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Nest-predator prevalence along a mountain birch–alpine tundra ecotone

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Abstract

Context. Nest predation is a major factor influencing life history and population dynamics of ground-nesting birds. The transitions between the northern boreal mountain birch forests and the low-alpine tundra are important habitats for the willow ptarmigan, *Lagopus lagopus* (Linnaeus, 1758). During the past decades, these landscapes have been extensively developed with cabin resorts in southern Norway, which has led to an increased number of roads and foot paths in relatively undisturbed habitats.

Aims. The aim of the present study was to investigate relative nest-predation rates in elevation gradients (ecotones) spanning from northern boreal mountain birch forests to low-alpine tundra in three locations with contrasting willow ptarmigan densities.

Methods. We conducted an artificial nest study by using baited track boards ($n = 108$). Track boards were placed along transects (200 m) in the following three habitat types: birch forest, edge habitat and low-alpine tundra. Predator prevalence was analysed in relation to study-design variables (location, habitat, study period) and the load of human infrastructure (i.e. distance to foot paths and roads), using generalised linear mixed-effect models assuming binomial distribution for the response variable.

Key results. Prevalence of avian predators was consistently high (range 38.2–85.3%), in contrast to much lower prevalence of mammalian predators (range 2.8–22.9%). Raven (*Corvus corax*) was the dominant nest predator, followed by hooded crow (*C. cornix*) and pine marten (*Martes martes*). Location, as contrasted by differences in willow ptarmigan density, was not significantly related to total relative predation rates. Species-specific predator prevalence was habitat specific and related to human infrastructure, but with opposite relative predation patterns between pine marten and raven. Hooded crow predation was similar across the ecotone and not related to human infrastructure.

Conclusions. Predator prevalence was habitat specific and affected by human infrastructure (distance to human foot paths). Our study confirmed that human activity might alter the predation rates by generalist species in these low-alpine environments.

Implications. We recommend that attractive willow ptarmigan habitat should be avoided when planning human infrastructure in alpine ecosystems. To reduce predation pressure in this ecosystem, it appears that generalist predators should be considered for management actions. Further research is needed to explain the underlying mechanism driving expansion of

generalist species into alpine habitats. Such knowledge is also important in developing alternative management actions with focus other than predator control.

Additional keywords: artificial nest, disturbance, hooded crow, infrastructure, pine marten, predator, raven, willow ptarmigan.

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Introduction

Predation on eggs and chicks is documented to be the overall most important cause of reproductive failure in willow ptarmigan (*Lagopus lagopus*) populations, resulting in lower recruitment, and is hence considered to be a limiting factor of population size (Myrberget 1984, 1985; Steen *et al.* 1988; Steen and Erikstad 1996; Munkebye *et al.* 2003). Willow ptarmigan populations in Norway appeared cyclic up to the mid-1980s, but have since then showed dampened oscillations and occur at lowered densities in many places (Holmstad *et al.* 2005; Pedersen and Eide 2010). Increased predation pressure, inflicted by expanding populations of nest predators (Prugh *et al.* 2009; Ritchie and Johnson 2009; Killengreen *et al.* 2011) and lack of cyclic smallrodent dynamics (Ims *et al.* 2008), are suggested as two of several possible explanations to the changes in willow ptarmigan population densities (Cotterill and Hannon 1999; Pedersen and Eide 2010; Henden *et al.* 2011). Other limiting factors are weather conditions, affecting the breeding success through forage availability for the hen and thereby the body condition and incubation rhythm, which again have an impact on predation risk (Erikstad and Andersen 1983; Erikstad 1986; Steen *et al.* 1988). Nest-predation risk varies in space and time, depending on factors such as habitat composition (Manzer and Hannon 2005), predator abundance and predator community structure (Angelstam 1986; Cotterill and Hannon 1999), foraging behaviour of the predator (Pulliainen 1981; Picman 1988; Seymour *et al.* 2004) and availability of alternative prey (Hagen 1952; Angelstam *et al.* 1984).

The northern boreal mountain birch forests and the low-alpine tundra are important habitats for willow ptarmigan (Andersen 1986; Hannon *et al.* 1998). During egg-laying and incubation, both poor and rich mountain birch forests and wet willow scrub are used to a large extent. Willow ptarmigan broods (i.e. 0–14 days of age) exploit similar habitats, but utilise the richer birch forest more than other habitat types. When the chicks become older, they move upwards into the low- and mid-alpine habitats in which all kinds of willow vegetation is used (Andersen 1986). To our knowledge, few studies have investigated how different predators utilise the ecotone between boreal forests and low-alpine tundra landscapes (but see Klausen *et al.* 2010), and how their presence affects nestpredation rates on ground-nesting willow ptarmigan, which is the dominating gallinaceous bird within these landscapes (Erikstad *et al.* 1982; Myrberget 1985; Hannon *et al.* 1998; Munkebye *et al.* 2003).

Willow ptarmigan is an important component in mountain birch-forest and alpine ecosystems, where the species is prey for various avian and mammalian nest predators (Erikstad *et al.* 1982; Myrberget 1985; Munkebye *et al.* 2003). Potential mammalian nest predators present in northern boreal forests and the lowalpine tundra are the generalist predators red fox (*Vulpes vulpes*; food- and habitat generalist) and pine marten (*Martes martes*; food generalist and habitat specialist), and the specialist predators stoat (*Mustela*

erminea) and least weasel (*M. nivalis*) (Angelstam *et al.* 1984; Parker 1984; Myrberget 1985; Shorrocks *et al.* 1998; Kauhala and Helle 2002; Munkebye *et al.* 2003). Potential avian generalist nest predators are raven, hooded crow and European magpie (*Pica pica*) (Parker 1984; Myrberget 1985; Munkebye *et al.* 2003). Avian predators rely on visual cues to locate nests, whereas mammalian predators mostly use olfactory cues to find nests (Rangen *et al.* 2000). A predator's ability to detect a nest is affected by the composition and structure of the vegetation; thus, nest cover can affect predation rates and predation risks (O'Reilly and Hannon 1989; Schieck and Hannon 1993; Wiebe and Martin 1998; Manzer and Hannon 2005). Visual cues are mostly limited by vegetation cover of the nest, whereas olfactory cues are limited by the vegetation surrounding the nest influencing how the odorant molecules from the nest spread in the terrain (Conover 2007).

