MASTER 2
EFCE

Ecologie Fonctionnelle, Comportementale et Evolutive

Effect of wolf (*Canis lupus*) establishment on moose (*Alces alces*) winter damage in young Scots pines (*Pinus sylvestris*) plantations

MSc thesis

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By,
Morgane GICQUEL

MSc supervisor(s):
Camilla WIKENROS
Johan MÅNSSON
Håkan SAND

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OUTLINE

INTRODUCTION

Ungulates, like other large herbivores, are keystone species because they act as ecosystem engineer and restructure communities and modify their functioning (Huntly, 1991; McShea & Rappole, 1992). They are an important link in food webs as they interact with plant communities by foraging, and also by being prey for carnivore species (Apollonio et al., 2010). Wild ungulates can induce different effects to vegetation because of their foraging behaviour, like grazing, browsing or bark-stripping, but also by other behaviours such as fraying, trampling or bedding. Sometimes foraging may stimulate growth and can increase seed production (McNaughton, 1983; Hester *et al.*, 2006), and may also enhance seed dispersal and seed establishment (Hulme, 1996; Gill & Beardall, 2001; Danell *et al.*, 2003). But at high foraging rates, it can hamper plant growth and alter other functions, sometimes leading the plant to death (Hester *et al.*, 2006; Skarpe & Hester, 2008). Therefore, high densities of wild ungulates can affect ecosystems, for example by changing plant species composition (Hobbs, 1996; Augustine & McNaughton, 1998; Augustine & Decalesta, 2003; Côté et al., 2004).

After a decline during the 19th century, wild ungulate populations are now recovering all over the globe, aided by active management and conservation actions (Augustine & Decalesta, 2003; Côté et al., 2004; Apollonio et al., 2010). The recent increase in ungulate density is also a source of conflict between different human interests, in particular between conservation, hunting, agriculture, livestock or forestry (Côté *et al.*, 2004). Damage caused by ungulates can lead to an important economic cost for agriculture and forestry, not only by the direct loss of the yield (Reimoser & Putman, 2011), but also by the costs generated by compensatory and management methods needed to avoid and/or reduce damage. Both forestry and agriculture are sources of vast incomes in Europe, as the output of crop production was 210 195 million Euro in 2016, and the output of forestry represented 48 392 million Euro in 2014 (Forti, 2017). In Sweden, one of the European countries with the largest forested area, forestry and logging activities are one of the main production activities, with a gross value amounted 4 622 million Euro in 2014 (Forti, 2017). Thus, the economic loss to forestry from wild ungulates damage is significant in this country. Here, particularly moose (*Alces alces*) cause damage by browsing and bark-stripping (Faber & Edenius, 1998; Bergqvist *et al.*, 2001). These damage lead to a reduction of timber production and quality (Gill, 1992), which represents an economic loss of at least 50 million Euro annually for forest owners (Liberg *et al.*, 2010).

To protect vulnerable forests from damage by moose, fences or supplementary feeding are common methods used, but the harvest is by far the most important method in order to reduce moose population in highly vulnerable areas, such as young forests (Côté *et al.*, 2004). But whereas

foresters usually want a significant decrease of moose population to avoid damage and thus money loss, hunters may want to maintain a large population to have good game seasons (Ezebilo *et al.*, 2012). Thus, foresters and hunters have to compromise the quotas of moose harvest within various hunting management units, with a particular number of male, female and calves to shoot (Bergman & Åkerberg, 2006).

Besides the ungulate density, other factors can play a role in the impact of moose to forest damage. The availability of forage can have an indirect impact on damage to vegetation caused by ungulates (Månsson, 2009). Browsing on deciduous species, often selected by ungulates, like rowan (*Sorbus aucuparia*), aspen (*Populus tremula*) or birch (*Betula sp*), has been viewed as favourable by foresters, because it reduces browsing pressure on valuable tree species, such as Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), as ungulates select for deciduous species (Andrén & Angelstam, 1993). However, the presence of deciduous trees in the stand can also attract ungulates in the area, and as the ungulate density increases, they will begin to browse less selected species as well, and thus increase the damage to valuable forest species (Andrén & Angelstam, 1993; Hörnberg, 2001; Ball & Dahlgren, 2002; Lavsund *et al.*, 2003; Edenius *et al.*, 2015). Also, Norway spruce is a species which is rarely selected (Bergqvist *et al.*, 2014), and thus if this cover increase it may lead to more damage on Scots pines. In addition, climatic conditions, such as snow depth, can influence browsing damage made by ungulates. Severe winters can affect ungulate populations negatively, resulting in less damage (Augustine & McNaughton, 1998; White *et al.*, 2003). But increased snow depth can also decrease forage availability for ungulates and thus push them to consume more twigs and bark leading to more damage on trees (Månsson, 2009). In addition, human disturbance, such as traffic, may push ungulates away resulting in decreased damage near roads (Augustine & Decalesta, 2003). But in case of large roads that are usually fenced to avoid vehicles-wildlife collisions, the damage level are higher near the roads (Ball & Dahlgren, 2002).

Since large carnivores are recently recolonizing Europe due to conservation efforts, e.g. protection and natural habitat restoration (Chapron *et al.*, 2014), there is now another factor to consider in the management of ungulates. By regulating prey populations large predators can have a major role in ecosystems that may result in cascading effects through the whole food web (Beschta & Ripple, 2009) for example by reducing ungulate population density and therefore also impact on vegetation (Bergerud *et al.*, 1983; Ripple *et al.*, 2001; White *et al.*, 2003; Beschta & Ripple, 2009). Large carnivores can also change the behaviour of prey, by changing their perception of predation risk which will be different according to the habitat characteristics, creating a “landscape of fear” (Laundré *et al.*, 2001; Kuijper *et al.*, 2013). Ungulates may change their foraging strategy, grouping behaviour, habitat use and movement rate, according to the presence of predators (Kie, 1999; Ripple *et al.*, 2001; Creel *et al.*, 2005; Creel & Winnie, 2005; Fortin *et al.*, 2005). The distribution

of ungulates across the landscape may change if they avoid the predator's territory core areas (Kuijper *et al.*, 2013). But in some studies, the presence of predators does not seem to induce any changes in prey anti-predator behaviour, even after a long time period (Sand *et al.*, 2006; Gervasi *et al.*, 2013; Nicholson *et al.*, 2014).

In this study, the focus will be on browsing damage induced by moose on Scots pines in south-central Sweden, an area that has been recently recolonized by wolves. The aim of this study is to improve the understanding of the consequences of predators' establishment for their prey impact on vegetation. Data on moose harvest density, moose browsing damage on Scots pines, wolf presence, forage availability (cover of deciduous trees and other tree species), snow depth, and road densities will be used. First, if the presence and the level of damage on Scots pines are linked to the presence of wolves will be assessed. Second, if the effect of the duration of wolf presence can explain further variation of the presence and the level of the damage on Scots pines will be tested.

This study predicts that the presence and level of moose damage to Scots pines will be lower (1) within established wolf territories and with increasing number of years with wolf presence, (2) in presence of deciduous species (rowan, aspen, willow, oak) and at high birch cover, (3) at high density of small and medium roads; but higher (4) at high moose density, (5) at high spruce cover, (6) at high snow depth, and (7) at high large road density.

MATERIALS & METHODS

1. Study area

The study was conducted in south-central Sweden, in the counties of Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland, and Örebro. In this area, the landscape is divided into different land use classes, including sub-boreal forests (69%), agricultural lands (11%), mires (10%) and urban areas (3%) (Nilsson & Cory, 2017). The sub-boreal forests are mostly composed of Norway spruce (*Picea abies*, 43%), Scots pine (40%) and birch (*Betula spp*., 11%) (Nilsson & Cory, 2017). Human density averaged 10.2 humans per km² in Dalarna, 15.8 in Gävleborg, 16.0 in Värmland, 53.0 in Västmanland, 71.0 in Västra Götaland and 35.1 in Örebro, representing a mean of 33.5 humans per km^2 in these six counties (Statistics Sweden, 2018). The high exploitation of forests leads to an extensive forest roads network, which with other roads, such as national, regional, and highways lead to a mean road density of 2.02 km/km² in these 6 counties (National Roads DataBase NVDB). The mean snow depth in cm was of 12.4 in Dalarna, 9.4 in Gävleborg, 2.0 in Västra Götaland, 5.9 in Värmland, 4.8 in Västmanland and 4.5 in Örebro, averaging 6.6 for the 6 counties during winters 2014 to 2017, for the period from October to April (Swedish Meteorological and Hydrological Institute, https://opendata-download-metobs.smhi.se/explore/).

The moose population size has been fluctuating in Sweden for centuries (Liberg *et al.*, 2010). Moose hunting was at first only reserved to the royal family, but this restriction was abolished in 1789 causing a moose population decrease (Liberg *et al.*, 2010). Intensive hunting but also overexploitation of forests, and expansion of agricultural lands (Côté *et al.*, 2004; Liberg *et al.*, 2010) almost led to the extinction of moose in Sweden (Bergman & Åkerberg, 2006). Then, during the 19th and 20th centuries, thanks to favourable management actions through conservation of their habitats, hunting regulation policies, new forestry practice involving intense clear-cutting creating more food for moose, and also the previous extirpation of their predators, moose population had been increasing and expanding (Hörnberg, 2001; Lavsund *et al.*, 2003; Liberg *et al.*, 2010).

Wolves were declared functionally extinct in Scandinavia in the 1960s. In the 1980s, two wolves from the Finnish-Russian population reproduced in a territory at the border between Sweden and Norway, thereby founded the current Scandinavian population (Wabakken *et al.*, 2001; Liberg *et al.*, 2005). Since then, the wolf population continued to increase in numbers and expanded their breeding range in Scandinavia, despite high inbreeding (Liberg *et al.*, 2005). In 2016-2017, the population was composed of 56 territories (including territorial pairs or packs (≥ 3 individuals) and half of the border territories) and estimated to 355 (95% CI = 281-461) individuals in Sweden (Svensson *et al.*, 2017). Wolves are the main predator of moose, which constitute more than 95% of their diet (Sand *et al.*, 2005). They prefer to prey on calves, and > 70% of moose killed by wolves are calves during winter and 90% during summer (Sand *et al.*, 2005, 2008).

2. Moose browsing damage survey

The moose browsing damage survey ("Älgbetesinventering" or ÄBIN) takes place each year during the spring (~April-June). The methodology was designed by the Swedish Forestry Board ("Skogsstyrelsen") and is performed by the Swedish forestry hired staff ("ÄBIN Ekonomisk Förening"). The objective is to estimate the proportion of damage made by moose on Scots pines during the preceding winter. The types of damage that are surveyed correspond to browsing of the apical shoot, stem breaking and bark-stripping (Figure 1). In this study, a total of 4086 squares of 1 x 1 km (hereafter squares) that were randomly distributed in the 6 counties and surveyed during 3 years (2015 to 2017) were used. For the analyses, only squares with presence of Scots pines were used, (n = 3284). Within all squares, young forest stands with an average tree height between 1 to 4 meters and containing at least 10% of pine trees were selected. In each stand 1 to 15 sample plots (stand size dependent) were randomly distributed and surveyed using a minimum distance of 80 meters between the plots. All sample plots had a 3.5 m radius (Rolander *et al.*, 2017). Within each plot, the following measurements were registered: number of damaged and undamaged stems of Scots pines, number of stems of spruce and birch, presence of highly selected tree species (hereafter RAWO) which include rowan, aspen, willow (*Salix caprea*) and oak (*Quercus robur*), and the

presence of deciduous trees that were competitive with pine. Then, to obtain the total number of damaged and undamaged pine stems of the different tree species at the square level, upscaling estimation was made from the plot to the stand level, and then from the stand to the square.

Figure 1. Different damage made by moose in young Scots pine forests. From left to right: browsing of the apical stem, stem breaking and bark-stripping. (modified from Rolander et al., 2017)

Using the same method as Bergqvist *et al.*, (2014) the proportion of browsed Scots pines was calculated as well as the estimated number of trees with recent browsing damage (made during the preceding winter) in the squares. The percentage of coverage of the other tree species was calculated by estimating the total number of that species divided by the estimated total number of trees. The proportion of plots containing RAWO was calculated by the number of plots surveyed in the square and containing RAWO divided by the total number of plots surveyed in that square (hereafter RAWO presence). The same type of calculation was made for the proportion of plots containing deciduous trees that were competitive with Scots pines (hereafter competitive RAWO).

3. Moose, wolf, habitats, snow depth and road densities

3.1. Moose

Moose hunting statistics were compiled from the Swedish Moose Hunting database provided by the website Älgdata (http://www.algdata.se). Moose hunting statistics were compiled both at the regional moose management scale ("Älgförvaltningsområden" or ÄFO, hereafter referred to as regional scale, average 1578 km², range 169-5231 km²), and at the local moose management scale ("Älgjaktområden" or ÄJO, hereafter referred to as local scale, average 93 km², range 1-3970 km²). Moose harvest density in each of these areas was calculated as the total number of moose harvested per km² (Figure 2c). The moose harvest density from the hunting season during the autumn/winter preceding the moose browsing survey was used as a proxy for moose density.

3.2. Wolf

The Scandinavian wolf population has been monitored since 1978, using foremost snow tracking, DNA analyses and combined with radio-telemetry for collared wolves. The main objective of the monitoring is to confirm the residence and breeding status of all territorial wolves (Wabakken *et al.*, 2001; Liberg *et al.*, 2012). Wolf territory polygons were calculated by using 100% Minimum Convex Polygon, according to presence indicators obtained from the monitoring (Svensson *et al.*, 2017). The centre point of each polygon was determined using ArcGIS 10.5 (ESRI, 2017). Based on these centre points, a buffer of 18 km radius representing the average wolf territory size, corresponding to 1017 km², were created (Mattisson *et al.*, 2013; Wikenros *et al.*, 2017).

As the wolf territory borders are not recorded by the monitoring, 3 different wolf indexes were created. First, all squares with available moose browsing data was categorized as 1) outside the average territory buffer (hereafter No wolf presence), 2) inside the average wolf territory buffer (hereafter Probable wolf presence) but outside the wolf territory polygon, or 3) inside the wolf territory polygon (hereafter Known wolf presence) (Figure 2b). Second, at both the regional and local scale, the proportion of area coverage of wolf territories (hereafter Wolf coverage) in each management area was estimated, by calculating the size of the area covered by average wolf territory buffers divided by the total size of the management area in km², using ArcGIS 10.5 (ESRI, 2017). Third, the duration of wolf presence (or Wolf duration) was determined, by counting how many years in total each square had been within the known wolf presence area.

