

# Spatial and temporal population dynamics in the mountain tundra – mesopredator and prey

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## Abstract

It is well known that competition, predation and fluctuating food resources can have strong effect on individual fitness and population dynamics. The complexity of natural systems can make it complicate to disentangle those processes, but environments with relatively simple food webs, and strong cyclic population dynamics offer contrasting conditions resembling experimental treatments. This thesis concerns the spatial and temporal implications of fluctuations in small rodent abundance on two trophic levels in a highly cyclic ecosystem, the Scandinavian mountain tundra. The first two chapters focus on plant biomass and spatiotemporal distribution in the Norwegian lemming (*Lemmus lemmus*), while the three last papers focus on the direct and indirect effects of small rodent fluctuations and territory quality on reproductive success, juvenile survival and group living in a lemming specialist mesopredator, the arctic fox (*Vulpes lagopus*). By developing, validating and applying a novel application of aerial photos for remote sensing of plant biomass (Chapter I), we found that food availability predicted lemming distribution during population peaks, but that they were more habitat specific during increase years when intraspecific competition was lower (Chapter II). Arctic fox reproduction is tightly connected to small rodent abundance but the effects of geographical variation in food availability is less well known. We used 17 years of population surveys of an arctic fox subpopulation in mid Sweden (*Helagsfjällen*) to investigate potential effects. During small rodent increase years, we found that arctic fox litter sizes were smaller in territories of intermediate plant productivity, compared to both more and less productive territories (Chapter III). This could be an effect of limited food availability together with increased presence of red foxes (*Vulpes vulpes*), a stronger and potentially lethal competitor. However, when small rodents peaked, and competition would be expected to decrease, we saw no effect of territory productivity. Based on a smaller data set concerning juvenile summer survival, we found that the mortality rate among juveniles born by first time breeding arctic fox females were more sensitive to low small rodent prey abundance (Chapter IV). We explain it with an increased predation pressure from top-predators that switch from small rodents to alternative prey when small rodents decline, as suggested by an observed positive effect on juvenile survival by adult presence on den sites. Arctic foxes are socially flexible, and several adults can share a den with the resident pair, potentially increasing juvenile survival and help in territorial defence. Returning to the 17-year data set, we tested the Resource Dispersion Hypothesis predicting that increased resource availability should increase group size (Chapter V). We found support for this prediction as group living increased during the small rodent peak phase. However, it remained unexpectedly high during the decrease phase, when resources are scarce. This could however be related to increased predation pressure, and an increasing benefit of group living.

**Keywords:** *population dynamics, cyclic, mountain tundra, arctic fox, Norwegian lemming, small rodents, mesopredator, predation, survival, reproduction.*

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MOUNTAIN TUNDRA – MESOPREDATOR AND PREY

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University

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*"Lenge har jag kjent det sånn at megen logikk på én gang er mistenkelig. En avhandling med allting dokumentert og soleklart skal absolutt ikke belønnes. Jag kjenner bestandig i fingertuppene mine at et sånt verk er en skurkaktighet, og at resultatet bestandig kunne være blitt alt mulig annet, med like stor utfoldelse av logikk i hvert enkelt tilfelle."*

Aksel Sandemose: *En flyktning krysser sitt spor: Espen Arnakkes kommentarer til Janteloven*. Oslo 1970.



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According to the ideas of Wallace and Darwin on natural selection, survival and successful reproduction are the currencies of evolution (Darwin and Wallace 1858; but see Davies 2013) making demography the link between ecology and evolution. Predation and competition are ecological processes that can have a profound effect on fitness and are therefore keys to understand the ecology of organisms. However, the overwhelming complexity of natural systems can be a major obstacle to disentangle the mechanisms that affect critical aspects of life history such as mating, reproductive output, juvenile survival and mortality.

Computer simulations and experimental studies in controlled conditions provide valuable tools in ecology that can reduce noise and allow for observation and quantification of some mechanisms underlying complex ecological processes. However, although valuable conclusions may be drawn, they are inevitably based on simplifications of the natural systems in which organisms actually live, interact and evolve. Observations from controlled environments therefore need to be compared with their less cooperative natural counterpart. For some species, the noisy and sometimes frustratingly complex outdoors provide the only environment where relevant processes can be studied. On the other hand, naturally occurring fluctuations in nature can function as field experiments, providing a great opportunity for field biologists.

Still, not all biomes are equally complex. Low-productivity ecosystems typically host less biodiversity, and therefore offer possibilities to study ecological processes that quickly get too complicated when primary productivity increase (Oksanen et al. 1981). Terrestrial arctic and subarctic ecosystems for example, are relatively simple (if arthropods are excluded; Schmidt et al. 2017). The vegetation is strikingly similar around the north pole (Walter 1973) and the diversity of vertebrate species is typically limited and functionally similar (Chester 2016). Additionally, cyclic small rodents are characteristic for many Arctic and Subarctic regions (Elton 1924). They are ecologically interesting in their own right, and the two first chapters of this thesis focus on the distribution of vegetation and the Norwegian lemming (*Lemmus lemmus*). But small rodents are also an important prey resource for many carnivores and birds of prey (Nyström et al. 2006; Hellström et al. 2014; Stoessel et al. 2018), and the fluctuations in rodent population size provide something resembling a replicated natural experiment for the vertebrate predator guild.

