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Do the predators of Yamal have a learning effect of artificial nests?

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Foreword

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1 Abstract

Many artificial nest studies that goes over several years place the nests in the same location each placement. Over the years there is a chance that the predators learn where the nests are placed and that can give skewed results. The goal of my study is to see if the predators learn where the nests are located. This was done over three study sites on the Yamal peninsula. In two of the study sites the nests where placed over 4 years with an early and late incubation timing. The last study site had 2 years and only one placement each year. Each time the nests where placed half of the nests where covered nests while the rest was uncovered. The results were tested using glmer in R. The results show an increase in predation over the years. The results also show a difference between the early and late incubation timing, but this difference decrease over the years. The increase over the years suggests that the predators do learn where the nests are placed each year since more nests are predated each year. The difference between the early and late predation of nests might be caused by the shift in search image for the predators, but the decrease in this difference suggests that the learning effect over the years negate this shift. Overall there is an indication that there is a learning effect for the predators and should be taken in to consideration when using multiannual artificial nests.

2 Introduction

One of the most important interactions in food webs is predation. Predation is the killing and consumption of another living being. This is one of the only ways for organisms to gain energy and survive. This starts from the consumption of plants, that are the ones giving an influx of energy to an ecosystem, to the top predator, that does not get predated. This means that predation is a deciding factor when it comes to the size of populations and the general structure of ecosystems (Campbell *et al.*, 2017). Predators fundamentally affect ecosystem structure by exerting top down control on the populations of their prey (Hairston, Smith and Slobodkin, 1960). Moreover, aspects of predator behaviour such as optimal foraging and their functional response to the abundance of different prey are central topics in ecology (Begon *et al.*, 2006). In addition to being a key direct interaction in food webs, predation can also mediate indirect interactions among species such as apparent competition. Apparent competition is when two different species that utilize different resources influence each other's growth rate through a shared predator. This means that if one of the prey species increase its population, the shared predator might also increase in abundance, and this might give an higher mortality rate for the second prey species (Muller *et al.*, 1997; Bêty *et al.*, 2002). Since both prey species can suffer from an increase in the population from the other prey species, as found in normal competition, Holt (1977) called this interaction apparent competition. This explanation is based on if the predator does not have a preferred prey. If the predator has a preferred prey and the population is large, the predation rate on the alternative prey will be low, allowing population growth. If, on the contrary, the population of the preferred prey decreases, predators will switch to an alternative prey (Moss and Watson, 2001; Šálek *et al.*, 2004).

Terrestrial arctic food webs are characterized by strong trophic interactions and relative few key species (Gilg *et al.*, 2003). Because of their simplicity, tundra food webs have been the object of numerous studies of both direct and indirect trophic interactions (e.g., 2-3 exemplar). An essential key group in tundra ecosystems are the small rodents, lemmings (genus *Lemmus* and *Dicrostonyx*) and voles (genus *Microtus* and *Myodes*), which exhibit characteristic, high amplitude, multiannual density fluctuations (Ims and Fuglei, 2005). The different species of lemmings are the only small rodents that live in the high Arctic, whereas low arctic communities are usually composed of both lemmings and voles (Ehrich *et al.*

2020). The small rodent cycles exhibit a period of three–five years; there is often a couple of years with relative low population numbers and then one year where the number of lemmings is extremely high, followed by a crash year (Ims and Fuglei 2005). Two of the predators most affected by the cycles is the snowy owl and the stoat, which both are very specialised on the rodents. Then there are several predators that are more loosely correlated to the cycles such as long-tailed skua (*Stercorarius longicaudus*) and arctic fox (*Vulpes lagopus*) (Schmidt *et al.*, 2012). This correlation between the predators and the rodents density fluctuations result in apparent competition with other groups of prey such as ground nesting birds.

The alternative prey hypothesis states that a generalist predator may switch from its primary prey to an alternative prey when the population of its primary prey is low (Lack, 1955; Angelstam, Lindström and Widén, 1984; Hörnfeldt, Löfgren and Carlsson, 1986; Moss and Watson, 2001; Šálek *et al.*, 2004). This means the generalist predator and its main prey, the small rodents, may be a major driver for the populations of alternative prey (Breisjøberget *et al.*, 2018). In the Arctic, this has for instance been shown by McKinnon, Berteaux, & Bêty, (2014). They tested whether predation pressure on shorebird nests would increase as the abundance of lemmings decreased. Using both real and artificial nests over a period of five years, they found that the predation risk was negatively correlated to high lemming numbers (McKinnon *et al.*, 2014). A similar relationship was demonstrated by Marcstrom, Kenward, & Engren, (1988) who had a 9 years experimental study in the Northern Baltic where the link between vole and tetraonid numbers was confirmed to be mediated by red foxes (*Vulpes vulpes*) and pine marten (*Martes martes*).

In recent years, bird populations have been declining on a global scale and especially the alpine and the Arctic tundra is affected (Melfoite *et al.*, 2013; Elsen and Tingley, 2015; Stephens *et al.*, 2016; Ims *et al.*, 2019). This is also where the climate is changing particularly rapidly (Bekryaev, Polyakov and Alexeev, 2010; Callaghan *et al.*, 2011). This decline has been related to increased nest predation. Thus Ims *et al.*, (2019) discussed and tested the effect of climate change on predation. The results showed that the predation risk increased with the increase in primary productivity. The predation risk was highest in the crash year of the lemming cycles, which is as expected based on the alternative prey hypothesis. As the climate changes and the primary productivity increases, the paper concludes that the predation will

also increase (Ims et al., 2019) and likely leading to a decrease in the populations of these vulnerable birds.

A method that is used to measure the predation pressure in the paper by Ims et al., (2019) and other papers, is artificial nests (Bêty *et al.*, 2001; McKinnon *et al.*, 2010; McKinnon, Berteaux and Bêty, 2014). Artificial nests are nests created by researchers that are made to look like the nests of the birds that are the subject of the study. The advantage of using artificial nests is that it is easier to control factors such as the type of habitat where they are located and date of deployment, which is not possible for real nests, and thus study specific contrasts in predation pressure. Artificial nest studies are often conducted over several years in the same place, in particular in studies relating predation rate to indirect effects of multiannual fluctuations in small rodent abundance (McKinnon and Bêty, 2009; Ims *et al.*, 2013, 2019; McKinnon *et al.*, 2013). Such a study design might lead to biased results because predators might learn where and when the artificial nests are deployed if the nests are placed at the same location each year.

The importance of predator learning when measuring predation pressure has been exemplified in a study by Pelech et al. (2010). They found that predation by red squirrels (*Tamiasciurus hudsonicus*) on artificial nests was not incidental, but likely due to that the squirrels learn to prey on nests and that the success ratio increased as they gained experience.

This assumption can also be made about the predation from avian predators such as corvids and skuas. For mammalian predators such as the arctic fox and stoat it is safe to assume that they might exhibit the same learning pattern as the red squirrel.

Another example of predator learning is discussed in the paper by Pöysä, Jalava, & Paasivaara (2016). Here they do not find the expected higher predation rate that is usually correlated with the drop in the lemming population, as predicted by the alternative prey hypothesis. They actually found the opposite of the prediction. They concluded that individual learning in the pine martin population, coupled with an efficient search image, overrode the positive indirect effects of high vole population in their system.

To what extent arctic predators learn to use artificial nests has not previously been addressed in the literature. However, several typical arctic nest predators such as corvids, skuas and

arctic foxes are known as species that remember locations and learn to use different cues (Rausch, 1995; Heinrich and Pepper, 1998; Niehaus, Ruthrauff and McCaffery, 2004).

The main aim of this study is to investigate whether there is evidence that arctic nest predators learn to use artificial nests, when artificial nest experiments are repeated at the same locations. Artificial nests were deployed according to a standardized protocol at three study sites. The study sites were located in the high Arctic, middle Arctic and low Arctic, in areas with different patterns of small rodent fluctuations. The experiment was repeated over several years and carried out twice during the breeding with an early and late replicate. I predicted that predation rate on artificial nests will be negatively related to small rodent abundance. Assuming that the predators learn where the artificial nests are, I predicted that predation rate will be higher during the second artificial nest deployment in each season and that predation rate would increase over the years.

3 Method

3.1 Study sites

All the sites lay in North-western Russia. Two of the study sites are on the Yamal Peninsula and one on Belyi Island (Figure 1). When Yamal Peninsula is mentioned from here on that includes Belyi Island. The study site on Belyi Island (73.31°N, 70.10°E) is in the high Arctic, the Sabetta study site (71.19 °N, 71.45 °E) is at the border between high Arctic and low Arctic and Erkuta (68.27 °N, 69.18 °E) study site is in the low Arctic.

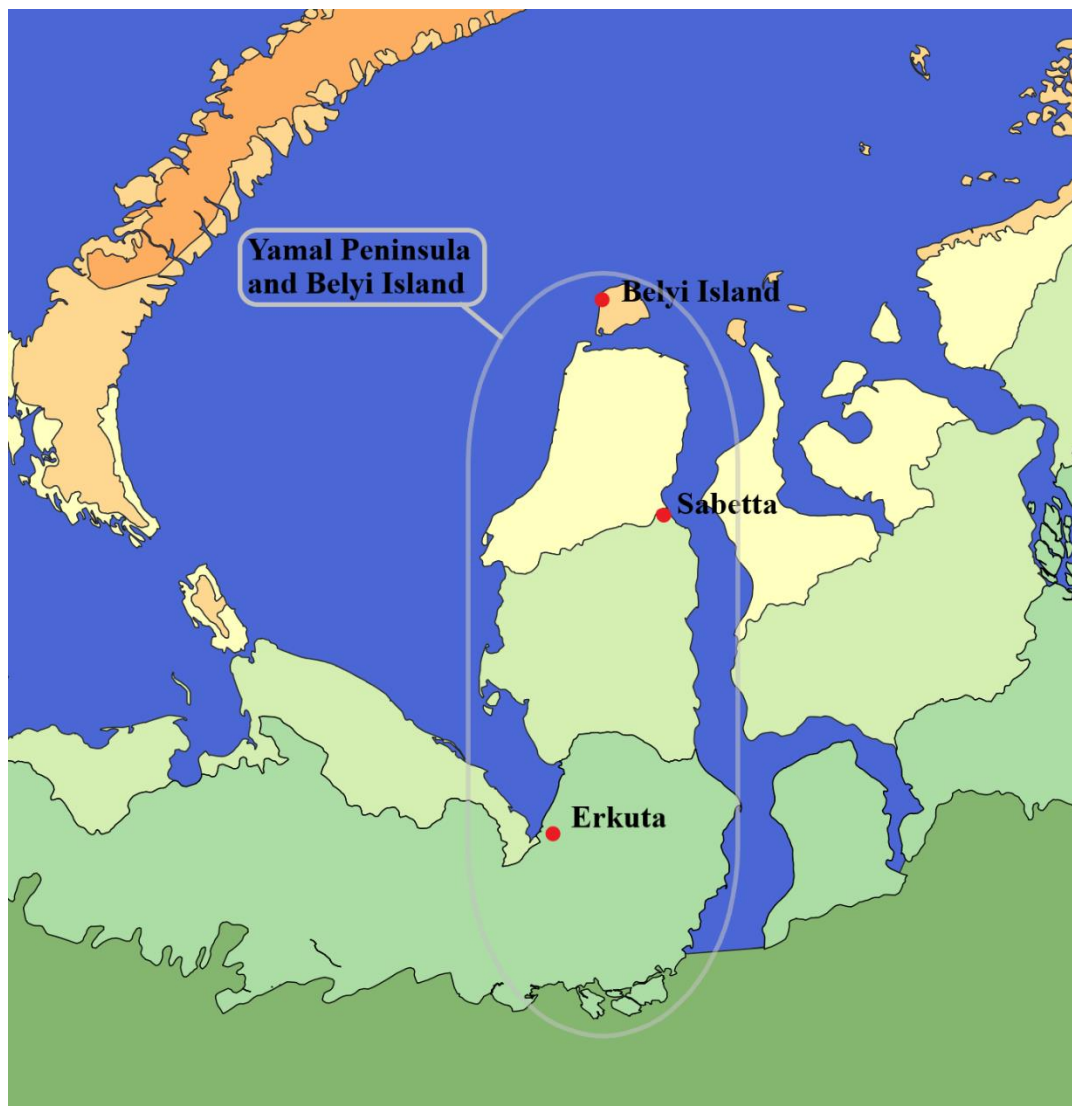


Figure 1 A map of the Arctic bioclimatic subzones (Walker et al. 2005) for Yamal Peninsula and surrounding areas with the three study sites.