3.3. Habitats

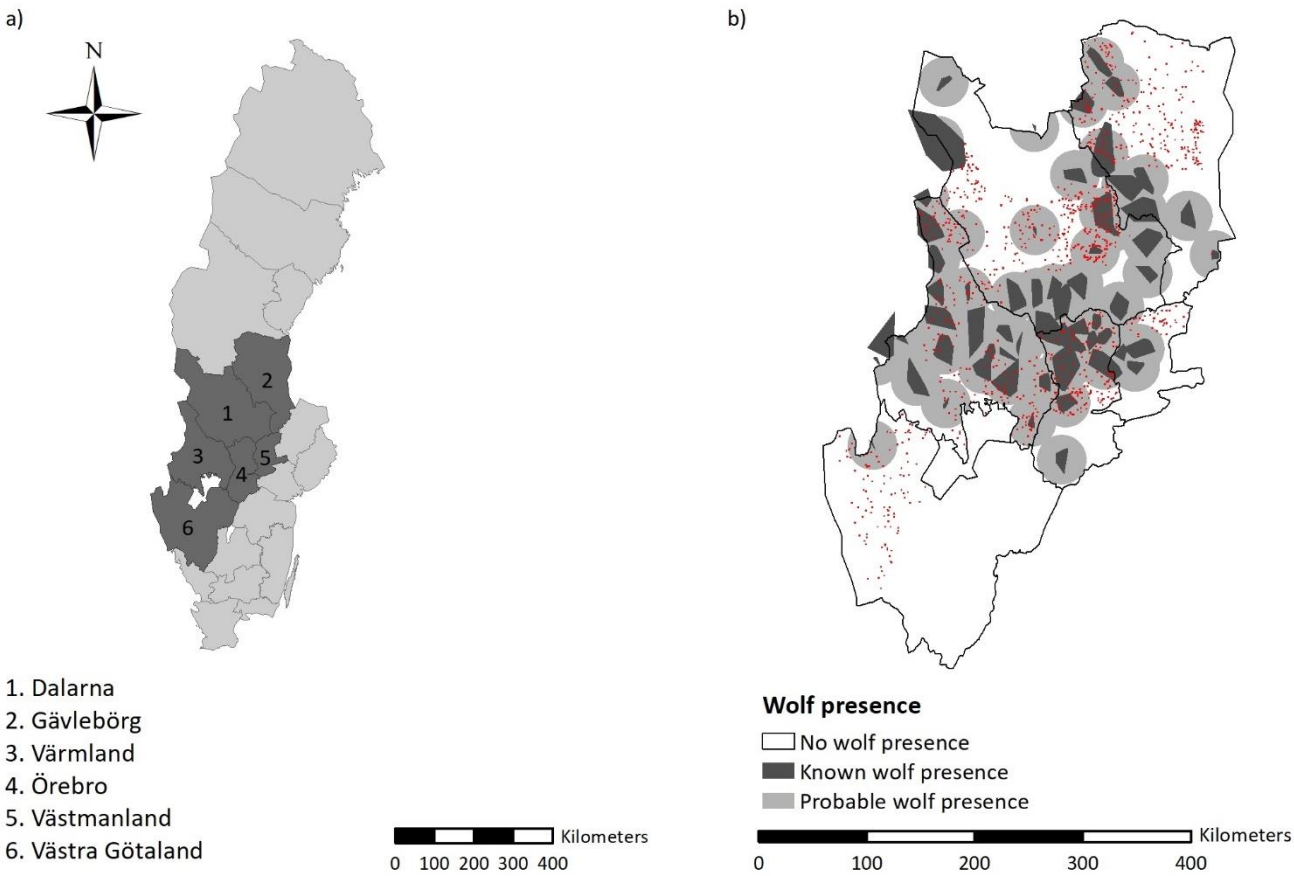
Corine Land Cover (CLC) 2012 version 18.5.1 (https://www.eea.europa.eu/data-and-maps/data/clc-2012-raster) was used to define the proportion of each land cover type for each square. Then, the proportion of the main land cover type was used to classify each square according to land cover type. Of the 3284 sampled squares, 2900 squares were located in forest-dominated landscape, 167 in grasslands, 95 in agricultural lands, 56 squares were overlapping continental waters, and 43 squares in marshes, with the rest of the 23 squares located in either open, heterogeneous, urban, industrial/commercial, or sea dominated landscapes (Figure 2d).

3.4. Snow depth

Snow depth data was obtained from the Swedish Meteorological and Hydrological Institute (SMHI, https://opendata-download-metobs.smhi.se/explore/). Snow data were compiled from 121 weather stations across the six counties, for winters (October to April) 2014-2015, 2015-2016 and 2016-2017. To estimate the snow cover (cm) across the six counties, the interpolation tool (Inverse Distance Weighted or IDW) from spatial analyst tools box in ArcGIS 10.5 was used (ESRI, 2017), using data from the 121 neighbouring stations (Figure 2e). Then, the mean snow depth for each square according to the actual year of survey was obtained.

3.5. Road densities

Three roads categories could be distinguished according to the National Roads DataBase (NVDB) (Trafikverket, 2006). Large roads correspond to highways and national roads (classes 0 to 2), medium roads regroup primary to tertiary roads (classes 3 to 6), and small roads represent local forest's or exploitation roads (classes 7 to 9) (Figure 2f). For these 3 categories, the density was calculated inside all the squares, by determining the total length of roads in km within the square and dividing it by the size of the square area (km road/km^2).



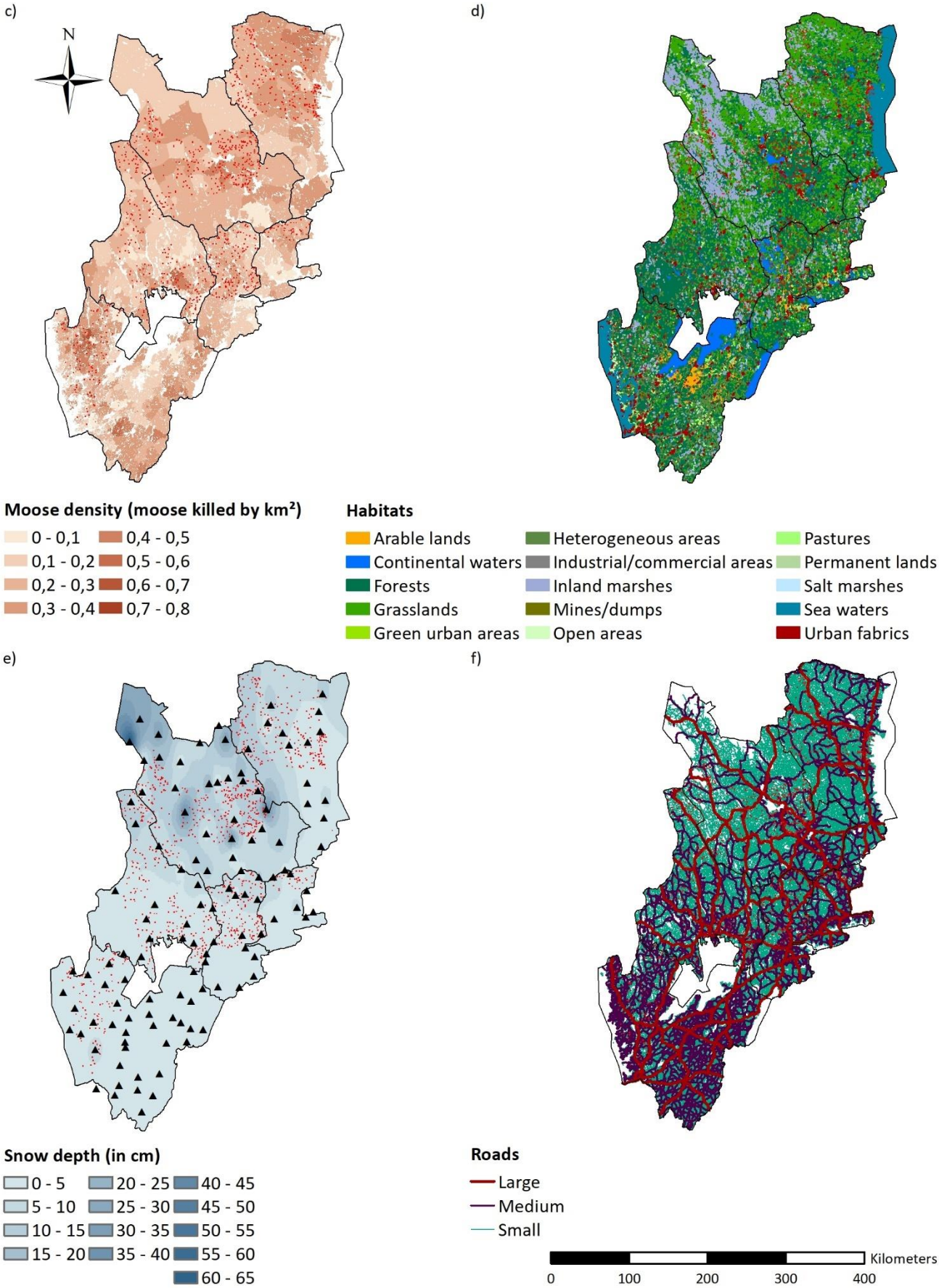


Figure 2. The maps are representing a) Sweden counties, dark grey the six counties that constituted the study area; b) wolf presence in the study area; c) moose densities, obtained from hunting data; d) habitats from Corine Land Cover (CLC) 2012, version 18.5.1 (https://www.eea.europa.eu/data-and-maps/data/clc-2012-raster); e) snow depth, estimated with interpolation (IDW), the triangles represent the 121 weather stations; and f) road network in the study area. All the data for map b, c and e were from the winter season 2016-2017. Red dots represent the squares surveyed during the moose browsing survey of 2017. Maps created using ArcGIS 10.5 (ESRI, 2017).

4. Statistical analyses

All the statistical analyses were conducted using R version 3.4.3 (R Core Team, 2017). All analyses were conducted for forest-dominated landscape squares only (n = 2900). General Linear Mixed Models (GLMM), using the "lme4" package (Bates *et al.*, 2018), with a binomial distribution and the presence of damage (yes or no) as a binary response variable. For the damage level (proportion 0 < x < 1) analysis, 0 and 1 proportion were deleted to be able to use a GLMM with a beta distribution reducing the dataset to 1655 squares (Figure 3), using the "glmmTMB" package (Magnusson *et al.*, 2017).

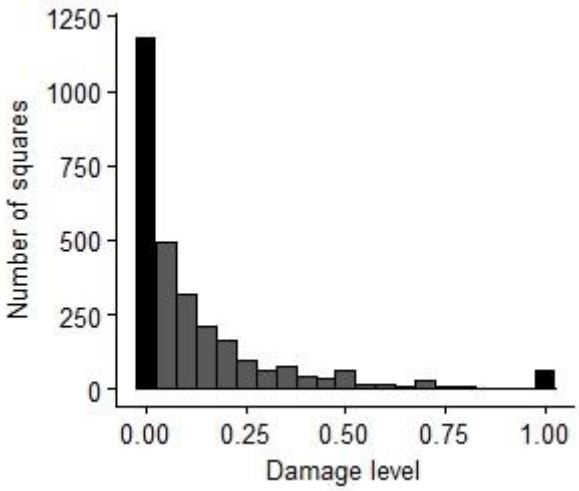


Figure 3. Histogram of the distribution of damage level for forested-dominated landscape squares (n = 2900) surveyed from 2015 to 2017, in the six counties of the study area (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) in Sweden. Grey bars represent the distribution of damage level without the zeros and ones (n = 1655).

For the variable representing the duration of wolf presence, squares that always were outside a wolf territory where deleted from the datasets, resulting in a sample size of n = 1436 for the damage presence; and a sample size of n = 873 for the damage level. Of the total 2900 squares that were surveyed in forest habitats, 432 were located inside a known wolf territory, 1000 were inside an area with the probable presence of wolf, and 1466 were outside. Over these 2900 squares, 1728 had damage Scots pines from moose, damage level ranging from 0.01 to 1 (Figure 3).

For all the analyses, wolf indexes were used independently as explanatory variables in different models; with wolf presence (3-level category: No wolf presence (0), Probable wolf presence (1), or Known wolf presence (2)), wolf coverage (proportion variable, range between 0 and 1), and wolf duration (continuous variable, range between 0 and 15). The RAWO presence and competitive RAWO were highly correlated ($p < 0.05$; rho < -0.5), so only RAWO presence was included in the analyses. In each model, variables such as one of the wolf indexes (see above), moose density (continuous variable, range 0-0.81), RAWO presence (proportion variable, range 0-1), spruce and birch cover (proportion variables, range 0-0.97, and 0-0.98, respectively), snow depth

(continuous variable, range 0.02-39.58), and small, medium and large road densities (continuous variables, range 0-6.24, 0-2.28, and 0-3.26, respectively) were used as explanatory variables.

All analyses were made both at the regional and local scale, with the wolf coverage index and moose density corresponding to the respective scale. The area code (either regional or local) was used as a random factor to account for spatial autocorrelation between the squares. The year at which the square was surveyed was also used as a random factor. The number of sample plots surveyed within each square was used to weight all analyses in relation to sample size.

For all analyses, models for every variables combination were compared using the Akaike Information Criterion (AIC) and AIC weights (wi) from the "MuMIn" package (Barton, 2018). Models with $\Delta AIC \leq 2$ were used to generate full model-averaged parameter estimates (Burnham & Anderson, 2002). AIC weights on model set with $\Delta AIC \leq 2$ were used to generate Relative Variable Importance weights (RVI) for each explanatory variable.

RESULTS

1. Regional scale

1.1. Presence of damage

Wolf presence models (at the square level)

Wolf presence was an important factor that affected the probability of presence of damage (RVI = 1; Table 1) with higher probability of damage within known wolf territories (0.19 ± 0.05 SE), as compared to probable wolf territory (-0.06 ± 0.04 SE) or outside wolf territories (Figure 4a; Table 1). All other variables were also important factors explaining the probability of damage (RVI = 0.85-1), except the presence of RAWO and large road density which were only present in one of the highest ranked models ($RVI_{RAWO\ presence}$ = 0.26, $RVI_{large\ roads}$ = 0.15; Table 1). The probability of the presence of damage decreased with increasing moose density and increased with increasing snow depth (Table 1). The variables related to forage availability showed a positive relationship with the probability of damage for the presence of RAWO and birch cover, but a negative relationship with spruce cover (Table 1). All categories including road density (small, medium and large) showed a negative relationship with the probability of the presence of damage (Table 1).

Wolf coverage models (at the moose management level)

Compared to the wolf presence index, wolf coverage had the opposite relationship on the probability of damages with a decrease in the probability of damage with an increase in wolf coverage (-0.04 ± 0.10 SE; Figure 4b; Table 1). Wolf coverage was of low relative importance and was present only in 2 of the 6 highest ranked models (RVI = 0.31; Table 1). Most other variables included had a similar effect as in the models with the wolf presence index except RAWO presence that had a higher importance (RVI = 0.47; Table 1).

Wolf duration models (at the square level)

Where wolves had been established for a relatively longer period of time there was a higher probability of damage as compared to units where they had established more recently (0.04 ± 0.008 SE; Figure 4c; Table 1). Wolf duration was an important variable (RVI = 1; Table 1). In these models, the importance of the different variables changed with respect to the models including wolf presence or wolf coverage indexes. In the highest ranked models, moose harvest density was the least important variable (RVI = 0.19; Table 1). Compared to models including wolf presence or wolf coverage indexes, RAWO presence and birch showed the opposite relationship (the probability of the presence of damage decreased with increasing RAWO and birch presence, Table 1).

