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Predator-prey interactions and alternative prey hypothesis – a comparative insight from the Arctic

Interakce predátor-kořist a hypotéza alternativní kořisti – komparativní vhléd z Arktidy

**Bachelor thesis**

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## **Prohlášení**

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## **Abstract in English**

Predator-prey interactions have changed substantially in recent decades, with vast consequences for entire Arctic ecosystem. Lemmings and voles represent the primary food source for predators in the Arctic, but they have vanished from many regions recently, with poorly understood implications for the remaining organisms. There are several local pieces of evidence that shorebird nests serve as alternative prey for Arctic predators during the lack of Arctic rodents, but a comparative perspective has been so far lacking.

Therefore, I compile a comparative look at the issue, summarizing the existing knowledge on the alternative prey hypothesis and its effect on shorebirds as common alternative prey in the Arctic. The alternative prey hypothesis seems to be supported more in the Russian Arctic than in the Canadian Arctic and the support for the hypothesis was probably stronger before year 2000 than after, possibly connected with disrupted cycles of Arctic rodent populations. Not well functioning alternative prey hypothesis could contribute to recently observed population declines of Arctic shorebirds. However, the higher abundances and functional cyclicality of Arctic rodents are again reappearing at some Arctic locations and the whole issue requires more detailed meta-analytical investigation. Diverse, mostly climate change-induced and not mutually exclusive factors can impact on the functionality of the alternative prey hypothesis.

## **Keywords**

alternative prey hypothesis, Arctic, climate change, lemmings, nest and chick predation, predator-prey interactions, population dynamics, shorebirds, voles, waders

## **Abstrakt v češtině**

Interakce mezi predátory a kořistí se v posledních desetiletích výrazně změnila, což má rozsáhlé důsledky pro celý Arktický ekosystém. Lumíci a hraboši představují hlavní potravní zdroj pro predátory v Arktidě, ale z mnoha oblastí v poslední době vymizeli, přičemž důsledky pro ostatní organismy zůstávají málo pochopené. Existují lokální důkazy o tom, že hnízda bahňáků slouží jako alternativní kořist pro arktické predátory během období nedostatku arktických hlodavců, nicméně srovnávací pohled na tento problém dosud chyběl.

Proto jsem v této práci srovnávací pohled na dané téma vytvořila. Shrnuji dosavadní poznatky o hypotéze alternativní kořisti a jejím vlivu na bahňáky jako běžnou alternativní kořist v Arktidě. Zdá se, že tato hypotéza je více podporována v ruské Arktidě než v té kanadské, a podpora této hypotézy byla pravděpodobně silnější před rokem 2000 než po něm, což může souviset s narušením populačních cyklů arktických hlodavců. Nefungující hypotéza alternativní kořisti by mohla rovněž přispívat k nedávno pozorovanému poklesu populací arktických bahňáků. Nicméně vyšší početnost a funkční cykličnost arktických hlodavců se opět objevují v některých oblastech Arktidy, a celá problematika si vyžaduje podrobnější metaanalytické zkoumání. Různé, převážně klimatickými změnami podmíněné a vzájemně se nevyklučující faktory mohou ovlivňovat funkčnost hypotézy alternativní kořisti.

## **Klíčová slova**

Arktida, bahňáci, hraboši, hypotéza alternativní kořisti, interakce predátor-kořist, lumíci, populační dynamika, predace hnízd a kuřat, změna klimatu



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# 1 Introduction

The Arctic region lies around the Arctic Ocean and is characterized by extreme environmental conditions, including persistently low temperatures, the widespread presence of permafrost and sea ice, prolonged periods of darkness during the polar night and continuous daylight during the Arctic summer. Despite its harshness, such environment supports a distinctive and specialized ecosystem, inhabited by a range of plant, animal, and human populations. Moreover, it is further enriched in the summer months by migratory animals, mostly birds, that use the Arctic as an area for reproduction. Although species richness remains relatively low compared to equatorial regions, the Arctic provides valuable opportunities for investigating ecological processes and species interactions under inhospitable conditions (ACIA, 2004).

Current world is rapidly changing due to ongoing climate change and various human-induced stressors (Gries et al., 2019; IPCC, 2021; Vitousek, 1994). The scale of global warming is particularly severe in the Arctic, where temperatures are rising almost twice as fast as in the rest of the world (ACIA, 2004). The actual ecosystem changes include the melting of glaciers, the thawing of permafrost, the decline of Arctic perennial sea ice cover, or for example the so-called greening and browning of the Arctic (ACIA, 2005; Comiso, 2002; Forbes et al., 2010; Gilg et al., 2012). These alterations affect vegetation as well as animals in the Arctic and the relatively simple Arctic food webs (Kaplan & New, 2006; McGuire et al., 2020; McKinnon et al., 2013; Meltofte et al., 2007).

Arctic rodents, especially lemmings and voles, along with the nests and chicks of birds that migrate to the Arctic to breed there during the summer months, represent common prey and a primary food source for many Arctic predators (Careau et al., 2007; Maher, 1970). An abundance of Arctic rodents naturally fluctuates across time in cycles, that are restricted to northern latitudes (Gilg et al., 2009; Larsen et al., 1996; Underhill, 1987). The cause of this cyclicity is the subject of many scientific works (Fauteux et al., 2015, 2016; Gauthier et al., 2024; Hanski et al., 1991). The phenomenon of population cyclicity is also a key component of the alternative prey hypothesis (Figure 1), which has primarily been studied in Arctic regions (Ježková et al., 2014). It explains the direct and indirect influence on other organisms through the abundance of these rodents and links the dynamics of primary prey and alternative prey through their shared predators (Aharon-Rotman et al., 2015; Macpherson, 1969; Schekkerman et al., 2004). Predation pressure on these two prey types varies based on the abundance of the

primary prey (Angelstam et al., 1984). Predator densities may increase due to overabundant main prey and when the abundance of these prey declines, other alternative food sources may become more important for predators (McKinnon et al., 2013). In the Arctic, lemming cycles are balanced by birds' eggs and young, that can serve as alternative prey for both avian and mammalian predators (Aharon-Rotman et al., 2015; Gilg et al., 2009; Underhill, 1987).

The hypothesis, named by Angelstam (1984) as the alternative prey hypothesis, concerning the greater predation rate of Arctic birds by Arctic Fox (*Alopex lagopus*) in areas without lemmings. Since the 20th century, the alternative prey hypothesis and predation of avian nests as alternative prey have been investigated in various places in the Arctic region. We have studies from the Eastern Hemisphere that support this hypothesis (Blomqvist et al., 2002; Ims et al., 2013; Summers et al., 1998), but mostly in the Western Hemisphere, there are several studies that do not support the relation between lemmings, predators, and alternative prey (Holmes, 1966; Smith, 2009; A. Stickney, 1991). Some studies even suggest that due to environmental changes, the cycles of lemmings and the survival of bird nests may not be so closely linked anymore (Kausrud et al., 2008; Machín et al., 2019). However, a comparative perspective on the issue of alternative prey hypothesis across the Arctic is so far lacking.

The inhospitable conditions of the Arctic are changed for a few months during the summer, turning the area into a temporary home for migratory birds from all over the world, which use a period of two to three months for breeding in the polar region (CHASM, 2004; Smith et al., 2010a). Around two hundred bird species (CAFF, 2013) contribute to the biodiversity of this region every summer. These seasonal Arctic migrants include many species of geese, ducks, divers, gulls or jaegers and seabirds. However, nearly a quarter of all bird species in the Arctic are made up of shorebirds belonging to the families Scolopacidae and Charadriidae (Henningsson & Alerstam, 2005). Shorebirds reach their greatest breeding diversity in these northern latitudes (Smith et al., 2020) and migrate to the Arctic from many places around the world, often covering thousands of kilometers (Smith et al., 2010a). They form an integral part of the Arctic and the Arctic food web (CHASM, 2004). The breeding success of shorebirds is influenced by many factors such as weather, snow cover, human pressure, the abundance of invertebrates, or the abundance of predators (Byrkjedal, 1980; Meltofte et al., 2007; Underhill et al., 1993). Moreover, shorebird nests and chicks can serve as alternative prey instead of arctic rodents (Roselaar, 1979; Troy, 1996; Zhemchuzhnikov et al., 2024), representing a suitable model group for investigating the alternative prey hypothesis across larger scales for five main reasons:

1. Distribution across the whole Arctic

Shorebirds exhibit a cosmopolitan distribution, with numerous species occurring throughout the circumpolar Arctic region in all Arctic terrestrial habitats (Billerman et al., 2025; Henningsson & Alerstam, 2005). As a result, we can investigate how this model group interacts across the Arctic.

2. Even densities across the landscape

Shorebirds' density varies significantly across different regions within the Arctic (Meltotte et al., 2007), but at the same time, they generally do not form colonies and are rather more evenly distributed in the landscape (Cunningham et al., 2016; Johnson et al., 2007), which is similar to the distribution of rodents in the Arctic (Le Vaillant et al., 2018). This can help us understand how the presence and absence of rodents influence different shorebird species across various regions of the Arctic.

3. Nesting in the tundra

Shorebirds place their nests directly on the ground in the Arctic tundra (Nol et al., 1997). Similar to Arctic rodents, they spend a lot of time on the ground and may experience predation pressure from shared predator species (Aharon-Rotman et al., 2015; Smith, 2003). The nests are also easier to trace and more accessible to scientists. Moreover, their nesting success in the Arctic tundra and the effect of predation can be effectively monitored.

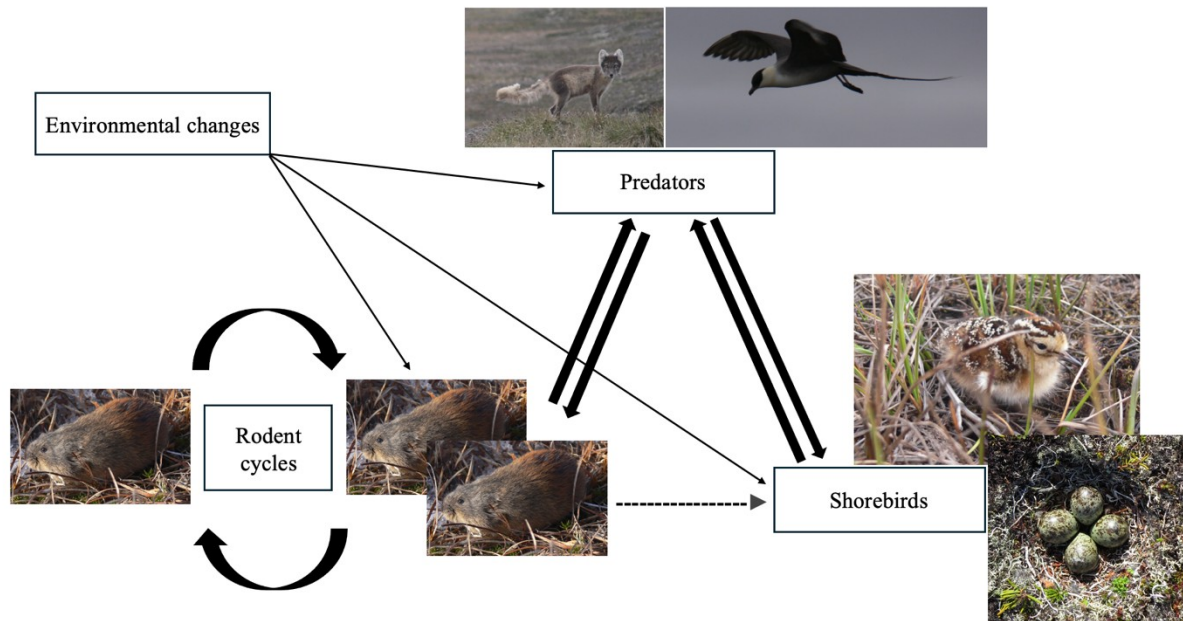
4. Body size

One type of anti-predatory strategy in shorebirds may involve imitating lemmings to distract predators from their nests (Larson, 1960). This may suggest that, in contrast to colonial and larger geese, shorebirds are more susceptible to detection by predators hunting small rodents in the tundra, as these rodents are similar in size to shorebirds (Macpherson, 1969).

5. High abundance

Shorebirds comprise a highly abundant and diverse avian group, with numerous species migrating to the Arctic region for breeding. According to (CHASM, 2004), the population of shorebirds in this area was estimated to number around 30 million individuals. While this figure may have fluctuated over time due to a range of ecological, environmental, and anthropogenic factors, shorebirds continue to be a key component of Arctic ecosystems. Their abundance and wide distribution, as well as numerous scientific studies, make them an ideal group for investigating various ecological and environmental issues in the Arctic, such as climate change, habitat loss,

migratory patterns, the impacts of lemming cycles, and importantly, the phenomenon of the alternative prey hypothesis.



