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Comparative use of forest habitats by roe deer and moose in a human-modified landscape in southeastern Norway during winter

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Abstract The negative impact of anthropogenic disturbance and land-use changes on large mammals is generally recognized within conservation biology. In southeastern Norway, both moose (*Alces alces*) and roe deer (*Capreolus capreolus*) occur throughout human-modified landscapes, facilitating an interesting comparative study of their habitat use. By using pellet group counts, we looked at the importance of forest structure, vegetation characteristics and human disturbance (e.g., distance to the nearest house, nearest paved road, and nearest edge between field and forest) in shaping the winter distribution of both species at multiple spatial scales, in non-agricultural habitats. Moose occurred more often in areas with higher densities of heather and *Vaccinium* sp. in the ground layer, and used areas with more open forest structure. The proportion of built-up areas, within a 1,000-m buffer, negatively influenced moose occurrence. Roe deer occurred more often in areas with deciduous trees and patches with juniper and *Vaccinium* sp. in the ground layer, used areas near roads less, but were significantly associated with areas near the field–forest ecotone. The proportion of built-up areas positively influenced roe deer distribution within a 2,500-m buffer. Roe deer seem to be able to persist in more human-dominated landscapes, possibly due to the availability of field–forest edges providing both high-

quality fodder and cover in close proximity. Moose, on the contrary, did not show any preference for areas associated with human disturbance, and their distribution was only associated with patches providing food.

Keywords *Capreolus capreolus* · *Alces alces* · Game management · Human activities · Pellet group counts

Introduction

Human-mediated disturbance has a profound and ongoing effect on habitats around the world (Loreau et al. 2001). Habitats, and consequently animal populations, are increasingly fragmented as a consequence of the human population increase, urbanization, expansion of transport infrastructure, habitat transformation, and agriculture intensification (e.g., Prugh et al. 2008). In such a developing world, areas of undisturbed wilderness are rapidly decreasing, compelling wild ungulates to integrate into human-modified environments, which represent novel and often rapidly changing habitats (Andersen et al. 1996).

During the past 300 years, Scandinavian forests have undergone dramatic changes, as industrial forestry has virtually eliminated old forests in the southern boreal zone (Niklasson and Granström 2000). These disturbances have often been cited among the factors responsible for the decrease in abundance of old-growth forest-specialist species [woodland caribou (*Rangifer tarandus caribou*), Vors et al. (2007); grey-sided vole (*Clethrionomys rufocanus*), Ecke et al. (2002)]. Modern large-scale forestry practices produce new landscape patterns and change vegetation composition, where some species can be favored and others reduced.

Populations of roe deer (*Capreolus capreolus*) and moose (*Alces alces*) have increased considerably during the last century and both species are now common throughout much of Scandinavia (Persson et al. 2000). The increase of both species has been attributed to

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changes in land use and more targeted hunting regulations (Lavsund et al. 2003). Moose are very abundant in the forests of Scandinavia (average winter density varies between 1 and 2 moose/km²; Lavsund et al. 2003), where they have benefited from the increase in forage provided by the modern clear-cut/regeneration system of forestry, although some studies have shown the potential for negative impacts of human disturbance (Jiang et al. 2009). Roe deer are closely associated with human-modified landscapes and the presence of agricultural fields in many parts of Europe, often utilizing the ecotone between forests and agricultural areas (McLoughlin et al. 2007; Panzacchi et al. 2009). Many studies have demonstrated their tolerance of human disturbance (e.g., Cederlund and Kjellander 1991). However, other studies have also shown the negative impacts of anthropogenic disturbance on roe deer, showing their avoidance of areas with very high human activity (Hewison et al. 2001), and that their behavioral response is flight when disturbed (Danilkin and Hewison 1996).

In the south of Norway, where both species are hunted, they are likely to view humans as potential predators (Lima and Dill 1990). Both species have a long history of sympatry with humans, and studies of impacts of human activity on both moose and roe deer have demonstrated both positive and negative effects on population density, behavior, and space use (Hewison et al. 2001; Neumann 2009; Panzacchi et al. 2009).

