PREDATION ON ARTIFICIAL NESTS IN RELATION TO HUMAN ACTIVITY AND WILLOW PTARMIGAN DENSITY ALONG LANDSCAPE GRADIENTS IN A BOREAL ECOSYSTEM

PREDASJON PÅ KUNSTIGE REIR I FORHOLD TIL MENNESKELIG AKTIVITET OG RYPETETTHET LANGS LANDSKAPSGRADIENTER I ET BOREALT ØKOSYSTEM

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Preface

Abstract

In a study conducted in five willow ptarmigan (*Lagopus lagopus*) areas in central Norway we found a total predation rate on artificial nests with common quail (*Coturnix coturnix*) eggs ranging from 39.8% to 50.7% over three years. The most dominating egg predators were ravens (*Corvus corax*), pine martens (*Martes martes*) and hooded crows (*Corvus cornix*). Predators that showed a low predation rate on the artificial nests were magpies (*Pica pica*), red foxes (*Vulpes vulpes*), stoats (*Mustela erminea*) and least weasels (*Mustela nivalis*). Evaluating the influence of human activity on the predation rates we found that the total predation rate increased with increasing road - and path density. Pine marten predation was negatively associated with density of roads and paths while raven predation was positively associated with density of roads and paths. The total predation rate increased with increasing settlement density. There was a negative relationship between raven predation and settlement density whereas there was a positive relationship between hooded crow predation and settlement density. In other words; the dominating mammalian species showed a negative association with overall human activity, while the two dominating corvid (*Corvus* spp.) species showed a positive association with overall human activity with the exception of ravens´ negative association with settlement density. It seems that in some way human activity and infrastructure facilitate access to resources for the corvid species; leading to higher corvid densities;- possibly leading to higher predation rates on nests in vicinity to settlement and infrastructure. We found however no relationship between total predation rate and willow ptarmigan density. This finding can be due to the difficulties of transferring predation rates on artificial nests to predation rates on natural nests where the predation rate by mammals probably is higher. Most of the predation from pine marten took place in birch habitat whereas most of the predation by corvids occurred in the more open low-alpine habitat and edge habitat. Although there was no clear relation between predation patterns on artificial nests and predator density measured using cameras, our results showed that we could expect higher densities of potential ptarmigan predators in association with human activity, settlement and infrastructure. Planning e.g. new cabin resorts areas, this should be taken into account, to avoid setting up resorts areas in high productive willow ptarmigan habitat. Small rodent abundance was positively related to total predation.

Sammendrag

I et forsøk gjennomført i fem lirypeområder (*Lagopus lagopus*) i Midt-Norge fant vi at totale predasjonsrater på falske reir med vaktelegg (*Coturnix coturnix*) varierte fra 39.8 % til 50.7 % over tre år. De vanligste eggpredatorene var ravn (*Corvus corax*), mår (*Martes martes*) og kråke (*Corvus cornix*). Noen predatorarter utførte lite predasjon på de falske reirene. Disse artene var skjære (*Pica pica*), rødrev (*Vulpes vulpes*), røyskatt (*Mustela erminea*) og snømus (*Mustela nivalis*). Da vi vurderte predasjonsratene opp mot menneskelige påvirkninger fant vi at den totale predasjonsraten økte i samsvar med økende tettheter av vei og sti. Det var en negativ sammenheng mellom predasjon fra mår og tettheter av vei og sti, mens det var en positiv sammenheng mellom predasjon fra ravn og disse variablene. Den totale predasjonsraten økte med økende tetthet av bygninger. Vi fant et negativt forhold mellom predasjon fra ravn og tetthet av bygninger, mens forholdet mellom predasjon fra kråke og tetthet av bygninger var positivt. Dette vil med andre ord si at den dominerende pattedyrarten (mår) var negativt påvirket av menneskelig aktivitet, mens de to dominerende kråkefuglene (*Corvus* spp.) var positivt påvirket av total menneskelig aktivitet, med unntak av ravnens negative sammenheng med tetthet av bygninger. Det kan virke som om menneskelig aktivitet og infrastruktur gir økt ressurstilgang til kråkefuglene, noe som fører til høyere tetthet av kråkefugl. Dette kan igjen føre til høyere predasjonsrater på reir i nærheten av bygninger eller annen infrastruktur. Den største andelen av predasjon fra mår ble utført i skogshabitatet mens den største andelen av predasjon fra kråkefugl ble utført i det mer åpne lavalpine habitatet og i skoggrensa. Vi fant derimot ingen sammenheng mellom total predasjonsrate og tetthet av lirype. Dette kan skyldes vanskelighetene med å overføre predasjonsrater på falske reir til predasjonsrater på ekte reir hvor predasjonen fra pattedyr sannsynligvis er høyere. Selv om vi ikke kunne se noen klar sammenheng mellom predasjon på falske reir og tetthet av predatorer målt ved hjelp av kameraer viste resultatene våre at vi kan forvente høyere tettheter av potensielle predatorer på ryper i nærheten av menneskelig aktivitet, bygninger og infrastruktur. Dette bør det tas hensyn til i planleggingen av for eksempel nye hytteområder for å unngå å oppføre slike hytteområder i områder hvor det er høy produksjon av liryper. Vi fant en positiv tilknytning mellom forekomst av smågnagere og total predasjon.

Contents

Introduction

Willow ptarmigan (*Lagopus lagopus*) population densities in northern Fennoscandia show considerable variation in time and space. It is believed that these fluctuations in population size are caused mainly by variations in reproductive success (e.g. Zwickel 1975, Myrberget 1985, Steen et al. 1988a), which in turn is dependent on factors related to predation and climate (Steen et al. 1988a). Predation on eggs and chicks is recognised as the most important factor influencing reproductive failure in populations of many tetraonid birds (Steen et al. 1988a, Wegge and Storaas 1990), but weather and temperature can also affect production of eggs and chicks (Erikstad and Andersen 1983, Steen et al. 1988b, Swenson et al. 1994). Steen and Erikstad (1996) ranked demographic parameters that affected the number of breeding willow ptarmigan hens by using sensitivity/elasticity analysis. They found that winter survival of juveniles had the largest impact followed by egg survival and chick survival that also had great impact. Cold and wet weather during the pre-laying period of Hazel grouse (*Bonasa bonasia*) influence the availability of nutritious food which may lead to reduced reproductive success (Swenson et al. 1994).

Human disturbances can act as a strong stressor in various species of wild animal populations in their natural habitats (Barja et al. 2007). A number of studies have investigated the impacts of human activities on bird populations (e.g. Andrén 1992, Kurki et al. 1998, Watson and Moss 2004, Marzluff and Neatherlin 2006). The human activity could for instance be related to agriculture, roads, paths, houses and cottages. Traffic and roads can have major ecological effects on animals (Forman and Alexander 1998, Spellerberg 1998), for instance trough direct losses of animal lives (hit by vehicles) or influence animals` movement patterns (Forman and Alexander 1998). Increasing numbers of outdoor recreationists lead to higher impacts on wildlife and wildlife habitat directly through disturbance of animals and less directly through discarded food and other items (Boyle and Samson 1985). In Norway, new cabin areas are opened and existing cabin areas are expanding to meet demands from the general public (Kaltenborn et al. 2005). Cabins in mountain areas are particularly popular, and this development has imposed concerns about the impacts on neighbouring natural ecosystems (Pedersen et al. 2006). Many of these cabins are placed in important willow ptarmigan areas in the transition zone between forests and treeless mountains which may enforce willow

ptarmigan habitat loss (Støen et al. 2010), and favour generalist predators such as foxes (*Vulpe*s spp.) and corvids (*Corvus* spp.) (Storch and Willebrand 1991). American crows (*Corvus brachyrhynchos*) and ravens (*Corvus corax*) in Washington State (USA) have higher reproduction near human settlement and recreation (Marzluff and Neatherlin 2006) and red fox (*Vulpes vulpes*) is potentially able to cause elevated predation pressure in landscapes fragmented by human activities (Kurki et al. 1998). Andrén (1992) suggested that increased corvid activity in fragmented landscapes can be due to many omnivores finding reliable food sources around farms and other human settlements. The red fox can use paths and roads for movements in the landscape, and there is often a greater activity of red fox in areas close to infrastructure and settlement (Røhnebæk 2004, Pedersen and Karlsen 2007). Asmyhr (2008) found a relationship between human activity and predation on artificial nests by some species. He found that pine marten (*Martes martes*) avoided (depredated less in) areas with human activity, while raven and hooded crow (*Corvus cornix*) depredated more in vicinity to human activity.

Potential avian predators of willow ptarmigan in the north boreal and low alpine zone are raven, hooded crow, black billed magpie (*Pica pica*) (Pedersen et al. 1983, Hjeljord 2008), goshawk (*Accipiter gentilis*), gyrfalcon (*Falco rusticolus*), eagle owl (*Bubo bubo*) and golden eagle (*Aquila chrysaetos*) (Hagen 1952). Raven, hooded crow and black billed magpie are primarily nest and chick predators (Hjeljord 2008), while goshawk, gyrfalcon, eagle owl and golden eagle prey upon juvenile and adult ptarmigan (Hagen 1952). Birds rely on their sight to locate food sources and some individuals can specialize on locating nests and thus be responsible for considerable egg losses within their territory or home range (Erikstad et al. 1982). Territorial hooded crows on Tranøy in the north of Norway apparently located ptarmigan nests by watching hens move to and from their nests (Erikstad et al. 1982). Territorial crows were the single most important nest predators on the island Tranøy, and nest losses decreased significantly when the territorial crows were removed (Erikstad et al. 1982). A corvid removal study was also conducted on another island in northern Norway, Karlsøy (Parker 1984). Here all hooded crows, ravens and magpies were removed over four years in a willow ptarmigan and black grouse habitat. The removal took place during nesting and early brooding of the tetraonids. During the study period estimated willow ptarmigan nest loss was lower in only 1 of 4 years, while production, nesting density and chick mortality were

unaffected. Parker (1984) stressed that the study was conducted during years with unusual high chick survival, high production and a rapid increase in willow ptarmigan breeding stocks, despite the high nest losses. Parker (1984) believed that the corvid removal might have led to different results during a period of willow ptarmigan decline.

Potential mammalian predators of willow ptarmigan in the northern boreal and low alpine zone are the specialists least weasel (*Mustela nivalis*) (Hjeljord 2008) and stoat (*M. erminea*), while the generalist predators are red fox, pine marten (Pedersen et al. 1983) and American mink (*M. lutreola*) (Hjeljord 2008). The least weasel, stoat and American mink are all predators mainly on ptarmigan eggs or chicks, while pine marten and red fox also prey on adult individuals. There is a link between predation on ptarmigan and ptarmigan density (Myrberget 1988, Steen et al. 1988a). That the red fox can have high influence on prey populations was observed during the epidemic outbreak of the sarcoptic mange (*Sarcoptes scabei*) in the mid 1970ties (Lindström et al. 1995, Smedshaug et al. 1999). During this period the red fox population experienced a considerable decline, while the hunting bag of central small game species like mountain hares (*Lepus timidus*) and grouse increased (Lindström et al. 1995, Smedshaug et al. 1999). In a one-year experimental study using artificial nests in three willow ptarmigan areas Asmyhr (2008) observed that predation on artificial nests were related to ptarmigan densities, with lowest predation rates where there were highest ptarmigan densities.

The willow ptarmigan is an alternative prey species to many predators in northern Fennoscandia which has voles (*Microtus* and *Myodes* spp.), lemmings (*Lemmus* and *Dicrostonyx* spp.) or other rodents as their main prey (Angelstam et al. 1984). The density fluctuations in willow ptarmigan populations in many areas within the northern boreal and low alpine zone are believed to be caused by varying predation pressure (Steen et al. 1988a), which in turn may be related to fluctuations in local abundance of voles and lemmings (Hagen 1952). When vole densities are low the nest losses are higher than at high vole densities (Angelstam et al. 1984, Myrberget 1984, Myrberget 1988, Steen et al. 1988a, Wegge and Storaas 1990). There also exists support for a hypothesis concerning rodent cycles being

subjected to a bottom-up control rather than controlled by predation (e.g. Selås 1997, Seldal et al. 1994). It is suggested that 3-4 year small rodent cycles are initiated by mast-induced changes in plant chemistry (Selås 1997), and thus only modified by predation (Selås 2006).

A commonly used method for studying the impact of different predator species on breeding success in birds is to use artificial nests with eggs (e.g. Angelstam 1986, Andrén 1992, Moore and Robinson 2004). There are however biases that should be considered when setting up experiments with artificial nests (e.g. Angelstam 1986, Willebrand and Marcström 1988, King et al. 1999, Moore and Robinson 2004). Moore and Robinson (2004) pointed out that differences between predation on artificial nests and natural nests can be caused by varying attraction to the two types of nests by different predator species. The difference in attraction versus avoidance of predator species on artificial nests could occur because predators access, locate and depredate eggs in different manners depending on whether the nest is natural or artificial. It is important to notice that it is not possible to make direct inferences about predation on natural nests based on predation on artificial nests (Zanette 2002).