During the past 20 years, many areas in the mountain birch forests and the low-alpine tundra have been extensively developed into large cabin resorts in Norway (Kaltenborn *et al.* 2007; Statistics Norway 2010), which has led to increased human infrastructure at higher elevations. Recent studies have documented generalist species such as red foxes and corvids using such altered habitats, thus demonstrating their attraction to such areas (e.g. red fox, Røhnebæk 2004; corvid species, Storch and Leidenberger 2003; Liebezeit *et al.* 2009; Røttereng and Simonsen 2010; Støen *et al.* 2010). Infrastructure such as roads and foot paths could potentially increase accessibility of nests to mammalian predators (Liebezeit *et al.* 2009). Although not explored, the attraction to cabin-resort areas could be related to increased access to easily available food resource, such as garbage, food remains or even increased abundance of rodents in the grassland often developed around cabins. External subsidies represent an input of energy and nutrients, which could have an impact on the ecosystem structure and function, thus potentially resulting in trophic cascades, such as increased spatial and temporal abundance of generalist predators (i.e. red fox and corvids), possibly leading to higher predation pressure (Dhindsa and Boag 1990; Pedersen *et al.* 2007).

The aim of the present study was to investigate relative nestpredation rates along elevation gradients (ecotones), spanning from northern boreal mountain birch forests to low alpine-tundra in three areas contrasted by a varying density of willow ptarmigan. More specifically, we investigated whether relative nest-predation rates were related to (1) habitat types in the gradient, (2) the load of human infrastructure and (3) the density of willow ptarmigan (i.e. higher predation rates in areas with low willow ptarmigan density). Thus, a consistent variation in relative predation rates and those predators responsible for nest predation could be expected.

Materials and methods

Study area

The study was performed in June 2007 in three mountain areas in Hedmark County in Norway (Fig. 1). We selected the following three study areas of contrasting willow ptarmigan density: (1) Raudfjellet (61°12'N, 11°00'E; low willow ptarmigan density in August 2003–2007 (8–21 birds km⁻²)); (2) Råtåsjøhøi (62°16'N, 09°47'E; medium willow ptarmigan density in August 2005–2007 (17–25 birds km⁻²)) and Åslia (62°36'N, 10°56'E; high willow ptarmigan density in August 2004–2007 (40–102 birds km⁻²)) (Fig. 1). The study areas were located in northern boreal mountain birch forests and low-alpine tundra in the cool-temperate climatic region (Moen 1999).

Vegetation composition and structure were different among the three locations, Åslia and Råtåsjøhøi being similar in characteristics, but different from Raudfjellet. Differences were most pronounced for the birch forest and edge habitat. The birch forests in Åslia and Råtåsjøhøi were dominated by tall birch trees (*Betula pubescens*) (4–10 m), junipers (*Juniperus communis*), willows (*Salix* spp.), various herbs and grasses (Poaceae spp.), in

contrast to smaller birch trees (0–2 m), coniferous trees (*Picea abies* and *Pinus sylvestris*) (2–4m) and bilberry (*Vaccinium myrtillus*) in Raudfjellet. The edge habitat had similar forest composition and structure as described above, but differed by dominance of grasses in Åslia and Råtåsjøhøi and of cotton grass (*Eriophorum* spp.) in Raudfjellet. Differences in the low-alpine tundra, although to less extent than with the other habitat types, were mainly related to dominance of dwarf birch (*Betula nana*) in Åslia and Råtåsjøhøi, in contrast to dominance of heath (Ericaceae spp.) and moss in Raudfjellet (Appendices 1–3).

The study locations were situated in the vicinity of local human settlements or cabin-resort areas, with road access and foot paths connecting the birch forest with alpine areas. These developments were situated at lower altitudes than our study ecotones. Only in Råtåsjøhøi, there was a road above the tree line, which divided the study area into two parts. Human foot-path networks intersected our study ecotones, most often leading to the closest summit above the tree line.

Study design

We used an experimental approach with artificial nests to investigate our research questions. Artificial nests on track boards were used to obtain spatial replication and controlled stratification which would not have been possible using natural nests. This type of study design yields information about spatial and temporal prevalence of egg-consuming predators, thus indicating relative predation-risk patterns for ground-nesting birds (Angelstam 1986; Storch 1991; Villard and Pärt 2004; Manzer and Hannon 2005; McKinnon *et al.* 2010). In each of the three study areas, we placed 12 transects (total of 36 transects) with three track boards (i.e. artificial nests) in each transect (total of 108 track boards). Transects represented a natural elevation gradient, with changing vegetation composition and structure from the birch forest through the edge habitat to the open low-alpine tundra (termed birch forest, edge, low-alpine, respectively; Fig. 1). Transects were placed approximately in a straight line at an angle of 90 degrees with the tree line and the track boards were placed at a distance of 100m between each track board; one in the birch forest, one at the edge (i.e. tree line where birch forest meets low-alpine habitat) and one in the open low-alpine habitat (Fig. 1). The tree line was defined as the border where there were scattered trees with height <2m (Børset 1962). Initially, transects were placed systematically, at a distance of 1 km from each other in the study areas; however, access by foot was constrained by topography and ruggedness, and as a result, the distance between transects varied between 700 and 1600 m.

