



**Reproductive success and survival of hen  
rock ptarmigan (*Lagopus muta*) during  
summer**

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**Faculty of Life and Environmental Sciences  
University of Iceland  
2012**



# **Reproductive success and survival of hen rock ptarmigan (*Lagopus muta*) during summer**

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90 ECTS thesis submitted in partial fulfillment of a  
*Magister Scientiarum* degree in Biology

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Reykjavík, May 2012

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**Bibliographic information:**

Aðalsteinn Örn Snæþórsson, 2012, *Reproductive success and survival of hen rock ptarmigan (Lagopus muta) during summer*, M.Sc. thesis, Faculty of Life and Environmental Sciences, University of Iceland, 42 pages.

Printing: Háskólaprent ehf.  
Reykjavík, Iceland, May 2012

## Abstract

The rock ptarmigan (*Lagopus muta*) is a common breeding bird in Iceland and the population shows fairly regular 10-year cycles. Independent of the cycle the population has been declining 4% annually for the last decades and the amplitude is markedly reduced. In this study two questions are addressed. One is whether generalist predators can cause the dampening of the population cycle and the decline of the population. The other is whether there is an age related difference in chick production, which is information needed to refine a population model of the ptarmigan in Iceland. Hens were trapped in two areas in Iceland, one in the north-east in 2009 and 2010 and the other close to the city Reykjavík in the south-west in 2007 and 2008. Two age groups were identified, birds from previous summer (yearlings) and older birds (adults). All hens were radio tagged and monitored once a week during May through August. Mortality causes were estimated as well as reproductive success. The result shows no statistical difference between age groups regarding survival of hens or number of chicks in August while the difference between areas was large. Survival and reproduction were higher in the north-east where the population increased 3.7-fold during the breeding season while in the south-west the population increase was only 1.6-fold. The proximate reason for this difference was high predation by generalist mammalian predators on hens in the south-west and low chick production.

## Útdráttur

Rjúpa (*Lagopus muta*) er algengur varpflugl á Íslandi og stofninn sýnir reglulegar sveiflur í fjölda. Hver sveifla tekur um 10 ár og margfaldast stofninn milli lágmarks- og hámarksára. Óháð sveiflunum hefur stofninn minnkað um 4% á ári síðustu áratugi og hámarksárið sífellt lægri. Í þessari rannsókn er leitað svara við tveimur spurningum. Önnur snýr að því hvort aukið afrán á kvenfuglum yfir sumartímann geti verið orsök breytinga í stofnsveiflunum. Hin snýr að því að afla upplýsinga um ungaframleiðslu eftir aldri en þær upplýsingar vantar til að hægt sé að bæta stofnlíkan sem gert hefur verið fyrir rjúpunna. Kvenfuglar rjúpunnar voru fangaðir á tveimur svæðum, á Suðvesturlandi 2007 og 2008 og Norðausturlandi 2009 og 2010 og þeir flokkaðir í tvo aldursflokka, árgamla fugla og tveggja ára og eldri. Útvarpssendar voru settir á fuglana og þeim fylgt eftir einu sinni í viku yfir vor og sumar. Afföll voru skráð sem og varpárangur. Ekki mældist marktækur munur á afföllum eða varpárangri eftir aldri en niðurstöðurnar sýna mikinn mun á milli svæða þar sem aföll kvenfugla voru mun meiri og varpafkoma slakari á Suðvesturlandi en Norðausturlandi. Eftir niðurstöðum þessara rannsókna að dæma þá 3,7 faldadist stofninn yfir sumartímann á Norðausturlandi en 1,6 faldadist á Suðvesturlandi sem er 2,3 faldur munur. Nærtækar skýringar þessa munar voru meira afrán spendýra á kvenfugla og minni ungaframleiðsla á Suðvesturlandi en á Norðausturlandi.



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# Acknowledgment

I want to thank my supervisors Ólafur Karl Nielsen, Tómas Grétar Gunnarsson and Páll Hersteinsson, who sadly passed away on 13 October 2011, for their help and support throughout the process of this study. I want to thank Tomas Willebrand for extremely valuable help on data analysis and good advice regarding the study and also his family for great hospitality and kindness during my visit in Norway.

I want to thank Yann Kolbeinsson who was my biggest help during the field work in the north-east, Ólafur Karl Nielsen and Sólrún Harðardóttir for trapping, banding and radio tracking hens in the south-west. I also thank Björg Þorleifsdóttir, Frederik Dahl, Hallgrímur Gunnarsson, Hlynur Aðalsteinsson, Iris Schwenkmeier, Jan Macher, Jón Hallur Jóhannsson, Maika Holzappel, Maria Hörnell-Willebrand, Már Höskuldsson, Ólafur Einarsson, Ólafur Torfason, Sigþrúður Stella Jóhannsdóttir, Snæþór Aðalsteinsson, Tomas Willebrand, Ute Stenkewitz and Þorvaldur Björnsson for help with field work. I thank Sigmar Metúsalemsson for making figures 1 and 2 in this thesis.

I want to thank all my co-workers at the North East Iceland Nature Center for good advice and help throughout my studies.

I want to give my wife, Sigþrúður Stella Jóhannsdóttir, and our two sons a special thank for their patience and support during this process and making this worthwhile.

This project was funded by the North East Iceland Nature Center, the Icelandic Institute of Natural History and The State Alcohol and Tobacco Company of Iceland (ÁTVR).



# 1 General Introduction

The rock ptarmigan (*Lagopus muta*) is the only grouse species in Iceland and plays an important role in the Icelandic ecosystem as being one of the most significant wild herbivores among the native vertebrate community. Further it is the most popular game bird in Iceland and a traditional Christmas food for a large proportion of the Icelandic nation. The population shows a fairly regular 10-year cyclic fluctuation in number of birds (Guðmundsson 1960, Garðarsson 1988, Nielsen and Pétursson 1995) and predation by the gyrfalcon (*Falco rusticolus*), which is a specialist predator preying on the ptarmigan, may play a role in driving the cycles (Nielsen 1999a).

Time series of ptarmigan abundance have been analysed and show a cyclic fluctuation with a period of 10–12 years and a decline of the population by 4% per year on average during 1981–2003 (Brynjarsdóttir et al. 2003). Further, the amplitude of the cycle has diminished mainly through lowering of the peaks. Population model for the ptarmigan in Iceland shows two delayed density dependent demographic factors explaining the cyclic behaviour. One is the excess juvenile autumn- and winter mortality which lags the ptarmigan population by 2–4 years and the other is a negative impact of population size on chick production which lags the ptarmigan population by 2 years (Magnússon et al. 2004, Magnússon 2005). In this study two questions are addressed. Firstly could increased mortality by generalist predators be causing the population decline and the collapse of the population cycle? Secondly do adult hens produce more chicks than yearlings as expected in the population model and if so to what extent? These two questions will be further addressed below.

## 1.1 The generalist predators

Many cyclic populations are now fluctuating at lower abundance than previously and among the reasons given is warmer climate and increased predation by generalist predators (Strann et al. 2002, Hornfeldt et al. 2005, Korpimäki et al. 2005, Ludwig et al. 2006, Ims et al. 2008, Brommer et al. 2010). It is unknown if this is operating in the Icelandic ptarmigan population, i.e. generalist predators preying on hens and chicks causing the dampening of the cycle.

Previous studies have shown ptarmigan in Iceland being highly productive with low predation on nests and chicks. In a study on Hrísey, an island of the north coast of Iceland, during the years 1963–1970 the mean clutch size varied between 10.4 and 11.7 eggs and the mean brood size in late July was between 7.3 and 9.3 chicks except in 1966 when the brood size was only 4.3 chicks due to cold weather in July (Garðarsson 1988). This is a much higher production than reported elsewhere for this species where the clutch size varies from 5.8 to 8.7 (Steen and Unander 1985, Watson et al. 1998, Cotter 1999, Scherini et al. 2003, Sawa et al. 2011) and brood size from 0.6 to 5.0 (Cotter 1999, Scherini et al. 2003). There are no mammalian predators on Hrísey but on the mainland there are arctic fox (*Alopex lagopus*) and American mink (*Neovison vison*). A high chick production has also been reported on the mainland where the mean brood size in early August was 8.1 in

north-east Iceland 1981–2003 and 7.4 in south-west Iceland 1995–2003 and on the average 95% of hens in these areas had chicks (Nielsen et al. 2004).

The survival of adult ptarmigan, both sexes, during summer in Hrísey was 77% on average. Most of the mortality was caused by gyrfalcon which mainly took territorial cocks in spring (Garðarsson 1988). Survival of hens is thus likely to have been higher although studies on gyrfalcons have shown that most of the ptarmigan killed on the mainland during midsummer are hens (Nielsen 2003).

During 2007 and 2008 hens were trapped and radio tagged in south-west Iceland, close to the capital of Reykjavík and monitored throughout the year. The results showed a much higher mortality of hens, nests and broods during summer than observed on Hrísey due to mammalian predation. This raises the question whether similar patterns of predation are established elsewhere. In this study the survival and reproductive success of hens during summer were measured in north-east Iceland and the results compared to the south-west. The reason for choosing the north-east is because of its importance for the ptarmigan population since it holds the highest breeding densities in Iceland (Guðmundsson 1960).