Accordingly, landscapes and main vegetation types are different for each site. For the Erkuta site the landscape has several types of vegetation. The landscape is relatively flat with some hills (ca.30m) and river cliffs (up to 40m high). There are also several lakes and rivers, connecting them to the main river Erkuta(Sokolov *et al.*, 2012; Sokolova *et al.*, 2014) with. The soil itself is mostly consistent of clay or a more sandy ground. The region has permafrost although the top layer of the permafrost melts during the summer. There are the wet and marshy habitats where it ranges from just a general wet ground to shallow pools of water that are about 30 cm deep. Here the vegetation consists of both mosses and different species of grass and in some cases small willow (*Salix* spp.) bushes covering it or growing close by to the body of water.

In Sabetta, the landscape consists of a humid and fertile river valley characterized by wetlands, and adjacent low hills with tundra dominated by prostrate shrubs, mosses and lichen. In protected places and close to small streams, low thickets of erect willows are growing (usually < 50 cm height). The shrub often do not exceed 2 meters in high in this region and as the latitude increases the hight of the shrub decreases thereby are the shrub lower in Sabetta.

On the high arctic and very flat Belyi Island there are extensive wetlands dominated by mosses and graminoids. Drier parts of the landscape are characterized by tundra communities with prostrate shrubs and forbs.

3.1.1.1 Small Rodents

There are several vole species on the Yamal Peninsula. The most numerous are Middendorff's vole (*Microtus middendorffii*) and narrow-headed vole (*M. gregalis*). There are also collared lemmings (*Dicrostonyx torquatus*) and Siberian lemming (*Lemmus sibiricus*) present on the peninsula at lower abundance (Sokolova *et al.*, 2014). On Belyi Island the only lemming is the Siberian lemming.

In each study area, annual small rodent abundance was assessed by snap trapping. Snap traps were arranged in small quadrats of 15 x 15 m with three traps in each corner (Sokolova *et al.* 2014). Traps were baited with rolled oats and raisins and deployed for two days (24 trap

nights per quadrat). The small rodent trapping on Belyi Island was done in wet marshes in 2016, and in 2017 the same habitat was utilized plus a drier prostrate shrub and graminoid tundra was used. The first two years (2015 and 2016) on Belyi Island the trapping was done in 2 units with 1 habitat in each unit and 6 quadrats in the habitat, totalling 12 quadrates for Belyi Island ($2 \times 1 \times 6 = 12$ quadrates). The third year there was still 2 units but extended to 2 habitats per unit and 4 quadrates in each habitat, totalling 16 quadrates for Belyi Island ($2 \times 2 \times 4 = 16$ quadrates).

In 2014, 2015 and 2017 the rodent trapping in Sabetta were done with 2 units with 3 habitats in each unit and 4 quadrates in each habitat, totalling 24 quadrates ($2 \times 3 \times 4 = 24$ quadrates). While in 2016, 2018 and 2019 the rodent trapping was done with 3 units with 3 habitats in each unit and 4 quadrates in each habitat, totalling 36 quadrates ($3 \times 3 \times 4 = 36$ quadrates). The three habitats were wet tundra, mesic dwarf shrub tundra on slopes and at the edge of willow thickets.

In Erkuta the trapping of rodents was done twice each year, the first in late June and the second in early August. It was done over 3 units with 3 habitats in each: low erect willows interspersed with meadow plants, wet marshy tundra and drier dwarf shrub tundra on slopes. In each habitat there was 6 quadrats, with a total of 54 quadrants in Erkuta (Sokolova *et al.*, 2014; Ehrich *et al.*, 2017).

3.1.1.2 Predators

The Common Raven (*Corvus corax*) can be found almost across the entire Northern Hemisphere. This includes the Yamal Peninsula where it is mainly a scavenger but is also one of the common predators on bird nests. The raven is a species which is known for its high intelligence, its ability to learn and solve puzzles (Heinrich and Bugnyar, 2005). It normally lives up to 50 years old (Boarman and Heinrich, 2020). Young ravens are roaming birds and aggregate at carcasses. The adults on the other hand are territorial and has established territories (Marzluf and Heinrich, 1991).

Hooded crows (*Corvus cornix*) are a comparatively new predator in the Arctic. It has been observed at the Erkuta site. Here nests have also been found, the first was found in 2014 (Sokolov *et al.*, 2016). The crow is also a highly intelligent scavenger and a generalist predator. There are studies which show that a crow which is in the same genus as ravens

can remember a specific person that was cruel to them for at least 2.7 years and even communicate this to other individuals so they as well remembered the face (Marzluff *et al.*, 2010). The hooded crow is not present in Sabetta and on Belyi Island as of yet.

The Arctic fox is one of the iconic predators of the arctic and is found across the entire Northern Arctic Hemisphere (Prestrud, 1991; Fuglestad *et al.*, 2006; Lai, Bêty and Berteaux, 2017). It is both a predator and a scavenger. Its main prey is considered to be lemming and voles, but it also feeds a lot on waterfowl and seabirds. For the latter two, it is mostly the nests that is preyed upon (Lai, Bêty and Berteaux, 2017). During the mating season they breed in monogamous pairs and raise their pups in underground dens. This entails that some of them are territorial during the mating season while others that has chosen to not mate are not.

Skuas can also be important nest predators. Pomarine skua (*Stercorarius pomarinus*) is very abundant on Belyi Island. Long-tailed skua and Arctic skua (*Stercorarius parasiticus*) are in the two other sites. The plots in Sabetta and Erkuta has skua nests close to the artificial nests, and the skuas have the same territories each year.

Then there are the Glaucous Gull (*Larus hyperboreus*) that is found on Belyi Island. The expected lifespan is 19 years, and it is a generalist predator and scavenger (Cornell University, 2019). They do feed on nests if the opportunity presents itself. In Sabetta and Erkuta there is the herring gull (*Larus heuglini*). Close to the Erkuta plot for artificial nests there was a gull colony.

3.2 The artificial nests

The entire study is a part of a coordinated international project, the Interactions Working Group (Gilg, Giroux and Meyer, 2018), that uses a standardised protocol with small variations. In accordance with this protocol, an artificial nest experiment was conducted twice per summer, once early during incubation and once late during incubation of local wader species. The nests placed each incubation timing was also divided in to covered and uncovered nests. The covered nests had a piece of the surrounding covering the nest while the uncovered nests had nothing covering them. The artificial nests were meant to look like the

nests of smaller waders of the genus *Calidris*. Common species were Temminck's stint (*Calidris temmickii*), Dunlin (*C. alpina*) and little stint (*C. minuta*). All three species were rather common in Sabetta, whereas Temminck's stint was the most abundant species in Erkuta and little stint the most abundant species on Belyi Island. In Belyi Island the experiment was replicated over 2 years in 2016-2017 and only one period, while in both Sabetta and Erkuta it was conducted every year from 2016 to 2019, 4 years.

From 2016 to 2018, the artificial nests in Erkuta were placed in the same area. In 2019, the experiment had to be moved because as Nenets put their camp directly on the study site (Figure 2). So, the plots in Erkuta has two different descriptions. The study site up to 2019 can be described as relatively flat area with humid tundra consisting of a thick moss layer, with graminoids and dwarf shrubs. The site in 2019 consisted of three different vegetation types. The first can be described as a dry ridge with little vegetation and patches of open ground. The second can be described as semidry with some tall grass and moss. The last can be described as wet, with a lot more grass and often a body of water nearby.

In Sabetta the artificial nests were deployed from 2016 to 2019 in an area comprising the same three landscapes elements in which small rodent trapping was carried out: wet tundra with a thick moss layer and graminoids, drier dwarf shrub tundra on slopes, and areas with erect willows up to ca 30 cm height (Figure 3).

On Belyi Island, the artificial nests were placed in the same area as the small rodent trapping, in humid tundra habitat consisting of a thick moss layer and graminoid vegetation. This habitat was used for breeding by Little Stints and Dunlin. Nests were deployed in 2016 and 2017 (due to logistic difficulties, field work could not be carried out at this site in later years) and placed in the same area in both years (Figure 4).

There was approximately 1-2 weeks between the early incubation and late incubation experiments, the exact dates changed depending on the year and the breeding pattern of the birds (Table 1).

Table 1 The placement dates of artificial nests for each study site and year. Nests were only placed once each year on Belyi Island, and twice for Sabetta and Erkuta (divided in early and late placement)

Site	Year	Dates	
		Early	Late
Belyi Island	2016	5 th of July	
	2017	8 th of July	
Sabetta	2016	21 st of June	3 rd of July
	2017	21 st of June	3 rd of July
	2018	22 nd of June	2 nd of July
	2019	26 th of June	6 th of July
Erkuta	2016	11 th of June	24 th of June
	2017	24 th of June	18 th of July
	2018	22 nd of June	15 th of July
	2019	25 th of June	6 th of July

The nests were placed 150 m apart, that means in a density 5-10 nest/km² to insure independence. We also avoided placing a nest if a predator was close by and observing. Half of the nests was covered by a small amount of moss or the vegetation type that was close to the nest. The reason behind this was to try and separate the visual avian predators and the sensitive predators such as the arctic fox. This was replicated over all sites (Sabetta, Erkuta and Belyi Island).

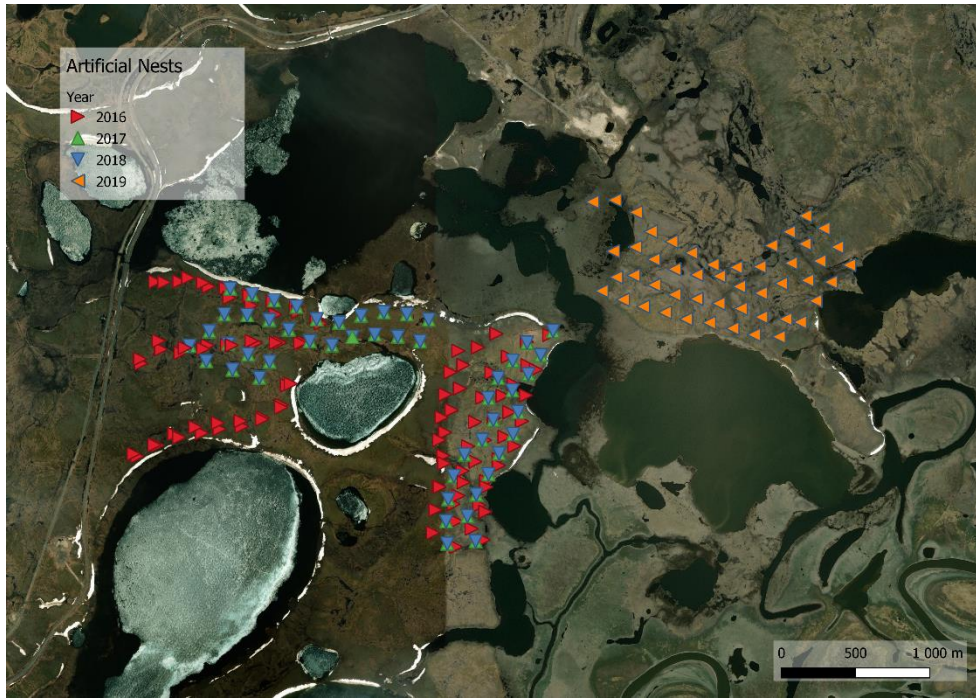


Figure 2. Locations of the artificial nests in Erkuta in the different years (satellite image obtained from QGIS).

