



**The wood mouse *Apodemus sylvaticus* in  
Iceland: population dynamics and limiting  
factors at the northern edge of the species'  
range**

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May 2014**



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Thesis submitted in partial fulfilment of a  
*Philosophiae Doctor* degree in Biology

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The wood mouse *Apodemus sylvaticus* in Iceland: population dynamics and limiting factors at the northern edge of the species' range

Short title: Limiting factors of the wood mouse

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# Abstract

The wood mouse is a suitable model species for studying potential limiting factors and population ecology at an edge of the distributional range. The species arrived in Iceland with the settlers during the 10<sup>th</sup> century but Iceland is north of the natural range of the species. No other rodent is found so widely in the wild. The species is found in vegetated areas all around Iceland and on some surrounding islands.

The aim of this research was to uncover the forces that act on population dynamics and demography of the Icelandic wood mouse population. For this purpose CMR surveys were conducted with regular five day censuses for three years in 2001 – 2003 and 2004 – 2005, of which the last year was in two contrasting habitats: grassland and woodland, both located in southwest Iceland. Live-trapping data from annual autumn surveys at the grassland since 1996 was also used for this project. In addition, mice were caught in snap-traps for autopsy, in order to estimate food composition from stomach contents and detect breeding activity by status of reproductive organs.

This study revealed strong evidence of density-independent control of the wood mouse population in the grassland where early winter temperature explained 74% of the variation of the autumn population density. At the woodland site, however, density-dependent factors were believed to act on the population as is the case near the centre of the species' range.

Wood mouse populations of both habitats fluctuated seasonally with a typical peak in abundance in autumn and low numbers in spring. The autumn population density at the grassland site was far lower than has been recorded elsewhere (3-8 mice/ha) but at the woodland site population density was around 25-30 mice/ha, resembling studies in other countries. Apparent monthly overwintering survival was stable around 60% at the woodland site but fluctuated between 40% and 80% with temperature during the early winter at the grassland site.

Food varied more by season than by habitat and in general, mice fed predominantly on seeds. Mice from the grassland were more likely than the woodland mice to feed on grass or other green material but such items were not found in stomachs from the woodland mice. Insects and other animal matter were eaten in large numbers during the spring in both habitats. Woodland mice appeared to have depleted the seed availability earlier in the spring than the grassland mice but began to feed on seeds before the grassland mice did in the summer. No selection for certain types of seed or animal matter was detected by stomach content analysis.

Mice of both habitats gained body mass during the winter and males were heavier than females in all periods. Woodland mice of both sexes were significantly heavier than the grassland mice in mid-winter, suggesting that the woodland mice were in somewhat

better condition than the grassland mice. According to the results of this comparative study the woodland seems a better habitat for wood mice than the grassland. Population density was manifold higher, monthly survival rate was stable and did not fluctuate with temperature, body mass was higher and food was most likely of a better quality. All these factors are important for sustaining a viable population.

During spring and early summer, low trapability resulted in small sample sizes and problems with population estimates and other statistical analysis. In the autumn, all generations were easily trapped and sample sizes were sufficient for age- and/or habitat-specific analysis.

The autumn trapped population (September and October) could be divided into four age groups, based on body mass and pelage colour. The largest mice (>23g) were regarded as overwintering (one year old) but individuals of both sexes in this oldest group disappeared from the population in October. The youngest group, weighing less than 17g in the autumn was assumed to be of the last born cohort of the summer. The first generation of the summer, born in May, was believed to be weighing 20-23g in the autumn and those individuals most likely managed to breed at least once in the summer of their own birth. The mid-cohort of the summer, weighing 17-20g in the autumn could also have become mature and possibly bred in the summer of their birth. The three summer born cohorts all gained weight throughout the winter and the females grew up to body mass of 25g before the onset of breeding in the spring. It appears that the females of the grassland have adopted a strategy in terms of maximizing their reproductive output with a trade-off between growth and breeding. Therefore, it appears that females cease growth when breeding and only gain weight during the non-breeding season which takes place during the toughest period of the year. Thus, females probably never reach the males in size.

As the population estimates rely on trap data, which is difficult to obtain during periods of low trapability, we developed a novel method to address this problem. We used the body mass data on autumn trapped mice, with a Bayesian approach, to reconstruct the population estimates during the summer. It made it possible to detect summer recruitment 100 days earlier than traditional population estimates could. This study suggests that it is possible to use body mass to estimate age. And that Bayesian analysis can be conducted on short lived small mammals. This study shows that live-trapping data obtained during periods of peak density can be a useful aid when describing population parameters of the previous months when sample sizes are too low for direct measurements. This is important for ethical reasons and when studying populations of rare and endangered species.

# Ágrip

Hagamúsinn er kjörin til rannsókna á takmarkandi þáttum og stofnvistfræði á nyrstu mörkum útbreiðslu. Hagamúsinn barst til Íslands með fyrstu mönnum á 10. öld en landið liggur norðar en náttúruleg mörk tegundarinnar. Engin önnur nagdýr lifa í villtri náttúru landsins og er hagamúsinn útbreidd á grónum svæðum um allt land og eyjum umhverfis landið.

Markmið rannsóknarinnar var að kanna hvaða þættir hafa áhrif á stofnvistfræði íslensku hagamúsarinnar. Í þeim tilgangi voru mýs veiddar, merktar og endurveiddar í reglubundum fimm daga veiðilotum í þrjú ár: 2001-2003 og 2004-2005. Síðasttalda árið var veitt jafnhliða á tveimur ólíkum búsvæðum: túnnum á Kjalarnesi og blönduðum laufskógi að Mógilsá, bæði á suðvesturlandi. Jafnframt var notast við niðurstöður árlegra haustveiða á Kjalarnesi frá árinu 1996. Einnig voru hagamýs veiddar í felligildrum og krufðar til að meta fæðuval með greiningu á magainnihaldi, og áætla tímgunarstöðu og frjósemi.

Rannsókn þessi leiddi í ljós sterkar vísbendingar um að stjórnun á hagamúsastofninum á Kjalarnesi væri óháð þéttleika, því að hitastig í upphafi vetrar réði mestu (74%) um stofnstærð næsta hausts. Í skóglendinu að Mógilsá voru hins vegar þéttleikaháðir þættir líklegri til að ráða stofnstærð hagamúsa eins og þekkt er á svæðum nær miðju útbreiðslusvæðis tegundarinnar.

Á báðum svæðum voru árstíðabundnar sveiflur í stofnstærð með háum þéttleika að haustlagi en lágum að vori. Haustþéttleiki á túnnum Kjalarness var með því lægsta sem mælt hefur (3-8 mýs/ha) en í skóglendinu var þéttleikinn um 25-30 mýs sem er svipað og þekktist erlendis. Áætlaðar lífslíkur yfir veturinn voru að jafnaði 60% á mánuði í skóglendinu en sveifluðust (40-80%) í takt við hitastig á Kjalarnesi.

Að jafnaði var meiri munur á fæðu milli árstíma en milli svæða og í heildina voru fræ aðalfæða músanna. Mýsnar á túnunum voru líklegri til að innbyrða gras og græna plöntuhluta en slíkt sást ekki í mögum músa úr skóglendinu. Skordýr og aðrir hryggleysingjar voru étin í miklum mæli á vorin á báðum svæðunum. Svo virtist sem skógarmýsnar yrðu fyrir uppiskroppa með fræ að vori en mýsnar á túnunum en jafnframt fyrri til að éta fræ aftur um sumarið. Út frá greiningu magainnihalds var ekki unnt að sýna fram á að mýsnar veldu sér ákveðna fæðu umfram aðra.

Mýs á báðum svæðum juku þyngd sína yfir veturinn og karlmýs voru þyngri en kvenmýs á öllum tímabilum. Mýs af báðum kynjum voru marktækt þyngri í skóginum en á túnnum um miðjan veturinn. Þetta bendir til þess að skógarmýsnar hafi verið í betra líkamsástandi en mýsnar á túnunum. Samkvæmt niðurstöðum á samanburði þessara tveggja búsvæða er skóglendið langtum hagstæðara fyrir hagamýs en túnin á Kjalarnesi. Þar er þéttleikinn

mun hærri, lífslíkur óháðar veðri og stöðugar, hærri líkamsþyngd og hugsanlega betri fæða. Allt eru þetta þættir sem skipta máli fyrir afkomu músanna.

Á vorin og snemmsumars reyndist afar erfitt að veiða nógu margar mús til að geta metið stofnstærð eða fyrir aðra tölfræðilega úrvinnslu. Um haustið veiddist hins vegar vel af músum á öllum aldri og hægt var að greina gögnin og gera ýmsa útreikninga eftir aldri og búsvæðum músanna.

Haustafli músa á Kjalarnesi (september og október) skiptist í fjóra aldurshópa, eftir þyngd og útliti. Þær þyngstu (>23g) voru líklega veturgamlar mús af báðum kynjum, og hurfu úr stofninum í október. Þær yngstu vógu undir 17g um haustið og voru taldar vera af síðustu kynslóðinni sem fæddist það sumarið. Fyrsta kynslóð sumarsins var talin vera þær mús sem vógu 20-23g um haustið og náðu líklega að tímgast a.m.k. einu sinni sama sumarið og þær fæddust. Þær sem vógu milli 17 og 20g um haustið voru taldar fæddar um mitt sumarið og líklega náðu sumar þeirra einnig að tímgast fyrir veturinn. Mús úr þessum þremur þyngdarhópum juku þyngd sína yfir veturinn og náðu kvenmýsnar sem lifðu veturinn svipaðri þyngd, um 25g, áður en tímgun hófst um vorið. Svo virðist sem kvendýrin á þessu svæði hafi þróað með sér leið til að hámarka tímgunargetu sína: að vaxa á veturna og tímgast á sumrin. Þær eru því að þyngjast yfir erfiðasta tíma ársins og ná aldrei körlunum í þyngd.

Þar sem stofnmatið er byggt á veiðigögnum sem svo erfitt reynist að ná þegar stofninn er lítill að vori voru notuð gögn um líkamsþyngd haustmúsa til að meta aldur þeirra og endurreikna stofnstærðina aftur í tímann með Bayesískri nálgun. Með þessari leið tókst að sýna fram á stofnvöxt um 100 dögum fyrr en með hefðbundnum stofnvistfræðilegum aðferðum sem við höfðum áður beitt.

Þessi rannsókn hefur sýnt fram á að hægt er að nota þyngd til að áætla aldur nagdýra út frá vaxtarkúrfum. Jafnframt að Bayesískar aðferðir duga til að áætla stofna smárna og skammlífra nagdýra sem veidd eru í lífgildirur. Þessar niðurstöður koma að miklu gagni við stofnmat og eru ekki síður áhugaverðar í ljósi verndunarsjónarmiða og þegar unnið er með fágætar tegundir.



*Dedication*

*This thesis is dedicated to my dear supervisor, friend and mentor,  
Professor Páll Hersteinsson (1951-2011). Who, with bright and optimistic (and endless)  
ideas, encouraged me to make an effort and shed some light on the basic question:*

*“How did this little mouse manage to deal with all the challenges faced to survive in  
Iceland, far north of the species range?”*

*- Well Páll, I did my best....*

# List of publications

This thesis is based on the following papers. Within the thesis, references to these papers will be by their Romanic numerals.

- **Paper I:** Unnsteinsdottir, E. R. and Hersteinsson, P. (2009). Surviving north of the natural range: the importance of density independence in determining population size. *Journal of Zoology*, **277**: 232–240.
- **Paper II:** Unnsteinsdottir, E. R. and Hersteinsson, P. (2011). Effects of contrasting habitats on population parameters and diet of *Apodemus sylvaticus* (Rodentia) in south-western Iceland. *Mammalia*, **75**: 13-21.
- **Paper III:** Unnsteinsdottir, E. R., Hersteinsson, P., Jonasson, J. P. and McAdam, B. J. (2014). Using Bayesian growth models to reconstruct small-mammal populations during low-trapping periods. *Journal of Zoology*, **292**: 206–211.

# Presentations of results from this study in international conferences

- E.R. Unnsteinsdóttir, J.P. Jonasson, B.J. McAdam & P. Hersteinsson† (2012). The use of autumn trapping data in determining summer populations and recruitment of *Apodemus sylvaticus*. The 13th International Conference on Rodent Biology (*Rodens et Spatium*). Rovaniemi (Finland) 16–20 July 2012. Poster (Abstract), p. 42.
- Ester Rut Unnsteinsdóttir & Páll Hersteinsson (2009). Effects of contrasting habitats on various population parameters of wood mice (*Apodemus sylvaticus*) in Iceland. Afmælisráðstefna Líffræðifélags Íslands. Reykjavík, 6–7 November 2009. Poster (Abstract), p. 151.
- Ester Rut Unnsteinsdóttir & Páll Hersteinsson (2008). The wood mouse (*Apodemus sylvaticus*) in treeless Iceland: Surviving north of the natural distribution range. The 11th International Conference on Rodent Biology (*Rodens et Spatium*). Myshkin (Russia) 24–28 July 2008. Oral presentation (Abstract).
- Ester Rut Unnsteinsdóttir (2008). Seasonal fluctuations in population ecology of wood mice in two contrasting habitats of SW-Iceland. Natural Science Symposium (Raunvísindadagur), Reykjavík 14–15 March 2008. Oral presentation (Abstract, in Icelandic).
- Unnsteinsdóttir E.R. & P. Hersteinsson (2003): Weight changes in *Apodemus sylvaticus* with seasons in Iceland. 4th European Vertebrate Pest Conference, Parma, Italy, 9-12 September 2003. Oral presentation (Abstract), p. 110.



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# 1 Introduction

*Apodemus sylvaticus* is a widely distributed small Eurasian rodent, commonly found in mainland European woodlands and thus referred to as *the wood mouse*. This study, however, focuses on population ecology of the species in a barren peninsula in south-western Iceland. On an isolated island in the North Atlantic, currently almost treeless, Icelandic nature has fostered this mouse for over 1100 years in atypical surroundings. In the following thesis, aspects of the demography and habitat ecology of the wood mouse in Iceland, north of the natural range, are addressed. The thesis takes the form of synopsis, complemented by three peer reviewed papers published in scientific journals and additional material that can become useful for future studies.

## 1.1 Species distributional range

Wallace (1902; in: Whittaker 2001) looked into distributional patterns of species of the earth and divided various regions according to them with lines. This is one of the earliest attempts to explain geographical distribution and limitations of species. One of these lines is the well-known „Wallace line“ south of New Guinea, marking distributional ranges of mammal species in the area. Often the reasons for the distributional limits are obvious, geographical barriers such as mountains, oceans and large rivers. In other cases, limits are less apparent (e.g. Brown & Lomolino 1998; Rosenzweig 2000; Whittaker 2001).

## 1.2 Northern populations

Species diversity is negatively associated with latitude (Rosenzweig 2000) partly due to the relationship between ecosystem productivity and plant growth season length. That is, at higher latitudes, the more unpredictable and harsh the climate becomes (e.g. Meiri & Dayan 2003). Northern regions indeed encounter strong fluctuations in climate. These areas are subject to substantial seasonality in temperature, daylight and productivity, which all play a role in limiting the distributional ranges of animals (e.g. Krebs 1994; Rosenzweig 2000). Temporal patterns in geophysical processes such as the ice ages, which are more pronounced at northern latitudes have been claimed to contribute to species richness patterns, through the age of ecological communities which may be less saturated than further south (see e.g. Ólafsdóttir et al. 2007).

Large scale weather systems of North Atlantic oceans have been described with The North Atlantic Oscillation (NAO). This index is based on the difference between sea level

pressure (SLP) in Iceland and the Azores (e.g. Hurrell 1995). The index values show large fluctuations in SLP, causing irregularities in temperature, precipitation and wind strength. Ecological impacts of these fluctuations have become apparent over the last decade or so (e.g. Post et al. 1999; Mysterud et al. 2001; Stenseth et al. 2002). Those who conduct studies on a smaller scale in time and space should thus be aware of the large and long-term impact such weather systems can have on local weather parameters.

About 150 years ago, Carl Bergmann suggested that warm blooded animals would be larger in northern areas than more southern individuals of the same species. This has been referred to as “the Bergmann’s rule” (Bergmann 1847; In: McNab 1971). In a review article with data from 94 bird- and 149 mammal species it was shown that 72% of the bird and 65% of the mammal species followed Bergmann’s rule (Meiri & Dayan 2003). In some studies, other factors such as prey size (Erlinge 1987) and precipitation (Yom-Tov & Geffen 2006) were shown to have significant effect on body size so that species did not follow the Bergmanns rule. In a more recent study, it was suggested that the geographical range of species, as well as availability and distribution of key resources such as food would play a significant role in determining body size of carnivores (Meiri, et al. 2007).

### **1.3 Islands**

Climate on islands tends to be dynamic in time and space so that organisms inhabiting islands have to have good adaptation ability (Whittaker 2001). As islands are unique and variable (MacArthur & Wilson 2001) different selective forces can be expected amongst species that manage to settle on islands. Indeed, populations that have become resident in isolated areas such as islands have been shown to differ from mainland populations of the same species. This dissimilarity has been termed *the island syndrome* and is reflected in larger body size, higher density and better survival but less reproductive output, low aggression and reduced dispersal (Adler & Levins 1994; Goltsman et al. 2005). Angerbjörn (1986) compared the body size of *Apodemus* populations from island populations in Europe. His results were that weather factors were irrelevant for body size of the island populations. Furthermore, larger body size could not be explained by island size and the distance from mainland did not affect body size in general but a trend was detected on the British Isles. However, he suggested that the body size of these species was mainly affected by intraspecific competition for food and/or predation pressure (Angerbjörn 1986).

## **1.4 Islands as natural experiments**

Islands have for long been subjects of work in the field of evolutionary biology and ecology. They are often referred to as “living laboratories” with ecosystems that reflect an evolutionary history which has been isolated in time and space. Examples such as the Juan Fernandez Islands off Chile, Galápagos, Krakatau and Hawaii are well known (e.g. Whittaker 2001). Geographically isolated terrestrial areas are not really islands but can be referred to as “habitat islands”, and are also useful in evolutionary studies (e.g. Drake et al. 2002; Ólafsdóttir et al. 2007). In addition, island models are suitable when studying changes and determining factors in closed populations since immigration and emigration is often negligible (e.g. Armstrong et al. 2002; Drake et al. 2002). Thus, population studies on islands can be seen as “natural experiments” where factors, such as interactions with other species, immigration and emigration have been removed. On the other hand, island ecosystems are often vulnerable with weak resilience to species introductions. Many examples are of introduced animals and diseases which have caused large problems for local fauna and flora, with costly management efforts (e.g. Howald et al. 2007; Wanless et al. 2007).



## 2 The model species

The wood mouse (*Apodemus sylvaticus* Linnaeus 1758) belongs to the mouse family (Muridae), the largest family of mammals, and the genus *Apodemus*. There are 10 species of *Apodemus* but only two of them are found in Northern Europe: the wood mouse and the yellow-necked mouse (*A. flavicollis* Melchior 1834; Corbet & Southern 1977).

The wood mouse is a relatively small rodent (adults weighing 20-30g) with big ears and eyes, brownish pelage on the dorsal site and whitish on the ventral site. Young and juveniles are evenly greyish until 5-9 weeks of age (Corbet & Southern 1977). The body length ranges from 95-106 mm and varies by location (Angerbjörn 1986) and the tail is a little shorter than the body. The wood mouse is distributed throughout most of continental Europe, from the Mediterranean Sea in the south to southern Scandinavia in the north and from the Iberian Peninsula in the west to western Asia in the east (Figure 1). It is also found throughout the British Isles and has been introduced by man in northern Africa and Iceland (Corbet & Southern 1977, Mitchell-Jones et al. 1999).

The wood mouse has a more southern distribution in Scandinavia than the yellow necked mouse (Angelstam et al. 1987). In contrast, the wood mouse is widely distributed in the British Isles and Ireland but the yellow necked mouse has a more southern distribution. Furthermore, the wood mouse in Great Britain is more commonly found in open areas than the yellow necked mouse (Mitchell-Jones et al. 1999). The geographical distribution of *Apodemus* in Scandinavia was studied in the late 1980's. In explaining distribution range large tree seeds turned out to be important for *A. flavicollis* but for *A. sylvaticus* the distribution of small seed forming shrubs was more important (Angelstam et al. 1987). Morphologically these two species look very similar but the yellow necked mouse has a yellowish spot on the neck that is lacking on the wood mouse (Corbet & Southern 1977). The former species is also a little larger, especially where the two species coexist (Angerbjörn 1986).

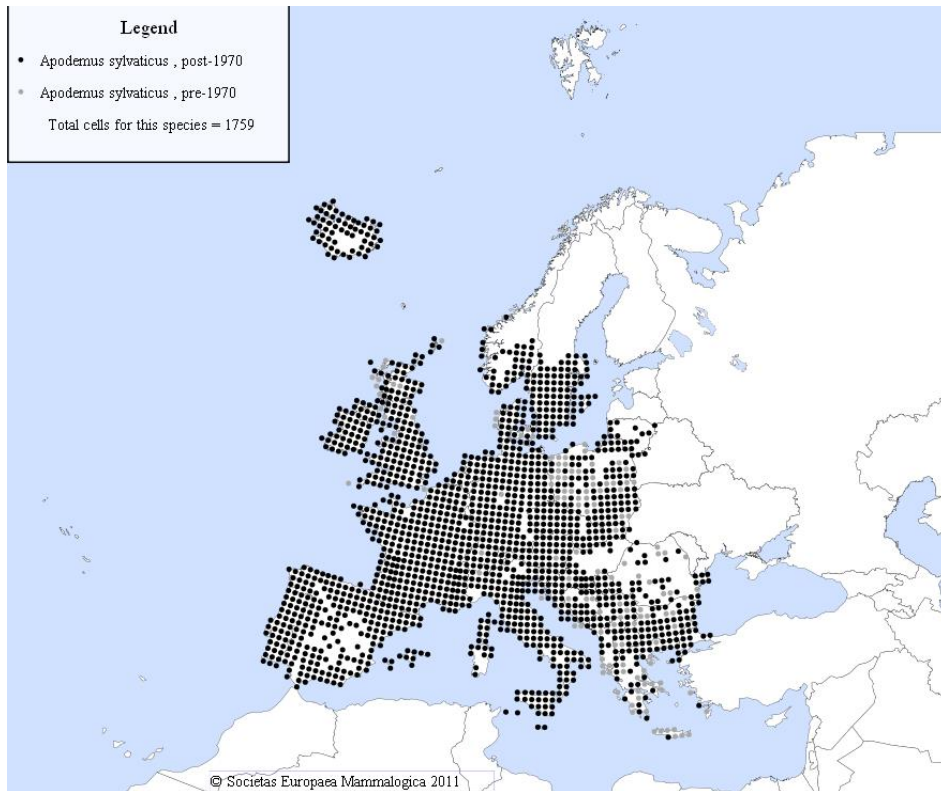


Figure 1. The distributional range of *Apodemus sylvaticus* in Europe (Societas Europaea Mammalogica).

The wood mouse is a typical “r-species” (as the opposite of so-called K-species) being a short lived, highly productive small mammal often found in unstable or unpredictable environments. The offsprings grow fast and reproduce early (Krebs 1994). These traits of the r-species should make it easier for the wood mouse to settle and adapt to various habitats in new areas.

## 2.1 The wood mouse in Iceland

The wood mouse most probably arrived in Iceland with the early settlers in the 10<sup>th</sup> century, both from Norway and British Isles (Lupton & Wykes 1938; Arnason 1974; Bengtson et al. 1986). The species is, in most areas, the only rodent living in the wild in Iceland, where it exists at its northern and western limits (Bengtson et al. 1989a,b). Wood mice are found in all vegetated areas in Iceland and on some of the larger islands around Iceland (Skírnisson 1993, 2004).

Few predator species prey upon wood mice in Iceland. The short-eared owl (*Asio flammeus*) which is rare in Iceland, with only about 100-200 breeding pairs in the whole country, is probably depending on the wood mouse as a main prey species (Nielsen 1997; Petersen 1999).

Mammalian carnivores in Iceland are the American mink (*Neovison vison*; Skirnisson 1980) and the arctic fox (*Vulpes lagopus*; Hersteinsson & Macdonald 1996). However, wood mice are not an important component of the diet of these species. The arctic fox is the only native terrestrial mammal in Iceland and had already settled long before humans arrived during the 10<sup>th</sup> century (Hersteinsson 1984; Hersteinsson et al. 2007). The feral mink was first imported for fur-farming during the 1930's and immediately escaped from captivity (Skirnisson & Petersen 1980).

There are three other rodent species found in Iceland, besides the wood mouse: house mouse (*Mus musculus*), brown rat (*Rattus norvegicus*) and rarely black rats (*Rattus rattus*). House mice are often found outdoors in urban areas and live outdoors in Vestmannaeyjar islands, south of Iceland, where there are no wood mice (Skirnisson 2004). Nevertheless, the wood mouse is the only small mammal that has managed to get established and survive in the wild in Iceland, independent of man (Saemundsson & Degerbøl 1939; Bengtson et al. 1976; Bengtson et al. 1989b).

The cool and short but bright summers (with long days) in Iceland as well as the long, dark winters and unfavourable climate with strong winds and frequently interchanging frost and thaw (Figure 3) are likely to affect the population characteristics of this small rodent, far north of its natural range.

Despite harsh conditions, the species seems to have adapted quite well to Icelandic nature (Bengtson et al. 1989a,b) and has managed to cope with changes in climate and vegetation such as deforestation and changes in agricultural practices through the centuries (e.g. Ólafsdóttir et al. 2001). Icelandic wood mice have probably been influenced by farming activities as well as woodland and soil restoration efforts, followed by milder climate in general during the last century, despite frequent but short cold periods in between (Jónsson 2008).

Prior to this research project, Icelandic studies on wood mouse population ecology were limited to a survey at an isolated Angelica (*Angelica archangelica*) stand in southern Iceland and a smaller comparative study in a birch wood (*Betula* spp.) in northern Iceland (Bengtson et al. 1976; 1986; 1989a,b). Earlier studies have been published on taxonomy and size (Saemundsson & Degerbøl 1939), external parasites and origin (Lupton & Wykes 1938) and protein polymorphism (Arnason 1974). The morphological study of

Sæmundsson and Degerbøl (1939) suggested that the Icelandic wood mouse differed from the species in other areas, especially due to sharper colours and larger size, and should thus be regarded as a subspecies: *Mus sylvaticus grandiculus* (Sæmundsson & Degerbøl 1939). Bengtson and colleagues (1976) also measured body mass and length (as well as other parameters) of Icelandic wood mice and despite being close to the largest sizes registered of the species they did not find them different enough to deserve a separate taxonomic status (Bengtson et al. 1976).

The study of wood mouse parasites revealed that the same parasite species that were found in Icelandic wood mice were known from Norway and the British Isles. Yet, one external parasitic flea, *Ctenophthalmus agyrtes*, found on a wood mouse in Iceland, turned out to be of the subspecies *agyrtes*. This subspecies is commonly found in Scandinavia, Germany, Austria and Switzerland. In Britain, however, this subspecies does not exist but another subspecies, *C. a. celticus*, is common. That subspecies has, on the other hand, not yet been found in Iceland (Lupton & Wykes 1938; Bengtson et al. 1986; Skirnisson 1993). Arnason (1974) compared protease structure from samples of *A. sylvaticus* from Iceland, Ireland and Norway. His results were contradictory since the esterase proteins of Icelandic and Norwegian samples resembled each other, but the transferrin proteins of Icelandic and Irish samples were identical (Arnason 1974). It can be expected that wood mice were introduced to Iceland many times through the centuries. To our knowledge, no genetic studies have been conducted to further examine the origin of the wood mouse in Iceland.

The fact that the wood mouse is at the northern and western limit of its distributional range in Iceland, makes it an excellent model species for studying the population ecology and potential limiting factors. Additionally, being the only rodent in the wild, competition with other rodent species can be excluded as a potential limiting factor. Iceland lacks woodlands and is devoid of trees that form large seeds (>2g), such as beech (*Fagus sylvatica*) and oaks (*Quercus spp.*), that have been shown to be important food resources for overwintering wood mice (Watts 1969; Montgomery & Montgomery 1990; Selås et al. 2002). It is thus interesting to see how competent the species is in finding good habitats that provide necessary food and shelter through the year in Iceland.

## **2.2 Variable environment**

During the last millenium, Iceland has undergone several periods of large changes in climate and vegetation. Cold periods, frequent volcanic eruptions with ash cover and river floods, heavy grazing by live-stock, deforestation and high levels of desertification (Ólafsdóttir et al. 2001; Hanna et al. 2004). Not to mention more recent large scale drainage of wetlands for agricultural activities in the 20<sup>th</sup> century (Ólafsson 1998) that



may have affected habitat quality for mice. Over the past 200 years, average temperature in Iceland has been rising at the rate of  $0.7^{\circ}\text{C}$  per century. The variation within this period is large, however, so that between 1800 and 1900 there were large fluctuations in annual mean temperature ranging from  $+0.5^{\circ}\text{C}$  (in 1812) up to  $+4.7^{\circ}\text{C}$  (in 1828). During the 20<sup>th</sup> century, however, the annual mean temperature never reached below  $+2^{\circ}\text{C}$ , not even during the “frosty winters” of 1918 and 1979 (Jónsson 2008). The species has overcome the task and managed to live “on the edge”, even at very high population densities in some habitats (Bengtson 1989a,b).



## 3 Population ecology

Population ecology addresses population changes and the interaction of demography with biotic and abiotic factors in time and space (e.g. Krebs 1994). Studies often aim to explain the mechanism behind population dynamics such as fluctuations in population growth rate which, on small mammals in northern regions often follow seasonal and/or multi-annual cycles (e.g. Krebs et al. 1973; Hanski et al. 1991; Ims et al. 2008).

### 3.1 Population density

A central issue of many small mammal studies is the question of abundance. A variety of conceptual and applied problems require reliable information on variation in population size in time and space. Some key ecological questions are related to changes, for example if populations are growing or shrinking, and seek to identify causes and/or consequences of such changes. Thus, numerous books and scientific papers have been published in order to develop and improve statistical methods of population estimates (e.g. Seber 1973; Pollock et al. 1990; Amstrup et al. 2010).

For small mammals, density is commonly estimated indirectly by the use of capture mark recapture (release) methods, often referred to as CMR. The Cormack-Jolly-Seber (CJS) approach is the basis of many CMR models, both for open and closed population analysis (e.g. Otis et al. 1978). Estimates are based on trapping histories and thus, the ability of trapping and re-trapping individuals (trapability) is important. Model assumptions have to be met in order to secure accuracy and reliability (Seber 1973; Blower et al. 1981; Krebs 1999; Southwood & Henderson 2000). Therefore, while some statisticians and ecologists are working towards improving statistical methods, others are looking into behavioural aspects of trap response such as sex biased trapability and temporal trapping heterogeneity (Tanton 1965; Watts 1969; Jensen et al. 1993; Krebs et al. 1994).

Various statistical methods have been developed to detect and deal with these problems (e.g. Otis et al. 1978; Nichols & Pollock 1983; Nichols 1986; Chao 1987; Pollock et al. 1990; Lebreton et al. 1992). The methods, however, rely on getting sufficient sample sizes (e.g. Chao et al. 2000), which can be difficult during periods of small population size and/or low trapability (e.g. Tanton 1965; Watts 1969).

For simplicity, and since trap data is often insufficient for meeting assumptions of statistical analysis despite all correcting efforts, so called Minimum Number known to be

Alive (MNA), has often been used to determine species abundance (see e.g. Pollock et al. 1990; Krebs 1999). This is also referred to as enumeration method and has been found to underestimate population size (e.g. Krebs 1999). For density, values are commonly given in “individuals per hectare” but trap index (number of individuals caught per trap per night) is also used (e.g. Krebs 1999; Southwood & Henderson 2000; Aplin et al. 2003).

Snap trapping has also been conducted in small mammal studies, most often to obtain specimens for autopsy but also for relative (indexed) population estimates (e.g. Krebs 1999; Southwood & Henderson 2000). These methods have the benefit of being easy, inexpensive and less time consuming than live trapping procedures. As the snap-trapping removes individuals from the population, it is particularly suitable for studies on species regarded as pests and those which are commercially exploited (e.g. Aplin et al. 2003). In most countries, governmental approval is needed for studies involving capture of wild animals.

The wood mouse is considered relatively trappable and density estimates are commonly based on live trapping and CMR analysis. MNA-based enumeration is also commonly used, especially during periods of low numbers (e.g. Montgomery 1989a). In many studies, information about temporal changes is more important than exact values on density. Thus for simplicity, changes in population growth rate are often based on MNA values, scaled as trap index (such as number of individuals caught by 100 trap-nights) rather than values from density estimates, based on CMR and scaled per area (e.g. Wilson et al. 1993; Montgomery 1989a). Index methods, however, also rely on constant trappability which is often an unrealistic assumption.

In northern Europe, the wood mouse generally goes through a seasonal cycle with low population density at the onset of the breeding season in early spring and a maximum at the end of the breeding season in late autumn (Flowerdew 1985; Montgomery 1989a; Wilson et al. 1993; Bengtson 1989a). Autumn population density varies both in space and time but there are no signs of inter-annual cyclic patterns (Montgomery 1989a; Gorman & Zubaid 1993).

