

RESEARCH ARTICLE

Highways associated with expansion of boreal scavengers into the alpine tundra of Fennoscandia

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Abstract

1. Habitat fragmentation may affect species distributions through, for example, altered resource availability and shifts in species interactions. Fragmentation by roads has had negative impacts on Fennoscandian alpine ecosystems, with reduction of habitats and connectivity for alpine species. Concurrently, infrastructure development causes influx of subsidies through roadkills and litter, which may facilitate expansion of boreal scavenging species, such as the red fox *Vulpes vulpes*, which may intensify negative interactions with alpine species. Hence, understanding the impact of subsidies within marginal alpine areas is imperative for successful conservation and management of particularly vulnerable alpine species.
2. We used snow tracking and camera traps in three alpine tundra areas in Norway to investigate whether the presence of boreal scavengers was positively associated with highways during winter, and if this contrasted the pattern of a critically endangered alpine species, the Arctic fox *Vulpes lagopus*. In summer, artificial nests were used to assess whether predation risk was related to proximity to highways.
3. During winter, the occurrence of red foxes was higher close to highways and decreased with increasing distance to highways, while the arctic fox showed no discernible pattern. Red fox occurrence increased with the number of edible items of anthropogenic origin located along highways, whereas arctic fox occurrence decreased.
4. The overall predation risk of artificial nests during summer was high (>31.2%) and increased with proximity to the highway in the area with highest traffic volume.
5. *Synthesis and applications.* Highways crossing alpine areas may attract boreal scavengers, possibly connected to increased access to subsidies of anthropogenic origin. Litter and food waste dominated available subsidies along highways in our study, and prevailing mitigating measures directed at reducing roadkill and movement restrictions may not be applicable to reduce negative effects of littering. We recommend actions focusing on informational campaigns, improved garbage disposal facilities and routines, and imposing fines for littering, to reduce negative impacts on vulnerable species. This is likely needed to achieve goals of 'no impact' from the physical loss of habitats due to road development.

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KEYWORDS

corvids, human impact, nest predation, range expansion, red fox, road ecology, scavengers, subsidies

1 | INTRODUCTION

The distribution of species is governed by mechanisms acting through time and space, such as climatic and environmental conditions, habitat quality and food availability, as well as dynamics within species communities (Krebs & Elwood, 2008; MacArthur, 1984). Changes to the factors limiting a species distribution may enforce range shifts, expansions or contractions (Hickling, Roy, Hill, Fox, & Thomas, 2006; Parmesan, 2006). Altered distributions may induce shifts within species communities and in predator–prey dynamics (Krebs & Elwood, 2008; Tylanakis, Didham, Bascompte, & Wardle, 2008), potentially leading to cascading effects (Ripple & Beschta, 2012). A well-known ecological cascade is extirpation of apex predators causing increased mesopredator abundance with subsequent decline in the abundance of prey species (O'Bryan, Holden, & Watson, 2019; Prugh et al., 2009).

Human land-use has been credited as the most important driver of habitat and biodiversity loss within terrestrial ecosystems (IPBES, 2019). Habitat fragmentation affects species distributions directly and indirectly through changes in environmental conditions, food availability or species interactions (Murcia, 1995), often resulting in increased mortality and reduced population viability (Lande, 1998; Laundré, Hernández, & Ripple, 2010). Fragmentation also produces new habitats, in particular edge habitats (Saunders, Hobbs, & Margules, 1991), which often have positive effects on opportunistic species and scavengers, for example through increased access to subsidies of anthropogenic origin such as food waste, road-kills and hunting remains. The input of external subsidies may increase carrying capacity, reproductive output and survival of scavengers in otherwise marginal habitats (Marzluff & Neatherlin, 2006; Storch & Leidenberger, 2003). Thus, human activities may cause opportunistic scavengers to increase in abundance and persist at the fringes of their geographic distribution, and shift or expand their distributional range, which may lead to increased interspecific interactions with neighbouring species (Courchamp, Langlais, & Sugihara, 2000).

Arctic and alpine ecosystems are often highlighted as the most sensitive to environmental changes (IPCC, 2018). Species within these low productivity ecosystems often have restricted geographic ranges with limited possibilities to move when the environment changes (Parmesan, 2006; Pauchard et al., 2009). In the Scandinavian alpine tundra development of infrastructure and cabin resorts has increased over the past decades (EEA, 2017). This may increase the availability of human-induced subsidies which in turn may attract opportunistic and scavenging species, such as red foxes and corvids, into otherwise low productive alpine habitats (Balestrieri, Remonti, & Prigioni, 2011; Storch & Leidenberger, 2003).