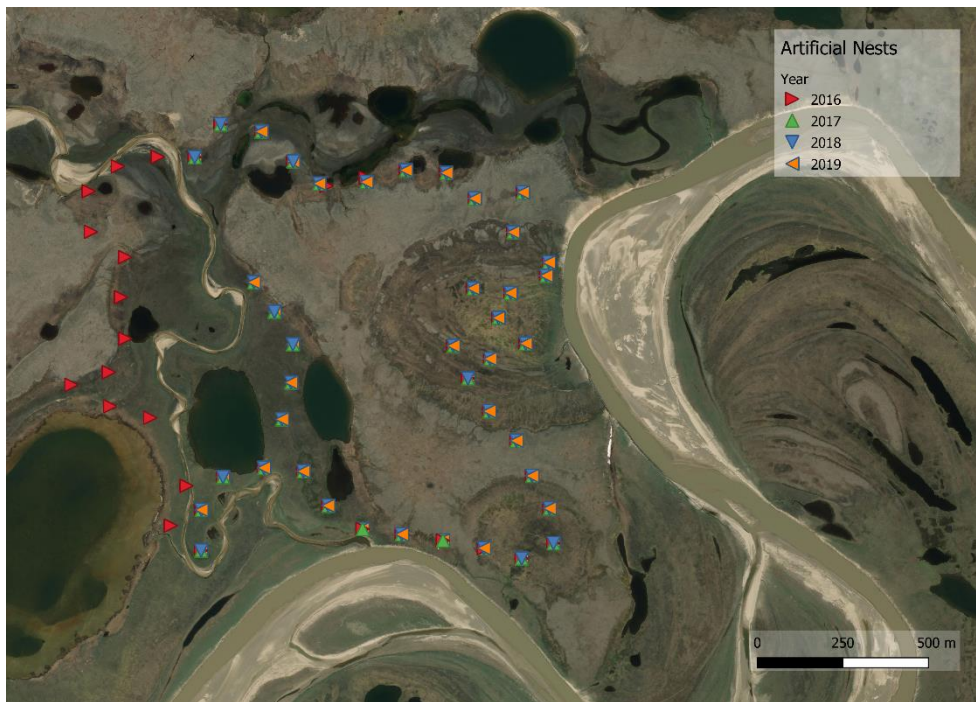


Figure 3. Locations of the artificial nests in Sabetta in the different years (satellite image obtained from QGIS).

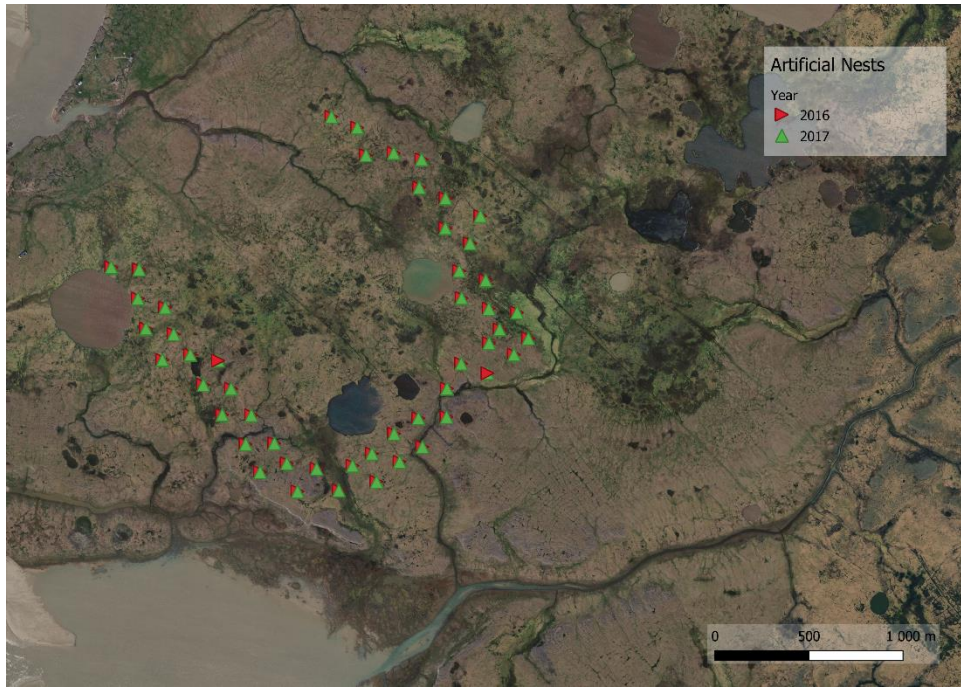


Figure 4. Locations of the artificial nests in Sabetta in the different years (satellite image obtained from QGIS).

Each artificial nest consisted of 4 European quail (*Coturnix coturnix*) eggs which were placed in a small depression in the tundra made from the heel of a rubber boot. The eggs were placed using rubber gloves and nothing, but the eggs and rubber boots touched the ground to avoid leaving scent marks which could attract predators. Two markers were placed by each nest. The first marker was placed two meters from the nest in the direction I came from. The second marker was placed 5 meters from the first marker so there is a straight line between the second marker through the first marker to the nest. For the covered nests the 2-meter stick was broken in half and one half was placed right behind the nest. This was not done for the uncovered nests. The marking sticks were barbecue wooden skewers. If a nest was predated the sticks were not used twice since they can be contaminated by smell and therefore found again by the predator. A GPS point was taken for each nest and each nest was checked after 48 hours and 96 hours. The state of the nest was recorded as predated, partially predated or intact at each check. After predation, the nest was inspected and possible traces left by a predator, such as eggshells or feces, were recorded.

There were also placed 3 artificial nests across the river from the camp 150 meters apart on the 6th of July. Close to each nest a wildlife camera was placed. The camera settings were set to

take a 10 second video every hour and to film each time the camera detected movement. The sensitivity was set to high in the hope that if a stoat predated the nest it would be captured on video. The cameras were out for 11 days before they were taken down.

3.3 Statistical analyses

All of the data was standardised in Excel, and all of the analyses was done in RStudio version 3.5.1 (Team, 2018). To summarize the data, I used only the last check, after 96 hours, to determine if the nest was predated or not. A nest was counted as predated if one or more eggs were missing after 96 hours. Overview graphs of the predation for each site were created in R, dividing the nests in to four categories for each year (categories: early uncovered, early covered, late uncovered, and late covered).

The small rodent data were summarized as mean number of individuals caught per 24 trap-nights each year. For Erkuta, the data were thus averaged between the June and August trapping session. All species were pooled. For Sabetta and Erkuta I also plotted as an overview graph.

All maps was created using QGIS and the satellite pictures was downloaded using the same software(QGIS Development Team, 2009). In the results maps points are the predated nests divided by year and incubation timing (early and late). These maps was to see if the same nests was predated each time.

Nest predation was analysed with generalized linear mixed models (GLMM) using a binomial error. All of the models were estimated with glmer from the lme4 package (Bates, Maechler, Bolker, & Walker, 2015, see appendix). Several candidate GLMMs were compared for each site. The same models where used for Erkuta and Sabetta. Here I started with a general model with all the explanatory variables as additive effects. Explanatory variables were nest type (covered or uncovered), incubation period (early or late), the small rodent trapping index, and year as a continuous variable to test whether predation increased over years. Continuous variables (small rodents and year) were scaled to improve model estimation. In the next model, I tested whether predation of the different nest types increased differently over the years (interaction between nest type and year). The next model assumed that predation on the two types of nests reacted differently to small rodent abundance (interaction between nest

type and small rodents). I then test to see if predation early and late in the incubation period changed differently over the years (interaction between incubation timing and year). In the last model, I removed incubation timing as explanatory variable and kept the three others as additive effect.

I created a location ID that will be called locID from here on. In Erkuta and Belyi Island this locID included the site, which year the nest was placed and the nest ID. For Sabetta only the site and nest ID was included since the nests here where placed in the exact same locations every year. LocID was included as a random factor in all models.

For Belyi Island there was only one model since I only have two years of data and it was therefore not possible to distinguish between the effect of year and small rodent abundance. This was a model with nest type and year as additive effects, locID as a random factor, and no interactions.

The most parsimonious model for each site was chosen based on AICc (Richards, 2005). The best model was the model with the lowest AIC, and models with a $\Delta AICc$ smaller than 2 was counted as an equal fit (Richards, 2005). Model fit was assessed by checking for overdispersion and graphically inspecting the distribution of absolute residuals and random effects. Finally, I checked for influential values by recalculating parameter estimates without a few extreme points. Then I plotted the predicted relationship, from the best fitted model, between rodent abundance and nest predation for the four categories of artificial nests (categories: early uncovered, early covered, late uncovered, and late covered).

4 Results

There was only one covered nest that was predated in Erkuta and that was in 2017.

Considering the raw data, there was an increase in predation over the years for both early and late incubation (Figure 5). From 2018 to 2019 the predation of early nests decreased, but the total predation increased due to more predation later in the season. In all years the predation rate decreased from early to late. The highest predation in one category was for early uncovered nests in 2018, when all nests were predated, but the overall highest predation rate was in 2019 (Figure 5).

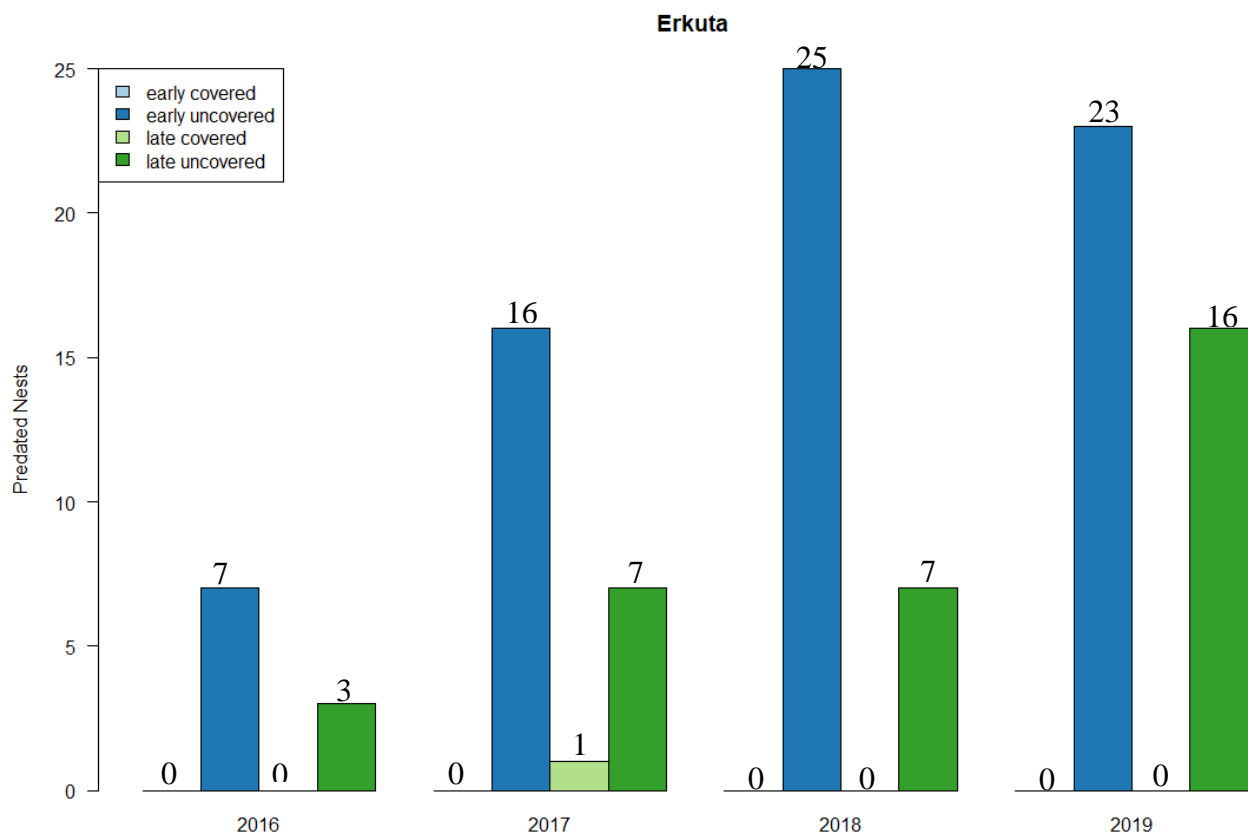


Figure 5 The number of artificial nests predated at Erkuta over years is shown for covered and uncovered nests in the early and late incubation period. There were 25 nests in each category each year.

