Roads, forestry, and wolves interact to drive moose browsing behavior in Scandinavia

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Abstract. As wild ungulate densities increase across Europe and North America, plant–herbivore interactions are increasingly important from ecological and economic perspectives. These interactions are particularly significant where agriculture and forestry occur and where intensive grazing and browsing by wild ungulates can result in economic losses to growing crops and trees. We studied plant–herbivore interactions in a moose (*Alces alces*)-dominant system where forestry is a primary economy, the primary and secondary road networks are extensive, and wolves (*Canis lupus*) are recolonizing. Wolves and humans use low-traffic, secondary roads, yet roadsides provide high-quality and quantity browse for moose. Foraging theory predicts that moose will respond to riskier landscapes by selecting habitats that reduce predation risk, sacrificing feeding time or food quality. As food becomes limiting, however, animals will accept higher predation risk in search of food. We predicted that road avoidance behavior would be strongest within wolf territories. In areas without wolves, moose should select roadsides for their high forage availability. To test these predictions, we measured moose browsing and counted pellet groups as a proxy for habitat use each spring in Norway and Sweden between 2008 and 2018, in areas with and without wolves and at different distances from primary and secondary roads. We used generalized linear mixed models to evaluate drivers of the probability of browsing occurrence and browsing pressure. We found that browsing occurrence increased closer to secondary roads but decreased closer to primary roads. We also found browsing patterns to vary among tree species. For Scots pine (*Pinus sylvestris*), the browsing occurrence was two times higher in young forests relative to non-young forests and decreased further from secondary roads. Wolf territory presence and probability had neutral or positive effect on browsing occurrence and pressure for all species. However, wolf territory presence had negative effects on browsing occurrence and pressure when interacting with secondary roads, young forest, or snow cover. We showed that roads can influence browsing patterns in Norway and Sweden. However, further research is needed, particularly in the face of continued infrastructure development in Scandinavia.

Key words: *Alces alces*; browsing; forestry; roads; Scandinavia; trophic cascades; ungulates; wolves.

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INTRODUCTION

Predation can have direct, lethal consequences to prey density and abundance (Gasaway et al. 1992, Messier 1994). Prey can also perceive predation risk from predators such as large carnivores and humans. Increasingly, behavioral effects of predation risk are shown to influence a variety of prey behaviors such as foraging, vigilance, patch use, diet, and habitat selection (Brown and Kotler 2004, Winnie and Creel 2007, LaManna and Martin 2016). For prey, there is often a trade-off between predation risk and food supply (Schmitz 2005) and ungulate prey move to vegetative cover in response to predators (Mysterud and Østbye 1999, Creel et al. 2005). Thus, we can expect that the spatial effects of predators on ungulate browsing patterns will be altered due to predator movements (behaviorally mediated trophic cascades; Schmitz et al. 1997).

Predators like wolves (*Canis lupus*) can contribute to the landscape of fear (Beyer et al. 2007, Ripple and Beschta 2012, Kuijper et al. 2013), particularly in protected areas (Hernández and Laundré 2005). However, large carnivores have become threatened globally (Ripple et al. 2014) and humans have a disproportionately large effect (direct and indirect) on wildlife behavior and mortality outside of protected areas. Cascading effects from predators on prey and plant–herbivore interactions (i.e., trophic cascades) have been documented in protected areas (Kuijper et al. 2013). Beyond the boundaries of protected areas, however, humans are the primary mortality factor and long histories of human-managed systems have resulted in reduced spatial landscape heterogeneity (Kuijper et al. 2016). Trophic cascades appear more difficult to elucidate outside protected areas (van Beeck Calkoen et al. 2018), which could have consequences to predator/prey relationships.

The trade-off between predation avoidance and foraging has long been recognized (Sih 1980, McNamara and Houston 1987). Predation and foraging are dynamic processes that vary in time and space, and their effects are context and scale-dependent (Oates et al. 2019). The risk allocation hypothesis states that predation risk and food availability interact: under food-limited conditions, animals will lose fat faster and enter risky areas earlier than in areas with abundant food

(Lima and Bednekoff 1999). Thus, as available food declines, animals will accept a higher predation risk in search of food (Sinclair and Arcese 1995). For browsing and grazing ungulates, however, only a small fraction of plant biomass is palatable and easily digested, and there is often a trade-off between food quantity and quality (Felton et al. 2018). Optimal foraging theory predicts that a foraging ungulate aims to maximize net energy consumption (Pyke et al. 1977). Consequently, food items with high nutrient or energy concentration or digestibility (i.e., high quality) would be of greater value to food-limited ungulates relative to low-quality food items. Seasonal constraints such as winter snow cover can drive changes in food availability, which can be population bottlenecks (Nordengren et al. 2003, Wiegand et al. 2008, Coltrane and Barboza 2010). Snow can also increase wolf predation risk because wolves have light foot loads relative to many ungulates, so they are able to catch ungulate prey easier in deep snow (Fuller 1991, Mech et al. 2001). As a result, we can expect ungulates to accept higher predation risk to obtain higher-quality items or seasonally during periods of food limitation.

Roads are among the most pervasive forms of human disturbance on the globe (Fahrig and Rytwinski 2009). Roads can increase habitat fragmentation, reduce gene flow, change species composition, facilitate the spread of invasive and exotic species, and increase wildlife mortality due to vehicle collisions (Pauchard and Alaback 2004, Fahrig and Rytwinski 2009, Holderegger and Di Giulio 2010). For ungulates, roads can also alter predator–prey relationships by increasing predator movements, encounter rates with prey, and prey vigilance levels (Eriksen et al. 2009, Dickie et al. 2017). High-traffic road sides also increase mortality risk from vehicle collisions (Seiler 2005, Laurian et al. 2008a, Eldegard et al. 2012). Thus, roads can contribute to a landscape of fear (Laundré et al. 2001), which is defined as the spatial variation in prey perception of predation risk (Gaynor et al. 2019). Yet, roads and road sides are attractive to ungulates because they can provide a human-shield from predators (Berger 2007), create nutrient pools (Laurian et al. 2008b), reduce movement costs especially during winter (Parker et al. 1984), and increase access to high-quality food such as

young, deciduous trees (Bowman et al. 2010). Because roads represent a trade-off between predation risk and food, we used primary (high-traffic, generally paved roads) and secondary roads (low-traffic, gravel roads) to test the risk allocation hypothesis. We predicted that, in areas with wolves, moose should avoid secondary roads under conditions where food is not limiting. In areas without wolves, moose should select roadsides for their high forage availability. Primary roads should be avoided due to collision risks.

We tested these predictions using a predator–ungulate–forest system in Sweden and south-central Norway where moose (*Alces alces*) are the dominant browsers, wolves are recolonizing portions of their former range (Wabakken et al. 2001), and commercial forestry is the primary land use. Forestry is the primary driver of landscape change in Scandinavia (Swedish Forest Agency 2014), and forest access roads occur at high densities (Sand et al. 2006*a*). Humans are the primary cause of annual moose mortality during a fall hunt (Sæther et al. 1996, Stubsjøen et al. 2000) but moose are the primary prey of wolves year-round (Sand et al. 2008, Wikenros et al. 2009). Interestingly, previous studies have not found a cascading effect of wolves through affecting moose browsing behavior (Nicholson et al. 2014, Wikenros et al. 2016, Månsson et al. 2017).

Moose can damage young commercial trees in the form of apical shoot browsing, bark browsing and rubbing, and stem breakage, which can negatively affect tree growth and morphology (Danell et al. 1994, Bergström and Danell 1995, Wallgren et al. 2013). Browsing damage is largely concentrated during winter when moose may congregate, food availability is reduced, and winter diets are dominated by young Scots pine (*Pinus sylvestris*). Browsing damage has resulted in conflicts between forest owners, who want to sell commercial timber, and moose hunters, who harvest over 115,000 moose annually in Norway and Sweden combined (harvest data from www. ssb.no and www.algdata.se). Here, we investigate how forestry, predators, and roads influence moose browsing behavior, which could have consequences to moose-forestry conflicts.