Most often predation rates are higher on artificial nests than on natural nests (Major and Kendal 1996, King et al. 1999, Burke et al. 2004). It is also established that natural nests are mainly depredated by mammalian predators while birds often are responsible for most artificial nests depredation (Willebrand and Marcström 1988, MacIvor et al. 1990). Artificial nests have greater conspicuousness than natural nests (King et al. 1999), and especially artificial nests with grease, as used in our study, may be easier to detect for a bird in the air, than for a mammal on the ground (Angelstam 1986). The smell of the grease or of the humans handling the nests could also make mammals sceptical and make them avoid the "grease-nests". It is also speculated that the hens scent and trail to the nest cause a higher mammalian predation rate on natural nests (Willebrand and Marcström 1988, O`Reilly and Hannon 1989, MacIvor et al.1990). Despite biases; there are several factors that make artificial nests experiments a very valuable research method. The technique is less time consuming than finding natural nests (O`Reilly and Hannon 1989, Burke et al. 2004), and makes it possible to gather large quantities of data on spatial and temporal predation on eggs from ground nesting birds without disturbing any incubating hen (Klausen et al. 2009). The advantage of using artificial nests, and especially "grease nests", is that it makes it possible to identify the predator (Angelstam 1986). This can be very difficult when it comes to predation on real nests

because there are usually no signs after successful predation (Angelstam 1986). Other advantages with the method is that it provides estimates on predator occurrence in it self (Miller and Hobbs 2000) as well as giving an opportunity to investigating their search patterns (O`Reilly and Hannon 1989), e.g. in relation to habitat and human influence. We argue that for detecting relationships between human activity and predation patterns from different predator species this is a useful method.

The aim of this study was to investigate species specific predation rates on artificial nests in different habitats (birch forest-, tree line- and low-alpine habitat) and in context to human activity and infrastructure, as well as differences in relative predator abundance measured by cameras with bait. These relationships were studied in five areas with dissimilar ptarmigan densities. We also included an index variable on small rodent abundance to control for possible influence of their abundance. Based on earlier studies we predict that: a) predation rates on artificial nests will be lower in areas with higher ptarmigan densities, b) avian predators will be more important than mammalian predators and account for most egg removal in the open low-alpine habitat, c) the different predators' predation rates will be correlated to human activity; pine marten will avoid human activity while corvids will be attracted to human activity, and d) according to the alternative prey hypothesis we expect predation rates to be lower when voles are abundant.

2. Materials and methods

2.1. Study areas

The study was completed in five areas in central Norway (Fig. 1). They are all mountainous areas located between 700 and 1140 m above sea level, with similarities in bedrock, vegetation and composition of the predator community. Mastukåsa/Åslia and Råtåsjøhø is situated in Hedmark County. The study site in Gåvålia is situated on the boarder between Oppland and Sør-Trøndelag County. Dindalen is located in Sør-Trøndelag County and Grødalen in Møre og Romsdal County. For comparable information about longitudes and latitudes, ptarmigan densities, mean June temperatures and precipitations, dominating bedrocks and vegetation in addition to the presence of potential ptarmigan predators, see Table 1. Moen (1999) characterized the northern boreal zone as a zone dominated by birch woodland and some stunted coniferous woodland. The coniferous woodland is comprised of Scots pine (*Pinus sylvestris*) (on dry ground) and Norway spruce (*Picea abies*). In the northern boreal zone you find aspen (*Populus tremula*), species of willow (*Salix* spp.) and rowan (*Sorbus aucuparia*) forming groups with scattered, low-growing trees. The zone has minerothropic mires covering large areas. The upper boundary of the northern boreal zone is placed at the climatic woodland limit which is defined as a line drawn through the uppermost, or northernmost, woodland stands, where the climate determines the uppermost extent of woodland (Moen 1999). But there is also an actual woodland limit that may be determined by topological factors, impact of man and soil factors. The actual woodland limit is often situated considerably lower than the climatic woodland limit. In our study we used the actual woodland limit, and called this the edge habitat. The low alpine zone is the zone above the woodland limit. The lack of woodland is the most important characteristic of the zone. This zone is characterized by bilberry heath (*Vaccinium myrtillus*), juniper (*Juniperus*), dwarf birch scrub (*Betula nana*) and willow communities (Moen 1999). The low alpine zone extend as far up as bilberry, blue heath (*Phyllodoce caerulea*) or scrub vegetation are found.

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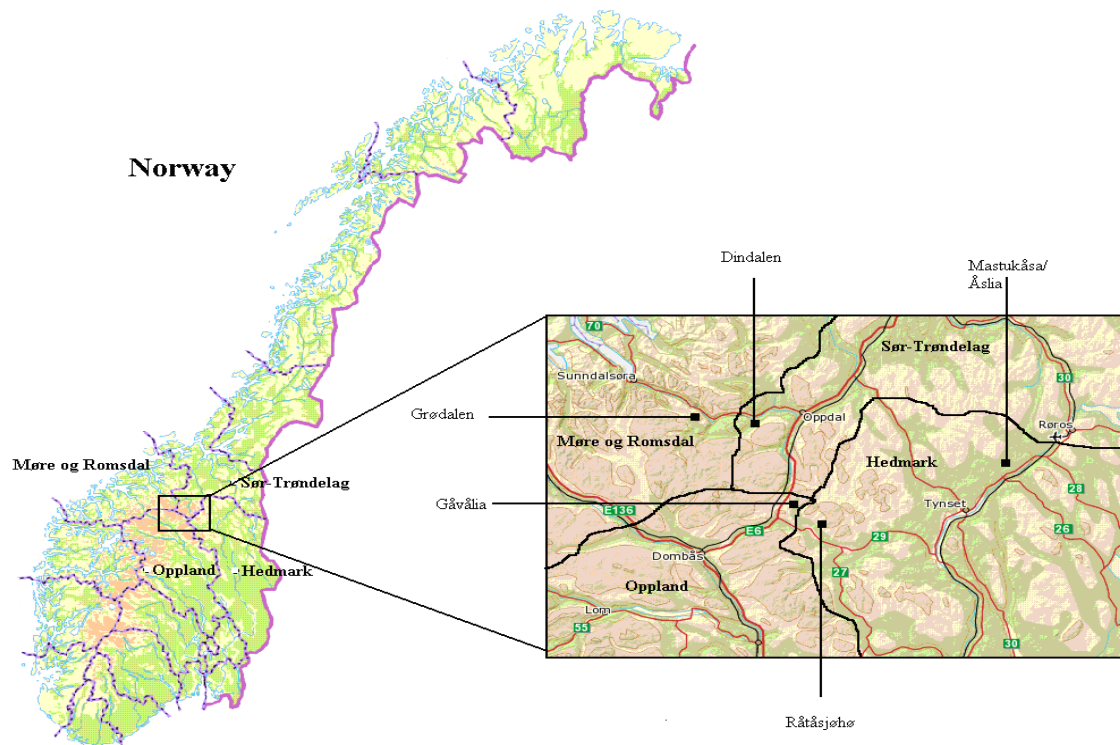
Figure 1: Map of Norway which illustrates the location of the counties in which the study areas are situated (Møre og Romsdal, Hedmark, Oppland and Sør-Trøndelag). Box to the right shows a more detailed map with approximate locations of the study areas (Dindalen, Mastukåsa/Åslia, Råtåsjøhø, Gåvålia and Grødalen). (NGU 2010 II).

Table 1. Longitudes- and latitudes, mean ptarmigan densities (2009), mean June temperatures and precipitations (Meteorologisk institutt 2010 I-IV), dominating bedrocks (NGU 2010 I) and vegetation in addition to the camera recorded presence of potential ptarmigan predators (2009) for all study areas.

	Råtåsjøhø	Mastukåsa/Åslia	Grødalen	Dindalen	Gåvålia
Latitude and longitude	62° 12` - 62° 15`N, 9° 44` – 9° 51`E	62° 35` - 62° 39`N, 10° 55` - 11° 01`E	62° 32` - 62° 35`N, 8° 52` - 8° 57`E	62° 31` - 62° 33`N, 9° 18` – 9° 24`E	62° 14` - 62° 17`N, 9° 37` - 9° 42`E
Estimated mean ptarmigan density/km²	24.0	18.0	5.0	25.0	9.0
Mean June temperature	10.0°C	10.3°C	12.3°C	10.5°C	10.5°C
Mean June precipitation	51 med mer	59 mm	42 mm	49 mm	49 mm
Dominating bedrock	Phyllite	Paragneiss	Migmatite	Migmatite	Igneous rock
Dominating vegetation	*Poaceae, Betula nana, Juniperus*	*Vaccinium myrtillus, Betula nana, Salix* spp.	*Poaceae, Ericaceae* without *Vaccinium myrtillis*	*Ericaceae*	*Poaceae, Betula nana*
Species (events per 14 camera trap days):					
Red fox	0.62	1.16	0.18	0.91	1.89
Pine marten	0.36	0.49	0.00	0.00	0.06
Hooded crow	1.61	4.24	0.00	5.46	3.15
Raven	0.00	0.13	0.00	0.70	2.40
Magpie	0.18	0.06	0.00	0.00	0.06

2.2. Study design

In each of the five study areas we distributed twelve transects, all consisting of three track boards, which were placed along the landscape gradient: birch – edge – low alpine. The transects were placed in a relatively straight line 90 degrees on the tree line, with one track board in the forest habitat, one at the edge (tree line) and one in the low alpine habitat (Fig. 2). The distance between each track board was approximately 100 m, which make the total length of one transect 200 m. Transects were originally placed at random in the landscape, and the distances between transects range from approximately 400 m to 3 km. The different distances between transects was adjusted to avoid the roughest terrain and from logistics reasons as we were depending on easy access to the individual transects by foot.
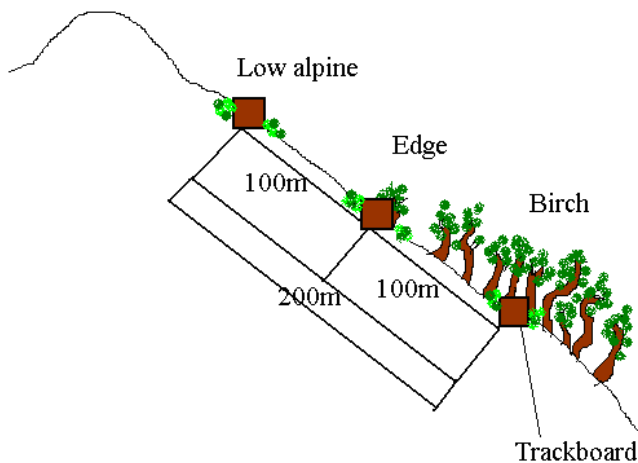
Figure 2: Transect design with position of the track boards along the landscape gradient (birch, edge and low alpine).

2.2.1. Artificial nests

The method of using baited track boards to examine predation has been developed by Angelstam (1986) and Andrén (1992). More recently this study design has for instance been used by Asmyhr (2008), Klausen et al. (2009) and Pedersen et al. (2009). The artificial nests

consisted of a track board, grease, soil and two common quail (*Coturnix coturnix*) eggs (Fig. 3). Common quail eggs and willow ptarmigan eggs have a similar colour and they are both heavily pigmented, but the willow ptarmigan eggs are larger in size than the common quail eggs (O`Reilly and Hannon 1989). The artificial nests are not supposed to imitate natural willow ptarmigan nests, they are simply just a tool to make it possible to identify potential egg predators and predation rates in the study areas. The track boards were made of Huntonitt and measured 60 times 60 cm and were about 3 mm thick. On each of the boards we smeared a thin layer, approximately 2-3 mm, of non-toxic lubrication grease (Mobile grease FM 102). This kind of grease is normally used for large scale kitchen machines. On top of the grease we strewed a thin layer of soil. The soil was supposed to cover the white grease to make the track board less visible. In the centre of each track board we put two common quail eggs. The grease had two functions; it made the eggs stick to the track board and also made it possible to see the footprints of potential predators. Transferring of human scent to the track boards could be a problem (Whelan et al. 1994). To reduce the transferring of human scent we used plastic gloves when we handled all the parts of the artificial nests. The position of each artificial nest was saved on a GPS unit (Garmin).

Figure 3: Left: Track board covered with grease and soil and baited with two common quail eggs. Right: Predated track board with one common quail egg missing and a foot print from the predator.

Each track board was checked for egg depredation after two consecutive trial periods. The first trial periods started during the first half of June in all three years. In year 2007 there were two study areas and hence 24 transects with a sum of 72 track boards while in year 2008 and

2009 there were five study areas and hence a total of 60 transects with a sum of 180 track boards. The total number of track boards for all years and both periods pooled was 864. The consecutive periods lasted for 10 days in 2007 and 7 days in 2008 and 2009. This change was done for practical reasons. A depredation event was recorded if one or both of the eggs of one board were missing or damaged. If there had been a depredation event we examined the footprints and noted which animal that could have caused the depredation. We used hand books for determining mammal tracks (Bang and Dahlstrøm 2000). Avian predators were determined according to Pedersen et al. (2009). If it was not possible for us to determine the predator species the predation was recorded as an unspecified predation event. Least weasel and stoat were pooled together in one group, since it is difficult to distinguish their foot print. In case of predation, new common quail eggs were placed on the track boards for the second trial period. If needed, additional grease and soil were added to the boards. Between the first trial period and the second trial period we moved all the artificial nests 50 m along the tree line (all nests in each transects were moved in the same direction), so the predators should not find the boards at the exactly same place as the first time. The moving of the nests was done because experiments have shown that predators can concentrate their food search in areas where earlier searches have been successful (O`Reilly and Hannon 1989). Nests disturbed by domesticated animals (mainly sheep) were registered as missing data (n=81) and not included in further analysis.