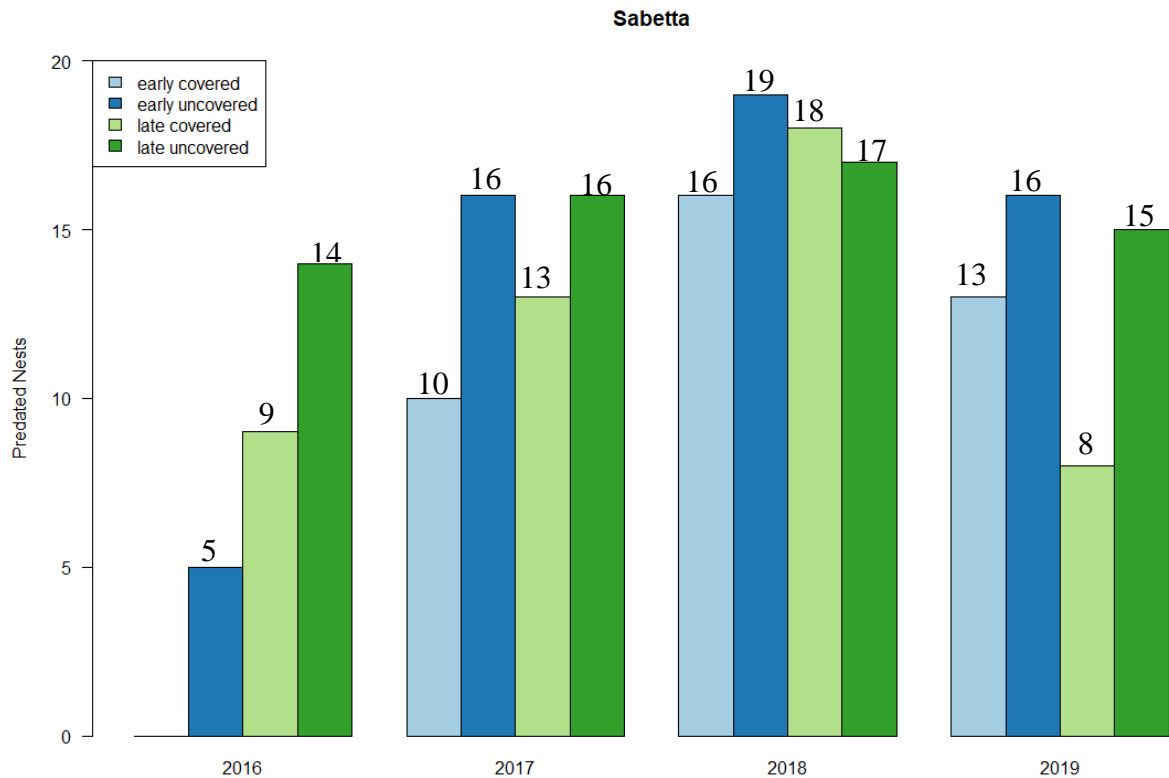


Figure 6 The number of artificial nests predated in Sabetta over years is shown for covered and uncovered nests in the early and late incubation period. There were 25 nests in each category in 2016. Early uncovered for the rest of the years there was 20 nests each year. In the rest of the categories there was 21 nests each of the remaining years.

In Sabetta, the raw data showed an increase of predation over the years up to 2018 and then a decrease from a total of 70 predated nests to 52 nests predated in 2019 (Figure 6). Most of the predation in 2016 was on the late nests, in particular the late uncovered nests. In 2017, predation was more spread out with the most predation on uncovered nests both early and late during the incubation period (Figure 6). In 2018, early covered nests were the most predated nests and had the highest predation of all of the years. In 2019, the predation early was higher than the late predation. The difference was created because when 2019 was compared to 2018 the late covered nests had a large decrease in predation compared to early covered, uncovered and late uncovered (Figure 6).

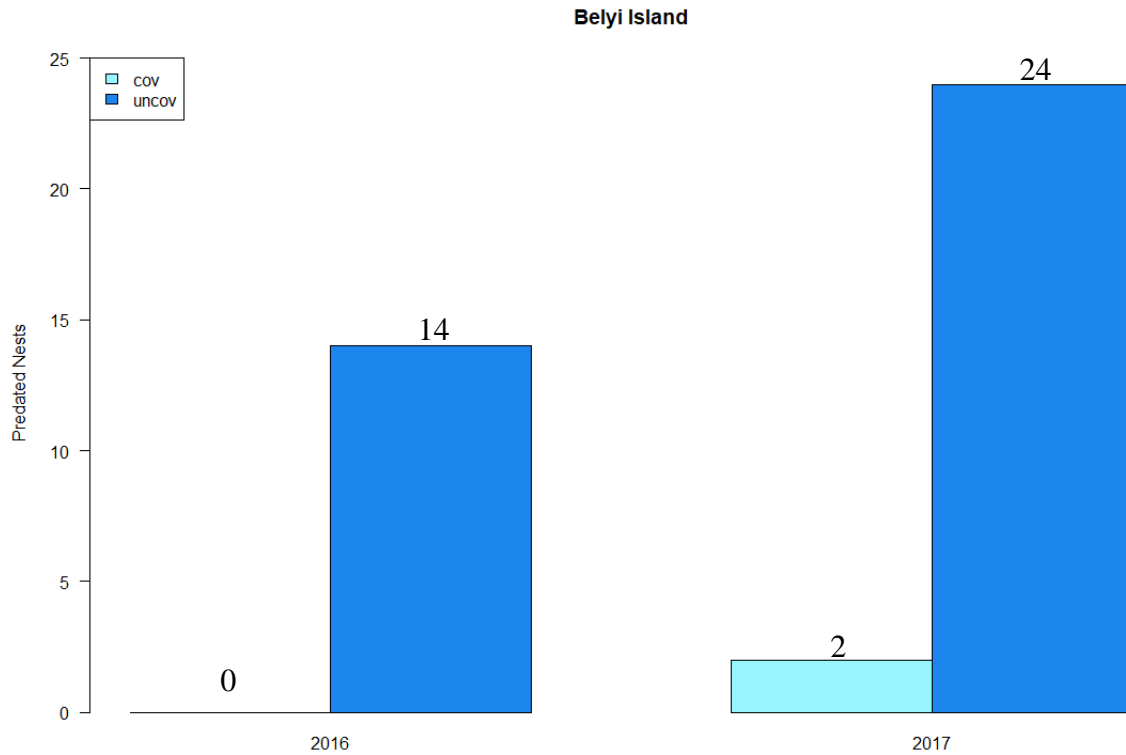


Figure 7 Bar plot of the predated covered and uncovered nests on Belyi Island each year. Only two covered nests were predated in 2017 while the uncovered nests was preyed on in both years. There were 25 nests in each category each year.

On Belyi Island there were 14 artificial nests predated in 2016 and 26 artificial nests were predated in 2017 (Figure 7). All the nests that where predated on Belyi Island where uncovered nests, except two in 2017 which were covered.

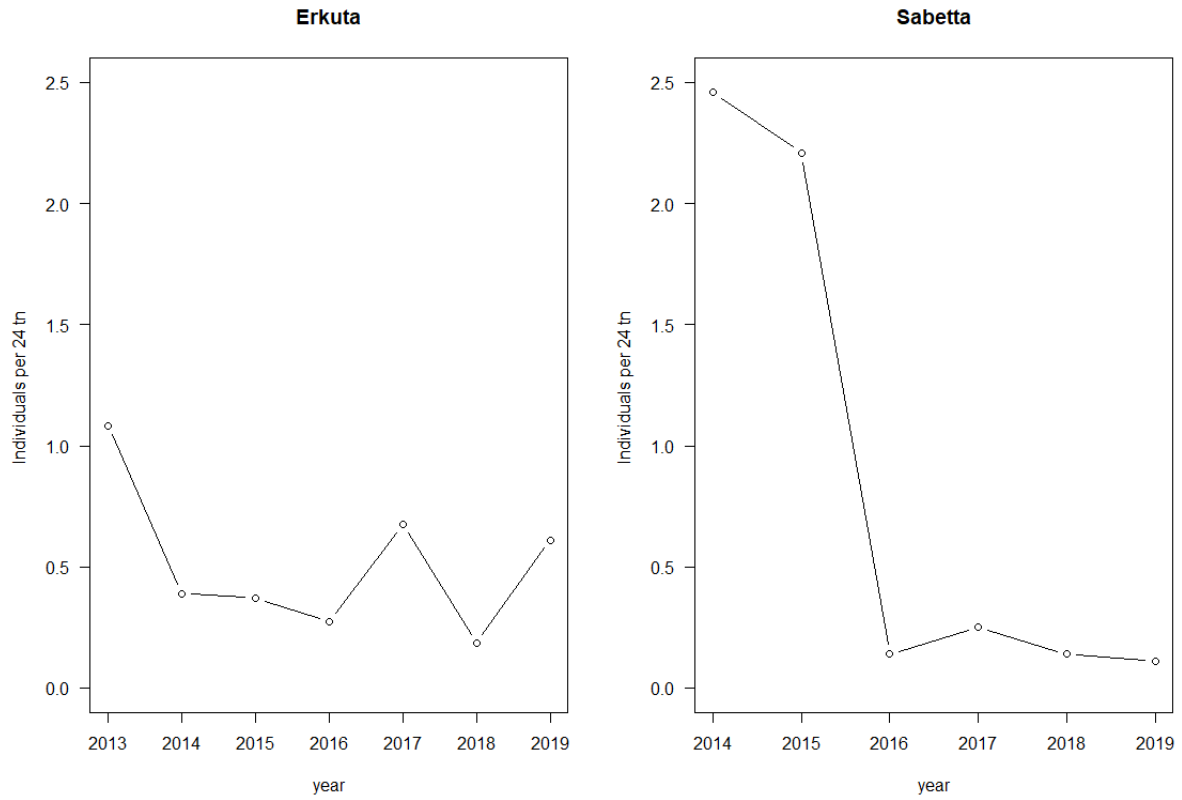


Figure 8 Mean number of small rodents caught per 24 trap nights per year (all species summed) for Erkuta and Sabetta. Artificial nests were deployed from 2016 to 2019.

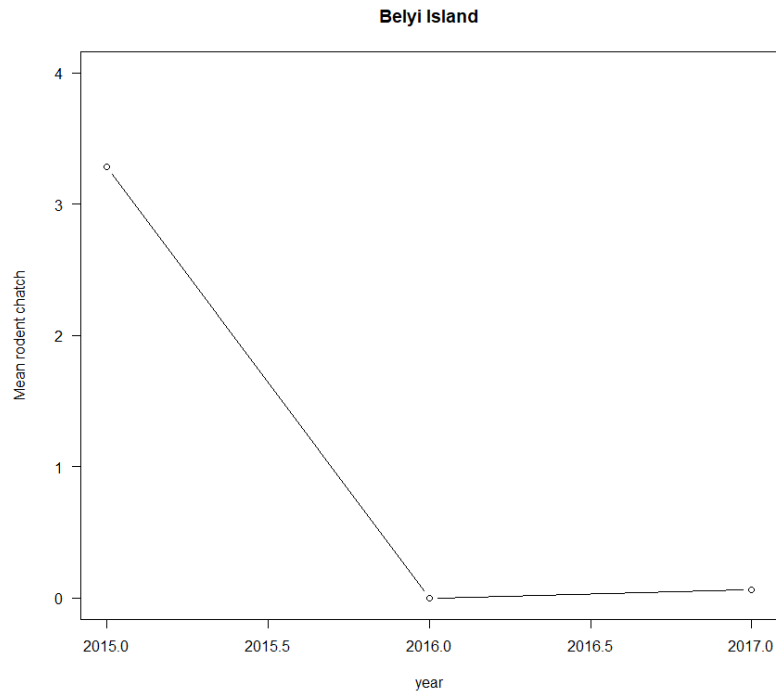


Figure 9 Mean number of small rodents caught per 24 trap nights per year (all species summed) for Belyi Island. Artificial nests were deployed from 2016 to 2017.

During the study period for artificial nests, the small rodent population was at a low in all study sites. On Belyi Island there was a peak in the small rodent population (2015) the year before the artificial nest study was started (Figure 9). In Sabetta, there had been a peak in the small rodent population in 2014, which was 2 years before the artificial nest study started. In Erkuta, the highest small rodent trapping index was observed in 2013, but density was not as high as in Sabetta in 2014 (Figure 8).

