UiT The Arctic University of Norway

Faculty of Biosciences, Fisheries and Economics

— Institute of Arctic and Marine Biology

Population cycles in small rodents seen through the lens of a wildlife camera

—

Eivind Flittie Kleiven

A dissertation for the degree of Philosophiae Doctor – April 2022

> *"To know that we know what we know, and that we do not know what we do not know, that is true knowledge."*
>
> — **Confucius**
>
> As quoted in *Walden (1854)* by Henry David Thoreau

Supervisors:
Rolf Anker Ims[1]
Nigel Gilles Yoccoz[1]
Eeva M. Soininen[1]
Frédéric Barraquand[2]

[1] UiT - The Arctic University of Norway, Department of Arctic and Marine Biology, Tromsø, Norway

[2] Institute of Mathematics of Bordeaux, CNRS and University of Bordeaux, Talence, France

Contents

Acknowledgements v

List of publications ix

Summary xi

Introduction 1
  1.1. Population cycles in small rodents 1
  1.2. Monitoring of rodents and small mustelids 6
  1.3. Population dynamics of rodents in the time of climate change 11
  1.4. The rise of camera traps in wildlife monitoring 12

Thesis Objectives 14
  2.1. Thesis context 14
  2.2. Thesis aim 16

Methods 18
  3.1. Study area 18
  3.2. The small mammal community 18
  3.3. Study design 20
  3.4. Data analysis 23

Results and discussion 26
  4.1. Study I 26
  4.2. Study II 27
  4.3. Study III 28
  4.4. Study IV 30

Model limitations 33
  4.5. Challenges with complex hierarchical occupancy models 33
  4.6. Estimating detection probability in the occupancy framework 35
  4.7. Mechanistic interpretation of occupancy model parameters 38

Conclusions and future perspectives 41

Bibliography 45

Paper I 62

Paper II 80

Paper III 124

Paper IV 158

Acknowledgements

The way to this thesis started already back in 2011. A younger me then gave up on his path to becoming and engineer with a stable income and a simple life, to instead take on a much more complicated path. I followed my curiosity about the large yearly variations in the tundra ecosystem, which in fact has been my preferred habitat every since I was very young. My journey leading up to the delivery of this thesis have not at all been a ”one mans show”. Already back in 2012 I joined the COAT-team to do fieldwork on Varanger for the first time (something I’ve kept doing every year since). Suddenly, I found my self surrounded by world-leading experts in the functioning of the very food-web that had fascinated me for so long. The yearly COAT fieldwork, and in particular all the inspiring discussions we had while doing it, fueled my motivation to pursue a scientific career.

As I now deliver this thesis I want to express my gratitude to everyone that have helped, supported and motivated me along the way. First of all I want to thank my amazing supervisor team. Rolf, for being so genuinely friendly and full of humor, while showing by example how to be a brilliant ecologist. I truly admire your never ending curiosity and enthusiasm for the wildlife surrounding us. I’m incredibly thankful for all the discussion we have had, you are a true inspiration. Nigel, for learning me so much about critical thinking, good science and rigorous data analysis. Eeva, for training me as a field ecologist already since 2013, all the good discussions we have had over the years and for learning me so much about good scientific writing (and grammar...). Last, but not least, Fred, for taking me in as your phd-student even long before you officially became my supervisor. This thesis would have looked very different without your expertise in theoretical ecology and statistics. I appreciate your care for the details, always pushing me to understand more about the methods we have applied. As a side note, the funding for this thesis was given to Rolf and Nigel as a gift from UiT after they won the RCN prize for outstanding research. I hope you are happy with it.

I also want to thank the co-author on the studies included in this thesis for fruitful collaborations. I want to thank Pedro for the effort and enthusiasm you have put into our collaboration. I am thankful for the many discussions we have had and for inspiring me to learn more about birds. I thank Jonas for allowing me to be a part of your supervisor team and for being a brilliant master student and a good friend. I thank Olivier for providing invaluable statistical advice whenever needed, and for all your positivity. I thank John-André for always coming by my office to check on me and for providing valuable advice on modelling in JAGS. Hanna, for the amazing work you have done setting up the automatic image annotation, without you I would probably still be looking at camera trap images. Siw and Ingrid for you dedication in the development of the small mammals camera tunnel, without which, this thesis would look pretty stupid.

Further, there are many more people to who I am grateful for making my life in the biology department (and elsewhere) more fun. Filippo, Martin and Jarad for all the amazing moments we have had together. I hope you some day can forgive me for advising you not to bring skins on your Finnmark expedition. Marita, for all the good times we have had and everything I have learned from you since the beginning of our biology studies. Torunn, for all the ski touring, dumpster diving and sushi dinners. Julia for your care for the people around you and for regularly feeding me chocolate. I'm grateful to Lorena, Xabi, Isabell, Emma, Stijn and Michelle for being great fellow young-ecologists. Further, I'm thankful to everyone in the Northern Population and Ecosystems group for a good working environment and for the many discussions by the coffee machine. In particular I want to thank Sissel and Laffen for always helping with all the practical challenges in the daily life at the department. Every research group should have someone like you.

I want to thank my friends in Tromsø that have made these years some of the best in my life. I'm grateful to Vetle, Andreas, Are and Olav for all the great outdoor-moments and many discussions about where to find the most ptarmigans and the biggest trout, which helped set off my interest for ecology. I also want to thank my childhood-friends in Lillehammer for making it feel like no time has passed whenever I'm home.

Last, and most important. I want to thank my family. Mamma, Pappa og Anne Kari (inkludert Tore, Emilie og Sunniva), jeg er uendelig takknemlig for all støtten dere alltid har vist meg. Fra dere har det bare vært gode ord selv om det kanskje har framstått som underlig at jeg har tilbragt de 10 siste juli-månedene på tundraen i Finnmark med lua tredd godt nedover ørene, i stede for på famileferie med dere. I also want to thank Giron, Nova and Gabrielle for always welcoming me back home with smiles, enthusiasm and by licking my face.

Eivind Flittie Kleiven
Tromsø, 2022

List of publications

This thesis is based on the following publications and manuscripts which in the text will be referred to by their roman number:

I
Mölle, J.P., Kleiven, E.F., Ims, R.A. & Soininen, E.M. (2021), **Using subnivean camera traps to study Arctic small mammal community dynamics during winter**, *Artic Science*, 1–7, doi.org/10.1139/as-2021-0006.

II
Kleiven, E.F., Barraquand, F., Gimenez, O., Henden, J.A., Ims, R.A., Soininen, E.M. & Yoccoz, N.G., **A dynamic occupancy model for interacting species with two spatial scales**, under review in *Journal of Agricultural, Biological and Environmental Statistics.*

III
Kleiven, E.F., Barraquand, F., Gimenez, O., Henden, J.A., Soininen, E.M., Böhner, H., Yoccoz, N.G., & Ims, R.A., **Seasonality and habitat-dependency in the strength of a predator-prey interaction**, Manuscript

IV
Kleiven, E.F., Nicolau, P. G., Sørbye, S.H., Aars, J., Yoccoz, N.G. & Ims, R.A., **Using camera traps to monitor vole population cycles**, Manuscript

Summary

Population cycles in small rodents have attracted attention from ecologists for more than a century. This spectacular phenomenon is crucial for the functioning of many northern food-webs and has intrigued ecologist because of its lessons for general ecology. Knowledge about the rodent cycle has, however, been hampered by the lack of reliable monitoring methods both for rodents and some of their assumed interactants (e.g. the small mustelids).

In resent decades, camera traps have become widely used in ecology as they provide a cost-efficient and non-invasive method for wildlife monitoring. In this thesis, consisting of four studies, I will investigate how camera trap tunnels tailored for small mammals can enhance rodent monitoring. First, in study I, I together with colleagues conducted the first large scale assessment of the applicability of tunnel-based camera traps to estimate population parameters in a small mammal community, including during a long Arctic winter. We showed that the camera trap provide estimates of rodent occupancy also under the snow during winter. Further we give recommendation on micro-scale placement of the traps to maximize technical functionality in order to avoid loss of data. Then, in study II, we expand on dynamic occupancy models for interacting species by including two nested spatial scales. This allows for camera trap-based investigation of the rodent-mustelid interaction on both a local and a landscape scale. Features of this interaction are assumed to be a key to understand the cause(s) of the rodent population cycles. In study III, we apply the statistical framework developed in study II to a dataset derived from the long-term monitoring program Climate-ecological Observatory for Arctic Tundra (COAT). Our results show that presence of mustelids increased the extinction probability of rodents on both a local and a landscape scale. Furthermore, we demonstrate a clear habitat dependence and indications of a season-dependency in the rodent-mustelid interaction strength. Finally, in study IV, we assess whether camera trap-based abundance indices can be used to study population dynamics of two rodent species (gray-sided vole (*Myodes rufocanus*) and tundra vole (*Microtus oeconomus*)). This was done by comparing camera trap-based abundance

indices to abundance estimated from capture-mark-recapture (CMR). For gray-sided voles a single camera trap provided reliable abundance indices with camera trap counts aggregated over 5-days. For tundra voles counts from four spatially replicated camera traps from a single day within the same local population needed to be aggregated to obtain a good correspondence to the abundance estimated from CMR. Such species-differences imply that the design of camera trap studies should be adapted to the species in focus. This study further highlight that camera traps yield much more temporally resolved abundance metrics than alternative methods.

To conclude, the work presented in this thesis demonstrates how camera trap-based rodent monitoring provides multiple improvements compared to previous methods. Camera traps are non-invasive avoiding the ethical issues kill-trapping are fraught with. Further, camera traps provide data year round — including from underneath the snow— on a fine temporal scale. In addition camera traps are not species specific and provide data on the whole small mammals community including small rodents, shrews and small mustelids. In addition, camera traps provide a reliable abundance index at least for two of the most ecologically important rodents species in northern Fennoscandia. Furthermore, this thesis present a statistical framework for investigating mustelid-rodent interactions based camera trap data and exemplify how this framework can improve on the knowledge on one of the longest standing mysteries in ecology.

Introduction

1.1 Population cycles in small rodents

Ecology and population cycles

One definition of Ecology is “the scientific study of the distribution and abundance of organisms and the interactions that determine distribution and abundance” (Begon and Townsend, 2020). In most populations of wild animals both distribution and abundance typically exhibit strong temporal variation. Hence, one of the key tasks for ecologists is to explain and predict this temporal variation. In the process of doing so, the attention of scientists was initially drawn to a specific phenomenon where some species were observed to fluctuate between highs and lows in abundance and distribution with regular intervals (Elton, 1924). Such regular multi-annual fluctuations are often referred to as populations cycles. Already in the early 1920’s the famous Lotka-Volterra model (Lotka, 1925; Volterra, 1926) demonstrated theoretically how population cycles can be created. Specifically, the predator-prey version of the Lotka-Volterra model demonstrated how interspecific interactions alone might create regular, multi-annual, oscillations in species abundance (i.e. population cycles). The first empirical evidence of existence of population cycles in wild animals were presented by Charles Elton in 1924, based on number of fur-bearing animals from Hudson Bay Company in Canada and observations of the Norwegian lemmings (*Lemmus lemmus*) in Fennoscandia, collected by the Norwegian zoologist Robert Collett (Elton, 1924). Since then, ecologists have considered population cycles one of nature’s great mysteries (Myers, 2018). Much work motivated by cyclic populations has been important in the development of current knowledge on variability in abundance and distribution of wildlife species.

The small rodent population cycles: why are they important?

Population cycles have been observed in many different groups of animals (e.g. mammals, insects (Myers and Cory, 2013) and birds (Martínez-Padilla et al., 2014)). However, population cycles in small rodents have received a particular attention in the scientific community because of their spectacular appearance. Further, they are crucial for the functioning of many boreal and tundra food webs (Ims and Fuglei, 2005). The violent boom and bust cycles of rodents cascade through the food-web, where grazing impact of the herbivorous rodents on tundra vegetation can be so strong that it can be seen from space during peak population densities (Olofsson et al., 2012). Furthermore, the rodent population dynamics are decisive for the survival, breeding density and reproductive success of most northern mammalian (Angerbjörn et al., 1999; Gilg et al., 2006) and avian predators (Hellström et al., 2014; Therrien et al., 2014). In addition, rodent populations peaks have an indirect positive effect on other prey species through shared predators. This is often referred to as the alternative prey hypothesis and makes existence of resident alternative prey populations possible where a high predation pressure would otherwise drive them to local extinction (Angelstam et al., 1984; Bety et al., 2002; McKinnon et al., 2014). In fact, indirect positive interactions between prey species that share predators have been theoretically demonstrated to be stronger in the presence of population cycles (Abrams et al., 1998). The alternative prey mechanism in cyclic northern food-webs are contributing to a latitudinal gradient in predation-pressure on ground nesting birds, which might help explaining bird migration (Gilg and Yoccoz, 2010; McKinnon et al., 2010).

The small rodent population cycles: what do we know?

Since Elton's introduction of the rodent population cycles to the scientific community thousands of scientific papers has been published on the topic. Almost a hundred years later, we can say that the understanding of this phenomenon has been considerably improved. Over the last 50-years, sometimes longer, ecologists have established and maintained long time series on the population dynamics of rodents (Hanski et al., 1993; Ekerholm et al., 2001; Hörnfeldt et al., 2005; Kausrud et al., 2008; Korpela et al., 2013; Ehrich et al., 2020). Based on these empirical investigations, the anatomy of rodent population cycles can be dissected into four phases (i.e. increase, peak, crash and low phase), each with distinct features (Krebs and Myers, 1974; Oli, 2019). The cycles typically consist of a gradual increase phase, leading to a peak followed by a step decline (i.e. the crash phase) (see e.g. figure 2 in Andreassen et al. (2021)). Fluctuating rodent populations are known for large temporal variability in population size (i.e. high cycle amplitude), where the increase from the low phase to the peak often is by 3 orders of magnitude, or more (Ims and Fuglei, 2005). However, for a given location, the cycle amplitude is highly variable between different cycle peaks (Kleiven et al., 2018). The periodicity of the rodents cycles is typically between 3 and 5 years and for a single location, remarkably consistent between cycles. In addition to multi-annual population cycles, northern rodents also have strong seasonal cycles. In northern areas rodents have a seasonal breeding cycle, following the plant productivity so that breeding mainly happen during summer and only exceptionally during winter (except for lemmings) (Andreassen et al., 2021). In addition, mortality might be increased during the long snowy winter when rodents are living in the subnivean space at the bottom of the snow pack (Korslund and Steen, 2006; Poirier et al., 2021). There are, in fact, indications of a latitudinal gradient in the periodicity of rodent population cycle, where northern rodent populations have longer periodicity than southern populations (Bjørnstad et al., 1995). Furthermore, there is also a latitudinal gradient in cyclicity in wildlife populations in general, and for rodents in particular, where population cycles are more pronounced in highly seasonal northern areas (Hansson and Henttonen, 1988; Kendall et al., 1998). I however, note that although population cycles in rodents also most common in northern areas they do also exist in some more temporal areas (see e.g. (Cornulier et al., 2013; Mougeot et al., 2019)). Empirical models that have accounted for seasonality have demonstrated that strong negative delayed-density dependency during winter is a direct cause for the multi-annual population cycles in rodents (Hansen et al., 1999; Stenseth et al., 2003). Theoretically, strong negative delayed-density dependence during winter can be caused by both bottom-up (plant-herbivore) and top-down (predator-prey) interactions. In a high arctic food-web lacking predators, Fauteux et al. (2021) found that bottom-up interactions was unlikely to cause multi-annual cycles with periodicity longer than 2 years. This is contrasting the 3-5 year multi-annual population cycles typically found in rodents, suggesting top-down effects to play an important role as cycle driving mechanisms.

Another striking feature in small rodent population fluctuations is that they are synchronized over much larger areas than can be expected from intrinsic population processes, like e.g. individual dispersal distance (Steen et al., 1996; Angerbjörn et al., 2001; Henden et al., 2009). This is particularly interesting as the scale and strength of synchrony might reflect how rodents are affected by different processes with different scales (Bjørnstad et al., 1999). Both predation (Ims and Andreassen, 2000) and stochastic weather events (Moran, 1953) have been found to play important roles in driving population synchrony. Furthermore, interspecific synchrony between sympatric small rodent populations are commonly observed (Krebs, 2013). This indicates that population processes for all species in a local small rodent community, often containing species with different diets (Soininen et al., 2013), social organization (Ims, 1987; Bondrup-Nielsen and Ims, 1988) and habitat preferences (Soininen et al., 2017), are affected by common factors.

The small rodent population cycles: Theoretical models and predator-prey interactions

Despite nearly a century of intense research on rodent populations dynamics and the accumulated knowledge summarized above there are still also some unanswered questions. While both theory and empirical investigation of long time series has showed that rodent population cycles are characterized by delayed density dependence in population growth rate, exactly what is causing this delayed density dependency has lead to intense debates among ecologists (Stenseth, 1999). A wide range of hypotheses has been proposed, but there is still no consensus on which is the most plausible (and even if a single one could be sufficient). I will not attempt to provide a complete review of all of them here, as this has been done very well elsewhere (see e.g. Oli (2019)). However, I shall point out like other authors that the connection between empirical and theoretical work for many of the hypothesised cycle driving mechanism has often been weak (Stenseth, 1999; Oli, 2019). This is a pity, as, to say it with the words of Haila and Järvinen (1982): “Sound naturalism is to ecology what legs are to a runner; but anti-theoretical naturalists are, quite naturally, like headless runners”. In fact, theoretical work has displayed the potential of different hypothesized mechanisms to function as cycle-driving mechanisms by enforcing strong delayed density dependence (Inchausti and Ginzburg, 1998; Turchin and Hanski, 2001; Turchin and Batzli, 2001). However, this thesis will mainly focus on the assumed key interaction between rodents and small mustelids. In fact predation for specialist predators was one of the first hypothesized cycle driving mechanisms with roots all the way back to the initial predator-prey modelling by Lotka (1925) and Volterra (1926). The specialist predator hypothesis postulated that resident specialist predators respond numerically to the increase in numbers of prey (i.e. rodents) with a time delay, for instance caused by delayed reproduction. In the northern areas the small rodents spend the long snowy winters in the sub-nivean space which protect them from avian and large mammalian predators. However, the small mustelids follow in the rodent runways also under the snow (Wilson et al., 1999; Ims and Fuglei, 2005). Many theoretical predator-prey models have therefore been tailored specifically for the rodent-mustelid interaction. This has been done by extending a two-dimensional differential equation system to include both the effect of generalist predators, the strong seasonality in northern ecosystems and environmental stochasticity (Turchin and Hanski, 1997; Hanski et al., 2001). When comparing the predicted rodent dynamics from these theoretical models to long time series on rodents in Fennoscandia the similarity is striking (Turchin and Hanski, 2001). Although this body of theoretical work clearly has demonstrated the potential of specialist predation from mustelids to drive the population cycles of rodents, empirical validation has so far been hampered by the lack of empirical data on rodents and mustelids to compare to theoretical model predictions.

1.2 Monitoring of rodents and small mustelids

There are three central questions needed to be addressed for successful wildlife monitoring (Yoccoz et al., 2001). First, the purpose of the monitoring needs to be clearly defined (”why monitor?”). In the case of rodents and mustelids I hope that at least one answer to ”why monitor” has been given already (i.e. to increase our understanding of the role of mustelids as a potential driver of the rodent population cycles). Second, depending on the purpose of the monitoring one needs to decide what to monitor. Most theoretical work on predator-prey interactions and cyclic populations have been focused on population abundance. However, if the aim of the monitoring is to study population dynamics, for instance by means of time series analyses (Stenseth, 1999; Cornulier et al., 2013; Barraquand et al., 2017) indices of abundance can be used if there is a proportionate relationship between true abundance and the abundance index (Hanski et al., 1994; Lambin et al., 2000; Yoccoz et al., 2001; Gilbert et al., 2021). In addition, insights about the rodent-mustelid interaction might be attained from a metapopulation framework, where species occupancy (i.e. presence/absence) can be used to study local and regional scale colonization and extinction dynamics (Hanski, 1998). Then the final question is how to monitor these variables (i.e. abundance, abundance indices or occupancy). Most wildlife species are observed imperfectly which might lead to biased population state estimate if not accounted for. For species abundance the detection error can be estimated by the use of capture-mark-recapture (CMR) methods. However, such methods are often very laborious, which lead most studies to apply indices of abundance as a cheaper alternative. It is then crucial that such indices are well calibrated with reliable abundance estimates to avoid biased inference. In the case of occupancy, the detection error can be estimated using repeated observations within a time period where the occupancy process is assumed to be closed (MacKenzie et al., 2002). A second issue that needs to be carefully considered is spatial variation and survey error (Yoccoz et al., 2001). Ecological monitoring can rarely monitor large areas entirely, hence it is important that the spatial design of the monitoring is appropriate to answer the question of interest.

Rodent monitoring					
Method	Variable	Effort	Temporal scale	Species	Example studies
Live trapping	abundance estimate	high	biannual	CL, BL, V	Fauteux et al. (2018)
Kill traps	abundance index	medium	biannual	all	Kleiven et al. (2018)
Nest count	abundance index	low	annual	CL, BL	Sittler (1995)
Sign index	abundance index	low	biannual	L, M	Vindstad et al. (2017)
Incidental observations	presence/ absence	low	annual	all	Bowler et al. (2020)

Table 1. This table list the most common monitoring methods for small rodents in northern areas as well as the typical state variables they give and temporal scale they are applied on. I note, however, that these are just examples and many other studies using these or similar monitoring methods for rodents exist. To some degree other studies also extract different state variables and are conducted on different temporal scales then what I display here. Abbreviations: L=*Lemmus sp.*, M=*Microtus sp.*, CL=Collared lemming, BL=Brown lemmning, V=all vole species.

One important reasons for the limited understanding of rodents population cycles, despite the huge effort over the last century, is the challenge of obtaining reliable estimates of rodent abundance and/or occupancy. CMR methods are only rarely applied for rodent monitoring, despite providing reliable abundance estimates. CMR is often considered too labour-intensive to be regularly applied in long-term monitoring programs (Fauteux et al., 2018; Ehrich et al., 2020). Kill traps (snap traps) are currently the most commonly monitoring methods applied for rodents (Turchin et al., 2000; Hörnfeldt et al., 2005; Korpela et al., 2013; Cornulier et al., 2013; Kleiven et al., 2018; Ehrich et al., 2020). They are cheap, give reliable information for species identification and give information on individual features, like sex, weight and reproductive status, and most importantly provide and abundance index, e.g. number of animals caught per 100 trap nights (Oksanen and Oksanen, 1992). However, snap-trapping share many of the labour intensive features of CMR-trapping, where traps have to be set and revisited. Therefore, snap-trapping of rodent are typically conducted once or twice (to capture the strong seasonality) a year when applied for long-term monitoring (Ehrich et al., 2020). Kill traps are also fraught with both ethical issues (Powell and Proulx, 2003) and questionable assumptions regarding sampling errors (Xia and Boonstra, 1992; Hanski et al., 1994). Snap-trapping also has an important limitation in that it has only rarely been attempted during winter, and these attempts has most often failed (Bilodeau et al., 2013). This has lead some researchers, especially in high Arctic sites, to use number of winter nests along fixed transects as an index of winter abundance (Sittler, 1995). However, while this density index has been found to correlate moderately well with rodent density in a high Arctic site (Fauteux et al., 2018), the method is not likely to be generalizable to low Arctic, or boreal areas. This because nests in low-arctic and boreal sites are mainly placed in hollows underground or in dense vegetation making them practically undetectable for human above-ground observers. Some studies have used signs of activity (feces or marks of grazing) as an index of abundance (Lambin et al., 2000; Vindstad et al., 2017). This index has been validated in at least one case (Lambin et al., 2000), however, while it might work well on some rodent species that leave clear traces (like e.g. Norwegian lemming and tundra vole) it is likely to perform poorer on species leaving less traces (like e.g. gray-sided vole). Some studies have applied incidental observations of presence/absence (Bowler et al., 2020) or counts (abundance index) to monitor the population state of rodents (Fauteux et al., 2018). However, again this index is mostly not validated. Both sign-based indices and incidental observations must be heavily confounded with activity. Rodents may exhibit density-dependent shifts in behavior (Semb-Johansson et al., 1979), which may confound such indices. In general, I argue that current methods available for monitoring of small rodents are poorly validated, have low temporal resolution and cannot be used during winter (with the exception of winter nest surveys in the high Arctic).

Mustelid monitoring				
Method	Variable	Effort	Temporal scale	Refs
Live trapping	abundance estimate	high	biannual	Mougeot et al. (2019)
Kill traps	abundance index	high	biannual	King and Powell (2006)
Snow tracking	abundance index	medium	annual	Oksanen et al. (1992)
Predated nests	abundance index	low	annual	Gilg et al. (2003)
Tracking tunnels	abundance index	medium	annual	Graham (2002)

Table 2. This table list the most common monitoring methods for small mustelids as well as the typical state variables they give and the temporal scale they are applied on. I note, however, that these are just examples and many other studies using these or similar monitoring methods for small mustelids exist. To some degree other studies also extract different state variables and are conducted on different temporal scales then what I display here.

Small mustelids are particularly difficult to monitor, even more so than small rodents. This is likely because they appear in low numbers (considerably lower numbers than rodents), are patchy, and sometimes unpredictably distributed, the traps are not active for long enough for mustelids to encounter them, and finally because mustelids actively avoid traps (King and Powell, 2006; King et al., 2009). To put it in numbers, King (1975) trapped only five common weasels in a total of 4032 trap-rounds in a deciduous woodland in Britain. Hence, trapping of mustelids with live or kill traps are only feasible for short intensive efforts and not for long-term monitoring. Finnish researches therefore developed a snow tracking density index by defining fixed transect that would be systematically checked after every snowfall (Korpimäki and Norrdahl, 1989b; Korpimäki et al., 1991; Oksanen and Oksanen, 1992). However, this method has several weaknesses that should lead us to search for alternatives. First, mustelids (particularly least weasel) are generally believed to follow rodents in their tunnels below the snow, which complicates the interpretation of numbers of tracks at the top of the snow layer (King and Powell, 2006)– the lack of supranivean activity might actually correspond to more subnivean activity. Second, it has been shown that the snow conditions affect the relative presence of mustelids on top of the snowpack and in the sub-nivean space, further biasing a tracking based density index (Jedrzejewski et al., 1995). Furthermore, this method can only be applied in snow-covered areas that are not too wind affected: heavy wind makes the snow so hard that tracks cannot be seen. On the barren Arctic tundra, mustelids have been monitored by the help of the ratio of mustelids predated rodent nests (Gilg et al., 2003; Gilg et al., 2006). While this might approximate mustelid densities in some high Arctic regions, it has, as far as I know not been properly validated and has the same problems with generalization to other areas as rodent nests are mainly found in large numbers on the high Arctic tundra. Furthermore, nest-indexes can only provide yearly abundance indexes masking short-term and seasonal variations. Tracking tunnels have been used to monitor small mustelids in places and season without snow (Graham, 2002). However, when mustelids appear in low numbers, like they most often do in northern areas, the number of tracking tunnels needed to obtain reliable estimates will be extremely laborious to operate (Choquenot et al., 2001). In addition, abundance indices from tracking tunnels does not seem to be linearly related their density as estimated from CMR (Graham, 2002). To summarize, the monitoring methods that exist for mustelids in northern areas are either extremely laborious, limited in what system they can be applied or generally poorly validated.

From the summary of available monitoring methods for small rodents and small mustelids above, the need for new methods to shed light on the role of mustelids in driving the rodent population cycles is clear. In general, one would need monitoring methods for both rodents and mustelids, which provide reliable information on population state variables (e.g. presence/absence and abundance) with a high temporal resolution matching that of the assumed interaction with reasonably low labour effort and costs.

1.3 Population dynamics of rodents in the time of climate change

The attention given to rodent population fluctuations has in the last decades been fuelled by emerging evidence of dampening or even disappearing of cycles caused by antropogenic climate change (Kausrud et al., 2008; Ims et al., 2008; Cornulier et al., 2013). The velocity of climate change is especially fast (Serreze and Barry, 2011) and its importance to wildlife particularly acute in northern regions (Post et al., 2009). Clear trends are already seen in both temperature which are increasing and the length of the snow covered season which is decreasing (Box et al., 2019). Climate change is increasing the frequency of extreme weather events (Diffenbaugh et al., 2017; Peeters et al., 2019), where increased frequnecy of phenomenons like rain-on-snow and winter warms spells has been found to have detrimental impacts on rodent populations as well as on whole northern food webs (Kausrud et al., 2008; Gilg et al., 2009; Hansen et al., 2013). Some pathways through which climate might impact northern rodent population are known, like e.g. hardening of the snow which affect the energy required for locomotion in the snow pack (Poirier et al., 2021) or formation of ground ice-layer blocking food plants (Aars and Ims, 2002; Korslund and Steen, 2006). However, climate impacts are complex and predicting their effects is difficult. For instance recent research implies that climate impacts might be contingent on which species' interactions that are most influential in the food web (Fauteux et al., 2021). The complexity of predicting climate effects are also illustrated by the sudden reappearance of the high amplitude rodent fluctuations Kausrud et al. (2008) predicted to disappear in the early 2000's (Wegge and Rolstad, 2018). I propose that better monitoring data on rodents and their local abiotic conditions on fine temporal and spatial scales, especially during the crucial winter period, will be needed to fully understand the potential pathways through which climate change will impact rodent population dynamics.

1.4 The rise of camera traps in wildlife monitoring

Over the last decades, the use of camera traps has seen a drastic increase in ecology as they provide a low-cost and non-invasive alternative to existing wildlife monitoring methods (Rowcliffe and Carbone, 2008). Camera traps provide multiple advancements to previous state-of-the-art monitoring methods. First, camera traps have the potential to providing temporally fine-scale observations (Sollmann, 2018). Second, camera traps can simultaneously provide data on a whole community of species (Ridout and Linkie, 2009). Third, camera traps have the potential to record local abiotic conditions, either by using additional sensors (e.g. temperature) or by assessing information in the images themselves (e.g. presence of snow or water). Camera trap studies have so far focused mainly on large mammals (Burton et al., 2015), however a camera trap approach was recently developed to monitor northern small mammal communities, also underneath the snow during winter (Soininen et al., 2015).

Camera traps, like any other monitoring method, detect species imperfectly. This means that it is possible that a focal species or individual goes undetected even though it is present. To avoid bias in population estimates it is crucial to account for this detection process (Chen et al., 2013). In state-of-the-art ecological modelling this is most reliably dealt with using capture-mark-recapture techniques where individual detection probability can be estimated. These methods do, however, require recognition of individuals, something which is for most species not possible from camera trap images. Therefore, instead, most camera trap studies choose to model presence/absence dynamics following the occupancy modelling framework developed by MacKenzie et al. (2002). In this framework the detection process is modelled using repeated samplings of the same population within a period, where the population is assumed to be closed (no change in species space-use). In the 20 years since its introduction the occupancy modelling framework has proven to be an effective way to obtain unbiased estimates on species distribution. This framework have been extended and generalized to deal with a broader range of ecological questions (see Guillera-Arroita, 2017 for an overview). As ecologists often are interested in explaining drivers of species distribution across time, one of the first extensions of occupancy models was to enable estimation of colonization and extinction dynamics over multiple temporal occasions (typically referred to as dynamic models) (MacKenzie et al., 2003; MacKenzie et al., 2017). As it is well recognised that interspecific interactions play important roles in driving colonization and extinction dynamics, dynamic occupancy models were then generalized to deal with multiple interacting species (Richmond et al., 2010; Waddle et al., 2010). Later these dynamic occupancy models for interacting species have been extended to deal with more than two species and to enable estimation of covariate effects on colonization and extinction parameters (Rota et al., 2016; Fidino et al., 2019).

Thesis Objectives

2.1 Thesis context

This thesis was conducted as a part of the long-term monitoring program Climate-ecological Observatory for Arctic Tundra (COAT) (see www.coat.no and Ims et al. (2013)). COAT is an adaptive, ecosystem-based observation system established aiming to unravel how climate change impacts Arctic tundra food webs. COAT applies a multi-dimensional monitoring system with multiple modules each centered around a food web compartment particularly important to the functioning of the food web or with high societal impact. At the core of each module is a conceptual model illustrating potential climate change and management impact pathways. As has been described in detail in the introduction, the population dynamics of small rodents are central to the functioning of most tundra food webs. Small rodents are therefore an important monitoring target of COAT, making them the center of one of the COAT modules. The conceptual model for the small rodent module incorporates climate impacts and interactions with specialist predators (i.e. small mustelids) as key targets for the module (Fig. 2.1).

In monitoring of the state variables in the conceptual models, COAT aims to apply an adaptive monitoring framework where improved knowledge or emergence of new technology or statistical methodology will lead to updated monitoring protocols (see Fig. 2.2). This thesis was conducted during the late implementation phase of COAT, as a part of the COAT tools + project. The overarching aim of COAT-tools + is to combine new monitoring technology with development of beyond state-of-the-art statistical methods to provide better monitoring of state variables in COAT. With this context, the aims of this thesis are described below.

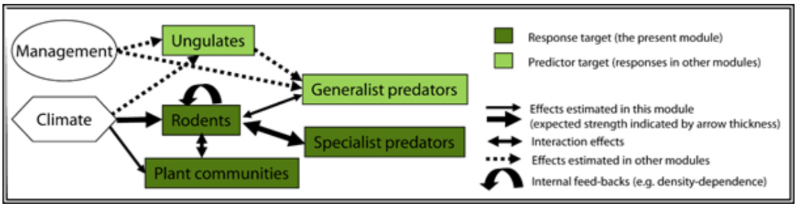


FIGURE 2.1. Conceptual model of the small rodent module in COAT. It displays potential climate and management impact pathways on small rodents at the same time as describing the most important food-web interaction affecting population dynamics of small rodents. The assumed relative importance of the different relations and interactions is proportionate to the boldness of the arrows. The figure is reproduced from Ims et al. (2013) with the permission from the authors.

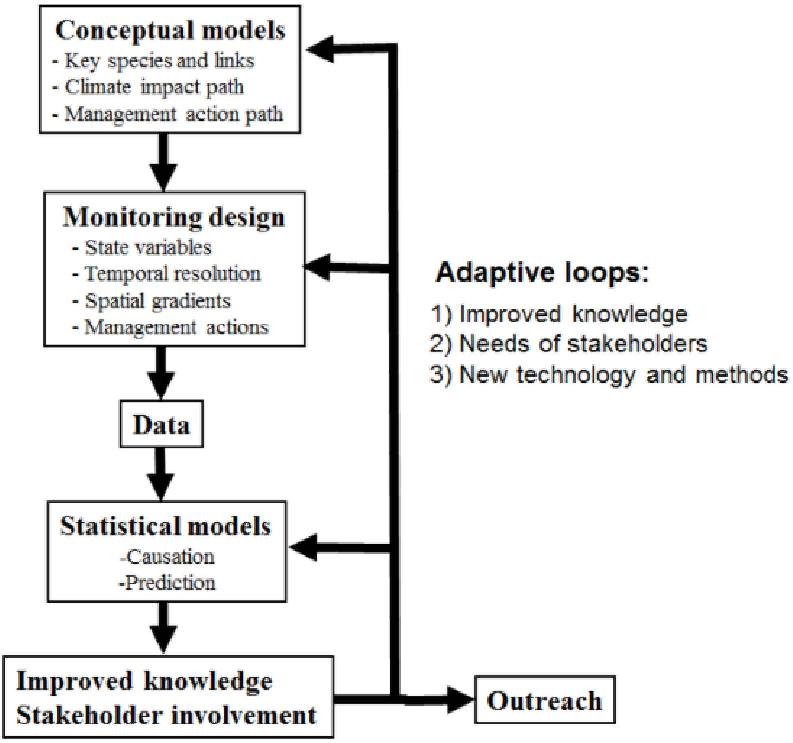


FIGURE 2.2. Figure describing the adaptive monitoring approach and specifically illustrating the implementation of new technology and methods. The figure is reproduced from Ims et al. (2013) with the permission from the authors.

2.2 Thesis aim

In this thesis I will assess the applicability of novel camera trapping technology to improve the monitoring of small rodents on the Arctic tundra. This will be combined with the development of a novel statistical framework for modelling of predator-prey interactions from camera trap-based population monitoring. This will be done by answering the following four questions:

Can camera traps provide reliable estimates of occupancy dynamics of northern rodent populations on an extensive spatial scale also during the long Arctic winter?

To answer this questions we do, in study I, the first extensive-scale assessment of technical functionality of the tunnel camera traps of Soininen et al. (2015) under harsh environmental conditions on the low Arctic tundra and investigate the camera traps ability to provide reliable information on the Arctic small mammal community.

Can camera trap data be used to study the interactions between predators and prey that operate on two different spatial scales within the occupancy modelling framework?

As interacting species in general, and predators and their prey in particular, often operate on different spatial scales monitoring programs focused on interacting species might be conducted on nested spatial scales. In study II, we will combine the frameworks of dynamic occupancy models for interacting species with multi-scale occupancy models by developing a dynamic occupancy models for interacting species with two nested spatial scales. We will further assess the reliability of the model in producing unbiased estimates of a simulated predator-prey interaction under different occupancy and detection scenarios.

What role does mustelids predation play on local and regional scale colonization and extinction dynamics of rodents and how does this predator-prey *interaction vary in space and time?*

Camera traps gives a unique opportunity to pin-point the assumed key mechanisms underlying rodent cycles. In study II we apply the dynamics occupancy models for interacting species with two spatial scales to COAT's spatially hierarchical camera trap-based rodent-mustelids dataset. In study III we investigate in more detail, and with more data, whether the mustelid-rodent interaction differ between seasons and habitats.

Can camera trap counts provide a reliable index of abundance for rodents?

Even though occupancy dynamics has been used to answer a wide range of ecological questions, it is less informative than studying abundance dynamics. We will therefore in study IV perform a calibration study by comparing camera trap-based species counts to density estimates derived from capture-mark-recapture (CMR) to investigate the potential of camera traps to provide a reliable index for abundance of small rodents.

Methods

3.1 Study area

The studies in this thesis were all conducted in northern Norway. Study I-III were conducted in COAT's long-term monitoring sites on the Varanger Peninsula in the Norwegian low-Arctic (70 °N and 27-30°E, Fig 3.5). The Norwegian low Arctic tundra consists of hilly plains dominated by dry dwarf shrub heaths (mostly common species are *Empetrum nigrum, Vaccinium spp.* and *Betula nana*) carved by river valleys and occasional mesic hummock tundra and mires with lusher vegetation and snowbeds dominated by mosses. The river valleys are dominated by willow thickets and particularly lush grasslands, while mesic hummock tundra and mires have high abundance of sedges and herbs. The Norwegian low-Arctic food-web is described in detail by Ims et al. (2013). Study IV is conducted in the forest-tundra transition zone, which is characterized by mountain birch forest with understory vegetation dominated by dwarf shrubs intermixed with grasses and herbs (Fig. 3.6). Both the tundra and the forest-tundra transition zone exhibit strong environmental seasonality with long snowy winters lasting 6-8 months.

3.2 The small mammal community

The Norwegian low Arctic tundra is inhabited by three rodent species: the Norwegian lemming, gray-sided vole (*Myodes rufucanus*) and tundra vole (*Microtus oeconomus*) (fig. 3.3). They all differ in their preferred habitat and diet. The Norwegian lemming is assumed to spend the summer in moist hummock tundra sites and move to snowbed sites during winter (Aho and Kalela, 1966; Koponen, 1970) (Fig. 3.4). During summer tundra voles co-occur with Norwegian lemmings in hummock tundra

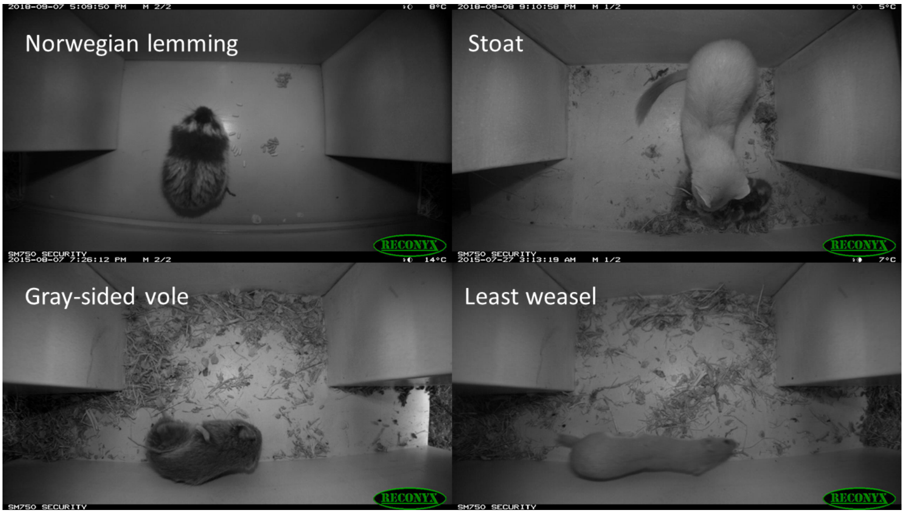


FIGURE 3.3. Camera trap images showing Norwegian lemming (upper left), gray-sided vole (lower left), stoat (upper right) and least weasel (lower right) captured by COAT's long-term monitoring system for small mammals on the Varanger peninsula.

sites (Tast, 1966), in addition to frequently inhabiting grassy meadow sites (Henden et al., 2011). The dwarf-shrub dominated vegetation both in the tundra and the mountain birch forest is the primary habitat of the gray-sided vole (Viitala, 1977). In addition to rodents, the small mammal community on the low Arctic tundra also consist of shrews (the common shrew *Sorex araneus*, masked shrew *Sorex caecutiens* and pygmy shrew *Sorex minutus*). The insectivorous shrews are ecologically very different from small rodents and their interaction with small mammals predators are debated, where some have suggested that shrews are not a preferred prey (Korpimäki, 1986; Korpimäki and Norrdahl, 1989a). In addition two species of small mustelids are present: the least weasel (*Mustela nivalis*) and stoat (*M. erminea*). Both the least weasel and the stoat are considered to be specialized predators on small rodents, still there are some species specific differences which might impact their interaction with rodents. The least weasel is in general considerably smaller than the stoat, however a large sexual dimorphism in body weight in both stoats and least weasels still cause overlap in body size between the two species (King and Powell, 2006). Furthermore, least weasels are known to reproduce up to three times a year (Sundell, 2003), increasing the potential for rapid shifts in population size. The stoat on the other hand has delayed implantation, which only make them able to reproduce once a year, lowering the potential for a quick increase in population size (King and Powell, 2006). The small mammal community in the northern birch forest is very similar to the one on the nearby low Arctic tundra. The main difference is that the most Arctic rodent species, the Norwegian lemming is only present in the northern birch forest during the peak phase of their population cycles when they disperse from the nearby tundra.

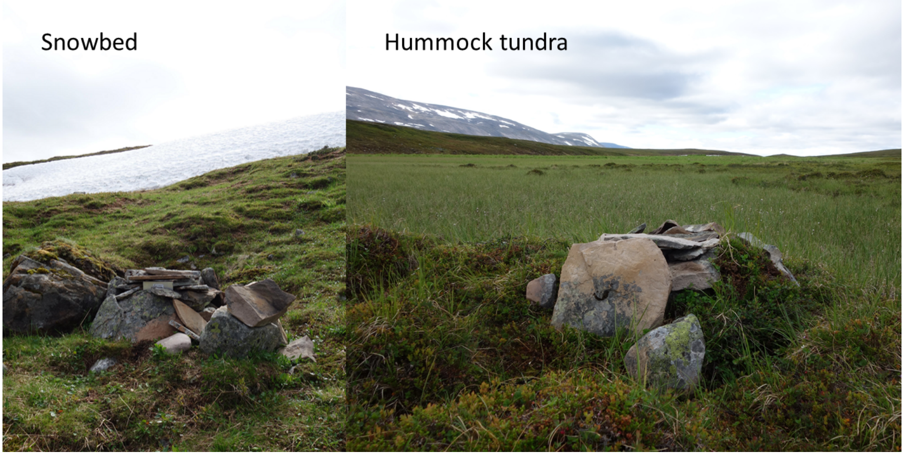


Figure 3.4. Images of two example sites with camera-tunnels. On the left in a snowbed site and on the right in a hummock tundra site. The camera tunnels are covered by stones to avoid drifting snow from entering the tunnel and block the view of the camera (see discussion on this study I).

3.3 Study design

Camera traps

The camera trap-based small mammals monitoring system in COAT is applying the tunnel camera traps presented by (Soininen et al., 2015). The key feature of this camera trap is that it applies an artificial tunnel, with small opening in each end with a larger cavity in the middle. Similar natural cavities are frequently used by rodents and mustelids. The camera has a wide-angle lens focused for photographing objects at relatively close range. The camera trap also has a wide-angle passive-infrared (PIR) detection sensor with a detection zone covering the whole tunnel, hence any animal entering the tunnel will trigger the camera. The cameras are set to capture two images every time they are triggered, and can only be triggered once per minute (i.e. 1 minute quite time after a trigger event).

Spatial design of COAT's long-term small mammal monitoring (study I-III)

Studies I-III use data from COAT's camera trap-based long-term monitoring system for small mammals on the low Arctic tundra. This monitoring system targets the two preferred habitats of the Norwegian lemming (i.e. hummock tundra and snowbeds). Snowbed sites were selected to include relatively rich vegetation consisting of mosses, graminoids, herbs and prostrate shrubs (*Salix herbacea and Vaccinium spp*). In addition, the snowbed sites was chosen to be in proximity of boulder fields that provide shelter to small mammals (Magnusson et al., 2013; Soininen et al., 2018). Hummock tundra sites were moist, bordering mires with lush vegetation containing sedges, herbs and erect shrubs (e.g. *Betula nana, Vaccinium spp.*) as well as hummocks providing shelter. Even though the monitoring targeted the Norwegian lemming, small mustelids (i.e. least weasel and stoat), voles and shrews are also commonly observed. To account for the contrasting movement ranges of mustelids and rodents the monitoring design includes two nested spatial scales (Fig. 3.5). Sites (i.e. camera traps) are spaced > 300 m apart and clustered in blocks, which again are spaced > 3000m apart. The sites are assumed to yield independent occupancy measures of rodents (i.e. different cameras should not overlap the home range of the same rodent individual) (Ims, 1987; Andreassen et al., 1998). In contrast all sites within the same block could potentially be within the home range of the same mustelid (Hellstedt and Henttonen, 2006). Hence colonization-extinction dynamics of mustelids on the site-scale will represent within home range movements, like e.g. foraging movements. The blocks are assumed to give independent measurement of mustelid occupancy. For rodents, colonization-extinction dynamics on the block scale will represent more their landscape-scale population dynamics.

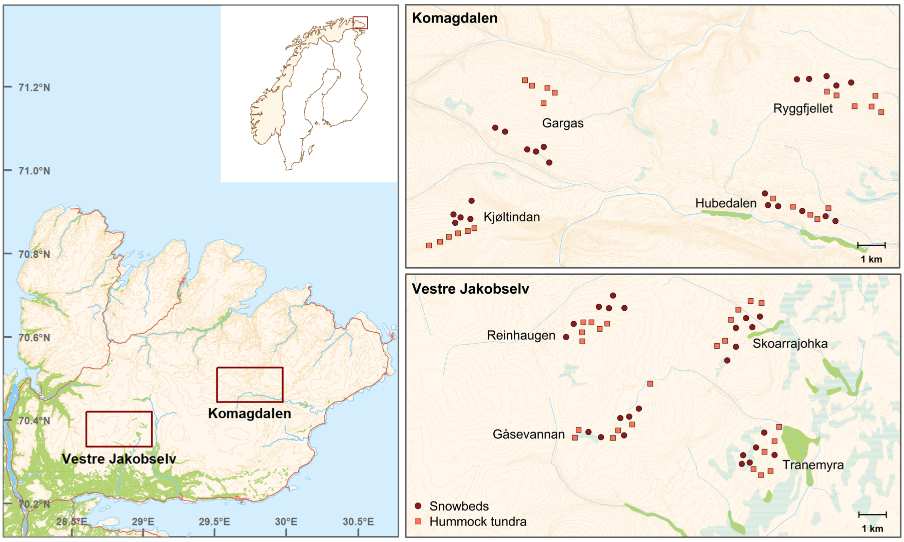


FIGURE 3.5. Maps of COAT's low-Arctic tundra study areas in Komagdalen and Vestre Jakobselv on the Varanger Peninsula. Dark brown circles represent camera trap sites in hummock tundra and light red squares represent sites in snowbeds. Figure reproduced from paper III with permission from the authors.

Spatial design of calibration study (study IV)

In study IV we took advantage of two existing long term monitoring-series of rodent population dynamics obtained from multiple CMR trapping grids in the mountain birch forest. One of the time-series focused on the gray-sided vole (region Porsanger) and the other on the tundra vole (region Håkøya) (see Fig. 3.6).

These are the two numerically dominant species of voles in the mountain birch forest and on the low Arctic tundra in northern Norway. In the beginning of the work with this thesis, in fall 2017 (Håkøya) and spring 2018 (Porsanger), we deployed one tunnel camera trap within each live trapping grid in both regions. These were maintained and checked yearly and live trapping conducted 3 and 5 times a year respectively for Porsanger and Håkøya. We used data from deployment in spring 2018 to end of 2020, to make sure that we covered all phases of the small rodent cycle.

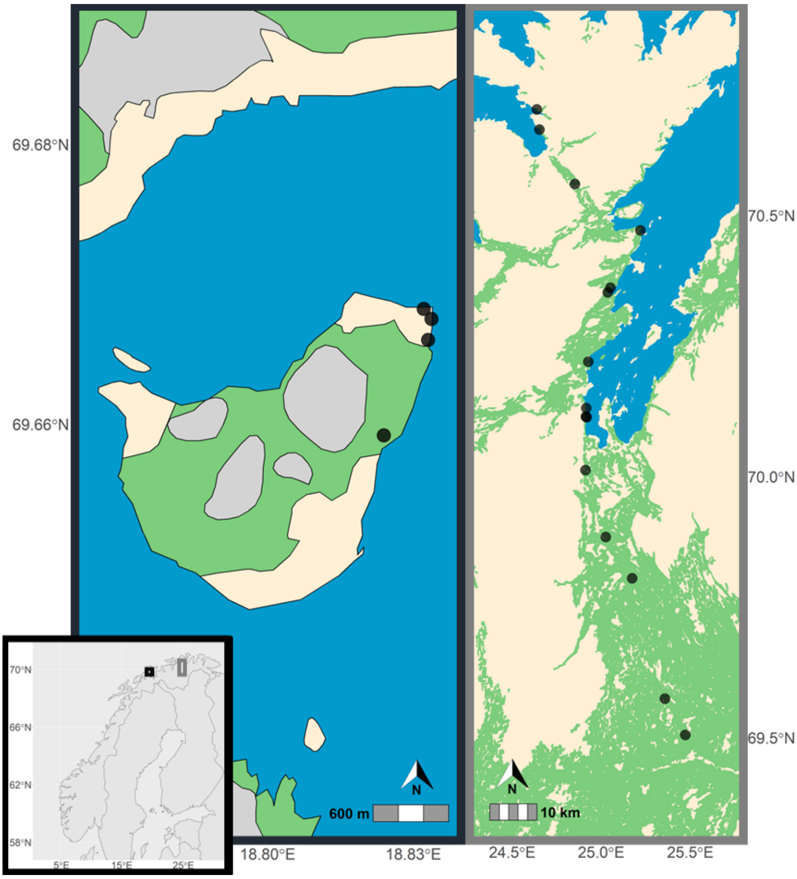


Figure 3.6. Maps of the CMR grids with camera traps used in study IV. Black circles represent CMR grids. Figure from paper IV with premission from the Authors.