We aimed to answer two research questions: (1) Is moose browsing reduced in areas with high predation risk, such as where wolves are present and areas close to primary roads, in accordance with a landscape of fear? (2) Is the trade-off between risk and foraging modified by forage value, that is, tree species of different selectivity? We used browsing selectivity rankings from previous literature (Shipley et al. 1998) as a proxy for food quality, and as the basis for our predictions (below) on browsing pressure and occurrence. Previous research has suggested that fine-scale evaluation may reveal a behavioral response by moose to recolonizing wolves (Nicholson et al. 2014). We thus evaluated these questions at the tree level, which corresponds to the fine-scale food selection an animal makes within a foraging patch and represents the fourth order of selection in the hierarchy of selection processes (Johnson 1980). Moose may browse one or two shoots on a tree and continue searching until they find a suitable tree to feed on (Shipley et al. 1998). Thus, we modeled the presence of browsed trees (browsing occurrence) as well as browsing pressure (ratio of browsed to available shoots per tree). We predicted the following: (P1) Moose will browse in areas close to secondary roads due to increased forage quantity and quality. However, because wolves use secondary roads, we expect ungulate browsing occurrence and pressure to decrease close to secondary roads when the probability of wolf territory occurrence is high; (P2) primary roads offer foraging opportunities but they represent an increased mortality risk. Thus, we expect that ungulates will avoid primary roads and browsing occurrence and pressure will decrease closer to primary roads; (P3) we expect browsing occurrence and pressure will increase with increasing snow coverage as the field layer and shrubs are concealed; (P4) we expect highly selected tree species to be of greatest value to ungulates; hence, ungulates would accept greater risk to attain them relative to species of lower selectivity. Thus, we expect a weaker effect of roads and wolves when ungulates browse highly selected species, relative to less selected ones.

METHODS

Study area

Our study area lies between 57.0°–66.4° N and 12.2°–22.2° E in Norway and Sweden (hereafter, Scandinavia; Fig. 1), with elevation ranging from

1 to 725 m above sea level. The area experiences cold, snowy winters (January average temperature $-1.9°C$; average snow depth 0.2 m; Swedish Meteorological and Hydrological Institute) and short, cool summers, though winters are less severe in the south relative to the north. Land cover is dominated by boreal and hemiboreal forests (Ahti et al. 1968), which are managed for timber and pulp production. Production forests, which are largely coniferous, typically undergo one or two thinning events to optimize commercial tree densities. Mature trees are harvested in clear-cuts up to 1000 ha, resulting in a mosaic of even-aged patches or stands of trees (Axelsson and Östlund 2001, Rytter et al. 2014). Regeneration occurs from planted trees or naturally from seed trees. Forestry has created a high-density network of secondary roads (mean road density 8.5 km/km^2) whereas primary roads are less common (mean road density 2.7 km/km^2; Sweden road data from www.lantmateriet.se; Norway data from www.geonorge.no). Road density is higher in the south (Fig. 1).

Common tree species include Scots pine, silver birch (*Betula pendula*), downy birch (*Betula pubescens*), Norway spruce (*Picea abies*), gray alder (*Alnus incana*), black alder (*Alnus glutinosa*), rowan (*Sorbus aucuparia*), goat willow (*Salix caprea*), and aspen (*Populus tremula*). The dwarf-shrub layer is typically dominated by heather (*Calluna vulgaris*), bilberry (*Vaccinium myrtillus*), and other Ericaceous species. In boggy areas, Sphagnum spp. mosses are dominant (Moen et al. 1998). Generally, rowan, aspen, and willow are highly selected by moose but are rare relative to Scots pine and birch (Shipley et al. 1998, Månsson et al. 2007). Scots pine is a primary food source for moose during winter due to its high abundance whereas spruce is more chemically defended and is rare in moose diets (Cederlund et al. 1980).

Since the industrialization of forest management in the 1960s, combined with changes in moose harvest strategies, moose densities peaked in the 1980s and 1990s with local winter densities of 5–6 individuals per km^2 (Lavsund et al. 2003). Average annual moose densities have since decreased and vary across our study area (0.50–2.6 moose/km^2; Sand et al. 2006*b*, Mattisson et al. 2013, Zimmermann et al. 2015, Pfeffer et al. 2018). Moose typically migrate from high-elevation mountainous areas to low-elevation valley bottoms to over-winter, where snow depths are reduced (Sweanor and Sandegren 1988, Bunnefeld et al. 2011, Singh et al. 2012). Assemblages of other ungulates vary across our study area. Roe deer (*Capreolus capreolus*), fallow deer (*Dama dama*), and red deer (*Cervus elaphus*) have higher densities in the south and along the coast (based on hunting statistics; www.algdata.se and www.viltdata.se). Carnivores include wolves, brown bears (*Ursus arctos*), wolverines (*Gulo gulo*), and Eurasian lynx (*Lynx lynx*). Wolves and bears prey on neonate calves in the spring and early summer, and moose are the main prey of wolves throughout the year (Swenson et al. 2007, Sand et al. 2008, Zimmermann et al. 2015). Wolf density in Scandinavia is lower (0.154 wolves/100 km^2; 95% credible intervals 0.151–0.159; Bischof et al. 2019) than in North America (0.3–5.4 wolves/100 km^2; Mech and Barber-Meyer 2015), yet wolf hunting success of moose is substantially higher in Scandinavia than in North America (Sand et al. 2006).

Data collection

Our data were collected during four projects: Forest and Moose (2012, 2015, and 2018) in Norway, and Vilt och Skog (2008–2009, 2011), Fortlöpande Miljöanalys (2012–2015), and Beyond Moose (2015–2018) in Sweden. All projects had common methods for counting ungulate pellet groups and assessing browsing at fixed monitoring plots. We systematically placed quadrats (500 × 500 m or 1000 × 1000 m) at 11 sites (Fig. 1). Within sites, quadrats were placed at minimum 1 km and maximum 3 km apart. Along each quadrat's border, we placed 16 circular plots every 100 m (Norway and Sweden) or 200 m (Sweden; Fig. 1).

Browsing surveys.—We assessed browsing from circular plots in the spring. Starting with the tree closest to the plot center, we identified the tree species, and counted the number of browsed and unbrowsed shoots from the previous growing season. We defined a shoot as woody tissue >1 cm long. We considered shoots <1 cm to be unavailable to moose because they are too small for processing. The number of available shoots is the sum of browsed and unbrowsed shoots. We registered browsing from the current winter season where browsed shoots were still wet with
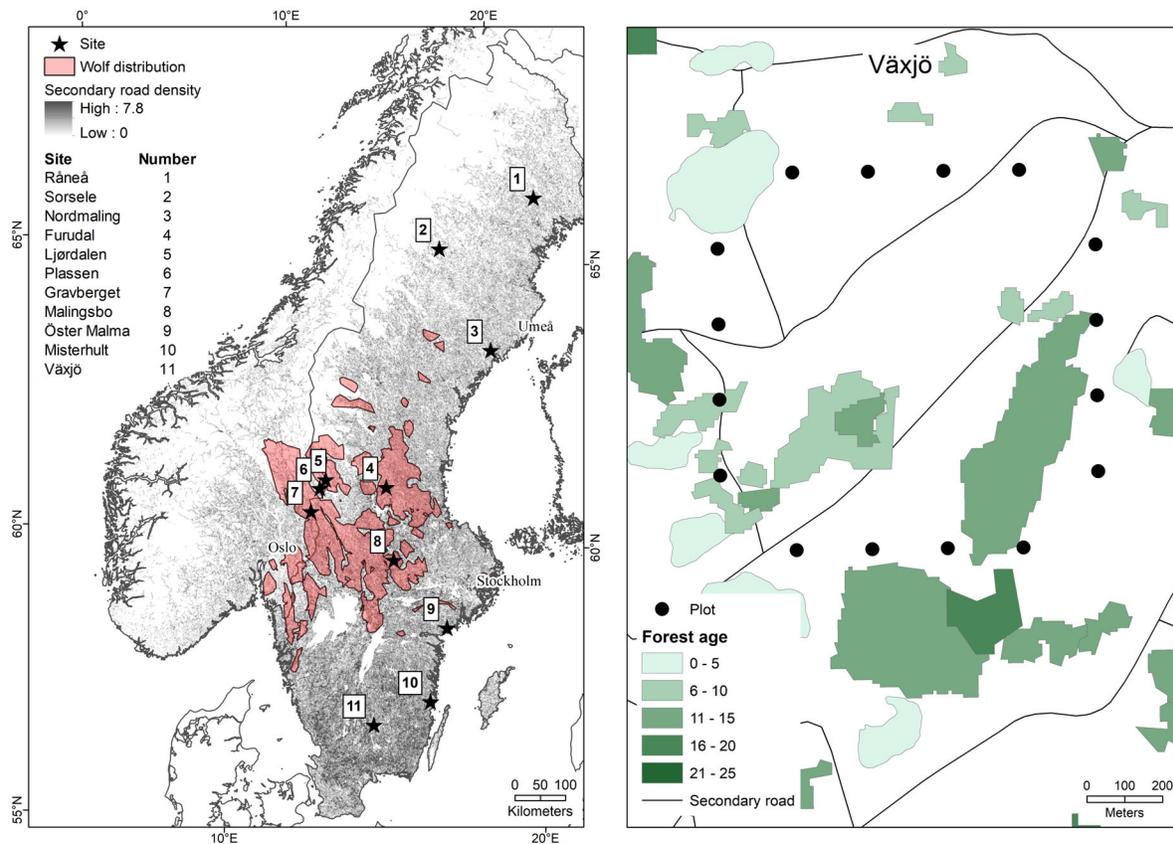
Fig. 1. Our study included 11 sites across a gradient of human-use, predator occurrence (left), and forestry activities (right) in Norway and Sweden. At right, 16 plots lie along the quadrat boundary. Wolf distribution data were derived from annual monitoring surveys (Wabakken et al. 2018). Secondary road density units are km/km^2.