Population density at peak abundance varies considerably by habitat type. Thus, deciduous woods in Great Britain generally have a high density, varying from about 20 mice/ha to >50 mice/ha, depending on the presence of other dominant rodent species. In grassland and arable land in England, wood mouse population density ranged between 15-20 mice/ha (Wilson et al. 1993). Gorman and Zubaid (1993) showed that peak population density in a maritime sand-dune system in Scotland was consistently in the range 10-12 mice/ha in 5 years of study while in deciduous woodland it was in the range 25-55 mice/ha.

Population density of small mammals is generally believed to correlate with food quality and availability, in particular seed abundance, both in space and time (Watts 1969; Bengtson et al. 1989b; Montgomery & Montgomery 1990; Gorman & Zubaid 1993; Zubaid & Gorman 1993). Montgomery (1989a) found that population growth rate from spring to autumn was density-dependent such that low population density in spring would result in a higher rate of growth and the autumn increase would continue for longer when initial population density was low. This means that low population density in spring resulting from unusually high non-density dependent mortality during winter due to shortage of food, predation, adverse weather or disease would be compensated for during the increase phase of summer and autumn.

### **3.2 Survival**

Survival is one of the key parameters of studies in population ecology. Survival rate represents the proportion of the population studied that is alive from one period to another. For long lived animals, survival is often described by the use of life-tables, an age-specific summary of the mortality rates acting on a given population. In CMR studies of small mammals, survival rates are commonly estimated by the use of open population CJS models (e.g. Seber 1973; Krebs 1999; Southwood & Henderson 2000).

Survival of the wood mouse has been shown to be, in general, 70-80% per month (Bengtson et al. 1989b; Wilson et al. 1993; Zubaid & Gorman 1993). According to this, total survival of overwintering mice, from October to May, would be as low as 8-20%. Thus, life expectancy is only a few weeks up to a year in natural habitats and very few reach two years of age (Corbet & Southern 1977).

Wood mice do not hibernate but store food in their nests for the winter and forage when they run out of food items (e.g. Hansson 1971). It is likely that survival can be affected by habitat quality as in poor habitats mice have to spend more time and/or cover larger area while foraging (Gorman & Zubaid 1993). Furthermore, habitats differ in quality by seasons and mice can enhance overwintering survival by moving seasonally between habitats (e.g. Tattersall et al. 2004). Survival can also differ between various age groups, e.g. the first generation born in the spring can suffer higher mortality than later generations born in the same summer (e.g. Watts 1969).

It is not clear if and how weather factors such as precipitation and/or temperature affect overwintering survival through food availability or directly through cold intolerance. Knowledge of which periods of the winter and what kind of habitats are critical for overwintering survival is therefore important for understanding the population dynamics and limiting factors of small mammals in northern regions. Still, as many mice die

throughout the winter and recruitment does not occur until spring, sufficient data can be difficult to obtain.

### **3.3 Breeding**

Murid rodents are small mammals which experience strong selective pressure to compensate for a short life span by rapid growth and high fecundity (Bronson 1989). Growth and breeding are, however, energy demanding physiological processes and thus limited by the amount and quality of available food. Consequently, natural selection could be expected to act on mice to mature as young as possible and breed before they die or environmental conditions become too hazardous for rearing young (Bronson 1989; Roff 2002). On the other hand, females should not risk breeding until they are physically prepared for an energy demanding gestation and lactation period. In areas where summers are short and the climate unfavourable, the female wood mouse may be forced to risk her own survival and even delay growth to maximize her reproductive success by giving birth to as many viable offspring as possible before winter sets in (e.g. French et al. 1975). This means that females are dependent on resources required for pregnancy and lactation: nesting sites and food. Males, however, mainly compete for receptive females and in some cases for breeding territories, rather than food. Thus, selection should favour larger males than females (Bronson 1989), perhaps through a longer growth period.

It has been suggested that female wood mice can breed as young as 10 weeks of age (Jonsson & Silverin 1997). This means that if female wood mice are born in May (first generation) they can become mature in July. If they mate, gestation takes 3-4 weeks and lactation 2-3 weeks (Flowerdew 1977). Thus, the second generation will be born in the beginning of, or mid-August. If this second generation of the summer is born in early August, they could also breed in the same season, at 10 weeks of age. This means that if females of the second generation manage to breed at the end of the summer, their young will be weaned in late October at first (in accordance to the 15-22 weeks process). If growth is delayed and females become mature before 10 weeks of age, their offspring can become independent earlier and thus have more chance to survive the winter than those born later. It has been shown that yellow-necked mice born in early spring have a higher survival rate during winter than mice born later in the summer (Bujalska and Grüm 2006). Litters born to females that were born earlier in the same year (in the same breeding season) may thus have low success even when this is possible.

It has been shown by experiments that food availability can affect growth and maturity and that breeding of both sexes can be delayed by reducing food. As soon as the food availability was increased again, females ovulated in a few days but males were less likely to respond (Bronson 1989). Additionally, according to a field study in Sweden, a

rich crop of seed mast in late summer was assumed to prolong breeding into the winter (Bergstedt 1965) and supplemental food experiments enhanced breeding to begin earlier in the spring than in areas without additional feeding.

The social system of the wood mouse is believed to be similar to the one of *Peromyscus maniculatus* (and *P. leucopus*) that has been thoroughly studied. These mice are commonly referred to as “deer mice” and have been termed as an ecological equivalent of *A. sylvaticus*, our wood mouse. Moreover, these two species look amazingly similar and are believed to share ecological and social characteristics (Montgomery 1989c). Deer mice are promiscuous and it is believed that females are territorial during the breeding season but that males have larger home ranges which include several female territories. Females are aggressive towards other females but not to males, especially the older ones which could possibly have fathered their offspring.

A study of two *P. maniculatus* populations in North America revealed great inter-population differences in breeding phenology that were assumed to be due to geographical locations (Bronson 1989). In Michigan, U.S.A., the breeding season extended seven months and age of maturity for females ranged from 5 to 25 weeks. The reason for this large range is that females that are born early in the breeding season can breed in the end of that same season and again next spring (if they survive the winter). Mice born late in the breeding season can not breed before the onset of winter and become the bulk of breeding individuals next spring. Another population of the same species, occurring in northern areas, near Great Slave Lake, Canada, has a much shorter breeding season of only 2-3 months. In that population, only one generation is born each summer. This summer-born generation does not manage to breed before the onset of winter and becomes the bulk of the breeding population next spring as very few older individuals survive the winter (Bronson 1989). A similar pattern was observed in compared populations of *A. sylvaticus* in South and North Iceland. In the southern population, females had three litters each summer but only one litter was born during the summer in the northern population (Bengtson et al. 1989a).

### **3.4 Diet**

In general, wood mice are considered granivorous and feed preferably on large tree seeds (e.g. Hansson 1985; Montgomery & Montgomery 1990). Animal matter, such as insect larvae, snails and worms, is also eaten by mice, especially when seeds are scarce. Thus, diet is seasonal in relation to availability. In low density areas of poor quality, mice have been shown to feed on, besides seeds, various invertebrates and even green plant material (Gorman & Zubaid 1993). In set-aside-land in Britain (agricultural land where no planting activity takes place in a “resting” period), vegetation cover is discontinuous and seed

formation poor. A study of wood mouse diet in such habitat revealed that a bulk of the diet was mostly grass (green material and stalks). Seeds were never more than around 20% of the diet (Rogers & Gorman 1995). In Iceland, diet was studied in a wood mouse population in an *Angelica* field where the main food items were *Angelica* seeds. This particular area seems of unusually high quality since the mice in this study were in good condition, survival rate was high and the mice breed up to three times in the summer. Furthermore, the density was extremely high,  $>100$  mice  $\text{ha}^{-1}$ , probably due to the abundance of nutritious *Angelica* seeds (Bengtsson et al. 1989a,b). Even though wood mice are not strictly granivorous, the distribution and abundance of seeds has been found to be strongly related to distributional limits of *Apodemus* species (Angelstam et al. 1987).

### **3.5 Growth**

Individual growth is often described by changes in body mass or length from birth to a certain life stage, for example maturity (e.g. Layne 1968; Gurnell & Rennolls 1983; Lin et al. 1993). Body mass can be an unreliable measurement when describing growth and/or determining age, compared to eye lens weight (see e.g. Adamczewska-Andrzejewska 1971; Vandorpe & Verhagen 1979). In contrast to eye lens weight though, body weight can be obtained while conducting Capture Mark Recapture studies and without harming or killing the animals. For *A. agrarius* in Poland, body mass was shown to change more rapidly in the early stages of growth than for example body length, with a steep curve during the first six weeks from birth. Body length however increased a little slower so that 20% of the final value was reached during the first three months of life (Adamczewska-Andrzejewska 1971). Growth pattern of wood mice follows the sigmoidal curve and the Gompertz growth model is believed to describe wood mouse growth quite well (e.g. Zullinger et al. 1984).

Different growth strategies have been observed for those born in early spring than those born later in the breeding season (Adamczewska-Andrzejewska 1971). This can be explained in the way that early born individuals do not suffer from competition with older generations and thus should have access to higher quality food and can therefore grow faster. Those born later in the summer or even in the autumn, grow up under higher density of mice and more competition for food resources that differ from the available food in the spring, plant food is less nutritious in late summer and seeds have ripened in autumn (e.g. Bergstrom & Rose 2004).



### **3.6 Habitat**

Population density of small mammals varies considerably by habitats (e.g. Gorman & Zubaid 1993; Wilson et al. 1993) suggesting that habitats are of different quality for sustaining viable populations. Therefore it is expected that habitats with good nest sites for the breeding season and shelter and high energy food during non-breeding periods of winter should be favoured. The need for various attributes of habitat would then be assumed to differ by sex and/or season so it is possible that in some cases, small mammals would be better off by moving seasonally in order to get the best out of each habitat at a time (see e.g. Todd et al. 2000; Tattersall et al. 2004).

Habitats can vary in quality from superior habitats that harbour populations with positive growth rates, often termed sources, to low-quality habitats with low survival and reproductive rate, termed sinks. Sink populations are not believed to persist without immigrants from adjacent source habitats (Pulliam 1988; Diffendorfer 1998; Hanski 1999). Thus, populations inhabiting sink habitats regularly become extinct.

It has been shown that available habitats in Icelandic nature can differ greatly in regard to food quality and availability, shelter and other important factors. There are habitats with the characteristics of a sink, with low carrying capacity (Bengtson et al. 1989a) and in which wood mice most likely became extinct many times throughout the centuries. In contrast, there would be habitats that could be regarded sources and acted as refuges when conditions became unfavourable during rough periods in Iceland during the past centuries.



## 4 Aims

Before this study, basic knowledge on the population ecology of the wood mouse in Iceland was mainly derived from a study in a dense angelica field of south Iceland (Bengtson et al. 1976, 1989a,b). The studies of Bengtson and colleagues, revealed an extremely high population density, high and stable survival and longevity of the studied individuals. The mice of the angelica field could breed up to three times in a summer and were trappable in all seasons. The fact that Iceland is at the northern edge of the wood mouse distributional range, gave the impression that the demography and population parameters in the angelica field did not describe a “typical” situation for Iceland. It was therefore interesting to see if the results of Bengtson and colleagues were representative of wood mouse populations in other areas more typical of the lowland habitats of Iceland.

### 4.1 Limiting factors (Paper I)

The first aim of this study was to describe seasonal patterns in population density and survival by following a wood mouse population inhabiting a typical grassland/coastline habitat in Kjalarnes SW-Iceland in order to compare them with values from the angelica field in south Iceland (Bengtson 1989a) and from other European areas, closer to the core of the species’ distributional range.

As the wood mouse population had been studied in Kjalarnes every autumn from 1995 (Páll Hersteinsson, unpubl. data) until the onset of this study in 2001, autumn trapping data was available and could be used. The second aim was to estimate autumn population size and density from the former dataset and the data collected in this study. The population estimates (and population growth rates) were then compared to available weather data and other important sources to detect factors that could be important in determining autumn population density. Since Iceland is at the northern edge of the species’ distributional range, it was predicted that density-independent factors, climate in particular, should be important in determining population density. In view of the cold summers, it was predicted that climate during the breeding season would be the most important predictor of autumn population density.

## **4.2 Contrasting habitats (Paper II)**

As it turned out already in the early stages that the wood mouse density in the grassland and coastal habitats of Kjalarnes was very low, the study was extended to another study area for comparison, the Mógilsá woodland. Therefore, the third aim was to compare population parameters in these two contrasting habitats. It was predicted that the woodland would be more favourable for the mice, resulting in higher population density and winter survival as well as better physical condition than mice in the open grassland site (see e.g. Gorman & Zubait 1993). It was also predicted that wood mice in the woodland site were feeding more on various seeds and berries than at the grassland site where they would feed more on green plant material, small grass seeds and invertebrates. The fourth aim was thus to determine the diet of wood mice and compare food types by seasons, habitats and sex.

## **4.3 Reconstructing population size (Paper III)**

As in other areas where this species is studied, the spring and early summer turned out to be difficult in regard to obtaining adequate sample sizes. Mice were not as keen to enter the traps as before and the young of the year seemed to learn from their mothers to be “trap shy”. As the majority of the mice trapped in the autumn were young, born in the summer of that year, inverse growth curves could be used to estimate when they were born. That would be a base for the new population estimates of the summer period of low trapping success. This is how the fifth aim was born: To find a way to use the ample autumn trapping data as an aid to describe population parameters of the previous months when low trapability prevented direct measurement. To be able to do this, we had to figure out if body mass measurements of live-trapped individuals could be used to estimate age. And to confirm that our data could be fitted into growth models to predict population density and detect recruitment during periods of low trapability.

# 5 Materials and methods

## 5.1 Study area

The study took place in two contrasting habitats in SW-Iceland: (1) The Kjalarnes study site, Brautarholt (64°13'58"N, 21°53'52"W) of 35 ha is located at the tip of a small peninsula in SW-Iceland, about 40 km north of the capital Reykjavík. It is composed of cultivated hayfields with ditches, uncultivated meadows and a narrow coastal habitat.

(2) The Mógilsá study site (64°12'34"N, 21°42'40"W) is an approximately 2,8 ha area composed of deciduous and coniferous woods, mixed with open areas, about 30 km north of Reykjavík and 13 km away from the Kjalarnes study area (Figure 2).

The former can be regarded as typical modern Icelandic landscape while the latter is more representative of recent development in land management and, indeed, it is probably also more similar to the landscape prior to deforestation in the early centuries of human settlement in the country. For clarification 23.800 km<sup>2</sup> of 88.000 km<sup>2</sup> land area (glaciers and lakes are excluded) is termed as vegetated area and Icelandic coastline is almost 5.000 km long (National land survey of Iceland, 2014).

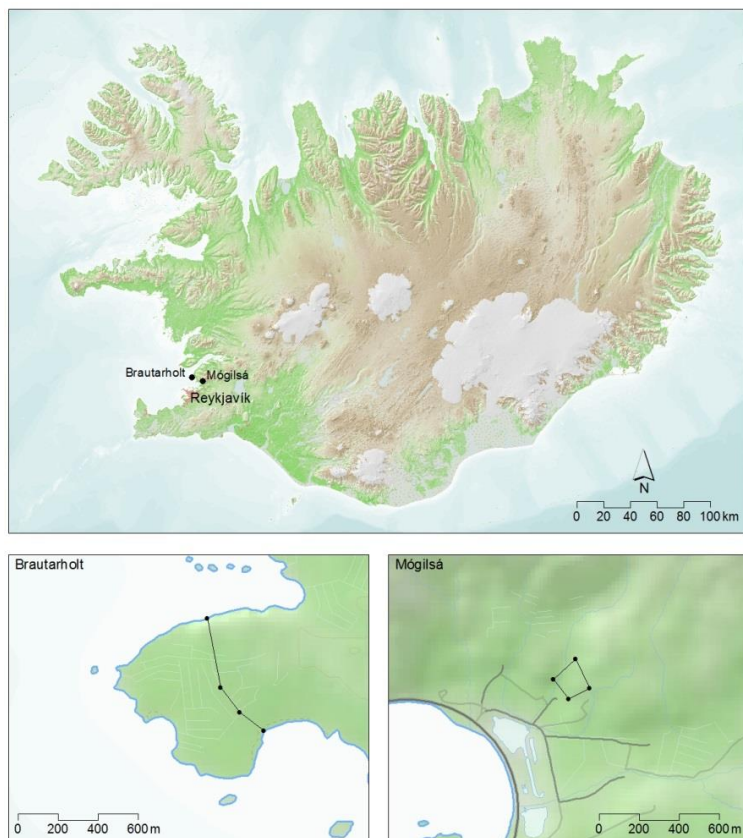


Figure 2. The location of the study areas in Iceland. Maps made by Hans H. Hansen at The Icelandic Institute of Natural History. Black lines show the boundaries of the study sites. Brautarholt is the Kjalarnes grassland site and Mógilsá is the woodland site.

## 5.2 Flora and fauna

Flora was examined with the use of 1x1m quadrates. The frames were randomly set out in various types of vegetated areas of the study site (Paper II). Plants were identified to species level if possible in order to get an overview of the vegetation composition of the area.

### *Kjalarnes grassland*

The largest part of Kjalarnes peninsula is a former bog, drained with ditches to grow a hayfield with grass sown during the 1950's (pers. comm. Páll Ólafsson, landowner). Vegetation cover is continuous and the main grass species are *Agrostis stolonifera*, *Alopecurus pratensis*, *Festuca richardsonii* and *Phleum pratense*. Along the ditches the grass was not cut, during the annual harvest, resulting in a 50cm zone of seed forming

grass on the ditch edges. The coastal vegetation is more discontinuous but characteristic plants are *Cakile arctica*, *Mertensia maritima*, *Matricaria maritima*, *Chamomila suaveolens*, *Leymus arenarius* and *Angelica archangelica*. In general, the vegetation is rather homogeneous and no fruit bearing plants were found in the grassland site, with an exception of few and scattered *Empetrum nigrum*. No farm animals were at the hayfield during the time of the study (with the exception of a few horses *Equus caballus* that were grazing in the area during autumn trapping 1996-1998).

The grassland macro-habitat was, by direct observations on topography and vegetation structure, divided into three main sub-habitat types: (1) ditch edges, (2) coast and (3) wild with rocky parts (Paper II).

#### *Mógilsá woodland*

The Mógilsá woodland is characterized by birch (*Betula pubescens*) as a dominating tree type, mixed with occasional coniferous trees such as Sitka spruce (*Picea sitchensis*) and willows (*Salix* spp.). The woodland floor is characterized by *Filipendula ulmaria* with occasional *Rubus saxatilis*, *Geum rivale*, *Equisetum pratense* and common grass species such as *Agrostis stolonifera*.

#### *Surface invertebrates*

Surface animals in both study areas were caught by the use of Barber pit traps, half filled with ethylene glycol that preserves the specimens from decomposing (Southwood & Henderson 2000). This examination was done in July 2005 in both Kjalarnes grassland and Mógilsá woodland simultaneously.

The pitfall traps were placed in the middle of each plant frame (Paper II). Captured surface animals were mainly dipterans, lepidoptera and coleopteran species, in larva, pupae and adult instars and spiders (arachnids). Other surface animals were earthworms (Lumbricidae), slugs and snails (pulmonata).

### **5.3 Predators and competitors**

As Iceland is an isolated island in the middle of the northern North Atlantic Ocean, the terrestrial mammal fauna is rather poor. In our study area we never observed any traces of arctic foxes but two minks were spotted at the grassland site during the study period. A house cat (*Felis catus*) or two were known to visit the woodland area regularly though they were never directly observed but their tracks could be followed in the snow during the winter.

Icelandic birds of prey are known to feed on mice in the autumn when rodents are in high abundance. There is however no one that could be regarded as specialized on small rodents, with the possible exception of the short-eared owl (*Asio flammeus*). Owls were spotted in the grassland area every now and then, especially around the ditches. Merlin (*Falco columbarius*) was also seen occasionally, they are known to feed on mice (Bengtson 1975; Nielsen 1986). Other birds that probably also feed on mice, such as raven (*Corvus corax*), arctic skua (*Stercorarius parasiticus*), and gyrfalcon (*Falco rusticolus*) were observed in our study area. Gulls could also prey on mice but only one gull species was seen in our study area, the lesser black-backed gull (*Larus fuscus*). Of all these, only the raven was commonly seen. None of these predatory birds were observed in the woodland study area. One other rodent species than wood mouse was trapped during this study, the house mouse. Two were caught in the live-traps at the woodland site and two-to three house mice were live-trapped in all the years of trapping at the grassland site. None of these house mice were recaptured.



## 5.4 Weather

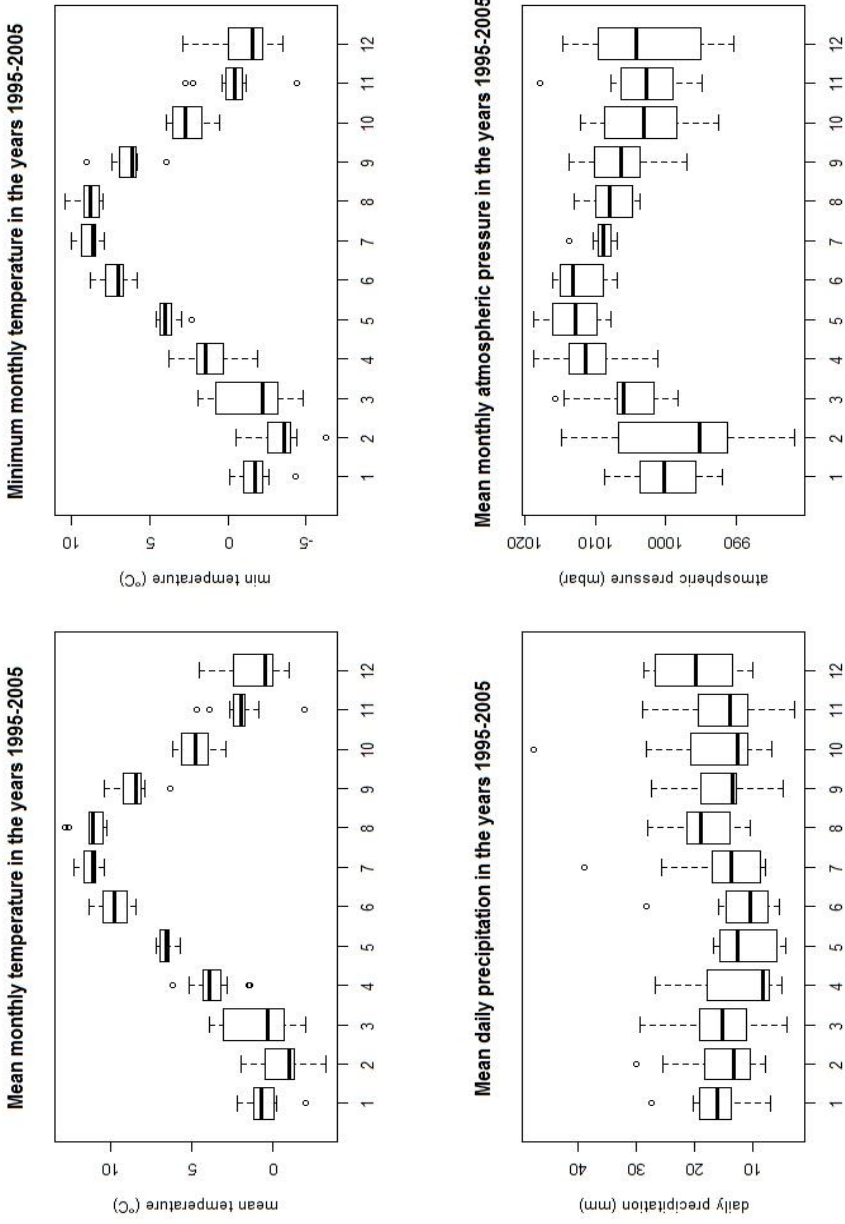


Figure 3. Main weather factors at Reykjavik weather station in the study period (1995-2005). Upper left: Monthly average temperature (°C). Upper right: Monthly average minimum temperature (°C). Lower left: Mean daily precipitation per month (mm). Lower right: Monthly mean atmospheric pressure (mbar). Data from the Icelandic Meteorological office.

Information on weather was obtained from The Icelandic Meteorological Office, recorded at Reykjavik weather station every 3rd hour. Mean temperature and precipitation were calculated as an average for each month (Figure 3). The weather conditions can be regarded as representative for the maritime climate of southwest Iceland. The average temperature in the years 1995-2005 varied from -3.3 to 4.5 °C in the coldest winter months (December–March) (The Icelandic Meteorological Office, 2013). Precipitation varied from 20 and 157 mm per month during the same period (Figure 3). As temperature fluctuates through the winter, precipitation varies from rain to snow. Furthermore, changeable thawing and freezing periods are common in this region, causing unstable snow layers through the winter (The Icelandic Meteorological Office, 2013).

Wind speed and/or direction were regarded as irrelevant factors for ground living creatures like mice. Figure 3 shows mean values of temperature, precipitation and minimum daily temperature during the study period.

## **5.5 Trapping procedure**

In Kjalarnes grassland, a permanent grid of 145 live traps was set out with an interval of about 45 m between traps (Figure 4). In Mógilsá woodland, 97 live-traps were set out on a grid with an interval of 20 m (Figure 5). Other studies of contrasting habitats have used different intervals between traps when comparing habitats assumed to have diverse density (e.g. Gorman & Zubaid 1993).

Live trapping was conducted in 5 days sessions approximately every 5th week from September 2001 to November 2003. In September 2004 – November 2005, live trapping sessions were carried out at 3-7 week intervals simultaneously in the Kjalarnes grassland and Mógilsá woodland.

Captured mice were individually marked with microtags under the skin at the neck and individuals were identified by the use of a pocket reader. Animals caught were weighed and information about sex and other notes (such as breeding status, visible injuries, part of tail missing) were registered.

In the traps, we placed a piece of sheep wool and rodent food to keep the animals warm and alive. During winter trapping, an extra 7 mm isolating cover was used for the traps to protect the animals from the cold. Traps were checked once every day and the whole process of checking, measuring and tagging took from two to ten hours each day, depending on the trapping effort.

Mice were also trapped in snap-traps in similar nearby habitats to determine breeding status and fertility by measurements of testes (size, sperm production), ovaries (ovulation) and uterus (placental scars), while food selection was determined from stomach contents. The snap-trapping procedure took up to four months in spring and summer periods, often with little or no results.

Trapping methodology was approved by The Icelandic Food and Veterinary Authority and The Icelandic Ministry of the Environment. We did not observe any negative effects of tagging during our study.

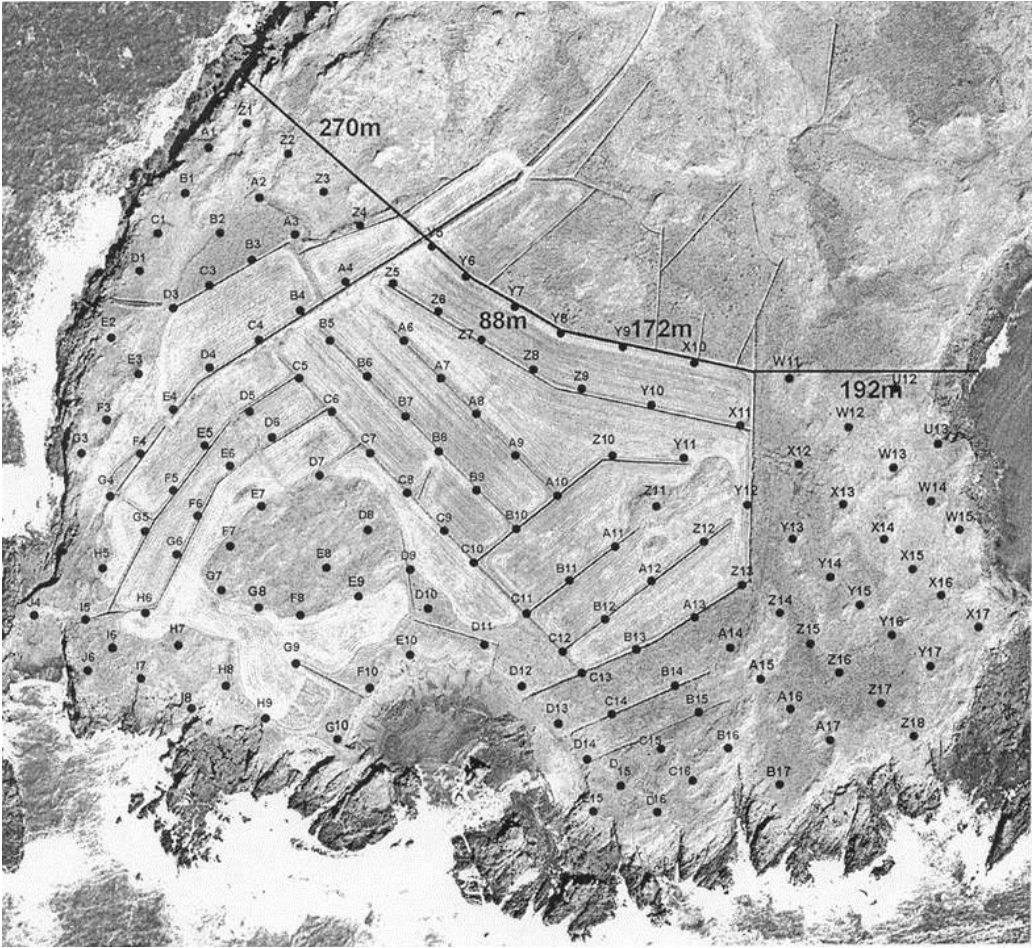


Figure 4. The Kjalarnes grassland study area. The black dots represent the locations of live-traps. In the earlier studies (1995-2000) trapping was only conducted in lines A-J. Snap traps were placed along the beach on both sides and two of the ditches that reach out of the area, away from the sea.



Figure 5. Locations of live-traps in the Mógilsá woodland are shown with black dots. The purple dots represent snap trap locations that were used in the weeks between the live-trapping censuses.

## 5.6 Datasets

The study is based on the following four datasets (see also Table AX3):

- (1) Annual live trapping with Capture Mark Recapture (CMR) procedure in 5 day censuses each autumn from 1996 to 2000 (with the exception of 1999). The mid date of autumn trapping for all years was October 3<sup>rd</sup>, ranging from September 25<sup>th</sup> to October 17<sup>th</sup>. Study area: Kjalarnes grassland, Traps: 120, interval: 40m, size of area: 30ha (Paper I).
- (2) Approximately monthly trapping for 5 consecutive days in Kjalarnes grassland. Live trapping with CMR procedure from September 2001 to October 2003 (21 censuses). Number of traps: 145, interval: 40m, size of area: 35ha (Paper I and III).
- (3) Live trapping with CMR procedure in 5 day sessions with approximately 7 weeks intervals from September 2004 to November 2005 (11 censuses) in Kjalarnes grassland. Traps: 120, interval: 40m, size of area: 30ha. Simultaneously, with one week delay, CMR sessions in Mógilsá woodland from September 2004 to October 2005 (10 censuses). Traps: 87, interval: 15m, size of area: 2.8ha. In May to July, in both habitat sites, live trapping was conducted in 3 day sessions with 2-3 weeks interval (Paper II and III).
- (4) Snap traps were set out in linear transects >100m away from the two live-trapping areas. The snap traps were situated in habitat types similar to the habitat types found within each of the two macro habitat sites, the grassland and the woodland. At each location, transect of 10-25 traps were set out with 10-15m apart and with 1-3 traps in each trap station. This was done during one to four weeks between (after) live-trapping censuses, in order to get mice for autopsy (Paper II and III).

## 5.7 Statistical analysis

Population estimates were based on Capture Mark Recapture (CMR) methods, where each animal was trapped, individually tagged, released and then re-trapped again.

Analysis was based on CMR models by Cormack, Jolly-Seber (CJS; Cormack 1964; Jolly 1965; Seber 1965) and used for density and survival estimates with a combination of open and closed system modelling (e.g. Pollock et al. 1990).

The following four assumptions are underlying the CJS models:

- Every individual, marked or unmarked, in the population at time  $i$  has the same probability of being captured.
- Every marked animal present in the population immediately after each sampling ( $i$ ) has the same probability of survival until the next sampling occasion ( $i+1$ ). Capturing and marking do not affect survival.
- Tags or marks are not lost or overlooked.
- Sampling must be at discrete time intervals and each release is made immediately after sampling.

Open population models allow variable levels of movements into and out of the population. In our study, the data did not provide adequate information to separate migration from births and deaths.

Population estimates (population size, recapture rate and survival) were performed using program MARK 4.3 (White & Burnham 1999). When too few mice were caught (mainly in June and July) for estimates based on CMR, we used MNA to estimate the population size (Blower et al. 1981). In order to improve the values from MNA during the periods of low trapability, Bayesian analysis was used to reconstruct population estimates.

To test for possible failure of the assumptions underlying the CJS models we used Test 2.CT and Test 3.SR (Lebreton et al. 1992) in Program U-care 2.2.5 (Choquet et al. 2006). Other statistical analyses were carried out using the software package R, 2.6.1 (© 2007 The R foundation for statistical computing).

### **5.7.1 CMR analysis (Paper I and II)**

The CMR data allows the estimation of survival rate, based on recaptures, using the capture history of the data (Pollock et al. 1990).

Population size for each capture period was estimated by the use of closed capture models and survival between capture periods by the use of open capture models. This combination of closed and open methods is termed “robust design” and was designed by Pollock et al. (1990).

Open capture models were developed from the CJS models that are believed to be well-defined stochastic models. The most important feature that characterizes the open capture models is that death and recruitment are included.