3.4 Data analysis

Study I-III

In study I-III we used data from COAT's long-term monitoring of small mammals to model occupancy dynamics. Study I used data from autumn 2014 to summer 2015, which was the first year of camera trap-based small mammal monitoring in COAT. During this initial year, much was learned about camera placement to avoid malfunctioning of cameras (see details about this in paper I). Hence, most camera traps were relocated accordingly during summer of 2015. Hence, the dataset from summer 2014 to 2015 is limited in ecological information and not directly comparable to the following years. We applied a dynamic single species occupancy model to test the ability of the data from COAT's tunnel trap to provide occupancy estimates for lemmings, voles and shrews during winter.

For study II we extended the existing occupancy modelling framework for interacting species (Rota et al., 2016; Fidino et al., 2019) to be able to account for the spatial hierarchical study design in the small mammal monitoring in COAT (see study II for a detailed description of the model). In a case study, to demonstrate the real-world applicability of the model, we analysed COAT's small mammal data collected from summer 2015 to summer 2019. As this model is considerably more complex compared to the model used in study I, we lumped the three rodent species and the two mustelid species to two functional groups (i.e. predators (mustelids) and prey (rodents)). We did not model any covariate effects on colonization or extinction probability, but did include a season effect on the detection probability of both functional groups. We did check the model performance by conducting a prior sensitivity analysis, parameter identifiability analysis as well as assessing the goodness-of-fit.

The same model was again applied in study III. This time we analysed data from COAT's small mammal monitoring from summer 2015 to summer 2021. We still used the same functional groups as in study II. We now focused on the estimation of the effect of one temporal (season) and one spatial (habitat) covariate on the colonization and extinction probabilities, while accounting for the seasonal effect on detection probability.

It be noted that the seasonality covariate differ between study II and study III. In study II we used temperatures measured in the camera traps to estimate beginning and end of winter, while we in study III defined the winter to be between 1sth of November and 1sth of July.

Study IV

In this study IV, we assess the adequacy of using camera-trap-based abundance indices, from the camera tunnels developed by Soininen et al. (2015), for monitoring population dynamics of the gray-sided vole and the tundra vole. We performed a calibration-regression analysis, with the camera trap-based indices (CT-indices), based on number of photos of a given species from single camera traps, as the exposure variable and CMR-based abundance estimates as the ground-truthing variable. In the case of tundra vole, for which several camera traps and grids were located within the same local population (Fig. 3.6), we assessed if aggregating data over several camera traps and grids could improved the fit of the calibration regression. As the camera traps provide continuous-time data, we assessed which temporal discretization of the data that gave the best calibration results (i.e, maximized the R^2). In addition, we performed inverse prediction to estimate vole abundance using the best CT-index.

Results and discussion

4.1 Study I

Study I represents the first large scale application of camera traps to estimate population parameters (i.e. occupancy state) of within a small mammal community. We learned that the micro-scale location of the traps was very important to assure best possible year-round technical functionality of the tunnel-trap developed by (Soininen et al., 2015). In particular, we found it necessary to avoid placement of camera tunnels in small depressions. At the same time camera tunnel entrances have to be appropriately sheltered to avoid snow from drifting into the open cavity of the tunnel blocking the camera lens. We give recommendations on how to avoid these problems, which we later have successfully implemented in COAT. On the other hand, we did not experience problems with frost, which has recently been reported from a camera trapping study on the High Arctic tundra (Pusenkova et al., 2021). This might be because our low-Arctic study area lacks permafrost and has a thick snow cover in winter (up to 4m thick (Soininen et al., 2017)). The functional camera traps recorded Norwegian lemmings, gray-sided voles, tundra voles, shrews and mustelids both during the snow-free and snow-covered period. The mustelid recording in this pilot study, however, were too few for occupancy modelling. For the three rodent species and shrews (the latter combined in one functional group), we were able to estimate weekly occupancy and detection probabilities. Estimated occupancy of both the rodents and shrews decreased at the onset of winter, but quickly stabilized at low to medium occupancy rates, before they increase following snow-melt in the spring. Regarding the estimated detection probabilities, shrews generally had lower detection probability than rodents and snow did not seem to have large negative effects on the detection probabilities. This suggests that camera traps can be used to monitor occupancy of small mammals, including under the snow during the long Arctic winters. The latter, is particularly important as monitoring of small mammals in the sub-nivean space previously has not been possible (Bilodeau et al., 2013).

A additional feature of camera traps is their ability to record not only biotic information (e.g. species presence), but also local-scale abiotic information on a fine temporal scale. In Study I, we demonstrate how information about the local-scale environmental conditions can be extracted from the images (e.g. presence of snow or water) as well as the temperature recorded by a sensor in the camera. This is particularly promising as local environmental conditions can cause both direct and lagged effects on populations processes, which is still often ignored in studies of small mammal ecology (Hallett et al., 2004).

4.2 Study II

We were able to successfully develop and validate a dynamic occupancy model for interacting species with two spatial scales, which was inspired by both the model for interacting species by Fidino et al. (2019) and the dynamic multi-scale occupancy model by Tingley et al. (2018). The model performed well in retrieving unbiased parameter values in a simulation study with varying scenarios of occupancy and detection probabilities. The contrasted scenarios in the simulation study attempted to investigate the data requirements of the spatially hierarchical occupancy model where parameter values were chosen according to previous knowledge from occupancy studies (Specht et al., 2017) and what could be expected about the parameters from a predator-prey interaction. When applying the model to the spatially hierarchical COAT monitoring dataset on rodents and mustelids, we found that the site-level extinction probability of rodents drastically increased when mustelids were present. Unfortunately, two block-level parameters (extinction probability of mustelids and colonization probability of rodents when mustelids were present) appeared to be unidentifiable based on the COAT dataset (using data from 2015-2019). This can be explained by the large amount of missing observations, strong seasonality in addition to multi-annual population fluctuations and low detection rates of the two functional groups. Furthermore, the fact that it is only the block parameters that appear to be unidentifiable can be explained. All observations come from the site-level, with the block-level parameters thus depending on the reconstruction of two latent states. Also, the nested study design implies that there are more sites than blocks, providing more data to estimate the site-level parameters than the block-level parameters. Considering the complexity of this model, it is likely to require large datasets to be able to identity all parameters. Hence we suggest that the challenges with parameter identifiability might be solved with more data. This was in fact later confirmed by study III were we have two more years of data.

On a more self-critical note, the identifiability issues we meet in the real world case study might indicate that the scenarios in the simulation study did not challenge the model enough in terms of detection rates and temporal heterogeneity in the data. Indeed, hierarchical occupancy models are becoming increasingly complex, however only seldom the exact data requirements of these models are assessed. See further discussions on more aspects on hierarchical occupancy modelling in section 5.1.

4.3 Study III

In study III we apply the dynamic occupancy model for interacting species with two spatial scales developed in study II to a temporally extended dataset from COAT's small mammals monitoring system (Fig. 4.7). Based on this almost 6-year dataset, which included two decrease phases of the rodent cycle, we investigated if the strength of the interaction between rodents and mustelids differed between two seasons (i.e. summer and winter) and habitats (i.e. hummock tundra and snowbed).

We found clear empirical evidence of a strong predator-prey interaction between rodents and mustelids, where mustelids increased the extinction probability of rodents on both the local spatial scale of sites (matching the home range size of rodents) and larger scale of blocks (matching the home range size of mustelids). Furthermore, we found a clear habitat dependency in the strength of the rodent-mustelid interaction in the sense that it was most pronounced in the snowbed habitat. While it seemed that the interaction was slightly stronger during summer than during the winter, the habitat effect was considerably stronger and more prevalent than the season effect. It should however, be noted that the analysis may not have been able to account for the profound seasonal transitions in the observed occupancy rates of mustelids, which did not match well our fixed definition of summers and winters (Fig. 4.7).

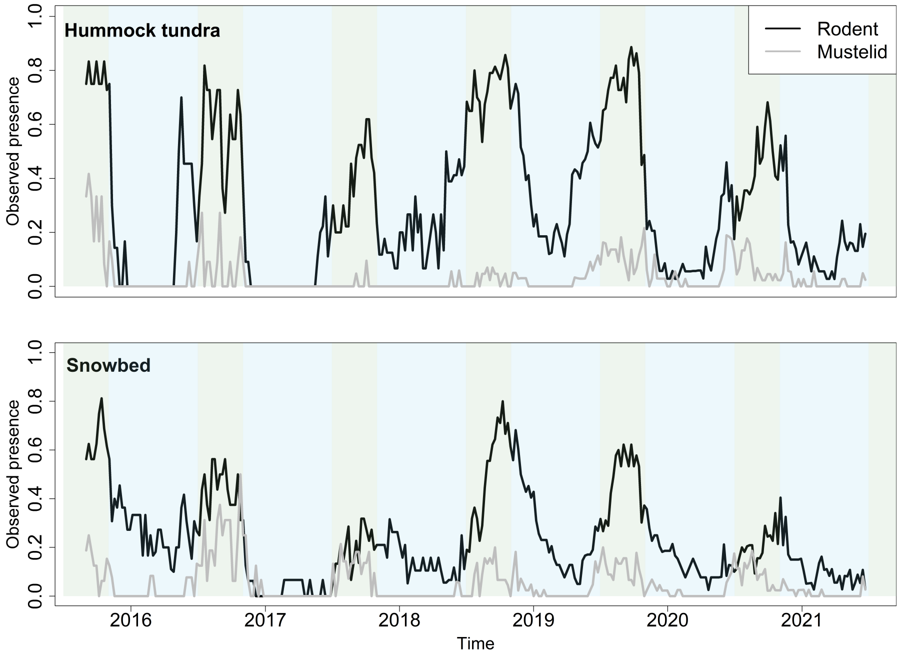


Figure 4.7. Temporal patterns in the proportion camera traps sites with weekly records of rodents (black lines) and mustelids (grey lines) in hummock tundra and snowbeds. Pale green background denote summer seasons (July 1-November 1), while the pale blue background denote the winter season.

The result of this study, should be seen more as a first glance into aspects of mustelid-rodent interactions that conventional monitoring methods have not been able to uncover, rather than giving definitive answers about the role of mustelids in generating population cycles in rodents. Indeed, there are several limitations to this study. First, it only included approximately only one and a half rodent cycle, which is problematic as rodent cycles are known for being inherently variable both in terms of amplitude and shape (Kleiven et al., 2018). Second, the study covered only two tundra habitats (i.e. snowbeds and hummock tundra) and not the more productive river valleys and tundra-forest transition zones, which may be important winter habitats for mustelids (Oksanen and Oksanen, 1992; Aunapuu and Oksanen, 2003). Third, local environmental conditions (e.g. physical snow properties) appear to be important determinants of space-use of rodents and mustelids during winter (Jedrzejewski et al., 1995; Poirier et al., 2021). Unfortunately, due to a lack of reliable local scale environmental information and a too sparse dataset to include additional covariates, we were not able to model such effects. Finally, the fixed definitions of seasons in this study may not have adequately accounted for the seasonal variation in environmental conditions affecting rodents and mustelids. Despite these limitations, the spatio-temporal variability in interaction strength between rodents and mustelids revealed by this study may have significant bearings on how mustelid affect the population dynamics of Arctic rodents (Sih, 1987). Overall, our study highlight the ability of camera trap-based monitoring systems to provide novel insights about an ecological phenomenon that have been out of reach of previous monitoring methods.

Future camera-trap studies that include more tundra habitats and span multiple rodent cycles are needed to work out the full role mustelids may potentially play in the generation of the population cycles of northern rodent populations. Such empirical studies should be accompanied by theoretical studies that assess the potential consequences of habitat- and season dependency in the interaction between mustelid and rodents.

4.4 Study IV

Overall the results from the index calibration in study IV show that camera traps have the ability to provide a reliable abundance index for both the gray-sided vole and the tundra vole. For the gray-sided vole, a single camera trap was able to provide a reliable abundance index when temporally aggregating camera trap counts over only 5 days. However for the tundra vole, abundance indices based on single camera traps performed much more poorly. It was needed to aggregate camera count over four camera traps within the same local tundra vole population to obtain a good correspondence between the camera-trap indices and the CMR-based abundance estimates. This difference is likely attributed to species differences in spatio-social organization of the vole populations (Ims, 1987; Bondrup-Nielsen and Ims, 1988). Female territoriality makes gray-sided voles more evenly distributed in space, while tundra vole females have spatially clustered kin-groups that are temporally unstable, as tundra vole females frequently shift home range, also within a breeding season (Tast, 1966). We suggest that the improved calibration performance in case of the tundra vole was obtained when aggregating the data over four local monitoring sites are caused by the smoothing out of this temporally fast and spatially small-scaled variability. This species difference stress the importance of conducting such calibration studies when applying new monitoring methods to new species. This is also interesting in the context of a more general discussion on index calibration studies. Index calibration is particularly challenging when true species abundance is not known (which is the case for most wildlife populations) as the error of the population abundance estimate (i.e. the ground-truth variable) may not be negligible (Gopalaswamy et al., 2015).

It is important that camera traps can produce ecologically relevant information on species abundance based on appropriate study design (i.e. temporal and spatial replications). While it is true that many ecological questions can successfully be studied by the use of presence-absence dynamics, some questions can only be answered using more informative state variables (like abundance). The approach of analysing predator-prey interaction between mustelids and rodents with occupancy models (study II and III) illustrated this point. With occupancy models one has to assume that mustelid predation is sufficient to drive rodents into either local or regional extinction. Furthermore, one has to assume that the presence of rodents is enough to drive mustelid colonization. However, mustelids might in fact impact rodent populations by reducing their abundance, without driving them to local or regional extinction. It is also possible that it is not the presence of rodents, but rather their abundance that affect the colonization probability of mustelids. Although as one zooms into smaller and smaller spatial scales, local abundance eventually transforms into presence-absence of single individuals. The site-scale considered in studies II and III is typically a little larger, as it potentially could include overlapping home ranges of several rodent individuals.

For these reasons I really think that the possibility of studying population dynamics of rodents by means of calibrated abundance indexes derived from camera traps will greatly improve our knowledge about rodent population dynamics and how such dynamics is affected by biotic and abiotic factors.

Model limitations

4.5 Challenges with complex hierarchical occupancy models

After being presented to the ecological community 20 years ago (MacKenzie et al., 2002; Tyre et al., 2003), occupancy models have been widely adopted by ecologists and generalized to answer a wide range of ecological questions (Guillera-Arroita, 2017). Occupancy models have been fitted both in a frequentist framework, using maximum likelihood (MacKenzie et al., 2002) and penalized maximum likelihood methods, and in the Bayesian framework (Royle and Kéry, 2007). Today a range of methods are available for Bayesian model fitting, where Markov Chain Monte Carlo (MCMC) simulations are likely the method most frequently used by ecologists. MCMC-simulations provide a full probability distribution for the estimated parameters (i.e. posterior distribution). Further, the Bayesian framework allow for inclusion of prior knowledge by including prior distributions for model parameters. The Bayesian framework is more flexible and is therefore often preferred by ecologists over the frequentist approach when performing non-standard statistical analysis (Clark, 2005; Dorazio, 2015). I find that ecological data have a tendency to be messy in terms of often containing various dependency structures, indirect observations and unaccounted for confounding factors. Hence, ecological data are rarely as clean as standard statistical methods typically assume. Context dependence (Catford et al., 2022), spatial autocorrelation (Johnson et al., 2013) and complex detection processes (Royle, 2006) are only a small subset of the challenges one might meet when analysing ecological data. Therefore, I find the need for case specific model modifications to be the rule rather than the exception in ecological data analysis. Ecological datasets are often relatively small as data collection often is laborious and expensive. Another advantage with Bayesian inference is that it is theoretically valid at any sample size. However, even though inference might be theoretically valid when there is little information in the data, more emphasis is given to the prior distribution (Dorazio, 2015). Hence, these sparse datasets often hamper the use of complex statistical models, therefore I see ecological data-analysis as a trade-off between accounting for the most prominent sources of bias, while at the same time avoiding models that are too complex for the data.

The advantages of now being able to fit complex Bayesian occupancy models, however, do not come without costs, which I have experienced in the work with this thesis. When models are extended with additional model parameters, typically the data requirements of the models also increase. This is can be problematic as ecological datasets often are relatively small. This is well demonstrated in this thesis. In study II, two block level parameters (extinction probability of mustelids and colonization probability of rodents when mustelids were present) in the spatially hierarchical occupancy model were unidentifiable from the COAT dataset from 2015-2019. However, when adding two more years to the dataset (2019-2021), which we did in study III, all block level parameters appeared to be identifiable. We note that while the COAT dataset appears to be relatively large seen in number of primary occasions it is poorer in term of actual species observations, in particularly so for the mustelids which are rare and elusive.

The opportunity to include prior information in the Bayesian framework is rarely taken by analysts of ecological data (Northrup and Gerber, 2018). This has been criticised, as e.g. Lemoine (2019) argue for the use of weakly informative priors. Moreover, prior distributions have to be specified carefully as even seemingly uninformative priors can have large unintended effects on the estimated posterior distributions (Seaman and Stamey, 2012). Another important challenge with complex hierarchical models analysed in a Bayesian framework is the lack of general methods for model checking. This has led ecological data analysts using complex occupancy models to most often ignore model checking (Conn et al., 2018), in stark difference to for example capture-mark-recapture models (Gimenez et al., 2018). To address these challenges in study II we performed a prior sensitivity analysis demonstrating that the model estimates were not sensitive to the prior distributions chosen (except for the two parameters we deemed to be unidentifiable). In addition, we extended on a model checking procedure proposed by Kéry and Royle (2020) for single species dynamic occupancy models with one spatial scale. To apply this approach we had to consider the two species (rodents and mustelids) separately and ignore the the two nested spatial scales in our data. We did a simple check of the applicability of this approach by first applying it to the simulation study from study II. Even though this is discussed briefly in the appendix of study II, I want to stress that this is not an extensive validation of this model checking procedure. The limitations already mentioned, e.g. ignoring the nested spatial structure, are likely to affect the performance of the model check. More work will definitively be needed to develop and validate reliable model checking methods for complex hierarchical multi-scale, multi-species occupancy models, and similar complex occupancy models.

A limitation with MCMC-methods is that they are often computationally intensive. For complex hierarchical models and large datasets this can often lead to long run times. For instance, the model in study III uses a week to run despite paralleling the separate chains (multiple chains are necessary to assess convergence in MCMC methods) of the MCMC analysis on separate cores when analysed using JAGS (Plummer, 2003). For other models and datasets it can be considerably longer. I note that more computationally efficient methods for analysis of hierarchical models in the Bayesian framework are available (e.g. NIMBLE (de Valpine et al., 2017) and Stan (Stan Development Team, 2021)).

4.6 Estimating detection probability in the occupancy framework

An important reason why occupancy models were so quickly adopted by the ecological community is their ability to account for imperfect detection in a practical and theoretically sound way. In the initial occupancy models detection probability was estimated from the pattern in multiple independent replicated observations (secondary occasions) of detection and non-detection at the same location within a time period where the focal population is assumed to be closed for changes in occupancy (i.e. primary occasion) (MacKenzie et al., 2002; Tyre et al., 2003). This is not entirely unproblematic in many ecological studies. Most populations are in fact not closed for the time periods typically considered in occupancy studies (7 days to 3 months) (Rota et al., 2009). If the closure assumption is not valid because species randomly move in and out of the area, the estimated occupancy can be considered as species activity to avoid unbiased ecological inference (Mackenzie, 2005; Latif et al., 2016). If the changes in occupancy during a primary occasion are non-random they can potentially lead to both positively and negatively biased occupancy estimates (Rota et al., 2009; Hines et al., 2010; Kendall et al., 2013; Otto et al., 2013). Which implications may this have for the studies presented in this thesis? Space-use of mustelids on the tundra is poorly understood. However, mustelids are known to cover large areas and frequently shift foraging grounds. Furthermore, they exhibit seasonal changes in space use, driven both by snow conditions, but also by their seasonal breeding cycle (Hellstedt and Henttonen, 2006). In addition they are both rare and elusive (King and Powell, 2006). This makes the weekly closure assumption unlikely to be a good approximation, at least for mustelids, with unknown consequences.

Furthermore, while we see a sharp decrease in the observed presence of both our functional groups (i.e. rodents and mustelids) at the beginning of every winter followed by a sharp increase around the beginning of every summer, the difference in the estimated detection probability both of rodents and mustelids is relatively small between summer and winter. Especially the sharp increase in observed presence in the spring, when most rodents have not yet started to reproduce, cannot be caused by a sharp increase in population size. We cannot completely rule out strong seasonal migration as a potential cause, as we do not cover all tundra habitats. Still, I find it quite plausible that at least a part of this sharp seasonal shifts in observed presence are caused by seasonal changes in the ecological interpretation of the occupancy measure (see Lele et al. (2013) for general discussion).

Replicated measures (i.e. secondary occasions) that are fully independent can be difficult to obtain, especially so when they should be close in time to avoid breaking the closure assumption. In addition, also repeated primary occasions (period within which closure is assumed) might be close in time. Many camera trap studies collect data in continuous time before arbitrary split them into primary and secondary occasions, which then often abut each other in time (see for e.g Bischof et al. (2014), Davis et al. (2017) and Kass et al. (2020), see Sollmann (2018) for further discussion of temporal dependencies in continuous camera trap data). Further, the requirement of temporally replicated observations limits the possibilities to model temporally fine-scaled processes. To illustrate the issue with independent sampling, think about the continuously sampled camera trap data from the small mammal monitoring in COAT which this thesis is based on. We have tried to obtain temporally independent secondary occasions by considering ecologically reasonable temporal windows (i.e. treating each day as a secondary occasion, as rodents have a circadian rhythm). In addition we have set the length of the primary occasion to match the expected time scale of the mustelid-rodent interaction. This is in itself particularly challenging as population dynamics of rodents and mustelids happen on different temporal scales. Furthermore, both secondary and primary occasions do still abut one another. This is clearly problematic. However, when data is continuously sampled, the only way it can be avoided in the classical occupancy framework is to leave out data. While that may make the modelling more theoretically sound, it will also drastically reduce the amount of data available.

4.7 Mechanistic interpretation of occupancy model parameters

Most of the theoretical understanding on predator-prey interactions in general, and the mustelid-rodent interaction in particular, comes from theoretical models focusing on population size (Hanski, 1998; Turchin et al., 2000; Turchin and Hanski, 2001; Turchin and Batzli, 2001). These models generally consider global rodent and mustelid populations and assume population processes to be spatially homogeneous. This contrasts dynamic occupancy models, which are frequently used for empirical investigation of predator-prey interactions (e.g. Magle et al. (2014), Bischof et al. (2014) and study II and III in this thesis). Dynamic occupancy models apply the theoretical metapopulation framework (Hanski, 1998), by analysing spatially explicit patterns in local colonization and extinction. Hence, the link between the findings from theoretical mustelid-rodent models focused on population size and dynamic occupancy models focused on local colonization and extinctions is not clear. In an attempt to close this gap we extended on the basic theoretical mustelid-rodent model from Hanski et al. (2001). The basic model can be defined as follows:

$$\frac{dN}{dt} = rN\left(1 - \frac{N}{K}\right) - \frac{CNP}{D + N} \tag{4.1}$$

$$\frac{dP}{dt} = sP\left(1 - \frac{QP}{N}\right) \tag{4.2}$$

Where the parameters are defined in table 3.

Parameter	Verbal description
N	Rodent population density
P	Mustelid population denisty
r	Rodent intrinsic rate of increase
s	Mustelid intrinsic rate of increase
K	Carrying capacity for rodent
C	The maximum predation rate
D	Mustelid's attack rate
Q	Constant related to carrying capacity of mustelid
B	Number of blocks (i.e. rodent sub-populations)
d	Rate of migration

TABLE 3. Verbal definition of parameters of Eqs 4.1-4.4.

We assumed four separate rodent sub-populations with a small proportion of density-dependent migration between the sub-populations (de Roos et al., 1998). All rodent sub-populations interacted with a global mustelid population. The individual mustelids are assumed to be distributed in the rodent sub-populations according to their relative sub-population size. Further we added seasonality in population growth rates according to Turchin and Hanski (1997). This gave the following model:

$$\frac{dN_i}{dt} = r_i\left(1 - e\ \sin(2\pi t)\right)N_i - \frac{rN_i^2}{K_i} - \frac{CN_i\frac{N_i}{\sum_{i=1}^{B} N_i}P}{D + N_i} - d\left(N_i - \frac{1}{B}\sum_{i=1}^{B} N_i\right) \tag{4.3}$$

$$\frac{dP}{dt} = s\left(1 - e\ \sin(2\pi t)\right)P - \frac{sQP^2}{\bar{N}} \tag{4.4}$$

The model resulted in predator-prey population cycles, similar to what is typically observed in rodents. We further tried to mimic the assumed detection process from the camera traps in COAT small mammals monitoring on the Varanger Peninsula (described in detail in section 3.3). First, we assigned individual rodents and mustelids to the area covered by single camera traps within each sub population (site). Then, individuals present at a site could be detected by the camera trap on a given day according to a species-specific detection probability. We then used this theoretical model to simulate a 10 year dataset from 12 camera trap sites in 4 blocks. This data was analysed by the use of the dynamic occupancy model for interactions species with two spatial scales.

Connecting the two frameworks was challenging. First, we realised that while the mechanistic model produced detection probabilities of individuals, these had to be translated into probabilities of detection of each species. When this was implemented, we then realised that the weekly closure assumption of the dynamic occupancy model required us to switch to a mechanistic model with constant state variables during a single week. When this new feature was again implemented, we were finally able to estimate detection probabilities but block-level colonization and extinction probabilities were not identifiable. Why exactly is still unclear. Site-level probabilities were identifiable, but the signature of predator-prey interactions was almost invisible (e.g. $\epsilon_{A|B}$ was barely under ϵ_A). One difficulty with the differential equations framework is that it rarely translates into extinction at block level, which is nonetheless required for estimating block-level parameters. It is a bit unclear why site-level parameters are so uninformative when fitted on the mechanistic model, but it might well be that local extinction is still too rare and that the continuous state variables N_i and P_i, even when sampled stochastically through multinomial or Poisson variables, have increases that do not quite resemble the colonization process in the statistical, dynamic occupancy model. In other words, the occupancy model resembles more a metapopulation framework than the local population framework of differential equation models. We have considered increasing the quantity of environmental stochasticity to have more frequent colonizations and extinctions, but perhaps a mathematical framework where these happen naturally would be better, like a probabilistic cellular automata (which in some cases can be related to classical differential theory, e.g. Hosseini (2003)). It would, however, be a much larger endeavour to do this in the spatially hierarchical setup described in this thesis.

Conclusions and future perspectives

The work presented in this thesis provides recommendations for maximizing the technical functionality of year-round small mammals camera tunnels on the Arctic tundra. In addition, we have extended state-of-the-art dynamic occupancy models for interacting species to account for the two nested spatial scales applied in the small mammal monitoring of COAT. Together, the temporally highly resolved camera trap data and the novel statistical methods show that mustelids increased rodents extinction probability on a local and a regional spatial scale. Furthermore, we were able to demonstrate a clear habitat dependency in the strength of the mustelid-rodent interaction. Further we have validated the performance of camera trap-based indices to assess abundance dynamics of two common species of rodents in Fennoscandia. We show that camera traps give reliable population estimates given that the right species-specific precautions (e.g. temporal and spatial aggregation) are taken.

Related to the conceptual model centered on rodent population dynamics in COAT, study II and III have directly improved ecological knowledge on the interaction between rodents and their specialist predators (i.e. the mustelids). Furthermore, the methodological framework developed in this thesis have paved the way for future analysis. So, when the time series from the COAT monitoring grow longer, encompass multiple rodent cycles as well as being extended to more tundra habitats, a lot more will be learned about the mustelid-rodent interaction. In addition, both occupancy and abundance of rodents can now be monitored on a fine temporal scale year round. This is important in the context of the conceptual model as it opens the door for more detailed investigations of rodent interactions also with the plant community and the generalist predator community (e.g. avian predators and foxes) as well as addressing abiotic impacts from a changing climate. For all these interactions and potential impacts, seasonal timing is important and previous understanding has been hampered by the low temporal resolution of the rodent state variables (Ims and Fuglei, 2005). Rodents are mainly available to generalist predators during summer, but their numerical response to rodent numbers (e.g. by deciding to breed or not) are likely affected by rodent spring densities (Angerbjörn et al., 1999), which have earlier not been known. Rodent-plant interactions are highly seasonal, where winter herbivory might have different impact on the plants compared to summer herbivory (Ravolainen et al., 2014). Furthermore, climate impacts might be highly seasonal and only detected on a very fine temporal scale (Hallett et al., 2004).

So what is the way forward? A key limitation in the modelling framework applied in this thesis, as in many other occupancy models analysing continuously sampled camera trap data, is the need to discretize the data into arbitrary chosen sampling occasions to account for the detection process. Further, the assumption of closure in the occupancy process during a primary occasion (5 - 7 days in this thesis) are likely especially problematic in highly mobile species like the small mustelids. Continuous time detection models have over the last decades started to emerge in the CMR framework (Chao, 2001; Schofield et al., 2018; Zhang and Bonner, 2020), however only very recently they have been developed for occupancy models (Kellner et al., 2022). If this proves successful it will be a key to take full advantage of the vast amount of wildlife camera data currently generated in continuous time. Continuous time detection models might solve the concerns I raise about the closure assumption and primary and secondary occasions close in time (in section 5.2). Furthermore, continuous time detection models will allow for investigation of drivers of temporally fine-scaled dynamics. This will be important to fully understand the potential impacts of climate change on Arctic small mammals as abrupt climatic events, like e.g. rain-on-snow which are becoming more frequent with anthropogenic climate change (Peeters et al., 2019), are assumed to have considerable impacts on small mammals (Kausrud et al., 2008; Ims et al., 2008; Stien et al., 2012; Cornulier et al., 2013; Fauteux et al., 2021).

High quality biotic data combined with state-of-the-art statistical methods are not by itself enough to investigate the impact of climate effects. Temporally fine-scaled data on relevant abiotic variables are also needed. In study I we show how camera trap images can provide information about some simple abiotic parameters (i.e. presence of snow or water). However, more informative environmental variables (e.g. physical snow properties like snow hardness and depth of the snow layer) that are important to small mammals (Kausrud et al., 2008; Poirier et al., 2021) are generally lacking from remote Arctic tundra sites. This is because direct local scale environmental observations are mostly missing and spatial extrapolation techniques are generally too imprecise. For these reasons, COAT have recently deployed a network of synoptic weather stations, which will supplement the local-scale camera trap temperature and simple abiotic observations. Collaboration with geophysicists will then be needed to combine these two sources of information to provide reliable and ecologically relevant local-scale abiotic state variables that directly affect the small mammal community.

Our empirical investigation of one of the longest standing and most discussed hypothesis about population cycle driving mechanisms in northern rodents — the specialist predation hypothesis — has demonstrated that mustelids impact on rodents are strong enough to increase extinction probability of rodents both on a local and a regional scale. Furthermore, it demonstrates a profound habitat-dependency in the strength of the rodent-mustelid interaction. I hope this reaches the attention of theoreticians. While seasonality already has been included for species-specific growth rates in theoretical mustelid-rodent models (see e.g. Hanski et al. (1993) and Hanski et al. (2001)), it is not clear what consequences season- and habitat-dependency in interaction strength will have for the potential of specialist predation to cause multi annual population cycles in rodents.

Study IV in this thesis has opened the door for camera trap-based counts to be used as an abundance index. This drastically enhances the information in camera trap-based small mammal time series like the one collected by COAT. Statistical models to estimate species interactions while at the same time accounting for imperfect detection exist. However, they are leaning on many of the same assumptions as the occupancy frame work (i.e. closed populations over fixed primary periods) (Dorazio et al., 2015; Roth et al., 2016). Hence, further extensions of abundance model for interaction species should be done to include continuous time detection and nested spatial scales. Furthermore, new studies will be needed to validate the camera trap-based abundance indices for mustelids and lemmings. Attempts to perform similar index-calibration analysis for these species are likely to meet the same constrains as we did, as reliable ground-truthing data is extremely challenging. However, this might be solved by resent advances in statistical frameworks to estimate abundance correct for detection probability from unmarked populations (Gilbert et al., 2021; Palencia et al., 2021) or detection rates (Ait Kaci Azzou et al., 2021). Alternatively abundance models for voles might be combined with occupancy models for mustelids, as we have already showed that the presence of the mustelids affect the extinction probability of rodents. In any case, I am convinced that these model developments combined with the unique camera trap dataset on small mammals collected in COAT will greatly improve the knowledge on the mustelid-rodent interaction, as well as about population cycles of rodents in general.

Long-term multi-dimensional observation programs like COAT, including both rodents, mustelids, environmental factors and other important biotic factors (e.g. plant biomass and breeding density of avian predators) will be key to compare the relative strength of the many factors affecting population dynamics of rodents. At the same time, statistical models tailored to unravel ecological mysteries based on camera trap data will continue to be extended and improved. These developments together will over the next decades revolutionize our understanding of tundra food web dynamics centered around small rodents, and how they will be affected by climate change.

Bibliography

Aars, J. and R. A. Ims (2002). Intrinsic and climatic determinants of population demography: The winter dynamics of tundra voles. *Ecology*, 83, 3449–3456.

Abrams, P. A., R. D. Holt and J. D. Roth (1998). Apparent Competition or Apparent Mutualism? Shared Predation When Populations Cycle. *Ecology*, 79(1), 201–212. ISSN: 00129658, 19399170.

Aho, J. and O. Kalela (1966). The spring migration of 1961 in the Norwegian lemming, Lemmus lemmus (L.), at Kilpisjärvi, Finnish Lapland. *Annales Zoologici Fennici*, 3(1), 53–65. ISSN: 0003455X, 17972450.

Ait Kaci Azzou, S., L. Singer, T. Aebischer, M. Caduff, B. Wolf and D. Wegmann (2021). A sparse observation model to quantify species distributions and their overlap in space and time. *Ecography*, 44(6), 928–940. DOI: `https://doi.org/10.1111/ecog.05411`.

Andreassen, H. P., K. Hertzberg and R. A. Ims (1998). Space-Use Responses to Habitat Fragmentation and Connectivity in the Root Vole Microtus oeconomus. *Ecology*, 79(4), 1223–1235. ISSN: 00129658, 19399170.

Andreassen, H. P., J. Sundell, F. Ecke, S. Halle, M. Haapakoski, H. Henttonen, O. Huitu, J. Jacob, K. Johnsen, E. Koskela, J. J. Luque-Larena, N. Lecomte, H. Leirs, J. Mariën, M. Neby, O. Rätti, T. Sievert, G. R. Singleton, J. van Cann, B. V. Broecke and H. Ylönen (2021). Population cycles and outbreaks of small rodents: ten essential questions we still need to solve. *Oecologia*, 195(3), 601–622. DOI: `10.1007/s00442-020-04810-w`.

Angelstam, P., E. Lindström and P. Widén (1984). Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, 62(2), 199–208. DOI: `10.1007/bf00379014`.

Angerbjörn, A., M. Tannerfeldt and S. Erlinge (1999). Predator–prey relationships: arctic foxes and lemmings. *Journal of Animal Ecology*, 68(1), 34–49. DOI: `https://doi-org.mime.uit.no/10.1046/j.1365-2656.1999.00258.x`.

Angerbjörn, A., M. Tannerfeldt and H. Lundberg (2001). Geographical and temporal patterns of lemming population dynamics in Fennoscandia. *Ecography*, 24(3), 298–308. DOI: `https://doi.org/10.1034/j.1600-0587.2001.240307.x`.

Aunapuu, M. and T. Oksanen (2003). Habitat selection of coexisting competitors: a study of small mustelids in northern Norway. *Evolutionary Ecology*, 17(4), 371–392.

Barraquand, F., S. Louca, K. C. Abbott, C. A. Cobbold, F. Cordoleani, D. L. DeAngelis, B. D. Elderd, J. W. Fox, P. Greenwood, F. M. Hilker, D. L. Murray, C. R. Stieha, R. A. Taylor, K. Vitense, G. S. Wolkowicz and R. C. Tyson (2017). Moving forward in circles: challenges and opportunities in modelling population cycles. *Ecology Letters*, 20(8), 1074–1092. DOI: `https://doi.org/10.1111/ele.12789`.

Begon, M. and C. R. Townsend (2020). *Ecology: from individuals to ecosystems.* John Wiley & Sons.

Bety, J., G. Gauthier, E. Korpimaki and J.-F. Giroux (2002). Shared Predators and Indirect Trophic Interactions: Lemming Cycles and Arctic-Nesting Geese. *Journal of Animal Ecology*, 71(1), 88–98. ISSN: 00218790, 13652656.

Bilodeau, F., A. J. Kenney, B. S. Gilbert, E. Hofer, G. Gauthier, D. G. Reid, D. Berteaux and C. J. Krebs (2013). Evaluation of a Technique to Trap Lemmings Under the Snow. *Arctic*, 66(1), 32–36. ISSN: 00040843.

Bischof, R., H. Ali, M. Kabir, S. Hameed and M. A. Nawaz (2014). Being the underdog: an elusive small carnivore uses space with prey and time without enemies. *Journal of Zoology*, 293(1), 40–48. DOI: `https://doi.org/10.1111/jzo.12100`.

Bjørnstad, O. N., W. Falck and N. C. Stenseth (1995). A geographic gradient in small rodent density fluctuations: a statistical modelling approach. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 262(1364), 127–133.

Bjørnstad, O. N., R. A. Ims and X. Lambin (1999). Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology and Evolution*, 14(11), 427–432. ISSN: 0169-5347. DOI: `https://doi.org/10.1016/S0169-5347(99)01677-8`.

Bondrup-Nielsen, S. and R. A. Ims (1988). Predicting Stable and Cyclic Populations of Clethrionomys. *Oikos*, 52(2), 178. DOI: `10.2307/3565245`.

Bowler, D. E., M. A. J. Kvasnes, H. C. Pedersen, B. K. Sandercock and E. B. Nilsen (2020). Impacts of predator-mediated interactions along a climatic gradient on the population dynamics of an alpine bird. *Proceedings of the Royal Society B: Biological Sciences*, 287(1941), 20202653. DOI: `10.1098/rspb.2020.2653`.

Box, J. E., W. T. Colgan, T. R. Christensen, N. M. Schmidt, M. Lund, F.-J. W. Parmentier, R. Brown, U. S. Bhatt, E. S. Euskirchen, V. E. Romanovsky, J. E. Walsh, J. E. Overland, M. Wang, R. W. Corell, W. N. Meier, B. Wouters, S. Mernild, J. Mård, J. Pawlak and M. S. Olsen (2019). Key indicators of Arctic climate change: 1971–2017. *Environmental Research Letters*, 14(4), 045010. DOI: `10.1088/1748-9326/aafc1b`.

Burton, A. C., E. Neilson, D. Moreira, A. Ladle, R. Steenweg, J. T. Fisher, E. Bayne and S. Boutin (2015). REVIEW: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52(3), 675–685. DOI: `https://doi.org/10.1111/1365-2664.12432`.

Catford, J. A., J. R. Wilson, P. Pyšek, P. E. Hulme and R. P. Duncan (2022). Addressing context dependence in ecology. *Trends in Ecology & Evolution*, 37(2), 158–170. ISSN: 0169-5347. DOI: `https://doi.org/10.1016/j.tree.2021.09.007`.

Chao, A. (2001). An overview of closed capture-recapture models. *Journal of Agricultural, Biological, and Environmental Statistics*, 6(2), 158–175.

Chen, G., M. Kéry, M. Plattner, K. Ma and B. Gardner (2013). Imperfect detection is the rule rather than the exception in plant distribution studies. *Journal of Ecology*, 101(1), 183–191. DOI: `https://doi.org/10.1111/1365-2745.12021`.

Choquenot, D., W. A. Ruscoe and E. Murphy (2001). Colonisation of new areas by stoats: time to establishment and requirements for detection. *New Zealand Journal of Ecology*, 25(1), 83–88. ISSN: 01106465, 11777788.

Clark, J. S. (2005). Why environmental scientists are becoming Bayesians. *Ecology Letters*, 8(1), 2–14. DOI: `https://doi.org/10.1111/j.1461-0248.2004.00702.x`.

Conn, P. B., D. S. Johnson, P. J. Williams, S. R. Melin and M. B. Hooten (2018). A guide to Bayesian model checking for ecologists. *Ecological Monographs*, 88(4), 526–542. DOI: `https://doi.org/10.1002/ecm.1314`.

Cornulier, T., N. G. Yoccoz, V. Bretagnolle, J. E. Brommer, A. Butet, F. Ecke, D. A. Elston, E. Framstad, H. Henttonen, B. Hörnfeldt, O. Huitu, C. Imholt, R. A. Ims, J. Jacob, B. Jędrzejewska, A. Millon, S. J. Petty, H. Pietiäinen, E. Tkadlec, K. Zub and X. Lambin (2013). Europe-Wide Dampening of

Population Cycles in Keystone Herbivores. *Science*, 340(6128), 63–66. DOI: `10.1126/science.1228992`.

Davis, A. J., R. McCreary, J. Psiropoulos, G. Brennan, T. Cox, A. Partin and K. M. Pepin (2017). Quantifying site-level usage and certainty of absence for an invasive species through occupancy analysis of camera-trap data. *Biological Invasions*, 20(4), 877–890. DOI: `10.1007/s10530-017-1579-x`.

de Valpine, P., D. Turek, C. Paciorek, C. Anderson-Bergman, D. Temple Lang and R. Bodik (2017). Programming with models: writing statistical algorithms for general model structures with NIMBLE. *Journal of Computational and Graphical Statistics*, 26, 403–417. DOI: `10.1080/10618600.2016.1172487`.

De Roos, A., E. McCauley and W. Wilson (1998). Pattern formation and the spatial scale of interaction between predators and their prey. *Theoretical Population Biology*, 53(2), 108–130.

Diffenbaugh, N. S., D. Singh, J. S. Mankin, D. E. Horton, D. L. Swain, D. Touma, A. Charland, Y. Liu, M. Haugen, M. Tsiang and B. Rajaratnam (2017). Quantifying the influence of global warming on unprecedented extreme climate events. *Proceedings of the National Academy of Sciences*, 114(19), 4881–4886. ISSN: 0027-8424. DOI: `10.1073/pnas.1618082114`.

Dorazio, R. M. (2015). Bayesian data analysis in population ecology: motivations, methods, and benefits. *Population Ecology*, 58(1), 31–44. DOI: `10.1007/s10144-015-0503-4`.

Dorazio, R. M., E. F. Connor and R. A. Askins (2015). Estimating the Effects of Habitat and Biological Interactions in an Avian Community. *PLOS ONE*, 10(8), 1–16. DOI: `10.1371/journal.pone.0135987`.

Ehrich, D., N. M. Schmidt, G. Gauthier, R. Alisauskas, A. Angerbjörn, K. Clark, F. Ecke, N. E. Eide, E. Framstad, J. Frandsen, A. Franke, O. Gilg, M.-A. Giroux, H. Henttonen, B. Hörnfeldt, R. A. Ims, G. D. Kataev, S. P. Kharitonov, S. T. Killengreen, C. J. Krebs, R. B. Lanctot, N. Lecomte, I. E. Menyushina, D. W. Morris, G. Morrisson, L. Oksanen, T. Oksanen, J. Olofsson, I. G. Pokrovsky, I. Y. Popov, D. Reid, J. D. Roth, S. T. Saalfeld, G. Samelius, B. Sittler, S. M. Sleptsov, P. A. Smith, A. A. Sokolov, N. A. Sokolova, M. Y. Soloviev and D. V. Solovyeva (2020). Documenting lemming population change in the Arctic: Can we detect trends? *Ambio*, 49(3), 786–800. DOI: `10.1007/s13280-019-01198-7`.

Ekerholm, P., L. Oksanen and T. Oksanen (2001). Long-Term Dynamics of Voles and Lemmings at the Timberline and above the Willow Limit as a Test of Hypotheses on Trophic Interactions. *Ecography*, 24(5), 555–568. ISSN: 09067590, 16000587.

Elton, C. S. (1924). Periodic Fluctuations in the Numbers of Animals: Their Causes and Effects. *Journal of Experimental Biology*, 2(1), 119–163. ISSN: 0022-0949. DOI: `10.1242/jeb.2.1.119`.

Fauteux, D., G. Gauthier, M. J. Mazerolle, N. Coallier, J. Bêty and D. Berteaux (2018). Evaluation of invasive and non-invasive methods to monitor rodent abundance in the Arctic. *Ecosphere*, 9(2), e02124. DOI: `https://doi.org/10.1002/ecs2.2124`.

Fauteux, D., A. Stien, N. G. Yoccoz, E. Fuglei and R. A. Ims (2021). Climate variability and density-dependent population dynamics: Lessons from a simple High Arctic ecosystem. *Proceedings of the National Academy of Sciences*, 118(37). ISSN: 0027-8424. DOI: `10.1073/pnas.2106635118`.

Fidino, M., J. L. Simonis and S. B. Magle (2019). A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species. *Methods in Ecology and Evolution*, 10(2), 233–244. DOI: `https://doi.org/10.1111/2041-210X.13117`.

Gilbert, N. A., J. D. J. Clare, J. L. Stenglein and B. Zuckerberg (2021). Abundance estimation of unmarked animals based on camera-trap data. *Conservation biology : the journal of the Society for Conservation Biology*, 35(1), 88–100. ISSN: 0888-8892. DOI: `10.1111/cobi.13517`.

Gilg, O., I. Hanski and B. Sittler (2003). Cyclic Dynamics in a Simple Vertebrate Predator-Prey Community. *Science*, 302(5646), 866–868. DOI: `10.1126/science.1087509`.

Gilg, O., B. Sittler and I. Hanski (2009). Climate change and cyclic predator–prey population dynamics in the high Arctic. *Global Change Biology*, 15(11), 2634–2652. DOI: `https://doi.org/10.1111/j.1365-2486.2009.01927.x`.

Gilg, O., B. Sittler, B. Sabard, A. Hurstel, R. Sané, P. Delattre and I. Hanski (2006). Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos*, 113(2), 193–216. DOI: `https://doi.org/10.1111/j.2006.0030-1299.14125.x`.

Gilg, O. and N. G. Yoccoz (2010). Explaining Bird Migration. *Science*, 327(5963), 276–277. DOI: `10.1126/science.1184964`.

Gimenez, O., J.-D. Lebreton, R. Choquet and R. Pradel (2018). R2ucare: An r package to perform goodness-of-fit tests for capture–recapture models.

Methods in Ecology and Evolution, 9(7), 1749–1754. DOI: `https://doi.org/10.1111/2041-210X.13014`.

Gopalaswamy, A. M., M. Delampady, K. U. Karanth, N. S. Kumar and D. W. Macdonald (2015). An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods in Ecology and Evolution*, 6(9), 1055–1066. DOI: `https://doi.org/10.1111/2041-210X.12351`.

Graham, I. M. (2002). Estimating weasel Mustela nivalis abundance from tunnel tracking indices at fluctuating field vole Microtus agrestis density. *Wildlife Biology*, 8(4), 279–287. DOI: `10.2981/wlb.2002.025`.

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography*, 40(2), 281–295. DOI: `https://doi.org/10.1111/ecog.02445`.

Haila, Y. and O. Järvinen (1982). The role of theoretical concepts in understanding the ecological theatre: a case study on island biogeography. *Conceptual issues in ecology*. Ed. by E. Saarinen. Springer, pp. 261–278.

Hallett, T. B., T. Coulson, J. G. Pilkington, T. H. Clutton-Brock, J. M. Pemberton and B. T. Grenfell (2004). Why large-scale climate indices seem to predict ecological processes better than local weather. *Nature*, 430(6995), 71–75. DOI: `10.1038/nature02708`.

Hansen, B. B., V. Grøtan, R. Aanes, B.-E. Sæther, A. Stien, E. Fuglei, R. A. Ims, N. G. Yoccoz and Å. Ø. Pedersen (2013). Climate Events Synchronize the Dynamics of a Resident Vertebrate Community in the High Arctic. *Science*, 339(6117), 313–315. DOI: `10.1126/science.1226766`.

Hansen, T. F., N. C. Stenseth and H. Henttonen (1999). Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. *The American Naturalist*, 154(2), 129–139.

Hanski, I. (1998). Metapopulation dynamics. *Nature*, 396(6706), 41–49.

Hanski, I., H. Henttonen and L. Hansson (1994). Temporal Variability and Geographical Patterns in the Population Density of Microtine Rodents: A Reply to Xia and Boonstra. *The American Naturalist*, 144(2), 329–342. ISSN: 00030147, 15375323.

Hanski, I., H. Henttonen, E. Korpimäki, L. Oksanen and P. Turchin (2001). Small-rodent dynamics and predation. *Ecology*, 82(6), 1505–1520. DOI: `https://doi.org/10.1890/0012-9658`.

Hanski, I., P. Turchin, E. Korpimäki and H. Henttonen (1993). Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, 364(6434), 232–235.

Hansson, L. and H. Henttonen (1988). Rodent dynamics as community processes. *Trends in Ecology & Evolution*, 3(8), 195–200. DOI: `10.1016/0169-5347(88)90006-7`.

Hellstedt, P. and H. Henttonen (2006). Home range, habitat choice and activity of stoats (Mustela erminea) in a subarctic area. *Journal of Zoology*, 269(2), 205–212. DOI: `https://doi.org/10.1111/j.1469-7998.2006.00072.x`.

Hellström, P., J. Nyström and A. Angerbjörn (2014). Functional responses of the rough-legged buzzard in a multi-prey system. *Oecologia*, 174(4), 1241–1254. DOI: `10.1007/s00442-013-2866-6`.

Henden, J.-A., R. A. Ims and N. G. Yoccoz (2009). Nonstationary spatio-temporal small rodent dynamics: evidence from long-term Norwegian fox bounty data. *Journal of Animal Ecology*, 78(3), 636–645. DOI: `https://doi.org/10.1111/j.1365-2656.2008.01510.x`.

Henden, J.-A., R. A. Ims, N. G. Yoccoz, R. Sørensen and S. T. Killengreen (2011). Population dynamics of tundra voles in relation to configuration of willow thickets in southern arctic tundra. *Polar Biology*, 34(4), 533–540. DOI: `10.1007/s00300-010-0908-7`.

Hines, J. E., J. D. Nichols, J. A. Royle, D. I. MacKenzie, A. M. Gopalaswamy, N. S. Kumar and K. U. Karanth (2010). Tigers on trails: occupancy modeling for cluster sampling. *Ecological Applications*, 20(5), 1456–1466. DOI: `https://doi.org/10.1890/09-0321.1`.

Hörnfeldt, B., T. Hipkiss and U. Eklund (2005). Fading out of vole and predator cycles? *Proceedings of the Royal Society B: Biological Sciences*, 272(1576), 2045–2049. DOI: `10.1098/rspb.2005.3141`.

Hosseini, P. R. (2003). How Localized Consumption Stabilizes Predator-Prey Systems with Finite Frequency of Mixing. *The American Naturalist*, 161(4), 567–585. DOI: `10.1086/368293`.

Ims, R., U. Jepsen J., A. Stien and N. G. Yoccoz (2013). *Science plan for COAT: Climate-ecological Observatory for Arctic Tundra.* Fram Centre Report Series 1. Fram Centre, Norway. ISBN: 978-82-999253-0-3.

Ims, R. A. and H. P. Andreassen (2000). Spatial synchronization of vole population dynamics by predatory birds. *Nature*, 408(6809), 194–196. DOI: `10.1038/35041562`.

Ims, R. A. and E. Fuglei (2005). Trophic Interaction Cycles in Tundra Ecosystems and the Impact of Climate Change. *BioScience*, 55(4), 311–322. ISSN: 0006-3568. DOI: `10.1641/0006-3568`.

Ims, R. A., J.-A. Henden and S. T. Killengreen (2008). Collapsing population cycles. *Trends in Ecology & Evolution*, 23(2), 79–86. ISSN: 0169-5347. DOI: `https://doi.org/10.1016/j.tree.2007.10.010`.

Ims, R. A. (1987). Responses in Spatial Organization and Behaviour to Manipulations of the Food Resource in the Vole Clethrionomys rufocanus. *Journal of Animal Ecology*, 56(2), 585–596. ISSN: 00218790, 13652656.