Artificial nests on baited track boards

Each artificial nest consisted of a 60x60 cm by 3-mm-thick chip board baited with two common quail (*Coturnix coturnix*) eggs placed in the middle of the board. The board was smeared with a thin layer of non-toxic lubrication grease (Mobile greaseFM102, 800 g; Exxon Mobil Corporation) and covered with soil, thus ensuring predators left tracks when removing the eggs (Angelstam 1986). Track boards were placed horizontally on the ground and slightly concealed at the edges by surrounding vegetation in the field layer. Latex gloves were used when handling the track boards and eggs to reduce human scent (Bowen *et al.* 1976). The nests were not marked on the ground, but were located by GPS positions (GARMIN eTrex) because corvids likely develop search images for permanent markers in the landscape (Picozzi 1975; Sonerud and Fjeld 1984, 1987).

The track boards were set out in early June, coinciding with the incubation period of many ground-nesting birds. Nests were exposed to predators for two consecutive trial periods of 10 days and each nest was rechecked after 10 days of exposure. Additional grease and soil were supplied, if needed, and the same procedure was carried out as in the first trial period. A nest was noted as depredated when ≥ 1 egg was missing and/or destroyed, and when foot

prints were set in the grease. Nests disturbed by domestic animals were recorded as missing data. Identification of mammalian predators was based on Østbye (2000), and avian predators were identified according to Pedersen *et al.* (2009). Stoat and least weasel were grouped together because their foot prints were difficult to distinguish from each other on the boards. We were aware that track boards as artificial nests are more conspicuous than are natural nests and may be easier to discover by avian predators using visual cues to locate prey than by mammalian predators using olfactory cues (Storaas 1988; Willebrand and Marcström 1988; Major and Kendal 1996; Moore and Robinson 2004; Thompson and Burhans 2004). However, because the present study was conducted to explore relative differences among three locations with contrasting willow ptarmigan densities, we assumed that the methodological constraints were similar across locations.

Predictors of human infrastructure

The load of human infrastructure around the individual track boards was characterised by the shortest distance from track board to human settlement (i.e. cabin-resort areas, individual houses, cabins and dairy farms and local settlements; mean = 1231 m, range = 200–3000); road (mean = 1263 m, range = 100–3000) and foot path (mean = 446 m, range = 0–1300), with a ruler tool in the Program Map Source (Garmin International Inc. 2007). The first two variables were highly correlated (Spearman's rank correlation coefficient $r = 0.87$, $P < 0.05$) and only the variable 'distance to road' was included in the statistical analysis.

Statistical methods

Total and species-specific relative predation rates were analysed using generalised linear mixed-effect models, assuming a binomial distribution for the response variable (Lewis 2004). Models were fitted in R (R Development Core Team 2010) using the lme4 package (Bates and Maechler 2007). Transects were treated as a random factor in the analysis and the following variables were included as fixed predictor variables: location (Raudfjellet, Råtåsjøhøi, Åslia), habitat (birch forest, edge, low-alpine), period (two consecutive trial periods of 10 days), distance to road and distance to foot path. All possible model combinations were tested, including biologically relevant interaction terms (i.e. location \times period, location \times habitat, period \times habitat). Model selection was performed using the Akaike's information criterion corrected for a small sample size (AICc) and AICc-weights (Anderson and Burnham 2002). When differences in delta AICc were ≤ 1 , the simplest model was selected for inference. Variable importance (VI) was assessed using the sum of the AICc weights for the 40 best models, including this variable (Anderson *et al.* 2001). Estimates of effect sizes are given as odds ratios (OR), with 95% confidence intervals (CI) for factorial study-design variables.

To investigate whether predators were correlated in space, we calculated Spearman's rank correlation coefficients on the basis of transect-specific predation (i.e. predation events summed over transect ($n = 36$) and period ($n = 2$)). Correlation coefficients were calculated on proportion data expressed as a number of predation events per transect (aggregated over habitats and study periods), divided by the total number of track boards available for predation (excluding track boards disturbed by domestic animals).

Results

Predator assemblage and overall predation rates

In all three locations and over both trial periods, 58.2% (121 of 208) of the artificial nests were preyed on by six identified predator species. Over both trial periods, 72.9% (51 of 70) of the artificial nests were preyed on by four identified predator species at Raudfjellet, 57.7% (41 of 71) by five identified predator species at Råtåsjøhøi and 43.3% (29 of 67) by five identified

predator species at Åslia (Table 1). In all three areas, there was an increase in total predation from the first to the second trial period (Table 1). Raven was the dominating predator at all study locations and over both trial periods, except for the second period at Raudfjellet where hooded crow dominated. The second-most dominating predator was hooded crow, followed by pine marten, stoat/least weasel, red fox and magpie (Table 1). In addition, some eggs were removed by domestic sheep (*Ovis aries*). Among the predators identified with certainty, we analysed statistically relative predation rates only for predators with ≤ 15 predation events (pine marten, raven and hooded crow).

Predictors of relative predator prevalence

Total predation was explained by a simple model including only additive effects of the variables period (VI = 1.00) and path (VI = 0.71) (Table 2). Total predation rates increased over trial periods (OR period, ORPeriod2/Period 1 = 4.64, CI = 2.16–9.98) and predation rates decreased significantly with increasing distance to path (logit estimate = -0.0030 , 95% CI = -0.0048 to -0.0005 , $P = 0.014$; Fig. 2). The density of willow ptarmigan was not significantly related to total relative predation rates as expected, because the variable 'location' was not included in the best model.