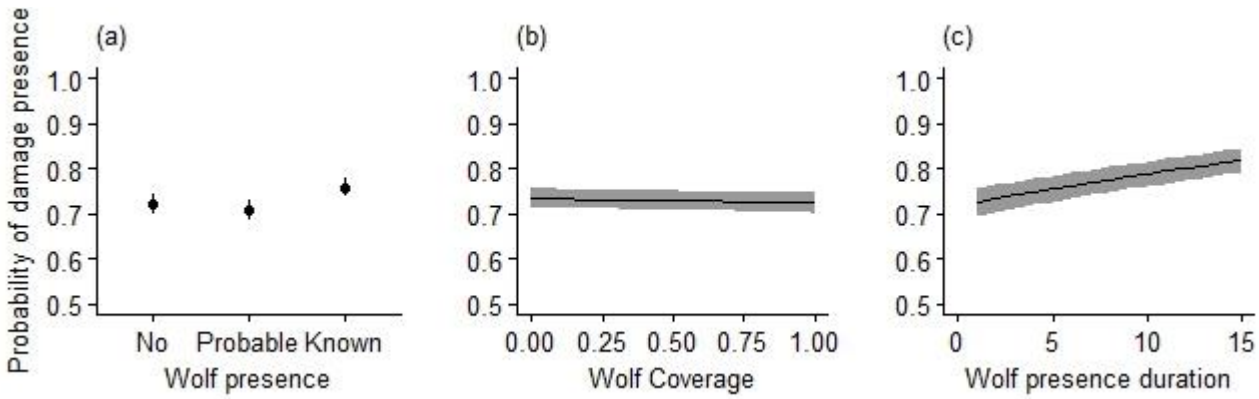


Figure 4. Probability of damage presence in relation to (a) wolf presence at the square (n = 2900), (b) wolf coverage of the regional units (n = 2900) and (c) wolf presence duration in years (n = 1486), in the six counties of study from 2015 to 2017. The dots and lines indicate the fitted values, with associated Standard Errors, from the full model averaged estimates (Table 1). Moose harvest density, RAWO presence, Spruce and birch cover, snow depth, and road densities are held constant at average.

1.2. Damage level

Wolf presence models (at the square level)

In these models, wolf presence was an important factor that affect the damage level (RVI = 0.78; Table 2). The damage level was lower within known wolf presence areas (-0.02 ± 0.02 SE) as compared to probable territories (0.02 ± 0.02 SE) or outside territories (Figure 5a; Table 2). However, all the other variables were important as well, except small roads density which was only present in one of the highest ranked models (RVI = 0.17; Table 2). The damage level was positively related to moose density, birch cover, snow depth, and spruce at the regional scale (Table 2). In contrast, RAWO presence was negatively related to the level of damage. In addition, a higher density of small and large road densities increased the damage level, whereas the density of medium roads decreased the damage level (Table 2).

Wolf coverage models (at the moose management units)

With the increase of wolf coverage, the damage level increased (0.05 ± 0.06 SE; Figure 5b). Wolf coverage was not an important variable explaining the variation of damage level compared to the other variables included in the highest ranked models (RVI = 0.55; Table 2). Similar to the models assessing damage presence probability, the wolf coverage gave the opposite relation

compared to the wolf presence index. For the other variables, the estimates were similar as when using the wolf presence index (Table 2).

Wolf duration models (at the square level)

The averaged model showed a weak negative effect of the wolf duration on damage level, (-6.28e-5 ± 9.56e-4 SE; Figure 5c). Wolf duration was also the least important variable only present in one of the 6 highest ranked models (RVI = 0.10; Table 2). In the highest ranked models with wolf duration index, the relative variable importance changed compared to models including wolf presence and coverage indexes (Table 2). Moose harvest density and small road density had low importance in the highest ranked models ($RVI_{moose\ density}$ = 0.59 and $RVI_{small\ roads}$ = 0.55; Table 2). All other included variables, had positive relationships, except large road density that when increasing, the damage level decreased (Table 2).

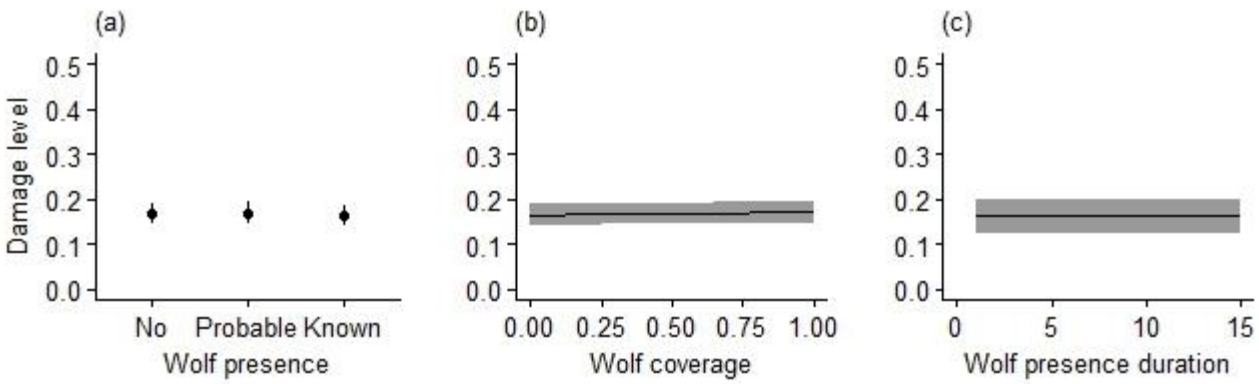


Figure 5. Damage level on Scots pines in relation to (a) wolf presence at the square (n = 1655), (b) wolf coverage of the regional units (n = 1655) and (c) wolf presence duration in years (n = 873), in the 6 counties of study from 2015 to 2017. The dots and lines indicate the fitted values, with associated Standard Errors, from the full model averaged estimates (Table 2). Moose harvest density, RAWO presence, Spruce and birch cover, snow depth, and road densities are held constant at average.

2. Local scale

2.1. Presence of damage

Wolf presence models (at the square level)

Wolf presence was an important factor, present in all of the highest ranked models (RVI = 1; Table 3) with the probability of damages higher within known wolf territory (0.29 ± 0.07 SE), as compared to probable wolf territory (-0.02 ± 0.06 SE) or outside wolf territory (Figure 6a; Table 3). For models including wolf presence index, all the variables were important, except RAWO presence and large roads density, which were included in only 1 model of the 4 highest ranked models ($RVI_{RAWO\ presence}$ = 0.25, $RVI_{large\ road}$ = 0.17; Table 3). Moose density was positively related to damage presence probability (Table 3). For the forage availability, both increasing RAWO presence, birch cover, as well as snow depth increased the probability of the presence of damage whereas spruce availability showed the opposite pattern (Table 3). Road densities showed different results, for small and medium roads, the increase of their density in the area led to a decrease of the probability of the presence of damage, but for large roads, it was the opposite relationship (Table 3).

Wolf coverage models (at the moose management units)

Opposite to the wolf presence, the probability of the presence of damage decreased with increasing wolf coverage (-0.58 ± 0.11; Figure 6b). Wolf coverage was among the most important variables in the highest ranked models (RVI = 1; Table 3). For the highest ranked models, RAWO presence was a more important variable compared to models with wolf presence index (RVI = 0.70), but large roads density was still of weak importance (RVI = 0. 20; Table 3). Otherwise, all the other variables had a high RVI. As for the models including wolf presence index, the other variables had the same relationship with the probability of the presence of damage (Table 3).

Wolf duration models (at the square level)

The wolf duration showed an increase of the probability of the presence of damage. When wolves were established for a long period of time there was a higher damage presence probability than when they were established only since a few years (0.04 ± 0.01 SE; Figure 6c; Table 3). In these models, all the different variables had the highest relative variable importance, except for the large road density (RVI = 0.40; Table 3). Compared to models including wolf presence or wolf coverage indexes, RAWO presence and birch cover showed a different relation, i.e. when increasing the probability of the presence of damage decreased (Table 3). For the other variables, such as moose density, roads densities, or snow depth there were no changes compared to models with either wolf presence or wolf coverage.

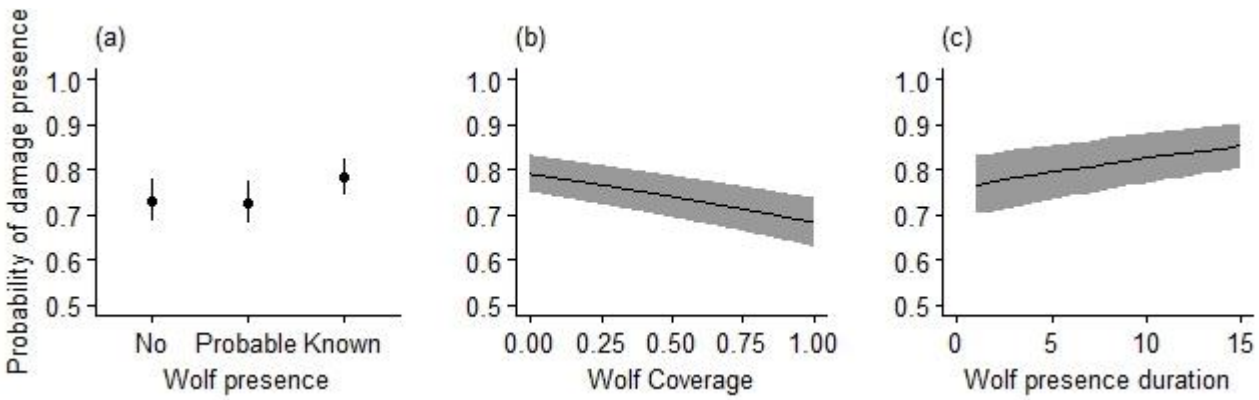


Figure 6. Probability of damage presence in relation to (a) wolf presence at the square (n = 2900), (b) wolf coverage of the local units (n = 2900) and (c) wolf presence duration in years (n = 1486), in the 6 counties of study from 2015 to 2017. The dots and lines indicate the fitted values, with associated Standard Errors, from the full model averaged estimates (Table 3). Moose harvest density, RAWO presence, Spruce and birch cover, snow depth, and road densities are held constant at average.

2.2. Damage level

Wolf presence models (at the square level)

The damage level of Scots pines was not affected by the wolf presence at the local scale (Table 4). All the other variables were still included in the best models, even if medium and large road densities showed relative variable importance values that were weaker ($RVI_{medium\ road}$ = 0.45 and $RVI_{large\ road}$ = 0.34; Table 4). Again, the damage level increased with the increase of moose density, spruce and birch cover at the local scale on Scots pines in young forests. In contrast,

RAWO presence decreased the damage level as did snow depth. For the road densities, the increase of small, medium and large road densities increased the damage level (Table 4).

Wolf coverage models (at the moose management units)

For the wolf coverage at the local scale, the damage level decreased when the coverage increased (-0.003 ± 0.02 SE; Figure 7a), but this variable was only present in one of the 6 highest ranked models (RVI = 0.13; Table 4). In the highest ranked models, almost all variables were of strong importance, except the medium and large roads densities ($RVI_{medium\ road}$ = 0.40 and $RVI_{large\ road}$ = 0.30; Table 4). For the other variables, moose density, forage availability variables, snow depth and roads densities showed the same effect sign as models using wolf presence index (Table 4).

Wolf duration models (at the square level)

In models with wolf duration, which was present in all the highest ranked models (RVI = 1; Table 4), the damage level was higher in areas with longtime wolf established territory (0.02 ± 0.004 SE; Figure 7c). Compared to previous wolf indexes models, the highest ranked models with wolf duration, showed that all the variables were of great importance, even medium and large road densities ($RVI_{medium\ road}$ = 0.62 and $RVI_{large\ road}$ = 1; Table 4). Moose density as well as RAWO presence, spruce and birch cover, snow depth and all the roads densities had the same pattern than in the models with wolf coverage index (Table 4).

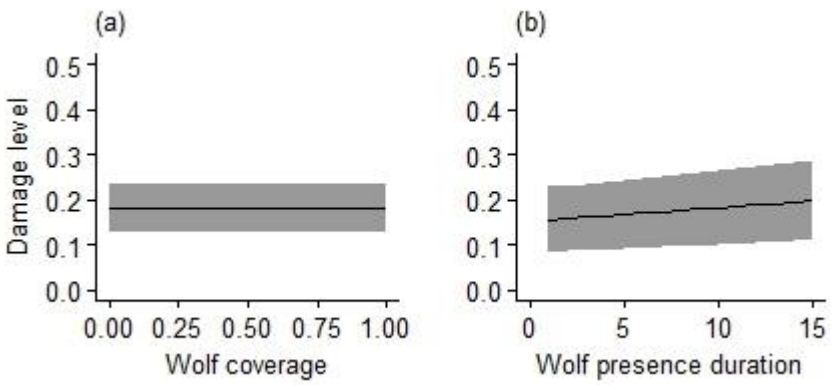


Figure 7. Damage level on Scots pine in relation to (a) wolf coverage of the local units (n = 1655) and (b) wolf presence duration in years (n = 873), in the 6 counties of study from 2015 to 2017. The lines indicate the fitted values, with associated Standard Errors, from the full model averaged estimates (Table 4). Moose harvest density, RAWO presence, Spruce and birch cover, snow depth, and road densities are held constant at average.

Table 1. Highest ranked candidate models (within ΔAIC ≤ 2, grey background) and intercept model relating the presence of moose damage on Scots pines to wolf presence (P: Probable wolf presence, K: Known wolf presence), wolf coverage, moose density, RAWO presence, spruce and birch cover, snow depth, small, medium and large road densities, at the regional scale. Year and regional units ID were used as random factors to account for year effects and repeated measure and spatial autocorrelation of squares. For each candidate model, degrees of freedom (df), AIC, the difference in AIC relative to the highest-ranked model (ΔAIC), and AIC weight (wi) are shown. For each variable, full model-averaged estimates (β) with standard error (SE), and Relative Variable Importance (RVI) are shown. Moose damage on Scots pines were surveyed in the 6 counties (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) in Sweden from 2015 to 2017. (Wolf presence and coverage: n = 2900, 512 models; Wolf duration: n = 1436, 512 models).