If prey population cycles are persistent enough, predators may evolve an ability to track them. This appears to be the case with the lemming-ecotype of the arctic fox (*Vulpes lagopus*), a lemming specialist characterised by cyclic population fluctuations due to the remarkable ability to instantly adjust litter size according to small rodent abundance (Tannerfeldt and Angerbjörn 1998). Depending on the region, some lemming-fox populations have access to alternative food resources, such as eggs from bird colonies or marine resources (Smith 1976; Samehlius et al. 2007). The Scandinavian population, however, is deprived of alternatives and rely almost entirely on small rodents, with the Norwegian lemming as the single most important. Together, the cyclic prey and the specialist predator constitute a study system suspiciously

resembling a text book example of predator-prey interactions, suitable to study how variation in prey abundance affects breeding, survival and ultimately fitness of a predator.

This predator-prey interaction is also the focus of the three last chapters of this thesis. This perspective is essential since small rodents do not only affect the arctic fox but more or less all vertebrate predators in the mountain tundra. Among those are some top predators that can switch to the arctic fox as an alternative prey (Nyström et al. 2006; Meijer et al. 2011). Taking intraguild predation into account however, the apparent simplicity of the mountain tundra ecosystem turns out to be decisive. A resource overlap between a mesopredator and a top predator makes it complicated to disentangle effects of basal prey availability and intraguild predation since they might be connected. Decreasing basal prey leads to both starvation and intraguild predation, which increase mortality of alternative prey (the mesopredator). With the reversed pattern to be expected when basal prey increase. Further, the close distance between mountain tundra and boreal forests increases the influx of southern species such as the red fox (*Vulpes vulpes*), increasing the complexity of the ecosystem, but also offering an opportunity to study the interactions between similar species at the limit of their distribution ranges. This is particularly relevant in the scope of global warming, as a model system of boreal invasion (Elmhagen et al. 2015).

Although challenging, this complexity makes the system more interesting, since the arctic fox as a study organism provides us with both a predator and a prey perspective. However, it also poses as a pedagogic challenge since the far-reaching effects of the small rodent cycle must be kept in mind as a backdrop to all processes, limiting the studies that can be made (Table 1) and leaving but conditional answers to presumably simple questions. To someone lacking a strong enough character to stay away from hackneyed quotations, it could even be tempting to conclude that “nothing in the mountain tundra makes sense, except in the light of the small rodent dynamics”.

*Table 1: Overview of how the small rodent cycle affects data availability, and in turn the possibilities to study different ecological processes.*

	<i>Low phase</i>	<i>Increase phase</i>	<i>Peak phase</i>	<i>Decrease phase</i>	<i>Chapter</i>
Lemming distribution	-	Possible	Possible	Bad	II
Litter size	-	Possible	Possible	Bad	III
Juvenile survival	-	Possible	Possible	Possible	IV
Group living	-	Bad	Possible	Possible	V

#### **Aims:**

The focus of this thesis has been to study how population abundance affects spatial variation in prey abundance (the Norwegian lemming) and how prey fluctuations affects different aspects related to breeding and survival in a specialist mesopredator, the arctic fox. To do this, a novel approach for remote assessment of plant productivity, based on high resolution colour infrared aerial photos, is brought forward in *Chapter I*. This method was applied in *Chapter II* where we developed a spatial model of lemming distribution during the increase and peak phase of their population cycle to investigate how intraspecific competition interacts with habitat preferences. In *Chapter III* we tested if reproductive output increased with territory quality in the light of interspecific competition. In *Chapter IV* we investigated how maternal breeding

experience, small rodent abundance and adult presence on den sites affected juvenile summer survival in the arctic fox. In *Chapter V* we tested the prediction of the Resource Dispersion Hypothesis that group living should increase with prey abundance and territory quality.