The red fox has been found to expand its distributional range northwards and upwards over the past decades in Fennoscandia, likely explained by both climate warming and an increase in human land-use (Elmhagen, Kindberg, Hellström, & Angerbjörn, 2015; Norén et al., 2015). Similarly, corvid populations have increased over the past decades (Vorisek, Gregory, Van Strien, & Meyling, 2008), possibly as a result of increased access to anthropogenic subsidies (Knight & Kawashima, 1993). This expansion of opportunistic scavengers into alpine areas may adversely affect alpine species such as the Arctic fox (Elmhagen et al., 2017). The arctic fox shares a broad niche overlap with the red fox (Elmhagen, Tannerfeldt, & Angerbjörn, 2002), however, being smaller and subdominant to the red fox it is likely to retreat in the face of an expanding red fox population (Hersteinsson & Macdonald, 1992).

Red foxes and corvids are common predators on ground nests and ground nesting birds (Pedersen, Asmyhr, Pedersen, & Eide, 2011) and studies suggest that nest predation rates increase in fragmented landscapes (Andrén, 1992; Keyser, Hill, & Soehren, 1998). Increased persistence, reproductive success and survival of opportunistic scavengers and predators through influx of anthropogenic subsidies may thus result in trophic cascades by increased competition and predation pressure, which may alter species communities and predator–prey dynamics. An increased understanding of how distribution of opportunistic scavengers relates to anthropogenic subsidies within low productivity habitats may thus aid conservation efforts of threatened alpine species and advice management how to prevent or reduce the negative impact of road development across marginal and sensitive habitats, such as the Scandinavian alpine tundra.

Here we investigated the ecological effects of highways crossing alpine areas in Norway. Based on the hypothesis that roads subsidize opportunistic scavengers through increased availability of food (i.e. litter, food waste and road kills), we expected (a) an increased occurrence of sub-alpine opportunistic scavengers (red fox and corvids), (b) a lower occurrence of alpine species (arctic foxes) and (c) a higher predation rate on artificial ground-nests, with increasing proximity to highways.

2 | MATERIALS AND METHODS

2.1 | Study area

We collected data in the late winter (March to April) and early summer (June) annually from 2016 to 2018 along highways in three alpine tundra areas in Norway (Figure 1a; see Table S1). The study areas were located within the lower alpine vegetation zone,