**Figure 1.** Schematic representation of the alternative prey hypothesis including key players: Arctic rodents, predators and shorebirds as well as the impact of environmental changes on it. Solid arrows represent direct interactions, dashed arrow indirect interaction. Only major interactions are illustrated for the simplicity of the figure. All photographs were taken by Vojtěch Kubelka.

## 2 Aims

I am going to fill the aforementioned knowledge gap by collating relevant literature and providing a comparative insight on the alternative prey hypothesis across the whole Arctic. Specifically, I am asking: Where and when is the alternative prey hypothesis working, in other words what are the spatial and temporal patterns? Which factors influence the alternative prey hypothesis functioning? What are the consequences for shorebirds, as the model alternative prey? Where are the gaps in our knowledge of alternative prey hypothesis?

## 3 Arctic shorebirds

Arctic shorebirds can be found throughout the circumpolar Arctic during the breeding season. About 40 different species of shorebirds in the Arctic tundra choose various habitats, most of them are found in wetlands and riparian areas (Brown et al., 2007; Smith et al., 2020), but also in the upland drained tundra (Billerman et al., 2025). Around the waters they feed mainly on small crustacea, chironomids, or tipulids, and in drained areas, they hunt spiders,

beetles, or look for seeds and arthropods in the soil (Baker, 1977; Holmes & Pitelka, 1968; Tulp & Schekkerman, 2001). However, the diet of chicks consists solely of arthropods that are either flying or surface-dwelling (Schekkerman et al., 2004).

Common species like the Dunlin (*Calidris alpina*), Sanderling (*Calidris alba*), or Red-necked Phalarope (*Phalaropus lobatus*), can be found in most places across the circumpolar Arctic. However, some species have more restricted breeding ranges. For example, the Bristle-thighed Curlew (*Numenius tahitiensis*) and Western Sandpiper (*Calidris mauri*) are found primarily in Alaska. Or European Golden Plover (*Pluvialis apricaria*) and Sharp-tailed Sandpiper (*Calidris acuminata*) are predominantly found breeding in the Arctic regions of the eastern hemisphere.

Many shorebird populations are decreasing globally (CHASM, 2004; Koleček et al., 2021; Smith et al., 2020) and this is additional reason from conservation perspective for selecting them as a model group for this study, as they are likely to be significantly affected by predator-prey interactions. Other potential drivers of their decline may include various climate change factors such as for example increasing presence of species that typically breed further south, for example, some predators, or with an expansion of scrub (Anderson et al., 2023; R. H. Fraser et al., 2014; Meltofte et al., 2007). Moreover, global warming may also be altering the conditions that have historically attracted birds to the Arctic, such as an abundant food supply or a lower number of parasites and diseases (Kubelka et al., 2022). Human pressure on the environment, coupled with climate change, can also significantly affect the quality of stopover sites used by migratory shorebirds on their way to the Arctic (Kubelka et al., 2022; Studds et al., 2017). An example of such a site, which is crucial for many migratory shorebird species, is the Yellow Sea, where tidal mudflats are located. Expanding urban development on the coast and the decreasing availability of food resources may make it harder for birds to restore their energy there during migration and it may contribute to population declines in shorebirds (Studds et al., 2017). However, it may also occur due to the decreasing availability of suitable breeding habitats for Arctic shorebirds (Swift et al., 2017). Wauchope et al. (2017) predicted that the Beringia region – currently home to the majority of shorebird species – will experience a huge decrease in the number of suitable breeding areas in the near future.

### **3.1 Breeding in the Arctic**

Shorebirds arrive in the Arctic in late May – early June, and at the end of this month, they start nesting, but first, they need to find a partner. There are two basic mating systems. In monogamy, also known as conservative strategy, birds return to the same breeding site each year

and often reunite with the same partner. This may lead to an earlier start of nesting compared to the second type (McGuire et al., 2020). They defend their territory, and both parents usually take turns incubating the eggs (Holmes, 1971). Biparental care of eggs is more likely to lead to successful hatching, due to more constant and aggressive defense against predators (Pitelka et al., 1974; Smith, 2009). In addition, partners can guard each other from predators (Kubelka, 2018) and together they can more easily chase predators and protect their nest (Larsen et al., 1996). However, frequent movements on the nest during parent changes and longer periods of an unattended nest may increase the risk of predation (Meyer et al., 2020). The pair can also produce a replacement clutch if the first nest is lost at the beginning of the breeding season (Jónsson & Gunnarsson, 2010; Pitelka et al., 1974; Tulp & Schekkerman, 2001; Underhill et al., 1993). However, chicks from replacement clutches may have lower chances of survival to adulthood (Saalfeld et al., 2021) and there is in many occasions not enough time for replacement clutch during short Arctic summer (Moltofte et al., 2007). The second type is called opportunistic and includes serial polygamy (polygyny or polyandry), and promiscuity. One sex (males in polygynous species and females in polyandrous species) defend territories that are suitable for mating or protect feeding areas for a certain period and the other sex is solely or predominantly responsible for incubation and chick rearing (Billerman et al., 2025; Pitelka et al., 1974). This strategy often results in the nest being unprotected from the cold Arctic temperatures or predators, relying solely on camouflaging the eggs in the tundra (Cantar & Montgomerie, 1985). Smaller shorebird species are typically observed to exhibit more frequent nest departures than larger species, on the other hand, these departures tend to be for shorter duration (Tulp et al., 2012). It is a common strategy in species such as the Little Stint (*Calidris minuta*) or White-rumped Sandpiper (*Calidris fuscicollis*) (Piersma et al., 2003; Pitelka et al., 1974), and that is because they can have more chicks than the conservative species when conditions are optimal. A special case is then Sanderling (*Calidris alba*), which can be either uniparental or biparental (Reneerkens et al., 2011). Both these mating systems, opportunistic and conservative, were supported by Saalfeld & Lanctot (2014).

Shorebirds do not form colonies like geese or seabirds but breed usually in more evenly distributed densities. They build their nest depressions on the ground in the Arctic tundra and lay there usually four eggs (Jónsson & Gunnarsson, 2010; Nol et al., 1997; Norton, 1972). However, when the number of nesting pairs becomes large, they are forced to nest closer together due to limited space in favorable locations (Saalfeld & Lanctot, 2014). Choosing a suitable nesting site in shorebirds is influenced by habitat preference, which can vary among species (Cunningham et al., 2016; Smith et al., 2007). For example, shorebird species that nest

in wetlands and stony shores tend to have a higher breeding success rate compared to those in mesic tundra (Léandri-Breton & Bêty, 2020; Lecomte et al., 2008). Zhemchuzhnikov et al. (2024) also support the impact of the habitat, namely the elevation of the nest, and McKinnon et al. (2013) pointed out the increased risk of predation near nesting geese. Moreover, some research shows that early nesting in areas with remaining snow may make it easier for predators to locate nests built on snow-free patches (Byrkjedal, 1980; McGuire et al., 2020). However, an earlier start of nesting may be advantageous for shorebirds that hide their nests in vegetation, such as the Redshank (*Tringa totanus*). Warmer spring temperatures, caused by global warming, can accelerate the growth of vegetation, thus providing better nest cover from predators (Laidlaw et al., 2020). Otherwise, Laidlaw et al. do not find an effect of habitat on predation risk in their research, similar to Smith et al. (2007) and Giroux et al. (2016). On the other hand, Giroux et al. confirm, that the presence of large numbers of breeding shorebirds can increase the risk of predation. But there are also species, like Black-bellied Plover (*Pluvialis squatarola*), that are worth nesting around for other species, because Black-bellied Plovers actively attack and repel predators (Larsen & Grundetjern, 1997). But attacking a predator and aggressiveness is only one of the final steps in the antipredatory strategies of shorebirds. Migration to the Arctic or the use of nest and egg crypsis also functions as an anti-predatory strategy (Kubelka, 2018; Larsen & Moldsvor, 1992). Additionally, some shorebird species nest in exposed areas of the tundra, which may enhance their ability to detect predators early (Amat & Masero, 2004; Dyrce et al., 1981). Synchronization of nest initiation can also serve as a strategy for nest protection, as a higher number of nests can spread the risk of predation and provide greater protection for individuals (Sandercock et al., 1999; Smith et al., 2010a).

However, in response to an imminent predator threat, many shorebird species remain on their nests motionless for as long as possible. They avoid drawing attention to themselves, they remain silent, rely on their camouflage and the predator may not even notice the potential prey during its search (Larson, 1960; Summers & Underhill, 1987). Shorebirds may also defend the nest by luring the predator away. They do this through injury-feigning behavior, pretending to be easy prey, as well as by making warning calls. They may also exhibit false incubating or feeding behaviors. Distracting displays are employed by species such as Eurasian Golden Plover (*Pluvialis apricaria*) or White-rumped Sandpiper (*Calidris fuscicollis*), although they may not always be fully effective. This is evidenced by the relatively low nesting success observed in these species, as reported in the studies by Machín et al. (2019) and Smith et al. (2007).

If necessary, shorebirds start with aggressive circling and scolding, and then they can launch an attack. It can occur in a group, referred to as group mobbing (Dyrce et al., 1981; Gochfeld, 1984; Kubelka, 2018; Smith et al., 2007). An attack on a predator can be fatal for the nesting parent, as even an adult bird may be preyed upon by predators such as the Arctic Fox (Bahr, 1989). This risk is more likely to be taken by parents with older nests, that have a higher probability of survival (Nguyen et al., 2006; Smith & Wilson, 2010b; Smith, 2009). In any case, they try to return to the nest as quickly as possible to warm up the eggs or chicks (Gochfeld, 1984).

The eggs take about 19 to 28 days to hatch (McKinnon & Bêty, 2009; Weiser et al., 2018), and even after hatching, the parents can protect the young from the Arctic temperatures and, especially, from predators while the chicks forage for food (Jónsson & Gunnarsson, 2010; Larson, 1960; Pitelka et al., 1974). Parents can escort their chicks and, in response to danger, use warning signals to direct them to disperse and crouch (Larsen & Moldsvor, 1992; Larson, 1960). In fact, predation may exert a more significant influence on chick survival in years characterized by high predator abundance and low lemming populations than factors such as food availability, rainfall, or temperature (Machín et al., 2018). The chicks reach the fledging stage after around 11 to 19 days (Cantar & Montgomerie, 1985; Meltofte et al., 2007) and soon after that, parents can start to migrate back to their wintering grounds, sometimes up to a month earlier than the young. In years of high predation pressure and a large number of failed nests, parents may migrate back south even earlier (Blomqvist et al., 2002).

#### **4 The alternative prey hypothesis and shorebirds**

The alternative prey hypothesis seeks to explain the relationship between a primary prey, a secondary or alternative prey species, and their shared predator. In the Arctic tundra, lemmings, along with voles to a lesser extent, typically serve as the primary prey (Angerbjörn et al., 1999; Ims et al., 2013). These small rodents experience cyclical population fluctuations, with periods of abundance followed by crashes, often in regular and somewhat predictable patterns (Kokorev & Kuksov, 2002). Population cycles, however, do not just impact the lemmings themselves, they have cascading effects throughout the Arctic ecosystem, particularly on predators (Macpherson, 1969; Pitelka et al., 1955). According to the hypothesis, when lemmings are abundant, predators such as Arctic Foxes, skuas, or Snowy Owls primarily prey on them (Summers & Underhill, 1987; Troy, 1996). Since lemmings are easier to find during population peaks, predators spend less time foraging and are less likely to find other potential

food sources (Beardsell et al., 2022). As a result, alternative prey such as the eggs and chicks of ground-nesting birds, like shorebirds, are under lower predation pressure during these times and have higher chances of survival (McKinnon et al., 2014). However, when Arctic rodents numbers decline, predators are forced to search more widely for food (Underhill et al., 1993). This increases the likelihood that they will encounter and prey upon the nests of these migratory birds (Beardsell et al., 2022; Zhemchuzhnikov et al., 2024). Thus, the abundance of lemmings and voles may have an indirect, but still significant influence on the breeding success and survival of Arctic-nesting birds. In this way, the alternative prey hypothesis highlights the interconnectedness of species within the Arctic food web and explains how changes in one population can impact other animals. However, this hypothesis is affected by multiple climate change-related factors, which are expected to intensify in the future, potentially leading to significant shifts in ecosystem dynamics (Fraser et al., 2014; Gallant et al., 2014; Gauthier et al., 2024).