Inchausti, P. and L. R. Ginzburg (1998). Small mammals cycles in northern Europe: patterns and evidence for a maternal effect hypothesis. *Journal of Animal Ecology*, 67(2), 180–194. DOI: `https://doi.org/10.1046/j.1365-2656.1998.00189.x`.

Jedrzejewski, W., B. Jedrzejewska and L. Szymura (1995). Weasel Population Response, Home Range, and Predation on Rodents in a Deciduous Forest in Poland. *Ecology*, 76(1), 179–195. DOI: `10.2307/1940640`.

Johnson, D. S., P. B. Conn, M. B. Hooten, J. C. Ray and B. A. Pond (2013). Spatial occupancy models for large data sets. *Ecology*, 94(4), 801–808. DOI: `https://doi.org/10.1890/12-0564.1`.

Kass, J. M., M. W. Tingley, T. Tetsuya and F. Koike (2020). Co-occurrence of invasive and native carnivorans affects occupancy patterns across environmental gradients. *Biological Invasions*, 22(7), 2251–2266. DOI: `10.1007/s10530-020-02254-0`.

Kausrud, K. L., A. Mysterud, H. Steen, J. O. Vik, E. Østbye, B. Cazelles, E. Framstad, A. M. Eikeset, I. Mysterud, T. Solhøy and N. C. Stenseth (2008). Linking climate change to lemming cycles. *Nature*, 456(7218), 93–97. DOI: `10.1038/nature07442`.

Kellner, K. F., A. W. Parsons, R. Kays, J. J. Millspaugh and C. T. Rota (2022). A Two-Species Occupancy Model with a Continuous-Time Detection Process Reveals Spatial and Temporal Interactions. *Journal of Agricultural, Biological and Environmental Statistics*. DOI: `10.1007/s13253-021-00482-y`.

Kendall, Prendergast and Bjørnstad (1998). The macroecology of population dynamics: taxonomic and biogeographic patterns in population cycles. *Ecology Letters*, 1(3), 160–164. DOI: `https://doi.org/10.1046/j.1461-0248.1998.00037.x`.

Kendall, W. L., J. E. Hines, J. D. Nichols and E. H. C. Grant (2013). Relaxing the closure assumption in occupancy models: staggered arrival and departure times. *Ecology*, 94(3), 610–617. DOI: `https://doi.org/10.1890/12-1720.1`.

Kéry, M. and J. A. Royle (2020). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 2: Dynamic and Advanced Models.* Academic Press.

King, C. M. and R. A. Powell (2006). *The natural history of weasels and stoats: ecology, behavior, and management.* Oxford University Press.

King, C. M. (1975). The Home Range of the Weasel (Mustela nivalis) in an English Woodland. *Journal of Animal Ecology*, 44(2), 639–668. ISSN: 00218790, 13652656.

King, C. M., R. M. McDonald, R. D. Martin and T. Dennis (2009). Why is eradication of invasive mustelids so difficult? *Biological Conservation*, 142(4), 806–816. ISSN: 0006-3207. DOI: `https://doi.org/10.1016/j.biocon.2008.12.010`.

Kleiven, E. F., J.-A. Henden, R. A. Ims and N. G. Yoccoz (2018). Seasonal difference in temporal transferability of an ecological model: near-term predictions of lemming outbreak abundances. *Scientific Reports*, 8(1). DOI: `10.1038/s41598-018-33443-6`.

Koponen, T. (1970). Age structure in sedentary and migratory populations of the Norwegian lemming, Lemmus lemmus (L.), at Kilpisjärvi in 1960. *Annales Zoologici Fennici*, 7(2), 141–187. ISSN: 0003455X, 17972450.

Korpela, K., M. Delgado, H. Henttonen, E. Korpimäki, E. Koskela, O. Ovaskainen, H. Pietiäinen, J. Sundell, N. G. Yoccoz and O. Huitu (2013). Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. *Global Change Biology*, 19(3), 697–710. DOI: `10.1111/gcb.12099`.

Korpimäki, E. (1986). Predation Causing Synchronous Decline Phases in Microtine and Shrew Populations in Western Finland. *Oikos*, 46(1), 124. DOI: `10.2307/3565390`.

Korpimäki, E. and K. Norrdahl (1989a). Avian and mammalian predators of shrews in Europe: regional differences, between-year and seasonal variation, and mortality due to predation. *Annales Zoologici Fennici*, 26(4), 389–400. ISSN: 0003455X, 17972450.

Korpimäki, E. and K. Norrdahl (1989b). Avian Predation on Mustelids in Europe 1: Occurrence and Effects on Body Size Variation and Life Traits. *Oikos*, 55(2), 205–215. ISSN: 00301299, 16000706.

Korpimäki, E., K. Norrdahl and T. Rinta-Jaskari (1991). Responses of stoats and least weasels to fluctuating food abundances: is the low phase of the vole cycle due to mustelid predation? *Oecologia*, 88(4), 552–561.

Korslund, L. and H. Steen (2006). Small rodent winter survival: snow conditions limit access to food resources. *Journal of Animal Ecology*, 75(1), 156–166. DOI: `https://doi.org/10.1111/j.1365-2656.2005.01031.x`.

Krebs, C. J. (2013). *Population fluctuations in rodents.* University of Chicago Press.

Krebs, C. J. and J. H. Myers (1974). Population Cycles in Small Mammals. Ed. by A. MacFadyen. Vol. 8. Advances in Ecological Research. Academic Press, pp. 267–399. DOI: `https://doi.org/10.1016/S0065-2504(08)60280-9`.

Lambin, X., S. J. Petty and J. L. Mackinnon (2000). Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology*, 69(1), 106–119. DOI: `https://doi.org/10.1046/j.1365-2656.2000.00380.x`.

Latif, Q. S., M. M. Ellis and C. L. Amundson (2016). A broader definition of occupancy: Comment on Hayes and Monfils. *The Journal of Wildlife Management*, 80(2), 192–194. DOI: `https://doi.org/10.1002/jwmg.1022`.

Lele, S. R., E. H. Merrill, J. Keim and M. S. Boyce (2013). Selection, use, choice and occupancy: clarifying concepts in resource selection studies. *Journal of Animal Ecology*, 82(6), 1183–1191. DOI: `https://doi.org/10.1111/1365-2656.12141`.

Lemoine, N. P. (2019). Moving beyond noninformative priors: why and how to choose weakly informative priors in Bayesian analyses. *Oikos*, 128(7), 912–928. DOI: `https://doi.org/10.1111/oik.05985`.

Lotka, A. J. (1925). *Elements of physical biology.* Williams & Wilkins.

MacKenzie, D. I., J. D. Nichols, J. A. Royle, K. H. Pollock, L. L. Bailey and J. E. Hines (2017). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence.* Elsevier.

Mackenzie, D. I. (2005). Was it there? Dealing with imperfect detection for species presence/absence data. *Australian & New Zealand Journal of Statistics*, 47(1), 65–74. DOI: `https://doi.org/10.1111/j.1467-842X.2005.00372.x`.

MacKenzie, D. I., J. D. Nichols, J. E. Hines, M. G. Knutson and A. B. Franklin (2003). Estimating site occupancy, colonization, and local extinction when species is detected imperfectly. *Ecology*, 84(8), 2200–2207. DOI: `https://doi.org/10.1890/02-3090`.

MacKenzie, D. I., J. D. Nichols, G. B. Lachman, S. Droege, J. Andrew Royle and C. A. Langtimm (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8), 2248–2255. DOI: `https://doi.org/10.1890/0012-9658`.

Magle, S. B., L. S. Simoni, E. W. Lehrer and J. S. Brown (2014). Urban predator–prey association: coyote and deer distributions in the Chicago metropolitan area. *Urban Ecosystems*, 17(4), 875–891. DOI: `10.1007/s11252-014-0389-5`.

Magnusson, M., A. Bergsten, F. Ecke, Ö. Bodin, L. Bodin and B. Hörnfeldt (2013). Predicting grey-sided vole occurrence in northern Sweden at multiple spatial scales. *Ecology and Evolution*, 3(13), 4365–4376. DOI: `https://doi.org/10.1002/ece3.827`.

Martínez-Padilla, J., S. M. Redpath, M. Zeineddine and F. Mougeot (2014). Insights into population ecology from long-term studies of red grouse Lagopus lagopus scoticus. *Journal of Animal Ecology*, 83(1), 85–98. DOI: `https://doi.org/10.1111/1365-2656.12098`.

McKinnon, L., P. Smith, E. Nol, J. Martin, F. Doyle, K. Abraham, H. Gilchrist, R. Morrison and J. Bêty (2010). Lower predation risk for migratory birds at high latitudes. *Science*, 327(5963), 326–327.

McKinnon, L., D. Berteaux and J. Bêty (2014). Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. *The Auk*, 131(4), 619–628. DOI: `10.1642/auk-13-154.1`.

Moran, P. (1953). The statistical analysis of the Canadian Lynx cycle. *Australian Journal of Zoology*, 1(3), 291. DOI: `10.1071/zo9530291`.

Mougeot, F., X. Lambin, R. Rodríguez-Pastor, J. Romairone and J.-J. Luque-Larena (2019). Numerical response of a mammalian specialist predator to multiple prey dynamics in Mediterranean farmlands. *Ecology*, 100(9), e02776. DOI: `https://doi.org/10.1002/ecy.2776`.

Myers, J. H. (2018). Population cycles: generalities, exceptions and remaining mysteries. *Proceedings of the Royal Society B: Biological Sciences*, 285(1875), 20172841. DOI: `10.1098/rspb.2017.2841`.

Myers, J. H. and J. S. Cory (2013). Population Cycles in Forest Lepidoptera Revisited. *Annual Review of Ecology, Evolution, and Systematics*, 44(1), 565–592. DOI: `10.1146/annurev-ecolsys-110512-135858`.

Northrup, J. M. and B. D. Gerber (2018). A comment on priors for Bayesian occupancy models. *PLOS ONE*, 13(2), 1–13. DOI: `10.1371/journal.pone.0192819`.

Oksanen, L. and T. Oksanen (1992). Long-term microtine dynamics in north Fennoscandian tundra: the vole cycle and the lemming chaos. *Ecography*, 15(2), 226–236.

Oksanen, T., L. Oksanen and M. Norberg (1992). Habitat Use of Small Mustelids in North Fennoscandian Tundra: A Test of the Hypothesis of Patchy Exploitation Ecosystems. *Ecography*, 15(2), 237–244. ISSN: 09067590, 16000587.

Oli, M. K. (2019). Population cycles in voles and lemmings: state of the science and future directions. *Mammal Review*, 49(3), 226–239. DOI: `https://doi.org/10.1111/mam.12156`.

Olofsson, J., H. Tømmervik and T. V. Callaghan (2012). Vole and lemming activity observed from space. *Nature Climate Change*, 2(12), 880–883. DOI: `10.1038/nclimate1537`.

Otto, C. R. V., L. L. Bailey and G. J. Roloff (2013). Improving species occupancy estimation when sampling violates the closure assumption. *Ecography*, 36(12), 1299–1309. DOI: `https://doi.org/10.1111/j.1600-0587.2013.00137.x`.

Palencia, P., J. M. Rowcliffe, J. Vicente and P. Acevedo (2021). Assessing the camera trap methodologies used to estimate density of unmarked populations. *Journal of Applied Ecology*, 58(8), 1583–1592. DOI: `https://doi.org/10.1111/1365-2664.13913`.

Peeters, B., Å. Ø. Pedersen, L. E. Loe, K. Isaksen, V. Veiberg, A. Stien, J. Kohler, J.-C. Gallet, R. Aanes and B. B. Hansen (2019). Spatiotemporal patterns of rain-on-snow and basal ice in high Arctic Svalbard: detection of a climate-cryosphere regime shift. *Environmental Research Letters*, 14(1), 015002. DOI: `10.1088/1748-9326/aaefb3`.

Plummer, M. (2003). JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. *Proceedings of the 3rd international workshop on distributed statistical computing.* Vol. 124. Vienna, Austria., pp. 1–10.

Poirier, M., D. Fauteux, G. Gauthier, F. Domine and J.-F. Lamarre (2021). Snow hardness impacts intranivean locomotion of arctic small mammals. *Ecosphere*, 12(11), e03835. DOI: `https://doi.org/10.1002/ecs2.3835`.

Post, E., M. C. Forchhammer, M. S. Bret-Harte, T. V. Callaghan, T. R. Christensen, B. Elberling, A. D. Fox, O. Gilg, D. S. Hik, T. T. Høye, R. A. Ims, E. Jeppesen, D. R. Klein, J. Madsen, A. D. McGuire, S. Rysgaard, D. E.

Schindler, I. Stirling, M. P. Tamstorf, N. J. Tyler, R. van der Wal, J. Welker, P. A. Wookey, N. M. Schmidt and P. Aastrup (2009). Ecological Dynamics Across the Arctic Associated with Recent Climate Change. *Science*, 325(5946), 1355–1358. DOI: `10.1126/science.1173113`.

Powell, R. A. and G. Proulx (2003). Trapping and Marking Terrestrial Mammals for Research: Integrating Ethics, Performance Criteria, Techniques, and Common Sense. *ILAR Journal*, 44(4), 259–276. DOI: `10.1093/ilar.44.4.259`.

Pusenkova, A., M. Poirier, D. Kalhor, T. Galstian, G. Gauthier and X. Maldague (2021). Optical design challenges of subnivean camera trapping under extreme Arctic conditions. *Arctic Science*, 1–16. DOI: `10.1139/as-2021-0012`.

Ravolainen, V. T., K. A. Bråthen, N. G. Yoccoz, J. K. Nguyen and R. A. Ims (2014). Complementary impacts of small rodents and semi-domesticated ungulates limit tall shrub expansion in the tundra. *Journal of Applied Ecology*, 51(1), 234–241. DOI: `https://doi.org/10.1111/1365-2664.12180`.

Richmond, O. M. W., J. E. Hines and S. R. Beissinger (2010). Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecological Applications*, 20(7), 2036–2046. DOI: `https://doi.org/10.1890/09-0470.1`.

Ridout, M. S. and M. Linkie (2009). Estimating overlap of daily activity patterns from camera trap data. *Journal of Agricultural, Biological, and Environmental Statistics*, 14(3), 322–337. DOI: `10.1198/jabes.2009.08038`.

Rota, C. T., M. A. R. Ferreira, R. W. Kays, T. D. Forrester, E. L. Kalies, W. J. McShea, A. W. Parsons and J. J. Millspaugh (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7(10), 1164–1173. DOI: `https://doi.org/10.1111/2041-210X.12587`.

Rota, C. T., R. J. Fletcher Jr, R. M. Dorazio and M. G. Betts (2009). Occupancy estimation and the closure assumption. *Journal of Applied Ecology*, 46(6), 1173–1181. DOI: `https://doi.org/10.1111/j.1365-2664.2009.01734.x`.

Roth, T., C. Bühler and V. Amrhein (2016). Estimating Effects of Species Interactions on Populations of Endangered Species. *The American Naturalist*, 187(4). PMID: 27028074, 457–467. DOI: `10.1086/685095`.

Rowcliffe, J. M. and C. Carbone (2008). Surveys using camera traps: are we looking to a brighter future? *Animal Conservation*, 11(3), 185–186. DOI: `https://doi.org/10.1111/j.1469-1795.2008.00180.x`.

Royle, J. A. and M. Kéry (2007). A Bayesian state-space formulation of dynamic occupancy models. *Ecology*, 88(7), 1813–1823.

Royle, J. A. (2006). Site Occupancy Models with Heterogeneous Detection Probabilities. *Biometrics*, 62(1), 97–102. DOI: `https://doi.org/10.1111/j.1541-0420.2005.00439.x`.

Schofield, M. R., R. J. Barker and N. Gelling (2018). Continuous-time capture–recapture in closed populations. *Biometrics*, 74(2), 626–635. DOI: `https://doi.org/10.1111/biom.12763`.

Seaman, J. W. and J. D. Stamey (2012). Hidden Dangers of Specifying Noninformative Priors. *The American Statistician*, 66(2), 77–84. ISSN: 00031305.

Semb-Johansson, A., R. Wiger and C. E. Engh (1979). Dynamics of Freely Growing, Confined Populations of the Norwegian Lemming Lemmus lemmus. *Oikos*, 33(2), 246. DOI: `10.2307/3544001`.

Serreze, M. C. and R. G. Barry (2011). Processes and impacts of Arctic amplification: A research synthesis. *Global and Planetary Change*, 77(1), 85–96. ISSN: 0921-8181. DOI: `https://doi.org/10.1016/j.gloplacha.2011.03.004`.

Sih, A. (1987). Prey refuges and predator-prey stability. *Theoretical Population Biology*, 31(1), 1–12.

Sittler, B. (1995). Response of stoats (Mustela erminea) to a fluctuating lemming (Dicrostonyx groenlandicus) population in North East Greenland: preliminary results from a long-term study. *Annales Zoologici Fennici*, 32(1), 79–92. ISSN: 0003455X, 17972450.

Soininen, E. M., J.-A. Henden, V. T. Ravolainen, N. G. Yoccoz, K. A. Bråthen, S. T. Killengreen and R. A. Ims (2018). Transferability of biotic interactions: Temporal consistency of arctic plant–rodent relationships is poor. *Ecology and Evolution*, 8(19), 9697–9711. DOI: `https://doi.org/10.1002/ece3.4399`.

Soininen, E. M., I. Jensvoll, S. T. Killengreen and R. A. Ims (2015). Under the snow: a new camera trap opens the white box of subnivean ecology. *Remote Sensing in Ecology and Conservation*, 1(1), 29–38. DOI: `https://doi.org/10.1002/rse2.2`.

Soininen, E. M., V. T. Ravolainen, K. A. Bråthen, N. G. Yoccoz, L. Gielly and R. A. Ims (2013). Arctic Small Rodents Have Diverse Diets and Flexible Food Selection. *PLoS ONE*, 8(6). Ed. by A. J. Munn, e68128. DOI: `10.1371/journal.pone.0068128`.

Soininen, E. M., L. Zinger, L. Gielly, N. G. Yoccoz, J.-A. Henden and R. A. Ims (2017). Not only mosses: lemming winter diets as described by DNA metabarcoding. *Polar Biology*, 40(10), 2097–2103. DOI: `10.1007/s00300-017-2114-3`.

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, 56(4), 740–749. DOI: `https://doi.org/10.1111/aje.12557`.

Specht, H. M., H. T. Reich, F. Iannarilli, M. R. Edwards, S. P. Stapleton, M. D. Weegman, M. K. Johnson, B. J. Yohannes and T. W. Arnold (2017). Occupancy surveys with conditional replicates: An alternative sampling design for rare species. *Methods in Ecology and Evolution*, 8(12), 1725–1734. DOI: `https://doi.org/10.1111/2041-210X.12842`.

Stan Development Team (2021). *Stan Modeling Language Users Guide and Reference Manual, Version 2.29.0.*

Steen, H., R. A. Ims and G. A. Sonerud (1996). Spatial and Temporal Patterns of Small-Rodent Population Dynamics at a Regional Scale. *Ecology*, 77(8), 2365–2372. DOI: `https://doi.org/10.2307/2265738`.

Stenseth, N. C., H. Viljugrein, T. Saitoh, T. F. Hansen, M. O. Kittilsen, E. Bølviken and F. Glöckner (2003). Seasonality, density dependence, and population cycles in Hokkaido voles. *Proceedings of the National Academy of Sciences*, 100(20), 11478–11483.

Stenseth, N. C. (1999). Population Cycles in Voles and Lemmings: Density Dependence and Phase Dependence in a Stochastic World. *Oikos*, 87(3), 427–461. ISSN: 00301299, 16000706.

Stien, A., R. A. Ims, S. D. Albon, E. Fuglei, R. J. Irvine, E. Ropstad, O. Halvorsen, R. Langvatn, L. E. Loe, V. Veiberg and N. G. Yoccoz (2012). Congruent responses to weather variability in high arctic herbivores. *Biology Letters*, 8(6), 1002–1005. DOI: `10.1098/rsbl.2012.0764`.

Sundell, J. (2003). Reproduction of the least weasel in captivity: basic observations and the influence of food availability. *Acta Theriologica*, 48(1), 59–72. DOI: `10.1007/bf03194266`.

Tast, J. (1966). The root vole, Microtus oeconomus (Pallas), as an inhabitant of seasonally flooded land. *Annales Zoologici Fennici*. Vol. 3. 3. JSTOR, pp. 127–171.

Therrien, J.-F., G. Gauthier, E. Korpimäki and J. Bêty (2014). Predation pressure by avian predators suggests summer limitation of small-mammal populations in the Canadian Arctic. *Ecology*, 95(1), 56–67. DOI: `https://doi.org/10.1890/13-0458.1`.

Tingley, M. W., A. N. Stillman, R. L. Wilkerson, C. A. Howell, S. C. Sawyer and R. B. Siegel (2018). Cross-scale occupancy dynamics of a postfire specialist in response to variation across a fire regime. *Journal of Animal Ecology*, 87(5), 1484–1496. DOI: `10.1111/1365-2656.12851`.

Turchin, P., L. Oksanen, P. Ekerholm, T. Oksanen and H. Henttonen (2000). Are lemmings prey or predators? *Nature*, 405(6786), 562–565. DOI: `10.1038/35014595`.

Turchin, P. and G. O. Batzli (2001). Availability of food and the population dynamics of arvicoline rodents. *Ecology*, 82(6), 1521–1534. DOI: `https://doi.org/10.1890/0012-9658(2001)082[1521:AOFATP]2.0.CO;2`.

Turchin, P. and I. Hanski (1997). An Empirically Based Model for Latitudinal Gradient in Vole Population Dynamics. *The American Naturalist*, 149(5). PMID: 18811252, 842–874. DOI: `10.1086/286027`.

— (2001). Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecology Letters*, 4(3), 267–276. DOI: `https://doi.org/10.1046/j.1461-0248.2001.00204.x`.

Tyre, A. J., B. Tenhumberg, S. A. Field, D. Niejalke, K. Parris and H. P. Possingham (2003). Improving precision and reducing bias in biological surveys: estimating false-negative error rates. *Ecological Applications*, 13(6), 1790–1801.

Viitala, J. (1977). Social organization in cyclic subarctic populations of the voles Clethrionomys rufocanus (Sund.) and Microtus agrestis (L.) *Annales Zoologici Fennici*, 14(2), 53–93. ISSN: 0003455X, 17972450.

Vindstad, O. P. L., J. U. Jepsen, M. Klinghardt, M. Ek and R. A. Ims (2017). Salvage logging of mountain birch after geometrid outbreaks: Ecological context determines management outcomes. *Forest Ecology and Management*, 405, 81–91. ISSN: 0378-1127. DOI: `https://doi.org/10.1016/j.foreco.2017.09.027`.

Volterra, V. (1926). Fluctuations in the Abundance of a Species considered Mathematically1. *Nature*, 118(2972), 558–560. DOI: `10.1038/118558a0`.

Waddle, J. H., R. M. Dorazio, S. C. Walls, K. G. Rice, J. Beauchamp, M. J. Schuman and F. J. Mazzotti (2010). A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications*, 20(5), 1467–1475. DOI: `https://doi.org/10.1890/09-0850.1`.

Wegge, P. and J. Rolstad (2018). Cyclic small rodents in boreal forests and the effects of even-aged forest management: Patterns and predictions from a long-term study in southeastern Norway. *Forest Ecology and Management*, 422, 79–86. ISSN: 0378-1127. DOI: `https://doi.org/10.1016/j.foreco.2018.04.011`.

Wilson, D. J., C. J. Krebs and T. Sinclair (1999). Limitation of Collared Lemming Populations during a Population Cycle. *Oikos*, 87(2), 382–398. ISSN: 00301299, 16000706.

Xia, X. and R. Boonstra (1992). Measuring temporal variability of population density: a critique. *The American Naturalist*, 140(5), 883–892.

Yoccoz, N. G., J. D. Nichols and T. Boulinier (2001). Monitoring of biological diversity in space and time. *Trends in Ecology & Evolution*, 16(8), 446–453. ISSN: 0169-5347. DOI: `https://doi.org/10.1016/S0169-5347(01)02205-4`.

Zhang, W. and S. J. Bonner (2020). On continuous-time capture-recapture in closed populations. *Biometrics*, 76(3), 1028–1033. DOI: `10.1111/biom.13185`.

Paper I

Using subnivean camera traps to study Arctic small mammal community dynamics during winter,

Artic Science, 1–7, doi.org/10.1139/as-2021-0006.

Canadian Science Publishing

ARTICLE

Using subnivean camera traps to study Arctic small mammal community dynamics during winter

Jonas P. Mölle, Eivind F. Kleiven, Rolf A. Ims, and Eeva M. Soininen

Abstract: Small rodents are a key indicator to understand the effect of rapidly changing winter climate on Arctic tundra ecosystems. However, monitoring rodent populations through the long Arctic winter by means of conventional traps has, until now, been hampered by snow cover and harsh ambient conditions. Here, we conduct the first extensive assessment of the utility of a newly developed camera trap to study the winter dynamics of small mammals in the Low Arctic tundra of northern Norway. Forty functional cameras were motion-triggered 20 172 times between September 2014 and July 2015, mainly by grey-sided voles (*Myodes rufocanus* (Sundevall, 1846)), tundra voles (*Microtus oeconomus* (Pallas, 1776)), Norwegian lemmings (*Lemmus lemmus* (Linnaeus, 1758)) and shrews (*Sorex* spp.). These data proved to be suitable for dynamical modelling of species-specific site occupancy rates. The occupancy rates of all recorded species declined sharply and synchronously at the onset of the winter. This decline happened concurrently with changes in the ambient conditions recorded by time-lapse images of snow and water. Our study demonstrates the potential of subnivean camera traps for elucidating novel aspects of year-round dynamics of Arctic small mammal communities.

Key words: lemmings, voles, occupancy modelling, snow, winter ecology.

Résumé : Les petits rongeurs constituent un indicateur clé pour comprendre l'effet du changement rapide du climat hivernal sur les écosystèmes de la toundra arctique. Cependant, le suivi des populations de rongeurs pendant le long hiver arctique au moyen de pièges conventionnels a jusqu'à présent été entravé par la couverture neigeuse et les conditions ambiantes difficiles. Les auteurs réalisent ici la première évaluation approfondie de l'utilité d'un nouveau piège photographique pour étudier la dynamique hivernale des petits mammifères dans la toundra du bas-arctique au nord de la Norvège. Quarante appareils photo fonctionnels ont été déclenchés par le mouvement 20 172 fois entre septembre 2014 et juillet 2015, principalement par des campagnols de Sundevall (*Myodes rufocanus* (Sundevall, 1846)), des campagnols nordiques (*Microtus oeconomus* (Pallas, 1776)), des lemmings norvégiens (*Lemmus lemmus* (Linnaeus, 1758)) et des musaraignes (*Sorex* spp.). Ces données se sont avérées appropriées pour la modélisation dynamique des taux d'occupation des sites spécifiques aux espèces. Les taux d'occupation de toutes les espèces enregistrées diminuaient abruptement et de façon synchrone au début de l'hiver. Ce déclin se produisait en même temps que les changements des conditions ambiantes enregistrés par les images de neige et d'eau prises à intervalles. Cette étude démontre le potentiel des pièges

---

Received 18 January 2021. Accepted 6 April 2021.

J.P. Mölle. Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, NO-9037 Tromsø, Norway; Department of Agriculture and Nutrition, Christian-Albrechts University, DE-24118 Kiel, Germany.

E.F. Kleiven, R.A. Ims, and E.M. Soininen. Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, NO-9037 Tromsø, Norway.

Corresponding author: Eivind F. Kleiven (e-mail: eivind.f.kleiven@uit.no).

Arctic Science **8:** 183–199 (2022) dx.doi.org/10.1139/as-2021-0006

photographiques subnivaux pour élucider de nouveaux aspects de la dynamique des communautés de petits mammifères de l'Arctique tout au long de l'année. [Traduit par la Rédaction]

Mots-clés : lemmings, campagnols, modélisation de l'occupation, neige, écologie hivernale.

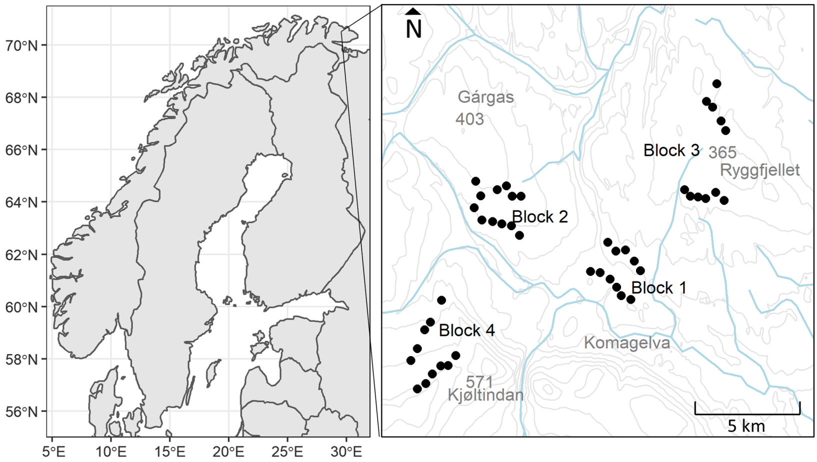
Introduction

The Arctic climate is changing with temperatures rising more than twice as fast as the global average (Davy and Outten 2020). This change in temperature drives profound changes in snow conditions during the long Arctic winter season (AMAP 2017). The changing cryosphere alters the characteristics of the tundra ecosystems, and investigation of the ecological consequences requires more effort (ACIA 2004; Post et al. 2009; Ims et al. 2013*a*). To better understand the ecosystem impacts of changing winter climate, it is crucial to specifically monitor species with key functions in the food web that can be expected to have a clear link to changes in winter climate (Christensen et al. 2013; Ims et al. 2013*b*). In many Arctic food webs, lemmings (*Lemmus* and *Dicrostonyx* spp.) and voles (*Myodes* and *Microtus* spp.) have such roles. Their high-amplitude population cycles have repercussions for the entire food web (Ims and Fuglei 2005), and these dynamics appear to change as a result of changes in the duration and physical properties of the snow layer (Kausrud et al. 2008; Gilg et al. 2009; Stien et al. 2012; Berteaux et al. 2017; Domine et al. 2018). Winter warm spells and rain-on-snow events appear to have a considerable negative effect on rodent survival rates by disrupting the insulating snow layer and causing that ground ice blocks habitat and food sources (Korslund and Steen 2006; Kausrud et al. 2008; Ims et al. 2011; Berteaux et al. 2017). However, this understanding is mainly based on indirect inferences from data collected during the snow-free period, and no direct assessment of wintertime dynamics of rodent populations within the Arctic has been published.

To understand how the environmental drivers affect the dynamics of cyclic small rodent populations it is essential to acquire high-quality monitoring data (Ims et al. 2008; Korpela et al. 2013). However, it is problematic to observe winter dynamics of Arctic and boreal small rodents as they live under the snow (Krebs 2013; Berteaux et al. 2017). Generally, the strength of the inferences about ecological mechanisms is limited by the temporal resolution of the data that can be generated (Krebs 2013). It is particularly essential to monitor small rodent dynamics with an adequate frequency (Ehrich et al. 2020) that matches the timing of abrupt climatic events (Domine et al. 2018). To fully understand small rodent cycles and keep track of their changing dynamics in Arctic ecosystems, new approaches are needed (Ehrich et al. 2020).

During the last few years, cheaper and more advanced camera technology has led to wide-scale implementation of camera trapping studies (Steenweg et al. 2017) and methodological adaptations of camera traps to specific ecosystem conditions and questions have been made (Nichols et al. 2010; Glen et al. 2013; Burton et al. 2015; Soininen et al. 2015). Camera traps require low fieldwork effort while providing a high sampling resolution (Kucera and Barrett 2011; Soininen et al. 2015). Camera traps are already applied in the monitoring of small mammals (Meek et al. 2012; Glen et al. 2013; Rendall et al. 2014; Villette et al. 2016), and a small-scale pilot study from the subarctic forest has presented a below-snow camera trap to study small rodents during winter (Soininen et al. 2015). Indeed, as the winter dynamics of small mammals may be subjected to rapid environmentally driven extinctions of local populations (e.g., Aars and Ims 2002), camera trap occupancy data may be particularly suitable for modelling such extinction–colonization dynamics at the landscape scale. Occupancy models are the established way to analyse

Fig. 1. Map of Fennoscandia (left panel) and zoom on the study area on Varanger Peninsula (right panel) with the 44 camera trap sites (black points) in four spatially segregated blocks arranged in an elevation gradient. Numbers denote the elevation (in metres) of the summits of the highest hills. Grey lines represent elevation contours and blue lines represent rivers. The base map was taken from https://kartkatalog.geonorge.no/metadata/n250-map-data/442cae64-b447-478d-b384-545bc1d9ab48 (Kartverket 2015).



camera trapping data when one cannot detect all individuals that are present (Nichols et al. 2010). Still, such methods for studying winter season dynamics of cyclically fluctuating rodent communities have not yet been published.

Here, we present the first extensive-scale assessment of camera traps as a method for investigating winter season dynamics of an Arctic small mammal community. We investigated how the camera trap developed by Soininen et al. (2015) performed both in terms of technical functionality under the harsh ambient winter conditions in Arctic tundra and in terms of animal detection rates under such conditions. Furthermore, we assessed how information about the particular environmental conditions potentially affecting rodent winter dynamics could be gained from the camera trapping data. Finally, a major aim of the study was also to assess the utility of the camera trap data for state-of-the-art statistical models (Nichols et al. 2010) to estimate species-specific occupancy rates.

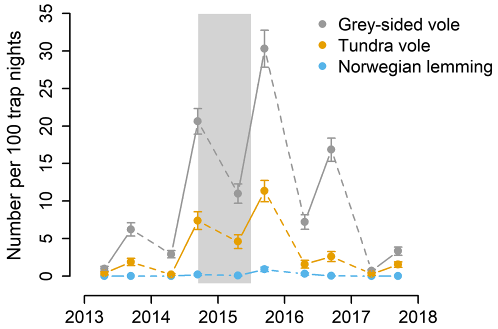
Methods

Study area

This study was conducted in a Low Arctic tundra landscape in the inner part of Varanger Peninsula, northeast Norway (70°N, 30°E) (Fig. 1). Hilly plains carved by river valleys shape the study area that is located on an elevation between 165 and 489 m a.s.l. The plains are characterised by dwarf-shrub dominated heaths (*Empetrum nigrum* L., *Vaccinium* spp., *Betula nana* L.), occasionally interspersed by mesic areas with mires and graminoid- or moss-dominated snow bed habitats. Upland areas are covered with boulder fields above the alpine limit of vascular plants, whereas lowland valleys have rivers lined by wet meadows and willow thickets (*Salix* spp.).

Monthly mean temperatures (period 1961–1990) at the nearest weather station (Båtsfjord, at 150 m a.s.l. and ca. 20 km from the nearest camera trap), range from −6.5 °C

Fig. 2. Seasonal and multi-annual dynamics of the three focal rodent species on the Varanger peninsula during the population cycle that encompassed the present camera trap study. Points denote the number of trapped rodents per 100 trap nights in early July and September each year. Solid lines denote changes over the 2-month summer periods (early July–early September), whereas broken lines denote changes over the 10-month periods (early September–early July) encompassing fall, winter, and spring. The light grey bar denotes the focal camera trap study period. The snap-trap data are from three sub-regions on Varanger Peninsula described by Ims et al. (2011). Each trapping period is based on 1176 trap-nights. The data are available from https://data.coat.no/dataset/v_rodents_snaptrapping_abundance_regional_v1 (COAT 2018).



in January to 11.0 °C in July and the annual mean precipitation amount is 545 mm (NMI 2020). The area is normally fully covered by snow at least from October to May (Malnes et al. 2016) with an average depth of 57 cm (Virtanen et al. 1999). However, the snow cover is very heterogeneous, and snow beds can be covered by 4 m of snow and persist until late July (Soininen et al. 2017).

Small mammal community

The study area is inhabited by three species of small rodents: Norwegian lemming (*Lemmus lemmus* (Linnaeus, 1758)), grey-sided vole (*Myodes rufocanus* (Sundevall, 1846)) and tundra vole (*Microtus oeconomus* (Pallas, 1776)). Norwegian lemmings spend the summer in habitats with moist hummock tundra or mires and move to snow beds on dry ground in the winter (Kalela 1957). During summer, they co-occur with tundra voles that also tend to shift habitat between summer and winter seasons (Tast 1966). Grey-sided voles prefer dwarf shrub habitats (Viitala 1977). The three species exhibit an interspecifically synchronous, high-amplitude four year cycle on Varanger peninsula (Ims et al. 2011; Kleiven et al. 2018; Soininen et al. 2018). The population cycle of the Norwegian lemming has an amplitude that is typically more variable than the vole cycles and sometimes the peaks of this species are missing in time series derived from snap trap monitoring (Ims et al. 2011).

The present study covers a 9.5-month period from mid-September 2014 to early July 2015. As is evident from large-scale and long-term monitoring of the small rodent community on the Varanger Peninsula based on snap-trapping (Kleiven et al. 2018), our study period encompassed the winter season preceding the peak phase summer of the rodent cycle (Fig. 2). According to the snap-trapping data, the grey-sided vole was clearly the numerically dominant species during our study period, whereas the Norwegian lemming was almost absent (Fig. 2).

Other small mammals in the study area that so far have not been systematically monitored are insectivorous shrews (the common shrew, *Sorex araneus* Linnaeus, 1758, masked shrew, *Sorex caecutiens* Laxmann, 1788, and pygmy shrew, *Sorex minutus* Linnaeus, 1766) and

Fig. 3. Typical camera trap placements in different habitats and relations to micro-topographic features. Mesic hummock tundra with paths and grazing signs of rodents (left panel). Snow bed in early July (centre panel). Hummock tundra where the camera was damaged by flooding during the spring thaw (right panel).

carnivorous small mustelids (ermine, *Mustela erminea* Linnaeus, 1758, and least weasel, *Mustela nivalis* Linnaeus, 1766).

Study design

The camera trap is described by Soininen et al. (2015). We replaced the wooden camera box, presented by Soininen et al. (2015), with an aluminium box to improve durability. We programmed the cameras (Reconyx SM 750 Hyperfire; Reconyx Inc., Holmen, Wisconsin, USA) to take two images for each motion-triggered event and to have a 1-min quiet period (i.e., delay) after each event to avoid an excessive number of photos. To verify whether the camera was functional and to monitor the ambient environmental conditions inside the camera trap, we programmed two additional time-lapse images per day (at 1:00 AM and PM). The cameras had a thermometer, and the temperature was recorded every time an image was taken.

During 15–17 September in 2014, 44 camera traps were set up to cover lemming habitats at different elevations in the study area. They were placed in four separate blocks ($n = 11$ trap sites in each block) (Fig. 1). Two of the blocks consisted primarily of snow bed sites (Fig. 1, blocks 3 and 4), whereas the two other blocks had heath, mesic hummock tundra, and mire sites (Fig. 1, blocks 1 and 2). Within each block, the traps were placed in two lines with 5–6 traps. The minimum distance between traps was 300 m to avoid the same rodent individual including more than one camera trap within its home range (Ims 1987; Andreassen et al. 1998) and, thus, to ensure that occupancy rates would be independent between the traps.

Criteria for the choice of location of traps within blocks were that the vegetation should include food plants preferred by lemmings (mosses and graminoids) (Soininen et al. 2017). Placed among micro-topographic structures (between stones or hummocks), the camera traps were integrated with natural pathways that rodents normally use for movements in tundra habitats. Stones from the surrounding environment were put on the sides and top of the camera traps to secure them from strong winds (Fig. 3).

Memory cards from all cameras were collected during 1–6 July in 2015 so that the entire study period covered approximately 290 days. Malfunctioning of cameras due to flooding and water damage or for other reasons was recorded.

Data analysis

Image data

Cameras with technical failure from the onset of the study were excluded from the analysis ($n = 4$). Images of all other cameras were classified using Reconyx MapView professional software (Reconyx Inc., Holmen, Wisconsin, USA). When a malfunctioning camera flash or snow/ice on the lens caused bad quality images and impeded their inspection, these images were excluded from the data set.

For the movement-sensor triggered images, we noted whether an image contained lemmings, tundra voles, and grey-sided voles, or "unknown vole" if the two vole species could not be distinguished. Mustelids and shrews were also recorded, but the latter without being able to distinguish the different species.

Based on the two time-lapse images per day, we recorded a daily score for the presence of snow and water (see Appendix A, Fig. 1A).

Snow was scored as:

(0) No snow present in the entrances of the camera traps,
(1) shallow snow present, but not sufficient to cover the trap entrances and, thus, not a closed snow layer that can harbour a rodent tunnel system,
(2) a closed snow layer that was higher than both of the 7 cm high entrances of the traps, or
(3) a lot of snow inside the trap to the extent that it potentially prevented the detection of animals tunnelling their way through the trap.

Water was scored as:

(0) No visible humidity inside the trap,
(1) big drops of water or generally wet surface of the floor of the trap,
(2) light flooding with water up to half the height of the trap entrances, or
(3) severe flooding with a water level more than half as high as the trap entrances or higher so that terrestrial animals were not able to enter the traps.

The scores with the value of 3 for both snow and water obstructed the observation of animals. To be able to include camera traps with such scores in the occupancy model, these covariate values were treated in the analysis as NAs.

In addition to images, the camera traps provide a temperature record for each image. Temperature recordings from time-lapse images provide site-level data that can be useful to estimate the length of the snow-covered season, or indicate insulating properties of the snow pack. However, as we recorded explicit data for snow and water within the camera boxes, we here provide temperature data only to illustrate its possible uses.

Occupancy modelling

Occupancy models determine the probability of a species presence, taking into account that some individuals may remain unobserved. This framework allows both occupancy probability and detection probability to be estimated as a function of covariates (MacKenzie et al. 2003). Here we used a dynamic (i.e., estimating changes over time) occupancy model over repeated sampling occasions to estimate occupancy of the three rodent species and shrews collectively over the entire study period (MacKenzie et al. 2003). Mustelids occurred too infrequently to be included. As our main interest here was to investigate the functionality of the camera traps, we modelled detection probability as a function of environmental covariates, and occupancy probability without covariates.

We defined primary sampling occasions as five-day units (59 primary sampling occasions in the study period). Five days was chosen to be in line with the recommended sample sizes of MacKenzie and Royle (2005) and so that this period would be short enough for the local population at a given trap site not to change considerably. The occupancy rates were estimated for these time units. Within the primary occasions (i.e., the five-day units), the presence or absence of the different species was recorded each day (secondary occasion). As the camera traps recorded relatively few numbers of lemmings, the records of all three rodent species and shrews were combined to model a single stronger data set. To be able to obtain species-specific parameter estimates (White et al. 2013), the model was extended by a "species dimension". The presence-absence observations (y) at site i in primary occasion (five-day unit) t and secondary occasion (day) j for species s, can be described with a Bernoulli distribution:

$$(1)\quad y_{i,t,j,s}|z_{i,t,s} \sim \text{Bernoulli}\,(z_{i,t,s}p_{i,t,s})$$

where $z_{i,t,s}$ denotes the true state of occurrence and $p_{i,t,s}$ the detection probability.

Detection probability (p): Through a logit link function, species-specific detection probabilities were modelled as a function of two categorical environmental covariates snow and water. The equation for detection probability was thus

$$(2)\quad \text{logit}(p_{i,t,s}) = pb1_{\text{snow}_{i,t,s}} + pb2_{\text{water}_{i,t,s}}$$

where $pb1$ and $pb2$ are the coefficients that describe the effect of the environmental covariates. As the three-level categorical covariates snow and water (see section "Image data") in eq. (2) are specified at the temporal resolution of primary occasions t (five-day periods), although they were recorded from time-lapse photos each day (i.e., at secondary occasions j), the scores for the covariates were set to the highest recorded value (0–2) per trap and secondary occasion. Records of NAs for the covariates at any given site (e.g., scores of 3) were replaced with the median of the scores of the other sites within a block.

Occupancy probability (Ψ): The initial occupancy probability (Ψ_1 = occupancy probability of small rodents in the first primary occasion) was modelled as

$$(3)\quad \text{logit}(\Psi_{i,t=1,s}) = a_s$$

where a_s is a species-specific intercept. The development of the occupancy changes over time (Ψ_{t+1}, here z) was modelled as a function of site colonization (γ) and extinction (ε) events:

$$(4)\quad z_{i,t,s} \sim \text{Bernoulli}(z_{i,t-1,s} \times (1-\varepsilon_s) + (1 - z_{i,t-1,s}) \times \gamma_s)$$

Extinction (ε) and colonization (γ) probability: Both were modelled similar to Ψ_1 with a logit link:

$$(5)\quad \text{logit}(\gamma_s) = gb_s$$

and

$$(6)\quad \text{logit}(\varepsilon_s) = eb_s$$

The model of the four parameters (p, Ψ, γ, and ε) was implemented using the R software (R Core Team 2019). The estimation of the parameters was done in a Bayesian framework, running a Markov chain Monte Carlo (MCMC) with JAGS. For the model to converge, three chains with 160 000 iterations were run and the first 10 000 iterations were discarded as burn-in and 40 000 was used as adaptations. The model was checked and indicated chain convergence as all $\hat{R}$ values were <1.1 (Gelman et al. 2013) and trace plots showed that the chains were mixed well. We ascertained that the model was fit for the data set by performing a posterior predictive check (Kéry 2010). All occupancy estimates are provided with 95% credible intervals based on their posterior distributions.

Results

Camera trap functionality and ambient conditions

Of the 40 cameras that were technically functional from the onset of the study, four ceased to function in autumn and a further 12 had water-induced hardware damage associated with flooding during the spring thaw period in May–June (Fig. 4). Thirteen traps were infiltrated by snow and five traps were flooded by water to the extent that it prohibited detection of animals (snow and water category 3) for shorter or longer periods during the winter and spring (Fig. 4).

The first snow was recorded in late September (Fig. 4). However, this shallow snow cover (snow 1) melted soon and caused some water (water 1) in most traps. A closed snow cover (snow 2) established quite simultaneously across the sites/blocks in mid-October. In the turn of October–November, snow 2 transitioned to snow 0/1, associated with the presence of water in some of the traps (Fig. 4). A permanently closed snow cover (snow 2) was present from early November until the spring thaw period when a lot of water (water 2 and 3) was prevalent in many of the traps (Fig. 4).

In total, the cameras recorded 60 547 images of which 40 346 were motion-triggered. The number of motion-triggered images per camera across the whole study period (290 days) ranged from 14 to 4726 with a mean of 506. Of the motion-triggered images, 10.4% did not show a presence of animals in the trap despite good-quality images. Moreover, 4.2% of the motion-triggered images were of such bad quality because of malfunctioning cameras, or ice or dew on the lens, that animals would not be visible even if they were present (Appendix A, Table A1). When rodents were recorded, the species could be identified in almost all cases, i.e., only 0.3% were classified as unknown voles (Appendix A, Table A1) that were discarded from the analysis.

The grey-sided vole was recorded most frequently (64.5% of the trigger images; Appendix A, Table A1) with the largest and most even spatial distribution across sites and blocks (Fig. 4). Tundra voles were the next-most frequent species and with most of the records aggregated on two of the blocks. The Norwegian lemming had the most restricted distribution of the rodents, whereas shrews appeared more scattered in time and space than the rodents (Fig. 4). Least weasels and ermines were recorded on three and two sites, respectively (Appendix A, Table A1).

Occupancy modelling

The estimated occupancy probabilities (Ψ) of all small mammal species decreased during October–November contemporary with the abrupt shift in ambient conditions in terms of a drop in temperature and the emergence of a closed snow cover (Fig. 5; see Appendix A, Table A2 for estimates of other parameters). Thereafter, the occupancy probabilities of the most prevalent species — the grey-sided vole — became remarkably stable for the rest of the winter and spring. Tundra vole occupancy continued to have a declining trend until the spring thaw when occupancy rates increased. The lemming exhibited a long period of complete absence after the decline in the early winter. Shrews had quite low occupancy rates with more short-term variability than the rodents.

The estimated detection probability ($p_{i.t.s}$) ranged between 0.065 and 0.909 depending on the species and ambient conditions (Fig. 6). Shrews had mostly lower detection probabilities than the rodents. The detection probabilities for the lemming were more affected by the ambient conditions than for the two vole species, with a peak associated with the

Fig. 4. Records of ambient conditions (snow and ice) and the presence of small mammals at 40 camera trap sites during the 9.5 month study period from mid-September 2014 to early July 2015. Each cell represents a five day sampling period per site. The sites (i.e., the rows) are grouped according to the four blocks shown in Fig. 1. For the snow and water panels, the white squares indicate occasions where the cameras were malfunctioning, i.e., not recording information of ambient conditions. For the animal species panels, the white squares also include images of bad quality and record snow 3 and water 3.