*Study organisms - Small rodents in general, lemmings in particular*

The drastic population fluctuations characterising some arctic and subarctic lemmings (*Lemmus sp.* and *Dicrostonyx sp.*) is a classic example of cyclic population dynamics (Elton 1924; Stenseth and Ims 1993). Their peculiar ability to increase from literally undetectable levels during low years of their population cycle to super abundant during peak years has intrigued people with an eye for ecological patterns for centuries. For example, Olaus Magnus (1555) mention a daring yet ecologically implausible hypothesis regarding lemmings raining from the sky in large numbers (apparently a go-to mechanism explaining rapid population increase in his times). He also reported positive effects of the lemming population growth on several predator populations (Magnus 1555). The fascination has last into modern times, and the unsupported rumours of lemmings committing mass suicide due to overpopulation inspired an American film production company to stage a lemming mass movement event and subsequent suicide by tossing individuals of (the non-migratory) *Dicrostonyx richardsoni* into a river in Calgary (Vallee and McKeown 1982; Henttonen and Kaikusalo 1993). The resulting film, a somewhat dubious nature documentary known as *The White Wilderness* (Algar 1958) was awarded by the Academy of Motion Picture Arts and Sciences. On the interactive side of entertainment, the popular computer game *Lemmings* (Jones and Dailly 1991) featured indifferent lemmings quickly falling off cliffs or drowning if the player failed to stop them. To be fair, it should be noted that debunking of the lemming suicide myths is also represented in mass media and pop culture (Vallee and McKeown 1982; Sykfont et al. 1998).

As many systems evoking naturalistic curiosity, the enigmatic population dynamics of cyclic northern small rodents have also interested researchers. Yet, although thoroughly studied for over one hundred years, the mechanisms underlying their fluctuations remain obscure (Stenseth and Ims 1993). And although Chitty (1960) already 60 years ago felt that he had to "...justify the addition of fresh speculations to a subject already overburdened with them", this surely have not prevented new speculations to flourish (Hansson and Henttonen 1985; Krebs and Korpimäki 1996; Kausrud et al. 2008). Much to my relief, the mechanisms underlying the small rodent fluctuations are not within the scope of this thesis (but see Chapter II). Not out of some misguided fear of keeping on piling speculations (Chitty could be considered quite a worthy role model for any ecologist), but because the small rodent dynamics, regardless of their underlying mechanisms, give rise to processes that can provide interesting perspectives to ecological questions. So, I chose to focus on the consequences rather than on the causes of the rodent fluctuations.

The terminology used in this thesis regarding rodents could be somewhat confusing and benefit from some clarification for readers that are not acquainted with the mountain tundra ecosystem. The term *small rodents* is used when referring to the functional group of cyclic, vole-like, tundra-living rodents. Species concerned in this thesis are: *Microtus agrestis*, *Microtus oeconomus*, *Myodes rufocanus* and *Lemmus lemmus*. All common prey species in the mountain tundra but with different local distribution and not necessarily synchronous dynamics. All species are included when small rodent abundance (trapping index) is discussed.

The Norwegian lemming is however a special case. It is a strict tundra species limited to the Fennoscandian mountain tundra, breeds during winter, can become superabundant, and is the most important prey for the arctic fox. The spatial distribution model for lemmings developed in *Chapter II* solely concern the Norwegian lemming (we trapped too few of the other species to allow spatial modelling) and hence, any relationship based on the model from *Chapter II* is only discussed from a lemming perspective.

If regular, the small rodent cycle commonly spans 3-5 years. In the text book 4-year cycle an increase year is followed by a peak year during which small rodents are super abundant. Then they decrease in numbers during the decline phase, followed by a low year when small rodents are literally undetectable. However, even when regular there are many other factors that can vary between cycles. Besides variation in peak amplitude, peaks can be interrupted and turn into declines instead. And declines can either be slow or abrupt. In addition, the population cycles in the mountain tundra and the surrounding boreal forest can be unsynchronised, resulting in different predator dynamics.

#### *Study organisms - The arctic fox*

The Scandinavian arctic fox population forms the remains of the once Fennoscandian population which underwent a severe reduction in the early 20<sup>th</sup> century due to fur over harvesting (Lönnberg 1927). Despite protection in the 1920's in Sweden and Norway, and in the 1940's in Finland, the species has not been able to recover on its own (Angerbjörn et al. 2013). The Scandinavian population was close to extinction around 1998-2000 due to an extended period of irregular and faint small rodent cycles (Angerbjörn et al. 2013), and the species is no longer breeding in Finland. However, the Scandinavian population has increased about 5-fold due to reoccurring regularity in the small rodent dynamics in combination with conservation measures (supplementary feeding, red fox culling). For instance, all litters studied in this thesis have been supplementary fed with dog food provided in feeding stations close to natal den sites. Feeding stations are put up at all dens where a litter is detected, and often already in early spring if there are signs of a pair inhabiting a den. Supplementary feeding has been shown to increase litter size (Tannerfeldt et al. 1994; Meijer et al. 2013), however, natural prey is still preferred, and despite provision of large quantities of supplementary food, foxes do not breed if small rodents are too few.

As mentioned above, there arctic fox can be divided into ecotypes (Bræstrup 1941). In contrast to the coastal ecotype that relies on fairly stable marine food resources and show little litter size variation between years, almost every aspect of the lemming-ecotype ecology is tightly linked to fluctuating small rodents (Bræstrup 1941). Most strikingly, arctic fox litter size depends on small rodent abundance without time lag, ranging from 1 to 18 cubs (Tannerfeldt and Angerbjörn 1998). However, despite yearly mating in the spring, arctic fox females hardly breed at all during the small rodent low phase (Fig 1, *Chapter III-V*), likely a good strategy since starvation commonly is a major cause of juvenile mortality in carnivores (Packer et al. 1988).