More than 100 years ago, Charles S. Elton described the four-year population cycle of lemmings and voles. Even back then, he was trying to understand why these population peaks and subsequent crashes occur (Evans, 1943). The functioning and impacts of these cycles have not only been studied in the Arctic (Ježková et al., 2014; Pearson, 1966), but it is the place where they have received the most attention (Kokorev & Kuksov, 2002; Maher, 1970). It has also been found that these cycles may not be strictly periodic and can even disappear over time (Krebs et al., 1995). At the same time, some scientists have shown that these fluctuations affect not only predators but also other organisms that may become alternative prey – geese, but most importantly shorebirds (Macpherson, 1969; Pitelka et al., 1955; Summers & Underhill, 1987). Larson (1960) confirms that in areas without lemmings, such as Spitsbergen, or during periods of lower lemming numbers, Arctic breeding birds are more likely to become prey for predators. The study of the alternative prey hypothesis, as named by Angelstam et al. (1984), has not always led scientists to the same conclusion that the hypothesis operates uniformly across all regions as originally described (Holmes, 1966; Meltofte et al., 2021; Smith et al., 2010a; Smith, 2009; A. Stickney, 1991). From my perspective, the study by McKinnon et al. (2013) is particularly important, as they divided prey into "alternative" and "incidental" categories. In the surroundings of geese breeding colonies, shorebirds can be regarded as incidental prey (McKinnon et al., 2013). This highlights the fact that relationships in the Arctic are more complex than previously thought (Aharon-Rotman et al., 2015). The alternative prey hypothesis, along with the ecological relationships and the environmental changes that influence it, continues to be a focus of research in recent years (Beardsell et al., 2022; Saalfeld et

al., 2021; Zhemchuzhnikov et al., 2024), and given the ongoing effects of climate change and its related impacts, it will be important to further investigate these relationships and changes within this ecosystem.

#### **4.1 Role of Arctic rodents**

The multi-year population cycles of lemmings have been recognized since the early 20th century. Given that lemmings, namely Collared Lemmings (*Dicrostonyx ssp.*) and Brown Lemmings (*Lemmus ssp.*) (Ehrich et al., 2020), are an important prey species for many Arctic predators, their population dynamics are of significant interest, particularly in the context of climate change and warming trends in the Arctic.

Lemmings are adapted to spend the long winter periods under the snow (Reid & Krebs, 1996), where they build their nests lined with grass (Gilg et al., 2003). Heterogeneous microtopography and the depth of snow are critical factors in selecting an appropriate nesting site for lemmings (Duchesne et al., 2011; Reid & Krebs, 1996). A sufficient snow layer offers thermal insulation, mitigating the effects of extreme winter temperatures and providing a stable microclimate for the nest. Additionally, snow can serve as a physical barrier, reducing the risk of predation by Arctic Foxes (Duchesne et al., 2011). These short-lived rodents can reproduce at elevated levels of stress hormones induced by the presence of predators (Fauteux et al., 2018), and are even capable of reproducing within their nests during some winters (Krebs, 2024). This facilitates a more rapid population increase during the summer season and helps compensate for their summer losses (Duchesne et al., 2011; Ims et al., 2011). However, climate change is resulting in elevated temperatures and increased winter precipitation, which can influence both the quantity and quality of snow cover. Rain in winter falls on snow and increases its temperature, which can lead to snowmelt. However, liquid water in the landscape may later refreeze, resulting in the formation of an ice layer on the soil surface. Moreover, with more precipitation, rainwater can reach the soil surface, where it freezes and further warms both the soil and the snow (ACIA, 2004; Gilg et al., 2009; Putkonen & Roe, 2003; Tulp & Schekkerman, 2001). These changes have the potential to reduce the survival of Arctic herbivores and to disrupt the natural life cycles of lemming populations, as the movement becomes much more difficult for lemmings in hard snow and during rain-on-snow events. It may become more difficult for them to access food resources in the future, as increased snow hardness will prolong the time and energy required for digging (ACIA, 2004; Kausrud et al., 2008; Poirier et al., 2021).

In contrast to winter habitat selection, summer habitat selection of lemmings is more strongly influenced by the availability and abundance of food resources (Predavec & Krebs, 2000) and the winter and summer distribution of lemmings in the Arctic may therefore differ (Le Vaillant et al., 2018). Food preference differs between Collared Lemmings, which consume mainly herbs and shrubs, and Brown Lemmings, which choose predominantly graminoids when available (Rodgers & Lewis, 1986).

The number of lemmings naturally goes through synchronized peak periods, followed by periods of lower density (Lecomte et al., 2008). That is probably due to the winter weather, or effects of predation (Gilg et al., 2006; Krebs, 2024), which can strongly modulate the cycles (Pitelka et al., 1955). The impact of predation was experimentally tested during the summer months by Fauteux et al. (2016), who set up a large enclosure against both avian and mammalian predators. They confirmed that predation can have a significant impact on the population dynamics of lemmings. Typical population cycles of lemmings are reported to span 3 – 4 years (Kokorev & Kuksov, 2002). However, Summers et al. (1998) have indicated that the cycles can be asynchronous, but more likely they are synchronized only regionally (Krebs, 2024). They can also disappear entirely from certain areas of the Arctic (Aharon-Rotman et al., 2015; Ehrich et al., 2020; Schmidt et al., 2012). Ims et al. (2011) and Kausrud et al. (2008) suggest that this may be due to global climate change. However, this is not supported by the results of Ehrich et al. (2020), who have not so far found the effect of global warming on lemmings. Moreover, Brommer et al. (2010) try to disprove the hypothesis that global warming is affecting these cycles, by confirming the return of vole cycles after several years of absence in southern Finland. According to the most geographically extensive study of lemming cyclicality in the Arctic, it has been shown that although lemming cycles are not always clearly 3 – 4 years, the cycles are still able to return after a period of non-cyclicality, even in today's warming world (Gauthier et al., 2024).

Lemmings serve as a primary prey species in the Arctic ecosystem and their population cycles exert a significant influence on the dynamics of arctic predators. Predators are influenced by the need to find other food sources when their main prey is less abundant and Snowy Owls, and sometimes even other avian predators, do not even begin to breed at lower population densities of lemmings (Fauteux et al., 2016; Gilg et al., 2006). However, even a high abundance of lemmings does not always lead to the initiation of breeding (Meltofte et al., 1981). In some areas, the reproduction of Arctic Foxes may also be coupled to lemming populations (Blomqvist et al., 2002; Schmidt et al., 2012). So, the density of lemmings can affect the abundance of predators, which can then also form indications of cyclic populations (Schmidt et al., 2012).

Overall breeding success for birds is better at higher lemming levels (Summers & Underhill, 1987). Alternative prey, which may experience increased predation pressure at lower lemming densities, also plays a role in sustaining population cycles. Voles or eggs of shorebirds, and geese may enable lemmings to escape the predator-pit, thereby allowing their population to increase again (Ims et al., 2011; Krebs et al., 1995).

## 4.2 Role of predators

Throughout almost the entire Arctic, we can encounter important predators that influence the survival and behavior of both Arctic rodents and nesting birds. This includes avian predators – e.g. Parasitic Jaeger (*Stercorarius parasiticus*), Long-tailed Jaeger (*Stercorarius longicaudus*), Snowy Owl (*Bubo scandiacus*) or Common Raven (*Corvus corax*) as well as mammalian predators – Arctic Fox (*Alopex lagopus*) or Eurasian Stoat (*Mustela erminea*) (Gilg et al., 2009; Meltofte et al., 1981; Smith et al., 2007; Smith & Wilson, 2010b).

The Arctic Foxes are distributed throughout the circumpolar region and represent a major predatory threat to lemmings and ground-nesting birds (Angerbjörn et al., 1999; Gilg & Yoccoz, 2010; Larson, 1960; Machín et al., 2019). They defend their breeding territories, which typically include a den, and the size of these home ranges varies in response to prey availability (Fuglei & Ims, 2008; Macpherson, 1969). Due to the soil characteristics of the tundra, suitable sites for fox dens are limited (Garrott et al., 1983). As a result, these dens are often used for multiple years and may be continually expanded over time (Macpherson, 1969). The location of a fox den is often easily identifiable (Garrott et al., 1983), as foxes frequently bring prey to the den site, disturbing the soil through digging the burrow and thereby creating localized conditions that favor plant growth (Johnson-Bice et al., 2023). Over time, these sites may become covered with unique vegetation, that is not found anywhere near the den and can subsequently attract other Arctic animals (Zhao et al., 2022). Through these habitat changes, foxes function as ecosystem engineers, generating biotic hotspots within the tundra landscape (Johnson-Bice et al., 2023; Zhao et al., 2022). Among the animals attracted to these vegetated den sites are species such as reindeer, which are not preyed upon by Arctic Foxes due to their large body size. As generalist predators, Arctic Foxes respond to the availability of a wide range of prey items (Smith, 2009). They feed on insects, hares, birds, and their eggs and on islands or near the coast, they also eat fishes and marine mammals (Elmhagen et al., 2000; Tannerfeldt & Angerbjörn, 1998). However, these are just alternative food resources, as their primary prey are small rodents (Elmhagen et al., 2000; Macpherson, 1969). The population cycles of lemmings can have a substantial influence on Arctic Fox reproduction, with litter sizes reaching up to 22

pups during peak lemming abundance (Fuglei & Ims, 2008; Gilg et al., 2009; Tannerfeldt & Angerbjörn, 1998). With low numbers of lemmings, litter size and survival of the young is reduced (Macpherson, 1969). Despite that, Elmhagen et al. (2000) reported no evidence of a relationship between lemming abundance and litter size.

Lemmings also influence the population dynamics of Arctic Foxes through their non-cyclic periods and prolonged absences from certain regions. The Arctic Fox is a relatively short-lived species, with an average lifespan of 3 to 4 years (Tannerfeldt & Angerbjörn, 1996). Although it reaches sexual maturity at approximately 9 months of age (Macpherson, 1969), prolonged periods of lemming scarcity can significantly impact its reproductive success and population viability. In response to the absence of lemmings, foxes may expand their range beyond their territories, adopt a wide-ranging search strategy, and potentially migrate northward and even south into the taiga biome, where foxes do not initiate breeding (Fuglei & Ims, 2008; Tannerfeldt & Angerbjörn, 1998; Underhill et al., 1993). Clermont et al. (2021) also emphasize that the spatial and temporal distribution of Arctic Foxes exhibits considerable variability, largely driven by fluctuations in the abundance and distribution of their primary prey. However, due to ongoing environmental changes, the Red Fox (*Vulpes vulpes*), which is larger than the Arctic Fox and exhibits similar behavior (Frafjord et al., 1989), may expand its range northward to the Arctic. This could also potentially affect the distribution of the Arctic Fox and negatively impact Arctic fauna (Gallant et al., 2014; Summers et al., 1998). Climate change may play an indirect role in the northward expansion of the Red Fox. The primary driver is likely increased human activity in the Arctic, such as expanding settlements, industrial development, and increased food availability through anthropogenic waste (Gallant et al., 2020; Stickney et al., 2014). This range expansion poses a significant threat to the Arctic Fox, as the Red Fox can occupy permanent dens, using anthropogenic food sources independently of lemming population cycles or alternative prey, and even preying upon Arctic Foxes and their whelps (Frafjord et al., 1989; Gallant et al., 2014; A. A. Stickney et al., 2014). Prolonged periods of low or absent lemming cyclicality may therefore strongly favor the expansion of this competitively dominant species, representing another threat for Arctic rodents as well as shorebirds nests and chicks as alternative prey.

Another important group of Arctic predators is birds, whose lives can also be significantly influenced by lemming population cycles. However, they affect lemmings for no longer than a few months during the summer breeding season (Angerbjörn et al., 1999). For both, the Long-tailed Jaeger and the Snowy Owl, lemmings represent a primary prey source and can therefore influence the survival of their offspring (Andersson, 1971; Macpherson, 1969;

Meltofte et al., 1981; Smith & Wilson, 2010b). In the absence of their primary prey, avian predators may resort to alternative food sources, such as the eggs of other ground-nesting bird species in the Arctic, including those of shorebirds (Pitelka et al., 1955; Tulp & Schekkerman, 2001). However, these avian predators may incidentally confer protective benefits to other birds, such as geese, by creating a 'protective umbrella' effect. This occurs through the active defense of nesting territories against other avian predators, reindeers, as well as foxes (Andersson, 1971), and such behavior may result in a localized reduction in predation pressure (Bêty et al., 2001; Larsen & Grundetjern, 1997; Underhill et al., 1993). Another way avian predators may respond to a low number of lemmings is by migrating to other parts of the Arctic (Angerbjörn et al., 1999; Therrien et al., 2014), a strategy that is generally easier for them than for mammalian predators. However, this may be disadvantageous, as it results in the loss of familiarity with their established breeding territories (Gilg et al., 2009; Therrien et al., 2014).

Lemming population cycles can influence predators to such an extent that the predators themselves may develop cyclic population dynamics (Smith et al., 2010a, 2020). Following a population peak and subsequent decline, predator numbers may continue to rise for some time, as they can start to use alternative food sources (Pearson, 1966). This suggests a shift to alternative food sources – commonly referred to as prey switching – with shorebirds and their chicks frequently serving as alternative prey (Maher, 1970; Summers & Underhill, 1987). The survival of these alternative prey species in the Arctic is therefore largely determined by the abundance of active predators in the area (Larsen et al., 1996). Collectively, these findings indicate that ongoing global environmental change is expected to significantly affect both lemming populations and breeding shorebirds in the future.