	Intercept	Wolf index		Moose density	RAWO presence	Cover		Snow depth	Road density			df	AIC	ΔAIC	wi
						Spruce	Birch		Small	Medium	Large				
Wolf Presence		X		X		X	X	X	X	X		11	30204.0		0.42
		X		X	X	X	X	X	X	X		12	30204.9	0.93	0.26
		X		X		X	X	X	X			10	30205.8	1.82	0.17
		X		X		X	X	X	X	X	X	12	30206.0	1.99	0.15
β	1.69	P = -0.06	K = 0.19	-2.55	0.02	-1.10	0.24	0.03	-0.15	-0.06	-0.001				
SE	0.26	0.04	0.05	0.86	0.05	0.09	0.08	0.006	0.02	0.05	0.03				
RVI		1.00		1.00	0.26	1.00	1.00	1.00	1.00	0.83	0.15				
Wolf Coverage				X		X	X	X	X	X		9	30231.5		0.27
				X	X	X	X	X	X	X		10	30231.9	0.34	0.22
		X		X		X	X	X	X	X		10	30232.5	0.98	0.16
		X		X	X	X	X	X	X	X		11	30232.7	1.19	0.15
				X		X	X	X	X	X	X	10	30233.4	1.85	0.11
				X	X	X	X	X	X			9	30233.5	2.00	0.10
β	1.74	-0.04		-2.70	0.04	-1.09	0.24	0.03	-0.15	-0.07	-0.003				
SE	0.27	0.10		0.87	0.06	0.09	0.08	0.006	0.02	0.04	0.02				
RVI		0.31		1.00	0.47	1.00	1.00	1.00	1.00	0.90	0.10				
Intercept model	X											1	30534.9		
Wolf Duration		X			X	X	X	X	X	X	X	11	14717.1		0.45
		X		X	X	X	X	X	X	X	X	12	14718.8	1.69	0.20
		X			X	X		X	X	X	X	10	14719.0	1.84	0.18
		X			X	X	X	X		X	X	10	14719.1	1.93	0.17
β	1.01	0.04		-0.13	-0.27	-1.72	-0.18	0.08	-0.04	-0.20	-0.39				
SE	0.27	0.008		0.60	0.10	0.13	0.13	0.01	0.03	0.06	0.18				
RVI		1.00		0.19	1.00	1.00	0.82	1.00	0.83	1.00	1.00				
Intercept model	X											1	15011.0		

Table 2. Highest ranked candidate models (within ΔAIC ≤ 2, grey background) and intercept model relating the moose damage level on Scots pines to wolf (P: Probable wolf presence, K: Known wolf presence), wolf coverage, moose density, RAWO presence, spruce and birch cover, snow depth, small, medium and large road densities, at the regional scale. Year and regional units ID were used as random factors to account for year effects and repeated measure and spatial autocorrelation of squares. For each candidate model, degrees of freedom (df), AIC, the difference in AIC relative to the highest-ranked model (ΔAIC), and AIC weight (wi) are shown. For each variable, full model-averaged estimates (β) with standard error (SE), and Relative Variable Importance (RVI) are shown. Moose damage on Scots pines were surveyed in the 6 counties (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) in Sweden from 2015 to 2017. (Wolf presence and coverage: n = 1655, 512 models; Wolf duration: n = 873, 512 models).

	Intercept	Wolf index		Moose density	RAWO presence	Cover		Snow depth	Road density			df	AIC	ΔAIC	wi
						Spruce	Birch		Small	Medium	Large				
Wolf Presence		X		X	X	X	X	X		X	X	13	-38608.5		0.37
		X		X	X	X	X	X		X		12	-38607.7	0.78	0.25
				X	X	X	X	X		X	X	11	-38607.5	1.02	0.22
		X		X	X	X	X	X	X	X	X	14	-38607.0	1.53	0.17
β	-3.07	P = 0.02	K = -0.02	1.69	-0.27	2.09	1.36	-0.006	0.001	-0.04	0.04				
SE	0.22	0.02	0.02	0.39	0.03	0.05	0.04	0.002	0.004	0.02	0.04				
RVI		0.78		1.00	1.00	1.00	1.00	1.00	0.17	1.00	0.75				
Wolf Coverage		X		X	X	X	X	X		X	X	12	-38607.9		0.29
				X	X	X	X	X		X	X	11	-38607.5	0.43	0.23
		X		X	X	X	X	X		X		11	-38606.4	1.54	0.13
		X		X	X	X	X	X	X	X	X	13	-38606.3	1.63	0.13
				X	X	X	X	X	X	X	X	12	-38606.0	1.96	0.11
				X	X	X	X	X		X		10	-38605.9	1.97	0.11
β	-3.10	0.05		1.73	-0.27	2.09	1.36	-0.006	0.001	-0.04	0.04				
SE	0.23	0.06		0.39	0.03	0.05	0.04	0.002	0.004	0.02	0.04				
RVI		0.55		1.00	1.00	1.00	1.00	1.00	0.24	1.00	0.76				
Intercept model	X											1	-35351.0		
Wolf Duration				X	X	X	X	X	X	X	X	12	-22305.1		0.26
				X	X	X	X	X		X	X	11	-22305.0	0.14	0.24
					X	X	X	X		X	X	10	-22304.7	0.40	0.21
					X	X	X	X	X	X	X	11	-22304.7	0.48	0.20
		X		X	X	X	X	X	X	X	X	13	-22303.2	1.95	0.10
β	-2.71	-6.28e-5		0.50	-0.19	2.16	1.21	-0.01	0.009	-0.06	-0.22				
SE	0.24	9.56e-4		0.60	0.04	0.06	0.05	0.003	0.01	0.03	0.08				
RVI		0.10		0.59	1.00	1.00	1.00	1.00	0.55	1.00	1.00				
Intercept model	X											1	-20372.0		

Table 3. Highest ranked candidate models (within ΔAIC ≤ 2, grey background) and intercept model relating the presence of moose damage on Scots pines to wolf presence (P: Probable wolf presence, K: Known wolf presence), wolf coverage, moose density, RAWO presence, spruce and birch cover, snow depth, small, medium and large road densities, at the local scale. Year and local units ID were used as random factors to account for year effects and repeated measure and spatial autocorrelation of squares. For each candidate model, degrees of freedom (df), AIC, the difference in AIC relative to the highest-ranked model (ΔAIC), and AIC weight (wi) are shown. For each variable, full model-averaged estimates (β) with standard error (SE), and Relative Variable Importance (RVI) are shown. Moose damage on Scots pines were surveyed in the 6 counties (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) in Sweden from 2015 to 2017. (Wolf presence and coverage: n = 2900, 512 models; Wolf duration: n = 1436, 512 models).

	Intercept	Wolf index		Moose density	RAWO presence	Cover		Snow depth	Road density			df	AIC	ΔAIC	wi
						Spruce	Birch		Small	Medium	Large				
Wolf Presence		X		X		X	X	X	X	X		11	27085.8		0.37
		X		X	X	X	X	X	X	X		12	27086.6	0.81	0.25
		X		X		X		X	X	X		10	27086.9	1.11	0.21
		X		X		X	X	X	X	X	X	12	27087.3	1.56	0.17
β	0.69	P = -0.02	K = 0.29	1.76	0.02	-1.49	0.13	0.05	-0.20	-0.21	0.009				
SE	0.28	0.06	0.07	0.36	0.05	0.11	0.10	0.009	0.02	0.05	0.04				
RVI		1.00		1.00	0.25	1.00	0.79	1.00	1.00	1.00	0.17				
Wolf Coverage		X		X	X	X	X	X	X	X		11	27091.6		0.50
		X		X		X	X	X	X	X		10	27092.6	1.06	0.30
		X		X	X	X	X	X	X	X	X	12	27093.4	1.81	0.20
β	0.90	-0.58		1.70	0.09	-1.47	0.19	0.05	-0.20	-0.22	0.007				
SE	0.29	0.11		0.36	0.08	0.11	0.09	0.009	0.02	0.05	0.04				
RVI		1.00		1.00	0.70	1.00	1.00	1.00	1.00	1.00	0.20				
Intercept model	X											1	27507.1		
Wolf Duration		X		X	X	X	X	X	X	X		11	13089.6		0.60
		X		X	X	X	X	X	X	X	X	12	13090.4	0.82	0.40
β	0.70	0.04		2.29	-0.25	-2.04	-0.26	0.08	-0.06	-0.35	0.11				
SE	0.43	0.01		0.60	0.11	0.15	0.13	0.01	0.03	0.07	0.20				
RVI		1.00		1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.40				
Intercept model	X											1	13365.8		

Table 4. Highest ranked candidate models (within ΔAIC ≤ 2, grey background) and intercept model relating the moose damage level on Scots pines to wolf presence (P: Probable wolf presence, K: Known wolf presence), wolf coverage, moose density, RAWO presence, spruce and birch cover, snow depth, small, medium and large road densities, at the local scale. Year and local units ID were used as random factors to account for year effects and repeated measure and spatial autocorrelation of squares. For each candidate model, degrees of freedom (df), AIC, the difference in AIC relative to the highest-ranked model (ΔAIC), and AIC weight (wi) are shown. For each variable, full model-averaged estimates (β) with standard error (SE), and Relative Variable Importance (RVI) are shown. Moose damage on Scots pines were surveyed in the 6 counties (Dalarna, Gävleborg, Värmland, Västmanland, Västra Götaland and Örebro) in Sweden from 2015 to 2017. (Wolf presence and coverage: n = 1655, 512 models; Wolf duration: n = 873, 512 models).

	Intercept	Wolf index	Moose density	RAWO presence	Cover		Snow depth	Road density			df	AIC	ΔAIC	wi
					Spruce	Birch		Small	Medium	Large				
Wolf Presence			X	X	X	X	X	X			10	-42777.7		0.36
			X	X	X	X	X	X	X		11	-42777.3	0.38	0.30
			X	X	X	X	X	X		X	11	-42776.4	1.32	0.19
			X	X	X	X	X	X	X	X	12	-42776.1	1.64	0.16
β	-2.79		0.75	-0.30	2.34	1.50	-0.007	-0.03	-0.01	-0.009				
SE	0.18		0.15	0.03	0.05	0.04	0.003	0.008	0.02	0.02				
RVI		-	1.00	1.00	1.00	1.00	1.00	1.00	0.45	0.34				
Wolf Coverage			X	X	X	X	X	X			10	-42777.7		0.31
			X	X	X	X	X	X	X		11	-42777.3	0.38	0.26
			X	X	X	X	X	X		X	11	-42776.4	1.32	0.16
			X	X	X	X	X	X	X	X	12	-42776.1	1.64	0.14
		X	X	X	X	X	X	X			11	-42775.9	1.76	0.13
β	-2.79	-0.003	0.75	-0.30	2.34	1.50	-0.007	-0.03	-0.01	-0.009				
SE	0.18	0.02	0.15	0.03	0.05	0.04	0.003	0.008	0.02	0.02				
RVI		0.13	1.00	1.00	1.00	1.00	1.00	1.00	0.40	0.30				
Intercept model	X										1	-39248.1		
Wolf Duration		X	X	X	X	X	X	X	X	X	13	-23814.2		0.62
		X	X	X	X	X	X	X		X	12	-23813.3	0.96	0.38
β	-3.00	0.02	1.33	-0.23	2.45	1.25	-0.01	-0.03	-0.03	-0.16				
SE	0.19	0.004	0.22	0.04	0.06	0.05	0.004	0.01	0.04	0.08				
RVI		1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.62	1.00				
Intercept model	X										1	-21752.9		

DISCUSSION

Wolf indexes were often among the important variables explaining the variation of damage presence and level, but other variables such as moose harvest density, foraging availability and snow depth were almost always more important explaining the variation with higher estimates and RVI values, especially in models at the local scale. Also, even if they were in the highest ranked models, wolf indexes showed estimates with standard errors overlapping zero for models made at the regional scale, which mean that they did not lead to a significant variation of the damage presence or level. Moreover, the sample size for the analyses was large, which can sometimes lead to the inclusion of variables in model selection that may only explain a small amount of the variation observed. Moreover, even though some variables may be considered important in a statistical sense these may not be considered biologically relevant. Indeed, even if significant, wolf indexes sometimes had a small effect on the response variable. For example, at the local scale, for the wolf presence index, the probability of the presence of damage was 0.73 when no wolves were present in the area and 0.78 for areas with known wolf presence.

1. A matter of scale?

Results between scales varied for some of the variables. For the damage presence models, wolf indexes showed the same pattern between regional and local scale, by increasing the probability of damage on Scots pines with known presence and increasing duration of wolf presence, and by decreasing the probability of damage with increasing wolf coverage at both the regional and local scale. In contrast, the relationship between moose density and damage was different between regional and local models. When using moose density at the regional scale, a higher moose density decreased the probability of damage, but when using moose density at the local scale, a higher moose density increased the probability of damage on Scots pines. This might be due to the fact that at the regional scale the data for moose density is too rough and thus not accurate for representing the actual moose density at the square level.

At the regional scale, wolf indexes showed an opposite relation such as if the probability of damage presence increased with a certain wolf index, the damage level decreased with other indexes. At the local scale, the pattern was the same between damage presence probability or damage level whatever was the wolf indexes. Only the wolf presence index shows no effect on damage level. Important, wolf presence and wolf coverage indexes represented different spatial scales. Whereas wolf presence was representing the presence or absence of wolves at the square level, wolf coverage represented either the regional or local scale, giving information more about the presence of wolves over a larger area. More precisely, wolf coverage represented the most probable areas of wolf presence, which may be different from the actual wolf presence areas. The

results of this study may indicate that the regional scale was too large to be able to distinguish any effects of wolf establishment on moose browsing behaviour and thus on damage on Scots pines.

2. Moose density and environmental factors

2.1. Moose density

If the focus is put on the local scale, this study results showed that the presence and level of damage on Scots pines increased with an increasing moose density. A lot of studies have shown a positive correlation between ungulate population density and damage level (Gill, 1992; Hörnberg, 1995; Faber & Edenius, 1998; Augustine & Decalesta, 2003; Côté *et al.*, 2004). Also, studies in Sweden have demonstrated that moose density is highly associated with moose browsing damage and when moose density increases, the damage on Scots pines increases as well (Andrén & Angelstam, 1993; Månsson, 2009; Bergqvist *et al.*, 2014). But if moose density is an important factor affecting damage in Scots pines young forests (Hörnberg, 1995; Bergqvist *et al.*, 2014), so are also other factors which can also influence the moose damage (Hörnberg, 2001).

2.2. Forage availability

In the present study, forage availability (of other species than pine), here assessed by the RAWO presence and by the cover of spruce and birch, showed to change the probability of the presence of damage as well as the damage level. For the presence of damage, RAWO presence and birch cover increased the probability to have damage on young Scots pines plantations. At the opposite, RAWO presence decreased the damage level on Scots pine. In contrast, the spruce cover had a negative relationship with damage presence, but like birch cover increased the level of damage. These results show that moose select for deciduous species, but their presence decreases the damage level on Scots pine, since moose may preferably eat the deciduous species. Spruce, on the contrary, push away moose from the area where they are dominant, and since they are less selected over pine, the damage increase on pines in an area where spruce cover is large. But in the Bergqvist *et al.* (2014) study, the increase of both rowan, aspen, willow and birch cover increases the proportion of damage to Scots pines. According to other studies, moose select for these deciduous species when there is some in the stand, but if there is not, they eat less selected species, which are mainly birch and pine (Andrén & Angelstam, 1993; Månsson *et al.*, 2007; Månsson, 2009). Then, if spruce and birch cover is important, meaning a low forage quality, moose have to increase their food intake and thus it increases the damage level on young pines (Månsson, 2009). However, this study focuses in damage done during the winter, and at that time the deciduous species do not have leaves. Also, moose may create more damage on Scots pine during winter in an area that are richer in deciduous species during the summer.