To get an idea of the influence the track board had on the predator's ability to find our artificial nests, eggs without track boards were also distributed in our study areas in 2009. These "extra eggs" were placed in pairs directly on the ground 20 m away from selected track boards, 90 degrees on the tree line. We positioned a total of 60 pairs with "extra eggs" in all areas and both periods pooled, and marked their location with small paper strips tied to nearby vegetation and saved the position on a GPS unit. The "extra eggs" were checked and moved along with the track boards from the first period to the second period.

Our study has great resemblance to the study of Asmyhr (2008), who completed his fieldwork in 2007. He used data from only one year in three separate study areas, while we used data

from three years (2007-2009) and five different study areas (Table 2). The data we used from 2007 is extracted from Asmyhrs` (2008) data. Asmyhr (2008) did not move the track boards from their position in the first period to a new position in the second period as we did. For practical reasons we also used shorter trial periods; Asmyhr (2008) had two consecutive periods on ten days, while we had two consecutive periods on seven days. We did not adjust for the different length of the trial periods in the analysis since no good method for doing such an adjustment is developed. In addition we used more predictor variables than Asmyhr (2008) in the model selection (see 2.2.7 Statistical tests).

Table 2: Study areas used by Asmyhr (2008) = X, study areas used in our study = Y. (We have not included Asmyhr's (2008) third study area Raudfjellet in this table because this area was not included in the field work of 2008 and 2009 and is hence not a part of our study).

	Råtåsjøhø	Mastukåsa/Åslia	Grødalen	Dindalen	Gåvålia
2007	XY	XY			
2008	Y	Y	Y	Y	Y
2009	Y	Y	Y	Y	Y

2.2.2. Presence of potential ptarmigan nest predators

To get a measure of relative predator abundance, two automatic cameras (Stealth Ocam, Prowler DVS, STC-DVSIR5) with bait were set up in each study area. The purpose of these specific cameras was to document the potential ptarmigan predator species and differences in their relative abundance within our study areas. The bait used to attract potential predators to the camera was roadkills of moose (*Alces alces*), roe deer (*Capreolus capreolus*) and red deer (*Cervus elaphus*). The distance between the camera pairs ranged from approximately 2.7 km to 5.3 km (average 4.7 km) depending on topography and where proper camera sites could be found. The camera studies were carried out from March to July/August in 2009.

The cameras were equipped with 2GB memory chips to ensure capacity to record every approaching animal, and were checked with 14-64 days intervals. Memory chips were

replaced with empty ones whenever cameras were checked, the bait was replaced if most of the meat had been eaten. We set the cameras to take a series of three pictures (2 second intervals between pictures) when triggered by movement, and we chose the lowest possible interval between picture series (1 minute). The date and time appear at the bottom of each picture. The appearance of a predator in the pictures was counted as a separate "event" when there was > 1hour between appearances by individuals of the same species. The total number of events by each predator was pooled for the entire period and for each area separately. To get a relative estimate of abundance we corrected for number of trap days. In order to compare camera events with predation events on the track boards we chose to present the data as "camera events per 14 trap days" because the track board study lasted for 14 days.

2.2.3. Human activity

As indices of human activity we measured distance from all track boards to the closest road, the closest path and the closest settlement. To estimate human activity we included indices of road density, path density and settlement density. Forman and Alexander (1998) claimed that road density, e.g. measured as length of roads in km/km², is a useful index of ecological effects of roads. For the density indices we measured variables on three scales from each track board; number of buildings, total length of paths and total length of roads within circles with radius 1 km, 3 km and 5 km from each track board.

To measure distances from track boards to closest building, closest path and closest road we used the program Map Source version 6.13.7 (1999-2008 Garmin Ltd. or its subsidiaries), with the maps Topo Adventures and Topo Pro for all study areas. In these instances the two types of maps gave the exact same results for distance to human activities. We measured the linear distance with a ruler tool.

To measure the density indices of human activity a GIS-program called PostGIS 1.5 (an extension of PostgreSQL 8.4) with N50 maps was used. The Euclidean 2 dimensional distances were measured.

Buildings included in the term settlements were houses, cabins, agriculture buildings, industrial buildings and campgrounds. The term path included unmarked trails (there were no

marked trails in the areas). The term roads included all roads denoted as roads in the N50 maps (e.g. European route E6 and national roads)

2.2.4. Ptarmigan density

In the latest years willow ptarmigan surveys have been conducted in selected areas in Norway (Solvang et al. 2007). The method used is counting of ptarmigan along census lines. Pointing dogs are used by the observers. The observers and the dogs are searching for ptarmigan along the line. In advance of the surveys the placement of the census lines has to be decided. It is important that the quality of the areas adjacent to the census lines reflects the quality of the study area as a whole.

Two different methods to measure ptarmigan density have been used by us to see if there is any relationship between ptarmigan density and predation rate on artificial nests. The first method called "Distance sampling" was used in the three study areas Råtåsjøhø, Mastukåsa/Åslia and Grødalen. When ptarmigan are being found using this method the distance from the line to the place of the ptarmigan residence are measured. The probability to observe ptarmigan are depending on the distance between the census lines and the ptarmigan. If the ptarmigan is positioned close to the census line the probability to observe it is higher than if it is positioned further away. For the density estimation three values need to be measured; the length of the census line, the distance from the line to an observation and the number of birds per observation. To estimate the ptarmigan densities a statistic program called "Distance sampling" is used (Buckland et al. 2007). The program shows consideration for the probability to observe ptarmigan in relation to distance between census lines and ptarmigan. Volunteers (often small game hunters and dog owners) have joined the ptarmigan surveys as observers, and the "Grouse Managament Project 2006-2011" has calculated the ptarmigan densities using the "Distance sampling" method.

In the study areas Dindalen and Gåvålia we obtained estimates on ptarmigan densities by the second approach. The estimates of ptarmigan density were conducted in relation to a monitoring program for terrestrial ecosystems (TOV) by NINA (Norwegian Institute for Nature Research) (Framstad and Kålås 2005). Also this method of measuring ptarmigan density uses census lines walked by observers with pointing dogs. To calculate ptarmigan

density using the methods of the TOV project the values needed is number of ptarmigan observed, the total length of the census line, the width of the census line and a coefficient of detectability of ptarmigan within the area. In this instance the width of the census line was set to 100 m and the detectability was set to 80% (Pedersen et al. 1999). In 2009 both methods were used in census of willow ptarmigan in Gåvålia giving approximately the same density estimates (Distance: 13 ptarmigan/km² and 3.3 chicks/hen, TOV: 16 ptarmigan/km² and 3.0 chicks/hen). For both methods the observers registered the number of juveniles and the number of adult ptarmigan. From these numbers the chick/hen-ratio is estimated.

2.2.5. Tree density

At each transect we used a "relascope like" method to estimate the number of trees within 360° radius of the transect line. We used a "home made" relascope with a small rectangular piece of hard plastic with the same width as the opening of the original relascope, tightened to a thin rope. Because we lost this measure instrument we had to use our outstretched arm (equivalent to the string), and our little finger acted as the blade in Gåvålia 2009. The trees that were visible when our finger was placed directly in front of them were counted, thus giving us a relative measurement of trees in the nearby area of the transect line. This was done every 10th m (a total of 21 stations along each transect), starting by the track board in the forest habitat and finishing by the track board in the low-alpine habitat. We pooled all tree species and had therefore only one category including both deciduous and coniferous trees. When performing the model selection we pooled the seven stations closest to each track board to get the tree density in the respective habitats. The use of different approaches for measuring tree density is not optimal, we believe however that the relative difference is good enough, and the results seem ecologically sound.

2.2.6. Small rodent abundance

The data on trapped small rodents per 100 trap days from Åmotsdalen was used as an index of small rodent abundance in our study. We got the data on small rodent abundance for Åmotsdalen 2009 from Erik Framstad (pers. comm.). Data from 2007 was extracted from Framstad (2008) while data from 2008 was extracted from Framstad (2009). Åmotsdalen is

situated in Oppdal municipality and is centred between the study areas with Mastukåsa/Åslia as the outlying study area with longest distance to Åmotsdalen. Year 2007 was a peak year in the small rodent populations with 65 small rodents per 100 trap days, whereas in 2008 no small rodents were trapped (low year) and in 2009 two small rodents were trapped per 100 trap days (low year). Small rodent population fluctuations at separate localities within regions occur with high degree of synchrony, (e.g.; Kalela 1962, Myrberget 1973, Korpimäki and Krebs 1996, Lambin et al. 2006), especially the high peaks in small rodent abundance are common over entire regions (Hjeljord 2008). In the study year 2009 we also recorded signs of small rodent activity systematically within all study areas, and in connection to each transects, to account for possible population differences (peak, crash, low); recording rodent tunnels, lairs, faeces as well as small rodent bite marks on vegetation on every m along a 50 m measuring tape (50 measuring units pr transect). Other studies using similar methods have shown that such small rodent activity is proportional to local abundance (Lambin et al. 2000). These signs of activity occurred in relatively equal frequencies between the study areas, and as this was only done in 2009, we used only the one regionally estimate on small rodent abundance i.e. in our study the data from Åmotsdalen.

2.2.7. Statistical tests

Lewis (2004) examined different types of statistical tests used to analyse artificial nest data. He concluded that logistic regression is the most appropriate form of the generalized linear models for analysing artificial nest data with a binary or proportional response variable. Based on Lewis (2004) we are using logistic regression to analyse our data. We performed the logistic regression in JMP® 4.0.0. (SAS Institute Inc 2000).

In our study the outcome variable was predation/not predation on the track boards. We were studying the outcome in six groups: total predation, predation by mammals, predation by birds, predation by pine martens, predation by ravens and predation by hooded crows. With exception from the first mentioned group we were studying predation in the different groups in relation to the overall predation. Total predation was studied in relation to all available track boards. The predictor variables were: year, location, period, habitat (birch, edge or low-alpine), distance to closest settlement, distance to closest path, distance to closest road,

ptarmigan density, chicks/hen, number of trees (using relascope from each track board), small rodent index, number of buildings within a circle with radius 1 km, 3 km and 5 km from each track board, total length of paths within a circle with radius 1 km, 3 km and 5 km from each track board and total length of roads within a circle with radius 1 km, 3 km and 5 km from each track board. I.e. we have three different scales for each predictor variable for human activity (1km, 3 km and 5km).

The predictor variables year and location was treated as random effects. Location turned out to be a biased and zeroed variable and was hence not included in any models (Hosmer and Lemeshow 2000). Distance to closest settlement and chicks per hen did not contribute enough to be included in any of the three best models to explain predation in the different groups. Number of buildings within a circle with radius 1 km, 3 km and 5 km from each track board were strongly correlated variables. Maximum one of these variables was included in each model. The same principle goes for the total length of paths within a circle with radius 1 km, 3 km and 5 km from each track board and the total length of roads within a circle with radius 1 km, 3 km and 5 km from each track board. To decide which scale to use on the predictor variables in the models we evaluated AICc-values for the full models and chose the scale that gave the models with the lowest AICc-value. We accepted the scale to be different for the different types of human activity variables (settlement, road and path) in each model if this gave the model with lowest AICc-value. We listed the three best models for each predator group and did not include new models with the only change being switching one scale of a human activity predictor variable with one of the other two scales for the same predictor variable giving a model with higher AICc-value. Variables with p-values < 0.1 in the multivariable models were considered to be included in the models. To avoid biased models we compared the size of the variable coefficients between univariable models and multivariable models (for univariable estimates see Appendix 1). If the variable coefficients had changed markedly in magnitude, or had changed from a positive to a negative value or opposite, the variable was not included in the model (Hosmer and Lemeshow 2000). We also compared the ratio of the size of the standard errors of the parameter estimates to the size of the parameter estimates and excluded variables with ratios greater than 0.6 or lower than -0.6. As a model-building strategy we used variable selection (Hosmer and Lemeshow 2000). When analysing predation rates we pooled all study areas and all years.

To select the best models we used Akaikes information criterion corrected for small sample

size (AICc) and Akaike weights (w AICc). In the tables listing the three best models for the predator groups in the result part we only show the predictor variables used in these models. The best model was the model with lowest AICc-value and highest w AICc-value. To assess the relative merits of the models we treated models with ΔAICc $\leq$ 2.0 as models with substantial support while models with ΔAICc $\geq$ 4.0 had substantial less support (Burnham and Anderson 2004). Based on advices from Anderson and Burnham (2002) we listed these values for each of the models in the result-part; the maximized log-likelihood (Max. logl.), number of estimable parameters (k), AICc-value, ΔAICc and the Akaike weights (w AICc). In addition we also listed p-values, estimates (reg. coef.), standard errors (SE) and variable importance (VI) of the predictor variables (Anderson and Burnham 2002).