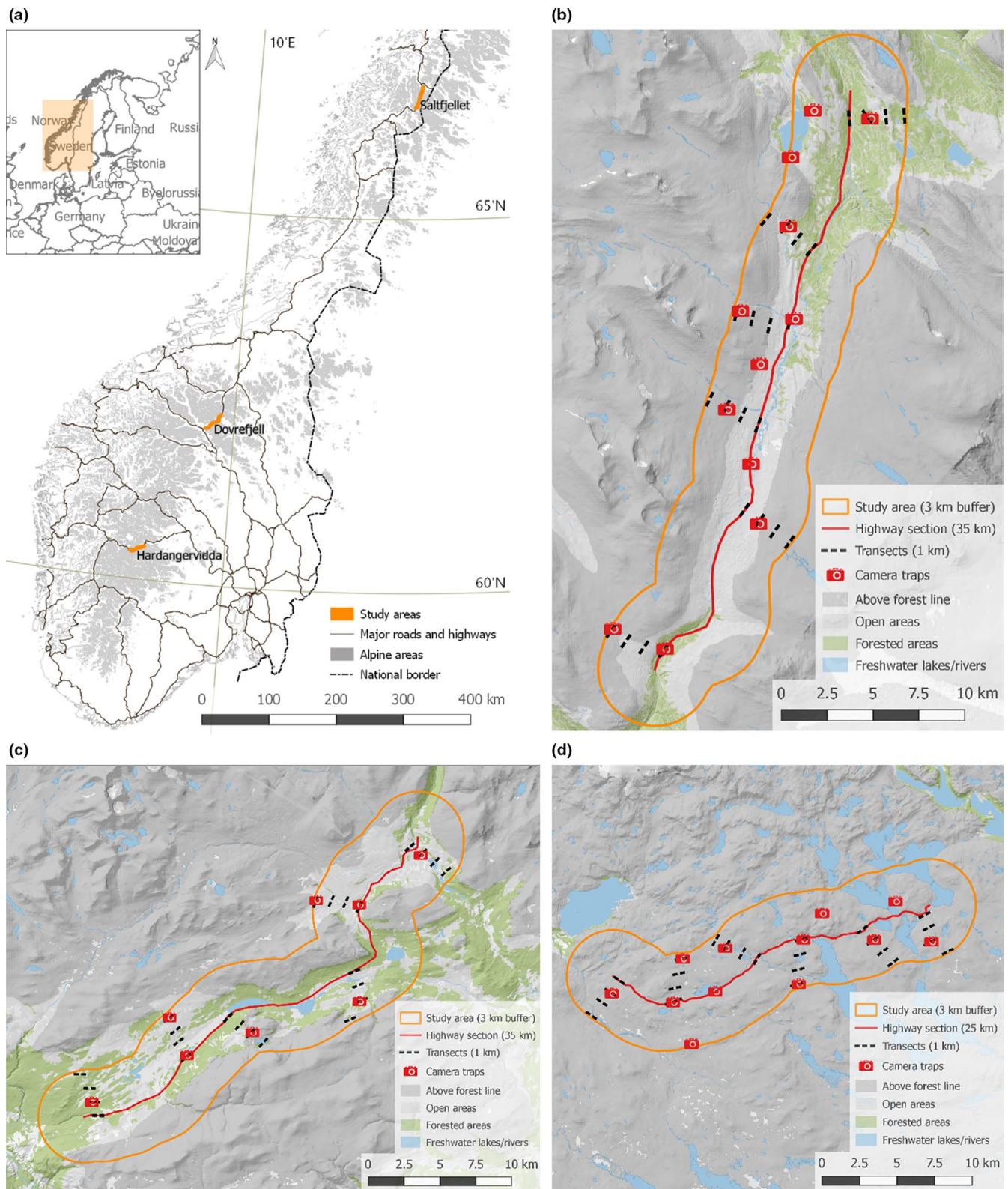


FIGURE 1 (a) Location of the surveyed highways through mountain passes in Norway, highlighted in orange; (b–d) Illustration of the placement of transects and camera traps along the surveyed road segments at Saltfjellet (b), Dovrefjell (c) and Hardangervidda (d)

dominated by willow shrubs *Salix* sp., juniper *Juniperus communis* and dwarf birch *Betula nana* (Moen, 1998). Dovrefjell was partly located within the northern boreal vegetation zone, with continuous clusters of mountain birch *Betula pubescens tortuosa* and

scattered clusters of pine *Pinus sylvestris*. Wild reindeer have perennial pastures at Dovrefjell and Hardangervidda, whereas semi-domesticated reindeer migrate into Saltfjellet in late spring. Alpine species within all study areas include arctic fox, golden eagle

Aquila chrysaetos, wolverine *Gulo gulo*, small rodents *Microtinae* spp. and ptarmigan *Lagopus* spp.

2.2 | Data collection

Each study area was divided into six sections of 1 km × 3 km (3 km²) along the highway (Figure 1b–d). Sections were semi-randomly selected, where the section had to be (a) located within the mountain pass, (b) physically accessible by foot/skis (i.e. excluding steep ridges) and not on a frozen lake (for safety concerns) and (c) >3 km apart to reduce overlap of species occurrence and risk of pseudoreplication. Each section contained four predefined 1-km transects running parallel to the road, located at 0, 1, 2 and 3 km from the road, totalling 24 km per study area (Figure 1b–d). One transect in the northernmost section at Saltfjellet was adjusted 100 m westward, and one transect at Dovrefjell was adjusted 750 m towards the southwest to avoid protected areas (Figure 1b,c). The next northernmost section at Saltfjellet was adjusted 200 m southwards to avoid a steep scree and reindeer herding area (Figure 1b).

2.2.1 | Snow tracking

We tracked red and arctic foxes along the transects on two occasions, approximately 14 days apart, and counted all crossing tracks. The field work was carried out on skis or by foot to reduce disturbance to local wildlife. We separated red and arctic fox tracks by (a) measuring the stride length and/or (b) following their tracks for some distance to analyse the gait. We assumed that regular trot indicated red fox (stride length 70–90 cm; 40–60 cm for arctic foxes), whereas a 'triple' trot indicated arctic foxes (stride length 87–100 cm; 122–150 cm for red foxes; Aronson & Eriksson, 1992).

2.2.2 | Camera trapping

Twenty-four baited camera traps (Reconyx HyperFire PC800 Professional; Reconyx, Inc.) were deployed during the first snow tracking occasion at selected transects, with eight cameras evenly distributed among proximity gradients within each study area (Figure 1b–d). Cameras were placed with a minimum distance of 3 km apart to reduce the chance of observing the same individual scavenger. To supplement our data, four extra cameras were placed outside the transects within each area at the same proximity gradient to the highways, except at Dovrefjell due to conflicts with wild reindeer migration. The cameras were set to a time-lapse of 5 min in addition to motion triggering and were active 14 days on average. Camera traps were baited with trimmings from slaughtered reindeer, frozen into blocks measuring approximately 60 cm × 40 cm × 15 cm and weighing 15–20 kg. At Hardangervidda in 2016 one camera was stolen and data could not be retrieved. In the same area in 2017 we failed to deploy two cameras due to adverse weather conditions.