2.3. Snow depth

Some other factors can also affect the forage availability, such as snow depth. Snow depth in this study also affects the presence and level of moose damage on Scots pines. As it was hypothesized that the damage presence and level should be higher at high snow depth, the results showed the opposite relationship for the damage level. According to other studies (White *et al.*, 2003; Ripple & Beschta, 2004; Månsson, 2009), the results should be the opposite. The more there is snow-days with more than 10 cm, the more moose select for young forest (<30 years) instead of old forest (>30 years) and this may increase the damage in Scots pines plantations (Månsson, 2009). In this study, it looks like moose indeed select for young forests when there is a lot of snow, as there is more probability to find damage there, but the damage are less intensive in these areas.

2.4. Road densities

Roads also have an impact on damage presence probability and damage level. As though, a high density of small and also medium roads in the area induced a lower damage presence and level. Thus, it indicates that moose avoid foraging in an area where there is a higher probability to encounter human activities, like hunting and forestry near small roads, and also avoid collisions on both small and medium roads. For the large road density, its increase leads to an increase in the probability of the presence of damage, and to a decrease of the damage level. This can indicate that moose may be attracted to an area where the large road density is high, but do not create a lot of damage here. A cause can be that the higher sodium concentration in the vegetation near large roads due to de-icing salt used in the winter attracts moose there (Ball & Dahlgren, 2002; Laurian *et al.*, 2008). Also, large roads are usually fenced in Sweden, and this can affect the migration of moose leading to an aggregation of moose along fenced roads (Ball & Dahlgren, 2002). But the fact that they do not create a lot of damage there may also suggest that because of traffic noise, they have to be more alert to detect predators (Laurian *et al.*, 2008).

3. The effect of wolf establishment

Predators can affect prey populations both directly and indirectly by inducing changes in their behaviours. Direct predation normally leads to a decrease of the moose damage in the areas with wolf presence, as shown by several studies on wolf-ungulate interactions in North America (Berger *et al.*, 2001; Ripple & Beschta, 2004). Furthermore, wolves may affect moose behaviours in a way that increases their foraging activities or food intake, habitat selection, grouping tendencies or movement rate (Creel & Christianson, 2008), as it been shown in study on elk (*Cervus elaphus*) in Yellowstone, where the reintroduction of wolves re-established a landscape of fear (Laundré *et al.*, 2001; Hernández & Laundré, 2005).

This study predicted that the wolf presence should lead to a decrease in the probability of presence and level of damage to Scots pines. However, the results showed the opposite relation,

where the moose damage presence and level are higher within wolf areas. The same type of contradictory result was observed with the number of years since a wolf territory is established, the moose browsing damage are more likely to occur in wolf territories that have been established during a relatively long time period. In contrast, at the landscape level (regional or local scale), increasing wolf coverage resulted in a reduction of the probability of the presence of damage, but no change for the damage level. However, this index was not an important variable in the highest ranked models.

In this study, damage presence probability is higher in presence of wolf which can mean that moose try to seek cover inside young pine forests which are dense compared to other forests (Kie, 1999), but the fact that there is a predation risk can change their vigilance behaviour, meaning that they do not create high damage because they have to be vigilant. In a study on elk in Montana, they did not show that there were any changes in the foraging-vigilance trade-off when there is a predation risk by wolf (Winnie & Creel, 2007). Others studies show a change in the elk foraging behaviour and vigilance because, in areas with wolves, individuals spend more time scanning their environment, especially females with calves (Laundré *et al.*, 2001; Childress & Lung, 2003).

Apart from wolf predation-risk, this foraging-vigilance trade-off can be affected by the size of prey groups (Childress & Lung, 2003). Indeed, grouping behaviour can be also be affected by the predation risk. A study from Creel & Winnie (2005) on elk shows that with predation risk, there is a change of the herd size. Indeed, kills happened more often in open landscape than in forest, and thus they gathered more in open habitats than in close ones. But in Creel & Winnie (2005) study, they found that under predation risk elk disaggregate, as it is better to be solitary to have less probability to be detected by a predator. Male elk show bigger herd size under wolf predation risk (Winnie & Creel, 2007). The same pattern was noticed in Sweden for male moose that formed larger groups in response to wolf presence (Månsson *et al.*, 2017). At the opposite, females elk with calves show a reduction of their herd size when wolves are around (Winnie & Creel, 2007). This can be explained by the fact that females with calves are more vulnerable to predation risks (Laundré *et al.*, 2001; Sand *et al.*, 2005, 2008), they adapt their behaviour by hiding and then decrease group size, especially in forest landscape. But in Sweden, there was no evidence that wolves can change the grouping behaviour of female moose with calves (Månsson *et al.*, 2017).

Predation risk can also alter the habitat selection of prey species. Creel *et al.* (2005) show that in presence of predators, elk use more coniferous forests than open grasslands. Thus, it might explain why moose can induce more damage in forest in presence of wolves. But, here again, in Sweden, nothing was found to confirm that wolves affect moose habitat selection and thus induce changes of perception of predation risk in moose (Nicholson *et al.*, 2014).

In some studies, the change in prey behaviour has been rapid in response to colonisation of large carnivores. For example, for the vigilance behaviour, elk females with calves increased only one year after the reintroduction of wolves in the area and then stabilized (Laundré *et al.*, 2001).

4. Direct predation and predation risk of humans versus predators

One other reason that can create this study results is that Sweden is a country where moose hunting is very important, as it represents 90% of the moose mortality and caused more than 50% of the mortality even in areas where wolves were established (Wikenros *et al.*, 2010; Sand *et al.*, 2012). Moreover, hunting risk may be more predictable temporally and spatially compared to the predation risk from a non-human predator. In the study of Proffitt *et al.* (2009), even if elk respond the same way from wolf-predation risk and human-predation risk, the level of the response was higher towards humans. In another study, it was found that the fear from humans was higher than the fear from other causes, like predators (Ciuti *et al.*, 2012). In the same study, even if the risk of human predation was low, elk still reacted towards it. For example, elk were more likely to respond towards hikers than bikers because they associated them to hunters. Another study looking at the level of stress in both elk and roe deer (*Capreolus capreolus*) show that they experienced more stress in area dominated by human activities (hunting, roads) than under the predation risk of predators (Zbyryt *et al.*, 2018). Also, the decrease of fitness observed following antipredator behaviours are very costly and can thus affect population dynamics with the same intensity that direct predation (Creel & Christianson, 2008).

Therefore, additional studies are needed to assess the effect of wolf and hunting direct predation on moose population to help to put in place management plans to handle moose-forestry conflicts. Maybe increase the disturbances even non-lethal could affect moose behaviours, especially foraging-vigilance trade-off and then lead directly and/or indirectly by a decrease of their fitness, to a decrease of damage.

CONCLUSION

This study does not bring any support towards the fact that wolf establishment can mitigate the moose-forestry conflict in Sweden. Expectations were orientated towards a decrease of the moose browsing damage on Scots pine plantations following wolf establishment in Sweden. But this is not the case, according to this study results and also another study done in Sweden (van Beeck Calkoen *et al.*, 2018). Moose population density as well as other environmental factors such as forage availability, human activities and/or forest management also affect the damage level, likely more than direct predation or predation risk from wolves. One solution is to increase moose harvest, especially within areas where there is a high moose density and where the stands are more vulnerable, according to the habitat characteristics.

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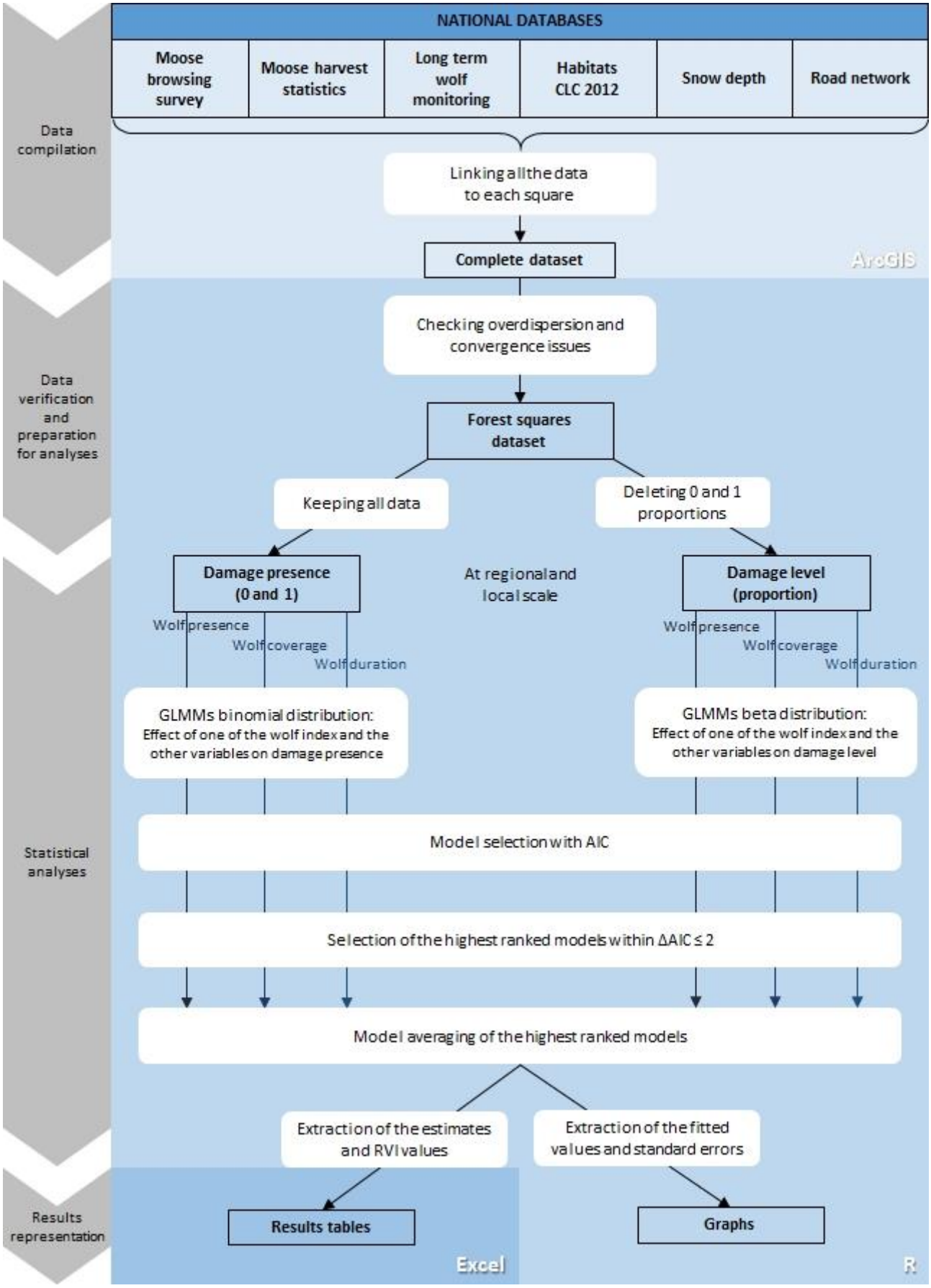
APPENDICES

Appendix 1. Pipeline analyse of the data compilation and analyses with the different software used.