resin, and the wood had not died or become gray (Ball and Dahlgren 2002). We restricted our analysis to trees ≥30 cm and ≤3 m tall to be consistent with field protocols across projects. The lower height represented average winter snow levels below which trees were not available for browsing during winter. The upper height represented the maximum browsing height for moose (Nichols et al. 2015). For the Forest and Moose project, we assessed browsing on up to 10 trees per species in 50-m^2 plots. For Swedish projects, we assessed browsing on one tree per species in 100-m^2 plots. In both cases, we chose trees closest to the plot center. The four common tree species to all project protocols were rowan, downy birch, silver birch, and Scots pine.

Pellet counts.—Because browsing pressure is highly correlated with animal abundance, we counted ungulate pellet groups (Neff 1968) in 100-m^2 circular plots during late spring. We used the number of pellet groups to represent the time animal(s) spent in a plot which Månsson et al. (2007) identified as an unbiased estimator of habitat use. Pellet counts occurred at the same plot center as browsing surveys. Although we were primarily interested in moose habitat use, we counted pellets for all ungulate species present. We identified ungulate species by morphological characteristics of the pellets and the number of pellets per group (Spitzer et al. 2019). To register a pellet group, >50% of the group needed to fall within the plot (Norway) or the center of the group was within the plot (Sweden). A minimum number of 20 moose pellets were required to register pellets as a group. We distinguished between fresh (current winter) and old

(prior to current winter) pellets. Typically, winter pellets were brown, in pellet form, and positioned on top of leaf litter and forest debris. Summer pellets were often in patty form, had leaf litter on top of pellets, or had mold or fungus growth (Zimmermann et al. 2015). For this analysis, we were only interested in winter pellets, which corresponded to winter browsing.

Wolf data.—Wolves in Scandinavia have been monitored annually with snow tracking, scat/DNA collection, and occasional VHF/GPS tracking (Liberg et al. 2012, Wabakken et al. 2018), with the goal to monitor reproduction events and breeding pairs. Despite extensive tracking efforts (mean km tracked annually = 3011.2 km; SD 1394.8; Milleret et al. 2017), data per territory were sparse for the spatio-temporal extent of our study (3–21 individual wolves collared each year in Sweden and Norway). Because home range estimators are biased at low spatial and temporal sampling (Burgman and Fox 2003, Börger et al. 2006, Mattisson et al. 2013), territory centers and boundaries were inestimable or unreliable for most packs (Appendix S1: Figs. S1, S2, S3). We instead used all available data to compute a centroid point location for each territory and year. We then used that centroid to rebuild the pack's territory by buffering each annual centroid by 18 km, which is the average radius of a wolf territory (1000 km^2) in Scandinavia (Mattisson et al. 2013). Because territory size is influenced by prey density, population density, intra- and interspecific competition, and habitat characteristics (McNab 1963, Mattisson et al. 2013, Allen et al. 2016), we accounted for density-dependence by not allowing territory boundaries to overlap (see description in Appendix S1). We created a wolf territory presence variable (Table 1), which was the presence of a wolf territory created from the above steps (Appendix S1: Fig. S4).

Due to limited tracking data, however, there was uncertainty in the territory boundary (see Milleret et al. 2017 for details). Therefore, we created a second wolf variable (probability of wolf territory occurrence; Table 1) by assigning a decreasing probability of territory occurrence as distance from the centroid increased. We used a probability because we were more confident that the areas closer to the centroid contained a wolf territory, compared to the areas far from a centroid. We assumed a parabolic decrease in

probability of wolf territory occurrence from the centroid to the buffer edge (Appendix S1: Fig. S2, S3). The probability stayed high in the first 9-km radius from the centroid but uncertainty increased further out. We based this assumption on the non-linear use of their territory by wolves, where they concentrate on a small core area and use the rest of the territory less intensely (Ciucci et al. 1997, Zimmermann et al. 2019). For example, Ciucci et al. (1997) found core territory use represented only 15% of the MCP home range. We extracted raster values (probability values 0–1) for each plot in each study year in Norway and Sweden at a 1000-m resolution, which represents a coarse-scale variable. Areas outside a wolf territory were assigned a null probability. Both wolf variables (wolf territory presence, probability of wolf territory occurrence) were calculated for the winter prior to browsing surveys from 08/2007 to 08/2017. Wolf territory presence was described previously in Milleret et al. (2017). Both wolf variables are described in full in Appendix S1.

Environmental data.—We extracted additional spatial data known to influence moose habitat use and selection (Table 1). We expected the number of days with snow coverage to correlate with winter severity (Foster et al. 1982), which would influence food availability and predation risk. The spatial coverage of weather stations was insufficient to interpolate snow depth for our study area, so we calculated the number of days per year per plot with snow cover from the Normalized Difference Snow Index from MODIS (500 m; Hall et al. 2006). The spatial resolution of the snow cover variable matches the quadrat, and we interpret this variable as such. We extracted elevation because it is negatively correlated with productivity (Danell et al. 1991b). We extracted percent canopy cover because open areas increase predation risk by wolves (Creel et al. 2005, Gervasi et al. 2013) and human hunters (Lone et al. 2014) but often provide the most food resources (Mysterud and Østbye 1999). Young forests provide high quantity and quality food for moose (Wallgren et al. 2013). We created a binary young forest (5–20 yr old) variable based on field-collected data in Norway, and national forest inventory data in Sweden. We included the presence of downy and silver birch, Scots pine, and rowan in the plot, as we could expect the presence of other browse

Table 1. Explanatory variables used in browsing occurrence and browsing pressure models.