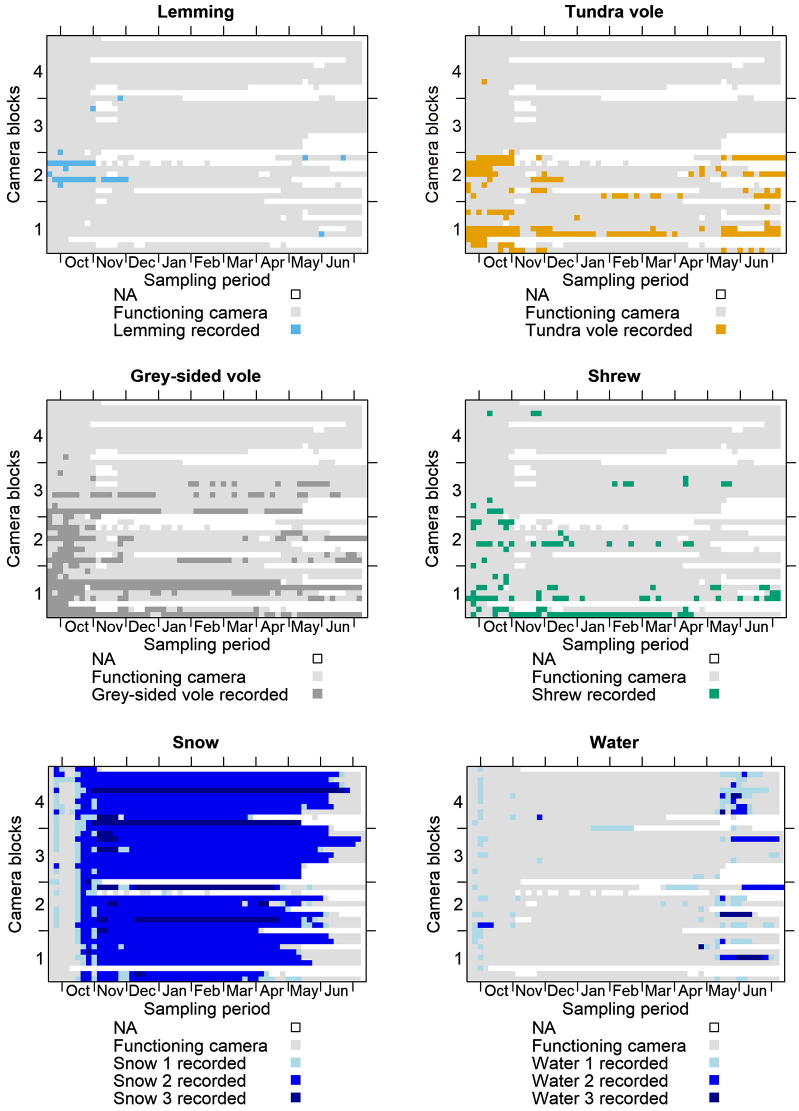
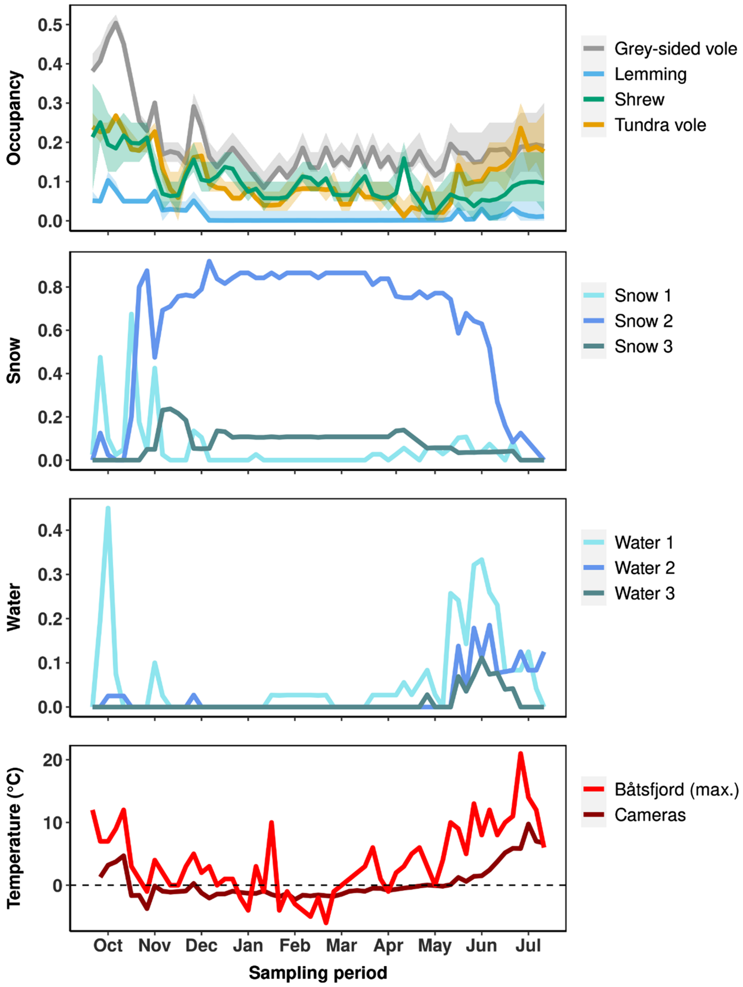
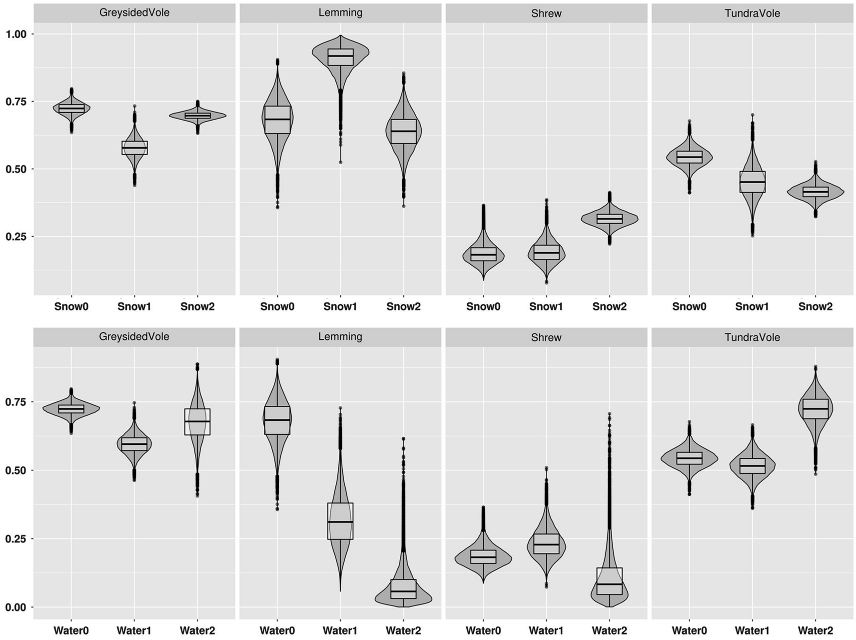


Fig. 5. Small mammal occupancy dynamics and ambient conditions per five-day units during the 9.5 month study period. Occupancy rates are the means of the posterior distribution of Ψ averaged over sites with functional camera traps. Water and snow are the proportion of functional camera traps (sites) with records of the three snow and water categories. Temperatures are highest recorded daily air temperature per five-day unit from the nearest weather station (Båtsfjord) and recorded by the camera traps (averaged over all functional traps).



appearance of shallow snow (snow 1) at the onset of the winter, and a sharp drop with the presence of water (water 1 and 2) in the traps. Of note, the development of a closed snowpack (snow 2) as compared with snow-free tundra (snow 0) only appeared to have a negative effect on the detection probability of the tundra vole (Fig. 6).

Fig. 6. Small mammal detection probabilities for the recorded categories of snow and water (see text for a description of the categories). The violin and box plots show estimated posterior distributions obtained from the dynamic occupancy model. The estimates for the three snow categories were obtained for water 0, whereas the estimates for three water categories were obtained for snow 0.



Discussion

We performed the first assessment of the applicability of camera traps for providing data on small mammal community dynamics during the Arctic winter. Whenever functional, the camera traps developed by Soininen et al. (2015) yielded data suitable for dynamical occupancy modelling with generally high detection probabilities — especially for the three rodent species that were present in our study area. The detection/non-detection data acquired from camera traps do not provide the kind of abundance estimates/indices that have been the standard way to study Arctic rodent population dynamics (Krebs 2013; Ehrich et al. 2020). However, at a landscape scale cyclically fluctuating rodents can be considered as metapopulations that are driven by local-scale extinction and colonization events (Glorvigen et al. 2013). The year-round data collection enabled by camera traps thus provides a means for assessing the link between such metapopulation events and potentially influential ambient events such as snowfalls, snowmelt, and flooding. Our camera traps provide daily site-specific data on such ambient events that can be used as covariates in occupancy models. This allows both to correct for their influence on the detection rates as done in the present study, and to estimate their impact on metapopulation processes (e.g., colonization and extinction rates) in future multi-annual studies. Ultimately, this approach will yield improved knowledge about how Arctic climate change impacts Arctic rodent community dynamics. Our results on snow and water indicate that such ambient conditions need to be modelled as species-specific parameters.

This study revealed some important challenges due to the severe ambient conditions in Arctic tundra during winter and spring that resulted in reduced camera trap functionality. Drifting snow caused some cameras to be clogged with snow to the extent that it hindered data capture for shorter or longer periods through the winter. An action that can reduce snow infiltration through the trap entrances, is to erect piles of stones around the camera traps (Appendix A, Fig. A2) functioning as snow fences, but still leaving gaps for passages of small mammals. In tundra areas without access to stones, the camera traps can be differently designed, for instance, with entrances formed as angled tubes that will likely prevent snow from clogging the main compartment of the trap.

Flooding due to melting snow, particularly during the spring thaw, permanently damaged a proportion of the cameras. This problem can be counteracted by avoiding placing the camera traps in topographic features such as small-scale depressions, where water is likely to accumulate. Waterproof cameras will prevent damage to hardware, but waterlogged traps will still hinder passages of terrestrial small mammals and cause loss of data — so sites that are vulnerable to such events should be avoided.

We experienced only minor problems with frost or dew on the camera lenses contrary to what has been reported from a High Arctic study site with very cold permafrost and profound vertical temperature gradients in the snow packs (Kalhor et al. 2019). The Varanger Peninsula has only sporadic warm permafrost (Farbrot et al. 2013) and we recorded subnivean temperatures that were only slightly below zero (Fig. 4). Hence, the camera traps used in the present study should be tested under a wider range of ambient conditions to verify their general functionality.

It is still uncertain whether data from camera traps will be able to yield the same numerical aspects of population arithmetic as conventional trapping data (removal sampling and capture–recapture). It is, however, promising to notice that the abundance relations between rodent species and the observed overwinter decrease obtained by camera trapping (Fig. 5) and snap-trapping (Fig. 2) show similar patterns. Furthermore, the occupancy estimates showed the characteristic drop at the onset of the winter previously found by mark–recapture trapping of boreal rodent populations (e.g., Merritt and Merritt 1978; Johnsen et al. 2018), indicating that occupancy estimation is able to show the main features of seasonal and multi-annual dynamics of cyclic rodent populations. However, we encourage future studies to assess how occupancy estimates compare with more conventional metrics of Arctic small mammal population dynamics — such as estimates or indices of population density and growth rate.

To conclude, we find that camera traps can be used to monitor small mammal community dynamics during the Arctic winter. In addition, the camera traps also collect environmental data that can be used to estimate climate-driven colonization and extinction events in Arctic small mammal communities. As the camera traps also provide simultaneous data on presence/absence of mustelids, future more long-term studies that cover all phases of the multi-annual cycle can provide new insights about how the dynamics of mustelids (predator) and rodents (prey) are linked. It is also noteworthy that our relatively modest sample of camera traps was able to capture the seasonal dynamics of the Norwegian lemming, a key species in the focal ecosystem (Ims et al. 2017), given that the lemmings were almost absent in the extensive sample of snap-trapped rodents. Hence, we conclude that subnivean camera traps bear great promise in terms of elucidating novel aspects of the community dynamics of Arctic small mammals and how these communities respond to climate change.

Acknowledgements

We thank I. Jensvoll and S. Killengreen for their substantial contributions to the development of the camera trap and to the fieldwork. We also thank D. Ehrich, X. Ancin, and K. Mæland for help with fieldwork, N. Yoccoz for advice with the analyses, and T. Diekötter for comments on an earlier version of this manuscript. S. Killengreen and D. Ehrich have maintained the long-term snap-trapping data, and we thank them and all their field assistants throughout the years. We also thank two anonymous reviewers for providing helpful comments on an earlier draft of the manuscript. This work is a contribution from the Climate-ecological Observatory for Arctic Tundra (COAT, www.coat.no). This research was supported by the Research Council of Norway (project nr. 245638), and Tromsø Research Fund (project COAT-Tools+).

Author contributions

Conceptualization R.A.I., E.M.S., E.F.K.; Data curation J.P.M., E.M.S.; Formal analysis J.P.M., E.F.K.; Funding acquisition R.A.I., E.M.S.; Investigation J.P.M., E.F.K., R.A.I., E.M.S.; Methodology J.P.M., E.F.K., R.A.I., E.M.S.; Project administration J.P.M., Visualization J.P.M., E.M.S., Writing — original draft J.P.M., Writing — review and editing J.P.M., E.F.K., E.M.S. and R.A.I.

Data availability

The data are available through the COAT data portal (https://data.coat.no/dataset/v_rodents_cameratraps_pilot_v1, doi: 10.48425/0077746).

References

Aars, J., and Ims, R.A. 2002. Intrinsic and climatic determinants of population demography: the winter dynamics of tundra voles. Ecology, **83**(12): 3449–3456. doi: 10.1890/0012-9658(2002)083[3449:IACDOP]2.0.CO;2.

ACIA. 2004. Impacts of a warming Arctic. Arctic Climate Impact Assessment (ACIA). Cambridge University Press, Cambridge, UK.

AMAP. 2017. Snow, water, ice and permafrost in the Arctic (SWIPA). Arctic Monitoring and Assessment Programme (AMAP). Oslo, Norway.

Andreassen, H.P., Hertzberg, K., and Ims, R.A. 1998. Space-use responses to habitat fragmentation and connectivity in the root vole *Microtus oeconomus*. Ecology, **79**(4): 1223–1235. doi: 10.1890/0012-9658(1998)079[1223:SURTHF]2.0.CO;2.

Berteaux, D., Gauthier, G., Domine, F., Ims, R.A., Lamoureux, S.F., Lévesque, E., and Yoccoz, N.G. 2017. Effects of changing permafrost and snow conditions on tundra wildlife: critical places and times. Arct. Sci. **3**(2): 65–90. doi: 10.1139/as-2016-0023.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., et al. 2015. Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. J. Appl. Ecol. **52**(3): 675–685. doi: 10.1111/1365-2664.12432.

Christensen, T., Payne, J., Doyle, M., Ibarguchi, G., Taylor, J., Schmidt, N.M., et al. 2013. The Arctic Terrestrial Biodiversity Monitoring Plan. CAFF International Secretariat, Akureyri, Iceland.

Climate-ecological Observatory for Arctic Tundra (COAT). 2018. v_rodents_snaptrapping_abundance_regional_v1: COAT project data. Available from https://data.coat.no/dataset/v_rodents_snaptrapping_abundance_regional_v1.

Davy, R., and Outten, S. 2020. The Arctic surface climate in CMIP6: status and developments since CMIP5. J. Clim. **33**(18): 8047–8068. doi: 10.1175/JCLI-D-19-0990.1.

Domine, F., Gauthier, G., Vionnet, V., Fauteux, D., Dumont, M., and Barrere, M. 2018. Snow physical properties may be a significant determinant of lemming population dynamics in the high Arctic. Arct. Sci. **4**(4): 813–826. doi: 10.1139/as-2018-0008.

Ehrich, D., Schmidt, N.M., Gauthier, G., Alisauskas, R., Angerbjörn, A., Clark, K., et al. 2020. Documenting lemming population change in the Arctic: can we detect trends? Ambio, **49**(3): 786–800. doi: 10.1007/s13280-019-01198-7. PMID: 31332767.

Farbrot, H., Isaksen, K., Etzelmüller, B., and Gisnås, K. 2013. Ground thermal regime and permafrost distribution under a changing climate in northern Norway. Permafr. Periglac. Process. **24**(1): 20–38. doi: 10.1002/ppp.1763.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A., and Rubin, D.B. 2013. Bayesian data analysis. 3rd ed. Chapman and Hall/CRC, Boca Raton, Fla., USA.

Gilg, O., Sittler, B., and Hanski, I. 2009. Climate change and cyclic predator–prey population dynamics in the high Arctic. Global Change Biol. **15**(11): 2634–2652. doi: 10.1111/j.1365-2486.2009.01927.x.

Glen, A.S., Cockburn, S., Nichols, M., Ekanayake, J., and Warburton, B. 2013. Optimising camera traps for monitoring small mammals. PLoS ONE, **8**(6): e67940. doi: 10.1371/journal.pone.0067940. PMID: 23840790.

Glorvigen, P., Andreassen, H.P., and Ims, R.A. 2013. Local and regional determinants of colonisation-extinction dynamics of a riparian mainland-island root vole metapopulation. PLoS ONE, **8**(2): e56462. doi: 10.1371/journal.pone.0056462. PMID: 23437137.

Ims, R.A. 1987. Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. J. Anim. Ecol. **56**(2): 585–596. doi: 10.2307/5070.

Ims, R.A., and Fuglei, E. 2005. Trophic interaction cycles in tundra ecosystems and the impact of climate change. Bioscience, **55**(4): 311–322. doi: 10.1641/0006-3568(2005)055[0311:TICITE]2.0.CO;2.

Ims, R.A., Henden, J.-A., and Killengreen, S.T. 2008. Collapsing population cycles. Ecol. Evol. **23**(2): 79–86. doi: 10.1016/j.tree.2007.10.010.

Ims, R.A., Yoccoz, N.G., and Killengreen, S.T. 2011. Determinants of lemming outbreaks. Proc. Natl. Acad. Sci. USA, **108**(5): 1970–1974. doi: 10.1073/pnas.1012714108. PMID: 21245340.

Ims, R.A., Ehrich, D., Forbes, B.C., Huntley, B., Walker, D.A., Wookey, P.A., et al. 2013*a*. Terrestrial ecosystems. *In* Arctic biodiversity assessment. Status and trends in Arctic biodiversity. *Edited by* H. Meltofte. Conservation of Arctic Flora and Fauna, Akureyri, Iceland. pp. 384–440, 560.

Ims, R.A., Jepsen, J.U., Stien, A., and Yoccoz, N.G. 2013*b*. Science plan for COAT: Climate-ecological observatory for Arctic Tundra. Fram Centre Report Series No. 1. Fram Centre, Tromsø, Norway.

Ims, R.A., Killengreen, S.T., Ehrich, D., Flagstad, Ø., Hamel, S., Henden, J.-A., et al. 2017. Ecosystem drivers of an Arctic fox population at the western fringe of the Eurasian Arctic. Polar Res. **36**(Suppl. 1): 8. doi: 10.1080/17518369.2017.1323621.

Johnsen, K., Devineau, O., and Andreassen, H.P. 2018. The effects of winter climate and intrinsic factors on survival of cyclic vole populations in southeastern Norway. Ann. Zool. Fenn. **55**(4–6): 173–185. doi: 10.5735/086.055.0604.

Kalela, O. 1957. Regulation of reproduction rate in subarctic populations of the vole, *Clethrionomys rufocanus* (Sund.). Ann. Acad. Sci. Fenn., Ser. A4: Biol. **34**: 1–60.

Kalhor, D., Pusenkova, A., Poirier, M., Gauthier, G., Galstian, T., and Maldague, X. 2019. Using near infrared for studying lemming subnival behavior in the high Arctic. Proceedings, **27**(1): 11. doi: 10.3390/proceedings2019027011.

Kartverket. 2015. N250. Norwegian Mapping Authority. Available from https://kartkatalog.geonorge.no/metadata/n250-map-data/442cae64-b447-478d-b384-545bc1d9ab48 [accessed 18 April 2021].

Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., et al. 2008. Linking climate change to lemming cycles. Nature, **456**(7218): 93–97. doi: 10.1038/nature07442. PMID: 18987742.

Kéry, M. 2010. Chapter 21 — Nonstandard GLMMs 2: binomial mixture model to model abundance. *In* Introduction to WinBUGS for ecologists. *Edited by* M. Kéry. Elsevier, Cambridge, Mass., USA. pp. 253–274. doi: 10.1016/B978-0-12-378605-0.00021-1.

Kleiven, E.F., Henden, J.-A., Ims, R.A., and Yoccoz, N.G. 2018. Seasonal difference in temporal transferability of an ecological model: near-term predictions of lemming outbreak abundances. Sci. Rep. **8**(1): 15252. doi: 10.1038/s41598-018-33443-6. PMID: 30323293.

Korpela, K., Delgado, M., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., et al. 2013. Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. Global Change Biol. **19**(3): 697–710. doi: 10.1111/gcb.12099.

Korslund, L., and Steen, H. 2006. Small rodent winter survival: snow conditions limit access to food resources. J. Anim. Ecol. **75**(1): 156–166. doi: 10.1111/j.1365-2656.2005.01031.x. PMID: 16903053.

Krebs, C.J. 2013. Population fluctuations in rodents. University of Chicago Press, Chicago, Ill., USA and London, UK.

Kucera, T.E., and Barrett, R.H. 2011. A history of camera trapping: methods and analyses. *In* Camera traps in animal ecology. *Edited by* A.F. O'Connell, J.D. Nichols, and K.U. Karanth. Springer Science & Business Media, Tokyo, Japan. pp. 9–26.

MacKenzie, D.I., and Royle, J.A. 2005. Designing occupancy studies: general advice and allocating survey effort. J. Appl. Ecol. **42**(6): 1105–1114. doi: 10.1111/j.1365-2664.2005.01098.x.

MacKenzie, D.I., Nichols, J.D., Hines, J.E., Knutson, M.G., and Franklin, A.B. 2003. Estimating site occupancy, colonization, and local extinction when a species is detected imperfectly. Ecology, **84**(8): 2200–2207. doi: 10.1890/02-3090.

Malnes, E., Karlsen, S.R., Johansen, B., Bjerke, J.W., and Tømmervik, H. 2016. Snow season variability in a boreal-Arctic transition area monitored by MODIS data. Environ. Res. Lett. **11**(12): 125005. doi: 10.1088/1748-9326/11/12/125005.

Meek, P.D., Fleming, P., and Ballard, G. 2012. An introduction to camera trapping for wildlife surveys in Australia. Invasive Animals Cooperative Research Centre, Canberra, Australia.

Merritt, J.F., and Merritt, J.M. 1978. Population ecology and energy relationships of *Clethrionomys gapperi* in a Colorado subalpine forest. J. Mammal. **59**(3): 576–598. doi: 10.2307/1380235.

Nichols, J.D., Karanth, K.U., and O'Connell, A.F. 2010. Science, conservation, and camera traps: methods and analyses. *In* Camera traps in animal ecology. *Edited by* A.F. O'Connell, J.D. Nichols, and K.U. Karanth. Springer Science & Business Media, Tokyo, Japan. pp. 45–56.

Norwegian Meteorological Institute (NMI). 2020. Weather Båtsfjord. Available from https://seklima.met.no/days/max(air_temperature_P1D)/custom_period/SN98360/nb/2014-09-15T17:29:00+02:00;2015-07-31T17:29:00+02:00 [accessed 18 February 2020].

Post, E., Forchhammer, M.C., Bret-Harte, M.S., Callaghan, T.V., Christensen, T.R., Elberling, B., et al. 2009. Ecological dynamics across the Arctic associated with recent climate change. Science, **325**(5946): 1355–1358. doi: 10.1126/science.1173113. PMID: 19745143.

R Core Team. 2019. R: a language and environment for statistical computing. Version 4.0.3. R Foundation for Statistical Computing, Vienna, Austria. Available from https://www.R-project.org/.

Rendall, A.R., Sutherland, D.R., Cooke, R., and White, J. 2014. Camera trapping: a contemporary approach to monitoring invasive rodents in high conservation priority ecosystems. PLoS ONE, **9**(3): e86592. doi: 10.1371/journal.pone.0086592. PMID: 24599307.

Soininen, E.M., Jensvoll, I., Killengreen, S.T., and Ims, R.A. 2015. Under the snow: a new camera trap opens the white box of subnivean ecology. Remote Sens. Ecol. Conserv. **1**(1): 29–38. doi: 10.1002/rse2.2.

Soininen, E.M., Zinger, L., Gielly, L., Yoccoz, N.G., Henden, J.-A., and Ims, R.A. 2017. Not only mosses: lemming winter diets as described by DNA metabarcoding. Polar Biol. **40**(10): 2097–2103. doi: 10.1007/s00300-017-2114-3.

Soininen, E.M., Henden, J.-A., Ravolainen, V.T., Yoccoz, N.G., Bråthen, K.A., Killengreen, S.T., and Ims, R.A. 2018. Transferability of biotic interactions: temporal consistency of arctic plant–rodent relationships is poor. Ecol. Evol. **8**(19): 9697–9711. doi: 10.1002/ece3.4399. PMID: 30386568.

Steenweg, R., Hebblewhite, M., Kays, R., Ahumada, J., Fisher, J.T., Burton, C., et al. 2017. Scaling-up camera traps: monitoring the planet's biodiversity with networks of remote sensors. Front. Ecol. Environ. **15**(1): 26–34. doi: 10.1002/fee.1448.

Stien, A., Ims, R.A., Albon, S.D., Fuglei, E., Irvine, R.J., Ropstad, E., et al. 2012. Congruent responses to weather variability in high Arctic herbivores. Biol. Lett. **8**(6): 1002–1005. doi: 10.1098/rsbl.2012.0764. PMID: 23015455.

Tast, J. 1966. The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. Ann. Zool. Fenn. **3**: 127–171.

Viitala, J. 1977. Social organization in cyclic subarctic populations of the voles *Clethrionomys rufocanus* (Sund.) and *Microtus agrestis* (L.). Ann. Zool. Fenn. **14**(2): 53–93.

Villette, P., Krebs, C.J., Jung, T.S., and Boonstra, R. 2016. Can camera trapping provide accurate estimates of small mammal (*Myodes rutilus* and *Peromyscus maniculatus*) density in the boreal forest? J. Mammal. **97**(1): 32–40. doi: 10.1093/jmammal/gyv150.

Virtanen, R., Oksanen, L., and Razzhivin, V. 1999. Topographic and regional patterns of tundra heath vegetation from northern Fennoscandia to the Taimyr Peninsula. Acta Bot. Fenn. **167**: 29–83.

White, A.M., Zipkin, E.F., Manley, P.N., and Schlesinger, M.D. 2013. Conservation of avian diversity in the Sierra Nevada: moving beyond a single-species management focus. PLoS ONE, **8**(5): e63088. doi: 10.1371/journal.pone.0063088. PMID: 23667579.

Appendix A

Fig. A1. Example images of recorded classes of snow and water described in the main text.

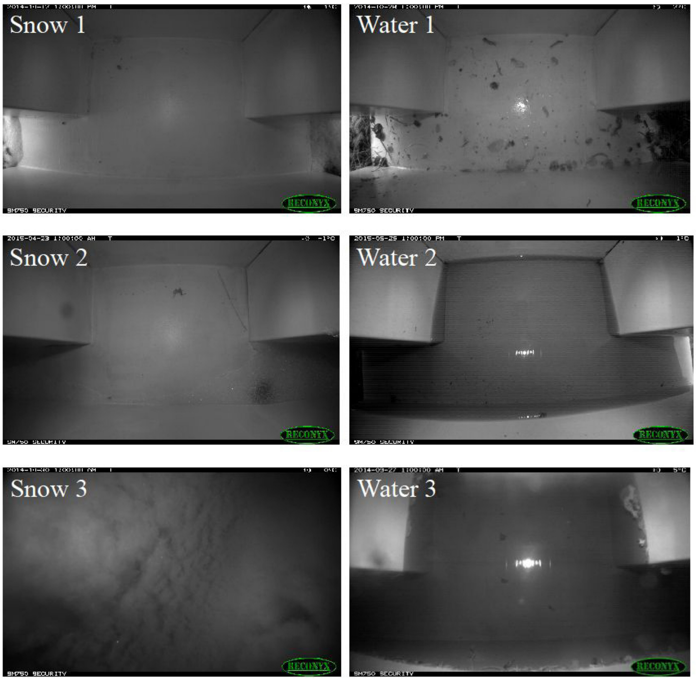


Fig. A2. Example of a camera trap embedded in a stone pile made to prevent infiltration of drifting snow that may clog the trap as shown in Fig. A1, Snow 3.

Table A1. Summary statistics of observations of presence of different image categories.

Observation	No. camera traps	No. five-day units	No. days	No. triggers
Lemming	10	31	92	830
Grey-sided vole	26	398	1336	13 019
Tundra vole	19	203	526	2596
Unknown vole	8	15	25	48
Shrews	23	148	278	716
Ermine	2	2	2	2
Least Weasel	3	7	10	15
Bad quality	14	96	172	845
Total	40	636	3238	20 172

Note: Row "total" refers to the number of sampling units that were available for observations, i.e., sum of active camera traps included in the study, total number of five-day units, camera trap and days, and the total number of movement trigger releases.

Table A2. Parameters estimates of colonization probability (γ), extinction probability (ε) and initial season occupancy (ψ) given as the means of the posterior distribution and 95% credible intervals (CI).

Parameter	Species	Posterior mean	95% CI
γ	Lemming	0.005	0.002–0.009
ε	Lemming	0.335	0.180–0.512
ψ	Lemming	0.058	0.010–0.146
γ	Grey-sided vole	0.042	0.032–0.052
ε	Grey-sided vole	0.192	0.154–0.234
ψ	Grey-sided vole	0.383	0.240–0.533
γ	Tundra vole	0.025	0.018–0.033
ε	Tundra vole	0.217	0.156–0.283
ψ	Tundra vole	0.241	0.121–0.386
γ	Shrew	0.026	0.018–0.036
ε	Shrew	0.263	0.185–0.346
ψ	Shrew	0.215	0.046–0.420

Paper II

A dynamic occupancy model for interacting species with two spatial scales

In review in Journal of Agricultural, Biological and Environmental Statistics

RESEARCH ARTICLE

A dynamic occupancy model for interacting species with two spatial scales

Authors:

Eivind Flittie Kleiven[1], Frederic Barraquand[2,3], Olivier Gimenez[4], John-André Henden[1], Rolf Anker Ims[1], Eeva M. Soininen[1] & Nigel Gilles Yoccoz[1]

[1] UiT - The Arctic University of Norway, Department of Arctic and Marine Biology, Tromsø, Norway

[2] CNRS, Institute of Mathematics of Bordeaux, Talence, France

[3] Integrative and Theoretical Ecology, LabEx COTE, University of Bordeaux, Pessac, France

[4] CEFE, Université Montpellier, CNRS, EPHE, IRD, Universite Paul Valéry Montpellier 3, Montpellier, France

Corresponding author email: eivind.f.kleiven@uit.no

Abstract

Occupancy models have been extended to account for either multiple spatial scales or species interactions in a dynamic setting. However, as interacting species (e.g., predators and prey) often operate at different spatial scales, including nested spatial structure might be especially relevant to models of interacting species. Here we bridge these two model frameworks by developing a multi-scale two-species occupancy model. The model is dynamic, i.e. it estimates initial occupancy, colonization and extinction probabilities—including probabilities conditional to the other species' presence. With a simulation study, we demonstrate that the model is able to estimate parameters without marked bias under low, medium and high average occupancy probabilities, as well as low, medium and high detection probabilities. We further evaluate the model's ability to deal with sparse field data by applying it to a multi-scale camera trapping dataset on a mustelid-rodent predator-prey system. Most parameters are accurately estimated, although very sparse observations of predators in our case study make two parameters unidentifiable at the largest spatial scale. More broadly, our model framework creates opportunities to explicitly account for the spatial structure found in many spatially nested study designs, and to study interacting species that have contrasted movement ranges with camera traps.

Keywords: co-occurrence, multi-scale, occupancy, predator-prey, spatial, species interactions

1 Introduction

Much of the data available to ecologists consists of species occurrences, which in turn have sparked the development of statistical models to analyse such data (Bailey *et al.*, 2014). Due to their ability to model species occurrences while accounting for imperfect detection and therefore unobserved species, occupancy models have become widely used in ecology (Bailey *et al.*, 2014; Guillera-Arroita, 2017). Initial formulations of occupancy models estimated species occupancy across multiple sites that were assumed to be spatially independent (MacKenzie *et al.*, 2002). However, this assumption is rarely met in the field (Johnson *et al.*, 2013), and failing to account for spatial dependencies will lead to overconfidence in estimated uncertainties, and might in some cases lead to bias in estimated effects of predictor variables (Guélat & Kéry, 2018).

There are numerous extensions of occupancy models to incorporate spatial dependencies. In static occupancy models, occupancy can be made dependent on the occupancy probability of neighboring sites (Bled *et al.*, 2011; Eaton *et al.*, 2014; Yackulic *et al.*, 2014; Broms *et al.*, 2016), while in dynamic models (i.e., models that explicitly estimate change over time), colonization probability can be made a function of latent occupancy status at nearby sites. Spatial dependencies may be formulated as explicit functions of distance or connectivity between sites (Sutherland *et al.*, 2014; Chandler *et al.*, 2015), or in the form of random spatial effects (Johnson *et al.*, 2013; Rota *et al.*, 2016b).

Data from many ecological studies exhibit multiple nested spatial scales, which mirrors the fact that population dynamics result from different processes occurring at multiple scales (Baumgardt *et al.*, 2019). Accordingly, recently developed multi-scale occupancy models enable analyses of data from designs with such a hierarchy of spatial scales (Nichols *et al.*, 2008; Aing *et al.*, 2011; Mordecai *et al.*, 2011; Kéry & Royle, 2015; Smith & Goldberg, 2020), and can be extended to dynamic versions to estimate colonization and extinction probabilities (Tingley *et al.*, 2018).

A parallel development of occupancy models—dynamic multi-species models— addresses how interacting species co-occur over time (MacKenzie *et al.*, 2004; Waddle *et al.*, 2010; Richmond *et al.*, 2010; Rota *et al.*, 2016a; MacKenzie *et al.*, 2017; Fidino *et al.*, 2019; Marescot *et al.*, 2020). These models have great potential to increase our knowledge of species interactions. However, interacting species in general, and predators and prey in particular, often move at different spatial scales (de Roos *et al.*, 1998; Fauchald *et al.*, 2000). Incorporating the multiple spatial scales of interacting species would therefore lead to more intuitive and ecologically meaningful model parameters as colonization and extinction parameters may represent different ecological processes on different spatial scales.

Here we build on dynamic multi-species models by MacKenzie *et al.* (2017) and Fidino *et al.* (2019), as well as the dynamic multi-scale occupancy model by Tingley *et al.* (2018) to develop a multi-scale dynamic two-species occupancy model. In this model, initial occupancy, colonization and extinction probabilities are estimated at two spatial scales, i.e. both at site level and at a block level, spanning a cluster of sites. After describing the model, we perform a simulation study to investigate potential issues of bias and precision under different scenarios. Finally, we apply the model to a camera trapping data set with two spatial scales to estimate the predator-prey interaction strength between small mustelids and small rodents.

2 Methods

2.1 Case study

The case study that motivated the development of this model was a camera trap dataset from the long-term monitoring program COAT (Climate-ecological Observatory for Arctic Tundra, Ims *et al.*, 2013). The camera trapping program targets small rodents and their (small) mustelid predators. Here rodents (grey-sided vole *Myodes rufocanus*, tundra vole *Microtus oeconomus* and Norwegian lemming *Lemmus lemmus*) constitute prey, while mustelids (stoat *Mustela erminea* and least weasel *Mustela nivalis*) constitute predators. Rodents and mustelids have for decades been known to exhibit a predator-prey interaction (Hanski *et al.*, 1991). However, estimating the prevalence and strength of that interaction has been difficult, as reliable data—especially on mustelids—have previously been lacking (King & Powell, 2006). The camera trap monitoring was started in the autumn of 2015 and consisted of 4 blocks, with 11 camera trap sites within each block. In the summer of 2018, the monitoring was expanded by 4 blocks, containing 12 camera trap sites each, to make up a total of 8 blocks. The camera traps, described by Soininen *et al.* (2015), are functional year-round in arctic tundra habitats (70°20'N 29°38'E , Mölle *et al.*, 2021). The sampling design has a multi-scale structure, where sites (camera traps), are spaced >300m apart, but clustered in blocks of 11 to 12 cameras covering two different habitats, snowbeds and hummock tundra (see Appendix S1). This spatial structure can be matched to the movement ranges of small rodents and mustelids, where sites represent independent samples of rodent presence and blocks represent independent samples of mustelid presence (Hellstedt & Henttonen, 2006). Since mustelid observations almost only occurred in the snowbed habitat, we chose to focus only on these sites, reducing the number of cameras to 5 - 6 per block. As the rodents are known to exhibit rapid local scale colonization-extinction dynamics (Andreassen & Ims, 2001) we here define a primary occasion as one week (i.e. 7 days) and secondary occasions as the days within that week. While mustelids have slower demographic processes than small rodents, they are assumed to show a spatially aggregative response (movement towards prey-rich areas) on a short time scale (i.e., changing foraging grounds from one week to the next, Hellstedt & Henttonen, 2006). As there were particularly few observations of least weasel and Norwegian lemming, the analysis could not be conducted at the species level. However, on the Arctic tundra, rodents and mustelids can be considered functional groups as both mustelid species prey on all rodent species. We therefore combine the data for the two functional groups in a multi-state occupancy dataset with 4 states (U = none of the species are observed, A = only small rodents observed, B = only small mustelids observed or AB = both small rodents and small mustelids are observed). When analyzing the data from the case study, we included all weeks from the beginning of the monitoring in 2015, resulting in a total of 203 weeks. The case study is viewed as an inspiration for the following model framework, which is nonetheless more general.

2.2 Model framework and latent ecological states

Compared to the classical occupancy model, we have added an additional spatial level so that we have $b \in \{1,...,B\}$ blocks, each of which contains $k \in \{1,...,K\}$ sampling sites. Each sampling site is surveyed over $t \in \{1,...,T\}$ sampling occasions (hereafter primary occasions). Between the primary occasions the populations are assumed to be open (i.e. the species can colonize or go extinct). Within each primary occasion each site is sampled J times, $j \in \{1,...,J\}$ being the index of the survey (hereafter secondary occasion). Between the secondary occasions the populations are assumed to be closed (the species are assumed to neither colonize nor go extinct at any site) . For each secondary occasion j, considering two species (or functional group), any given site can then either be observed as unoccupied ($y_{b,k,t,j} = U$), occupied by species A only ($y_{b,k,t,j} = A$), occupied by species B only ($y_{b,k,t,j} = B$) or occupied by both species A and B ($y_{b,k,t,j} = AB$). These replicated samples within primary occasions, during which the populations are assumed to be closed, allow for the estimation of the detection process (MacKenzie *et al.*, 2017). The true latent state of each site (k) during each primary occasion (t) in a given block (b) can then be described with a latent variable $z_{b,k,t}$, that can take on any of the same 4 states. In this model we also consider an ecological process on the block level by describing a latent block state, $x_{b,t}$, that can take on any of the same four states as the latent site level state (U, A, B, or AB). This process occurs on a larger spatial scale than the site level, and will for instance in our case study represent the spatial scale of dispersal (e.g. changing home ranges) for mustelids, compared to the site level which represents the foraging movements within their home range. The site states will then depend on the state of the block they belong to (e.g. if a block is unoccupied by a given species, all sites within that block also have to be unoccupied by that species, although the converse is not true).

2.3 Transition model

After initial states have been modelled as a random categorical variable (see Appendix S1 for details), transitions between states are modelled with the transition probability matrices $\mathbf{\Theta}$ for the block level and $\mathbf{\Phi}(\boldsymbol{x}_{b,t})$ for the site level, with the latter depending on the block state (see Fig. 1 for an illustration of the spatial setup and the model structure).

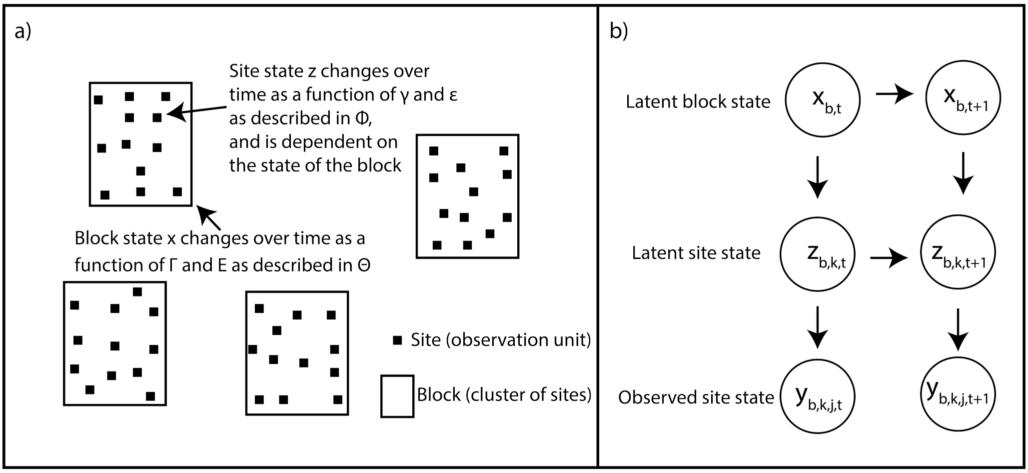


Figure 1: Conceptual diagram of the design and model structure. Panel (a) describes the multi-scale structure of the design, data sampling and state variables (probabilities) with clusters of sites nested in 4 blocks. Parameters γ and ε denote site level colonization and extinction probabilities, respectively, and Φ denotes the site transition probability matrix. Parameters Γ and E are the block level colonization and extinction probabilities, respectively, and Θ denotes the block level transition probability matrix. The diagram in panel (b) shows the conditional dependencies among the state variables in the model for observation j in primary occasion t at site k in block b.

It is assumed that the site colonization (γ) and extinction (ε) probabilities are dependent on the site state in the previous time step ($z_{k,b,t-1}$) as well as the block state in the same time step ($x_{b,t}$). The latter is assumed because site level colonization is only possible whenever the given species is already present in the block. Because site transition probabilities are dependent on the block state in the same time step ($\Phi(x_{b,t})$), it is possible that both a block and sites within that block are colonized in the same time step. However, because sites do not cover all available habitat within the block, blocks are not forced to go extinct even though all sites within that block are extinct. Hence, the model allows for a block to remain occupied even when all of its sites go extinct. On the other hand, when a block goes extinct, all of its sites are forced to go extinct (i.e. if $x_{b,t}$ = U then $z_{b,k,t}$ = U). The state transitions of a given species are only dependent on the presence of the other species in the previous time step. For that reason, it is important that the temporal resolution of the primary occasions correspond to the time scale relevant for the interaction of interest.

The transition probability matrix ($\boldsymbol{\Theta}$) for blocks (b) can be written as follows, with block level transition parameters defined in Table 1,

$$\boldsymbol{\Theta} = \begin{array}{ccc} & & \text{To block state} \\ & & \begin{array}{cccc} U & A & B & AB \end{array} \\ \text{From block state} & \begin{array}{c} \text{U} \\ \text{A} \\ \text{B} \\ \text{AB} \end{array} & \begin{pmatrix} (1-\Gamma_A)(1-\Gamma_B) & \Gamma_A(1-\Gamma_B) & (1-\Gamma_A)\Gamma_B & \Gamma_A\Gamma_B \\ E_A(1-\Gamma_{B|A}) & (1-E_A)(1-\Gamma_{B|A}) & E_A\Gamma_{B|A} & (1-E_A)\Gamma_{B|A} \\ (1-\Gamma_{A|B})E_B & \Gamma_{A|B}E_B & (1-\Gamma_{A|B})(1-E_B) & \Gamma_{A|B}(1-E_B) \\ E_{A|B}E_{B|A} & (1-E_{A|B})E_{B|A} & E_{A|B}(1-E_{B|A}) & (1-E_{A|B})(1-E_{B|A}) \end{pmatrix} \end{array} \tag{1}$$

Parameter	Verbal description
Γ_A	Probability that species A colonize a block at time t given that species B was absent at t-1
$\Gamma_{A\|B}$	Probability that species A colonize a block at time t given that species B was present at t-1
Γ_B	Probability that species B colonize a block at time t given that species A was absent at t-1
$\Gamma_{B\|A}$	Probability that species B colonize a block at time t given that species A was present at t-1
E_A	Probability that species A goes extinct in a block at time t given that species B was absent at t-1
$E_{A\|B}$	Probability that species A goes extinct in a block at time t given that species B was present at t-1
E_B	Probability that species B goes extinct in a block at time t given that species A was absent at t-1
$E_{B\|A}$	Probability that species B goes extinct in a block at time t given that species A was present at t-1

Table 1: Verbal definition of block level transition parameters.

Since the site transition probabilities depend on the block level state ($x_{b,t}$) we create one site transition matrix for each possible block state in the following way with site level transition parameters defined in Table 2:

$$\Phi(x_{b,t} = U) = \begin{array}{cc} & \text{To site state} \\ & \begin{array}{cccc} U & A & B & AB \end{array} \\ \text{From site state} \begin{array}{c} \mathrm{U} \\ \mathrm{A} \\ \mathrm{B} \\ \mathrm{AB} \end{array} & \begin{pmatrix} 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \\ 1 & 0 & 0 & 0 \end{pmatrix} \end{array} \tag{2}$$

$$\Phi(x_{b,t}=A)=\begin{array}{ccc} & & \text{To site state} \\ & & \begin{array}{cccc} U & A & B & AB \end{array} \\ \text{From site state} & \begin{array}{c} \text{U} \\ \text{A} \\ \text{B} \\ \text{AB} \end{array} & \begin{pmatrix} (1-\gamma_A) & \gamma_A & 0 & 0 \\ \varepsilon_A & (1-\varepsilon_A) & 0 & 0 \\ (1-\gamma_{A|B}) & \gamma_{A|B} & 0 & 0 \\ \varepsilon_{A|B} & (1-\varepsilon_{A|B}) & 0 & 0 \end{pmatrix} \end{array} \tag{3}$$

$$\Phi(x_{b,t}=B)=\begin{array}{ccc} & & \text{To site state} \\ & & \begin{array}{cccc} U & A & B & AB \end{array} \\ \text{From site state} & \begin{array}{c} \text{U} \\ \text{A} \\ \text{B} \\ \text{AB} \end{array} & \begin{pmatrix} (1-\gamma_B) & 0 & \gamma_B & 0 \\ (1-\gamma_{B|A}) & 0 & \gamma_{B|A} & 0 \\ \varepsilon_B & 0 & (1-\varepsilon_B) & 0 \\ \varepsilon_{B|A} & 0 & (1-\varepsilon_{B|A}) & 0 \end{pmatrix} \end{array} \tag{4}$$

$$\Phi(x_{b,t}=AB)=\begin{array}{ccc} & & \text{To site state} \\ & & \begin{array}{cccc} U & A & B & AB \end{array} \\ \text{From site state} & \begin{array}{c} \text{U} \\ \text{A} \\ \text{B} \\ \text{AB} \end{array} & \begin{pmatrix} (1-\gamma_A)(1-\gamma_B) & \gamma_A(1-\gamma_B) & (1-\gamma_A)\gamma_B & \gamma_A\gamma_B \\ \varepsilon_A(1-\gamma_{B|A}) & (1-\varepsilon_A)(1-\gamma_{B|A}) & \varepsilon_A\gamma_{B|A} & (1-\varepsilon_A)\gamma_{B|A} \\ (1-\gamma_{A|B})\varepsilon_B & \gamma_{A|B}\varepsilon_B & (1-\gamma_{A|B})(1-\varepsilon_B) & \gamma_{A|B}(1-\varepsilon_B) \\ \varepsilon_{A|B}\varepsilon_{B|A} & (1-\varepsilon_{A|B})\varepsilon_{B|A} & \varepsilon_{A|B}(1-\varepsilon_{B|A}) & (1-\varepsilon_{A|B})(1-\varepsilon_{B|A}) \end{pmatrix} \end{array} \tag{5}$$

Parameter	Verbal description
γ_A	Probability that species A colonize a site at time t given that species B was absent at t-1 and that the given block was colonized by species A at time t
$\gamma_{A\vert B}$	Probability that species A colonize a site at time t given that species B was present at t-1 and that the given block was colonized by species A and B at time t
γ_B	Probability that species B colonize a site at time t given that species A was absent at t-1 and that the given block was colonized by species B at time t
$\gamma_{B\vert A}$	Probability that species B colonize a site at time t given that species A was present at t-1 and that the given block was colonized by species B and A at time t
ε_A	Probability that species A goes extinct in a site at time t given that species B was absent at t-1 and that the given block was colonized by species B at time t and t-1
$\varepsilon_{A\vert B}$	Probability that species A goes extinct in a site at time t given that species B was present at t-1 and that the given block was colonized by species A at time t and t-1 and species B at time t
ε_B	Probability that species B goes extinct in a site at time t given that species A was absent at t-1 and that the given block was colonized by species B at time t and t-1
$\varepsilon_{B\vert A}$	Probability that species B goes extinct in a site at time t given that species A was present at t-1 and that the given block was colonized by species B at time t and t-1 and species A at time t

Table 2: Verbal definition of site level transition parameters.

Then the full model for both block- and site-level states can be written as

$$\begin{aligned} x_{b,t} \vert (x_{b,t-1}, \Gamma, E) &\sim \text{Categorical}(\Theta_{x_{b,t-1},\bullet}) \text{ for } t = 2, ..., T \\ z_{k,b,t} \vert (x_{b,t}, z_{k,b,t-1}, \gamma, \varepsilon) &\sim \text{Categorical}(\Phi(x_{b,t})_{z_{k,b,t-1},\bullet}) \text{ for } t = 2, ..., T. \end{aligned} \tag{6}$$

The indices $x_{b,t-1}$ describe the specific row in $\mathbf{\Theta}$ which has value $x_{b,t-1}$ and $z_{k,b,t-1}$ the row in $\mathbf{\Phi}$ which has value $z_{k,b,t-1}$, while $\bullet$ refers to all columns of that row.

2.4 Detection model

All observations on which the model relies on are coming from the site level. Hence, the detection probability can be modelled similarly to other two-species occupancy models. Models to estimate detection probabilities of one species dependent on the presence (Rota *et al.*, 2016a) or the detection of the other species (Miller *et al.*, 2012; Fidino *et al.*, 2019) exist. It is possible that such detection-interactions also exist for mustelids and rodents. However, as we have no indications that they do, for simplicity, we assumed that the detection of each species is independent of both the presence and detection of the other species. In the simulation study we also assumed that the detection probability is constant over sites, blocks and temporal occasions. However, note that a temporal binary covariate is added to the detection model in the empirical case study (see related section below). Let p_A and p_B be the detection probabilities of species A and B at a given site, the detection probability matrix (λ) can then be defined as

$$\lambda = \text{True state} \begin{array}{c} \\ U \\ A \\ B \\ AB \end{array} \overset{\text{Observed state}}{\begin{array}{cccc} U & A & B & AB \\ \left(\begin{array}{c} 1 \\ 1-p_A \\ 1-p_B \\ (1-p_A)(1-p_B) \end{array}\right. & \begin{array}{c} 0 \\ p_A \\ 0 \\ p_A(1-p_B) \end{array} & \begin{array}{c} 0 \\ 0 \\ p_B \\ (1-p_A)p_B \end{array} & \left.\begin{array}{c} 0 \\ 0 \\ 0 \\ p_A p_B \end{array}\right) \end{array}} \tag{7}$$

The observation at site k in block b at visit j during time t ($y_{k,b,j,t}$) can then be described by the following equation:

$$y_{k,b,j,t} | (x_{b,t}, z_{k,b,t}) \sim \text{Categorical}(\lambda_{z_{k,b,t},\bullet}) \tag{8}$$

with $z_{k,b,t}$ being the chosen row of the detection matrix (λ) to draw the observed state.

2.5 Simulation study

We conducted a simulation study to evaluate the performance of our model by examining potential issues of bias and variance in parameter estimates of colonization, extinction and detection. The spatiotemporal structure of the simulated data was largely inspired by our empirical case study (see section below for a more detailed explanation). Hence, we simulated data for 8 blocks, each containing 12 sites. We chose weeks as primary occasions and days within each week as secondary occasions corresponding to the expected rate of the dynamics of the empirical case study (Andreassen & Ims, 2001). We simulated data for 50 weeks (approximately one year). The chosen parameters values were also inspired by the predator-prey case study (e.g. E_A <E_B. See all parameter values in Appendix S1). To investigate how contrasting scenarios affected bias of parameters, we simulated data where both species had low (lo), medium (mo) and high (ho) average occupancy probability (with medium detection probability). In addition we simulated data where both species had low (ld), medium (md) and high (hd) detection probabilities (with medium occupancy probability, for more details, see Appendix S1). For each scenario, we simulated and analyzed 50 replicate datasets. The models were analyzed in a Bayesian framework using the JAGS software (Plummer, 2003) with the `jagsUI` package (Kellner, 2015) in `R v4.0.3` (R Core Team, 2020). We note that the model is a hidden Markov model and could also be fitted in a maximum likelihood framework using the Forward algorithm (McClintock *et al.*, 2020). We specified Uniform$(0,1)$ prior distributions for the detection, colonization and extinction probabilities and Uniform$(0,0.5)$ prior distributions for the initial occupancy probabilities. The MCMC algorithm was run with an adaptation phase (initial phase where the Bayesian sampler can adapt to increase efficiency) of a 1000 iterations. No additional iterations was discarded as burn-in. The model was run for 5000 iterations with a thinning of 10 (keep every 10 values in the chain to construct the posteriors) (Gelman *et al.*, 2013). Convergence was assessed by having a $\hat{R}$ <1.1 for all key parameters (Gelman *et al.*, 2013) and from graphical investigation of traceplots.

2.6 Analysing the empirical case study

All images of the two functional groups (i.e. rodents and mustelids) were identified by means of an algorithm for automatic classification of camera trap images. The MLWIC R-package (Tabak *et al.*, 2019) was used to train the algorithm (see Appendix S1 for more details). The resulting dataset describes, for each secondary occasion (day), if each functional group was detected or not. The blocks were established at different times, which resulted in inclusion of missing data since more than half of the sites were only observed for the last 47 weeks.

This study system exhibits strong seasonality that needs to be accounted for. However, there is a lack of detailed environmental data representative of the seasonality in this area. Therefore, we used temperature measurements from the camera traps to estimate the onset of winter (defined as the first day after summer with a daily mean temperature < 0) and the time of snow melt (defined as the first day in spring with daily mean > 0) for each camera trap individually. Such partitioning of the year will account for most of the seasonal changes affecting detection, as the winter period is mostly snow-covered, forcing small mammals into the subnivean space at the bottom of the snow pack, while the summer season is mostly snow-free. Indeed, presence of snow is known to impact the detection probability of small rodents on the Arctic tundra (Mölle *et al.*, 2021). Season was therefore included as a covariate on detection probabilities (p_A and p_B) through a logit-link function. The model was analyzed similarly to the simulation model.