In the model selection part of the results the predictor variable terms "road", "path" and "settlement" are used for the distance from track boards to the closest road, path and settlement respectively. The terms "settlement 1km", "path 1km", "road 1km", "settlement 3km" etc. are used for the number of buildings within circles with the given radius from each track board and the total length of paths and roads within circles with the given radius from each track board respectively.

To reveal if there was any relationship between total predation rate and ptarmigan density in the different study areas in the various years we performed a simple linear regression in JMP 4.0.0. The outcome variable was total predation rate and the predictor variable was ptarmigan density.

3. Results

3.1. Predator assemblage

In all study areas and all years pooled five different predator species were identified as predators on the track boards. In addition, stoats or least weasels or both had been on the track boards, but it was not possible to distinguish these two species. We also included a group with unknown predators where we could not identify the species. There were not enough predation events by red fox (n=8), stoats/least weasels (n=9) and magpies (n=15) to perform any model selection on predation by these species separately. Raven (n=109) was the most common predator followed by pine marten (n=73) and hooded crow (n=72). Depredation rates pooled for all years by the different predator species in the study areas is presented as percentage of available nests in the study areas depredated (Fig. 4). A more thorough summary of the data on predation by the different species distributed on location, habitat and year is given in Appendix 2.
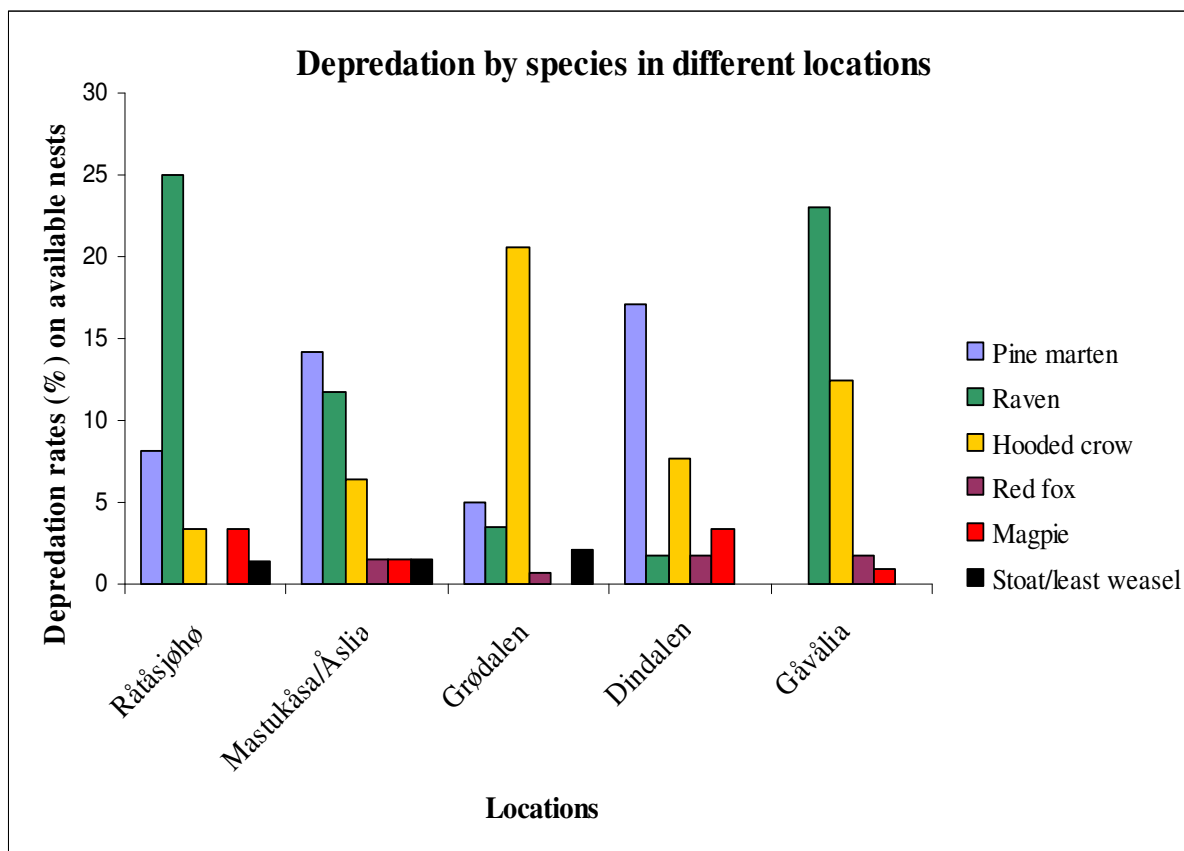
Figure 4: Depredation rates (%) by our identified species pooled over all years on the different study locations.

Of the available nests in the different habitats; 42.4% (n=255) were depredated in the birch habitat, 40.6% (n=256) were depredated in the edge habitat and 44.9% (n=272) were depredated in the low alpine habitat. The different predator species had different depredation rates depending on the type of habitat. Most of the pine marten depredation was done in the birch habitat, while most of the raven and hooded crow depredation was done in the low alpine habitat (Fig. 5).
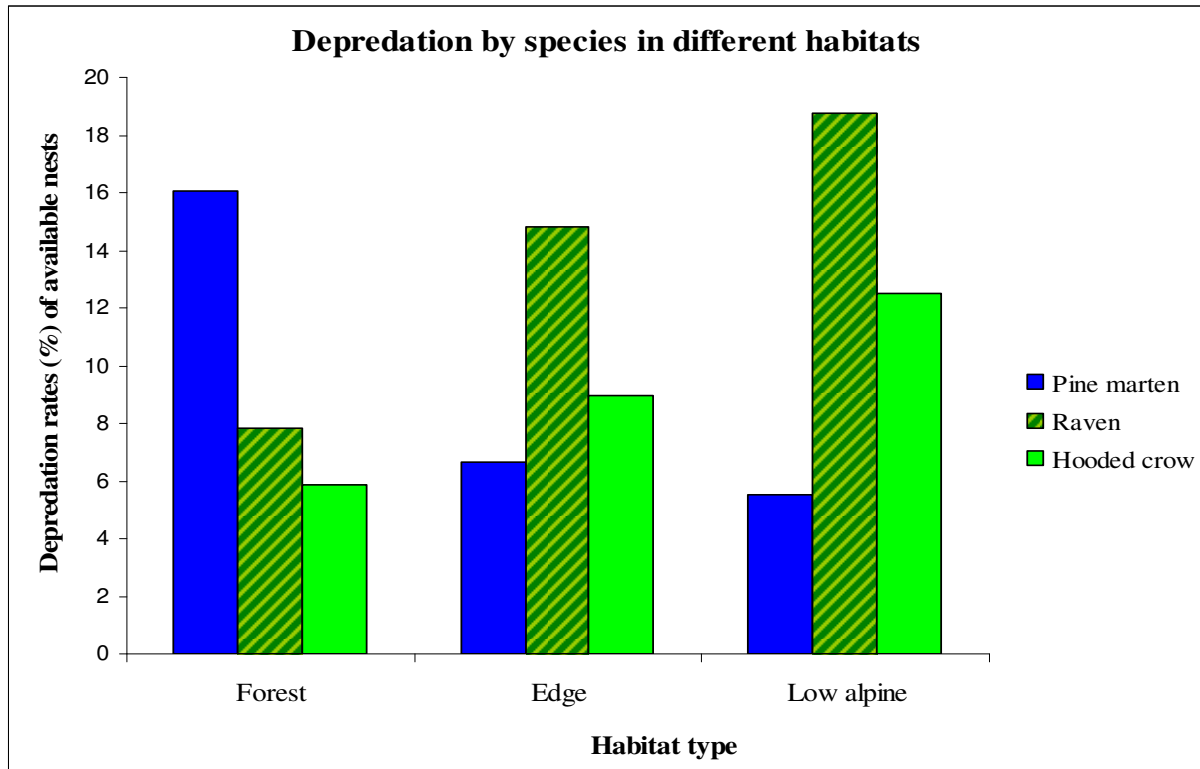
Figure 5: Depredation rate by pine marten, raven and hooded crow in the different habitats.

There was also a yearly difference in predation rates of available nests by the three dominating predator species pooled together for all study areas (Fig. 6). Of the available nests in the different years pine martens depredated 12.3 % (n=138) in 2007, 12.9% (n=326) in 2008 and 4.4 % (n=319) in 2009. Raven depredated 27.5 % (n=138) in 2007, 13.5 % (n=326) in 2008 and 8.5 % (n=319) in 2009, while hooded crow depredated 2.9 % (n=138) in 2007, 5.5 % (n=326) in 2008 and 15.7 % (n=319) in 2009.
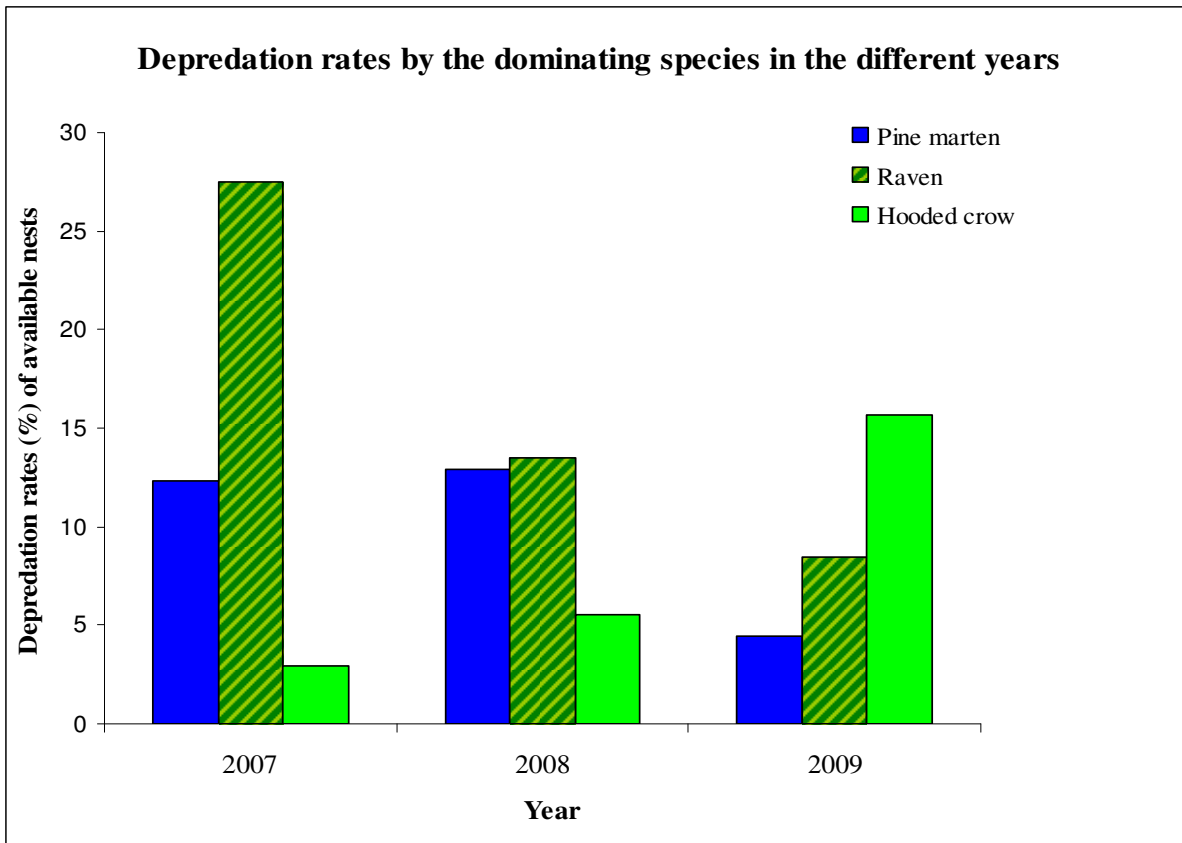
Figure 6: Yearly variations in depredation rates (%) of available nests by the dominating predator species.

None of the "extra eggs" placed in the vicinity of the track boards were subjected to predation.

3.2. Presence of potential nest predators

A comparison between the total number of predation events on the track boards and total number of camera events by each predator species showed no consistent relationships (Table 3). Within some of the study areas there was however some concurrence between these two datasets.

Table 3: Number of predation- and camera events per 14 trap days in the different study areas and by the different predator species in 2009. The predation- and camera events are adjusted to present the respectively proportions of events over each study area.