## 1.2 Age related production

The population model is based on data on ptarmigan in north-east Iceland 1981–2004 and time series analysis on the number of ptarmigan (Nielsen 1996, 1999a, b, Brynjarsdóttir et al. 2003, Nielsen et al. 2004). The full population model is described in the following equation:

$$N^t = e^{-Z_2^t} \left\{ e^{-Z_{x,w}^t} (\gamma N^{t-1} + \lambda e^{-Z_2^{t-1}} N^{t-2} - \epsilon N^{t-2}) + N^{t-1} \right\}$$

Where the year starts in May 1 and the parameters are defined as:

$N^t$  = number of birds at the end of winter in year  $t$

$N^{t-1}$  = number of birds at the end of winter in year  $t - 1$

$N^{t-2}$  = number of birds at the end of winter in year  $t - 2$

$e^{-Z_2^t}$  = yearly adult survival rate from spring in year  $t - 1$  to spring in year  $t$

$e^{-Z_{x,w}^t}$  = the excess juvenile autumn and winter mortality

$e^{-Z_2^{t-1}}$  = yearly adult survival rate from spring in year  $t - 2$  to spring in year  $t - 1$

$\gamma$  = number of female chicks in August per yearling hen divided by survival of hen during summer.

$\lambda$  = the excess number of female chicks in August produced by ad hens divided by survival of hen during summer.

$\epsilon$  = additional chick removal caused by gyrfalcon predation on hens in late summer. Orphaned chicks will perish.

In order to limit the number of parameters the two  $N^{t-2}$  terms in the equation were combined, in other words the  $\varepsilon$  parameter was included in the  $\lambda$  parameter. This gives new and simpler population model where the new expanded  $\lambda$  parameter is used:

$$N^t = e^{-Z_2^t} \left\{ e^{-Z_{x,w}^t} (\gamma N^{t-1} + \lambda e^{-Z_2^{t-1}} N^{t-2}) + N^{t-1} \right\}$$

A parameter estimation was conducted by using the time series analysis of the data from north-east Iceland. This estimation gave the value 6.8 (SE = 1.95, t = 4.9, p < 0.001) for  $\gamma$  and -3.7 (SE = 1.6, t = -2.22, p = 0.04) for  $\lambda$ . There are two outliers in the dataset for excess juvenile mortality rate and though there is no prior reason for excluding them parameter estimation was also conducted without these outliers. Removing the outliers improved the model fit and gave the values 4.2 for  $\gamma$  (SE = 0.33, t = 12.5, p < 0.001) and -2.5 for  $\lambda$  (SE = 0.60, t = -4.13, p < 0.001). A parameter estimation was done for  $\lambda = 0$  and also with constraint about the output of the second peak but neither gave a better fit than the original model and the estimation shows that the  $\lambda$  parameter has to be negative for sustained cycles (Magnússon et al. 2004).

Looking at these parameter estimations it is worth inspecting how much the values approach the truth and what they are telling us. Let us first check the  $\gamma$  parameter which is defined as:

$$\gamma = \frac{S_{Y,1}^t \beta_1^t}{S_{AD,S}^t}$$

The numerator is the number of female chicks per yearling hen in August and the denominator is the survival of hens during summer. By using the average number of 8.1 chicks per hen in August as observed in north-east Iceland during 1981–2003 (Nielsen et al. 2004), the average adult survival of 77% as observed for ptarmigan in Hrísey (Garðarsson 1988) and assuming equal sex rate among chicks a value of 5.3 is obtained. This value is lower than the value from the original model but higher than the value obtained when the outliers were excluded. When taken into account that most of the mortality on Hrísey was due to predation on cocks in spring (Garðarsson 1988) it may suggest that survival of females could be somewhat higher than used here. On the other hand Hrísey is an island without any mammalian predators but on the mainland there are both arctic fox and American mink which could reduce the survival of hens. This study will give us an estimate of the  $\gamma$  parameter based on the survival of hens on the mainland.

The original  $\lambda$  parameter is defined as:

$$\lambda = \frac{S_{Y,2}^t \beta_2^t - S_{Y,1}^t \beta_1^t}{S_{AD,S}^t}$$

The numerator is the excess number of female chicks produced by adult hens and the denominator is the survival of hens during summer. Before estimation the  $\varepsilon$  parameter was added to the  $\lambda$  parameter giving a new expanded parameter. The fact that the expanded  $\lambda$  parameter has to be negative means that the  $\varepsilon$  parameter is larger than the original  $\lambda$  parameter. In other words, chicks that vanish because their mothers die during summer are more numerous than the chicks produced by adult hens in excess to the chicks produced by

yearlings. There is no data available on age related production by ptarmigan in Iceland but this information is needed to be able to separate  $\lambda$  and  $\varepsilon$  parameters. So the second question in this study is whether adult hens are producing more chicks than yearlings.

In order to be able to answer these two study questions hens were trapped and radio tagged in north-east Iceland during spring. The birds were then monitored once a week during summer and data on survival and reproductive success as obtained and compared to data collected in the south-west.



## **2 Reproductive success and survival of hen rock ptarmigan during summer**

## 2.1 Introduction

The mechanism behind regular increase and decrease phases in animal populations have attracted a wide interest in ecology (Berryman 2002). The 10-year cycle of the snowshoe hare (*Lepus americanus*) in North-America is a well known example (Keith 1963, Krebs 1995, Krebs et al. 2001), but other species such as microtine rodents, lemmings (Lemmini), mountain hares (*Lepus timidus*), ptarmigan and woodland grouse (Tetraoninae) have all populations that fluctuate in cyclic patterns (Andreev 1988, Hansson and Henttonen 1988, Keith and Rusch 1988, Linden 1988, Newey et al. 2007). What drives the cycles probably varies between species and communities, but most cases are thought to involve trophic interactions and delayed feed-back mechanism (Kendall et al. 1999, Turchin 2003). Many populations of grouse and voles, previously cyclic, now fluctuate at a lower abundance and various potential causes have been addressed like warmer climate and increased predation by generalist predators like red foxes (*Vulpes vulpes*) and mustelids (Strann et al. 2002, Hornfeldt et al. 2005, Korpimaki et al. 2005, Ludwig et al. 2006, Ims et al. 2008, Brommer et al. 2010).

Populations of ptarmigan and woodland grouse are well represented among cyclic populations. In Fennoscandia the periodicity of grouse cycles is commonly 3–6 years (Hornfeldt 1978, Andren et al. 1985, Lindstrom et al. 1995), and the proposed mechanism is predation on eggs and chicks by generalist predators (Hagen 1952, Lack 1954). When microtines abound, predation on grouse is reduced, but when the microtines crash the generalist predators shift to grouse. This is the so-called alternative prey hypothesis where predation on alternative prey is dependent on population status of the main prey. Woodland grouses and red grouse (*Lagopus lagopus scotica*) populations have been shown to have 6–7 year periodicity (Williams 1985, Linden 1988). In Iceland and Scotland the rock ptarmigan (*Lagopus muta*) shows a 10-year cycle (Guðmundsson 1960, Nielsen and Pétursson 1995, Watson et al. 1998).

The rock ptarmigan (here after ptarmigan) is common and widely distributed in Iceland. The 10-year cycle of the population is particularly interesting as the ptarmigan is the only grouse species occurring and the dominant herbivore in upland areas, no microtines, lemmings or lagomorphs occur. Other grazers include domestic animals like sheep (*Ovis aries*) and horses (*Equus caballus*), introduced reindeer (*Rangifer tarandus*) and geese (*Anser sp.*). The gyrfalcon (*Falco rusticolus*) is a specialized ptarmigan predator and shows a delayed numerical response to changes in ptarmigan numbers and could be one of the agents driving the cycle (Nielsen 1999a). Other ptarmigan predators in Iceland are generalists of which the arctic fox (*Alopex lagopus*) is probably the most effective (Hersteinsson and Macdonald 1996).

Studies on ptarmigan were conducted on the island of Hrísey, north Iceland in 1963–1970 and showed that most of the mortality during spring and summer was due to gyrfalcon predation on territorial cocks in spring and on juveniles in late summer while hens suffered little predation (Garðarsson 1971, 1988). Nest predation was negligible and mean clutch size varied from 10.4 to 11.7 eggs. Survival of chicks was also high in all years, 7.3–9.3 chicks per hen in late July, except when bad weather in July 1966 affected chick survival yielding only 4.3 chicks per hen in late summer. This high and stable production could not be linked to the fluctuation of the population. There are no mammalian predators on Hrísey so the situation there is not typical for the whole of Iceland. Winter losses of juveniles

were higher than of adults and were divided in two periods. Early losses of juveniles, in September-October, were caused by a delayed density dependent factor and late losses, in November-April, by a density dependent factor. These winter losses of juveniles were assumed to be the demographic driver of the 10-year cycle (Garðarsson 1971, 1988).