In addition, we performed a prior sensitivity analysis by running the model with 3 different sets of priors. The first set contained flat uniform priors ($\sim$ Uniform$(0,1)$) except for the detection probabilities, which were given a Normal$(0,1)$ prior distributions since they are defined on a logit scale. For the second set we used centered priors by using a Beta$(4,4)$ distribution for all priors, again except for the detection probabilities which now were given a Logistic$(0,1)$ prior distribution. The third set of priors was specified to be skewed towards our ecological expectations, by using either a Beta$(2,4)$ or Beta$(4,2)$ depending on the expected relationships in a predator-prey system. Detection probabilities were given a Normal$(-0.5, 1)$ prior distribution on the logit scale (see Appendix S1). The prior sensitivity analysis was also used to investigate identifiability by additionally estimating prior-posterior overlap (Gimenez *et al.*, 2004). To assess the goodness of fit we calculated a Bayesian p-value as described by Kéry & Royle (2020) (see details in Appendix S1). To reach convergence with the field dataset we needed to run the model for 20 000 iterations, with 5 000 steps of adaptation. In addition we discarded the first 1000 iterations as burn-in and used a thinning of 20. We note that this was slightly longer than for the simulation study.

3 Results

3.1 Simulation study

All colonization and extinction probabilities at both spatial scales were estimated without bias for most data scenarios (Fig. 2 and Tables S5-S7 in Appendix S1). However, in the low detection scenario there was a slight positive bias in the block extinction probability of species B when species A were absent (E_B, 21% bias) and in the block extinction of species A when B were present ($E_{A|B}$, 20% bias), see Fig. 2. Both detection probabilities (p_A and p_B) were estimated without any apparent bias (Fig. S12 in Appendix S1). The initial values were also estimated without any obvious bias except for ψ_{AB} under the low occupancy and low detection scenario (Fig. S13 in Appendix S1).

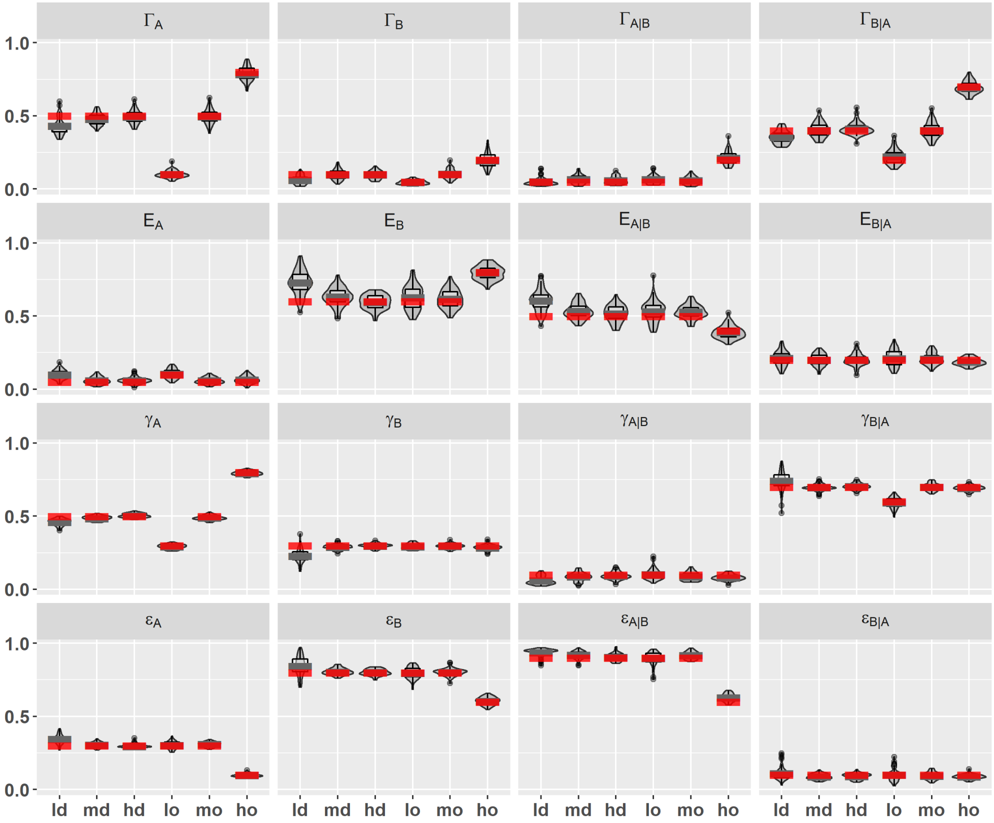


Figure 2: Violin plots and boxplots of the posterior means of site and block colonization (γ and Γ) as well as extinction probabilities (ε and E), from 50 simulation replicates. The thick red bar indicates the true parameter values while the thick grey bar indicates the average of the posterior means from the 50 simulated replicates. The x-axis displays the 6 different data scenarios: low, medium and high detection probability of both species (ld, md, hd) and low, medium and high average site occupancy probability of both species (lo, mo, ho).

3.2 *Empirical case study*

Rodents generally had a higher detection probability than mustelids, and mustelids were less detectable during winter than in summer (for detection probabilities, see Appendix S1).

For rodents, we found a clear indication of strong mustelid impacts at the site level, as mustelid presence increased the site level rodent extinction probability from 0.09 to 0.33 (an increase of 0.23 with 95% CRI (0.12-0.36)). For colonization/extinction probabilities that did not show marked effects, see Fig. 3. At the block level, on the other hand, rodent extinction appeared unaffected by the presence of mustelids in the block. Meanwhile, the estimated effects of rodents on mustelids were small and uncertain (Table S9 in Appendix S1). We note, however, that two of the block-level parameters (i.e. block-level colonization of rodents when mustelids were present ($\Gamma_{A|B}$) and block-level extinction of mustelids alone (E_B)) were estimated with a large uncertainty. They were also quite sensitive to prior choice and probably unidentifiable in practice, according to the prior-posterior overlap (Appendix S1, section 4). This makes ecological inference about these parameters impossible for our case study (See Tables S8 and S9 in Appendix S1 for numerical values of estimates of all colonization and extinction probabilities, and the differences between them, with corresponding credible intervals).

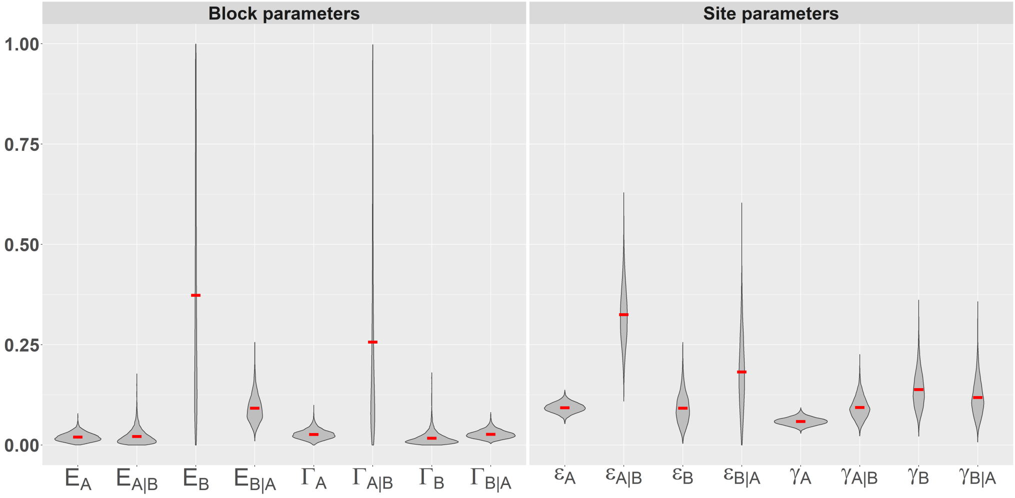


Figure 3: Violin plots of the estimated posterior distribution of site and block colonization (γ and Γ) and extinction probabilities (ε and E) for the case study. Subscript A denotes small rodents and B denote small mustelids. Red bars indicate posterior means.

4 Discussion

We constructed a dynamic multi-scale occupancy model for interacting species. Through simulations, we demonstrated that the model is able to produce unbiased estimates of colonization and extinction parameters under most scenarios of average presence and detection. We find the current extension of the dynamic multi-species occupancy framework to nested spatial scales useful for two reasons. First, it is possible to explicitly account for the spatial structures found in many spatially nested study designs. This should reduce bias and increase precision in parameter estimates. Second, it makes it possible to investigate the joint colonization and extinction dynamics of species pairs that have contrasted movement ranges, where the daily movement range of one species (e.g., the predator) is equivalent to the dispersal distance for another species (e.g., the prey). Analysing data from a multi-scale monitoring program of two species with contrasted movements ranges (cf. our mustelid-rodent case study) with a single scale model would make little sense. Not only would this violate the assumption of spatial independence, it would also compromise inference in terms of ecologically meaningful model parameters. Indeed, the two spatial scales represent different ecological processes for predator and prey: the spatial scale of short distance colonization for rodents (between sites) corresponds to the scale of within-home range movements for mustelids (e.g. foraging), while the spatial scale of long distance colonization for rodents (between blocks) correspond for mustelids to the scale of between-home range movements (e.g. changing territories). Our work therefore helps to bridge the gap between the separate developments of multi-scale dynamic occupancy models (Tingley *et al.*, 2018) and dynamic multi-species occupancy models (MacKenzie *et al.*, 2017; Fidino *et al.*, 2019).

The simulation study showed that all model parameters are estimated without any considerable bias in most data scenarios (see Appendix S1 Table S6). The exception is the low detection scenario where small biases appeared for the block extinction probability of A when B is present ($E_{A|B}$) and in block extinction probability of B when A is absent (E_B). A likely explanation is that when few blocks are occupied with species B, there are also few blocks that have the potential to go extinct. Furthermore, the block-level parameters appear to vary more between models than the site-level parameters. This could result from all observations coming from the site-level, with the block-level parameters thus depending on the reconstruction of two latent states. Also, the nested study design has logically more sites than blocks, providing more data to estimate the site-level parameters than the block-level parameters. If an auxiliary data stream constituted of indices of block presence (e.g. snow track data for mustelids) could be constructed, it could be fed to a joint model to increase the precision on estimated block-level parameters. In the current model framework, the simulation study demonstrates that care has to be taken when analysing data on species with low detection probability. We encourage further work on the data requirements of similarly complex multi-scale occupancy models, possibly with more informed priors and/or additional data streams. We consider this simulation exercise as opening doors rather than providing definitive answers.

Our real-world case study incorporates some of the classical empirical challenges that ecologists have to deal with. First, the dataset has a high proportion of missing data and detection probability differs between the functional groups. Second, the dataset comes from an ecosystem with both strong seasonality and multi-year cyclicity, which likely affects the detection, colonization and extinction probabilities. Third, we use functional groups instead of species, potentially adding some unexplained variability in the data. Moreover, we treated blocks as if they were identical, which is likely to be an oversimplification. Even without addressing these challenges specifically in the model (with the exception of a seasonal covariate on detection probability), the model seems to be able to identify most parameters. However, it is evident that some parameters ($\Gamma_{A|B}$ and E_B) are estimated with large uncertainties, to a degree where it limits the ecological inferences that can be made (Fig. 3). Why $\Gamma_{A|B}$ and E_B are the parameters that are not practically identifiable can be explained. First, these are block-level parameters, and by design fewer transitions between states occur at block level (since there are less blocks than sites). These are also predator-related parameters, conditional on predator presence, and there were fewer observations of mustelids than of rodents (see Table S4 in Appendix S1). It is expected that predators have fewer observations than prey as they usually are at lower density. However, mustelids are also known to be especially difficult to observe (King & Powell, 2006). Our empirical case study appears thus to constitute the minimal data requirements for this model. It is likely that a longer time series would increase parameter precision (Guillera-Arroita *et al.*, 2014), especially in the case study system where the population dynamics are ruled by 4-year population cycles. Other predator-prey systems where the predator is more conspicuous might also make it easier to identify all parameters including at block level.

Despite the abovementioned challenges, the model gave some evidence of a predator-prey interaction between mustelids and rodents (Hanski *et al.*, 1993; Norrdahl & Korpimäki, 2000). On the site level, mustelid presence lead to a four-fold increase in rodent extinction probability, which is probably due to direct effects (killing) and indirect effects (predator avoidance) of predation by mustelids. This result is coherent with the hypotheses that mustelids are able to induce population crashes in boreal and arctic rodent populations (Hanski *et al.*, 1993). Most of the current observational evidence for this hypothesis comes from indirect observations of mustelids (snow tracks Korpela *et al.*, 2014 and winter nests Gilg *et al.*, 2003) and spatially aggregated rodent counts once or twice per year: we provide here some support for the predation hypothesis from direct observations of mustelid and rodent individuals, at spatial and temporal scales commensurate to those of theoretical models.

We note that numerous extensions to this model could be possible. Although we only included a simple binary covariate (season) for the detection probabilities in the case study, the model could be extended to include both temporal and spatial covariates on initial occupancy, colonization and extinction probabilities by including a multinomial logit link function following earlier multi-species occupancy models (Rota *et al.*, 2016a; Fidino *et al.*, 2019; Kéry & Royle, 2020). Our model also has the potential to be extended to more species (similar to models by Rota *et al.* 2016a and Fidino *et al.* 2019) or spatial levels. However, complicating the model further (e.g. by increasing number of species) may require regularization (shrinkage of some parameters) or variable selection (Hutchinson *et al.*, 2015; McElreath, 2015).

To conclude, we developed a dynamic occupancy model for interacting species at two spatial scales, which estimates initial occupancy, colonization and extinction probabilities as well as detection probabilities. Applied to northern rodent population dynamics, the model provided evidence consistent with the predation hypothesis, while accounting for the fact that interactions between predators and prey arise from processes occurring at two nested spatial scales.

5 Data Availability

All data and code used in this manuscript are available at UiT Open Research Data (doi.org/10.18710/ZLW59W).

References

Aing, C., Halls, S., Oken, K., Dobrow, R. & Fieberg, J. (2011). A bayesian hierarchical occupancy model for track surveys conducted in a series of linear, spatially correlated, sites. *Journal of Applied Ecology*, 48, 1508–1517.

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

Bailey, L.L., MacKenzie, D.I. & Nichols, J.D. (2014). Advances and applications of occupancy models. *Methods in Ecology and Evolution*, 5, 1269–1279.

Baumgardt, J.A., Morrison, M.L., Brennan, L.A. & Campbell, T.A. (2019). Developing rigorous monitoring programs: Power and sample size evaluations of a robust method for monitoring bird assemblages. *Journal of Fish and Wildlife Management*, 10, 480–491.

Bled, F., Royle, J.A. & Cam, E. (2011). Hierarchical modeling of an invasive spread: the eurasian collared-dove streptopelia decaocto in the united states. *Ecological Applications*, 21, 290–302.

Broms, K.M., Hooten, M.B., Johnson, D.S., Altwegg, R. & Conquest, L.L. (2016). Dynamic occupancy models for explicit colonization processes. *Ecology*, 97, 194–204.

Chandler, R.B., Muths, E., Sigafus, B.H., Schwalbe, C.R., Jarchow, C.J. & Hossack, B.R. (2015). Spatial occupancy models for predicting metapopulation dynamics and viability following reintroduction. *Journal of Applied Ecology*, 52, 1325–1333.

de Roos, A.M., McCauley, E. & Wilson, W.G. (1998). Pattern formation and the spatial scale of interaction between predators and their prey. *Theoretical Population Biology*, 53, 108 – 130.

Eaton, M.J., Hughes, P.T., Hines, J.E. & Nichols, J.D. (2014). Testing metapopulation concepts: effects of patch characteristics and neighborhood occupancy on the dynamics of an endangered lagomorph. *Oikos*, 123, 662–676.

Fauchald, P., Erikstad, K.E. & Skarsfjord, H. (2000). Scale-dependent predator-prey interactions: The hierarchical spatial distribution of seabirds and prey. *Ecology*, 81, 773–783.

Fidino, M., Simonis, J.L. & Magle, S.B. (2019). A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species. *Methods in Ecology and Evolution*, 10, 233–244.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A. & Rubin, D.B. (2013). *Bayesian data analysis*. CRC press.

Gilg, O., Hanski, I. & Sittler, B. (2003). Cyclic dynamics in a simple vertebrate predator-prey community. *Science*, 302, 866–868.

Gimenez, O., Viallefont, A., Catchpole, E.A., Choquet, R. & Morgan, B.J. (2004). Methods for investigating parameter redundancy. *Animal Biodiversity and Conservation*, 27, 561–572.

Guillera-Arroita, G. (2017). Modelling of species distributions, range dynamics and communities under imperfect detection: advances, challenges and opportunities. *Ecography*, 40, 281–295.

Guillera-Arroita, G., Lahoz-Monfort, J.J., MacKenzie, D.I., Wintle, B.A. & McCarthy, M.A. (2014). Ignoring imperfect detection in biological surveys is dangerous: A response to 'fitting and interpreting occupancy models'. *PLOS ONE*, 9, 1–14.

Guélat, J. & Kéry, M. (2018). Effects of spatial autocorrelation and imperfect detection on species distribution models. *Methods in Ecology and Evolution*, 9, 1614–1625.

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

Hanski, I., Turchin, P., Korpimäki, E. & Henttonen, H. (1993). Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, 364, 232–235.

Hellstedt, P. & Henttonen, H. (2006). Home range, habitat choice and activity of stoats (mustela erminea) in a subarctic area. *Journal of Zoology*, 269, 205–212.

Hutchinson, R.A., Valente, J.J., Emerson, S.C., Betts, M.G. & Dietterich, T.G. (2015). Penalized likelihood methods improve parameter estimates in occupancy models. *Methods in Ecology and Evolution*, 6, 949–959.

Ims, R., Jepsen J., U., Stien, A. & Yoccoz, N.G. (2013). *Science plan for COAT: Climate-ecological Observatory for Arctic Tundra*. Fram Centre Report Series 1. Fram Centre, Norway.

Johnson, D.S., Conn, P.B., Hooten, M.B., Ray, J.C. & Pond, B.A. (2013). Spatial occupancy models for large data sets. *Ecology*, 94, 801–808.

Kellner, K. (2015). jagsui: a wrapper around rjags to streamline jags analyses. *R package version*, 1.

Kéry, M. & Royle, J.A. (2015). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 1: Prelude and Static Models*. Academic Press.

Kéry, M. & Royle, J.A. (2020). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 2: Dynamic and Advanced Models*. Academic Press.

King, C.M. & Powell, R.A. (2006). *The natural history of weasels and stoats: ecology, behavior, and management*. Oxford University Press.

Korpela, K., Helle, P., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., Pietiäinen, H., Sundell, J., Valkama, J. & Huitu, O. (2014). Predator-vole interactions in northern europe: the role of small mustelids revised. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20142119.

MacKenzie, D.I., Bailey, L.L. & Nichols, J.D. (2004). Investigating species co-occurrence patterns when species are detected imperfectly. *Journal of Animal Ecology*, 73, 546–555.

MacKenzie, D.I., Nichols, J.D., Lachman, G.B., Droege, S., Andrew Royle, J. & Langtimm, C.A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83, 2248–2255.

MacKenzie, D.I., Nichols, J.D., Royle, J.A., Pollock, K.H., Bailey, L. & Hines, J.E. (2017). *Occupancy estimation and modeling: inferring patterns and dynamics of species occurrence*. Elsevier.

Marescot, L., Lyet, A., Singh, R., Carter, N. & Gimenez, O. (2020). Inferring wildlife poaching in southeast asia with multispecies dynamic occupancy models. *Ecography*, 43, 239–250.

McClintock, B.T., Langrock, R., Gimenez, O., Cam, E., Borchers, D.L., Glennie, R. & Patterson, T.A. (2020). Uncovering ecological state dynamics with hidden markov models. *Ecology letters*, 23, 1878–1903.

McElreath, R. (2015). *Statistical rethinking: A Bayesian course with examples in R and Stan*. CRC press.

Miller, D.A.W., Brehme, C.S., Hines, J.E., Nichols, J.D. & Fisher, R.N. (2012). Joint estimation of habitat dynamics and species interactions: disturbance reduces co-occurrence of non-native predators with an endangered toad. *Journal of Animal Ecology*, 81, 1288–1297.

Mölle, J.P., Kleiven, E.F., Ims, R.A. & Soininen, E.M. (2021). Using subnivean camera traps to study arctic small mammal community dynamics during winter. *Arctic Science*, pp. 1–17.

Mordecai, R.S., Mattsson, B.J., Tzilkowski, C.J. & Cooper, R.J. (2011). Addressing challenges when studying mobile or episodic species: hierarchical Bayes estimation of occupancy and use. *Journal of Applied Ecology*, 48, 56–66.

Nichols, J.D., Bailey, L.L., O'Connell Jr., A.F., Talancy, N.W., Campbell Grant, E.H., Gilbert, A.T., Annand, E.M., Husband, T.P. & Hines, J.E. (2008). Multi-scale occupancy estimation and modelling using multiple detection methods. *Journal of Applied Ecology*, 45, 1321–1329.

Norrdahl, K. & Korpimäki, E. (2000). The impact of predation risk from small mustelids on prey populations. *Mammal Review*, 30, 147–156.

Plummer, M. (2003). Jags: A program for analysis of bayesian graphical models using gibbs sampling. In: *Proceedings of the 3rd international workshop on distributed statistical computing*. Vienna, Austria., vol. 124, pp. 1–10.

R Core Team (2020). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Richmond, O.M.W., Hines, J.E. & Beissinger, S.R. (2010). Two-species occupancy models: a new parameterization applied to co-occurrence of secretive rails. *Ecological Applications*, 20, 2036–2046.

Rota, C.T., Ferreira, M.A.R., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W. & Millspaugh, J.J. (2016a). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7, 1164–1173.

Rota, C.T., Wikle, C.K., Kays, R.W., Forrester, T.D., McShea, W.J., Parsons, A.W. & Millspaugh, J.J. (2016b). A two-species occupancy model accommodating simultaneous spatial and interspecific dependence. *Ecology*, 97, 48–53.

Smith, M.M. & Goldberg, C.S. (2020). Occupancy in dynamic systems: accounting for multiple scales and false positives using environmental dna to inform monitoring. *Ecography*, 43, 376–386.

Soininen, E.M., Jensvoll, I., Killengreen, S.T. & Ims, R.A. (2015). Under the snow: a new camera trap opens the white box of subnivean ecology. *Remote Sensing in Ecology and Conservation*, 1, 29–38.

Sutherland, C.S., Elston, D.A. & Lambin, X. (2014). A demographic, spatially explicit patch occupancy model of metapopulation dynamics and persistence. *Ecology*, 95, 3149–3160.

Tabak, M.A., Norouzzadeh, M.S., Wolfson, D.W., Sweeney, S.J., Vercauteren, K.C., Snow, N.P., Halseth, J.M., Di Salvo, P.A., Lewis, J.S., White, M.D., Teton, B., Beasley, J.C., Schlichting, P.E., Boughton, R.K., Wight, B., Newkirk, E.S., Ivan, J.S., Odell, E.A., Brook, R.K., Lukacs, P.M., Moeller, A.K., Mandeville, E.G., Clune, J. & Miller, R.S. (2019). Machine learning to classify animal species in camera trap images: Applications in ecology. *Methods in Ecology and Evolution*, 10, 585–590.

Tingley, M.W., Stillman, A.N., Wilkerson, R.L., Howell, C.A., Sawyer, S.C. & Siegel, R.B. (2018). Cross-scale occupancy dynamics of a postfire specialist in response to variation across a fire regime. *Journal of Animal Ecology*, 87, 1484–1496.

Waddle, J.H., Dorazio, R.M., Walls, S.C., Rice, K.G., Beauchamp, J., Schuman, M.J. & Mazzotti, F.J. (2010). A new parameterization for estimating co-occurrence of interacting species. *Ecological Applications*, 20, 1467–1475.

Yackulic, C.B., Reid, J., Nichols, J.D., Hines, J.E., Davis, R. & Forsman, E. (2014). The roles of competition and habitat in the dynamics of populations and species distributions. *Ecology*, 95, 265–279.

Appendix S1: A dynamic occupancy model for interacting species with two spatial scales

1 Model specification

1.1 Initial occupancy state

It is necessary to define in what state the blocks and sites are in the first primary occasion (or initial state). Since all observations are exclusively done at the site level and there is no information regarding the site state before the first sampling season, the initial latent site state ($z_{k,b,t=1}$) is modeled as the following categorical random variable (generalized Bernoulli), where k denotes site, b block and t primary occasion

$$z_{k,b,t=1} \sim \text{Categorical}(\psi_b) \tag{1}$$

where ψ_b is a vector describing the initial state probabilities of sites within a given block. To assure that the initial state probabilities sum to one, one state probability is obtained through subtraction. Then the initial state probability vector (ψ_b) can be written as

$$\begin{array}{rccccc} & & \text{U} & \text{A} & \text{B} & \text{AB} \\ \psi_b = & [& (1-\psi_{A_b}-\psi_{B_b}-\psi_{AB_b}) & \psi_{A_b} & \psi_{B_b} & \psi_{AB_b}] \end{array} \tag{2}$$

where ψ_{A_b}, ψ_{B_b} and ψ_{AB_b} are the probabilities that a site within a given block will be in state A, B or AB respectively in the first primary occasion. Since there are no direct observations of the latent block state, it is assumed that the initial latent block state ($x_{b,t=1}$) is solely a function of the states of the sites within the given block (e.g. if at least one site is in state A and no sites are in state B or AB, then the block state is A).

We note that the initial state model presented above is rather simplistic. The reason for this is that the mustelid-rodent case study has a limited number of spatial replicates, compared to the relatively large number of primary occasions. Also the ecological interest in this example is mainly in the dynamical part of the model. In other cases where there is a stronger ecological interest in the initial states we recommend implementing a initial state model where site state are dependent on block states, in line with the way we model transition probabilities.

2 Simulation study

To investigate how detection and occupancy probability affect bias we simulate data from 6 sets of parameter values: 3 sets with varying detection probability and 3 sets with varying occupancy probability. See exact parameter values in Table S1. The parameters values for all scenarios was chosen to reflect a predator-prey setting, e.g. $\Gamma_A > \Gamma_{A|B}$ and $\epsilon_A < \epsilon_{A|B}$. Moreover, varying detection and occupancy scenarios was based on a review of occupancy studies by Specht *et al.* (2017) defining common species as occupancy > 0.5, rare species as occupancy < 0.3 and cryptic species as detection probability < 0.3.

Parameter	*ld*	*md*	*hd*	*lo*	*mo*	*ho*
Γ_A	0.5	0.5	0.5	0.1	0.5	0.8
Γ_B	0.1	0.1	0.1	0.05	0.1	0.2
$\Gamma_{A\|B}$	0.05	0.05	0.05	0.05	0.05	0.2
$\Gamma_{B\|A}$	0.4	0.4	0.4	0.2	0.4	0.7
E_A	0.05	0.05	0.05	0.1	0.05	0.05
E_B	0.6	0.6	0.6	0.6	0.6	0.8
$E_{A\|B}$	0.5	0.5	0.5	0.5	0.5	0.4
$E_{B\|A}$	0.2	0.2	0.2	0.2	0.2	0.2
p_A	0.2	0.5	0.9	0.5	0.5	0.5
p_B	0.1	0.5	0.8	0.5	0.5	0.5
γ_A	0.5	0.5	0.5	0.3	0.5	0.8
γ_B	0.3	0.3	0.3	0.3	0.3	0.3
$\gamma_{A\|B}$	0.1	0.1	0.1	0.1	0.1	0.1
$\gamma_{B\|A}$	0.7	0.7	0.7	0.6	0.7	0.7
ϵ_A	0.3	0.3	0.3	0.3	0.3	0.1
ϵ_B	0.8	0.8	0.8	0.8	0.8	0.6
$\epsilon_{A\|B}$	0.9	0.9	0.9	0.9	0.9	0.6
$\epsilon_{B\|A}$	0.1	0.1	0.1	0.1	0.1	0.1
$\psi_{U,t=1}$	0.5	0.5	0.5	0.6	0.5	0.4
$\psi_{A,t=1}$	0.25	0.25	0.25	0.2	0.25	0.3
$\psi_{B,t=1}$	0.15	0.15	0.15	0.15	0.15	0.2
$\psi_{AB,t=1}$	0.1	0.1	0.1	0.05	0.1	0.1

Table S1: Description of parameter values used in the simulation study under the 6 different scenarios. We use low, medium and high detection probability (ld, md, hd) and low, medium and high occupancy probability (lo, mo, ho).

We also plotted the trends in the simulated observed occupancy probability at site level (Figure S1). This helps to clearly describe the actual data that was used, and show that the contrasted scenarios give the expected gradient in observed occupancy, where the low detection and low occupancy scenarios result in the lowest number of observations, while the medium detection and occupancy also gives an intermediate number of observation. High occupancy and detection result in the highest number of observations, so that the simulated datasets all serve their purpose.

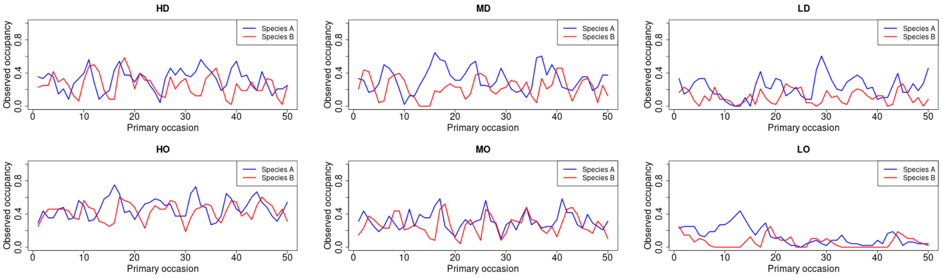


Figure S1: Description of proportion of sites observed as occupied in different primary occasions (weeks) in the different simulations scenarios. The red line indicate the observed occupancy of species A, while the blue line indicate the observed occupancy of species B.

3 Camera trapping data

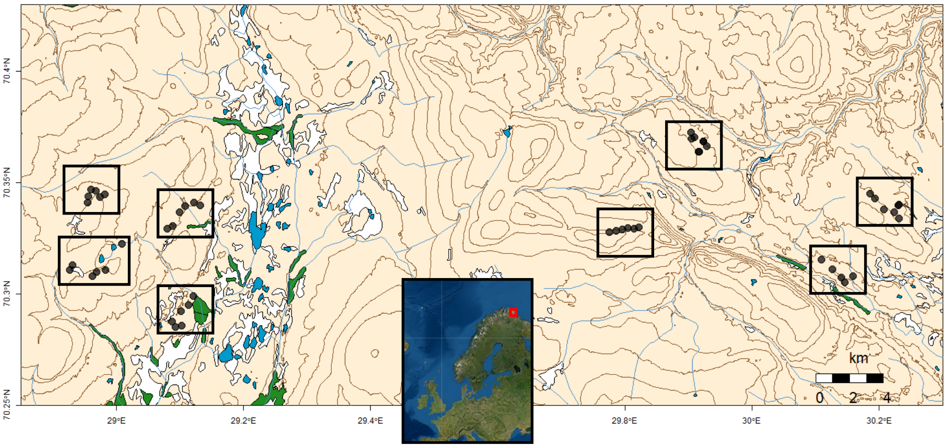


Figure S2: Map of the study area (Varanger peninsula, in northern Norway, red box), describing the spatial setup of the sampling design from the empirical case study. Black dots mark camera trapping sites and black boxes highlight blocks of camera traps.

To illustrate the real world applicability of our model we apply it to a camera trap data set from the long-term monitoring program COAT (Climate-ecological Observatory of the Arctic Tundra) on small rodents (grey-sided vole, tundra vole and norwegian lemming) and small mustelids (stoat and least weasel) on the Norwegian part of the low-arctic tundra. This monitoring program was started in autumn of 2015 and then consisted of 4 blocks of camera trap sites, with 11 sites with-in each block. In the summer of 2018 it was extended with 4 more blocks containing 12 sites within each block, to then make it a total of 8 blocks. The two groups of interest (i.e., small rodents and small mustelids) have different home ranges, so the spatial hierarchy in the sampling is designed so that sites (>300m apart) do not overlap the home range of the same individuals of small rodents, while they do so for small mustelids. The blocks are spaced out so that they do not overlap the home range of an individual of neither small rodents nor small mustelids (>3000m apart). At each camera trap site there is a tunnel containing a camera trap with a PIR-sensor places in a natural runway for small mustelids and small rodents. The cameras is out and active year round and monitors the animals in continuous time by capturing two consecutive pictures any time the PIR-sensor is triggered (see Soininen *et al.* (2015) for further details on camera site setup). All pictures captures by the cameras was automatically classified with the MLWIC R-package (Tabak *et al.*, 2019). The model was trained with a total of 47029 pictures from 8 different classes (see table S2 for details). The class “bad quality” was used for images where the quality is so low that it is likely that and animal could go undetected even though it was present (e.g. if the camera is full of snow or water). Such images were treated as missing observations in the data analysis. This training dataset was manually classified by experts (see Table S2 for classes and number of training pictures).

Class ID	Number of pictures
Bad quality	6695
Bird	1448
Empty	9001
Least Weasel	749
Lemming	8047
Shrew	8333
Stoat	3181
vole	9575
Total	47029

Table S2: Classes used for the training of the image classification model. In the right column, we show how many images were included in each category of the training data.

We used a separate test data consisting of 4425 expert classified images to validate the model. From these, the model classified 97.2% correctly.

The animals exhibit a day rhythm in activity patterns (Soininen *et al.*, 2015) hence we choose to discretize the data into weeks (periods of 7 days) as primary occasions and every day within a week as secondary occasions. We combine the data for the two species to a multi-state occupancy data set with 4 states (U = none of the species are observer, A = only small rodents observed, B = only small mustelids observed or AB = both small rodents and small mustelids are observed). To analyze this data we included all weeks from the beginning of the monitoring in 2015, making it a total of 203 weeks. This will include much missing data, since more then half of the sites were only observed for the last 47 weeks.

The data is from a seasonal system, with long snowy winters. In addition there is a multiyear dynamics with 3 to 5-years population cycles (Ims & Fuglei, 2005). This is visible in the observed data (see Fig. S3 and S4). Note that the number of observed sites increased during the study.

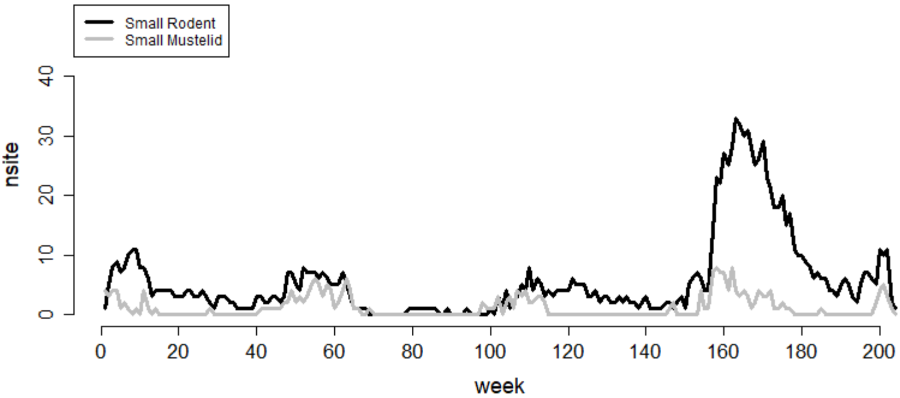


Figure S3: Number of occupied sites in the case study plotted against weeks (primary occasions). The black line indicate small rodents and the gray line indicates small mustelids

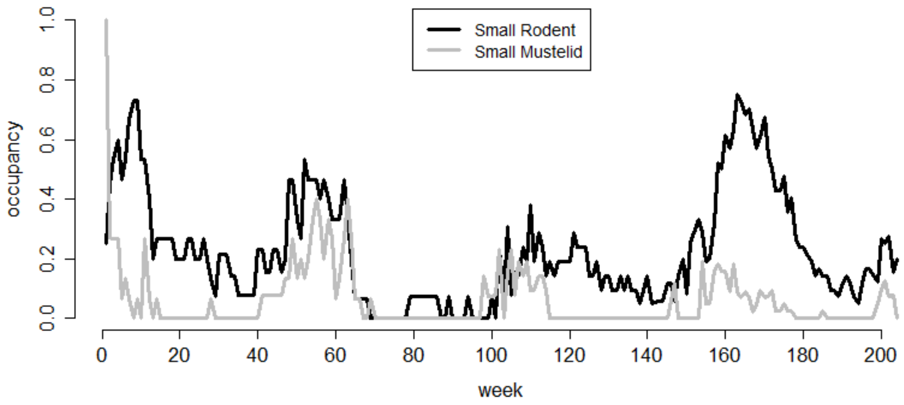


Figure S4: Proportion of active sites that were observed as occupied by either small rodents (black line) or small mustelids (gray line) in a given week (primary occasion).

Table S3 gives the number of transitions observed between the blocks states. It highlight that even though the case study cover many primary occasions, it does in fact not observe that many block level state transitions, especially so for states involving mustelids. We also see that some transitions are more common that others, something that potentially can give a hint about the data requirement of such a model.

$$
\begin{array}{cc}
 & \text{To site state} \\
\text{From site state} &
\begin{array}{c|cccc}
 & \mathrm{U} & \mathrm{A} & \mathrm{B} & \mathrm{AB} \\
\hline
U & 398 & 42 & 15 & 1 \\
A & 39 & 335 & 15 & 14 \\
B & 15 & 17 & 54 & 9 \\
AB & 0 & 14 & 13 & 12
\end{array}
\end{array}
$$

Table S3: This table gives the number of observed block state transition in the case study. A is used to indicate rodents and B to indicate mustelids.

4 Model checking for case study

4.1 Evaluating goodness of fit

Goodness-of-fit (GOF) testing is challenging for complex occupancy models analysed in a Bayesian framework and is often ignored in the ecological litterature (Conn *et al.*, 2018). However, some approaches have been developed to investigate the GOF for simple dynamic occupancy models (Kéry & Royle, 2020) and community occupancy models (Zipkin *et al.*, 2012). To assess the GOF in our case study analysis, we adopted the approach presented by Kéry & Royle (2020). This approach considers separate fit statistics for the open (between primary occasions) and closed (within primary occasions) part of the model. To be in line with Kéry & Royle (2020) we tested the GOF only on site level and did separate tests for the two species. The test for the open part of the model was done by calculating the number of observed and expected transitions between model states for each species separately. While for the closed part of the model, observed and expected detection frequencies at individual sites were calculated for the two species separately. A replicated dataset under the model was simulated. Both the observed and replicated datasets were compared to the expected number of transitions and detection frequencies to calculate χ^2 discrepancies as follows:

$$\chi^2_{\text{transition}} = (O_{\text{transition}} - E_{\text{transition}})^2 / E_{\text{transition}} \tag{3}$$

$$\chi^2_{\text{frequency}} = (O_{\text{frequency}} - E_{\text{frequency}})^2 / E_{\text{frequency}} \tag{4}$$

where $O_{\text{transition}}$ is the observed number of transitions between states, $E_{\text{transition}}$ is the number of transitions between states expected under the model (calculated from data simulated under the model), $O_{\text{frequency}}$ is the observed detection frequency within a primary occasion and $E_{\text{frequency}}$ is the detection frequency within a primary occasion expected under the model (calculated from the data simulated under the model).

As it is not clear how one would interpret the results of the GOF-test for the dynamic two-species occupancy model with nested spatial scales, we first applied the GOF-test on a data set simulated under the model (mid occupancy scenario from the simulation study) to investigate how the test would preform under ideal circumstances (see Fig. S5). However, we do stress that this is not a complete investigation of how this GOF-test performs for complex occupancy models. Furthermore, we want to highlight that more work is needed to understand the sensitivity of GOF-tests for complex occupancy models and how the outputs of these tests should be interpreted (Kéry & Royle, 2020).

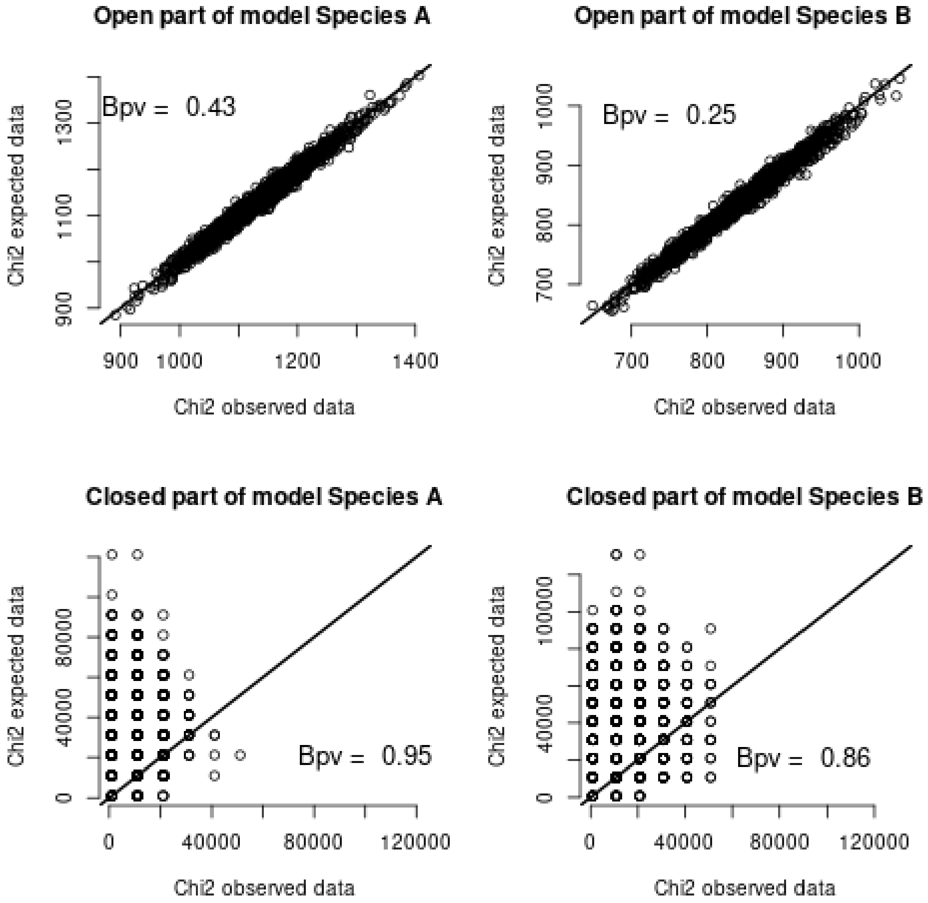


Figure S5: Goodness-of-fit check of the open and closed parts of the model based on data simulated under the model for the two different species groups (rodents (A) and mustelids (B)). The Bayesian p-value (Bpv) is the proportion of points above the 1:1 line.

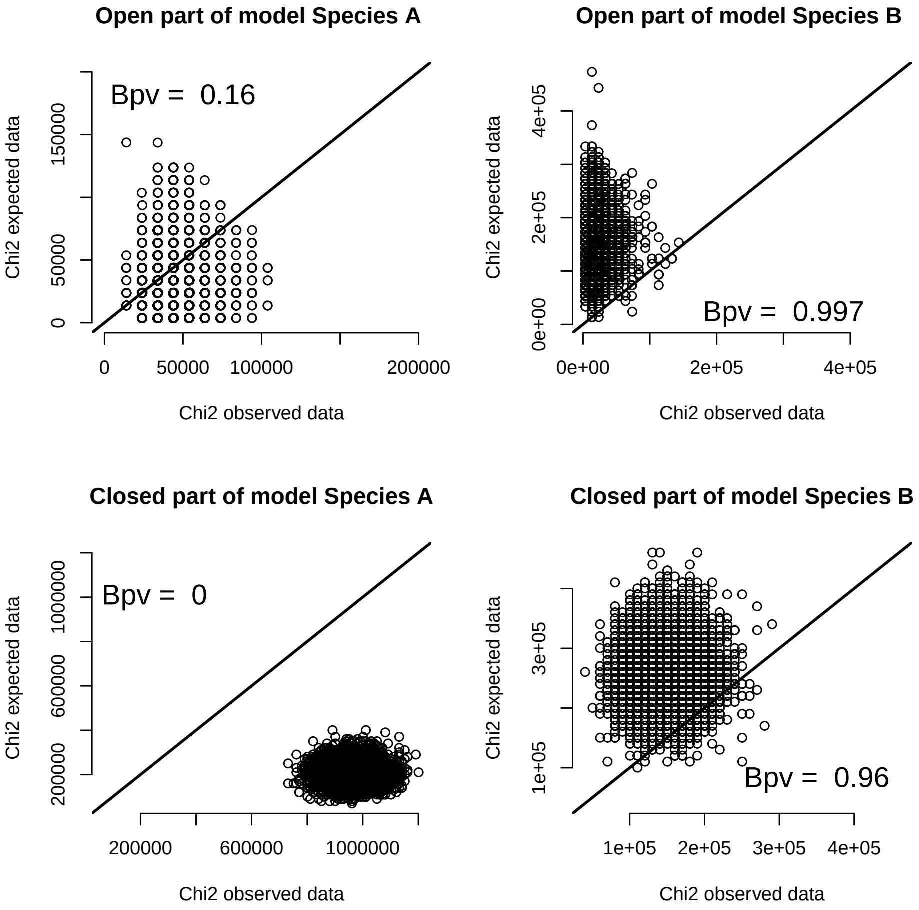


Figure S6: Goodness-of-fit check of the open and closed parts of the model based on the observed data for the two different species groups (rodents (A) and mustelids (B)). The Bayesian p-value (Bpv) is the proportion of points above the 1:1 line.

We see from figure S5 and S6 that with the case study data, the χ^2 discrepancies between the replicated and observed data are a little more different from each other than for data simulated under the theoretical model. The large discrepancy is for species A in the closed part of the model. This could indicate that there are factors affecting the detection probability of rodents that we do not account for. However, regarding the open part of the model for both functional groups, and for the closed part of the model for mustelids, we see that there is not a considerable difference between what is expected under ideal circumstances (data simulated under the model) and what we see with the case study data.

4.2 Prior sensitivity analysis

To ensure that the parameters were not estimated only from the prior distribution we performed a prior sensitivity analysis. This was done by running the model with three different sets of priors (see table S4) and comparing parameter estimates. This prior sensitivity analysis can also be used to investigate parameter identifiability by estimating the prior-posterior overlap.

Parameter	previously used priors	centered prior set	skewed prior set
Γ_A	Uniform(0,1)	Beta(4,4)	Beta(2,4)
$\Gamma_{A\|B}$	Uniform(0,1)	Beta(4,4)	Beta(2,4)
Γ_B	Uniform(0,1)	Beta(4,4)	Beta(2,4)
$\Gamma_{B\|A}$	Uniform(0,1)	Beta(4,4)	Beta(2,4)
E_A	Uniform(0,1)	Beta(4,4)	Beta(2,4)
$E_{A\|B}$	Uniform(0,1)	Beta(4,4)	Beta(4,2)
E_B	Uniform(0,1)	Beta(4,4)	Beta(4,2)
$E_{B\|A}$	Uniform(0,1)	Beta(4,4)	Beta(2,4)
γ_A	Uniform(0,1)	Beta(4,4)	Beta(4,2)
$\gamma_{A\|B}$	Uniform(0,1)	Beta(4,4)	Beta(2,4)
γ_B	Uniform(0,1)	Beta(4,4)	Beta(2,4)
$\gamma_{B\|A}$	Uniform(0,1)	Beta(4,4)	Beta(4,2)
ϵ_A	Uniform(0,1)	Beta(4,4)	Beta(2,4)
$\epsilon_{A\|B}$	Uniform(0,1)	Beta(4,4)	Beta(4,2)
ϵ_B	Uniform(0,1)	Beta(4,4)	Beta(4,2)
$\epsilon_{B\|A}$	Uniform(0,1)	Beta(4,4)	Beta(2,4)
α_{A0}	Normal(0,1)	logistic(0,1)	Normal(0.5,1)
α_{B0}	Normal(0,1)	logistic(0,1)	Normal(-0.5,1)
ψ_1	Uniform(0,0.5)	Beta(4,4)	Beta(2,4)
ψ_2	Uniform(0,0.5)	Beta(4,4)	Beta(2,4)
ψ_2	Uniform(0,0.5)	Beta(4,4)	Beta(2,4)

Table S4: This table gives details on what priors were used for the prior sensitivity analysis. α_{A0} and α_{B0} are the intercept in the logit link function for the detection probabilities p_A and p_B. These are parameters are on the logit scale. ψ_1, ψ_2 and ψ_3 are the initial state probabilities for the states A, B and AB. Γ and E are the colonization and extinction probabilities on block level while γ and ϵ are the colonization and extinction probabilities on site level. All initial state, colonization and extinction probabilities are defined on the probability scale. Exact definitions of these with subscripts can be found in table 1 and 2 in the main text.

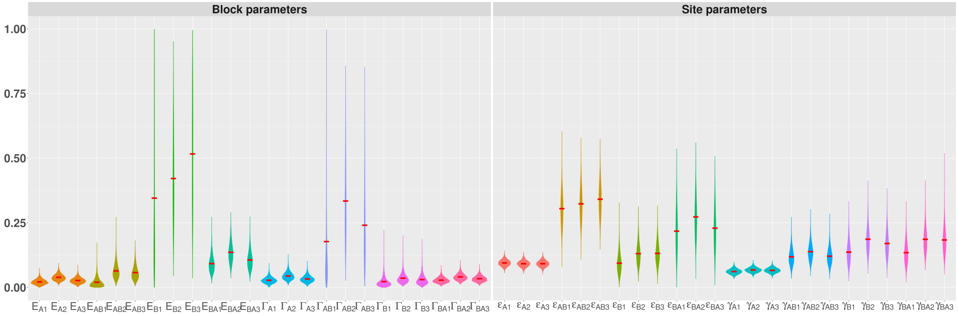


Figure S7: Violin plot of the colonization and extinction probabilities estimates with the different sets of priors. The red bar indicate the posterior mean. In the x-axis label 1-3 indicate the prior set used.

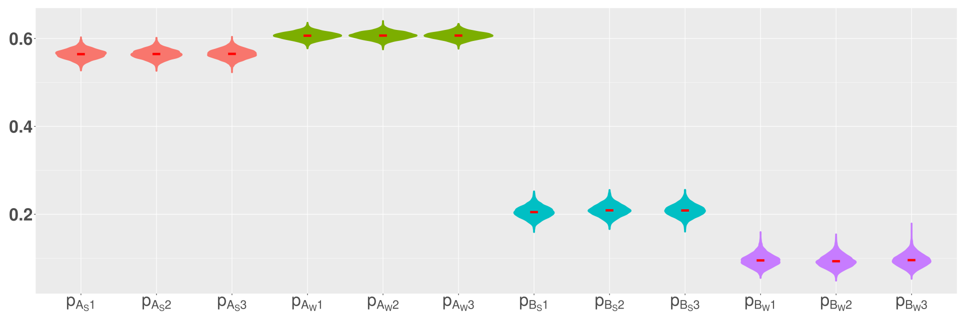


Figure S8: Violin plot of the detection probabilities estimates with the different sets of priors. The red bar indicate the posterior mean. In the x-axis label 1-3 indicate the prior set used.

We see from figure S7 and S8 that the estimates detection, colonization and extinction probabilities seem to have little sensitivity to the priors distributions, except for $\Gamma_{A|B}$ and E_B where the posterior seems to change slightly depending on the prior distribution.

4.3 Parameter identifiability

To check parameter identifiability we investigated the overlap of the prior and posterior distributions. This was done for all colonization, extinction and detection parameters for the same 3 sets of prior distributions that were used in the prior sensitivity analysis (see table S4). The results are shown in figure S9, S10 and S11, where we see that all parameters except E_B and $\Gamma_{A|B}$ appear to be identifiable. For E_B and $\Gamma_{A|B}$ the posterior is very similar to the prior distribution, especially so for prior sets 2 and 3. This indicates that these parameters are not identifiable from this data.