It was assumed that the population was closed during the short sampling period (5 days), with recruitment and deaths negligible. The population size for each capture period was estimated using model  $M_t: \{Np(t)=c(t)\}$  (Otis et al. 1978; Pollock et al. 1990) in program MARK V-4.3 (White & Burnham 1999) with the sin link function on  $p$  and  $c$  and the log link function on  $N$ . The notation  $p$  is the probability of initial capture,  $c$  is the probability of recapture,  $t$  is the time and  $N$  is the abundance.

Effective trapping area at Kjalarnes was determined by adding a strip of land on the eastern border of the study site, which width equalled the radius of a circular home range of caught mice. Home range was calculated as the average minimum convex polygon range of trap locations of all mice caught six or more times during the time of the study. The effective trapping area was used when converting population size to population density (mice per ha).

### 5.7.2 Survival (Paper I and II)

Survival rate between capture periods (censuses) was estimated by the use of open capture models, developed from the CJS models.

Basic equation for the survival estimate:

$$\hat{\phi}_i = \frac{\hat{M}_{i+1}}{\hat{M}_i - \hat{m}_i + R_i}$$

Where  $\hat{\phi}_i$  is estimated survival at time  $i$ ,  $\hat{m}_i$  is the number of marked individuals caught at time  $i$  and  $\hat{M}_i$  is estimated number of marked individuals in the population at time  $i$  and  $R_i$  is the number of marked individuals released at time  $i$ . The values  $\hat{N}_i$  and  $\hat{M}_i$  cannot be estimated for the first and last capture occasions and  $\phi_i$  cannot be estimated for the last two capture occasions.

Monthly survival analysis was based on recapture data from September to June during each year of monthly monitoring (2001–2002, 2002–2003 and 2004–2005), using program MARK (V-4.3).

For model selection, we began with the most complex model, containing the variables of interest. In relation to our hypothesis, we assumed time and sex differences in survival and recapture probabilities. Model selection was made by Akaike's information criterion (AIC) and based on AICc weights due to



small sample sizes in some months (Burnham & Anderson 2002). The most parsimonious models to explain variation in the data (lowest AICc weight) were used for presentation. In other cases, results of averaging the equally best fitting models were used to describe the survival rates (Paper I and II).

### 5.7.3 Bayesian analysis (Paper III)

Growth was modelled using a Gompertz growth curve (e.g. Zullinger et al. 1984) with a hierarchical parameter structure (parameters for population, sex and individual). Birth dates were then estimated based on (backtracked) growth. This resulted in posterior distributions for growth asymptote and parameters (for population, sex and each individual) and birth date. The posterior distribution of birthdays was used to estimate the pattern of change of the population size of a typical cohort through the year. We could detect the first pregnancies and first cohort of the summer by live- and snap trap data (Table AX1 and AX2). First confirmed pregnant females were trapped in April (Figure 6) and the first young appeared in traps in May. Thus, we set the first day of the summers' recruitment as May 15<sup>th</sup>. Cohorts were modelled as starting from a population size of 0 at the beginning of the year (Figure AX2). Births were added for each day of the year in proportion to the sum of the posterior densities of the birthdays of the mice. Fixed mortality rates were then applied to model death of the mice in each cohort. Model fitting was performed by an R script that assembled the data set before using the BRugs library (BRugs library version 0.8-1; Lunn et al. 2009) to fit the model in OpenBugs and extract the chains of estimates (version 3.2.2 rev 1063; OpenBUGS Project Management Group; Thomas et al. 2006).

The model estimates several unknown variables. The Gompertz growth model is a hierarchical model with parameters for population, sex and individual, specifically there is a population average growth asymptote,  $K_\mu$ , and rate,  $\alpha_\mu$ ; sex specific asymptotes and rate,  $K_{\text{male}}$ ,  $K_{\text{female}}$ ,  $\alpha_{\text{male}}$ ,  $\alpha_{\text{female}}$ ; and for each mouse,  $m$ , individual asymptote and rate,  $K_m$ ,  $\alpha_m$ . The random variation in the growth model is characterised by precision parameters,  $\tau_{K,\text{sex}}$ ,  $\tau_{\alpha,\text{sex}}$ ,  $\tau_K$ ,  $\tau_\alpha$ ,  $\tau$ . Each mouse has an unknown birthday  $b_m$ .

#### *Model Equations*

The expected size of a mouse on a day of observation depends upon its age and the individual growth parameters for that mouse, following the Gompertz growth model and with a fixed birth size  $w_0 = 1.5\text{g}$ , for all observations  $i$ :

$$E(w_i) = K_{m_i} \times \exp(\log(w_0 / K_{m_i}) \times \exp(\alpha_{m_i} \times (d_i - b_{m_i})))$$

The residual variation between  $E(w_i)$  and  $w_i$  has a lognormal distribution with precision  $\tau$

$$w_i \sim \ln N(\log(E(w_i)), \tau)$$

#### *The Bayesian model*

The implementation of the Bayesian model simultaneously estimates growth parameters and possible birth dates for each mouse. For each observation,  $i$ , of any mouse the input to the model is a mouse ID ( $m_i$ ), weight on day of observation ( $w_i$ ), and day of the year ( $d_i$ ). For every mouse ID,  $m$ , we also know the mouse sex,  $s_m \in \{\text{female, male}\}$ .

For a full description of the models, equations and fitting, see the supplementary information with paper III.

### **5.7.4 Body mass and diet (Paper II)**

#### *Body mass*

Two-way analysis of variance (ANOVA) was used to measure variable differences in mean body mass in each trapping session, between habitats (woodland vs. grassland) and between sexes within habitats in each trapping month. We did not distinguish between age classes in any season but during the breeding season apparently pregnant females were excluded from body mass comparisons (Figure 6).

#### *Diet analysis*

The data on stomach contents was compared between the grassland and the woodland for each trapping month. The results were presented by seasons as follows: winter (December to March), spring (April to May), summer (June to August) and autumn (September to November). During analysis, the food was divided into four main types: seeds, green plant material, larva/pupae and adult

arthropods. The proportions of each food type were compared by months and habitats by two-way ANOVA.

In all habitats and seasons, there were stomachs which had no detectable traces of one or more food type, causing problem in statistical analysis. Therefore, before analysis, the 0s were replaced by 0.0001, a proportion that is an order of magnitude less than the smallest proportion recorded (0.001). We also had a few stomachs that included only one food type (100%); the 1s were thus replaced by 0.9999. Furthermore, the proportional data was arc sine transformed in order to attain normality in the data.

In addition, multivariate analysis of variance (MANOVA) was conducted to identify possible differences of food consumption by sex and time within each habitat type separately.

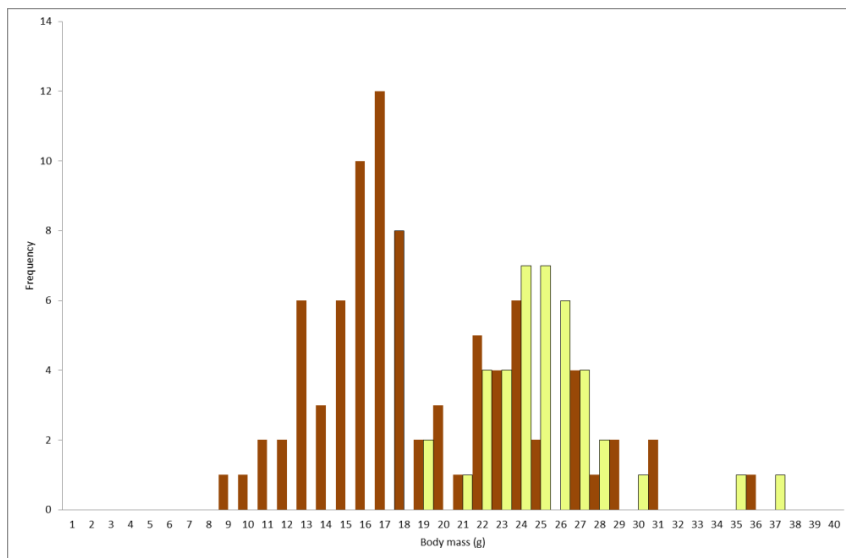


Figure 6. Frequency distribution of body mass of grassland females in September (red columns, n=84) and April (yellow columns, n=40). The body mass distribution in April represents adult weight. Note that six females were heavier than 30g, three in each month. These are most likely pregnant and indeed, females of both habitats weighing >25g can also be pregnant (Table AX1).



# 6 Results and discussions

## 6.1 Limiting factors (Paper I)

Population dynamics of the wood mice in our study showed the same seasonal pattern as is known in other areas with a peak in the autumn and small numbers at the onset of breeding in the spring. Autumn population density at the grassland site turned out to be very low, ranging from 2.7 to 8.9 mice ha<sup>-1</sup> while spring densities ranged from 0.4 to 0.8 mice ha<sup>-1</sup>. No regular cyclicality was observed in the annual autumn population size during the study period. Apparent monthly survival probabilities ranged from 0.4 to 0.7 per month in autumn and 0.7 to 0.9 in winter. Thus, the autumn-to early winter appeared to be more critical than mid-winter in regard to survival probabilities. Our results suggested that low temperature in early winter (October–December) was most strongly related to population density in the following autumn, explaining 74% of the variation in autumn population density (Figure 7). Differential mortality in early winter resulted in variation in spring population size at the grassland site.

There was a slight sex difference in apparent monthly survival, both during the autumn and in the spring at the onset of breeding (Table AX4). Thus, longevity appears to be different for the sexes at the grassland site since males have lower survival and a shorter life-span (Figure 8). This could mean that males put all the effort in mating with as many females as possible during the spring (they are scattered due to low population density) and then die or disperse. The females, however, will have to survive and stay in the area through gestation and lactation periods in order to maximise their reproductive output.

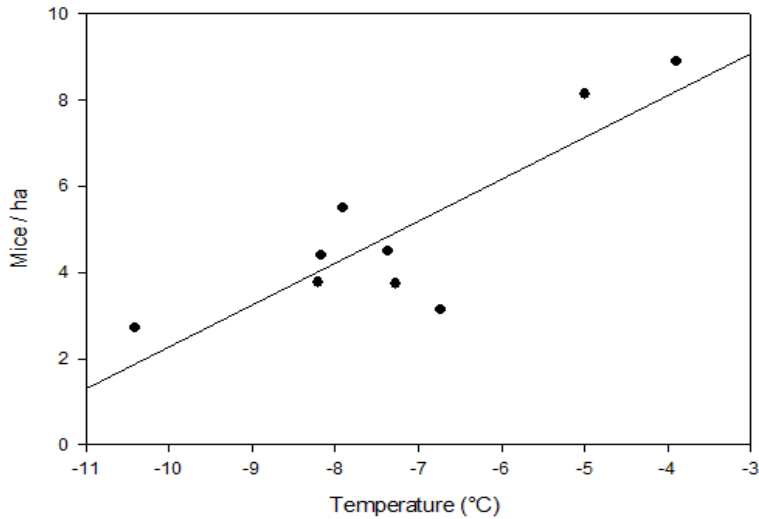


Figure 7. The correlation between the autumn population density and mean minimum temperature of October to December in the previous winter ( $R^2=0.74$ ; slope 1.0005; SE=0.22, d.f.=1, 7; p-value=0.003).

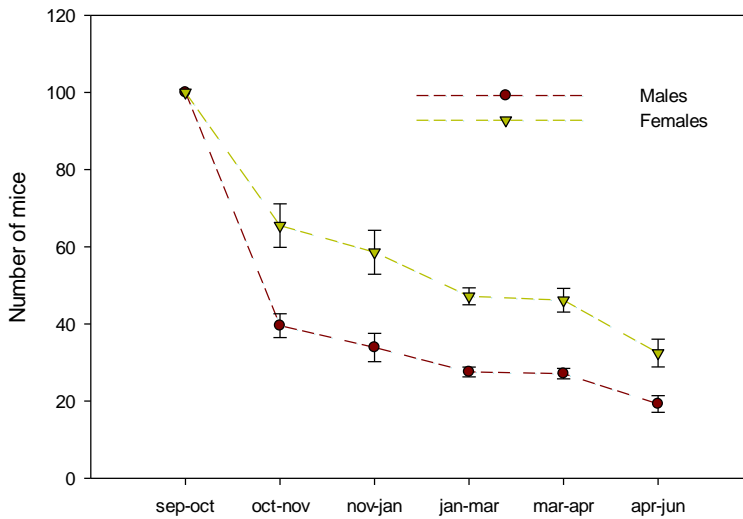


Figure 8. A simple model of longevity of grassland male and female wood mice from September 2002 to June 2003. The model is based on estimated monthly survival throughout the winter by a given initial population with 100 individuals of each sex in September 2002. Yellow triangles and line represent females, red dots and line represent males.

## 6.2 Contrasting habitats (Paper II)

Estimated population density was up to 10 times higher at the woodland site than in the grassland but seasonal dynamics were the same, with peak density in autumn and low density in spring. Apparent monthly survival varied greatly throughout the winter in the grassland, ranging from 39% to 78%, but was stable at around 60% throughout the winter in the woodland. Low sample size during the spring and summer prevented survival estimates in the breeding season.

Sex ratio was male biased in all trap censuses except during the autumn at the grassland site. In April, more than twice as many males than females were captured at the grassland site. On average, males were heavier than females in all trapping months throughout the winter. The variation in weight was, however, great in September, with the exception of woodland males (Figure 9).

Both sexes gained weight through the winter in both study areas (Figure 9) in agreement with former studies in Iceland (Bengtson et al. 1976). Males in woodland added 46% and males in grassland added 49% to their average weight from September to April. In the same time period, females gained on the average 36% in body mass at the grassland site but at the woodland site, female body mass increased by 21% from September to April. This difference between females may reflect that woodland females were older and thus closer to maximum weight than the grassland females during the autumn, as was the case with females in the angelica field of S-Iceland (Bengtson et al. 1976). Furthermore, during mid-winter (December and January), woodland mice of both sexes were heavier than mice at the grassland site (males in January:  $F=28;df=1,79;p<<0.0001$ , Females in December:  $F=5.8;df=1,37;p=0.02$ ).

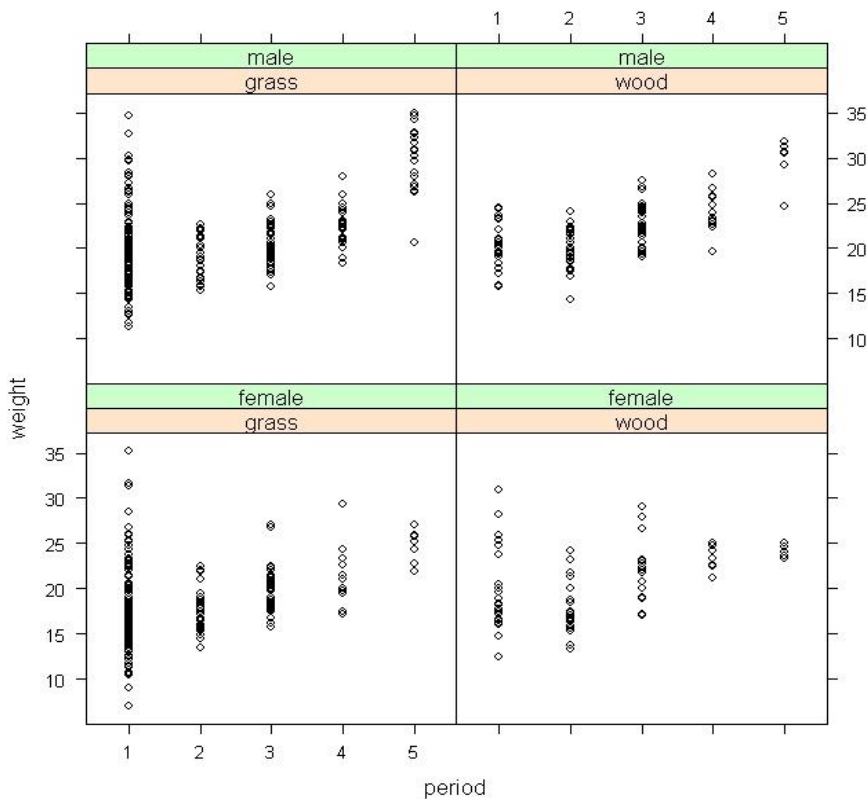


Figure 9. Raw data from body mass measurements at the grassland (left) and woodland (right) sites. Trapping censuses 1-5 represent the trapping months: September 2004 (1), November (2), December (3), January 2005 (4) and April (5). The body mass distribution in September is wider at the grassland for both sexes, indicating broader age distribution at the grassland site. Interestingly, in October (census 2), the oldest (heaviest) individuals of both sexes disappear from the population at the grassland site. The woodland site has no heavy (old) males in the autumn and different growth patterns are observed at the woodland site than at the grassland.

Interestingly, the grassland population size was largest in November but the autumn peak was reached in September at the woodland site. This could mean that breeding was extended into the autumn in the former habitat but was ceased in the woodland. If this is right, breeding is most likely density dependent in the woodland. This can also explain why woodland females were heavier than females at the grassland site and perhaps in a better body condition in the autumn if they have had more time to recover from energy costly gestation and lactation (Bronson 1989). Relative testes size, however, suggests that in both



habitats some males were biologically prepared for potential breeding during the autumn (Figure AX1 in Appendix).

A steep decline in population growth rate at the woodland site between September and October (Table AX3) can be a signal of emigration or a significant drop in population size but apparent survival was the same between all censuses so dispersal is a more likely explanation. Interestingly, the heaviest mice of the autumn disappeared from the population in October, with the exception of woodland males but they seem to have disappeared before the autumn peak (Figure 9). In September 30% of captured mice at the grassland site were of the youngest generation of summer born mice (<17g) and 19% of the October trapped mice. Most recaptured mice of this cohort had reached 20g by December in the same year. In April, significant sex difference in body mass was observed in both habitats (grassland:  $F=14.1$ ;  $df=1, 25$ ;  $p=0.0009$ ; woodland:  $F=24.99$ ;  $df=1, 10$ ;  $p=0.0005$ ) along with a sudden and considerable increase in weight among most of the males (Paper II). A similar increase in weight among females of both habitats took place in May, apparently due to pregnancy (Figure 9).

Stomach content analyses showed that the mice fed predominantly on seeds in all seasons except in the spring when arthropod larvae were the most common food type. Food varied more by season than by habitat, but evidently mice from the woodland were less likely to feed on green material and showed more seasonal fluctuations in volume of seed consumption.

No selection of special seed type was detected from the stomach content analyses. However, a cafeteria experiment with six mice (three of each sex) from the grassland area, held in captivity, suggested that mice selected some seed types over others. For example, when the mice could choose between seeds of the grass species *P. pratense*, *Deschampsia cespitosa* and *F. richardsonii* (<1mm) and seeds of the coastal sea sandwort *Honckenya peploides* (2mm), seeds from *P. pratense* were actively selected (Ester Rut Unnsteinsdóttir, unpublished data).

### **6.3 Reconstructing population size (Paper III)**

Using data from autumn live-trapping of several years, growth curves could be adjusted to individual body weights to predict their birth dates (Figure 10). We were able to estimate population density and recruitment during the period of low trapability by comparing the predicted birth dates with other data sources,

such as first pregnancy dates and the body mass of first young that were trapped in the summer. With given values of mortality, potential patterns of population growth were predicted.

We found that former density estimates from our own study, based on MNA (Paper I) underestimated population density during the period of low trapability in spring and early summer. Furthermore, the population increase of the summer appeared to begin approximately 100 days earlier than was observed by CMR analysis and MNA. Thus, even with the most cautious model, assuming high mortality, significant population increase could be observed already at the end of May instead of August (Figure 10). Importantly, it is possible to use body weight of live-trapped individuals of small mammals to estimate age and predict population estimates during periods of low sample sizes and trapability problems.

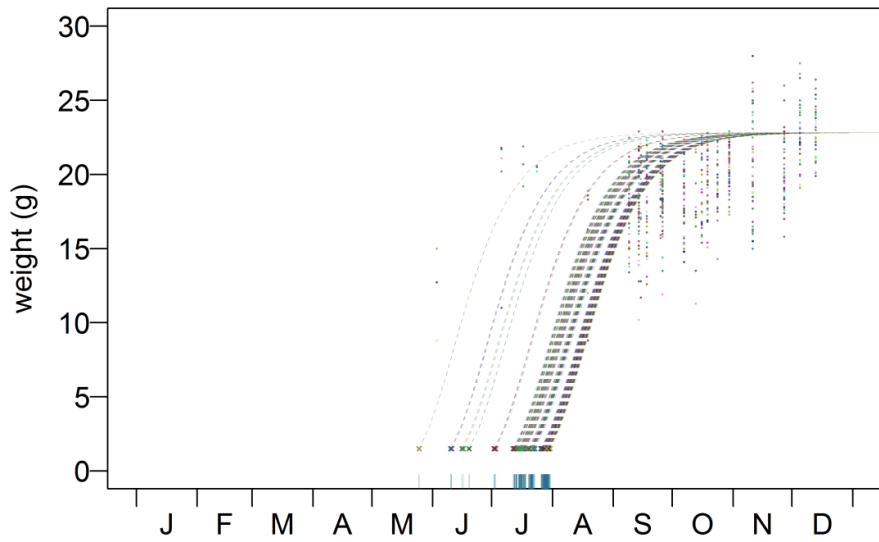


Figure 10. During the period of small population size in combination of low trapability, data is too scarce for proper analysis (May to August). During periods of high population density, individuals of various cohorts are available. Dots on the graph show individual captures during the study, the stipled lines represent potential growth curves of example individual mice from autumn catch. The x's represent predicted birthdates of each backtracked mouse.



## 7 Conclusions

The wood mouse would not have reached as far north as Iceland, crossing the ocean on its way, without human intervention. Iceland is north of the species' natural distribution range, an isolated island with unpredictable weather, low primary productivity and a short growing season of plants. Perhaps against the odds, the wood mouse has made a living in the harsh environment of Iceland, in the absence of competition from other rodents. This is a known case for other rodents that have been brought by humans to remote islands in north-west Europe, for example *Microtus levi* on Spitsbergen (Yoccoz et al. 1993; Stien et al. 2012).

Density estimates in the grassland of our study area were low compared to other habitats in northern Europe where population density has been recorded (Flowerdew 1985; Montgomery 1989a; Wilson et al. 1993). Population density in the mixed woodland of our study was ten times higher than at the grassland site in all seasons (Paper II). In a study in an open habitat of a maritime sand dune system in Scotland, assumed to have low carrying capacity, the population density was 50-90% higher than at the grassland of our study (Gorman & Zubaid 1993). At the Angelica field of south Iceland, autumn density values were five to ten times higher than at the grassland of our study (Bengtson et al. 1989a). These results suggest a striking contrast between habitat qualities within Iceland. Habitat patches of high quality can play an important role in maintaining the population despite being located north of the natural distributional range of the species (Angelstam et al. 1987).

It is not known if (or how) human-made structures, such as farmhouses of turf-and-rocks, were important for the success of the Icelandic wood mouse. Icelanders were few (only a few tens of thousands) and patchily distributed through the centuries. Farm activities were rather simple with low industrial impact before the latter half of the 20<sup>th</sup> century. Wood mice are, however, known for seeking shelter in buildings during the autumn and early winter. Therefore it is possible that the Icelandic wood mouse population has benefitted from human activities through the centuries.

In early winter, the wood mouse population in the grassland of our study was composed largely of newly recruited subadults. Some of the females bred in late summer and lactation extended into the autumn so they may have been physically unprepared for the onset of winter. Therefore a large proportion of the wood mouse population would not have been able to store sufficient food supplies and have to go out foraging regardless of the weather, facing the threat of hypothermia and/or risk of predation. Storing food in the nest is therefore vital for overwintering survival and access to food items suitable for storing can play an important role. In the grassland site of our study no tree seeds are available and very few plant species produce seeds large enough to make it possible for the mice to quickly accumulate large stores for the winter. This can be one of the reason why the open grassland of Kjalarnes peninsula is so poor in comparison to the woodland, the angelica field and other habitats within the natural range of the species (Watts 1969; Flowerdew 1985; Bengtson et al. 1989a,b; Montgomery 1989a,b; Wilson et al. 1993).

As the mice were young, inexperienced and with high energy demands, low survival at the onset of winter could be reflecting that some of them were simply not prepared for the cold temperature as they would not have selected habitat suitable for overwintering and/or stored sufficient food. Recent telemetry studies in arable farmlands suggest that wood mice move between micro habitats in accordance with seasonal changes in availability concerning disturbance, shelter and food abundance (Todd et al. 2000). Furthermore, on a smaller scale, mice have been shown to avoid open areas and select actively for certain food items, in accordance to breeding activities of the sexes due to differences in nutritional and energetic demands (Tew et al. 2000). Indeed, in this study, the last trapping census of the winter (April) is characterized by sex-biased trapping and rapid decline in male survival (Table AX3), at least at the grassland site.

Even though this study was unsuccessful in describing habitat selection throughout the winter statistically, it is clear from our results that various Icelandic habitat types differ in quality for sustaining viable wood mouse populations. Contrasting habitats of various sizes have most likely acted in a source-sink manner through time. Thus, it can be expected that wood mice have died out in some areas with low carrying capacity and re-colonized from adjacent source areas later on. Importantly, high environmental variability is often related to negative population growth and low density (e.g. Lewontin & Cohoen 1969; Barraquand et al. 2014). The Kjalarnes grassland resembles poor

habitat for wood mice with low carrying capacity and rapid population turnover. Nevertheless, the grassland mice seem to have compensated by increased breeding effort as some of the females appear to have given birth to up to three litters in the same summer, which is also the case in the angelica field in south Iceland (Bengtson et al. 1989a). The variation in body mass of autumn trapped mice in the woodland did not give the impression that there were as many generations as in the grassland (Figure 9).

The estimated birth dates from the Bayesian analysis of growth curves from body weight of live trapped mice were within the range of first potential births of the season as the first confirmed pregnancy of the spring was in late April (Table AX1). Thus, according to the potential length of gestation and lactating periods (Flowerdew 1977) the first generation of the summer would have been born in late April to early May and become trappable in mid-May or the first week of June (Figure AX2). In the three years of our study, one young (9,8g) was live-trapped in mid-May (2003) and six young (<14g) were trapped in early June (2002 and 2003). By dissecting mice from snap-traps, we found that three females had more placental scars than the previously published litter size of 4-9 (Bengtson et al. 1989a). This strongly suggests that some female mice had more than one litter in the season. Furthermore, two small females (body length of 7-8cm, in which we found placental scars, were almost certainly breeding in the summer of their own birth; one of them had probably also given birth to two litters (11 placental scars). According to this, at least some mice born in spring were able to breed twice before the onset of winter (Table AX1). As we assume that body size (length/weight) is a sign of age, these small females were believed to have been born in mid-summer. If so, the second cohort was also able to breed before winter.

The fact that more than one generation of females were participating in the summer breeding can at least partly explain the rapid population increase in the autumn, in agreement with other studies of this species (Flowerdew 1985; Montgomery 1989a; Wilson et al. 1993; Čiháková & Frynta 1996). Studies in southern Sweden and southern Iceland suggest that, in good conditions, female wood mice born in spring can breed up to three times in the same summer (Bergstedt 1965; Bengtson et al. 1989a).

The body mass of the wood mice in our study was in accordance with values from other studies in Iceland (Bengtson et al. 1976) and we did not find any evidence that Icelandic wood mice were symbolic for the island syndrome, with

higher body mass than continental populations (e.g. Sæmundsson & Degerbøl 1939; Angerbjörn 1986; Adler & Levins) nor do they follow the Bergmann rule (Meiri & Dayan 2003). As only a few overwintering mice survived (or were recaptured) during or after the second summer of their life, it is possible that only a small fraction of the wood mouse population of Kjalarnes grassland ever reach full adult size. Indeed, of all the male mice ( $n = 886$ ) trapped during the ten years of this study only 11 males exceeded 30g. These males were regarded to have lived two summers and reached a full body size. Females are more difficult to measure since pregnancy causes difficulty in estimating body mass. It appears, however, that females cease growth in breeding periods but gain weight only during the winter.

Breeding strategies have been suggested to differ in northern and southern areas in the way that southern populations have more litters per breeding season than the northern areas. This has been explained by milder climate and longer growth period for plants in southern areas. Wood mice in an angelica stand of south Iceland could indeed breed up to three times in one summer but only one litter was born in a birch wood of north Iceland (Bengtson 1989b). Strangely, the females at the grassland habitat of our study appeared to have bred two- to three times, despite the indication that the grassland site was poor in quality with low density and survival rates. From our study, it seems likely that females have adopted strategies that can maximize the breeding effort with trade-offs between growth and breeding. It would be interesting to look further into habitat related differences in growth and breeding strategies of the species and how weather can act on these factors. Unfortunately low trapability during the breeding season prevented sufficient sample sizes.

Stomach content analysis can give a good picture of diet and changes in food habits in time and space. It would, however be complimenting to look at stable isotopes (see e.g. Angerbjörn et al. 1994; Magnúsdóttir et al. 2014) in order to see if mice switch actively between plant and animal related food types with changes in breeding activity or other seasonal changes that might act differently on the sexes.

It would also be interesting to look into the population genetics of the species in various regions of Iceland. As large rivers may have acted as barriers, some populations may have become genetically isolated as has been shown to be the case for the arctic fox (Norén et al. 2009). Also, if sources and sinks occur in



Iceland, it is interesting to see from what types of habitats mouse populations re-colonized in periods followed by severe decline in the population.

A better understanding of the spatial distribution of the species in Iceland and what characterises better habitats in comparison to poorer ones would be very valuable. Especially during the winter, since weather seems to have so strong effects on overwintering survival, at least in some habitat types. This can be done for example by setting out plots in various habitat types and conduct live-trapping studies suited for the purpose (e.g. Montgomery 1989b). By comparing population growth rates between various habitat types, source-sink relationship, immigration/emigration, seasonal dispersal and/or population control could be identified.

Since so few mice were trapped in the spring and early summer, it still remains unanswered how life-history strategies act on the mice during the breeding season. It can be expected that females would become residential and have smaller home ranges since they were breeding and bound to their nest sites. On the other hand, it is likely that in April to May, males that have already mated with the females in the area would seek further and disperse in order to look for other acceptable females. Thus, dispersal or at least home range size at this time of the year would be assumed to differ by sex. This could be studied with the use of radio collars (e.g. Wolton 1983), that is if the mice would enter traps during this period. Perhaps future studies will figure out how to solve the seasonal problem of low trapability and then we could capture mice for any studies of interest. Until then, we have to get the best out of what we have and figure out the patterns in the long term.

Although more questions have arisen during the study period than have been answered, I hope that the results of this study have shed some light on the population ecology of the Icelandic wood mouse and that we now have a somewhat better idea how the wood mouse can manage so well in the land of volcanoes, sands, lavafields, coastal habitats and farmlands – with the absence of proper woodlands, the favourite habitats of the species near the core of its natural range.



# References

- Adamczewska-Andrzejewska, K.A. (1971). Methods of age determination in *Apodemus agrarius* (Pallas 1771). *Ann. Zool. Fennici* 8:68-71.
- Adler, G. H., & Levins, R. (1994). The island syndrome in rodent populations. *Quarterly Review of Biology* 69:473-490.
- Amstrup, S. C., McDonald, T. L., & Manly, B. F. (eds.). (2010). *Handbook of capture-recapture analysis*. Princeton University Press.
- Angelstam, P., Hansson, L., & Pehrsson, S. (1987). Distribution borders of field mice *Apodemus*: the importance of seed abundance and landscape composition. *Oikos* 50: 123-130.
- Angerbjörn, A. (1986). Gigantism in island populations of wood mice (*Apodemus*) in Europe. *Oikos* 47:47-56.
- Angerbjörn, A., Hersteinsson, P., Lidén, K., & Nelson, E. (1994). Dietary variation in arctic foxes (*Alopex lagopus*)-an analysis of stable carbon isotopes. *Oecologia*, 99(3-4), 226-232.
- Aplin, K. P., Brown, P. R., Jacob, J., Krebs, C. J. & Singleton, G. R. (2003). *Field methods for rodent studies in Asia and the Indo-Pacific*: Australian Centre for International Agricultural Research. Australia, Canberra. 220 pp.
- Armstrong, D. P., Davidson, R. S., Dimond, W. J., Perrott, J. K., Castro, I., Ewen, J. G., Griffiths, R. & Taylor, J. (2002). Population dynamics of reintroduced forest birds on New Zealand islands. *Journal of Biogeography* 29: 609-621.
- Arnason, A. (1974). Protein polymorphism in northern populations of field mice (*Apodemus sylvaticus* L.). PhD thesis, University of Strathclyde, Glasgow.
- Barraquand, F., Høye, T. T., Henden, J. A., Yoccoz, N. G., Gilg, O., Schmidt, N. M., Sittler, B. & Ims, R. A. (2013). Demographic responses of a site-faithful and territorial predator to its fluctuating prey: long-tailed skuas and arctic lemmings. *Journal of Animal Ecology*.
- Bengtson, S. A. (1975). Jaktbeteende hos en isländsk population av stenfalk. *Fauna Flora* 70: 8-12 (In Swedish with English summary).
- Bengtson, S. A., Nilsson, A., Nordström, S. & Rundgren, S. (1976). Body weights of *Apodemus sylvaticus* in Iceland. *Acta Theriologica* 21: 389-399.
- Bengtson, S. A., Brinck-Lindroth, G., Lundqvist, L., Nilsson, A. & Rundgren, S. (1986). Ectoparasites on small mammals in Iceland: origin and population characteristics of a species-poor insular community. *Ecography* 9: 143-148.