### **4.3 Role of shorebirds**

Arctic shorebirds are migratory species that seasonally fly to the Arctic tundra to breed there. During this period, their eggs and chicks may serve as an additional or alternative resource for local predators (Clermont et al., 2021; Smith & Wilson, 2010b; A. Stickney, 1991). The abundance of these Arctic predators can therefore significantly affect their breeding success (Naves et al., 2008). Surprisingly, Weiser et al. (2018) found that high predator abundance affected nesting success in only one species – the Western Sandpiper (*Calidris mauri*). Rodents, as the main prey, should also have an impact, according to the alternative prey hypothesis (Blomqvist et al., 2002; McKinnon et al., 2014). Smith et al. (2007) also assumed a correlation between the reduced abundance of lemmings and increased shorebird nest mortality due to predation. As a result, certain shorebird species, such as the Red Knot (*Calidris canutus*) and

Sanderling (*Calidris alba*), select their breeding sites based on the presence of lemmings. They can perceive predation pressure and avoid those locations. So, in regions like Svalbard, where lemmings are absent, these shorebird species are also not found as common breeders (Fredga et al., 1999; Gilg & Yoccoz, 2010). However, A. Stickney (1991) and Weiser et al. (2018) did not observe a significant influence of rodents on shorebirds.

The eggs of shorebirds are less energetically profitable than lemmings for predators, and even compared to goose eggs, they are calorically less advantageous (Bahr, 1989; McKinnon et al., 2013, 2014). If a nest is found by the Arctic Fox, all the eggs present are typically depredated by immediate consumption of the eggs on-site or the removal and caching of the eggs for later consumption (Bahr, 1989). The presence of the shell and protective membranes increases the processing time of the egg but also helps delay its decomposition in the cache, making it energetically advantageous for Arctic Foxes to transport the eggs over longer distances (Careau et al., 2007; Samelius et al., 2007). A. Stickney (1991) even reports that with the start of the bird breeding season, Arctic Foxes switched to eggs, despite the presence of higher densities of rodents. Arctic Foxes are likely influenced by the fact that cached eggs can serve as a food resource during the winter months (Careau et al., 2007).

Nest predation is a significant threat to shorebirds in the Arctic (Smith et al., 2007), profoundly influencing their behavioral patterns (Gochfeld, 1984). Some species, such as Whimbrels (*Numenius phaeopus*), actively defend their territories and nests from predators. This is also related to their large size, which enables them to confront larger avian predators (Jónsson & Gunnarsson, 2010). Defensive behavior in birds can lead to the formation of a 'protective umbrella' effect, where the presence of aggressive species provides safety for other species within the same area (Dyrce et al., 1981). In the case of the aggressive Long-tailed Jaeger, this protective effect is closely tied to the availability of their primary prey – lemmings (Larsen & Grundetjern, 1997). As lemming populations decline, the jaegers may become unreliable 'umbrellas' due to reduced food availability and it can be hazardous for other species, such as Bar-tailed Godwit (*Limosa lapponica*) to nest near them. Less aggressive species can nest in association with these species and have significantly higher nesting success compared to that of the more aggressive species, as confirmed by Larsen & Moldsvor (1992) study in northern Norway. However, according to Jónsson & Gunnarsson (2010) study in Iceland, the Bar-tailed Godwit is not less aggressive; rather, it targets smaller predators due to its relatively smaller size compared to the Whimbrel. Moreover, they did not find evidence supporting a dependence of Bar-tailed Godwits on Whimbrels. The differential aggressiveness observed by Jónsson & Gunnarsson and Larsen & Moldsvor in Bar-tailed Godwits may be attributable to the

absence of lemmings in Iceland (Fredga et al., 1999). Shorebird species nesting in areas lacking alternative prey, such as rodents, typically exhibit higher levels of aggression toward predators (Larsen et al., 1996).

Shorebirds, as relatively long-lived birds (Moltofte et al., 2007), may be caught in cycles (Roselaar, 1979), similar to Arctic predators, which may influence shorebird nest success due to the scarcity of primary prey – lemmings (Troy, 1996). If lemming cycles occur every 3-4 years, shorebirds could potentially benefit from improved breeding success in subsequent years when primary prey becomes abundant again. However, if there are long periods of non-cyclicity (Krebs et al., 1995), or if lemmings were to disappear from the Arctic in the future due to climate change, it could have significant consequences for the dynamics of shorebird populations. To date, the longest documented period of non-cyclicity of Arctic rodents has been recorded in Kilpisjärvi, Finland, lasting approximately 27 years (Gauthier et al., 2024).

#### **4.4 Spatial patterns**

The alternative prey hypothesis has been investigated across numerous Arctic sites (Figure 2); however, the relationship between predators, primary prey, and alternative prey has not been supported across all regions. Among the regions where this hypothesis has been supported is Russia, specifically on the Taimyr Peninsula, where Summers & Underhill (1987), and later also Underhill et al. (1993) demonstrated a dependence of both shorebird and goose nesting success on lemming abundance. Another study conducted on this peninsula by Tulp & Schekkerman (2001) confirmed that predation can significantly impact shorebirds even at low predator densities, particularly when lemming abundance is low. Blomquist (2002) used data from the Taimyr Peninsula for his study and emphasized that population fluctuations in shorebirds and geese are more pronounced in this region compared to species with broader breeding ranges across Russia. Zhemchuzhnikov et al. (2024), also worked in this region of Central Russian Arctic, observed an increased influence of predation during periods of low lemming abundance. However, he as well identified nest elevation as an important factor, suggesting that predators may more frequently encounter shorebird nests located at lower elevations, where lemmings are also typically found. It is important to note that in recent decades, there has been a significant lack of long-term monitoring of lemming populations in Russia and although data collection still takes place in some areas of the Russian Arctic (Soloviev & Tomkovich, 2025), current studies from this region remain very limited. This represents a major concern in the context of ongoing Arctic warming (CAFF, 2013; Ehrich et al., 2020).



**Figure 2.** Spatial distribution of studies conducted in the Arctic related to the alternative prey hypothesis with shorebirds as the alternative prey. Green tones represent bioclimatic subzones as delineated and adapted by CAFF (2013). Bird pictograms indicate locations where studies involving shorebirds or shorebirds and geese were conducted and examined the alternative prey hypothesis. I searched for these articles on Google Scholar using selected keywords – 'the alternative prey hypothesis', 'shorebirds', 'waders' and 'Arctic'. This search provided over 4,600 publications. From these, I selected around 400 studies for closer investigation. Out of them, 26 publications held relevant information on the alternative prey hypothesis with shorebirds or shorebirds and geese as alternative prey, and those studies are depicted in this figure. For a broader view, I also read studies that focused specifically on geese, other bird species, or small mammals that may also serve as alternative prey; however, these were not included in the core literature review. The keywords were also translated into three languages to make sure I found as many articles on the topic as possible. The important languages for me were Russian, French, and Danish because they are used widely in the Arctic region. In relevant articles, I also investigated the referenced publications, as well as I did check newer citations of those articles on Google Scholar. I downloaded relevant publications from electronic databases.

Successful testing of the alternative prey hypothesis and the relationship between lemmings and shorebirds has also been conducted in North America (Bahr, 1989; Lamarre et al., 2017; Perkins et al., 2007; Robinson et al., 2014; Troy, 1996). Bêty et al. (2001), through their findings highlighted the relationship between lemming abundance and nesting birds' success at

the Bylot Island, Canada. McKinnon et al. (2013) also conducted their study on this island and found that low lemming abundance was associated with increased predator activity near large goose colonies, where they placed artificial shorebird nests and observed higher predation rates of those nests. In North America, however, the alternative prey hypothesis has not been supported consistently across all study sites. For example, (Flemming et al., 2019; Reiter & Andersen, 2011; Smith, 2009; A. Stickney, 1991) are among the studies that did not find support for this hypothesis. Some studies from the Western Hemisphere have neither supported nor refuted the alternative prey hypothesis or its connection to lemming dynamics, primarily due to a lack of spatially consistent data on predation rates and lemming numbers over time (Fraser et al., 2013; Holmes, 1966). There could be numerous reasons why the alternative prey hypothesis has not been supported in some areas and why it may increasingly be rejected in the future. These include a greater effort by predators to store food resources – such as bird eggs – for the winter months; a generally higher availability of diverse food sources; and the effects of climate change – particularly the northward expansion of the Red Fox, the overabundance of geese (as discussed later in this chapter), and the collapse of lemming cycles.

However, the alternative prey hypothesis has also been tested and supported in other regions (Figure 2), such as Greenland (Gilg et al., 2006). On the other hand, Meltofte et al. (2008, 2021) also investigated the relationship between lemming abundance and nest survival in Zackenberg, Greenland, but found no significant correlation. It could be due to the fact that there are two distinct populations of Arctic Foxes in Greenland, which varied in their dependence on lemming abundance (Schmidt et al., 2012). While the population at Zackenberg, which does not rely exclusively on lemmings, showed no reproductive response to changes in lemming density (Larson, 1960), the population on Traill Island exhibited reproductive success that was strongly associated with fluctuations in lemming numbers. Two distinct populations of Arctic Foxes are also found in Iceland (Hersteinsson, 1992). However, the alternative prey hypothesis has not been tested in this region, likely due to the complete absence of lemmings (Fredga et al., 1999). Arctic Foxes in Iceland rely on different food sources and their populations do not exhibit the typical population cycles observed in other regions (Hersteinsson, 1992).

The loss of bird nests due to predation is a significant threat, whether in the Arctic (Smith et al., 2007) or in more southern regions (Amat & Masero, 2004). Nevertheless, the alternative prey hypothesis has primarily been studied and supported in polar and subpolar regions, as noted by Ježková et al. (2014). In their study from central Europe, they rejected the alternative prey hypothesis. The same conclusion was reached in a study done by Pöysä et al. (2016) in southern Finland. The clear pattern predicted by the alternative prey hypothesis may become

less apparent or may not operate at all in more temperate areas. This may be due to the fact that, at lower latitudes relative to the Arctic Circle, there is a greater availability of alternative prey for predators (Ježková et al., 2014) and as a result, a higher number of predators can be sustained in these regions (Léandri-Breton & Bêty, 2020). However, with the increased availability of anthropogenic food resources associated with agricultural practices (Yu et al., 2017), populations of Snow Geese (*Anser caerulescens*) and Ross's Geese (*Anser rossii*) have expanded significantly in North America (Kerbes et al., 2014). These species form large breeding colonies in the Arctic, which may attract higher numbers of predators and influence their temporal and spatial distribution. Moreover, it poses a threat to shorebirds and other bird species that are already highly vulnerable and experiencing population declines (Flemming et al., 2019; Lamarre et al., 2017; McKinnon et al., 2013). Large flocks of grazing geese in the tundra may provoke nest defense behavior in shorebirds, potentially increasing opportunities for predators near the geese to locate and depredate unattended shorebird nests (Flemming et al., 2019). In addition, large flocks of geese may attract predators, which can more easily detect shorebird nests in heavily grazed vegetation (Gauthier et al., 2006). Furthermore, goose-induced changes to vegetation structure may alter invertebrate communities that serve as an important food source for shorebirds (Sherfy & Kirkpatrick, 2003). Substantial increases in goose populations and their impacts on Arctic ecosystems have been primarily documented and described in North America. In contrast, the Eastern Hemisphere population growth in these regions began later, around the 1980s, and such massive goose colonies are not found there. In some parts of Eurasia, particularly in Central Asia, goose populations may actually be declining. However, data mostly remain limited or insufficient to draw firm conclusions (Aharon-Rotman et al., 2015; CAFF, 2013, 2018; Rozenfeld et al., 2021; Smith et al., 2020). Whether overabundant geese are the main reason, why shorebird populations are declining, has yet to be confirmed (Flemming et al., 2019), however, it is in the Nearctic region where many populations of Arctic shorebirds are currently in decline (CAFF, 2013). Nonetheless, such a situation would meet both conditions proposed by McKinnon et al. (2014) concerning the site-specific variation in the influence of lemmings: shorebirds are considered incidental prey in areas with overabundant geese, and these areas also exhibit high nest densities. Moreover, according to Clermont et al. (2021) and Alisauskas et al. (2024), foxes select their habitat partially based on the abundance of geese in the area. Although lemming cycles may still drive fluctuations in Arctic Fox populations (Alisauskas et al., 2024), hyperabundant geese could provide a concentrated and predictable food source that reduces the need for foxes to range widely across the tundra in search of prey (Beardsell et al., 2022). As a result, foxes are less

likely to encounter and depredate shorebird nests. Under such circumstances, the indirect effect of lemming abundance on shorebirds may be negligible in regions with overabundant geese colonies.