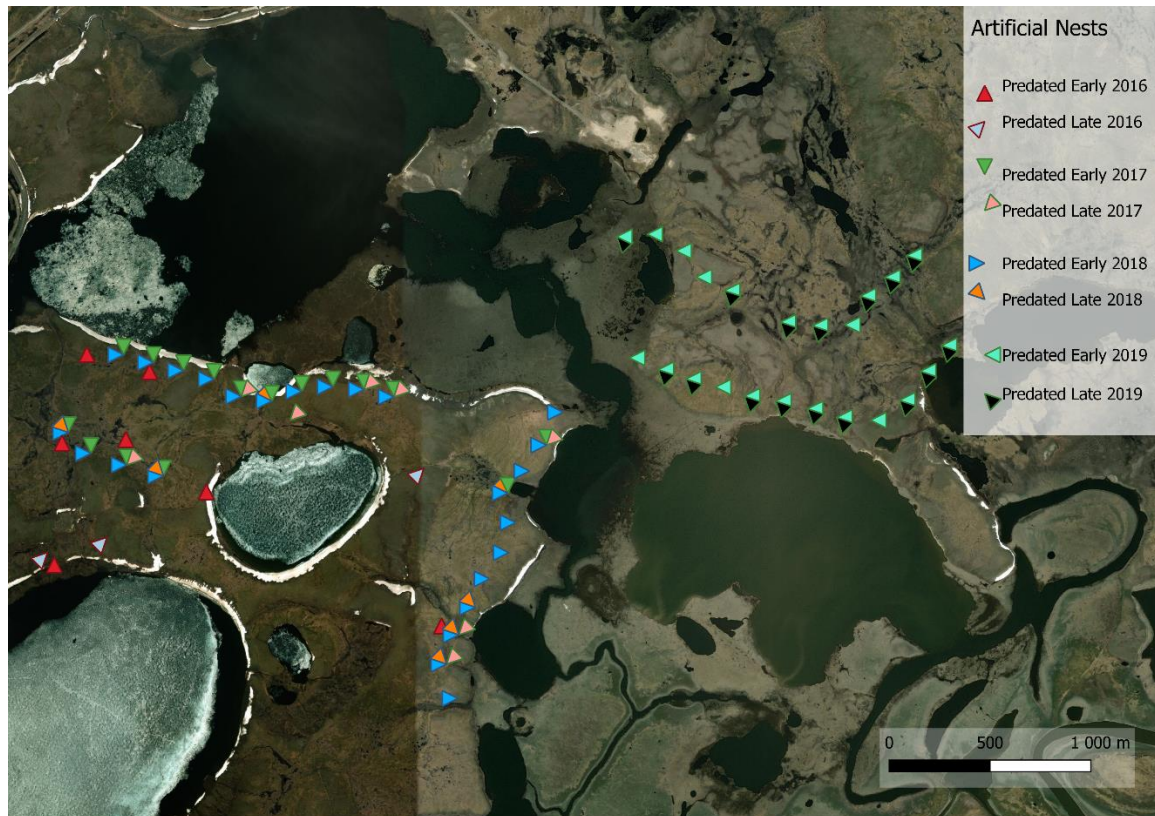


Figure 10 Map over the predated points over the years in Erkuta. Points come from the coordinates registered during placement of nests (satellite image obtained from QGIS).

Regarding the spatial pattern of nest predation, in Erkuta it was difficult to see whether the same nests were predated each year, but 18 of the same nests were predated in 2017 and 2018 in addition two of the same nests from 2016, that were also predated in 2017 and 2018 (Figure 10). In Erkuta there was not a single late nest that was not also predated earlier in the year except two nests in 2016 (Figure 10).

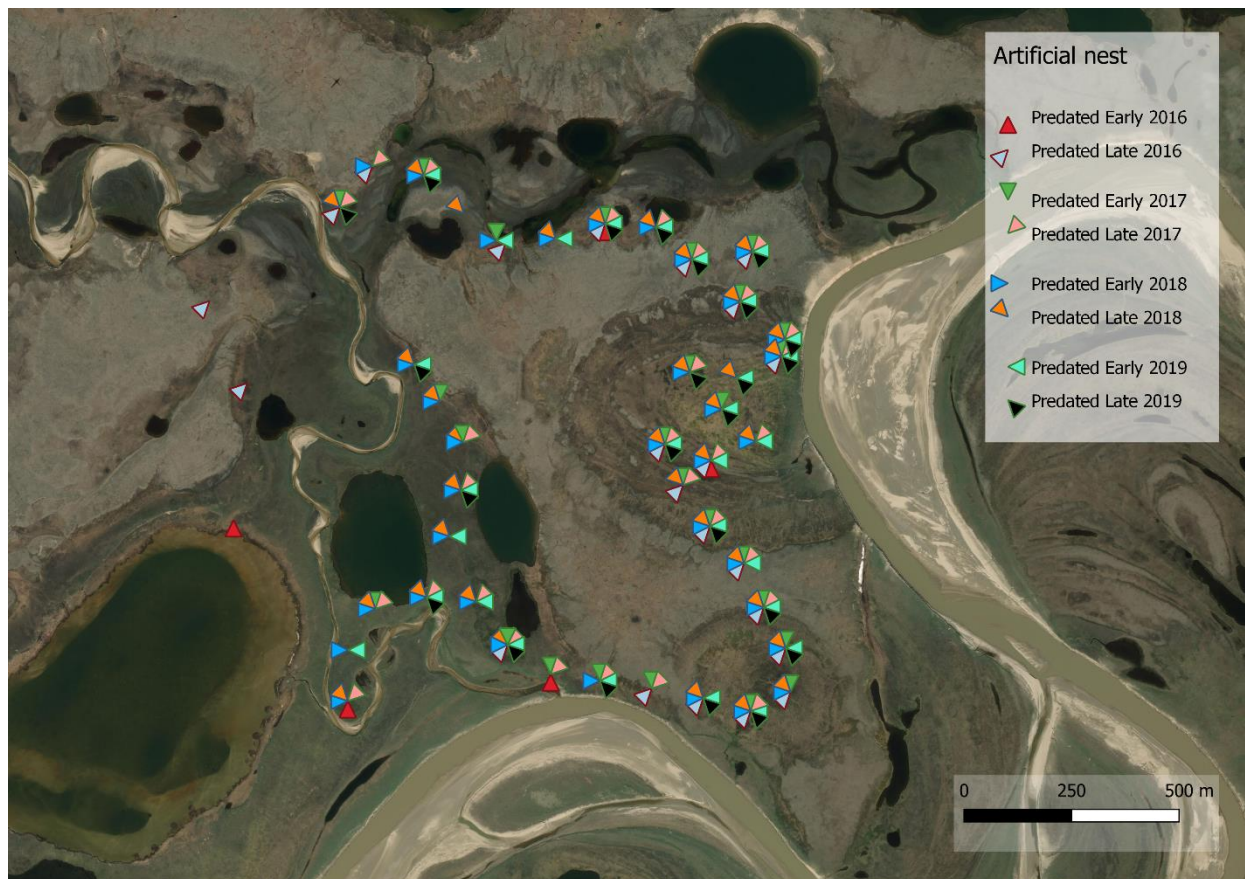


Figure 11 Map over the predated points over the years in Sabetta. Points come from the coordinates registered during placement of nests (satellite image obtained from QGIS).

In Sabetta all of the nests that was predated in 2016 and placed again in other years were predated in the following years as well. 11 of the same nests were predated all of the years and in every period except for the early incubation in 2016. Excluding the nests that were also predated in 2016, there were 10 new nests that were predated in all of the years from 2017 to 2019 (Figure 11).

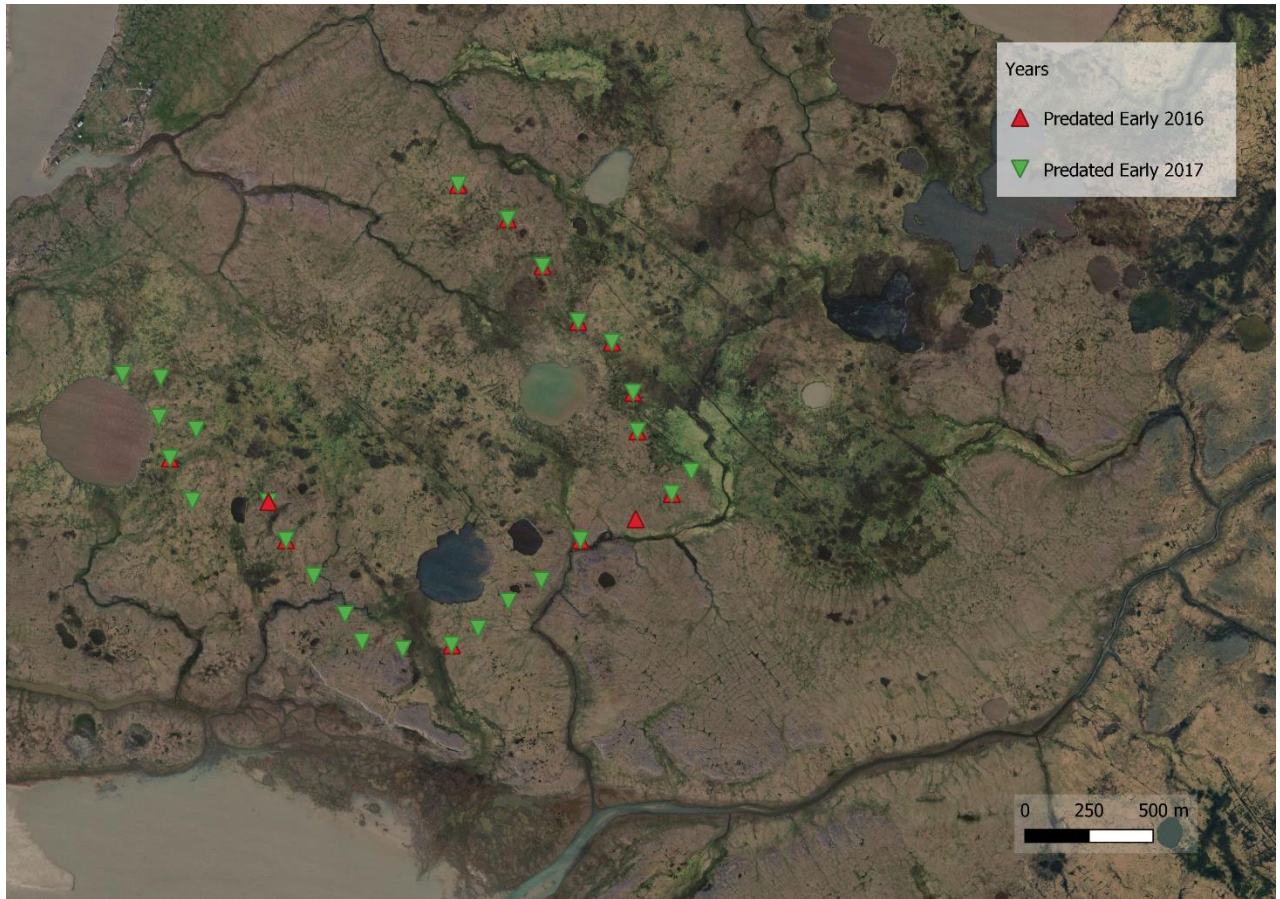


Figure 12 Map over the predated points over the years in Belyi Island. Points come from the coordinates registered during placement of nests (satellite image obtained from QGIS).

All of the nests predated in 2016 except for one was also predated in 2017 on Belyi Island. (Figure 12).