Most carnivores are hard to study, since they are shy for humans and mainly active when dark. This is true also for the arctic fox in winter and during lemming low years, when they do not breed. However, when the arctic fox does breed, the situation becomes quite different. Both adults and juveniles are not particularly shy towards humans and generally tolerate observers as close as 100 m from the den site, which in combination with the bright summer nights of Scandinavia allow for detailed focal observations 24 h a day. The foxes are tied to the den site during breeding and at least one adult is often present at the den. Cubs emerge around the end of June and stay on the den at least until late august. They are usually highly active at least a couple of hours per day, facilitating litter size assessment.

To be able to follow individuals we trap and ear tag foxes in the study area with unique colour combinations. Cubs are relatively easy to trap although there can be substantial variation between den sites and usually gets harder later in the season. Handling during trapping and tagging induces stress, but tagged juveniles are often seen playing around shortly after tagging. Trap-happiness is also fairly common, and sometimes problematic since more daring individuals prevent siblings from being caught. Adults are generally less prone to be trapped, more stressed during handling, and as a rule not re-trappable.

Conservation measures are scientifically interesting from two perspectives. Seen from the applied perspective, a successful method can be used to conserve other threatened species, and

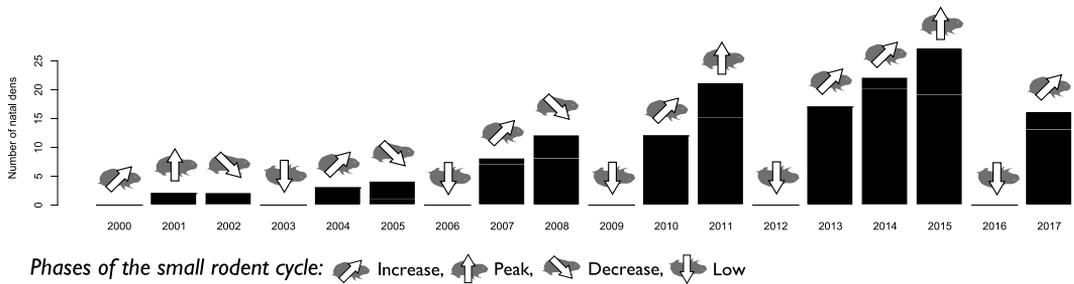


Figure 1: Population dynamics of small rodents and the Swedish arctic fox (*Vulpes lagopus*) sub-population of Helagsfjällen 2000–2017.

field observations can be used to make conservation efforts more efficient. From a theoretical point of view on the other hand, conservation measures can function as experimental treatments to manipulate natural systems and test ecological hypotheses. Due to their primary purpose of conservation, they may not provide ideal control treatments and randomised setups. However, properly handled in analyses, they can still increase the value of conservation efforts from a scientific perspective.

#### Study organisms - Some other predators

The arctic fox is not the sole vertebrate predator in the mountain tundra ecosystem, and although few others are as specialised, all respond to small rodent fluctuations. The number of larger carnivores is strictly controlled in the study areas as, although an apparent wilderness, the sparsely populated Swedish mountain tundra constitute a summer pasture fundamental to reindeer husbandry. Too high densities of, for example, Wolverine (*Gulo gulo*) and lynx (*Lynx lynx*) can have a severe negative impact on reindeer herding, and wolves (*Canis lupus*) are immediately relocated or culled if entering reindeer herding areas (Prop 2012/13:191). Among larger avian predators, the golden eagle (*Aquila chrysaetos*) and the white-tailed eagle (*Haliaeetus albicilla*) are the most important, while Snowy owl (*Bubo scandiacus*) only breed at lemming peaks.

In addition to the local mesopredators, i.e. the arctic fox and lesser mustelids, the guild consists of the red fox (*Vulpes vulpes*), which can breed in the mountains but often with limited success. However, the short geographic distance between mountain tundra and the surrounding boreal forest where red foxes successfully breed facilitates a steady influx of spill over dispersing individuals (Elmhagen et al. 2015). Canids are often intolerant to each other (Palomares and Caro 1999), and the red fox is a dominant competitor regarded as one of the major threats to the arctic fox, able to kill both adults and cubs. Arctic foxes have been shown to avoid breeding in areas where red foxes are common (Tannerfeldt et al. 2002; Herfindal et al. 2010), and can therefore be excluded from suitable breeding habitat even if there is no fatal interaction.