Variable	Abbreviated name	Units	Scale	Data source
Base model covariates				
Available shoots	Available	Number of browsed and unbrowsed shoots	Tree	field collected
Downy birch presence	Downy birch	Presence (1)/absence (0) of downy birch	Plot	field collected
Silver birch presence	Silver birch	Presence (1)/absence (0) of silver birch	Plot	field collected
Scots pine presence	Pine	Presence (1)/absence (0) of Scots pine	Plot	field collected
Rowan presence	Rowan	Presence (1)/absence (0) of rowan	Plot	field collected
Moose pellet group counts	Moose	Number of moose pellet groups	Plot	field collected
Canopy cover	Canopy	0 (no forest)–1 (full canopy)	25 m	Copernicus Land Monitoring Service
Elevation	Elevation	m	25 m	Copernicus Land Monitoring Service
Hypothesis-driven covariates				
Euclidian distance to nearest primary road	Primary road	m	Vector†	National road inventory (SWE: Lantmäteriet; NOR: Geonorge)
Euclidian distance to nearest secondary road	Secondary road	m	Vector	National road inventory (SWE: Lantmäteriet; NOR: Geonorge)
Young forest	Young forest	Presence (1)/absence (0) of young forest	Vector	SWE: Swedish Forest Agency (Skogsstyrelsen); NOR: field collected
Snow cover	Snow	Number of snow days/year	500 m	MODIS (Hall et al. 2006)
Probability of wolf territory occurrence	Wolf probability	0 (low probability)–1 (high probability)	1000 m	Wabakken et al. 2018
Presence of wolf territory	Wolf presence	Presence (1)/absence (0) of wolf territory	1000 m	Wabakken et al. 2018

† Vectors are spatial features that represent points, polygons, or lines. The spatial resolution is defined by the precision of the x, y coordinates, but the original resolution of these coordinates is often not preserved.

species could alter browsing behavior (Danell et al. 1991a). Last, we calculated the distance to roads in meters as the Euclidian distance to nearest primary and secondary roads. See Table 1 for variable details. Spatial extractions were done in ArcMap version 10.3.1 (Environmental Systems Research Institute 2011).

STATISTICAL ANALYSIS

Browsing occurrence

We modeled tree browsing occurrence with a logistic regression (0, unbrowsed; 1, browsed) separately for the four species: silver birch, downy birch, rowan, and Scots pine. It was important to separate browse species because forage mass differs between species. For example, Scots pine in winter has up to 20 times the mass of the other browse species (Shipley et al. 1998). It is difficult to

define forage quality based on a single metric of digestibility, nutrient content, or defense compounds (Bergström and Danell 1987). Instead, we refer to quality as an index based on food selection ranks following Shipley et al. (1998; rowan > silver birch > downy birch ≥ Scots pine).

We included the presence of other palatable species, elevation, canopy cover, and moose pellet group counts in all candidate models. We refer to these as "base model covariates." We then added up to three variables per model related to our research questions (young forest, secondary road, primary road, wolf) as additive or interactive terms, resulting in 25 candidate models (Table 2). Hereafter, we refer to moose pellet group counts as "habitat use" (see definition above in pellet counts subsection). To account for differences in study design structure and sampling years, we included two random

intercepts: plot nested within site (site/plot) and year. We mean-centered and scaled continuous predictor variables to SD = 2 so scaled coefficients from continuous variables are comparable to unscaled binary predictor coefficients (Gelman and Hill 2006). We checked for collinearity using Pearson correlation coefficients. All values > 0.7 were considered correlated and were not included in the same model (Dormann et al. 2013).

We used generalized linear mixed models (GLMM) with a binomial family (logit link) in package glmmTMB (Brooks et al. 2017). We used Akaike information criteria (AIC) to identify the most parsimonious model(s) and model-averaged parameter effect sizes based on AIC weights (Burnham et al. 2011) using the modavg function in package AICcmodavg (Mazerolle 2019). We excluded models with interaction terms from model averaging (Cade 2015). Prediction curves were created from top-ranked models only. We evaluated model fit by visualizing the scaled residuals simulated from the fitted model with package DHARMa (Hartig 2020). All analyses were completed in program R version 3.6.1 (R Core Team 2018). We report results by tree species in the ranked order of selectivity.

Browsing pressure

We modeled browsing pressure by using the number of browsed shoots per tree as our response variable and the log-transformed number of available shoots per tree as an offset. We used zero-inflated negative binomial models (logit link binomial, log-link count) with the identical fixed (Table 1) and random effect variables as the model for browsing occurrence for the conditional count and zero-inflated process models. The zero-inflation formula describes the probability of excess zeros (Brooks et al. 2017), which differs from the logistic regression. We followed the same variable standardizing, model fitting, selection, averaging, and diagnostics described above for browsing occurrence models. We did not include an offset for the binomial model.

RESULTS

From 2012 to 2018, we visited 51,527 plots to count pellet groups and assess browsing. Most plots (78%) had no pellets present (median = 0). On average, moose pellet group counts were highest among ungulate species (mean = 0.004, SE = 5.9e-05) but pellet counts varied strongly by site (Appendix S1: Fig. S5). Fallow deer were present in our study area, but inconsistencies in field data collection across years resulted in an excess of NA values. Because roe deer and red deer detections were constrained to three sites, and model fitting was difficult, moose were the only ungulate species included as explanatory variables. Distances from plots to the nearest secondary (min = 0 m, max = 2248 m) and primary roads (min = 1 m, max = 5929 m) varied. Across years, 17% of plots on average intersected with wolf territories.

Table 2. Candidate models for evaluating browsing occurrence and browsing pressure.

Model number	Description
1	Young forest × wolf probability
2	Young forest + wolf probability
3	Young forest × secondary road
4	Young forest + secondary road
5	Young forest + primary road
6	Wolf probability × secondary road
7	Wolf probability + secondary road
8	Wolf probability + primary road
9	Snow × secondary road
10	Snow + secondary road
11	Snow + primary road
12	Snow × wolf probability
13	Snow + wolf probability
14	Wolf probability × secondary road × young forest
15	Wolf probability × secondary road × snow
16	Young forest × wolf presence
17	Young forest + wolf presence
18	Wolf presence × secondary road
19	Wolf presence + secondary road
20	Wolf presence + primary road
21	Snow × wolf presence
22	Snow + wolf presence
23	Wolf presence × secondary road × young forest
24	Wolf presence × secondary road × snow
25	Null model (base model covariates only)

Notes: Browsing occurrence is the probability of a tree being browsed (0, unbrowsed; 1, browsed). Browsing pressure is the number of browsed shoots per tree with the log-transformed number of available shoots as an offset. In addition to the listed variables below, all models included base model covariates moose pellet groups, elevation, canopy cover, and the presence of other palatable species. See Table 1 for variable definitions.

We recorded 29,314 individual tree measurements. Deciduous species occurred less frequently in plots than Scots pine (in order of selectivity): rowan (14%; n = 4,235), silver birch (13%; n = 3,740), downy birch (37%; n = 10,800), and Scots pine (36%; n = 10,539). Overall browsing pressure was low (mean = 0.06; SD = 0.18). Mean browsing pressure was highest for rowan (Fig. 2). Minimum and maximum distance to nearest secondary and primary roads did not vary substantially between species: rowan (secondary 1–2040 m; primary 1–5700 m), downy birch (secondary 1–2248; primary 0–5928 m), silver birch (secondary 1–1869; primary 4–5578 m), and Scots pine (secondary 0–2248 m; primary 1–5794 m).

