to 79% of the total number ringed. Of those birds, 784 individuals (11.85%) were recovered, and 177 birds (2.77%) were recaptured at least once (Table 1).

We estimated and compared age dependent (adult and juvenile) average annual survival for:

1) Dataset 1: Three time periods. The 3 periods were subsets of the 86 years (1927-2013) study period. The reason behind the subgrouping was changes in the characteristics of

the population cycle. The first period (1927-1960) was characterized by large population cycle peaks. During the second period (1961-1980), the population exhibited a reduced peak in 1966 and no visible cycle in the 1970s. The third period (1981-2013) was characterised by a general decrease in population abundance and shortening of the cycle length (Nielsen 1999a, b, Nielsen et al. 2004).

2) Dataset 2: Increase and decrease phases of the population cycle. For this, we could only use ringing data for years 1950-2013 when reliable census data of population were also available. The censuses were conducted in the spring in northeast Iceland, on territorial males. We used these data as a reference since the ptarmigan population changes are synchronized across the country (Nielsen 1996b, Nielsen et al. 2004). We determined the increase and decrease phases of the population by visually inspecting the census trajectories. The increase phase was defined as the years from when the density trajectory rises from the trough until just before it reaches the peak years, while the decrease phase was defined from the first year of decline just before the trough years. We excluded the periods 1970–1980 and 2000–2013 from this analysis because there was no apparent population cycle in the 1970s (Nielsen 1999b), and because the period of the cycle interval changed abruptly in the 2000s (Sturludottir 2015, Nielsen unpublished data).
3) Dataset 3: An overall data that aggregate all the aforementioned periods and cycle phases. We modelled this one simply for the sake of getting an overall estimate of all parameters per age.

For dataset 1, we knew that the survival probability (Magnússon et al. 2004) and fidelity probability (Borecha et al. 2018) of the species were age. But we did not know how these probabilities developed over time in the three periods. In addition, we had no prior knowledge whether or not the species recovery and recapture probabilities were age-dependent. But we knew that there was no recapture effort during the study and we only obtained a few recapture histories per period. Due to that we assumed that both adults and juveniles had similar recapture probability, but we allowed it (the recapture) to be either period-dependent or constant. All in all, we considered 35 combinations of models, in which the periods either had a separate age-dependent survival, recovery, and fidelity probabilities, or common juvenile and/or adult probability of these parameters. We also explored models in which the recovery was non-age-dependent but either period-dependent or constant.

For dataset 2, we analysed the ring-recapture and recovery histories of both adult and juvenile individuals that were ringed during the particular population cycle phase. We assessed models where survival, recovery, and fidelity were either constant or phase and/or age dependent. As it was mentioned above, we kept the recapture probability either constant or phase dependent. In total, we explored 19 models. We present all parameter estimates of the highest ranked model. Nevertheless, we could not make use of the adult estimates, as we could not know for certain in which population cycle phase they had hatched. However, including the adult data in the analysis allowed us to obtain estimates for the juveniles, because juvenile survival is unidentifiable from juvenile ringing data alone (Anderson et al. 1985, Mazzetta 2010).

For dataset 3, we analysed the ring-recapture and dead recovery histories of all birds ringed during the study period. We evaluated only one model, in which survival was age and year dependent, recovery and fidelity were age-dependent, and capture was constant. From this model, we only present the survival estimates in the results section. We fitted this model to merely estimate the overall average survival probabilities of both age classes. Thus, we did not do model selection.

We used multistate capture-recapture-recovery model fitted in the Bayesian framework (Kéry and Schaub 2012) to estimate the parameters (see A2). We converted the individual capture histories to a multistate m-array format which allows the application of the multinomial likelihood (Lebreton et al. 2009). The use of this likelihood instead of the state-space likelihood (Kéry and Schaub 2012) has computational benefits and allows using Deviance Information Criterion (DIC) for model selection, because the model is not hierarchical (Barry et al. 2003, Kéry and Schaub 2012).

We used a fixed time effect (years pooled) model to estimate the parameters of the periods and cycle phases, and time effect for overall survival probability. We used uninformative priors with uniform distribution for all parameters. We checked for parameter identifiability by evaluating the overlap area of priors with posterior estimates (Gimenez et al. 2009, Kéry and Schaub 2012). We used JAGS (Plummer 2003), which was called from R (R Core Team 2016). We ran three chains, extracted every other observations (thinning), and discarded the first 800 (burn-in) of the chains for each model (Kéry 2010, Kéry and Schaub 2012). On average, all models were run over 2000 iterations, and we assessed the chain convergence both visually and with the Rhat $\approx 1.01$ for each parameter (Kéry 2010, Kéry and Schaub 2012). We selected the best model using the rule of a minimum difference in $\Delta$DIC of two models. We presented the parameters' mean and 95% Credible Intervals (CIs), and we considered whether the intervals overlapped assess statistical significance.

# Results

Most recoveries were obtained during the hunting season (October–November). The raw data shows that hunting was the main cause of recovery/mortality followed by gyrfalcon predation (Table 1). There was no age related difference with respect to recovery causes. Among the recovered individuals of known age and sex, females lived the longest. The oldest recovered female was 14 years old and the oldest male was seven years old.

## Age and period effect

The highest DIC-ranked model encompassed full age and period dependent survival and fidelity probabilities, age and period dependent recovery, and constant recapture probabilities (Table 2). The parameter estimates from this model are presented on Figure 3. The juvenile survival was lower than the adult survival in all three periods, and the two age groups had opposing survival probability trends over the periods. The difference, however, was more pronounced in 1961-1980 and 1981-2013. The estimates show that between 1961 and 1980 adult survival was at its highest (mean survival probability ± se = 0.58 ± 0.05) whereas juvenile survival was at its lowest (mean survival probability ± se = 0.12 ± 0.03). During the period that followed i.e. 1981-2013, the difference in their survival narrowed slightly when adult survival decreased somewhat (survival probability ± se = 0.51 ± 0.03) and juvenile survival increased (mean survival probability ± se= 0.24 ± 0.03.). Yet, adult survival was better during this period than during the earliest period i.e. 1927-1960 (mean adult survival probability ± se = 0.39 ± 0.05) while juvenile survival was lower (mean juvenile survival probability = 0.30 ± 0.06).

The average recovery probability of the juveniles during the first two periods was similar, and equal to that of the adults i.e. 0.10 ± 0.01 (Fig. 3). Nevertheless, the recovery of juveniles increased abruptly to 0.15 ± 0.01 in the latest period. The average recapture rates with both age groups pooled, were lower than their recovery rates during 1927-1960 and 1981-2013 but the highest (0.23 ± 0.06) in 1961-1980. On the other hand, the average fidelity probabilities of adults were significantly higher than that of the juveniles except in 1961-1980, when juvenile fidelity was slight higher (0.70 ± 0.18) than that of the adults (0.51 ± 0.10).

## Cycle phases

The highest DIC-ranked model is where the survival probability was age and phase dependent, the fidelity, and recapture probabilities were constant, and the recovery was phase dependent (Table 3). The juvenile average survival probability was lower during the decrease phase (0.13 ± 0.2) than during the increase phase (0.18 ± 0.02) (Table 4). The recovery probability, with ages pooled, was correspondingly better during the increase phase (0.15 ± 0.01) than during the decrease (0.12 ± 0.01). The fidelity estimate was 0.98 ± 0.02 whereas the recapture was 0.08 ± 0.01. This latter parameter estimate is similar to what we obtained for whole dataset.

## Overall estimates

The average annual survival, fidelity, recovery, and recapture probability over the whole study period was not different than the estimates obtained per period (Fig. 4, Fig A1). The adult survival and fidelity probabilities were two times higher than those of the juveniles (mean juvenile survival ± se= 0.23 ± 0.03; mean adult survival ± se = 0.48 ± 0.02; mean juvenile fidelity ± se = 0.54 ± 0.12; mean adult fidelity ± se = 0.97 ± 0.02).

# Discussion

## Age-dependent survival rates

Our age-dependent survival probability estimates for the Icelandic rock ptarmigan do not show a strong decline over the study period. We had expected to see a reduced annual survival probability for 1981–2013 compared with the previous two periods. This would contribute to explain the shorter cyclic fluctuation and lower abundance of the population. However, the average annual survival rate for this period turned out to be the second highest estimate for adults and the highest for juveniles. An earlier population model suggested that adult average survival probability above 0.50 is required for the 10-12 year population cyclic to continue (Magnússon et al. 2004, Nielsen et al. 2004). In our case, the average annual survival probability of adults was 0.58 ⍰ 0.05 at most, and it was already less than 0.50 during 1927-1960, when the population abundance was higher and the population was cycling.

The observed discrepancy between our results and the previous population change models could be due to sampling location difference, type of data, and/or type of estimate (i.e. time dependent or not). The population data that was used earlier was collected in the northeast of Iceland (Nielsen et al. 2004) and relied on adult and juvenile site fidelity (Magnússon et al. 2004). Both the north and northeast of Iceland are regarded as a core rock ptarmigan breeding region in the country (Gudmundsson 1960). However, we think the site fidelity assumption is not easily justifiable for the species as dispersal is a common phenomenon (Greenwood and Harvey 1982, Martin et al. 2000, Hörnell-Willebrand et al. 2014). As for our current study, 82% of the ringed ptarmigans were from the north and northeast, but our recovery data covered the entire country and spanned 86 years. In addition, our estimates are averages over extended periods (⍰ 20 years), unlike the previous estimates, which assessed survival probabilities per year. Furthermore, the previous estimates only evaluated the 1981-2003 period whereas we also looked at two previous periods that had higher population abundance and a cycling population. It is possible that there were trends within the periods. Understandably, it is expected for the survivals to vary across years due to stochastic effects (Kéry and Schaub 2012), the periodic population cycle of the species, and/or our uneven sampling efforts. We did not estimate yearly survival probabilities within each period because we had limited recoveries and recaptures within each year to enable us get reliable estimates per year per age for each period. The results we obtained from the pooled time-effect model also do not indicate the claimed 0.50 adult average survival probability. Consequently, it is difficult to compare our survival estimates to the apparent survival estimates from previous studies.

Given the biology of the Icelandic rock ptarmigan population, we believe that the survival of juveniles and any factors that affects it plays a greater role in the population dynamics than the survival of adults. Such a conclusion was already drawn before (Gardarsson 1988, Nielsen 1999b). The juvenile survival was lower in the two earlier periods than in the last one, which does add up with the development of the population and the conclusion of Magnusson et al. (2004). It has been shown that population growth rates are more sensitive to juvenile survival in willow ptarmigan (Steen and Erikstad 1996), and white-tailed ptarmigan *Lagopus leucura* (Wilson and Martin 2012). As for Iceland, there is a strong correlation between the proportion of juveniles in the breeding population and the population changes (Nielsen 1999b, Magnússon et al. 2004), which implies that the population dynamics is driven by the juveniles. The rock ptarmigan in Iceland has a relatively high reproductive effort already as yearlings. On average, a hen can have 7–8 chicks in late summer (Gardarsson 1988, Nielsen et al. 2004) and circa 95% of the hens reproduce successfully (Nielsen et al. 2004). For species with such life-histories, the juveniles contribute more than the adults to the population growth rate (Gaillard et al. 1989, Sæther et al. 1996, Sæther and Bakke 2000, Sandercock et al. 2005).

Juvenile average annual survival probabilities were lower than adult survival probabilities, predominantly after 1960, which is consistent with previous estimates of apparent survival. Adult and juvenile survival probabilities developments were opposite over the three periods. That is, when the juvenile survival was high, the adult survival was low and vice versa. Based on these results, we disagree with Magnusson et al. (2004) when they speculate that the causes of mortality were the same for both age groups, and, proportionally, they both were affected equally by the causes. Lower juvenile survival as compared to adult survival is the general rule for all grouse (Myrberget 1975, Lindstrom 1994, Hannon and Martin 2006). This is especially apparent when the first month after hatching is included in the calculations. Nonetheless, this first month was not well covered in our dataset as most of the juveniles were ringed in September. We assumed that those three months old birds had equal survival rates as birds ringed one to two months earlier. This is justified by generally low juvenile mortality during the first six weeks in the life of the chicks (Gardarsson 1988, Nielsen et al. 2004, Snæþórsson 2012).

The main reason suggested for the population decline after 1981 was increased harvest and/or predation (Magnússon et al. 2004). Our recovery probability estimates for both age groups were equal except for the last time period, when more juveniles were recovered. Bear in mind that our sample size was higher in the last period than in the other two periods. Our raw data show that raptor predation was the second most important cause of recovery/mortality following hunting. This trend was also reported in Norwegian willow grouse population (Myrberget 1975). It is not straightforward to draw conclusions on the importance of different mortality causes from proportion of recovery causes (Schaub and Pradel 2004). It has been suggested that in game species, the juveniles are generally more exposed to hunting than adults (Gardarsson 1988, Freeman and Morgan 1992). Asmyhr et al. (2012) found out that juvenile willow ptarmigan are more vulnerable to hunting than adults when they occur in aggregate. In Iceland, the proportion of rock ptarmigan juvenile in brood in July did not differ from that in the harvest data during October–December (Nielsen 1999b). Studies elsewhere on ptarmigan also did not find any age related differences in vulnerability to hunting (Hannon and Martin 2006, Hörnell-Willebrand et al. 2006), but these study are restricted to few grouse species.

Predation is the major natural cause of ptarmigan mortality (Nielsen 1999a, Valkama et al. 2005, Hannon and Martin 2006). In Iceland, the gyrfalcon depends on rock ptarmigan year-around and preys heavily on them (Nielsen and Cade 1990, Nielsen 1999a, Brynjarsdóttir et al. 2003, Nielsen 2011a). Another important predator is the arctic fox *Vulpes lagopus* (Gardarsson 1988, Hersteinsson and Macdonald 1996, Ellgutter 2017), and raven *Corvus corax* (Nielsen 1996a, Nielsen 1999a). It is then reasonable to assume that most of the non-recovered ptarmigans were killed by predators. A comparison of ring-recovery and radio-tracking study on the little-owl *Athene noctua* showed that predation mortality is largely undetected because the rings are never retrieved, which underestimates the predation mortality rates (Naef-Daenzer et al. 2017). Understandably, different causes of mortality have different degree of detection (Schaub and Pradel 2004), and hunting tends to have a high report rate as compared to other mortality causes (Souchay and Schaub 2016).

The widest difference in average annual survival between juveniles and adults was during 1961-1980. This was the period when there was no visible population cycle after 1966. In this period, the recapture probability of the population was the highest. Survival is negatively related to recovery as unrecovered birds could partly imply survival (Freeman and Morgan 1992, Mazzetta 2010). But in our case, it does not seem that recovery was the reason for the juvenile and adult survival difference but perhaps site fidelity was. The survival and fidelity probabilities were in opposite trend for both age classes. The adults survived better when they were less sedentary, and they survived less well when they were more sedentary. It was the opposite for the juveniles: they survived better when they were less sedentary, and survived less well when they were more sedentary. Nonetheless, the site fidelity probabilities of both age classes were relatively equivalent in this period.

### Cycle phase and survival rates

We found that the average juvenile survival probability was higher during the increase phase of the cycle than during the decrease phase. The same pattern was observed in territorial male counts in the spring. The estimates were deterministic and juvenile survival was lower during the decrease (0.08) than during the increase (0.15) whereas adults survival was the opposite i.e. 0.38 and 0.41, respectively (Nielsen 1999b). These results are also consistent with what was seen in snowshoe hare populations, where adult hares suffered higher mortality rate in the decline phase than during the rest of the periods (Krebs et al. 1986, Hodges 1999). For hare populations, the main causes of mortality during the decline phase were predation (Krebs et al. 1995, Boonstra et al. 1998, Hodges 1999), and starvation (Boutin et al. 1986). Similarly, the predation pressure of the gyrfalcon on the ptarmigan population is the highest during the peak phase and the lowest during the low phase of the population cycle in Iceland (Nielsen 1999a).

## Conclusion

Our results indicate that the population survival probabilities has neither decreased nor increased consistently over the years. They also do not hint at why the population started declining. As our second expectation, however, the juveniles survived better during the increase phase than the decrease phase. Juveniles and adults had opposite survival development over the three periods, but their survival differences was the widest when the population cycle was flat. Recently, a few studies have shown that population cycles are not as stable over long periods as previously thought (Henden et al. 2009). For instance, Henden et al. (2009) showed that the collapsing population cycles of Norwegian foxes had happened before.

The absence of rodents and hares in the Icelandic ecosystems make the system unique and brings the rock ptarmigan problem close to the level of rodents and hares. External factors such as climate (Cornulier et al. 2013), latitude, and hunting are what the Icelandic, North American and Fennoscandia ecosystems have in common. Answers are perhaps hidden in these common factors. Hunting was more prevalent in earlier periods than in recent years in Icelandic rock ptarmigan. This implies that unless hunting interacts with climate and land-use changes, it might not provide the full explanation. Climate change did not show satisfactory correlation with rodent population development (Ims et al. 2008, Brommer et al. 2010). But rock ptarmigan are known to be sensitive to climate change (Kozma et al. 2016). Therefore, we suggest that the change in rock ptarmigan population cycle and abundance in Iceland should be assessed in relation to factors such as changes in climate, land-use, hunting, and predator communities. Acknowledging land-use changes when doing population abundance surveys is essential as the sampling areas have been held constant for long period. In addition, switching the effort of ringing towards radio collaring and satellite tracking could shed a better light on the winter survival and causes of mortality.

## Acknowledgements

We would like to thank all the people that have taken part in ringing of rock ptarmigan in Iceland and all those that have turned in recoveries. We also extend our gratitude to the staffs of the bird ringing office of the Icelandic Institute of Natural History, for processing and archiving the data and make it available to us for analysis. We are in debt to Olivier Devineau for his comments on our modelling efforts.

## Reference

Anderson, D. R., K. P. Burnham, and G. C. White. 1985. Problems in estimating age-specific survival rates from recovery data of birds ringed as young. Journal of Animal Ecology **54**:89-98.

Angelstam, P., E. Lindstrom, and P. Widen. 1985. Synchronous short-term population fluctuations of some birds and mammals in Fennoscandia - occurrence and distribution. Holarctic Ecology **8**:285-298.

Asmyhr, L., T. Willebrand, and M. Hörnell-Willebrand. 2012. Successful adult willow grouse are exposed to increased harvest risk. Journal of Wildlife Management **76**:940-943.

Barry, S. C., S. P. Brooks, E. A. Catchpole, and B. J. T. Morgan. 2003. The analysis of ring-recovery data using random effects. Biometrics **59**:54-65.

Boonstra, R., C. J. Krebs, and N. C. Stenseth. 1998. Population cycles in small mammals: The problem of explaining the low phase. Ecology **79**:1479-1488.

Borecha, D. E., T. Willebrand, and O. K. Nielsen. 2018. Males stay at home while females touring: Dispersal and migration pattern of Icelandic rock ptarmigan *Lagopus muta*. Page 43. Inland Norway University of Applied Sciences, Elverum.

Boutin, S., C. J. Krebs, R. Boonstra, M. R. T. Dale, S. J. Hannon, K. Martin, and A. R. E. Sinclair. 1995. Population changes of the vertebrate community during a snowshoe hare cycle in Canada boreal forest. Oikos **74**:69-80.

Boutin, S., C. J. Krebs, A. R. E. Sinclair, and J. N. M. Smith. 1986. Proximate causes of losses in a snowshoe hare population. Canadian Journal of Zoology **64**:606-610.

Brommer, J. E., H. Pietiainen, K. Ahola, P. Karell, T. Karstinen, and H. Kolunen. 2010. The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through 'climatic forcing'. Global Change Biology **16**:577-586.

Brynjarsdóttir, J., S. H. Lund, K. G. Magnússon, and Ó. K. Nielsen. 2003. Analysis of time series for rock ptarmigan and gyrfalcon populations in north-east Iceland. University of Iceland, Reykjavík.

Burnham, K. P. 1993. A theory for combined analysis of ring recovery and recapture data. Pages 199-213 *in* J.-D. N. Lebreton, Philip M. , editor. Marked individuals in the study of bird population. Birkhauser Verlag, Basel, Boston & Berlin.

Catchpole, E. A., S. N. Freeman, B. J. T. Morgan, and M. P. Harris. 1998. Integrated recovery/recapture data analysis. Biometrics **54**:33-46.

Clobert, J., and J. D. Lebreton. 1991. Estimation of demographic parameters in bird population. Pages xvi, 683 *in* C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Bird population studies: Relevance to conservation and management. Oxford University Press, Oxford, New York, Tokyo.

Cornulier, T., N. G. Yoccoz, V. Bretagnolle, J. E. Brommer, A. Butet, F. Ecke, D. A. Elston, E. Framstad, H. Henttonen, B. Hornfeldt, O. Huitu, C. Imholt, R. A. Ims, J. Jacob, B. Jedrzejewska, A. Millon, S. J. Petty, H. Pietiainen, E. Tkadlec, K. Zub, and X. Lambin. 2013. Europe-Wide dampening of population cycles in keystone herbivores. Science **340**:63-66.

Cortez, M. H., and J. S. Weitz. 2014. Coevolution can reverse predator-prey cycles. Proceedings of the National Academy of Sciences of the United States of America **111**:7486-7491.

Ellgutter, J. A. C. 2017. An analysis of dietary variation in Icelandic arctic fox *Vulpes lagopus* over a period of 30 years using stable isotopes. Norges Arktiske Universitet, Tromsø.

Elton, C., and M. Nicholson. 1942. Fluctuations in numbers of the muskrat *Ondatra zibethica* in Canada. Journal of Animal Ecology **11**:pp. 96-126.

Freeman, S. N., and B. J. T. Morgan. 1992. A modeling strategy for recovery data from birds ringed as nestlings. Biometrics **48**:217-235.

Gaillard, J. M., D. Pontier, D. Allaine, J. D. Lebreton, J. Trouvilliez, and J. Clobert. 1989. An analysis of demographic tactics in birds and mammals. Oikos **56**:59-76.

Gardarsson, A. 1988. Cyclic population changes and some related events in rock ptarmigan in Iceland. Pages 300-329 *in* A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press and Fitzhenry & Whiteside Limited, Minneapolis and Markham.

Gimenez, O., B. J. T. Morgan, and S. P. Brooks. 2009. Weak identifiability in models for mark-recapture-recovery data.*in* D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modelling demographic processes in marked populations. Springer, New York.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics **13**:1-21.

Gudmundsson, F. 1960. Some reflections on ptarmigan cycles in Iceland. Pages 259-265 *in* Proceedings of the XII International Ornithological Congress, Helsinki.

Hagen, Y. 1952. Rovfuglene og viltpleien. Gyldendal Norsk Forlag, Oslo. In Norwegian.

Hannon, S. J., and K. Martin. 2006. Ecology of juvenile grouse during the transition to adulthood. Journal of Zoology **269**:422-433.

Hanski, I., and H. Henttonen. 1996. Predation on competing rodent species: A simple explanation of complex patterns. Journal of Animal Ecology **65**:220-232.

Henden, J.-A., R. A. Ims, and N. G. Yoccoz. 2009. Nonstationary spatio-temporal small rodent dynamics: Evidence from long-term Norwegian fox bounty data. Journal of Animal Ecology **78**:636-645.

Henden, J. A., R. A. Ims, N. G. Yoccoz, and S. T. Killengreen. 2011. Declining willow ptarmigan populations: The role of habitat structure and community dynamics. Basic and Applied Ecology **12**:413-422.