Although moose and roe deer are known to thrive in human-dominated landscapes in Scandinavia, the impact of the magnitude and extent of anthropogenic disturbances on their habitat use at different scales are not well understood. Such an understanding is of particular relevance in countries such as Norway because roe deer and moose are recreationally and economically important species for their trophy and meat value. Understanding the potential direct and cascading effects of predator recovery and further human disturbance will require a solid understanding of basic ecological issues, such as the way in which these species are distributed in the landscape. Furthermore, because of an ongoing global debate concerning the impacts of human land-use changes on wildlife there is a need to quantify some of the seemingly trivial “basic knowledge” concerning the tolerance of Scandinavian cervids for human disturbance to permit comparative analyses and identification of the key features that influence this tolerance.

Generally, cervid habitat use is described as being mainly determined by the presence of both food and cover (e.g., Tufto et al. 1996). In Norway, winter conditions can have a significant influence on the habitat selection of ungulates (Ratikainen et al. 2007; van Beest et al. 2010). To understand how moose and roe deer exploit their winter environment, we examined winter habitat use by these two herbivores at different spatial scales. We focused on winter habitat use, which in northern ecosystems is a period of nutritional and physiological stress when resource access decisions are likely to be very important. Our aim was to identify

habitat variables that are relevant, at different spatial scales, for moose and roe deer occurrence in a human-modified landscape in southeastern Norway. Based on previous studies (see above) we expected that both species would make less use of areas near roads, while they will be differently affected by the landscape composition (e.g., proportion of urban areas and proportion of agricultural field). Furthermore, we expected that both species would make more use of areas with greater forage and/or cover availability.

Materials and methods

Study area

The study was conducted in southeastern Norway, in the counties of Østfold and Akershus (Aurskog-Høland, Enebakk, Høbol, Ski, Askim, Vestby, Spydeberg and Trøgstad municipalities), situated between 59° and 60°N; 11° and 12°E (Fig. 1). The study area is dominated by commercially exploited boreal forest, mainly composed of Norwegian spruce (*Picea abies*), Scots pine (*Pinus sylvestris*), hoary alder (*Alnus incana*) and birch (*Betula pubescens*), and is intensively managed for timber and pulp. The forests are harvested by clearcutting, but the average size of the clear cuts is typically in the order of a few hectares only. The forests in the study area are fragmented by farmlands, especially along valley bottoms. Human population density in the various municipalities within the study area, measured on January 1, 2009, varied between 64 and 107 people km⁻², that live in a dispersed manner throughout the landscape (Statistics Norway).

Sampling survey

The data were collected along 21 transects. The transects were placed throughout the study area in a stratified (by altitude) manner. Each transect consisted of a 1 × 1 × 1 km triangle, which is an efficient field design (the start point and end point are on the same place) (Lindén et al. 1996). Following Wahlström and Liberg (1995), at each 100-m interval we delimited a circular 10-m² plot to record the number of pellet groups of each species. Plots were cleaned after inspection, overcoming the need for any assumption regarding fecal persistence period (decay rate) (Aulak and Babinskawerka 1990). Throughout the entire field period, each plot was visited five times: in spring (April–May) 2007, 2008, and 2009, and autumn (September) 2007 and 2008. With this, we avoided the period when vegetation was too high in summer and the ground being covered by snow in winter. Plots were cleaned in autumn, before the spring season, and analysis only included data collected in spring (with the accumulated pellets reflecting winter habitat use). The global position system (GPS) location of each plot was recorded on the first visit, allowing the precise

Fig. 1 Map of Norway (*left*) highlighting the counties where the field survey was done (*right* Østfold and Akerhusus counties). On the *right*, there is the distribution of the sampling plots



re-location of plots on posterior visits. Furthermore, a small colored marker was placed on the center of the plot and the nearest tree was marked to help the plot recognition. A pellet group was defined as containing six or more individual pellets following Mayle et al. (2000) and identified as being produced at the same defecation event (similar size, shape, texture, and color). Discrimination between pellets of both species was possible because they clearly differ in size. A total of 598 plots per season were examined within our study area. Plots that fell on lakes and agricultural fields were avoided by field workers and were not included in the analysis. In total, 32 plots were rejected (5% of the total plots). Although fields are likely to be used by both species, especially roe deer, it was not possible to sample fields in spring. In some cases this was because of the risk of damaging the crops, while in many cases it was because the fields were freshly ploughed in spring, which would remove all accumulated pellets. There was therefore no practical or unbiased way to assess the relative use of fields. At each plot, we firstly assessed the presence of moose and roe deer by recording the number of pellets, and then recorded habitat vari-