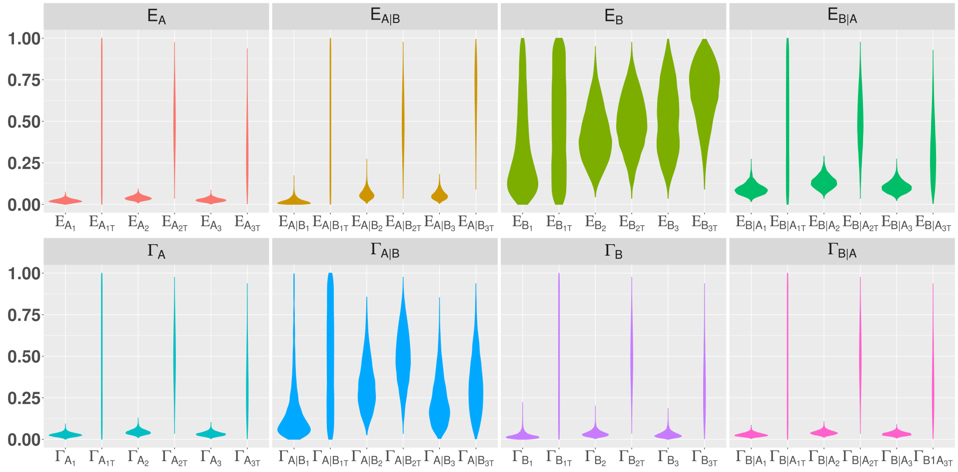


Figure S9: Violin plot of both prior (indicated by subscript T) and posterior distributions for block colonization and extinction parameters with the different sets of priors. Subscript 1:3 indicate the prior set used.

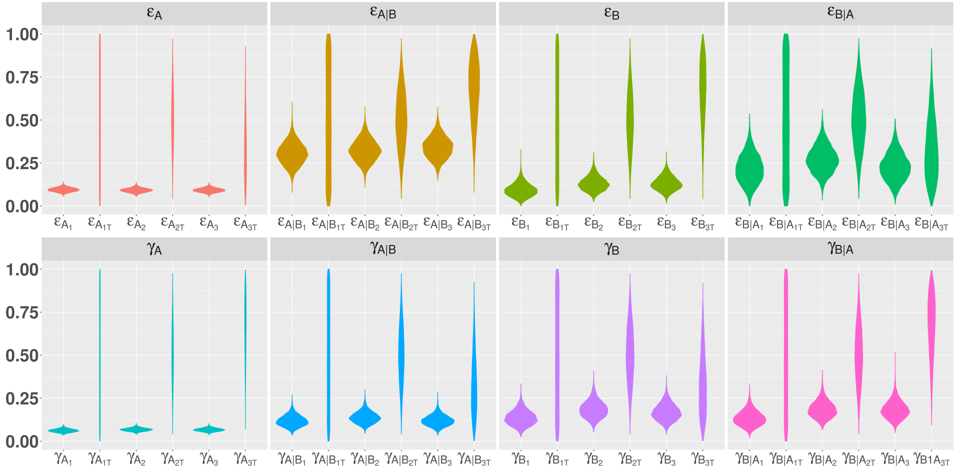


Figure S10: Violin plot of both prior (indicated by subscript T) and posterior distributions for site colonization and extinction parameters with the different sets of priors. Subscript 1:3 indicate the prior set used.

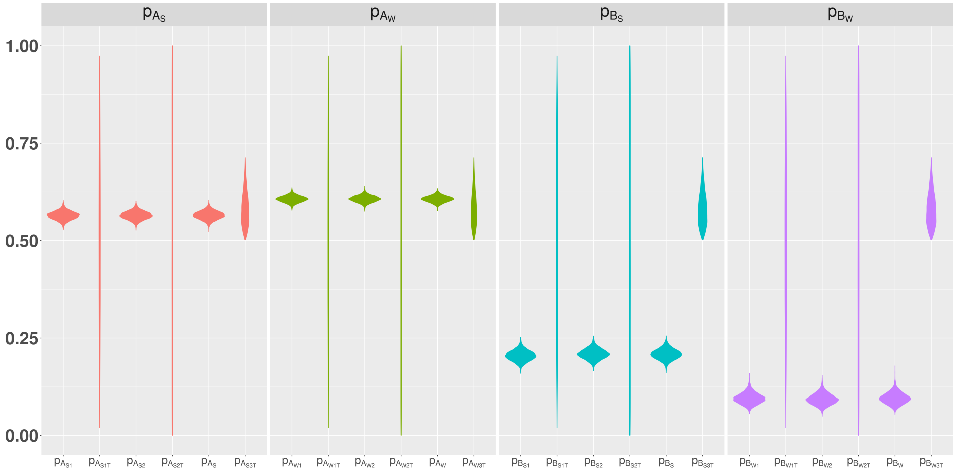


Figure S11: Violin plot of both prior (indicated by subscript T) and posterior distributions for block colonization and extinction parameters with the different sets of priors. Subscript S and W refer to summer and winter estimates, while 1:3 indicate the prior set used.

5 Results

5.1 Simulation study

In this section we give a more detailed description of the simulation results.

Table S7 and S6 give the results from the simulation study. We see that the model is able to estimate most parameters without bias. Some small biases appear, especially so under the low detection probability scenario.

	low det			mid det			high det		
Parameter	true	mean	sd	true	mean	sd	true	mean	sd
Γ_A	0.50	0.43	0.06	0.50	0.48	0.04	0.50	0.49	0.05
$\Gamma_{A\|B}$	0.05	0.05	0.03	0.05	0.07	0.03	0.05	0.06	0.02
Γ_B	0.10	0.06	0.03	0.1	0.10	0.03	0.10	0.10	0.03
$\Gamma_{B\|A}$	0.40	0.36	0.04	0.4	0.40	0.05	0.40	0.41	0.04
E_A	0.05	0.10	0.03	0.05	0.06	0.02	0.05	0.06	0.02
$E_{A\|B}$	0.50	0.61	0.08	0.50	0.53	0.05	0.50	0.52	0.06
E_B	0.60	0.73	0.08	0.60	0.63	0.06	0.60	0.60	0.05
$E_{B\|A}$	0.20	0.21	0.04	0.20	0.20	0.04	0.20	0.20	0.04
γ_A	0.50	0.46	0.02	0.50	0.49	0.02	0.50	0.50	0.01
$\gamma_{A\|B}$	0.10	0.06	0.03	0.10	0.08	0.03	0.10	0.09	0.03
γ_B	0.30	0.23	0.05	0.30	0.29	0.02	0.30	0.30	0.02
$\gamma_{B\|A}$	0.70	0.74	0.07	0.70	0.70	0.02	0.70	0.70	0.02
ϵ_A	0.30	0.34	0.03	0.30	0.31	0.02	0.30	0.30	0.01
$\epsilon_{A\|B}$	0.90	0.94	0.03	0.90	0.92	0.03	0.90	0.91	0.03
ϵ_B	0.80	0.84	0.07	0.80	0.81	0.02	0.80	0.80	0.02
$\epsilon_{B\|A}$	0.10	0.11	0.04	0.10	0.09	0.02	0.10	0.09	0.02

Table S5: Results from the 3 scenarios with varying detection probabilities in the simulation study given as mean and standard deviation of the posterior means from the 50 replicated sets.

	low occ			mid occ			high occ		
Parameter	true	mean	sd	true	mean	sd	true	mean	sd
Γ_A	0.10	0.10	0.02	0.50	0.50	0.05	0.80	0.79	0.05
$\Gamma_{A\|B}$	0.05	0.07	0.03	0.05	0.06	0.03	0.20	0.21	0.05
Γ_B	0.05	0.05	0.01	0.10	0.10	0.03	0.20	0.19	0.05
$\Gamma_{B\|A}$	0.20	0.22	0.05	0.40	0.40	0.06	0.70	0.69	0.04
E_A	0.10	0.10	0.03	0.05	0.06	0.02	0.05	0.07	0.02
$E_{A\|B}$	0.50	0.53	0.07	0.50	0.53	0.05	0.40	0.39	0.04
E_B	0.60	0.63	0.08	0.60	0.62	0.06	0.80	0.79	0.05
$E_{B\|A}$	0.20	0.21	0.06	0.20	0.21	0.04	0.20	0.19	0.03
γ_A	0.30	0.29	0.02	0.50	0.49	0.02	0.80	0.79	0.01
$\gamma_{A\|B}$	0.10	0.10	0.04	0.10	0.09	0.03	0.10	0.08	0.02
γ_B	0.30	0.29	0.02	0.30	0.29	0.02	0.30	0.29	0.02
$\gamma_{B\|A}$	0.60	0.59	0.04	0.70	0.70	0.02	0.70	0.69	0.02
ϵ_A	0.30	0.30	0.03	0.30	0.31	0.02	0.10	0.10	0.01
$\epsilon_{A\|B}$	0.90	0.90	0.05	0.90	0.92	0.02	0.60	0.63	0.03
ϵ_B	0.80	0.80	0.04	0.80	0.80	0.02	0.60	0.61	0.03
$\epsilon_{B\|A}$	0.10	0.10	0.04	0.10	0.09	0.02	0.10	0.09	0.02

Table S6: Results from the 3 scenarios with varying occupancy probabilities in the simulation study given as mean and standard deviation of the posterior means from the 50 replicated sets.

	low det		mid det		high det		low occ		mid occ		high occ	
Par	bias	rel.	bias	rel.	bias	rel.	bias	rel.	bias	rel.	bias	rel.
Γ_A	0.07	14%	0.02	4%	0.01	2%	0	0	0	0	0.01	1%
$\Gamma_{A\|B}$	0	0	0.02	40%	0.01	20%	0.02	40%	0.01	20%	0.01	5%
Γ_B	0.04	40%	0	0%	0	0%	0	0%	0	0%	0.01	5%
$\Gamma_{B\|A}$	0.04	10%	0	0%	0.01	3%	0.02	10%	0	0%	0.01	1%
E_A	0.05	50%	0.01	20%	0.01	20%	0	0%	0.01	20%	0.02	40%
$E_{A\|B}$	0.11	22%	0.03	6%	0.02	4%	0.03	6%	0.03	6%	0.01	3%
E_B	0.13	22%	0.03	5%	0	0%	0.03	5%	0.02	3%	0.01	1%
$E_{B\|A}$	0.01	5%	0	0%	0	0%	0.01	5%	0.01	5%	0.01	5%
γ_A	0.04	8%	0.02	4%	0	0%	0.01	3%	0.01	2%	0.01	1%
$\gamma_{A\|B}$	0.04	40%	0.02	20%	0.01	10%	0	0%	0.01	10%	0.02	20%
γ_B	0.07	23%	0.01	3%	0	0%	0.01	3%	0.01	3%	0.01	3%
$\gamma_{B\|A}$	0.04	6%	0	0%	0	0%	0.01	1%	0	0%	0.01	1%
ϵ_A	0.04	13%	0.01	3%	0	0%	0	0%	0.01	3%	0	0%
$\epsilon_{A\|B}$	0.04	4%	0.02	2%	0.01	1%	0	0%	0.02	2%	0.03	5%
ϵ_B	0.04	5%	0.01	1%	0	0%	0	0%	0	0%	0.01	2%
$\epsilon_{B\|A}$	0.01	10%	0.01	10%	0.01	10%	0	0%	0.01	10%	0.01	10%

Table S7: Comparison of the true and estimated parameter values in the simulation study. The table gives the absolute and relative bias.

From Figure S12 and S13 we see that detection probabilities (p_A and p_B) and initial occupancy probabilities ($\psi_{A_{t-1}}$, $\psi_{B_{t-1}}$ and $\psi_{AB_{t-1}}$) are estimated without bias.

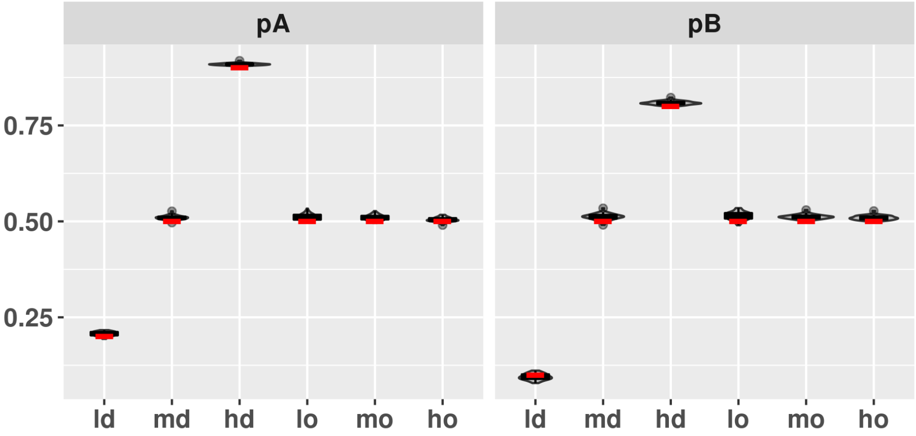


Figure S12: Violin plot and boxplot of the posterior mean of detection probability (p_A and p_B) from the 50 simulations. The red bar indicates the true parameter values. x-axis displays the 6 different data scenarios (low, medium and high detection probability: ld, md, hd, and low, medium and high occupancy probability: lo, mo,ho).

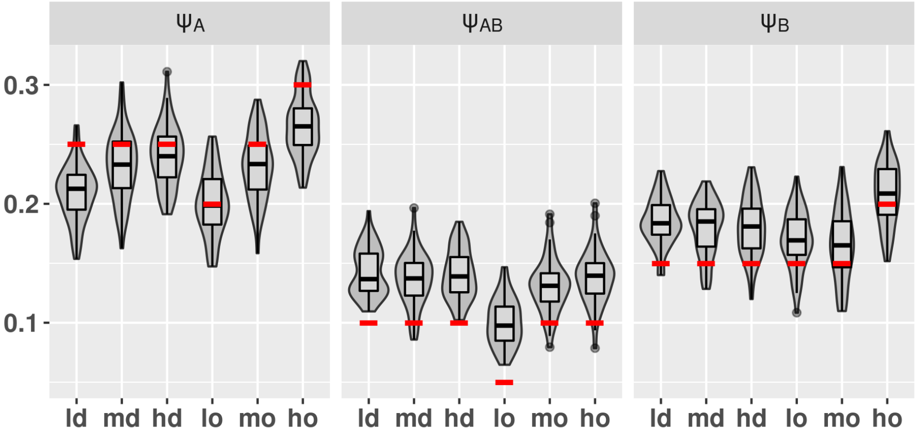


Figure S13: Violin plot and boxplot of the posterior mean of initial occupancy ($\psi_{t=1}$) from the 50 simulations. The red bar indicates the true parameter values. x-axis displays the 6 different data scenarios (low, medium and high detection probability: ld, md, hd, and low, medium and high occupancy probability: lo, mo,ho).

5.2 Case study

This section gives detailed results on the case study. Table S8 gives more details on the estimated colonization and extinction parameters in the case study while table S9 gives more information on the estimated differences between colonization and extinction parameters depending on the presence or absence of the other species. Figure S14 displays the difference in detection probability between the two species groups and the two seasons as described in the main text.

Parameter	mean	sd	95% CI
Γ_A	0.027	0.012	0.007 0.054
$\Gamma_{A\|B}$	0.257	0.234	0.013 0.874
Γ_B	0.018	0.016	0.001 0.057
$\Gamma_{B\|A}$	0.027	0.011	0.011 0.052
E_A	0.020	0.011	0.003 0.043
$E_{A\|B}$	0.022	0.019	0.001 0.070
E_B	0.374	0.269	0.029 0.947
$E_{B\|A}$	0.092	0.034	0.039 0.170
γ_A	0.059	0.009	0.042 0.079
$\gamma_{A\|B}$	0.094	0.027	0.047 0.154
γ_B	0.139	0.046	0.064 0.238
$\gamma_{B\|A}$	0.119	0.045	0.046 0.220
ϵ_A	0.093	0.012	0.070 0.117
$\epsilon_{A\|B}$	0.326	0.072	0.194 0.476
ϵ_B	0.092	0.038	0.030 0.175
$\epsilon_{B\|A}$	0.183	0.089	0.028 0.367

Table S8: Results from the case study given as mean and standard deviation from the posterior distribution in addition to the 95% credible intervals.

Parameter	mean	95% CI
γ_A - $\gamma_{A\|B}$	-0.033	-0.087 0.009
γ_B - $\gamma_{B\|A}$	0.020	-0.076 0.115
ϵ_A - $\epsilon_{A\|B}$	- 0.229	-0.360 -0.115
ϵ_B - $\epsilon_{B\|A}$	-0.086	-0.259 0.062
Γ_A - $\Gamma_{A\|B}$	-0.146	-0.756 0.008
Γ_B - $\Gamma_{B\|A}$	-0.012	-0.037 0.023
E_A - $E_{A\|B}$	0.001	-0.040 0.028
E_B - $E_{B\|A}$	0.218	-0.065 0.810

Table S9: Estimated differences between dependent and independent colonization and extinction probabilities with 95% credible intervals.

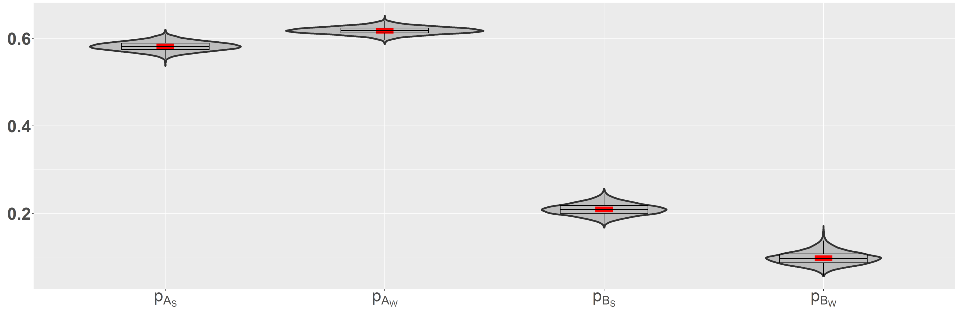


Figure S14: Violin plot of the posterior mean of detection probability (p_A and p_B) for summer (S) and winter (W) in black. The red bar indicates the mean of the posterior distribution.

Figure S15 shows the estimated initial occupancy probabilities from the case study ($\psi_{t=1}$). In blocks b1 to b4 we see some variation both between blocks, where blocks b2 and b4 have a higher occupancy. Note that ψ_1 is occupancy probability of species A only, ψ_2 is occupancy probability of species B only and ψ_3 is the probability that both species A and B occupy a given site. Block b2 has high occupancy probability of species A (ψ_1) and b4 has high occupancy probability of species B (ψ_3). Please also note that we do not have any observations from blocks b6-b8 in the initial season, and that we do not include any spatial covariates in the model.

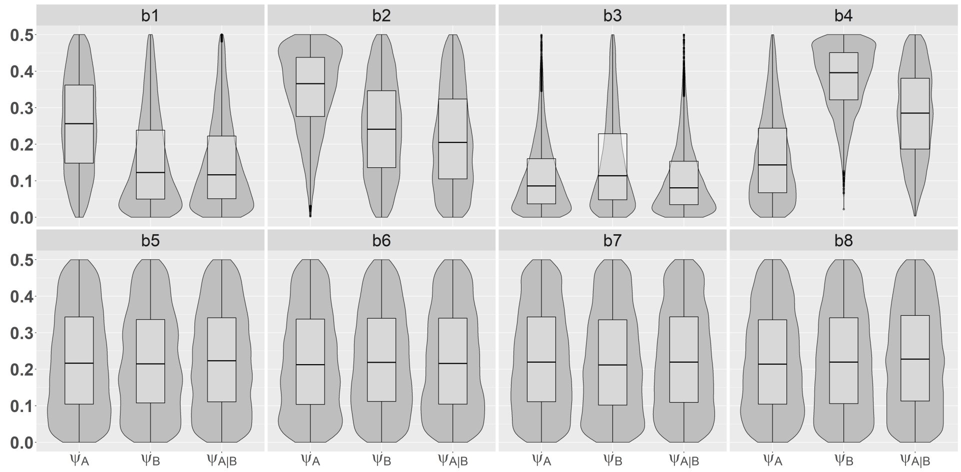


Figure S15: Violin plot and boxplot of the posterior mean of initial occupancy ($\psi_{t=1}$) for each of the 8 blocks (b1-b8).

References

Conn, P.B., Johnson, D.S., Williams, P.J., Melin, S.R. & Hooten, M.B. (2018). A guide to bayesian model checking for ecologists. *Ecological Monographs*, 88, 526–542.

Ims, R.A. & Fuglei, E. (2005). Trophic Interaction Cycles in Tundra Ecosystems and the Impact of Climate Change. *BioScience*, 55, 311–322.

Kéry, M. & Royle, J.A. (2020). *Applied Hierarchical Modeling in Ecology: Analysis of distribution, abundance and species richness in R and BUGS: Volume 2: Dynamic and Advanced Models*. Academic Press.

Soininen, E.M., Jensvoll, I., Killengreen, S.T. & Ims, R.A. (2015). Under the snow: a new camera trap opens the white box of subnivean ecology. *Remote Sensing in Ecology and Conservation*, 1, 29–38.

Specht, H.M., Reich, H.T., Iannarilli, F., Edwards, M.R., Stapleton, S.P., Weegman, M.D., Johnson, M.K., Yohannes, B.J. & Arnold, T.W. (2017). Occupancy surveys with conditional replicates: An alternative sampling design for rare species. *Methods in Ecology and Evolution*, 8, 1725–1734.

Tabak, M.A., Norouzzadeh, M.S., Wolfson, D.W., Sweeney, S.J., Vercauteren, K.C., Snow, N.P., Halseth, J.M., Di Salvo, P.A., Lewis, J.S., White, M.D., Teton, B., Beasley, J.C., Schlichting, P.E., Boughton, R.K., Wight, B., Newkirk, E.S., Ivan, J.S., Odell, E.A., Brook, R.K., Lukacs, P.M., Moeller, A.K., Mandeville, E.G., Clune, J. & Miller, R.S. (2019). Machine learning to classify animal species in camera trap images: Applications in ecology. *Methods in Ecology and Evolution*, 10, 585–590.

Zipkin, E.F., Grant, E.H.C. & Fagan, W.F. (2012). Evaluating the predictive abilities of community occupancy models using auc while accounting for imperfect detection. *Ecological Applications*, 22, 1962–1972.

Paper III

Seasonality and habitat-dependency in the strength of a predator-prey interaction,

Manuscript

MANUSCRIPT

Seasonality and habitat-dependency in the strength of a predator-prey interaction

Authors:

Eivind Flittie Kleiven[1], Frederic Barraquand[2,3], Olivier Gimenez[4], John-André Henden[1], Eeva M. Soininen[1], Hanna Böhner[1], Nigel Gilles Yoccoz[1] & Rolf Anker Ims[1],

[1] UiT - The Arctic University of Norway, Department of Arctic and Marine Biology, Tromsø, Norway

[2] CNRS, Institute of Mathematics of Bordeaux, Talence, France

[3] Integrative and Theoretical Ecology, LabEx COTE, University of Bordeaux, Pessac, France

[4] CEFE, Université Montpellier, CNRS, EPHE, IRD, Universite Paul Valéry Montpellier 3, Montpellier, France

Corresponding author email: eivind.f.kleiven@uit.no

Abstract

The interaction between small mustelids (stoats and weasels) and their preferred prey (small rodents) is hypothesized to be the key driver of the renown population cycles of boreal and Arctic rodents. However, although the role of this predator-prey interaction may depend on how its strength varies between seasons (summer and winter) and habitats, such dependencies have not been empirically investigated due to methodological constraints. Based on a recently developed camera trap tailored for monitoring small mammals year-round, and a new dynamic occupancy model for analysing spatial structured trophic interaction, we assessed whether there was evidence for season- and habitat-dependence in mustelid-rodent interactions in low-arctic tundra. We analysed a data set from a spatially extensive monitoring system consisting of replicated landscape blocks with nested camera sites located in two key rodent habitats (snowbeds and hummock tundra). The 6-year monitoring period included two cyclic phases of declines in the rodent populations, in which predator-prey interactions could be expected to be strong. We found evidence for a predator-prey interaction on a weekly time scale both on the block and site level. The interaction was most consistent and strong in terms of increased weekly extinction probabilities of rodents in presence of mustelids. At the site level, for which the occupancy model allowed for season- and habitat-dependent estimates, the predator-prey interaction was strongest in the snowbed habitat. Overall, the impact of mustelids on rodent population dynamics was likely most important in summer as the mustelids occurred most frequently in this season. We conclude that our study demonstrates that camera-trap-based monitoring systems open opportunities for a much more spatially and temporally nuanced knowledge of mustelid-rodent interactions. We propose that future camera trap studies could be advanced by (1) developing more refined and flexible criteria for defining different seasons than the arbitrary and inflexible definitions used in most studies, (2) investigating species-specific interactions such as partial effects of weasels and stoats on lemming and voles and (3) including all habitats that may be involved in landscape-scale predator-prey interactions.

1 Introduction

While the interaction between small mustelids and rodents for decades has been hypothesized to be the key driver of the renown, multi-annual population cycles of boreal and Arctic small mammals (Hansson & Henttonen, 1988; Hanski *et al.*, 1991, 1993; Ims & Fuglei, 2005; Krebs, 2013; Boonstra *et al.*, 2016), recent reviews have concluded that new approaches are needed to obtain more empirical information about critical features of this predator-prey interaction (Myers, 2018; Oli, 2019; Andreassen *et al.*, 2021). A crucial feature of the northern population cycles, already highlighted by Charles Elton a century ago (Elton, 1924), is seasonality. Indeed, modern-time analyses of long-term population time series have suggested that season-specific biotic interactions should be invoked to explain these cycles (Hansen *et al.*, 1999; Stenseth *et al.*, 1998, 2003; Fauteux *et al.*, 2021). Accordingly, Andreassen *et al.* (2021) proposed that how seasonality interacts with predation and other biotic drivers of cyclic rodent population dynamics is an essential question that remains to be solved.

There are several reasons why the rodent-mustelid interaction may be season dependent. The impact of mustelid predation may be particularly important in the winter season, because weasels (*Mustela nivalis*) and stoats (*M. erminea*) are the only predators capable of following the rodents down in the subnivean space (Norrdahl & Korpimäki, 1995). On the other hand, the mustelid-rodent interaction may be particularly influential in summer as there are indications that reproducing rodent females are most vulnerable to weasel predation (Hanski *et al.*, 2001). Moreover, some rodent species are known to change habitats between summer and winter (e.g. Tast (1966); Kalela (1971)). Thus, if predation risk is habitat dependent (Jacob & Brown, 2000; Sundell & Ylönen, 2008), there may be an interaction between seasonality and habitat use that influences the dynamics of predator-prey interactions (Schmitz *et al.*, 2017).

Seasonality is incorporated in some mathematical models of rodent-mustelid interactions (Turchin & Hanski, 1997; Hanski *et al.*, 2001; Klemola *et al.*, 2003). However, these models are based on the the simplifying assumptions that only the population growth rates are season-specific and, hence, that the parameters of the functional and numerical response that determine the the strength of the interaction are independent of season. Moreover, the interaction is assumed to be spatially homogeneous (i.e. no habitat dependence). Empirical studies have on other hand been hampered by methodological constraints. A few field studies have obtained information on predation rates based on radio-tagged rodents in summer (Norrdahl & Korpimäki, 1995), however this approach appears inapplicable to the subnivean life-style of small mammals in winter. Data on mustelids have mostly been obtained by means of track-surveys of supranivean activity one or a few times during the winter (Oksanen *et al.*, 1992; Aunapuu & Oksanen, 2003) or by inspecting rodent winter nest for signs of mustelids at the end of the winter (Gilg *et al.*, 2003; Vigués *et al.*, 2021). Such data have been used to infer mustelid habitat use in winter (Oksanen *et al.*, 1992) and moreover to parameterize mathematical (winter nests, (Gilg *et al.*, 2003)) or statistical population dynamics models (snow-tracking, Sundell *et al.* (2013); Korpela *et al.* (2014)). However, we are not aware of any empirical studies that have been able to address how rodent-mustelid interactions may depend on both habitat and season.

The use of camera traps has recently opened opportunities to obtain multi-species data on temporal and spatial scales that have not been possible by previous monitoring methods (Burton *et al.*, 2015; Tobler *et al.*, 2015; Sollmann, 2018). Moreover, statistical approaches (i.e. occupancy models) have been developed to enable estimation of inter-specific interactions in terms of conditional extinction and colonization probabilities based on camera trap data (Rota *et al.*, 2016; Fidino *et al.*, 2019). In the present study we apply a dynamical occupancy model developed by Kleiven *et al.* (2021) to an unique data set from a landscape-scale, years-round, camera-trap-based monitoring system that targets an Arctic small mammal community. Our main aim is to assess whether the interaction between rodents and mustelids are dependent on season and habitat.

2 Methods

2.1 Study area and species

This study was conducted in low-arctic tundra on Varanger Peninsula, NE Norway (70°20'N 29°38'E; Fig. 1). The species of the small mammal community focal to the present study includes three species of rodents (Norwegian lemming *Lemmus lemmus*, gray-sided vole *Myodus rufocanus* and tundra vole *Microtus oeconomus*) and two species of mustelids (stoat and least weasel) (Mölle *et al.*, 2021; Kleiven *et al.*, 2021). Although the habitat use of the three rodent species differ, their 4-5 year population cycles exhibit profound inter-specific synchrony on Varanger Penisula (Soininen *et al.*, 2018; Kleiven *et al.*, 2018) and in alpine-arctic tundra elsewhere in Fennoscandia (Turchin *et al.*, 2000; Kausrud *et al.*, 2008; Olofsson *et al.*, 2012). It has been suggested that shared mustelid predation is the cause of this synchrony (Sundell & Ylönen, 2008). Consequently, we will in this study treat rodents and mustelids as two functional groups (prey and predators) like have been done in several previous theoretical and empirical analyses of mustelid-rodent interactions (Hanski *et al.*, 1993; Sundell *et al.*, 2013; Korpela *et al.*, 2014).

2.2 Study design

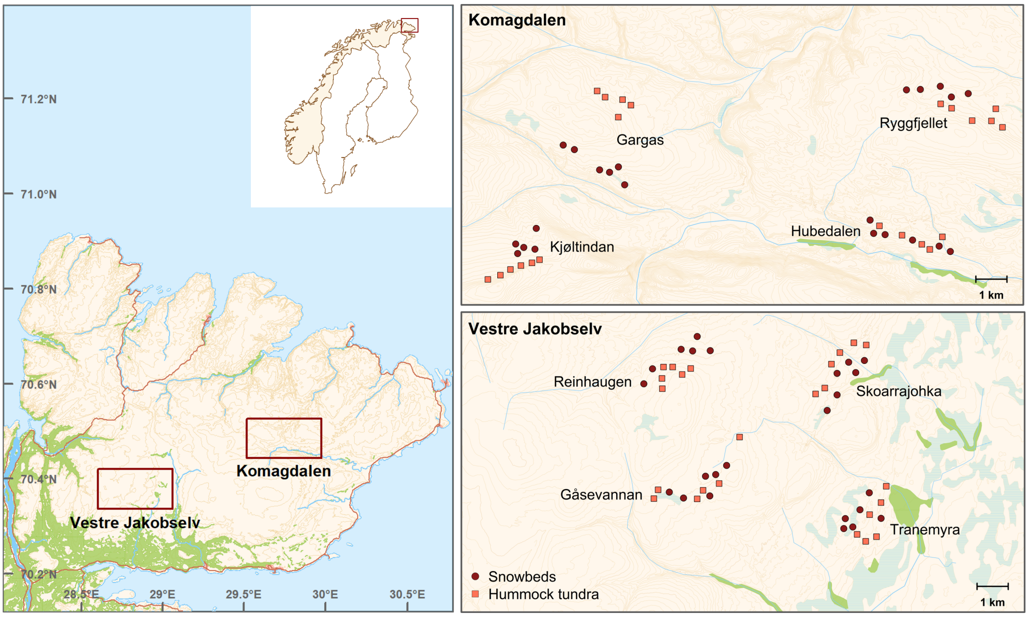


Figure 1: Maps of the study area. Left: Varanger Peninsula in NE Norway with the two study sub-areas Vestre Jakobselv and Komagdalen denoted as rectangles. Right: The spatial setup of the camera trap monitoring system within the two sub-areas. Brown circles denote camera trap sites in hummock tundra, while red squares denote camera trap sites in snow beds. Green shades represent areas with tall shrubs or sub-arctic forest

We used data from the camera-trap-based small mammal monitoring system of the Climate-ecological Monitoring for Arctic Tundra (COAT, Ims *et al.* (2013)). The monitoring system included the two habitats (snowbeds and hummock tundra) that were assumed focal to the Norwegian lemming (Aho & Kalela, 1966; Koponen, 1970). The snowbed sites were selected based on the criterion that they should harbour fairly rich vegetation consisting of mosses, graminoids, herbs and prostrate shrubs (*Salix herbacea* and *Vaccinium* spp.) as well as they should be adjoining boulder fields that could provide shelter to small mammals in summer (Magnusson *et al.*, 2013; Soininen *et al.*, 2018). The selected hummock tundra sites were typically moist (often bordering mires) and contained lush vegetation of sedges, herbs and erect shrubs (e.g. *Betula nana, Vaccinium* spp.) as well as hummocks providing shelter to small mammals. Within each of the selected sites one tunnel-based camera trap of the version developed by Soininen *et al.* (2015), and with the camera setting described by Mölle *et al.* (2021)), was established.

To account for the different movement ranges of rodents and mustelids the monitoring system has a hierarchical structure, where multiple camera sites are clustered in blocks (see Fig. 1). Camera traps within a block are > 300m apart. Each block contain 11-12 camera traps and blocks are > 3km apart. In September 2015 the camera traps were deployed in 4 blocks in Komagdalen with 5 or 6 cameras in each of the two habitats (i.e. hummock tundra and snowbeds) within each block. In August 2018 the monitoring system was extended by an additional 4 blocks in Vestre Jakobselv with 6 cameras in each of the two habitats. Hence, when fully established the monitoring system amounts to a total of 8 blocks and 93 camera trap sites. For more details on the camera trap setup and functionality see Mölle *et al.* (2021) and Kleiven *et al.* (2021).

2.3 Data analysis

We trained a neural network model for automatic classification of camera trap images. We then used this model to automatically classify all images with respect to presence of rodents and mustelids as well to identify periods when certain camera traps were not functional (for more information see https://data.coat.no/dataset/v_rodents_cameratraps_image_classification_lemming_blocks_v1). Malfunctioning camera traps were most prevalent during winters (Mölle *et al.*, 2021) and such traps/sites were excluded from the data set for those periods they could not record images. In total, the dataset consists of 109 601 functional camera trap days spanning a period of 304 weeks (i.e. primary occasions) and nearly 6 years (from September 2015 to July 2021). According to a snap-trap-based rodent monitoring on Varanger Peninsula (cf. https://www.coat.no/en/Small-rodent), our study period included two cyclic phases of rodent population declines (2015-2017 and 2019-2021) in which the mustelid-rodent interaction could be expected to be strong.

The data was analysed by means of the dynamic occupancy model developed by Kleiven *et al.* (2021) for interacting species at two nested spatial scales (i.e. blocks and sites). This model allows for the estimation of scale-specific colonization (Γ and γ, for block and site level respectively) and extinction (E and ε, for block and site level) probabilities dependent on the presence of the other functional group, in two habitats and seasons. We used the estimated difference in these probabilities (i.e. contrast estimates) in absence and presence of the other functional group as a measure of the strength of the predator-prey interaction (Emmerson & Raffaelli, 2004; Wootton & Emmerson, 2005).

To account for the detection process, we discretized the camera trap data by considering every week (i.e. 7-day period) primary occasions, between which the populations are assumed to be open (i.e. sites can become colonized and go extinct). The length of the primary occasions was assumed to match the fast population processes in rodents, i.e. leading to rapid site-scale, colonization-extinction dynamics (Andreassen & Ims, 2001). Mustelids have slower demographic processes, but are assumed to alter frequently site-scale hunting grounds (Hellstedt & Henttonen, 2006). Every day within a week is considered secondary occasions (i.e. temporal replicates), between which the population is assumed to be closed (i.e. no colonization nor extinction occur). The secondary occasions are used to estimate the detection probability.

The site and block level states can be estimated as any of the following four states: none of the species present (U), only rodents present (R), only mustelids present (M) or both rodents and mustelids present (RM). The site state depends on the block state, as a block would need to be occupied before a site within that block can become occupied. However, the model does not assume the reverse to be true, meaning that a block can remain occupied even when all sites within that block are extinct. Ecologically this means that the sum of the sites within a block does not cover the entire block, hence it is possible for a species to be present in the area outside of the sites but still within the block. For a more detailed model description see Kleiven *et al.* (2021).

On the site-level we included (through a logit link function) habitat and season as functional group-specific covariates on the extinction and colonization probabilities and season as a covariate on the functional group-specific detection probabilities. We did not include covariates on the block-level extinction and colonization probabilities, because initial analysis revealed that the dataset was insufficient to estimate all possible covariate combinations. Similar to other analyses of season dependency in boreal and Arctic rodents populations (Hansen *et al.*, 1999; Stenseth *et al.*, 1998, 2003; Fauteux *et al.*, 2021), we defined a fixed schedule for the two seasons; i.e. the summer season as the 4-month period between July 1 and November 1 and the remaining 8-month period of the year as the winter season.

The model was analysed in a Bayesian framework using the JAGS software (Plummer, 2003) with the `jagsUI` package (Kellner, 2015) in `R v4.1.2` (R Core Team, 2021). The MCMC chains was run for 20 000 iterations with a thinning of 10 where we discarded the first 5000 as burn-in. We used an adaptation phase of 5000 iterations. Convergence was assessed by having a $\hat{R}$ <1.1 for all key parameters (Gelman *et al.*, 2013) and from graphical investigation of traceplots.

3 Results

3.1 Occupancy data

Rodents were recorded in 19 196 camera trap days of which the largest proportion was recorded in the hummock tundra during the summer season (Table 1). Mustelids were recorded in 1 100 camera trap days with clearly the largest proportion in snowbeds during summer.

Habitat	Season	
	Winter	Summer
Hummock tundra	135 / 3845 (31981)	288 / 7489 (18579)
Snowbed	157 / 3337 (38769)	520 / 4525 (20272)

Table 1: Number of camera trap days with mustelids and rodents in the total data set according to season (winter and summer) and habitat (snowbeds and hummock tundra). The numbers are given as mustelid/rodents (total number of camera trap days).

The weekly proportions of camera sites with recorded presence of rodents and mustelids exhibited violent fluctuations between the two seasons (Fig. 2). For rodents these seasonal fluctuations were larger in hummock tundra than in the snowbed habitat due to higher peaks in summers and sometimes absence of recordings in winters. The multi-annual component of the rodent fluctuations were much smoother than the seasonal component. However, gradual decline phases over the years 2015-2017 and 2019-2021 were apparent, thus mirroring the pattern evident in the snap-trap-based series (Fig. 6 in Appendix A). The relatively much smaller proportions of camera trap days in mustelids exhibited a weaker multi-annual component, especially in the snowbed habitat. The most conspicuous pattern in the mustelid occupancy data was the long periods with absence of recordings in the winters.

Some of the seasonal differences in the raw occupancy data (Fig. 2) can be attributed to moderately reduced detection probabilities in winter for both rodents and mustelids (Fig.3). The daily detection probabilities were substantially higher for rodents than for mustelids.

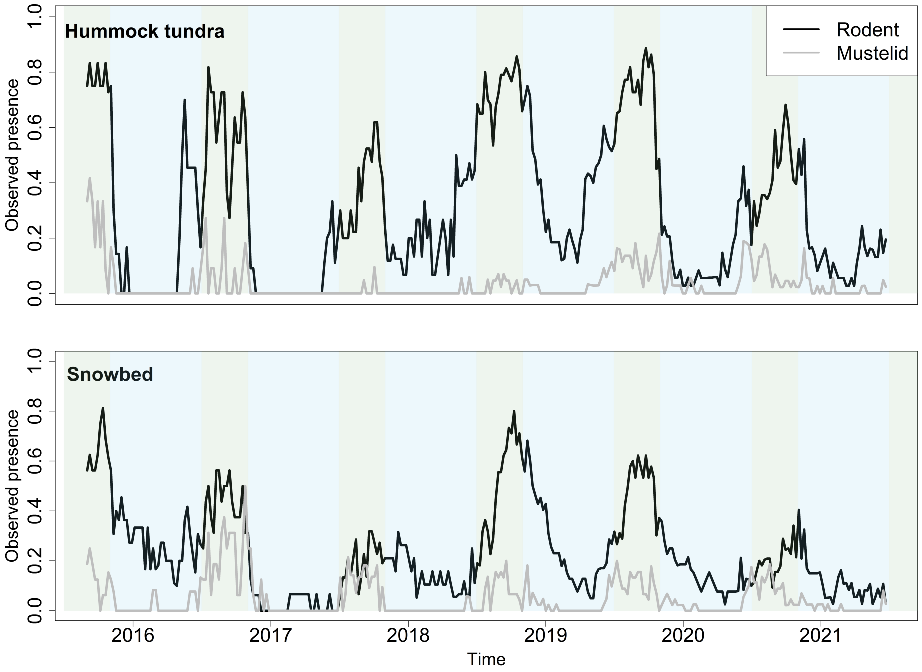


Figure 2: Temporal patterns in the proportion camera traps sites with weekly presence of rodents (black lines) and mustelids (gray lines) in hummock tundra and snowbeds. Pale green background denote summer seasons (July 1- November 1), while the pale blue background denote the winter seasons.

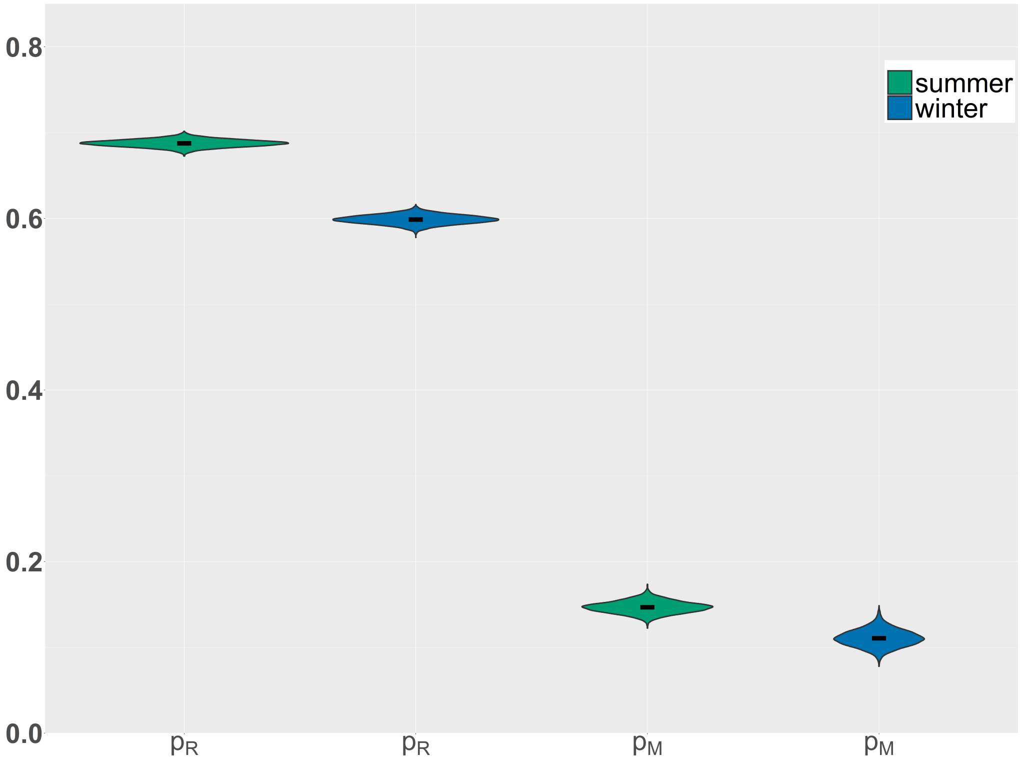


Figure 3: Violin plots of the estimated posterior distributions for the daily detection probabilities of rodents (P_A) and mustelids (P_B) in the two seasons. The black bar denotes the posterior mean.

3.2 Colonization and extinction probabilities

Several of the estimated block-level probabilities, which could not be made conditional on season and habitat, had large uncertainties especially for mustelids (Fig. 4). This limited which inferences could be made about rodent-mustelid interactions at this scale. However, the weekly rodent extinction probability increased from 0.005 (E_R) when mustelids were absent to 0.048 ($E_{R|M}$) when mustelids were present (an increase of 0.043 with 95% CI [0.013 - 0.075]). The other contrasted parameters that could indicate predator-prey interactions had credible intervals that included zero (see Tab. 3 Appendix C).

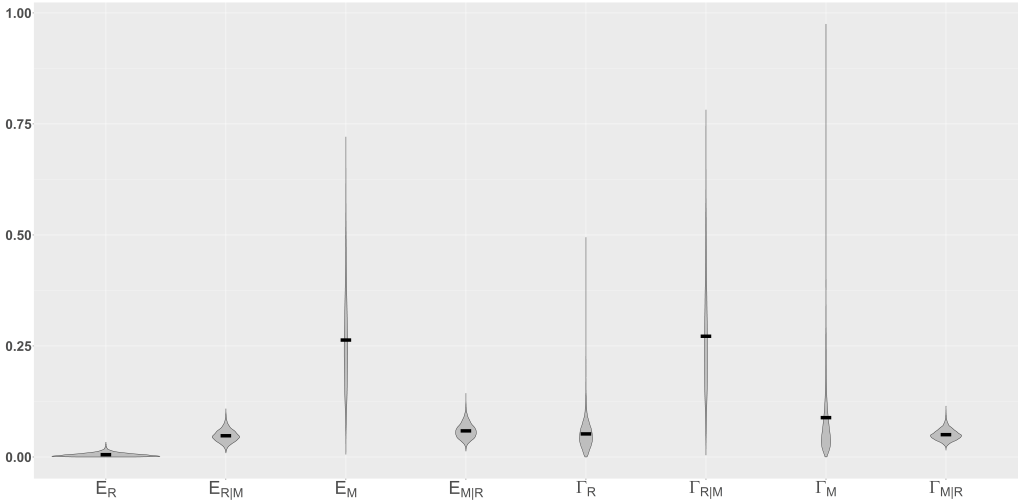


Figure 4: Violin plots of posterior distributions of block-level colonization (Γ) and extinction probabilities (E). The subscript R denotes rodents and M mustelids. Estimates for each functional group are provided both in case of absence (i.e subscript R or M) and in presence of the other functional group (i.e. subscript $R|M$ for rodents in presence of mustelids and $M|R$ for mustelids in presence of rodents). The black bars show the posterior means.

At the site level, the evidence for predator-prey interactions was most evident in the snowbed habitat in terms of extinction probabilities (Fig. 5). In this habitat, presence of mustelids increased the weekly extinction probability of rodents from 0.11 (ε_R) to 0.37 ($\varepsilon_{R|M}$) (i.e. an increase of 0.26 with 95% CI [0.13 - 0.40]) in summer and from 0.15 to 0.30 (an increase of 0.15 with 95% CI [0.001 - 0.304]) in winter. Somewhat curiously, in summer the extinction probability of mustelids in the snowbeds also increased in presence of rodents; i.e. from 0.07 (ε_M) to 0.34 ($\varepsilon_{M|R}$) (an increase of 0.27 with 95% CI [0.11-0.43]). The other habitat- and season-specific parameter contrasts that could be interpreted as resulting from predator-prey interaction were uncertain (i.e. credible intervals included zero; see Tab. 4 in Appendix C). However, there was a tendency for higher mustelid colonization probabilities when rodents were present in both habitats and seasons (Fig. 5).

Independent of predator-prey interactions, the effect of season and habitat was most pronounced in case of the rodent colonization probabilities (γ_R). These were higher in the summers than in the winters and moreover, higher in the hummock tundra than in the snowbed habitat (Fig. 5). In addition, the extinction probability of rodents (ε_R) tended to be higher in winter than in summer (see Fig. 5). For mustelids, effects of habitat and season on extinction and colonization probabilities were less clear, partly owing more uncertain estimates. However, the extinction probabilities (ε_M) may have been higher in hummock tundra than in the snowbed habitat (Fig. 5).

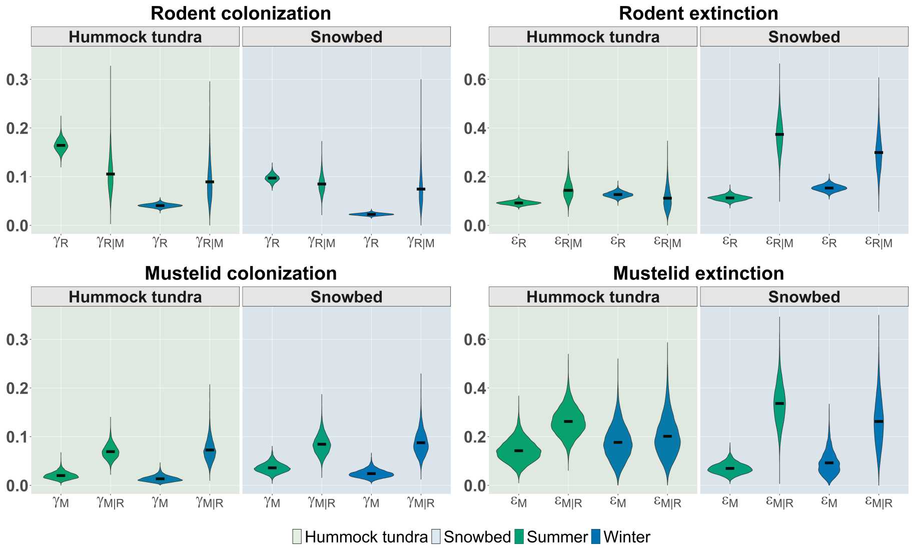


Figure 5: Violin plots of habitat- and season-specific posterior distributions site-level colonization (γ) and extinction probabilities (ε). The subscript R denotes rodents and M mustelids. Estimates for each functional group are provided both in case of absence (i.e subscript R or M) and in presence of the other functional group (i.e. subscript $R|M$ for rodents in presence of mustelids and $M|R$ for mustelids in presence of rodents). Dark green violins denote estimates from the summer season, while dark blue violins denote estimates from the winter season. The black bars denote the posterior means.

4 Discussion

The predator-prey interaction between mustelids and rodents has been perceived as a key driver of the population cycles in northern rodents (Henttonen *et al.*, 1987; Hanski *et al.*, 2001; Korpimäki *et al.*, 2002). However, it has been difficult to obtain direct empirical estimates of this interaction, mostly due to lack of data that fit the temporal and spatial scales of both interactants. Small rodents, and likely also the least weasel, have multivoltine life cycles. This combined with profound climatic seasonality may give rise to rapid and/or episodic interactions not captured by conventional population survey methods (e.g. snap-trapping or snow-track surveys) conducted once or twice per year. By using data derived from a continuous, camera-trap-based monitoring system recently established in arctic tundra landscapes, we have now estimated the strength of the mustelid-rodent interaction on a weekly time scale, year round. By applying a dynamical occupancy model specifically tailored to the hierarchical spatial structure of these monitoring data, we found evidence for a rapid (i.e. week-scale) predator-prey interaction. This interaction was most consistent in terms of increased probability of extinction of rodents in presence of mustelids, as this effect was found on both spatial scales considered (block and site). At the site-scale the strength of the interaction was habitat dependent as it was only found to be significant in the snowbeds, which was also the habitat where mustelids were most frequently recorded. Mustelids were generally recorded much less frequently in winter than in summer, but whenever they were present their impact on rodent extinction probability in the snowbeds was also apparent in winter. Although the interaction strengths, here assessed in terms of conditional extinction and colonization probabilities, appeared to be somewhat more prevalent and stronger in summer than in winter, our study does not provide clear evidence for any season dependency in the strength of mustelid-rodent interaction.