Predation by pine marten was explained by the second-best model ($\Delta AICc = 0.24$) including additive effects of the variables location (VI = 0.98), habitat (VI = 1.00) and path (VI = 0.93) (Table 2). There was no statistically significant difference in predation rates from pine marten among the locations (OR Råtasjøhøi/Åslia = 2.80, range = 0.74–10.50); no predation from pine marten in Raudfjellet). Predation rates by pine marten were clearly higher in birch-forest habitat (OR birch forest/low-alpine = 25.59, CI = 2.78–235.10), whereas almost no predation took place in the two other habitats (Table 2). Pine marten predation rates increased significantly with an increasing distance to foot path (logit estimate = 0.0024, 95% CI = 0.0006–0.0042, $P = 0.008$; Fig. 2).

Raven predation was explained by a model including the variables habitat (VI = 0.98) and path (VI = 0.59) (Table 2). The raven had the highest predation rates in the low-alpine habitat, whereas in the birch-forest and edge habitats, respectively, predation by raven was similar to or significantly less than that in the low-alpine habitat (OR birch forest/lowalpine = 0.22, CI = 0.08–0.62, OR edge/low-alpine habitat = 0.22, CI = 0.08–0.62). Predation rates by raven, although not statistically significant, decreased with increasing distance to path (logit estimate = -0.0025 , 95% CI = -0.0051 – -0.0009 , $P = 0.063$; Fig. 2).

Predation by hooded crow was explained by a model including the variables period (VI = 1.00) and habitat (VI = 0.79) (Table 2). Almost all predation by the hooded crow occurred in the second trial period (see Table 2). There was no statistically significant difference in predation rates by hooded crow between birchforest and low-alpine habitats (birch forest/low-alpine, OR=0.04, range = 0.00–5.32). The edge habitat tended to have the highest predation rates (OR edge/low-alpine = 1.98, range = 0.23–16.70), although the difference was not statistically significant.

Spatial relation between predator species

There was a significant and negative association in transect-specific predation rates of raven and pine marten ($r = -0.48$, $P < 0.05$). There was no evidence for spatial association in transect-specific predation rates between any other predator species.

Discussion

Generalist predators, dominated by raven, followed by hooded crow and pine marten, were the overall most numerous predators observed in the study. Predator prevalence was habitat specific, with opposite relative predation patterns between the forest dwelling pine marten,

and the open-tundra dwelling raven. Similarly, the species displayed opposite predation patterns related to human infrastructure, raven predation increasing closer to foot paths and *vice versa* for pine marten. Hooded crow predation was similar across the elevation gradient and was not related to human infrastructure. Location, as contrasted by differences in the density of willow ptarmigan, was not significantly related to relative predation rates in the statistical models, as we expected.

Total relative predation rates found in the present study were of magnitude similar to what was found in former nest-predation studies of willow ptarmigans (Appendix 4). The predators were dominated by generalist, corvids (raven and hooded crow) and pine marten. Predation rates by other mammalian predators such as red fox, stoat and least weasel were low compared with those by avian predators. There could be several reasons for this, including the following: (1) the study year appeared to be a low abundance year for small rodents, which probably led to lower densities of mammalian predators (i.e. both red fox (Lindström and Hörnfeldt 1994) and mustelids (Hellstedt *et al.* 2006) are known to respond numerically, with a time lag of 1 year, and functionally to population dynamics of cyclic boreal voles); (2) differences in hunting mode and search pattern between mammalian and avian predators (visual *v.* olfactory cues; Sonerud and Fjeld 1984; Storaas 1988; Thompson and Burhans 2004); (3) failure of mammals detecting a nest due to lack of an incubating bird with scent (Willebrand and Marcström 1988); and/or (4) there might be an inherent bias in the artificial-nest method that underestimates the importance of mammals as nest predators (see Materials and methods). Likewise, a lack of an incubating bird can potentially elevate predation rates by small-sized corvids (Nguyen *et al.* 2006), although this is not likely for the medium-sized hooded crow. It is reasonable to believe that the present artificial-nest study might be biased towards avian predators, although this was not quite consistent because we observed similar predation rates by hooded crow and pine marten. Thus, the relative prevalence of the predator species across the ecotones and locations is likely to be similar and comparable.

The two most significant explanatory variables for prevalence of pine marten and raven were habitat and distance to foot path. Predation by pine marten took place at similar rates in the birch-forest habitats of Råtasjøhøi and Åslia, with a medium and high density, respectively, of willow ptarmigan, whereas no predation was observed in Raudfjellet (low density). The characteristics of the birch-forest habitat (see Fig. 2) were similar between the two locations (i.e. Råtasjøhøi and Åslia), but different from the forest habitat at Raudfjellet. The two first-mentioned locations were dominated by tall birch forest with more variation in the shrub and field layer than there was in the smaller-birch and coniferous forest, with only bilberry in the field layer, at Raudfjellet. Pine marten is foremost a forest-dwelling species, dependent on cavities in trees for dens, and avoids areas with no overhead cover (Pulliainen 1981; Brainerd *et al.* 1995; Brainerd and Rolstad 2002); thus, the habitat at Raudfjellet may be less suitable for pine marten. Red fox is known to be a limiting factor for pine marten abundance (Smedshaug *et al.* 1999) and numbers of predation events from pine marten could reflect the density of red fox in the study areas. Despite the low prevalence of red fox, four of five predation events from red fox were in Raudfjellet where no predation from pine marten took place, whereas at Råtasjøhøi, which had the highest prevalence of pine marten, there was no predation from red fox. The sample size of red fox was, however, too low for statistical analysis.