2.2.3 | Nest predation

We placed artificial nests along the transects in early summer (June) each year to assess the relative predation risk of ground-nests of alpine birds (cf. McKinnon et al., 2010). Each nest, containing one quail egg and one artificial egg, handmade from modelling clay to mimic a quail egg, was placed for every 250 m along each transect for a total of five nests per transect (20 per road section/120 per study area). Plastic gloves were used when handling the eggs to reduce contamination by human scent. The nests were marked using yellow, white or red bands. Eggs were collected after 14–21 days. Bite marks on the artificial egg revealed the predator, recorded as either avian or mammal. About 12.3% of the nests were missing both eggs, whereas 6.4% of the nests were missing the quail egg with the artificial egg untouched, and the predator could not be identified. We therefore considered the overall relative predation risk rather than species-specific predation.

2.2.4 | Quantification of subsidies

In late winter, we inventoried road verges in each study area, parallel to snow tracking transects, for edible food items of anthropogenic origin and road-kills, following the procedure described by Lyngen (2016). Due to logistical reasons and adverse weather conditions we were unable to inventory all road verges in 2017 and 2018, and therefore only present results from 2016. Based on the number of inventoried food items, we quantified the potential amount of subsidies available to scavengers, i.e. the original items weight in grams.

2.2.5 | Explanatory variables

We included the number of *cabins* within a 1,500-m radius around each transect to assess if this proxy of human activity would affect red or arctic fox occurrence (see Table S1). The radius was selected as a maximum to avoid spatial autocorrelation between road sections. As our focus was on species occurring in mixed boreal/alpine habitats, we included the *relative distance to the forest line*, calculated as the average elevation of each transect divided by the overall forest line elevation of the study area. The rodent cyclic phase was used as an indication of *relative rodent abundance*, categorically represented by 'low', 'increasing', 'peak' or 'crash' phases, as the rodent phase governs activity and breeding success in arctic foxes, varying also in abundance in the diet of both arctic and red foxes (Elmhagen et al., 2002; Killengreen et al., 2011). None of the included variables showed signs of multicollinearity or strong correlations, as determined from a variance inflation factor (VIF) analysis with a threshold of VIF > 10, and a Pearson's correlation test with a threshold of $r > 0.7$ (see Tables S8 and S13; cf. Dormann et al., 2013). We added traffic volume, i.e. the average number of vehicles per day (VPD) for each study area and year (see Table S1), as traffic volume may indicate the amount of subsidies generated

along highways. VPD was, however, moderately confounded with other explanatory variables ($VIF = 4.3$; $r = 0.75$), and we excluded VPD from further analysis.

2.3 | Statistical analyses

2.3.1 | Snow tracking

We included only the tracking occasion each year with the most favourable tracking conditions in the analysis, i.e. where snow covered the entirety of the transects, >12 hr since the snow fall, and wind speeds preferably <5 m/s during tracking, to minimize the effects of varying weather conditions. We included *snow age* as an offset parameter in the models, as snow age (i.e. the days since last snowfall) may affect the number of tracks imprinted in the snow as well as the precision in track identification (see Table S2). As some transects had active camera traps prior to the second tracking occasion, we added *camera trap presence* as a covariate in the models (1 camera present, 0 camera absent) to account for the effect of aggregation of animals at baits.

The number of tracks of red and arctic foxes per km (i.e. one transect length) was analysed as a count model with a negative binomial distribution with a log link function to account for overdispersion and reduce bias in standard error estimation. We used the function 'glmmTMB' from the *TITULAR* package (Brooks et al., 2017), and fit the models using restricted maximum likelihood (REML) in R version 3.6.1 (R Core Team, 2019). *Site ID*, corresponding to a transect within a given study area, was included as a random effect (intercept only) to account for dependency between samples. We included the distance from the transects to the highway (continuous variable; 0–3 km), the number of *cabins*, *relative distance to forest line* and *relative rodent abundance* as predictors. *Area* was included as a covariate to account for heterogeneity between study areas. *Species*, a factor separating red and arctic fox tracks, was included in interaction with *distance to road*, *relative distance to the forest line*, *relative rodent abundance* and *cabins*, as we predicted species-specific responses to these variables.

As our main interest was assessing the occurrence of red and arctic foxes relative to the distance to highways, all candidate models including *distance to road* also included the interaction *species* $\times$ *distance to road*. We used AIC_c (Burnham & Anderson, 1998) to rank the models, where models with $\Delta AIC_c < 2$ compared to the one with the lowest AIC_c were considered good candidate models. The top ranked model (i.e. the model with lowest AIC_c) was utilized for predicting and visualizing parameter estimates. Predictions were based on the study area of Hardangervidda, with a relative distance to forest line of 1.00, distance to roads of 0 km, and the rodent increase phase. Cabins, snow age and camera trap presence were set to their numerical means.