ables within the plot. Pellet groups lying on the boundary of plots were alternately counted and ignored (Mayle et al. 2000). Pellet group counts is a technique widely applied in studies of ungulate habitat use (e.g., Neff 1968; Borkowski and Ukalska 2008). Although it has been criticized by some authors (Collins and Urness 1981), when it is compared to other methods to infer habitat use patterns (e.g., such as radio-telemetry), it has been found that the results are similar (Guillet et al. 1995). Furthermore, other authors (Loft and Kie 1988; Edge and Marcum 1989) have found that pellet group counts accurately indicate which habitat receives the greatest and least amount of use.

Habitat data

For each sampling plot, a series of local scale- and broad-scale variables were quantified. Local-scale variables were collected within each 10-m² plot, whereas broad-scale variables (i.e., within a radius of 1,000 m and of 2,500 m from the center of the plot) were derived

from 1:50000 digital maps using geographic information system (ArcMap ArcGIS 9 ESRI Inc, Redlands, CA, USA). Digital land-use data were provided by the official Norwegian Mapping Authority (Statens Kartverk). These maps are vector-based and contain information on forest, agricultural land, water, roads, paths, human settlements, single houses, and built-up areas. Variables (see Table 1) were selected based on the literature and the authors' predictions. Habitat structure was assessed by vegetation cover for each of the three vertical strata: tree cover (> 2 m), shrub cover (0.5–2 m) and ground cover (< 0.5 m) and by means of visual estimations, these vertical strata were assigned to one of four classes: no cover; sparse, medium, and dense. Cover of common juniper *Juniperus communis*, rowan *Sorbus aucuparia*, moss, grass/forbs, common heather *Calluna vulgaris* and *Vaccinium* sp. were estimated visually using a five-point scale: 0, 0%; 1, 1–25%; 2, 26–50%; 3, 51–75% and 4, > 75%. These food items have already been demonstrated to be part of roe deer and moose diet (Cederlund and Nyström 1981; Sæther and Heim 1993; Sand et al. 1995; Mysterud et al. 1997). In Scandinavia, the winter diet of moose is typically composed of twigs of Scots pine and various deciduous tree species (van Beest et al. 2010). Percentages of these browse species were not collected, as moose data was included as an ad hoc procedure in our analysis of habitat use. Forest age class was estimated based on cutting ages, following the standard used by the National Forestry Inventory in Norway (Landskogstakseringen 1971). Five categories

of stands were identified: clear cuts (class I), young plantations (class II), pole-sized stands (class III), medium-aged stands (class IV) and older mature stands (class V). To analyze the effects of human disturbance, distances were measured from the center of each plot to the nearest border of the following features: nearest human house, nearest paved roads and nearest edge between a forest and a field. Roads included in the study area consist of highways, national roads, and local roads, with daily high traffic density. Roe deer and moose find concealment in dense stands. Therefore, visual obstruction provided by vegetation is essential for hiding cover. Visual protection, provided by cover, was estimated by measuring lateral visibility (m). An index of horizontal visibility (m) was estimated by placing a cover board, 80 cm high, in the center of the plot. Then, in a random direction, the minimum distance required for the board to be completely hidden was noted (Mysterud 1996). Cover is also important as protection from adverse weather: dense canopy stands provide shelter against adverse weather conditions. Canopy cover was estimated using Lemmon's densiometer (Mysterud and Østbye 1999). Holding the densiometer horizontally, measures were taken in all directions (north, south, east, and west) at each plot, then the values were averaged to obtain a percentage canopy cover value for each sampling unit. Using ArcMap, circular buffers, with radii of 1,000 and 2,500 m, were created and several broad-scale variables were calculated. For each buffer, the proportion of fields and urban (built-up) areas, with respect to

Table 1 Description of the variables used to model roe deer and moose distribution in Østfold and Akershus counties, southeastern Norway (2007–2009)