SPECIES	METHOD	AREA				
		Råtåsjøhø	Mastukåsa/Åslia	Grødalen	Dindalen	Gåvålia
Red fox	Camera	0,22	0,19	1,00	0,13	0,25
	Track board	0,00	0,15	0,00	0,00	0,00
Pine marten	Camera	0,13	0,08	0,00	0,00	0,01
	Track board	0,40	0,69	0,03	0,00	0,00
Hooded crow	Camera	0,58	0,70	0,00	0,77	0,42
	Track board	0,20	0,15	0,82	0,75	0,38
Raven	Camera	0,00	0,02	0,00	0,10	0,32
	Track board	0,10	0,00	0,15	0,00	0,58
Magpie	Camera	0,06	0,01	0,00	0,00	0,01
	Track board	0,30	0,00	0,00	0,25	0,04

The red fox occurred on the cameras in all five areas, while red fox predation was only recorded in Mastukåsa/Åslia. Mastukåsa/Åslia and Råtåsjøhø were the two areas were pine marten events occurred both on the track boards and on the pictures. Hooded crows were recorded both by cameras and on track boards in all areas except from in Grødalen, where events were only recorded on track boards. Number of predation events of hooded crow in Grødalen was also the highest recorded in this study. Raven occurred on both cameras and track boards only in Gåvålia, but occurred in all areas either on track boards or camera. Magpie events were recorded by both methods only in Gåvålia and Råtåsjøhø, but occurred also on track boards in Dindalen and on cameras in Mastukåsa/Åslia

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3.3. Total predation

The total predation rate over all study areas and all years pooled was 42.7% (n=783). The three best models to explain total predation included the predictor variables year, period, road, small rodent index, settlement 1 km, path 5 km and road 3 km (Table 4). All the three best models have substantial support compared to each other (ΔAICc ≤ 2.0).

Table 4: The three best models explaining total predation ranked from best to third best (the best model is indicated in bold letters). Settl. = settlement, Small rod. = small rodent index.

Model	Max logl.	k	AICc	ΔAICc	w (AICc)	Variable	Reg. coef.	SE	P-value	VI
1	-518,45	6	1049,01	**0,00**	0,26	Year	-0,244268	0,104379	0,0189	0,59
						Period (1)	-0,194869	0,073970	0,0082	1,00
						Road	-0,000341	0,000149	0,0199	1,00
						Settl. 1km	0,004661	0,002441	0,0546	0,67
						Road 3km	0,000016	0,000009	0,0650	0,26
						Constant	490,00	209,67		
2	-518,69	6	1049,49	0,48	0,20	Year	-0,262798	0,103108	0,0106	0,59
						Period (1)	-0,195437	0,073952	0,0080	1,00
						Road	-0,00035	0,000147	0,0153	1,00
						Settl. 1km	0,004261	0,002491	0,0853	0,67
						Path 5km	0,000009	0,000005	0,0874	0,49
						Constant	527,35	207,09		
3	-519,72	5	1049,52	0,51	0,20	Period (1)	-0,190954	0,073772	0,0094	1,00
						Road	-0,000380	0,000148	0,0086	1,00
						Small rod.	0,008801	0,003038	0,0037	0,41
						Settl. 1km	0,005329	0,002415	0,0261	0,67
						Constant	-0,162633	0,168728		

The total predation rate decreased over the years from 50.7% (n=138) in 2007, to 42.0% (n=326) in 2008 and to 39.8% (n=319) in 2009. In the first trial periods the predation rates were lower (38.1%, n=383) than in the second trial periods (47.0%, n=400). There was a negative association between distance to road and predation. The average distance from a depredated track board to the closest road was 838 m (±27 SE), while the average distance from a track board that was not depredated to the closest road was 967 m (±29). The year with the highest small rodent index (year 2007) had the highest predation rate. The numbers of

buildings within a circle with radius 1 km from each track board was positively associated with predation. The average number of buildings within these circles at depredated track boards was 21 (±2), while at not depredated track boards the number of buildings was 14 (±1). Total length of paths within a circle with radius 5 km from each track board was positively associated with predation. The average total length of paths within these circles at depredated track boards was 39.53 km (±0.80), while the average total length of paths was 36.55 km (±0.69) at not depredated track boards. Total length of roads within a circle with radius 3 km from each track board was also positively associated with predation. The average total length of roads within these circles at depredated track boards was 30.74 km (±0.45), while the average total length of paths was 28.82 km (±0.45) at not depredated track boards.

3.4. Mammalian predation

In the category mammalian predation we included the species pine marten, red fox and stoat/least weasel. Predation from mammals occurred at 11.5% of the available track boards (n=783) over all years and all study areas pooled together. The three best models to explain the mammalian depredation among the depredation events included the predictor variables year, habitat, path, number of trees registered (using relascope) and paths 3 km (Table 5). Model 2 and 3 have considerably less support (ΔAICc $\geq$ 4.0) than model 1. Therefore we will only discuss model 1 as a good model explaining predation by mammals.

Table 5: The three best models explaining predation by mammals ranked from best to third best (the best model is indicated in bold letters). Hbt. = habitat, Nu. trees = number of trees registered (using relascope).

Model	Max logl.	k	AICc	ΔAICc	w (AICc)	Variable	Reg. coef.	SE	P-value	VI
1	-159,88	6	331,87	**0,00**	0,89	Year	-0,766779	0,195143	0,0001	1,00
						Hbt. alpine	-0,552250	0,204267	<0,0001	0,96
						Hbt. birch	0,915134	0,190469	<0,0001	0,96
						Path	0,000576	0,000214	0,0070	0,94
						Path 3 km	-0,000089	0,000021	<0,0001	0,99
						Constant	1539,66	391,82		
2	-163,52	5	337,12	5,25	0,06	Year	-0,627000	0,183678	0,0005	1,00
						Hbt. alpine	-0,567690	0,203631	<0,0001	0,96
						Hbt. birch	0,928802	0,187818	<0,0001	0,96
						Path 3 km	-0,000102	0,000020	<0,0001	0,99
						Constant	1259,58	368,86		
3	-164,11	5	338,30	6,43	0,04	Year	-0,883869	0,197583	<0,0001	1,00
						Path	0,000686	0,000211	0,0010	0,94
						Nu. trees	0,014365	0,003571	0,0001	0,04
						Path 3 km	-0,000084	0,000021	<0,0001	0,99
						Constant	1774,19	396,69		

Depredation rates by mammals among all depredation events decreased over the years. In 2007 the mammalian depredation rate was 32.9% (n=70), in 2008 the rate was a bit higher with 35.0% (n=137) while in 2009 the rate sank to 15.0% (n=127). Mammals showed selectivity in habitat use in relation to depredation rate. Of the track boards depredated by mammals (n=90) 53.3% were situated in the birch forest, 23.3% were situated in the edge habitat and 23.3% were situated in the low alpine habitat. There was a positive relationship between distance to closest path and depredation on track boards. The average distance from a track board depredated by mammals to the closest path was 828 m (±81). Total length of paths within a circle with radius 3 km from each track board was negatively associated with depredation rates. The average total length of paths within these circles at track boards depredated by mammals was 13.16 km (±0.72).

3.5. Avian predation

In the category avian predation we included the species raven, hooded crow and magpie. Over all study areas and all years 25.0% of the available track boards (n=783) were depredated by avian predators. The three best models explaining avian predation among the depredated track boards included the predictor variables period, habitat, path 1 km and road 1 km (Table 6). Model 3 has considerably less support (ΔAICc $\geq$ 4.0) than model 1 and model 2. Therefore we will only discuss model 1 and model 2 as good models explaining predation by birds.

Table 6: The three best models explaining total predation by avian predators ranked from best to third best (the best model is indicated in bold letters). Hbt. = habitat.

Model	Max logl.	k	AICc	ΔAICc	w (AICc)	Variable	Reg. coef.	SE	P-value	VI
1	-197,22	5	404,52	**0,00**	0,68	Period (1)	0,231108	0,124277	0,0611	0,68
						Hbt. alpine	0,537828	0,171171	<0,0001	1,00
						Hbt. birch	-0,756673	0,171942	<0,0001	1,00
						Path 1km	0,000397	0,000073	<0,0001	1,00
						Constant	-0,522161	0,198088		
2	-198,98	4	406,01	1,49	0,32	Hbt. alpine	0,538253	0,170318	<0,0001	1,00
						Hbt. birch	-0,746444	0,170899	<0,0001	1,00
						Path 1km	0,000386	0,000072	<0,0001	1,00
						Constant	-0,531930	0,197242		
3	-203,73	5	417,54	13,02	0,00	Period (1)	0,218730	0,121485	0,0700	0,68
						Hbt. alpine	0,556798	0,168144	<0,0001	1,00
						Hbt. birch	-0,765705	0,168618	<0,0001	1,00
						Road 1km	0,000240	0,000055	<0,0001	0,00
						Constant	-0,512834	0,230786		

In the first trial period 63.0% of all depredated track boards (n=146) were predated by birds while in the second trial period 55.3% of all depredated track boards (n=188) were predated by birds. Of the track boards predated by birds (n=196) 22.4% was situated in birch habitat, 33.7% in edge habitat and 43.9% in low alpine habitat. Avian depredation was positively related to average length of paths within a circle with radius 1 km from each track board. The average total length of paths within these circles at track boards depredated by avian was 2.87

km (±0.13).

3.6. Predation by pine martens

Of the available track boards (n=783) over all study areas and all years 9.3% was depredated by pine martens. To explain the pine marten depredation among the depredation events the three best models included the predictor variables year, habitat, path, number of trees registered (using relascope), path 3 km and road 1 km (Table 7). Model 1 and model 2 have substantial evidence compared to each other (ΔAICc $\leq$ 2.0), while model 3 has less support (ΔAICc=3.28).

Table 7: The three best models explaining predation by pine marten ranked from best to third best (the best model is indicated in bold letters). Hbt. = habitat, Nu. trees = number of trees registered (using relascope).

Model	Max logl.	k	AICc	ΔAICc	w (AICc)	Variable	Reg. coef.	SE	P-value	VI
1	-138,09	7	290,32	**0,00**	0,43	Year	-0,756117	0,215682	0,0005	1,00
						Hbt. alpine	-0,648604	0,229539	<0,0001	0,48
						Hbt. birch	0,966297	0,205986	<0,0001	0,48
						Path	0,000622	0,000231	0,0071	0,96
						Path 3km	-0,000077	0,000026	0,0033	0,90
						Road 1km	-0,000151	0,000089	0,0914	1,00
						Constant	1518,17	433,05		
2	-139,13	6	290,37	0,05	0,42	Year	-0,926960	0,222234	<0,0001	1,00
						Path	0,000702	0,000228	0,0021	0,96
						Nu. trees	0,019086	0,004122	<0,0001	0,52
						Path 3km	-0,000058	0,000026	0,0225	0,90
						Road 1km	-0,000251	0,000094	0,0078	1,00
						Constant	1860,63	446,17		
3	-141,76	5	293,60	3,28	0,08	Year	-0,911729	0,218669	<0,0001	1,00
						Path	0,000731	0,000229	0,0014	0,96
						Nu. trees	0,019661	0,004074	<0,0001	0,52
						Road 1km	-0,000356	0,000085	<0,0001	1,00
						Constant	1829,49	439,00		

The depredation rate by pine martens among all the depredation events decreased over the years. In 2007 the pine marten depredation rate was 24.3% (n=70), in 2008 the rate was 30.7% (n=137) and in 2009 the rate was 11.0% (n=127). In other words there was not a

decline in depredation rate from 2007 to 2008, but there was a big decline to the year 2009. The pine martens showed a preference in type of habitat to conduct depredation. Of the track boards with predation events performed by pine martens (n=73) 56.2% of the track boards were situated in birch habitat, 23.3% were situated in edge habitat and 20.5% were situated in low alpine habitat. Depredation rate by pine martens increased with distance to closest path. The average distance to the closest path from track boards predated by pine martens was 900 m (±91) (Table 8). Number of trees estimated from each track board using relascope was positively associated with depredation rate by pine martens. The average number of trees estimated using relascope at track boards predated by pine martens was 45 (±5). Total average length of paths within a circle of 3 km from each track board was negatively associated with predation rate by pine martens. The average total length of paths within these circles at track boards depredated by pine martens was 12.53 km (±0.79). Total length of roads within a circle with radius 1 km from each track board was also negatively associated with predation rate by pine martens. The average total length of roads within these circles at track boards depredated by pine martens was 2.69 km (±0.26).

Table 8: Settlement 1 km, path 1 km, road 1 km etc. are the average number of settlements and average length of paths and roads within circles with the given radius from each track board respectively. Settlement, path and road are the distance from a depredated track board to the closest situated settlement, path and road. The average numbers of the variables for all track boards depredated by the three most common species in our study are listed; the standard errors are given in parenthesis.

	Raven	Pine marten	Hooded crow
Settlement 1 km	11 (±2)	17 (±4)	44 (±6)
Settlement 3 km	95 (±9)	121(±15)	211 (±21)
Settlement 5 km	270 (±18)	318 (±19)	379 (±28)
Path 1 km	3.17 km (±0.17)	1.56 km (±0.20)	2.59 km (±0.19)
Path 3 km	18.78 km (±0.51)	12.53 km (±0.79)	17.01 km (±0.77)
Path 5 km	44.95 km (±10.42)	31.58 km (±1.88)	41.07 km (±1.68)
Road 1 km	4.13 km (±0.19)	2.69 km (±0.26)	4.68 km (±0.26)
Road 3 km	32.91 km (±0.70)	27.67 km (±1.05)	31.28 km (±0.95)
Road 5 km	93.08 km (±2.01)	77.39 km (±2.96)	77.83 km (±2.33)
Settlement	1.02 km (±0.04)	934 m (±63)	692 m (±51)
Path	461 m (±47)	900 m (±91)	557 m (±79)
Road	955 m (±40)	963 m (±68)	650 m (±54)

3.7. Predation by ravens

Ravens depredated 13.9% of the available track boards (n=783) all years and all study areas pooled. To explain the depredation rate by ravens among all depredation events these predictor variables were included in the three best models: year, habitat, ptarmigan density, small rodent index, settlement 3 km, path 1 km and road 5 km (Table 9). Model 1 and model 2 have great support compared with each other. Model 3 is also accepted (ΔAICc=2.88), but this model has less support than the two best models.