Hersteinsson, P., and D. W. Macdonald. 1996. Diet of arctic foxes *Alopex lagopus* in Iceland. Journal of Zoology **240**:457-474.

Hodges, K. E. 1999. The ecology of snowshoe hares in northern boreal forests. Pages 117-161 *in* L. F. Ruggiero, K. B. Aubry, S. W. Buskirk, G. M. Koehler, C. J. Krebs, K. S. McKelvey, and J. R. Squires, editors. Ecology and conservation of lynx in the united states. United States Department of Agriculture, Forest Service Rocky Mountain Research Station, Fort Collins.

Holmstad, P. R., P. J. Hudson, V. Vandvik, and A. Skorping. 2005. Can parasites synchronise the population fluctuations of sympatric tetraonids? - Examining some minimum conditions. Oikos **109**:429-434.

Hudson, P. J., A. P. Dobson, and D. Newborn. 1998. Prevention of population cycles by parasite removal. Science **282**:2256-2258.

Hörnell-Willebrand, M., V. Marcstrom, R. Brittas, and T. Willebrand. 2006. Temporal and spatial correlation in chick production of willow grouse *Lagopus lagopus* in Sweden and Norway. Wildlife Biology **12**:347-355.

Hörnell-Willebrand, M., T. Willebrand, and A. A. Smith. 2014. Seasonal movements and dispersal patterns: Implications for recruitment and management of willow ptarmigan *Lagopus lagopus*. Journal of Wildlife Management **78**:194-201.

Hörnfeldt, B. 1978. Synchronous population fluctuations in voles, small game, owls, and Tularemia in Northern Sweden. Oecologia **32**:141-152.

Ims, R. A., J.-A. Henden, and S. T. Killengreen. 2008. Collapsing population cycles. Trends in Ecology and Evolution **23**:79-86.

Kendall, B. E., J. Prendergast, and O. N. Bjørnstad. 1998. Trophic interactions and population growth rates describing patterns and identifying mechanisms. Ecology Letters **1**:160-164.

Kéry, M. 2010. Introduction to WinBUGS for Ecologists: Bayesian approach to regression, ANOVA, mixed models and related analyses. Elsevier, Amsterdam.

Kéry, M., and M. Schaub. 2012. Bayesian population analysis using WinBUGS: A hierarchical perspective. Elsevier Inc., Amsterdam.

Kobayashi, A., and H. Nakamura. 2013. Chick and juvenile survival of Japanese rock ptarmigan *Lagopus muta japonica*. Wildlife Biology **19**:358-367.

Kozma, R., P. Melsted, K. P. Magnússon, and J. Höglund. 2016. Looking into the past – The reaction of three grouse species to climate change over the last million years using whole genome sequences. Molecular Ecology **25**:570-580.

Krebs, C. J. 1996. Population cycles revisited. Journal of Mammalogy **77**:8-24.

Krebs, C. J. 2011. Of lemmings and snowshoe hares: The ecology of Northern Canada. Proceedings of the Royal Society B-Biological Sciences **278**:481-489.

Krebs, C. J., S. Boutin, R. Boonstra, A. R. E. Sinclair, J. N. M. Smith, M. R. T. Dale, K. Martin, and R. Turkington. 1995. Impact of food and predation on the snowshoe hare cycle. Science **269**:1112-1115.

Krebs, C. J., B. S. Gilbert, S. Boutin, A. R. E. Sinclair, and J. N. M. Smith. 1986. Population biology of snowshoe hares. 1. Demography of food-supplemented populations in the Southern Yukon, 1976-84. Journal of Animal Ecology **55**:963-982.

Laine, K., and H. Henttonen. 1983. The role of plant production in microtine cycles in Northern Fennoscandia. Oikos **40**:407-418.

Lebreton, J. D., K. P. Burnham, J. Clobert, and D. R. Anderson. 1992. Modeling survival and testing biological hypotheses using marked animals - A unified approach with case-studies. Ecological Monographs **62**:67-118.

Lebreton, J. D., B. J. T. Morgan, R. Pradel, and S. N. Freeman. 1995. A simultaneous survival rate analysis of dead recovery and live recapture data. Biometrics **51**:1418-1428.

Lebreton, J. D., J. D. Nichols, R. J. Barker, R. Pradel, and J. A. Spendelow. 2009. Modeling individual animal histories with multistate capture-recapture models. Advances in Ecological Research **41**:87-173.

Lehikoinen, A., M. Green, M. Husby, J. A. Kalas, and A. Lindstrom. 2014. Common montane birds are declining in northern Europe. Journal of Avian Biology **45**:3-14.

Lindstrom, J. 1994. Tetraonid population studies - State of the art. Annales Zoologici Fennici **31**:347-364.

Liu, R. S., S. A. Gourley, D. L. DeAngelis, and J. P. Bryant. 2012. Modeling the dynamics of woody plant-herbivore interactions with age-dependent toxicity. Journal of Mathematical Biology **65**:521-552.

Ludwig, G. X., R. V. Alatalo, P. Helle, H. Linden, J. Lindstrom, and H. Siitari. 2006. Short- and long-term population dynamical consequences of asymmetric climate change in black grouse. Proceedings of the Royal Society B-Biological Sciences **273**:2009-2016.

Magnússon, K. G., J. Brynjarsdóttir, and Ó. K. Nielsen. 2004. Population cycles in rock ptarmigan *Lagopus muta*: modelling and parameter estimation. Science Institute, Reykjavík.

Martin, K., P. B. Stacey, and C. E. Braun. 2000. Recruitment, dispersal, and demographic rescue in spatially-structured white-tailed ptarmigan populations. The Condor **102**:503-516.

Mazzetta, C. 2010. Age specificity in conditional ring-recovery models. Journal of Agricultural, Biological, and Environmental Statistics **15**:435-451.

Moss, R., and A. Watson. 2001. Population cycles in birds of the grouse family (Tetraonidae). Advances in Ecological Research **32**:53-111.

Myrberget, S. 1975. Age distribution, motality and migration of willow grouse *Lagopus lagopu*s on Senja, North Norway. Astarte **8**:29-35.

Naef-Daenzer, B., F. Korner-Nievergelt, W. Fiedler, and M. U. Grüebler. 2017. Bias in ring-recovery studies: Causes of mortality of little owls *Athene noctua* and implications for population assessment. Journal of Avian Biology **48**:266–274.

Nielsen, O. K. 1996a. Rock ptarmigan censuses in northeast Iceland 1981 to 1994. Náttúrufræðingurinn **65**:137–151. In Icelandic with English summary.

Nielsen, Ó. K. 1996b. Rock Ptarmigan censuses in Northeast Iceland 1981 to 1994. Natturufraedingurinn **65**:137-151. In Icelandic with English summary.

Nielsen, Ó. K. 1999a. Gyrfalcon predation on ptarmigan: numerical and functional responses. Journal of Animal Ecology **68**:1034-1050.

Nielsen, Ó. K. 1999b. Vöktun rjúpnastofnsins. Nattúrufræðistofnunar Island, Reykjavik. In Icelandic with English summary.

Nielsen, Ó. K. 2011a. Gyrfalcon population and reproduction in relation to rock ptarmigan numbers in Iceland. Pages 21-48 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and Ptarmigan in a Changing World. The Peregrine Fund, Boise, Idaho.

Nielsen, Ó. K. 2011b. Harvest and population change of rock ptarmigan in Iceland.*in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and Ptarmigan in a Changing World. The Peregrine Fund, Boise, Idaho, USA.

Nielsen, Ó. K., J. Brynjarsdóttir, and K. G. Magnússon. 2004. Vöktun rjúpnastofnsins 1999-2003 Nattúrufræðistofnunar Island, Reykjavik. In Icelandic with English summary.

Nielsen, Ó. K., and T. J. Cade. 1990. Seasonal changes in food habits of gyrfalcons in NE-Iceland. Ornis Scandinavica **21**:202-211.

Nielsen, Ó. K., and G. Pétursson. 1995. Population fluctuations of gyrfalcon and rock ptarmigan: Analysis of export figures from Iceland. Wildlife Biology **1**:65-71.

Novoa, C., J.-F. Desmet, J.-F. Brenot, B. Muffat-Joly, M. Arvin-Berod, J. Resseguier, and B. Tran. 2011. Demographic traits of two alpine populations of rock ptarmigan. Page 355 *in* B.

K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, Conservation, and Management of Grouse. University of California Press, Berkeley.

O'Donoghue, M., S. Boutin, C. J. Krebs, G. Zuleta, D. L. Murray, and E. J. Hofer. 1998. Functional responses of coyotes and lynx to the snowshoe hare cycle. Ecology **79**:1193-1208.

Petersen, A., and G. A. Gudmundsson. 1998. Seventy-five years of bird-ringing in Iceland. Bliki **19**:49-56. In Icelandic with English summary.

RCoreTeam. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Sandercock, B. K., K. Martin, and S. J. Hannon. 2005. Life history strategies in extreme environments: Comparative demography of arctic and alpine ptarmigan. Ecology **86**:2176-2186.

Schaub, M., and R. Pradel. 2004. Assessing the relative importance of different sources of mortality from recoveries of marked animals. Ecology **85**:930-938.

Schaub, M., and J. A. Royle. 2014. Estimating true instead of apparent survival using spatial Cormack-Jolly-Seber models. Methods in Ecology and Evolution **5**:1316-1326.

Schwarz, C. J. 1993. Estimating migration rates using tag-recovery data. Pages 255-264 *in* J. D. Lebreton and P. M. North, editors. Marked individuals in the study of bird population. Birkhäuser Verlag, Basel, Boston, Berlin.

Selås, V. 1997. Cyclic population fluctuations of herbivores as an effect of cyclic seed cropping of plants: The mast depression hypothesis. Oikos **80**:257-268.

Sirkia, S., A. Linden, P. Helle, A. Nikula, J. Knape, and H. Linden. 2010. Are the declining trends in forest grouse populations due to changes in the forest age structure? A case study of capercaillie in Finland. Biological Conservation **143**:1540-1548.

Snæþórsson, A. Ö. 2012. Reproductive success and survival of hen rock ptarmigan *Lagopus muta* during summer. University of Iceland, Reykjavik.

Souchay, G., and M. Schaub. 2016. Investigating rates of hunting and survival in declining european lapwing populations. Plos One **11**.

Steen, H., and K. E. Erikstad. 1996. Sensitivity of willow grouse *Lagopus lagopus* population dynamics to variations in demographic parameters. Wildlife Biology **2**:27-35.

Stenkewitz, U., O. K. Nielsen, K. Skirnisson, and G. Stefansson. 2016. Host-parasite interactions and population dynamics of rock ptarmigan. Plos One **11**.

Storch, I. 2007. Grouse: Status survey and conservation action plan 2006-2010 IUCN, Gland, Switzerland and Fordingbridge, UK.

Sturludóttir, E. 2015. Statistical analysis of trends in data from ecological monitoring. Univeristy of Iceland, Reykjavik.

Sæther, B.-E., and O. Bakke. 2000. Avian life history variation and contribution of demographic traits to the population growth rate. Ecology **81**:642-653.

Sæther, B.-E., T. H. Ringsby, and E. Roskaft. 1996. Life history variation, population processes and priorities in species conservation: Towards a reunion of research paradigms. Oikos **77**:217-226.

Valkama, J., E. Korpimaki, B. Arroyo, P. Beja, V. Bretagnolle, E. Bro, R. Kenward, S. Manosa, S. M. Redpath, S. Thirgood, and J. Vinuela. 2005. Birds of prey as limiting factors of gamebird populations in Europe: A review. Biol. Rev. **80**:171–203.

Watson, A., and R. Moss. 2008. Grouse: The natural history of British and Irish species. Collins, Hong Kong.

Weeden, R. B., and A. Watson. 1967. Determining the age of rock ptarmigan in Alaska and Scotland. Journal of Wildlife Management **31**:825-826.

Williams, C. K., A. R. Ives, R. D. Applegate, and J. Ripa. 2004. The collapse of cycles in the dynamics of North American grouse populations. Ecology Letters **7**:1135-1142.

Wilson, S., and K. Martin. 2012. Influence of life history strategies on sensitivity, population growth and response to climate for sympatric alpine birds. Bmc Ecology **12**.

# Figures

Figure 1. Ringing and recovery sites for rock ptarmigan (n = 8916) in Iceland in 1927-2013. The labels and the arrow base indicate the ringing sites while the arrow location shows the recovery sites.

Figure 2. The number of ringed and recovered rock ptarmigan over the study years (1927-2013) in Iceland.

Figure 3. The average annual survival, fidelity, recovery, and recapture posterior probabilities of the highest DIC-ranked model for adult and juvenile Icelandic rock ptarmigan during the three periods i.e. 1927-1960, 1961-1980, and 1981-2013. The graph shows the average estimates for each of the three periods and the corresponding 95% CIs.

Figure 4. Temporal variability of average annual survival probability of adult and juvenile rock ptarmigan overall data (periods pooled) modelled by random time/year effect, 1927-2013. Note no model selection was performed for this estimates.

Table 1. The causes of recovery of rock ptarmigan in Iceland during three periods: 1927-1960; 1961-1980; and 1981-2013. Adult recoveries encompass all individual ringed as adults as well as those ringed as juvenile and recovered as adults. “Collision” stands for mortality caused by human infrastructure (hit wires, fence, glass, machines, etc.), and “Unknown” reason for (unknown, ring only or leg with ring only found).

| **Mortality causes** | **Juvenile** | | | **Adult** | | |
|---|---|---|---|---|---|---|
| | 1927–1960 | 1961–1980 | 1981–2013 | 1927–1960 | 1961–1980 | 1981–2013 |
| Unknown | 2 | 15 | 32 | 1 | 7 | 10 |
| Collision | 9 | 15 | 19 | 4 | 7 | 7 |
| Shot | 52 | 67 | 269 | 37 | 14 | 75 |
| Predated by wild mammal | 4 | 0 | 1 | 1 | 0 | 1 |
| Predated by dog/cat | 1 | 5 | 3 | 1 | 0 | 0 |
| Predated by raptor | 2 | 10 | 87 | 1 | 3 | 22 |
| Ringed (Recovery %) | 995 (7) | 1295 (9) | 3686 (11) | 129 (35) | 119 (26) | 391 (29) |

Table 2. The evaluated age - and period dependent survival (phi), fidelity (f), recovery (r), and recapture (p) models and their DIC rank for Icelandic rock ptarmigan, 1927-2013. The dot (.) stands for the constant and the star (*) refers for multiplication.

| **#** | **Model** | **DIC** | **dDIC** | **#Parameter** | **Deviance** |
|---|---|---|---|---|---|
| 1 | phi(age*period), f(age*period), r(age*period(adult.), p(period) | 1819.03 | 0 | 20 | 1799.93 ± 6.19 |
| 2 | phi(age*period), f(age*period), r(age*period), p(period) | 1822.09 | 3.06 | 22 | 1798.64 ± 6.86 |
| 3 | phi(age*period (adult.)), f(age*period), r(age*period), p(period) | 1825.15 | 6.12 | 20 | 1804.89 ± 6.39 |
| 4 | phi(age*period), f(age*period), r(age*period(adult.), p(.) | 1826.64 | 7.61 | 18 | 1807.49 ± 6.19 |
| 5 | phi(age*period), f(age*period), r(period), p(period) | 1826.95 | 7.92 | 19 | 1807.84 ± 6.19 |
| 6 | phi(age*period), f(age*period), r(age*period), p(.) | 1827.27 | 8.24 | 20 | 1807.66 ± 6.27 |
| 7 | phi(age*period (juvenile.)), f(age*period), r(age*period), p(period) | 1829.79 | 10.76 | 20 | 1809.43 ± 6.38 |
| 8 | phi(age*period (juvenile.)), f(age*period), r(age*period), p(.) | 1830.04 | 11.01 | 18 | 1812.37 ± 5.97 |
| 9 | phi(age*period), f(age*period(adult.)), r(age*period(adult.), p(period) | 1830.65 | 11.62 | 18 | 1814.61 ± 5.68 |
| 10 | phi(age*period), f(age*period(adult.)), r(age*period(adult.), p(.) | 1831.82 | 12.79 | 16 | 1815.28 ± 5.76 |
| 11 | phi(age*period (adult.)), f(age*period), r(age*period), p(.) | 1832.78 | 13.75 | 18 | 1814.22 ± 6.10 |
| 12 | phi(age*period), f(age*period), r(.), p(period) | 1833.30 | 14.27 | 17 | 1817.90 ± 5.55 |
| 13 | phi(age*period), f(age*period), r(age), p(period) | 1833.68 | 14.65 | 18 | 1816.25 ± 5.92 |
| 14 | phi(age*period), f(age*period), r(period), p(.) | 1834.00 | 14.97 | 18 | 1816.06 ± 5.987 |
| 15 | phi(age*period), f(period), r(period), p(period) | 1836.58 | 17.55 | 16 | 1820.36 ± 5.7 |
| 16 | phi(age*period), f(age*period), r(age), p(.) | 1837.62 | 18.59 | 16 | 1821.36 ± 5.71 |
| 17 | phi(age*period), f(age*period), r(age*period(juvenile.), p(period) | 1838.28 | 19.25 | 20 | 1818.15 ± 6.35 |
| 18 | phi(age*period), f(age*period), r(age*period(juvenile.), p(.) | 1840.27 | 21.24 | 18 | 1822.45 ± 5.98 |
| 19 | phi(age*period), f(age*period), r(.), p(.) | 1840.32 | 21.29 | 15 | 1826.34 ± 5.29 |
| 20 | phi(age*period), f(age*period(juvenile.)), r(age*period(juvenile.), p(period) | 1843.28 | 24.25 | 18 | 1824.22 ± 6.17 |
| 21 | phi(age*period), f(period), r(.), p(period) | 1845.26 | 26.23 | 14 | 1830.58 ± 5.42 |
| 22 | phi(age*period), f(age), r(age*period), p(.) | 1846.34 | 27.31 | 15 | 1831.75 ± 5.42 |

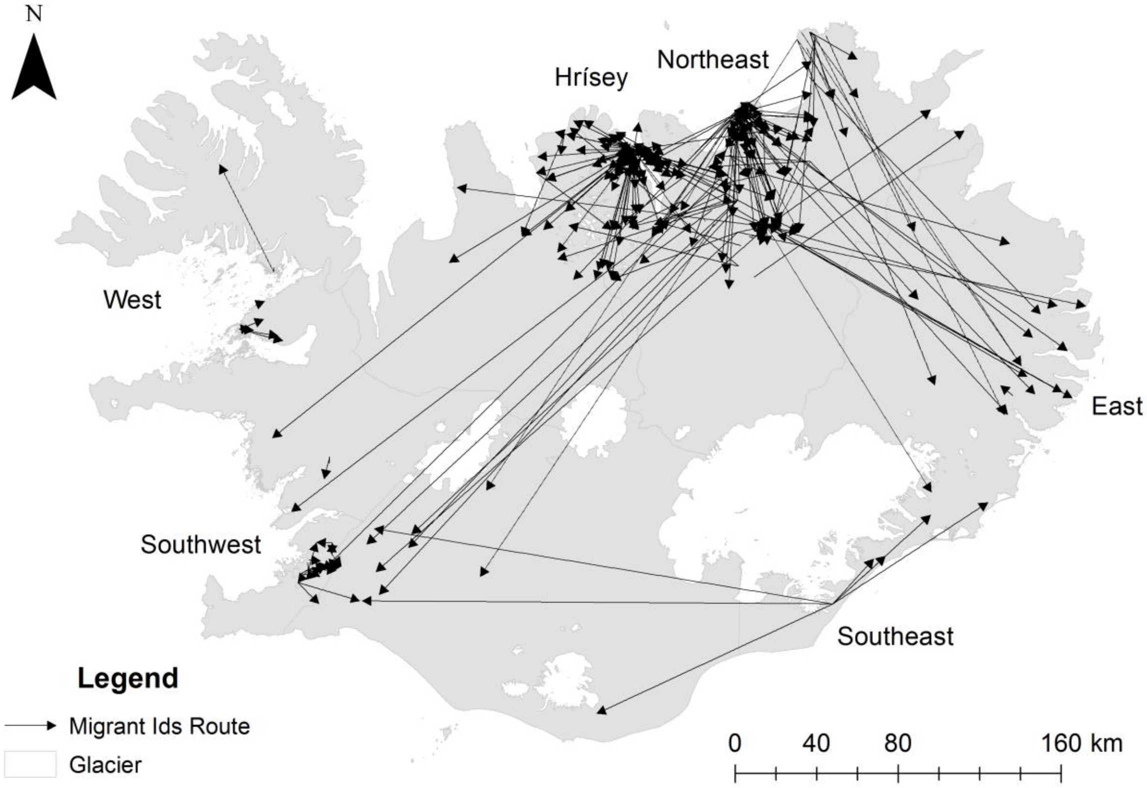
| | | | | | |
|---|---|---|---|---|---|
| 23 | phi(age*period), f(age), r(age*period(adult.)), p(.) | 1851.17 | 32.14 | 14 | 1838.56 ± 5.027 |
| 24 | phi(age*period), f(age), r(age*period(juvenile.)), p(period) | 1854.87 | 35.84 | 16 | 1839.09 ± 5.62 |
| 25 | phi(age*period), f(age), r(period), p(.) | 1861.44 | 42.41 | 13 | 1849.20 ± 4.96 |
| 26 | phi(age*period), f(age*period(juvenile.)), r(age*period(juvenile.), p(.) | 1863.73 | 44.70 | 16 | 1848.47 ± 5.527 |
| 27 | phi(age*period), f(period), r(.), p(.) | 1866.63 | 47.60 | 12 | 1856.40 ± 4.52 |
| 28 | phi(age*period), f(age), r(age*period(juvenile.)), p(.) | 1866.86 | 47.83 | 14 | 1854.08 ± 5.06 |
| 29 | phi(age*period), f(age), r(age), p(.) | 1867.46 | 48.43 | 11 | 1857.05 ± 4.56 |
| 30 | phi(age*period), f(age), r(age), p(.) | 1868.57 | 49.54 | 12 | 1857.47 ± 4.71 |
| 31 | phi(age*period), f(age), r(.), p(.) | 1869.71 | 50.68 | 10 | 1859.80 ± 4.465 |
| 32 | phi(age), f(age), r(age), p(.) | 1872.72 | 53.69 | 8 | 1865.14 ± 3.70 |
| 33 | phi(age*period), f(age), r(.), p(.) | 1873.01 | 53.98 | 11 | 1864 ± 4.21 |
| 34 | phi(age*period), f(.), r(.), p(.) | 1873.63 | 54.60 | 10 | 1864.24 ± 4.34 |
| 35 | phi(age), f(age), r(.), p(.) | 1874.61 | 55.58 | 7 | 1867.66 ± 3.74 |

Table 3. The evaluated age dependent survival (phi), fidelity (f), recovery (r), and recapture (p) models and their DIC rank for the decrease and increase phases of rock ptarmigan population cycle data, 1927-2013, Iceland. The dot (.) stands for the constant, and the star (*) refers for multiplication.

| # | **Model** | DIC | dDIC | #Parameter | Deviance |
|---|---|---|---|---|---|
| 1 | phi(phase*age), f(.), r(phase), p(.) | 976.86 | 0 | 9 | 968.20 ± 4.19 |
| 2 | phi(phase*age), f(.), r(phase*age), p(.) | 980.27 | 3.41 | 11 | 969.56 ± 4.63 |
| 3 | phi(phase*age), f(phase*age), r(phase), p(phase) | 981.70 | 4.83 | 13 | 967.87 ± 5.26 |
| 4 | phi(phase*age), f(phase), r(phase), p(phase) | 981.89 | 5.02 | 11 | 970.55 ± 4.77 |
| 5 | phi(phase*age), f(.), r(.), p(.) | 981.98 | 5.12 | 8 | 974.62 ± 3.84 |
| 6 | phi(phase*age), f(phase*age), r(phase), p(.) | 982.05 | 5.19 | 14 | 967.48 ± 5.40 |
| 7 | phi(age), f(.), r(age), p(.) | 982.13 | 5.27 | 9 | 974.75 ± 3.86 |
| 8 | phi(phase*age), f(phase*age), r(phase*age), p(phase) | 982.46 | 5.60 | 15 | 967.26 ± 5.52 |
| 9 | phi(age), f(.), r(.), p(.) | 982.56 | 5.69 | 8 | 974.70 ± 3.97 |
| 10 | phi(phase*age), f(age), r(age), p(.) | 983.56 | 6.70 | 10 | 974.76 ± 4.20 |
| 11 | phi(phase*age), f(phase*age), r(.), p(.) | 984.60 | 7.73 | 11 | 974.31 ± 4.54 |
| 12 | phi(age), f(age), r(age), p(.) | 987.45 | 10.58 | 8 | 981.58 ± 3.43 |
| 13 | phi(age), f(.), r(.), p(.) | 987.52 | 10.66 | 6 | 981.56 ± 3.46 |
| 14 | phi(phase), f(.), r(phase*age), p(.) | 1030.76 | 53.89 | 10 | 1021.26 ± 4.36 |
| 15 | phi(phase), f(.), r(phase), p(.) | 1080.93 | 104.07 | 7 | 1073.65 ± 3.82 |
| 16 | phi(.), f(.), r(.), p(.) | 1083.92 | 107.05 | 5 | 1079.39 ± 3.01 |
| 17 | phi(phase), f(phase), r(phase), p(phase) | 1084.33 | 107.46 | 9 | 1074.21 ± 4.50 |
| 18 | phi(phase), f(age), r(age), p(.) | 1085.53 | 108.67 | 8 | 1079.83 ± 3.38 |
| 19 | phi(phase), f(.), r(age), p(.) | 1085.95 | 109.09 | 7 | 1079.82 ± 3.51 |

Table 4. The mean and 95% CIs of the posterior estimates of the highest DIC-ranked model for the increase and decrease phases of rock ptarmigan population.