The mustelid-rodent interaction was only clear in snowbed habitat. This may be explained in terms of species-specific habitat use within the two functional groups. The stoat was the most frequently recorded mustelid in the snowbeds, while the least weasels tended to be recorded relatively more often in hummock tundra (see Fig. 8, in Appendix B). While the least weasel is regarded to be the most specialized rodent predator (Sundell & Ylönen, 2008), little is so far known about the relative impact of the two mustelids on rodent populations. Lemmings were as expected proportionately more frequently recorded than voles in snowbeds, while the hummock tundra was proportionally dominated by voles (see Fig 7, Appendix B). As lemmings may be more vulnerable to predation than voles (Oksanen *et al.*, 2008), this difference in habitat use of tundra rodents may explain the higher impact of mustelid presence on rodent extinction rates in snowbeds. Surprisingly, the extinction probability of mustelids in snowbeds was also found to increase when rodents were present. We suggest that this is likely an artefact of the high extinction rate of rodents in presence of mustelids. If a mustelid eradicates the rodents on a site within a primary occasion (i.e. within a week), and then leaves this site before the next primary session, this will appear as a mustelid extinction event conditional on presence of rodents. This highlights a general challenge of multi-species occupancy models in terms of defining a length of the primary occasions that are equally suitable for different species that are included in the model.

Northern small mammals exhibit strong seasonal variability in the demographic processes governing their population dynamics (Hansen *et al.*, 1999; Stenseth *et al.*, 2003; Andreassen *et al.*, 2021). Reproduction occurs mainly in summer. Hence for the rodents, we found (as could be expected) colonization probabilities to be highest in summer and extinction probabilities to be highest in winters. The probability estimates for the mustelids were more uncertain and not significantly different between seasons. However, the occupancy data suggested that there was also a profound seasonal dynamics in the mustelids as they were mostly present during summer (Table 1). Sharp declines and increases in weekly habitat occupancy data were especially prevalent in the transitions (i.e. the shoulder seasons) between summer and winters (Fig. 5). This may have obscured (i.e. cancelled out) seasonal differences in extinction and colonization probabilities, which were assumed to be constant within the two seasons in our model. The profound seasonal fluctuations in mustelid habitat occupancy, that appeared to be most prevalent in the stoat (see Fig. 8, Appendix B), may indicate that their movements become restricted in the subnivean space - at least in the two habitats included the present study. Previous snow tracking studies of mustelid in tundra landscapes have found that they prefer more productive habitats (e.g. meadows) in river valleys (Aunapuu & Oksanen, 2003). In tundra areas that are in close proximity to the boreal forest, mustelids tend to spend the winter in the forest-tundra transition zone (Oksanen *et al.*, 1992). Hellstedt & Henttonen (2006) suggested that mustelid space use is season dependent, both due to their seasonal breeding cycle and due to changing environmental conditions (e.g. presence of snow). Hence, such seasonal variability in habitat use of mustelids, where they mainly spend the winters in habitats not covered by this study, may have limited our ability to reveal important features of their landscape-scale interactions with rodents. We also note that our estimates of interaction strength, in terms of extinction and colonization probabilities conditional on weekly co-occurrences of both interactants, are not directly compatible with those parameters that are used to assess the impact of mustelids in empirical and theoretical models on rodent population dynamics.

We regard our study as more of a first glance into the spatial and temporal components of the rodent-mustelid interaction, rather than aiming for definitive answers about the role of this interaction in northern rodent cycles. Population cycles are inherently, temporally variable in their shapes and amplitudes (Krebs, 2013), and this study encompassed only one and a half cycle. This limits our ability to generalize our findings. Also, lumping different rodent and mustelid species into two functional group limits possible generalizations, as both population and detection processes are likely species specific. The same is true regarding the lack of detailed environmental covariates included in the analysis. For instance, boreal and Arctic small mammals have been found to be very sensitive to the physical properties of the snow pack (Jedrzejewski *et al.*, 1995; Poirier *et al.*, 2021). Unfortunately, lack of reliable local-scale environmental information combined with a too sparse dataset to include additional covariates, made it impossible to model such effects. Furthermore, our fixed definition of summer and winter seasons did not match very well the observed seasonal dynamics in the occupancy data. This regards especially the transition from winter to summer that also appeared to differ between habitats and years (Fig 2). Future analysis should attempt to use more flexible definitions of climate seasonality, for instance, based on site-level environmental data derived from the temperature sensors of the camera traps (Mölle *et al.*, 2021). Finally, the ability of mustelids to drive rodents to local and regional extinction might be dependent on the phase of the rodent population cycle (Norrdahl & Korpimäki, 1995), something we where unable to account for .

Despite these limitations, our study have provided insight about aspects of mustelid-rodent interactions that until now have been constrained by available monitoring technologies. Most clearly we found that the strength of the interaction is habitat dependent in Arctic tundra. Our study indicates that the impact of mustelids on rodent population dynamics is likely season dependent too, due to the strong seasonal fluctuation in presence of the mustelids in the two habitats encompassed by the camera-based monitoring system. Future landscape-scale, species-specific analyses based on camera trap monitoring data that span a wider range of habitats and multiple rodent cycles will be needed to fully elucidate which role mustelids play in the generation of northern rodent cycles. More generally, this study demonstrate how novel technology can shed new light on long-standing mysteries in ecology.

References

Aho, J. & Kalela, O. (1966). The spring migration of 1961 in the norwegian lemming, lemmus lemmus (l.), at kilpisjärvi, finnish lapland. *Annales Zoologici Fennici*, 3, 53–65.

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

Andreassen, H.P., Sundell, J., Ecke, F., Halle, S., Haapakoski, M., Henttonen, H., Huitu, O., Jacob, J., Johnsen, K., Koskela, E., Luque-Larena, J.J., Lecomte, N., Leirs, H., Mariën, J., Neby, M., Rätti, O., Sievert, T., Singleton, G.R., van Cann, J., Broecke, B.V. & Ylönen, H. (2021). Population cycles and outbreaks of small rodents: ten essential questions we still need to solve. *Oecologia*, 195, 601–622.

Aunapuu, M. & Oksanen, T. (2003). Habitat selection of coexisting competitors: a study of small mustelids in northern norway. *Evolutionary Ecology*, 17, 371–392.

Boonstra, R., Andreassen, H.P., Boutin, S., Hušek, J., Ims, R.A., Krebs, C.J., Skarpe, C. & Wabakken, P. (2016). Why do the boreal forest ecosystems of northwestern europe differ from those of western north america? *BioScience*, 66, 722–734.

Burton, A.C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J.T., Bayne, E. & Boutin, S. (2015). Review: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52, 675–685.

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

Emmerson, M.C. & Raffaelli, D. (2004). Predator–prey body size, interaction strength and the stability of a real food web. *Journal of Animal Ecology*, 73, 399–409.

Fauteux, D., Stien, A., Yoccoz, N.G., Fuglei, E. & Ims, R.A. (2021). Climate variability and density-dependent population dynamics: Lessons from a simple high arctic ecosystem. *Proceedings of the National Academy of Sciences*, 118.

Fidino, M., Simonis, J.L. & Magle, S.B. (2019). A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species. *Methods in Ecology and Evolution*, 10, 233–244.

Gelman, A., Carlin, J.B., Stern, H.S., Dunson, D.B., Vehtari, A. & Rubin, D.B. (2013). *Bayesian data analysis*. CRC press.

Gilg, O., Hanski, I. & Sittler, B. (2003). Cyclic dynamics in a simple vertebrate predator-prey community. *Science*, 302, 866–868.

Hansen, T.F., Stenseth, N.C. & Henttonen, H. (1999). Multiannual vole cycles and population regulation during long winters: An analysis of seasonal density dependence. *The American Naturalist*, 154, 129–139. PMID: 29578785.

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

Hanski, I., Henttonen, H., Korpimäki, E., Oksanen, L. & Turchin, P. (2001). Small-rodent dynamics and predation. *Ecology*, 82, 1505–1520.

Hanski, I., Turchin, P., Korpimäki, E. & Henttonen, H. (1993). Population oscillations of boreal rodents: regulation by mustelid predators leads to chaos. *Nature*, 364, 232–235.

Hansson, L. & Henttonen, H. (1988). Rodent dynamics as community processes. *Trends in Ecology & Evolution*, 3, 195–200.

Hellstedt, P. & Henttonen, H. (2006). Home range, habitat choice and activity of stoats (mustela erminea) in a subarctic area. *Journal of Zoology*, 269, 205–212.

Henttonen, H., Oksanen, T., Jortikka, A. & Haukisalmi, V. (1987). How much do weasels shape microtine cycles in the northern fennoscandian taiga? *Oikos*, 50, 353.

Ims, R., Jepsen J., U., Stien, A. & Yoccoz, N.G. (2013). *Science plan for COAT: Climate-ecological Observatory for Arctic Tundra*. Fram Centre Report Series 1. Fram Centre, Norway.

Ims, R.A. & Fuglei, E. (2005). Trophic Interaction Cycles in Tundra Ecosystems and the Impact of Climate Change. *BioScience*, 55, 311–322.

Jacob, J. & Brown, J.S. (2000). Microhabitat use, giving-up densities and temporal activity as short- and long-term anti-predator behaviors in common voles. *Oikos*, 91, 131–138.

Jedrzejewski, W., Jedrzejewska, B. & Szymura, L. (1995). Weasel population response, home range, and predation on rodents in a deciduous forest in poland. *Ecology*, 76, 179–195.

Kalela, O. (1971). Seasonal trends in the sex ratio of the grey-sided vole, clethrionomys rufocanus (sund.). In: *Annales Zoologici Fennici*. JSTOR, pp. 452–455.

Kausrud, K.L., Mysterud, A., Steen, H., Vik, J.O., Østbye, E., Cazelles, B., Framstad, E., Eikeset, A.M., Mysterud, I., Solhøy, T. & Stenseth, N.C. (2008). Linking climate change to lemming cycles. *Nature*, 456, 93–97.

Kellner, K. (2015). jagsui: a wrapper around rjags to streamline jags analyses. *R package version*, 1.

Kleiven, E.F., Barraquand, F., Gimenez, O., Henden, J.A., Ims, R.A., Soininen, E.M. & Yoccoz, N.G. (2021). A dynamic occupancy model for interacting species with two spatial scales. *bioRxiv*.

Kleiven, E.F., Henden, J.A., Ims, R.A. & Yoccoz, N.G. (2018). Seasonal difference in temporal transferability of an ecological model: near-term predictions of lemming outbreak abundances. *Scientific Reports*, 8.

Klemola, T., Pettersen, T. & Stenseth, N.C. (2003). Trophic interactions in population cycles of voles and lemmings: A model-based synthesis. Academic Press, vol. 33 of *Advances in Ecological Research*, pp. 75–160.

Koponen, T. (1970). Age structure in sedentary and migratory populations of the norwegian lemming, lemmus lemmus (l.), at kilpisjärvi in 1960. *Annales Zoologici Fennici*, 7, 141–187.

Korpela, K., Helle, P., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., Pietiäinen, H., Sundell, J., Valkama, J. & Huitu, O. (2014). Predator–vole interactions in northern europe: the role of small mustelids revised. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20142119.

Korpimäki, E., Norrdahl, K., Klemola, T., Pettersen, T. & Stenseth, N.C. (2002). Dynamic effects of predators on cyclic voles: field experimentation and model extrapolation. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 269, 991–997.

Krebs, C.J. (2013). *Population fluctuations in rodents*. University of Chicago Press.

Magnusson, M., Bergsten, A., Ecke, F., Bodin, Ö., Bodin, L. & Hörnfeldt, B. (2013). Predicting grey-sided vole occurrence in northern sweden at multiple spatial scales. *Ecology and Evolution*, 3, 4365–4376.

Mölle, J.P., Kleiven, E.F., Ims, R.A. & Soininen, E.M. (2021). Using subnivean camera traps to study arctic small mammal community dynamics during winter. *Arctic Science*, pp. 1–17.

Myers, J.H. (2018). Population cycles: generalities, exceptions and remaining mysteries. *Proceedings of the Royal Society B: Biological Sciences*, 285, 20172841.

Norrdahl, K. & Korpimäki, E. (1995). Mortality factors in a cyclic vole population. *Proceedings of the Royal Society of London. Series B: Biological Sciences*, 261, 49–53.

Oksanen, T., Oksanen, L., Dahlgren, J. & Olofsson, J. (2008). Arctic lemmings, lemmus spp. and dicrostonyx spp.: integrating ecological and evolutionary perspectives. *Evolutionary Ecology Research*, 10, 415–434.

Oksanen, T., Oksanen, L. & Norberg, M. (1992). Habitat use of small mustelids in north fennoscandian tundra: A test of the hypothesis of patchy exploitation ecosystems. *Ecography*, 15, 237–244.

Oli, M.K. (2019). Population cycles in voles and lemmings: state of the science and future directions. *Mammal Review*, 49, 226–239.

Olofsson, J., Tømmervik, H. & Callaghan, T.V. (2012). Vole and lemming activity observed from space. *Nature Climate Change*, 2, 880–883.

Plummer, M. (2003). Jags: A program for analysis of bayesian graphical models using gibbs sampling. In: *Proceedings of the 3rd international workshop on distributed statistical computing*. Vienna, Austria., vol. 124, pp. 1–10.

Poirier, M., Fauteux, D., Gauthier, G., Domine, F. & Lamarre, J.F. (2021). Snow hardness impacts intranivean locomotion of arctic small mammals. *Ecosphere*, 12, e03835.

R Core Team (2021). *R: A Language and Environment for Statistical Computing*. R Foundation for Statistical Computing, Vienna, Austria.

Rota, C.T., Ferreira, M.A.R., Kays, R.W., Forrester, T.D., Kalies, E.L., McShea, W.J., Parsons, A.W. & Millspaugh, J.J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7, 1164–1173.

Schmitz, O.J., Miller, J.R.B., Trainor, A.M. & Abrahms, B. (2017). Toward a community ecology of landscapes: predicting multiple predator–prey interactions across geographic space. *Ecology*, 98, 2281–2292.

Soininen, E.M., Henden, J.A., Ravolainen, V.T., Yoccoz, N.G., Bråthen, K.A., Killengreen, S.T. & Ims, R.A. (2018). Transferability of biotic interactions: Temporal consistency of arctic plant–rodent relationships is poor. *Ecology and Evolution*, 8, 9697–9711.

Soininen, E.M., Jensvoll, I., Killengreen, S.T. & Ims, R.A. (2015). Under the snow: a new camera trap opens the white box of subnivean ecology. *Remote Sensing in Ecology and Conservation*, 1, 29–38.

Sollmann, R. (2018). A gentle introduction to camera-trap data analysis. *African Journal of Ecology*, 56, 740–749.

Stenseth, N.C., Bjørnstad, O.N. & Saitoh, T. (1998). Seasonal forcing on the dynamics of clethrionomys rufocanus: modeling geographic gradients in population dynamics. *Population Ecology*, 40, 85–95.

Stenseth, N.C., Viljugrein, H., Saitoh, T., Hansen, T.F., Kittilsen, M.O., Bølviken, E. & Glöckner, F. (2003). Seasonality, density dependence, and population cycles in hokkaido voles. *Proceedings of the National Academy of Sciences*, 100, 11478–11483.

Sundell, J., O'Hara, R.B., Helle, P., Hellstedt, P., Henttonen, H. & Pietiäinen, H. (2013). Numerical response of small mustelids to vole abundance: delayed or not? *Oikos*, 122, 1112–1120.

Sundell, J. & Ylönen, H. (2008). Specialist predator in a multi-species prey community: boreal voles and weasels. *Integrative Zoology*, 3, 51–63.

Tast, J. (1966). The root vole, microtus oeconomus (pallas), as an inhabitant of seasonally flooded land. In: *Annales Zoologici Fennici*. JSTOR, vol. 3, pp. 127–171.

Tobler, M.W., Zúñiga Hartley, A., Carrillo-Percastegui, S.E. & Powell, G.V.N. (2015). Spatiotemporal hierarchical modelling of species richness and occupancy using camera trap data. *Journal of Applied Ecology*, 52, 413–421.

Turchin, P. & Hanski, I. (1997). An empirically based model for latitudinal gradient in vole population dynamics. *The American Naturalist*, 149, 842–874.

Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T. & Henttonen, H. (2000). Are lemmings prey or predators? *Nature*, 405, 562–565.

Vigués, J., Menci, S., Wilkinson, C., Vaillant, M.L., Angerbjörn, A. & Norén, K. (2021). A beacon of dung: using lemming (lemmus lemmus) winter nests and DNA analysis of faeces to further understand predator–prey dynamics in northern sweden. *Polar Biology*, 44, 2269–2276.

Wootton, J.T. & Emmerson, M. (2005). Measurement of interaction strength in nature. *Annual Review of Ecology, Evolution, and Systematics*, 36, 419–444.

A Snap trapping

A long-term snap-trapping-based monitoring program is run on the Varanger Peninsula (Kleiven *et al.*, 2018). The time series derived from this monitoring program yield independent information on the population dynamics of rodents during the study period (2015-2021) and shows that it includes two cyclic decrease phases over the years 2015-2017 and 2019-2020, respectively (Fig. 6).

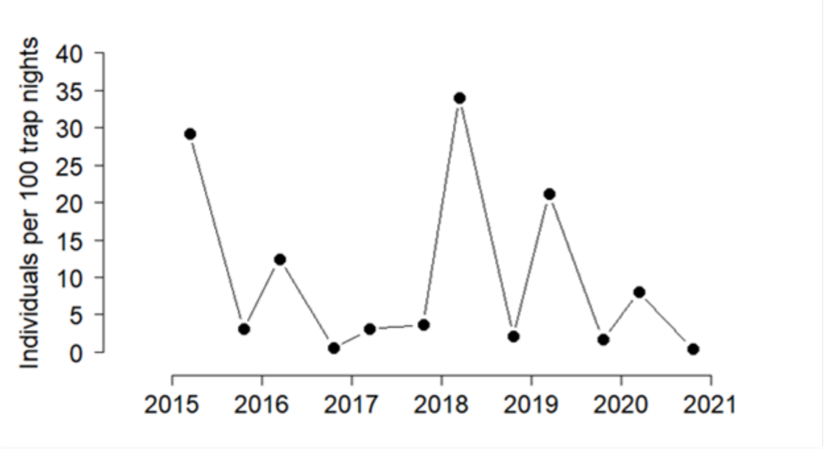


Figure 6: Time series plots of two population density indices (late June and early September) per year derived from the snap trapping monitoring system on the Varanger Peninsula.

B Data

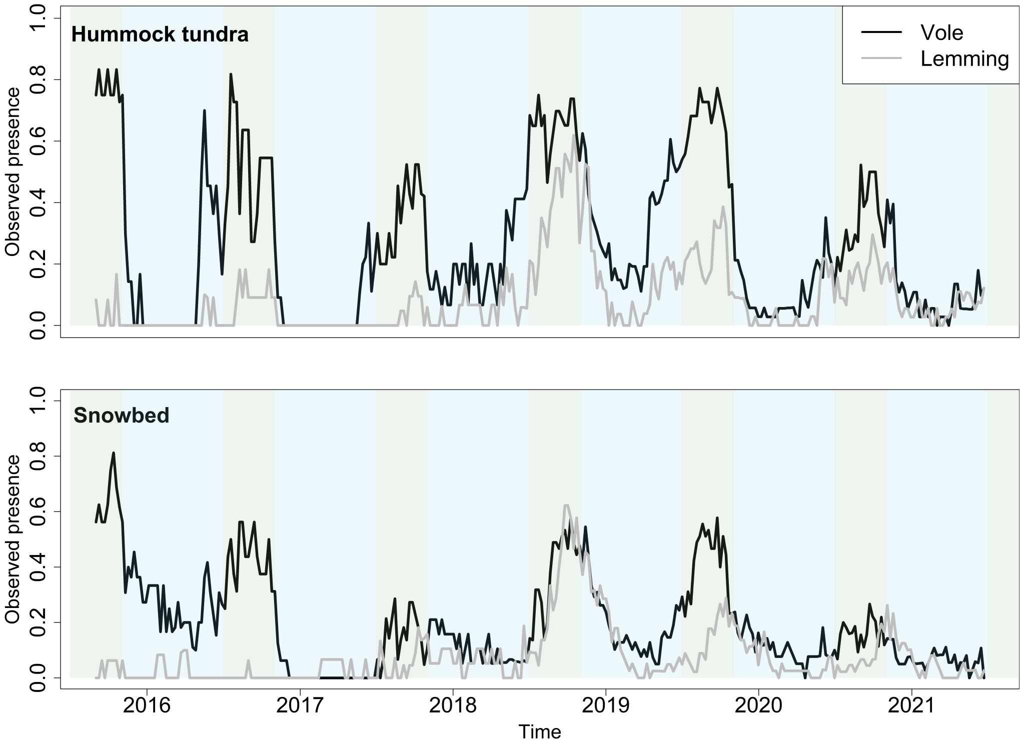


Figure 7: Temporal patterns in the proportion camera traps sites with weekly presence of lemmings (grey lines) and voles (black lines) in hummock tundra and snowbeds. Pale green background denote summer seasons (July 1- November 1), while the pale blue background denote the winter seasons. Note that only sites from the 4 blocks in Komagdalen were functional before summer 2018.

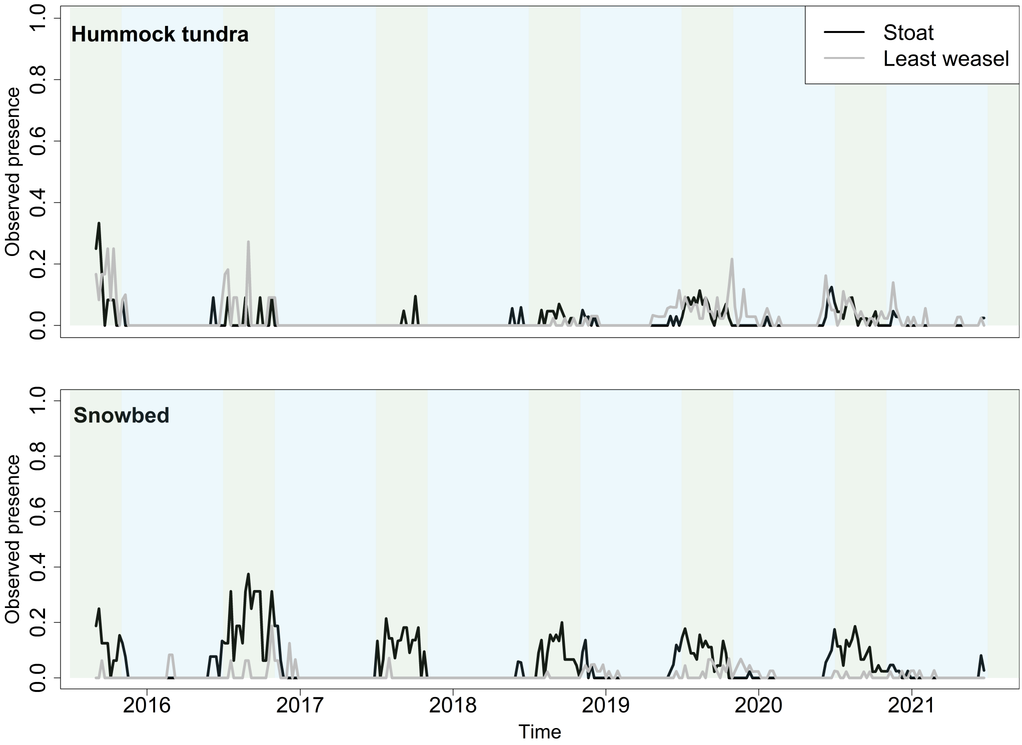


Figure 8: Temporal patterns in the proportion camera traps sites with weekly presence of least weasels (grey lines) and stoats (black lines) in hummock tundra and snowbeds. Pale green background denote summer seasons (July 1- November 1), while the pale blue background denote the winter seasons. Note that only sites from the 4 blocks in Komagdalen were functional before summer 2018.

C All occupancy model parameters

C.1 Block level parameters

Parameter	mean	sd	95% CI
Γ_R	0.052	0.033	0.006 0.124
$\Gamma_{R\|M}$	0.272	0.122	0.080 0.544
Γ_M	0.089	0.105	0.008 0.389
$\Gamma_{M\|R}$	0.050	0.012	0.029 0.079
E_R	0.005	0.004	0.0002 0.016
$E_{R\|M}$	0.048	0.014	0.023 0.079
E_M	0.264	0.107	0.090 0.505
$E_{M\|R}$	0.059	0.017	0.031 0.096

Table 2: Means, standard deviations and 95% credible intervals based the posterior distributions of block level colonization (Γ) and extinction probabilities (E) of rodents (R) and mustelids (M) dependent on the presence of the other functional group.

C.1.1 interaction strength

Parameter	mean	95% CI
Γ_R - $\Gamma_{R\|M}$	-0.220	-0.512 0.017
Γ_M - $\Gamma_{M\|R}$	0.038	-0.049 0.333
E_R - $E_{R\|M}$	-0.043	-0.075 -0.013
E_M - $E_{M\|R}$	0.205	0.021 0.452

Table 3: Estimated differences (i.e. contrasts) between independent (i.e. rodents and mustelids in absence of the other) and dependent (i.e. rodents and mustelids in presence of the others) colonization and extinction probabilities with 95% credible intervals.

C.2 Site level parameters

C.2.1 interaction strength

Parameter	Habitat	Season	mean	95% CI
γ_R - $\gamma_{R\|M}$	Hummock tundra	Summer	0.059	-0.020 0.123
γ_R - $\gamma_{R\|M}$	Hummock tundra	Winter	-0.049	-0.133 0.011
γ_R - $\gamma_{R\|M}$	Snowbed	Summer	0.012	-0.030 0.048
γ_R - $\gamma_{R\|M}$	Snowbed	Winter	-0.052	-0.127 -0.001
ε_R - $\varepsilon_{R\|M}$	Hummock tundra	Summer	- 0.052	-0.129 0.011
ε_R - $\varepsilon_{R\|M}$	Hummock tundra	Winter	0.015	-0.094 0.094
ε_R - $\varepsilon_{R\|M}$	Snowbed	Summer	- 0.261	-0.399 -0.131
ε_R - $\varepsilon_{R\|M}$	Snowbed	Winter	- 0.146	-0.305 -0.001
γ_M - $\gamma_{M\|R}$	Hummock tundra	Summer	-0.049	-0.083 -0.019
γ_M - $\gamma_{M\|R}$	Hummock tundra	Winter	-0.059	-0.108 -0.021
γ_M - $\gamma_{M\|R}$	Snowbed	Summer	-0.048	-0.094 -0.008
γ_M - $\gamma_{M\|R}$	Snowbed	Winter	-0.063	-0.116 -0.021
ε_M - $\varepsilon_{M\|R}$	Hummock tundra	Summer	-0.120	-0.268 0.026
ε_M - $\varepsilon_{M\|R}$	Hummock tundra	Winter	-0.025	-0.251 0.186
ε_M - $\varepsilon_{M\|R}$	Snowbed	Summer	-0.267	-0.432 -0.111
ε_M - $\varepsilon_{M\|R}$	Snowbed	Winter	-0.170	-0.396 0.042

Table 4: Estimated differences (i.e. contrasts) between independent (mustelid or rodents in absence of the other) and dependent (mustelid or rodents in presence of the other) colonization and extinction probabilities with 95% credible intervals at the site level.

C.2.2 Rodent parameters

Parameter	Habitat	Season	Mean	sd	95% CI
γ_R	Hummock tundra	Summer	0.164	0.012	0.142 0.188
γ_R	Hummock tundra	Winter	0.041	0.004	0.034 0.048
γ_R	Snowbed	Summer	0.097	0.007	0.083 0.112
γ_R	Snowbed	Winter	0.023	0.002	0.018 0.028
$\gamma_{R\|M}$	Hummock tundra	Summer	0.105	0.034	0.048 0.180
$\gamma_{R\|M}$	Hummock tundra	Winter	0.090	0.037	0.031 0.173
$\gamma_{R\|M}$	Snowbed	Summer	0.085	0.018	0.054 0.123
$\gamma_{R\|M}$	Snowbed	Winter	0.075	0.032	0.025 0.148
ε_R	Hummock tundra	Summer	0.092	0.008	0.078 0.108
ε_R	Hummock tundra	Winter	0.127	0.011	0.106 0.149
ε_R	Snowbed	Summer	0.113	0.011	0.093 0.135
ε_R	Snowbed	Winter	0.154	0.013	0.130 0.179
$\varepsilon_{R\|M}$	Hummock tundra	Summer	0.144	0.034	0.085 0.217
$\varepsilon_{R\|M}$	Hummock tundra	Winter	0.112	0.046	0.040 0.215
$\varepsilon_{R\|M}$	Snowbed	Summer	0.374	0.066	0.249 0.509
$\varepsilon_{R\|M}$	Snowbed	Winter	0.300	0.073	0.160 0.451

Table 5: Means, standard deviations and 95% credible interval based on the posterior distribution of all rodent parameters at the site level.

C.2.3 Mustelid parameters

Parameter	Habitat	Season	Mean	sd	95% CI
γ_M	Hummock tundra	Summer	0.020	0.007	0.009 0.036
γ_M	Hummock tundra	Winter	0.014	0.006	0.005 0.028
γ_M	Snowbed	Summer	0.036	0.010	0.019 0.058
γ_M	Snowbed	Winter	0.024	0.008	0.011 0.042
$\gamma_{M\|R}$	Hummock tundra	Summer	0.069	0.014	0.045 0.100
$\gamma_{M\|R}$	Hummock tundra	Winter	0.073	0.022	0.037 0.120
$\gamma_{M\|R}$	Snowbed	Summer	0.085	0.019	0.050 0.126
$\gamma_{M\|R}$	Snowbed	Winter	0.089	0.024	0.047 0.141
ε_M	Hummock tundra	Summer	0.143	0.045	0.064 0.239
ε_M	Hummock tundra	Winter	0.177	0.069	0.056 0.325
ε_M	Snowbed	Summer	0.070	0.021	0.032 0.117
ε_M	Snowbed	Winter	0.093	0.047	0.023 0.205
$\varepsilon_{M\|R}$	Hummock tundra	Summer	0.263	0.058	0.160 0.383
$\varepsilon_{M\|R}$	Hummock tundra	Winter	0.202	0.081	0.067 0.386
$\varepsilon_{M\|R}$	Snowbed	Summer	0.337	0.081	0.188 0.500
$\varepsilon_{M\|R}$	Snowbed	Winter	0.263	0.098	0.088 0.470

Table 6: Means, standard deviations and 95% credible interval based on the posterior distribution of all mustelid parameters at the site level.

Paper IV

Using camera traps to monitor vole population cycles Manuscript

Manuscript

Using camera traps to monitor vole population cycles

Eivind Flittie Kleiven[1,*], Pedro Guilherme Nicolau[2,*], Sigrunn Holbek Sørbye[2], Jon Aars[3], Nigel Gilles Yoccoz[1], and Rolf Anker Ims[1]

[1]Department of Arctic and Marine Biology, Faculty of Biosciences, Fisheries and Economics, UiT The Arctic University of Norway, N-9037, Tromsø

[2]Department of Mathematics and Statistics, Faculty of Science, UiT The Arctic University of Norway, N-9037, Tromsø

[3]Norwegian Polar Institute, Fram Centre, Tromsø 9296, Norway

[*]These authors have contributed equally.

Abstract

Camera traps have become increasingly popular as a labor-efficient and non-invasive tool to study animal ecology. Despite rodents being the most abundant and specious order of living mammals, camera trap studies have mainly focused on larger mammals. Here we investigate the suitability of camera-trap-based abundance indices to monitor population cycles of two species of voles with key functions in boreal and Arctic ecosystems. The targeted species — gray-sided vole (*Myodes rufocanus*) and tundra vole (*Microtus oeconomus*) – differ with respect to habitat use and spatial-social organization, which allow us to assess whether such species-traits influence the accuracy of the abundance indices. For both species, multiple live-trapping grids yielding capture-mark-recapture (CMR) abundance estimates, were matched with single tunnel-based camera traps (CT) intended to yield abundance indices. The study encompassed three years with contrasting abundances and phases of the population cycle. First, we used linear regressions to calibrate CT-indices based on photo counts over different time-windows as a function of CMR-derived abundance estimates. Then, we performed inverse regressions to predict CMR-abundances from CT-indices. We found that CT-indices (for windows showing best goodness-of-fit) from single camera traps predicted adequately the CMR-based estimates for the gray-sided vole, whereas such predictions were generally poor for the tundra vole. However, aggregating photo counts over several nearby camera traps yielded also reliable abundance indices for the tundra vole. The two species differed also with respect to the optimal time-window for the CT-indices, which was 1 day for the tundra vole and 5 days for the gray-sided vole. Such species differences imply that the design of camera trap studies of rodent population dynamics should to be adapted to the species in focus. Overall, tunnel-based camera traps yield much more temporally resolved abundance metrics than alternative methods. This gives a potential for revealing new aspects of the multi-annual population cycles of voles as well as other small mammal species they interact with in boreal and Arctic ecosystems.

Key words: Rodents, Index-calibration regression, inverse prediction, camera trap, population monitoring

1 Introduction

During the last decade, the use of camera traps has increased drastically in animal ecology as this provides a non-invasive and cost efficient alternative to traditional census methods (Wearn and Glover-Kapfer, 2019). In studies of mammals, the use of camera traps has so far largely focused on large-sized species (Burton et al., 2015). Nonetheless, smaller-sized rodents represent the most abundant and specious order of mammals (Wilson and Reeder, 2005). Many rodent species are cryptic, and hence resource-demanding, or otherwise difficult to study by means of conventional methods. Hence, camera traps specifically adapted to study small rodents may advance our ability to investigate their ecology (Rendall et al., 2014). Studying the population dynamics of small rodents is important for several reasons (Krebs, 2013). Many rodent species pose risks to humans as vectors of zoonoses (Meerburg et al., 2009a; Capizzi et al., 2014) or by damaging crops (Meerburg et al., 2009b; Andreassen et al., 2021). Moreover, voles and lemmings exert key ecosystem functions, especially in northern biomes where they exhibit multi-annual population cycles (Ims and Fuglei, 2005). Therefore, accurate monitoring of boreal and Arctic small rodent populations is fundamental to studies of ecosystem dynamics (Legagneux et al., 2014; Boonstra et al., 2016) and to the successful conservation of endangered species that are directly (Ims et al., 2018) or indirectly affected by their population dynamics (Marolla et al., 2019; Henden et al., 2021). Many boreal and Arctic rodent monitoring programs are still based on kill-traps (snap-traps), providing counts as indices of abundance (Turchin et al., 2000; Hörnfeldt et al., 2005; Korpela et al., 2013; Cornulier et al., 2013; Kleiven et al., 2018; Ehrich et al., 2019). However, kill-trapping is fraught with both ethical issues (Powell and Proulx, 2003) and questionable assumptions regarding sampling errors (Hanski et al., 1994). Live-trap-based, capture-mark-recapture (CMR) monitoring is less invasive and allows to account for sampling errors (Krebs et al., 2011). However, live-trapping requires much effort from qualified personnel and is therefore rarely sufficiently long-term and spatially extensive to support monitoring programs. In addition, several species display very low trappability in live-traps and are thus inadequately monitored by capture-recapture methods (Boonstra and Krebs, 1978; Jensen et al., 1993). In general, existing monitoring programs of rodent populations are logistically limited in terms of their coarse temporal resolution. In northern ecosystems such monitoring is usually restricted to two trapping sessions per year (Cornulier et al., 2013). This implies an important limitation due to the multivoltine life histories and the fast population dynamics of voles and lemmings. Camera traps may potentially resolve such constraints by providing means for spatially extensive and continuous year-round monitoring, even in climatically harsh and remote boreal and Arctic regions (Soininen et al., 2015; Mölle et al., 2021).

Camera traps are today most commonly used to analyze presence-absence dynamics (i.e. occupancy probability) (MacKenzie et al., 2002; Bailey et al., 2014). However, presence-absence is a less informative population state variable than abundance, especially when density-dependent population regulatory mechanisms are of concern. Hence, the use of camera traps to estimate abundance is increasing. Most of these studies have however focused on marked (or otherwise distinguishable) individuals (Gilbert et al., 2021; Palencia et al., 2021). For many species, such as small rodents, it is not feasible to either mark or distinguish individuals by clues that are visible in camera trap images. Moreover, design constraints make presence-absence-based abundance estimators less applicable in the case of unmarked small mammals.

If the aim is to study population dynamics, for instance by means of time series analyses (Stenseth, 1999; Cornulier et al., 2013; Barraquand et al., 2017), simple indices of abundance can be used if there is a proportionate relationship between true abundance and the abundance index (Hanski et al., 1994; Lambin et al., 2000; Yoccoz et al., 2001; Gilbert et al., 2021). Counts of motion triggered photos appear to be a promising abundance index for large- to medium-sized mammals (Palmer et al., 2018). Recent studies suggest that this may also be the case for some small rodent species (Villette et al., 2015; Parsons et al., 2021). However, as of yet, such camera-based abundance indices have not been validated for rodent species that exhibit multi-annual population cycles, for instance, boreal and Arctic voles. Furthermore, previous works have been limited in scope and have not assessed the uncertainty associated with using camera-trap indices to estimate population abundance. A potential challenge in the case of such population dynamics is that there may be density- and/or cyclic phase-dependent aspects of their performance (sensu Stenseth (1999)) that may influence the reliability of camera-trap (CT) indices.

Proper calibration of CT-based abundance indices as a function of CMR-based abundance estimates is challenging. Generally, calibration consists of modelling the measurable response variable (e.g. a population index) as a function of a ground-truthing variable that typically is assumed to be measured accurately (e.g. a population state variable measured without error). Once a calibration function is established, it can be used in inverse regression to predict the state variable for a given value of the response variable (Eisenhart, 1939). The goodness of the fit of the regression may be assessed using the ordinary coefficient of determination (R^2). In most ecological studies, the true state of a population is not known and must be estimated with some error, for instance, based on CMR trapping. As the error of the population state estimate (i.e. the ground-truth variable) may not be negligible, this becomes a more difficult calibration problem because the uncertainty of the true abundance can bias the estimation of the population state (Gopalaswamy et al., 2015). Thus it is important to assess the accuracy of prediction after establishing a calibration function (Diefenbach et al., 1994), to ensure high precision of the abundance predictions, which can sometimes be too low (Jennelle et al., 2002). Furthermore, camera trap-based abundance indices have been criticized for not being generalizable to other species or sampling sites (Jennelle et al., 2002). It is therefore important to investigate potential differences in the performance of the abundance index for different species, i.e., to assess out-of-sample predictive ability of the index-calibration models.

In this study, we assess the suitability of camera-trap-based abundance indices for studying population dynamics of the gray-sided vole (*Myodes rufocanus*) and the tundra vole (*Microtus oeconomus*). Both species are renowned for their multi-annual cycles (Hansen et al., 1999; Turchin et al., 2000; Cornulier et al., 2013) and key roles in boreal and sub-arctic ecosystems (Ims and Fuglei, 2005; Boonstra et al., 2016). The two vole species are also known to differ profoundly in their habitat use and spatial-social organization (Ims, 1987a; Bondrup-Nielsen and Ims, 1990), which provides a case for assessing whether such species-specific traits influence camera trap-based abundance indices (CT-indices). For both species, we used time series of spatio-temporally matched CT-indices and CMR-estimates, spanning a wide range of abundances and different phases of the population cycle. We followed a two-step calibration approach. First, we fitted calibration regressions, with the CT-indices, based on photo counts from single camera traps, as the exposure variable and CMR-based abundance estimates as the ground-truthing variable. In the case of tundra vole, for which several camera traps were used within the same local population, we also assessed to what extent aggregating data over several camera traps improved the fit of the calibration regression, i.e., treating the cameras as spatial replicates. As the camera traps provide continuous-time data, we assessed which temporal resolution (i.e. time-window) of the camera trap data was optimal, in the sense of providing the best goodness-of-fit calibration regression (i.e, maximized the R^2). As the second step, we performed inverse prediction to estimate vole abundance using the optimal CT-index, and evaluated the predictive performance of the model using k-fold cross-validation, bias and a classification metric for three abundance classes.

2 Methods

2.1 Study areas and species

The data were obtained from two study areas in sub-arctic Norway (Figure 1), where long-term monitoring of vole population is ongoing by means of CMR-trapping. Regional-scale population dynamics of gray-sided vole were monitored in Porsanger (N 70.05°, E 24.97°) with multiple trapping stations spaced along a 170 km transect (Nicolau et al., 2020). The sampling was conducted in mountain birch forest, where the gray-sided vole is the most common species within a community with four other rodent species (Yoccoz and Ims, 2004). The phases of the 4-year population cycle exhibit a great deal of spatial synchrony across the sampled region. In case of the tundra vole, local population dynamics were monitored within an area of $1km^2$ on the small oceanic island Håkøya (N 69.67°, E 18.83°). The tundra vole is here the only rodent species present. The population is distributed on patches of coastal meadows (Soininen et al., 2015), which is the preferred habitat for this species in Arctic and boreal ecosystem (Tast, 1966; Soininen et al., 2018).

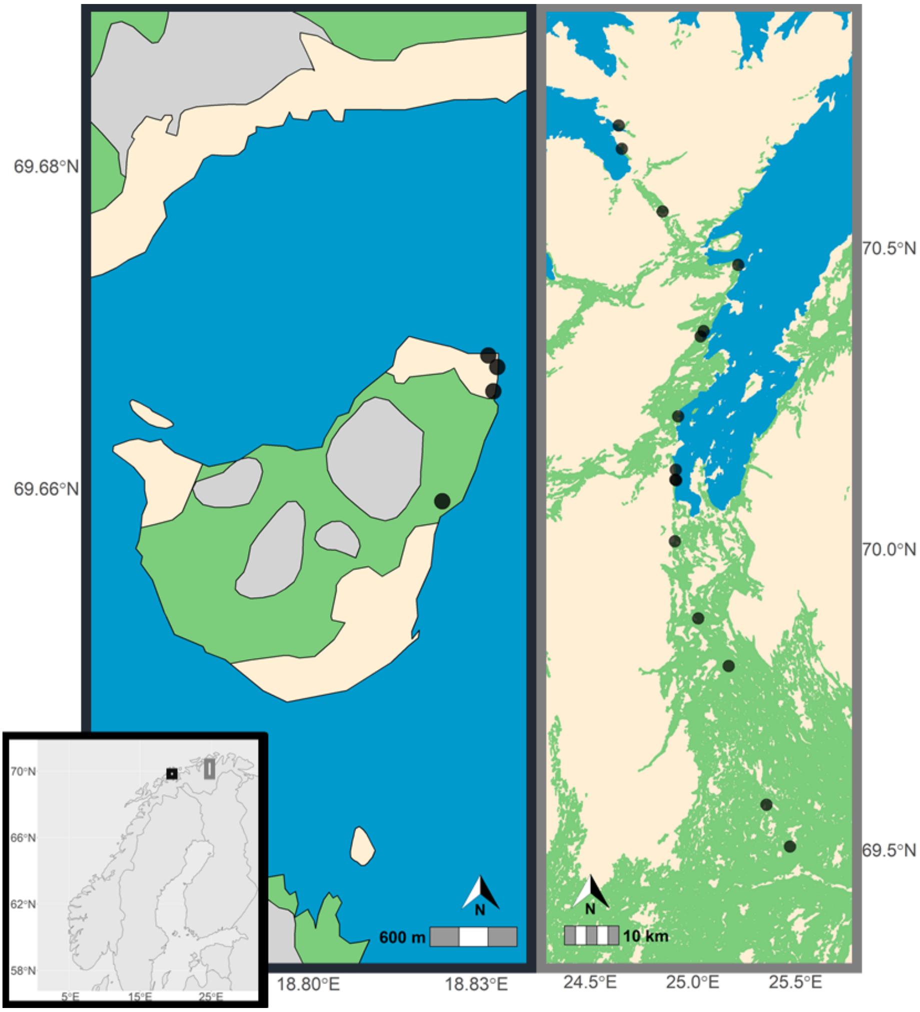


Figure 1: Maps of the study areas. Bottom left: regional map of Fennoscandia with the two study areas marked with different colored rectangles (Håkøya in black and Porsanger in gray). Left: Håkøya study area for the tundra vole. Right: Porsanger study area for the gray-sided vole. Black dots denote sampling stations, green hue is forest, light yellow corresponds to non-forested areas on dry ground (e.g. alpine or coastal heaths), gray is mire and the blue is sea. Notice the different scale of the two study area maps.

2.2 Sampling design

2.2.1 CMR-trapping

CMR-trapping was conducted with baited Ugglan No. 2 live traps during the snow-free seasons in the years 2018-2020. Unless previously marked, trapped animals were marked with a passive induced transponder (PIT)-tag, and the individual covariates *weight* and *sex* were recorded.

For the gray-sided vole monitoring, the trapping was conducted on 15 trapping stations spaced along the study transect (Figure 1). Each trapping station consisted of a standardized grid with 16 live traps, covering an area of about 0.5 ha (Ehrich et al., 2009). In each of the three years, trapping was conducted in three sessions: middle of June, beginning of August and middle of September. During each session, the trapping was conducted over two consecutive days trapping days, following a trap-setting day (see Ehrich et al. (2009) for more details).

For the tundra vole monitoring, trapping was conducted in variably shaped and sized coastal meadow patches. For the purpose of the present study, we defined 4 sampling stations with sizes (approximately 0.5) and trapping grids (10-20 live traps) that were comparable to the sampling stations of the gray-sided vole monitoring. However, in contrast to the widely spaced trapping stations in the regional-scale monitoring of the gray-sided vole, the adjacent tundra vole trapping stations were considered to cover the same local population. CMR-trapping of tundra voles was conducted monthly from June to October (i.e., five trapping sessions) in each of the three years. As the trappability of tundra voles is lower than that of gray-sided voles (Øvrejorde, 2007), the tundra vole trapping was conducted over three consecutive days per session. Trappability was further enhanced by pre-baiting the live-traps one day prior to the first trap-night.

2.2.2 CMR-based abundance estimation

To address the sampling error associated with capture heterogeneity, abundances were estimated using the capture histories of each of the trapped individuals. Specifically, individual capture probabilities were assumed to have a temporal effect (model M_{th} in Otis et al. (1978)). We then fitted a multinomial regression model, where the logit-transformed probabilities of the capture histories were modelled in terms of the individual variables *weight* and *sex*. In addition, the predictor included independent random effects for stations, to account for spatially-varying capture heterogeneity. Finally, the CMR-based abundances ($N_{s,t}$) were estimated using the Horvitz-Thompson estimator (Horvitz and Thompson, 1952), for each station s and trap season t (Huggins and Hwang, 2011). This corresponds to the CR-INLA framework presented in Nicolau et al. (2020). Finally, we standardized the abundance estimates according to the number of live traps per trapping location.

2.2.3 Camera trapping and abundance indices

In November 2017 (tundra vole) and June 2018 (gray-sided vole), a single camera trap was placed within each of the CMR-grids, for a total of 15 camera traps in Porsanger and 4 in Håkøya. We used the tunnel trap developed by (Soininen et al., 2015) and with the specific camera settings described in Mölle et al. (2021) and Appendix A.2.

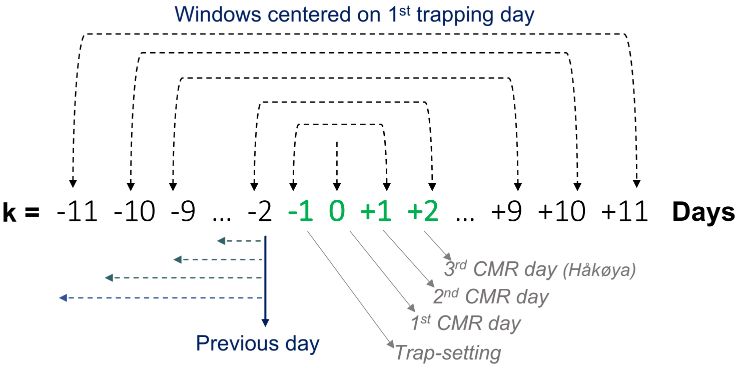


Figure 2: Schematic representation of the time-windows used to aggregate photo counts for the camera trap-based abundance indices. Days related to the CMR-trapping are presented in green, with day 0 corresponding to the first capture day (following trap-setting on the previous day; day -1), followed by one (gray-sided vole) or two (tundra vole) capture days. Two types/groups of time-windows are defined: CMR-encompassing, centered on first CMR day and thus including all days with activated live traps, shown by the upper set of of vertical arrows; and CMR-preceding, for the days preceding the trap-setting day, shown by the set of bottom left vertical arrows.

We use a range of time-windows of daily photo counts to derive CT-indices (Figure 1). Let X_k, $k = -11, \dots, 11$, denote the number of photos counted at day k relative to the first day of CMR-trapping ($k = 0$). The different temporal windows I denote intervals of d days. Each CT-index is then defined as the average CT-counts per day for a given I, given by $Y_I = \frac{1}{d} \sum_{k \in I} X_k$.

We define two types/groups of time-windows, depending on whether the window encompassed the CMR-trapping or preceded it. We make this distinction to account for the potential confounding effect of entrapment of animals during CMR-trapping (i.e. considering that animals in live traps cannot be camera trapped). For the CMR-preceding intervals, we assessed the windows $I = [k, -2]$, where $k = -11, \dots, -2$. For the CMR-encompassing intervals, we used the windows $I = [-k, k]$, where $k = 0, \dots, 11$.

2.3 Calibration analysis

For each time-window, we calibrated the CT-indices from the single camera trap per sampling station against the temporally matching CMR-based abundances estimates for the same station. For gray-sided voles, the dataset includes in total 115 calibration points, while there are 60 calibration points for the tundra voles (see Appendix A.1). As the 4 trapping stations for the tundra vole covered the same local population, we additionally perform a calibration analysis with the abundance indices and estimates averaged over all stations, which yields 15 calibration points.

2.3.1 Calibration Regression

Let $Y_{I,s,t}$ denote the CT-index for a given temporal window I, measured at station s and trap season t. A linear relationship between the CT-index and the CMR-abundance ($N_{s,t}$) is best fitted on a log-scale. A linear regression model is thus formulated by

$$\log(Y_{I,s,t}+1) = \beta_0 + \beta_1 \log(N_{I,s,t}+1) + \varepsilon_{I,s,t}, \tag{1}$$

where β_0 and β_1 are coefficients to be estimated to define the calibration line for each temporal window I. The set $\{\varepsilon_{I,s,t}\}$ denotes error terms that are assumed to be independent and normally distributed with homogeneous variance. The number 1 was added to ensure positive arguments of the log-function. The ordinary coefficient of determination R^2 is used as a measure of the goodness-of-fit.

2.3.2 Inverse prediction and model validation

For a simple linear regression model, the prediction interval for the explanatory variable can be calculated by inverting the corresponding prediction interval for the response variable. Here, we used the R-package `investr` (Greenwell and Schubert Kabban, 2014) to compute the Wald 95% prediction interval for a new observation, $\hat{x}_0 = \frac{\hat{y}_0 + \hat{\beta}_0}{\hat{\beta}_1}$, where $\hat{x}_0$ is the CMR-abundance estimate using the observed CT-index $\hat{y}_0$, and $\hat{\beta}_0$ and $\hat{\beta}_1$ denote estimates of the coefficients.

To assess the predictive performance of the calibration model with the time-window with the highest R^2 value, we employ a k-fold cross-validation approach. Specifically, we remove all calibration points for a given station and estimate the coefficients of (1) using the remaining stations. We then predict the CMR-abundances given the corresponding CT-index of the excluded station. This is repeated for all stations, thus being equivalent to a 15-fold cross-validation approach for the gray-sided vole and a 4-fold cross-validation approach for tundra voles. For the spatially aggregated tundra vole calibration, performing cross-validation is not feasible (only 15 calibration points at a single spatial location).

Different measures of predictive performance are computed. These include coverage of the 95% prediction interval for the explanatory variables log CMR-abundances, the mean absolute error and the root mean squared error. Additionally, we define an ecological classification metric (ECM) which intends to provide qualitative information on predictions that are functionally relevant for a cyclic populations (i.e. cycle phases). We define the following three population density categories: low-abundances (low phase of the cycle), intermediate abundances and high abundances (high phase). The high and low abundances are defined as the 25% and 75% quantiles of the respective sample distributions for each species. The ECM is thus defined as the proportion of times the true observed log-abundance value and the predicted value belong to the same category. The analysis was conducted in R 4.0.3 (R Core Team 2020).