Abbreviation	Variable description
Patch-scale variables (in 10-m ² radius circle)	
Tree layer (height > 200 cm)	
TREECOV	Tree cover: 0, 1–25, 26–50, 51–75, > 75%.
TREECOMP	Mixed (pine and spruce), pine, spruce, open, deciduous
STANDAGE	Class I, class II, class III, class IV and class V (according to Landskogstakseringen 1971)
Shrub layer (height 50–200 cm)	
SHRUBCOV	Shrub cover: no cover, sparse, medium-density, dense
CONCOV	% Conifer (spruce and pine)
DECCOV	% Deciduous
JUNCOV	% <i>Juniperus communis</i>
ROMCOV	% <i>Sorbus aucuparia</i>
Ground layer (height < 50 cm)	
GROUNDCOV	Shrub cover: no cover, sparse, medium-density, dense
MOSSCOV	% Moss cover
GRAMCOV	% Grass/forbs cover
CALCOV	% <i>Calluna vulgaris</i> cover
BERCOV	% <i>Vaccinium</i> sp. cover
VISINDEX	Measure of lateral visibility (m)
Human disturbance variables	
DROAD	Distance (m) to the closest road
DHOUSE	Distance (m) to the closest settlement
DEDGE	Distance (m) to the closest edge field/forests
Broad-scale variables (in 1 and 2.5-km radius circle)	
PURBAN_1	Proportion of urban area inside a 1-km radius
PURBAN_2	Proportion of urban area inside a 2.5-km radius
PFIELD_1	Proportion of agricultural fields inside a 1-km radius
PFIELD_2	Proportion of agricultural fields inside a 2.5-km radius

forest, were calculated as [field area/(forest + field + urban) areas] and [urban area/(forest + field + urban) areas]. The three land-cover classes summed up to 1. Urban areas included houses, buildings, and industrial areas.

Statistical analyses

Habitat use by moose and by roe deer was quantified through species-specific generalized linear mixed model (GLMM; Faraway 2006) procedures. Continuous variables were square root transformed in order to mitigate the effects of extreme values (Rossiter et al. 2001). Before any regression analysis, all continuous variables were standardized (giving zero mean and variance of one) to avoid the effect of different measurement scales and to facilitate direct comparison. We checked for multicollinearity by computing pairwise Pearson correlation tests. Whenever a correlation exceeded 0.6 (Acevedo et al. 2005), the variable with lower biological meaning was dropped. To avoid artificially increasing the explanatory power in our analysis through the inclusion of redundant variables, we first construct three sub-models using TREECOV, TREECOMP, STANDAGE, SHRUBCOV, GROUNDGOV, and VISINDEX variables (habitat structure model), CONCOV, DECCOV, JUNCOV, ROMCOV, MOSSCOV, GRAMCOV, CALCOV, BERCOV variables (vegetation model) and DROAD, DHOUSE, DDGE, PURBAN_1, PURBAN_2, PFIELD_1, PFIELD_2 variables (landscape model). Thus, we used logistic regressions from the general linear model (GLM) framework to identify minimal subsets of factors that best explain moose and roe deer presence-absence. Therefore, for each species, we used the stepAIC function in R (library MASS; Venables and Ripley 1999), to identify sub-groups of variables, in order to reduce multicollinearity. StepAIC performs stepwise variable selection that adds or removes predictors to produce a model that minimizes Akaike's information criterion (AIC). Finally, we constructed a global model with the variables that explained a significant ($p < 0.05$) amount of variance of moose and roe deer data. Following Hosmer and Lemeshow (1989), the model (both sub-models and global model) was a binary response analysis using binomial error and the logit link function. The response variable was the presence or absence of moose or roe deer. Transect identity was included as a random factor to control for the lack of independence of segments within them and to avoid pseudoreplication arising from repeated sampling of the same transect (Hurlbert 1984). The models were fitted using the lmer function in lme4 library (Bates and Sarkar 2006) in R (version 2.8.1; R Development Core Team 2006). To construct the global model, we used a backward stepwise procedure for model simplification. In order to select the best model, we evaluated the parsimony relative to predictive efficiency of all possi-

ble subsets of uncorrelated candidate variables using an information theoretical-approach (Burnham and Anderson 1998). Such a procedure compares the suitability of a set of candidate models according to their AIC values. In this framework, we generated models and they were ranked according to AIC values, where model with the lowest AIC is the best one. We also reported the Δ AIC value in order to compare the difference between each model and the best model. As a rule of thumb, a Δ AIC < 2 suggests substantial evidence for the model (and consequently for the variables included), values between 3 and 7 indicate that the model has considerably less support, whereas a Δ AIC > 10 indicates that the model is very unlikely (Burnham and Anderson 1998). The level of significance was set at 0.05 for all statistical tests.