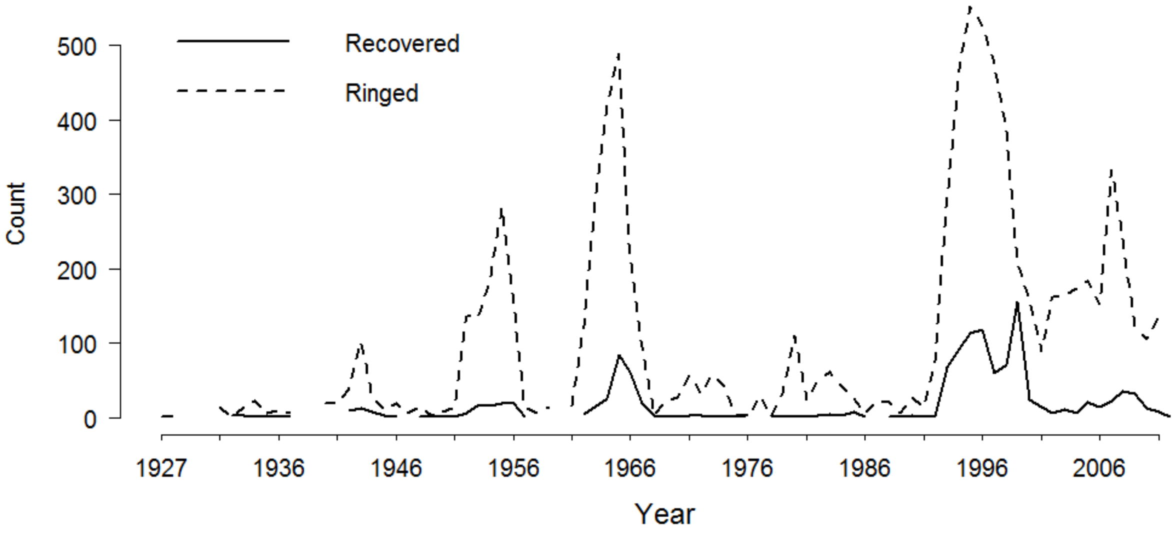
| Parameter | Age | Phase | Mean | SD | 2.5% | 97.5% |
|---|---|---|---|---|---|---|
| Survival | Juvenile | Decrease | 0.13 | 0.02 | 0.09 | 0.18 |
| Survival | Juvenile | Increase | 0.18 | 0.02 | 0.15 | 0.23 |
| Fidelity | Constant | Constant | 0.98 | 0.02 | 0.92 | 1.00 |
| Recovery | Constant | Decrease | 0.12 | 0.01 | 0.01 | 0.13 |
| Recovery | Constant | Increase | 0.15 | 0.01 | 0.13 | 0.16 |
| Recapture | Constant | Constant | 0.08 | 0.01 | 0.06 | 0.10 |



712

713 Figure 1

714



715

716 Figure 2

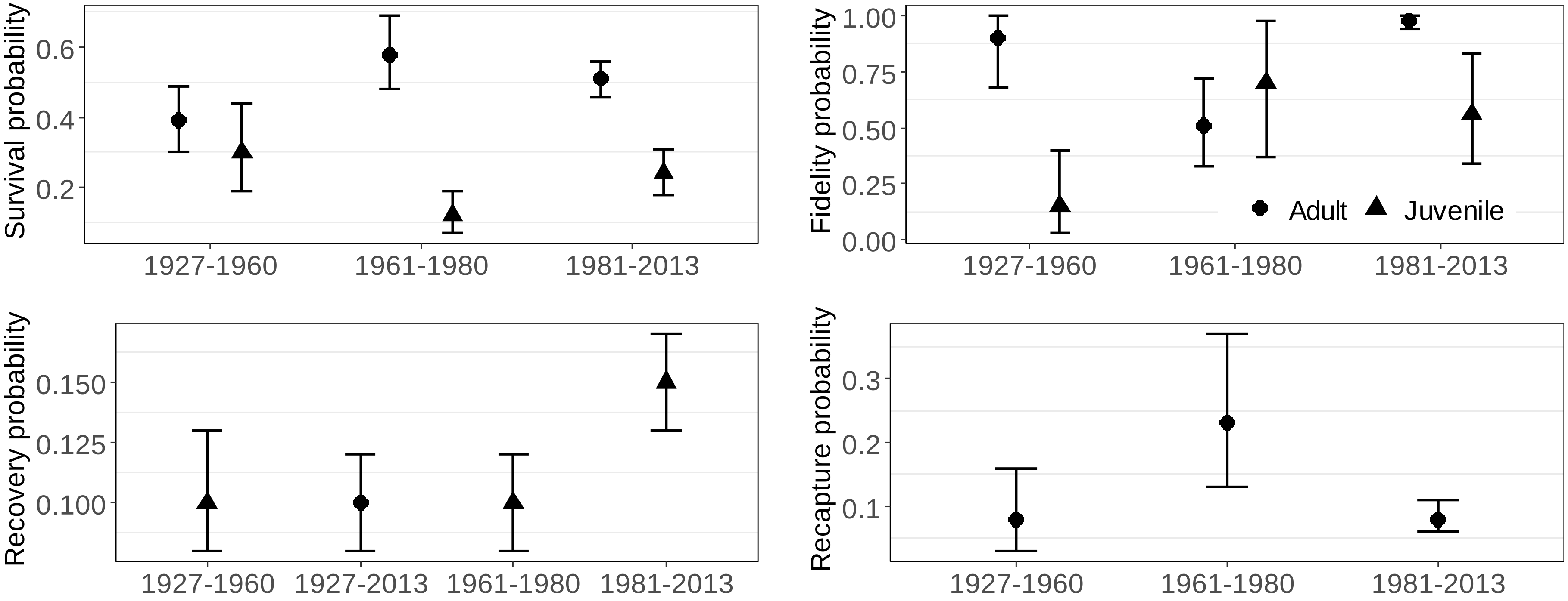

Survival probability
0.6
0.4
0.2
1927-1960
1961-1980
1981-2013
Fidelity probability
1.00
0.75
0.50
0.25
0.00
● Adult
▲ Juvenile
1927-1960
1961-1980
1981-2013
Recovery probability
0.150
0.125
0.100
1927-1960
1927-2013
1961-1980
1981-2013
Recapture probability
0.3
0.2
0.1
1927-1960
1961-1980
1981-2013

Figure 3

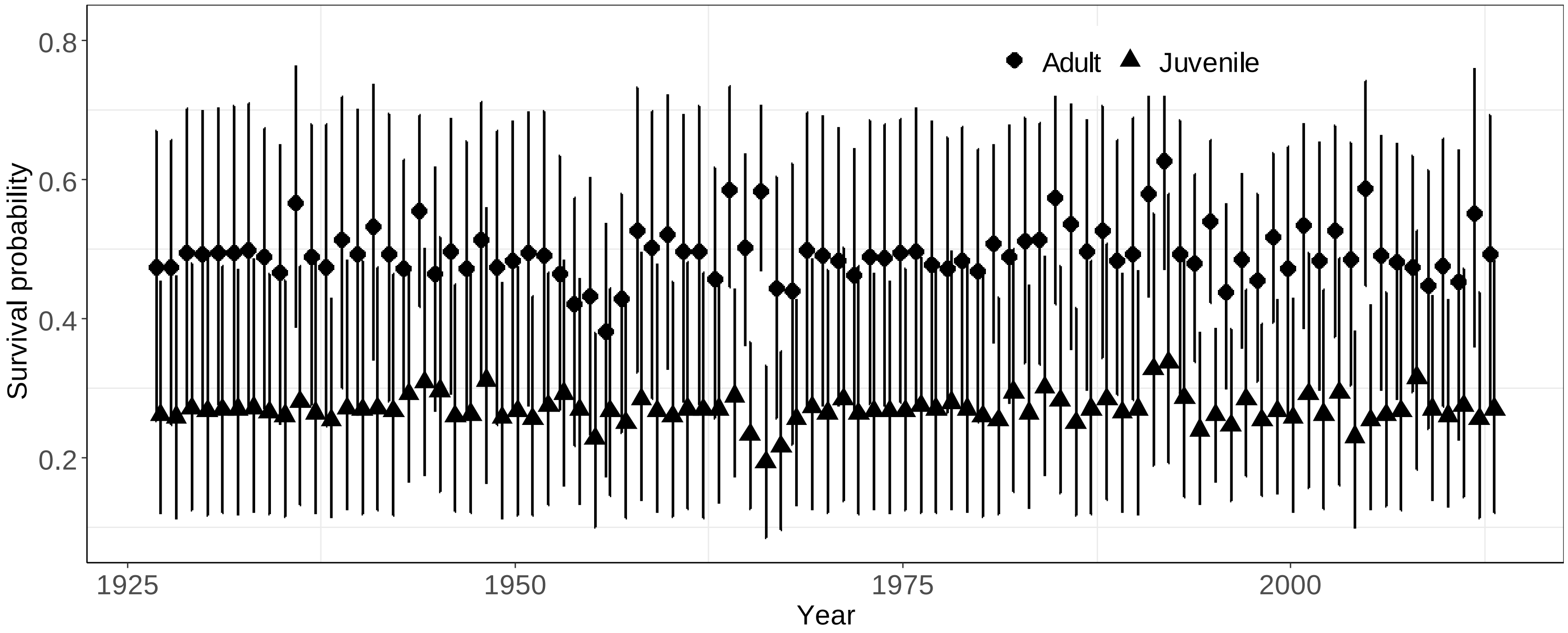
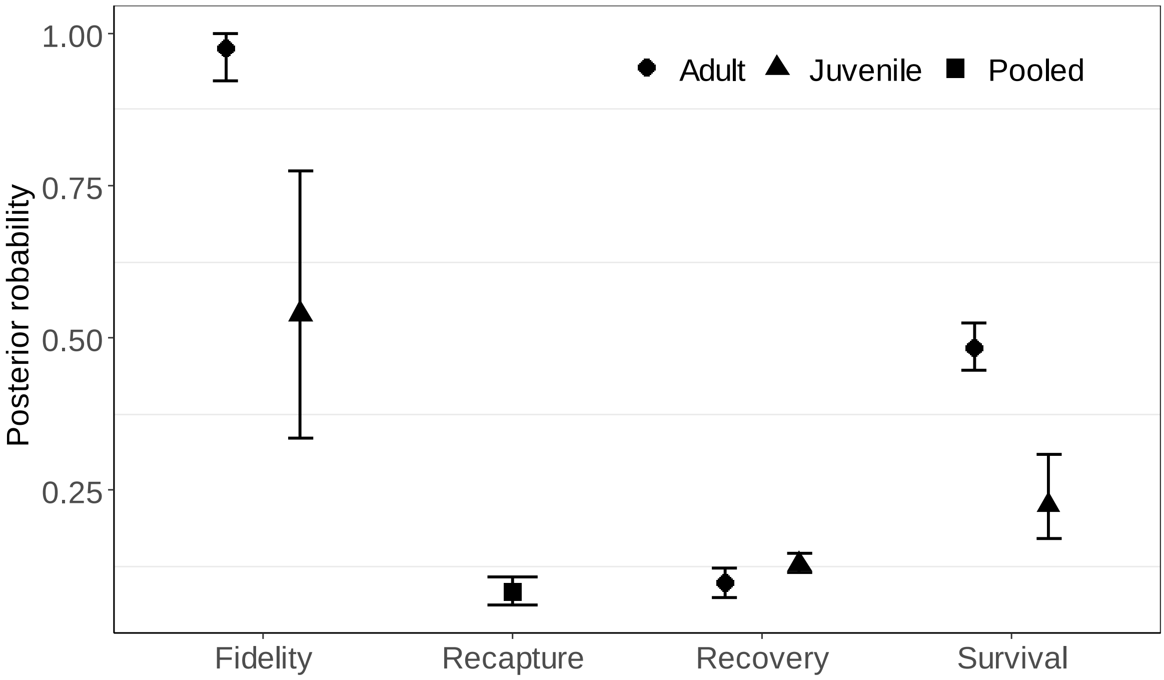

Survival probability
0.8
0.6
0.4
0.2
1925
1950
1975
2000
Year
Adult
Juvenile

Figure 4

# Appendix



A1. The average annual survival, fidelity, recovery, and recapture posterior probabilities of adult and juvenile rock ptarmigan overall data (periods pooled), 1927-2013. The error bar shows the average estimates for each of the parameters and the corresponding 95% CIs. Note no model selection was performed for this estimates.

A2. The script for the multistate joint capture-recapture-recovery model fitted in the Bayesian framework using JAGS.

```
cat(file = "xxxx.jags", "
model {
   for (t in 1:(n.occasions-1)){
   sj[t] <- mean.sj[period[t]]
   sa[t] <- mean.sa[period[t]]
   fj[t] <- mean.fj[period[t]]
   fa[t] <- mean.fa[period[t]]
   rj[t] <- mean.rj[period[t]]
   ra[t] <- mean.ra[period[t]]
   p[t] <- mean.p[period[t]]

   for (i in 1:2){
```

```
mean.sj[i] ~ dunif(0, 1)
mean.sa[i] ~ dunif(0, 1)
mean.fj[i] ~ dunif(0, 1)
mean.fa[i] ~ dunif(0, 1)
mean.rj[i] ~ dunif(0, 1)
mean.ra[i] ~ dunif(0, 1)
mean.p[i] ~ dunif(0, 1)
}

for (t in 1:(n.occasions-1)){
psi[1,t,1] <- 0
psi[1,t,2] <- sj[t]*fj[t]
psi[1,t,3] <- 1-sj[t]
psi[1,t,4] <- 0
psi[1,t,5] <- sj[t]*(1-fj[t])
psi[1,t,6] <- 0

psi[2,t,1] <- 0
psi[2,t,2] <- sa[t]*fa[t]
psi[2,t,3] <- 0
psi[2,t,4] <- 1-sa[t]
psi[2,t,5] <- sa[t]*(1-fa[t])
psi[2,t,6] <- 0

psi[3,t,1] <- 0
psi[3,t,2] <- 0
psi[3,t,3] <- 0
psi[3,t,4] <- 0
psi[3,t,5] <- 0
psi[3,t,6] <- 1

psi[4,t,1] <- 0
psi[4,t,2] <- 0
psi[4,t,3] <- 0
psi[4,t,4] <- 0
psi[4,t,5] <- 0
psi[4,t,6] <- 1

psi[5,t,1] <- 0
psi[5,t,2] <- 0
psi[5,t,3] <- 0
psi[5,t,4] <- 1-sa[t]
psi[5,t,5] <- sa[t]
psi[5,t,6] <- 1

psi[6,t,1] <- 0
psi[6,t,2] <- 0
```

```
   psi[6,t,3] <- 0
   psi[6,t,4] <- 0
   psi[6,t,5] <- 0
   psi[6,t,6] <- 1

   po[1,t] <- 0
   po[2,t] <- p[t]
   po[3,t] <- rj[t]
   po[4,t] <- ra[t]
   po[5,t] <- 0
   po[6,t] <- 0
   for (s in 1:ns){
   dp[s,t,s] <- po[s,t]
   dq[s,t,s] <- 1-po[s,t]
   } # s
   for (s in 1:(ns-1)){
   for (m in (s+1):ns){
   dp[s,t,m] <- 0
   dq[s,t,m] <- 0
   } # s
   } # m
   for (s in 2:ns){
   for (m in 1:(s-1)){
   dp[s,t,m] <- 0
   dq[s,t,m] <- 0
   } # s
   } # m
   } # t

   for (t in 1:((n.occasions-1)*ns)){
   marr[t,1:(n.occasions*ns-(ns-1))] ~ dmulti(pr[t, ], rel[t])
   }

   for (t in 1:(n.occasions-2)){
   U[(t-1)*ns+(1:ns), (t-1)*ns+(1:ns)] <- ones
   for (j in (t+1):(n.occasions-1)){
   U[(t-1)*ns+(1:ns), (j-1)*ns+(1:ns)] <- U[(t-1)*ns+(1:ns), (j-2)*ns+(1:ns)] %*% psi[,t,] %*%
dq[,t,]
   }
   }
   U[(n.occasions-2)*ns+(1:ns), (n.occasions-2)*ns+(1:ns)] <- ones
   for (t in 1:(n.occasions-2)){
   pr[(t-1)*ns+(1:ns),(t-1)*ns+(1:ns)] <- U[(t-1)*ns+(1:ns),(t-1)*ns+(1:ns)] %*% psi[,t,] %*%
dp[,t,]
   for (j in (t+1):(n.occasions-1)){
   pr[(t-1)*ns+(1:ns), (j-1)*ns+(1:ns)] <- U[(t-1)*ns+(1:ns), (j-1)*ns+(1:ns)] %*% psi[,j,] %*%
dp[,j,]
```

```
  }
  }
  pr[(n.occasions-2)*ns+(1:ns), (n.occasions-2)*ns+(1:ns)] <- psi[,n.occasions-1,] %*%
dp[,n.occasions-1,]
  for (t in 2:(n.occasions-1)){
  for (j in 1:(t-1)){
  pr[(t-1)*ns+(1:ns),(j-1)*ns+(1:ns)] <- zero
  } #j
  } #t
  for (t in 1:((n.occasions-1)*ns)){
  pr[t,(n.occasions*ns-(ns-1))] <- 1-sum(pr[t,1:((n.occasions-1)*ns)])
  } #t
  }
  ")
```

# Paper II

**Title**: Males stay at home while females are touring: Migration and dispersal patterns of Icelandic rock ptarmigan *Lagopus muta*

DEGITU ENDALE BORECHA, Department of Forestry and Wildlife Management, Faculty of Applied Ecology and Agricultural Sciences, Campus Evenstad, Inland Norway University of Applied Sciences, N-2480, Koppang, Norway

OLAFUR K. NIELSEN, The Icelandic Institute of Natural History, P.O. Box 125, 212 Garðabær, Iceland

# Abstract

The flow of individuals between populations, through dispersal and migration, has the potential to synchronise fluctuations in population abundance between areas. Here, we studied the migration and natal and breeding dispersal of the Icelandic rock ptarmigan, *Lagopus muta*, in order to examine 1) the extent to which populations from different regions exchanged individuals, and 2) the consequence of such movements for the age and sex structure of the population. We used an 86-year dataset of ringed birds with information on recoveries (i.e. observed dead due to hunting or predation), and recaptures or resightings collected in five regions of Iceland namely Hrísey, northeast, west, southwest, and southeast. We considered these regions as sub-populations of the whole country's population. Along with this, we used a 39-year dataset of the number of aged and sexed individuals from the harvest collected in nine "hunting" regions of the country. We detected very few dispersing rock ptarmigan individuals. Some ptarmigan from Hrísey showed natal dispersal, and some individuals from the northeast area showed breeding dispersal. We also found that parts of the sub-populations migrated while the parts of the individuals stayed on the breeding ground year-round (partial migration), and individual groups showed a difference in the distance they migrated (differential migration). These migration patterns were stronger on Hrísey and in the northeast regions, and created regional sex and age segregation of rock ptarmigan during winter. The finding of sexual segregation was supported by the hunting statistics, which showed an unbalanced sex ratio across regions in winter. We discuss whether these dissimilar movements might expose inconsistent harvest among sub-populations. If so, we would recommend that the hunting quotas in these regions were adjusted accordingly.

# Introduction

In the northern hemisphere many populations show regular changes in density, often resulting in multiannual population cycles (Elton 1924, Kendall et al. 1998, Turchin et al. 2003). These multiannual changes in abundance are often synchronised over large areas (Moran 1953, Hansson and Henttonen 1985, Hanski et al. 1991, Bjørnstad et al. 1995). The spatial synchronization of population dynamics may be enhanced by density-dependent dispersal (Jenkins et al. 1963, Ranta et al. 1995, Ranta et al. 1998, Bjørnstad et al. 1999). Dispersal is defined as the process of individuals' emigration from a home site, immigration and settlement in a new home site, and their transfer between these two home sites (Stenseth and Lidicker 1992, Ims and Yoccoz 1997). Any type of individual movement, dispersal and/or migration, between populations can play a crucial role in altering the distribution of individuals and the dynamics of populations (Clobert and Lebreton 1991, Cheke and Tratalos 2007, Dingle and Drake 2007, Ronce 2007, Faccio et al. 2013).

Dispersal is related to life history stages, i.e. natal dispersal is the displacement of juveniles from their site of origin to their first breeding location (Greenwood 1980, Matthysen 2012), and breeding dispersal is the movement between two different breeding events (Greenwood and Harvey 1982, Lambin 1997). A multitude of proximate factors of dispersal have been suggested (Lidicker and Stenseth 1992), such as population density and intraspecific competition (Howard 1960, Liberg and Schantz 1985, Johnson and Gaines 1990, Ims and Andreassen 2000), ultimately due to differential resource distribution in a heterogeneous landscape (Roff 1975, Amarasekare 1998, Holt and Barfield 2001), and/or inbreeding avoidance (Bengtsson 1978, Pusey 1987).