Statistical analysis

Rowan.—The top-ranked browsing occurrence model included the interaction snow:wolf presence:secondary road and was 2.7 times more supported by the data (based on AIC weights) than the next-ranked model (Appendix S1: Table S1). The interaction showed that with a higher number of snow days and wolf territory presence, browsing occurrence increased further
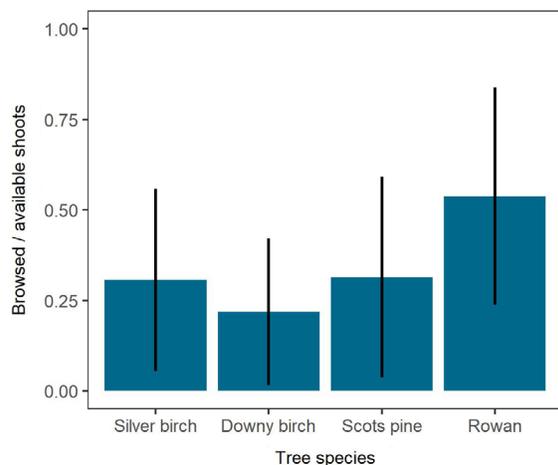
Fig. 2. Bar chart showing mean browsing pressure across all tree species for Norway and Sweden (2008–2018). We calculated browsing pressure as the number of browsed shoots divided by the number of available shoots per individual tree. For visualization, we excluded unbrowsed trees. Bars represent standard error.

from secondary roads. With lower snow coverage days and wolf territory presence, browsing occurrence decreased further from secondary roads. The two-way interaction of secondary roads:wolf presence showed that browsing occurrence increased further from secondary roads when wolf territories were present, whereas the opposite occurred when wolf territories were absent (Fig. 3). Model-averaged parameter estimates indicated that moose habitat use (β = 0.33; 95% CI = 0.19, 0.47), wolf territory presence (β = 0.23; 95% CI = −0.12, 0.59; Fig. 4), presence of silver birch (β = 0.17; 95% CI = −0.01, 0.34), and secondary roads (β = −0.11, 95% CI = −0.27, 0.06; Figs. 4, 5) had a positive effect on browsing occurrence on rowan. The presence of Scots pine (β = −0.17; 95% CI = −0.34, −0.01), elevation (β = −0.46; 95% CI = −0.83, −0.09), and distance to primary road (β = 0.21; 95% CI = 0.04, 0.37; Figs. 4, 5) had a negative effect on rowan browsing occurrence. Rowan browsing occurrence was 2.3 times higher and 1.5 lower along secondary and primary roadsides, respectively, relative to the maximum distance from each road type (Fig. 5). For all models, no variables were correlated above |0.7|. All correlation coefficients are presented in Appendix S1: Fig. S6.

There were no clear top models for rowan browsing pressure (Appendix S1: Table S2). Model-averaged parameter estimates showed moose habitat use had a positive effect (β = 0.19; 95% CI = 0.10, 0.28) and downy birch presence (β = −0.14; 95% CI = −0.25, −0.03) had a negative effect on rowan browsing pressure.

Silver birch.—For silver birch browsing occurrence, there were no clear top models (Appendix S1: Table S1). Model-averaged parameter estimates indicated a positive effect of moose habitat use (β = 1.03; 95% CI = 0.83, 1.23) and secondary roads (β = −0.12; 95% CI = −0.28, 0.05; Figs. 4, 5), and a negative effect of primary roads (β = 0.20; 95% CI = 0.02, 0.37; Figs. 4, 5) and downy birch presence (β = −0.27; 95% CI = −0.44, −0.10) on browsing occurrence. Browsing occurrence was 1.26 times higher at the highest probability of wolf territory occurrence relative to a zero probability. Silver birch browsing occurrence was 1.4 times higher and 1.6 times lower along secondary and primary roadsides,
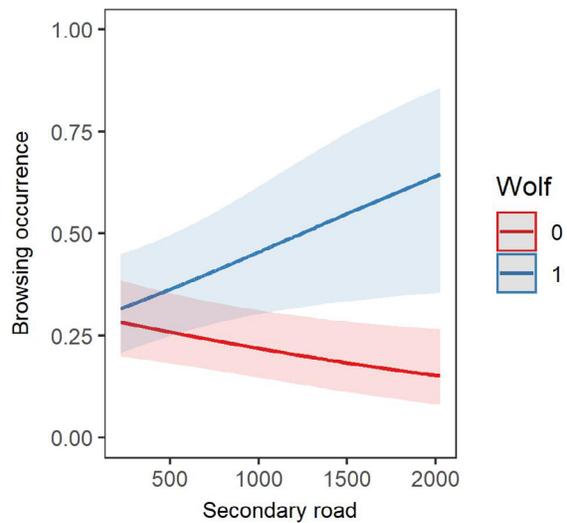
Fig. 3. Predictive plot for the interaction secondary road:wolf from the top-ranked rowan browsing occurrence model. Wolf territory absence = 0 and presence = 1. Low road values (in meters) are close to secondary roads, while high values are far from secondary roads. Predictions were from the top-ranked browsing occurrence model. Data are from Norway and Sweden from 2008 to 2018. Ribbons represent 95% confidence intervals.

respectively, relative to the maximum distance from each road type (Fig. 5).

For silver birch browsing pressure, the top model was 2.6 times more likely than the second-ranked model (Appendix S1: Table S2). Model-averaged parameter estimates indicated a strong positive effect of moose habitat use (β = 0.15; 95% CI = 0.05, 0.24) and a negative effect of young forests (Fig. 6) on browsing pressure.

Downy birch.—The top downy birch browsing occurrence model was 2.3 times more likely than the next-ranked model (Appendix S1: Table S1). This model contained the additive terms young forest and primary roads. Model-averaged parameter estimates indicated a positive effect of moose habitat use (β = 0.47; 95% CI = 0.37, 0.57) and secondary roads (β = −0.03, 95% CI = −0.17, 0.11; Figs. 4, 5), but a negative effect of primary roads (β = 0.22; 95% CI = 0.09, 0.34; Figs. 4, 5) and elevation (β = −0.54; 95% CI = −0.89, −0.20) on browsing occurrence. Browsing occurrence was 1.37 times higher at the highest probability of wolf territory occurrence

relative to a zero probability. Downy birch browsing occurrence was 1.1 higher and 1.8 times lower along secondary and primary roadsides, respectively, relative to the maximum distance from each road type (Fig. 5).

There were no clear top models for downy birch browsing pressure (Appendix S1: Table S2). Model-averaged covariates included negative effect of elevation (β = −0.46; 95% CI = −0.71, −0.20) and Scots pine presence (β = −0.11; 95% CI = −0.25, 0.04) on browsing pressure.

Scots pine.—The top Scots pine browsing occurrence model was two times more likely than the second-ranked model (Appendix S1: Table S1). This model included interaction terms young forest:secondary road where browsing occurrence was higher in young forests but declined further from secondary roads. Outside young forests, browsing occurrence on Scots pine was lower and the road effect was dampened (Appendix S2: Fig. S4). Model-averaged parameter estimates showed a positive effect of moose habitat use (β = 0.77; 95% CI = 0.67, 0.87), the presence of young forest (β = 0.49; 95% CI = 0.30, 0.69; Fig. 4), silver birch (β = 0.38; 95% CI = 0.24, 0.51), and downy birch (β = 0.42; 95% CI = 0.29, 0.54) on Scots pine browsing occurrence (Fig. 4). Browsing occurrence increased closer to secondary roads (β = −0.22; 95% CI = −0.36, −0.08) but decreased closer to primary roads (β = 0.19; 95% CI = 0.06, 0.31; Figs. 4, 5). Pine browsing occurrence was 1.6 times higher and 1.9 times lower along secondary and primary roadsides, respectively, relative to the maximum distance from each road type (Fig. 5).