Results

Moose

Moose were relatively well distributed across the study area. Indeed, moose pellet groups were found in 241 of the 598 plots (40.3%). The stepAIC function retained the following variables: TREECOMP, TREECOV (habitat structure model), CALCOV, BERCOV (vegetation model), PFIELD_2, PURBAN_1 (landscape model).

According to the AIC values, the final model for moose occurrence included as predictors tree cover, *Calluna vulgaris* cover, *Vaccinium* sp. cover, and the proportion of urban areas within a 1,000-m buffer (b, Table 2). Moose occurrence was positively associated with *Calluna vulgaris* cover and *Vaccinium* sp. cover, whereas it was negatively associated with tree cover and the proportion of urban areas within a 1,000-m buffer (Table 3).

Roe deer

Roe deer showed a more restricted distribution and pellet groups were only observed in 125 of 598 plots (20.9%). The stepAIC function retained the following variables: DECCOV, JUNCOV, ROMCOV, CALCOV, BERCOV (vegetation model), DROAD, DEDGE, PURBAN_2 (landscape model).

According to the AIC values, the final model for roe deer occurrence included as predictors deciduous cover, juniper cover, *Vaccinium* sp. cover, distance to roads, distance to edge and the proportion of urban areas within a 2,500-m buffer (b, Table 4). Roe deer occurrence was positively associated with deciduous cover, juniper cover, *Vaccinium* sp. cover, distance to roads and the proportion of urban areas within a 2,500-m buffer, whereas it was negatively associated with the distance to forest-field edges (Table 5).

Table 2 Number of model parameters (k), the Akaike information criterion (AIC), and the difference between the AIC of each selected model (Δ AIC) for the alternative models describing moose occurrence ($n = 241$) in Østfold and Akershus counties, southeastern Norway (2007–2009)

Models	k	AIC	Δ AIC
Full model			
(a) TREECOMP + TREECOV + CALCOV + BERCOV + PFIELD_2 + PURBAN_1	6	756.8	8.9
Alternative models			
(b) TREECOV + CALCOV + BERCOV + PURBAN_1	3	747.9	0
(c) TREECOV + CALCOV + BERCOV + PURBAN_1 + PFIELD_2	4	749.9	2

For explanation of variables, see Table 1

Table 3 Generalized linear mixed final model for winter moose occurrence in Østfold and Arkesus counties, southeastern Norway (2007–2009), with binomial error distribution and log link function using the most parsimonious model and its levels of significance

	Estimate \pm SE	z value	p value
Moose			
Intercept	-0.545 ± 0.206	-2.645	<0.008
TREECOV	-0.815 ± 0.356	2.292	0.020
CALCOV	0.403 ± 0.098	4.100	<0.001
BERCOV	0.368 ± 0.099	3.691	<0.001
PURBAN_1	-0.487 ± 0.187	-2.600	0.009

For explanation of variables, see Table 1

Discussion

Winter is a critical period for cervid species that live at high latitudes, as low temperatures and short days increase the amount of energy needed for thermoregulation while reducing the availability of high-quality food; in addition, snow increases the cost of mobility and limits access to food (Mysterud 1996). Hence, during this time, deer have to balance between the available resources to achieve the most favorable energy balance (Dussault et al. 2005) and it is expected that winter should be a period where animals are forced to be more selective when it comes to habitat use. In general, our results support the general view that animals select their habitats using different criteria at different spatial scales, which is particularly true when working with highly mobile and medium to high sized species such as moose and roe deer (Senft et al. 1987).

Several parameters that characterize our human-dominated study landscape affected the occurrence of both roe deer and moose, but in somewhat different ways at the different scales. The proportion of urban areas at a 2,500-m scale positively influenced the occurrence of roe deer. This correlation is likely connected to environmental productivity gradients, since it has been shown that human settlements are generally situated on more fertile grounds (Pautasso 2007). In addition, during winter, roe deer home ranges are often located in proximity to the small-scale artificial feeding stations (Odden et al. 2006) which are often set up to increase winter survival (see Gundersen et al. 2004).