Migration, on the other hand, is an adaptation to temporary, unsynchronised changes in habitat suitability across the landscape (Ketterson and Nolan 1983, Dingle 1996, Dingle and Drake 2007). The changes normally result in reoccurring seasonal movements of groups of individuals of certain species or populations between breeding and wintering areas (Alerstam and Hogstedt 1982, Dingle and Drake 2007). Populations can be partly migratory when only part of the population migrates while the rest remains behind on the breeding ground (Lack 1944, Terrill and Able 1988, Dingle and Drake 2007). Populations can also show differential migration patterns where individuals show a difference in their departure time and/or in the distance they move (Terrill and Able 1988, Dingle and Drake 2007). Some populations show both partial and differential migrations (Terrill and Able 1988). These two migration types have been explained as a measure of breeding adaptation and/or a result of social structure such as physical or age dominance of some individuals over others (Myers 1981, Ketterson and Nolan 1982, 1983).

Both dispersal and migration abilities may vary according to an individual's age and sex (Terrill and Able 1988, Ronce 2007), and have consequences for the age and sex structure of local populations (Ketterson and Nolan 1983, Terrill and Able 1988, Dingle and Drake 2007). In birds, females generally travel further than males during both natal and breeding dispersal (Greenwood 1980, Greenwood and Harvey 1982, Wolff and Plissner 1998). This is holds true for most grouse populations (Giesen and Braun 1993, Caizergues and Ellison 2002, Montadert and Léonard 2011, Hörnell-Willebrand et al. 2014).

In Iceland, rock ptarmigan, *Lagopus muta*, populations have previously shown 10-12-year population cycles, which were synchronised across the country (Nielsen 1995b, 1996). In addition, the number of rock ptarmigan shot has shown partial spatial sexual segregation in certain regions (Gardarsson 1988), implying that the population may exhibit differential and/or partial migration. Seasonal migration is common in ptarmigan (Irving et al. 1967, Hoffman and Braun 1975, Fuglei et al. 2017), invariably resulting in sexual segregation (Weeden 1964, Schwab et al. 2005). The highest density of rock ptarmigan in Iceland is found in the north and northeast regions (Gudmundsson 1960, Nielsen 1993). In these two regions, males dominate the hunting bag data; i.e. 80-90% males (Gardarsson 1988). In contrast, females constitute 70% of the harvest in the south, west, and southwest parts of the country (Gardarsson 1988). However, there is no empirical research that documents migration and dispersal characteristics of this species in Iceland. Therefore, it is not clear how and to what extent the regional populations are connected, which is necessary information for the sustainable management of these game populations.

In this paper, we analyse recapture-resighting and recovery histories of 8 916 ringed rock ptarmigan in Iceland to quantify dispersal and migration patterns. We estimated (1) the natal and breeding dispersal distances across age and sex classes; and (2) the migration distance across regions and age-sex classes. We expected to find a high rate of natal dispersal, especially from the most densely populated northern populations to the rest of the country. We also expected to see differences in both dispersal and migration across regions by sex and age classes, resulting in sexual segregation during winter.

# Methods

## Study area

Iceland is an island (103 000 km$^2$) situated in the Atlantic just south of the Arctic Circle, and has an altitudinal ranges from sea-level up to 2 100 meters above sea level (masl). Most of the continuous mountain areas are located in the north and the northeast regions, where the elevation reaches 1 300 masl. The country lies within the northern boreal zone but alpine tundra habitat is more dominant than forest (Hagen et al. 2013). Over 11% of the country is covered by glaciers (Björnsson and Pálsson 2008), and the interior is either sparsely vegetated or barren lava field. Mosses *Rhacometrium* spp, and shrub heath vegetation constitute more than half of all vegetation cover (Aradóttir and Eysteinsson 2005, Hagen et al. 2013). Heathland is common in the dryer northeast part of Iceland, where the vegetation commonly consists of crowberries, *Empetrum nigrum,* and small shrubs like dwarf birch, *Betula nana,* and tea-leaved willow, *Salix phylicifolia,* (Nielsen 1995b). In these parts, downy birch, *B. pubescens,* form small woodlands, but exotic tree species have been planted in many parts of Iceland as part of reforestation efforts (Aradóttir and Eysteinsson 2005). Along the coast and in the valleys there are farms and cultivated areas. In the wetter southwest, the vegetation in the low hills (> 50 masl) is dominated by grasses and flowering plants with scattered patches of shrubs, trees and some extensive forestry plantations.

High densities of gyrfalcon, *Falco rusticolus*, occur in the northern region (Gardarsson 1988, Nielsen 1996, Nielsen 2011). Arctic fox, *Vulpes lagopus,* is at its highest density in western Iceland (Hersteinsson and Macdonald 1996, Ellgutter 2017). Ravens, *Corvus corax*, occur all across the country (Skarphedinsson et al. 1990, Nielsen 1996). Unlike those of most Nordic countries, Icelandic ecosystems lack microtine rodents (Microtinae) and hares (Leporidae) (Gardarsson 1988, Nielsen 1999).

Rock ptarmigan have been ringed extensively in five regions (Fig. 1), as follows:

1) Hrísey Island in the north (66°00’N, 18°24’W), which is a low-lying island (< 100 masl), 7.67 km$^2$ in size. Its shortest distance to the mainland is ca. 3.5 km.
2) Northeast (NE) around Tjörnes (66°10’N, 17°10’W) and Myvatn (65°36’N, 17°00’W).
3) Southeast (SE) around Kvisker (63°59’N, 16°26’W).
4) Southwest (SW) in areas surrounding Reykjavik (64°08’N, 21°56’W).
5) West (W) in areas near Dagverðarnes (65°10’N, 22°29’W).

These ringing locations were selected systematically to be in high ptarmigan density areas, but also logistically restricted to locations that were easily accessed by the ringing team, and near where the ringers lived. In all of our analyses and interpretation of the results, we considered the ptarmigan in these ringing locations as sub-populations while all ptarmigan from across the whole country were considered to belong to a single population.

## Data

We used two types of rock ptarmigan data: (1) from the bird-ringing program in Iceland managed by the Icelandic Institute of Natural History; and (2) hunting statistics or bag data (number of harvested males and females), were collected by the same institution (Fig. 2). The ringing data consisted of the date of all ringed and recaptured, resighted and/or dead recovered (i.e. dead due to hunting, predation, collision etc.) birds since the initiation of the program in 1921 (Petersen and Gudmundsson 1998). Ringing data used here covered 86 years; i.e. 1927-2013.

## Ringing data

All the captures and recaptures took place during daylight hours. Birds were spotted by walking within the habitat, and they were captured with various trapping methods including snaring, drop netting, mist netting, and driving birds into corrals (Nielsen 1995a). The captured birds were immediately put in a blind, weighed, ringed, and released. Most birds were ringed with a standard engraved aluminium leg ring or wing ring. Recaptures and resights were purely incidental since no effort was made specifically to recapture or resight ringed birds.

In total, 8 916 birds (17% adults and 83% juveniles; 30% females, 31% males, and 39% individuals of unknown-sex) were ringed. The number of rock ptarmigan ringed each year varied due to both ringing effort and the cyclic changes in abundance of the ptarmigan population. Most birds were ringed in May-September with a peak in September. However, 322 individuals (137 females, 159 males, and 26 individuals of unknown-sex) were ringed in winter i.e. October-March, mostly in the SW (47%), and on Hrísey (43%). Individuals of unknown-sex were mostly 3-5 week-old chicks, ringed between the end of July and the beginning of August.

For this paper, we included recoveries and recaptures or resightings until the end of 2013, and ringing until the end of 2012. We excluded individuals which: (1) had inaccurate recovery date; (2) inaccurate recovery or ringing locations; (3) were not aged at ringing (n = 3); (4) were recovered or recaptured within the same season as the ringing (e.g. those that died within a month after ringing); or (5) were of unknown-sex (used only for the migration analysis).

Sex was determined at capture for birds older than 5 weeks; younger birds could not be sexed. The sex of some of the unsexed ringed birds was determined when they were recaptured or recovered or killed (for bag data). Prior to 1967, rock ptarmigan were aged by plumage pattern, body size and growth of primaries, but from 1967 and onwards, the pigmentation of the primary feathers was used (Weeden and Watson 1967). As rock ptarmigan chicks hatch at the end of June in Iceland (Gardarsson 1988), we defined the 1st of July as the beginning of the bird´s calendar year.

### Bag data

Previously, the ptarmigan hunting season was from mid-October to mid-December in Iceland. Currently, hunting is more restricted, and a large area in the SW has been closed to hunting since 2003. Hunting on Hrísey has never been allowed. The bag data (hunting statistics) that used for this analysis included 49 832 aged and sexed harvested rock ptarmigan based on collected wings during 1964-2002 in 9 different regions of Iceland (Appendix 1).

## Data analysis

### Dispersal

Rock ptarmigan start their spring movement in late March and their autumn movement is over by late September. We analysed natal dispersal for juveniles ringed between July-September of their first summer/autumn, and recovered, recaptured or resighted between April-August the following year.

For breeding dispersal, we used individuals ringed in April-September when they were ≥ 10 months old and recovered, recaptured or resighted in April-August in subsequent years. We presented the median and range (minimum and maximum) of natal dispersal distance because 94% (114 out of 121) of the individuals did not disperse. Similarly, we presented the median breeding dispersal distance and range, grouped by sex, because 86% (158 out of 177) of the individuals did not disperse (0 km distance).

## Migration

For the migration analysis, we considered all birds ringed between April-September and recovered in October-March. We grouped the migration data into two, namely: 1) Individuals recovered, recaptured or resighted in the first winter after ringing; and 2) Individuals recovered, recaptured or resighted in any winter after ringing; including the first group i.e. those recovered in the first winter after ringing (Fig. 2). We made this distinction to explore the effect of age on migration distance, which was only possible for first group data (#1; above) since the juveniles became adults after their first winter. Additionally, as data from other regions were scarce, we restricted the first group data (# 1; above) analysis only to Hrísey and the NE sub-populations (Fig. 2).

We calculated the shortest linear distance (Euclidean distance) between the ringing and the recovery, recapture or resight locations. We used generalized linear models to analyse migration distances. Since our data were right skewed, we used a Gamma distribution with an inverse link function. We tested the effect of age, sex, ringing location, and their interactions on the migration distance. We considered the age effect for the first group migration data only (see above).

We checked the model assumptions and model fit using graphic bootstrap generalized linear model diagnostics from the package ‘boot’ (Davison and Hinkley 1997, Canty and Ripley 2016) in the statistical software R (R Core Team 2016). All models were compared using the Akaike Information Criteria (AIC) (Akaike 1973), and we selected the best model using a delta-AIC of 2-points. For those models with less than 2 delta AIC, we compared their AIC weight and selected the model with the greatest weight. We did all the analysis with R 3.3.0 (R Core Team 2016).

### Bag data

In order to determine sexual distribution (sex composition) of the harvested birds in the different regions during the harvest season, we compared the proportions of males and females in the harvested birds’ data with a chi-square test.

## Results

Of the 8 916 ringed ptarmigan, 1 249 dead individuals were recovered and 271 were recaptured or resighted at least once (Table 1). Among these, 26 rock ptarmigan were both recaptured and recovered. Most of the re-encounters (i.e. recovers, recaptures and resights) were ringed on Hrísey (59%), followed by the NE (22%), and the SW (10%) regions.

### Natal dispersal

A total of 121 rock ptarmigan (30 females, 50 males, 41 of unknown sex) could be used in the analysis of natal dispersal. Only 7 of the 121 individuals (2 females, 2 males, and 3 of unknown sex) dispersed more than 1 km away from their natal sites (6%; Table 2). The two females dispersed 1 km, and 8 km and the two males 1 km and 2 km. The rest of the individuals, 94% (n = 114), were recaptured or recovered where they were ringed with a median dispersal distance of zero km. With the exception of one individual that was ringed in NE (unknown sex), all dispersing ptarmigan were hatched on Hrísey.

Most of the re-encounters resulted from recapture (41) or predation (43); 67% of the predated birds were males (Table 2). None were recaptured more than once, and none of the individuals that dispersed were recaptured.

## Breeding dispersal

A total of 177 rock ptarmigan (120 females and 57 males) could be used in the analysis of breeding dispersal (Table 2). Recaptures accounted for 73% of the re-encounters, and 77% of the recaptured birds were females. Predation was the main cause of mortality among the recovered individuals (55%). Only 11% of the individuals (13 males, and 6 females) were observed ≥ 1 km from their ringing location (median dispersal distance was zero km).

The majority of the rock ptarmigan that dispersed ≥ 1 km were ringed in the NE (n = 15) while the other four were on Hrísey. The longest observed distance was 4 km, by an adult male from the NE. None of the females were observed further than 2 km from the ringing site.

## Undefined long distance dispersal

In addition, we observed nine juveniles (3 females, 2 males, and 5 of unknown sex individuals; 6 Hrísey, 2 NE, and 1 W) which dispersed more than 1 km. Three of the individuals of unknown sex were recovered 11-69 km away from their natal site (from NE = 69 km, Hrísey = 37 km, and W = 11 km). But all these were recovered after their first year with no recapture in between. Hence, it was not possible to differentiate between natal or breeding dispersal in these cases.

## Observed migratory patterns

We recorded a total of 608 ringed rock ptarmigan (557 juveniles, and 51 adults; 322 males and 286 females) during the migration period. None of these individuals were recaptured; all were recovered dead. The causes of death were hunting (67%), predation (25%), unknown (7%), and collision (1%). Out of these 608 birds, a total of 506 (83%) individuals were found dead within the first winter after ringing. Out of the 557 birds ringed as juveniles that were found dead, 461 (83%) died during the first winter after ringing, i.e. as juveniles during their first winter.

The birds ringed in the NE and, to some extent on Hrísey, fanned out in all directions including to the two southern ringing regions (SE and SW). The birds ringed in the SW and in the W region did not appear to migrate as many as the birds ringed in other regions (Fig. 1). There was not a single individual that migrated from south to north, or to Hrísey.

## Migration in the first winter after ringing

The migration distance of rock ptarmigan that were recovered in the first winter after ringing was best explained by the individuals' ringing region, and the interaction between age and sex (Table 3 & A2; Fig. 3). Birds of both sexes from the NE (mean ± se: adult males = 56.27 ± 19.74 km, adult females = 79.10 ± 21.75 km) migrated further than birds from Hrísey (mean ± se: adult males = 12.70 ± 1.34 km, adult females = 13.59 ± 1.22 km; Fig. 3). In addition, juvenile males migrated less far distance than adult males irrespective of region while there was no difference between juvenile and adult females within each region. Among juveniles, there was also a difference in migration distance between males and females, as juvenile females migrated further than the juvenile males from the same region. The estimated longest average migration distance for juvenile females was 81.71 ± 25.07 km (mean ± se km), and

23.73 ± 3.79 km (mean ± se km) for juvenile males. This difference was not observed among adult birds.

### All migration data irrespective of age

The migration distance of all rock ptarmigans ringed in all the five regions and recovered in any of the winters after ringing, was best explained by sex and ringing region (Fig. 4, Table 4). The estimated migration distances depicted similar patterns to those of migration distances of individuals recovered within their first winter. The model estimated that females migrated further (mean ± se = 25.47 ± 2.65 km) than the males (mean ± se = 13.53 ± 1.32 km), and this was most apparent in the NE and on Hrísey, where there were most data. Females from the NE migrated over the greatest average distances (mean ± se = 92.21 ± 17.66 km; compared to males in NE: 27.57 ± 3.84 km). Both males and females ptarmigan from the SW, and the W regions migrated proportionally similar, and shorter average distances. On average, males from the W region migrated the shortest average distances (mean ± se = 3.80 ± 1.84 km).

## Bag data

The bag data showed a biased sex ratio among nine “hunting” regions (*chi-square* = 2162.4, df = 8, *p-value* < 0.001, two-tailed test; Fig. 5). The areas in the north, especially the core breeding region of the NE, showed the lowest proportion of females, whereas areas outside the north had more females than males.

# Discussion

Many grouse populations are of interest to conservationists and game managers, but there is limited knowledge about their spatial dynamics. Without movement data, it is difficult to set an ecologically relevant spatial scale for management (Willebrand and Hörnell 2001, Tack et al. 2012). Below we discuss the observed patterns of rock ptarmigan dispersal and migration in Iceland.

## Dispersal

We did not observe as high a rate of dispersal activity as we had expected. Only 6% and 11% of the recovered rock ptarmigan dispersed more than 1 km in natal and breeding dispersal, respectively. When we compared those individuals that dispersed the longest distances, however, females dispersed further than males during natal dispersal, whereas males moved further than females during breeding dispersal. It was mainly the ptarmigan from the Hrísey region that dispersed natally, and those from the NE that dispersed for breeding. No individual was recaptured outside the region where they had been ringed.

It is possible that we underestimated the bird’s dispersal potential as our method of study was unable to identify where individuals were between re-encounters. Higher percentage of our re-encounter means were recapture, which indicates that our methods were biased toward the ringing locations. We also observed some long distance dispersals that we could not define as natal or breeding dispersal. Essentially, natal dispersal could be embedded within breeding dispersal if the ringed birds were not re-encountered within a year. In addition, bear in mind that 83% of the recovered dead juveniles were found within their first winter before they got a chance to disperse. Furthermore, it has been shown that juveniles that have already dispersed tend to revisit their natal area in the form of migration (Herzog and Keppie 1980, Schroeder and Braun 1993). If this observation also holds for rock ptarmigan, it is possible that juvenile Icelandic rock ptarmigan do disperse long distances, but that we have failed to observe them due to our methods of study.

Even though rock ptarmigan have been well studied, their natal and breeding dispersal are still poorly understood (Montadert and Léonard 2011). A genetic study in the Alps pinpointed that male rock ptarmigan are philopatric than the females (Caizergues et al. 2003). However, a mark-recapture-resight and recover study conducted in Svalbard showed that none of the resighted juvenile rock ptarmigan were observed where they were ringed (Unander and Steen 1985). Breeding dispersal is a rare event in birds (Unander and Steen 1985, Martin et al. 2000), and it is believed to be caused by breeding failure (Greenwood and Harvey 1982, Montadert and Léonard 2011) among females (Middleton et al. 2006), and/or by food shortage (Greenwood and Harvey 1982) . It is also uncommon to observe males switching breeding grounds as often as females. This is especially interesting in rock ptarmigan because the males do not help raising chicks, and thus might not switch breeding site because of a failed breeding attempt.

Natal dispersal distance could be correlated with population density when individuals surrounded by many siblings disperse further than those surrounded by fewer relatives (Reed and Oring 1993, Tinbergen 2005). The Hrísey and the NE regions have higher rock ptarmigan densities than the other regions studied (Gudmundsson 1960, Gardarsson 1988), and individuals of these two regions were the only ones that we observed dispersing. Hence, dispersal seems to be a density-dependent. Density or crowdedness may, however, deter immigration and affect dispersal success (Andreassen and Ims 2001, Lambin et al. 2001). That might explain why no individuals immigrated to the Hrísey, and NE ringing regions.

## Migration

### Partial migration

It has been suggested that, as a general rule, a bird which is recovered or recaptured within 5 km of its ringing site should be considered sedentary (Clobert and Lebreton 1991). In addition, the winter home range of rock ptarmigan varies from 13.84-41.63 km$^2$, while the breeding season home range is around 0.50-0.57 km$^2$ (Favaron et al. 2006). Accordingly, 5 km should be a suitable value to distinguish between resident and migratory movements among rock ptarmigan.

Using this definition of migration, the Icelandic rock ptarmigan population has partially migratory sub-populations. This was certainly the case on Hrísey, in the NE, and in the SE regions, where a portion of the ringed individuals were recovered in winter beyond 5 km of their ringing locations, while rock ptarmigan in the SW and in the W remained on their breeding ground year round.

Partial migration of rock ptarmigan has also been reported in Svalbard (Unander and Steen 1985), and Alaska (Weeden 1964). Chapman et al. (2011) stated that, with the exception of arctic tern, *Sterna paradisaea,* and snow geese, *Chen caerulescens*, most populations of every other species are composed of both resident and migratory individuals, in all types of habitats ranging from the tropics (Boyle 2008, 2011) to the arctic tundra (Unander and Steen 1985). The speculated reasons for partial migration overlap with those of differential migration (see below). The only difference in our partial migration was that sex was not important (see Chapman et al. 2011). We think sub-population densities seemed to explain our migratory observations, in which partial migration occurred in higher density sub-populations (Chapman et al. 2011). Alternatively, this could also be because these sub-populations have been studied for longer and have a larger sample size.

### Differential migration

As expected, we found migration differences between sex- and age classes, i.e. differential migration patterns, in which females migrated longer distances than males, irrespective of age, but juveniles migrated less far distance than adults. These differences in migration distances between sex and age categories provide the basis for segregation on wintering grounds. The existence of spatial sexual segregation was supported by our analysis of long-term hunting bag statistics. Previously, Gardarsson (1988) illustrated that the hunting bag in the northern regions was male biased whereas it was female biased in the southern and western parts of the country. Our analyses confirm Gardarsson's observation. In addition, our results suggest that the northern males were most likely juveniles and some of the southern females may have come from the northern regions. It is possible; however, that both the age and the sexual segregation were limited to the NE, Hrísey, and SE regions as the average migration distances were nearly equal between sexes in the other two regions.

Differential migration is a reasonably common occurrence in migratory species (Cristol et al. 1999), including in many grouse species. For example, the white-tailed ptarmigan *Lagopus leucurus* (Hoffman and Braun 1975), the sage grouse *Centrocercus urophasianus* (Beck 1977), the spruce grouse *Falcipennis canadensis* (Herzog and Keppie 1980), the willow ptarmigan *Lagopus lagopus* (Gruys 1993, Hörnell-Willebrand et al. 2014), the greater prairie-chicken *Tympanuchus cupido* (Bergerud and Gratson 1988, Schroeder and Braun 1993), and the black grouse *Tetrao tetrix* (Willebrand 1988, Borecha et al. 2017), where the males winter closer to their breeding grounds than the females. The only exception is the dusky grouse, *Dendragapus obscurus,* in which males migrate further than females (Cade and Hoffman 1993).

It appears that winter sexual segregation and differential migration are closely interconnected. Many species with differential migration patterns show partial or full sexual segregation in winter. Even though their distances were not measured, a number of other grouse populations have shown partial sexual segregation in winter (see Weeden 1964, Irving et al. 1967). This segregation could also be marked in seasons other than winter (see Gruys 1993).

Ketterson and Nolan (1983) and Myers (1981) hypothesised that differential and partial migration were the result of one or more of the following factors: breeding resource limitation, unequal tolerance of winter temperature due to body size differences, and/or sexual differences in survival during migration. We did not have estimates of differential survival between sexes and could not evaluate the two last hypotheses. However, we argue that differential and partial migration of Icelandic male rock ptarmigan was a result of breeding resource limitation. Male Icelandic rock ptarmigan are both territorial, and bigger in size (Nielsen et al. 2013), and migrated shorter distances than females. The variability and limited availability of suitable breeding grounds forced the territorial individuals to stay near their breeding grounds year around (Kokko and Lundberg 2001). Thus, males had more to lose than females by migrating. This difference in preferences gave rise to a spatial separation between the two sexes.

### Regional differences

The fact that the most northerly sub-populations showed stronger migration tendencies than the other regions indicates that latitude may be part of the explanation. It is a universal trend for individuals dwelling at northern latitudes to migrate longer distances than those that inhabit lower latitudes (Newton 2008, Gow and Wiebe 2014). Latitude universally dictates climate parameters, and, in the case of Iceland, is also correlated with differences between the regions in the predator community and habitat quality.