The top browsing pressure model was 10 times more likely than the second-ranked model (Appendix S1: Table S2). This model included the interaction of wolf presence:secondary road: young forest. Browsing pressure outside wolf territories was relatively unchanged whether close to or far from secondary roads, or in young forests or not. Inside wolf territories, browsing pressure decreased in young forests when further from secondary roads. Browsing pressure increased further from secondary roads when outside young forests (Fig. 7). Model-averaged parameter estimates showed a positive effect of the presence of silver birch (β = 0.14; 95% CI = 0.002, 0.29) and a negative effect of
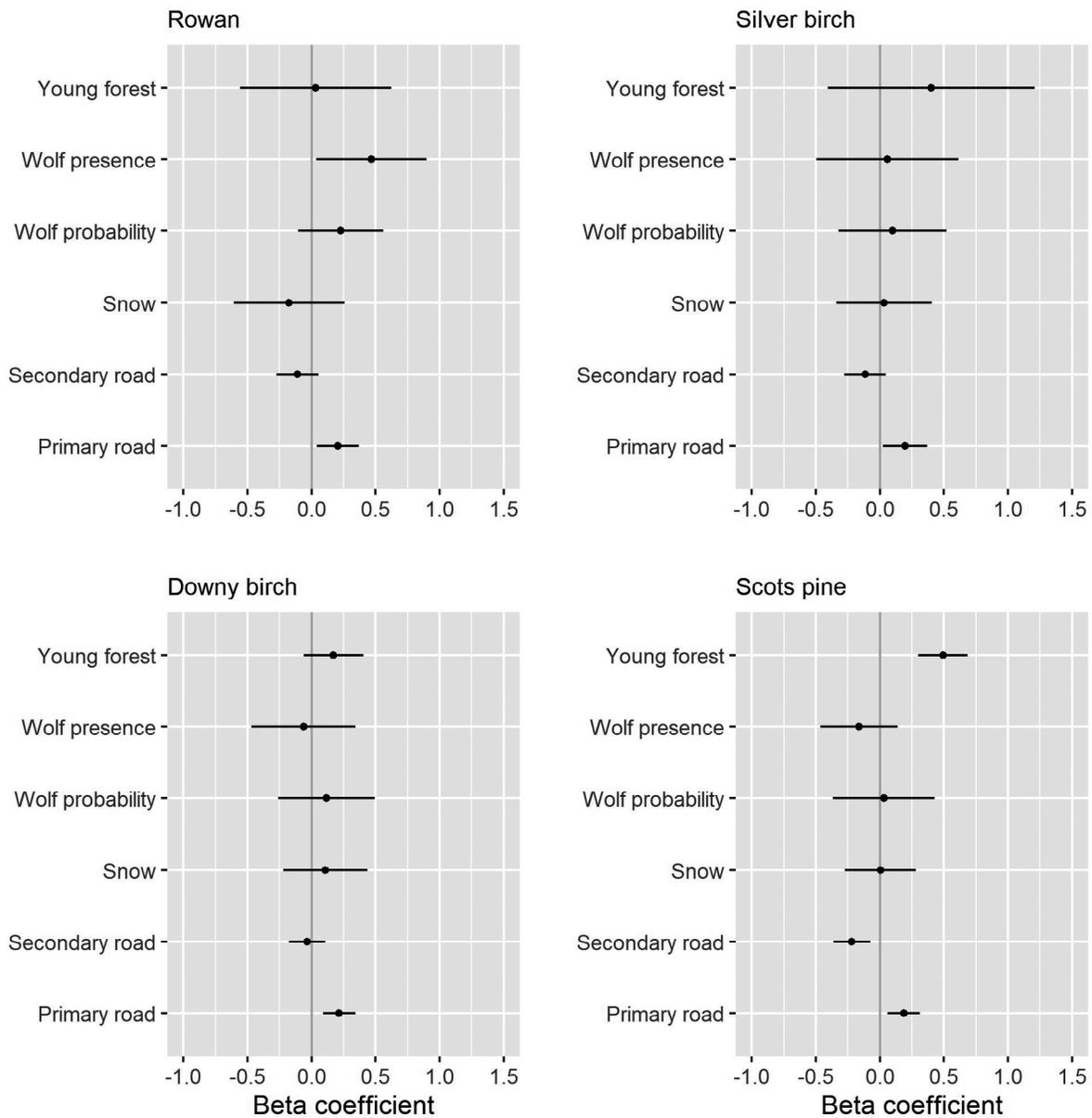
Fig. 4. Forest plots of model-averaged main effect coefficients from browsing occurrence models. Estimates are from binomial models. Reference categories for binary variables (wolf presence, young forest) are 0. Bars represent 95% confidence intervals.

elevation ($\beta = -0.58$; 95% CI $= -0.92$, -0.24) on Scots pine browsing pressure.

DISCUSSION

We tested the importance of roads, young forests, and wolves on moose browsing occurrence and browsing pressure at a fine spatial scale and large spatial extent. Primary and secondary roads were important explanatory variables for moose browsing occurrence and pressure on all tree species. Generally, for all tree species, browsing occurrence and pressure decreased close to primary roads but browsing occurrence
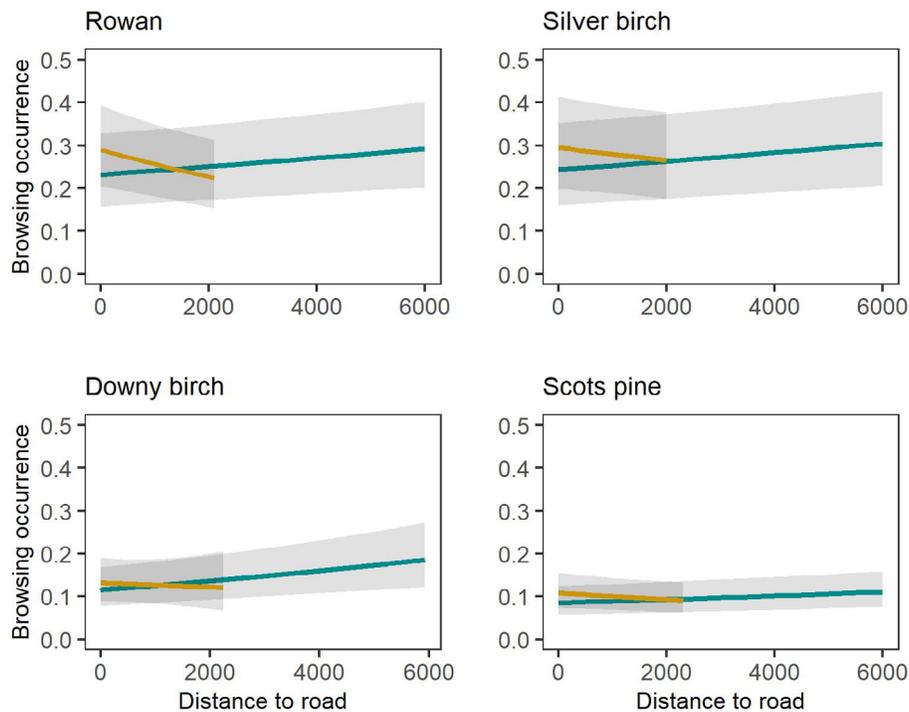
Fig. 5. Predictive plots for the relationship between browsing occurrence and distance to secondary (yellow line) and primary roads (green line) for all four tree species. Low road values (in meters) are close to roads, while high values are far from roads. Plots are from highest ranked models that contain secondary and primary roads for each species. See Appendix S1: Table S1 for model rankings. Data are from Norway and Sweden from 2008 to 2018. Ribbons represent 95% confidence intervals.

increased close to secondary roads (P1, P2). We also found a neutral to positive effect of wolf territory presence and probability on browsing occurrence and pressure. However, wolf effects became negative when they interacted with food and risk variables like snow cover, distance to roads, and presence of young forest (P1). We found little support for days with snow cover increasing browsing occurrence and pressure (P3) and tree species with differing selectivity rankings explaining differences in road and wolf effects (P4).

Our results showed reduced browsing occurrence close to primary roads and increased browsing occurrence close to secondary roads, as expected. Primary roads can increase chances of moose-vehicle collisions and are barriers to moose migration (Ball et al. 2001, Seiler et al. 2003), with vehicle speed, traffic volume, and fencing being primary deterrents (Seiler 2005). For all tree species, we found browsing

occurrence was 1.6–1.9 times lower along primary roadsides relative to the furthest point from primary roads. This supports a behavioral response from moose to avoid risky primary roads. Indeed, road avoidance behavior results in indirect habitat loss, which can often be a bigger driver than direct habitat loss (Dwinnell et al. 2019). This can reduce nutritional carrying capacity, reduce fitness, and lead to population declines (McLoughlin et al. 2006). While Scandinavian moose densities are among the highest in the world (Lavsund et al. 2003), little emphasis is placed on the fitness consequences of road development in Scandinavia.