Table 9: The three best models explaining predation by ravens ranked from best to third best (the best model is indicated in bold letters). Hbt. = habitat, Settl. = settlement, Small rod. = small rodent index, Pt. dens. = ptarmigan density.

Model	Max logl.	k	AICc	ΔAICc	w (AICc)	Variable	Reg. coef.	SE	P-value	VI
1	-163,35	7	340,84	**0,00**	0,59	Year	-0,446498	0,185273	0,0152	0,61
						Hbt. alpine	0,530723	0,186798	0,0002	0,91
						Hbt. birch	-0,824260	0,214490	0,0002	0,91
						Settl. 3km	-0,005542	0,001317	<0,0001	0,97
						Path 1km	0,000383	0,000090	<0,0001	1,00
						Road 5km	0,000020	0,000007	0,0033	0,97
						Constant	893,82	372,17		
2	-164,15	7	342,44	1,60	0,27	Hbt. alpine	0,529179	0,186144	0,0002	0,91
						Hbt. birch	-0,814838	0,213488	0,0002	0,91
						Small rod.	0,010618	0,005121	0,0382	0,27
						Settl. 3km	-0,005788	0,001316	<0,0001	0,97
						Path 1km	0,000398	0,000090	<0,0001	1,00
						Road 5km	0,000019	0,000007	0,0049	0,97
						Constant	-2,957220	0,584318		
3	-164,79	7	343,72	2,88	0,14	Hbt. alpine	0,529384	0,185807	0,0002	0,91
						Hbt. birch	-0,823336	0,212594	0,0002	0,91
						Pt. dens.	0,021651	0,012507	0,0826	0,12
						Settl. 3km	-0,004635	0,001451	0,0007	0,97
						Path 1km	0,000389	0,000089	<0,0001	1,00
						Road 5km	0,000024	0,000007	0,0003	0,97
						Constant	-3,822870	0,715569		

Raven depredation rate among all depredation events decreased over the years. In 2007 the raven depredation rate was 54.3% (n=70), in 2008 the rate was 32.1% (n=137) and in 2009 the rate was 21.3% (n=127). Predation rate by ravens was differing between the different types of habitats. Of the track boards predated by ravens (n=109) 16.9% was situated in the birch habitat, 36.9% was situated in the edge habitat and 46.2% was situated in the alpine habitat. Raven depredation was positively associated with the ptarmigan density. On track boards depredated by ravens the ptarmigan density in the area was on average 27 ptarmigan per km² (±1). Most of the raven depredation took place in the small rodent peak year (2007). That makes the raven depredation positively associated with the small rodent index, at track boards depredated by ravens the average small rodent index was 23 small rodents per trap day (±3). Depredation by ravens was negatively associated with the numbers of buildings within a circle with radius 3 km from each track board. At track boards depredated by ravens the average number of buildings was 95 (±9). There was a positive relationship between average lengths of paths within a circle with radius 1 km from each track board and raven depredation rate. The average lengths of paths within these circles at track boards predated by ravens were 3.17 km (±0.17). Raven depredation was also positively associated with length of roads within circles with radius 5 km from each track board. The average length of roads within these circles at track boards predated by ravens was 93.08 km (±2.01).

3.8. Predation by hooded crows

Over all years and study areas pooled 9.2% of the available track boards (n=783) were depredated by hooded crows. The three best models explaining predation by hooded crows among the depredated track boards included the predictor variables year, habitat, settlement 1 km, settlement 3 km and road 1 km (Table 10). Model 2 and 3 have considerably less support (ΔAICc ≥ 4.0) than model 1. Therefore we will only discuss model 1 further on as a good model explaining predation by hooded crows.

Table 10: The three best models explaining predation by hooded crows ranked from best to third best (the best model is indicated in bold letters). Hbt. = habitat, Settl. = settlement.

Model	Max logl.	k	AICc	ΔAICc	w (AICc)	Variable	Reg. coef.	SE	P-value	VI
1	-140,22	5	290,52	**0,00**	0,90	Year	1,184979	0,248217	<0,0001	1,00
						Hbt. alpine	0,562029	0,205906	0,0067	0,92
						Hbt. birch	-0,621047	0,240148	0,0067	0,92
						Settl. 1 km	0,015335	0,003444	<0,0001	0,88
						Constant	-2381,66	498,54		
2	-144,70	3	295,43	4,91	0,08	Year	1,161799	0,242889	<0,0001	1,00
						Settl. 3km	0,013970	0,003364	<0,0001	0,08
						Constant	-2334,99	487,84		
3	-143,79	5	297,66	7,14	0,03	Year	1,379049	0,243222	<0,0001	1,00
						Hbt. alpine	0,482303	0,200205	0,0193	0,92
						Hbt. birch	-0,540469	0,230187	0,0193	0,92
						Road 1km	0,000224	0,000063	0,0003	0,03
						Constant	-2771,92	488,56		

Depredation rates by hooded crows among all depredation events increased over the years. In 2007 the hooded crow depredation rate was 5.7% (n=70), in 2008 the rate was 13.1% (n=137) and in 2009 the rate was 39.4% (n=127). Hooded crow showed selectivity in choice of habitat for predation events. Of all depredation by hooded crows (n=72) 20.1% was performed in birch habitat, 31.9% in edge habitat and 47.2% in alpine habitat. Depredation by hooded crows was positively associated with the number of buildings within a circle with radius 1 km from each track board. The average number of buildings within these circles at track boards predated by hooded crow was 44 (±6).

3.9. Relationship between total predation rate and ptarmigan density

The simple linear regression showed no relationship between total predation rate and ptarmigan density (n=12, R^2 =0.6%, p=0.814) among all study areas and all years (Fig. 7 and Table 11).

Table 11: M/Å = Mastukåsa/Åslia, R=Råtåsjøhø, D=Dindalen, Grø=Grødalen and Gå=Gåvålia. Estimated mean ptarmigan density/km² and total predation rates (%) on the available nests in different locations and different years.

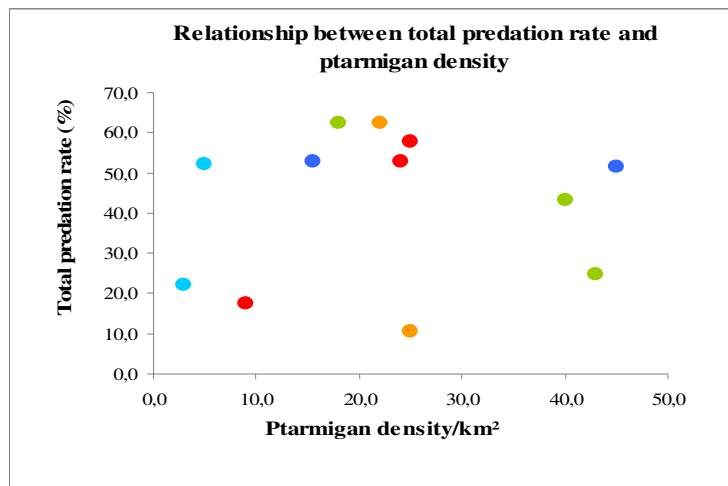| Year	Location	Mean ptarmigan density/km²	Total predation rate (%)
2007	M/Å	40,0	43,3
2007	R	25,0	57,7
2008	M/Å	43,0	24,6
2008	R	24,0	52,9
2008	D	22,0	62,3
2008	Grø	3,0	22,2
2008	Gå	45,0	51,7
2009	M/Å	18,0	62,5
2009	R	9,0	17,4
2009	D	25,0	10,7
2009	Grø	5,0	52,2
2009	Gå	15,5	52,8

Figure 7: Plot of ptarmigan density/km² versus total predation rate for all study areas and all years. Red circles are Råtåsjøhø, green circles are Mastukåsa/Åslia, turquoise circles are Grødalen, orange circles are Dindalen and blue circles are Gåvålia.

4. Discussion

4.1. The methodological approach; using artificial nests

Artificial nest experiments have been claimed to favour avian predators, and has been proven to sometimes exclude certain mammalian predators (Willebrand and Marcström 1988, MacIvor et al. 1990). Two out of three main predators in our experiments were birds (raven and hooded crow), and these two species together were responsible for more than 54.2% of all predation events. Red fox is also believed to be an important predator on small game species, but out of all our identified species it were responsible for the smallest amount of depredated nests, and occurred as egg predator only in one area in 2009. However, red fox camera events occurred in all areas, thus determining that this species exist in the study areas at least part of the year. It is very likely that some red foxes still inhabit the study areas during spring and summer, even though they are not captured by any cameras during this period. This supports the assumption that some mammalian predators may be more sceptic of robbing artificial "grease-nests". Conversely, the pine marten was responsible for the second most predation in our study, emphasizing the importance of the great variations in scepticism, foraging behaviour and ability to locate nests that exist between the mammalian species. A study conducted in northern Norway by Klausen et al. (2009) found a low predation rate by red fox on track boards, similar to our results. This is contrary to another similar experimental study in northern Norway where red fox caused high predation rates (Pedersen et al. 2009). Klausen et al. (2009) suggested that the discrepancy in red fox depredation between these two studies can be caused by different phases of the vole cycle. The study of Klausen et al. (2009) appeared to be conducted in a pre-peak year for voles in the region, whereas predators are expected to have the highest predation rates on alternative prey (such as ground nests) in the decline phase of small rodents (Hagen 1952, Angelstam et al. 1984). Our study did however also include a year with a decline phase of small rodents (year 2008), but still the red fox predation rate was very low (1.5%, n=326). This could possibly be due to differences in the shyness of the red fox between our study area and the study area of Pedersen et al. (2009). The red foxes in our area may have been hunted more by humans, and therefore be more sceptical to objects associated with humans. If we had been able to get more red fox predation in this study, we could have been able to determine the relationship between occurrence of red fox and human activity in our study areas. These data were however not obtained, since the number of red fox predation events was too few, and we are left with merely speculations

related to this subject.

It is important to note that none of the "extra eggs" were predated during the study in 2009. They were placed directly on the ground 20 m away from the nearest track board, and were of the same type as the eggs used in the rest of the project. The lack of predation on the "extra eggs" clearly points out that these natural looking artificial nests are more difficult to locate than eggs displayed on a track board. Lack of predation incidents could be tied to the absence of an incubating hen, since predators probably use the hen to locate real nests (Willebrand and Marcström 1988, O`Reilly and Hannon 1989, MacIvor et al.1990). Our track boards may compensate for this by being so clearly visible in the landscape. The scent of the grease could also attract mammalian predators using olfactory cues, but the extra eggs did in our opinion have a quite notable scent and should therefore have attracted predators if scent is the key factor for attraction. As the extra eggs were not subjected to predation at all, we believe this indicate that it is the presence of an incubating hen that attracts most of the mammalian predators. The track boards seemed less visible from the sides than from directly above to the human eye, and would perhaps therefore also be easiest for avian predators to discover as they search for food from the sky.

4.2. Presence of potential ptarmigan nest predators

Our results showed no clear relationship between observations by the field cameras and predation events. Three of the areas had both the highest (or lowest) number of predation events and the highest (or lowest) number of camera events registered for the same species. Gåvålia, Mastukåsa/Åslia and Råtåsjøhø had the highest number of combined events of raven, pine marten and magpie respectively, while Grødalen and Dindalen had the lowest amount of events for both methods with the species magpie and pine marten respectively. There was, however, no area that showed the same trend for more than one species, nor did one particular species show the same trend for more than one area. It is nevertheless interesting to observe that in respect to determining what potential ptarmigan predators that can be found in the different areas, the two methods do to some extent complement each other. Camera events are recorded when predation events are absent (and vice versa) for all species in all areas except from pine marten in Dindalen and magpie in Grødalen where no event of any kind is

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documented. In respect to red fox, which is registered by cameras repeatedly in all areas, it is obvious that it is present in the study areas even though it has not been recorded at the track boards. Red foxes should have no more trouble in locating artificial nests than pine martens, so there are probably other factors that explain why it has shown this behaviour in our study. The recordings of hooded crow events in Grødalen are also interesting when considering that this is the area with most hooded crow predation and the only area completely without camera registrations of this species.

Another bias related to our camera study is that recordings of predators decreased extensively when approaching spring, and only a very few registrations were made from April to July (Eide et al. unpublished). This implies that the total number of camera events does not necessarily mirror the presence of predators in the areas during the reproductive period of willow ptarmigan. The diet of animals is limited when snow is covering the ground and may therefore draw predators to constant and easy-accessed food sources like our baits, thus portraying an uncharacteristic composition- or density of the predator community. Some predators also have different behaviour in the different seasons (e.g hooded crows that appear in flocks during winter, but hold territories when reproducing).