Climate parameters such as snow depth and/or temperature may explain ptarmigan movement. Snow depth and ptarmigan migration have been shown to be correlated in other grouse populations such as red grouse (Mossop 1988) and sage grouse (Beck 1977),as well as rock ptarmigan in Alaska and Italy (Christie et al. 2014, Ferrarini et al. 2017), wherein mild snow seems to discourage migration (Bergerud and Gratson 1988, Gruys 1993). If it does not restrict accessibility of food, deep snow limits the availability of vegetation cover for hide (Bergerud and Gratson 1988, Mossop 1988, Tape et al. 2010). In our case, it is warmer with lesser snow depth in southern Iceland, particularly in the SW, than in the northern regions (http://en.vedur.is/). This may explain why the SW sub-population is sedentary, and the area is used as a wintering ground by some birds from the NE and the SE sub-populations. The SE is located slightly further south than the SW, but the former region is located close to a vast glacier.

The reason why there is a higher density of rock ptarmigan in the northern regions of Iceland could be explained by the greater availability of ptarmigan forage and/or better habitat quality in the area (Gudmundsson 1960, Nielsen 1993). These regions also host higher densities of gyrfalcon, a resident specialist rock ptarmigan predator, than the rest of the country (Gardarsson 1988, Nielsen 1996, Nielsen 2011). These factors seem to overlap with the observed migration pattern of the rock ptarmigan.

An interesting difference between the NE and Hrísey sub-populations was the difference in hunting pressure between them. Some rock ptarmigan may have preferred to remain on the island over winter, where hunting was not allowed. Hunting disturbance is known to shape individuals' location choice and distribution (Frid and M. Dill 2001, Tolon et al. 2009), and several grouse species respond to hunting and other human disturbances by shifting to more secure sites (Storch 2013). Behaviourally, rock ptarmigan are less shy of people on Hrísey than individuals in the other part of the country. Hrísey rock ptarmigan behave almost like domestic chickens, landing on roofs and feeding in gardens of local houses. This is evidently an adaptation to the long-term absence of hunting. Japanese rock ptarmigan, which have almost never been hunted, show the most similar behaviour to the Hrísey sub-population (Nakamura 2010).

## Conclusion and management implication

We found no evidence to suggest that Icelandic rock ptarmigan sub-populations were connected by dispersal. Instead, we found that the species had a high migration potential that may connect the sub-populations at least through shared resources during winter. Thus, we cannot rule out the suggestion that migration plays a role in the ptarmigan population's synchrony across Iceland. Three sub-populations, namely NE, Hrísey, and SE, showed both partial and differential migration that resulted in sexual segregation in winter. The segregation was particularly strong in the NE, and on Hrísey, which also showed age segregation. These results also seem to point out that density has an effect on individuals' dispersal and migration levels. As sub-populations affect each other through movement, winter management strategies in one area affect the spring-summer sub-populations in other regions. We, therefore, recommend that management authorities adjust the hunting of rock ptarmigan according to regional differences in migration patterns. In addition, anticipate the possibility of uneven sex and age distribution whenever using the hunting statistics and population census for any future analysis or management issues since it might conceal an essential fact, and mislead the management. We also suggest implementing either radio- or satellite-tracking in combination with the ringing in the future research to map the dispersal potential of the birds in better precision.

## Acknowledgements

This paper would not materialize without the unreserved supervision and comments of Harry Peter Andreassen. We thank you Harry. We are also grateful to both Olivier Devineau and Jos Milner for investing their time on reviewing the manuscript. In addition, we would like to thank all the people that have taken part in ringing of the rock ptarmigan and all those that have turned in recoveries. We also extend our gratitude to the staffs of the bird ringing office of the Icelandic Institute of Natural History, for processing and archiving the data and make it available to us for analysis.

## References

Akaike, H. 1973. Information theory as an extension of the maximum likelihood principle. Pages 267-281 *in* B. N. Petrov and F. Csaki, editors. Second International Symposium on Information Theory. Akadamiai Kiado, Budapest.

Alerstam, T., and G. Hogstedt. 1982. Bird migration and reproduction in relation to habitats for survival and breeding. Ornis Scandinavica **13**:25-37.

Amarasekare, P. 1998. Interactions between local dynamics and dispersal: Insights from single species models. Theoretical Population Biology **53**:44-59.

Andreassen, H. P., and R. A. Ims. 2001. Dispersal in patchy vole populations: Role of patch configuration, density dependence, and demography. Ecology **82**:2911-2926.

Aradóttir, Á., and T. Eysteinsson. 2005. Restoration of birch woodlands in Iceland. Pages 195-209 *in* J. A. Stanturf and P. Madsen, editors. Restoration of Boreal and Temperate Forests, CRC Press.

Beck, T. D. I. 1977. Sage grouse flock characteristics and habitat selection in winter. Journal of Wildlife Management **41**:18-26.

Bengtsson, B. O. 1978. Avoiding inbreeding: at what cost? Journal of Theoretical Biology **73**:439-444.

Bergerud, A. T., and M. W. Gratson. 1988. Survival and breeding strategies of grouse. Pages 473-577 *in* A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press, Minneapolis.

Björnsson, H., and F. Pálsson. 2008. Icelandic glaciers. Jökull **58**:365-386.

Bjørnstad, O. N., W. Falck, and N. C. Stenseth. 1995. Geographic Gradient in Small Rodent Density-Fluctuations - a Statistical Modeling Approach. Proceedings of the Royal Society B-Biological Sciences **262**:127-133.

Bjørnstad, O. N., R. A. Ims, and X. Lambin 1999. Spatial population dynamics: Analyzing patterns and processes of population synchrony. Trends in Ecology & Evolution **14**:427-432.

Borecha, D. E., T. Willebrand, and O. K. Nielsen. 2017. Lek site defines annual spatial use of male black grouse *Tetrao tetrix*. Ornis Fennica **94**:150-160

Boyle, W. A. 2008. Partial migration in birds: tests of three hypotheses in a tropical lekking frugivore. Journal of Animal Ecology **77**:1122-1128.

Boyle, W. A. 2011. Short-distance partial migration of Neotropical birds: a community-level test of the foraging limitation hypothesis. Oikos **120**:1803-1816.

Cade, B. S., and R. W. Hoffman. 1993. Differential migration of blue grouse in Colorado. Auk **110**:70-77.

Caizergues, A., A. Bernard-Laurent, J. F. Brenot, L. Ellison, and J. Y. Rasplus. 2003. Population genetic structure of rock ptarmigan Lagopus mutus in Northern and Western Europe. Molecular Ecology **12**:2267-2274.

Caizergues, A., and L. N. Ellison. 2002. Natal dispersal and its consequences in black grouse *Tetrao tetrix*. Ibis **144**:478-487.

Canty, A., and B. Ripley. 2016. boot: Bootstrap R (S-Plus) functions.*in* 1.3-18, editor.

Chapman, B. B., C. Bronmark, J. A. Nilsson, and L. A. Hansson. 2011. The ecology and evolution of partial migration. Oikos **120**:1764-1775.

Cheke, R. A., and J. A. Tratalos. 2007. Migration, patchiness, and population processes illustrated by two migrant pests. Bioscience **57**:145-154.

Christie, K. S., M. S. Lindberg, R. W. Ruess, and J. A. Schmutz. 2014. Spatio-temporal patterns of ptarmigan occupancy relative to shrub cover in the Arctic. Polar Biology **37**:1111-1120.

Clobert, J., and J. D. Lebreton. 1991. Estimation of demographic parameters in bird population. Pages xvi, 683 *in* C. M. Perrins, J. D. Lebreton, and G. J. M. Hirons, editors. Bird population studies: Relevance to conservation and management. Oxford University Press, Oxford, New York, Tokyo.

Cristol, D. A., M. B. Baker, and C. Carbone. 1999. Differential migration revisited: Latitudinal segregation by age and sex class. Pages 33-88 *in* V. Nolan, E. D. Ketterson, and C. F. Thompson, editors. Current Ornithology. Springer, Boston, USA.

Davison, A. C., and D. V. Hinkley. 1997. Bootstrap methods and their applications. Cambridge University Press, Cambridge.

Dingle, H. 1996. Migration: The biology of life on the move Oxford University Press, ProQuest Ebook Central.

Dingle, H., and V. A. Drake. 2007. What is migration? Bioscience **57**:113-121.

Ellgutter, J. A. C. 2017. An analysis of dietary variation in Icelandic arctic fox *Vulpes lagopus* over a period of 30 years using stable isotopes. Norges Arktiske Universitet, Tromsø.

Elton, C. S. 1924. Periodic fluctuations in the numbers of animals : their causes and effects. British Journal of Experimental Biology **2**:pp. 119-163.

Faccio, S. D., M. Amaral, C. J. Martin, J. D. Lloyd, T. W. French, and A. Tur. 2013. Movement patterns, natal dispersal, and survival of peregrine falcons banded in New England. Journal of Raptor Research **47**:246-261.

Favaron, M., G. C. Scherini, D. Preatoni, G. Tosi, and L. A. Wauters. 2006. Spacing behaviour and habitat use of rock ptarmigan *Lagopus mutus* at low density in the Italian Alps. Journal of Ornithology **47**:618-628.

Ferrarini, A., J. M. Alatalo, and M. Gustin. 2017. Climate change will seriously impact bird species dwelling above the treeline: A prospective study for the Italian Alps. Science of the Total Environment **590–591**:686-694.

Frid, A., and L. M. Dill. 2001. Human-caused disturbance stimuli as a form of predation risk. 6 **1**.

Fuglei, E., M. A. Blanchet, S. Unander, R. A. Ims, and A. O. Pedersen. 2017. Hidden in the darkness of the Polar night: A first glimpse into winter migration of the Svalbard rock ptarmigan. Wildlife Biology:1-8.

Gardarsson, A. 1988. Cyclic population changes and some related events in rock ptarmigan in Iceland. Pages 300-329 *in* A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press and Fitzhenry & Whiteside Limited, Minneapolis and Markham.

Giesen, K. M., and C. E. Braun. 1993. Natal dispersal and recruitment of juvenile white-tailed ptarmigan in Colorado. Journal of Wildlife Management **57**:72-77.

Gow, E. A., and K. L. Wiebe. 2014. Males migrate farther than females in a differential migrant: an examination of the fasting endurance hypothesis. Royal Society Open Science **1**:140346.

Greenwood, P. J. 1980. Mating systems, philopatry and dispersal in birds and mammals. Animal Behaviour **28**:1140-1162.

Greenwood, P. J., and P. H. Harvey. 1982. The natal and breeding dispersal of birds. Annual Review of Ecology and Systematics **13**:1-21.

Gruys, R. C. 1993. Autumn and winter movements and sexual segregation of willow ptarmigan. Arctic **46**:228-239.

Gudmundsson, F. 1960. Some reflections on ptarmigan cycles in Iceland. Pages 259-265 *in* Proceedings of the XII International Ornithological Congress, Helsinki.

Hagen, D., K. Svavarsdóttir, C. Nilsson, A. Tolvanen, K. Raulund-Rasmussen, Á. Aradóttir, A. M. Fosaa, and G. Halldórsson. 2013. Ecological and Social Dimensions of Ecosystem Restoration in the Nordic Countries.

Hanski, I., L. Hansson, and H. Henttonen. 1991. Specialist predators, generalist predators, and the microtine rodent cycle. Journal of Animal Ecology **60**:353-367.

Hansson, L., and H. Henttonen. 1985. Gradients in density variations of small rodents: The importance of latitude and snow cover. Oecologia **67**:394-402.

Hersteinsson, P., and D. W. Macdonald. 1996. Diet of arctic foxes *Alopex lagopus* in Iceland. Journal of Zoology **240**:457-474.

Herzog, P. W., and D. M. Keppie. 1980. Migration in a local population of spruce grouse. Condor **82**:366-372.

Hoffman, R. W., and C. E. Braun. 1975. Migration of a wintering population of white-tailed ptarmigan in Colorado. Journal of Wildlife Management **39**:485-490.

Holt, R. D., and M. Barfield. 2001. On the relationship between the ideal free distribution and the evolution of dispersal. Page 85:96 *in* J. Clobert, E. Danchin, A. A. dhondt, and J. D. Nichols, editors. Dispersal. Oxford University Press, Oxford.

Howard, W. E. 1960. Innate and environmental dispersal of individual vertebrates. The American Midland Naturalist **63**:152-161.

Hörnell-Willebrand, M., T. Willebrand, and A. A. Smith. 2014. Seasonal movements and dispersal patterns: Implications for recruitment and management of willow ptarmigan *Lagopus lagopus*. Journal of Wildlife Management **78**:194-201.

Ims, R. A., and H. P. Andreassen. 2000. Spatial synchronization of vole population dynamics by predatory birds. Nature **408**:194-196.

Ims, R. A., and N. G. Yoccoz. 1997. Studying transfer processes in metapopulations: Emigration, migration, and colonization. Pages 247-265 *in* I. Hanski and M. E. Gilpin, editors. Metapopulation Biology. Academic Press, San Diego.

Irving, L., G. C. West, L. J. Peyton, and S. Paneak. 1967. Migration of willow ptarmigan in arctic Alaska. Arctic **20**:77-85.

Jenkins, D., A. Watson, and G. R. Miller. 1963. Population studies on red grouse *Lagopus lagopus scoticus* in northeast Scotland. Journal of Animal Ecology **32**:317-376.

Johnson, M. L., and M. S. Gaines. 1990. Evolution of dispersal - Theoretical-models and empirical tests using birds and mammals. Annual Review of Ecology and Systematics **21**:449-480.

Kendall, B., J. Prendergast, and O. N Bjørnstad. 1998. The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles.

Ketterson, E. D., and V. Nolan. 1982. The role of migration and winter mortality in the life history of a temperate-zone migrant, the dark-eyed junco, as determined from demographic analyses of winter populations. The Auk **99**:243-259.

Ketterson, E. D., and V. Nolan. 1983. The evolution of differential bird migration. Pages 357-402 *in* R. F. Johnston, editor. Current Ornithology. Springer US, Boston, MA.

Kokko, H., and P. Lundberg. 2001. Dispersal, migration, and offspring retention in saturated habitats. The American Naturalist **157**:188-202.

Lack, D. 1944. The problem of partial migration. British Birds **37**:122-130.

Lambin, X. 1997. Home range shifts by breeding female Townsend's voles (Microtus townsendii ): a test of the territory bequeathal hypothesis. Behavioral Ecology and Sociobiology **40**:363-372.

Lambin, X., J. Aars, and S. B. Piertney. 2001. Dispersal, intraspecific competition, kin competition and kin faciliation: A review of the empirical evidence. Pages 110-122 *in* J. Clobert, E. danchin, A. A. dhondt, and J. D. Nichols, editors. Dipersal. Oxford University Press, Oxford.

Liberg, O., and T. v. Schantz. 1985. Sex-biased philopatry and dispersal in birds and mammals: The Oedipus hypothesis. The American Naturalist **126**:129-135.

Lidicker, W. Z., and N. C. Stenseth. 1992. To disperse or not to disperse: who does it and why? Pages 21-36 *in* N. C. Stenseth and W. Z. Lidicker, editors. Animal Dispersal: Small mammals as a model. Springer Netherlands, Dordrecht.

Martin, K., P. B. Stacey, and C. E. Braun. 2000. Recruitment, dispersal, and demographic rescue in spatially-structured white-tailed ptarmigan populations. The Condor **102**:503-516.

Matthysen, E. 2012. Multicausality of dispersal: a review. Page 462 *in* J. Clobert, M. Baguette, T. G. Benton, and J. M. Bullock, editors. Dispersal Ecology and Evolution. Oxford University Press, Oxford.

Middleton, H. A., C. A. Morrissey, and D. J. Green. 2006. Breeding territory fidelity in a partial migrant, the American dipper Cinclus mexicanus. Journal of Avian Biology **37**:169-178.

Montadert, M., and P. Léonard. 2011. Natal dispersal affects population dynamics of hazel grouse in heterogeneous landscapes. Pages 89-103 *in* B. K. Sandercock, K. Martin, and G. Segelbacher, editors. Ecology, conservation, and management of grouse. University of California Press, Berkeley, Los Angeles, London.

Moran, P. 1953. The statistical analysis of the Canadian Lynx cycle. Australian Journal of Zoology **1**:291-298.

Mossop, D. H. 1988. Winter survival and spring breeding strategies of willow ptarmigan. Pages 330-378 *in* A. T. Bergerud and M. W. Gratson, editors. Adaptive strategies and population ecology of northern grouse. University of Minnesota Press and Fitzhenry & Whiteside Limited, Minneapolis and Markham.

Myers, J. P. 1981. A test of three hypotheses for latitudinal segregation of the sexes in wintering birds. Canadian Journal of Zoology **59**:1527-1534.

Nakamura, H. 2010. Why Japanese rock ptarmigan never fear humans. Grouse News **40**:32-35.

Newton, I. 2008. The migration ecology of birds. Elsevier, London, UK.

Nielsen, O. K. 1993. Initiation of territoriality among Icelandic rock ptarmigan in spring. Náttúrufræðingurinn **63**:29-37, In Icelandic with English summary.

Nielsen, O. K. 1995a. Rock ptarmigan banding in Iceland. Bliki **15**:63-66, In Icelandic with English summary.

Nielsen, O. K. 1995b. Rock ptarmigan density and heathland vegetation in Suður-Þngeyjarsýsla, NE-Iceland. Náttúrufræðingurinn **65**:81-102, In Icelandic with English summary.

Nielsen, O. K. 1996. Rock ptarmigan censuses in northeast Iceland 1981 to 1994. Náttúrufræðingurinn **65**:137–151, In Icelandic with English summary.

Nielsen, Ó. K. 1999. Vöktun rjúpnastofnsins. Nattúrufræðistofnunar Island, Reykjavik, In Icelandic with English summary.

Nielsen, Ó. K. 2011. Gyrfalcon population and reproduction in relation to rock ptarmigan numbers in Iceland. Pages 21-48 *in* R. T. Watson, T. J. Cade, M. Fuller, G. Hunt, and E. Potapov, editors. Gyrfalcons and Ptarmigan in a Changing World. The Peregrine Fund, Boise, Idaho.

Nielsen, Ó. K., N. d. Pelsmaeker, and G. A. Guðmundsson. 2013. Rock ptarmigan *Lagopus muta* health studies in northeast Iceland 2012: Morphology and body reserves. Náttúrufræðistofnun íslands, Garðabær.

Petersen, A., and G. A. Gudmundsson. 1998. Seventy-five years of bird-ringing in Iceland. Bliki **19**:49-56, In Icelandic with English summary.

Pusey, A. E. 1987. Sex-biased dispersal and inbreeding avoidance in birds and mammals. Trends in Ecology & Evolution **2**:295-299.

Ranta, E., V. Kaitala, J. Lindstrom, and H. Linden. 1995. Synchrony in population-dynamics. Proceedings of the Royal Society B-Biological Sciences **262**:113-118.

Ranta, E., V. Kaitala, and P. Lundberg. 1998. Population variability in space and time: The dynamics of synchronous population fluctuations. Oikos **83**:376-382.

RCoreTeam. 2016. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Reed, J. M., and L. W. Oring. 1993. Philopatry, site fidelity, dispersal, and survival of spotted sandpipers. The Auk **110**:541-551.

Roff, D. A. 1975. Population stability and the evolution of dispersal in a heterogeneous environment. Oecologia **19**:217-237.

Ronce, O. 2007. How does it feel to be like a rolling stone? Ten questions about dispersal evolution. Annual Review of Ecology Evolution and Systematics **38**:231-253.

Schroeder, M. A., and C. E. Braun. 1993. Partial migration in a population of greater prairie-chickens in northeastern Colorado. Auk **110**:21-28.

Schwab, F. E., P. P. S. Neal, and S. Nash. 2005. Age and Sex Segregation of Wintering Willow Ptarmigan in Labrador. Northeastern Naturalist **12**:113-118.

Skarphedinsson, K. H., O. K. Nielsen, S. Thorisson, S. Thorstensen, and S. A. Temple. 1990. Breeding biology, movements, and persecution of ravens in Iceland. Acta Naturalia Islandica **33**:1-45.

Stenseth, N. C., and W. Z. Lidicker. 1992. Animal dispersal: Small mammals as a model. Chapman and Hall, London.

Storch, I. 2013. Human disturbance of grouse - Why and when? Wildlife Biology **19**:390-403.

Tack, J. D., D. E. Naugle, J. C. Carlson, and P. J. Fargey. 2012. Greater sage-grouse *Centrocercus urophasianus* migration links the USA and Canada: a biological basis for international prairie conservation. Oryx **46**:64-68.

Tape, K. D., R. Lord, H.-P. Marshall, and R. W. Ruess. 2010. Snow-mediated ptarmigan browsing and shrub expansion in arctic Alaska. Ecoscience **17**:186-193.

Terrill, S. B., and K. P. Able. 1988. Bird migration terminology. Auk **105**:205-206.

Tinbergen, J. M. 2005. Biased estimates of fitness consequences of brood size manipulation through correlated effects on natal dispersal. Journal of Animal Ecology **74**:1112-1120.

Tolon, V., S. Dray, A. Loison, A. Zeileis, C. Fischer, and E. Baubet. 2009. Responding to spatial and temporal variations in predation risk: space use of a game species in a changing landscape of fear. Canadian Journal of Zoology **87**:1129-1137.

Turchin, P., S. N. Wood, S. P. Ellner, B. E. Kendall, W. W. Murdoch, A. Fischlin, J. Casas, E. McCauley, and C. J. Briggs. 2003. Dynamical effects of plant quality and parasitism on population cycles of larch budmoth. Ecology **84**:1207-1214.

Unander, S., and J. B. Steen. 1985. Behaviour and social structure in Svalbard rock ptarmigan *Lagopus mutus* hyperboreus. Ornis Scandinavica **16**:198-204.

Weeden, R. B. 1964. Spatial separation of sexes in rock and willow ptarmigan in winter. The Auk **81**:534-541.

Weeden, R. B., and A. Watson. 1967. Determining the age of rock ptarmigan in Alaska and Scotland. Journal of Wildlife Management **31**:825-826.

Willebrand, T. 1988. Demography and ecology of a black grouse *Tetrao tetrix* L. population. Uppsala University Uppsala.

Willebrand, T., and M. Hörnell. 2001. Understanding the effects of harvesting willow ptarmigan *Lagopus lagopus* in Sweden. Wildlife Biology **7**:205-212.

Wolff, J. O., and J. H. Plissner. 1998. Sex biases in avian natal dispersal: An extension of the mammalian model. Oikos **83**:327-330.

# Figures

Figure 1. The direction of migration for all recovered Icelandic rock ptarmigan (n = 608) during 1927-2013 is indicated by arrows. 1a) The 5 ringing regions i.e. Hrísey (island), northeast (NE), southeast (SE), southwest (SW), and west (W), and their locations, noted by their labels and the arrow bases. 1b). The location of Hrísey; the only island among the five ringing regions.

Figure 2. Types of data, and the organization of the data that we used in the paper. We used rock ptarmigan ring-recapture/resight and dead recovery histories that were collected in 1927-2013, and the bag data (harvest statistics) that were collected during 1964-2002 in Iceland. We used the ring-recapture/resighiting and recovery data to assess both dispersal and migration patterns whereas the bag data were used to describe the spatial sex structure.