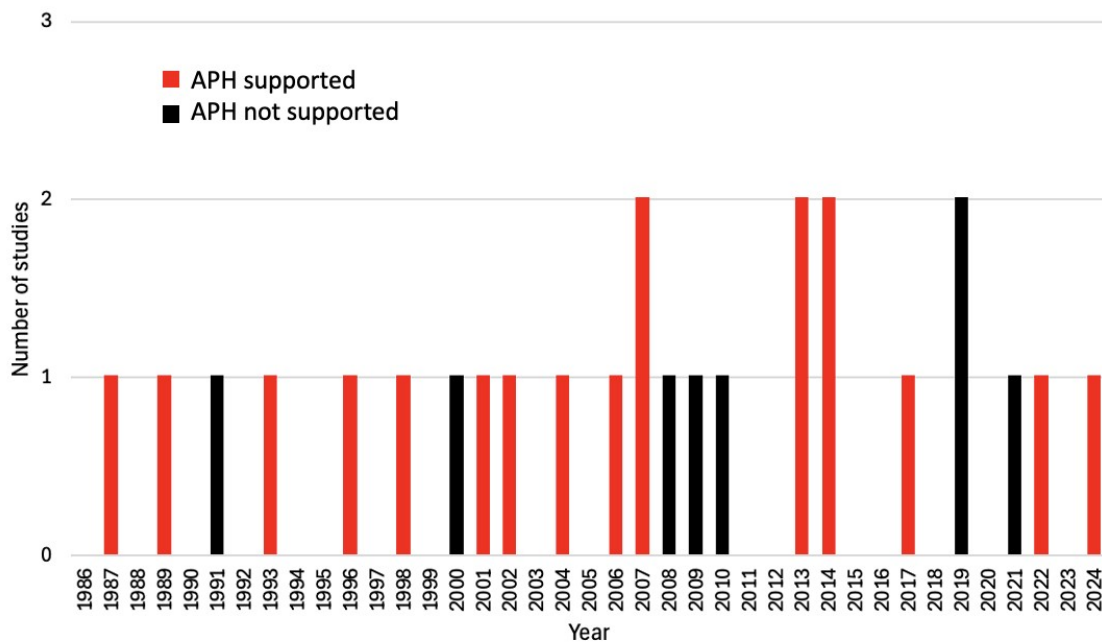
#### **4.5 Temporal patterns**

The alternative prey hypothesis has been studied, refined, and supported since the second half of the 20th century (Figure 3), during which lemming populations were generally described as cyclic, typically following 3-4 year cycles (Aharon-Rotman et al., 2015; Angerbjörn et al., 1999; Hanski et al., 1991; Kaikusalo & Angerbjörn, 1995). However, in some parts of the Arctic, particularly in Europe and Greenland, a collapse of these more or less regular population cycles was recorded around the turn of the century (Elmhagen et al., 2000; Fuglei & Ims, 2008; Gilg et al., 2009; Kausrud et al., 2008; Schmidt et al., 2012). A collapse also occurred in parts of North America around the year 2000, although many populations there remained cyclic (Ehrich et al., 2020; Gauthier et al., 2024; Krebs, 2024; Krebs et al., 1995). One of the sites in Canada where lemming cyclicity has persisted is Bylot Island (Gauthier et al., 2024), where several successful studies related to the alternative prey hypothesis have also been conducted (Bêty et al., 2001; McKinnon et al., 2013) (Figure 3). Giroux et al. (2012) also supported prey-switching behavior toward geese during lemming population crashes on this island. In response to the reduced availability of their primary prey, Arctic Foxes increasingly occupied dens located near goose colonies. However, the study did not address the survival rates of shorebirds under low lemming abundance, leaving a gap in understanding the broader implications of prey-switching on the entire prey community. Beardsell et al. (2022) conducted a relatively recent long-term study on Bylot Island demonstrates a persistent cyclic pattern in lemming population dynamics. In addition, the study offers valuable contributions to the understanding of the alternative prey hypothesis by elucidating how temporal variations in lemming abundance can modulate predator foraging behavior. Nonetheless, even on this island, the relationship between lemming abundance and nest predation can vary across different sites (Smith, 2009).

Some of the key studies supporting the alternative prey hypothesis were conducted in Siberia, on the Taimyr Peninsula, during the second half of the 20th century (Summers & Underhill, 1987; Underhill et al., 1993). Studies that do not primarily focus on lemming cycles may apply different data collection methods and, due to other research objectives – such as monitoring fox and bird populations – may not allocate sufficient time to collecting lemming data (Ehrich et al., 2020). Nevertheless, according to a long-term study by (Kokorev & Kuksov, 2002), which included systematic lemming monitoring, clear 3 – 4 year synchronized

population cycles were observed on the Taimyr Peninsula and this was supported two years later by Schekkerman et al. (2004). Ehrich et al. (2017) reported that, due to the absence of lemming peak years since 2000 in Erkuta, Russia (Ehrich et al., 2020; Gauthier et al., 2024), Arctic Foxes have shifted their foraging focus toward the increasingly abundant vole populations. Unlike lemmings, voles have benefited from recent climate change, leading to more favorable conditions for their survival. Voles also exhibit low-amplitude population fluctuations, which contributed to greater temporal stability in the Arctic Fox population observed during the study period. In addition to small rodents, shorebirds may continue to serve as alternative food sources during the summer, while reindeer carcasses can provide an important supplementary resource during winter (Elmhagen et al., 2000; Kaikusalo & Angerbjörn, 1995; Meltofte et al., 2007). After year 2000, more studies found no support for the alternative prey hypothesis (Figure 3), which might be linked to the recently disrupted cyclicities of Arctic rodents. However, more detailed investigation (locality by locality and year by year) is needed to shed light on this issue.

Another temporal variability might occur within breeding season. The use of shorebird nests as an alternative food source for Arctic Foxes may vary over the course of the breeding season. This dependence may be influenced by the amount of snow and the distribution of snow-free patches, which can create isolated 'islands' where the nests of early-breeding shorebirds are easily located by predators (Machín et al., 2019; McGuire et al., 2020; Meltofte et al., 1981) and it may lead to low survival of these early nests (Smith & Wilson, 2010b). Even the presence of lemmings during this period may not be sufficient to prevent predation of shorebird nests by Arctic Foxes (Meltofte et al., 1981; A. Stickney, 1991). However, if eggs are laid after the tundra is snow-free, the presence of lemmings may have a substantial effect. Schekkerman et al. (2004) found that shorebird nest predation remained low while lemmings were still active on the surface. After the summer burrows had thawed out and lemmings were able to return underground again, nest predation increased. However, after lemming reproduction in summer burrows, their numbers on the surface may increase again, which could mean greater safety for birds' nests later in the season (Meltofte et al., 1981). Nevertheless, nest survival throughout the short Arctic breeding season likely varies between years and locations, depending on the presence and abundance of predators and lemmings (McGuire et al., 2020; Smith et al., 2007).



**Figure 3.** Scientific interest in alternative prey hypostasis across time. The number of all articles found about shorebirds or shorebirds and geese in relation to the alternative prey hypothesis between 1987 and 2024. Most studies are long-term and the year was determined by the publication date. Studies supporting the alternative prey hypothesis are shown in red, while those not supporting it are shown in black. For the selection of the studies, see details in the Figure 2.

#### 4.6 Climate change impact on the alternative prey hypothesis

In the short term, climate change might bring some benefits to shorebirds nesting in the Arctic. Parents incubate their nests and protect them from low Arctic temperatures, which requires a large proportion of their daily energy expenditure (Piersma et al., 2003). Similarly, chicks use a significant amount of energy for thermoregulation. Therefore, rising temperatures in the Arctic could reduce these energetic costs for shorebirds, increase their reproductive effort and potentially enhance their survival (Robinson et al., 2014; Weiser et al., 2018). However, by 2070, these favorable breeding conditions are projected to decline significantly (Wauchope et al., 2017). Climate change is also expected to influence various other factors that may further reduce shorebird survival, despite their considerable efforts through behavioral flexibility (McGuire et al., 2020). For example, it is likely to affect the functioning of the alternative prey hypothesis. Kausrud et al. (2008) suggest that phases of non-cyclic dynamics or weakened cycles of lemmings may be driven by climate change. However, Gauthier et al. (2024) find no conclusive evidence to support this hypothesis at present, as the currently available data are insufficient to confirm such an effect. Lemming cycles continue to persist, and the phenomenon of disappearance does not yet appear to be widespread. A similar conclusion was reached by

Brommer et al. (2010), who observed a return of vole population cycles in southern Finland after a five-year collapse, even in the context of ongoing climate change. On the other hand, Gauthier et al. (2024) acknowledge that climate change and associated environmental shifts are likely to have a significant impact on lemming cycles in the future – for example, due to rain-on-snow events (for more details, see Chapter 4.1 Role of Arctic rodents). Moreover, the loss of lemmings in the future could also affect the composition of vegetation, thus contributing to the greening of the Arctic (Gilg et al., 2012).

Arctic Foxes, which are key components of the Arctic ecosystem, primary predators of cyclic lemmings, and legally protected animals in many parts of the Arctic, may also be increasingly affected by climate change. For instance, elevated anthropogenic influence in Arctic regions and winter mortality of large herbivores, as a result of reduced food availability on icy pastures (Ehrich et al., 2017), may create more resources not only for Arctic Foxes but also for the increasingly common Red Foxes (Gilg et al., 2012). They are expanding northward into the Arctic from southern regions and may have negative effects on Arctic Foxes, as they (Ehrich et al., 2017; Kaikusalo & Angerbjörn, 1995) (Ehrich et al., 2017; Kaikusalo & Angerbjörn, 1995). Climate change is also associated with an extended duration of ice-free periods at sea. This may influence another major Arctic predator, the Polar Bear (*Ursus maritimus*), which is expected to increasingly forage in Arctic terrestrial ecosystems (Prop et al., 2015). This predator may be drawn to Arctic Fox dens and could negatively affect them. In addition, Polar Bears may prey on the nests of ground-nesting birds, such as geese, which could serve as alternative prey for Arctic Foxes (Gilg et al., 2012; Prop et al., 2015; Zhao et al., 2022). Other bird species, such as shorebirds, may then become more frequent prey for the foxes.

## **5 Future perspectives on the alternative prey hypothesis research**

Testing the alternative prey hypothesis does not always occur under the same conditions. Whether it is a method of collecting data on the number of lemmings (Ehrich et al., 2020; Gauthier et al., 2024) or the use of artificial nests, which differ from natural ones in predation rates (McKinnon et al., 2013; Nguyen et al., 2006). Experimental artificial nests are particularly useful for researching shorebird species that nest uniparentally and are more likely used as a controlled measure (Giroux et al., 2016), as they lack parental protection against predators and are not at risk of being detected due to parental movements around the nest (Gochfeld, 1984; Meyer et al., 2020). Additionally, the increased presence of scientists in the field, either searching for real nests or placing artificial ones, may contribute to higher predation rates of

nests (Lecomte et al., 2008; Tulp & Schekkerman, 2001). Therefore, using a temperature probe in the nest (Meyer et al., 2020), or cameras near the nest, provides an effective solution for monitoring. According to McKinnon & Bêty (2009), the cameras do not affect nest predation. Moreover, the data interpretation in the two largest databases also differs significantly. The “Arctic Shorebird Demographics Network” provides clearly defined numerical values (Brown et al., 2025), whereas the “Arctic Birds – The International Breeding Conditions Survey on Arctic Birds” database relies on more subjective categorical descriptions, e.g. low, average or high (Soloviev & Tomkovich, 2025).

Future studies investigating the functioning of the alternative prey hypothesis should continue with long-term monitoring of lemming cycles, particularly in Russia, where such datasets remain limited. They should also aim to apply the most consistent field methods possible (Gauthier et al., 2024). Studies should also continue during the winter months, when lemmings live beneath the snow, which is undergoing significant changes due to climate change (Duchesne et al., 2011; Poirier et al., 2021). It would also be valuable to monitor predators over the long term, ideally using GPS and accelerometer tracking (Beardsell et al., 2022). Snow plays a crucial role in the lives of many Arctic animals, both through its presence and absence (CAFF, 2013). Therefore, it is essential to continue measuring its properties, particularly its density and hardness (Gauthier et al., 2024). Ongoing monitoring of Arctic shorebirds is also important, as they are threatened not only during their migration to the Arctic but also at their breeding grounds (Kubelka et al., 2022; Wauchope et al., 2017). Climate change, combined with anthropogenic impacts, could have devastating consequences for this entire ecosystem in the future, where remain significant knowledge gaps, even in areas that are relatively well-studied (CAFF, 2013).

In my Master's research, I would like to go further in this direction. I will conduct a comparative study, compiling a matrix of abundance of Arctic rodents, abundance of predators and the breeding success of shorebirds at the same locality during same year. I will enrich such dataset with own data from Utsjoki location in the Arctic Finland. Additionally, I will extract climatic characteristics for each year and location from open climatic data sources. Such fine scale investigation at level of given locations and given years will enable to evaluate comprehensively the functionality of alternative prey hypothesis across the Arctic. I plan to use primary research articles and the two previously mentioned databases, particularly the "Arctic Birds", which, although limited by the interpretation of its data, still includes ongoing summer observations, mainly from a few locations in Russia. Those resources will help to cover the spatial gaps depicted in the Figure 2. At the same time, I will continue searching for primary

sources in languages other than English, something I have found to be a challenging task while writing this thesis. Moreover, I also plan to build connections with researchers who focus on similar topics. These collaborations could help me access literature in their native languages and, more importantly, support joint efforts in monitoring and data collection to make future research as accurate and consistent as possible.