Mysterud and Østbye (1999) found that roe deer increasingly selected feeding sites closer to human settlement as snow depth increased. In contrast, the proportion of urban areas at a 1,000-m scale negatively influenced the occurrence of moose. This could be due to the fact that in the south of Norway, moose populations experience a strong harvest pressure, and it is likely that hunting induces avoidance responses similar to those caused by non-human predators (Frid and Dill 2002). Roe deer are also subjected to a relatively high hunting pressure in the study area (Statistics Norway), but as this species is at the northern limit of its distribution range during winter, the trade-off between avoidance of human-dominated areas and the need to feed on high-quality foods associated with proximity to human settlements is relaxed, and roe deer are compelled to accept a closer proximity to human-dominated areas in order to survive (Mysterud et al. 1997). A previous study based on radio-monitored roe deer in the study area (Ratikainen et al. 2007) showed that the distance between bed sites, foraging sites, and human activities decreased as the winter progressed, especially for the more energetically constrained family groups (i.e., females with fawns). The study also showed no support for the hypothesis that roe deer changed habitat use to reduce their vulnerability to lynx predation (Ratikainen et al. 2007), as the risk of starvation especially at the end of winter was higher than that of predation. For moose, on the contrary, the risk of starvation does not seem of any real importance, and the species can therefore afford to avoid human-dominated areas. It could also be due to the greater size of moose that makes it harder for them to seek concealment in cover, forcing them to utilize increased distance from disturbance sources as a strategy. Furthermore, Nikula et al. (2004) showed that moose winter home ranges included less agricultural land and human settlements than expected at random. A final factor that could explain the species differences is the fact that moose have a greater tolerance to snow than roe deer.

Several studies in boreal regions have found a positive correlation between moose occurrence and young forests, clear cuts, and young pine plantations (Cederlund and Okarma 1988; Cederlund 1989). However, in our study, this evidence was not so clear, although our results indicate that moose pellets were more abundant

Table 4 Number of model parameters (k), the Akaike information criterion (AIC), and the difference between the AIC of each selected model (Δ AIC) for the alternative models describing roe deer occurrence ($n = 125$) in Østfold and Arkesus counties, southeastern Norway (2007–2009)

Models	k	AIC	Δ AIC
Full model			
(a) DECCOV + JUNCOV + BERCOV + ROMCOV + CALCOV + DROAD + DEDGE + PURBAN_2	8	580.7	2.8
Alternative models			
(b) DECCOV + JUNCOV + BERCOV + DROAD + DEDGE + PURBAN_2	6	577.9	0
(c) DECCOV + JUNCOV + BERCOV + DROAD + DEDGE + PURBAN_2 + ROMCOV	7	578.7	0.8
(d) DECCOV + BERCOV + DROAD + DEDGE + PURBAN_2	5	579.4	1.5

For explanation of variables, see Table 1

Table 5 Generalized linear mixed final model for winter roe deer occurrence in Østfold and Arkesus counties, southeastern Norway (2007–2009), with binomial error distribution and log link function, using the most parsimonious model and its levels of significance

	Estimate \pm SE	z value	p value
Roe deer			
Intercept	-1.538 ± 0.154	-9.964	< 0.001
DECCOV	0.304 ± 0.106	2.865	0.004
JUNCOV	0.200 ± 0.103	1.947	0.052
BERCOV	0.272 ± 0.116	2.340	0.019
DROAD	0.264 ± 0.130	2.024	0.043
DEEDGE	-0.380 ± 0.142	-2.667	0.008
PURBAN_2	0.470 ± 0.154	3.052	0.002

For explanation of variables, see Table 1

in areas with a lower density of tree cover, which corresponds to clear cuts or open forest patches. Moose occurred more often in patches with higher densities of heather and bilberry as ground cover, a pattern already demonstrated by Cederlund and Nyström (1981) who demonstrated that these food items were also important for roe deer. The biological significance of *Calluna vulgaris* in the moose habitat model deserves careful consideration. Even though it was statistically significant, it is not biologically meaningful, since heather is not a typical browse for moose. However, it is likely that heather did not have an effect per se, but rather an indirect association with Scots pine, since the former is usually associated with Scots pine. Roe deer occurrence was positively related to the presence of deciduous plant patches, which have been shown to be an important determinant of winter habitat use by roe deer in other areas (Borkowski and Ukalska 2008).