*Table 2 The candidate generalized linear mixed models (GLMM) explaining predation on artificial nests in Erkuta For each model the explanatory variables are shown (+ indicates additive effects and * indicates an interaction), the number of parameters (K), AICc*

	Candidate GLMM for Erkuta	K	AICc	Δ AICc
1	nest type8 + incubation timing + rodent index+ year + (1 locID)	6	229.85	1.16
2	nest type * year + rodent index + incubation timing + (1 locID)	7	229.35	0.66
4	nest type + rodent index + year * incubation timing + (1 locID)	7	228.68	0
5	nest type + rodent index + year + (1 locID)	5	265.73	37.04

For Erkuta, the model with an interaction between nest type and small rodents could not be estimated, because there was only a single covered nest that was predated. According to AICc, the best model for Erkuta was the model with an interaction between year and incubation timing (model 4 on Table 2). The next best model included and interaction between nest type and year (Δ AICc =0.66). The model without incubation timing was much less suitable (Δ AICc = 37,04). Despite the fact that model 1 might be a better model based on the small difference in AIC and smaller number of factors, model 4 was used for further testing and plotting since it tests for an interaction that was interesting to examine (results from the other 2 models can be found in the appendix).

Table 3 The candidate generalized linear mixed models (GLMM) explaining predation on artificial nests in Sabetta. For each model the explanatory variables are shown (+ indicates additive effects and * indicates an interaction), the number of parameters (K), AICc and the difference in AICc to the best model ($\Delta AICc$)

	Candidate glmer Models Sabetta	K	AIC	$\Delta AICc$
1	nest type8 + incubation timing + rodent index+ year + (1 locID)	6	396.66	16.15
2	predation ~ nest type * year + rodent index + incubation timing + (1 locID)	7	398.66	18.14
3	predation ~ nest type * rodent index + year + incubation timing + (1 locID)	7	398.69	18.18
4	Predation ~ nest type + rodent index + year * incubation timing + (1 locID)	7	380.52	0.00
5	predation ~ nest type + rodent index + year + (1 locID)	5	446.26	65.75

According to AICc, the best model for Sabetta was the model with an interaction between year and incubation timing (Table 3). The next best model included and interaction between nest type and year ($\Delta AICc = 18.14$). The model without incubation timing was much less suitable ($\Delta AICc = 65.75$) supporting that there was a difference in predation rate between the early and late incubation period.

Table 4 Estimates from the glmer test of model 4 in Erkuta which tests if the different incubation timings have a separate increase.

Results of Model 4 Erkuta				
Random effect				
Groups	Variance	Std.Dev.		
locID (Intercept)	0.159	0.399		
Number of obs: 400, groups: locID, 250				
Fixed Effects				
	Estimate	Std.Error	z-value	P-value
(Intercept)	-5.816	1.157	-5.028	<0.001
Nest type uncovered	6.918	1.266	5.464	<0.001
Rodent index	0.623	0.839	0.742	0.458
Year	1.606	0.371	4.333	<0.001
Incubation timing late compared to early	-2.091	0.460	-4.549	<0.001
The difference between incubation timing late and early over the years	-0.647	0.427	-1.514	0.130

The results from the best model for Erkuta (table 4) showed that there was an increase in predation rate with 1.606 (SE=0.371, $p<0.001$) over the years, and that the uncovered nests were predated more than the covered nests. The model also estimated that there was a decrease of predation later in the season, but it also estimates that this difference in early and late decrease over the years (Table 4).

Table 5 Results from the glmer test of model 4 in Sabetta which tests if the different incubation timings have a separate increase.

Results of Model 4 Sabetta				
Random effects				
Groups	Variance	Std.Dev.		
locID (Intercept)	1.183	1.088		
Number of obs: 346, groups: locID, 57				
Fixed Effects				
	Estimate	Std.Error	z-value	P-value
(Intercept)	-0.429	0.329	-1.302	0.193
Nest type uncovered compared to covered	1.250	0.423	2.956	0.003
Rodent index	0.593	0.159	3.729	<0.001
Year	1.719	0.257	6.687	<0.001
Incubation timing late compared to early	0.523	0.280	1.860	0.063
The difference between incubation timing late and early over the years	-1.209	0.299	-4.049	<0.001

The results from model 4 in table 5 for Sabetta shows similar trends as the models from Erkuta, but to different degrees. While in Erkuta the estimates of predation of uncovered nests compared to covered nests are at 6.918 (estimate on the logit scale; SE = 1.266, $p < 0.001$), the estimate for Sabetta is positive and significant with 1.250 (SE = 0.423, $p = 0.003$). The results in table 4 from Erkuta does not show a significant impact of the small rodent

population in Erkuta. In table 5 for Sabetta on the contrary the small rodent population is estimated to have a positive effect on the predation of artificial nests. The results shown in table 5, show that there was an increase of predation over the years. There is not a significant estimated difference between early and late placement of the artificial nests in Sabetta. Although the results show that there is less of an estimated difference over the years.

Table 6 Results from the glmer test of model 2 on Belyi Island which uses Year

Results of Model 2 Belyi Island				
Random effects				
Groups	Variance	Std.Dev.		
locID (Intercept)	0.137	0.370		
Number of obs: 100, groups: locID, 100				
Fixed Effects				
	Estimate	Std.Error	z-value	P-value
(Intercept)	-8.767	3.487	-2.514	0.012
Nest type uncovered	5.893	2.307	2.555	0.011
Year	3.108	1.384	2.246	0.025

The results from model 2 for Belyi Island there is also an increase in the predation of the uncovered nests compared to the covered nests, and it shows a significant increase to the predation over the 2 years it was measured (Table 6).

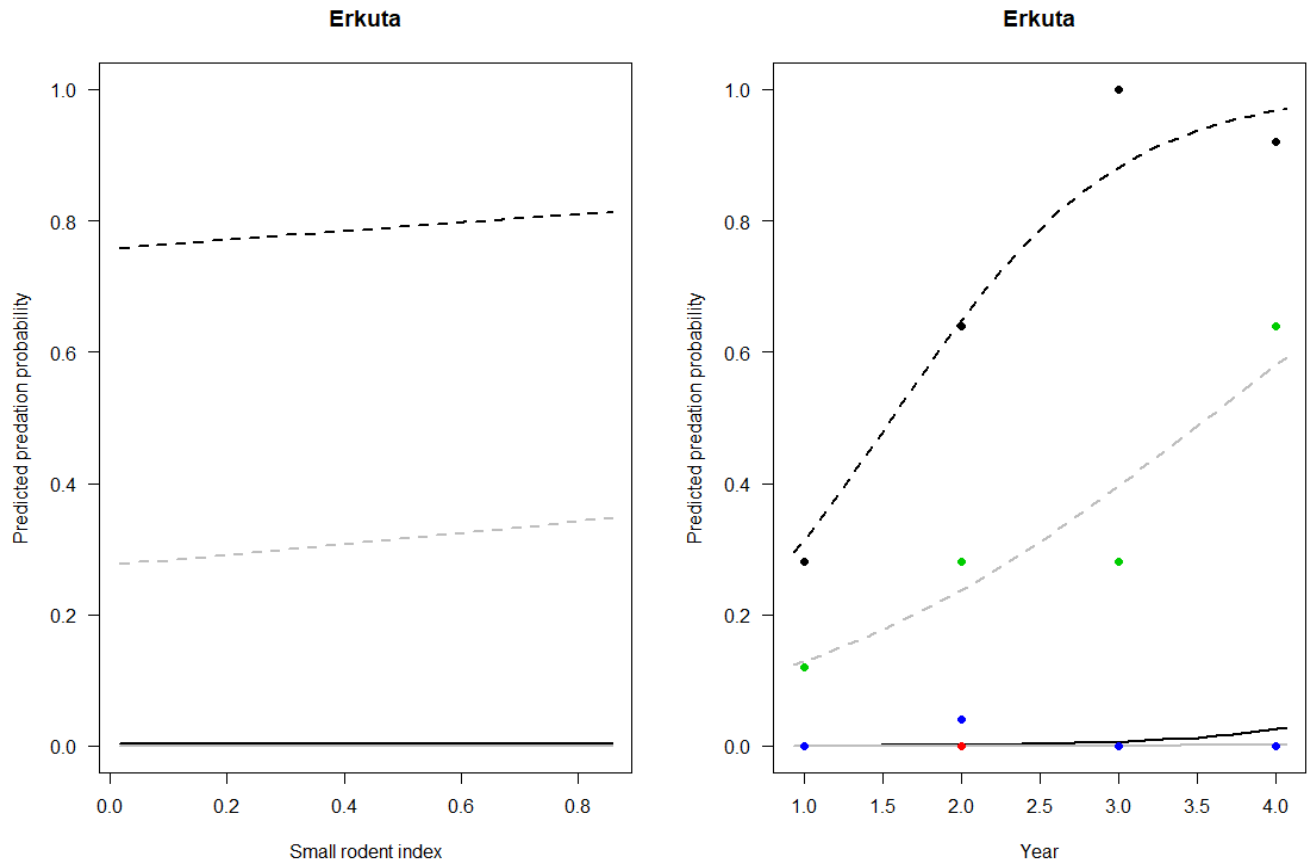


Figure 13 a) Prediction graph showing predation probability in Erkuta using model 4 with the small rodent index. The black stapled line is for early uncovered nests. The fully black line is early covered nests. The grey stapled line is for late uncovered nests. The fully grey line is for late covered nests.

b) Prediction graph showing predation probability in Erkuta using model 4 with over the years. Black dots are average early uncovered predation each year, red dots are observed early covered predation each year, green dots are observed late uncovered predation each year, Blue dots are observed late covered predation each year. The black stapled line is for early uncovered nests. The fully black line is early covered nests. The grey stapled line is for late uncovered nests. The fully grey line is for late covered nests.

The predicted predation in Erkuta was increasing for the uncovered nests both in the early and late incubation period. In relation to the small rodent index the increase was very small, but over the years the predicted predation increases significantly (Figure 13 a and b). They covered nests do not have an increase or any prediction at all in Erkuta since there was only one covered nest in Erkuta that was predated in the late season in 2017.

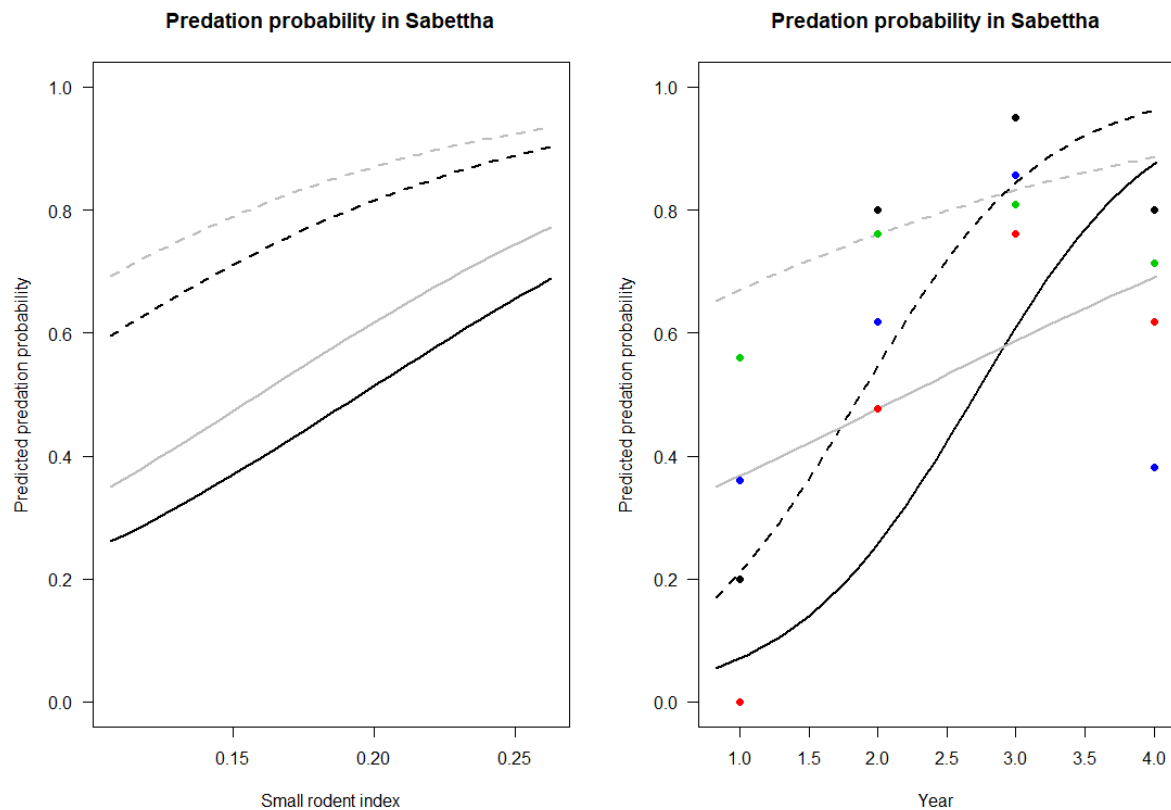


Figure 14 a) Prediction graph showing predation probability in Sabetta using model 4 with a small rodent index. The black stapled line is for early uncovered nests. The fully black line is early covered nests. The grey stapled line is for late uncovered nests. The fully grey line is for late covered nests.

b) Prediction graph showing predation probability in Sabetta using model 4 with over the years. Black dots are average early uncovered predation each year, red dots are observed early covered predation each year, green dots are observed late uncovered predation each year, Blue dots are observed late covered predation each year. The black stapled line is the predicted predation rate for early uncovered nests. The fully black line is the predicted predation rate for early covered nests. The grey stapled line is the predicted predation for late uncovered nests. The fully grey line is the predicted predation for late covered nests.