Later studies have confirmed constant and high chick production between years and areas. Mean brood size in north-east Iceland 1981–2003 was 8.1 chicks (range 4.6–9.6) and in south-west Iceland 1995–2003 7.4 chicks (range 4.2–8.4) (Nielsen et al. 2004). The only exception being years with cold spells during late June and early July. A population model for the ptarmigan in Iceland based on demographic data from the north-east part of the country from 1981–2004 indicated that a winter mortality rate, specific for the juvenile cohort, was the primary lag effect that drove the cycle in a demographic sense. Another lag factor that emerged from the model was the negative impact of spring population size on chick production. In order to minimize the number of parameters, this factor is a combination of two others, one of which is age related chick production and the other one is additional chick removal presumably caused by gyrfalcon predation on hen in late summer (Magnússon et al. 2004). Age related chick production or hen survival during summer on the mainland has not been studied in Iceland but these factors are essential for improving the population model.

In this study the survival of hen ptarmigan and reproductive rates, were studied in two regions in Iceland. One study area was in the north-east and one in the south-west. North-east Iceland is regarded as the “heart” of the rock ptarmigan range in Iceland with large continuous breeding habitats and high densities (Guðmundsson 1960), the south-west is more peripheral breeding grounds with less extensive and more patchy breeding habitats, and generally lower densities. The population in the north-east is partly migratory where most hens leave the area in the autumn to spend the winter elsewhere within the country but the population in the south-west is sedentary. The south-west region has been closed to hunting since 2002. The following questions are addressed: what is the survival rate, reproductive rate and mortality causes of hen rock ptarmigan on mainland Iceland during the breeding season. Further do these factors differ between age groups or areas of high and moderate ptarmigan densities?

## 2.2 Methods

### 2.2.1 Study areas

There were two study areas, one in the south-west and the other in the north-east of Iceland. The south-west study area is in the hills and lava fields bordering the east side of the capital city Reykjavik and neighbouring communities, Mosfellsbær, Kópavogur, Garðabær and Hafnarfjörður (Figure 1). The vegetation in the low hills (altitude 50 m above sea level) is typical of sparsely vegetated heathland in Iceland and is grown with grasses and flowering plants and a scatter of scrubs and some extensive forestry plantations. The variation in vegetation gradually decreases as altitude increases further east until it is dominated by mosses with a scatter of grasses, sedges and flowering plants at Mosfellsheiði (altitude 300 m above sea level). The study area is a part of a larger area closed to ptarmigan hunting since 2002. Ptarmigan, both sexes, are sedentary in this region. Monitoring of cocks in spring has been conducted on two plots, Heiðmörk where a 21 year average gave 3.0 cocks/km<sup>2</sup> (range = 1.5–5.5, CV = 40%) and Úlfarsfell with a 9 year average of 3.4 cocks/km<sup>2</sup> (range = 2.5–5.0, CV = 25%). Brood counts have been done within the general study area giving a 9 year average of 7.4 chicks per hen in August (range 4.2–8.4) and 94% of the hens having chicks (Nielsen et al. 2004). Arctic fox and mink (*Neovison vison*) are found on the study area and domestic cats (*Felix domesticus*) are common in the suburban parts. Avian nest predators include the raven (*Corvus corax*) and the lesser black-backed gull (*Larus fuscus*). The gyrfalcon is a winter visitor only.

In the north-east, ptarmigan were studied at the west side of Tjörnes Peninsula, and in the valleys and hills to the south, leading up to Lake Mývatn which is 50 km inland and 300 m above sea level (Figure 2). Farm and cultivated areas are along the coast and in the valleys but most of the study area is heathland used for sheep grazing. Hummocks are prominent on the heath and the dominant plants are of the heather family (Ericaceae) and small scrubs like dwarf birch (*Betula nana*) and tea-leaved willow (*Salix phylicifolia*). Ptarmigan have been monitored on four plots within this area since 1981. On Tjörnes density was very high or 14.4 cocks/km<sup>2</sup> on average (n = 23, range = 5.8–30.8, CV = 47%). The density then decreases inland and was down to 4.4 cocks/km<sup>2</sup> (range = 0.4–11.8, CV = 65%) close to Mývatn. Brood counts in August gave 8.1 chick/hen (n = 23, range 4.6–9.6) on average and 95% of hens with chicks (Nielsen 1999b, Nielsen et al. 2004). Ptarmigan hens in the north-east study area are partly migratory, some spending the winter in the eastern part of Iceland. They start leaving their breeding grounds in late August and return in late April while the cocks spend the winter within the region (Garðarsson 1988). The gyrfalcon breeds in the area and is an important predator of ptarmigan (Nielsen 1999a). Arctic fox and mink breed within the area but the populations of these species are kept low by hunting. The domestic cat is found at farms and within the village of Húsavík. Common nest predators are raven and arctic skua (*Stercorarius parasiticus*).

### 2.2.2 Trapping, tagging and tracking

Ptarmigan hens were found by scanning with binoculars, either from a car or on foot. Once found, an attempt was made to trap the hen using a drop net. The net was 2.5 × 4.0 m in size and two persons held it up in the air by using four 6 m long fishing poles with reels. The lines (60 m) from the reels were tied to the corners of the net using swivels. During trapping the two trappers approached the hen holding up the poles and reeling out the lines

to a preferable length. Because of the slack of the lines the maximum operable distance between the two trappers was approx. 80 m. The trappers facing each other then walked sideways towards the target hen holding the net as high above the ground as possible. When the hen was underneath the net the trappers lowered it over the bird.. The hen then usually tried to fly and got tangled in the net. A third person was usually participating and giving angular aiming instructions to the trappers from a good vantage point. The wind had a great effect on trapping success as it made it harder to control the net and also the hens were more likely to fly off when the net was beating in wind. Incubating hens sit very tight and do not flush until almost touched. They were also trapped by placing a net over them.

The captured hen was placed in a bag and weighed to the nearest 10 g using a SALTER Brecknell digital scale. *Head size* was measured from the tip of the bill to the nape by using digital vernier calipers ( $\pm 0.01$  mm). *Wing length* was measured to the nearest mm as the distance between the wrist joint and the tip of the longest primary feather with wing folded and primaries flattened and extended against a ruler with a vertical stop at 0 mm (Stiles and Altshuler 2004). Two age groups were recognized: yearlings and adults; yearlings were hens hatched the previous year and adults were in their third calendar year or older. Age determination was based on the pigmentation of the primary feathers (Weeden and Watson 1967). All trapped individuals were marked with a numbered aluminium leg ring and a transmitter (11 g, model RI-2BM from Holohil Systems Ltd, Canada). The transmitter was attached by using an adjustable elastic necklace. The lifetime of the batteries was 12 months. Each transmitter was equipped with a motion-sensitive switch which doubled the transmitters pulse rate when motionless for 12 hours enabling the tracker to know in advance if a hen was alive or dead.

Location and fate of radio tagged hens in the north-east study area was monitored once a week from the day of capture in April and May until September when most of the hens had left the brood rearing areas. In the south-west study area hens were monitored weekly during spring and summer and then irregularly through winter. In this study, only data from May 1 to August 31 from both areas was used. Individuals were located using STR\_1000 Suretrack telemetry receiver from Lotek Engineering Inc., Canada. Each individual was approached on foot until seen.

In the south-west study area a total of 31 hen ptarmigan were trapped and radio tagged during February through April 2007 of which 30 (17 yearlings and 13 adults) were alive and tracked during the study period from May 1 to August 31. In 2008 a total of 6 hens (3 yearlings and 3 adults) were tracked, 3 of them were survivors from previous year and 3 were trapped in March 2008 (Table 1). In the north-east study area a total of 52 hen ptarmigan were trapped in 2009 (34 yearlings and 18 adults), and 44 hens in 2010 (37 yearlings and 7 adults). Most of the hens (90) were trapped in late April and the first 3 weeks of May. Six hens were trapped in June while incubating, 1 in 2009 and 5 in 2010. Transmitters were removed from 9 hens at the end of August and the beginning of September 2009 leaving 30 hens with transmitters of which 6 returned with active transmitters the following spring. One of them was not tracked in 2010 because of location but the others were recaptured during incubation to renew transmitters giving a total of 95 hens which were tracked in the north-east area during the two years (Table 1).

In order to minimise tagging effect a hen had to survive at least one week to be entered to the dataset. In the north-east study area 4 hens failed to do so, 3 were killed by bird and 1

was hit by a car. In June 2007 and 2009 an aeroplane was used to locate hens that had dispersed after tagging on the south-west and north-east study areas respectively.

Many studies have been carried out on the effect of radio transmitters on bird survival and breeding success, some showing negative effect (Erikstad 1979, Guthery and Lusk 2004) and others no effect (Hagen et al. 2006, Terhune et al. 2007). A study on ptarmigan in Canada showed no effect of necklace transmitter weighing 2.3% of body mass on the survival of cocks during breeding season while transmitters weighing 3.6% of the body mass had negative effect (Cotter and Gratto 1995). In Scotland a dummy necklace transmitters (2.1% of body mass) did not have effect on survival or breeding success by red grouse (Thirgood et al. 1995). It is therefore concluded that the transmitters used in this study, weighing 2.3% of the body weight, should not have negative effect and the data represent natural mortality rates.