2.3.2 | Camera trapping

Images were analysed manually according to a predefined template (see Appendix S1). We recorded the status of the bait

(present, absent (i.e. consumed) or unavailable due to snow cover) to assess when the bait was acting as an attractant to animals. Observations of occurring species were coded as daily detections (1) or non-detections (0) for each camera trap site for the first 14 days of camera trapping per year. The study area of Saltfjellet only had 8 days of camera trapping in 2016 due to adverse weather conditions.

Data were fitted with multi-season occupancy models (MacKenzie, Nichols, Hines, Knutson, & Franklin, 2003) for each species using the package *UNMARKED* (Fiske & Chandler, 2011) in R. We used the same explanatory variables as for the snow tracking data analysis with the addition of *bait status*, *daily* and *nightly temperature* (average per camera trap site per day, obtained from each camera's internal temperature logger) and *daily snow depth* (see Table S1).

We aimed to compare results from camera traps and snow tracking to further test our predictions. Unfortunately, only two cameras captured arctic foxes throughout our study. Furthermore, none of the fitted models for red or arctic fox occupancy in relation to highways passed a goodness-of-fit (GOF) test (MacKenzie & Bailey, 2004), thus rendering the comparison of camera trap and snow tracking data moot. We therefore decided to only include analysis of corvids. We corrected the candidate models ($\Delta AIC_c < 2$) with the overdispersion parameter ($\hat{c}$) from the GOF test and used the top-ranked corrected model, i.e. the model with lowest $\Delta QAIC_c$, for predicting and visualizing model parameter estimates.

2.3.3 | Nest predation

Each artificial nest was coded as depredated (1) or not depredated (0) for each study area and year. Data were fitted with generalized linear mixed models with a binomial distribution and logit link-function to model the proportion of depredated nests. The explanatory variables were identical to the snow tracking data analysis, excluding *species*, *snow age* and *camera trap presence*. We included the interaction between *distance to road* $\times$ *area*, as we expected area-specific differences in relative predation risk. We used AIC_c to rank candidate models, where the top ranked model was used for predicting and visualizing parameter estimates.

3 | RESULTS

We snow-tracked 309 km (126, 72 and 111 km in 2016, 2017 and 2018, respectively) out of a potential of 432 km, where 216 km of tracking data were retained in the analysis after discarding occasions with unfavourable tracking conditions. On average, we found 3.4 ± 0.8 (mean $\pm$ 2 SE) tracks per km of red fox and 1.0 ± 0.5 tracks per km of arctic fox over all study areas and years (see Figure S1, Table S2). We included 1,103 of a total of 1,833 camera trap days in the occupancy analyses. The average percentage of daily visits was

10.8% for red foxes, 4.7% for arctic foxes and 32.2% for corvids (see Table S3). The nest predation data included 985 artificial nests of which 307 were depredated (31.2%) over all study areas and years, with 8.5 ± 0.3 (mean ± 2 SE) nests depredated on average per area and year (see Figure S2; Table S2).

3.1 | Occurrence of scavengers in relation to highways

Distance to highways and its interaction with species were included in the two highest ranked models (cumulative AIC_c weight = 0.686) explaining variation in tracks of red and arctic foxes during winter (see Table S4). The ΔAIC_c to the best model without *distance to road* $\times$ *species* was 1.94. According to the top ranked model, red fox occurrence increased with proximity to roads, whereas a weak non-significant negative relationship was found for arctic fox (Figure 2a; see Table S5). The predicted occurrence for both species decreased with an increasing number of cabins (Figure 2b). Red fox occurrence decreased, while arctic fox did not vary, with increasing relative distance to the forest line (Figure 2c). Red fox occurrence was significantly higher than arctic fox in rodent crash years, with a slightly increased occurrence of red fox compared to arctic fox in rodent increase and peak phases (Figure 2d). Red fox occurrence was highest at Dovrefjell and lowest at Saltfjellet, with no arctic fox tracks detected at Dovrefjell (see Table S2; Figure S1).

After correcting for overdispersion ($\hat{c} = 1.52$) our top ranked occupancy model for corvids ($\Delta AIC_c = 3.89$ from second ranked model; see Table S9) included only the *relative distance to forest line* as predictor for occupancy (ψ), where the probability of site occupancy decreased with increasing relative distance to the forest line (see Figure S3a, Table S10). The probability of detection (ρ) was higher when *bait* was present than absent or unavailable, increased with increasing *day temperature*, and decreased with increasing *snow depth* (see Figure S3b–d; Table S10). Site occupancy of corvids was generally high (0.80), but varied between years (0.81, 0.87 and 0.70 in 2016–2018 respectively).