Figure 3. The estimated means and 95% CIs of the best-AIC model of migration distances (i.e. the ringing region and the interaction of sex and age) for the Hrísey and northeast rock ptarmigan (n = 476), which were recovered the following winter after ringing, 1927-2013, Iceland.

Figure 4. The estimated average migration distances and 95% CIs for the highest AIC-ranked model, for all ptarmigans (n = 608), which were recovered in any winter after the ringing between 1927 and 2013 in Iceland.

Figure 5. The average proportion ± SE of male rock ptarmigan in hunting bags from nine (9) “hunting” regions in Iceland, 1964-2002. N = North, NE = Northeast, Northwest, NW-P = Northwest peninsula, S = South, SE = Southeast, SW = Southwest, E = East, and W = West.

Table 1. Number of total ringed, and then recovered dead or recaptured/resighted rock ptarmigan per ringing sub-population by age, during the period 1927-2013 on Iceland. The age is defined at time of ringing. For the sake of simplicity, number of male and female juveniles presented here are grouped together, and resighted individuals (n = 7) are presented as recaptures. Note that an individual could have been both recaptured and recovered (n = 26), but does not appear more than once in the recapture column if it was resighted or recaptured more than once. NE = northeast, SW = southwest, SE = southeast, and W = West.

| | Ringed | | | Recovered dead | | | Recaptured/resighted | | |
|---|---|---|---|---|---|---|---|---|---|
| | Juvenile | Adult | | Juvenile | Adult | | Juvenile | Adult | |
| Region | | Female | Male | | Female | Male | | Female | Male |
| Hrísey | 3921 | 389 | 182 | 665 | 33 | 34 | 106 | 45 | 14 |
| NE | 2123 | 310 | 393 | 227 | 41 | 31 | 18 | 11 | 3 |
| SW | 266 | 29 | 34 | 133 | 7 | 5 | 2 | 0 | 1 |
| SE | 873 | 106 | 87 | 38 | 9 | 7 | 46 | 11 | 13 |
| W | 174 | 18 | 11 | 18 | 0 | 1 | 0 | 1 | 0 |
| Sum | 7357 | 852 | 707 | 1081 | 90 | 78 | 172 | 68 | 31 |
| Total | | 8916 | | | 1249 | | | 271 | |

Table 2. Causes of re-encounter (recapture, resight or recovery) of Icelandic rock ptarmigan during their natal (n = 121) and breeding (n = 177) dispersal, summarized by number of individuals per sex, 1927-2013. Numbers in brackets refer to individuals that were recaptured, resighted or recovered >1 km away from their ringing locations.” Collision” refers to mortality caused by human infrastructure (hit wires, fences, roads, machinery etc.), “Unknown” due to unidentified cause (ring only or leg with ring only found), and “Predated” for predation by raptor, raven, wild mammals or unknown predator, and “Recapture” for both recaptures and resighting (resight: n = 1).

| Re-encounter reason | Female | Male | Unknown | Total | Female | Male | Total |
|---|---|---|---|---|---|---|---|
| | **Natal** | | | | **Breeding** | | |
| Recaptured | 7 (0) | 8 (0) | 26 (0) | 41 (0) | 99 (4) | 29 (9) | 128 (13) |
| Predated | 8 (1) | 29 (1) | 6 (1) | 43 (3) | 15 (1) | 12 (3) | 27 (4) |
| Unknown | 13 (0) | 9 (0) | 4 (1) | 26 (1) | 5 (0) | 7 (2) | 12 (2) |
| Collision | 2 (1) | 4 (1) | 5 (1) | 11 (3) | 5 (0) | 5 (0) | 10 (0) |
| Total | 30 (2) | 50 (2) | 41 (3) | 121 (7) | 124 (5) | 53 (14) | 177 (19) |

Table 3. The assessed migration distance Gamma models and their AIC rank for Hrísey and NE rock ptarmigan (n = 476), which were recovered during the first winter after ringing, 1927-2013, Iceland.

| # | Model | AIC | ΔAIC | AICweight |
|---|---|---|---|---|
| 1 | Region + Sex*Age | 3452.2 | 0 | 0.36 |
| 2 | Sex*Region*Age | 3452.3 | 0.1 | 0.33 |
| 3 | Region*Sex + Sex*Age | 3453.9 | 1.7 | 0.15 |
| 4 | Region*Sex + Sex*Age + Region*Age | 3455.3 | 3.1 | 0.07 |
| 5 | Sex + Region | 3456.1 | 3.9 | 0.05 |
| 6 | Region + Sex + Age | 3457.3 | 5.1 | 0.03 |
| 7 | Region*Sex + Age | 3458.8 | 6.6 | 0.01 |
| 8 | Region | 3478.8 | 26.6 | <0.001 |
| 9 | Sex + Age | 3560.7 | 108.5 | <0.001 |
| 10 | Age | 3576 | 123.8 | <0.001 |
| 11 | Sex | 3613.3 | 161.1 | <0.001 |

Table 4. The assessed migration distance Gamma models for all the recovered Icelandic rock ptarmigans (n = 608) during any winter after ringing, 1927-2013, Iceland.

| # | Model | AIC | ΔAIC | AICweight |
|---|---|---|---|---|
| 1 | Sex + Region | 4509.9 | 0 | 0.65 |
| 2 | Sex * Region | 4511.2 | 1.3 | 0.35 |
| 3 | Sex | 4556.4 | 46.5 | <0.001 |
| 4 | Region | 4735.1 | 225.1 | <0.001 |

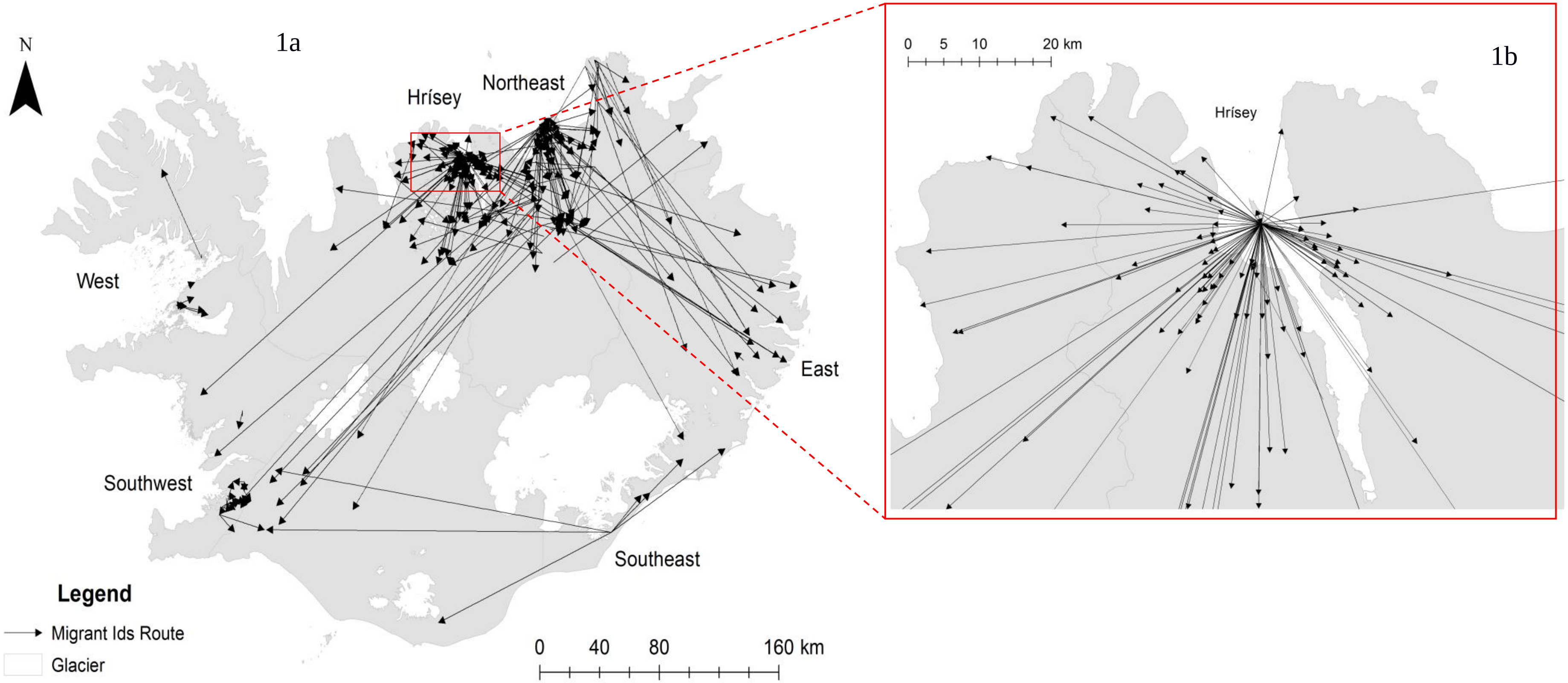

N
1a
Hrísey
Northeast
West
East
Southwest
Southeast
Legend
Migrant Ids Route
Glacier
0 40 80 160 km
0 5 10 20 km
1b
Hrísey

Figure 1

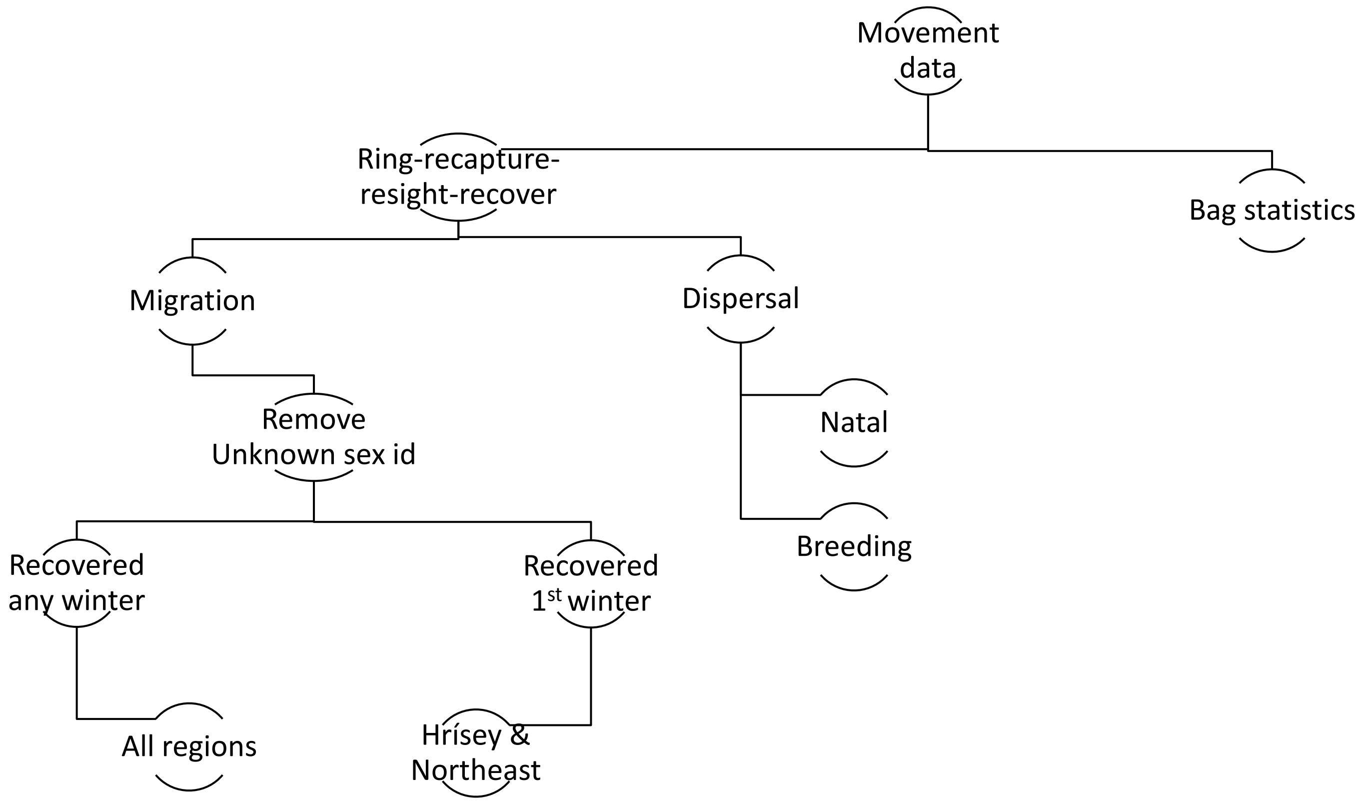

Movement data
Ring-recapture-resight-recover
Bag statistics
Migration
Dispersal
Remove Unknown sex id
Natal
Breeding
Recovered any winter
Recovered 1st winter
All regions
Hrísey & Northeast

Figure 2

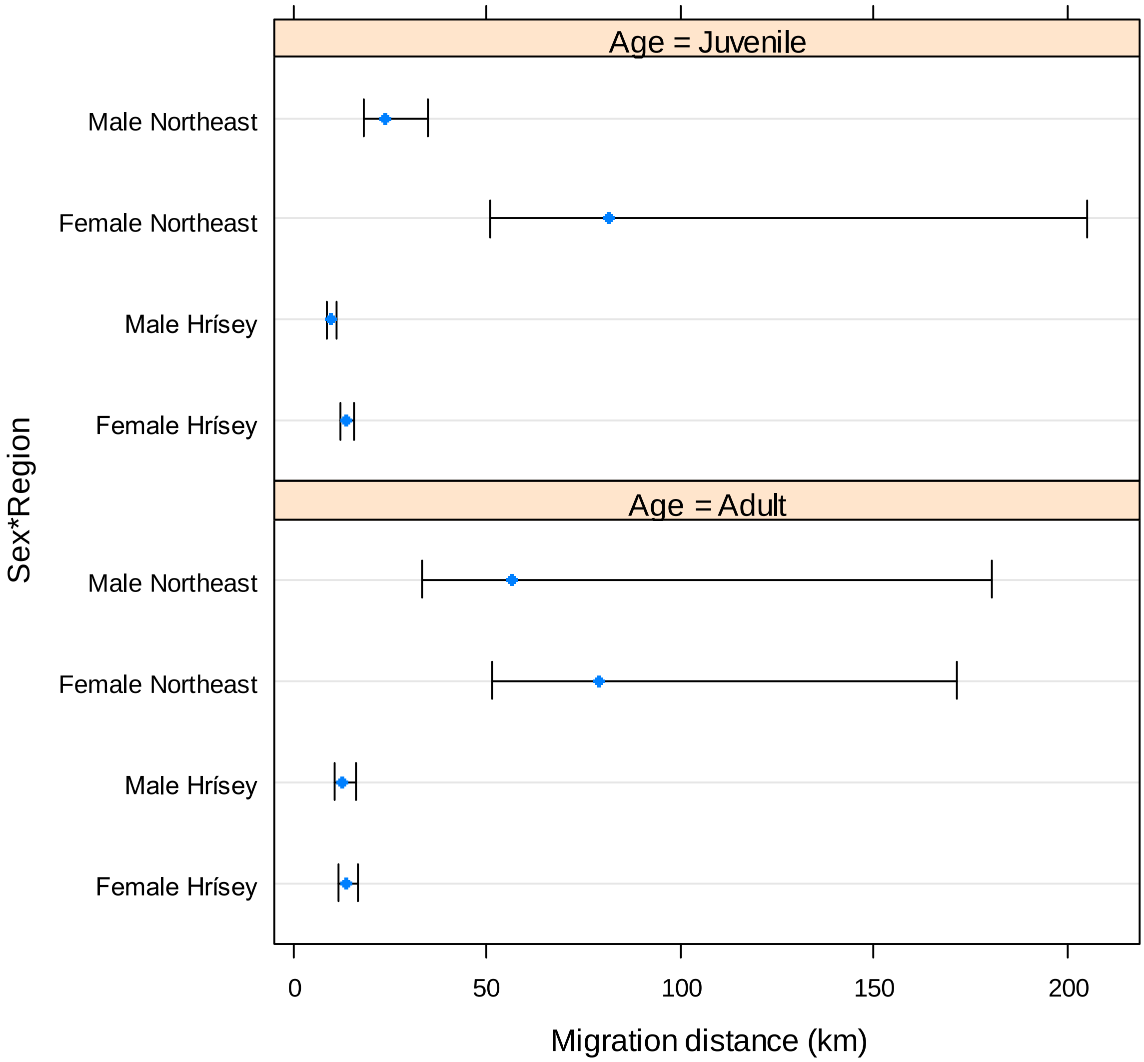

Age = Juvenile
Male Northeast
Female Northeast
Male Hrísey
Female Hrísey
Age = Adult
Male Northeast
Female Northeast
Male Hrísey
Female Hrísey
Sex*Region
0
50
100
150
200
Migration distance (km)

Figure 3

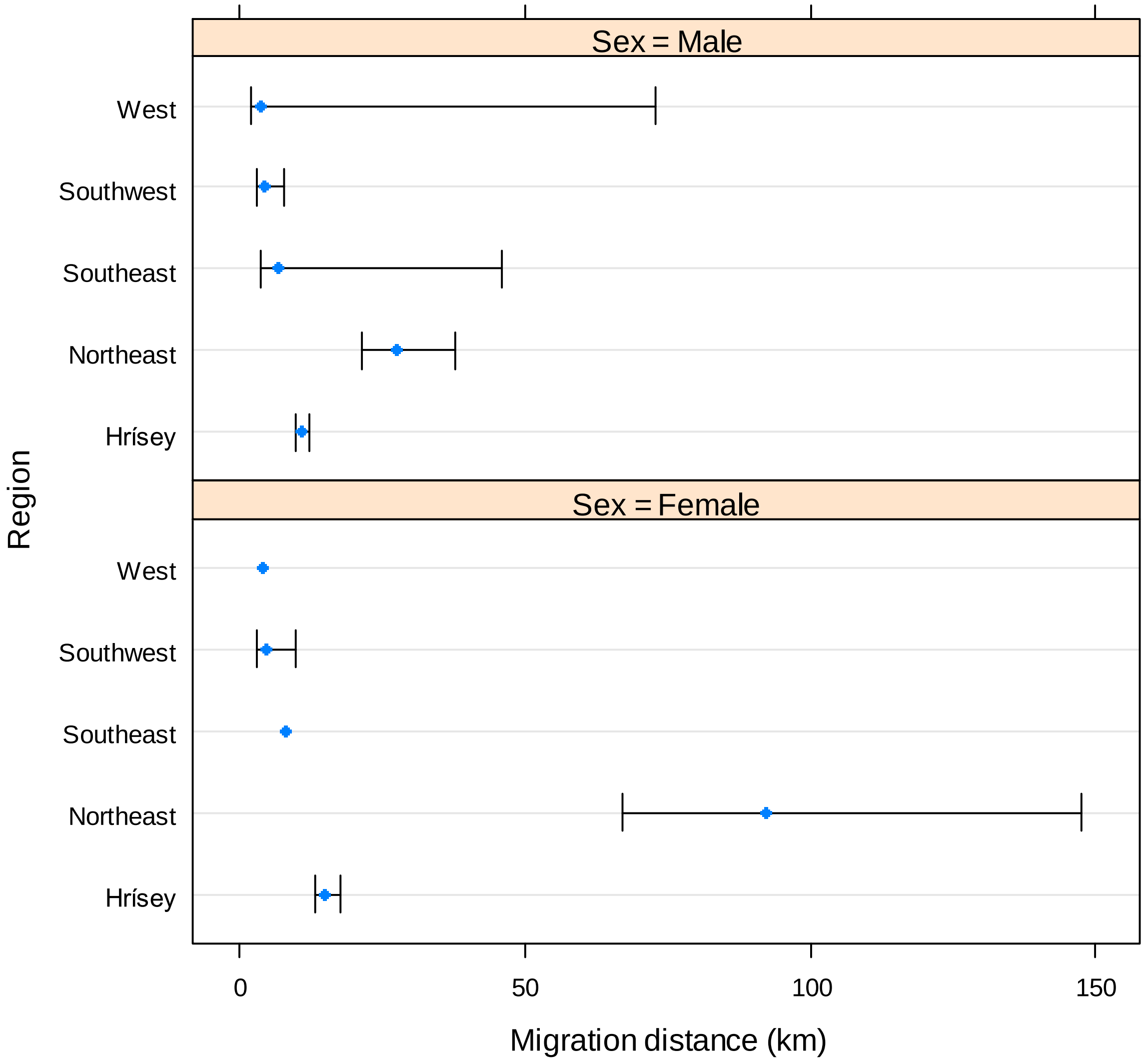

Sex = Male
West
Southwest
Southeast
Northeast
Hrísey
Sex = Female
West
Southwest
Southeast
Northeast
Hrísey
Region
0
50
100
150
Migration distance (km)

Figure 4

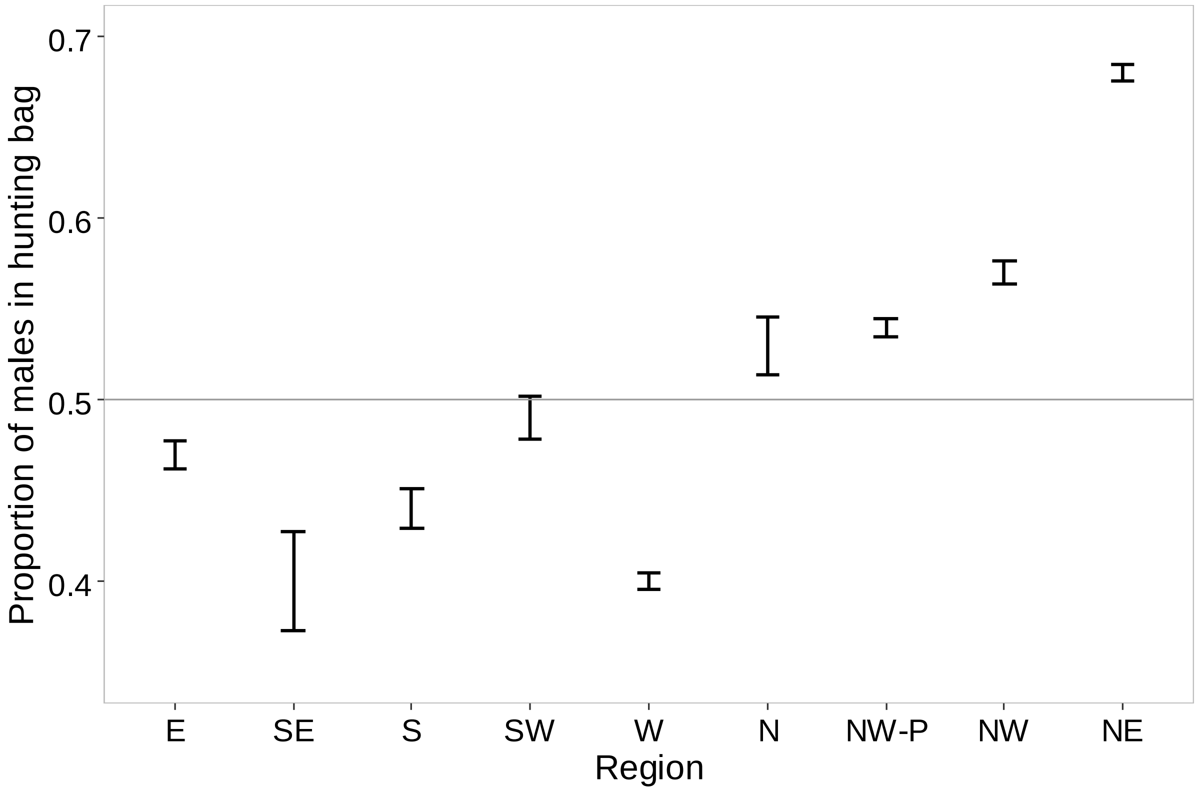

Proportion of males in hunting bag
0.7
0.6
0.5
0.4
E
SE
S
SW
W
N
NW-P
NW
NE
Region