In contrast to the response to primary roads, we found browsing occurrence was 1.1–2.3 times higher along secondary roadsides relative to the furthest point from the road. Moose could use secondary roads for travel but often these linear features are perceived as risky, especially when predators are present (Dickie et al. 2020), so we
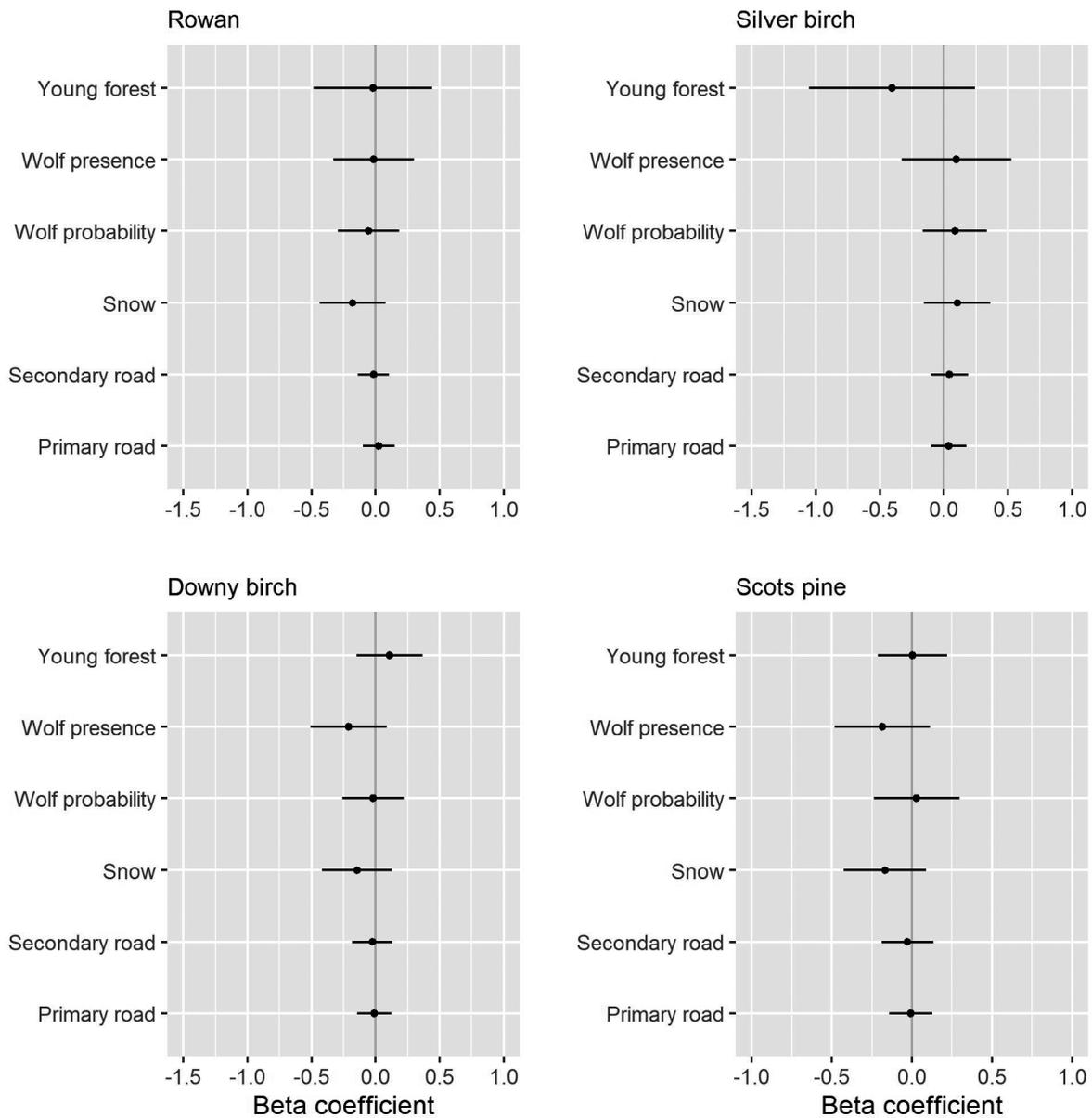
Fig. 6. Forest plots of model-averaged main effect coefficients from browsing pressure models. Estimates are from the conditional part of zero-inflated negative binomial models. Reference categories for binary variables are 0. Bars represent 95% confidence intervals.

would expect some degree of road avoidance behavior. A more plausible explanation for the positive effect of secondary roads is that roads change an herbivore's food landscapes without adding the burden of high vehicle traffic. For example, roadside mowing and ditching can increase plant diversity, specifically birch density

(Zielińska et al. 2013, Jakobsson et al. 2018). Forests in Scandinavia are typically low in structural and species diversity because deciduous tree densities are reduced during pre-commercial thinning. Roads and clear-cuts offer one of the few disturbance events to stimulate early successional deciduous tree growth. We could thus
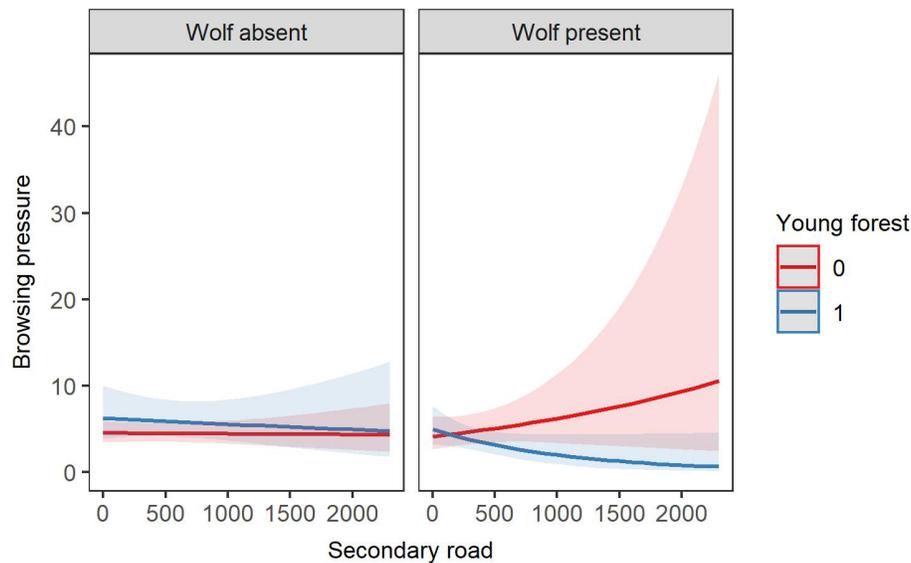
Fig. 7. Predictive plot for the interaction between secondary road:young forest:wolf territory presence from the top Scots pine browsing pressure model. Low road values (in meters) are close to secondary roads, while high values are far from secondary roads. Young forest presence = 1 and absence = 0. Data are from Norway and Sweden from 2008 to 2018. Ribbons represent 95% confidence intervals.

expect a relationship between roads and deciduous tree density, which could positively influence browsing occurrence and pressure. This is a plausible explanation for the positive main effect of secondary roads, though we could not detect any trend between tree density and distance to roads in Norway (Appendix S1: Fig. S7). Tree density data were not available for Sweden.

While secondary roadsides can offer food subsidies and easy travel routes, they also represent a spatial mortality risk to moose because they are also used by predators and humans. This could result in temporal or spatial road avoidance under certain situations (Mathisen et al. 2018). Indeed, we found rowan browsing occurrence increased further from secondary roads where wolf territories were present (Fig. 3), which suggests that secondary roadsides could be perceived as risky when predators are present. Globally and locally, roads increase the distance and speed at which wolves travel (Zimmermann et al. 2014, Dickie et al. 2017); in Scandinavia, wolves travel almost twice as fast on roads versus off roads. This could increase detection rates of prey and motivate moose to spend time away from roads despite roadsides offering attractive

foods. Additionally, multi-predator systems (including humans as predators) could have contrasting, additive, or multiplicative effects on the ungulate prey. For example, Lone et al. (2014) found that roe deer predation risk was greatest in rugged terrain where lynx and human hunters overlapped, creating areas of additive predation risk. Similarly, because secondary roads are used by wolves and humans, they could also be areas of additive (or additional) moose predation risk.