3.2 | Nest predation

Distance to highways and its interaction with study areas was included in the two top ranked models (cumulative AIC_c weight = 0.764; ΔAIC_c between the two models = 2.03) explaining the variation in nest predation risk (see Table S11). The ΔAIC_c to the best model without *distance to road* $\times$ *area* was 2.94. Accordingly, the predation risk increased in proximity to roads at Dovrefjell, while this pattern was reversed at Hardangervidda, with a weak non-significant increase in proximity to roads at Saltfjellet (Figure 3; see Table S12). The predation risk was significantly higher in rodent crash years compared to low or increasing rodent abundance (see Figure S4a). Predation risk increased with increasing relative distance to the forest line (see Figure S4b).

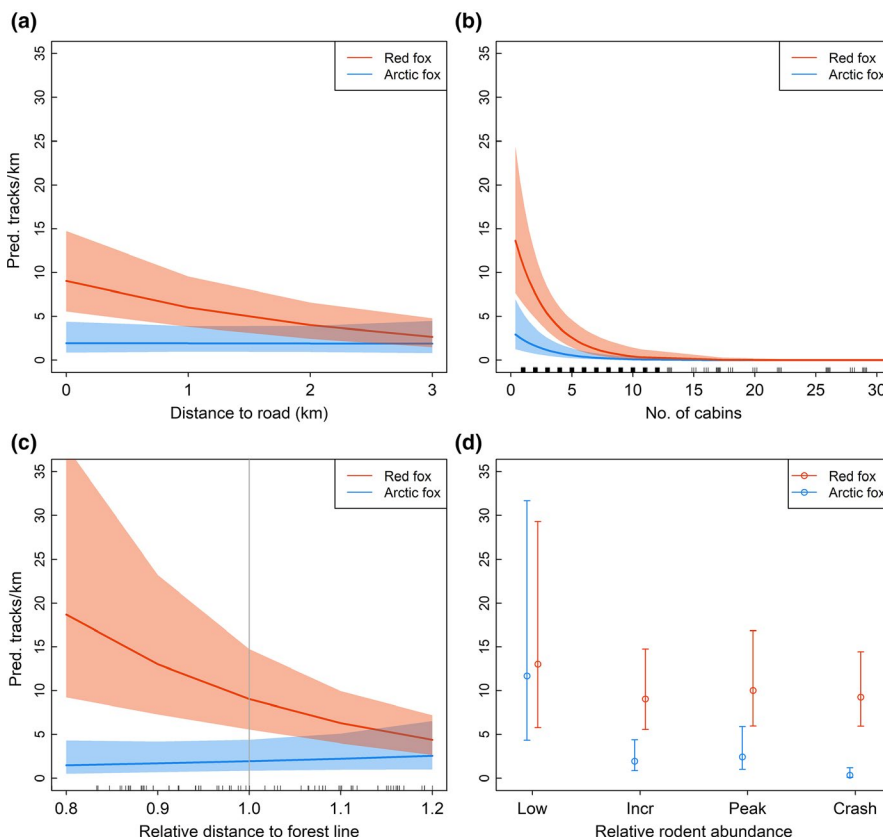


FIGURE 2 Predicted number of tracks per km for red (red line) and arctic (blue line) foxes (a) in proximity to highways, (b) in relation to the number of cabins, (c) relative to the distance to forest line (grey vertical line) and (d) in relation to relative rodent abundance. Shaded areas in (a–c) and vertical lines in (d) represent 95% Wald-type confidence intervals. Points in (d) are the predicted mean number of tracks per km

FIGURE 3 Predicted probability of nest predation in proximity to highways within each study area. Points represent mean probability of predation. Bars represent 95% confidence intervals estimated from parametric bootstrapping ($n = 1,000$). Predictions were based on a relative distance to forest line of 1.00 and for the rodent peak phase