Appendix 2. Script used for the analyses using R software.

```
##############################################################################
#                           SCRIPT  Wolf/Moose/Forest                        #
##############################################################################

rm(list=ls()) # clear R environment

# Set the working directory
setwd("~/Master/Master 2/Master thesis/Statistics/Final Script")

# Load the packages
library(lme4) # Package used to run glmer function
library(MuMIn) # Package to run dredge function
library(glmmTMB) # Package to run glmTMB function allowing to do beta
regression
library(lmerTest) # Package to get more details in the summary output of glmer
library(fitdistrplus) # Package to identify the best distribution according to
the data
library(ggplot2) # Package to be able to do graphs
library(gridExtra) # Package to be able to arrange several graphs on the same
page
library(readr) # Package to be able to import csv dataset

# Loading the dataset
Dataset_WMF <- read_delim("Dataset_WMF.csv", ";", escape_double = FALSE,
      col_types = cols(Damage_Pres = col_integer(), MainHabitat =
      col_factor(levels = c("Forests", "ArableLands", "Open",
      "ContinentalWaters", "Grasslands", "GreenUrban", "Heterogeneous",
      "IndustrialCommercial", "Marshes", "Sea", "Urban")), Year =
      col_factor(levels = c("2015","2016","2017")), Wolf_Presence =
      col_factor(levels = c("0","1", "2"))), locale = locale(decimal_mark =
      ","), na = "NA", trim_ws = TRUE)

head(Dataset_WMF) # Showing the columns name of the dataset
summary(Dataset_WMF) # Showing a summary of the dataset

############################ CHECKING CORRELATIONS ############################

#### Correlation between RAWO variables ####
cor.test( ~ RAWO_Compet + RAWO_Presence,
          data=Dataset_WMF,
          method = "spearman",
          continuity = FALSE,
          conf.level = 0.95)
# Significant and highly correlated -> rho = -0.52
# => Keep only RAWO Presence!

#### Correlation between Road densities ####
cor.test( ~ MediumRoads_Dens + SmallRoads_Dens,
          data=Dataset_WMF,
          method = "spearman",
          continuity = FALSE,
          conf.level = 0.95)
# Significant but poorly correlated -> rho = 0.08

cor.test( ~ MediumRoads_Dens + LargeRoads_Dens,
          data=Dataset_WMF,
          method = "spearman",
          continuity = FALSE,
          conf.level = 0.95)
# Significant but poorly correlated -> rho = 0.04

cor.test( ~ LargeRoads_Dens + SmallRoads_Dens,
          data=Dataset_WMF,
          method = "spearman",
          continuity = FALSE,
          conf.level = 0.95)
# Significant but poorly correlated -> rho = 0.12
# => Low correlation between roads density variables
# => Keep all of them!
```

```
#### Spruce and Birch cover ####
cor.test( ~ Spruce_Cover + Birch_Cover,
          data=Dataset_WMF,
          method = "spearman",
          continuity = FALSE,
          conf.level = 0.95)
# Significant but poorly correlated -> rho = -0.09
# => Keep both of them!

#### RAWO_Presence & other tree cover ####
cor.test( ~ RAWO_Presence + OtherTree_Cover,
          data=Dataset_WMF,
          method = "spearman",
          continuity = FALSE,
          conf.level = 0.95)
# Significant but poorly correlated -> rho = -0.42
# => Keep both of them!

############################## DATASETS CREATION ##############################

plot(Dataset_WMF$MainHabitat) # Plotting the main habitat for each square
# => Not balanced, so I will only focus on forested habitats

#### Forests ####
ForestSq = Dataset_WMF[Dataset_WMF$MainHabitat == "Forests",] # Creating the
dataset with only squares present in the forested habitats
# N = 2900

## Proportion ##
Forest_Prop = ForestSq[ForestSq$Damage_Prop!=0,] # Removing values of 0 for
Damage proportion in the dataset
Forest_Prop = Forest_Prop[Forest_Prop$Damage_Prop!=1,] # Removing values of 1
for Damage proportion in the dataset
# N = 1655
hist(Forest_Prop$Damage_Prop)
# Verifying if the beta distribution fit the data the best
fit_b <- fitdist(Forest_Prop$Damage_Prop,"beta")
plot(fit_b)

## Duration ##
Forest_Duration = ForestSq[ForestSq$WolfPoly_Duration!=0,] # Removing the
squares that were never within a wolf territory
# N = 1436
Forest_Duration_Prop = Forest_Duration[Forest_Duration$Damage_Prop!=0,]
Forest_Duration_Prop =
Forest_Duration_Prop[Forest_Duration_Prop$Damage_Prop!=1,]
# N = 873

### Beta family ###
# Script allowing to use the beta distribution in glmmTMB function
beta_family <- function(link="logit") {
  return(list(family="beta",link=link,
              variance=function(mu,phi) {
                mu*(1-mu)/(1+phi)
              },
              initialize=expression({
                if (any(y <= 0 | y >= 1))
                  stop("y values must be 0 < y < 1")
              }))}

################################## FORESTS ##################################

##################################### AFO #####################################

###### Presence / Absence of damage ######

#### Wolf presence ####
# GLMMS with binomial distribution, 2 random factors and 1 variable as weight
Pres_AFO_WP <- glmer(Damage_Pres ~ Wolf_Presence + RAWO_Presence + SnowDepth_cm
+ AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens + LargeRoads_Dens +
Spruce_Cover + Birch_Cover + (1|Year) + (1|AFO_ID), weights=Plot_Inv, data =
ForestSq, na.action=na.fail, family = binomial(link = "logit"))
```

```
# Graphic representations of the residuals to know if they follow the binomial
distribution
qqnorm(residuals(Pres_AFO_WP))
hist(residuals(Pres_AFO_WP))
# Summary of the model
summary(Pres_AFO_WP)
Generalized linear mixed model fit by maximum likelihood (Laplace
Approximation) ['glmerMod']
 Family: binomial  ( logit )
Formula: Damage_Pres ~ Wolf_Presence + RAWO_Presence + SnowDepth_cm +
    AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens + LargeRoads_Dens +
    Spruce_Cover + Birch_Cover + (1 | Year) + (1 | AFO_ID)
   Data: ForestSq
Weights: Plot_Inv

     AIC      BIC   logLik deviance df.resid
 30206.9  30284.5 -15090.4  30180.9     2887

Scaled residuals:
    Min      1Q  Median      3Q     Max
-11.963  -2.668   1.053   1.929   9.447

Random effects:
 Groups Name        Variance Std.Dev.
 AFO_ID (Intercept) 0.531010 0.72870
 Year   (Intercept) 0.005379 0.07334
Number of obs: 2900, groups:  AFO_ID, 61; Year, 3

Fixed effects: # Give the relationship of the different variable with the
response variable
                  Estimate Std. Error z value Pr(>|z|)
(Intercept)       1.646622   0.262663   6.269 3.63e-10 ***
Wolf_Presence1   -0.067357   0.043839  -1.536 0.124430
Wolf_Presence2    0.188769   0.054353   3.473 0.000515 ***
RAWO_Presence     0.063813   0.061599   1.036 0.300236
SnowDepth_cm      0.031961   0.006341   5.040 4.65e-07 ***
AFO_MooseDens    -2.549709   0.863195  -2.954 0.003139 **
SmallRoads_Dens  -0.145082   0.016853  -8.608  < 2e-16 ***
MediumRoads_Dens -0.072197   0.038779  -1.862 0.062640 .
LargeRoads_Dens  -0.004748   0.069104  -0.069 0.945228
Spruce_Cover     -1.080050   0.092974 -11.617  < 2e-16 ***
Birch_Cover       0.263134   0.077684   3.387 0.000706 ***
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Correlation of Fixed Effects:
            (Intr) Wlf_P1 Wlf_P2 RAWO_P SnwDp_ AFO_MD SmlR_D MdmR_D LrgR_D
Sprc_C
Wolf_Prsnc1 -0.068
Wolf_Prsnc2 -0.068  0.573
RAWO_Presnc -0.227 -0.088 -0.106
SnowDpth_cm -0.185 -0.069 -0.059 -0.016
AFO_MoosDns -0.843  0.042  0.053  0.005 -0.003
SmllRds_Dns -0.110 -0.033 -0.027  0.126 -0.009 -0.009
MedmRds_Dns -0.049 -0.003  0.005  0.088  0.030  0.002 -0.021
LargRds_Dns -0.044 -0.004  0.039  0.022  0.033  0.040 -0.115 -0.007
Spruce_Covr -0.200 -0.032 -0.041  0.253  0.059  0.012  0.068  0.033  0.039
Birch_Cover -0.234 -0.031 -0.023  0.372  0.083 -0.005  0.031  0.014 -0.001
0.367
convergence code: 0
Model failed to converge with max|grad| = 0.00157594 (tol = 0.001, component 1)

# Function to perform a model selection base on AIC values with the model
created above
dAFO_WP = dredge(Pres_AFO_WP, rank="AIC")
# Selection of the highest ranked models within a deltaAIC < or = to 2
subset(dAFO_WP, delta<=2)
Global model call: glmer(formula = Damage_Pres ~ Wolf_Presence + RAWO_Presence
+
    SnowDepth_cm + AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
    LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1 | Year) +
    (1 | AFO_ID), data = ForestSq, family = binomial(link = "logit"),
```

```
    weights = Plot_Inv, na.action = na.fail)
---
Model selection table
    (Int) AFO_MsD Brc_Cvr   LrR_Dns  MdR_Dns RAS_Prs SmR_Dns  SnD_cm Spr_Cvr
Wlf_Prs df
492 1.708  -2.552  0.2331           -0.07574         -0.1475 0.03209  -1.104
+ 11
508 1.646  -2.547  0.2631           -0.07221 0.06388 -0.1452 0.03198  -1.080
+ 12
484 1.693  -2.549  0.2304                            -0.1486 0.03248  -1.102
+ 10
496 1.709  -2.555  0.2332 -0.006345 -0.07572         -0.1473 0.03207  -1.104
+ 12
logLik     AIC    delta weight
-15090.98 30204.0492  0.00  0.416
-15090.45 30204.9508  0.93  0.262
-15092.89 30205.8484  1.82  0.168
-15090.98 30206.0496  1.99  0.154
Models ranked by AIC(x)
Random terms (all models):
‘1 | Year’, ‘1 | AFO_ID’
> subset(dAFO_WP, delta<=2)
Global model call: glmer(formula = Damage_Pres ~ Wolf_Presence + RAWO_Presence
+
    SnowDepth_cm + AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
    LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1 | Year) +
    (1 | AFO_ID), data = ForestSq, family = binomial(link = "logit"),
    weights = Plot_Inv, na.action = na.fail)
---
Model selection table
    (Int) AFO_MsD Brc_Cvr   LrR_Dns  MdR_Dns RAS_Prs SmR_Dns  SnD_cm Spr_Cvr
Wlf_Prs df    logLik     AIC
492 1.708  -2.552  0.2331           -0.07574         -0.1475 0.03209  -1.104
+ 11 -15090.98 30204.0
508 1.646  -2.547  0.2631           -0.07221 0.06388 -0.1452 0.03198  -1.080
+ 12 -15090.45 30204.9
484 1.693  -2.549  0.2304                            -0.1486 0.03248  -1.102
+ 10 -15092.89 30205.8
496 1.709  -2.555  0.2332 -0.006345 -0.07572         -0.1473 0.03207  -1.104
+ 12 -15090.98 30206.0
    delta weight
492  0.00  0.416
508  0.93  0.262
484  1.82  0.168
496  1.99  0.154
Models ranked by AIC(x)
Random terms (all models):
‘1 | Year’, ‘1 | AFO_ID’

# Model averaging of these highest ranked models
PresMA_AFO_WP = model.avg(get.models(dAFO_WP,subset=delta<=2))
# Summary of the averaged model
summary(PresMA_AFO_WP)
Call:
model.avg(object = get.models(dAFO_WP, subset = delta <= 2))
Component model call:
glmer(formula = Damage_Pres ~ <4 unique rhs>, data = ForestSq,
     family = binomial(link = "logit"), weights = Plot_Inv,
     na.action = na.fail)

Component models: # Show the highest ranked models used in this model
averaging, with AIC, deltaic and weight values
         df    logLik      AIC delta weight
1246789  11 -15090.98 30203.97  0.00   0.42
12456789 12 -15090.45 30204.89  0.93   0.26
126789   10 -15092.89 30205.79  1.82   0.17
12346789 12 -15090.98 30205.96  1.99   0.15
```

```
Term codes:
   AFO_MooseDens      Birch_Cover  LargeRoads_Dens MediumRoads_Dens
               1                2                3                4
   RAWO_Presence  SmallRoads_Dens     SnowDepth_cm     Spruce_Cover
               5                6                7                8
   Wolf_Presence
               9

Model-averaged coefficients:
(full average) # Give the coefficient for the ‘full’ average, that assumes that
a variable is included in every model, but in some models the corresponding
coefficient (and its respective variance) is set to zero
                   Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       1.6891908  0.2588005   0.2589079   6.524  < 2e-16
AFO_MooseDens    -2.5505746  0.8630207   0.8633824   2.954 0.003135
Birch_Cover       0.2405492  0.0748359   0.0748662   3.213 0.001313
MediumRoads_Dens -0.0621186  0.0449945   0.0450061   1.380 0.167517
SmallRoads_Dens  -0.1470331  0.0166966   0.0167036   8.802  < 2e-16
SnowDepth_cm      0.0321197  0.0063416   0.0063443   5.063    4e-07
Spruce_Cover     -1.0975032  0.0913201   0.0913579  12.013  < 2e-16
Wolf_Presence1   -0.0643485  0.0437512   0.0437695   1.470 0.141516
Wolf_Presence2    0.1936269  0.0541619   0.0541846   3.573 0.000352
RAWO_Presence     0.0167499  0.0422355   0.0422454   0.396 0.691743
LargeRoads_Dens  -0.0009761  0.0271924   0.0272038   0.036 0.971378

(Intercept)      ***
AFO_MooseDens    **
Birch_Cover      **
MediumRoads_Dens
SmallRoads_Dens  ***
SnowDepth_cm     ***
Spruce_Cover     ***
Wolf_Presence1
Wolf_Presence2   ***
RAWO_Presence
LargeRoads_Dens

(conditional average) # Give the coefficient for the ‘conditional’ average,
that only averages over the models where the parameter appears.
                  Estimate Std. Error Adjusted SE z value Pr(>|z|)
(Intercept)       1.689191   0.258801    0.258908   6.524  < 2e-16
AFO_MooseDens    -2.550575   0.863021    0.863382   2.954 0.003135
Birch_Cover       0.240549   0.074836    0.074866   3.213 0.001313
MediumRoads_Dens -0.074626   0.038714    0.038730   1.927 0.053999
SmallRoads_Dens  -0.147033   0.016697    0.016704   8.802  < 2e-16
SnowDepth_cm      0.032120   0.006342    0.006344   5.063    4e-07
Spruce_Cover     -1.097503   0.091320    0.091358  12.013  < 2e-16
Wolf_Presence1   -0.064349   0.043751    0.043769   1.470 0.141516