Our results show that roe deer occurrence was positively correlated with proximity to the closest edge between forest and field. Roe deer are browsers and their main food is often located at ecotones (Said and Servanty 2005). Forest edges bordering agricultural fields provide a diversity of abundant and high-quality food but also provide protective cover in close proximity. Consequently, edges provide a good interspersed cover and forage for roe deer (Myysterud and Østbye 1999). Moreover, previous studies have reported a link between forest edges use and individual reproductive output, e.g., McLoughlin et al. (2007) showed a positive association

between forest edges and reproductive success in roe deer females and Miyashita et al. (2008) showed that an increase in forest edge would increase female sika deer (*Cervus nippon*) probability of pregnancy. Our results also suggest that roe deer avoided areas near roads, which is consistent with previous findings on established populations in different countries for a range of cervid species (e.g., Rowland et al. 2000; Hewison et al. 2001; Coulon et al. 2008; Jiang et al. 2009).

Roe deer are an important prey species of the European lynx (*Lynx lynx*) (Odden et al. 2006) and red fox (*Vulpes vulpes*) (Panzacchi et al. 2008) and both roe deer and moose are an important prey species for wolves (*Canis lupus*) where they are present (Sand et al. 2005). Because both carnivores have recently re-colonized this human-dominated ecosystem, detailed models of ungulate abundance and habitat use are required. The emerging predator–prey system in the boreal forest of southeastern Norway differs dramatically from most other well-studied systems (for example in Yellowstone or Alaska) because it is played out entirely in human-modified ecosystems. Our findings concerning the differential response of moose and roe deer to human land use is likely to also influence the way in which wolves and lynx will interact with humans. Because their main prey is roe deer, it is likely that lynx will be forced to hunt in areas characterized with a greater human presence, which could in turn have impacts on these predator species vulnerabilities to human caused mortality and disturbance.

Although our results are purely correlational, they suggest that the presence of these deer species is compatible with the existing forms of intensive forest exploitation. Both species appeared to be more affected by the fine-scale details of vegetation structure and the large-scale landscape matrix (roads, urban areas, forest–field edges), than the forestry management (stand) scales. In forest areas, highly dense forage is often more limiting than cover, and therefore both moose and roe deer seem likely to profit from forest cutting since it promotes plant diversity (Vospernik and Reimoser 2008). Even though a uniform regeneration might be temporarily suitable for moose, it is likely to be disadvantageous for roe deer who meet their preferences best in a fine-scaled mosaic distribution of habitat types (Vospernik and Reimoser 2008). Unfortunately, we are aware that our explanatory variables and the scales were

somewhat coarse to understand and extract specific preferences for roe deer and moose in a human-modified landscape in southeastern Norway and we recognize the existence of other factors not considered in this study. We suspect that our sample size, despite being statistically high, might have limited our ability to discern and fully understand some of the variables selected. We believe that some of the variables selected can be functions of the scale used in this study, reflecting analytical artefacts to a greater extent than actual roe deer and moose true biological patterns. To account for the potential biases created by having different land cover categories within each buffer, we used correlation analysis to determine whether land-use cover variables measured in the different buffers were correlated between them. Clearly, these are not independent variables: an increase in one land-cover category necessarily requires a decrease in another land-cover category. However, the potential bias is more likely to be important when habitat categories are correlated, which were not in our case. Notwithstanding the limitations connected to the methodology, we believe that this study provides a preliminary and general overview of the differential responses of these species to large-scale land use. Future studies could use fine-scaled movement data (e.g., from GPS collars) combined with finer-scaled map data to identify in detail the habitat use on temporal and spatial scales in relation to human disturbance.

Of wider interest, our study demonstrates that two species of cervid are able to persist close to humans in intensively managed production landscapes. This is an important message for global wildlife conservation, particularly when recent studies (Licona et al. 2010; Singh et al. 2010) from the developing world show that ungulate presence is often inversely related to human activity. The difference in findings between regions could be more due to the impacts of human exploitation and the precise nature of human disturbance (e.g., the presence of free-ranging dogs) rather than the actual human presence or land use per se.

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