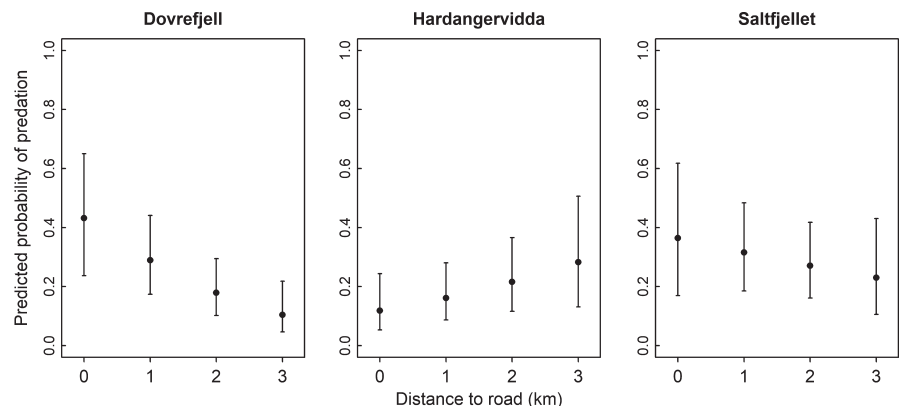
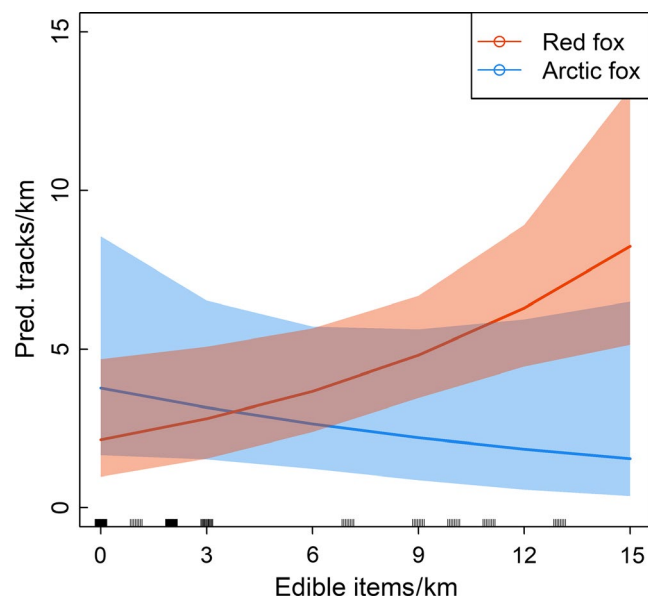


FIGURE 4 Predicted number of tracks of red (red line) and arctic (blue line) fox per km in relation to the number of edible items of anthropogenic origin per km found along road verges. The shaded areas represent 95% Wald-type confidence intervals

3.3 | Quantification of subsidies

Our inventory of 18 km of road verges in late winter 2016 revealed a total of 110 edible items of anthropogenic origin, with an overall average of 6.5 ± 2.6 (mean $\pm$ 2 SE) items per km (see Table S6). Common items were fruit (32.7%), sweets and crisps (27.3%), remains of fast food (8.2%) and bakery goods (3.6%). Only three roadkills were found during the inventory (two willow ptarmigans *Lagopus lagopus*, one hooded crow *Corvus cornix*), amounting to 94.1 ± 136.4 (mean $\pm$ 2 SE) g per km based on estimated weight of the animal.

An ad hoc negative binomial model was fitted to the snow tracking data from 2016, with *species* $\times$ *edible items* as the only predictor for the observed number of tracks, while also correcting for *area-specific variation* and *camera trap presence* (see Table S7). We found that red fox occurrence increased with an increasing number of edible items, while arctic fox occurrence decreased (Figure 4).

4 | DISCUSSION

In accordance with our predictions, we found that a major boreal scavenger, the red fox, utilized areas close to highways more actively than areas further from the highways during winter towards and into alpine tundra areas, whereas arctic foxes showed no explicit pattern. This suggests that roads indeed may serve as landscape features that benefit boreal generalist species and facilitate their presence in otherwise low productive habitats. Several studies highlight the importance of subsidies in the advancement of boreal generalists into alpine and arctic tundra (Gallant, Lecomte, & Berteaux, 2019; Restani, Marzluff, & Yates, 2001; Sokolov, Sokolova, Ims, Brucker, & Ehrich, 2016), and roads are known to be an important source of subsidies for scavengers or carrion-feeders (Knight, Knight, & Camp, 1995; Oxley, Fenton, & Carmody, 1974). Although traffic volume, and thus the potential amount of generated subsidies, in our study areas was relatively low compared to other studies (e.g. Gagnon, Theimer, Boe, Dodd, & Schweinsburg, 2007), we still found evidence for increased activity from boreal scavengers along highways crossing marginal alpine areas.

The red fox is territorial with home range sizes varying according to habitat productivity and food availability (Walton, Samelius, Odden, & Willebrand, 2017). Home ranges may extend upwards from boreal forests to include parts of low productive alpine tundra (Cagnacci, Meriggi, & Lovari, 2004). Favourable food abundance may allow increased use of such habitats, and subsidies associated with highways represent one such food source. However, this source is quite limited in space and our results indeed suggest that most of the red fox activity was within 1–2 km from the highways. Utilization of areas close to roads was generally higher for red foxes than arctic foxes in years where rodent abundance crashed, implying that external subsidies may be important for red foxes within alpine areas during winter and when abundance of natural prey is low, where carcasses and food of anthropogenic origin may sustain the red fox population (Gallant et al., 2019; Killengreen et al., 2011).

We expected a similar pattern for corvids as for red foxes, as corvids have been found to utilize anthropogenic resources where available, particularly in winter (Restani et al., 2001; Storch & Leidenberger, 2003). The spatial scale of this study may, however,

have been too small to reveal any spatial patterns in relation to highways in highly mobile species such as corvids. Due to topographical and logistical reasons, however, we were unable to extend our study further away from highways. Additionally, as we pooled all corvids in our analysis, forest-associated species such as hooded crows and magpies *Pica pica* may have contributed to the dominating effect of distance to forest in corvid occupancy.