- Bengtson, S. A., Nilsson, A. & Rundgren, S. (1989a). Population structure and dynamics of wood mouse *Apodemus sylvaticus* in Iceland. *Holarct. Ecol.* 12: 351–368.
- Bengtson, S. A., Nilsson, A. & Rundgren, S. (1989b). Unforeseen disruption of wood mouse population dynamics after food reduction: a field experiment. *Oikos* 56: 379–385.
- Bergstedt, B. (1965). Distribution, reproduction, growth and dynamics of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linné) in southern Sweden. *Oikos*, 16: 132-160.
- Bergstrom, B. J. & Rose, R. K. (2004). Comparative life histories of Georgia and Virginia cotton rats. *J. Mammal.* 85: 1077–1086.
- Blower, J. G., Cook, L. M. & Bishop, J. A. (1981). Estimating the size of animal populations. London: George Allen and Unwyn.
- Bronson, F. H. (1989). Mammalian reproductive biology. Chicago: University of Chicago Press.
- Brown, J. H. & Lomolino, M. V. 1998. Biogeography 2nd edn. Sinauer Associates Inc, Massachusetts. 691 pp.
- Bujalska, G. & Grüm, L. (2005). Reproduction strategy in an island population of yellow-necked mice. *Popul. Ecol.* 47: 151–154.
- Burnham, K. P. & Anderson, D. R. (2002). Model selection and multimodel inference, 2nd edn. New York: Springer-Verlag.
- Chao, A. (1987). Estimating the population size for capture-recapture data with unequal catchability. *Biometrics* 43: 783-791.
- Chao, A., Chu, W. & Hsu, C-H. (2000). Capture-Recapture When Time and Behavioral Response Affect Capture Probabilities. *Biometrics* 56: 427-433.
- Čiháková, J. & Frynta, D. (1996). Abundance fluctuations in *Apodemus* spp. and *Clethrionomys glareolus* (Mammalia: Rodentia): a seven year study in an isolated suburban wood. *Acta Soc. Zool. Bohem.* 60: 3–12.
- Choquet, R., Reboulet, A. M., Pradel, R. & Lebreton, J. D. (2006). U-care (utilities–capture–recapture) user’s guide. CEFE/CNRS (ed.). Montpellier, France.
- Corbet, G. B. & Southern, H. N. (1977). The handbook of British mammals. Oxford: Blackwell publications. London: Blackwell. 520 pp.
- Cormack, R. M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* 51: 429–438.
- Dias, P. C. (1996). Sources and sinks in population biology. *Trends in Ecology & Evolution* 11: 326-330.

- Diffendorfer J. E. (1998). Testing models of source-sink dynamics and balanced dispersal. *Oikos* 81: 417-433.
- Drake, D., Mulder, C. P. H., Towns, D. R. & Daugherty, C.H. (2002). The biology of insularity: an introduction. *Journal of Biogeography* 29:563-569.
- Erlinge, S. (1987). Why do European stoats *Mustela erminea* not follow Bergmann's rule? *Ecography* 10: 33-39.
- Finerty, J. P. (1980). The population ecology of cycles in small mammals. *Mathematical theory and biological fact*. New Haven: Yale University Press.
- Flowerdew, J. R. (1977). Wood mouse *Apodemus sylvaticus*. In: *The handbook of British mammals*: 206-217. Corbet, G.B. & Southern, H.N. (Eds). London: Blackwell. 520 pps.
- Flowerdew, J. R. (1985). The population dynamics of wood mice and yellow necked mice. *Symp. Zool. Soc. Lond.* 55: 315-338.
- French, N.R., Stoddart, D.M. & Bobek, B. (1975). Patterns of demography in small mammal populations. In: Golley, F.B., Petruszewicz, K. & Ryszkowski, L. (eds) *Small mammals their productivity and population dynamics*. International Biological Programme, 5. Cambridge University Press, London. 451pp.
- Goltsman, M., Kruchenkova, E. P., Sergeev, S., Volodin, I., & Macdonald, D. W. (2005). 'Island syndrome' in a population of Arctic foxes (*Alopex lagopus*) from Mednyi Island. *Journal of Zoology* 267: 405-418.
- Gorman, M.L. & Zubaid, A. (1993). A comparative study of the ecology of woodmice *Apodemus sylvaticus* in two contrasting habitats: deciduous woodland and maritime sand-dunes. *J. Zool. (Lond.)* 229: 385-396.
- Gurnell J. & Rennolls K. (1983). Growth in field and laboratory populations of wood mice (*Apodemus sylvaticus*). *J. Zool.* 200:355-365.
- Haldane, J.B.S. (1956). The relation between density regulation and natural selection. *Proc. Roy. Soc. Lond. Ser. B.* 24: 306-308.
- Hanna, E., Jónsson, T. & Box, J.E. (2004). An analysis of Icelandic climate since the nineteenth century. *Int. J. Climatol.* 24: 1193-1210.
- Hansson, L. 1971, *Small Rodent Food, Feeding and Population Dynamics: A Comparison between Granivorous and Herbivorous Species in Scandinavia*. *Oikos* 22: 183-198.
- Hansson, L. 1985. The food of bank voles, wood mice and yellow necked mice. *Symp. Zool. Soc. Lond.* 55: 141-168.
- Hanski, I., Hansson, L. & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* 60: 353-367.
- Hanski, I. (1999). *Metapopulation ecology*. Oxford University Press Inc., New York.

- Hersteinsson P. (1984). The behavioural ecology of the Arctic fox (*Alopex lagopus*) in Iceland. Oxford University.
- Hersteinsson, P. & Macdonald, D. W. (1996). Diet of arctic foxes (*Alopex lagopus*) in Iceland. *Journal of Zoology*, 240(3), 457-474.
- Hersteinsson, P., Nyström, V., Jóhannsson, J.H., Guðjónsdóttir, B. & Hallsdóttir, M. (2007). Elstu þekktu leifar melrakka á Íslandi (In Icelandic with English abstract). *Náttúrufræðingurinn* 76: 13-21.
- Howald, G., Donlan, C., Galván, J. P., Russell, J. C., Parkes, J., Samaniego, A., Wang, Y., Veitch, D., Genovesi, P., Pacal, M., Saunders, A. & Tershy, B. (2007). Invasive rodent eradication on islands. *Conservation Biology* 21: 1258-1268.
- Hurrell, J.W. (1995). Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science* 269: 676-679.
- Ims, R. A., Henden, J.-A. & Killengreen, S. (2008). Collapsing population cycles. *Trends Ecol. & Evol.* 23: 79-86.
- Jensen P.M., Stenseth N.C. & Framstad E. (1993). Trapability of the Norwegian lemming (*Lemmus lemmus*). In: Ims R.A. & Stenseth N.C. (eds). *The biology of Lemmings*. The Linnean Society of London (pg. 547-554).
- Jolly, G.M. (1965). Explicit estimates from capture–recapture data with both death and immigration-stochastic model. *Biometrika* 52: 225–247.
- Jonsson, P. & Silverin, B. (1997). The estrous cycle in female wood mice (*Apodemus sylvaticus*) and the influence of the male. *Ann. Zool. Fennici* 34: 197-204.
- Jónsson, T. (2008). Past temperature conditions in Iceland. Online articles in climatology, nr. 1213. <http://en.vedur.is/climatology/articles/nr/1213>. January 17th 2014.
- Kanda, L. L. (2005), Winter energetics of Virginia opossums *Didelphis virginiana* and implications for the species' northern distributional limit. *Ecography* 28: 731–744.
- Korpimäki, E., Brown, P.R., Jacob, J. & Pech, R.P. (2004). The puzzles of population cycles and outbreaks of small mammals solved? *BioScience* 54: 1071–1079.
- Krebs, C. J. (1994). *Ecology: the experimental analysis of distribution and abundance* (Vol. 4). New York: HarperCollins College Publishers.
- Krebs, C.J. (1999). *Ecological Methodology* (2<sup>nd</sup> ed.). Addison-Wesley Educational Publishers, Inc. New York, USA. 620 pp.
- Krebs, C. J., Gaines, M. S., Keller, B. L., Myers, J. H., & Tamarin, R. H. (1973). Population Cycles in Small Rodents Demographic and genetic events are closely coupled in fluctuating populations of field mice. *Science*, 179(4068): 35-41.
- Krebs, C. J., Singleton, G. R., & Kenney, A. J. (1994). Six reasons why feral house mouse populations might have low recapture rates. *Wildlife Research* 21: 559-567.

- Layne J.N. (1968). Ontogeny. In: King J.A. (ed.) *Biology of Peromyscus (Rodentia)*. Am. Soc. Mammal. 2:148–253.
- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* 62: 67–118.
- Lewontin, R. C., & Cohen, D. (1969). On population growth in a randomly varying environment. *Proceedings of the National Academy of Sciences*, 62(4), 1056-1060.
- Lin, L. K., Nishino, T., & Shiraishi, S. (1993). Postnatal Growth and Development of the Formosan Wood Mouse *Apodemus semotus*. *J. Mamm. Soc. Japan* 18: 1-18.
- Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009). The BUGS project: evolution, critique, and future directions. *Stat. Med.* 28: 3049–3067.
- Lupton, P. & Wykes, U. (1938). The field mice of Iceland. *J. Anim. Ecol.* 7: 22–26.
- MacArthur, R. H. & Wilson, E. O., 2001, 13th edn. *The Theory of Island Biogeography*; With a new preface by Edward O. Wilson. Princeton Landmarks in Biology. Princeton University Press, 2001.
- McNab, B. K. (1971). On the ecological significance of Bergmann's rule. *Ecology* 52: 845-854.
- McNab, B.K. (1983). Energetics, body size, and the limits to endothermy. *J. Zool. (Lond.)* 199: 1–29.
- Meiri, S. & Dayan, T. (2003). On the validity of Bergmann's rule. *Journal of Biogeography* 30: 331-351.
- Meiri, S., Yom - Tov, Y., & Geffen, E. (2007). What determines conformity to Bergmann's rule? *Global Ecology and Biogeography* 16: 788-794.
- Mitchell-Jones, A. J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J. B. M., Vohralik, V. & Zima, J. (1999). *The Atlas of European Mammals*. London: T and AD Poyser Natural History.
- Montgomery, W. I. (1989a). Population regulation in the wood mouse, *Apodemus sylvaticus*. I. Density dependence in the annual cycle of abundance. *J. Anim. Ecol.* 58: 465–475.
- Montgomery, W. I. (1989b). Population regulation in the wood mouse, *Apodemus sylvaticus*. II. Density dependence in spatial distribution and reproduction. *J. Anim. Ecol.* 58: 477–494.
- Montgomery, W. I. (1989c). *Peromyscus* and *Apodemus*: patterns of similarity in ecological equivalents. In: Kirkland, G.L. and Layne, J.N. (eds) *Advances in the study of Peromyscus*, 293-366. Texas Tech University Press. pp. 366.
- Montgomery, S. S. J. & Montgomery W. I. (1990). Intrapopulation variation in the diet of the wood mouse *Apodemus sylvaticus*. *J. Zool. Lond.* 222: 641–651.

- Mysterud, A., Stenseth, N. C., Yoccoz, N. G., Langvatn, R., & Steinheim, G. (2001). Nonlinear effects of large-scale climatic variability on wild and domestic herbivores. *Nature* 410(6832): 1096-1099.
- National land survey of Iceland: [www.lmi.is/en/](http://www.lmi.is/en/). Visited on February 26<sup>th</sup> 2014.
- Nichols, J. D. (1986). On the use of enumeration estimators for interspecific comparisons, with comments on a “trapability” estimator. *Journal of Mammalogy* 67: 590-593.
- Nichols, J. D. & Pollock, K. (1983). Estimation methodology in contemporary small mammal Capture-Recapture Studies. *Journal of Mammalogy* 64: 253-260.
- Nielsen, Ó.K. (1986). Population ecology of the gyrfalcon in Iceland with comparative notes on the Merlin and the Raven. PhD thesis. Cornell University, Cornell.
- Nielsen, Ó.K. (1997). Observations on winter food habits of short-eared owl *Asio flammeus* in Iceland (In Icelandic with English summary). *Náttúrufræðingurinn* 67: 85–88.
- Norén, K., Angerbjörn, A. & Hersteinsson, P. (2009). Population structure in an isolated Arctic fox, *Vulpes lagopus*, population: the impact of geographical barriers. *Biological journal of the Linnean Society* 97: 18-26.
- Obrtel, R. & Holisova, V. (1979). Food eaten by *Apodemus sylvaticus* in a spruce monoculture. *Fol. Zool.* 28: 299.
- Ólafsdóttir, G. Á., Snorrason, S. S. & Ritchie, M. G. (2007). Morphological and genetic divergence of intralacustrine stickleback morphs in Iceland: a case for selective differentiation? *Journal of Evolutionary Biology* 20: 603–616.
- Ólafsdóttir, R., Schlyter, P. & Haraldsson, H. (2001). Simulating Icelandic vegetation cover during the Holocene. Implications for long-term land degradation. *Geogr. Ann.* 83: 203–215.
- Ólafsson, J. S. (1998). Icelandic wetlands, conservation and utilization (in Icelandic). University of Iceland Press, Reykjavik. 283 pp.
- Otis, D. L., Burnham, K. P., White, G. C. & Anderson, D. R. (1978). Statistical Inference from Capture Data on Closed Animal Populations. *Wildlife Monographs* 62: 3-135.
- Petersen, Æ. (1999). Fuglar Íslands (e. Icelandic Birds). Reykjavik (In Icelandic).
- Plesner-Jensen, S. (1996). Juvenile dispersal in relation to adult densities in wood mice *Apodemus sylvaticus*. *Acta Theriol.* 41: 177-186.
- Pollock K. H., Nichols J. D., Brownie C. & Hines J. E. (1990). Statistical inference for capture-recapture experiments. *Wildl. Monogr.* 107: 3-97.
- Post, E., Peterson, R. O., Stenseth, N. C. & McLaren, B. E. (1999). Ecosystem consequences of wolf behavioural response to climate. *Nature*, 401: 905-907.



- Pulliam, H. R. (1988). Sources, sinks, and population regulation. *American Naturalist* 132: 652-661.
- Roff, D. A. (2002). *Life history evolution*. Sinauer Associates, Inc. Sunderland, Massachusetts, USA.
- Rogers, L.M. & Gorman, M.L. (1995). The diet of the wood mouse *Apodemus sylvaticus* on set-aside land. *J. Zool. Lond.* 235: 77–83.
- Rosenszweig, M. L., 2000. *Species diversity in space and time*. Cambridge University Press.
- Seber, G. A. F. (1965). A note on the multiple-recapture census. *Biometrika* 52: 249–292
- Seber, G. A. F. (1973). *The estimation of animal abundance and related parameters*. J. W. Arrowsmith Ltd. Bristol. 506 pp.
- Selås, V., Framstad, E., & Spidsø, T. K. (2002). Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. *Journal of Zoology* 258: 459-468.
- Scholander, P. F., Hock, R., Walters, V. & Irving, L. (1950). Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.* 99: 259–271.
- Skirnisson, K. (1980). “Food habits of mink (*Mustela vison* Schreber) at River Sog, South Iceland.” *Náttúrufræðingurinn* 50: 46-56 (In Icelandic with an English summary).
- Skirnisson, K. (1993). Nagdýr á Íslandi (in Icelandic). pp. 327-346 in: Hersteinsson, P. & Sigbjarnarson, G. (eds) *Villt Íslensk Spendýr* (e. Wild Icelandic Mammals). Reykjavík.
- Skirnisson, K. (2004). Hagamús (in Icelandic). In: Hersteinsson, P. (ed) *Íslensk spendýr* (e. Icelandic mammals). Reykjavík.
- Skirnisson, K. & Petersen, A. (1980). pp. 80-94 in: Einarsson, Á. (ed). *Minkur* (in Icelandic). *Villt spendýr. Rit Landverndar, 7*. Reykjavík.
- Societas Europaea Mammalogica. <http://www.european-mammals.org>, May 2nd 2013.
- Southwood, T. R. E. & Henderson, P. A. (2000). *Ecological methods*. Blackwell Science Ltd. London. 575 pp.
- Stenseth, N. C., Myrsetrud, A., Ottersen, G., Hurrell, J. W., Chan, K. S., & Lima, M. (2002). Ecological effects of climate fluctuations. *Science* 297(5585): 1292-1296.
- Stien, A., Ims, R. A., Albon, S. D., Fuglei, E., Irvine, R. J., Ropstad, E., ... & Yoccoz, N. G. (2012). Congruent responses to weather variability in high arctic herbivores. *Biology letters*, 8(6), 1002-1005.

- Sæmundsson, B. & Degerbøl, M. (1939). Mammalia. The Zoology of Iceland 4: 1-52. Copenhagen.
- Sæther, B. E., Sutherland, W. J. & Engen, S. (2004). Climate influences on avian population dynamics. *Adv. Ecol. Res.* 35: 185–209.
- Sæther, B. E., Grötan, V., Tryjanowski, P., Barbraud, C., Engen, S. & Fulin, M. (2006). Climate and spatio-temporal variation in the population dynamics of a long distance migrant, the white stork. *J. Anim. Ecol.* 75: 80–90.
- Tanton, M. T. (1965). Problems of Live-Trapping and Population Estimation for the Wood Mouse, *Apodemus sylvaticus* (L.). *J. Anim. Ecol.* 34: 1-22.
- Tattersall, F. H., Macdonald, D. W., Hart, B. J. & Manley, W. (2004). Balanced dispersal or source-sink - do both models describe wood mice in farmed landscapes? *Oikos* 106: 536-550.
- Tew, T. E., Todd, I. A. & Macdonald, D. W. (2000). Arable habitat use by wood mice (*Apodemus sylvaticus*). 2. Microhabitat. *Journal of Zoology* 250: 305-311.
- Todd I. A., Tew T. E. and Macdonald D. W. (2000). Arable habitat use by wood mice (*Apodemus sylvaticus*). 1. Macrohabitat. *Journal of Zoology* 250: 299-303.
- Thomas, A., O'Hara, B., Ligges, U. & Sturtz, S. (2006). Making BUGS open. *R News* 6: 12–17.
- Van Horne, B. (1983). Density as a Misleading Indicator of Habitat Quality. *The Journal of Wildlife Management* 47: 893-901.
- Vandorpe, E., & Verhagen, R. (1979). An age reference model for the wood mouse, *Apodemus sylvaticus* (Linnaeus, 1758), by use of the lens technique. *Annal. Soc. Roy. Zool. Belg.* 109: 133-140.
- Wanless, R. M., Angel, A., Cuthbert, R. J., Hilton, G. M., & Ryan, P. G. (2007). Can predation by invasive mice drive seabird extinctions? *Biology Letters* 3: 241-244.
- Watts, C. H. S. (1969). The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Whytham Woods, Berkshire. *J. Anim. Ecol.* 38: 285–304.
- White, G. C. & Burnham, K. P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study (Supplement)* 46: 120–138.
- Whittaker, R. J. (2001). *Island Biogeography*. Oxford University press.
- Wilson, W. L., Montgomery, W. I. & Elwood, R. W. (1993). Population regulation in the wood mouse *Apodemus sylvaticus* (L.). *Mammal Rev.* 23: 73–92.
- Wolton, R. J. (1983). The Activity of free-ranging wood mice *Apodemus sylvaticus*. *Journal of Animal Ecology* 52: 781:794.

- Yoccoz, N. G., Ims, R. A., & Steen, H. (1993). Growth and reproduction in island and mainland populations of the vole *Microtus epiroticus*. *Canadian Journal of Zoology*, 71(12), 2518-2527.
- Yom-Tov, Y., & Geffen, E. (2006). Geographic variation in body size: the effects of ambient temperature and precipitation. *Oecologia* 148: 213-218.
- Zubaid, A. & Gorman, M. L. (1993). The effect of supplementary feeding upon the sizes of the home ranges of woodmice *Apodemus sylvaticus* living on a system of maritime sand-dunes. *J. Zool. (Lond.)* 231: 233–237.
- Zullinger, E. M., Ricklefs, R. E., Redford, K. H., & Mace, G. M. (1984). Fitting sigmoidal equations to mammalian growth curves. *J. Mammal.* 65: 607-636.



# Appendix

Unpublished data or analysis, collected in the study.

Table AX1 Breeding information from autopsies on females.

DATA FROM SNAP-TRAPPING PROCEDURE:

Month	Habitat	Body mass	Body leng	lact mice	Plac sc	Embryos
Apr	Coast	25.1	83	0		6
Apr	Coast	25.5	100	0		6
Sep	Coast	24.1	90	0	4	
Sep	Coast	26.8	94	1	4	
Sep	Coast	30.9	105	1	13+	
Sep	Coast	33.9	104	0	5	
Oct	Coast	24.5	105	0	4	
Oct	Coast	25.0	108	0	5	
<b>N =</b>	<b>45</b>		<b>n =</b>	<b>2</b>	<b>6</b>	<b>2</b>
Jun	Grassl	*	89	0		7
Aug	Grassl	25.0	79	1		
Aug	Grassl	29.1	105	1	6	
Sep	Grassl	20.7	98	0		5
Sep	Grassl	23.8	88	0	9	
Sep	Grassl	29.5	92	1	4	
Sep	Grassl	30.4	107	1	8	
Sep	Grassl	*	135	1	9	
Oct	Grassl	19.4	72	1	6	
Nov	Grassl	20.7	70	0	11+	
Dec	Grassl	26.1	108	0	6	
<b>N =</b>	<b>51</b>		<b>n =</b>	<b>6</b>	<b>8</b>	<b>2</b>
Aug	Wood	17.4	83	1		
Aug	Wood	35.5	112	1	9	7
Sep	Wood	26.8	102	0	16+	
Oct	Wood	25.4	106	0	2	
Oct	Wood	27.4	108	0	3	
<b>N=</b>	<b>29</b>		<b>n =</b>	<b>2</b>	<b>4</b>	<b>1</b>

Table AX 2. Breeding activity of mice from live-traps 2004-2005.

Woodland						
		<i>FEMALES</i>			<i>MALES</i>	
Trapping period		Lactating	Pregnant	Perf vag	Scrotal	N
2004	Sep	2	1	3	6	55
	Oct					56
	Dec					54
2005	Jan			2	1	19
	Apr			5	4	12
	May			1	3	9
	Jun		2		3	8
	Jul	2	2			2
	Sep	1	1		1	20
	Oct					57

Grassland						
		<i>FEMALES</i>			<i>MALES</i>	
Trapping period		Lactating	Pregnant	Perf vag	Scrotal	N
2004	Sep	13	3	12	18	93
	Oct					63
	Dec					82
2005	Jan			7		51
	Apr			8	17	60
	May				2	3
	Jun	1			3	4
	Jul					5
	Sep	5			5	33
	Oct				1	37

Figure AX 1. Relative testis length of dissected males from snap traps.

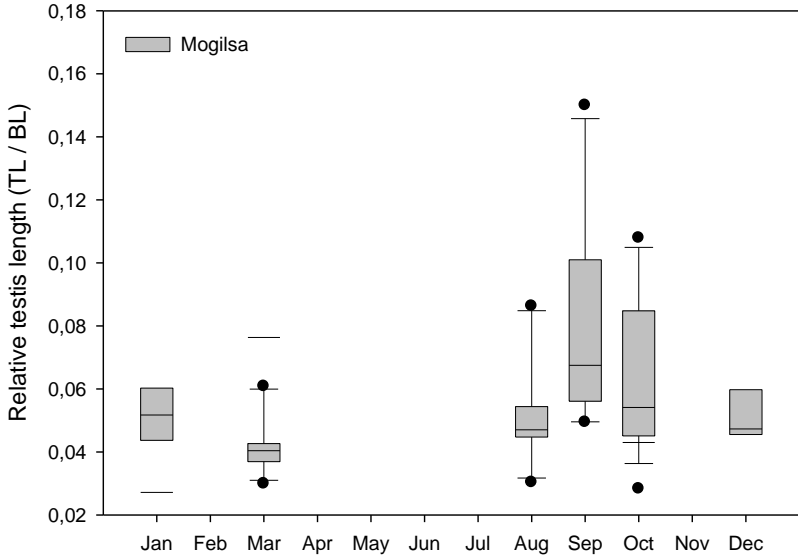
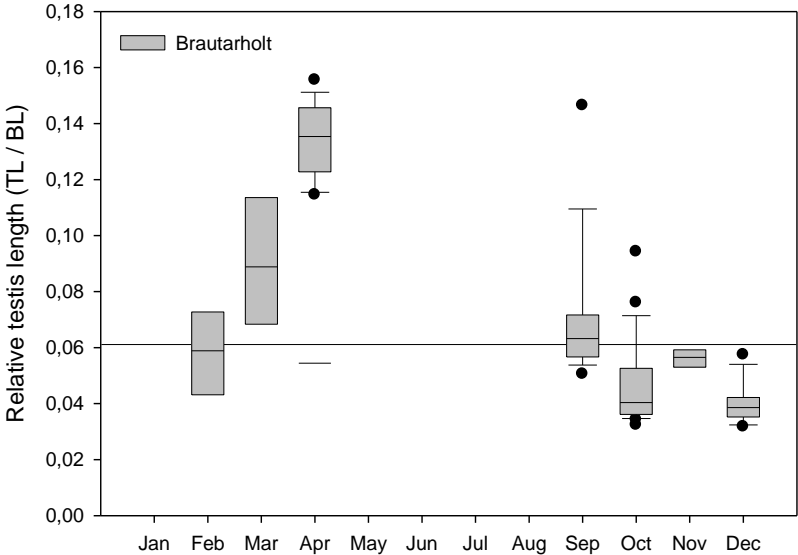




Table AX3. Various population parameters and sample statistics from (a) Kjalarnes grassland, (b) Mogilsa woodland from September 2004 to April 2005. The term trap cases explains how often males and females are trapped in the census. Below is the same table with data from Kjalarnes grassland trapping from September 2001-October 2003.

Census Month	Individual mice (females)	Sex ratio males/females	Mean body mass (females)	SE Bm males (females)	Trap cases males (females)	Estimated survival / mon	Estimated population density m/ha	Per capita growth rate /mon
<i>a) Grassland</i>								
1 Sep.	40(52)	0.8	20.1(18.2)	0.36(0.37)	61(74)		3.1 +/- 0.8	
2 Oct.	29(38)	0.8	18.9(17.3)	0.41(0.31)	71(84)	0.4	2.8 +/- 0.16	-0.13
3 Nov.	45(36)	1.3	20.3(19.7)	0.32(0.39)	109(93)	0.78	3.3 +/- 0.14	0.13
4 Jan.	26(25)	1	22.2(21.1)	0.44(0.93)	86(72)	0.75	2.0 +/- 0	-0.24
5 Apr.	19(8)	2.4	29.8(24.8)	0.83(0.60)	42(17)	0.67	1.1 +/- 0.13	-0.25
<i>b) Woodland</i>								
1 Sep.	31(24)	1.3	20.4(19.9)	0.43(0.94)	38(37)		30.8 +/- 8.42	
2 Oct.	31(25)	1.2	19.8(17.7)	0.38(0.55)	83(70)	0.61	19.8 +/- 0.76	-0.47
3 Nov.	34(19)	1.8	22.9(21.6)	0.38(0.79)	85(38)	0.63	19.7 +/- 1.31	-0.01
4 Jan.	11(8)	1.4	24.1(23.4)	0.97(0.52)	27(17)	0.58	6.8 +/- 0	-0.54
5 Apr.	7(5)	1.4	29.9(24.2)	0.93(0.31)	17(13)	0.64	4.3 +/- 0	-0.24

Census	Month	Individual males (females)	Sex ratio males /females	Mean body mass males (females)	SE mass males (females)	Trap cases males (females)	Estimated survival / mon	Population density m/ha	95% CL Pop dens	Per capita growth rate /mon
1	Sep. 01	40(29)	1.38	19.3(19.4)	3.94(6.35)	52(39)		3.91	1.122	
2	Oct. 01	68(61)	1.11	19.3(18)	3.89(4.54)	113(102)	0.40(0.65)*	5.50	0.304	0.36
3	Nov. 01	52(45)	1.16	21.1(18.9)	3.44(2.89)	92(92)	0.56(0.86)**	3.95	0.364	-0.28
4	Jan. 02	15(11)	1.36	23.1(22.3)	1.80(2.21)	26(28)	0.51(0.81)**	0.91	0.112	-0.58
5	Mar. 02	23(17)	1.35	25.6(21.8)	2.79(1.51)	45(40)	0.48(0.98)**	1.40	0.129	0.26
6	Apr. 02	16(17)	0.94	28.8(26.0)	2.42(4.12)	35(43)	0.11(0.47)*	1.12	0.076	-0.16
7	Jun. 02	6(6)	1.00	29.2(28.7)	3.28(2.80)	11(10)	0.71(0.70)***	0.45	0.140	-0.83
8	Jul. 02	4(3)	1.33	21.4(25.17)	1.94(2.45)	4(3)		0.20	MNA	
9	Aug. 02	10(16)	0.63	19.5(22.42)	5.64(6.81)	16(30)		1.30	0.446	0.41
10	Sep. 02	51(57)	0.89	18.4(19.7)	2.74(5.03)	84(99)		4.49	0.532	1.42
11	Oct. 02	43(45)	0.96	19.5(18.5)	2.30(2.80)	65(65)	0.54	3.62	0.469	-0.19
12	Dec. 02	31(25)	1.24	23.1(20.1)	2.30(1.63)	67(64)	0.69	1.94	0.125	-0.35
13	Jan. 03	23(24)	0.96	23.2(21.3)	2.38(1.99)	48(65)	0.85	1.60	0.094	-0.18
14	Feb. 03	25(31)	0.81	23.8(22.0)	2.75(2.19)	55(74)	0.9	1.96	0.138	0.17
15	Apr. 03	22(24)	0.92	29.9(23.6)	2.55(2.57)	38(60)	0.8	0.80	0.151	-0.67
16	May. 03	7(14)	0.50	31.6(27.8)	2.58(2.39)	13(29)	0.71	0.81	0.148	0.01
17	Jun. 03	17(15)	1.13	26.8(26.9)	7.90(5.65)	24(27)		0.67	MNA	
18	Jul. 03	8(3)	2.67	26.0(26.1)	5.73(3.43)	9(3)		1.73	MNA	
19	Aug. 03	23(26)	0.88	20.5(20.1)	6.89(9.52)	29(34)		3.04	1.128	0.51
20	Sep. 03	72(86)	0.84	19.3(18.9)	2.67(3.01)	103(122)		8.13	1.274	0.53
21	Oct. 03	92(72)	1.28	21.1(20.2)	1.92(2.47)	145(132)		6.62	0.618	-0.18

\* males(females), \*\* transients(residents), \*\*\* March-April residents; males(females)

# Some idea of the process in the summer – a timeline diagram...

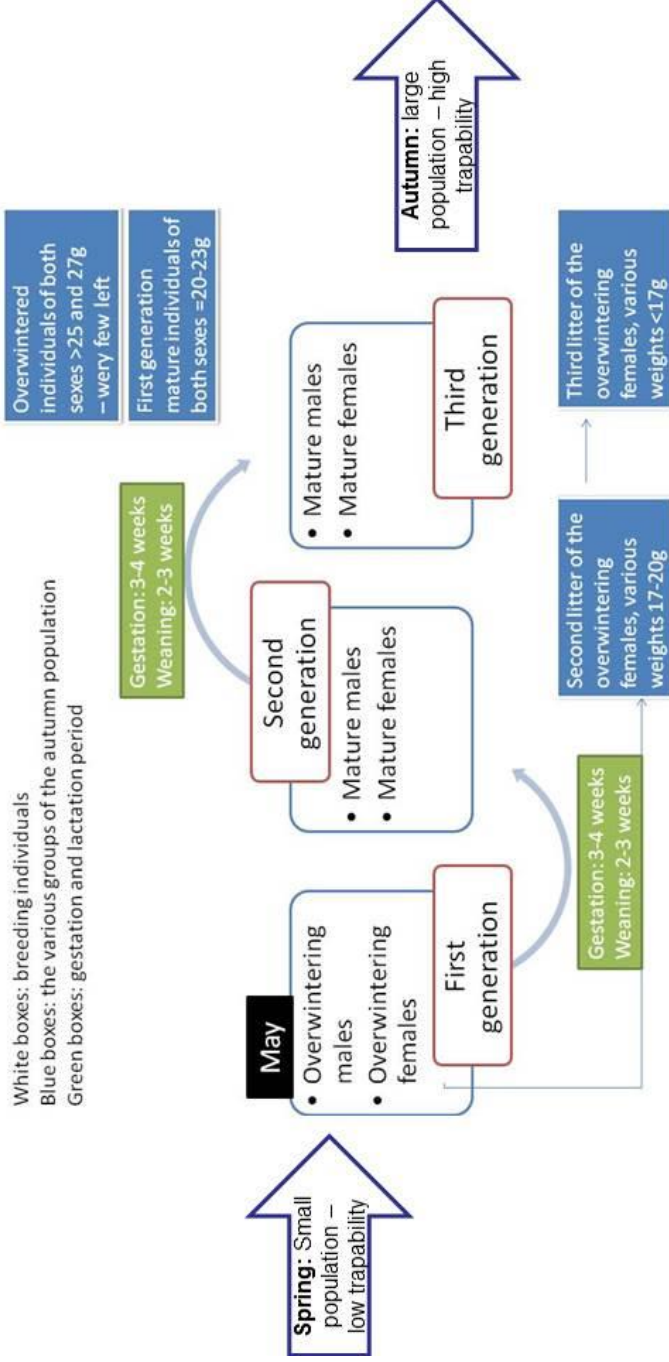


Figure AX2. A diagram of the potential population composition and recruitment process during the breeding season.