Wolf_Presence2    0.193627   0.054162    0.054185   3.573 0.000352
RAWO_Presence     0.063884   0.061583    0.061609   1.037 0.299766
LargeRoads_Dens  -0.006345   0.069086    0.069115   0.092 0.926851

(Intercept)      ***
AFO_MooseDens    **
Birch_Cover      **
MediumRoads_Dens .
SmallRoads_Dens  ***
SnowDepth_cm     ***
Spruce_Cover     ***
Wolf_Presence1
Wolf_Presence2   ***
RAWO_Presence
LargeRoads_Dens
---
Signif. codes:  0 ‘***’ 0.001 ‘**’ 0.01 ‘*’ 0.05 ‘.’ 0.1 ‘ ’ 1

Relative variable importance: # Give the RVI for variable according to their
presence and importance in the highest ranked models
```

```
                      AFO_MooseDens Birch_Cover SmallRoads_Dens
Importance:           1.00          1.00        1.00
N containing models:     4             4           4
                      SnowDepth_cm Spruce_Cover Wolf_Presence
Importance:           1.00         1.00         1.00
N containing models:     4            4            4
                      MediumRoads_Dens RAWO_Presence LargeRoads_Dens
Importance:           0.83             0.26          0.15
N containing models:     3                1             1

#### Wolf coverage ####
Pres_AFO_WC <- glmer(Damage_Pres ~ AFO_WOLF_cover + RAWO_Presence +
SnowDepth_cm + AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = ForestSq, family = binomial(link = "logit"),
na.action=na.fail)
qqnorm(residuals(Pres_AFO_WC))
hist(residuals(Pres_AFO_WC))
summary(Pres_AFO_WC)

dAFO_WC = dredge(Pres_AFO_WC, rank="AIC")
subset(dAFO_WC, delta<=2)
PresMA_AFO_WC = model.avg(get.models(dAFO_WC,subset=delta<=2))
summary(PresMA_AFO_WC)

Intercept_AFO_pres <- glmer(Damage_Pres ~ 1 + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = ForestSq, family = binomial(link = "logit"), na.action
= na.fail)
# Give the AIC values of the previous model
AIC(Intercept_AFO_pres)

#### Wolf Duration ####
Pres_AFO_WD <- glmer(Damage_Pres ~ WolfPoly_Duration + RAWO_Presence +
SnowDepth_cm + AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = Forest_Duration, na.action=na.fail, family =
binomial(link = "logit"))
qqnorm(residuals(Pres_AFO_WD))
hist(residuals(Pres_AFO_WD))
summary(Pres_AFO_WD)

dAFO_WD = dredge(Pres_AFO_WD, rank="AIC")
subset(dAFO_WD, delta<=2)
PresMA_AFO_WD = model.avg(get.models(dAFO_WD,subset=delta<=2))
summary(PresMA_AFO_WD)

Intercept_AFO_WD_pres <- glmer(Damage_Pres ~ 1 + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = Forest_Duration, na.action=na.fail, family =
binomial(link = "logit"))
AIC(Intercept_AFO_WD_pres)

###### Proportion of damage ######

#### Wolf Presence ####
# Utilisation of the function glmmTMB with beta distribution and 2 random
factors and 1 variable as a weight
Prop_AFO_WP <- glmmTMB(Damage_Prop ~ Wolf_Presence + RAWO_Presence +
SnowDepth_cm + AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = Forest_Prop, family = beta_family)
qqnorm(residuals(Prop_AFO_WP))
hist(residuals(Prop_AFO_WP))
summary(Prop_AFO_WP)

dAFO_WP_prop = dredge(Prop_AFO_WP, rank="AIC")
subset(dAFO_WP_prop, delta<=2)
PropMA_AFO_WP = model.avg(get.models(dAFO_WP_prop,subset=delta<=2),fit=T)
summary(PropMA_AFO_WP)

#### Wolf coverage ####
Prop_AFO_WC <- glmmTMB(Damage_Prop ~ AFO_WOLF_cover + RAWO_Presence +
SnowDepth_cm + AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
```

```
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = Forest_Prop, family = beta_family)
qqnorm(residuals(Prop_AFO_WC))
hist(residuals(Prop_AFO_WC))
summary(Prop_AFO_WC)

dAFO_WC_prop = dredge(Prop_AFO_WC, rank="AIC")
subset(dAFO_WC_prop, delta<=2)
PropMA_AFO_WC = model.avg(get.models(dAFO_WC_prop,subset=delta<=2))
summary(PropMA_AFO_WC)

Intercept_AFO_prop <- glmmTMB(Damage_Prop ~ 1 + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = Forest_Prop, family = beta_family)
AIC(Intercept_AFO_prop)

#### Wolf Duration ####
Prop_AFO_WD <- glmmTMB(Damage_Prop ~ WolfPoly_Duration + RAWO_Presence +
SnowDepth_cm + AFO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = Forest_Duration_Prop, family = beta_family)
qqnorm(residuals(Prop_AFO_WD))
hist(residuals(Prop_AFO_WD))
summary(Prop_AFO_WD)

dAFO_WD_prop = dredge(Prop_AFO_WD, rank = "AIC")
subset(dAFO_WD_prop, delta<=2)
PropMA_AFO_WD = model.avg(get.models(dAFO_WD_prop,subset=delta<=2))
summary(PropMA_AFO_WD)

Intercept_AFO_WD_prop <- glmmTMB(Damage_Prop ~ 1 + (1|Year) + (1|AFO_ID),
weights=Plot_Inv, data = Forest_Duration_Prop, family = beta_family)
AIC(Intercept_AFO_WD_prop)

##################################### AJO #####################################

###### Presence / Absence of damage ######

#### Wolf presence ####
Pres_AJO_WP <- glmer(Damage_Pres ~ Wolf_Presence + RAWO_Presence + SnowDepth_cm
+ AJO_MooseDens + SmallRoads_Dens + MediumRoads_Dens + LargeRoads_Dens +
Spruce_Cover + Birch_Cover + (1|Year) + (1|AJO_ID), weights=Plot_Inv, data =
ForestSq, na.action=na.fail, family = binomial(link = "logit"))
qqnorm(residuals(Pres_AJO_WP))
hist(residuals(Pres_AJO_WP))
summary(Pres_AJO_WP)

dAJO_WP = dredge(Pres_AJO_WP, rank="AIC")
subset(dAJO_WP, delta<=2)
PresMA_AJO_WP = model.avg(get.models(dAJO_WP,subset=delta<=2))
summary(PresMA_AJO_WP)

#### Wolf coverage ####
Pres_AJO_WC <- glmer(Damage_Pres ~ AJO_WOLF_cover + RAWO_Presence +
SnowDepth_cm + AJO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = ForestSq, family = binomial(link = "logit"),
na.action=na.fail)
qqnorm(residuals(Pres_AJO_WC))
hist(residuals(Pres_AJO_WC))
summary(Pres_AJO_WC)

dAJO_WC = dredge(Pres_AJO_WC, rank="AIC")
subset(dAJO_WC, delta<=2)
PresMA_AJO_WC = model.avg(get.models(dAJO_WC,subset=delta<=2))
summary(PresMA_AJO_WC)

Intercept_AJO_pres <- glmer(Damage_Pres ~ 1 + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = ForestSq, family = binomial(link = "logit"), na.action
= na.fail)
AIC(Intercept_AJO_pres)
```

```
#### Wolf Duration ####
Pres_AJO_WD <- glmer(Damage_Pres ~ WolfPoly_Duration + RAWO_Presence +
SnowDepth_cm + AJO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = Forest_Duration, na.action=na.fail, family =
binomial(link = "logit"))
qqnorm(residuals(Pres_AJO_WD))
hist(residuals(Pres_AJO_WD))
summary(Pres_AJO_WD)

dAJO_WD = dredge(Pres_AJO_WD, rank="AIC")
subset(dAJO_WD, delta<=2)
PresMA_AJO_WD = model.avg(get.models(dAJO_WD,subset=delta<=2))
summary(PresMA_AJO_WD)

Intercept_AJO_WD_pres <- glmer(Damage_Pres ~ 1 + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = Forest_Duration, na.action=na.fail, family =
binomial(link = "logit"))
AIC(Intercept_AJO_WD_pres)

###### Proportion of damage ######

#### Wolf Presence ####
Prop_AJO_WP <- glmmTMB(Damage_Prop ~ Wolf_Presence + RAWO_Presence +
SnowDepth_cm + AJO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = Forest_Prop, family = beta_family)
qqnorm(residuals(Prop_AJO_WP))
hist(residuals(Prop_AJO_WP))
summary(Prop_AJO_WP)
dAJO_WP_prop = dredge(Prop_AJO_WP, rank="AIC")
subset(dAJO_WP_prop, delta<=2)
PropMA_AJO_WP = model.avg(get.models(dAJO_WP_prop,subset=delta<=2),fit=T)
summary(PropMA_AJO_WP)

#### Wolf coverage ####
Prop_AJO_WC <- glmmTMB(Damage_Prop ~ AJO_WOLF_cover + RAWO_Presence +
SnowDepth_cm + AJO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = Forest_Prop, family = beta_family)
qqnorm(residuals(Prop_AJO_WC))
hist(residuals(Prop_AJO_WC))
summary(Prop_AJO_WC)

dAJO_WC_prop = dredge(Prop_AJO_WC, rank="AIC")
subset(dAJO_WC_prop, delta<=2)
PropMA_AJO_WC = model.avg(get.models(dAJO_WC_prop,subset=delta<=2))
summary(PropMA_AJO_WC)

Intercept_AJO_prop <- glmmTMB(Damage_Prop ~ 1 + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = Forest_Prop, family = beta_family)
AIC(Intercept_AJO_prop)

#### Wolf Duration ####
Prop_AJO_WD <- glmmTMB(Damage_Prop ~ WolfPoly_Duration + RAWO_Presence +
SnowDepth_cm + AJO_MooseDens + SmallRoads_Dens + MediumRoads_Dens +
LargeRoads_Dens + Spruce_Cover + Birch_Cover + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = Forest_Duration_Prop, family = beta_family)
qqnorm(residuals(Prop_AJO_WD))
hist(residuals(Prop_AJO_WD))
summary(Prop_AJO_WD)

dAJO_WD_prop = dredge(Prop_AJO_WD, rank = "AIC")
subset(dAJO_WD_prop, delta<=2)
PropMA_AJO_WD = model.avg(get.models(dAJO_WD_prop,subset=delta<=2))
summary(PropMA_AJO_WD)

Intercept_AJO_WD_prop <- glmmTMB(Damage_Prop ~ 1 + (1|Year) + (1|AJO_ID),
weights=Plot_Inv, data = Forest_Duration_Prop, family = beta_family)
AIC(Intercept_AJO_WD_prop)
```

```
################################### GRAPHS ###################################

#################################### AFO ######################################

###### Damage presence ######
# Create a new data frame with the fixed variable used in the analyse, with the
one of interest with all the different possibilities, and the other set to the
average
AFOwP = expand.grid(Wolf_Presence=c("0","1","2"),
RAWO_Presence=mean(ForestSq$RAWO_Presence),
SnowDepth_cm=mean(ForestSq$SnowDepth_cm),
AFO_MooseDens=mean(ForestSq$AFO_MooseDens),
SmallRoads_Dens=mean(ForestSq$SmallRoads_Dens),MediumRoads_Dens=mean(ForestSq$M
ediumRoads_Dens), LargeRoads_Dens=mean(ForestSq$LargeRoads_Dens),
Spruce_Cover=mean(ForestSq$Spruce_Cover),Birch_Cover=mean(ForestSq$Birch_Cover)
)
# Calculation of the prediction from the full model averaging coefficient using
the new data frame
AFOwPpred = predict(PresMA_AFO_WP, AFOwP, type="response", re.form=NA, se=T,
full=T)
# Extraction of the fitted and standard error values
AFOwP$fit = AFOwPpred$fit
AFOwP$se = AFOwPpred$se.fit

# Making the graph using ggplot function
AFOWolfPGraph <- ggplot() +
  scale_x_discrete(labels = c("No", "Probable", "Known")) + # Set the x scale
  ylim(0.5, 1) + # Set the y scale
  geom_point(data=AFOwP, aes(x=Wolf_Presence, y=fit), size=1.5) + # Display
fitted values
  geom_linerange(data=AFOwP, aes(x=Wolf_Presence, ymin=fit-se, ymax=fit+se)) +
# display standard errors values for each fitted values
  labs(y = "Probability of damage presence", x = "Wolf presence",size=18) +
# display the x and y axis labels
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10)) +
# Parameter for changing the theme of the graphs
  ggtitle("(a)")
# Display a title to the graph

AFOwC =
expand.grid(AFO_WOLF_cover=seq(min(Forest_Prop$AFO_WOLF_cover),max(Forest_Prop$
AFO_WOLF_cover),0.01), RAWO_Presence=mean(Forest_Prop$RAWO_Presence),
SnowDepth_cm=mean(Forest_Prop$SnowDepth_cm),
AFO_MooseDens=mean(Forest_Prop$AFO_MooseDens),
SmallRoads_Dens=mean(Forest_Prop$SmallRoads_Dens),MediumRoads_Dens=mean(Forest_
Prop$MediumRoads_Dens), LargeRoads_Dens=mean(Forest_Prop$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Prop$Spruce_Cover),Birch_Cover=mean(Forest_Prop$Birch_
Cover))
AFOwCpred = predict(PresMA_AFO_WC, AFOwC, type="response", re.form=NA, se=T,
full=T)
AFOwC$fit = AFOwCpred$fit
AFOwC$se = AFOwCpred$se.fit

AFOWolfCGraph <- ggplot() +
  scale_x_continuous(breaks=c(0,0.25,0.5,0.75,1) , limits=c(0,1)) +
  scale_y_continuous(limits=c(0.5,1)) +
  geom_ribbon(data=AFOwC, aes(x=AFO_WOLF_cover, ymin=fit-se, ymax=fit+se),
alpha=0.5) +
  geom_line(data=AFOwC, aes(x=AFO_WOLF_cover, y=fit)) +
  labs(y = "", x = "Wolf Coverage",size=10) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
```

```
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10)) +
  ggtitle("(b)")

AFOwDPres =
expand.grid(WolfPoly_Duration=seq(min(Forest_Duration$WolfPoly_Duration),max(Fo
rest_Duration$WolfPoly_Duration),1),
RAWO_Presence=mean(Forest_Duration$RAWO_Presence),
SnowDepth_cm=mean(Forest_Duration$SnowDepth_cm),
AFO_MooseDens=mean(Forest_Duration$AFO_MooseDens),
SmallRoads_Dens=mean(Forest_Duration$SmallRoads_Dens),MediumRoads_Dens=mean(For
est_Duration$MediumRoads_Dens),
LargeRoads_Dens=mean(Forest_Duration$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Duration$Spruce_Cover),Birch_Cover=mean(Forest_Duratio
n$Birch_Cover))
AFOwDPred = predict(PresMA_AFO_WD, AFOwDPres, re.form=NA, se=T,
type="response")
AFOwDPres$fit = AFOwDPred$fit
AFOwDPres$se = AFOwDPred$se.fit

AFOWolfDurationGraph <- ggplot() +
  scale_x_continuous(breaks=c(0,5,10,15) , limits=c(0,15)) +
  scale_y_continuous(limits=c(0.5,1)) +
  geom_ribbon(data=AFOwDPres, aes(x=WolfPoly_Duration, ymin=fit-se,
ymax=fit+se), alpha=0.5) +
  geom_line(data=AFOwDPres, aes(x=WolfPoly_Duration, y=fit)) +
  labs(y = "", x = "Wolf presence duration",size=18) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title = element_text(size=10)) +
  ggtitle("(c)")

# Arrange the 3 previous graphs together in the same plot
grid.arrange(AFOWolfPGraph, AFOWolfCGraph, AFOWolfDurationGraph, ncol=3)
# Output see Figure 4

###### Damage level ######
AFOwPProp = expand.grid(Wolf_Presence=levels(Forest_Prop$Wolf_Presence),
RAWO_Presence=mean(Forest_Prop$RAWO_Presence),
SnowDepth_cm=mean(Forest_Prop$SnowDepth_cm),
AFO_MooseDens=mean(Forest_Prop$AFO_MooseDens),
SmallRoads_Dens=mean(Forest_Prop$SmallRoads_Dens),MediumRoads_Dens=mean(Forest_
Prop$MediumRoads_Dens), LargeRoads_Dens=mean(Forest_Prop$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Prop$Spruce_Cover),Birch_Cover=mean(Forest_Prop$Birch_
Cover), Year=levels(Forest_Prop$Year), AFO_ID=levels(Forest_Prop$AFO_ID),
Plot_Inv=1)
AFOwPPropPred = predict(PropMA_AFO_WP, AFOwPProp, se.fit=T, type ="response")
AFOwPProp$fit = AFOwPPropPred$fit
AFOwPProp$se = AFOwPPropPred$se.fit
# Aggregate the fitted values so it doesn't take into account random factors
AFOwPPropagg <-
aggregate(list(fit=AFOwPProp$fit,se=AFOwPProp$se),by=list(Wolf_Presence=AFOwPPr
op$Wolf_Presence),mean)