Arctic foxes are regularly killed by traffic in Fennoscandia (52 reported cases 2008–2019 in Norway; NEA, 2019), suggesting that they utilize roads as part of foraging or scavenging behaviour, or cross or follow roads during dispersal, as found for other mammalian scavengers (Coffin, 2007). However, studies have shown that arctic foxes tend to avoid structures like cabins and cabin-clusters, possibly due to higher activity of competitors such as the red fox (Selås, Johnsen, & Eide, 2010). The increased occurrence of anthropogenically subsidized red foxes along highways within our study areas may have increased competition and acted as a dispersal barrier for arctic foxes (Herfindal et al., 2010).

The nest predation experiment, used as a proxy for summer occurrence of scavengers, revealed an increase in relative predation risk in proximity to highways at Dovrefjell. This was expected, as several studies have found similar predation patterns from generalist species in areas with high human activity (Pedersen et al., 2011; Støen, Wegge, Heid, Hjeljord, & Nellemann, 2010). Although we did not differentiate between predator species in the models, we found that corvids depredated 98% of the nests where the predator could be identified, similar to the findings of Klausen, Pedersen, Yoccoz, and Ims (2010). Both avian and mammalian scavengers locate nests by visual cues, such as incubating females fleeing from the nests (Erikstad, Blom, & Myrberget, 1982), whereas mammalian scavengers may locate nests using olfactory cues. Our use of coloured bands to identify the nests, or human scent from placing the nests, may have made the nests easier to locate by scavengers, especially for avian scavengers in open habitats above the forest line.

Analyses supported the impression of area-specific occurrences and predation risk, where expected patterns were more pronounced at Dovrefjell. Here, both traffic volume and the number of cabins were higher than in the other study areas, likely contributing to an increased amount of anthropogenic subsidies available to scavengers. Furthermore, less snow in late winter within Dovrefjell may have allowed access to subsidies earlier in the winter season, which may benefit scavengers particularly in cold winters and when rodent abundance is low (Bartoń & Zalewski, 2007; Killengreen et al., 2011). Expected patterns weakened at Saltfjellet and became unclear at Hardangervidda, where the overall distance to forest increased, with lower traffic volume and number of cabins, deeper snow and longer winters. Although this heterogeneity among study areas was accounted for in our analysis, the apparent gradient through the boreal-alpine ecotone and into alpine tundra may have implications for expansion of generalist species in light of forecasted climate warming and increased infrastructure development within tundra areas (cf. Elmhagen et al., 2017).

5 | CONCLUSIONS

Our findings revealed an increased occurrence of boreal scavengers close to highways, possibly linked to availability of anthropogenic subsidies. Highways may thus facilitate scavengers that would naturally occur at lower densities in marginal habitats. Expansion of boreal scavengers can have severe implications for alpine species through increased competition and predation, causing e.g. conflict with conservation efforts of threatened species. Cautious and knowledge-based land-use planning, e.g. avoiding placement of infrastructure, or considering wildlife passages, within sensitive wildlife habitats crossing montane areas, could reduce negative effects of landscape fragmentation followed by infrastructure development.

Litter and food waste dominated the available subsidies along highways in our study, presenting other challenges than e.g. roadkill and movement restrictions, which are often the focus in road ecology studies (e.g. van der Grift et al., 2013). Efforts aimed at reducing roadkill, such as wildlife passages, will likely not have the desired mitigating effects on littering, and prevailing road ecology research may not provide required solutions (e.g. van der Ree, Jaeger, van der Grift, & Clevenger, 2011). However, building public awareness on the adverse effects of littering, directed towards vehicle drivers, cabin owners and tourists within particularly sensitive areas, may be a mitigating first step. Proper garbage disposal facilities at rest-stops, intensive and systematic removal of litter along roads, or imposing fines, may be required to reduce negative effects of roads on vulnerable species. This is likely needed to achieve goals of 'no impact' from the physical loss of habitats due to road development, which would also diminish loss of landscape connectivity for alpine species.

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AUTHORS' CONTRIBUTIONS

N.E.E. and L.R.-E. conceived the idea and designed the methodology together with I.H. and H.J.; L.R.-E. and J.S. led the collection of the data; L.R.-E. analysed the data under supervision by I.H., and in discussion with all authors; L.R.-E. wrote the manuscript together with J.S., with comments and contributions from all co-authors. All authors approved the final manuscript for publication.

DATA AVAILABILITY STATEMENT

Data available via the Dryad Digital Repository <https://doi.org/10.5061/dryad.rr4xgxd62> (Rød-Eriksen, Skrutvold, Herfindal, Jensen, & Eide, 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

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