While browsing occurrence increased close to secondary roads for most tree species (except downy birch; Fig. 4), young forests intensified the positive effect of secondary roads for Scots pine (Fig. 7). For the commercially valuable Scots pine, the presence of young forest stands alongside secondary roads nearly doubled Scots pine browsing occurrence ($P = 0.20$) compared with a recently clear-cut, or forests older than 20 yr ($P = 0.11$; Appendix S2: Fig. S4). Much of Scandinavia's productive areas are used for agriculture and forestry. During winter, young pine forests are selected by moose for the abundance of high quantity and quality foods. However, intensive browsing can lead to a delay in stand maturity, irregular growth, or tree death (Wallgren et al.

2013, Herfindal et al. 2015). This is the center of the conflict between forest owners who want commercially valuable timber, and moose hunters, who want to sustain high harvest rates. Many forest roads in Scandinavia are being upgraded to allow for larger machinery (Flisberg et al. 2014), and new roads are being built for access to wind turbines, a growing energy source in Scandinavia (IEA Wind TCP 2018). While overall browsing occurrence along roadsides was low, the high-density secondary road network in Scandinavia could be facilitating intensive moose browsing. This could have long-term consequences to forestry and moose-forestry conflicts by intensifying moose browsing along roadsides.

Our browsing pressure estimates were comparable to previous Scandinavian studies. For example, browsing pressure estimates 1–10 km from supplemental feeding stations (where they did not find effects of feeding stations) from Mathisen et al. (2014) were 44% for rowan (2 SE = 9.0; 1.5 times higher than our average), 34% for silver birch (2 SE = 9.0; 1.3 times higher than our average), 27% for downy birch (2 SE = 6.0; 1.3 times higher than our average), and 33% for Scots pine (2 SE = 7.0; 1.2 times higher than our average). For both their study and ours, rowan experienced the highest browsing pressure (Fig. 2). Rowan is highly selected by moose, and high browsing impacts on rowan may have strong negative effects on plant and animal biodiversity (Shipley et al. 1998, Månsson et al. 2007). Indeed, Speed et al. (2013a, b) found height growth was restricted when 20–45% of rowan shoots and 30% of Scots pine shoots were browsed. For our study, 42% (n = 740) of Scots pine measured had ≥30% of shoots browsed. For rowan, 89% (n = 1,077) had ≥20% of shoots browsed and 57% (n = 691) had ≥45% of shoots browsed. We note the effect of browsing pressure on individual tree growth and development depends on many factors such as site productivity, tree species, or predation pressure, which make browsing pressure estimates difficult to generalize and compare. While our study was designed to quantify changes in moose browsing, and not changes in the plant community in relation to the presence of wolves, we recommend future research in Scandinavia to focus on the cascading effects of carnivores on plant biomass or recruitment.

Browsing occurrence and pressure represent different aspects of ungulate ecology but are poorly differentiated in the browsing literature. Given the data and our models, we found much clearer signals for browsing occurrence relative to browsing pressure. According to Shipley et al. (1998), moose utilize only 20% of available bites along a foraging path, taking only one or two bites per tree. In this case, we can think of browsing occurrence as one of many steps in the forage selection process: First, the moose needs to be present, then it encounters a tree, takes a bite or two, but may later reject the tree from further browsing. In contrast, browsing pressure reflects that moose have sampled the tree and chose to continue feeding on it. Browsing pressure is perhaps the more ecologically meaningful metric, as we can estimate the amount of forage removed from a tree/patch/landscape. However, browsing pressure had a low signal-to-noise ratio in our study. There were multiple potential sources of variation, including differences in tree morphology or uncertainty in our count estimates. For example, maximum counts for the number of browsed and available shoots reached 250 and 1028, respectively. These are high values, and although we used clicker-counters, human error likely contributed to some of this unknown error. For example, Prater (1979) found observers counting birds from photographs (i.e., true values known) consistently overestimated when counting small groups of birds but underestimated when counting large groups. For counting shoots on a tree, this could result in the systematic underestimation of the number of shoots on larger trees and overestimation of smaller trees. Shoot counting could be improved by using double observer surveys to quantify and correct for the uncertainty (Morrison 2016). Feedback sessions where all technicians count the same tree and learn from the group average could also be useful (Wintle et al. 2013).

Similar to Ausilio (2018) and van Beeck Calkoen et al. (2018), we found browsing occurrence increased with increasing probability of wolf territory occurrence (Fig. 4): For downy and silver birch, browsing occurrence was 1.37 and 1.26 times higher at the highest probability of wolf territory occurrence relative to a zero probability. This counterintuitive finding could result from wolves and moose being displaced by humans to

less productive areas, which results in high wolf-utilization areas having lower tree densities, or wolves aligning their territories with areas of higher moose densities. Unlike previous studies, however, we found that for rowan, browsing occurrence decreased close to secondary roads when wolf territories were present and the number of snow days were high. With a lot of snow, wolves may be more likely to use forest roads; alternatively, it may be easier for moose to move in the forest rather than on unplowed forest roads with deep snow. Similarly, browsing pressure was three times higher away from secondary roads when wolves were present and browsing occurred in clear-cut, or forests older than 20 yr. In contrast, browsing pressure was 1.4 times higher close to secondary roads when browsing occurred in young forests and wolves were present (Fig. 7). This finding lends tentative support for the risk allocation hypothesis that given roads represent a mortality risk, as we have shown above, moose are still attracted to roadsides when food sources are abundant. However, moose are less willing to accept this level of risk if the food reward is diminished, as is typically the case in mature forests. We note the high uncertainty with these estimates and are cautious in our interpretation.

Overall, however, wolf effects were lower than we expected. Part of this uncertainty could be because the wolf territory variable represents a coarser resolution (500 and 1000 m) than all other variables. At finer spatial resolutions, we would expect a stronger effect with reduced uncertainty. Another explanation for uncertain wolf effects is that our dataset is biased toward areas without wolves, so an excess of zeros in our wolf variables could mask underlying patterns. Post hoc, we ran browsing occurrence and pressure models with data only from sites within wolf distribution. Wolf effects become stronger (Appendix S2: Figs. S1, S2) but most other variables increased in uncertainty. Important interactions, such as the interaction of wolf territory presence and distance to secondary roads, remained present but estimates became more uncertain (Appendix S2: Figs. S3, S4). See Appendix S2 for post hoc results.

Our results of weak wolf effects are consistent with other European studies where the effects of wolves have been more difficult to elucidate than in North America, possibly because of reduced landscape heterogeneity and dampened effects of predators relative to the effects of humans (Schmidt and Kuijper 2015). In Scandinavia, previous research has also suggested that moose may be naïve to wolves as predators. Sand et al. (2006) found wolf hunting success of moose to be 2–9 times higher in Scandinavia relative to North America, which they argue is an artifact of mortality contributions from humans (high) and large carnivores (low). In North America, wolves were never extirpated from the moose's distribution (or only for short periods; e.g., 40–50 yr) whereas moose in Scandinavia have lived without large carnivores for 120–150 yr. Because of this carnivore-free period, Sand et al. (2006) and others (Berger et al. 2001) argue that moose have relaxed their aggressive anti-predator response in favor of a flee response. Last, another possible reason for a weak wolf effect could be because moose are widely hunted with dogs in Scandinavia. Hunting dogs bark at moose, and hunters are more successful at shooting moose that stand their ground, which is an advantageous anti-predator response to wolves. However, it is the fleeing moose that often escape human hunters and may thus be favored in selection. Hunting is a widely popular activity in Scandinavia with almost 115,000 moose shot annually, so human hunters potentially exert a stronger selection pressure relative to wolves.

To conclude, we found browsing occurrence and pressure effects varied by tree species. We found neutral to positive effects of wolves. Wolf effects became more certain and positive when they interacted with other factors such as snow cover, young forests, and roads. Whether these effects are large enough to shape tree recruitment or community patterns remains unknown. We found browsing occurrence increased close to secondary roads but decreased close to primary roads. The presence of young forests near secondary roads nearly doubled moose browsing occurrence for Scots pine, which could have consequences for moose-forestry conflicts. There are many secondary roads in Scandinavia, and even more to be built. We assert that forest and wildlife managers need to consider how an increasing network of secondary roads facilitates intensive moose browsing.

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