AFOWolfPPropGraph <- ggplot() +
  scale_x_discrete(labels = c("No", "Probable", "Known")) +
  ylim(0, 0.5) +
  geom_point(data=AFOwPPropagg, aes(x=Wolf_Presence, y=fit), size=1.5) +
  geom_linerange(data=AFOwPPropagg, aes(x=Wolf_Presence, ymin=fit-se,
ymax=fit+se)) +
  labs(y = "Damage level", x = "Wolf presence",size=18) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
```

```
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10)) +
  ggtitle("(a)")

AFOwCProp = expand.grid(AFO_WOLF_cover=seq(0,1,0.05),
RAWO_Presence=mean(Forest_Prop$RAWO_Presence),
SnowDepth_cm=mean(Forest_Prop$SnowDepth_cm),
AFO_MooseDens=mean(Forest_Prop$AFO_MooseDens),
SmallRoads_Dens=mean(Forest_Prop$SmallRoads_Dens),MediumRoads_Dens=mean(Forest_
Prop$MediumRoads_Dens), LargeRoads_Dens=mean(Forest_Prop$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Prop$Spruce_Cover),Birch_Cover=mean(Forest_Prop$Birch_
Cover), Year=levels(Forest_Prop$Year), AFO_ID=levels(Forest_Prop$AFO_ID),
Plot_Inv=1)
AFOwCPropPred = predict(PropMA_AFO_WC, AFOwCProp, se.fit=T, type ="response")
AFOwCProp$fit = AFOwCPropPred$fit
AFOwCProp$se = AFOwCPropPred$se.fit
AFOwCPropagg <-
aggregate(list(fit=AFOwCProp$fit,se=AFOwCProp$se),by=list(AFO_WOLF_cover=AFOwCP
rop$AFO_WOLF_cover),mean)

AFOWolfCPropGraph <- ggplot() +
  xlim(0, 1) +
  ylim(0, 0.5) +
  geom_ribbon(data=AFOwCPropagg, aes(x=AFO_WOLF_cover, ymin=fit-se,
ymax=fit+se), alpha=0.5) +
  geom_line(data=AFOwCPropagg, aes(x=AFO_WOLF_cover, y=fit)) +
  labs(y = "", x = "Wolf coverage",size=18) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10)) +
  ggtitle("(b)")

AFOwDProp = expand.grid(WolfPoly_Duration=seq(1,15,1),
RAWO_Presence=mean(Forest_Prop$RAWO_Presence),
SnowDepth_cm=mean(Forest_Prop$SnowDepth_cm),
AFO_MooseDens=mean(Forest_Prop$AFO_MooseDens),
SmallRoads_Dens=mean(Forest_Prop$SmallRoads_Dens),MediumRoads_Dens=mean(Forest_
Prop$MediumRoads_Dens), LargeRoads_Dens=mean(Forest_Prop$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Prop$Spruce_Cover),Birch_Cover=mean(Forest_Prop$Birch_
Cover), Year=levels(Forest_Prop$Year), AFO_ID=levels(Forest_Prop$AFO_ID),
Plot_Inv=1)
AFOwDPropPred = predict(PropMA_AFO_WD, AFOwDProp, se.fit=T, type ="response")
AFOwDProp$fit = AFOwDPropPred$fit
AFOwDProp$se = AFOwDPropPred$se.fit
AFOwDPropagg <-
aggregate(list(fit=AFOwDProp$fit,se=AFOwDProp$se),by=list(WolfPoly_Duration=AFO
wDProp$WolfPoly_Duration),mean)

AFOWolfDPropGraph <- ggplot() +
  scale_x_continuous(breaks=c(0,5,10,15) , limits=c(0,15)) +
  scale_y_continuous(limits=c(0,0.5)) +
  geom_ribbon(data=AFOwDPropagg, aes(x=WolfPoly_Duration, ymin=fit-se,
ymax=fit+se), alpha=0.5) +
  geom_line(data=AFOwDPropagg, aes(x=WolfPoly_Duration, y=fit)) +
  labs(y = "", x = "Wolf presence duration",size=18) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
```

```
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10)) +
  ggtitle("(c)")

grid.arrange(AFOWolfPPropGraph, AFOWolfCPropGraph, AFOWolfDPropGraph, ncol=3)
# Output see Figure 5

##################################### AJO ####################################

###### Damage presence ######
AJOwP =
expand.grid(Wolf_Presence=c("0","1","2"),RAWO_Presence=mean(ForestSq$RAWO_Prese
nce),SnowDepth_cm=mean(ForestSq$SnowDepth_cm),AJO_MooseDens=mean(ForestSq$AJO_M
ooseDens),SmallRoads_Dens=mean(ForestSq$SmallRoads_Dens),MediumRoads_Dens=mean(
ForestSq$MediumRoads_Dens), LargeRoads_Dens=mean(ForestSq$LargeRoads_Dens),
Spruce_Cover=mean(ForestSq$Spruce_Cover),Birch_Cover=mean(ForestSq$Birch_Cover)
)
AJOwPpred = predict(PresMA_AJO_WP, AJOwP, type="response", re.form=NA, se=T,
full=T)
AJOwP$fit = AJOwPpred$fit
AJOwP$se = AJOwPpred$se.fit

AJOWolfPGraph <- ggplot() +
  scale_x_discrete(labels = c("No", "Probable", "Known")) +
  ylim(0.5, 1) +
  geom_point(data=AJOwP, aes(x=Wolf_Presence, y=fit), size=1.5) +
  geom_linerange(data=AJOwP, aes(x=Wolf_Presence, ymin=fit-se, ymax=fit+se)) +
  labs(y = "Probability of damage presence", x = "Wolf presence",size=18) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10))  +
  ggtitle("(a)")

AJOwC =
expand.grid(AJO_WOLF_cover=seq(min(Forest_Prop$AJO_WOLF_cover),max(Forest_Prop$
AJO_WOLF_cover),0.01), RAWO_Presence=mean(Forest_Prop$RAWO_Presence),
SnowDepth_cm=mean(Forest_Prop$SnowDepth_cm),
AJO_MooseDens=mean(Forest_Prop$AJO_MooseDens),
SmallRoads_Dens=mean(Forest_Prop$SmallRoads_Dens),MediumRoads_Dens=mean(Forest_
Prop$MediumRoads_Dens), LargeRoads_Dens=mean(Forest_Prop$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Prop$Spruce_Cover),Birch_Cover=mean(Forest_Prop$Birch_
Cover))
AJOwCpred = predict(PresMA_AJO_WC, AJOwC, type="response", re.form=NA, se=T,
full=T)
AJOwC$fit = AJOwCpred$fit
AJOwC$se = AJOwCpred$se.fit

AJOWolfCGraph <- ggplot() +
  xlim(0, 1) +
  ylim(0.5, 1) +
  geom_ribbon(data=AJOwC, aes(x=AJO_WOLF_cover, ymin=fit-se, ymax=fit+se),
alpha=0.5) +
  geom_line(data=AJOwC, aes(x=AJO_WOLF_cover, y=fit)) +
  labs(y = "", x = "Wolf Coverage",size=10) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10))  +
  ggtitle("(b)")
```

```
AJOwDPres =
expand.grid(WolfPoly_Duration=seq(min(Forest_Duration$WolfPoly_Duration),max(Fo
rest_Duration$WolfPoly_Duration),1),
RAWO_Presence=mean(Forest_Duration$RAWO_Presence),
SnowDepth_cm=mean(Forest_Duration$SnowDepth_cm),
AJO_MooseDens=mean(Forest_Duration$AJO_MooseDens),
SmallRoads_Dens=mean(Forest_Duration$SmallRoads_Dens),MediumRoads_Dens=mean(For
est_Duration$MediumRoads_Dens),
LargeRoads_Dens=mean(Forest_Duration$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Duration$Spruce_Cover),Birch_Cover=mean(Forest_Duratio
n$Birch_Cover))
AJOwDPred = predict(PresMA_AJO_WD, AJOwDPres, re.form=NA, se=T,
type="response")
AJOwDPres$fit = AJOwDPred$fit
AJOwDPres$se = AJOwDPred$se.fit

AJOWolfDurationGraph <- ggplot() +
  scale_x_continuous(breaks=c(0,5,10,15) , limits=c(0,15)) +
  ylim(0.5, 1) +
  geom_ribbon(data=AJOwDPres, aes(x=WolfPoly_Duration, ymin=fit-se,
ymax=fit+se), alpha=0.5) +
  geom_line(data=AJOwDPres, aes(x=WolfPoly_Duration, y=fit)) +
  labs(y = "", x = "Wolf presence duration",size=18) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10)) +
  ggtitle("(c)")

grid.arrange(AJOWolfPGraph,AJOWolfCGraph, AJOWolfDurationGraph, ncol=3)
# See output Figure 6

###### Damage level ######
Forest_Prop$AJO_ID = as.factor(Forest_Prop$AJO_ID)
AJOwCProp = expand.grid(AJO_WOLF_cover=seq(0,1,0.05),
RAWO_Presence=mean(Forest_Prop$RAWO_Presence),
SnowDepth_cm=mean(Forest_Prop$SnowDepth_cm),
AJO_MooseDens=mean(Forest_Prop$AJO_MooseDens),
SmallRoads_Dens=mean(Forest_Prop$SmallRoads_Dens),MediumRoads_Dens=mean(Forest_
Prop$MediumRoads_Dens), LargeRoads_Dens=mean(Forest_Prop$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Prop$Spruce_Cover),Birch_Cover=mean(Forest_Prop$Birch_
Cover), Year=levels(Forest_Prop$Year), AJO_ID=levels(Forest_Prop$AJO_ID),
Plot_Inv=1)
AJOwCPropPred = predict(PropMA_AJO_WC, AJOwCProp, se.fit=T, full=T, type
="response")
AJOwCProp$fit = AJOwCPropPred$fit
AJOwCProp$se = AJOwCPropPred$se.fit
AJOwCPropagg <-
aggregate(list(fit=AJOwCProp$fit,se=AJOwCProp$se),by=list(AJO_WOLF_cover=AJOwCP
rop$AJO_WOLF_cover),mean)

AJOWolfCPropGraph <- ggplot() +
  xlim(0, 1) +
  ylim(0, 0.5) +
  geom_ribbon(data=AJOwCPropagg, aes(x=AJO_WOLF_cover, ymin=fit-se,
ymax=fit+se), alpha=0.5) +
  geom_line(data=AJOwCPropagg, aes(x=AJO_WOLF_cover, y=fit)) +
  labs(y = "Damage level", x = "Wolf coverage",size=18) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10)) +
```

```
  ggtitle("(a)")

AJOwDProp = expand.grid(WolfPoly_Duration=seq(1,15,1),
RAWO_Presence=mean(Forest_Prop$RAWO_Presence),SnowDepth_cm=mean(Forest_Prop$Sno
wDepth_cm), AJO_MooseDens=mean(Forest_Prop$AJO_MooseDens),
SmallRoads_Dens=mean(Forest_Prop$SmallRoads_Dens),MediumRoads_Dens=mean(Forest_
Prop$MediumRoads_Dens), LargeRoads_Dens=mean(Forest_Prop$LargeRoads_Dens),
Spruce_Cover=mean(Forest_Prop$Spruce_Cover),Birch_Cover=mean(Forest_Prop$Birch_
Cover), Year=levels(Forest_Prop$Year), AJO_ID=levels(Forest_Prop$AJO_ID),
Plot_Inv=1)
AJOwDPropPred = predict(PropMA_AJO_WD, AJOwDProp, se.fit=T, type ="response")
AJOwDProp$fit = AJOwDPropPred$fit
AJOwDProp$se = AJOwDPropPred$se.fit
AJOwDPropagg <-
aggregate(list(fit=AJOwDProp$fit,se=AJOwDProp$se),by=list(WolfPoly_Duration=AJO
wDProp$WolfPoly_Duration),mean)

AJOWolfDPropGraph <- ggplot() +
  scale_x_continuous(breaks=c(0,5,10,15) , limits=c(0,15)) +
  scale_y_continuous(limits=c(0,0.5)) +
  geom_ribbon(data=AJOwDPropagg, aes(x=WolfPoly_Duration, ymin=fit-se,
ymax=fit+se), alpha=0.5) +
  geom_line(data=AJOwDPropagg, aes(x=WolfPoly_Duration, y=fit)) +
  labs(y = "", x = "Wolf presence duration",size=18) +
  theme(axis.ticks = element_line(colour = "#000000", size = 0.2), axis.line =
element_line(colour = "#000000", size = 0.2),
        panel.grid.major = element_blank(),panel.grid.minor = element_blank(),
        panel.background = element_blank(),
        axis.title.x = element_text(size=10),
        axis.title.y = element_text(size=10),
        axis.text.x = element_text(size=10,colour = "#000000"),
        axis.text.y = element_text(size=10,colour = "#000000"),
        plot.title =element_text(size=10)) +
  ggtitle("(b)")

grid.arrange(AJOWolfCPropGraph, AJOWolfDPropGraph, ncol=2)
# See output Figure 7
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EFFET DE L'ETABLISSEMENT DU LOUP (*CANIS LUPUS*) SUR LES DEGATS HIVERNAUX DES ELANS (*ALCES ALCES*) DANS LES PLANTATIONS DE JEUNES PINS SYLVESTRES (*PINUS SYLVESTRIS*)

Les ongulés sauvages sont en conflit avec les activités humaines, comme l'agriculture, l'élevage ou la foresterie, car ils créent des pertes économiques. En Suède, l'un des pays européens avec la plus grande superficie boisée, la foresterie est l'une des principales activités de production. L'établissement récent des loups en Suède peut aussi bien que d'autres facteurs tels que la densité d'élans, la disponibilité de nourriture, la couverture neigeuse et la densité des routes affecter les dégâts de broutage des élans. L'établissement du loup devrait réduire la présence et le niveau des dégâts. Les données ont été recueillies au moyen d'enquêtes annuelles sur les dégâts causés par les élans, la surveillance à long terme de la population suédoise de loups et les bases de données nationales sur la chasse aux élans, les habitats, les conditions climatiques et le système routier en Suède de 2015 à 2017. Les analyses ont été faites à la fois à l'échelle régionale et locale. La présence et la durée depuis l'établissement des loups ont montré une augmentation des dégâts sur les plantations de pins sylvestres, de même que la densité d'élans. Les différentes espèces d'arbres ont donné des résultats différents, les espèces à feuilles caduques augmentant la présence de dégâts mais diminuant le niveau de dégâts, et la couverture de sapins montrant l'effet inverse. L'augmentation de la couverture neigeuse augmente la présence de dégâts mais diminue leur intensité. Les densités des différentes classes de routes augmentent la présence de dégâts et réduisent les dégâts. L'établissement des loups a eu l'effet contraire à celui attendu sur les dégâts occasionnés par les élans. Ainsi, l'établissement des loups n'affecte pas les dégâts par les élans. Selon ces études antérieures et celle-ci, il n'y a donc pas de soutien pour le fait que l'établissement de loups puisse atténuer le conflit entre les élans et la foresterie en Suède.

MOTS-CLES - *risque de prédation, recolonisation des prédateurs, densité des proies, dégâts de broutage des élans, conflit entre humains et animaux sauvages*

EFFECT OF WOLF (*CANIS LUPUS*) ESTABLISHMENT ON MOOSE (*ALCES ALCES*) WINTER DAMAGE IN YOUNG SCOTS PINES (*PINUS SYLVESTRIS*) PLANTATIONS

Wild ungulates are in conflict with human activities, such as agriculture, livestock or forestry, because they create economic losses. In Sweden, one of the European countries with the largest forested area, forestry is one of the main production activities. The recent wolf establishment in Sweden can as well as other factors like moose density, foraging availability, snow depth, and road densities affect moose browsing damage. The establishment of wolf is expected to decrease both damage presence and level. Data was collected through annual moose browsing damage survey, long-term wolf monitoring and national databases of moose harvest statistics, habitats, snow depth and road network in Sweden from 2015 to 2017. The analyses were made both at regional and local scales. Wolf presence and duration showed an increase of the damage presence and level in young Scots pine plantations, like the moose density. Different forage tree species showed different results, with deciduous species increasing the damage presence but decreasing damage level, and spruce cover showing the opposite effect. Increased snow depth increased the damage presence but decreased the damage level. Road densities increase leads to a lower damage presence and a lower damage level. Wolf establishment had the opposite effect than expected on moose browsing damage. Thus, wolf establishment did not affect moose browsing damage. According to these previous studies and this study, there is no support towards the fact that wolf establishment can mitigate the moose-forestry conflict in Sweden.

KEY WORDS - *predation risk, recolonization of predators, prey density, moose browsing damage, wildlife-human conflict*