### **2.2.3 Death causes**

Four different types of mortalities were recognized: (a) depredated by a mammal; (b) depredated by a bird; (c) depredated by an unknown predator; and (d) killed by collision. Distinction between the different causes was based on examination of the carcass and the scene.

Mammalian kills were recognized on bite marks on the carcass, if intact, and the transmitter antenna. Also when the bird had been eaten the calamus of the primaries was bitten off. In some cases the carcass had been transported to a den. Three species of mammals in Iceland are capable of killing ptarmigans, the arctic fox, mink and the domestic cat.

A kill made by a bird was identified by lots of plucked feathers at the place where the transmitter was found. Feathers included primaries, secondaries, rectrices and contour feathers all plucked from the body. Also, intestines were frequently found and sometimes the remains of the head but usually the carcass had been carried away. If skeletal remains were found the keel of the sternum had usually been bitten through. The gyrfalcon is by far the most effective bird that preys upon ptarmigans in Iceland but raven also kills ptarmigan.

The mortality type “unknown predator” was used in cases when it was not possible categorize whether a hen had been depredated by a mammal or a bird.

Some hens were found dead by fence or road and it was obvious that they had been killed colliding with vehicles or wires. Some of these carcasses were intact but others had been scavenged upon. One driver hitting ptarmigan reported the incident to the research crew.

### **2.2.4 Breeding success**

In this study six variables were used for estimating of breeding success: (a) laying rate; (b) clutch size; (c) nest success; (e) renest rate; (d) brood size at hatch; (f) brood size at fledging.

*Laying rate* is the proportion of hens alive during the breeding season that lay eggs. Hens never discovered on nest throughout the summer were considered not to have laid eggs.

Laying rate might be underestimated since hens were only checked once a week and nesting attempts could go unnoticed if the clutch was lost early and the hen did not renest or second clutch was also lost early.

*Clutch size* is the total number of eggs laid in a nest. In the north-east study area each hen was flushed from the nest once during incubation to determine the clutch size. To reduce the risk of nest abandonment this was done late in the incubation period, usually two weeks after the hen was first observed on nest. Hens were not flushed if weather conditions were harsh and in those cases egg shells and unhatched eggs left in nest after hatching were used to estimate clutch size. In the south-west study area clutch size was determined only after hatch by counting egg shells and unhatched eggs.

*Nest success* was defined as the proportion of nests started where at least one chick hatched and left the nest. This was determined by visiting the nest after hatching to search for egg shells. In case of complete nest failure an attempt was made to discover the reason. If all the eggs had been removed from the nest a raid was assumed but no attempt was made to distinguish between different nest raiders.

*Renest rate* is the proportion of hens that renest and attend a second nest if first nesting attempt was not successful.

*Brood size at hatch* is the number of chicks leaving the nest. It was considered equal to number of empty egg shell minus dead chicks in nest and only estimated for successful nest.

*Brood size at fledging* is the number of chicks/hen at the beginning of August when the chicks were 5–6 weeks old. This was done by flushing the whole family and counting the number of chicks. At this time the chicks can easily be distinguished from the hen by size and darker wings. If a radio tagged hen was accompanied with other families making it impossible to distinguish which chicks belonged to the radio tagged hen the brood count was postponed until next visit. All hens alive at the time of count were included regardless of nest success or nest attendance.

Ptarmigan hens usually abandon the nest if flushed during the egg laying period. The 2 hens flushed accidentally from nest by the researcher and subsequently abandoning their nests were excluded in all analysis of nest success and reproduction.

### **2.2.5 Statistical analysis**

All statistical analysis and graphics were done in R (R Development Core Team 2011). Generalized linear models (glm function in R) were used to model the effects of age and area on the response variable. For head and wing sizes the error structure was based on normal distribution and for laying rate, nest success and proportion of hens killed during incubation the error structure was based on binomial distribution. For clutch size and brood size at hatch the error structure was based on Poisson distribution but for brood size at fledge a glm with quasi-Poisson errors was used since Poisson produced overdispersion. For all instances both models with and without interaction term were tested. If a model with interaction was not significantly different (Chi-square test in anova) from model without interaction it was rejected and the simpler model used. For all models assumptions were checked visually by plotting (a) residual vs. predicted values, (b) normal Q-Q plot,

(c) scale-location and (d) residuals vs. leverage. For all tests the level of significance was set at  $\alpha = 0.05$ .

Weight of ptarmigan is not constant through the year (Steen and Unander 1985) and hens in this study were trapped at different time of the year, late winter in the south-west and in spring in the north-east making it impossible to compare weight of hens between areas. A plot of the weight of trapped hens (see Figure 3) shows a rather stable weight in late winter but rapid weight gaining in spring so the difference between age groups was tested separately for each area using a glm and date of tagging as a predictor. One outlier was removed from the data when testing the glm model for weight in the north-east. This particular hen was yearling and weighted much less than other at the same time (430 g while three others yearlings trapped at the same day were 510–530 g and the model predicted 554 g for yearlings at this day). It did never fly during trapping but ran away when released while all other hens flew. This hen was included in calculations of survival and breeding success.

For the survival analysis the date data was first modified by using the statistical package lubridate (Grolemund and Wickham 2011). Cox proportional hazard models were used to evaluate the difference in survival between areas and age groups, based on Kaplan-Meier survival function (Kaplan and Meier 1958) with staggered entry of individuals into the population (Pollock et al. 1989). The calculations were done with the statistical package Survival (Therneau 2011) and to check whether the data met the assumptions for Cox proportional hazards the function `cox.zph` was used. The significance of survival models was evaluated with Wald test. To calculate instantaneous hazard rate the package epiR was used (Stevenson 2011). The instantaneous hazard rate was plotted by time in order to illustrate trend and LOWESS (locally weighted scatterplot smoothing) was used to make the curve smooth. A smoothing factor of 0.65 was used which means that 65 percent of the neighbouring data was used to determine the LOWESS plotting position for each day.



## 2.3 Results

### 2.3.1 Morphology and mass

There was no statistical difference between areas or age groups with respect to head size but a significant interaction term implied that yearlings had bigger heads than adults in south-west but smaller in north-east (glm, family = normal, age:  $t = 1.30$ ,  $p = 0.20$ , area:  $t = 1.45$ ,  $p = 0.15$ , age-area interaction:  $t = -2.03$ ,  $p = 0.04$ ). A glm model without interaction showed no statistical difference between area or age groups though adults had longer wings in both areas (age:  $t = -1.82$ ,  $p = 0.07$ , area:  $t = -0.36$ ,  $p = 0.72$ , Table 2). Since there was no difference between areas in head size or wing length the data for body mass from both areas was pooled to show the trend over time (Figure 3). The mass was stable in late winter but a rapid gain in weight in May prior to egg laying was evident. There was no overlap in trapping time between the two study areas. All hens in the south-west were captured in late winter when the body mass was stable and all hens in the north-east were trapped in spring when body mass was increasing so separate glm models were built for the each area testing the influence of date of capture and age of hens on body weight. The model for hens in the south-west showed that the adult hens weighed significantly more than yearlings and date of year (in late winter) had no effect on the weight (age:  $-3.96$ ,  $p < 0.001$ , date:  $-0.64$ ,  $p = 0.53$ ) adding an interaction term did not improve the model. In the north-east a glm model with interaction term showed that yearlings weighed significantly less on arrival at the breeding grounds in late April and gained weight significantly faster than adults resulting in similar weight at the start of egg laying (Table 3).

### 2.3.2 Survival and mortality causes

The Cox-proportional hazard model using area and age as explanatory variables was significant (Wald test = 11.92,  $df = 2$ ,  $p = 0.0026$ ). Adding an interaction term between area and age did not improve the model (Anova,  $\chi^2 = 2.28$ ,  $p = 0.13$ ), so the simpler model using only area and age was used. Difference in survival between the two study areas was highly significant ( $z = -3.28$ ,  $p = 0.001$ ), it was higher in the north-east than in the south-west, 0.842 (SE = 0.039) and 0.609 (SE = 0.082) respectively for age groups pooled. Age was not statistically significant ( $z = 1.59$ ,  $p = 0.11$ ). In the north east the survival rate was 0.894 (SE = 0.0578) for adults and 0.820 (SE = 0.050) for yearlings, while in the south-west survival rates for adult and yearling hens was 0.745 (SE = 0.111) and 0.500 (SE = 0.112) respectively (Figure 4).

Predation was the only mortality cause in the south-west study area, where mammals accounted for 79%, birds 7% and unknown predators 14% (Table 4). In the north-east area both predation and collisions were important mortality factors, 43% were due to collisions, 36% mammals and 21% raptors. Collisions were mostly with cars on the main road that runs through the study area; one bird collided with a fence. In the north-east predation occurred only in June and July leaving collisions as the only mortality factor in August. All hens killed by cars nested close to roads. The average distance between nest and road for hens killed was 69 m (sd = 69,  $n = 4$ , range 5–160 m).

A graph of instantaneous hazard rate shows that hens in both areas are at greatest risk in June or during the incubation and the early brood period (Figure 5). All of the 5 mammalian kills in the north-east occurred during egg laying or incubation of which 4

were by arctic fox and all of the birds were transported to the same fox den. The average distance between the den and the nests where the hens were taken was 2.8 km (sd = 0.5, n = 3). The 5th hen was most likely killed by a domestic cat. It was nesting less than 100 m from a farm and was found dead during incubation close to nest with bite marks on neck and had been left intact and uncovered.