Raven predation was higher in the low-alpine habitat than in the birch-forest and edge habitats, whereas the hooded crow showed no statistically significant difference among the habitats. Šàlek *et al.* (2004) argued that the spatial pattern of a dominant generalist predator species explains the predation pattern on artificial nests, and Andrén *et al.* (1985) found that predation on artificial nests was correlated with corvid population abundance. Thus, the

spatial predation pattern by raven and hooded crow probably reflected the species' habitat use (Sandvik 1998; Smedshaug *et al.* 2002; Klausen *et al.* 2010). The high prevalence of ravens in the present study is most probably due to overall higher occurrence in alpine environments. In contrast to a similar study in northern Norway, where the hooded crow was the overall most important predator (Klausen *et al.* 2010), we observed very few artificial nests depredated by hooded crow in our study, which simply could be related to differences in population abundance between the study regions.

We expected location, with contrasting densities of willow ptarmigan, to be a predictor of predation rates; expecting higher nest-predation rates in the low-density area. However, we found no evidence by statistical modelling to support this hypothesis for total nest-predation rates (predator community pooled) or any of the species (see also O'Reilly and Hannon 1989). We suggest that the most likely explanation for the lack of this relation is the discrepancy between the predation rates of artificial nests and the predation rates on real nests (e.g. Storaas 1988; Willebrand and Marcström 1988; Thompson and Burhans 2004). Nest predation can also vary tremendously among years in boreal birch forests and the low-alpine habitats and is often linked to the stage of the small-rodent cycle (Myrberget 1985; Carignan and Villard 2002; Munkebye *et al.* 2003). Thus, several authors have recommended multi-annual studies in areas with cyclic fluctuations in small-rodent population because predation rates are expected to differ among different phases of the cycle (Yahner 1996; Carignan and Villard 2002; Šálek *et al.* 2004). The present study spanned across only one season and a multi-annual study would probably give more insight into how the densities of willow ptarmigan are related to predation rates of artificial nests.

Pine marten and raven showed opposite predation patterns in relation to human infrastructure (distance to foot path); namely, raven was positively related whereas pine marten was negatively related to the distance to foot path. Interestingly, the hooded crow, which has been found to be an important predator in Subarctic birch forests (e.g. Erikstad *et al.* 1982; Pedersen *et al.* 2009; Klausen *et al.* 2010), showed no association to human infrastructure, in contrast to recent work of Støen *et al.* (2010) who documented higher predation rates related to cabin-resort areas. Although, most predation events from hooded crow were in the area with the highest density of cabins, the low sample size may have biased the results. Miller and Hobbs (2000) suggested that avoidance of foot paths by mammalian predators might be related to scents from canines (i.e. dogs taken for walks). Also wild predators, such as the red fox, often use foot paths for movement in the landscape, resulting in less frequent use of paths by pine marten because of the antipredator behaviour of the latter (Lindström 1989). Such foot paths occur in higher densities around cabin-resort areas (Røhnebæk 2004), which could explain less frequent use of these areas by pine marten. Corvids, in contrast, have the ability to habituate to humans and are likely to search for subsidies (i.e. leftover food and garbage) provided by recreationalists using the foot paths connected to cabin-resort areas (Dhindsa and Boag 1990; Taugbøl *et al.* 2001).

Management implications

Our study confirmed that predator prevalence was habitat specific and the crucial human effect was the presence of foot paths in relatively undisturbed habitats. The present study is yet another example demonstrating that human infrastructure affects predation rates of generalist species in an alpine ecosystem (see also Røhnebæk 2004; Selås *et al.* 2010; Støen *et al.* 2010). Spatial food subsidies, possibly leading to higher nest predation from generalists such as corvids, may result in trophic cascades by increased spatial and temporal abundance of generalist predators (Marzluff and Neatherlin 2006; Støen *et al.* 2010; Killengreen *et al.* 2011). We recommend that attractive willow ptarmigan habitat should be avoided when planning large cabin-resorts areas and corresponding infrastructure. To reduce predation

pressure in this ecosystem, it appears that generalist predators should be considered for management actions. Further research is needed to explain the underlying mechanism driving expansion of generalist species into alpine habitats (Liebezeit *et al.* 2009; Selås *et al.* 2010). Such knowledge would be important also in developing alternative management actions with focus other than only predator control because both mammalian and avian predators are difficult and effort-demanding to control at large spatial and temporal scales (Parker 1984; Marcström *et al.* 1988).