## **6 Conclusions**

The Arctic is undergoing rapid ecological transformations, driven by a wide range of factors that directly and indirectly affect many components of this ecosystem. Different parts of the Arctic belong to different countries and therefore may have been, and continue to be, subject to varying regulations and laws, which can affect Arctic wildlife in different ways. Moreover, birds migrating to the Arctic may also be influenced by human activities and climate change occurring in many other countries along their migratory routes. Some of these factors have also been examined in this review, as they are closely related to the functioning of the alternative prey hypothesis.

The main findings of this review indicate that lemming population dynamics and cyclicity are still not fully understood and that, despite their disappearance in some areas over extended periods, these rodents may return to the ecosystem and once again play their important ecological role. Another important point is an additional indirect effect on shorebirds, namely the presence of geese, which in some areas may become overabundant and significantly impact the whole Arctic ecosystem as well as the survival of shorebird eggs and chicks.

Generally, the alternative prey hypothesis seems to be supported more in the Russian Arctic than in the Canadian Arctic and the support for the hypothesis was probably stronger before 2000 than after 2000, possibly connected with disruption of Arctic rodent population cycles in last decades. Not well functioning alternative prey hypothesis could contribute to recently observed population declines of Arctic shorebirds. However, the higher abundances and functional cyclicity of Arctic rodents are again returning at some Arctic locations and the whole issue requires more detailed meta-analytical investigation. Various, mostly climate change-induced and not mutually exclusive factors as rain-on-snow event during winter, new predator species expanding to the Arctic or suitable breeding habitat shrinkage can impact on the functionality of alternative prey hypothesis in complex ways.

For future, the standardized data collection is desired as well as continuation of long-term studies, which are especially valuable. Moreover, new techniques such as GPS tracking of

predators or alternative prey can provide valuable insights into predator–prey interactions in the Arctic, which remains an important and relevant research field, particularly in light of the ongoing environmental changes and conservation needs for endangered Arctic wildlife.

## 7 References

- ACIA. (2004). *Impacts of a Warming Arctic*. Cambridge University Press.
- ACIA. (2005). *Arctic climate impact assessment*. Cambridge University Press.
- Aharon-Rotman, Y., Soloviev, M., Minton, C., Tomkovich, P., Hassell, C., & Klaassen, M. (2015). Loss of periodicity in breeding success of waders links to changes in lemming cycles in Arctic ecosystems. *Oikos*, *124*(7), 861–870.
- Alisaukas, R. T., Kellett, D. K., Samelius, G., & Slattery, S. M. (2024). Geese as keystone species in the Low Arctic of central Canada: the Karrak Lake Research Station. *Arctic Science*, *10*(4), 778–798.
- Amat, J. A., & Masero, J. A. (2004). Predation risk on incubating adults constrains the choice of thermally favourable nest sites in a plover. *Animal Behaviour*, *67*(2), 293–300.
- Anderson, C. M., Fahrig, L., Rausch, J., Martin, J. L., Daufresne, T., & Smith, P. A. (2023). Climate-related range shifts in Arctic-breeding shorebirds. *Ecology and Evolution*, *13*(2), 1–10.
- Andersson, M. (1971). Breeding behaviour of the Long-Tailed Skua (*Stercorarius longicaudus*) (Vieillot). *Scandinavian Journal of Ornithology*, *2*(1), 35–54.
- Angelstam, P., Lindström, E., & Widén, P. (1984). Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia. *Oecologia*, *62*, 199–208.
- Angerbjörn, A., Tannerfeldt, M., & Erlinge, S. (1999). Predator-prey relationships: Arctic Foxes and lemmings. *Journal of Animal Ecology*, *68*(1), 34–49.
- Bahr, J. (1989). *The hunting ecology of Arctic Foxes (Alopex lagopus) near Cape Churchill, Manitoba* [Master's Thesis]. University of Manitoba.
- Baker, M. C. (1977). Shorebird food habits in the Eastern Canadian Arctic. *The Condor*, *79*(1), 56–62.
- Beardsell, A., Gravel, D., Clermont, J., Berteaux, D., Gauthier, G., & Bêty, J. (2022). A mechanistic model of functional response provides new insights into indirect interactions among arctic tundra prey. *Ecology*, *103*(8), 1–16.
- Bêty, J., Gauthier, G., Giroux, J.-F., & Korpimäki, E. (2001). Are goose nesting success and lemming cycles linked? Interplay between nest density and predators. *Oikos*, *93*(3), 388–400.
- Billerman, S. M., Keeney, B. K., Kirwan, G. M., Medrano, F., Sly, N. D., Smith, M. G., Editors. (2025). *Birds of the World*. Cornell Laboratory of Ornithology, Ithaca, NY, USA.
- Blomqvist, S., Holmgren, N., Åkesson, S., Hedenström, A., & Pettersson, J. (2002). Indirect effects of lemming cycles on sandpiper dynamics: 50 years of counts from southern Sweden. *Oecologia*, *133*(2), 146–158.

- Brommer, J. E., Pietiäinen, H., Ahola, K., Karell, P., Karstinen, T., & Kolunen, H. (2010). The return of the vole cycle in southern Finland refutes the generality of the loss of cycles through “climatic forcing”. *Global Change Biology*, *16*(2), 577–586.
- Brown, S., Bart, J., Lanctot, R. B., Johnson, J. A., Kendall, S., Payer, D., & Johnson, J. (2007). Shorebird abundance and distribution on the coastal plain of the Arctic National Wildlife Refuge. *The Condor*, *109*(1), 1–14.
- Brown, S., Lanctot, R., Sandercock, B., Gates, R., Liebezeit, J., & Smith, P. (2025). Arctic Shorebird Demographics Network (ASDN).
- Byrkjedal, I. (1980). Nest predation in relation to snow-cover – a possible factor influencing the start of breeding in shorebirds. *Ornis Scandinavica*, *11*(3), 249–252.
- CAFF. (2013). Arctic Biodiversity Assessment: Status and trends in Arctic biodiversity: Synthesis.
- CAFF. (2018). A global audit of the status and trends of Arctic and Northern Hemisphere goose population. Conservation of Arctic Flora and Fauna International Secretariat.
- Cantar, R. V., & Montgomerie, R. D. (1985). The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. *Behaviour*, *95*(3–4), 261–289.
- Careau, V., Giroux, J. F., & Berteaux, D. (2007). Cache and carry: hoarding behavior of Arctic Fox. *Behavioral Ecology and Sociobiology*, *62*, 87–96.
- CHASM. (2004). Shorebirds Expert Network Monitoring Plan. Monitoring Arctic-nesting Shorebirds: An International Vision for the Future. Conclusions from The Pan-Arctic Shorebird/Wader Monitoring and Research Workshop, Denmark, 3-6 December 2003.
- Clermont, J., Woodward-Gagné, S., & Berteaux, D. (2021). Digging into the behaviour of an active hunting predator: Arctic Fox prey caching events revealed by accelerometry. *Movement Ecology*, *9*(58), 1–12.
- Comiso, J. C. (2002). A rapidly declining perennial sea ice cover in the Arctic. *Geophysical Research Letters*, *29*(20), 1–4.
- Cunningham, J. A., Kesler, D. C., & Lanctot, R. B. (2016). Habitat and social factors influence nest-site selection in Arctic-breeding shorebirds. *Auk*, *133*(3), 364–377.
- Duchesne, D., Gauthier, G., & Berteaux, D. (2011). Habitat selection, reproduction and predation of wintering lemmings in the Arctic. *Oecologia*, *167*, 967–980.
- Dyrce, A., Witkowski, J., & Okulewicz, J. (1981). Nesting of ‘timid’ waders in the vicinity of ‘bold’ ones as an antipredator adaptation. *Ibis*, *123*(4), 542–545.

- Ehrich, D., Cerezo, M., Rodnikova, A. Y., Sokolova, N. A., Fuglei, E., Shtro, V. G., & Sokolov, A. A. (2017). Vole abundance and reindeer carcasses determine breeding activity of Arctic Foxes in low Arctic Yamal, Russia. *BMC Ecology*, *17*(32), 1–13.
- 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., ... Solovyeva, D. V. (2020). Documenting lemming population change in the Arctic: Can we detect trends? *Ambio*, *49*(3), 786–800.
- Elmhagen, B., Tannerfeldt, M., Verucci, P., & Angerbjörn, A. (2000). The Arctic Fox (*Alopex lagopus*): an opportunistic specialist. *Journal of Zoology*, *251*(2), 139–149.
- \*Evans, F. C. (1943). Voles, mice and lemmings: problems in population dynamics. *The Journal of Wildlife Management*, *7*(2), 238–240.
- Fauteux, D., Gauthier, G., & Berteaux, D. (2015). Seasonal demography of a cyclic lemming population in the Canadian Arctic. *Journal of Animal Ecology*, *84*(5), 1412–1422.
- Fauteux, D., Gauthier, G., & Berteaux, D. (2016). Top-down limitation of lemmings revealed by experimental reduction of predators. *Ecology*, *97*(11), 3231–3241.
- Fauteux, D., Gauthier, G., Berteaux, D., Palme, R., & Boonstra, R. (2018). High Arctic lemmings remain reproductively active under predator-induced elevated stress. *Oecologia*, *187*(3), 657–666.
- Flemming, S. A., Nol, E., Kennedy, L. V., Bédard, A., Giroux, M. A., & Smith, P. A. (2019). Spatio-temporal responses of predators to hyperabundant geese affect risk of predation for sympatric-nesting species. *PLoS ONE*, *14*(8), 1–16.
- Forbes, B. C., Fauria, M. M., & Zetterberg, P. (2010). Russian Arctic warming and “greening” are closely tracked by tundra shrub willows. *Global Change Biology*, *16*(5), 1542–1554.
- Frafjord, K., Becker, D., & Angerbjörn, A. (1989). Interactions between Arctic and Red Foxes in Scandinavia – predation and aggression. *Arctic*, *42*(4), 354–356.
- Fraser, J. D., Karpanty, S. M., Cohen, J. B., & Truitt, B. R. (2013). The red knot (*Calidris canutus rufa*) decline in the western hemisphere: Is there a lemming connection? *Canadian Journal of Zoology*, *91*(1), 13–16.
- Fraser, R. H., Lantz, T. C., Olthof, I., Kokelj, S. V., & Sims, R. A. (2014). Warming-induced shrub expansion and lichen decline in the Western Canadian Arctic. *Ecosystems*, *17*(7), 1151–1168.
- Fredga, K., Fedorov, V., Jarrell, G., & Jonsson, L. (1999). Genetic diversity in arctic lemmings. *Ambio*, *28*(3), 261–269.

- Fuglei, E., & Ims, R. A. (2008). Global warming and effects on the Arctic Fox. *Science Progress*, *91*(2), 175–191.
- Gallant, D., Lecomte, N., & Berteaux, D. (2020). Disentangling the relative influences of global drivers of change in biodiversity: A study of the twentieth-century Red Fox expansion into the Canadian Arctic. *Journal of Animal Ecology*, *89*(2), 565–576.
- Gallant, D., Reid, D. G., Slough, B. G., & Berteaux, D. (2014). Natal den selection by sympatric Arctic and Red foxes on Herschel Island, Yukon, Canada. *Polar Biology*, *37*, 333–345.
- Garrott, R. A., Eberhardt, L. E., & Hanson, W. C. (1983). Arctic Fox den identification and characteristics in northern Alaska. *Canadian Journal of Zoology*, *61*, 423–426.
- Gauthier, G., Ehrich, D., Belke-Brea, M., Domine, F., Alisauskas, R., Clark, K., Ecke, F., Eide, N. E., Framstad, E., Frandsen, J., Gilg, O., Henttonen, H., Hörnfeldt, B., Kataev, G. D., Menyushina, I. E., Oksanen, L., Oksanen, T., Olofsson, J., Samelius, G., ... Schmidt, N. M. (2024). Taking the beat of the Arctic: are lemming population cycles changing due to winter climate? *Proc. R. Soc. B*, *291*, 1–10.
- Gauthier, G., Giroux, J.-F., & Rochefort, L. (2006). The impact of goose grazing on arctic and temperate wetlands. *Acta Zoologica Sinica*, *52*, 108–111.
- Gilg, O., Hanski, I., & Sittler, B. (2003). Cyclic dynamics in a simple vertebrate predator-prey community. *Science*, *302*(5646), 866–868.
- Gilg, O., Kovacs, K. M., Aars, J., Fort, J., Gauthier, G., Grémillet, D., Ims, R. A., Meltofte, H., Moreau, J., Post, E., Schmidt, N. M., Yannic, G., & Bollache, L. (2012). Climate change and the ecology and evolution of Arctic vertebrates. *Annals of the New York Academy of Sciences*, *1249*(1), 166–190.
- Gilg, O., Sittler, B., & Hanski, I. (2009). Climate change and cyclic predator-prey population dynamics in the high Arctic. *Global Change Biology*, *15*(11), 2634–2652.
- Gilg, O., Sittler, B., Sabard, B., Hurstel, A., Sané, R., Delattre, P., & Hanski, I. (2006). Functional and numerical responses of four lemming predators in high arctic Greenland. *Oikos*, *113*(2), 193–216.
- Gilg, O., & Yoccoz, N. G. (2010). Explaining bird migration. *Science*, *327*, 276–277.
- Giroux, M. A., Berteaux, D., Lecomte, N., Gauthier, G., Szor, G., & Bêty, J. (2012). Benefiting from a migratory prey: spatio-temporal patterns in allochthonous subsidization of an arctic predator. *Journal of Animal Ecology*, *81*(3), 533–542.
- Giroux, M.-A., Trottier-Paquet, M., Bêty, J., Lamarre, V., & Lecomte, N. (2016). Is it safe to nest near conspicuous neighbours? Spatial patterns in predation risk associated with the density of American Golden-Plover nests. *PeerJ*, *4*, 1–13.