# Paper I

*Limiting factors*



# Surviving north of the natural range: the importance of density independence in determining population size

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## Keywords

*Apodemus sylvaticus*; climate; population dynamics; range edge; wood mouse.

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## Abstract

The relative importance of density-dependent and -independent processes in determining population density has been predicted to vary according to whether the population concerned is located near the centre or the periphery of the species' range. Thus, density-independent processes should be more pronounced near the periphery. The long-tailed wood mouse *Apodemus sylvaticus* in Iceland is at the northern and western edge of its geographical range. We estimated the autumn population density in an open habitat in south-western Iceland in 9 years out of 10 during 1996–2005 in order to monitor the annual maximum population size. Furthermore, we estimated population density and survival at *c.* 5-week intervals from September 2001 to October 2003 and from September 2004 to November 2005 in order to reveal the causes of variation in maximum population size. The estimated autumn population density was low, ranging from 2.7 to 8.9 mice ha<sup>-1</sup> while spring densities ranged from 0.4 to 0.8 mice ha<sup>-1</sup>. Apparent monthly survival probabilities ranged from 0.4 to 0.7 per month in autumn and 0.7 to 0.9 in winter. Our results suggest that low temperature in early winter (October–December) is the major determinant of population density in the following autumn, explaining 74% of the variation in autumn population density. No significant correlation was found between either the NAO index or the NAO winter index and variation in wood mouse population density in autumn. Differential mortality in early winter results in variation in spring population size. This study shows clear evidence of density-independent control of a mammal population at the edge of its geographical range as opposed to the mostly density-dependent control previously recorded near its centre of distribution.

## Introduction

Ecologists have long tried to understand the population processes that determine the edge of a mammal population's geographical range. Where there are no physical barriers, climate has often been implicated as a limiting factor, because the limits to the distribution of species often coincide with climatic conditions (Krebs, 1994; Rosenzweig, 1995; McNab, 2002; Gaston, 2003). The size and growth rate of a population are determined by the interaction of density-independent factors, such as climatic variation, and density-dependent processes, such as intraspecific competition (Enright, 1976), and may act differentially on individual sex and age classes (Milner, Elston & Albon, 1999; Mysterud *et al.*, 2000) and according to season (Stenseth, Bjørnstad & Saitoh, 1998). Density-independent climatic processes often act through resource availability (Enright, 1976; Forchhammer *et al.*, 1998; Mysterud *et al.*, 2000). Ice formation in the subnivean space is a major determinant of winter survival in voles in Fennoscandia, especially by restricting their movements and reducing plant biomass available to

them (Aars & Ims, 2002; Korslund & Steen, 2006). It has recently been shown that several climatic variables will often act in concert, explaining why the NAO (Hurrell, 1995) is frequently better correlated with inter-annual variation in population size than individual climatic variables (Post *et al.*, 1997; Hallet *et al.*, 2004; Stenseth & Mysterud, 2005).

Haldane (1956) was one of the first to predict that the contribution of stochastic density-independent processes would be generally of greater importance in this regard at or near the edge of a population's distribution range than at its centre, particularly where the range edge is determined by climate. This has since been confirmed by a number of studies (e.g. García & Arroyo, 2001; Sanford, 2002; Williams, Ives & Applegate, 2003).

Sæther, Sutherland & Engen (2004) showed that the density-independent effects of climate on population size in birds can be sub-divided into effects of climate during the breeding season on the one hand and in the non-breeding season on the other. In mammals, a longer non-breeding season in northern areas has been shown to reduce winter survival in cotton rats *Sigmodon hispidus* (Bergstrom &

Rose, 2004), deer mice *Peromyscus maniculatus* (Bronson, 1989) and raccoon dogs *Nyctereutes procyonoides* (Helle & Kauhala, 1991), and thus affect the northern limits to their distribution, but winter climate as such has not been shown to affect these populations.

The wood mouse *Apodemus sylvaticus* L. is distributed throughout most of continental Europe, from the Mediterranean Sea in the south to southern Scandinavia in the north and from the Iberian Peninsula in the west to western Asia in the east. It is also found throughout the British Isles and has been introduced by humans in northern Africa and Iceland (Corbet & Harris, 1991; Mitchell-Jones *et al.*, 1999). In northern Europe, its seasonal cycle is characterized by a low population density at the outset of the breeding season in early spring and a maximum at the end of the breeding season in late autumn (Flowerdew, 1985; Bengtson, Nilsson & Rundgren, 1989a; Montgomery, 1989a; Wilson, Montgomery & Elwood, 1993; Čiháková & Frynta, 1996). Autumn population density varies considerably and is generally correlated with food availability, in particular seed abundance, both in space and in time (Watts, 1969; Montgomery, 1989b; Montgomery & Montgomery, 1990; Montgomery *et al.*, 1991; Gorman & Zubaid, 1993; Zubaid & Gorman, 1993). Thus, deciduous woods generally have a high density, varying from about 20 to >50 mice ha<sup>-1</sup>, depending on the dominant species, while in grassland and arable land in England the wood mouse population density was 15–20 mice ha<sup>-1</sup> (Wilson *et al.*, 1993). Gorman & Zubaid (1993) showed that the peak population density in a maritime sand-dune system in Scotland was consistently 10–12 mice ha<sup>-1</sup> in 5 years of study while in deciduous woodland it was 25–55 mice ha<sup>-1</sup>. Importantly, Montgomery (1989a) found that the population growth rate from spring to autumn was density dependent such that a low population density in spring would result in a higher rate of growth and the autumn increase would continue for longer when the initial population density was low, and that population density at the onset of the breeding season accounted for about a quarter of the variation in autumn peak abundance.

Wood mice arrived in Iceland with early settlers from Scandinavia and the British Isles in the 9th and 10th centuries (Lupton & Wykes, 1938; Arnason, 1974; Bengtson *et al.*, 1986). The species became successfully established throughout lowland Iceland, well north of its natural range, as the only non-commensal rodent species (Bengtson, Nilsson & Rundgren, 1989b). Only two other rodent species have become established, the house mouse *Mus musculus* L. and brown rat *Rattus norvegicus* L., both of which are commensal. At the time of settlement, birch woods *Betula pubescens* were common in lowland regions in Iceland. Since then, the forest cover has been drastically reduced and is now about 1–2% of the country. The typical vegetation cover in lowland areas is now open grassland due to agricultural practices (Ólafsdóttir, Schlyter & Haraldsson, 2001; Haraldsson & Ólafsdóttir, 2003).

While winters are not very cold for the latitude due to the warming effects of the Gulf Stream (–1 to +1 °C in

January), summers are distinctly colder (8–11 °C in July) (Hanna, Jónsson & Box, 2004) than elsewhere in the geographical range of the species. It was thus of interest to study wood mouse population processes in Iceland in comparison with populations closer to the centre of the species' range. We predicted that density-independent factors, climate in particular, should dominate among variables determining variation in population density. In view of the cold summers, we predicted that climate during the breeding season would be the most important predictor of autumn population density.

## Methods and materials

### Study area

The study area is located at the tip of Kjalarnes Peninsula in south-western Iceland (64°14.035'N, 21°54.017'W). It is composed of cultivated hayfields with drainage ditches, uncultivated meadows and a narrow coastal habitat (Fig. 1), being surrounded on three sides by the sea. The approximate length of the ditches is 4.5 km and the length of the coastline 3.5 km. The fields are harvested once every summer, usually in late July or in early August.

The live trapping area was located *c.* 2 km from the nearest building. Besides long-tailed wood mice, 10 house mice were the only rodents trapped during the study. No cats *Felis catus* or arctic foxes *Vulpes lagopus* were known to be in the area but birds of prey were occasionally observed (e.g. short-eared owl *Asio flammeus* L.), and one to two feral minks *Mustela vison* Schreber were trapped annually in the general area (G. Björnsson, pers. comm.). There are no monitoring programmes on predatory species in the area and therefore no information is available that could be related to the population dynamics of wood mice.

### Trapping

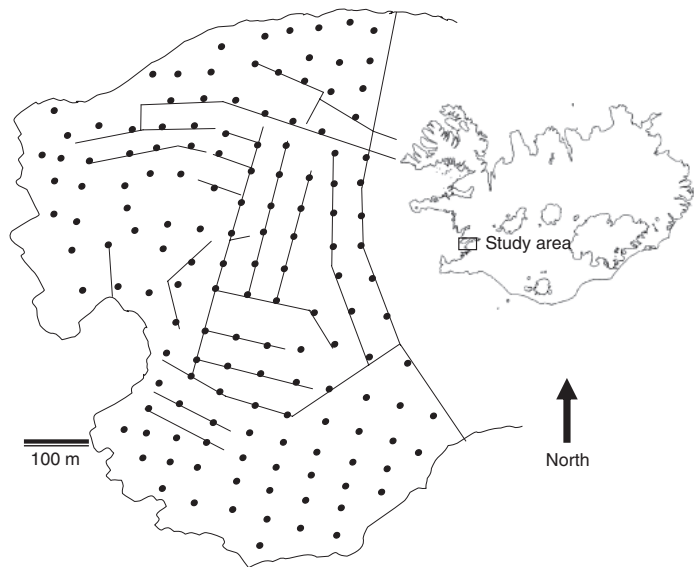
A grid of 145 Longworth live traps (©BTR, Penlon Ltd., Abingdon, Oxfordshire, UK) was set out in an area of 35 ha with a trap interval of about 45 m (Fig. 1). Some Icelandic wool (Ístex ehf, Blönduós, Iceland) and commercial rodent feed (Special Diet Services, Witham, Essex, UK) were placed in the traps.

Annual live trapping for density estimation was conducted in 5-day sessions (capture periods) each autumn between 1996 and 2005, except 1999. The mean date for all years was 3 October but varied between 25 September and 17 October.

Seasonal capture periods to record variation in population density and survival took place approximately every fifth week from September 2001 to October 2003 (21 capture periods) and from September 2004 to November 2005 (11 capture periods).

Captured mice were individually marked, originally by tattoo on the legs and tail, but from autumn 2000 with microtags (Indexel<sup>®</sup> Merial, Lyon, France) such that they





**Figure 1** Map of the study area and location in south-western Iceland ( $64^{\circ}14.035'N$ ,  $21^{\circ}54.017'W$ ). Dots and lines indicate individual trap stations and ditches, respectively.

could be identified by the use of a pocket reader (Pocketreader<sup>®</sup>, Destron Fearing, St Paul, Minnesota, USA). Animals caught were weighed (precision 0.1 g) and information about sex and reproductive status was noted before releasing them at the same location at which they had been trapped.

Trapping methodology was approved by The Icelandic Food and Veterinary Authority and The Icelandic Ministry of the Environment. We did not observe any negative effects of tagging during our study.

### Meteorological data

Meteorological data were obtained from The Icelandic Meteorological Office ([http://andvari.vedur.is/vedurfar/yfirlit/medaltalstoflur/Stod\\_001\\_Reykjavik.ManMedal.txt](http://andvari.vedur.is/vedurfar/yfirlit/medaltalstoflur/Stod_001_Reykjavik.ManMedal.txt)) for Reykjavik, a station that can be regarded as representative for the maritime climate of southern and western Iceland, and is located 11 km south of the study area. During the period of study, the mean temperature ranged from  $-3.3$  to  $4.5^{\circ}\text{C}$  (median:  $0.35^{\circ}\text{C}$ ) in mid-winter (December–March) and from  $8.4$  to  $12.8^{\circ}\text{C}$  (median:  $10.8^{\circ}\text{C}$ ) in mid-summer (June–August). Monthly precipitation ranged from 20.5 to 157.5 mm (median: 78.3 mm) in winter and from 16.1 to 101.1 mm (median: 59.8 mm) in summer. The mean wind speed ranged from  $3.3$  to  $7.5\text{ m s}^{-1}$  (median:  $5.6\text{ m s}^{-1}$ ) in winter and from  $2.6$  to  $5.9\text{ m s}^{-1}$  (median:  $4.0\text{ m s}^{-1}$ ) in summer. Hours of sunshine ranged from 1.3 to  $165.4\text{ h month}^{-1}$  (median:  $38.3\text{ h month}^{-1}$ ) in winter and  $74.8$  to  $272.1\text{ h month}^{-1}$  (median:  $158.2\text{ h month}^{-1}$ ) in summer.

Various weather variables were weighed against autumn density and monthly survival as well as the NAO winter

index (The Climate Analysis Section, NCAR, Boulder, CA, USA; <http://www.cgd.ucar.edu/cas/jhurrell/indices.html>).

### Statistical analysis

The trapping protocol follows a robust design as suggested by Pollock *et al.* (1990), and population size for each capture period (closed captures) and survival between capture periods (open captures) were estimated using program MARK 4.3 (White & Burnham, 1999). Other statistical analyses were carried out using the software package R, 2.6.1 (© 2007 The R foundation for statistical computing).

### Population estimates

We assumed that the population was closed during the short sampling period (5 days), with recruitment and deaths negligible. The population size for each capture period was estimated using model  $M_i$ ;  $\{Np(t) = c(t)\}$  (Otis *et al.*, 1978; Pollock *et al.*, 1990) in program MARK with the sin link function on  $p$  and  $c$  and the log link function on  $N$ . The notation  $p$  is the probability of initial capture,  $c$  is the probability of recapture,  $t$  is the time and  $N$  is the abundance.

When too few mice were caught (mainly in June and July) for estimates based on CMR, we used minimum number known to be alive to estimate the population size (Blower, Cook & Bishop, 1981).

We determined the effective trapping area by adding a strip of land on the eastern border of the study site, whose width equalled the radius of a circular home range of caught mice. Home range was calculated as the average minimum convex polygon range of trap locations of all mice caught six or more times during the time of the study. The effective

trapping area was used when converting population size to population density (mice ha<sup>-1</sup>).

## Survival

Monthly survival analysis was based on recapture data from September to June during each year of monthly monitoring (2001–2002, 2002–2003 and 2004–2005), using program MARK. Low sample size made survival analysis during summer impossible. Furthermore, with only one exception, each late summer and early winter trapping consisted solely of a new cohort of mice born the very same summer.

To test for possible failure of the assumptions underlying the CJS models for survival estimates (Cormack, 1964; Jolly, 1965; Seber, 1965), we used Test 2.CT and Test 3.SR (Lebreton *et al.*, 1992) in Program U-care 2.2.5 (Choquet *et al.*, 2006).

The results of Test 3.SR suggested a significant proportion of transients in the first year, 2001–2002 (for males:  $\chi^2 = 14.24$ , d.f. = 5,  $P = 0.014$ ; and females:  $\chi^2 = 11.81$ , d.f. = 4,  $P = 0.02$ ), but not for the other years. Transients are defined as individuals that were never recaptured after the initial capture–mark–release or that have considerably low survival from initial capture until first recapture. Transient individuals could also have died after release or emigrated out of the study area but we are unable to distinguish between those possibilities and so their fates remain unknown. Hence, resident individuals are those previously captured, marked and remaining in the population until the next capture period (Lebreton *et al.*, 1992; Pradel *et al.*, 1997). Therefore, first intervals represent a mixture of transient and resident animals but the later intervals mainly have residents. Test 2.CT was significant for trap response in males:  $\chi^2 = 12.85$ , d.f. = 2,  $P = 0.002$  and close to significance in females:  $\chi^2 = 5.28$ , d.f. = 2,  $P = 0.07$  in the last year (2004–2005), but not in the other years. To adjust for transients we used age-specific models (Lebreton *et al.*, 1992) to differentiate between survival estimates for those newly marked (first recapture) and those previously marked (residents). These models are also useful for identifying possible handling effects on animals at first capture (Brownie & Robson, 1983). Because we were dealing with relative age but not real age, we used *m*2 to denote that the model has two ‘relative age groups’: those recaptured for the first time and those recaptured subsequently; the slash bar distinguishes between them. Time-dependent models include *t* for time and sex-dependent models include *s* for sex. Survival is symbolized with ‘ $\Phi$ ’ and recapture rate with *p*.

We started with the most complex model, containing the variables of interest. In relation to our hypothesis, we assumed time and sex differences in survival and recapture probabilities. By simplifying each section of the model systematically, we worked through to the null model, assuming constant survival and recapture probability. In all, we fitted 12 models for 2002–2003 and 2004–2005 but 36 models for 2001–2002 due to the above-mentioned problems. By comparing the models, we could see the effects of varying parameters of *p* and  $\Phi$ , with or without ‘age’

effects, according to time (*t*) and sex (*s*) or left to remain constant (.).

Model selection was made by Akaike’s information criterion (AIC) and based on AIC<sub>c</sub> weights due to small sample sizes in some months (Burnham & Anderson, 2002). The most parsimonious models to explain variation in the data (lowest AIC<sub>c</sub> weight) were used for presentation.

In all 3 years, some of the first models were similar (AIC<sub>c</sub> < 2) and thus, results for survival and recapture are based on model averaging (Burnham & Anderson, 2002), performed in program MARK. Averaged models represent apparent monthly survival and recapture rate estimates and standard errors of the values.

Number of capture periods and interval length between capture periods differed between years; thus, all interval lengths were transformed into months (31 days) to be comparable.

## Weather

The following weather variables: minimum temperature, maximum temperature, temperature differences, precipitation and wind speed, were used as predictors in a stepwise multiple regression analysis with population parameters (monthly survival and autumn population density) as the dependent variables. A series of regression analyses were carried out with and without interactive terms. Monthly values for each weather variable were either used separately or pooled to seasons when used as predictors in the models. Preliminary check indicated an interaction term between temperature differences and minimum or maximum temperature, and therefore we only used one of these variables in each model.

When comparing the weather data, we divided the year into two seasons, winter and summer, roughly coinciding with the non-reproductive period of the mice (October–April) and the reproductive period (May–September), respectively. The seasons were further subdivided into early winter (October–December), late winter (January–April), early summer (May–July) and late summer (August–September).

Model selection was made by performing stepwise AIC in program R, and the most parsimonious model was used in explaining the association between weather and either autumn population density or monthly survival.

## Results

### Annual variation in autumn population density

Population density in autumn showed little variation between years (Fig. 2) with the exception of 2 peak years, occurring at a 5-year interval. Estimated population densities ( $\pm$  SE) were the highest in autumn 1998 ( $8.9 \pm 0.59$  mice ha<sup>-1</sup>) and 2003 ( $8.1 \pm 0.65$  mice ha<sup>-1</sup>). The lowest autumn densities were in the years 2004 and 2005 ( $3.1 \pm 0.41$  and  $2.7 \pm 0.63$  mice ha<sup>-1</sup>, respectively).

### Effect of weather on autumn population density

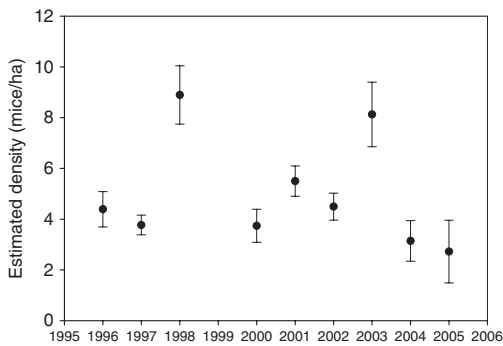
There was a clear positive correlation between minimum temperature in early winter (October–December) and population density the following autumn ( $R^2 = 0.74$ ; slope = 1.0005; SE = 0.22; d.f. = 1, 7;  $P$ -value = 0.003).

No correlation was found between autumn population density and temperature variables (minimum or maximum) in other seasons, nor with wind speed, precipitation or hours of sunshine in any season during the preceding 12 months. Interacting models, including all or some weather variables, did not improve the overall performance of the simplest and most parsimonious model.

No significant association was found between the NAO index or the NAO winter index and the maximum autumn population density of the wood mice.

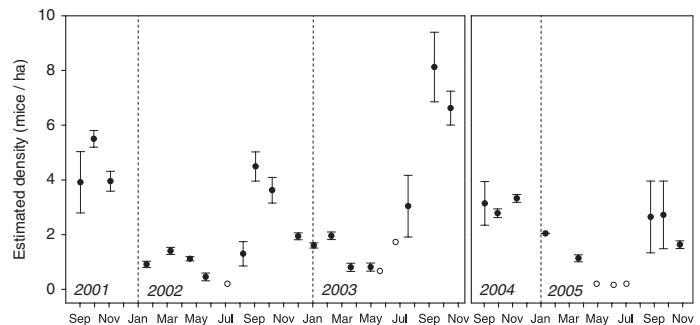
### Seasonal population dynamics

Seasonal fluctuations showed the typical northern European pattern of wood mouse autumn maximum and spring minimum population density (Fig. 3). Absolute densities ranged between  $0.5 \pm 0.07$  (2002) and  $0.8 \pm 0.08$



**Figure 2** Estimated autumn population density of wood mice *Apodemus sylvaticus* at the study area, Kjalarnes Peninsula, south-western Iceland, in 1996–2005. No estimate is available for 1999. Vertical bars show 95% confidential limits.

**Figure 3** Estimated population density of wood mice *Apodemus sylvaticus* at the study area at Kjalarnes Peninsula, south-western Iceland, September 2001 to October 2003 and September 2005 to October 2005. Vertical bars show 95% confidential limits. The open dots mark estimates using minimum number known to be alive. Dotted vertical lines correspond to January each trapping year.



(2003) mice  $\text{ha}^{-1}$  during the spring minima and  $2.7 \pm 0.63$  (2005) and  $8.1 \pm 0.65$  (2003) mice  $\text{ha}^{-1}$  in the autumn maxima. In all 3 years, the population density decreased quite rapidly at the onset of winter and then more slowly until the spring minimum was reached. From the small population in spring, the approximately sevenfold increase up to the autumn maxima took about 4 months.

### Seasonal variation in survival

The model results for survival analysis (Table 1) were similar for the winters 2002–2003 and 2004–2005 but considerably different for the first year (2001–2002). Transient or ‘age-specific’ models were most important the first winter, showing both a sex- and a time-specific difference in survival, but no time differences in recapture. The sex effects were stronger for the ‘transients’ (left side of the slash bar), but time effects were stronger for the ‘residents’ (right side of the slash bar).

The winters 2002–2003 and 2004–2005 had the same three most relevant models, none of which had sex effects but all had time effects in survival. Recapture was more or less constant or differed by sex (Table 1).

Apparent monthly survival in the first intervals (mixture of transient and resident animals) was almost half as low as the later intervals (resident animals) for both sexes in the year 2001–2002. Monthly survival values ( $\pm$  SE) in the first interval were  $0.40 \pm 0.08$  for males and  $0.65 \pm 0.09$  for females, while for all resident animals, survival probability ranged from 0.80 to 0.98 throughout the winter (Table 2a).

In the winter 2002–2003, apparent monthly survival ranged from 0.54 to 0.90, lowest at the onset of winter and highest in mid-winter (Table 2b). In the winter 2004–2005, monthly survival was as low as 0.39 at the onset of winter but increased up to 0.75–0.79 in mid-winter. In late winter, survival declined again and was 0.17 in the spring (Table 2c).

### Discussion

In this study, we have found evidence of density-independent control of a mammal population at the edge of its geographical range as opposed to the mostly density-dependent control recorded near its centre of distribution. Furthermore, the variation in autumn population density is

**Table 1** The four most parsimonious models from the set of candidate models for survival estimates each year, selected within program MARK (White & Burnham, 1999) by AIC<sub>c</sub> weight

Model	AIC <sub>c</sub>			
	$\delta$ AIC <sub>c</sub>	weight	Par	Deviance
<i>September 2001 to June 2002</i>				
{ $\Phi$ ( $m2-t^*s/t$ ) $p$ ( $m2-s/.$ )}	0.00	0.27	20	80.82
{ $\Phi$ ( $m2-t^*s/t$ ) $p$ ( $m2-s/s$ )}	0.07	0.26	21	78.63
{ $\Phi$ ( $m2-s/t^*s$ ) $p$ ( $m2-s/s$ )}	0.90	0.17	16	90.63
{ $\Phi$ ( $m2-t^*s/t$ ) $p$ ( $m2-s/t$ )}	1.56	0.12	24	73.25
<i>September 2002 to June 2003</i>				
{ $\Phi$ ( $t$ ) $p$ (.)}	0.00	0.40	8	230.21
{ $\Phi$ ( $t$ ) $p$ ( $s$ )}	0.53	0.31	9	228.64
{ $\Phi$ ( $t$ ) $p$ ( $t$ )}	1.54	0.19	14	219.01
{ $\Phi$ (. ) $p$ ( $t$ )}	4.26	0.05	8	234.46
<i>September 2004 to June 2005</i>				
{ $\Phi$ ( $t$ ) $p$ (.)}	0.00	0.58	7	74.09
{ $\Phi$ ( $t$ ) $p$ ( $s$ )}	1.08	0.34	8	73.06
{ $\Phi$ ( $t$ ) $p$ ( $t$ )}	4.69	0.06	12	68.10
{ $\Phi$ ( $t^*s$ ) $p$ (.)}	8.46	0.01	13	69.68

The slash bar distinguishes between animals recaptured after the first interval and those recaptured in later intervals;  $m2$  indicates that there are two groups. The \* indicates that both time ( $t$ ) and sex ( $s$ ) effects were important, and the . is the sign of a constant (neither time nor sex effects). AIC, Akaike's information criterion.

**Table 2** Apparent monthly survival based on model averaging on the models with  $\Delta$ AIC<sub>c</sub> < 2 (see Table 1)

		$\Phi \pm SE$			
		First interval	Later intervals	$\Phi \pm SE$	
<i>(a) September 2001 to June 2002 – males</i>				<i>(b) September 2002 to June 2003</i>	
Sep–Oct	0.40 ± 0.08			Sep–Oct	0.54 ± 0.07
Oct–Nov	0.56 ± 0.07	0.86 ± 0.11		Oct–Dec	0.69 ± 0.05
Nov–Jan	0.51 ± 0.08	0.81 ± 0.05		Dec–Jan	0.85 ± 0.06
Jan–Mar	0.49 ± 0.21	0.98 ± 0.05		Jan–Feb	0.90 ± 0.07
Mar–Apr	0.11 ± 0.01	0.71 ± 0.11		Feb–Apr	0.80 ± 0.07
Apr–Jun	–	–		Apr–May	0.71 ± 0.09
				May–Jun	–
<i>September 2001 to June 2002 – females</i>				<i>(c) September 2004 to June 2005</i>	
Sep–Oct	0.65 ± 0.09			Sep–Oct	0.39 ± 0.06
Oct–Nov	0.57 ± 0.07	0.89 ± 0.10		Oct–Nov	0.79 ± 0.06
Nov–Jan	0.43 ± 0.13	0.80 ± 0.05		Nov–Jan	0.75 ± 0.05
Jan–Mar	–	0.98 ± 0.07		Jan–Apr	0.65 ± 0.06
Mar–Apr	0.47 ± 0.16	0.70 ± 0.11		Apr–May	0.17 ± 0.07
Apr–Jun	–	–		May–Jun	–

The apparent survival ( $\Phi$ ) is displayed for transient (first interval) as well as resident (later intervals) males and females for the winter 2001–2002 (a), but there were no such differences in apparent survival for the other years (b, c). AIC, Akaike's information criterion.

mainly determined in the non-breeding season but not by the conditions in the breeding season.

Density-independent effects of climate have been shown to affect population parameters of various species of birds and mammals in temperate and cold-temperate regions in the northern hemisphere, in particular near the northern edge of their distribution. Furthermore, these density-independent processes have been subdivided into those acting during the breeding and the non-breeding season, respectively (Sæther *et al.*, 2004, 2006).

Climate is generally the most prominent density-independent factor operating but frequently a number of climatic variables may act in concert, making it difficult to pinpoint a single causal climatic variable. Neither NAO nor the NAO winter index was found to explain autumn population fluctuations of the Icelandic wood mouse. In any case, climate in Iceland does not correlate well with the NAO, presumably because Iceland lies near one dipole of the NAO (Hanna *et al.*, 2004).

Most rodent populations north of 60°N are subject to regular fluctuations or cycles (Finerty, 1980; Hanski, Hansson & Henttonen, 1991; Hansson & Henttonen, 1998; Korpimäki *et al.*, 2004; Lima, Berryman & Stenseth, 2006). Populations at or below 60°N can fluctuate greatly in abundance but usually without cyclicity, presumably due to a greater diversity of generalist predators in the south (Hansson & Henttonen, 1998; Bujalska & Grüm, 2005).

The variations observed in the autumn population size of Icelandic wood mice at our study site might at first give the impression of regular cycles (Fig. 2). The results of this study show no evidence of any cyclicity. However, in the open habitats of Iceland, a country devoid of proper woods (Ólafsdóttir *et al.*, 2001), and at the western and northern edge of the geographical range of the species (Bengtson *et al.*, 1989b), minimum temperature in early winter (October–December) is the major determinant of population density the following autumn. An association of this order between weather factors and population density does not leave much room for density dependence in winter mortality, summer mortality or reproduction in the following breeding season, in contrast to the situation in Britain where density dependence in wood mouse population dynamics is generally prominent (Montgomery, 1989a,b).

Autumn population density of wood mice in our study area was low compared with most habitats in northern Europe where population density has been recorded (Flowerdew, 1985; Montgomery, 1989a; Wilson *et al.*, 1993). Even in an open habitat of a maritime sand-dune system in Scotland, the population density was considerably higher (Gorman & Zubaid, 1993). Most studies on the population dynamics of wood mice near the core of its distribution range have shown that the population density is a function of food availability, in particular the abundance of tree seeds (Montgomery & Montgomery, 1990).

Wood mice store food in their burrows, particularly large seeds and acorns and to some extent snails and beetles (Jennings, 1975). In our study area of barren meadows and hay fields with drainage ditches, no tree seeds are available

and there are few plant species producing seeds large enough to make it possible for the mice to quickly accumulate large stores for the winter. However, seeds were the main constituent of the diet through the winter and arthropods only increased in the diet in spring (E. R. Unnsteinsdottir & P. Hersteinsson, in prep.). It thus appears that food limitation is not the cause of increased mortality in early winter in cold temperatures, although the relatively small seeds available may take a long time for the mice to harvest and store and to get their fill during foraging.

Wood mice do not hibernate and as insulation generally scales positively with body size (Scholander *et al.*, 1950) while metabolic rate scales inversely with body mass (McNab, 1983), they have a high area-specific thermal conductance and are likely to experience conditions in winter in which the energetic demand of maintaining a constant body temperature and weight may exceed the rate at which food can be obtained. In early winter, wood mouse populations are composed largely of newly recruited sub-adults and as these are the smallest individuals in the population, they are also the most vulnerable to cold conditions. A juvenile mouse born in September in our study area and becoming independent in October–November would probably not yet have been able to store sufficient food supplies to survive long spells of cold weather without foraging. The mice would thus be forced to forage regardless of the weather, with starvation and hypothermia being a constant threat. Alternatively, they might postpone foraging in cold weather, as has been shown to be the case with Virginia opossums *Didelphis virginiana* that do not forage at temperatures below  $-4^{\circ}\text{C}$  (Brocke, 1970 cited by Kanda, 2005). In the absence of food stores, starvation would result for the wood mice. It is possible that some of our 'transients' are individuals that have not been able to store food and thus forced out foraging. Those individuals could be in a poor physical condition and therefore more likely to suffer from the handling effect (Brownie & Robson, 1983), and thus have lower apparent survival than those recaptured later. It is also possible that the young mice are simply not large enough to be able to survive cold spells in early winter. It has been shown that body mass is adjusted to a certain mean so as to maximize winter survival in tundra voles *Microtus oeconomus* in south-eastern Norway (Aars & Ims, 2002).

Krebs, Singleton & Kenney (1994) found, using radio telemetry and live trapping methods, that low trappability during the breeding season and nomadic movements during the non-breeding seasons explained largely the low recapture rates in a feral house mouse *Mus domesticus* population in Australia. This phenomenon may explain some of our results, but because the sex  $\times$  transient effect only occurred in 1 year out of 3, this can only be a speculation.

For northern small mammals, mass loss during the winter is a well-known phenomenon (Iverson & Turner, 1974; Hansson, 1990, 1991, 1992, 1995). In our study, the mice gained weight throughout the winter in all 3 years of regular monitoring (Unnsteinsdottir & Hersteinsson, 2003). It is therefore possible that different mechanisms act on the

population demography of the Icelandic wood mouse, than drive other small mammal communities in northern areas. For a better knowledge and understanding, a longer time series, including further survival estimates, is required.

In Britain and on the mainland of Europe, the maximum autumn population size is generally reached in November (Montgomery, 1989a; Čiháková & Frynta, 1996), about 1–2 months later than in our study area. Winter climate is milder in Britain than in Iceland and this may explain why there seems to be little direct effect of weather on population density in Britain. This also means that the reproductive period is considerably longer in Britain, allowing a potentially greater density-dependent compensation for high mortality in winter, as the variable proportion of reproductive females in June and September observed by Montgomery (1989b) suggests. It is possible that in our study area we never observed mice at the carrying capacity of the area due to density-independent mortality in early winter and the relatively short reproductive period.

This study of a population at its range limits provides a new insight into the mechanisms driving dynamics and limitation of a population living at the edge of the species' distribution and how these mechanisms may differ from those operating near the distribution core.