In the south-west, 4 of 28 hens were killed during incubation while in the north-east 5 of 88 were killed during incubation and all of them were yearlings. There was no significant difference between age groups or areas in the proportion of birds killed during incubation according to a glm model with error structure based on binomial distribution (age: z-value = -1.032, p = 0.30; area: z-value = -1.632, p = 0.10). Adding an interaction term did not improve the model.

### **2.3.3 Breeding success**

#### Laying rate

Two hens alive during egg laying were never observed on nest, one in each study area. Both were adults, paired and sedentary the whole summer. The remaining hens, 28 (14 adults and 14 yearlings) in the south-west study area and 88 (25 adults and 63 yearlings) in the north-east study area laid eggs and attended nest. This gives a laying rate of 97% in the south-west and 99% in the north-east (Table 5).

#### Clutch size

The overall mean clutch size was 10.6 eggs (Table 5). A glm model for the effect of area and age group on clutch size with Poisson error structure did not show any statistical difference (age: z = -0.56, p = 0.57; area: z = -0.27, p = 0.79). Adding an interaction term did not improve the model.

#### Nest success

The nest success for first nesting attempt was higher in the north-east than in the south-west or 84% and 57% respectively. In the south-west the nest success was identical between age groups while in the north-east all adult hens had successful nest and 78% of the yearlings. A glm model of the effect of area and age groups on nest success with binomial error structure gave statistically significant difference between areas but the difference between age groups was not statistically significant at  $\alpha = 0.05$  (area: z = -3.19, p = 0.001, age: z = -1.92, p = 0.055). In both study areas most (92% in the south-west and 86% in the north-east) nest losses were due to predation on hens and nests, but humans accidentally destroyed one nest in the south-west and two in the north-east study area.

#### Brood size at hatch

Mean brood size at hatch was 9.8 chicks (Table 5). There was no area or age related difference in mean brood size at hatch according to a glm model based on Poisson error structure (age: z value = -0.57, p = 0.57; area: z value = -0.201, p = 0.84). Adding an interaction term did not improve the model.

#### Renest rate

Of the 8 hens that lost their first nest in the south-west only 2 (25%) re-nested but in the north-east 8 (89%) of the 9 hens re-nested. Nest success for all second nesting attempts was 100%. This raises the total nest success in north-east to 93% and in south-west to 64%

### Brood size at fledging

Brood counts in early August showed that 95% of hens in the north-east and 61% of hens in the south-west had chicks. A glm model with binomial error distribution where the effect of age group and areas on the proportion of hens with chicks were tested showed only the area as factor (age:  $z$  value = 0.17,  $p$  = 0.86, area:  $z$  value = -3.44,  $p$  < 0.001). Adding an interaction term did not improve the model. There were also fewer chicks/hen in the south-west study area than on the north-east study area or 3.3 (SE = 0.7,  $n$  = 18) and 6.3 chicks/hen (SE = 0.4,  $n$  = 79) respectively (Table 5). In the north-east study area adult hens had a higher number of chicks than yearlings, 6.9 (SE = 0.7,  $n$  = 25) and 6.0 chicks/hen (SE = 0.5,  $n$  = 54) respectively, the opposite was true on the south-west study area or 4.4 (SE = 0.2,  $n$  = 9) and 2.4 chicks/hen (SE = 0.9,  $n$  = 9) for yearlings and adults respectively (Table 5). The result of a glm model with quasi-Poisson errors where the effect of area and age groups on number of chicks were tested gave only statistically significant difference between areas but not age groups or interaction between age and area (age:  $t$  value = -0.972,  $p$  = 0.33, area:  $t$  value = -3.131,  $p$  = 0.002, age-area interaction:  $t$  value = 1.641,  $p$  = 0.10).

During brood counts 22 (61%) of the 36 hens were alive on the south-west study area while 85 (89%) of 95 hens on the north-east study area. Both hens that were not observed on nest were alive at brood count. Assuming equal sex ratio among live chicks the increase in the number of hens during the breeding season can be calculated. The ratio “hens alive in August” per “hen alive in May” was calculated, where hens alive in August included both hens and female chicks. The results indicate 2.3 times greater increase in the north-east study area than in the south-west or 1.63 hens in August per hen in May in the south-west study area and 3.71 in the north-east (Table 6).

## 2.4 Discussion

This study shows that Icelandic ptarmigans generally have a large clutch size but mortality of hens and chicks was very different between the 2 study sites. The ptarmigan population in the north-east shows more similarity to the population on the island Hrísey than the south-west population regarding summer mortality of hens and chick production. The generalist mammalian predators affecting ptarmigan hens in the south-west are not causing high mortality in the north-east, although present. The reason can be either variation in the density of mammals or that hens in the south-west are for some reason more vulnerable to mammal predation. The areas are different with regard to vegetation and weather conditions, and probably also food abundance. This difference is most likely the cause of different ptarmigan densities between areas and can affect predation patterns as well, e.g. through cover for nests and chicks but most of the hens were killed during egg laying or incubation. Since hens were trapped at different time of year in different areas, comparison of body condition is impossible but similar clutch size in both areas may however indicate similar body condition prior to egg laying.

There is no data on the density of mammals in either area but there are some possible reasons which could cause higher number of predators in the south-west. (1) The north-east area is typical farmland and control of mammalian predators is more of a priority in the rural areas where farmers are raising sheep and managing eider (*Somateria mollissima*) colonies. Most sightings of mammalian predators are reported to local hunters in the rural areas. (2) The mammalian predators can be attracted to the urban areas in search of easy food resulting in higher densities in neighbouring areas (Pedersen et al. 2011). (3) Domestic cats, some of which are semi-wild, are likely to be more numerous close to urban areas. It is thus very important to estimate the density of mammals in these areas to evaluate if difference in predation pressure is causing the different mortality.

Predation by birds was low in both areas, causing loss of one hen in south-west and three in north east. The population model states that the ptarmigan population size two years earlier has a negative impact on the chick production. The reason is considered to be the gyrfalcon predation on hens during midsummer causing loss of their broods (Magnússon et al. 2004). Since gyrfalcons are not nesting in the south-west little predation was expected but not in the north east where hens are a substantial part of the gyrfalcon's diet during midsummer (Nielsen 2003). The occupancy rate of gyrfalcon's territories in 2009 and 2010 in north-east Iceland was 61.4% and 60.2% respectively which is close to the average 61.9% (sd = 7.8). The laying rate was slightly above average, 62.7% in 2009 and 60.0% in 2010 (average = 57.3%, sd = 10.9) (Nielsen 2011). Higher predation on hens in the north east would be expected according to the number of gyrfalcons but only 3 out of 95 hens were killed by gyrfalcons in 2009 and 2010. Gyrfalcon territories are scarce on Tjörnes which might be the cause of the low predation and perhaps one of the reasons for the high density of ptarmigan there.

In the north-east, collisions with cars had substantial effects on the survival while none of the hens in south-west died in collisions. The reason is likely to be due to the trapping location and the importance of collisions in the north-east is undoubtedly overestimated. All road kills happened in 2009 when hens were trapped close to the highway. In 2010 trapping was conducted further away from the road resulting in no road kills that year.

There was no difference in clutch sizes between age groups which confirms previous analysis for ptarmigan in Iceland (Magnússon et al. 2004). This is contrary to the rock ptarmigan in Svalbard where yearlings have smaller clutch sizes than adult hens. The reason is believed to be due to difference in body condition. Yearlings weigh less than adults and there is a positive correlation between clutch size and hen body weight at the start of incubation (Steen and Unander 1985). In this study we found that yearlings weigh less in late winter than adults do but gain weight more rapidly in May resulting in a similar weight at the start of egg laying. This fast gain in weight enables yearlings to lay same number of eggs as adults.

The average clutch size of 10.6 eggs is similar as previously reported from Hrísey where clutch sizes varied from 10.4 to 11.7 eggs (Garðarsson 1988). This is higher than reported for rock ptarmigan populations elsewhere: from Canada 8.7 eggs (Cotter 1999), Svalbard, adult hens 8.4 and yearlings 5.8 eggs (Steen and Unander 1985), Italian Alps 6.8 eggs (Scherini et al. 2003), Scotland 6.5 eggs (Watson et al. 1998) and Japan, 6.0 eggs (Sawa et al. 2011).

All hens in the north-east that lost their nests renested except one which had its nest destroyed by a dog. The eggs had been broken and were scattered around but a few were left in the nest causing the hen to attend it throughout the summer. It was quite opposite in the south-west where only a quarter of the hens that lost their first nest renested, all of them adults. Because of high predation in the south-west it is possible that some renesting attempts went unnoticed since hens were only checked once a week. The total nest survival in the north-east (both nesting attempts combined) was very high (93%) where all hens surviving incubation had successful nests except one. The total nest survival in the south-west (64%) is more similar to what has been found for other population of this species: Japan 61% and 75% (Sawa et al. 2011), Canada 64% (Cotter 1999), Italian Alps 50% (Scherini et al. 2003) and Svalbard 44–48% (Steen and Unander 1985).