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Figures

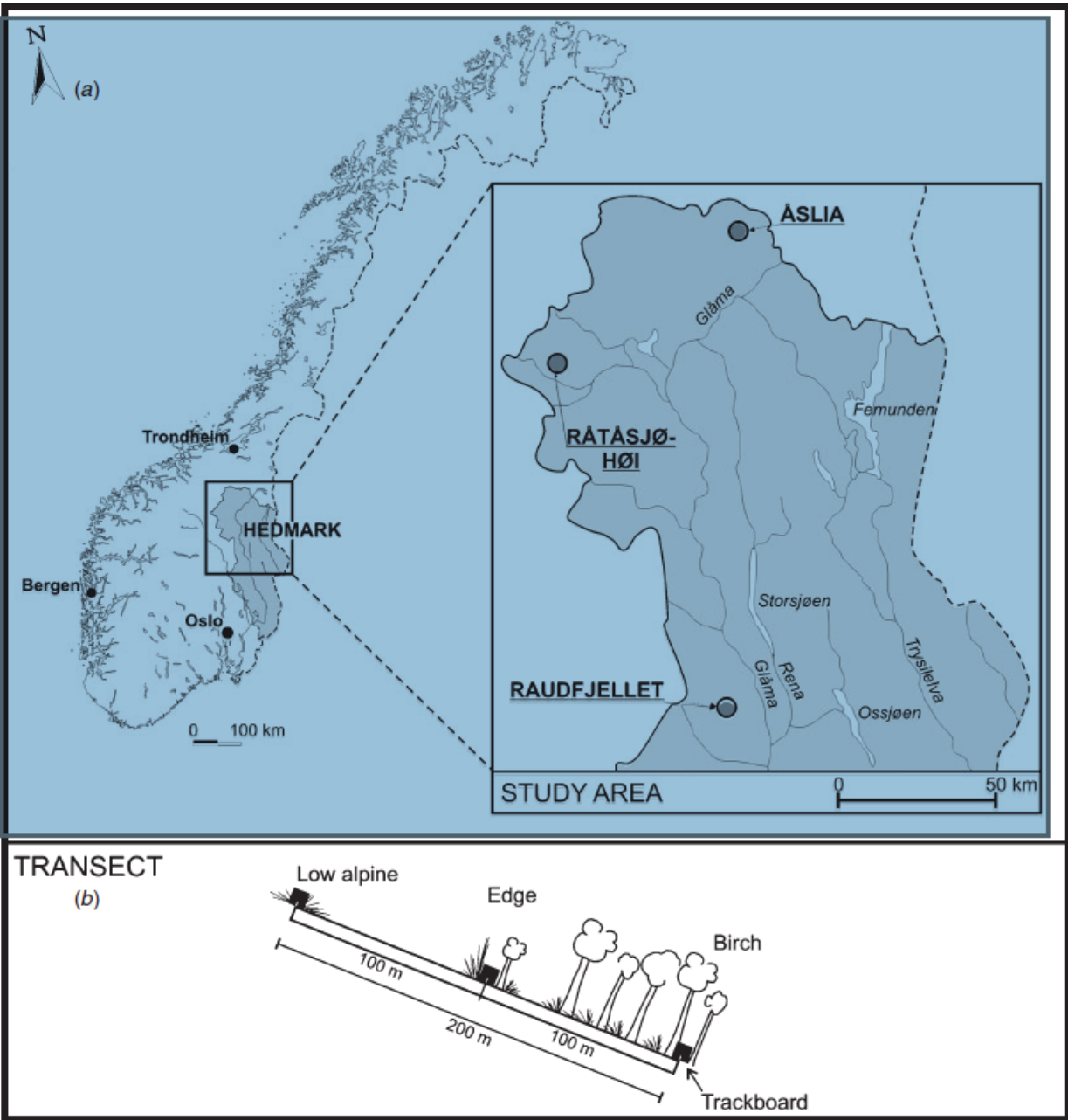


Fig. 1. (a) Map of Norway with Hedmark County (grey) and inset showing approximate location of the three study areas (Åslia, Råtåsjøhøi and Raudfjellet). (b) Track-board placement (■) along the elevation gradient, spanning from boreal mountain birch-forest to the low-alpine habitat.