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## References

- Aars, J. & Ims, R.A. (2002). Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. *Ecology* **83**, 3449–3456.
- Arnason, A. (1974). *Protein polymorphism in northern populations of field mice (Apodemus sylvaticus L.)*. PhD thesis, University of Strathclyde, Glasgow.
- Bengtson, S.-A., Brinck-Lindroth, G., Lundqvist, L., Nilsson, A. & Rundgren, S. (1986). Ectoparasites on small mammals in Iceland: origin and population characteristics of a species-poor insular community. *Ecography* **9**, 143–148.
- Bengtson, S.A., Nilsson, A. & Rundgren, S. (1989a). Population structure and dynamics of wood mouse *Apodemus sylvaticus* in Iceland. *Holarct. Ecol.* **12**, 351–368.

- Bengtson, S.A., Nilsson, A. & Rundgren, S. (1989b). Unforeseen disruption of wood mouse population dynamics after food reduction: a field experiment. *Oikos* **56**, 379–385.
- Bergstrom, B.J. & Rose, R.K. (2004). Comparative life histories of Georgia and Virginia cotton rats. *J. Mammal.* **85**, 1077–1086.
- Blower, J.G., Cook, L.M. & Bishop, J.A. (1981). *Estimating the size of animal populations*. London: George Allen and Unwyn.
- Brocke, R.H. (1970). *The winter ecology and bioenergetics of the opossum, Didelphis marsupialis, as distributional factors in Michigan*. PhD thesis, Michigan State University.
- Bronson, F.H. (1989). *Mammalian reproductive biology*. Chicago: University of Chicago Press.
- Brownie, C. & Robson, D.S. (1983). Estimation of time-specific survival rates from tag-resighting samples: a generalization of the Jolly-Seber Model. *Biometrics* **39**, 437–453.
- Bujalska, G. & Grüm, L. (2005). Reproduction strategy in an island population of yellow-necked mice. *Popul. Ecol.* **47**, 151–154.
- Burnham, K.P. & Anderson, D.R. (2002). *Model selection and multimodel inference*, 2nd edn. New York: Springer-Verlag.
- Choquet, R., Reboulet, A.M., Pradel, R. & Lebreton, J.D. (2006). *U-care (utilities–capture–recapture) user's guide*. CEFE/CNRS (Ed.). Montpellier, France.
- Čiháková, J. & Frynta, D. (1996). Abundance fluctuations in *Apodemus* spp. and *Clethrionomys glareolus* (Mammalia: Rodentia): a seven year study in an isolated suburban wood. *Acta Soc. Zool. Bohem.* **60**, 3–12.
- Corbet, G.B. & Harris, S. (1991). *The handbook of British mammals*. Oxford: Blackwell publications.
- Cormack, R.M. (1964). Estimates of survival from the sighting of marked animals. *Biometrika* **51**, 429–438.
- Enright, J.T. (1976). Climate and population regulation. The biogeographers dilemma. *Oecologia (Berl.)* **24**, 295–310.
- Finerty, J.P. (1980). *The population ecology of cycles in small mammals. Mathematical theory and biological fact*. New Haven: Yale University Press.
- Flowerdew, J.R. (1985). The population dynamics of wood mice and yellow necked mice. *Symp. Zool. Soc. Lond.* **55**, 315–338.
- Forchhammer, M.C., Stenseth, N.C., Post, E. & Langvatn, R. (1998). Population dynamics of Norwegian red deer: density-dependence and climatic variation. *Proc. Roy. Soc. Lond. Ser. B.* **265**, 341–350.
- García, J.T. & Arroyo, B.E. (2001). Effect of abiotic factors on reproduction in the centre and periphery of breeding ranges: a comparative analysis in sympatric harriers. *Ecography* **24**, 393–402.
- Gaston, K.J. (2003). *The structure and dynamics of geographic ranges*. Oxford: Oxford University Press.
- Gorman, M.L. & Zubaid, A. (1993). A comparative study of the ecology of woodmice *Apodemus sylvaticus* in two contrasting habitats: deciduous woodland and maritime sand-dunes. *J. Zool. (Lond.)* **229**, 385–396.
- Haldane, J.B.S. (1956). The relation between density regulation and natural selection. *Proc. Roy. Soc. Lond. Ser. B.* **24**, 306–308.
- Hallet, T.B., Coulson, T., Pilkington, J.G., Clutton-Brock, T.H., Pemberton, J.M. & Grenfell, B. (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature* **430**, 71–75.
- Hanna, E., Jónsson, T. & Box, J.E. (2004). An analysis of Icelandic climate since the nineteenth century. *Int. J. Climatol.* **24**, 1193–1210.
- Hanski, I., Hansson, L. & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *J. Anim. Ecol.* **60**, 353–367.
- Hansson, L. (1990). Ultimate factors in winter weight depression of small mammals. *Mammalia* **54**, 397–404.
- Hansson, L. (1991). Regional and individual variation in body growth in winter of bank voles *Clethrionomys glareolus*. *Acta Theriol.* **36**, 357–362.
- Hansson, L. (1992). Fitness and life history correlates of weight variation in small mammals. *Oikos* **64**, 479–484.
- Hansson, L. (1995). Size dimorphism in microtine rodent populations: characteristics of growth and selection against large-sized individuals. *J. Mammal.* **76**, 867–872.
- Hansson, L. & Henttonen, H. (1998). Rodent fluctuations in relation to seasonality in Fennoscandia and Hokkaido. *Res. Popul. Ecol.* **40**, 127–129.
- Haraldsson, H.V. & Ólafsdóttir, R. (2003). Simulating vegetation cover dynamics with regards to long-term climatic variations in sub-arctic landscapes. *Glob. Planet Change* **38**, 313–325.
- Helle, E. & Kauhala, K. (1991). Distribution history and present status of the raccoon dog in Finland. *Holarct. Ecol.* **14**, 278–286.
- Hurrell, J.W. (1995). Decadal trends in the North Atlantic oscillation: regional temperatures and precipitation. *Science* **269**, 676–679.
- Iverson, S.L. & Turner, B.N. (1974). Winter weight dynamics in *Microtus pennsylvanicus*. *Ecology* **55**, 1030–1041.
- Jennings, T.J. (1975). Notes on the burrow systems of woodmice (*Apodemus sylvaticus*). *Not. Mam. Soc.* **31**, 500–504.
- Jolly, G.M. (1965). Explicit estimates from capture–recapture data with both death and immigration–stochastic model. *Biometrika* **52**, 225–247.
- Kanda, L.L. (2005). Winter energetics of Virginia opossums *Didelphis virginiana* and implications for the species' northern distributional limits. *Ecography* **28**, 731–744.
- Korpimäki, E., Brown, P.R., Jacob, J. & Pech, R.P. (2004). The puzzles of population cycles and outbreaks of small mammals solved? *BioScience* **54**, 1071–1079.
- Korslund, L. & Steen, H. (2006). Small rodent winter survival: snow conditions limit access to food resources. *J. Anim. Ecol.* **75**, 156–166.
- Krebs, C.J. (1994). *Ecology. The experimental analysis of distribution and abundance*. New York: Harper Collins, College Publishers.

- Krebs, C.J., Singleton, G.R. & Kenney, A.J. (1994). Six reasons why feral house mouse populations might have low recapture rates. *Wildl. Res.* **21**, 559–567.
- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.
- Lima, M., Berryman, A.A. & Stenseth, N.C. (2006). Feedback structures of northern small rodent populations. *Oikos* **112**, 555–564.
- Lupton, P. & Wykes, U. (1938). The field mice of Iceland. *J. Anim. Ecol.* **7**, 22–26.
- McNab, B.K. (1983). Energetics, body size, and the limits to endothermy. *J. Zool. (Lond.)* **199**, 1–29.
- McNab, B.K. (2002). *The physiological ecology of vertebrates*. New York: Cornell University Press.
- Milner, J.M., Elston, D.A. & Albon, S.D. (1999). Estimating the contributions of population density and climatic fluctuations to interannual variation in survival of Soay sheep. *J. Anim. Ecol.* **68**, 1235–1247.
- Mitchell-Jones, A.J., Amori, G., Bogdanowicz, W., Krystufek, B., Reijnders, P.J.H., Spitzenberger, F., Stubbe, M., Thissen, J.B.M., Vohralik, V. & Zima, J. (1999). *The atlas of European mammals*. London: T and AD Poyser Natural History.
- Montgomery, S.S.J. & Montgomery, W.I. (1990). Intrapopulation variation in the diet of the wood mouse *Apodemus sylvaticus*. *J. Zool. (Lond.)* **222**, 641–651.
- Montgomery, W.I. (1989a). Population regulation in the wood mouse, *Apodemus sylvaticus*. I. Density dependence in the annual cycle of abundance. *J. Anim. Ecol.* **58**, 465–475.
- Montgomery, W.I. (1989b). Population regulation in the wood mouse, *Apodemus sylvaticus*. II. Density dependence in spatial distribution and reproduction. *J. Anim. Ecol.* **58**, 477–494.
- Montgomery, W.I., Wilson, W.L., Hamilton, R. & McCartney, P. (1991). Dispersion of the wood mouse, *Apodemus sylvaticus*: variable resources in time and space. *J. Anim. Ecol.* **60**, 179–192.
- Mysterud, A., Yoccoz, N.G., Stenseth, N.C. & Langvatn, R. (2000). Relationships between sex ratio, climate and density in red deer: the importance of spatial scale. *J. Anim. Ecol.* **69**, 959–974.
- Ólafsdóttir, R., Schlyter, P. & Haraldsson, H. (2001). Simulating Icelandic vegetation cover during the Holocene. Implications for long-term land degradation. *Geogr. Ann.* **83**, 203–215.
- Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed populations. *Wildl. Monogr.* **62**, 3–135.
- Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, E. (1990). Statistical inference for capture recapture experiments. *Wildl. Monogr.* **107**, 1–97.
- Post, E., Stenseth, N.C., Langvatn, R. & Fromentin, J.-M. (1997). Global climate change and phenotypic variation among red deer cohorts. *Proc. Roy. Soc. Lond. Ser. B* **264**, 1317–1324.
- Pradel, R., Hines, J.E., Lebreton, J.D. & Nichols, J.D. (1997). Capture–recapture survival models taking account of transients. *Biometrics* **53**, 60–72.
- Rosenzweig, M.L. (1995). *Species diversity in space and time*. Cambridge: Cambridge University Press.
- Sanford, E. (2002). Community responses to climate change: links between temperature and keystone predation in a rocky intertidal system. In *Wildlife responses to climate change*: 165–200. Schneider, S.H. & Root, T.L. (Eds). Washington: Island Press.
- Scholander, P.F., Hock, R., Walters, V. & Irving, L. (1950). Adaptation to cold in arctic and tropical mammals and birds in relation to body temperature, insulation, and basal metabolic rate. *Biol. Bull.* **99**, 259–271.
- Seber, G.A.F. (1965). A note on the multiple-recapture census. *Biometrika* **52**, 249–292.
- Stenseth, N.C., Bjørnstad, O.N. & Saitoh, T. (1998). Seasonal forcing on the dynamics of *Clethrionomys rufocanus*: modeling geographic gradients in population dynamics. *Res. Popul. Ecol.* **40**, 85–95.
- Stenseth, N.C. & Mysterud, A. (2005). Weather packages: finding the right scale and composition of climate in ecology. *J. Anim. Ecol.* **74**, 1195–1198.
- Sæther, B.E., Grötan, V., Tryjanowski, P., Barbraud, C., Engen, S. & Fulin, M. (2006). Climate and spatio-temporal variation in the population dynamics of a long distance migrant, the white stork. *J. Anim. Ecol.* **75**, 80–90.
- Sæther, B.E., Sutherland, W.J. & Engen, S. (2004). Climate influences on avian population dynamics. *Adv. Ecol. Res.* **35**, 185–209.
- Unnsteinsdottir, E.R. & Hersteinsson, P. (2003). Weight changes in *Apodemus sylvaticus* with seasons in Iceland. *4th European Vertebrate Pest Management Conference*, University of Parma, Italy, 9–12 September 2003, p. 110 (abstract).
- Watts, C.H.S. (1969). The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Whytham Woods, Berkshire. *J. Anim. Ecol.* **38**, 285–304.
- White, G.C. & Burnham, K.P. (1999). Program MARK: survival estimation from populations of marked animals. *Bird Study* **46** (Suppl.), 120–138.
- Williams, C.K., Ives, A.R. & Applegate, R.D. (2003). Population dynamics across geographical ranges: time-series analyses of three small game species. *Ecology* **84**, 2654–2667.
- Wilson, W.L., Montgomery, W.I. & Elwood, R.W. (1993). Population regulation in the wood mouse *Apodemus sylvaticus* (L.). *Mammal Rev.* **23**, 73–92.
- Zubaid, A. & Gorman, M.L. (1993). The effect of supplementary feeding upon the sizes of the home ranges of woodmice *Apodemus sylvaticus* living on a system of maritime sand-dunes. *J. Zool. (Lond.)* **231**, 233–237.





# **Paper II**

*Contrasting habitats*



# Effects of contrasting habitats on population parameters and diet of *Apodemus sylvaticus* (Rodentia) in south-western Iceland

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## Abstract

Population parameters, body mass and diet of *Apodemus sylvaticus* were compared in two nearby study sites in south-western Iceland: open grassland and mixed woodland. Live trapping was conducted at approximately 5 week intervals from September 2004 to October 2005. In addition, mice were caught in snap-traps every month to estimate food composition from stomach contents. Estimated population density was up to 10 times higher in the woodland than in grassland but seasonal dynamics were the same, with peak density in autumn and low density in spring. Apparent monthly survival varied greatly throughout the winter in the grassland, ranging from 39% to 78%, but was stable at around 60% in the woodland. Mice fed predominantly on seeds in all seasons, with an exception during the spring when arthropod larvae were the most common food type. Food varied more by seasons than by habitats, but evidently mice from the woodland were less likely to feed on green material and showed more seasonal fluctuations in seed consumption. During mid-winter, woodland mice of both sexes were heavier than mice in the grassland. To some extent, the observed differences in density, survival, weight and diet could be reflecting differences in habitat quality in the two contrasting habitat types.

**Keywords:** body weight; contrasting habitats; diet; Iceland; population parameters; Rodentia.

## Introduction

Many studies on small mammals have found that spatial variation in population density correlates to abundance and quality of food resources (Hansson 1971, Montgomery and Montgomery 1990, Gorman and Zubaid 1993, Wilson et al. 1993, Zubaid and Gorman 1993). Although population density does not necessarily reflect habitat quality, at least in fragmented habitats (Wheatley et al. 2002), it has been

shown that local and regional abundance of some small mammal species can be related to the abundance and distribution of preferred food types, such as seeds (Angelstam et al. 1987). Studies involving supplemental food experiments (Zubaid and Gorman 1993) or food removal (Bengtson et al. 1989a) are often short on a temporal scale (<1 year) and usually lead to increased population density, although not always, due to the interaction of other variables than food enrichment, such as emigration, territoriality and predation (Yunger 2002).

Large tree seeds (>2 g), such as acorns, have been shown to play an important role in winter survival for *Apodemus* species (Watts 1969, Montgomery and Montgomery 1990, Selås et al. 2002, Saitoh et al. 2007) which can be an important factor determining autumn population density. Iceland lacks oak (*Quercus* sp.), beech (*Fagus sylvatica*) and other trees producing large seeds. Thus, shortage of woodlands and the cold and wet climate in Iceland can be considered unfavourable, compared to other habitats of the species in northern Europe. By contrast, the wood mouse (*Apodemus sylvaticus*) appears to be rather skilful in finding sufficient food and surviving in a variety of habitat types throughout Iceland. The species is the only rodent living in the wild in Iceland since it was brought to the country by the early settlers around 1100 years ago (Lupton and Wykes 1938, Degerbøl 1939, Arnason 1974, Bengtson et al. 1986) and have become well-established and widespread throughout most vegetated areas (Skirnisson 2004).

Contrasting habitats have, however, resulted in dissimilar population density of wood mice in Iceland, suggesting considerable variation in the biology of the species in the country (Bengtson et al. 1989a). We have shown that autumn population density of wood mice in open grassland in south-western Iceland is low, approximately 3–9 mice ha<sup>-1</sup> (Unnsteinsdóttir and Hersteinsson 2009), compared to both birchwoods in northern Iceland and *Angelica* fields in southern Iceland (Bengtson et al. 1989b), as well as most habitats in northern Europe where population density has been recorded to be above 20 mice ha<sup>-1</sup> (Watts 1969, Flowerdew 1985, Montgomery 1989, Wilson et al. 1993). Even in an open habitat of a maritime sand dune system in Scotland, the population density was considerably higher, exceeding 10 mice ha<sup>-1</sup> every autumn in 6 years of study (Gorman and Zubaid 1993). The sand dune population turned out to be food limited because a supplemental food experiment resulted in a 6- to 7-fold increase in population density (Zubaid and Gorman 1993).

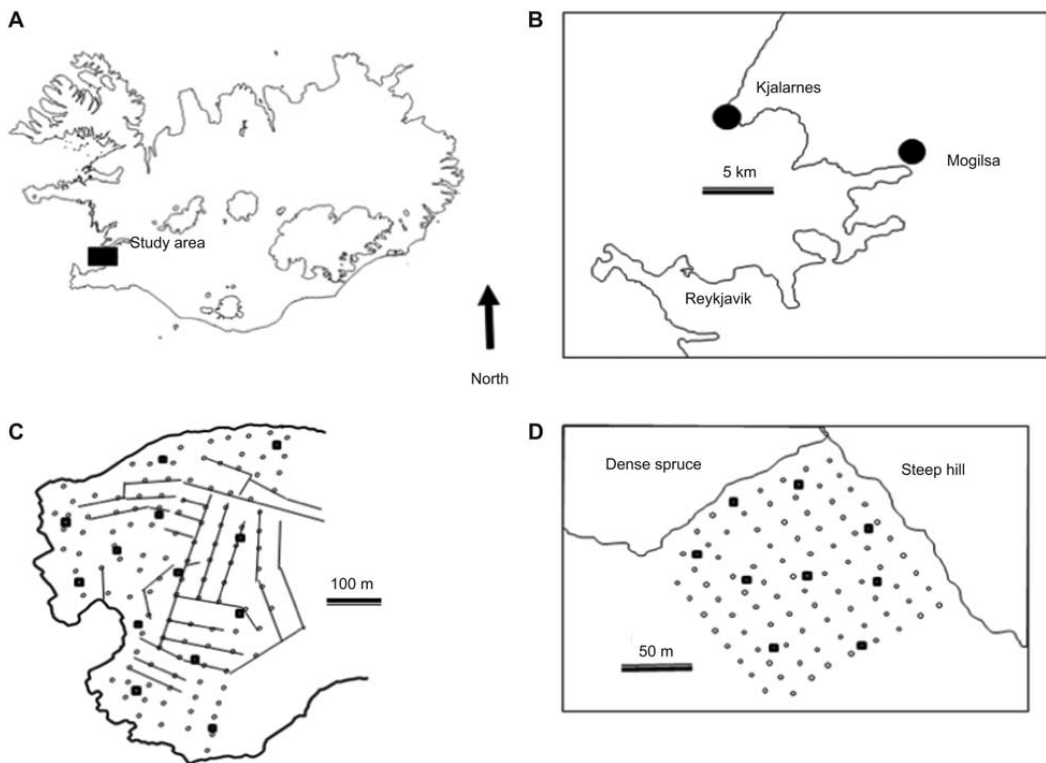
Bearing in mind these differences in population density and the low abundance in the open grassland, we decided to

investigate if a wood mouse population in a nearby mixed woodland would show other results. We assumed that the low population density in the grassland would be the result of low habitat quality. The grassland can be regarded as typical modern Icelandic landscape, whereas the woodland is more representative of recent development in land management and, indeed, is probably also more similar to the landscape prior to deforestation in the early centuries of human settlement in the country (Olafsdottir et al. 2001). We predicted (1) that the woodland would be more favourable for the mice, resulting in higher population density and winter survival as well as better physical condition and that this would be in relation to differences in food habits, exposure to predators and cold weather of these two wood mouse populations. We also predicted that (2) wood mice in the woodland site were feeding more on various seeds and berries than at the grassland site where they would feed more on green plant material, small grass seeds and invertebrates. Finally, we predicted that (3) that the mice at the woodland site were in a better physical condition during winter than the mice at the grassland site, i.e., we expected mice in the woodland site to be heavier than at the grassland site.

## Study area

The Kjalarnes grassland study site at the farm Brautarholt in south-western Iceland (64.2339°N, 21.9003°W) has previously been described rather thoroughly (Unnsteinsdottir and Hersteinsson 2009). It is composed mostly of hayfields with ditches, bordered on three sides by the sea (Figure 1). Furthermore, the hayfields were harvested at least once every summer during our study but there was no grazing by farm animals. On an approximately 50-cm wide zone on each side of the ditches, the grass was not cut and formed seeds annually that constitutes an important food source for the mice.

The Mogilsa woodland study site (64.2055°N, 21.7050°W) is located 13 km south-east of the Kjalarnes grassland site (Figure 1). It is a 2-ha mixed woodland bordered by a steep slope on one side and a dense spruce plantation on the other. The third border of the study site is delineated by a ditch and grassland, but on the fourth side the woodland continues towards the nearest buildings, located approximately 200 m from the study site. Both study sites, only 13 km apart, can be considered within the same weather system (Unnsteins-



**Figure 1** A map of Iceland, showing (A) the location of the study area, (B) the positions of Kjalarnes grassland (64.2339°N, 21.9003°W) and Mogilsa woodland (64.2055°N, 21.7050°W), (C) and (D) the live trap (o) and plant frame (□) locations in Kjalarnes grassland and Mogilsa woodland, respectively.

dottir and Hersteinsson 2009), although microclimate is assumed to differ.

## Materials and methods

### Live trapping

In the grassland, a grid of 120 Longworth live traps (©BTR, Penlon Ltd., Abingdon, Oxfordshire, UK) was set out with a trap interval of approximately 45 m and in the woodland we placed 87 traps with an interval of approximately 15 m. Such unequal interval between live traps, when comparing contrasting habitats, has been used where different population densities can be expected (Gorman and Zubaid 1993).

Live trapping was conducted in 5-day sessions (capture periods) in each study area, every 5–7 weeks from September 2004 to November 2005 (in all 21 capture periods), except in May–July, when trapping was conducted in 3-day sessions with approximately 3-week intervals. Live traps were checked daily during capture periods.

Captured wood mice were individually marked with microtags (Indexel<sup>®</sup>, Merial, Lyon, France) such that they could be identified by the use of a pocket reader (Pocketreader<sup>®</sup>, Destron Fearing, St. Paul, MN, USA). Relevant information such as sex, weight and reproductive status were recorded. The trapping process was approved by The Icelandic Food and Veterinary Authority and The Icelandic Ministry of the Environment.

### Snap trapping

Wood mice were caught in snap-traps located on linear transects >200 m away from the live-trapping sites and situated in two different habitats: (1) along ditches and coastline (Kjalarnes grassland) and (2) in mixed woodland (Mogilsa woodland). In each transect, there were 10–25 trap stations positioned 10–15 m apart. At each station we placed one to three traps, depending on the season.

Snap-trapping took place with approximately 4–7 week intervals and lasted for as long as it took to obtain at least 16 individuals, a sufficient sample to ascertain the major food types eaten (Obertel and Holisova 1977). The traps were checked daily. Each snap-trap was placed inside a Longworth live-trap to prevent accidental trapping of birds. No bait was used for snap-traps. Trapped mice were kept at -30°C until they were dissected. No tagged animal from the live-trapping sites were ever trapped in the snap-traps.

### Flora and fauna

Vegetation was examined by the use of 1×1 m quadrates spread throughout the study area (see locations in Figure 1). Thirteen frames were examined in the homogeneous grassland and nine frames in the woodland. Plants within frames were identified to species level and ranked, based on abundance and frequency in frames, throughout the study area. Samples were taken of leaves and seeds as reference material to compare to stomach contents of the dissected mice.

Pitfall traps were placed in the middle of the location of every plant frame, after vegetation analysis, to estimate the composition of surface invertebrates. The traps were laid out in July 2005 and kept for 2 weeks (checked weekly), half-filled with ethylene glycol to preserve specimens from decomposing (Southwood and Henderson 2000). Similar ranking was done for invertebrates as was used for the vegetation description, based on abundance and frequency of species within the habitats. Samples from pitfall traps were kept as reference material for comparison with animal related items found in mouse stomachs.

In addition to wood mice, two juvenile house mice (*Mus musculus*) were trapped in live traps in the woodland. No house mice were trapped in the grassland during this study, although they were trapped occasionally in the previous grassland study (Unnsteinsdottir and Hersteinsson 2009). Mammalian predators in Iceland are the American mink (*Neovison vison*) and the arctic fox (*Vulpes lagopus*), as well as house cats (*Felis catus*), which are common in urban areas. There were signs of one to two minks in the grassland area and one to two cats in the woodland area during the time of study, but no indication of arctic foxes. Of the Icelandic birds of prey, only the short-eared owl can be regarded as a rodent specialist (Nielsen 1997) but they are rare and none were observed during the study. Merlin (*Falco columbarius*) was spotted occasionally around the woodland area during the time of the study in Iceland; they mostly prey on passerines and they are also known to take wood mice (Bengtson 1975, Nielsen 1986). Ravens (*Corvus corax*), arctic skua (*Stercorarius parasiticus*) and gyrfalcons (*Falco rusticolus*) are known to prey on mice as a supplementary diet, but none of them can be regarded a mouse-specialist. Of these three species, only ravens were observed in our study area.

### Diet analysis

Diet of the wood mice was analysed by examining stomach contents using relative area methods based on Hansson (1970), Gorman and Zubaid (1993) and Rogers and Gorman (1995).

During dissection, stomachs were removed and kept in a freezer at -30°C until analysed. After thawing, each stomach was carefully opened and the ingredients washed out with distilled water and then sieved through a 250 µ grid to remove units that were too small for identification. The food particles >250 µ, were spread out in a Petri dish with a millimetre scale.

Microscopic analysis of the food particles was made by comparing them to prepared samples (animals, plants, seeds) from the area and by the use of an identification key and a checklist (animals: Olafsson 1991; seeds: Bertsch 1941). Plant material was assigned as either seed or green (leaf/stalk). Seeds were identified to family level when possible and green matter as either monocotyledonous or dicotyledonous by cell structure. Animal items were identified to family level and arthropods further grouped by developmental stage as either larvae/pupae or adult.

Area cover of each food category was estimated in mm<sup>2</sup> (with an accuracy of 0.5 mm<sup>2</sup>) and then transformed into percentile proportion of the total area cover of the particular stomach content. Unidentified particles were dyed with Lucol solution (Fluka Chemie GmbH, Buchs, Switzerland), which produces a blue colour when in contact with starch and this made it possible to distinguish seed contents from animal matter.

### Statistical analysis

**Population size** The trapping procedure followed a robust design according to Pollock et al. (1990) and thus we presumed that, during each 5-day sampling period, the population was closed and recruitment and deaths of minor importance. Population size for each capture period was estimated using the model  $Mt: \{N, p(t)=c(t)\}$  (Otis et al. 1978, Pollock et al. 1990, Chao and Huggins 2005) with the MARK V-4.3 program (White and Burnham 1999). The notation  $p$  is the probability of initial capture,  $c$  is the probability of recapture,  $t$  is time and  $N$  is abundance. We used  $\sin$  link function on  $p$  and  $c$  and  $\log$  link function on  $N$ .

In summer months, when we trapped only for 3 days and very few mice were caught (May, June and July), we used MNA (Minimum Number known to be Alive) to estimate population size (Blower et al. 1981).

**Survival** Survival estimation was based on open population analysis on recapture data from September 2004 to April 2005, using the MARK program. Before modelling the data, we used Test 2.CT and Test 3.SR in the U-CARE V-2.2.5 program (Choquet et al. 2003) to test for possible failure of the principal assumptions of the Cormack, Jolly, Seber (CJS) models used for survival estimates (Cormack 1964, Jolly 1965, Seber 1965, Lebreton et al. 1992). The grassland data revealed significant trap-happiness for males:  $\chi^2=12.85$ ,  $df=2$ ,  $p=0.002$ ; this was almost significant for females:  $\chi^2=5.28$ ,  $df=2$ ,  $p=0.07$  (Test 2.CT). The results of Test 3.SR for transients were negative for both habitats. We define transients as individuals that were never recaptured after the initial capture-mark-release or those who have considerably low survival from initial capture until first recapture. Transient individuals could also have died after release or emigrated out of the study area. As we are unable to distinguish between those possibilities, their fates remain unknown.

Goodness of fit was made by adjusting chi-hat ( $\check{c}$ ), based on 500 bootstrap samples on the general model ( $\mathcal{P}(s^*t)=p(s^*t)$ ) in accordance with our hypotheses that the survival and recapture rate was sex ( $s$ )- and time ( $t$ )-dependent. Thus, the grassland data was adjusted with  $\check{c}=1.45$  and woodland data with  $\check{c}=2.05$ . For each habitat we ran 12 models, assuming time, sex or constant (.) effects on survival and recapture rate. Model selection was made by Akaike's information criterion (AIC) and based on QAICc weights in the MARK program. The similar models (QAICc  $\leq 2$ ), of the most parsimonious models to explain variation in the data, were averaged (Burnham and Anderson 2002). Periods between trapping surveys differed in length and thus all

intervals were transformed into months (31 days) to be comparable.

**Stomach contents** The data on stomach contents was compared between the grassland and the woodland for each trapping month. The results were presented by seasons as follows: winter=December to March, spring=April to May, summer=June to August and autumn=September to November.

During analysis, the food was divided into four main types: seeds, green plant material, larva/pupae and adult arthropods. The proportions of each food type were compared by months and habitats with the use of two-way analysis of variance (ANOVA). In all habitats and seasons there were stomachs which had no detectable traces of one or more food type. Before analysis, the 0s were replaced by 0.0001, a proportion that is an order of magnitude less than the smallest proportion recorded (0.001). We also had a few stomachs that included only one food type (100%); the 1s were thus replaced by 0.9999. Furthermore, the data was arc sine transformed to attain normality.

**Body mass** Two-way ANOVA was used to measure variable differences in mean body mass in each trapping session, between habitats (woodland vs. grassland) and between sexes within habitats in each trapping month. We did not distinguish between age classes in any season but during the breeding season apparently pregnant females were excluded from weight comparisons.

Statistical analysis on stomach contents and body mass were carried out using the software package R, 2.6.1 (© 2007 R Development Core Team 2007).

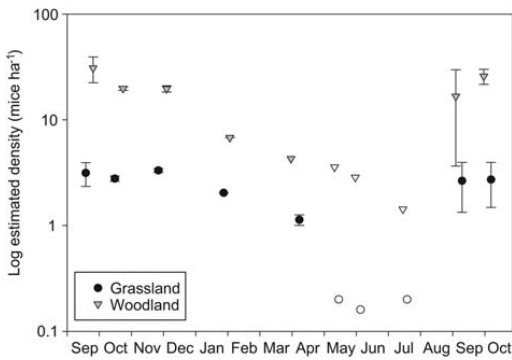
## Results

### Population size

Population estimates revealed almost 10-fold higher autumn density in the woodland site than in the grassland site (Figure 2). Autumn maxima in Kjalarnes grassland were  $3.14 \pm 0.41$  mice ha<sup>-1</sup> in 2004 and  $2.72 \pm 0.63$  mice ha<sup>-1</sup> in 2005. In the Mogilsa woodland, autumn maxima were  $30.8 \pm 4.3$  mice ha<sup>-1</sup> and  $25.8 \pm 2.2$  mice ha<sup>-1</sup> in 2004 and 2005, respectively. In both habitats, the populations declined rapidly at the onset of winter and reached a minimum in the spring. In the spring, the population densities were 1.13 mice ha<sup>-1</sup> and 4.29 mice ha<sup>-1</sup> in the grassland and woodland sites, respectively (April). It is possible that minimum population density in spring became even lower because sampling size was too small in spring and early summer for capture mark [release] recapture (CMR) analysis.

### Survival

According to the three most parsimonious models in the grassland site (explaining 90% of the variation), survival differed by season but not by sex (Table 1). The four most parsimonious models for the woodland (explaining 75% of



**Figure 2** Estimated population density by CMR of wood mice in Kjalarnes grassland (●) and Mogilsa woodland (▲) from September 2004 to October 2005. In May–July 2005 (open symbols) estimates were made by minimum number known to be alive (MNA) in both habitats. No trapping took place in January, March and August 2005.

the variation) resulted in constant survival with rather weak time and sex effects (Table 1). The three and four above-mentioned models had similar fit to the data ( $QAICc \leq 2$ ) and thus were averaged in the MARK program. Average models gave apparent monthly survival ( $\Phi$ ) and recapture

**Table 1** The three and four most parsimonious and similar models ( $QAICc \leq 2$ ) from the set of 12 models that were fitted to the data for survival estimates in each habitat.

Model	$\Delta QAICc$	$QAICc$ w	Par	QDeviance
Grassland				
{ $\Phi(t) p(.)$ }	0.00	0.510	5	40.335
{ $\Phi(t) p(s)$ }	1.92	0.196	6	40.161
{ $\Phi(t) p(s)$ }	1.92	0.196	6	40.161
Woodland				
{ $\Phi(.) p(.)$ }	0.00	0.339	2	19.226
{ $\Phi(s) p(.)$ }	1.63	0.150	3	18.779
{ $\Phi(t) p(.)$ }	1.74	0.142	5	14.673
{ $\Phi(.) p(s)$ }	2.06	0.121	3	19.211

Data were adjusted by  $\check{c}=1.45$  for the grassland and  $\check{c}=2.05$  for the woodland. Selection was based on Akaike's information criterion (AIC) within the MARK program (White and Burnham 1999). (*t*) indicates time effects, (*s*) that there are sex effects on survival and (.) indicates constant (neither time nor sex) effects; w, weight.