The difference in survival of chicks between areas is striking. Brood size at hatch was the same in both areas but at fledge about five weeks later chicks/hen in the south-west were only half of what was found in the north-east. These findings contradict the result of the annual brood census conducted in these areas which shows high production and no statistically significant difference between areas (Nielsen et al. 2004). In this study 94.9% of the hens had chicks during brood count in the north-east and the average number of chicks/hen was 6.3. The annual brood census for these same years in the north east yielded 91.9% of hens with chicks and the average of 6.4 chicks/hen or almost the same values as in this study (number of hens = 223, Ó.K. Nielsen, unpublished data). On the other hand in the south-west 61.1% of the hens in this study had chicks at brood count and the average was 3.3 chicks/hen. The annual brood census for the same years in the south-west yielded 88.9% hens with chicks and an average of 6.5 chicks/hen (number of hens = 63, Ó.K. Nielsen, unpublished data). The difference in brood size between this study and the regular census is statistically significant ( $\chi^2= 4.3$ ,  $df = 1$ ,  $p = 0.04$ ). Since the annual brood census and the radio tagged hens in the south-west were both within the same area a question rises of what can cause this difference. The first question is whether different methods can cause this difference. The annual brood census is conducted by walking through habitats where the probability of finding hens is high and when detected hen and chicks are flushed and counted. One explanation could be that hens with few or no chicks are overlooked in the census since they are harder to detect as has been shown for other grouse species (Brittas and Karlbom 1990). There was no difference in brood sizes between the annual brood

census and the brood size of the tagged hens in the north-east which suggests that this method is applicable, at least within the typical range of brood sizes recorded in this study. Another possibility is negative effect of the observer in the south-west though no such effects were observed in the north-east. Thirdly, the tagged hens, though in the same area as the annual brood count, were located closer to the urban area on average, making disturbance due to humans and dogs more likely.

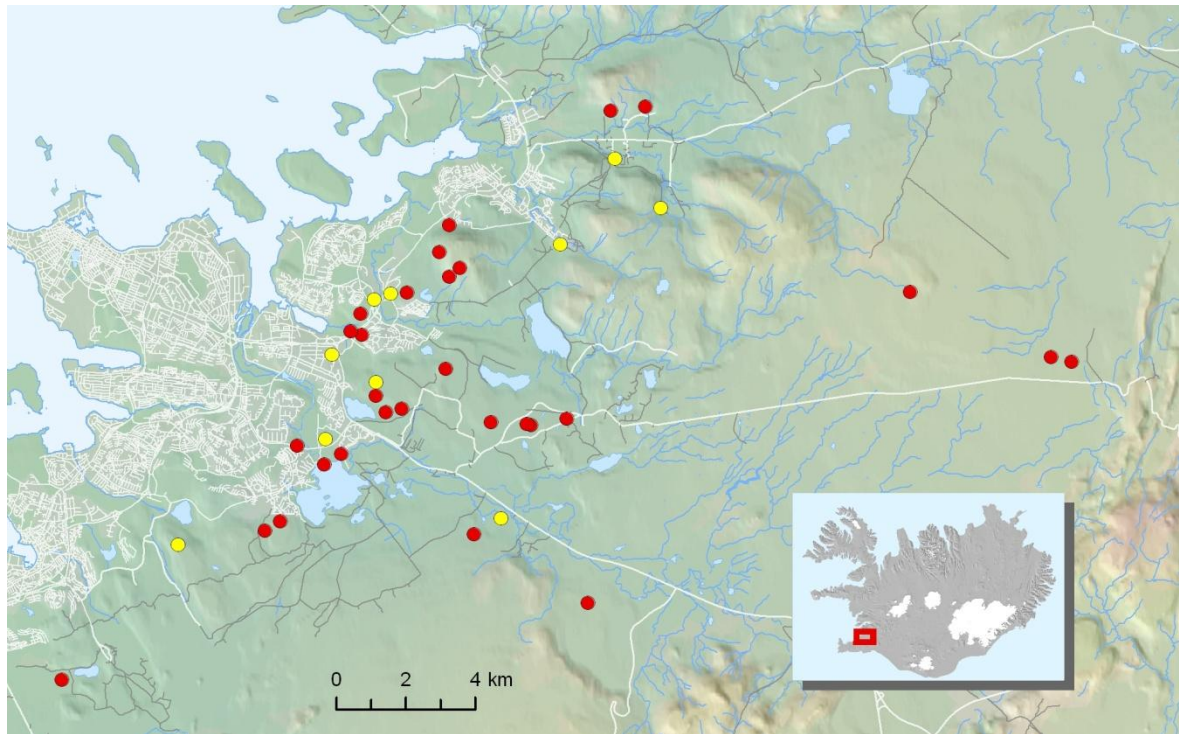
The reason for loss of chicks was not examined so it is not clear what caused higher mortality of chicks in the south-west. The hens in the south-west are suffering from higher predation than in north-east and the same might be the case with the chicks. The areas are different both in terms of vegetation and climate which can affect the survival of chicks. Further being close to urban area there are more disturbance in the south-west due to humans and dogs.

Another thing of interest is difference in brood survival between hen age groups in the south-west. A priori one would think that older and more experienced hens would be more successful in raising chicks as in the north-east where adult hens had higher number of chicks in August. In the south-west the opposite was recorded and yearlings were producing more chicks. Because of small sample size this was not statistically significant but needs further investigation. Perhaps the high predation pressure in the south-west is selecting for hens that take less risk in defending broods and such hens due to disproportional survival, thus becoming more prevalent in the adult cohort compared with the juvenile cohort.

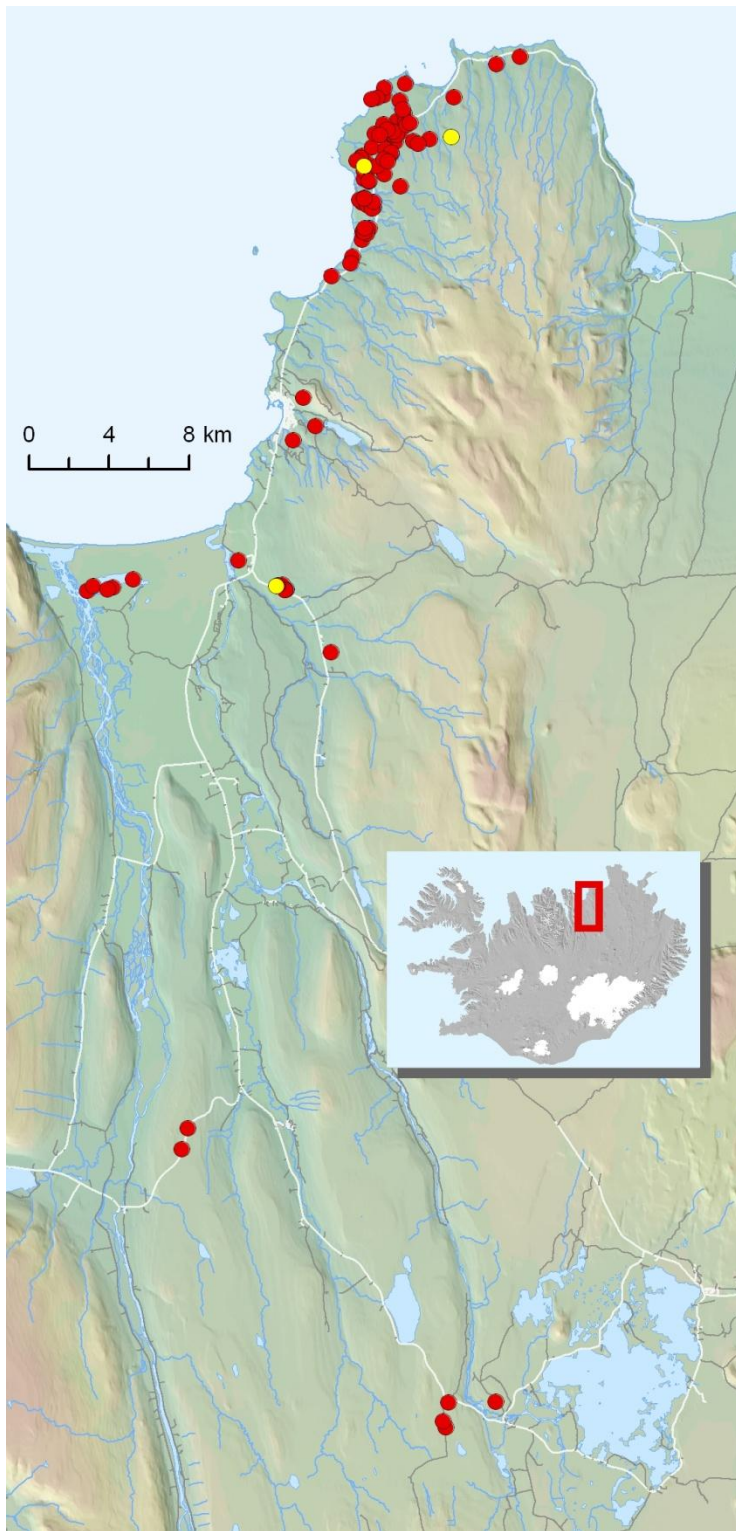
#### **2.4.1 Conclusion**

The 2.3-times higher production in the north-east was driven by much higher predation by generalist mammalian predators on hens and smaller brood size in the south-west area. The reason for higher predation by mammals in the south-west is not clear and needs further investigation. There was no difference between age groups regarding to survival or reproductive rates.