There is an increase in predation probability with an increase in rodent density. Here the uncovered nests have a higher probability to be predated both early and late compared to the covered nests. The late nests have a slightly higher probability to be predated than the early nests. This does seem to even out for the uncovered nests (Figure 14a).

There is an increase in predation probability with the increase in years in Sabetta. Here the early nests have a steeper increase for both the covered and uncovered nests, than the late covered and late uncovered nests. At the start there is a large spread in the predation probability between the different parameters. These differences decrease over the years. Although the early covered nests have the least probability to be predated at the start, the increase in predation risk over the years give it almost the same probability to be predated as

the late uncovered nests. The early uncovered nests also have a similar increase as the early covered nests, although they end up being the nests that are most likely to be predated (Figure 14b).

The observed predation for each year follows the curve of predicted predation to a certain degree, but there is a clear difference in 2019. Where the predicted predation is much higher than the actual average predation (Figure 14b).



Figure 15 Hooded Crow in Erkuta holding an egg from an artificial nest. Screenshot from video.

All the 3 artificial nests placed with wildlife cameras where all of them captured Hooded Crows predated the nest (Figure 15).

5 Discussion

The results from repeated artificial nest experiments at three sites showed an increase in predation over the years, in accordance with what would be expected if predators would learn where and when the nests are deployed. In Erkuta the early nests were predated more than the

late nests. In Sabetta the early and late nests were predated more equally. The points of predation in the maps show that there were several nests that after the first time they were predated they were predated they were predated all the other placements. Where uncovered nests were predated more than covered nests. The summary of the best fitted model for each site shows that there is an increase in predation over the years and a difference in the predation from early too late. It also shows that that difference is decreasing over the years. The results also show that the predation increase with an increase in the rodent index in Sabetta but not in Erkuta. This is also shown in the graphs presented in the results.

As predation decrease with incubation timing this might indicate that the shift in search image of predators is stronger than the learning from the artificial nests. But this was only shown in Erkuta and Sabetta. On Belyi Island the nests were only placed once per year so it hasn't been tested for incubation timing. The shift in search image has also been shown in other papers (Husby and Hoset, 2018). Here the predation by birds showed the same pattern as found in this study in Erkuta that my early nests were predated more than the late nests. The reason this same trend was not found in Sabetta might be due to the higher population of foxes in Sabetta. As the study from Husby & Hoset (2018) concluded that the foxes is not as seasonal in the predation of nests, the predation will be more evenly spread out.

Although this might be the case for the first years the results also indicate that the difference in early and late predation is decreasing. This indicates that the shift in search image might not be reflected as the predators learn where the artificial nests are located.

As expected, the uncovered nests had a higher predation pressure than the covered nests. This might be due to avian predators are more numerical and therefore finding more nests than mammalian predators. It might also be that the avian predators cover a larger search area that overlaps more than mammalian predators, and thereby more avian predators are present than mammalian predators. The numerical difference between mammalian and avian predators is especially evident when you compare Erkuta to Sabetta. As in Erkuta almost no covered nests where predated while in Sabetta they are almost equal to the uncovered nests. One difference between Erkuta and Sabetta is that there are more artic foxes in Sabetta. In Erkuta, there were on average 2.11(sd=1.93) active dens per 100 km² during the years of the study, whereas in Sabetta there were on average 5.14 (sd=3.35) active dens per 100 km² (Ehrich, personal communication, June 29, 2020). This difference in number of foxes might explain some of the

difference in predation of the covered artificial nests. As the avian predators are more visual hunters and the mammalian predators rely more on scent, this might also be a factor that is reflected in the results. This means that the avian predators are most likely to predate the uncovered while the mammalian predators might predate both covered and uncovered nests. It was also mentioned in the paper by Ims et al., (2019) that the extent the nests was visible was a factor in regards to the predicted predation.

In 2019 the study site was moved 3,43 km east. So, in Erkuta one could expect the predation in 2019 to go down, but the results do not entirely reflect this. This can be considered in the same area as most of the predators in the Arctic have a bigger search area for food than 3,43 km. There are studies showing that arctic foxes that is breeding have a home range of around 7km² (McKinnon, Berteaux and Bêty, 2014). The fact that the artificial nests also still was placed around the same lake where the same seagull colony was for all the years might also be a factor. The new placement of the artificial nests was also close to an arctic skua nest just as for the old placement. So, when all of these factors are viewed together, they can be summed up to that the number of predators and in general the predator population have not changed much from previous years.

On Belyi Island the artificial nest experiment was only conducted twice so even though it does show an increase in predation over the years this might not be as significant. In the case of Belyi Island the increase over the two years might be a coincidence, but since the same trend is shown in both of the other two study sites it might still show the indication for a learning effect.

When it comes to the predation pressure in regard to the rodent cycles for the study sites the results reflected an increase in predation pressure with an increase in rodent population. Although this do go against the alternative prey hypothesis, it might be explained by the fact that there was no rodent years during the artificial nest study, and thereby the trend that was discovered with rodents might not be valid since without a rodent year one will not be able to measure if there is a shift in predation. The counterargument for this is that the study sites do not have a large rodent population even during the rodent years. So the shift that might occur in other locations might not be a factor for these study sites. This is contrary to most Arctic systems where the lemming population is a driving force of predation pressure and is a key

species (Bêty *et al.*, 2001, 2002, 2014; Ims and Fuglei, 2005; Ims *et al.*, 2013; McKinnon, Berteaux and Bêty, 2014). The relative stable predation pressure despite the lemming cycles was also shown in the paper by Pöysä *et al.*, (2016). Where they also concluded that the predators had learned where the nests were placed. If there was no learning effect from the placement of artificial nests and since the rodent population was so small during the experiment, one would expect that there was a more constant predicted predation that do not have an increase over the years, regardless of if it was high or low. Another expectation one could have is that the predation the first year should have been the highest, since the first year is the year after the rodent peak, as shown in Ims *et al.*(2019). However, both of these assumptions were not reflected in the results. There was a significant increase of predation over the years and the first year had the lowest predation over all sites. This does go against alternative prey hypothesis, but as mentioned earlier the rodent population for all study sites on Yamal and its fluctuation is small when compared to other study sites in the artic, such as in Ims *et al.* (2019).

There is also a clear indication that there is a learning effect when it comes to which nests was predated in Sabetta. If there was no learning effect one would expect the nests to be predated more sporadically and not in such an orderly fashion for each year. Although there is a high predation rate in Sabetta overall there should still be even more spread if there was no learning effect. There should be more seasons missing and even entire years should not be counted in the predation dots (Figure 11).

In Erkuta it was proven using wildlife cameras placed above artificial nests that hooded crows is a predator for the artificial nests. As it is the only species that predated on the artificial nests with cameras. Although these cameras were placed closer to camp and were out several more days than the other artificial nests and thereby, they might not be very representative.

In the end we do see an increase of predation across the study sites over the years, and a decrease in the difference between early and late predation. This gives my hypothesis some merit, and there might be a learning effect from the artificial nests. Although to further confirm this the time series of the experiment should be continued for some time. Preferably until all sites have a peak in the rodent population. This is to get a more accurate estimation of predation pressure related to the rodents since my results cannot show what happens during a

rodent peak. During this time the Erkuta site should also have the same placement of nests. It would also be interesting to have a second plot for artificial nests in each site that changes where it is placed each year to better see if the predators is actually learning where the nests are or if they have a bigger focus on following the people that place them. This question comes form that I expected the predation in 2019 in Erkuta to go down, but it did not. Thou further research is needed both in these study areas and maybe on a larger scale. The predators seem to be learning where the nests are. Although, this might be specific to my study area it should be tested for and taken into consideration when other studies use multiannual placement of artificial.

6 Sources

- Angelstam, P., Lindström, E. and Widén, P. (1984) 'Role of predation in short-term population fluctuations of some birds and mammals in Fennoscandia', *Oecologia*. doi: 10.1007/BF00379014.
- Bates, D. *et al.* (2015) 'Fitting Linear Mixed-Effects Models Using lme4', *Journal of Statistical Software*, 67(1), pp. 1–48. doi: 10.18637/jss.v067.i01.
- Begon, M., Townsend, C. R. and Harper, J. L. (2006) *Ecology: From Individuals to Ecosystems*. 4th edn. Oxford: BLACKWELL PUBLISHING.
- Bekryaev, R. V., Polyakov, I. V. and Alexeev, V. A. (2010) 'Role of polar amplification in long-term surface air temperature variations and modern arctic warming', *Journal of Climate*, 23(14), pp. 3888–3906. doi: 10.1175/2010JCLI3297.1.
- Bêty, J. *et al.* (2001) 'Are goose nesting success and lemming cycles linked? Interplay between nest density and predators', *Oikos*, 93(3), pp. 388–400. doi: 10.1034/j.1600-0706.2001.930304.x.
- Bêty, J. *et al.* (2002) 'Shared predators and indirect trophic interactions: Lemming cycles and arctic-nesting geese', *Journal of Animal Ecology*, 71(1), pp. 88–98. doi: 10.1046/j.0021-8790.2001.00581.x.
- Bêty, J. *et al.* (2014) 'Fading indirect effects in a warming arctic tundra', *Current Zoology*, 60(2), pp. 189–202. doi: 10.1093/czoolo/60.2.189.
- Boarman, W. I. and Heinrich, B. (2020) 'Common Raven (*Corvus corax*)', *Birds of the World*. Cornell Laboratory of Ornithology. doi: 10.2173/bow.comrav.01.
- Breisjøberget, J. I. *et al.* (2018) 'The alternative prey hypothesis revisited: Still valid for willow ptarmigan population dynamics', *PLoS ONE*, 13(6), pp. 1–14. doi: 10.1371/journal.pone.0197289.
- Callaghan, T. V. *et al.* (2011) 'Multi-decadal changes in tundra environments and ecosystems: Synthesis of the international Polar year-back to the future project (IPY-BTF)', *Ambio*, 40(6), pp. 705–716. doi: 10.1007/s13280-011-0179-8.

Campbell, N. A. *et al.* (2017) 'Biology, A Global Approach', in Winickoff, B. N. and Burner, P. (eds) *Biology, A Global Approach. 11th edition*. 11th edn. New York: Pearson, pp. 1273–1275.

Cornell University (2019) *The Cornell Lab of Ornithology, All About Birds, Cornell Lab of Ornithology, Ithaca, New York*. Available at:
https://www.allaboutbirds.org/guide/Glaucous_Gull/overview (Accessed: 15 May 2020).

Ehrich, D. *et al.* (2017) 'Vole abundance and reindeer carcasses determine breeding activity of Arctic foxes in low Arctic Yamal, Russia', *BMC Ecology*. BioMed Central, 17(1), pp. 1–13. doi: 10.1186/s12898-017-0142-z.

Elsen, P. R. and Tingley, M. W. (2015) 'Global mountain topography and the fate of montane species under climate change', *Nature Climate Change*, 5(8), pp. 772–776. doi: 10.1038/nclimate2656.

Fuglesteig, B. N. *et al.* (2006) 'Seasonal variations in basal metabolic rate, lower critical temperature and responses to temporary starvation in the arctic fox (*Alopex lagopus*) from Svalbard', *Polar Biology*, 29(4), pp. 308–319. doi: 10.1007/s00300-005-0054-9.