**Table 2** Estimated survival at Kjalarnes grassland and Mogilsa woodland from September 2004 to April 2005.

Months	Kjalarnes grassland				Mogilsa woodland			
	Males	SE	Females	SE	Males	SE	Females	SE
Sep–Oct	0.39	0.07	0.39	0.07	0.61	0.06	0.59	0.07
Oct–Nov	0.78	0.07	0.78	0.07	0.63	0.06	0.61	0.06
Nov–Jan	0.75	0.05	0.75	0.05	0.58	0.06	0.57	0.07
Jan–Apr	0.67	0.07	0.67	0.07	0.64	0.07	0.63	0.07

Values are based on model averaging of the models from Table 1. Estimated values are shown on a monthly basis from one trapping month to another. SE, standard error.

rate (*p*), in each habitat and trapping session, during the winter (Table 2).

In the grassland, monthly survival was low for both sexes at the onset of winter (39%) but substantially higher (75–78%) during mid-winter, dropping to 67% in late winter-early spring. In the woodland, monthly survival remained around 60% throughout the winter. Recapture rate was stable, 70–76% in the grassland and 88% in the woodland.

## Flora and fauna

In the grassland, the vegetation was characterised by several dominating grass species and patchy dicotyledonous plant species throughout the area. Vegetation cover was continuous and the main monocotyledons included *Agrostis* spp., *Alopecurus pratensis*, *Festuca richardsonii* and *Phleum pratense*, all of which are common in Icelandic hayfields (Thorvaldsson 1997). The coastline vegetation was more discontinuous and characteristic plants included *Cakile arctica*, *Mertensia maritima*, *Matricaria maritima*, *Chamomila suaveolens*, *Leymus arenarius* and *Angelica archangelica*.

The woodland was dominated by 2–3 m high birch (*Betula pubescens*), mixed with 1–2 m high willows (*Salix* spp.) and >4 m high Sitka spruce (*Picea sitchensis*). The woodland floor was characterised by *Filipendula ulmaria*, *Ranunculus acris* and *Geranium sylvaticum* with occasional *Rubus saxatilis*, *Equisetum pratense* and *Galium boreale*.

In both habitats, the surface invertebrate fauna was of similar composition but differed slightly in structure. Thus *Coleoptera frigida* and Tipulidae were more frequent at the grassland than the woodland site. Lepidoptera was dominant in both habitats, Coleopterans were more frequent in the woodland, and spiders (Arachnids) were common in both habitats. Earthworms (Oligochaeta), slugs and snails (Gastropoda) were also found within both habitats, but were less common than the arthropods.

## Stomach contents

Seeds were found in 95–100% of stomachs in summer and autumn. During the winter, most stomachs from the grassland site and approximately half from the woodland site included seeds. In the spring, only a quarter of stomachs from woodland but the majority of stomachs from the grassland contained seeds (Table 3). In the grassland, seeds from *Stellaria* sp. were somewhat common as well as a mixture of various grass seeds, although no particular species dom-

inated. In the woodland, seeds of meadowsweet (*Filipendula ulmaria*) and willow herbs (*Epilobium* spp.) were the most common seed types found in stomachs.

Green plant material was found in similar proportions of stomachs in woodland and grassland during spring and autumn, respectively. In the woodland during summer, a quarter of stomachs contained green plant material, whereas all stomachs in the grassland had green plant material. In the winter, a minority of woodland stomachs but almost half of grassland stomachs contained green plant material (Table 3). In the grassland, green plant material consisted mainly of mass fractions, whereas at the woodland site tiny flowers of *Galium* sp. were common.

Animal matter was found in over half of the stomachs in all seasons, probably in accordance to seasonal availability. Thus, arthropod larvae/pupae were found in most stomachs in the spring. In the summer, less than half of the woodland and two-thirds of the grassland stomachs included larvae/pupae. During the autumn, the frequency of larvae/pupae in stomachs was much reduced at both sites. In the winter, larva/pupae were found in three-quarters of woodland stomachs, approximately twice as common as that in grassland stomachs. Adult arthropods were more frequent in stomachs from grassland than woodland in the summer (Table 3). *Lepidoptera* larvae were the absolute majority of animal remains found in stomachs in all habitats.

The results of the ANOVA models indicate that the variance in food habits is better explained by the seasons than habitats (Figure 3). More seeds were found in stomachs during the autumn than in other seasons ( $F=32.53$ ;  $df=3, 237$ ;  $p<0.001$ ). Some habitat interactions were found for seeds during summer and winter. Thus, more seeds were found in woodland than grassland stomachs during summer ( $F=23.21$ ;  $df=1, 23$ ;  $p<0.001$ ). During winter, seeds were found in higher proportions in stomachs from the grassland than in the woodland ( $F=6.85$ ;  $df=1, 67$ ;  $p=0.0109$ ). The stomachs from the woodland contained significantly more green material than the grassland stomachs in the autumn ( $F=9.88$ ;  $df=1, 107$ ;  $p=0.00216$ ) but it was the opposite in other seasons, whereas green plant material was more frequent in stomachs from grassland mice than woodland mice in summer ( $F=18.63$ ;  $df=1, 23$ ;  $p<0.001$ ) and in winter ( $F=3.94$ ;  $df=1, 67$ ;  $p=0.0512$ ). In the grassland, larvae/pupae were most frequent in stomachs from the spring but in the woodland, larva/pupae were also common at winter. The woodland stomachs contained a significantly higher proportion of larvae/pupae in winter than the stomachs from the grassland ( $F=41.69$ ;  $df=1, 67$ ;  $p<0.0001$ ). ANOVA models did not reveal any habitat or seasonal differences in proportions of adult arthropods in stomachs.

### Body mass

Sex differences in body mass were evident in most months from autumn to spring, but there were also differences in body mass between habitats (Table 4). There were weak interactive terms between sex and months, but no other interactive terms were found, either between period, habitat or sex.

Males at the grassland site were significantly heavier than females in September ( $F=13.01$ ;  $df=1, 284$ ;  $p=0.0004$ ), October ( $F=10.35$ ;  $df=1, 68$ ;  $p=0.002$ ) and April ( $F=14.1$ ;  $df=1, 25$ ;  $p=0.0009$ ). In the woodland, males were significantly heavier than females in October ( $F=9.873$ ;  $df=1, 53$ ;  $p=0.003$ ) and April ( $F=24.99$ ;  $df=1, 10$ ;  $p=0.0005$ ).

There were significant habitat differences in body mass of both sexes throughout the winter. Thus, woodland males were heavier than grassland males in December ( $F=28.04$ ;  $df=1, 79$ ;  $p=1.042e-06$ ) and January ( $F=5.791$ ;  $df=1, 37$ ;  $p=0.02$ ). Woodland females were somewhat heavier than grassland females throughout the winter, but the difference was only significant in December ( $F=5.686$ ;  $df=1, 56$ ;  $p=0.02$ ).

### Discussion and conclusion

The 10-fold difference in population density between the grassland and the woodland suggests a considerable contrast in habitat quality. Such differences have been found previously between wood mouse populations in two contrasting habitat types in Iceland where wood mice in a birch forest in northern Iceland had a lower population density than a population in a highly productive *Angelica* stand in southern Iceland (Bengtson et al. 1989b). This difference was mainly attributed to variation in food abundance, but could also be ascribed to different quality of food.

The open grassland of Kjalarnes peninsula seems to be poor in comparison to the natural range of the species in Britain, with autumn maximum population density among the lowest recorded for this species (Unnsteinsdottir and Hersteinsson 2009). In the birch wood of Mogilsa, however, the population density was similar to what has been recorded elsewhere (Watts 1969, Flowerdew 1985, Montgomery 1989, Wilson et al. 1993).

The variation in survival in the grassland site throughout the winter supports the results of a previous study on the importance of weather rather than food abundance for survival of wood mice in this area (Unnsteinsdottir and Hersteinsson 2009). In early winter, when survival was low, the population consisted mainly of juveniles that were still small and had probably not yet stored enough food for the winter, both of which makes them more vulnerable to cold temperatures in early winter. Bengtson et al. (1989b) also found that autumn juvenile mortality in an *Angelica* stand in southern Iceland was correlated with cold temperature. In mid-winter, when survival was high, the animals are believed to share burrows (Wolton 1983) and to have food stored underground, thus minimising exposure to harsh weather and predation. In spring, survival at the grassland site decreased again as the mice have to spend additional time out in the open fields foraging to meet the increased energy demands of reproduction.

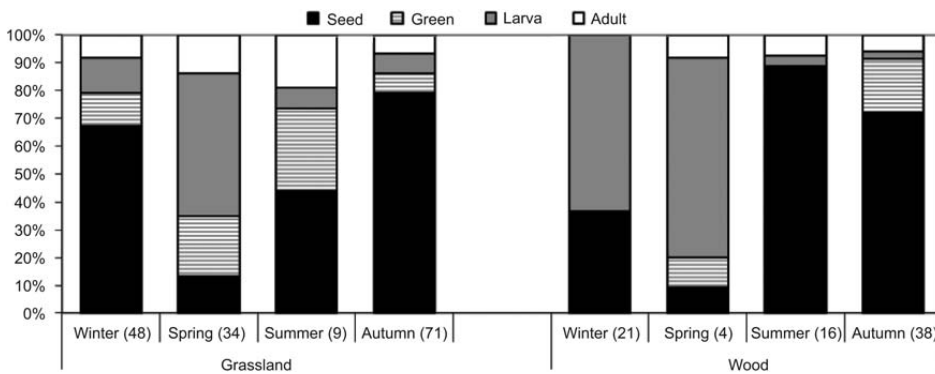
In contrast to the variable survival in grassland, survival was stable in the woodland, indicating that cold temperature in early winter and spring is less important in the woodland than in the grassland. This is possibly related to better body



**Table 3** Proportion (%) of stomachs containing each of the four food categories in each season and habitat type.

Season	Habitat	Seed	Green	Larva	Adult
Spring	Grassland (34)	71	71	91	68
	Wood (4)	25	75	100	75
Summer	Grassland (9)	100	100	67	89
	Wood (16)	100	25	44	63
Autumn	Grassland (71)	97	63	30	51
	Wood (38)	95	74	11	39
Winter	Grassland (48)	92	42	38	65
	Wood (21)	52	14	76	29

Larva and adult mean invertebrate larvae and adults. Sample sizes (number of stomachs from each habitat and season) are given within parentheses.

**Figure 3** Percent of each food type in stomachs by habitats and seasons. Numbers within parentheses represent the sample size. Green represents all green plant material including leaves and stalks, Adult represent all invertebrates other than larvae/pupae.

condition because the woodland mice were heavier than the grassland mice. More importantly, the woodland probably provides a better shelter from predators and adverse weather conditions than open grassland.

In both habitats, mice were feeding predominantly on seeds in autumn and animal matter, mainly arthropod larvae and pupae, in spring. This is in accordance with many previous studies (Watts 1968, Obrtel and Holisova 1979, Hansson 1985, Montgomery 1989, Montgomery and Montgomery

1990). In all seasons there were traces of green plant material in stomachs but these were negligible, except for the grassland site, where green material was eaten in considerable amount, both in spring and summer. This supports the notion that the grassland is a less favourable habitat for wood mice than the woodland, in agreement with the findings of Rogers and Gorman (1995) in set-aside land in northeast Scotland where green plant material and grass were important in the diet of wood mice.

**Table 4** Mean body mass (g) of live-trapped mice from Kjalarnes grassland and Mogilsa woodland in September 2001 to April 2002.

Month	Grass	SE	n	Wood	SE	n
<b>Males</b>						
Sep	20.1	±0.36	140	20.4	±0.43	31
Oct	18.9	±0.41	28	19.8	±0.37	30
Dec	20.3	±0.32	47	22.9	±0.38	34
Feb	22.2	±0.44	27	24.1	±0.67	12
Apr	29.8	±0.83	19	29.9	±0.93	7
<b>Females</b>						
Sep	18.2	±0.37	146	19.9	±0.94	24
Oct	17.3	±0.31	42	17.7	±0.55	25
Dec	19.7	±0.39	39	21.6	±0.79	19
Feb	21.1	±0.93	13	23.4	±0.52	7
Apr	24.8	±0.60	8	24.2	±0.31	5

n, number of trapped individuals of each habitat, season and sex; SE, standard error of the mean.

The mice in the grassland of our study area had access to seeds throughout the year, because seeds were found in 80–100% of their stomachs in all seasons. The mice in the woodland site, however, seemed to exhaust the seed resources during winter due to high population density, switching to animal matter earlier than the mice in the grassland. This could result in density dependent competition for food in spring.

The seeds in the diet mainly reflected the availability of seeds in each location. Thus, the mice showed no apparent choice of seed types in either habitat and were feeding on most seeds available in each season. The same was true for animal matter, as larvae and pupae were most common in the diet in spring when they are plentiful. Furthermore, adult arthropods (e.g. Diptera) were more common at the grassland than woodland site, both in stomachs and pitfall traps.

An overall decrease in mean body mass from September to October is due to the disappearance of the oldest and heaviest individuals and recruitment of trappable juveniles into the population. Lower body mass at the grassland site than in the woodland site, in some months, is a further indication of different habitat quality. This is in agreement with previous studies in Scotland (Zubaid and Gorman 1991, Rogers and Gorman 1995, Corp et al. 1999) and Iceland (Bengtson et al. 1976).

Even though wood mice are highly adaptable with regard to habitat and food abundance (Halle 1993) and have managed to become established in the relatively unfavourable environment of Iceland, this study reveals that Icelandic woodlands are vastly superior habitats compared to grassland. Our results furthermore suggest that different mechanisms can drive population dynamics in the two habitat types through variation in winter mortality and food habits. Although winter mortality due to density independent forces prevent seed depletion in barren grasslands (Unnsteinsdóttir and Hersteinsson 2009), the high density woodland population can suffer from intra-specific food competition as seeds become scarce in late winter. This could result in density dependent population control in the woodland, as is common among wood mice in Britain. Possibly the two contrasting habitats, woodland and grassland, act in a source-sink manner (Bengtson et al. 1989b, Tattersall et al. 2004). This is of importance in light of the deforestation following human settlement in Iceland when a favourable woodland habitat was largely replaced by open grassland and even deserts in some areas (Olafsdóttir et al. 2001). Owing to regulations and planned efforts to restore woodlands (Gunnarsdóttir et al. 2008), conditions for wood mice in Iceland could be considerably improved in the future.

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## References

- Angelstam, P., L. Hansson and S. Pehrsson. 1987. Distribution borders of field mice *Apodemus*: the importance of seed abundance and landscape composition. *Oikos* 50: 123–130.
- Arnason, A. 1974. Protein polymorphism in northern populations of field mice (*Apodemus sylvaticus* L.). PhD thesis. University of Strathclyde, Glasgow.
- Bengtson, S.-A. 1975. Jaktbeteende hos in isländsk population av stenfalk. *Fauna Flora* 70: 8–12 (in Swedish with English summary).
- Bengtson, S.-A., A. Nilsson, S. Nordström and S. Rundgren. 1976. Body weights of *Apodemus sylvaticus* in Iceland. *Acta Theriol.* 21: 389–399.
- Bengtson, S.-A., G. Brinck-Lindroth, L. Lundqvist, A. Nilsson and S. Rundgren. 1986. Ectoparasites on small mammals in Iceland: origin and population characteristics of a species-poor insular community. *Ecography* 9: 143–148.
- Bengtson, S.-A., A. Nilsson and S. Rundgren. 1989a. Unforeseen disruption of wood mouse population dynamics after food reduction: a field experiment. *Oikos* 56: 379–385.
- Bengtson, S.-A., A. Nilsson and S. Rundgren. 1989b. Population structure and dynamics of wood mouse *Apodemus sylvaticus* in Iceland. *Holarct. Ecol.* 12: 351–368.
- Bertsch, K. 1941. Früchte und Samen. Ein Bestimmungsbuch zur Pflanzenkunde der vorgeschichtlichen Zeit. In: (H. Reinert, ed.) *Handbücher der praktischen Vorgeschichtsforschung* (Band 1). Verlag Ferdinand Enke, Stuttgart. pp. 247 (in German).
- Blower, J.G., L.M. Cook and J.A. Bishop. 1981. Estimating the size of animal populations. George Allen and Unwyn, London. pp. 128.
- Burnham, K.P. and D.R. Anderson. 2002. Model selection and multimodel inference (2nd edn). Springer-Verlag, New York. pp. 488.
- Chao, A. and R.M. Huggins. 2005. Modern closed-population capture-recapture models. In: (C. Armstrong, T.L. McDonald and B.F.J. Manly, eds.) *Handbook of capture-recapture analysis*. Princeton University Press, Oxford. pp. 58–87.
- Choquet, R., A.M. Reboulet, R. Pradel, O. Gimenez and J.D. Lebreton. 2003. U-CARE user's guide, version 2.0. Mimeographed document. CEFE/CNRS, Montpellier (<ftp://ftp.cefe.cnrs-mop.fr/biom/Soft-CR/>).
- Cormack, R.M. 1964. Estimates of survival from the sighting of marked animals. *Biometrika* 51: 429–438.
- Corp, N., M.L. Gorman and J.R. Speakman. 1999. Daily energy expenditure of free-living male wood mice in different habitats and seasons. *Funct. Ecol.* 13: 585–593.
- Degerbøl, M. 1939. The field mouse of Iceland, its systematic position (*Apodemus sylvaticus grandiculus* subsp. nov.) and biology. In: (B. Saemundsson, ed.) *The zoology of Iceland IV*. Vol. 76. pp. 39–52.
- Flowerdew, J.R. 1985. The population dynamics of wood mice and yellow necked mice. *Symp. Zool. Soc. Lond.* 55: 315–338.

- Gorman, M.L. and A. Zubaid. 1993. A comparative study of the ecology of woodmice *Apodemus sylvaticus* in two contrasting habitats: deciduous woodland and maritime sand-dunes. *J. Zool. Lond.* 229: 385–396.
- Gunnarsdóttir, E.O., G. Guðjónsson and H. Óskarsson (eds). 2008. Ársrit 2007 (Annual report 2007). Skógrækt ríkisins (The Iceland Forest Service, Reykjavík). pp. 1–76 (in Icelandic).
- Halle, S. 1993. Wood mice (*Apodemus sylvaticus* L.) as pioneers of recolonization in a reclaimed area. *Oecologia* 94: 120–127.
- Hansson, L. 1970. Methods of morphological diet micro-analysis in rodents. *Oikos* 21: 255–266.
- Hansson, L. 1971. Small rodent food, feeding and population dynamics. *Oikos* 22: 183–198.
- Hansson, L. 1985. The food of bank voles, wood mice and yellow-necked mice. *Symp. Zool. Soc. Lond.* 55: 141–168.
- Jolly, G.M. 1965. Explicit estimates from capture-recapture data with both death and immigration-stochastic model. *Biometrika* 52: 225–247.
- 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. *Ecol. Monogr.* 62: 67–118.
- Lupton, P. and U. Wykes. 1938. The field mice of Iceland. *J. Anim. Ecol.* 7: 22–26.
- Montgomery, W.I. 1989. Population regulation in the wood mouse *Apodemus sylvaticus*. I. Density dependence in the annual cycle of abundance. *J. Anim. Ecol.* 58: 465–475.
- Montgomery, S.S.J. and W.I. Montgomery. 1990. Intrapopulation variation in the diet of the wood mouse *Apodemus sylvaticus*. *J. Zool. Lond.* 222: 641–651.
- Nielsen, O.K. 1986. Population ecology of the gyrfalcon in Iceland with comparative notes on the Merlin and the Raven. PhD thesis. Cornell University, Cornell.
- Nielsen, O.K. 1997. Observations on winter food habits of short-eared owl *Asio flammeus* in Iceland. *Náttúrufræðingurinn* (The Naturalist) 67: 85–88 (in Icelandic with an English summary).
- Obrtel, R. and V. Holisova. 1977. Sufficient sample size for analysis of small rodent diets. *Zool. Listy* 26: 193–205.
- Obrtel, R. and V. Holisova. 1979. Food eaten by *Apodemus sylvaticus* in a spruce monoculture. *Fol. Zool.* 28: 299.
- Olafsdóttir, R., P. Schlyter and H. Haraldsson. 2001. Simulating Icelandic vegetation cover during the Holocene. Implications for long-term land degradation. *Geogr. Ann.* 83: 203–215.
- Olafsson, E. 1991. A checklist of Icelandic insects. *Fjölrit Náttúrufræðistofnunar* (The Icelandic Institute of Natural History) 17: 1–69.
- Otis, D.L., K.P. Burnham, G.C. White and D.R. Anderson. 1978. Statistical inference from capture data on closed populations. *Wildl. Monogr.* 62: 7–135.
- Pollock, K.H., J.D. Nichols, C. Brownie and E. Hines. 1990. Statistical inference for capture recapture experiments. *Wildl. Monogr.* 107: 1–97.
- R Development Core Team. 2007. The R Foundation for Statistical Computing. Available at: <http://www.r-project.org/>.
- Rogers, L.M. and M.L. Gorman. 1995. The diet of the wood mouse *Apodemus sylvaticus* on set-aside land. *J. Zool. Lond.* 235: 77–83.
- Saitoh, T., J. Osawa, T. Takanishi, S. Hayakashi, M. Ohmori, T. Morita, S. Uemura, J.O. Vik, N.C. Stenseth and K. Maekawa. 2007. Effects of acorn masting on population dynamics of three forest-dwelling rodent species in Hokkaido, Jpn. *Popul. Ecol.* 49: 249–256.
- Seber, G.A.F. 1965. A note on the multiple-recapture census. *Biometrika* 52: 249–292.
- Selås, V., E. Framstad and T.K. Spidsø. 2002. Effects of seed masting of bilberry, oak and spruce on sympatric populations of bank vole (*Clethrionomys glareolus*) and wood mouse (*Apodemus sylvaticus*) in southern Norway. *J. Zool. Lond.* 258: 459–468.
- Skirnisson, K. 2004. Hagamús (Wood mouse). In: (P. Hersteinsson, ed.) Icelandic mammals, Reykjavík. pp. 262–269 (in Icelandic).
- Southwood, T.R.E. and P.A. Henderson. 2000. Ecological methods. Blackwell Science Ltd, London. pp. 575.
- Tattersall, F.H., D.W. Macdonald, B.J. Hart and W. Manley. 2004. Balanced dispersal or source-sink – do both models describe wood mice in farmed landscapes? *Oikos* 106: 536–550.
- Thorvaldsson, G. 1997. Gróður í íslenskum túnum (Vegetation in Icelandic hayfields). *Náttúrufræðingurinn* (The Naturalist) 67: 45–52 (in Icelandic).
- Unnsteinsdóttir, E.R. and P. Hersteinsson. 2009. Surviving north of the natural range: the importance of density-independence in determining population size. *J. Zool. Lond.* 277: 232–240.
- Watts, C.H.S. 1968. The foods eaten by wood mice (*Apodemus sylvaticus*) and bank voles (*Clethrionomys glareolus*) in Wytham woods, Berkshire. *J. Anim. Ecol.* 37: 25–41.
- Watts, C.H.S. 1969. The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Wytham woods, Berkshire. *J. Anim. Ecol.* 38: 285–304.
- Wheatley, M., K.W. Larsen and S. Boutin. 2002. Does density reflect habitat quality for north American red squirrels during a spruce-cone failure? *J. Mamm.* 83: 716–727.
- White, G.C. and K.P. Burnham. 1999. Program MARK: survival estimation from populations of marked animals. *Bird Study* (Supplement) 46: 120–138.
- Wilson, W.L., W.I. Montgomery and R.W. Elwood. 1993. Population regulation in the wood mouse *Apodemus sylvaticus* (L.). *Mamm. Rev.* 23: 73–92.
- Wolton, R.J. 1983. The activity of free-ranging wood mice *Apodemus sylvaticus*. *J. Anim. Ecol.* 52: 781–794.
- Yunger, J.A. 2002. Response of two low-density populations of *Peromyscus leucopus* to increased food availability. *J. Mamm.* 83: 267–279.
- Zubaid, A. and M.L. Gorman. 1991. The diet of wood mice *Apodemus sylvaticus* living in a sand dune habitat in north-east Scotland. *J. Zool. Lond.* 225: 227–232.
- Zubaid, A. and M.L. Gorman. 1993. The effect of supplementary feeding upon the sizes of the home ranges of wood mice *Apodemus sylvaticus* living on a system of maritime sand-dunes. *J. Zool. Lond.* 231: 233–237.



# **Paper III**

*Reconstructing population size*



# Using Bayesian growth models to reconstruct small-mammal populations during low-trapping periods

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## Keywords

Bayesian analysis; small mammals; growth curves; population density.

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## Abstract

Small-mammal populations that fluctuate in size often undergo periods of low trappability, which could be an important factor contributing to low-density estimates based on trapping efforts.

Age cohort analysis is commonly used to estimate population parameters of animals that are harvested. The method is based on known age at death that can be used for Bayesian hierarchical growth models. It is interesting to see if similar methods, hitherto conducted on long-living species, can be used on live-trapping data on short-lived and fast-growing small mammals.

Using data from live-trapping surveys of *Apodemus sylvaticus* in Iceland, we adjusted growth curves to individual body weights to predict their birth dates. The estimated birth dates were used to estimate population density and recruitment. These were then compared with other data sources.

We found out that density estimates, based on numerical methods [modified nodal analysis (MNA)], underestimated population density during the period of low trappability and that recruitment occurred up to 100 days earlier than was observed by capture-mark-recapture (CMR) analysis and MNA.

This study suggests that cohort analysis can be conducted on short-lived small mammals during periods when estimates based on CMR or numerical analysis fail because of low sample sizes. Furthermore, it is possible to use body weight of live-trapped individuals to estimate age. This is important in terms of ethics and conservation as such methods can be conducted without harming or killing the animals. We believe that live-trapping data obtained during a peak period in population density can be a useful aid when describing population parameters of previous months when low trappability prevents direct measurements.

## Introduction

Population dynamics of small mammals often vary in a regular pattern throughout the year, in association with breeding activity. In low-density habitats, populations can become extremely small at the onset of breeding during spring, followed by a slow increase in population density and a rapid rise at the end of the breeding season in autumn (Hansson, 1969; Watts, 1969; Bengtson, Nilsson & Rundgren, 1989; Montgomery, 1989; Čiháková & Frynta, 1996; Unnsteinsdottir & Hersteinsson, 2009). Small-mammal population estimates are generally derived from capture-mark-recapture (CMR) analysis based on the Jolly–Seber model method (e.g. Otis *et al.*, 1978). The so called robust design (Pollock, 1982; Kendall, Pollock & Brownie, 1995) expands the capacity of the Jolly–Seber in estimating a variety of population parameters in open systems over time. Various methods are available to detect and correct heterogeneous capture and

recapture probabilities (e.g. Otis *et al.*, 1978; Nichols & Pollock, 1983; Nichols, 1986; Chao, 1987; Pollock *et al.*, 1990; Lebreton *et al.*, 1992). These methods are, however, based on sufficient sample sizes (e.g. Chao, Chu & Hsu, 2000), which can be difficult to obtain during periods of low trappability, and the problem can be augmented if the periods coincide with low population density, for example, in the early breeding season. Many studies and experiments have attempted to explain the behavioural reasons for low trappability and/or recapture rate (Tanton, 1965; Watts, 1969; Anderson, 1989; Jensen, Stenseth & Framstad, 1993; Krebs, Singleton & Kenney, 1994; Montgomery, Wilson & Elwood, 1997; Quin *et al.*, 2000), but in general, the problems still remain unsolved.

Indirect population estimates based on modelling of demographic parameters and known age 'at capture' have commonly been conducted on fish and other exploited species stocks (see, e.g. Fryxell, Mercer & Gellately, 1988; Magnusson, 1995). Zhang, Lessard & Campbell (2009)

suggested that data from CMR studies can give information on growth, and therefore also age, that are compatible for Bayesian estimates of population parameters. Furthermore, recent studies suggest that these methods can also be conducted on terrestrial animals, where growth curves were based on direct measurements in the field (Armstrong & Brooks, 2013). We believe that these methods can also be useful when studying small-mammal populations, which suffer from seasonal periods of low trappability.

In a previous study on wood mice *Apodemus sylvaticus* L. at a barren peninsula in south-western Iceland, population density was extremely low in the spring and early summer. Low sample sizes prevented proper estimates of population parameters as assumptions for CMR analysis were not met and could not be corrected for. In contrast, capture numbers were considerably high and various generations of mice were trapped during the autumn peak (Unnsteinsdottir & Hersteinsson, 2009). Growth curves and age determination of small mammals from laboratory and field studies are available and useful for Bayesian hierarchical growth models while describing demographic parameters of previous months (Layne, 1968; Adamczewska-Andrzejewska, 1971; Bengtson *et al.*, 1976; Vandorpe & Verhagen, 1979; Gurnell & Rennolls, 1983; Lin, Nishino & Shiraishi, 1993). From information on body weight measurements of autumn-trapped mice, we can estimate the age of each individual mouse and, therefore, its birth date. This makes it possible to use Bayesian modelling to predict recruitment during summer and reconstruct density estimates. In this study we suggest that cohort analysis can be conducted on short-lived small mammals with clear and discrete generations when estimates based on CMR or numerical analysis fail because of low sample sizes. Furthermore, we suggest that body weight measurements of live-trapped individuals can be used to estimate age in the field. Hence, we make an effort to use the ample autumn trapping data as an aid to describe population parameters of the previous months when low trappability prevents direct measurement.

## Materials and methods

### Trapping data

This study is based on data from CMR surveys in 35 ha open grassland area at the tip of Kjalarnes peninsula of south-western Iceland (64°14.035'N, 21°54.017'W). Live trapping was conducted in 5-day sessions, *c.* every 5 weeks, from September 2001 to October 2003 and from September 2004 to October 2005. Live-trapped mice were weighed and tagged, and breeding status was estimated. Trapping methods, individual tagging and handling of captured and recaptured mice have been described in an earlier paper (Unnsteinsdottir & Hersteinsson, 2009). Trapping methodology was approved by the Icelandic Food and Veterinary Authority and the Icelandic Ministry of the Environment. We did not observe any negative effects of tagging during our study.

### Growth curves and birth dates

We used a Bayesian model to simultaneously estimate growth parameters and birth dates of observed mice from capture dates and observed weight of the mice. A full description of the model, including the computer code for the implementation, can be found in Supporting Information Figure S1. A briefer description concentrating on input data and results is given here.

### Data preparation

In order to model a cohort of mice over the early life period of low-trapping returns and to avoid the complexity of overwintering, the data were prepared by selecting a subset of the observed mice, which is intended to contain mice less than 1 year old (and hence expected to fit a continuous asymptotic growth model rather than losing weight and dropping back below the asymptote during winter) and to exclude pregnant females (whose weight gain will move them away from the growth curve for non-pregnant mice). The criteria applied were that included data points must be for the first year in which the mouse was observed, be observed after May 15 (estimated as first day on which the current year of cohort might be trapped) and be no heavier than 25 g before the end of October (to exclude larger mice that might be more than 1 year old). All observations matching the criteria were pooled from all years (2001–2005); hence, we model the dynamics of a typical cohort rather than any specific year class. Each observation consisted of mouse ID number, sex of mouse, weight on day of observation and day of the year on which the observation was made.

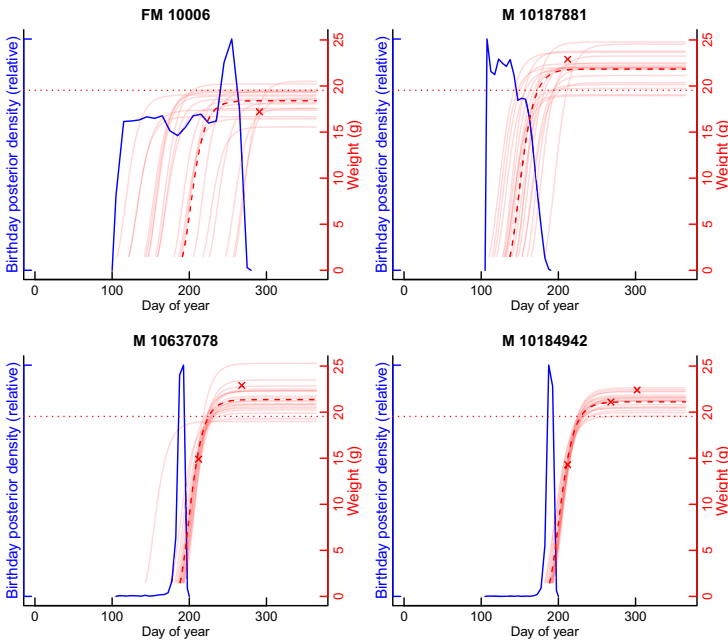
### Bayesian model

Growth was modelled using a Gompertz growth curve (e.g. Zullinger *et al.*, 1984; Lin *et al.*, 1993; Oh & Mori, 1998; Jaheen, 2003) with a hierarchical parameter structure (parameters for population, sex and individual). Birth dates were estimated based on growth. This resulted in posterior distributions for growth asymptote and rate parameters (for population, sex and each individual) and birth date. For a full description of the model fitting, see Supporting Information Figure S2.