Figure 5

# Appendix

Appendix 1. Number of aged and sexed rock ptarmigan from harvest data collected during hunting season in 1964-2002 in 9 “hunting” regions of Iceland.

| Regions | Females | Males | Sum | % Males |
|---|---|---|---|---|
| East | 2191 | 1933 | 4124 | 47 |
| Northeast | 3628 | 7825 | 11453 | 68 |
| North | 459 | 519 | 978 | 53 |
| Northwest | 2617 | 3457 | 6074 | 57 |
| Southeast | 197 | 131 | 328 | 40 |
| South | 1120 | 879 | 1999 | 44 |
| Southwest | 900 | 876 | 1776 | 49 |
| Northwest peninsula | 4628 | 5473 | 10101 | 54 |
| West | 7800 | 5199 | 12999 | 40 |

Appendix 2. The untransformed (inverse Gamma) parameters of the best model for migration distance of rock ptarmigan that were recovered within their first winter after ringing, 1927-2013, Iceland.

| | Estimate | Std. Error |
|---|---|---|
| (Intercept) | 0.10310 | 0.00554 |
| RegionNortheast | -0.06096 | 0.00509 |
| SexFemale:AgeAdult | -0.02950 | 0.00664 |
| SexMale:AgeAdult | -0.02437 | 0.00801 |
| SexFemale:AgeJuvenile | -0.02990 | 0.00605 |

Appendix 3.The untransformed (inverse Gamma) parameters of the best model for migration distance of all ptarmigan that were recovered in any winter after ringing, 1927-2013, Iceland.

| | Estimate | Std. Error |
|---|---|---|
| (Intercept) | 0.06614 | 0.00377 |
| SexMale | 0.02543 | 0.00410 |
| RegionNortheast | -0.05530 | 0.00394 |
| RegionSoutheast | 0.05525 | 0.05023 |
| RegionSouthwest | 0.13677 | 0.04153 |
| RegionWest | 0.17179 | 0.10034 |

# Paper III

**Ornis Fennica 94: 150–160. 2017**

# Lek site defines annual spatial use of male Black Grouse (*Tetrao tetrix*)

Degitu Endale Borecha*, Tomas Willebrand & Olafur K. Nielsen

*D. E. Borecha, Department of Forestry and Wildlife Management, Faculty of Applied Ecology and Agricultural Sciences, Campus Evenstad, Inland Norway University of Applied Sciences, N-2480, Koppang, Norway. Corresponding author's e-mail: degitu.borecha@inn.no*
*T. Willebrand, Department of Forestry and Wildlife Management, Faculty of Applied Ecology and Agricultural Sciences, Campus Evenstad, Inland Norway University of Applied Sciences, N-2480, Koppang, Norway*
*O. K. Nielsen, The Icelandic Institute of Natural History, P.O. Box 125, 212 Garðabær, Reykjavik, Iceland*

*Received 13 June 2016, accepted 10 March 2017*

Adult male Black Grouse (*Tetrao tetrix*) are assumed to use the same lek throughout their life-span and juveniles are rarely observed settling far from their natal areas. Here we report results on a study of lek site fidelity in male Black Grouse using mark-recapture, radio-telemetry, and lek observations between 1984 and 1992. Data were collected at two sites in central Sweden with six and two leks, respectively. A total of 306 Black Grouse (230 full-grown adult and juvenile males, and 76 chicks) were captured and tagged. We found that all recaptured males tagged as chicks ($n = 7$) were caught on the lek closest to their initial capture site. Twenty-six percent ($n = 59$) of individuals ringed as full-grown were recaptured at least once in the subsequent springs. Fewer individuals attended leks during the mating period than the premating period ($t_{(15)} = 3.06$, $P = 0.008$). Juvenile males were closer to the lek in the premating period (95% confidence interval = 0.45–0.65 km) than in the mating period (0.73–1.13 km), in contrast to adults, which were closer to leks in the mating period (0.44–0.61 km) than the premating period (0.80–0.95 km). Inter-lek movement probability of the birds was 15% ($n = 9$) in the study area. Male Black Grouse remain close to their lek all year round and their recruitment is local. This indicates that leks consist of well-defined local populations, which have limited interactions with other leks.

## 1. Introduction

Dispersal in grouse has not been extensively studied, but there appears to be a marked sex difference in natal dispersal distances, where males are recruited more locally than females (Schroeder 1986, Martin & Hannon 1987, Small & Rusch 1989). This reduces the risk of inbreeding, especially if kin recognition is poor. Black Grouse (*Tetrao tetrix*) have a lek mating system (Bradbury & Gibson 1983), in which males contest to be selected by females during the mating period. The

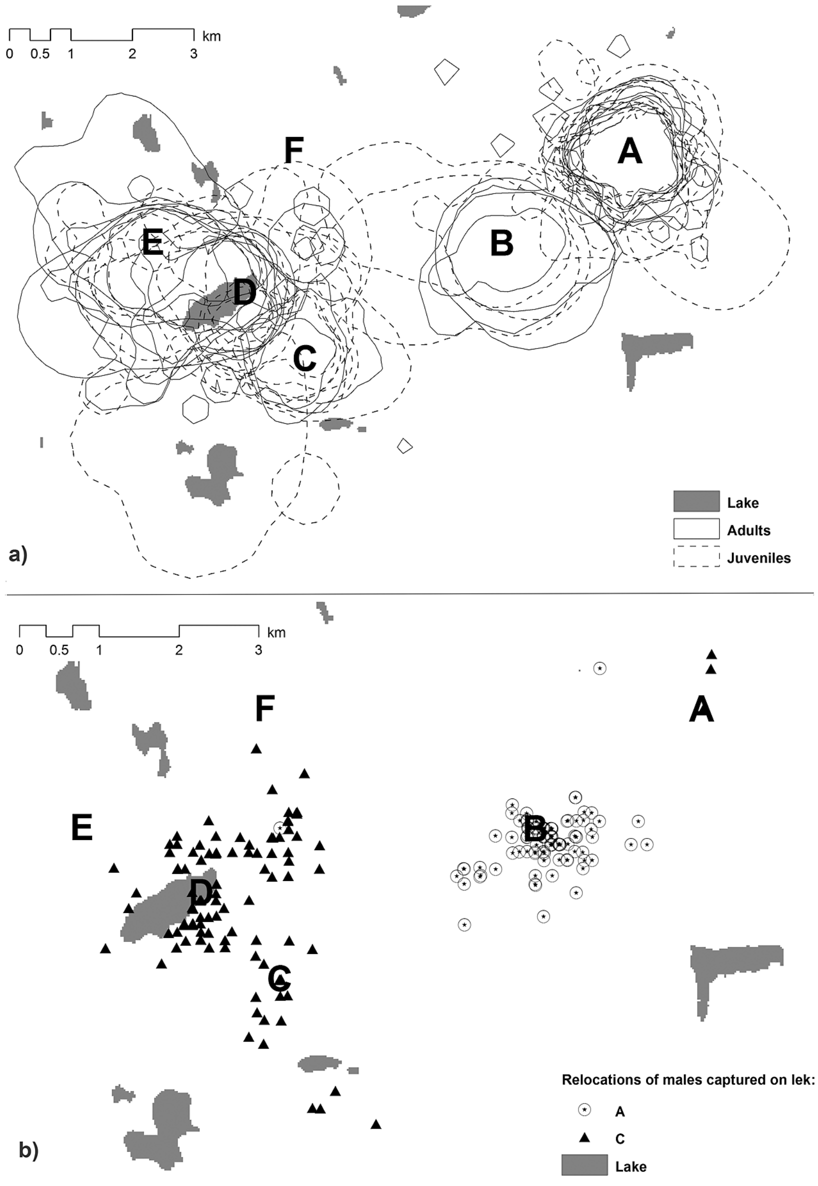


Fig. 1. Map showing home ranges and movements of male Black Grouse around lek A–F at study Site 1, Sweden, 1984–1987. a) Annual home ranges of 25 adults and 24 juveniles Black Grouse males captured at lek A–E. b) Relocations of one adult and five juvenile radio-collared Black Grouse males that have changed lek sites. One adult and two juveniles were recaptured at a new lek, and three juveniles had ≥ 50% of their relocations closer to another lek than where they were initially caught. Small open circle with dot and dark triangle indicate individuals' capture lek. One juvenile and one adult (both recaptured and radio-tracked) moved from lek-A to lek-B (2.6 km), one juvenile (both recaptured and radio-tracked) moved from lek-C to lek-A (6.3 km), and three juveniles (radio-track only) from lek-C to lek-D (1.5 km).

males display in open forest habitats in spring and to a lesser extent in autumn (Rintamäki *et al.* 1999). The leks are commonly 1–2 km apart (Alatalo *et al.* 1992, Rolstad *et al.* 2009). Females visit the leks during a brief period in spring to mate and large leks attract relatively more females than small ones (Alatalo *et al.* 1992, Hovi *et al.* 1997, Isvaran & Ponkshe 2013). A high proportion of adult males appear to be faithful to a lek throughout their life (Alatalo *et al.* 1992), which is also common in sympatric Capercaillie (*T. urogallus*) (Wegge & Larsen 1987) as well as Greater Sage-Grouse (*Centrocercus urophasianus*) (Schroeder & Robb 2003, Gibson *et al.* 2014) and Sharp-tailed Grouse *(Tympanuchus phasianellus)* (Drummer *et al.* 2011). Furthermore, leks of Black Grouse within a large study area hold genetically closely related males (Höglund *et al.* 1999); but see (Lebigre *et al.* 2008).

Juvenile male Black Grouse are rarely observed settling on leks further than 2 km from their natal areas (Caizergues & Ellison 2002, Warren &

Baines 2002). An observational study in Finland has shown that juvenile male Black Grouse sometimes visit leks other than their origin lek before settling, and can also permanently move to another lek (Alatalo *et al.* 1992). Similar lek exploratory behaviour of juvenile males has also been detected in Capercaillie (Wegge & Larsen 1987, Storch 1997, Gjerde *et al.* 2000), Sage-Grouse (Emmons & Braun 1984), and Ruff (*Philomachus pugnax*) (Widemo 1997). It has been suggested that young males are recruited to their father's lek in order to increase the lek's size, which would improve their indirect fitness despite their low chance of mating success (Kokko & Lindström 1996).

The aim of this study is to quantify lek site fidelity of male Black Grouse among neighbouring leks using data from 230 marked full-grown individuals and 76 chicks in two areas in Sweden. The overall question is whether male Black Grouse at a lek site can be considered as a separate group, or if there is a significant exchange of males between lek sites. We predict that male chicks, marked before fledging, should be recruited to the lek closest to the capture site. Adult males should not change lek sites and should remain close to their lek. We expect to see a maximum number of males displaying during the peak mating week.

## 2. Material and methods

### 2.1. Study area

We studied male Black Grouse in two areas in the boreal forest of central Sweden, specifically Boda (Site 1) between 1984 and 1987, and Länstersjön (Site 2) between 1990 and 1992. These sites were 200 km apart. Site 1 was an area of 32 km$^2$ located in Gävleborg County (approx. 61° N, 15° E) while Site 2 was an area of 19 km$^2$ located in Västernorrland County (approx. 62° N, 14° E). Both areas consisted of intensively managed Pine (*Pinus sylvestris* and *P. contorta*), and Norway Spruce (*Picea abies*) forests. Site 2 had substantially younger forest stands than Site 1.

At Site 1, five Black Grouse leks (A–E) were located in spring 1984 (Fig. 1). The average distance ± SD between neighbouring leks was 2.40 ± 0.80 km. One of those leks, lek-D, was on a frozen lake. A new lek (lek-F) was formed in spring 1985. By spring 1987, lek-E showed no activity, most likely due to the increasing canopy closure of the Pine plantation on the lek site. Males that were displaying on lek-D were moving to lek-E, the nearest lek, whenever the lake ice melted. Every late winter–spring during the four-year study period, we were actively searching for new leks within and nearby the study site by listening for calling males and searching for display tracks on the snow. We did not find any other lek within 2.50 km radius outside these six leks. However, we observed one solitary displaying male. At Site 2, we studied two leks, both of which were located in late winter of 1990. These leks were 1.10 km apart, and no other leks were located within a 2.50 km radius during the study period.

### 2.2. Data

We collected data on movements of male Black Grouse using three methods: (1) capture-mark-recapture, (2) radio-telemetry, and (3) lek counts.

(1) Capture-mark-recapture
These data were grouped in three categories:

(A) Males captured on leks. We captured 208 full-grown (juvenile and adult) males in March–May over the study period on leks at both Site 1 and Site 2 using drop-traps covered with soft net. Seventy-four percent of these individuals (103 juveniles and 50 adults) were captured at Site 1, while the remaining 28% (27 juveniles and 28 adults) were caught at Site 2 (Table 1). A total of 55 males from Site 1 were captured on lek-A, the largest lek (Fig. 1). We captured the individuals by randomly scattering 10–15 numbers of drop-traps in a compact plastic net of *circa* 20 cm high fence that we installed around each lek. We made sure the traps were the only openings in the fence. These traps were designed to be triggered by a nylon string when the birds walked under it (Willebrand 1988, Willebrand 1992). Males were caught leaving or entering the leks by foot through these trap-gates. We set the traps and the fences each day before midnight and collected them after the display was over in the morning. The fence was placed well outside the lek to reduce disturbance. One to two persons stayed in hides adjacent to each lek until the next morning so that any trapped birds were tagged or checked and released as soon as possible.

(B) Males captured in snow-burrows. We captured 22 full-grown males (16 juveniles and 6 adults) in snow-burrows during winter outside the leks at Site 1. Captures in the snow-burrows were aided by locating radio-collared males that were previously captured on a lek. We used a snowmobile to approach the located snow-burrows, and placed a net (175×175 cm; a 7 cm mesh) over the snow-burrow. Males captured in snow-burrows were assigned to the same lek as the radio-located males from a known lek. The males that were not accompanied by known males were assigned to the lek closet to the capture site.

All captured males in categories A and B ($n = 230$; 66% juveniles) were tagged with aluminium leg rings. The captured individuals were aged according to the form and pigmentation of their primary feathers (Helminen 1963). We defined males ≤ 18 months (until end of December of their second year) of age as juveniles and > 18 months as adults. We performed the captures every year during the study period with the recaptures occurring when we carried out these captures.

(C) Chicks captured before the brood break up. At Site 1, 76 chicks of < 21 days old, of both sexes, were captured and wing-tagged between the 2nd–3rd weeks of June in 1984–85. The chicks were too young to determine sex or to fit leg rings.

(2) Radio-telemetry

Among the captured and ringed full-grown males of Site 1, we fitted 113 males with 15–17 gram radio collars from Biotrack, UK with a minimum battery lifetime of 10 months. Out of the 113 radio-collared males, we obtained ≥ 20 positions for 54 individuals (33 juveniles and 21 adults) and used that data to evaluate movements and home ranges. Of these 33 juveniles, seven were captured in January–February in snow-burrows. We did not have any radio-collared juveniles that were tagged before brood break up. A subset of 15 males (7 juveniles and 8 adults) was used to estimate short-term (intensive tracking) home ranges by relocating them at least three times a day for 7–11 days. We managed to change the collar of nine males ≥ two times during the recaptures. Consequently, four males were tracked for four subsequent years, five for three years, 26 individuals for two years, and the rest of the 19 individuals for ≤ one year. We recorded a position by triangulation every other week throughout a year. The coordinates of the positions were extracted to the closest 100 m. All radio tracking occurred during daylight hours, 06:00–18:15.

(3) Lek counts

The number of males on leks at Site 1 were systematically counted from a well-camouflaged hiding spot in late winter–spring (February until May), and in autumn, lekking activities were recorded from 16th September to 1st October. During the late winter–spring display period, we further distinguished between premating (1985: 1/2–6/5; 1986: 1/2–1/5; 1987: 1/2–28/4 day/month) and mating (1985: 7/5–20/5; 1986: 2/5–20/5; 1987: 29/4–20/5 day/month) periods. Here, the mating period was the time when females are observed mating on the leks. Throughout the study, we observed each leks 4–12 days per month during the winter–spring pre-mating period, and every day during the mating period for three years. Non-lekking periods were defined as 1st June–15th September, and 1st November–31st January.

## 2.3. Analysis

We calculated the shortest distance of all radio locations to all lek sites. For each individual, we used the proportion of spring relocations when closest to its capture lek as a measure of site fidelity. We considered that an individual had changed lek when it was recaptured in spring at a lek other than the initial capture lek and/or if it showed weak site tenacity *i.e.*, when ≥ 50% of the spring relocations were nearer to another lek other than that of its first capture. Thus, both mark-recapture and radio tracking data were used to record how many leks an individual visited.

Table 1. Mark-recapture histories of male Black Grouse in successive springs after initial capture, Sweden, 1984–1992. The birds' age (juvenile & adult) are shown in the brackets.

| Location | Initial capture | 1st spring | 2nd spring | 3rd spring |
|---|---|---|---|---|
| Site 1 | 175 (117 & 58) | 43 (17 & 26) | 7 (2 & 5) | 3 (1 & 2) |
| Site 2 | 55 (27 & 28) | 16 (9 & 7) | 1 (1 & –) | – |

The *maximum number of males observed* (discrete, response) on each lek was used to test if more males were present during the *mating period* (categorical) than *premating period* (categorical). The difference between the two periods was tested in a *pairwise t*-test. We fitted a random intercept generalized linear mixed model with identity link normal distribution error to determine the effect of *age* (*adult* and *juvenile;* independent variable) and *period* (*premating*, *mating*, *autumn lekking*, and *non-lekking;* independent variable) on *average distance* (continuous, dependent variable) of each individual's relocations to its capture lek. We treated the *individuals* as a random effect (random intercept), and the *period* and *age* as fixed effects. We fitted all the models with Maximum Likelihood (ML) for model selections and then refitted the highest ranked model with Restricted Maximum Likelihood (REML). All models were compared using the corrected Akaike Information Criteria (AICc) (Akaike 1973, Burnham & Anderson 2002), and we selected the best model using the rule of a minimum difference in ΔAICc of two.

Short-term, seasonal, and annual home ranges were calculated using kernel estimates with optimum bandwidth (Worton 1989, Seaman & Powell 1996, Kie *et al.* 2010), excluding the 5% most peripheral positions. Individuals used to calculate short-term home ranges had a median of 32 relocations (range = 21–47 relocations) obtained as explained above. For the seasonal home ranges, we included individuals that had at least 20 relocations (median = 25 relocations, range = 20–54 relocations) in a season, whereas for annual home ranges we included individuals with a minimum of 30 relocations during a year (median = 47 relocations, range = 30–85 relocations) (Seaman *et al.* 1999). We reported both area and median overlap (%) of the individuals' home ranges. We treated lek-D and lek-E as one (E/D) for annual home range overlap analysis due to the individuals' displacement as stated above. We evaluated the overlap of short-term home ranges of males of lek-A only since most of the intensively tracked individuals belonged to this lek ($n = 8$).

We carried out all analysis using R 3.2.0 (R Core Team 2015) and we used ArcGIS (ESRI 2010) to produce Fig. 1. For all three home range analyses, we used package adehabitatHR (Calenge 2006) with dependent data classes provided by package sp (Bivand *et al.* 2008). We used the package lme4 (Bates *et al.* 2014) for the mixed modelling. We used package AICcmodavg to get AICc estimate (Mazerolle 2016). We used 0.05 *P*-value for all statistical tests and interpretation, and presented the 95% confidence interval where applicable.

## 3. Results

### 3.1. Inter-lek movement

Seven males of 76 ringed chicks were recaptured the following spring on the lek closest to their natal area. Twenty-six percent of 230 full-grown males (33 juveniles and 26 adults) were recaptured at least once in the subsequent springs (Table 1). Nine of these males (7 juveniles and 2 adults) were recaptured on a lek other than where they were first caught. The rest were recaptured on the same lek where they were initially captured. All but one of those males that changed leks were originally captured on a lek in spring, the other being a juvenile male captured in a snow-burrow in January. Two juveniles moved from lek-A to lek-B (2.6 km), and one juvenile from lek-C to lek-A (6.3 km). From these observations, the inter-lek movement probability of males was 15% (95% confidence interval = 6–25%). More juveniles than adults changed lek but the difference was not statistically significant (*prop.test*: $\chi^2 = 1.14$, $P = 0.29$).

Radio-locations from three of the seven recap-

Table 2. Annual and seasonal 95% kernel home range estimates of radio-collared Black Grouse males from Site 1 in Sweden, 1984–1987. The extensive estimates refer to the biweekly relocations while the intensive estimates to at least 3 daily relocations for 7–11 consecutive days. Results are presented as median (*minimum–maximum; n*) in km$^2$.

| | Extensive | Extensive | Intensive | Intensive |
|---|---|---|---|---|
| Season | Adult | Juvenile | Adult | Juvenile |
| Spring | 2.4 (1.8–10.0; 12) | 6.1 (4.6–7.5; 2) | 3.4 (2.8–3.9; 2) | 8.1 (5.4–10.9; 2) |
| Summer | 1.4 (1.2–2.6; 9) | 1.6 (1.0–4.0; 6) | 2.1 (0.5–2.5; 4) | 0.5 (0.4–2.0; 3) |
| Fall | 1.9 (0.9–8.3; 12) | 2.3 (1.3–8.3; 5) | 1.4 (0.5–6.2; 6) | 0.8 (0.6–1.1; 3) |
| Winter | 4.4 (3.2–5.0; 5) | – | 2.1 (1.9–5.3; 3) | – |
| Annual | 3.5 (1.5–9.2; 25) | 4.9 (2.3–12.0; 24) | – | – |

tured juveniles that moved to a new lek site revealed that they were ≤ 100 m of the new lek's centre during the following spring (Fig. 1b). Combining both radio tracking and recapture data, one of the juveniles changed leks twice in the same spring. It was one of the juvenile males that were captured in a snow-burrow. This individual travelled 6.30 km to a second lek, after visiting another lek in between. Of the other six juveniles that changed lek, four moved 2.50 km, one moved 1.10 km, and the othter one moved 1.50 km to the new lek. The two adults that moved to a new lek changed to the nearest lek (1.10 and 1.50 km, respectively).

Additional information on the inter-lek movement was also obtained from those males that were radio-collared but never recaptured. Three juveniles of the 54 radio tracked males (6%) had ≥ 50% of their spring relocations closer to a neighbouring lek than to their initial capture lek (Fig. 1b). All of these males moved from lek-C to lek-D (1.5 km). These juveniles occasionally revisited their capture lek, lek-C. Four males, including one of these males, visited at least two leks other than their capture lek.

### 3.2. Home range and lek fidelity

Home ranges of adults and juveniles were, to a large extent, similar in size, except during spring when the juveniles' home ranges were two times larger than the adults' both in the extensive and intensive tracking (Table 2). Note that the home ranges from the intensive tracking were not substantially smaller than the seasonal home ranges that obtained during a three month period. Small sample size made it difficult to test for seasonal effect, but annual home ranges did not statistically differ between adults and juveniles ($t_{(41)} = -1.86$, $P = 0.07$, *pairwise t*-test; Table 2).