Gilg, O., Giroux, M.-A. and Meyer, N. (2018) 'Arctic Interactions Working Group Protocol', (April), pp. 1–28.

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

Hairston, N. G., Smith, F. E. and Slobodkin, L. B. (1960) 'Community Structure, Population Control, and Competition Author (s): Nelson G. Hairston, Frederick E. Smith, Lawrence B. Slobodkin Published by: The University of Chicago Press for The American Society of Naturalists Stable URL: <http://www.jsto>', *The American Naturalist*, 94(879), pp. 421–425.

Heinrich, B. and Bugnyar, T. (2005) 'Testing problem solving in ravens: String-pulling to reach food', *Ethology*, 111(10), pp. 962–976. doi: 10.1111/j.1439-0310.2005.01133.x.

Heinrich, B. and Pepper, J. W. (1998) 'Influence of competitors on caching behaviour in the common raven, *Corvus corax*', *Animal Behaviour*, 56(5), pp. 1083–1090. doi: 10.1006/anbe.1998.0906.

- Holt, R. D. (1977) 'Predation, apparent competition, and the structure of prey communities', *Theoretical Population Biology*, 12(2), pp. 197–229. doi: 10.1016/0040-5809(77)90042-9.
- Hörnfeldt, B., Löfgren, O. and Carlsson, B. G. (1986) 'Cycles in voles and small game in relation to variations in plant production indices in Northern Sweden', *Oecologia*. doi: 10.1007/BF00378761.
- Husby, M. and Hoset, K. S. (2018) 'Seasonal variation in nest predation rates in boreal forests', *Journal of Ornithology*. Springer Berlin Heidelberg, 159(4), pp. 975–984. doi: 10.1007/s10336-018-1563-y.
- Ims, R. A. *et al.* (2013) 'Indirect food web interactions mediated by predator-rodent dynamics: Relative roles of lemmings and voles', *Biology Letters*, 9(6). doi: 10.1098/rsbl.2013.0802.
- Ims, R. A. *et al.* (2019) 'Arctic greening and bird nest predation risk across tundra ecotones', *Nature Climate Change*. Springer US, 9(8), pp. 607–610. doi: 10.1038/s41558-019-0514-9.
- Ims, R. A. and Fuglei, E. (2005) 'Trophic Interaction Cycles in Tundra Ecosystems and the Impact of Climate Change', *BioScience*, 55(4), p. 311. doi: 10.1641/0006-3568(2005)055[0311:ticite]2.0.co;2.
- Lack, D. (1955) 'The Natural Regulation of Animal Numbers', *The Journal of Wildlife Management*, 19(4), p. 487. doi: 10.2307/3797467.
- Lai, S., Bêty, J. and Berteaux, D. (2017) 'Movement tactics of a mobile predator in a meta-ecosystem with fluctuating resources: the arctic fox in the High Arctic', *Oikos*, 126(7), pp. 937–947. doi: 10.1111/oik.03948.
- Marcstrom, V., Kenward, R. E. and Engren, E. (1988) 'The Impact of Predation on Boreal Tetraonids During Vole Cycles: An Experimental Study', *The Journal of Animal Ecology*, 57(3), p. 859. doi: 10.2307/5097.
- Marzluff, J. M. *et al.* (2010) 'Lasting recognition of threatening people by wild American crows', *Animal Behaviour*. Elsevier Ltd, 79(3), pp. 699–707. doi: 10.1016/j.anbehav.2009.12.022.
- Marzluff, J. M. and Heinrich, B. (1991) 'Foraging by common ravens in the presence and

absence of territory holders: an experimental analysis of social foraging', *Animal Behaviour*, 42(5), pp. 755–770. doi: 10.1016/S0003-3472(05)80121-6.

McKinnon, L. *et al.* (2010) 'Lower predation risk for migratory birds at high latitudes', *Science*, 327(5963), pp. 326–327. doi: 10.1126/science.1183010.

McKinnon, L. *et al.* (2013) 'Predator-mediated interactions between preferred, alternative and incidental prey in the arctic tundra', *Oikos*, 122(7), pp. 1042–1048. doi: 10.1111/j.1600-0706.2012.20708.x.

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

McKinnon, L. and Bêty, J. (2009) 'Effect of camera monitoring on survival rates of High-Arctic shorebird nests', *Journal of Field Ornithology*, 80(3), pp. 280–288. doi: 10.1111/j.1557-9263.2009.00231.x.

Meltofte, H. *et al.* (2013) *Arctic Biodiversity Assessment - Scientific report*. Edited by H. Meltofte. Akureyri, Iceland: The Conservation of Arctic Flora and Fauna. Available at: http://www.abds.is/publications/search?tag=aba_2013.

Moss, R. and Watson, A. (2001) 'Population cycles in birds of the grouse family (Tetraonidae)', *Advances in Ecological Research*. Academic Press Inc., pp. 53–111. doi: 10.1016/s0065-2504(01)32011-1.

Muller, A. C. B. *et al.* (1997) 'Apparent Competition between Two Aphid Species Published by : British Ecological Society Apparent competition between two aphid species', *Journal of Animal Ecology*, 66(1), pp. 57–64.

Niehaus, A. C., Ruthrauff, D. R. and McCaffery, B. J. (2004) 'Response of Predators to Western Sandpiper Nest Exclosures', *Waterbirds*, 27(1), pp. 79–82. doi: 10.1675/1524-4695(2004)027[0079:roptws]2.0.co;2.

Pelech, S. A., Smith, J. N. M. and Boutin, S. (2010) 'A predator's perspective of nest predation: Predation by red squirrels is learned, not incidental', *Oikos*, 119(5), pp. 841–851. doi: 10.1111/j.1600-0706.2009.17786.x.

Pöysä, H., Jalava, K. and Paasivaara, A. (2016) 'Generalist predator, cyclic voles and cavity nests: testing the alternative prey hypothesis', *Oecologia*. Springer Berlin Heidelberg, 182(4), pp. 1083–1093. doi: 10.1007/s00442-016-3728-9.

Prestrud, P. (1991) 'Adaptations by the arctic fox (*Alopex lagopus*) to the polar winter', *Arctic*, 44(2), pp. 132–138. doi: 10.2307/40511073.

QGIS Development Team (2009) 'QGIS Geographic Information System', *Open Source Geospatial Foundation Project*. Open Source Geospatial Foundation Project.

Rausch, R. (1995) *Life cycle patterns and geographic distribution of Echinococcus species, Echinococcus and Hydatid disease*. Edited by R. . A. Thompson and A. J. Lymbery.

Wallingford, Oxfordshire, UK: CAB International. Available at:

<http://ci.nii.ac.jp/naid/10018775603/en/> (Accessed: 11 November 2018).

Richards, S. A. (2005) 'Testing ecological theory using the information-theoretic approach: Examples and cautionary results', *Ecology*, 86(10), pp. 2805–2814. doi: 10.1890/05-0074.

Šálek, M. *et al.* (2004) 'Predation on artificial nests in relation to the numbers of small mammals in the Krušné hory Mts, the Czech Republic', *Folia Zoologica*, 53(3), pp. 312–318.

Schmidt, N. M. *et al.* (2012) 'Response of an arctic predator guild to collapsing lemming cycles', *Proceedings of the Royal Society B: Biological Sciences*, 279(1746), pp. 4417–4422. doi: 10.1098/rspb.2012.1490.

Sokolov, A. A. *et al.* (2016) 'Emergent Rainy Winter Warm Spells May Promote Boreal Predator Expansion into the Arctic', *JSTOR*, 69(2), pp. 121–129.

Sokolov, V. *et al.* (2012) 'Bird Communities of the Arctic Shrub Tundra of Yamal: Habitat Specialists and Generalists', *PLoS ONE*, 7(12), pp. 1–12. doi: 10.1371/journal.pone.0050335.

Sokolova, N. A. *et al.* (2014) 'Small rodents in the shrub tundra of Yamal (Russia): Density dependence in habitat use?', *Mammalian Biology*. Elsevier GmbH, 79(5), pp. 306–312. doi: 10.1016/j.mambio.2014.04.004.

Stephens, P. A. *et al.* (2016) 'Consistent response of bird populations to climate change on two continents', *Science*, 352(6281), pp. 84–87.

Team, R. C. (2018) 'R: A Language and Environment for Statistical Computing'. Vienna,

7 Appendix

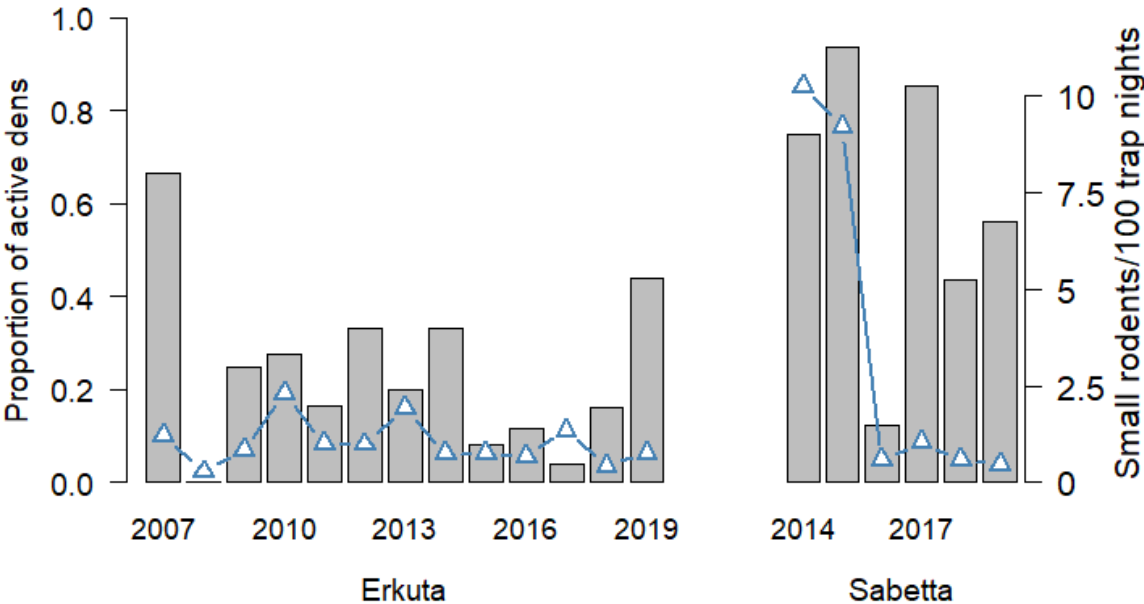


Figure 16 Bar plot of the proportions of active dens in Erkuta and Sabetta. With small Rodent population per 100 trap nights marked with triangles and lines to demonstrate the population trends

Table 7 Estimates from the glmer test of model 2 in Erkuta which tests with no interactions.

Results of Model 1 Erkuta				
Random effect				
Groups	Variance	Std.Dev.		
locID (Intercept)	0.159	0.399		
Number of obs: 400, groups: locID, 250				
Fixed Effects				
	Estimate	Std.Error	z-value	P-value
(Intercept)	-5.394	1.094	-4.930	<0.001
Nest type uncovered	6.526	1.186	5.504	<0.001
Rodent index	0.083	0.176	0.471	0.637
Year	1.148	0.242	4.750	<0.001
Incubation timing late compared to early	-2.025	0.455	-4.449	<0.001

Table 8 Estimates from the glmer test of model 2 in Erkuta which tests if the different nest types have a separate increase.

Results of Model 2 Erkuta				
Random effect				
Groups	Variance	Std.Dev.		
locID (Intercept)	0.308	0.555		
Number of obs: 400, groups: locID, 250				
Fixed Effects				
	Estimate	Std.Error	z-value	P-value
(Intercept)	-4.966	1.162	-4.275	<0.001
Nest type uncovered	6.152	1.242	4.952	<0.001
Rodent index	0.094	0.184	0.511	0.610
Year	-0.506	1.098	-0.461	0.645
Incubation timing late compared to early	-2.123	0.494	-4.298	<0.001
The difference between nest type covered and uncovered over the years	1.743	1.133	1.539	0.124