### Estimating population size

The posterior distribution of birthdays was used to estimate the pattern of change of the population size of a typical cohort through the year. Typical cohorts were modelled as starting from a population size of 0 at the beginning of the year. Births were added for each day of the year in proportion to the sum of the posterior densities of the birthdays of the mice. Fixed mortality rates were then applied to model death of the mice in each cohort. Each modelled cohort used a different fixed mortality rate (high, 5% per day; medium, 2% per day; low, 1% per day) chosen from the range of estimates of monthly survival from previous studies in Iceland (Bengtson *et al.*, 1989).





**Figure 1** Example individual mice. Actual date and observed size marked as red crosses (one cross for each observation); pink lines are a set of growth curves randomly sampled from the posterior distribution of growth parameters for that mouse; red dotted line is growth curve obtained from median of posterior distribution of growth parameters; blue line is probability density function for posterior distribution of birthdates for that mouse; right-hand axis is for growth curves and mouse size; left-hand axis is for probability density. For clarification, day 100 is April 10, day 200 is July 19 and day 300 is October 27.

## Model fitting

Model fitting was performed by an R script (R version 3.0.1; The R Foundation for Statistical Computing, Vienna, Austria) that assembled the dataset before using the BRugs library (BRugs library version 0.8-1; Lunn *et al.*, 2009) to fit the model in OpenBUGS (version 3.2.2 rev 1063; OpenBUGS Project Management Group; Thomas *et al.*, 2006) and extract the chains of estimates. An initial 1000 iterations were used to burn in the chain, then 10 000 iterations thinned by every 10 observations yielded 1000 sets of estimates of each parameter.

## Results

### Bayesian model

The Bayesian model was fitted to 1201 observations of 907 mice (maximum of four observations per mouse). Full details of the model results can be found in Supporting Information Figure S2.

### Posterior parameters

The model parameters and 95% Bayesian confidence intervals are given in Supporting Information Table S1. There was no difference between average growth asymptote among sexes, but the average growth rate was slightly higher for females (Supporting Information Figure S2).

Figure 1 shows the results of fitting the model to the data on individual mice, one female and three males, with different

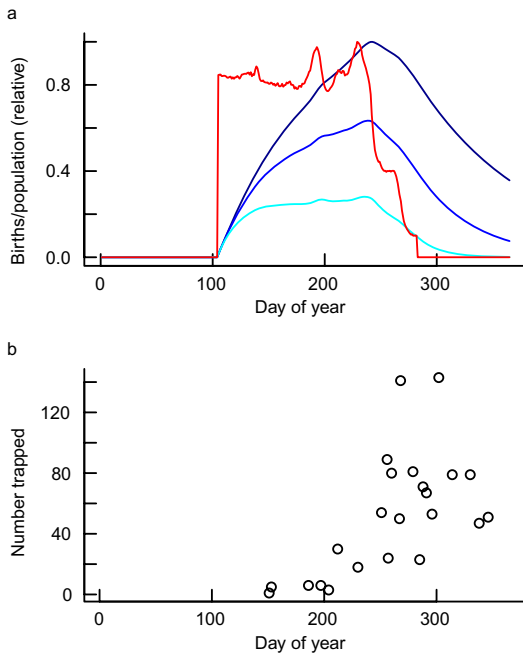
numbers of observation. This shows a selection of possible growth curves for each mouse as well as the median model parameters and the posterior range of possible birth dates for that mouse. As expected, with more observations birth date distribution was narrower.

### Estimated birth dates and population growth

The population dynamics obtained for a single cohort through the year based on the results of the model fitting are shown in Fig. 2a. The population size of a cohort on each day of the year, based on estimated birth dates from the model fitting, differed according to the amount of fixed mortality. As such with high daily mortality (5%), the population reached its maximum number around day 150 and stayed high until day 250. With lower daily mortality levels, the peak was later in the year (autumn) and shorter (Fig. 2a blue lines). There was a discrepancy between the number of trapped mice each day and the relative population size of cohorts at all rates of mortality, with trapped mice in lower number roughly from day 150 until 250 compared with the relative population estimates (Fig. 2b).

## Discussion

The estimated birth dates from the Bayesian analysis of growth curves from body weight of live-trapped mice were



**Figure 2** (a) Population size of cohort over the year simulated from birthday posteriors and estimated mortalities. The red line shows birth rate on a relative scale, obtained from summed posterior densities of birthdays. Various blue lines show population size of the modelled typical cohort under different daily mortality rates: high (5%, upper blue line), medium (2%, mid-blue line) and low (1%, low blue line). (b) Total number of mice trapped on each day of the year in which sampling took place (pooled over all years).

within the range of first potential births of the season. These birthdays were then used as parameters in 'the new population estimates' during the period of low sample sizes. Recruitment of the population could thus be estimated up to 100 days earlier and with more accuracy than with the numerical methods. The evident gap between the estimated relative and trapped numbers strongly point that the individuals were present in June until early September.

Watts (1969) denoted that the rapid increase of the population later in the breeding season could be related to a great improvement of juvenile survival and somewhat adult survival in the autumn. It has also been suggested that *A. flavicollis* born in early spring have higher survival rate during winter than mice born later in summer (Bujalska & Grüm, 2006). According to the estimates of our study, autumn peak occurred when daily mortality was low (1%). Clear autumn peaks like those observed in this population could thus be the results of high summer survival. However, low trappability during spring and early summer makes it difficult to determine survival and/or detect dispersal of

young mice in this period; by live-trapping data, this problem has been discussed in former studies (e.g. Plesner-Jensen, 1996). No winter breeding has been recorded for *A. sylvaticus* in Iceland. In our study, the first confirmed pregnancy in spring was in late April (E. R. Unnsteinsdottir, pers. obs. unpubl. data). Thus, according to the potential length of gestation and lactating periods (Flowerdew, 1977), the first generation of the summer would have been born in late April to early May and become trappable in mid-May or the first week of June. In 3 years of our study, one young (9.8 g) was live trapped in mid-May (2003) and six young (<14 g) were trapped in early June (2002 and 2003). By dissecting mice that died in traps, we found that three females had more placental scars (Rolan & Gier, 1967) than the previously published litter size of 4–9 (Bengtson *et al.*, 1989). This strongly suggests that each of them had more than one litter in the season. Two small females (body length of ~7 cm) in which we found placental scars were almost certainly breeding in the summer of their own birth; one of them had also given birth to two litters (11 placental scars). According to this, at least some mice born in spring were able to breed twice before the onset of winter. As we assume that body size (length/weight) is a sign of age, these small females were believed to have been born in mid-summer. If so, the second cohort was also able to breed before winter. The fact that more than one generation of females were participating in the summer breeding can at least partly explain the rapid population increase in the autumn, in agreement with other studies on this species (Flowerdew, 1974; Montgomery, 1989; Wilson, Montgomery & Elwood, 1993; Čiháková & Frynta, 1996). Studies in southern Sweden and southern Iceland suggested that, in good conditions, female wood mice born in spring could breed up to three times in the same summer (Bergstedt, 1965; Bengtson *et al.*, 1989). Tanton (1965) did not support the idea that the rapid population growth during autumn was explained simply by high rate of late summer breeding activities. He suggested that the most important factor explaining low population estimates during the early breeding season was low trappability, but did not exclude the role of immigration in the rapid population increase during fall. Watts (1969) noted that a rapid increase in a wood mouse population at the end of the breeding season exceeded an expected reproductive capacity of the females 'known to be alive' in the population. According to this, mice did not enter traps during a certain period of the early breeding season but became trappable later on. Indeed, at the end of the breeding season, wood mice of various generations become trappable, and estimates based on CMR analysis become reliable.

In this paper we suggest that cohort analysis can be conducted on short-lived small-mammal species with clear and discrete generations. Further understanding of the mechanisms behind the population growth will improve the use of these methods. Furthermore, we have shown that it is possible to use body weight of live-trapped individuals to estimate age. This is important in terms of ethics and conservation as such methods can be conducted without harming or killing the animals. We believe that live-trapping data obtained during a

peak period in population density can be a useful aid when describing population parameters of previous months when low trappability prevents direct measurements.

## Acknowledgements

This paper is dedicated in memory of late Prof. Pall Hersteinsson who sadly passed away during the process of writing. The study was financed by the Research Fund of the Icelandic Centre for Research, the Research Fund of the University of Iceland and the Assistantship Fund of the University of Iceland, the Norwegian Government Scholarship Pool and the University of Tromsø, Norway. Landowners at Brautarholt and Iceland Forest Service offered their land for the study. Ístex, an Icelandic wool factory, donated wool for insulating the live traps. Students at the biology department took part in live-trapping surveys. We wish to thank Arnthor Gardarsson, Tomas G. Gunnarsson and Rolf A. Ims for valuable comments and advice while writing this paper.

## References

- Adamczewska-Andrzejewska, K.A. (1971). Methods of age determination in *Apodemus agrarius* (Pallas 1771). *Ann. Zool. Fenn.* **8**, 68–71.
- Anderson, P.K. (1989). Dispersal in rodents: a resident fitness hypothesis. *Spec. Publ. Amer. Soc. Mammal.* **9**, 1–141.
- Armstrong, D.P. & Brooks, R.J. (2013). Application of hierarchical biphasic growth models to long-term data for snapping turtles. *Ecol. Modell.* **250**, 119–125.
- Bengtson, S.-A., Nilsson, A., Nordström, S. & Rundgren, S. (1976). Body weights of *Apodemus sylvaticus* in Iceland. *Acta Theriol.* **21**, 389–399.
- Bengtson, S.-A., Nilsson, A. & Rundgren, S. (1989). Population structure and dynamics of wood mouse *Apodemus sylvaticus* in Iceland. *Hol. Ecol.* **12**, 351–368.
- Bergstedt, B.O. (1965). Distribution, reproduction, growth and dynamics of the rodent species *Clethrionomys glareolus* (Schreber), *Apodemus flavicollis* (Melchior) and *Apodemus sylvaticus* (Linne) in southern Sweden. *Oikos* **16**, 132–160.
- Bujalska, G. & Grüm, L. (2006). Winter survival of *Apodemus flavicollis* in Crabapple island (NE Poland). *Hyst. Ital. J. Mammal.* **17**, 173–177.
- Chao, A. (1987). Estimating the population size for capture–recapture data with unequal catchability. *Biometrics* **43**, 783–791.
- Chao, A., Chu, W. & Hsu, C.-H. (2000). Capture–recapture when time and behavioural response affect capture probabilities. *Biometrics* **56**, 427–433.
- Čiháková, J. & Frynta, D. (1996). Abundance fluctuations in *Apodemus* spp. and *Clethrionomys glareolus* (Mammalia: Rodentia): a seven year study in an isolated suburban wood. *Acta Soc. Zool. Bohem.* **60**, 3–12.
- Flowerdew, J.R. (1974). Field and laboratory experiments on the social behaviour and population dynamics of the wood mouse (*Apodemus sylvaticus*). *J. Anim. Ecol.* **43**, 499–511.
- Flowerdew, J.R. (1977). Wood mouse *Apodemus sylvaticus*. In *The handbook of British mammals*: 206–217. Corbet, G.B. & Southern, H.N. (Eds). London: Blackwell.
- Fryxell, J.M., Mercer, E. & Gellately, B. (1988). Population dynamics of Newfoundland moose using cohort analysis. *J. Wildl. Mgmt.* **52**, 14–21.
- Gurnell, J. & Rennolls, K. (1983). Growth in field and laboratory populations of wood mice (*Apodemus sylvaticus*). *J. Zool. (Lond.)* **200**, 355–365.
- Hansson, L. (1969). Spring populations of small mammals in central Swedish Lapland in 1964–68. *Oikos* **20**, 431–450.
- Jaheen, Z.F. (2003). A Bayesian analysis of record statistics from the Gompertz model. *Appl. Math. Comput.* **145**, 307–320.
- Jensen, P.M., Stenseth, N.C. & Framstad, E. (1993). Trappability of the Norwegian lemming (*Lemmus lemmus*). In *The biology of lemmings*: 547–554. Ims, R.A. & Stenseth, N.C. (Eds). London: The Linnean Society of London.
- Kendall, W.L., Pollock, K.H. & Brownie, C. (1995). A likelihood-based approach to capture–recapture estimation of demographic parameters under the robust design. *Biometrics* **51**, 293–308.
- Krebs, C.J., Singleton, G.R. & Kenney, A.J. (1994). Six reasons why feral house mouse populations might have low recapture rates. *Wildl. Res.* **21**, 559–567.
- Layne, J.N. (1968). Ontogeny. In *Biology of Peromyscus (Rodentia)*: 148–253. King, J.A. (Ed.). Stillwater, USA: Am. Soc. Mammal., 2.
- Lebreton, J.D., Burnham, K.P., Clobert, J. & Anderson, D.R. (1992). Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecol. Monogr.* **62**, 67–118.
- Lin, L.K., Nishino, T. & Shiraishi, S. (1993). Postnatal growth and development of the Formosan wood mouse *Apodemus semotus*. *J. Mamm. Soc. Japan* **18**, 1–18.
- Lunn, D., Spiegelhalter, D., Thomas, A. & Best, N. (2009). The BUGS project: evolution, critique, and future directions. *Stat. Med.* **28**, 3049–3067.
- Magnusson, K.G. (1995). An overview of the multispecies VPA – theory and applications. *Rev. Fish Biol. Fish.* **5**, 195–212.
- Montgomery, W.I. (1989). Population regulation in the wood mouse, *Apodemus sylvaticus*. I. Density dependence in the annual cycle of abundance. *J. Anim. Ecol.* **58**, 465–475.
- Montgomery, W.I., Wilson, W.L. & Elwood, R.W. (1997). Spatial regulation and population growth in the wood mouse *Apodemus sylvaticus*: experimental manipulations of males and females in natural populations. *J. Anim. Ecol.* **66**, 755–768.
- Nichols, J.D. (1986). On the use of enumeration estimators for interspecific comparison, with comments on a ‘Trappability’ estimator. *J. Mammal.* **67**, 590–593.
- Nichols, J.D. & Pollock, K.H. (1983). Estimation methodology in contemporary small mammal capture–recapture studies. *J. Mammal.* 253–260.

- Oh, H.S. & Mori, T. (1998). Growth, development and reproduction in captive of the large Japanese field mouse, *Apodemus speciosus* (Rodentia, Muridae). *J. Fac. Agric. Kyushu Univ.* **43**, 397–408.
- Otis, D.L., Burnham, K.P., White, G.C. & Anderson, D.R. (1978). Statistical inference from capture data on closed animal populations. *Wildl. Monogr.* **62**, 3–135.
- Ouin, A., Paillat, G., Butet, A. & Burel, F. (2000). Spatial dynamics of wood mouse (*Apodemus sylvaticus*) in an agricultural landscape under intensive use in the Mont Saint Michel Bay (France). *Agric. Ecosyst. Environ.* **78**, 159–165.
- Plesner-Jensen, S. (1996). Juvenile dispersal in relation to adult densities in wood mice *Apodemus sylvaticus*. *Acta Theriol.* **41**, 177–186.
- Pollock, K.H. (1982). A capture–recapture design robust to unequal probability of capture. *J. Wildl. Mgmt.* **46**, 752–757.
- Pollock, K.H., Nichols, J.D., Brownie, C. & Hines, J.E. (1990). Statistical inference for capture–recapture experiments. *Wildl. Monogr.* **107**, 3–97.
- Rolan, R.G. & Gier, H.T. (1967). Correlation of embryo and placental scar counts of *Peromyscus maniculatus* and *Microtus ochrogaster*. *J. Mammal.* **48**, 317–319.
- Tanton, M.T. (1965). Problems of live-trapping and population estimation for the wood mouse, *Apodemus sylvaticus* (L.). *J. Anim. Ecol.* **34**, 1–22.
- Thomas, A., O'Hara, B., Ligges, U. & Sturtz, S. (2006). Making BUGS open. *R News* **6**, 12–17.
- Unnsteinsdottir, E.R. & Hersteinsson, P. (2009). Surviving north of the natural range: the importance of density independence in determining population size. *J. Zool. (Lond.)* **277**, 232–240.
- Vandorpe, E. & Verhagen, R. (1979). An age reference model for the wood mouse, *Apodemus sylvaticus* (Linnaeus, 1758), by use of the lens technique. *Ann. Soc. R. Zool. Belg.* **109**, 133–140.
- Watts, C.H.S. (1969). The regulation of wood mouse (*Apodemus sylvaticus*) numbers in Wytham woods, Berkshire. *J. Anim. Ecol.* **38**, 285–304.
- Wilson, W.L., Montgomery, W.I. & Elwood, R.W. (1993). Population regulation in the wood mouse *Apodemus sylvaticus* (L.). *Mamm. Rev.* **23**, 73–92.
- Zhang, Z., Lessard, J. & Campbell, A. (2009). Use of Bayesian hierarchical models to estimate northern abalone, *Haliotis kamtschatkana*, growth parameters from tag–recapture data. *Fish. Res.* **95**, 289–295.
- Zullinger, E.M., Ricklefs, R.E., Redford, K.H. & Mace, G.M. (1984). Fitting sigmoidal equations to mammalian growth curves. *J. Mammal.* **65**, 607–636.

## Supporting information

Additional Supporting Information may be found in the online version of this article at the publisher's web-site:

**Figure S1.** Prior probability density distribution of parameters and example growth curves: (a) prior density of population mean growth asymptote, (b) density of Exp(20) (solid line) and Exp(30) (dashed line) used for unknown standard deviations, and (c) example of Gompertz growth curves with asymptotic size as population mean and rate  $\alpha = -0.008$  (upper line, fast growth) and  $\alpha = -0.064$  (lower line, slow growth).

**Figure S2.** Posterior probability density distributions for (a)  $K_{\mu}$  and (b) rate  $\alpha_{\mu}$ . Histogram of posterior distribution, smoothed kernel density plot as solid black line, prior distribution as dashed line, and male and female specific parameter  $K_{\text{male}}$  and  $K_{\text{female}}$  posterior distributions as blue and red, respectively.

**Table S1.** Median and 95% Bayesian confidence intervals for model parameters.

## Using Bayesian Models to Reconstruct Small Mammal Populations

E.R. Unnsteinsdottir, P. Hersteinsson, J.P. Jonasson, B.J. McAdam

Journal of Zoology

### Supplementary Information

This supplementary information gives full details of the growth and birth model. Some details are replicated from the main paper, so that this may be read as a stand-alone document.

### Methods

#### Bayesian Model

The implementation of the Bayesian model simultaneously estimates growth parameters and possible birth dates for each mouse. For each observation,  $i$ , of any mouse the input to the model is a mouse ID ( $m_i$ ), weight on day of observation ( $w_i$ ), and day of the year ( $d_i$ ). For every mouse ID,  $m$ , we also know the mouse sex,  $s_m \in \{\text{female, male}\}$ .

#### Unknowns

The model estimates several unknown variables. The Gompertz growth model is a hierarchical model with parameters for population sex and individual, specifically there is a population average growth asymptote,  $K_\mu$ , and rate,  $\alpha_\mu$ ; sex specific asymptotes and rate,  $K_{\text{male}}, K_{\text{female}}, \alpha_{\text{male}}, \alpha_{\text{female}}$ ; and for each mouse,  $m$ , individual asymptote and rate,  $K_m, \alpha_m$ . The random variation in the growth model is characterised by precision parameters,  $\tau_{K, \text{sex}}, \tau_{\alpha, \text{sex}}, \tau_K, \tau_\alpha, \tau$ . Each mouse has an unknown birthday  $b_m$ .

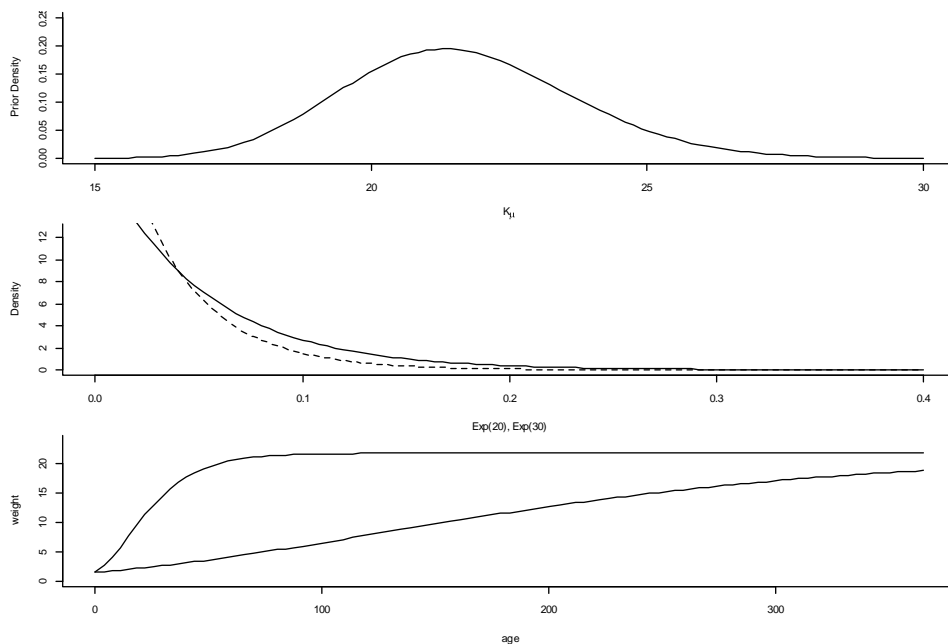
#### Priors

Prior distribution of population mean growth asymptote is based on measured size of individuals observed after day 330 (assumed to be near or fully grown), mean of logs  $\overline{\log(w)} = 3.06$  (equating to weight 21.3g), and standard deviation  $\sigma_{\log(w)} = 0.099$ . According to the Gompertz growth model, all weights should have a log normal distribution

$$K_\mu \sim \ln \text{N}(\overline{\log(w)}, 1/\sigma_{\log(w)}^2)$$

(‘ln N’ denotes the lognormal distribution parameterised by log of mean and precision. All probability distributions are parameterised here as in the OpenBugs implementations, the probability density function of this distribution is shown in Figure S1a)

## Using Bayesian Models to Reconstruct Small Mammal Population



**Figure S1:** Prior probability density distribution of parameters and example growth curves: (a) prior density of population mean growth asymptote; (b) density of  $\text{Exp}(20)$  (solid line) and  $\text{Exp}(30)$  (dashed line) used for unknown standard deviations; (c) example Gompertz growth curves with asymptotic size as population mean and rate  $\alpha = -0.008$  (upper line, fast growth) and  $\alpha = -0.064$  (lower line, slow growth).

Prior distribution of population mean growth rate is assumed to be uniform with limits chosen such that a mouse reaches 90% of asymptotic size after between 50 and 400 days.

$$\alpha_{\mu} = U(-0.064, -0.008)$$

The variation in growth between the sexes is characterised by the unknown precision parameters  $\tau_{K,sex}$  and  $\tau_{\alpha,sex}$ . These are given priors based on an exponential distribution of the corresponding standard deviation (distribution  $\text{Exp}(20)$  is exponential with has an expected value of 0.05, see Figure S1b, solid line)

$$\sigma_{K,sex}, \sigma_{\alpha,sex} \sim \text{Exp}(20)$$

$$\tau_{K,sex} = 1 / \sigma_{K,sex}^2$$

$$\tau_{\alpha,sex} = 1 / \sigma_{\alpha,sex}^2$$

$$K_{\text{male}}, K_{\text{female}} \sim \ln N(\log(K_{\mu}), \tau_{K,sex})$$

$$\alpha_{\text{male}}, \alpha_{\text{female}} \sim N(\alpha_{\mu}, \tau_{\alpha,sex})$$

In principal, this can be extended for any number of population components with differing growth parameters.

Individual mice vary from their sex mean growth parameters in the same manner

$$\sigma_K, \sigma_\alpha \sim \text{Exp}(20)$$

$$\tau_K = 1 / \sigma_K^2$$

$$\tau_\alpha = 1 / \sigma_\alpha^2$$

$$K_m \sim \text{ln N}(\log(K_{s_m}), \tau_K) \text{ for all } m$$

$$\alpha_m \sim \text{ln N}(\log(\alpha_{s_m}), \tau_\alpha) \text{ for all } m$$

And finally, growth is stochastic so there is an unknown variation between the individual growth curve and individual observations of weight, controlled by unknown precision  $\tau$ . As variation around the growth curve for an individual is likely to be smaller than variation between individuals, we use a narrower prior (dotted line on Figure S1b).

$$\sigma \sim \text{Exp}(30)$$

$$\tau = 1 / \sigma^2$$

The possible birthdays of each mouse are assumed to be uniformly distributed from the start of the breeding season (20<sup>th</sup> April=day 110, known from dissection of trapped mice, used as  $\text{minbirthday}_m$  for all mice  $m$ ) and the day before the first observation of that mouse ( $\text{maxbirthday}_m$ ). An alternative approach used by Zhang et al (2009) is to use a Gamma distribution for age at first capture in order to exclude the possibility of trapping at very young age, and of individuals being exceptionally old. We do not consider that we have sufficient information to set a prior for such a Gamma distribution, and the short breeding season is likely to be the dominant effect.

$$b_m \sim \text{U}(\text{minbirthday}_m, \text{maxbirthday}_m)$$

### Model Equations

The expected size of a mouse on a day of observation depends upon its age and the individual growth parameters for that mouse, following the Gompertz growth model and with a fixed birth size  $w_0 = 1.5\text{g}$ , for all observations  $i$ :

$$E(w_i) = K_{m_i} \times \exp(\log(w_0 / K_{m_i}) \times \exp(\alpha_{m_i} \times (d_i - b_{m_i})))$$

The residual variation between  $E(w_i)$  and  $w_i$  has a lognormal distribution with precision  $\tau$

$$w_i \sim \text{ln N}(\log(E(w_i)), \tau)$$

Example growth curves for high and low growth rates are shown in Figure S1c,d

### OpenBugs Implementation

The model is described using the OpenBugs model below

```
MouseModel {
```

## Using Bayesian Models to Reconstruct Small Mammal Population

```
# The unknowns are:
# - population growth asymptote and rate: Kmu, alphaMu
# - sex specific growth asymptote and rate: Ksex[s], alphaSex[s]
# - level of sex variation: tauKSex, tauAlphaSex
# - individual growth asymptote and rate: K[m], alpha[m]
# - level of individual variation: tauK, tauAlpha
# - level of observation variation: tau
# - mice's birthdays, birth[m]

# known values (observations given as input) are:
# - mouse observed on each observation: mouse[i]
# - weight at each observation: weight[i]
# - day of each observation: day[i]
# - sex of each mouse: sex[m]
# - range of possible birthdays for each mouse:
#   minBirthday[m], maxBirthday[m]
# - number of observations: observations
# - number of mice: mice

# PRIORS

# K distributed log-normally according to 'adult' data
# This is the precision of the log of K in the data
log.KPrecision <- 1/(adultLogWeightSD * adultLogWeightSD)
Kmu ~ dlnorm(adultMeanLogWeight, log.KPrecision)
log.Kmu <- log(Kmu)

# alpha is the growth rate,
# to reach 90% of asymptote in 50 days alpha=-0.064
# to reach 90% of asymptote in 400 days, alpha=-0.008
# > 20 * exp(log(1.5/20) * exp(-0.064 * 50))
# [1] 17.99596
```



## Using Bayesian Models to Reconstruct Small Mammal Population

```
# > 20 * exp(log(1.5/20) * exp(-0.008 * 400))
# [1] 17.99596
alphaMu ~ dunif(-0.064, -0.008)

# SEX SPECIFIC K AND ALPHA.
sigmaKSex ~ dexp(20) # expected value 0.05
                    # corresponds roughly to lg variation of 20g mean
tauKSex <- 1/(sigmaKSex*sigmaKSex)
sigmaAlphaSex ~ dexp(20) # expected value 0.05
                # scale corresponds to scale of alphaMu
tauAlphaSex <- 1/(sigmaAlphaSex*sigmaAlphaSex)
for(s in 1:2){
  Ksex[s] ~ dlnorm(log.Kmu, tauKSex)
  log.Ksex[s] <- log(Ksex[s])
  alphaSex[s] ~ dnorm(alphaMu, tauAlphaSex)
}

# tau is the unknown precision of the growth curve
# this is 1/variance of residuals
# our prior for tau is that large values should be more likely
# (i.e. smaller variance)
sigmaK ~ dexp(20) # expected value 0.05
tauK <- 1/(sigmaK*sigmaK)
sigmaAlpha ~ dexp(20) # expected value 0.05
tauAlpha <- 1/(sigmaAlpha*sigmaAlpha)
sigma ~ dexp(30) # expected value 0.05
          # could try smaller variation between samples
          # than between mice (e.g. 30)
tau <- 1/(sigma*sigma)

# individual growth
for(m in 1:mice){
  # individual K and alpha sampled from distributions for sex of mouse
  K[m] ~ dlnorm(log.Ksex[sex[m]], tauK)
```

## Using Bayesian Models to Reconstruct Small Mammal Population

```
alpha[m] ~ dnorm(alphaSex[sex[m]], tauAlpha)I(-0.100, -0.020)

  # individual growth rate
}

# birthday distributed normally through the breeding season
# but not after first observation of the mouse!
for(m in 1:mice){
  birthday[m] ~ dunif(minBirthday[m], maxBirthday[m])
}

# GROWTH MODEL
for(i in 1:observations){

  # age
  age[i] <- (day[i] - birthday[mouse[i]])

  # expected weight (given birthday, alpha and K)
  expectedWeight[i] <- K[mouse[i]] *
    exp( log(birthWeight/K[mouse[i]]) *
        exp(alpha[mouse[i]] * age[i]) )
  log.expectedWeight[i] <- log(expectedWeight[i])

  # residuals (not needed but useful for debugging)
  #residual[i] <- expectedWeight[i] - weight[i]

  # error in expected weight
  weight[i] ~ dlnorm(log.expectedWeight[i], tau)

} # end for(i in observations)

} # end MouseModel
```

### Model Fitting

Model fitting was performed by an R script that assembled the data set before using the BRugs library to fit the model in OpenBugs and extract the chains of estimates. An initial 10000 iterations

were used to burn-in the chain, then 50000 iterations thinned by every 10 observations yielded 5000 sets of estimates of each parameter.

A copy of the OpenBugs data file can be obtained from [NEED TO PUT THE DATA ONLINE](#)

## Results

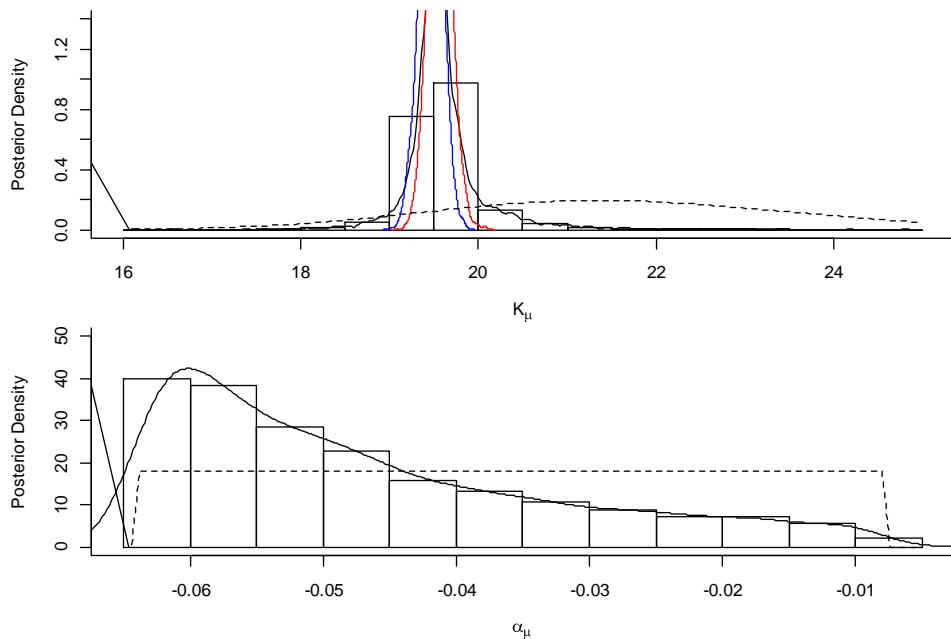
### Posterior Parameters

Table S1 shows median and 95% Bayesian confidence intervals for model parameters.

Variable	2.5%	50%	97.5%
$K_\mu$	18.9	19.5	20.8
$\tau_K$	71.2	85.3	105
$\alpha_\mu$	-0.063	-0.051	-0.012
$\tau_\alpha$	11500	789000	24100000
$K_{\mu,\text{female}}$	19.3	19.6	19.8
$K_{\mu,\text{male}}$	19.2	19.5	19.7
$\alpha_{\text{female}}$	-0.097	-0.091	-0.086
$\alpha_{\text{male}}$	-0.093	-0.088	-0.080
$\tau$	124	155	192

**Table S1:** median and 95% Bayesian confidence intervals for model parameters

Figure S2 shows posterior probability densities of parameters, and example growth curves.



**Figure S2:** Posterior probability density distributions for (a)  $K_\mu$  and (b) rate  $\alpha_\mu$ . Histogram of posterior distribution, smoothed kernel density plot as solid black

## Using Bayesian Models to Reconstruct Small Mammal Population

line, prior distribution as dashed line, and male and female specific parameter  $K_{\text{male}}$ ,  $K_{\text{female}}$  posterior distributions as blue and red respectively.

Figure 1 in the paper shows posterior distributions of growth curves and possible birth dates for example mice with different numbers of observations.

### **Estimated Birth Dates and Population Growth**

Figure 2 in the paper shows the overall distribution of birth dates of the observed mice, and cohort population size based on these birth dates and different values of estimated daily mortality.