## 2.5 Figures

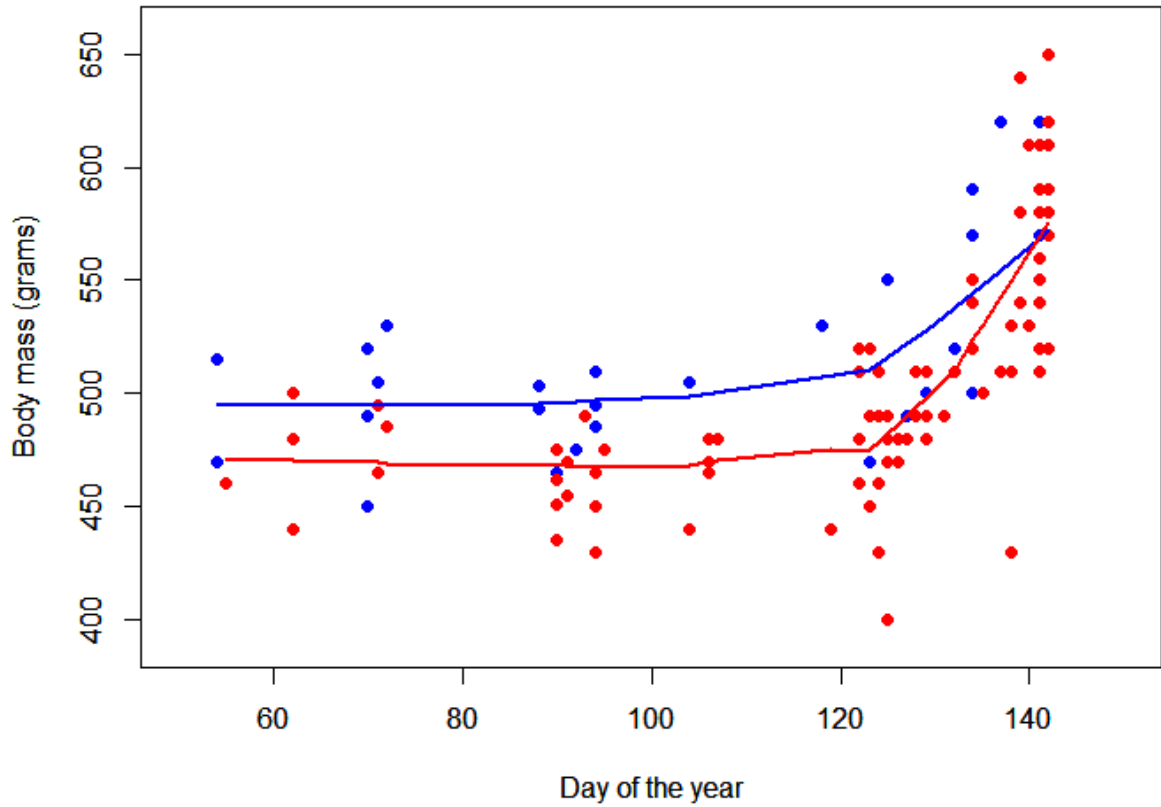


*Figure 1. Rock ptarmigan study area in south-west Iceland, 2007 and 2008. Red dots are nest sites of radio tagged hens and a place where non nesting hen stayed during summer. Yellow dots are the place of death for hens killed before nesting.*



*Figure 2. Rock ptarmigan study area in north-east Iceland, 2009 and 2010. Red dots are nest sites of radio tagged hens and a place where non nesting hen stayed during summer. Yellow dots are the place of death for hens killed before nesting.*





*Figure 3. Body mass of hen rock ptarmigan trapped in Iceland during 2007 through 2010. Blue are adults and red yearlings. Dots are individual measurements but the lines show the time trend. The lines are made by lowess (a none parametric curve fitter).*

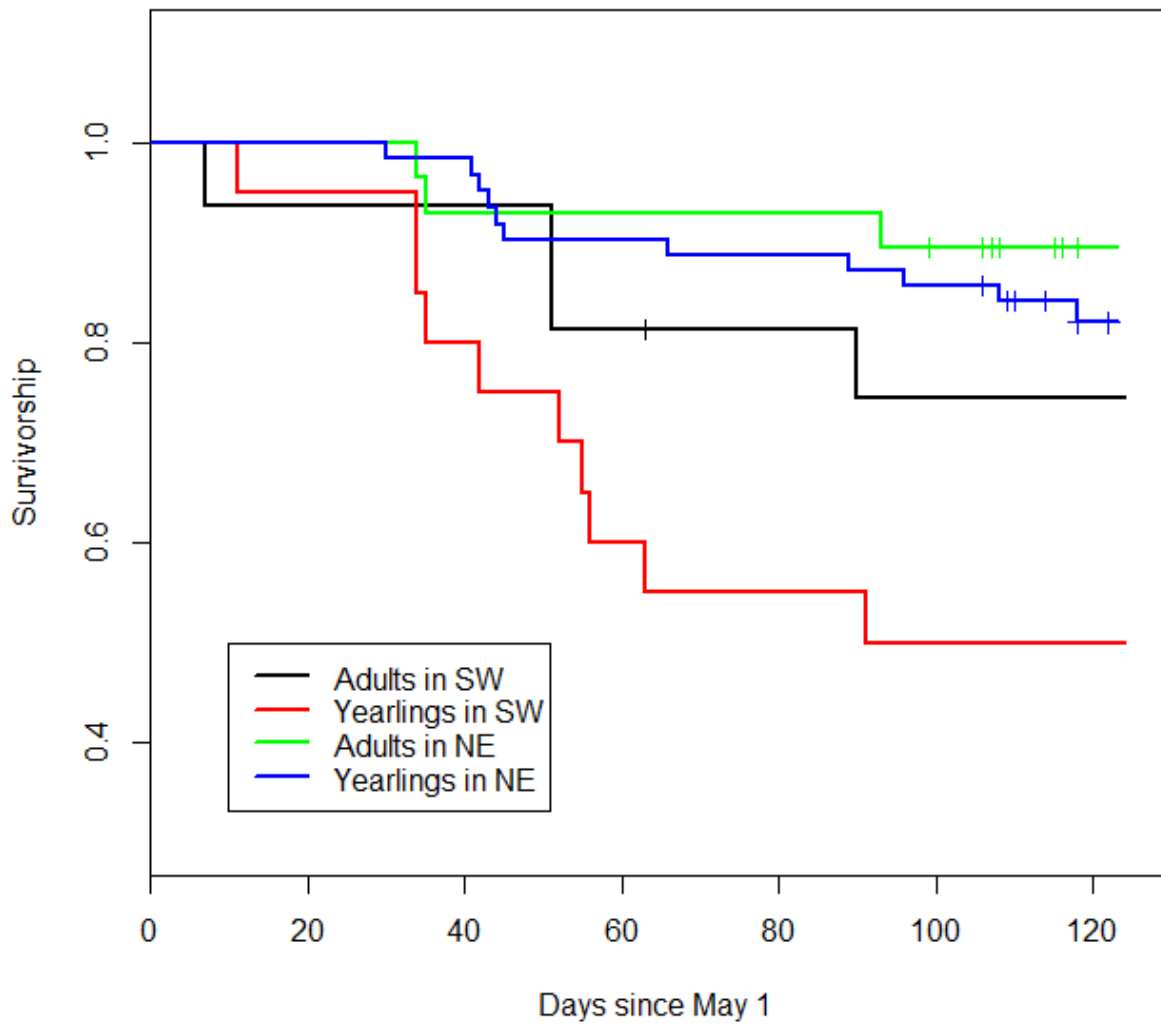
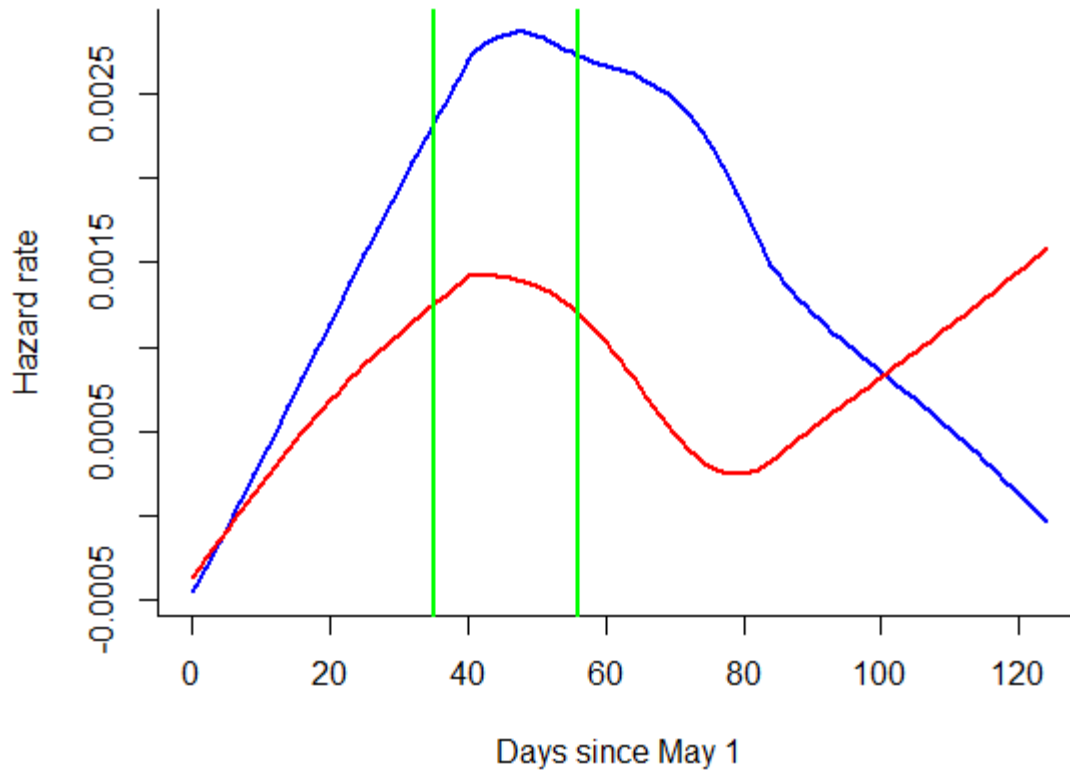