- Gochfeld, M. (1984). Antipredator behavior: Aggressive and distraction displays of shorebirds (J. Burger & B. L. Olla, Eds.). Plenum Press.
- Gries, T., Redlin, M., & Ugarte, J. E. (2019). Human-induced climate change: the impact of land-use change. *Theoretical and Applied Climatology*, *135*, 1031–1044.
- Hanski, I., Hansson, L., & Henttonen, H. (1991). Specialist predators, generalist predators, and the microtine rodent cycle. *Journal of Animal Ecology*, *60*(1), 353–367.
- Henningsson, S. S., & Alerstam, T. (2005). Patterns and determinants of shorebird species richness in the circumpolar Arctic. *Journal of Biogeography*, *32*(3), 383–396.
- Hersteinsson, P. (1992). Demography of the Arctic Fox (*Alopex lagopus*) population in Iceland. *Wildlife 2001: Populations*, 954–964.
- Holmes, R. T. (1966). Breeding Ecology and Annual Cycle Adaptations of the Red-Backed Sandpiper (*Calidris alpina*) in Northern Alaska. *The Condor*, *68*(1), 3–46.
- Holmes, R. T. (1971). Density, habitat, and the mating system of the Western Sandpiper (*Calidris mauri*). *Oecologia*, *7*(2), 191–208.
- Holmes, R. T., & Pitelka, F. A. (1968). Food overlap among coexisting sandpipers on Northern Alaskan Tundra. *Systematic Zoology*, *17*(3), 305–318.
- Ims, R. A., Henden, J. A., Thingnes, A. V., & Killengreen, S. T. (2013). Indirect food web interactions mediated by predator-rodent dynamics: relative roles of lemmings and voles. *Biology Letters*, *9*, 1–4.
- Ims, R. A., Yoccoz, N. G., & Killengreen, S. T. (2011). Determinants of lemming outbreaks. *Proceedings of the National Academy of Sciences of the United States of America*, *108*(5), 1970–1974.
- IPCC. (2021). Human Influence on the Climate System. In: *Climate Change 2021: The Physical Science Basis. Contribution of Working Group I to the Sixth Assessment Report of the Intergovernmental Panel on Climate Change*, 423–552.
- Ježková, M., Svobodová, J., & Kreisinger, J. (2014). Dynamics of rodent abundance and ground-nest predation risks in forest habitats of Central Europe: No evidence for the alternative prey hypothesis. *Folia Zoologica*, *63*(4), 269–280.
- Johnson, J. A., Lanctot, R. B., Andres, B. A., Bart, J. R., Brown, S. C., Kendall, S. J., & Payer, D. C. (2007). Distribution of breeding shorebirds on the Arctic Coastal Plain of Alaska. *Arctic*, *60*(3), 277–293.
- Johnson-Bice, S. M., Roth, J. D., & Markham, J. H. (2023). A cosmic view of “tundra gardens”: satellite imagery provides a landscape-scale perspective of Arctic Fox ecosystem engineering. *Ecosystems*, *26*, 1670–1684.

- Jónsson, J. E., & Gunnarsson, T. G. (2010). Predator chases by breeding waders: interspecific comparison of three species nesting in Iceland. *Wader Study Group Bulletin*, 117(3), 145–149.
- Kaikusalo, A., & Angerbjörn, A. (1995). The Arctic Fox population in Finnish Lapland during 30 years, 1964-93. *Annales Zoologici Fennici*, 32, 69–77.
- Kaplan, J. O., & New, M. (2006). Arctic climate change with a 2°C global warming: Timing, climate patterns and vegetation change. *Climatic Change*, 79, 213–241.
- 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(7218), 93–97.
- Kerbes, R. H., Meeres, K. M., & Alisauskas, R. T. (2014). Surveys of nesting lesser Snow Geese and Ross's Geese in Arctic Canada, 2002 – 2009. Arctic Goose Joint Venture Special Publication. U.S. Fish and Wildlife Service, Washington, D.C. and Canadian Wildlife Service, Ottawa, Ontario.
- Kokorev, Y. I., & Kuksov, V. A. (2002). Population dynamics of lemmings *Lemmus sibirica* and *Dicrostonyx torquatus*, and Arctic Fox *Alopex lagopus* on the Taimyr peninsula, Siberia, 1960-2001. *Ornis Svecica*, 12(3), 139–145.
- Koleček, J., Reif, J., Šálek, M., Hanzelka, J., Sottas, C., & Kubelka, V. (2021). Global population trends in shorebirds: migratory behaviour makes species at risk. *The Science of Nature*, 108(9), 1–8.
- Krebs, C. J. (2024). Lemming population fluctuations around the Arctic. *Proceedings of the Royal Society B*, 291, 1–4.
- Krebs, C. J., Boonstra, R., & Kenney, A. J. (1995). Population dynamics of the Collared Lemming and the Tundra Vole at Pearce Point, Northwest Territories, Canada. *Oecologia*, 103(4), 481–489.
- Kubelka, V. (2018). Significance of predation for breeding ecology and conservation in shorebirds [PhD thesis]. Charles University in Prague.
- Kubelka, V., Sandercock, B. K., Székely, T., & Freckleton, R. P. (2022). Animal migration to northern latitudes: environmental changes and increasing threats. *Trends in Ecology and Evolution*, 37(1), 30–41.
- Laidlaw, R. A., Gunnarsson, T. G., Méndez, V., Carneiro, C., Þórisson, B., Wentworth, A., Gill, J. A., & Alves, J. A. (2020). Vegetation structure influences predation rates of early nests in subarctic breeding waders. *Ibis*, 162(4), 1225–1236.

- Lamarre, J. F., Legagneux, P., Gauthier, G., Reed, E. T., & Bêty, J. (2017). Predator-mediated negative effects of overabundant Snow Geese on arctic-nesting shorebirds. *Ecosphere*, *8*(5), 1–13.
- Larsen, T., & Grundetjern, S. (1997). Optimal choice of neighbour: predator protection among tundra birds. *Journal of Avian Biology*, *28*(4), 303–308.
- Larsen, T., & Moldsvor, J. (1992). Antipredator behavior and breeding associations of Bar-tailed Godwits and Whimbrels. *The Auk*, *109*(3), 601–608.
- Larsen, T., Sordahl, T. A., & Byrkjedal, I. (1996). Factors related to aggressive nest protection behaviour: a comparative study of Holarctic waders. *Biological Journal of the Linnean Society*, *58*, 409–439.
- Larson, S. (1960). On the influence of the Arctic Fox *Alopex lagopus* on the distribution of Arctic birds. *Oikos*, *11*(2), 276–305.
- Le Vaillant, M., Erlandsson, R., Elmhagen, B., Hörnfeldt, B., Eide, N. E., & Angerbjörn, A. (2018). Spatial distribution in Norwegian Lemming *Lemmus lemmus* in relation to the phase of the cycle. *Polar Biology*, *41*(7), 1391–1403.
- Léandri-Breton, D. J., & Bêty, J. (2020). Vulnerability to predation may affect species distribution: plovers with broader arctic breeding range nest in safer habitat. *Scientific Reports*, *10*(5032), 1–8.
- Lecomte, N., Careau, V., Gauthier, G., & Giroux, J. F. (2008). Predator behaviour and predation risk in the heterogeneous Arctic environment. *Journal of Animal Ecology*, *77*(3), 439–447.
- Machín, P., Fernández-Elipe, J., Hungar, J., Angerbjörn, A., Klaassen, R. H. G., & Aguirre, J. I. (2019). The role of ecological and environmental conditions on the nesting success of waders in sub-Arctic Sweden. *Polar Biology*, *42*(8), 1571–1579.
- Machín, P., Fernández-Elipe, J., & Klaassen, R. H. G. (2018). The relative importance of food abundance and weather on the growth of a sub-arctic shorebird chick. *Behavioral Ecology and Sociobiology*, *72*(42), 1–12.
- Macpherson, A. H. (1969). The dynamics of Canadian Arctic Fox populations. *Canadian Wildlife Service Report Series, No. 8.*, 52pp.
- Maher, W. J. (1970). The Pomarine Jaeger as a Brown Lemming predator in Northern Alaska. *The Wilson Bulletin*, *82*(2), 130–157.
- McGuire, R. L., Lanctot, R. B., Saalfeld, S. T., Ruthrauff, D. R., & Liebezeit, J. R. (2020). Shorebird reproductive response to exceptionally early and late springs varies across sites in Arctic Alaska. *Frontiers in Ecology and Evolution*, *8*(577652), 1–19.

- McKinnon, L., Berteaux, D., & Bêty, J. (2014). Predator-mediated interactions between lemmings and shorebirds: A test of the alternative prey hypothesis. *Auk*, *131*(4), 619–628.
- McKinnon, L., Berteaux, D., Gauthier, G., & Bêty, J. (2013). Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra. *Oikos*, *122*(7), 1042–1048.
- McKinnon, L., & Bêty, J. (2009). Effect of camera monitoring on survival rates of High-Arctic shorebird nests. *Journal of Field Ornithology*, *80*(3), 280–288.
- Meltofte, H., Elander, M., & Hjort, C. (1981). Ornithological observations in Northeast Greenland between 74°30' and 76°00' lat., 1976. *Meddelelser Om Grønland, Bioscience*, *3*, 52 pp.
- Meltofte, H., Hansen, J., & Rigét, F. (2021). Trends in breeding performance in wader populations at Zackenberg, high Arctic Greenland, in relation to environmental drivers 1996–2018. *Polar Biology*, *44*(10), 1939–1954.
- Meltofte, H., Høye, T. T., & Schmidt, N. M. (2008). Effects of food availability, snow and predation on breeding performance of waders at Zackenberg. *Advances in Ecological Research*, *40*, 325–343.
- Meltofte, H., Piersma, T., Boyd, H., Mccaffery, B., Ganter, B., Golovnyuk, V. V., Graham, K., Gratto-Trevor, C. L., Morrison, R. I. G., Nol, E., Rösner, H.-U., Schamel, D., Schekkerman, H., Soloviev, M. Y., Tomkovich, P. S., Tracy, D. M., Tulp, I., & Wennerberg, L. (2007). Effects of climate variation on the breeding ecology of Arctic shorebirds. *Meddelelser om Grønland, Bioscience*, *59*, 48 pp.
- Meyer, N., Bollache, L., Dechaume-Moncharmont, F. X., Moreau, J., Afonso, E., Angerbjörn, A., Bêty, J., Ehrich, D., Gilg, V., Giroux, M. A., Hansen, J., Lanctot, R. B., Lang, J., Lecomte, N., McKinnon, L., Reneerkens, J., Saalfeld, S. T., Sabard, B., Schmidt, N. M., ... Gilg, O. (2020). Nest attentiveness drives nest predation in arctic sandpipers. *Oikos*, *129*(10), 1481–1492.
- Naves, L. C., Lanctot, R. B., & Taylor, A. (2008). How often do Arctic shorebirds lay replacement clutches? *Wader Stud. Group Bull.*, *115*, 2–9.
- Nguyen, L. P., Abraham, K. F., & Nol, E. (2006). Influence of Arctic Terns on survival of artificial and natural Semipalmated Plover nests. *Waterbirds: The International Journal of Waterbird Biology*, *29*(1), 100–104.
- Nol, E., Sullivan Blanken, M., & Flynn, L. (1997). Sources of variation in clutch size, egg size and clutch completion dates of Semipalmated Plovers in Churchill, Manitoba. *The Condor*, *99*(2), 389–396.
- Norton, D. W. (1972). Incubation schedules of four species of Calidridine sandpipers at Barrow, Alaska. *The Condor*, *74*, 164–176.