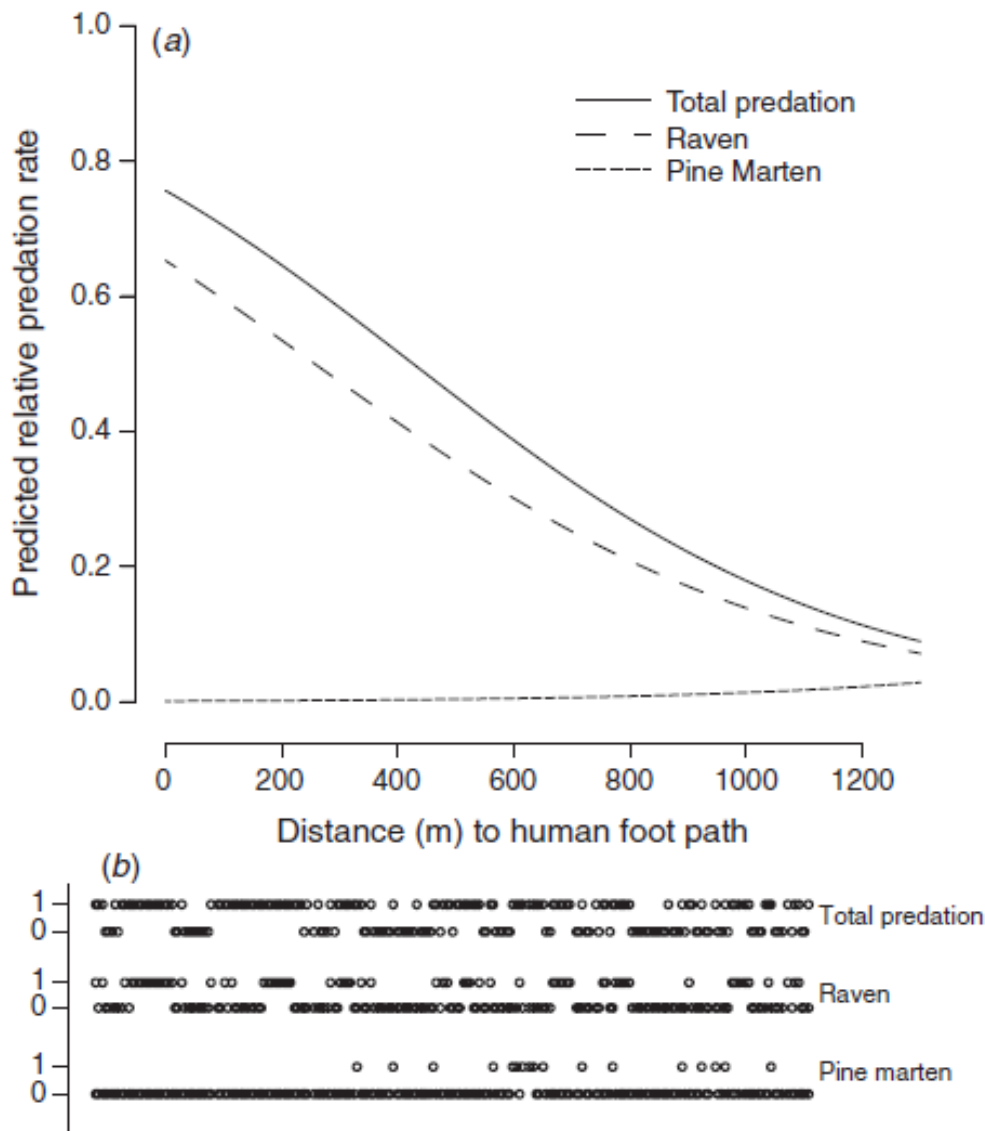


Fig. 2. (a) Relationship between predicted predation rates for total predation (i.e. all species combined), raven and pine marten from the selected models and the explanatory variable distance to foot paths. (b) Observed values (0 = no predation; 1 = predation) for all predators combined (total predation), raven and pine marten predation.

Tables

Table 1. Summary of species-specific predation by location (Raudfjellet (low willow ptarmigan density), Råtåsjøhøi (medium willow ptarmigan density) and Åslia (high willow ptarmigan density)), period (Period 1 and Period 2) and track-board placement (birch-forest habitat (b), edge habitat (e) and low-alpine habitat (l))

Treatments refer to eggs available for predation, excluding eggs removed by domestic animals. Total predation, treatments, total mammalian predation (%), total avian predation (%) and total predation (%) were calculated per trial period

Predator community	Raudfjellet						Råtåsjøhøi						Åslia					
	Period 1			Period 2			Period 1			Period 2			Period 1			Period 2		
	b	e	l	b	e	l	b	e	l	b	e	l	b	e	l	b	e	l
Red fox (<i>Vulpes vulpes</i>)	–	–	–	1	2	1	–	–	–	–	–	–	–	1	–	–	–	–
Pine marten (<i>Martes martes</i>)	–	–	–	–	–	–	2	1	–	5	1	1	3	–	–	2	2	–
Stoat/least weasel (<i>Mustela ermine/M. nivalis</i>)	–	1	–	–	–	–	1	–	1	–	1	–	–	–	1	1	–	–
Raven (<i>Corvus corax</i>)	6	4	8	4	3	3	2	3	4	3	3	6	2	3	3	1	3	5
Hooded crow (<i>C. cornix</i>)	–	1	–	3	5	5	–	–	–	–	1	1	–	–	–	–	1	1
European magpie (<i>Pica pica</i>)	–	–	–	–	–	–	–	2	–	1	1	–	–	–	–	–	–	–
Unidentified predator	1	–	–	–	1	–	–	–	–	–	–	1	–	–	–	–	–	–
Domestic sheep	–	–	–	1	–	1	–	–	–	–	1	–	2	–	–	2	1	–
Total predation	21			30			16			25			13			16		
Treatments	36			34			36			35			34			33		
Total mammalian predation (%)	2.8			11.1			13.9			22.9			14.7			15.2		
Total avian predation (%)	58.8			70.6			30.6			45.7			23.5			33.3		
Total predation (%)	61.1			85.3			44.4			71.4			38.2			48.5		

Table 2. The three best models for total predation (all predator species combined), pine marten, raven and hooded crow predation, including the following predictor variables: location, period, habitat, distance to road (Road) and distance to foot path (Path) according to Δ AICc and AICc weights (w)
No interactions were included in the candidate models. The best model is indicated in bold letters. n = number of predation events; np = number of parameters estimated; x = variable included in models; – = variable not included in models

Predator	np	Location	Period	Habitat	Road	Path	Δ AICc	AICc (w)
Total predation	4	–	x	–	–	x	0.00	0.41
($n = 121$)	5	–	x	–	x	x	2.04	0.15
	6	x	x	–	–	x	2.65	0.11
Variable importance		0.28	1.00	–	0.22	0.82		
Pine marten	8	x	x	x	–	x	0.00	0.36
($n = 17$)	7	x	–	x	–	x	0.24	0.31
	9	x	x	x	x	x	2.17	0.12
Variable importance		0.98	0.52	1.00	0.26	0.93		
Raven	5	–	–	x	–	x	0.00	0.18
($n = 68$)	4	–	–	x	x	x	0.08	0.18
	6	–	–	x	x	–	0.88	0.12
Variable importance		–	–	0.98	0.50	0.59		
Hooded crow	5	–	x	x	–	–	0.00	0.33
($n = 18$)	6	–	x	x	x	–	1.68	0.14
	6	–	x	x	–	x	2.00	0.12
Variable importance		–	0.79	1.00	0.35	0.27		

Appendix

Appendix 1. Habitat characteristics along the ecotone

Wemappedvertical vegetation structure to assess variation in structure along the elevation gradient. Dominating vegetation variables (Appendix 2) were registered within a circle of 3.14m² every 10malong the habitat gradient, providing a total of 21 sampling stations. Variables were classified in the following layers: bottom (ground level), field (<1 m), shrub (0–2m) and tree layer (0–2m, 2–4m and 4–10 m). We summarised the vegetation variables by habitat in each transect by calculating average values for respective variables in each habitat. The vegetation variables were processed by fuzzy coding according to Chevenet *et al.* (1994) to identify the structure of the vegetation composition in each layer, and the resulting frequencies were further analysed by a principle component analysis (PCA) (Jongman *et al.* 1995) with respect to instrumental variables (PCAIV) (Rao 1964) in the ade4 package forR (Chessel *et al.* 2004; RDevelopment CoreTeam2010). This constrained analysis explained only the variation among the vegetation variables resulting from the instrumental variables, location (Raudfjellet, Råtåsjøhøi, Åsli) and habitat (birch forest, edge, low-alpine)