4.3. Human activities

4.3.1. Roads

When correcting for the effect of year and period, the total predation increased with decreasing distance to roads, and in the best model also with increasing road density within 3 km from the artificial nests. This result was probably due to a higher risk of predation by avian predators, especially ravens. Among the track boards that were depredated, we found a positive relationship between raven predation and road density. Carrion feeders, as ravens, often move along roads in search of road kills (Austin 1971, Forman & Alexander 1998). The association we found between raven predation and road density can be due to ravens searching for road kills and therefore staying in areas close to roads. Common ravens were also the most frequently observed avian scavenger along a Canadian railway (Wells et al. 1999). In our study raven was the most common predator on the artificial nests. According to

Andrén (1992), data from Angelstam et al. (1984) and Angelstam (1986) indicate that raven is a much more important nest robber than could be expected from its relative density. He argued that it may pay for predators like ravens, which have a large home range and encounter many nests, to develop a search image for bird's nests and become a nest robber specialist during the brooding time of their prey (Andrén 1992). If the ravens in our study areas had developed such a search image for track boards, this may explain the high predation rate by ravens.

While we found a positive association between raven predation and road density, the best model for hooded crow predation did not include road as a predictor variable. We believe this finding is caused by larger home ranges used by ravens than by hooded crows (Hjeljord 2008). This give ravens a greater opportunity to search for carcasses along long road distances. The ravens, in comparison to the other corvids, do also to a greater extent act as a carnivore (Hjeljord 2008).

For pine marten there was a negative association between predation rate and the density of roads within 1 km from the track boards. However, since we tested this against all other predated nests, we cannot conclude that pine martens actually avoid roads. Pine martens do avoid open areas, possibly as an anti-predation behavior trait to avoid potential large predator species moving along roads (Lindström 1989). Several large predator species travel along roads that have little vehicular or people traffic (Forman & Alexander 1998). For prey species high road densities give higher risk of meeting predators and people (Forman et al. 2003). Roads can thus act as barriers for pine martens (Van Langevelde et al. 2009). It is also possible that the old forest areas, which pine martens are especially connected to (Lindström 1989), are mainly situated further away from roads. In a study from Kainuu in Eastern Finland Helle and Nikula (1995) found a significantly lower road density in areas with the most pine marten tracks than in areas with less pine marten tracks. Noises from traffic can affect animals stress levels and lead to avoidance of areas with the loudest noise levels (May et al. 2007). Ideally a measure of traffic volume could have been used in the models for the road influence on predation rate from different species. On the other hand, Helle and Nikula (1995) argued that it is not necessarily the amount of traffic per se that play the most important role in

whether or not animals avoid roads, but the local change in habitats and/or the increased activity in the areas by people. Most roads in their study were forestry roads that people might use to get easy access to areas for fishing, hunting and berry picking.

4.3.2. Paths

In the second best model for overall predation, there was a positive relationship between the predation risk and the length of paths within 5 km from the artificial nests. There was a positive relationship between raven predation rate and path density and a negative association between pine marten predation rate and path density. In addition, pine marten predation showed a positive association with distance to the closest path. We therefore conclude that also the positive relationship with paths in one of the overall predation models was due to increased egg predation by ravens. This is in accordance with the finding of Miller and Hobbs (2000) that birds attacked more nests near trails than away from trails, whereas mammals avoided robbing nests near trails. Miller and Hobbs (2000) hypothesized that the mammalian avoidance of trails can be partly due to canine scent from dogs taken for a walk by the owners on the trails. If the red fox uses paths for movements in the landscape, the pine marten avoidance of paths can also be an antipredator behavior trait to avoid red fox (Lindström 1989). Corvids on the other hand have the ability to habituate to human activity (Knight et al. 1987). Maybe also the trails work as a source of food for the ravens through garbage from the recreationalists.

4.3.3. Settlement

In all models, the total predation increased with increasing density of settlements within 1 km from the track board. Hooded crows seemed to be the predators responsible for this pattern. Among nests that were depredated, we found a positive association between settlement density and hooded crow depredation, while we found a negative association between settlement density and raven predation. A possible negative association for ravens might be a result of "shyness". Ravens are considered to be typical wilderness birds that mainly avoid high settlement density and areas connected with a high human density (Haftorn 1971, Olstad

and Sørensen 1981). The raven is, in contrast to the other corvids, vulnerable to persecution and hunting from humans which can explain this "shyness" (Olstad and Sørensen 1981). The hooded crow, on the other hand, is found in close association with humans. When land is cultivated and the settlement density is increased the hooded crow is getting better living conditions (Olstad and Sørensen 1981).

Our findings regarding the hooded crow are in correspondence with the study of Marzluff and Neatherlin (2006). They found a strong association between American crow abundance and proximity to human settlements and campgrounds. The abundance and survival of American crows increased with decreased distance to these human activities. Ravens were moderately abundant both close to and further away from settlements and campgrounds, and their survivorship only mildly increased close to settlements and campgrounds (Marzluff and Neatherlin 2006). It turned out that crows relied more on anthropogenic food than ravens. Marzluff and Neatherlin (2006) found that crows made long, unidirectional movements from core use areas to distant anthropogenic food sources while ravens made multi-directional movements from core use areas to interior forests, rivers and clear cuts. The reason for these differences can be different behaviour of the two species. Crows can acquire knowledge of anthropogenic foods during flocking and migration away from their breeding areas to roosting sites (Smedshaug 2000), while ravens usually remain in their breeding territories (Olstad and Sørensen 1981). Crows also allowed intrusion by conspecifics into their breeding home ranges unlike ravens (Marzluff and Neatherlin 2006). Adult ravens strongly defend food sources (Marzluff and Heinrich 1991) and make it a risk to challenge this defence. If the positive association between American crows and human activities is transferable to hooded crows it may explain the positive association we found between settlement density and hooded crow depredation. Also a study from the Bavarian Alps, Germany, found that crows are attracted to settlement (Storch and Leidenberger 2003). This study examined the presence of corvids at cabin areas and control areas seldom visited by humans. Carrion crows (*Corvus corone*), magpies and jays (*Garrulus glandarius*) were significantly more numerous near huts than in control areas. Ravens, on the other hand, were present in most control and hut areas alike.

Red foxes have been found to be more active in vicinity to cabins (Røhnebæk 2004). The red fox predation rate on the track boards in our study was too low to be analyzed, but in vicinity

to cabins red foxes can probably be responsible for substantial predation on natural nests. A study performed in Ringsakfjellet examined the relationship between recreational cabin areas and red fox activity and found that red foxes showed significantly more tracks in vicinity to cabins (Røhnebæk 2004).

4.4. Predation rates in relation to ptarmigan density

We found no relationship between ptarmigan density and total predation rate on the artificial nests. Asmyhr (2008) found a negative correlation between ptarmigan density and predation rate, but he performed his research in three study areas only, and in only one year. We measured the ptarmigan density using two different methods. Only for Gåvålia in 2009 we had data on ptarmigan density using both the distance method and the method used for getting the TOV-data (see section 2.2.4.). Here, the ptarmigan density was relative similar regardless of the method used.

To check if the lack of relationship between ptarmigan density and predation on artificial nests was due to the differences in methodology of estimating ptarmigan density, we performed a simple linear regression using only data from the study areas where the distance method was applied (i.e. Råtåsjøhø, Mastukåsa/Åslia and Grødalen). Still there was no relationship between total predation rate and ptarmigan density. But there may be other complicating factors linked to the artificial nest method that restrict us from finding such relationships. The difficulty of transferring predation rate on artificial nests to predation rate on natural nests is perhaps the most likely explanation. The predation rate by mammals is probably higher on natural nests in our study areas. For instance, the predation rate from red fox on the artificial nests was very low.

4.5. Habitat and tree density

We found that most of the pine marten depredation events took place in the forest habitat and believe this is consistent with the general view of pine marten as a habitat specialist associated primarily with forest (e.g. Pulliainen 1981, Angelstam 1986, Brainerd 1990, Storch et al. 1990, Baltrûnaitë 2006). The population dynamics of pine martens seem to be governed by

the availability of old-growth forest and occurrence of other predators (Lindström 1989). Pine martens are probably vulnerable to predation by eagle owls from the sky on illuminated nights in late winter and spring because they are easily detected on the white snow. In addition, the access to food may also be an important factor explaining the pine martens habitat choice (Brainerd 1990, Brainerd and Rolstad 2002). Pereboom et al. (2008) found that pine martens stayed close to the forest edge when venturing out into more open fields and are thus dependent on presence of trees in close vicinity. Brainerd and Rolstad (2002) found that pine martens in Varaldskogen (Norway) and Grimsö (Sweden) strongly avoided open habitats. This corresponds to our findings of pine marten predation rates being positively correlated with birch habitat and negatively correlated to low alpine habitat. However, occasionally pine marten has been observed in alpine habitat well above the tree-line preying on willow ptarmigan nests in Gåvålia (H. C. Pedersen, pers. comm.). Our results showed that pine marten predation rates were positively correlated with number of trees in immediate closeness to the track boards, which may relate to the findings of pine martens consistently preferring taller (spruce-dominated) forest and avoiding open habitats throughout the year in the study of Brainerd and Rolstad (2002). The red fox is often a habitat generalist which could have evened out the apparent separation in habitat choice between avian and mammalian predators. It is reason to believe that this species would have utilized all habitats, thus affecting the overall predation rates and illustrating the common agreement of mammalian predators being important nest robbers.

As hypothesized, corvids were responsible for most predation in the open low alpine habitat during this study. The models "avian predation", "predation by ravens" and "predation by hooded crows" all show that avian predation rates in this study is negatively correlated with birch habitat and positively correlated with open low-alpine habitat. This was expected on the basis of the study design and the artificial nests' conspicuousness which is believed to favor avian predators.

4.6. Variations in predation rates among study areas

We were not able to implement the variable "location" in the model selection, but Fig. 4 in

section 3.1, illustrates that there were high variation in the predation rates by raven, pine marten and hooded crow in the various locations. These variations can be caused by factors like differences in access to prey or other food sources (Angelstam 1986), varying hunting pressure, or a number of other ecological issues that could be different between the study areas. The time frame of this study did not allow us to explore this in further detail. But as an example we found that most of the predation by hooded crows took place in the study area Grødalen. This can be related to the high density of settlements in this area (mostly cabins). The mean "settlement density" in Grødalen, at every spatial scale (1km, 3 km and 5km), was much higher than the "settlement densities" in the other study areas. It is possible that hooded crows can utilize food scraps left in the areas with settlement (Marzluff and Neatherlin 2006). A large tourist cabin called "Vangshaugen fjellstue" (a cabin managed by "Kristiansund og Nordmøre turistforening") is situated in close vicinity to our track boards in this location, and waste and food remains distributed by tourist visiting this cabin, and probably going for walks in the nearby areas, can thus provide food that crows can utilize.

4.7. The significance of small rodent abundance, year and period

The main reason for including year as a random factor in the models was to control for possible effects of variations in methodology, predator abundance or activity, and the availability of alternative food, when testing for the impact of human activity on predation rates. We found that the predation rates decreased over all three years. In 2007, each trial period lasted for 10 days, whereas in 2008 and 2009, each trial period lasted only for seven days. We therefore think that some of the high predation rates in 2007 might have been caused by the different durations of the trail periods.

The decrease in predation rates over the years was mainly caused by decreased predation by raven and pine marten. Pedersen et al. (2009) also found a decrease in raven depredation, but this decrease only took place between the last two years of their study. Both our study and the study of Pedersen et al. (2009) found an increase in hooded crow predation from the first year to the second year, and then a dramatic increase from the second year to the third year. There is evidence for the ability of predator species to develop searching images when they are

preying upon nests (Sonerud 1985, Sonerud and Fjeld 1987, Andrén 1992). Hence, we should expect total predation rates to be positively correlated with year of the study, as was possibly the case for hooded crow. Since we found the opposite result for marten and raven, we conclude that searching image from one year to another was not important for these predators.

In 2007, small rodent populations showed a strong peak in central Norway, from Jotunheimen/Dovre to Børgefjell (Framstad 2009). According to the alternative prey hypothesis, predation on bird eggs should be less frequent in rodent peak years (Hagen 1952, Angelstam et al. 1984). However, our data showed the highest predation rate in 2007. The eggs on the track boards are probably much easier to detect than are natural nests. If the predators involved show a numerical response to rodent density, this may in fact lead to increased predation on artificial nests, which are easier prey than small rodents.

We found that the predation rate increased from the first period to the second period. For the predator group avian (raven, hooded crow and magpie pooled) we found a small increase in predation rate from period 1 to period 2, but this increase was smaller than the increase in mammal predation and predation from unknown predators, therefore the regression coefficient for avian predation in period 1 is positive. Pedersen et al. (2009) did not find a consistent increase in predation within years for any of the corvid species, and argued that their findings were not consistent with a memory effect acting as the main cause of the temporally variable avian predation rates. Pedersen et al. (2009) suggested that compositional changes within the predator community took place and influenced the predation rates during the study periods and years. The results of our study may reflect the different predators' ability to develop search images for artificial nests. But increased predation during summer may also reflect that the hunting activity of the predators, mainly pine martens, increases, due to increased food demand of their broods.