Figure 4. Kaplan-Meier survivor function of hen rock ptarmigan in Iceland from May through August. Black line are adults and red line yearlings in the south-west study area, 2007 and 2008 while green line are adults and blue line yearlings in the north-east study area, 2009 and 2010.



*Figure 5. Instantaneous hazard rate/day for hen rock ptarmigan in south-west (blue) and north-east (red) Iceland during 2007–2010. The lines have been smoothed by lowess smoothing factor  $f = 0.65$ . The green horizontal lines bracket the incubation period, the 1<sup>st</sup> line shows mean start of incubation and the 2<sup>nd</sup> mean time of hatch.*

## 2.6 Tables

*Table 1. Number and age of rock ptarmigan hens used in survival analysis in south-west and north-east Iceland 2007–2010.*

<i>Area</i>	<i>Year</i>	<i>Adults</i>	<i>Yearlings</i>	<i>Total</i>
South-west	2007	13	17	30
	2008	3	3	6
	Total	16	20	36
North-east	2009	18	31	49
	2010	11	35	46
	Total	29	66	95

*Table 2. Mean head size and wing length of rock ptarmigan hens trapped in south-west and north-east Iceland 2007–2010. SE is standard error of the mean and n is sample size.*

<i>Variable</i>	<i>Area</i>	<i>Adults</i>	<i>Yearlings</i>
		mean $\pm$ SE (n)	mean $\pm$ SE (n)
Head size (mm)	NE	52.03 $\pm$ 0.29 (25)	51,56 $\pm$ 0.13 (70)
	SW	51.48 $\pm$ 0.26 (16)	52,03 $\pm$ 0.19 (24)
Wing length (mm)	NE	191.4 $\pm$ 0.7 (25)	190.5 $\pm$ 0.5 (66)
	SW	192.3 $\pm$ 0.9 (16)	190.3 $\pm$ 0.7 (24)

Table 3. The results of a generalized linear model where time of year and age were used to explain weight gain in spring by hen rock ptarmigan in north-east Iceland. The data is from April 29 to May 23 in 2009 and 2010.

	Estimate	t	P
Adults weight at April 29 (g)	487	35.0	< 0.001 ***
Adults weight gain/day	3.6	4.1	< 0.001 ***
Yearlings difference in weight at April 29 (g)	-47	-2.9	0.001 **
Yearlings difference in weight gain/day	2.1	2.0	0.05 *

Table 4. The mortality factors affecting hen rock ptarmigan in May through August in south-west Iceland 2007 and 2008 and north-east Iceland 2009 and 2010. Given is the number of hens that died during the tracking period, from 1<sup>st</sup> of May through August and in parentheses is percentage.

Mortality factor	South-west study area			North-east study area		
	Adult	Yearling	Total	Adult	Yearling	Total
Mammal predation	3 (75%)	8 (80%)	11 (79%)	0 (0%)	5 (45%)	5 (36%)
Bird predation	0 (0%)	1 (10%)	1 (7%)	2 (67%)	1 (9%)	3 (21%)
Unknown predator	1 (25%)	1 (10%)	2 (14%)	0 (0%)	0 (0%)	0 (0%)
Collision	0 (0%)	0 (0%)	0 (0%)	1 (33%)	5 (45%)	6 (43%)

*Table 5. Breeding success of hen rock ptarmigan in two study areas in Iceland, south-west 2007 and 2008 and north-east 2009 and 2010. Data is presented as mean  $\pm$  SE or percentage and the sample size in parenthesis.*

	South-west study area			North-east study area		
	Adult	Yearling	Total	Adult	Yearling	Total
Laying rate	93% (15)	100% (14)	97% (29)	96% (26)	100% (63)	99% (89)
Clutch size	11.0 $\pm$ 0.4 (8)	9.9 $\pm$ 0.5 (7)	10.5 $\pm$ 0.3 (15)	10.8 $\pm$ 0.3 (25)	10.6 $\pm$ 0.2 (50)	10.6 $\pm$ 0.2 (75)
Nest success	57% (14)	57% (14)	57% (28)	100% (25)	78% (63)	84% (88)
Renest rate	50% (4)	0% (4)	25% (8)	-	89% (9)	89% (9)
Brood size at hatching	10.5 $\pm$ 0.4 (8)	8.7 $\pm$ 0.6 (6)	9.7 $\pm$ 0.4 (14)	9.9 $\pm$ 0.4 (25)	9.8 $\pm$ 0.3 (45)	9.8 $\pm$ 0.3 (70)
Brood size at fledging	2.4 $\pm$ 0.9 (9)	4.2 $\pm$ 1.2 (9)	3.3 $\pm$ 0.7 (18)	6.9 $\pm$ 0.7 (25)	6.0 $\pm$ 0.5 (54)	6.3 $\pm$ 0.4 (79)

*Table 6. The production of rock ptarmigan in two study areas in Iceland. The data in the south-west is from 2007 and 2008 and in north-east from 2009 and 2010. The calculated number of hens in August per hen in May is based on assumed equal sex ratio among the chicks and includes both adult hens alive and estimated number of female offspring.*

<i>Study area</i>	<i>Number of hens in May</i>	<i>Number of hens alive at brood count in August</i>	<i>Average brood size</i>	<i>Number of hens in August per hen in May</i>
South-west	36	22	3.3	1.63
North-east	95	85	6.3	3.71

### 3 General discussion

The first question was whether generalist mammalian predators could be causing the dampening of the population cycles of the ptarmigan. The high predation by mammals in the south-west indicates this possibility but the low predation pressure in the north-east does not support it. For the rest of the country there is no information on predation making it difficult to answer this question with certainty. Although predation was the main proximate cause of variation in survival between the study areas it cannot be excluded that predation is ultimately driven by unknown factors like vegetation structure or supply of other prey than ptarmigans rather than predator density. Estimates of predation and density of mammals from more sites are needed to validate this.

The second question had to do with the population model and parameter estimation. Let us first look at the  $\gamma$  parameter and use data from the north-east. In the north-east yearlings had 6.0 chicks on the average and the survival was 0.842 which gives the value for  $\gamma$  as 3.6 which is much lower than the estimation using the original model ( $\gamma = 6.8$ ) but only a little lower than obtained using the original model without outliers ( $\gamma = 4.2$ ). This supports the removal of the outliers from the model evaluation. Further the  $\gamma$  parameter, calculated from data obtained in the south-west has similar value or 3.4 (4.1 chicks/yearling and survival rate of 0.609) as in north-east giving support for the estimation of  $\gamma$  in the population model.

The  $\lambda$  parameter is more complicated as the extended parameter was estimated i.e. combination of the original  $\lambda$  parameter and the  $\varepsilon$  parameter. The original  $\lambda$  is the excess chicks produced by adult hens divided by survival and this study shows no statistical difference in chick production between age groups. This means the original  $\lambda$  is zero which leaves only the  $\varepsilon$  part in the extended parameter. The parameter estimation for the extended  $\lambda$  was then only estimating  $\varepsilon$  which has been explained as the additional chick removal caused by gyrfalcon predation on hens in late summer. The estimation for  $\lambda$  gave the value of -3.7 for original model and -2.5 when outliers had been removed. These are quite high negative values compared to the  $\gamma$  parameter which indicates high loss of chicks due to gyrfalcons preying on ptarmigan hens. The result from this study does not support this since only one hen in the south-west and three in north-east were killed by gyrfalcons. Perhaps hens in these study areas are less vulnerable to gyrfalcon predation than in Iceland in general. There are no gyrfalcons nesting close to the south-west area and in the north-east most hens were at Tjörnes where density of nesting gyrfalcons is low.

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