#### General methodology

The data underlying this thesis has mainly been collected during summer fieldwork in the Scandinavian mountains within the frame of the *Swedish arctic fox project*. Feet has been the

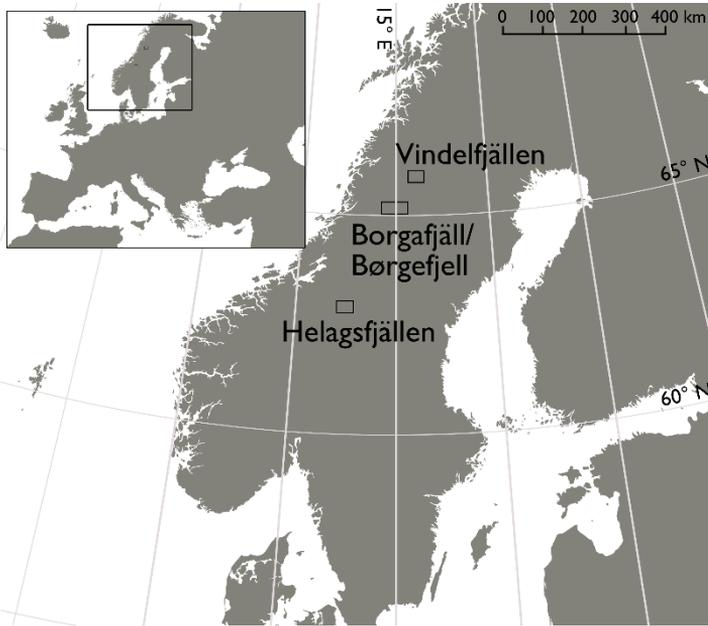


Figure 2: Overview of the different study sites covered in this thesis.

main mean of transportation in remote and exposed mountain areas where food for up to two weeks, camping and research equipment must be carried in backpacks.

All arctic fox data analysed in this thesis was recorded from the Swedish arctic fox sub population in the area of Helagsfjällen (Fig. 2) in mid Sweden. Practically all known arctic fox dens were visited during yearly summer inventories in July. Staff of the Swedish arctic fox project and volunteering fieldworkers camped 100 – 300 m away from active dens to detect breeding, assess litter sizes and identify tagged individuals. We trapped foxes using baited Tomahawk live traps, and ear tagged them with individual unique colour combinations (Dalton Rototags) that allowed us to identify individuals from more than 100 m distance (using spotting scopes) and follow them from year to year. Ear tags were also useful during assessment of litter and group size. During the tagging procedure, a small piece of skin was collected and used for genetic analysis (used to detect co-breeding in *Chapters III* and *V*).

Small rodent inventories were done using baited snap traps (raisins or peanut butter) following systematic setups. The data used to assess small rodent abundance in *Chapter III-IV* was collected within the Swedish arctic fox project, while the spatial model of lemming distribution (*Chapter II*) also included data collected by the Norwegian Institute for Nature research and The Swedish University of Agricultural Sciences and the areas of Vindelfjällen and Borgafjäll/Børgefjell (Fig. 2).

Vegetation samples used for ground truthing to evaluate the method in *Chapter I* were collected in Helagsfjällen and Vindelfjällen (Fig. 2). Orthophotos produced by the Swedish mapping, cadastral and land registration authority as well as different satellite images were used in *Chapter I* and *Chapter II*. In *Chapter III* and *Chapter V* we did not rely on the method from *Chapter I* since it was still unpublished and we did not need the high resolution. Instead we used the conventional satellite sources to assess primary productivity (used as a proxy for herbivore presence, and denoted *territory quality* in *Chapter III* and *Chapter V*).

## Results

*Chapter I:* The Normalised Differentiated Vegetation Index is a standard method to assess plant biomass using satellite images. Colour infrared aerial photos on the other hand are used for visual interpretation and, due to technical differences compared to satellite images, considered unfit for vegetation indices. However, in *Chapter I* we showed that we were able to assess plant biomass in mountain tundra by applying the standard NDVI-algorithm to high resolution colour infrared orthophotos (orthogonal image derived from aerial photos). Our method performed similarly to the conventional satellite method and the results were highly correlated. There was however an absolute shift between the values obtained from the different methods. This shift remained constant between the study areas and we therefore believe that it holds no ecological meaning and can be compensated for by adding a constant. Compared to standard satellite imagery, orthophotos has several benefits such as high resolution (0.5 m) and lower sensitivity to bad weather. We suggest that the use of colour infrared orthophotos can be expanded from visual interpretation to becoming a useful remote sensing tool operating on the scale between global satellite images and small drones intended for specialised local use.

*Chapter II:* Within species competition can have strong effects on habitat use and local distribution. When competition is low we would expect habitat use to reflect preferred habitat while increasing densities should weaken the ecological signal of habitat preference as individuals are forced to increase their presence in suboptimal territories. We used the large fluctuations in population density observed in the Norwegian lemming (*Lemmus lemmus*) as a natural experimental treatment of shifting competition levels and compared spatial distribution during the increase and the peak phase of the population cycle. Our spatial distribution models, based on snap trap data from large areas of the Scandinavian mountain tundra, showed that food plant biomass alone explained lemming distribution during the peak phase. Lemmings were more habitat specific in the increase phase when they were more likely to be found in terrain that was less sensitive to flooding. We included the result from the lemming model in the spatial analysis of *Chapter III* and *Chapter V*.