3 Results

3.1 Abundance estimates and indices

Annual means of the CMR-based abundance estimates reveal the phases/years of population increase (2018), peak (2019) and crash (2020) for both vole species (Figure 3). The distributions of the standardized abundance estimates and indices were similar between the species (Table 1). Moreover, neither the overall means nor the variance in the CT-indices differed notably between species or time windows (Table 1 and Figure 4). However, there was a difference in the temporal autocorrelations of daily CT-counts between the two species. While the estimated auto-correlations decreased linearly over time with relatively little scatter for the gray-sided vole, the estimated auto-correlations for the tundra vole showed a steeper decrease over the first 4 days before it leveled off with a large scatter. Furthermore, for the gray-sided vole, there was an increase in the mean number of photos taken the days right after the trapping experiment, which could suggest a possible interaction between the two methodologies.

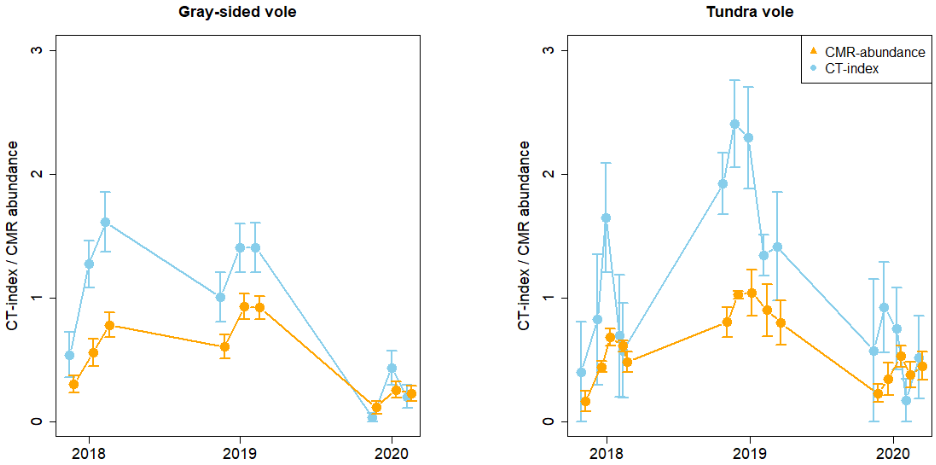


Figure 3: Population dynamics over trapping seasons (within-years) and years based on log-scale CT-abundance indices (blue circles) and log CMR-abundance estimates standardized by number of traps (orange circles). The indices and estimates represent means with standard error bars over all trapping stations for the two species. The optimal time-windows for the CT-index are used for both species (see Figure 5).

Table 1: Distribution statistics (arithmetic mean, standard deviation and range) for the standardized log-transformed abundances estimates (CMR-based; log(abundance/N traps) and CT-indices (log(CT-counts)/(N days)) used in the calibration regression models. The CT-indices are given for the time-window that provided the best fitting calibration regression (see Figure 5).

Metric	Statistic	Gray-sided vole	Tundra vole
CMR-estimates	Mean	0.54	0.59
	STDev	0.44	0.34
	Range	0-1.63	0-1.59
CT-indices	Mean	0.93	1.13
	STDev	0.84	0.94
	Range	0-3.10	0-3.22

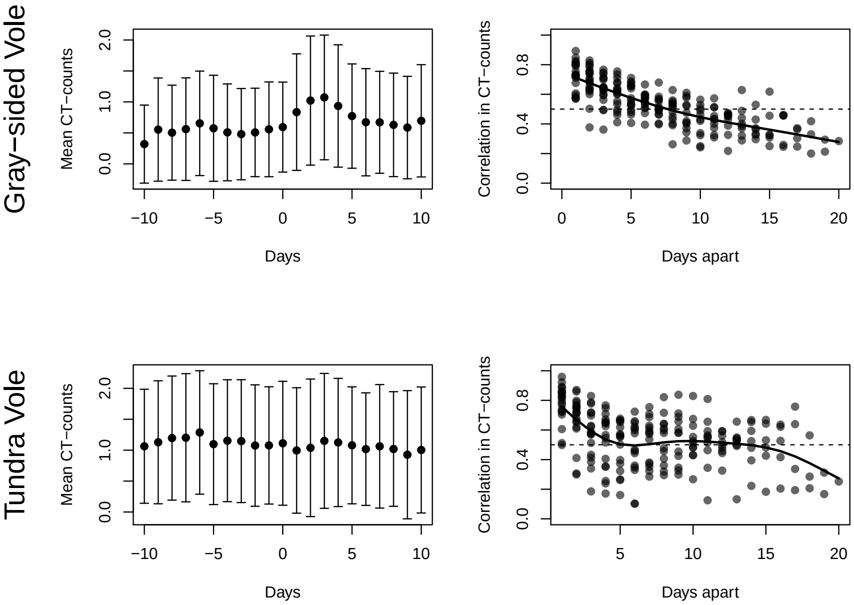


Figure 4: CT-count variation and temporal correlations. Left panels: mean of all the log CT-counts on each day relative to the trapping experiment (according to Fig.2), with standard deviation bars. Right panels: temporal auto-correlations in daily CT-counts per trap and trapping session as a function of temporal distance, i.e., days apart. The solid lines are non-parametric smooth regression lines from the `smooth.spline` function of the `stats` R-package (version 4.0.3).

3.2 Linear calibration regression

The linear calibration regressions based on the single camera trap per trapping station yielded R^2-values that greatly differed between the two species. The R^2–values for all time-windows are substantially higher for the gray-sided vole than the tundra vole (Figure 5). For the gray-sided vole, all time-windows for the CMR-encompassing group yielded similarly good fits (all $R^2 > 0.5$ except for $Y_{[0,0]}$). The best fitting calibration model ($R^2 = 0.58$, coefficients: $\beta_0 = 0.15$; $\beta_1 = 1.44$) was obtained for the 5-day time-window that encompassed the live-trapping session ($Y_{[-2,2]}$). This regression model fulfilled the assumptions regarding log-scale linearity. For the tundra vole, the best fit ($R^2 = 0.21$, coefficients: $\beta_0 = 0.37$; $\beta_1 = 1.28$) was obtained for the CT-index based on the single day before the onset of the live-trapping ($Y_{[-2,-2]}$). For the other time-windows (all $R^2 < 0.2$) the difference between the two groups of time-windows was small. When the data were aggregated over four adjacent sampling stations for the tundra vole population, the fit of the calibration function improved substantially ($R^2 = 0.81$, Coefficients: $\beta_0 = -0.16$; $\beta_1 = 2.17$, Figure 6).

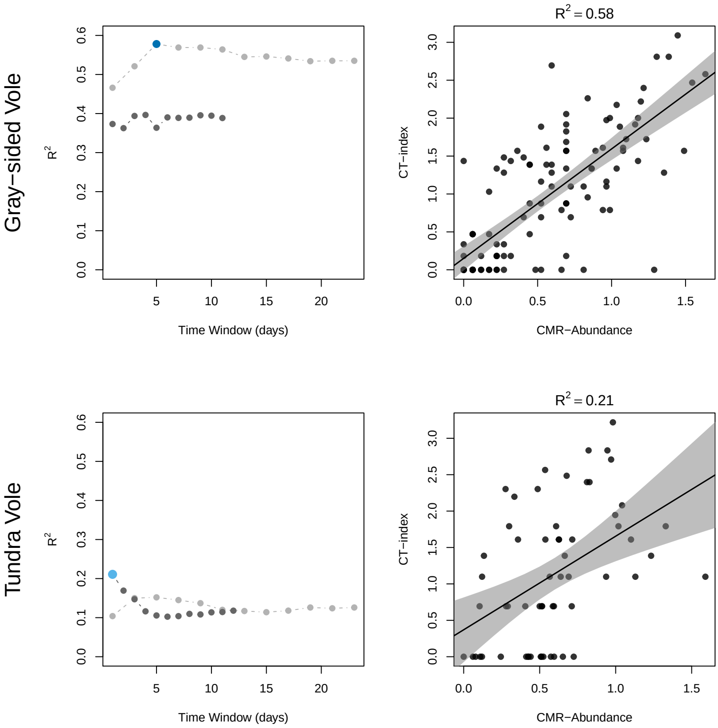


Figure 5: Statistics for linear calibration regressions. Left panels: R^2 values for the calibration linear regressions fitted to the two groups of time-windows (CRM-encompassing: light gray symbols and CMR-preceding: dark gray symbols). The highest R^2 values for each species is marked with an enlarged blue dot. Right panels: Data points and regression lines with 95% confidence intervals for the species-specific linear calibration models that yielded the highest R^2.

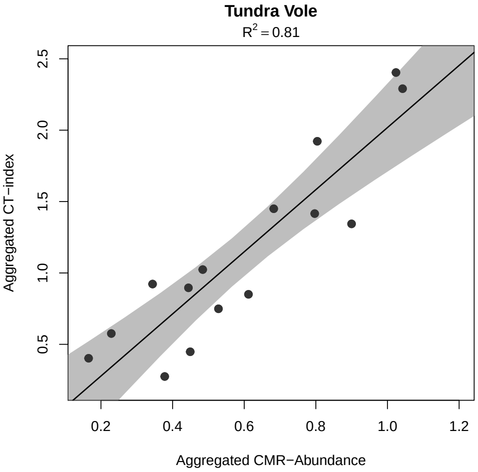


Figure 6: Calibration regression for tundra vole using aggregated data across all stations for the best fitting time-window ($Y_{[-2,-2]}$). Coefficients: $\beta_0 = -0.16$; $\beta_1 = 2.17$; p-value < 0.001.

3.3 Inverse prediction and validation

As could be expected from the differences in the goodness-of-fit of the calibration regression (i.e. the R^2 values), the prediction intervals derived by the inverse regression were wider for the tundra vole than for the gray-sided vole (Figure 7). The RMSE value (indicating the width of the interval) was almost twice as high as for the tundra vole compared to the gray-sided vole, and the bias was about three times higher (Table 2). In terms of classifying abundances based on the single camera traps with respect to the three abundance classes (cf. ECM metrics in Table 2), two thirds of the instances were correctly classified for the gray-sided vole, compared to roughly one third for the tundra vole.

Table 2: Prediction metrics for the models with highest R^2 for both the gray-sided Vole ($Y_{[-2,2]}$) and the tundra vole ($Y_{[-2,-2]}$).

Species	**Coverage**	**ECM$_A$**	**Bias**	**RMSE**
Gray-sided vole	0.957	0.661	-0.004	0.385
Tundra vole	0.933	0.350	0.013	0.701

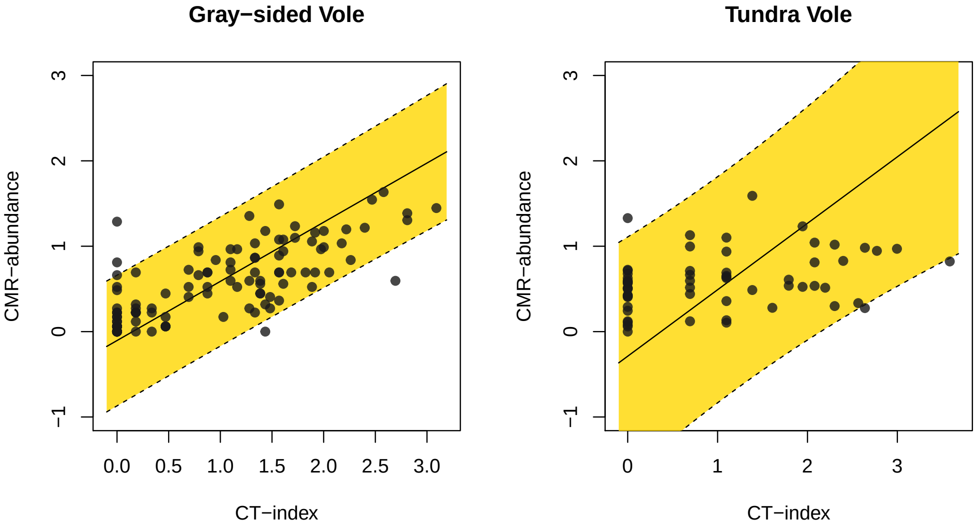


Figure 7: Inverse prediction plots for the CT-index windows yielding the best goodness-of-fit for each region, on the log scale. The Wald 95% confidence intervals are colored in yellow, and the data points are plotted in black dots.

4 Discussion

We have here assessed the adequacy of using photo counts, from the tunnel-camera trap developed by Soininen et al. (2015), as abundance metrics to study population dynamics of two ecologically important vole species that exhibit multi-annual cycles in boreal and Arctic ecosystems. Our assessment employed a two-step calibration approach, in which different temporally-scaled CT-indices from single camera traps were used as exposure variables calibrated against CMR-based abundance estimates from local live-trap grids, as the ground-truthing variable. In order to be adequate, abundance indices are required to have proportional (e.g. linear) relationships to the true abundance as well as reasonable precision. Considering that count-based camera trap indices (i.e. the number of motion-triggered animal passages) also reflect animal behavior (e.g. spacing behavior; *sensu* Krebs (1996)), which for long has been known to be density and phase dependent in cyclic vole populations (Chitty, 1960; Krebs, 2013), the assumption regarding proportionality can be violated.

While the proportionality assumption (on the log-scale) appeared to be met for both vole species, the precision of the abundance indices based on single camera traps differed considerably between them. For the gray-sided vole, the CT-indices from the single camera traps correlated well with the CMR-abundance estimates from the matched live-trapping grids, whereas equivalent correlation for the tundra vole was poorer. Accordingly, validation metrics of the inverse regressions showed that the abundance predictions based on single camera traps were substantially better for the gray-sided vole than the tundra vole. Compared with two previous calibration studies of non-cyclic vole populations in boreal America, the goodness of fit of the calibration regression for the cyclic gray-sided vole population ($R^2 = 0.58$) performed equally good (Villette et al., 2015) or better (Parsons et al., 2021). The two American studies employed a different camera trap; i.e. open cameras mounted in front of the entrance of baited live traps. Moreover, these previous studies used aggregated CT-indices over 15-16 (Villette et al., 2015) and 16-20 camera traps (Parsons et al., 2021) per live-trapping grid, which was twice the size of our grids. The fact that we obtained at least an equally good calibration for gray-sided vole with a single camera trap, and an even better calibration ($R^2 = 0.81$) for the tundra vole when aggregating the data over only 4 camera traps, indicates that our unbaited tunnel-based traps are more efficient in capturing voles.

The differences in goodness-of-fit of the calibrations (and thus also precision of the abundance predictions) of gray-sided voles and tundra voles are reflected by the different optimal time-windows and the temporal auto-correlations of CT-counts for the two species. The optimized time-window for the gray-sided vole was longer (5 days including the live trapping days) and less temporally distinct (high R^2-values for wide range of time-windows) than for the tundra voles. The best time-window for the tundra vole was based on a single day just prior to the onset of the live-trapping sessions. Accordingly, the auto-correlations of the daily camera counts dropped faster and had a generally higher scatter for the tundra vole than the gray-sided vole. We believe this can be explained by the fact that the two vole species differ with respect to how their populations are spatio-socially organized (Ims, 1987b; Bondrup-Nielsen and Ims, 1990). Due to female territoriality, gray-sided voles are more evenly spaced within their habitat than tundra voles where females form spatially clustered kin-groups. These local tundra vole kin-groups are temporally unstable since females frequently shift home ranges (Tast, 1966). Consequently, local-scale abundance dynamics of tundra voles is typically characterized with a high turnover (Andreassen and Ims, 2001) and weak auto-correlations (Ims and Andreassen, 1999). The much improved fit of the tundra vole calibration regression, when based on 4 instead of 1 camera trap, is most likely due to the effect of smoothing out the large small-scale spatio-temporal variability. This result underlines the benefit of spatially replicating camera traps within the same location/local population, which has also been highlighted by other authors (Kolowski et al., 2021). However, our study also shows that only a few tunnel-based camera traps may be needed to get adequate abundance indices for both vole species. In fact, a single camera trap was able to capture the main features of the cyclic dynamics of gray-sided vole. This indicates there may be a potential for conducting spatially extensive monitoring, for instance in order to estimate patterns of large-scale spatial population synchrony (Bjørnstad et al., 1999), even with a limited number of camera traps available.

We believe that the greatest asset of the tunnel-based camera trap employed in our study is its ability to yield population metrics year-round, with a finer temporal resolution than any other presently available method. For small rodents with multi-annual cycles, the transitions between the different cyclic phases (e.g. between peak and crash) can be very rapid and take place at any time of the year (Krebs, 2013). By providing reliable abundance indices for time-windows as short as a few days, camera traps radically enhance our options for identifying the drivers of cyclic rodent dynamics. Strongly density-dependent interactions and rapid community-level dynamics have for long been assumed to be driving rodents cycles (Hansson and Henttonen, 1988; Turchin and Hanski, 2001; Barraquand et al., 2017). Assumed key interactions – such as those between voles and small mustelids – have been beyond the reach of thorough investigations owing to difficulty of obtaining adequately scaled data for both interactants simultaneously (King and Powell, 2006). Our tunnel-based camera traps recorded substantial data (i.e. relatively high number of photo counts) for all members of the small mammal community in both study areas, including small mustelids (least weasel *Mustela nivalis* and stoat *Mustela erminea*), Norwegian lemmings (*Lemmus lemmus*) and shrews (*Sorex* spp.) (see also (Mölle et al., 2021) and Appendix B.3). While species-interactions based on camera trap data can be analysed based on absence-presence records within an occupancy modelling framework ((Rota et al., 2016; Fidino et al., 2019)), abundance metrics are more informative as they allow analyses of the density-dependent interactions that appear to drive population cycles (Stenseth, 1999). New studies are needed to validate camera trap-based abundance indices for species such as mustelids and lemmings. As true ground-truthing variables for such species (especially mustelids (King and Powell, 2006)) are extremely difficult to obtain, there may be alternatives to use other statistical frameworks to obtain detectability corrected abundance indices (Gilbert et al., 2021; Palencia et al., 2021). Such frameworks may also be used derive unbiased abundance indices from camera-trap data during the boreal and Arctic winter, when deep snow and harsh climatic condition hinder calibration studies of the kind we have performed in this study. Hence, although our study highlights the potential of tunnel-based camera traps to likely advance studies of cyclic rodent populations, it also illustrates the need for performing species- and context-specific validation studies.

References

Andreassen, H. P. and Ims, R. A. (2001). Dispersal in patchy vole populations: role of patch configuration, density dependence, and demography. *Ecology*, 82(10):2911–2926.

Andreassen, H. P., Sundell, J., Ecke, F., Halle, S., Haapakoski, M., Henttonen, H., Huitu, O., Jacob, J., Johnsen, K., Koskela, E., Luque-Larena, J. J., Lecomte, N., Leirs, H., Mariën, J., Neby, M., Rätti, O., Sievert, T., Singleton, G. R., van Cann, J., Broecke, B. V., and Ylönen, H. (2021). Population cycles and outbreaks of small rodents: ten essential questions we still need to solve. *Oecologia*, 195(3):601–622.

Bailey, L. L., MacKenzie, D. I., and Nichols, J. D. (2014). Advances and applications of occupancy models. *Methods in Ecology and Evolution*, 5(12):1269–1279.

Barraquand, F., Louca, S., Abbott, K. C., Cobbold, C. A., Cordoleani, F., DeAngelis, D. L., Elderd, B. D., Fox, J. W., Greenwood, P., Hilker, F. M., Murray, D. L., Stieha, C. R., Taylor, R. A., Vitense, K., Wolkowicz, G. S., and Tyson, R. C. (2017). Moving forward in circles: challenges and opportunities in modelling population cycles. *Ecology Letters*, 20(8):1074–1092.

Bjørnstad, O. N., Ims, R. A., and Lambin, X. (1999). Spatial population dynamics: analyzing patterns and processes of population synchrony. *Trends in Ecology & Evolution*, 14(11):427–432.

Bondrup-Nielsen, S. and Ims, R. A. (1990). Reversed sexual size dimorphism in microtines: Are females larger than males or are males smaller than females? *Evolutionary Ecology*, 4(3):261–272.

Boonstra, R., Andreassen, H. P., Boutin, S., Hušek, J., Ims, R. A., Krebs, C. J., Skarpe, C., and Wabakken, P. (2016). Why do the boreal forest ecosystems of northwestern Europe differ from those of western North America? *BioScience*, 66(9):722–734.

Boonstra, R. and Krebs, C. J. (1978). Pitfall trapping of *Microtus townsendii*. *Journal of Mammalogy*, 59(1):136–148.

Burton, A. C., Neilson, E., Moreira, D., Ladle, A., Steenweg, R., Fisher, J. T., Bayne, E., and Boutin, S. (2015). Review: Wildlife camera trapping: a review and recommendations for linking surveys to ecological processes. *Journal of Applied Ecology*, 52(3):675–685.

Capizzi, D., Bertolino, S., and Mortelliti, A. (2014). Rating the rat: global patterns and research priorities in impacts and management of rodent pests. *Mammal Review*, 44(2):148–162.

Chitty, D. (1960). Population processes in the vole and their relevance to general theory. *Canadian Journal of Zoology*, 38(1):99–113.

Cornulier, T., Yoccoz, N. G., Bretagnolle, V., Brommer, J. E., Butet, A., Ecke, F., Elston, D. A., Framstad, E., Henttonen, H., Hörnfeldt, B., Huitu, O., Imholt, C., Ims, R. A., Jacob, J., Jędrzejewska, B., Millon, A., Petty, S. J., Pietiäinen, H., Tkadlec, E., Zub, K., and Lambin, X. (2013). Europe-wide dampening of population cycles in keystone herbivores. *Science*, 340(6128):63–66.

Diefenbach, D. R., Conroy, M. J., Warren, R. J., James, W. E., Baker, L. A., and Hon, T. (1994). A test of the scent-station survey technique for bobcats. *The Journal of Wildlife Management*, 58(1):10–17.

Ehrich, D., Schmidt, N. M., Gauthier, G., Alisauskas, R., Angerbjörn, A., Clark, K., Ecke, F., Eide, N. E., Framstad, E., Frandsen, J., Franke, A., Gilg, O., Giroux, M.-A., Henttonen, H., Hörnfeldt, B., Ims, R. A., Kataev, G. D., Kharitonov, S. P., Killengreen, S. T., Krebs, C. J., Lanctot, R. B., Lecomte, N., Menyushina, I. E., Morris, D. W., Morrisson, G., Oksanen, L., Oksanen, T., Olofsson, J., Pokrovsky, I. G., Popov, I. Y., Reid, D., Roth, J. D., Saalfeld, S. T., Samelius, G., Sittler, B., Sleptsov, S. M., Smith, P. A., Sokolov, A. A., Sokolova, N. A., Soloviev, M. Y., and Solovyeva, D. V. (2019). Documenting lemming population change in the Arctic: can we detect trends? *Ambio*, 49(3):786–800.

Ehrich, D., Yoccoz, N. G., and Ims, R. A. (2009). Multi-annual density fluctuations and habitat size enhance genetic variability in two northern voles. *Oikos*, 118(10):1441–1452.

Eisenhart, C. (1939). The interpretation of certain regression methods and their use in biological and industrial research. *The Annals of Mathematical Statistics*, 10(2):162–186.

Fidino, M., Simonis, J. L., and Magle, S. B. (2019). A multistate dynamic occupancy model to estimate local colonization–extinction rates and patterns of co-occurrence between two or more interacting species. *Methods in Ecology and Evolution*, 10(2):233–244.

Gilbert, N. A., Clare, J. D. J., Stenglein, J. L., and Zuckerberg, B. (2021). Abundance estimation of unmarked animals based on camera-trap data. *Conservation biology : the journal of the Society for Conservation Biology*, 35(1):88—100.

Gopalaswamy, A. M., Delampady, M., Karanth, K. U., Kumar, N. S., and Macdonald, D. W. (2015). An examination of index-calibration experiments: counting tigers at macroecological scales. *Methods in Ecology and Evolution*, 6(9):1055–1066.

Greenwell, B. M. and Schubert Kabban, C. M. (2014). investr: An R package for inverse estimation. *The R Journal*, 6(1):90.

Hansen, T. F., Stenseth, N. C., and Henttonen, H. (1999). Multiannual vole cycles and population regulation during long winters: an analysis of seasonal density dependence. *The American Naturalist*, 154(2):129–139. PMID: 29578785.

Hanski, I., Henttonen, H., and Hansson, L. (1994). Temporal variability and geographical patterns in the population density of microtine rodents: A reply to Xia and Boonstra. *The American Naturalist*, 144(2):329–342.

Hansson, L. and Henttonen, H. (1988). Rodent dynamics as community processes. *Trends in Ecology & Evolution*, 3(8):195–200.

Henden, J.-A., Ehrich, D., Soininen, E. M., and Ims, R. A. (2021). Accounting for food web dynamics when assessing the impact of mesopredator control on declining prey populations. *Journal of Applied Ecology*, 58(1):104–113.

Hörnfeldt, B., Hipkiss, T., and Eklund, U. (2005). Fading out of vole and predator cycles? *Proceedings of the Royal Society B: Biological Sciences*, 272(1576):2045–2049.

Horvitz, D. G. and Thompson, D. J. (1952). A generalization of sampling without replacement from a finite universe. *Journal of the American Statistical Association*, 47(260):663–685.

Huggins, R. and Hwang, W.-H. (2011). A review of the use of conditional likelihood in capture-recapture experiments. *International Statistical Review*, 79(3):385–400.

Ims, R. and Andreassen, H. (1999). Demographic synchrony in fragmented populations. In Barrett, G. and Peles, J., editors, *The ecology of small mammals at the landscape level: experimental approaches*, pages 129–145. Springer-Verlag.

Ims, R. A. (1987a). Male spacing systems in microtine rodents. *The American Naturalist*, 130(4):475–484.

Ims, R. A. (1987b). Responses in spatial organization and behaviour to manipulations of the food resource in the vole *Clethrionomys rufocanus*. *The Journal of Animal Ecology*, pages 585–596.

Ims, R. A. and Fuglei, E. (2005). Trophic interaction cycles in tundra ecosystems and the impact of climate change. *BioScience*, 55(4):311–322.

Ims, R. A., Killengreen, S. T., Ehrich, D., Flagstad, Ø., Hamel, S., Henden, J.-A., Jensvoll, I., and Yoccoz, N. G. (2018). Ecosystem drivers of an Arctic fox population at the western fringe of the Eurasian Arctic. *Polar Research*, 36((sup1)).

Jennelle, C. S., Runge, M. C., and MacKenzie, D. I. (2002). The use of photographic rates to estimate densities of tigers and other cryptic mammals: a comment on misleading conclusions. *Animal Conservation*, 5(2):119–120.

Jensen, P., Stenseth, N., and E., F. (1993). Trappability of the norwegian lemming (*Lemmus lemmus*). In Stenseth, N. and R.A., I., editors, *The Biology of Lemmings*, pages 547–554. Academic Press, London.

King, C. M. and Powell, R. A. (2006). *The natural history of weasels and stoats: ecology, behavior, and management*. Oxford University Press.

Kleiven, E. F., Henden, J.-A., Ims, R. A., and Yoccoz, N. G. (2018). Seasonal difference in temporal transferability of an ecological model: near-term predictions of lemming outbreak abundances. *Scientific Reports*, 8(1).

Kolowski, J. M., Oley, J., and McShea, W. J. (2021). High-density camera trap grid reveals lack of consistency in detection and capture rates across space and time. *Ecosphere*, 12(2):e03350.

Korpela, K., Delgado, M., Henttonen, H., Korpimäki, E., Koskela, E., Ovaskainen, O., Pietiäinen, H., Sundell, J., Yoccoz, N. G., and Huitu, O. (2013). Nonlinear effects of climate on boreal rodent dynamics: mild winters do not negate high-amplitude cycles. *Global Change Biology*, 19(3):697–710.

Krebs, C. J. (1996). Population cycles revisited. *Journal of Mammalogy*, 77(1):8–24.

Krebs, C. J. (2013). *Population fluctuations in rodents*. University of Chicago Press.

Krebs, C. J., Boonstra, R., Gilbert, S., Reid, D., Kenney, A. J., and Hofer, E. J. (2011). Density estimation for small mammals from livetrapping grids: rodents in northern Canada. *Journal of Mammalogy*, 92(5):974–981.

Lambin, X., Petty, S. J., and Mackinnon, J. L. (2000). Cyclic dynamics in field vole populations and generalist predation. *Journal of Animal Ecology*, 69(1):106–119.

Legagneux, P., Gauthier, G., Lecomte, N., Schmidt, N. M., Reid, D., Cadieux, M.-C., Berteaux, D., Bêty, J., Krebs, C. J., Ims, R. A., Yoccoz, N. G., Morrison, R. I. G., Leroux, S. J., Loreau, M., and Gravel, D. (2014). Arctic ecosystem structure and functioning shaped by climate and herbivore body size. *Nature Climate Change*, 4(5):379–383.

MacKenzie, D. I., Nichols, J. D., Lachman, G. B., Droege, S., Andrew Royle, J., and Langtimm, C. A. (2002). Estimating site occupancy rates when detection probabilities are less than one. *Ecology*, 83(8):2248–2255.

Marolla, F., Aarvak, T., Øien, I. J., Mellard, J. P., Henden, J.-A., Hamel, S., Stien, A., Tveraa, T., Yoccoz, N. G., and Ims, R. A. (2019). Assessing the effect of predator control on an endangered goose population subjected to predator-mediated food web dynamics. *Journal of Applied Ecology*, 56(5):1245–1255.

Meerburg, B. G., Singleton, G. R., and Kijlstra, A. (2009a). Rodent-borne diseases and their risks for public health. *Critical Reviews in Microbiology*, 35(3):221–270. PMID: 19548807.

Meerburg, B. G., Singleton, G. R., and Leirs, H. (2009b). The Year of the Rat ends — time to fight hunger!. *Pest Management Science*, 65(4):351–352.

Mölle, J. P., Kleiven, E. F., Ims, R. A., and Soininen, E. M. (2021). Using subnivean camera traps to study arctic small mammal community dynamics during winter. *Arctic Science*, pages 1–17.

Nicolau, P. G., Sørbye, S. H., and Yoccoz, N. G. (2020). Incorporating capture heterogeneity in the estimation of autoregressive coefficients of animal population dynamics using capture–recapture data. *Ecology and Evolution*, 10(23):12710–12726.

Otis, D. L., Burnham, K. P., White, G. C., and Anderson, D. R. (1978). Statistical inference from capture data on closed animal populations. *Wildlife Monographs*, (62):3–135.

Øvrejorde, A. (2007). Calibrating abundance indices of small rodents in subarctic tundra. *MSci thesis, Univ. of Tromsø*.

Palencia, P., Rowcliffe, J. M., Vicente, J., and Acevedo, P. (2021). Assessing the camera trap methodologies used to estimate density of unmarked populations. *Journal of Applied Ecology*, 58(8):1583–1592.

Palmer, M. S., Swanson, A., Kosmala, M., Arnold, T., and Packer, C. (2018). Evaluating relative abundance indices for terrestrial herbivores from large-scale camera trap surveys. *African Journal of Ecology*, 56(4):791–803.

Parsons, M. A., Orloff, A. E., and Prugh, L. R. (2021). Evaluating livetrapping and camera-based indices of small-mammal density. *Canadian Journal of Zoology*, 99(6):521–530.

Powell, R. A. and Proulx, G. (2003). Trapping and marking terrestrial mammals for research: Integrating ethics, performance criteria, techniques, and common sense. *ILAR Journal*, 44(4):259–276.

Rendall, A. R., Sutherland, D. R., Cooke, R., and White, J. (2014). Camera trapping: A contemporary approach to monitoring invasive rodents in high conservation priority ecosystems. *PLoS ONE*, 9(3):e86592.

Rota, C. T., Ferreira, M. A. R., Kays, R. W., Forrester, T. D., Kalies, E. L., McShea, W. J., Parsons,

A. W., and Millspaugh, J. J. (2016). A multispecies occupancy model for two or more interacting species. *Methods in Ecology and Evolution*, 7(10):1164–1173.

Soininen, E. M., Henden, J.-A., Ravolainen, V. T., Yoccoz, N. G., Bråthen, K. A., Killengreen, S. T., and Ims, R. A. (2018). Transferability of biotic interactions: Temporal consistency of arctic plant–rodent relationships is poor. *Ecology and Evolution*, 8(19):9697–9711.

Soininen, E. M., Jensvoll, I., Killengreen, S. T., and Ims, R. A. (2015). Under the snow: a new camera trap opens the white box of subnivean ecology. *Remote Sensing in Ecology and Conservation*, 1(1):29–38.

Stenseth, N. C. (1999). Population cycles in voles and lemmings: Density dependence and phase dependence in a stochastic world. *Oikos*, 87(3):427–461.

Tabak, M. A., Norouzzadeh, M. S., Wolfson, D. W., Sweeney, S. J., Vercauteren, K. C., Snow, N. P., Halseth, J. M., Di Salvo, P. A., Lewis, J. S., White, M. D., Teton, B., Beasley, J. C., Schlichting, P. E., Boughton, R. K., Wight, B., Newkirk, E. S., Ivan, J. S., Odell, E. A., Brook, R. K., Lukacs, P. M., Moeller, A. K., Mandeville, E. G., Clune, J., and Miller, R. S. (2019). Machine learning to classify animal species in camera trap images: applications in ecology. *Methods in Ecology and Evolution*, 10(4):585–590.

Tast, J. (1966). The root vole, *Microtus oeconomus* (Pallas), as an inhabitant of seasonally flooded land. In *Annales Zoologici Fennici*, volume 3, pages 127–171. JSTOR.

Turchin, P. and Hanski, I. (2001). Contrasting alternative hypotheses about rodent cycles by translating them into parameterized models. *Ecology Letters*, 4(3):267–276.

Turchin, P., Oksanen, L., Ekerholm, P., Oksanen, T., and Henttonen, H. (2000). Are lemmings prey or predators? *Nature*, 405(6786):562–565.

Villette, P., Krebs, C. J., Jung, T. S., and Boonstra, R. (2015). Can camera trapping provide accurate estimates of small mammal (*Myodes rutilus* and *Peromyscus maniculatus*) density in the boreal forest? *Journal of Mammalogy*, 97(1):32–40.

Wearn, O. R. and Glover-Kapfer, P. (2019). Snap happy: camera traps are an effective sampling tool when compared with alternative methods. *Royal Society Open Science*, 6(3):181748.

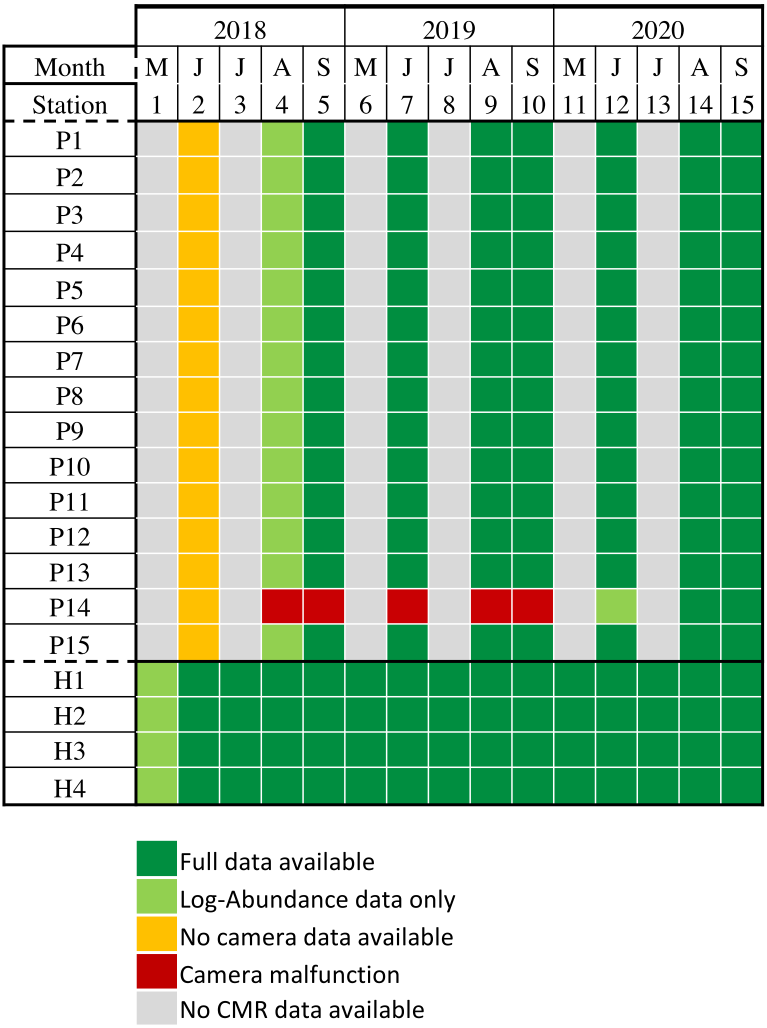
Wilson, D. E. and Reeder, D. M. (2005). *Mammal species of the world: a taxonomic and geographic reference*, volume 2. JHU Press.

Yoccoz, N. G. and Ims, R. A. (2004). Spatial population dynamics of small mammals: some methodological and practical issues. *Animal Biodiversity and Conservation*, 27(1):427–435.

Yoccoz, N. G., Nichols, J. D., and Boulinier, T. (2001). Monitoring of biological diversity in space and time. *Trends in Ecology and Evolution*, 16(8):446–453.

A Supplementary Methods

A.1 Temporal distribution of data sampling



	2018					2019					2020				
Month	M	J	J	A	S	M	J	J	A	S	M	J	J	A	S
Station	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15
P1	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P2	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P3	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P4	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P5	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P6	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P7	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P8	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P9	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P10	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P11	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P12	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P13	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
P14	⬜	🟧	⬜	🟥	🟥	⬜	🟥	⬜	🟥	🟥	⬜	🟢	⬜	🟩	🟩
P15	⬜	🟧	⬜	🟢	🟩	⬜	🟩	⬜	🟩	🟩	⬜	🟩	⬜	🟩	🟩
H1	🟢	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
H2	🟢	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
H3	🟢	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩
H4	🟢	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩	🟩

🟩 Full data available
🟢 Log-Abundance data only
🟧 No camera data available
🟥 Camera malfunction
⬜ No CMR data available

Figure 8: Temporal distribution of the index-calibration data for each of the stations for the different regions.

A.2 Camera Trap sampling

We used *Reconyx*^{TM} SM750 Hyperfire^{TM} (Reconyx Inc., Holmen, WI, USA) with a passive infrared (PIR) motion sensor. Each camera trap was placed at the roof of an artificial metal tunnel, facing down. These tunnels were deployed in natural small mammal runways without any kind of lure, simulating natural tunnels/cavities which small mammals typically enter. For a more detailed description of the small mammal camera setup see (Soininen et al., 2015) and (Mölle et al., 2021). At Porsanger, where the capture-recapture was done in standardized trapping grids, the camera traps were always deployed close to the center of the grid. At Håkøya, where the shape of the capture-recapture grids did not follow a structured design, the camera traps were deployed within the trapping grid.

This methodology allowed us to collect continuous camera trap data from the small rodent populations monitored by the capture-recapture design, with a total of 15 camera traps (and capture-recapture grids) in Porsanger and 4 in Håkøya. The camera traps collected data continuously and were checked once a year to replace batteries and collect memory cards. To avoid multiple camera trap counts from the same trigger event and to save power so that battery would not run out before next check, the cameras were set to not be triggered more than once per minute.

A.2.1 Camera trap image annotations

Once collected, all the camera trap images were annotated using the `MLWIC` package in R (Tabak et al., 2019) for automatic image classification. We set the classification threshold at 95% confidence for positive identification of a species in a photo. For the images from Håkøya, an area only inhabited by a single vole species, the images were classified to species level with high accuracy. For the Porsanger dataset, which contains multiple vole species, it was not possible to obtain sufficient classification results using the `MLWIC` package, as it did not separate different species of voles accurately (only possible at genus level). Therefore, we manually annotated the images for the Porsanger analysis to species level.

B Supplementary Results

In this section we present the calibration model coefficients for the different CT-indices tested in this study, as well as the predictive metrics, separately for the Gray-sided Vole (B.1) and for the Tundra Vole (B.2). Finally, we show the photo counts of all the species detected in the camera traps (B.3).

B.1 Gray-sided Vole

B.1.1 Linear Regression Coefficients

Table 3: Coefficients for region Porsanger for all the CMR-encompassing windows.

Window	β_0 (± **s.e.**)	β_1 (± **s.e.**)	p-value (β_1)	R^2
$Y_{[0,0]}$	0.05 ± 0.1	1.45 ± 0.15	< 0.001	0.466
$Y_{[-1,1]}$	0.14 ± 0.09	1.41 ± 0.13	< 0.001	0.521
$Y_{[-2,2]}$	0.15 ± 0.08	1.44 ± 0.12	< 0.001	0.578
$Y_{[-3,3]}$	0.16 ± 0.08	1.39 ± 0.11	< 0.001	0.569
$Y_{[-4,4]}$	0.16 ± 0.08	1.34 ± 0.11	< 0.001	0.569
$Y_{[-5,5]}$	0.15 ± 0.08	1.32 ± 0.11	< 0.001	0.564
$Y_{[-6,6]}$	0.16 ± 0.08	1.28 ± 0.11	< 0.001	0.545
$Y_{[-7,7]}$	0.16 ± 0.08	1.27 ± 0.11	< 0.001	0.546
$Y_{[-8,8]}$	0.16 ± 0.08	1.25 ± 0.11	< 0.001	0.541
$Y_{[-9,9]}$	0.16 ± 0.08	1.24 ± 0.11	< 0.001	0.534
$Y_{[-10,10]}$	0.15 ± 0.08	1.23 ± 0.11	< 0.001	0.535
$Y_{[-11,11]}$	0.14 ± 0.07	1.2 ± 0.11	< 0.001	0.535

Table 4: Coefficients for region Porsanger for all the CMR-preceding windows.

Window	β_0 (± **s.e.**)	β_1 (± **s.e.**)	p-value (β_1)	R^2
$Y_{[-2,-2]}$	-0.01 ± 0.09	1.05 ± 0.13	< 0.001	0.3732
$Y_{[-3,-2]}$	0.05 ± 0.08	0.96 ± 0.12	< 0.001	0.3626
$Y_{[-4,-2]}$	0.04 ± 0.08	0.98 ± 0.11	< 0.001	0.3938
$Y_{[-5,-2]}$	0.04 ± 0.08	0.99 ± 0.12	< 0.001	0.3964
$Y_{[-6,-2]}$	0.06 ± 0.09	0.98 ± 0.12	< 0.001	0.3636
$Y_{[-7,-2]}$	0.07 ± 0.08	1.03 ± 0.12	< 0.001	0.3901
$Y_{[-8,-2]}$	0.09 ± 0.08	1.02 ± 0.12	< 0.001	0.3889
$Y_{[-9,-2]}$	0.09 ± 0.08	1.01 ± 0.12	< 0.001	0.3894
$Y_{[-10,-2]}$	0.09 ± 0.08	1.03 ± 0.12	< 0.001	0.3955
$Y_{[-11,-2]}$	0.08 ± 0.08	1 ± 0.12	< 0.001	0.3945

B.1.2 Predictive Performance

Table 5: Predictive performance of the calibration models for Porsanger, using the CT-index for the CMR-encompassing windows to predict log-abundance.

Window	Coverage	ECM	Bias	RMSE
$Y_{[0,0]}$	0.957	0.617	-0.008	0.483
$Y_{[-1,1]}$	0.957	0.600	-0.007	0.431
$Y_{[-2,2]}$	0.957	0.661	-0.004	0.385
$Y_{[-3,3]}$	0.957	0.652	-0.004	0.394
$Y_{[-4,4]}$	0.948	0.670	-0.003	0.394
$Y_{[-5,5]}$	0.948	0.652	-0.004	0.399
$Y_{[-6,6]}$	0.957	0.609	-0.005	0.415
$Y_{[-7,7]}$	0.957	0.617	-0.004	0.415
$Y_{[-8,8]}$	0.948	0.609	-0.005	0.421
$Y_{[-9,9]}$	0.948	0.617	-0.005	0.427
$Y_{[-10,10]}$	0.939	0.609	-0.005	0.427
$Y_{[-11,11]}$	0.939	0.626	-0.005	0.427

Table 6: Predictive performance of the calibration models for Porsanger, using the CT-index for the CMR-preceding windows to predict log-abundance.

Window	Coverage	ECM	Bias	RMSE
$Y_{[-2,-2]}$	0.930	0.617	-0.011	0.599
$Y_{[-3,-2]}$	0.948	0.548	-0.011	0.611
$Y_{[-4,-2]}$	0.983	0.548	-0.009	0.571
$Y_{[-5,-2]}$	0.965	0.557	-0.009	0.568
$Y_{[-6,-2]}$	0.965	0.574	-0.009	0.605
$Y_{[-7,-2]}$	0.957	0.591	-0.007	0.570
$Y_{[-8,-2]}$	0.948	0.591	-0.007	0.574
$Y_{[-9,-2]}$	0.948	0.591	-0.007	0.573
$Y_{[-10,-2]}$	0.957	0.609	-0.007	0.566
$Y_{[-11,-2]}$	0.957	0.583	-0.007	0.566

B.2 Tundra Vole

B.2.1 Linear regression coefficients

Table 7: Coefficients for region Håkøya for all the CMR-encompassing windows.

Window	β_0 (± **s.e.**)	β_1 (± **s.e.**)	p-value (β_1)	R^2
$Y_{[0,0]}$	0.43 ± 0.25	0.96 ± 0.37	0.012	0.104
$Y_{[-1,1]}$	0.46 ± 0.24	1.13 ± 0.35	0.002	0.150
$Y_{[-2,2]}$	0.53 ± 0.23	1.1 ± 0.34	0.002	0.152
$Y_{[-3,3]}$	0.58 ± 0.23	1.1 ± 0.34	0.003	0.145
$Y_{[-4,4]}$	0.64 ± 0.22	1.0 ± 0.33	0.004	0.137
$Y_{[-5,5]}$	0.70 ± 0.22	0.91 ± 0.32	0.007	0.120
$Y_{[-6,6]}$	0.71 ± 0.22	0.89 ± 0.32	0.008	0.117
$Y_{[-7,7]}$	0.73 ± 0.22	0.87 ± 0.32	0.008	0.114
$Y_{[-8,8]}$	0.72 ± 0.22	0.89 ± 0.32	0.007	0.118
$Y_{[-9,9]}$	0.72 ± 0.21	0.91 ± 0.31	0.005	0.126
$Y_{[-10,10]}$	0.72 ± 0.21	0.89 ± 0.31	0.006	0.124
$Y_{[-11,11]}$	0.73 ± 0.21	0.89 ± 0.31	0.005	0.126

Table 8: Coefficients for region Håkøya for all the CMR-preceding windows.

Window	β_0 (± **s.e.**)	β_1 (± **s.e.**)	R^2	p-value (β_1)
$Y_{[-2,-2]}$	0.37 ± 0.22	1.28 ± 0.33	0.2109	< 0.001
$Y_{[-3,-2]}$	0.54 ± 0.22	1.09 ± 0.32	0.1692	0.001
$Y_{[-4,-2]}$	0.61 ± 0.21	1.00 ± 0.32	0.1471	0.002
$Y_{[-5,-2]}$	0.68 ± 0.22	0.88 ± 0.32	0.1162	0.008
$Y_{[-6,-2]}$	0.71 ± 0.21	0.83 ± 0.32	0.1056	0.011
$Y_{[-7,-2]}$	0.75 ± 0.22	0.82 ± 0.32	0.1025	0.013
$Y_{[-8,-2]}$	0.75 ± 0.22	0.84 ± 0.32	0.1039	0.012
$Y_{[-9,-2]}$	0.76 ± 0.22	0.86 ± 0.32	0.1097	0.010
$Y_{[-10,-2]}$	0.78 ± 0.22	0.85 ± 0.32	0.1082	0.010
$Y_{[-11,-2]}$	0.76 ± 0.22	0.87 ± 0.32	0.1136	0.008

530 B.2.2 Predictive performance

Table 9: Predictive performance of the calibration models for Håkøya, using the CMR-encompassing windows.

Window	Coverage	ECM	Bias	RMSE
$Y_{[0,0]}$	0.933	0.283	0.022	1.109
$Y_{[-1,1]}$	0.933	0.367	-0.003	0.860
$Y_{[-2,2]}$	0.933	0.333	0.003	0.886
$Y_{[-3,3]}$	0.950	0.300	0.013	0.921
$Y_{[-4,4]}$	0.967	0.300	0.012	0.942
$Y_{[-5,5]}$	0.950	0.267	0.037	1.040
$Y_{[-6,6]}$	0.950	0.250	0.045	1.073
$Y_{[-7,7]}$	0.950	0.250	0.038	1.077
$Y_{[-8,8]}$	0.950	0.250	0.026	1.050
$Y_{[-9,9]}$	0.950	0.250	0.020	0.996
$Y_{[-10,10]}$	0.933	0.283	0.011	0.988
$Y_{[-11,11]}$	0.933	0.283	0.010	0.987

Table 10: Predictive performance of the calibration models for Håkøya, using the CMR-preceding windows.

Window	Coverage	ECM	Bias	RMSE
$Y_{[-2,-2]}$	0.933	0.350	0.013	0.701
$Y_{[-3,-2]}$	0.967	0.383	0.017	0.793
$Y_{[-4,-2]}$	0.950	0.317	0.034	0.891
$Y_{[-5,-2]}$	0.950	0.283	0.070	1.072
$Y_{[-6,-2]}$	0.983	0.267	0.084	1.178
$Y_{[-7,-2]}$	0.983	0.217	0.065	1.164
$Y_{[-8,-2]}$	0.983	0.217	0.059	1.127
$Y_{[-9,-2]}$	0.967	0.233	0.048	1.075
$Y_{[-10,-2]}$	0.983	0.233	0.028	1.056
$Y_{[-11,-2]}$	0.967	0.233	0.022	1.021

B.3 Other species

The camera traps provide information on more species than the two vole species used in this calibration. Figure 9 displays counts of all species observed in the camera during the course of the study. In Porsanger, the Norwegian Lemming (*Lemmus lemmus*) is regularly observed (it is absent on Håkøya). This is a rodent species that has been considered particularly difficult to trap, and in fact no lemmings have been trapped by the live traps during this study (and only one during the previous 20 years in the same grids). Shrews are also observed in about the same numbers as voles in both study regions. Moreover, small mustelids (stoat (*Mustela erminea*) and least weasel (*Mustela nivalis*)) are also frequently observed in the regions where they exist (least weasel is not present on Håkøya).

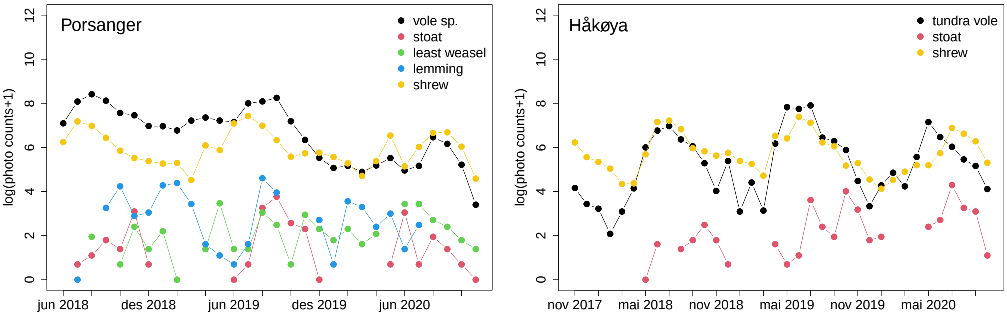


Figure 9: Number of trigger events for all species recorded by the camera traps as a monthly total for the two regions Håkøya and Porsanger, using automated classification data.