Males stayed close to their leks all year round, and annual home ranges of individuals from the same lek overlapped to a large extent (Fig. 1a). The median overlap among the home ranges of males from lek-A, B, C, and D/E was 71%, 64%, 71%, and 59%, respectively. Annual home ranges of two of the three radio-tracked emigrated juveniles showed a limited overlap with males of their first capture lek (median < 1%), but substantial overlap with males of their new lek site (median = 27%; 67%). The overlap of home ranges between males from different leks was small; the highest overlap was between males at lek-C and lek-D/E (median = 27%). For all the other combinations of lek sites, the median home range overlap was less than one percent. Short-term summer, autumn and winter home ranges of eight males at lek-A all overlapped and the median overlap was 45%.

Age (adult and juvenile), period (premating, mating, non-lekking, and autumn lekking), and their interaction, were important in explaining the individuals' relocation distance to the capture leks (Fig. 2). This full mixed model gave the lowest AICc (1102), with ΔAICc = 30 from the next best model (AICc = 1132), which was an additive of period and age. The model with age only had the highest (AICc = 1170). While the adults were closer to the leks during mating period, the juveniles were closer to the lek during premating. The two age groups had comparable distances from their leks during the autumn lekking and non-

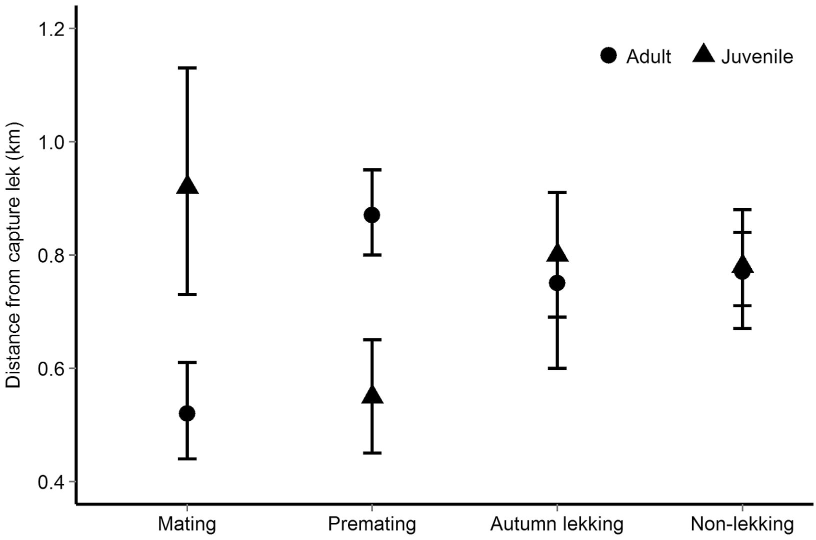


Fig. 2. The mean ± SE km relocations distance of radio-collared male Black Grouse to the capture leks, Sweden, 1984–1987. Age (adult and juvenile), period (premating, mating, autumn lekking, and non-lekking) and their interaction gave the lowest AICc (1102) with DAICc = 30 from the second best model (AICc = 1132) in the mixed model.

lekking periods. Note that the juveniles in the autumn lekking refer to 1.5 year old males. Furthermore, counts of males on the leks showed that more males were observed on the leks during the early lekking period compared to when females arrived at the leks to mate in spring (mean difference = 4, $t_{(15)} = 3.06$, $P = 0.008$, *pairwise t*-test).

The maximum relocation distance from the centre of the capture lek was 5.60 km (March) for an adult and 6.80 km (June) for a juvenile. A juvenile captured in a snow-burrow and fitted with a radio-collar was never recorded attending a lek. It was observed displaying alone in a tree-top after dispersing about 6.5 km from the point of capture.

## 4. Discussion

This is the only study, to our knowledge, that has produced data on male Black Grouse movement dynamics in relation to neighbouring lek sites, across consecutive years. We have shown that males displaying at a lek site stay close to their lek throughout the year, and have substantial overlap with each other's home ranges. The overlap of males from neighbouring lek sites was small, and only a few males changed leks. All males tagged as chicks and recaptured the following spring were recaptured at the lek closest to their natal area, a result that indicates that most males are recruited locally. Few chicks survive until next spring as mortality is high, *i.e.*, 70–80% (Willebrand 1992, Bowker *et al.* 2007, Ludwig *et al.* 2010). Assuming an even sex ratio of tagged chicks and a 30% survival, our seven recaptures correspond to more than 60% of the surviving male chicks.

High site tenacity of male Black Grouse has been reported in France (Caizergues & Ellison 2002), UK (Baines 1996, Warren & Baines 2002), and Norway (Gregersen & Gregersen 2014). Black Grouse males within a lek are somewhat more closely related than males among leks (Lebigre *et al.* 2008) and clusters of related males have been found on Capercaillie leks in Russia (Segelbacher *et al.* 2007), and on Lesser Prairie-Chicken (*Tympanuchus pallidicinctus*) leks in New Mexico, USA (Bouzat & Johnson 2004). This has also been observed in other lekking bird species such as White-Bearded Manakin (*Manacus manacus*) (Shorey *et al.* 2000), and Peacock (*Pavo cristatus*) (Petrie *et al.* 1999). Likewise, juvenile Red Grouse (*Lagopus lagopus scotica*) males are tolerated by their relatives when settling at a territory (Watson *et al.* 1994, MacColl *et al.* 2000).

Our results showed an unexpected, significant decline, rather than an increase, in the number of males observed on the leks from late winter-spring to the period of mating in early May. The reduction occurred at a time when juvenile males began to spend more time away from the lek centres, which resulted in larger home ranges. It is known that yearling Black Grouse males avoid active lekking and hostility by staying on the edge of the lek (Koivisto 1965, Alatalo *et al.* 1996). High lek attendance and active lekking would enhance mating success (Alatalo *et al.* 1991, Rintamäki *et al.* 1995, Höglund *et al.* 1997). However, juvenile Black Grouse males have a minor chance of copulation even if they have established a territory on a lek (Kervinen *et al.* 2012). We propose that juvenile males have a better chance to mate by searching for females in the surroundings of the leks. We have observed a single displaying male with three females, and mating with at least one of them. It is also documented that, compared to adults, a lower percentage of juvenile Sage-Grouse males attended leks when the number of visiting females were the highest (Emmons & Braun 1984, Walsh *et al.* 2004), and that none of the juveniles affiliated with a lek were detected to mate (Bird *et al.* 2013). Likewise, Capercaillie (Wegge & Larsen 1987), and Little Bustard (*Tetrax tetrax*) (Ponjoan *et al.* 2012) yearlings and sub-adults have wider home ranges than adults during mating period.

The lek activity both in autumn and in spring occurs when juvenile females disperse, with limited dispersal movements in the intervening winter period (Willebrand 1988, Caizergues & Ellison 2002, Warren & Baines 2002). In Willow Ptarmigan (*Lagopus lagopus*), a large proportion of female recruits have their natal area more than 10 km away from where they settle to breed (Hörnell-Willebrand *et al.* 2014). We expect a similar pattern in Black Grouse (Warren & Baines 2002, Lebigre *et al.* 2008). At Site 1, four radio-collared juvenile Black Grouse females that survived from autumn to late spring dispersed 5.10–8.00 km from their natal area (Willebrand 1988), a distance that made them pass one-two leks.

One important function of the lek mating system is to provide cues for females in selection of males (Höglund & Alatalo 1995), but we suggest that leks also function to attract females that go through natal dispersal in autumn and spring. High site fidelity of males makes it possible for dispersing females to use lek size and activity as a cue of the area's quality for chick production and survival. Although juvenile males have little success in obtaining a central territory in their first spring, they could increase their indirect fitness through kin selection, by helping their adult relatives to attract females by contributing to a high activity on their "natal" lek (Kokko & Lindström 1996). Attracting dispersing females would also increase the chance for juveniles to mate with females outside the lek. It is, therefore, advantageous for juvenile males to remain in the group of lekking males because females that have made a breeding attempt will return to breed the next year (Willebrand 1988, Marjakangas *et al.* 1997). Furthermore, an annual mortality of about 50% (Willebrand 1988, Bowker *et al.* 2007) will create several opportunities for juvenile male to fill up in vacant territories on the lek (Kokko *et al.* 1998).

## 5. Conclusions

Our findings suggest that the Black Grouse males at a lek consist of a well-defined local male population, and have a limited interaction with males from other leks. Displaying Black Grouse males can be audible for 2–3 km (personal observation) and males at one lek are probably aware of one or more neighbouring leks. Males appear to be recruited locally, and there is a high likelihood that they remain on the same lek until the following year. Adult males, in particular, remain close to their lek all year round. This is different from other lekking grouse males such as Sage Grouse (Bradbury *et al.* 1989, Leonard *et al.* 2000) and Capercaillie (Rolstad *et al.* 1988, Hjeljord *et al.* 2000) that stay away from lek sites during the non-breeding period, even though they too are faithful to a lek site in spring. For management purposes, counting Black Grouse males on leks in spring during the premating period instead of the mating week may give more reliable abundance estimates.

*Acknowledgements.* We would like to extend our genuine gratitude for both The Swedish Environmental Protection Agency and Svenska Jägareförbundet for funding our research. We also owe a great deal to both Gert Olsson and Gert Mattsson for their gracious help during the data collection.

### Orrtuppars spelplats bestämmer deras rörelsemönster

Orrtuppar antas komma tillbaka till samma spelplats år efter år, medan juvenila tuppar antas etablera sig på den spelplats som ligger närmast det område där de kläcktes. Här presenterar vi resultat från en undersökning av orrtuppars ortstrohet till en och samma spelplats genom att analysera data från fångst/återfångst, orrtuppar märkta med sändare och direkta spelplatsobservationer under perioden 1984 till 1992. Vi samlade data från två områden i centrala Sverige med vardera sex och två spelplatser. Totalt fångades och märktes 306 orrar (230 vuxna orrtuppar och 76 kycklingar).

Alla vingmärkta kycklingar ($n = 7$) återfångades på den spelplats som var närmast till märkningsplatsen. 26 % ($n = 59$) av de vuxna tupparna återfångades minst en gång under efterföljande år. Färre tuppar observerades på spelplatser under de dagar när hönor kom för att para sig än tidigare under våren ($t_{(15)} = 3.06, P = 0.008$). Under den tidiga perioden var juvenila tuppar närmare spelplatsen (95 % C.I. = 0.45–0.65 km) jämfört med perioden för parning (95 % C.I.= 0.73–1.13 km). I fråga om adulta tuppar var förhållandet det motsatta: de var närmare spelplatsen under dagarna för parning (95 % C.I. = 0.44–0.61 km) än under den tidigare perioden (95 % C.I. = 0.80–0.95 km).

Vi fann att endast 15 % ($n = 9$) av tupparna i den här studien bytte spelplats. Resultaten visar att orrtuppar på en spelplats utgör en väl definierad social grupp med begränsat utbyte med andra spelplatsgrupper och att rekryteringen av nya tuppar i huvudsak sker från den närmaste omgivningen.

## References

Akaike, H. 1973: Information theory as an extension of the maximum likelihood principle. — In second international symposium on information theory (ed. Petrov, B. N. & Csaki, F.): 267–281. Akadamiai Kiado, Budapest.

Alatalo, R. V., Hoglund, J. & Lundberg, A. 1991: Lekking in the Black Grouse: A test of male viability. — Nature 352: 155–156.

Alatalo, R. V., Hoglund, J., Lundberg, A., Rintamäki, P. T. & Silverin, B. 1996: Testosterone and male mating success on the Black Grouse leks. — Proceedings of the Royal Society B-Biological Sciences 263: 1697–1702.

Alatalo, R. V., Hoglund, J., Lundberg, A. & Sutherland, W. J. 1992: Evolution of Black Grouse leks: female preferences benefit males in larger leks. — Behavioral Ecology 3: 53–59.

Baines, D. 1996: Seasonal variation in lek attendance and lekking behaviour by male Black Grouse (*Tetrao tetrix*). — Ibis 138: 177–180.

Bates, D., Maechler, M., Bolker, B. & Walker, S. 2014: lme4: Linear mixed-effects models using Eigen and S4. — R package version 1.1-7. http://CRAN.R-project.org/package=lme4.

Bird, K. L., Aldridge, C. L., Carpenter, J. E., Paszkowski, C. A., Boyce, M. S. & Coltman, D. W. 2013: The secret sex lives of Sage-Grouse: multiple paternity and intraspecific nest parasitism revealed through genetic analysis. — Behavioral Ecology 24: 29–38.

Bivand, R. S., Pebesma, E. J. & Gomez-Rubio, V. 2008: Applied spatial data analysis with R. — Springer, NY.

Bouzat, J. L. & Johnson, K. 2004: Genetic structure among closely spaced leks in a peripheral population of Lesser Prairie-Chickens. — Molecular Ecology 13: 499–505.

Bowker, G., Bowker, C. & Baines, D. 2007: Survival rates and causes of mortality in Black Grouse (*Tetrao tetrix*) at Lake Vyrnwy, North Wales, UK. — Wildlife Biology 13: 231–237.

Bradbury, J. W. & Gibson, R. M. 1983: Leks and mate choice. — In Mate Choice (ed. Bateson, P): 109–138. Cambridge University Press, Cambridge.

Bradbury, J. W., Vehrencamp, S. L. & Gibson, R. M. 1989: Dispersion of displaying male Sage Grouse: 1. Patterns oftemporal variation. — Behavioral Ecology and Sociobiology 24: 1–14.

Burnham, K. P., & Anderson, D. R. 2002: Model selection and inference: A practical information theoretic approach. 2nd edition. — Springer, New York.

Caizergues, A. & Ellison, L. N. 2002: Natal dispersal and its consequences in Black Grouse (*Tetrao tetrix*). — Ibis 144: 478–487.

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: 516–519.

Drummer, T. D., Corace, R. G. & Sjogren, S. J. 2011: Sharp-Tailed Grouse lek attendance and fidelity in Upper Michigan. — Journal of Wildlife Management 75: 311–318.

Emmons, S. R. & Braun, C. E. 1984: Lek attendance of male Sage Grouse. — Journal of Wildlife Management 48: 1023–1028.

ESRI 2010: ArcGIS Desktop Version 10. — Environmental Systems Research Institute.

Gibson, D., Blomberg, E. J., Atamian, M. T. & Sedinger, J. S. 2014: Lek fidelity and movement among leks by male Greater Sage-Grouse (*Centrocercus urophasianus*): A capture–mark–recapture approach. — Ibis 156: 729–740.

Gjerde, I., Wegge, P. & Rolstad, J. 2000: Lost hotspots and passive female preference: the dynamic process of lek formation in Capercaillie (*Tetrao urogallus*). — Wildlife Biology 6: 291–298.

Gregersen, H. & Gregersen, F. 2014: Wildlife cameras effectively survey Black Grouse (*Lyrurus tetrix*) leks. — Ornis Norvegica 37: 1–6.

Helminen, M. 1963: Composition of the Finnish population of Capercaillie (*Tetrao urogallus*) and Black Grouse (*Lyrurus tetrix*) in the autumns of 1952–1961 as revealed by a study of wings. — Papers on Game Research 23: 1–124.

Hjeljord, O., Wegge, P., Rolstad, J., Ivanova, M. & Beshkarev, A. B. 2000: Spring–summer movements of male Capercaillie (*Tetrao urogallus*): A test of the “landscape mosaic” hypothesis. — Wildlife Biology 6: 251–256.

Hovi, M., Alatalo, R. V., Halonen, M. & Lundberg, A. 1997: Responses of male and female Black Grouse to male vocal display. — Ethology 103: 1032–1041.

Höglund, J. & Alatalo, R. V. 1995: Leks. — Princeton University Press, Princeton.

Höglund, J., Alatalo, R. V., Lundberg, A., Rintamäki, P. T. & Lindell, J. 1999: Microsatellite markers reveal the potential for kin selection on Black Grouse leks. — Proceedings of the Royal Society of London Series B-Biological Sciences 266: 813–816.

Höglund, J., Johansson, T. & Pelabon, C. 1997: Behaviourally mediated sexual selection: Characteristics of successful male Black Grouse. — Animal Behaviour 54: 255–264.

Hörnell-Willebrand, M., Willebrand, T. & Smith, A. A. 2014: Seasonal movements and dispersal patterns: Implications for recruitment and management of Willow Ptarmigan (*Lagopus lagopus*). — Journal of Wildlife Management 78: 194–201.

Isvaran, K. & Ponkshe, A. 2013: How general is a female mating preference for clustered males in lekking species? A meta-analysis. — Animal Behaviour 86: 417–425.

Kervinen, M., Alatalo, R. V., Lebigre, C., Siitari, H. & Soulsbury, C. D. 2012: Determinants of yearling male lekking effort and mating success in Black Grouse (*Tetrao tetrix*). — Behavioral Ecology 23: 1209–1217.

Kie, J. G., Matthiopoulos, J., Fieberg, J., Powell, R. A., Cagnacci, F., Mitchell, M. S., Gaillard, J. M. & Moorcroft, P. R. 2010: The home-range concept: are traditional estimators still relevant with modern telemetry technology? — Philosophical Transactions of the Royal Society B-Biological Sciences 365: 2221–2231.

Koivisto, I. 1965: Behavior of the Black Grouse (*Lyrurus tetrix* (L)) during the spring display. Volume 26. — Finnish Game Research, Helsinki.

Kokko, H., Lindstrom, J., Alatalo, R. V. & Rintamäki, P. T. 1998: Queuing for territory positions in the lekking Black Grouse (*Tetrao tetrix*). — Behavioral Ecology 9: 376–383.

Kokko, H. & Lindström, J. 1996: Kin selection and the evolution of leks: Whose success do young males maximize? — Proceedings of the Royal Society of London Series B-Biological Sciences 263: 919–923.

Lebigre, C., Alatalo, R. V., Forss, H. E. & Siitari, H. 2008: Low levels of relatedness on Black Grouse leks despite male philopatry. — Molecular Ecology 17: 4512–4521.

Leonard, K. M., Reese, K. P. & Connelly, J. W. 2000: Distribution, movements and habitats of Sage Grouse (*Centrocercus urophasianus*) on the Upper Snake River Plain of Idaho: changes from the 1950s to the 1990s. — Wildlife Biology 6: 265–270.

Ludwig, G. X., Alatalo, R. V., Helle, P. & Siitari, H. 2010: Individual and environmental determinants of early brood survival in Black Grouse (*Tetrao tetrix*). — Wildlife Biology 16: 367–378.

MacColl, A. D. C., Piertney, S. B., Moss, R. & Lambin, X. 2000: Spatial arrangement of kin affects recruitment success in young male Red Grouse. — Oikos 90: 261–270.

Marjakangas, A., Valkeajarvi, P. & Ijas, L. 1997: Female Black Grouse (*Tetrao tetrix*) shift nest site after nest loss. — Journal Fur Ornithologie 138: 111–116.

Martin, K. & Hannon, S. J. 1987: Natal philopatry and recruitment of Willow Ptarmigan in north central and northwestern Canada. — Oecologia 71: 518–524.

Mazerolle, M. J. 2016: AICcmodavg: Model selection and multimodel inference based on (Q)AIC(c). — R package version 2.1-0. https://cran.r-project.org/package=AICcmodavg.

Petrie, M., Krupa, A. & Burke, T. 1999: Peacocks lek with relatives even in the absence of social and environmental cues. — Nature 401: 155–157.

Ponjoan, A., Bota, G. & Manosa, S. 2012: Ranging behaviour of Little Bustard males (*Tetrax tetrax*) in the lekking grounds. — Behavioural Processes 91: 35–40.

R Core Team 2015: R: A language and environment for statistical computing 3.2.0. — R Foundation for Statistical Computing Vienna, Austria. http://www.R-project.org/.

Rintamäki, P. T., Alatalo, R. V., Hoglund, J. & Lundberg, A. 1995: Mate sampling behavior of Black Grouse females (*Tetrao Tetrix*). — Behavioral Ecology and Sociobiology 37: 209–215.

Rintamäki, P. T., Karvonen, E., Alatalo, R. V. & Lundberg, A. 1999: Why do Black Grouse males perform on lek sites outside the breeding season? — Journal of Avian Biology 30: 359–366.

Rolstad, J., Wegge, P. & Larsen, B. B. 1988: Spacing and habitat use of Capercaillie during summer. — Canadian Journal of Zoology-Revue Canadienne De Zoologie 66: 670–679.

Rolstad, J., Wegge, P., Sivkov, A. V., Hjeljord, O. & Storaunet, K. O. 2009: Size and spacing of grouse leks: comparing Capercaillie (*Tetrao urogallus*) and Black Grouse (*Tetrao tetrix*) in two contrasting Eurasian boreal forest landscapes. — Canadian Journal of Zoology-Revue Canadienne De Zoologie 87: 1032–1043.

Schroeder, M. A. 1986: The fall phase of dispersal in juvenile Spruce Grouse. — Canadian Journal of Zoology-Revue Canadienne De Zoologie 64: 16–20.

Schroeder, M. A. & Robb, L. A. 2003: Fidelity of Greater Sage-Grouse (*Centrocercus urophasianus*) to breeding areas in a fragmented landscape. — Wildlife Biology 9: 291–299.

Seaman, D. E., Millspaugh, J. J., Kernohan, B. J., Brundige, G. C., Raedeke, K. J., & Gitzen, R. A. 1999: Effects of sample size on kernel home range estimates. — Journal of Wildlife Management 63:739–747.

Seaman, D. E. & Powell, R. A. 1996: An evaluation of the accuracy of kernel density estimators for home range analysis. — Ecology 77: 2075–2085.

Segelbacher, G., Wegge, P., Sivkov, A. V. & Hoglund, J. 2007: Kin groups in closely spaced Capercaillie leks. — Journal of Ornithology 148: 79–84.

Shorey, L., Piertney, S., Stone, J. & Hoglund, J. 2000: Fine-scale genetic structuring on *Manacus manacus* leks. — Nature 408: 352–353.

Small, R. J. & Rusch, D. H. 1989: The natal dispersal of Ruffed Grouse. — Auk 106: 72–79.

Storch, I. 1997: Male territoriality, female range use, and spatial organisation of Capercaillie (*Tetrao urogallus*) leks. — Wildlife Biology 3: 149–161.

Walsh, D. P., White, G. C., Remington, T. E. & Bowden, D. C. 2004: Evaluation of the lek-count index for Greater Sage-Grouse. — Wildlife Society Bulletin 32: 56–68.

Warren, P. K. & Baines, D. 2002: Dispersal, survival and causes of mortality in Black Grouse (*Tetrao tetrix*) in northern England. — Wildlife Biology 8: 91–97.

Watson, A., Moss, R., Parr, R., Mountford, M. D. & Rothery, P. 1994: Kin landownership, differential aggression between kin and non-kin, and population fluctuations in Red Grouse. — Journal of Animal Ecology 63: 39–50.

Wegge, P. & Larsen, B. B. 1987: Spacing of adult and subadult male common Capercaillie during the breeding season. — Auk 104: 481–490.

Widemo, F. 1997: The social implications of traditional use of lek sites in the Ruff (*Philomachus pugnax*). — Behavioral Ecology 8: 211–217.

Willebrand, T. 1988: Demography and ecology of a Black Grouse (*Tetrao tetrix* L.) population. — Uppsala University Uppsala.

Willebrand, T. 1992: Breeding and age in female Black Grouse (*Tetrao-Tetrix*). — Ornis Scandinavica 23: 29–32.

Worton, B. J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. — Ecology 70: 164–168.