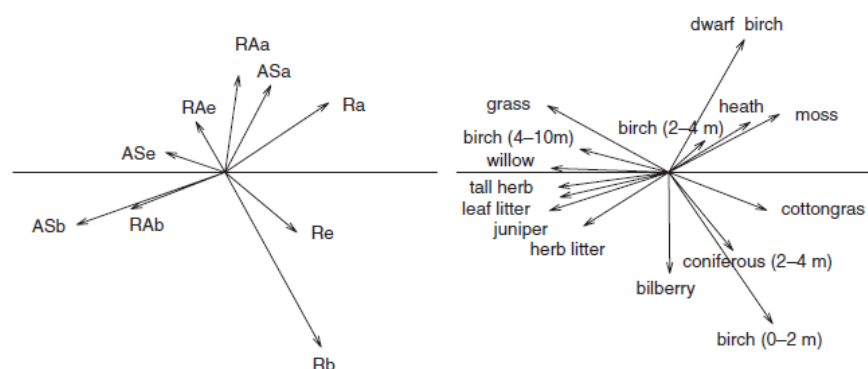
Appendix 2. Classification of vegetation variables (*n* = 15) in four vertical layers

Category	Species/species group
Bottom layer (at ground)	Moss and lichen Herb litter Leaf litter
Fieldlayer (<1 m above ground)	Bilberry (<i>Vaccinium myrtillus</i>) Grass (Poaceae spp.) Heath (Ericaceae spp.) ^A Tall herb Cottongrass (<i>Eriophorum</i> spp.)
Shrub layer (0–2 m above ground)	Dwarf birch (<i>Betula nana</i>) Juniper (<i>Juniperus communis</i>) Willow (<i>Salix</i> spp.)
Tree layer (0–10 m above ground)	Birch (<i>Betula pubescens</i>) (0–2 m) Birch (2–4 m) Birch (4–10 m) Coniferous (<i>Picea abies</i> and <i>Pinus sylvestris</i>) (2–4 m)

^AEricaceae without *Vaccinium myrtillus*.

Appendix 3. Correlation between the instrumental variables, habitat and location (Panel 1), and the first two axes of PCAIV (the first axis explained 48.4% and the second axis 27.5%) on the vegetation variables (Panel 2)

The first axis of the PCA on the vegetation variables (*n* = 15) (Panel 2) explained 26.9% and the second axis 13.4% of the variation in the dataset. The length of the vector is an estimate of the impact it has on the different axes. Instrumental variables were location (Åsli (AS), Råtåsjøhøi (RA), Raudfjellet (R)) and habitat (birch forest (b), edge (e), low-alpine (l))



Appendix 4. List of selected willow ptarmigan (*Lagopus lagopus*) nest-predation studies using natural and artificial nests^A

The list is sorted alphabetically by the first author of the article. Single values indicate 'mean values' across years and brackets [] indicate 'range' of nest-predation rates

Location	Latitude, longitude	Habitat	Year	Total predation (%)	Avian predation (%)	Mammalian predation (%)	Natural nest	Artificial nest	Reference
Evenes and Skånland, Norway	68°30'N, 16°40'E	Mountain birch	2002	[45.3–63.7]	[22.2–30.4]	[24.3–36.3]	–	x	Einarsen <i>et al.</i> 2008
Tranøy, Norway	69°09'N, 17°25'E	Mountain birch, bog and shrub	1975–1978	37	–	–	x	–	Erikstad <i>et al.</i> 1982
Chilkat Pass, British Columbia, La Perouse Bay, Manitoba, Canada	59°50'N, 136°30'W; 58°24'N, 94°24'W	Subalpine tundra	1979–1986	[6–86]	–	–	x	–	Hannon <i>et al.</i> 1988; see also O'Reilly and Hannon 1989 for a similar study
Troms, Norway	69°N, 18–19°E	Mountain birch, low-alpine	2007	[47.4–77.5]	[44.7–67.5]	[0.0–10.0]	–	x	Klausen <i>et al.</i> 2010
Dovre fjell, Norway	62°17'N, 09°39'E	Mountain birch, low-alpine	1978–1992	15.0 (0.0–50.0)	–	–	x	–	Munkebye <i>et al.</i> 2003
Tranøy, Norway	69°09'N, 17°25'E	Mountain birch, bog and shrub	1960–1980	21.6	–	–	x	–	Myrberget 1984, 1985
Glen Esk, north-eastern Scotland	–	Heather, moorland	1994–1995	22.4	–	–	x	–	Park <i>et al.</i> 2002 ^B
Evenes/Skånland, Norway	68°30'N, 16°40'E	Mountain birch	2003–2005	[57.3–96.7]	[28.1–95.6]	[1.1–52.8]	–	x	Pedersen <i>et al.</i> 2010
Dovre fjell, Norway	62°17'N, 09°39'E	Mountain birch, low-alpine	1981–1985	[0.0–37.5]	–	–	x	–	Rørvik <i>et al.</i> 1999
Sjusjøen, Norway	61°15'N, 10°40'E	Mountain birch, coniferous, low-alpine	2007	63	–	–	–	x	Støen <i>et al.</i> 2010

^ASearch words on ISI per medio August 2011: '*Lagopus lagopus* and nest predation'; '*Lagopus lagopus* and egg predation'; '*Lagopus lagopus* and artificial nest'.

^BReport loss of egg, brood or adult bird combined for *Lagopus lagopus scoticus*.