*Chapter III:* Reproductive output, regardless of breeding strategy, depends on the resources available for the reproducing individual. For territorial animals we could therefore expect investment in juveniles to increase with territory quality. However, good territories could also attract competitors and predators, suggesting that there could be a trade-off between territory quality and stress. The arctic fox is able to produce large litters when conditions are favourable, and litter size has been shown to increase with supplementary feeding. We therefore used arctic fox litter size (during the small rodent increase and peak phase) to investigate the effect of habitat quality on reproduction. We found a second-degree positive effect of increased territory quality (plant biomass) during the increase phase, however, the smallest litters were produced in territories of intermediate quality. This could be related to a generally higher abundance of the dominant red fox (*V. vulpes*) in intermediate and highly productive areas, resulting in increased stress levels. We suggest that those negative effects of increased competition are outweighed by positive effects in high quality territories, while low competition and supplementary feeding allow arctic foxes to do well in low quality habitats. During the peak phase there was no spatial variation, suggesting that higher prey abundance decrease interspecific competition, and allow for larger investments overall.

*Chapter IV:* Juvenile survival varies between species with different breeding strategies, between populations within a species, and between years and individuals within a population. In *Chapter IV* we assessed indirect effects of basal prey abundance on juvenile summer survival in the

arctic fox based on 5 years of breeding data. To achieve this, we used supplementary feeding as a way to limit the direct effect of starvation. Juvenile survival was positively related to small rodent densities, however, there were little variation among females with breeding experience. Instead, the decrease in survival associated with low small rodent abundance was only visible among first time breeding females. However, starvation seems like an unlikely explanation. Instead, we suggest that a decline in small rodent abundance set off a prey switch in top predators and that first-time breeders are unable to successfully handle the increased predation pressure. Based on behavioural data collected during 2 years of the study, we found that juvenile survival decreased if juveniles spent more active time unattended at the den, suggesting that parental guarding can reduce predation. However, we found no difference in attendance between experienced and first-time breeders.

*Chapter V:* According to the Resource Dispersion Hypothesis, territorial animals should defend a territory that can provide enough resources to sustain them also when conditions are poor. With increasing food availability however, resources should be enough to sustain a larger group of individuals in socially flexible species, potentially increasing inclusive fitness and reducing the cost of territory defence. Based on 17 years of breeding data, we tested the predictions of the Resource Dispersion Hypothesis by investigating if group living in the arctic fox followed the small rodent cycle, and if group living was more common in more productive territories. As predicted, groups were more common during the peak phase compared to the increase phase. However, group living did not decline during the decrease phase when prey decrease. Hersteinsson's model on the other hand, predicts that group size should be common despite high territory sharing costs if predation pressure is high, as suggested by the observations in *Chapter IV*. During the peak phase, groups were more common in more productive territories. During decline years, this effect did not show. However, when we tested for an effect of local variation in lemming abundance based on the model from *Chapter II*, there were weak indications of a potential positive effect during the decrease phase.

## Conclusions

The chapters presented in this thesis investigate how population dynamics affected spatial distribution in Norwegian lemmings and how basal prey dynamics and territory quality affected survival and reproduction in the Arctic fox, directly and indirectly. The effects of temporal fluctuations were profound, and all effects of spatial variation had to be studied in relation to those.

Generally, the effects of spatial and individual variation (distribution in lemmings, territory quality and breeding experience in the arctic fox) decreased with increasing small rodent abundance. This is reasonable from a mesopredator perspective, as widely available basal prey should lax competition and reduce intraguild predation. These two processes effectively result in mesopredator release, despite that top predators and stronger competitors remain in the system. When basal prey is less abundant, conditions should become more critical, and the observed effects of local and individual variation associated with the increase and decrease phase indicate that that was also the case. An exception was the inverted pattern seen in group living, which however could be explained by increasing intra guild predation and competition during the decrease phase.

Overall, our results point out how direct beneficial effects of increased resources (in general and locally) are modified by intraguild processes, resulting in indirect effects due to shared basal prey.

## Future work

There are some perspectives of this thesis that would be interesting to investigate further, but as Pilson's law ("It always takes longer", Pilson 1980) allows no exceptions, some data is still in

the process of being collected. The very act of predation is short in time, irregular and by its nature unpredictable. It is therefore hard to reliably quantify the threat from larger predators through manual observations. Many animals do however warn juveniles and other conspecifics through vocalisation when they feel threatened, and in some species those sounds are specific depending on the threat. During the field season of 2018 I mounted stationary wildlife microphones to record arctic fox warning calls to test if they can be used to measure conceived predation risk, and as a proxy for abundance of larger predators. Such data could be used for spatial modelling of predators and predation pressure. For arctic fox dens specifically, and over larger areas in general.