5. Conclusion

In this three-year study using artificial nests, we found yearly total predation rates ranging from 39.8% to 50.7%. The most common predators were ravens, pine martens and hooded crows, which depredated 13.9%, 9.3% and 9.2% of available track boards respectively. We found no relationship between ptarmigan density and total predation rate on artificial nests, probably related to the fact that the experiment failed to reflect natural predation fully. Predation rates varied between the habitats; birds were clearly the most common predators in the low-alpine habitat, whereas pine martens were responsible for most of the predation in the birch habitat, while the nests in the edge habitat was predated by several species. Predation rates increased with influence of human activity for most predators, except for pine marten. We had however too few data to make conclusions about red fox.

Our findings indicate that development of infrastructure in mountainous areas may result in increased corvid density, thus probably also causing increased predation pressure in the surrounding areas. Small game species such as willow ptarmigan may therefore be subjected to population decrease in close vicinity to settlements in mountainous areas. When planning to develop e.g. new cabin resort areas, important willow ptarmigan habitat should be avoided. Around existing settlements measures could probably prevent establishment of predators. It is reason to believe that human activity give access to additional food resources which result in higher predator densities. Awareness of this could motivate actions, e.g. establishing renovation plans also in second home areas. To reveal the true predation rates of potential ptarmigan predators we propose that research should be done by using real ptarmigan nests in combination with field cameras, although expenses and efforts has to be considerably increased.

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Appendix 1

Estimates and p-values for the predictor variables in univariable models, for all predator groups and predator species. P-values $<$ 0.0500 are indicated in bold letters.

Total predation	Estimate	p-value
Year	-0.198860	**0.0450**
Period	-0.182150	**0.0119**
Habitat alpine	0.091520	0.6133
Habitat birch	-0.010167	0.6133
Closest settlement	0.000026	0.8702
Closest path	-0.000171	0.1171
Closest road	-0.000423	**0.0013**
Ptarmigan density	0.005198	0.3292
Chicks/hen	0.037214	0.2602
Num of trees rel.	0.002478	0.2061
Small rodents	0.006114	**0.0376**
Settlement dens. 1km.	0.006666	**0.0025**
Settlement dens. 3km.	0.001310	**0.0331**
Settlement dens. 5km.	-0.000163	0.6863
Path dens. 1 km.	0.000052	0.1919
Path dens. 3 km.	0.000026	**0.0178**
Path dens. 5 km.	0.000014	**0.0049**
Road dens. 1 km.	0.000089	**0.0047**
Road dens. 3 km.	0.000024	**0.0031**
Road dens. 5 km.	0.000003	0.3003

Mammal predation	Estimate	p-value
Year	-0.524758	**0.0015**
Period	0.020335	0.8700
Habitat alpine	-0.514578	**<0.0001**
Habitat birch	0.832876	**<0.0001**
Closest settlement	0.000142	0.5994
Closest path	0.000613	**0.0006**
Closest road	0.000428	0.0854
Ptarmigan density	0.013618	0.1627
Chicks/hen	0.080539	0.1216
Num of trees rel.	0.009501	**0.0026**
Small rodents	0.005128	0.2658
Settlement dens. 1km.	-0.003332	0.3393
Settlement dens. 3km.	-0.000204	0.8226
Settlement dens. 5km.	0.000663	0.2751
Path dens. 1 km.	-0.000278	**0.0001**
Path dens. 3 km.	-0.000091	**<0.0001**
Path dens. 5 km.	-0.000040	**<0.0001**
Road dens. 1 km.	-0.000232	**0.0001**
Road dens. 3 km.	-0.000045	**0.0028**
Road dens. 5 km.	-0.000012	**0.0242**

Avian predation		
	Estimate	p-value
Year	0.122123	0.4103
Period	0.159606	0.1559
Habitat alpine	0.521427	**<0.0001**
Habitat birch	-0.724095	**<0.0001**
Closest settlement	-0.000103	0.6731
Closest path	-0.000581	**0.0007**
Closest road	-0.000013	0.9543
Ptarmigan density	-0.011419	0.1959
Chicks/hen	0.032025	0.5060
Num of trees rel.	-0.011817	**0.0001**
Small rodents	0.006361	0.1429
Settlement dens. 1km.	0.002542	0.4046
Settlement dens. 3km.	0.000552	0.5012
Settlement dens. 5km.	0.000264	0.6328
Path dens. 1 km.	0.000379	**<0.0001**
Path dens. 3 km.	0.000092	**<0.0001**
Path dens. 5 km.	0.000039	**<0.0001**
Road dens. 1 km.	0.000222	**<0.0001**
Road dens. 3 km.	0.000053	**0.0001**
Road dens. 5 km.	0.000019	**0.0002**

Pine marten predation		
	Estimate	p-value
Year	-0.479892	**0.0065**
Period	-0.032501	0.8079
Habitat alpine	-0.601913	**<0.0001**
Habitat birch	0.871744	**<0.0001**
Closest settlement	0.000247	0.3937
Closest path	0.000732	**0.0001**
Closest road	0.000647	**0.0148**
Ptarmigan density	0.014938	0.1529
Chicks/hen	0.065827	0.2378
Num of trees rel.	0.010280	**0.0019**
Small rodents	0.002095	0.6756
Settlement dens. 1km.	-0.005029	0.1959
Settlement dens. 3km.	-0.000714	0.4754
Settlement dens. 5km.	0.000474	0.4678
Path dens. 1 km.	-0.000362	**<0.0001**
Path dens. 3 km.	-0.000101	**<0.0001**
Path dens. 5 km.	-0.000045	**<0.0001**
Road dens. 1 km.	-0.000325	**<0.0001**
Road dens. 3 km.	-0.000059	**0.0003**
Road dens. 5 km.	-0.000014	**0.0201**

Raven predation		
	Estimate	p-value
Year	-0.733504	**<0.0001**
Period	0.009773	0.9338
Habitat alpine	0.457302	**0.0003**
Habitat birch	-0.693389	**0.0003**
Closest settlement	0.000887	**0.0006**
Closest path	-0.000655	**0.0013**
Closest road	0.000722	**0.0025**
Ptarmigan density	0.032593	**0.0005**
Chicks/hen	0.209582	**<0.0001**
Num of trees rel.	-0.016193	**<0.0001**
Small rodents	0.018015	**<0.0001**
Settlement dens. 1km.	-0.016167	**0.0001**
Settlement dens. 3km.	-0.003454	**0.0004**
Settlement dens. 5km.	-0.001258	**0.0338**
Path dens. 1 km.	0.000368	**<0.0001**
Path dens. 3 km.	0.000099	**<0.0001**
Path dens. 5 km.	0.000044	**<0.0001**
Road dens. 1 km.	0.000080	0.1089
Road dens. 3 km.	0.000050	**0.0007**
Road dens. 5 km.	0.000031	**<0.0001**

Hooded crow predation		
	Estimate	p-value
Year	1.310840	**<0.0001**
Period	0.126075	0.3452
Habitat alpine	0.393851	**0.0321**
Habitat birch	-0.479722	**0.0321**
Closest settlement	-0.001411	**<0.0001**
Closest path	-0.000193	0.3635
Closest road	-0.001144	**0.0001**
Ptarmigan density	-0.062253	**<0.0001**
Chicks/hen	-0.420310	**<0.0001**
Num of trees rel.	-0.002029	0.5771
Small rodents	-0.024888	**0.0001**
Settlement dens. 1km.	0.017602	**<0.0001**
Settlement dens. 3km.	0.004735	**<0.0001**
Settlement dens. 5km.	0.002343	**0.0003**
Path dens. 1 km.	0.000073	0.3153
Path dens. 3 km.	0.000024	0.2392
Path dens. 5 km.	0.000009	0.3122
Road dens. 1 km.	0.000195	**0.0006**
Road dens. 3 km.	0.000010	0.5238
Road dens. 5 km.	-0.000012	**0.0341**

Appendix 2

Summary of predation by different species distributed on locations, habitats (B=birch habitat, E=edge habitat and L=low-alpine habitat) and years. Treatments are the number of track boards available for predation, i.e. track boards not disturbed by domestic animals. Mast./Å. = Mastukåsa/Åslia, Tot. = total, pred. = predation.

Predator community	Location and habitat														
	Råtåsjøhø			Mast./Å.			Grødalen			Dindalen			Gåvålia		
	B	E	L	B	E	L	B	E	L	B	E	L	B	E	L
2007															
Red fox	0	0	0	0	1	0									
Pine marten	7	2	1	5	2	0									
Stoat/least weasel	1	1	1	1	0	1									
Raven	5	6	10	3	6	8									
Hooded crow	0	1	1	0	1	1									
Magpie	1	3	0	0	0	0									
Unidentified	0	0	1	0	0	0									
Total predation	**41**			**29**											
Treatments	**71**			**67**											
Tot. mammal pred. (%)	**18,3**			**14,9**											
Tot. avian pred. (%)	**38,0**			**28,4**											
Tot. pred. (%)	**57,7**			**43,3**											
2008															
Red fox	0	0	0	0	0	0	0	0	1	1	1	0	1	0	1
Pine marten	2	1	0	8	3	2	2	3	1	8	4	8	0	0	0
Stoat/least weasel	0	0	0	0	0	0	0	0	1	0	0	0	0	0	0
Raven	6	10	14	0	0	0	0	0	0	0	0	2	3	4	5
Hooded crow	0	1	2	0	0	2	1	1	0	0	3	3	1	1	3
Magpie	0	0	0	0	0	0	0	0	0	3	0	0	0	0	0
Unidentified	0	0	0	0	1	0	2	1	3	1	2	2	6	4	2
Total predation	**36**			**16**			**16**			**38**			**31**		
Treatments	**68**			**65**			**72**			**61**			**60**		
Tot. mammal pred. (%)	**4,4**			**20,0**			**11,1**			**36,1**			**3,3**		
Tot. avian pred. (%)	**48,5**			**3,1**			**2,8**			**18,0**			**28,3**		
Tot. pred. (%)	**52,9**			**24,6**			**22,2**			**62,3**			**51,7**		
2009															
Red fox	0	0	0	2	0	0	0	0	0	0	0	0	0	0	0
Pine marten	4	0	0	4	2	3	1	0	0	0	0	0	0	0	0
Stoat/least weasel	0	0	0	0	1	0	1	0	1	0	0	0	0	0	0
Raven	0	0	1	1	3	3	1	3	1	0	0	0	2	6	6
Hooded crow	1	1	0	1	5	3	9	8	10	0	0	3	2	1	6
Magpie	1	1	1	1	2	0	0	0	0	1	0	0	1	0	0
Unidentified	0	0	2	7	3	4	0	1	0	0	2	0	1	2	1
Total predation	**12**			**45**			**36**			**6**			**28**		
Treatments	**69**			**72**			**69**			**56**			**53**		
Tot. mammal pred. (%)	**5,8**			**16,7**			**4,3**			**0,0**			**0,0**		
Tot. avian pred. (%)	**8,7**			**26,4**			**46,4**			**7,1**			**45,3**		
Tot. pred. (%)	**17,4**			**62,5**			**52,2**			**10,7**			**52,8**		

Summary of predation by different species distributed on habitats (B=birch habitat, E=edge habitat and L=low-alpine habitat), periods and years. Treatments are the number of track boards available for predation, i.e. track boards not disturbed by domestic animals. Tot. = total, pred. = predation.

Predator community	Periode and habitat					
	Period 1			Period 2		
	B	E	L	B	E	L
2007						
Red fox	0	1	0	0	0	0
Pine marten	5	1	0	7	3	1
Stoat/least weasel	1	0	2	1	1	0
Raven	4	6	7	4	6	11
Hooded crow	0	0	0	0	2	2
Magpie	0	2	0	1	1	0
Unidentified	0	0	0	0	0	1
Total predation	**29**			**41**		
Treatments	**70**			**68**		
Tot. mammal pred. (%)	**14,3**			**19,1**		
Tot. avian pred. (%)	**27,1**			**39,7**		
Tot. pred. (%)	**41,4**			**60,3**		
2008						
Red fox	1	0	2	1	1	0
Pine marten	10	4	5	10	7	6
Stoat/least weasel	0	0	0	0	0	1
Raven	6	8	11	3	6	10
Hooded crow	2	3	6	0	3	4
Magpie	2	0	0	1	0	0
Unidentified	0	1	0	9	7	7
Total predation	**61**			**76**		
Treatments	**166**			**160**		
Tot. mammal pred. (%)	**13,3**			**16,3**		
Tot. avian pred. (%)	**22,9**			**16,9**		
Tot. pred. (%)	**36,7**			**47,5**		
2009						
Red fox	1	0	0	1	0	0
Pine marten	3	1	2	6	1	1
Stoat/least weasel	0	1	0	1	0	1
Raven	2	2	2	1	10	10
Hooded crow	5	9	10	8	6	12
Magpie	1	3	1	3	0	0
Unidentified	5	2	6	3	6	1
Total predation	**56**			**71**		
Treatments	**147**			**172**		
Tot. mammal pred. (%)	**5,4**			**6,4**		
Tot. avian pred. (%)	**23,8**			**29,1**		
Tot. pred. (%)	**38,1**			**41,3**		