- Pearson, O. P. (1966). The prey of carnivores during one cycle of mouse abundance. *Journal of Animal Ecology*, 35(1), 217–233.
- Perkins, D. E., Smith, P. A., & Gilchrist, H. G. (2007). The breeding ecology of Ruddy Turnstones (*Arenaria interpres*) in the eastern Canadian Arctic. *Polar Record*, 43(225), 135–142.
- Piersma, T., Lindström, Å., Drent, R. H., Tulp, I., Jukema, J., Morrison, R. I. G., Reneerkens, J., Schekkerman, H., & Visser, G. H. (2003). High daily energy expenditure of incubating shorebirds on High Arctic tundra: a circumpolar study. *Functional Ecology*, 17(3), 356–362.
- Pitelka, F. A., Holmes, R. T., & MacLean Jr., S. F. (1974). Ecology and evolution of social organization in Arctic Sandpipers. *American Zoologist*, 14(1), 185–204.
- Pitelka, F. A., Quentin Tomich, P., & Treichel, G. W. (1955). Ecological relations of jaegers and owls as lemming predators near Barrow, Alaska. *Ecological Monographs*, 25(1), 85–117.
- Poirier, M., Fauteux, D., Gauthier, G., Domine, F., & Lamarre, J. F. (2021). Snow hardness impacts intranivean locomotion of arctic small mammals. *Ecosphere*, 12(11), 1–14.
- Pöysä, H., Jalava, K., & Paasivaara, A. (2016). Generalist predator, cyclic voles and cavity nests: testing the alternative prey hypothesis. *Oecologia*, 182(4), 1083–1093.
- Predavec, M., & Krebs, C. J. (2000). Microhabitat utilisation, home ranges, and movement patterns of the Collared Lemming (*Dicrostonyx groenlandicus*) in the central Canadian Arctic. *Canadian Journal of Zoology*, 78(11), 1885–1890.
- Prop, J., Aars, J., Bårdsen, B. J., Hanssen, S. A., Bech, C., Bourgeon, S., de Fouw, J., Gabrielsen, G. W., Lang, J., Noreen, E., Oudman, T., Sittler, B., Stempniewicz, L., Tombre, I., Wolters, E., & Moe, B. (2015). Climate change and the increasing impact of Polar Bears on bird populations. *Frontiers in Ecology and Evolution*, 3(33), 1–12.
- Putkonen, J., & Roe, G. (2003). Rain-on-snow events impact soil temperatures and affect ungulate survival. *Geophysical Research Letters*, 30(4), 1188.
- Reid, D. G., & Krebs, C. J. (1996). Limitations to collared lemming population growth in winter. *Canadian Journal of Zoology*, 74(7), 1284–1291.
- Reiter, M. E., & Andersen, D. E. (2011). Arctic foxes, lemmings, and Canada goose nest survival at Cape Churchill, Manitoba. *The Wilson Journal of Ornithology*, 123(2), 266–276.
- Reneerkens, J., Grond, K., Schekkerman, H., Tulp, I., & Piersma, T. (2011). Do uniparental sanderlings *Calidris alba* increase egg heat input to compensate for low nest attentiveness? *PLoS ONE*, 6(2), e16834.
- Robinson, B. G., Franke, A., & Derocher, A. E. (2014). The influence of weather and lemmings on spatiotemporal variation in the abundance of multiple avian guilds in the Arctic. *PLoS ONE*, 9(7), 1–9.

- Rodgers, A. R., & Lewis, M. C. (1986). Diet selection in Arctic lemmings (*Lemmus sibericus* and *Dicrostonyx groenlandicus*): food preferences. *Canadian Journal of Zoology*, 64(12), 2717–2727.
- Roselaar, C. S. (1979). Fluctuaties in aantallen Krombekstrandlopers *Calidris ferruginea*. *Watervogels*, 4, 202–211.
- Rozenfeld, S. B., Volkov, S. V., Rogova, N. V., Kirtaev, G. V., & Soloviev, M. Y. (2021). The impact of changes in breeding conditions in the Arctic on the expansion of the russian population of the Barnacle Goose (*Branta leucopsis*). *Biology Bulletin*, 48(9), 1528–1540.
- Saalfeld, S. T., Hill, B. L., Hunter, C. M., Frost, C. J., & Lanctot, R. B. (2021). Warming Arctic summers unlikely to increase productivity of shorebirds through renesting. *Scientific Reports*, 11(15277), 1–13.
- Saalfeld, S. T., & Lanctot, R. B. (2014). Conservative and opportunistic settlement strategies in Arctic-breeding shorebirds. *Auk*, 132(1), 212–234.
- Samelius, G., Alisauskas, R. T., Hobson, K. A., & Larivière, S. (2007). Prolonging the arctic pulse: long-term exploitation of cached eggs by Arctic Foxes when lemmings are scarce. *Journal of Animal Ecology*, 76(5), 873–880.
- Sandercock, B. K., Lank, D. B., & Cooke, F. (1999). Seasonal declines in the fecundity of arctic-breeding sandpipers: different tactics in two species with an invariant clutch size. *Journal of Avian Biology*, 30(4), 460–468.
- Schekkerman, H., Tulp, I., Calf, K. M., & de Leeuw, J. J. (2004). Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2002. Wageningen, Alterra, Alterra-rapport 922.
- Schmidt, N. M., Ims, R. A., Høye, T. T., Gilg, O., Hansen, L. H., Hansen, J., Lund, M., Fuglei, E., Forchhammer, M. C., & Sittler, B. (2012). Response of an arctic predator guild to collapsing lemming cycles. *Proc. R. Soc. B*, 279, 4417–4422.
- Sherfy, M. H., & Kirkpatrick, R. L. (2003). Invertebrate response to Snow Goose herbivory on moist-soil vegetation. *Wetlands*, 23(2), 236–249.
- Smith, P. A. (2003). Factors affecting nest site selection and reproductive success of tundra nesting shorebirds [Master's thesis]. The University of British Columbia.
- Smith, P. A., Gilchrist, H. G., Forbes, M. R., Martin, J. L., & Allard, K. (2010a). Inter-annual variation in the breeding chronology of arctic shorebirds: Effects of weather, snow melt and predators. *Journal of Avian Biology*, 41(3), 292–304.
- Smith, P. A., Grant Gilchrist, H., & Smith, J. N. M. (2007). Effects of nest habitat, food, and parental behavior on shorebird nest success. *The Condor*, 109(1), 15–31.

- Smith, P. A., McKinnon, L., Meltofte, H., Lanctot, R. B., Fox, A. D., Leafloor, J. O., Soloviev, M., Franke, A., Falk, K., Golovatin, M., Sokolov, V., Sokolov, A., & Smith, A. C. (2020). Status and trends of tundra birds across the circumpolar Arctic. *Ambio*, *49*, 732–748.
- Smith, P. A., & Wilson, S. (2010b). Intraseasonal patterns in shorebird nest survival are related to nest age and defence behaviour. *Oecologia*, *163*(3), 613–624.
- Smith, P. Allen. (2009). Variation in shorebird nest survival: proximate pressures and ultimate constraints [PhD thesis]. Carleton University.
- Soloviev, M., & Tomkovich, P. (2025). The International Breeding Conditions Survey on Arctic Birds.
- Stickney, A. (1991). Seasonal patterns of prey availability and the foraging behavior of Arctic Foxes (*Alopex lagopus*) in a waterfowl nesting area. *Canadian Journal of Zoology*, *69*, 2853–2859.
- Stickney, A. A., Obritschkewitsch, T., & Burgess, R. M. (2014). Shifts in fox den occupancy in the greater Prudhoe Bay area, Alaska. *Arctic*, *67*(2), 196–202.
- Studds, C. E., Kendall, B. E., Murray, N. J., Wilson, H. B., Rogers, D. I., Clemens, R. S., Gosbell, K., Hassell, C. J., Jessop, R., Melville, D. S., Milton, D. A., Minton, C. D. T., Possingham, H. P., Riegen, A. C., Straw, P., Woehler, E. J., & Fuller, R. A. (2017). Rapid population decline in migratory shorebirds relying on Yellow Sea tidal mudflats as stopover sites. *Nature Communications*, *8*, 1–7.
- Summers, R. W., & Underhill, L. G. (1987). Factors related to breeding production of Brent Geese *Branta b. bernicla* and waders (Charadrii) on the Taimyr Peninsula. *Bird Study*, *34*(2), 161–171.
- Summers, R. W., Underhill, L. G., & Syroechkovski Jr., E. E. (1998). The breeding productivity of Dark-bellied Brent Geese and Curlew Sandpipers in relation to changes in the numbers of Arctic Foxes and lemmings on the Taimyr Peninsula, Siberia. *Ecography*, *21*(6), 573–580.
- Swift, R. J., Rodewald, A. D., & Senner, N. R. (2017). Breeding habitat of a declining shorebird in a changing environment. *Polar Biology*, *40*(9), 1777–1786.
- Tannerfeldt, M., & Angerbjörn, A. (1996). Life history strategies in a fluctuating environment: establishment and reproductive success in the Arctic Fox. *Ecography*, *19*(3), 209–220.
- Tannerfeldt, M., & Angerbjörn, A. (1998). Fluctuating resources and the evolution of litter size in the Arctic Fox. *Oikos*, *83*(3), 545–559.
- Therrien, J.-F., Gauthier, G., Pinaud, D., & Bêty, J. (2014). Irruptive movements and breeding dispersal of Snowy Owls: a specialized predator exploiting a pulsed resource. *Journal of Avian Biology*, *45*(6), 536–544.
- Troy, D. M. (1996). Population dynamics of breeding shorebirds in Arctic Alaska. *International Wader Studies*, *8*, 15–27.

- Tulp, I., & Schekkerman, H. (2001). Studies on breeding shorebirds at Medusa Bay, Taimyr, in summer 2001. Wageningen, Alterra, Green World Research. 110 pp.
- Tulp, I., Schekkerman, H., & de Leeuw, J. (2012). Eggs in the Freezer: Energetic Consequences of Nest Site and Nest Design in Arctic Breeding Shorebirds. *PLoS ONE*, 7(6), 1–9.
- Underhill, L. G. (1987). Changes in the age structure of Curlew Sandpiper populations at Langebaan Lagoon, South Africa, in relation to lemming cycles in Siberia. *Transactions of the Royal Society of South Africa*, 46(3), 209–214.
- Underhill, L. G., Prÿs-Jones, R. P., Syroechkovski Jr., E. E., Groen, N. M., Karpov, V., Lappo, H. G., van Roomen, M. W. J., Rybkin, A., Schekkerman, H., Spiekman, H., & Summers, R. W. (1993). Breeding of waders (Charadrii) and Brent Geese *Branta bernicla bernicla* at Pronchishcheva Lake, northeastern Taimyr, Russia, in a peak and a decreasing lemming year. *Ibis*, 135(3), 277–292.
- Vitousek, P. M. (1994). Beyond Global Warming: Ecology and Global Change. *Ecology*, 75(7), 1861–1876.
- Wauchope, H. S., Shaw, J. D., Varpe, Ø., Lappo, E. G., Boertmann, D., Lanctot, R. B., & Fuller, R. A. (2017). Rapid climate-driven loss of breeding habitat for Arctic migratory birds. *Global Change Biology*, 23(3), 1085–1094.
- Weiser, E. L., Brown, S. C., Lanctot, R. B., Gates, H. R., Abraham, K. F., Bentzen, R. L., Bêty, J., Boldenow, M. L., Brook, R. W., Donnelly, T. F., English, W. B., Flemming, S. A., Franks, S. E., Gilchrist, H. G., Giroux, M. A., Johnson, A., Kendall, S., Kennedy, L. V., Koloski, L., ... Sandercock, B. K. (2018). Effects of environmental conditions on reproductive effort and nest success of Arctic-breeding shorebirds. *Ibis*, 160(3), 608–623.
- Yu, H., Wang, X., Cao, L., Zhang, L., Jia, Q., Lee, H., Xu, Z., Liu, G., Xu, W., Hu, B., & Fox, A. D. (2017). Are declining populations of wild geese in China ‘prisoners’ of their natural habitats? *Current Biology*, 27(10), 376–377.
- Zhao, S. T., Johnson-Bice, S. M., & Roth, J. D. (2022). Foxes engineer hotspots of wildlife activity on the nutrient-limited Arctic tundra. *Global Ecology and Conservation*, 40, 1–9.
- Zhemchuzhnikov, M. K., Lameris, T. K., Soloviev, M. Y., Golovnyuk, V. V., ten Horn, J., Kutcherov, D. A., Popovkina, A. B., Sukhova, M. A., Zhemchuzhnikova, E. A., & van Gils, J. A. (2024). Food web interactions of two breeding Arctic shorebird species, little stint *Calidris minuta* and red knot *Calidris canutus*, are shaped by their elevational distribution. *Polar Biology*, 47(3), 247–261.

\* secondary citation