During the last field season, we also received funding for small enough GPS-collars to fit on adult arctic foxes. This offers us a new level of detail in movement data, giving us the possibility to answer many ecological questions, some already touched upon in this thesis.

### **Acknowledgements**

The single author name printed on the cover is of course misleading as all research, at least in ecology, is a team effort. Besides the people directly involved in data collection, the creative process, writing, analysis (my dear co-authors) and administration (not credited in the field of academia), a positive working environment is vital for any kind of work. On this account I am thankful to all the fun and friendly people at Zootis and in the field that have made my time as a PhD-student very pleasant. I should avoid writing a too ambitious acknowledgement due to the risk of forgetting somebody that definitely should be in. However, I want to mention a few in particular and would like to start with my inimitable supervisor Anders "Sleven" Angerbjörn. Always supportive at heart, you have encouraged me to find my own ways and keep a healthy sceptical mind, not least against authorities, including yourself. This is something I have also learned from my two "older academic siblings" Karin Norén and Tomas Meijer, whose moral support has been vital, and if it was not for Tomas suggestion to write my master thesis within the Arctic fox project I would never have gotten in to the *counting of foxes* for real. I am also very happy that Johan Wallén, who thought me to trap rodents when I was a young aspiring field worker, has become an indispensable and knowledgeable close co-worker. After a couple of years as the sole PhD-student in the project I got my "younger academic siblings" Malin Larm and Malin Hasselgren. Besides their contributions to the work and company I am grateful for Malin Larm's patient mind that allow her to almost put up with my talkativeness during field work, and I appreciate Malin Hasselgren's snappy replies during any discussion. I should also mention Peter Hellström that in addition to some statistical support always is a welcome visit at the department. The same goes for my assistant supervisor Bodil Elmhagen and Marianne Pasanen-Mortensen. Although not a *rävräkna* at all, it feels natural to include Helena Mellström and her relieving irreverent attitude.

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## Svensk sammanfattning

Ekologi är av naturen ett snårigt ämne, där en uppsjö olika skeenden samtidigt påverkar samspellet mellan olika arter. Till viss del går det att använda kontrollerade experiment och datorsimuleringar för att skaffa sig en uppfattning om hur olika saker hänger ihop och i vilken utsträckning de påverkar varandra. Men sådana iakttagelser måste ändå jämföras med den mindre samarbetsvilliga naturen, där livsformer i slutändan är hänvisade till att leva, växelverkar och utvecklas.

Fjällvärlden är ur det perspektivet ett på många sätt lämpligt studiesystem eftersom det är förhållandevis enkelt till sin sammansättning. Smågnagarna, kanske framförallt fjällämmeln, har en avgörande inverkan på de ekologiska förloppen i fjällekosystemen. De präglas av drastiska och, i skolboksexemplen, regelbundna svängningar i antal. Och eftersom de utgör en av de absolut viktigaste bytesdjursgrupperna för så gott som alla rovlevande ryggradsdjur i fjällvärlden, ger dessa skiftningar kraftiga återverkningar på hela ekosystemet. Skiftande förhållanden i naturliga system kan i sin tur fungera som naturliga experiment och möjliggöra undersökningar av ekologiska samband och skeenden som inte går att studera under mer stabila förhållanden.

Den här avhandlingen lägger sin vikt på två av fjällvärldens mest karaktäristiska arter: fjällämmeln (Kapitel I och II) och fjällräven (Kapitel III–V). Fjällrävarna i Fennoskandia (Finland, Norge och Sverige) är specialiserade på smågnagare, och fortplantningen är helt styrd av tillgången på bytesdjur. Under smågnagarnas lågår föds inga valpar, medan en kull i gengäld kan bestå av upp till 18 stycken under ett toppår. Under uppgångsåren är kullarna stora i förhållande till födotillgången, medan dödligheten kan vara enorm under nedgångsår. Ett skäl är matbrist, ett annat större rovdjur och rovfåglar som förlitar sig på fjällrävsvalpar som föda om det blir ont om smågnagare. Det nordiska beståndet är på så vis helt beroende av återkommande toppar hos smågnagarna. Men dessvärre inte bara det. En kraftig överbeskattning av beståndet på grund höga pälspriiser i början av 1900-talet gjorde den fennoskandiska fjällräven utrotningshotad, och trots fridlysning sedan 1920-talet i Sverige och Norge (1940-talet i Finland) har den inte förmått återhämta sig på egen hand. Med hjälp av bevarandeinsatser (stödfodring och skydds jakt på rödräv) har beståndet i Sverige och Norge dock mångdubblats sedan millennieskiftet. Det största hotet kvarstår dock, ett varmare klimat, vilket med största sannolikhet har negativ inverkan på smågnagarna och riskerar att öka förekomsten av rödräv ovanför trädgränsen. Avhandlingens kapitel belyser olika delar av fjällekologin men har beröringspunkter med den här problematiken.

*Kapitel I* är en metodstudie där vi visar att vi kunde använda högupplösta flygfoton för att uppskatta fotosyntetiserande växtlighet på ett sätt som liknar dagens satellitbaserade standardförfarande. I *Kapitel II* tillämpade vi metoden och utformade en modell över fjällämmelns rumsliga utbredning under beståndens uppgångsår och toppår. Lämmlarna var mer utpräglade i sin utbredning under uppgångsår, då de var vanligare i vad vi tolkar som mer skyddade områden. Under toppåren var tillgången på föda den viktigaste förklaringsmekanismen. I *Kapitel III* undersökte vi om kullstorlek hos fjällräv ökar med revirkvalitet med hänsyn tagen till förekomsten av rödräv. Det fanns ett samband under uppgångsår, men kullarna var minst i medelgodta revir, vilket skulle kunna förklaras med ökad stress och ökade kostnader för revirförsvar på grund av konkurrens från rödräv. I dåliga revir fanns få rödrävar, och i bra revir minskade förmodligen konkurrensen på grund av ökad födotillgång. I *Kapitel IV* fann vi att valpöverlevnaden var lägre under år med färre smågnagare. På grund av stödfodringen kunde detta dock inte förklaras med svält, och det drabbade i första hand valpar till förstgångsfödande honor. En möjlig förklaring är att andra rovdjur, såsom kungsörn, i brist på smågnagare utövar ett större tryck på fjällrävsvalpar och att oerfarna honor på något vis är sämre rustade att hantera detta. Denna förklaring får ett visst stöd i och med att dödligheten var större hos valpar som tillbringade mer tid ensamma uppe på lyan. Detta var dock i sin tur inte kopplat till erfarenhet.

I *Kapitel V* undersökte vi hur tillgången på smågnagare och revirkvalitet påverkar grupplevande hos fjällräv. Ökad födotillgång borde innebära att rävar som hävdar ett revir är mer benägna att tillåta andra vuxna rävar att dela deras revir. Vi fann en ökning i grupplevande under toppår jämfört med under uppgångsår. Men det visade sig att grupplevande förblev vanligt även under nedgångsår, då födotillgången återigen minskar. Detta skulle dock kunna förklaras med ett ökat rovdjurstryck och att fördelarna med grupplevande väger upp kostnaderna.

Informationen som ligger till grund för avhandlingen har samlats in i flera fjällområden, i huvudsak i Sverige men också i Norge (figur 2). Det mesta arbetet har skett inom ramen för *Svenska fjällrävsprojektets* årliga inventeringar och har samlats in av personal och frivilliga i samarbete med länsstyrelsens naturbevakare. Min tjänst har möjliggjorts tack vare finansiering från Fjällräven AB.

The thesis is based on the following chapters, which are referred to in the text by their Roman numerals:

- I **Erlandsson, R.**, Stoessel, M., Skånes, H., Wennbom, M & Angerbjörn, A. An innovative use of orthophotos – Possibilities to assess plant productivity from colour infrared aerial orthophotos. *Manuscript*
- II Le Vaillant, M., **Erlandsson, R.**, Elmhagen, B., Hörnfeldt, B., Eide, N.E., & Angerbjörn, A. (2018). Spatial distribution in Norwegian lemming *Lemmus lemmus* in relation to the phase of the cycle. *Polar Biology*.
- III **Erlandsson, R.** & Angerbjörn, A. – Limitations of a weaker competitor – Implications of territory quality on the reproductive output of a tundra specialist. *Manuscript*
- IV **Erlandsson, R.**, Meijer, T., Wagenius, S., & Angerbjörn, A. (2017). Indirect effects of prey fluctuation on survival of juvenile arctic fox (*Vulpes lagopus*): a matter of maternal experience and litter attendance. *Canadian Journal of Zoology* 95(4): 239–246.
- V **Erlandsson, R.**, Hasselgren, M., Angerbjörn, A. & Norén, K. The resource dispersion hypothesis – a test with a cyclic mesopredator. *Manuscript*

#### Candidate contributions to thesis chapters\*

	I	II	III	IV	V
Conceived the study	Substantial	Minor	Substantial	Substantial	Substantial
Designed the study	Substantial	Minor	Substantial	Substantial	Substantial
Collected the data	Substantial	Significant	Substantial	Substantial	Substantial
Analysed the data	Substantial	Minor	Substantial	Substantial	Substantial
Manuscript preparation	Substantial	Significant	Substantial	Substantial	Substantial

#### \* Contribution Explanation

Minor: contributed in some way, but contribution was limited.

Significant: provided a significant contribution to the work.

Substantial: took the lead role and performed the majority of the work.