修士論文

スカンジナビアに生息するオオカミの縄張りを形づける要因

Landscape features and moose density shape
wolf territory borders in Scandinavia

2021 年 3 月 20 日

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Abstract

Territorial animals are living in a space where there are suitable habitats and necessary resources to sustain them. The location, shape and size of a territory are affected by environmental factors. Using 26 wolf territories included 38 wolves from 2001 to 2020, I tested the influences of landscape features which might shape winter territories of wolves (*Canis lupus*) in Scandinavia. I estimated the wolf territories with two methods; 100% MCP and 95% LoCoH-k. Along the estimated borders of each territory, I generated two buffers of different width (1 km and 2.5 km). I then defined the area within the buffers as the borders of each territory, and the remaining area within each territory but outside of the buffers as the center of each territory. Moreover, I divided the borders areas of each territory into two additional categories, depending on the presence or absence of neighboring wolf territories: border areas with neighboring territories and border areas without neighboring territories. I generated random points inside of wolf territories and explained the location (center or border, neighboring border or non-neighboring border) of the points with landscape features (prey density, house density, road density, distance to water, slope and land covers) by fitting into generalized linear mixed-effects model. I recognized more differences between home range estimators than between widths of border. The borders of territory tended to have higher density of anthropogenic features and closer to water than the centers of territory. Moreover, I found that the neighboring wolf territory borders were located where wolves were not interested.

要旨

縄張りを形成する動物は、その動物にとって必要な条件が整った環境を選択して縄張りを形成するため、縄張りの場所や大きさ、形は環境要素による影響を受ける。本研究では、スカンジナビアに生息するオオカミの縄張りの形に影響を及ぼすと思われる環境要素について調べた。また、隣接するオオカミの存在による影響の検証も行った。2001～2020 年の間に得た GPS 首輪を装着した 38 頭のオオカミの位置情報から、95% LoCoH と 100% MCP の二つの行動圏推定法を用いて 26 個の縄張りを推定した。これらの縄張り境界沿いに、両側へ幅 1 km と 2.5 km のバッファーを生成し、これらを縄張りの境界部、残りの部分を中心部と定義した。さらにこの境界部を、近隣に生息するオオカミと隣接しているか（隣接部）、しいていないか（非隣接部）の 2 つに分類した。縄張り中心部と外縁部にそれぞれ 1,000 個のランダム

ポイントを生成して、これらのランダムポイントに環境要素（土地被覆、建物密度、舗装道路密度、林道密度、獲物の生息密度、川や湖までの距離、傾斜角）を取り込んだ。これらのランダムポイントが、縄張りの中心部もしくは外縁部にあるのか、隣接部もしくは非隣接部にあるのかを目的変数とし、環境要素を説明変数として一般化線形混合効果モデルに当てはめた。解析結果から、境界部の幅による違いよりも、行動圏推定方法による違いが顕著に見られた。スカンジナビアのオオカミの縄張りは、人工物の密度が低い場所を中心とし、縄張りの外郭は人工物の密度が高く、川や湖に沿っていることが示唆された。また、縄張り同士の隣接部は、比較的オオカミにとって利用価値のない場所が含まれていることが示された。

Key words: *Alces alces*, *Canis lupus*, prey density, Scandinavia, territory

1. Introduction

Every animal uses a home range that includes places for foraging, mating and caring for young, and when an animal defends its home range against conspecifics, the home range is called territory (Burt 1943). Grant (1968) suggested that if territory sizes are similar and neighbors equally spaced, then the shape of territories will be hexahedral. In reality, the shape of territories seem to be affected by two main factors: the habitat and the distribution of resources within it, which in turn are influenced by the presence of neighbors (Adams 2001; Grant 1968).

Resources are not evenly distributed in the landscape, and this heterogeneity may be important for the alignment and shape of territories. One could think of two scenarios, where the first is that a territorial animal tries to monopolize a resource concentration in the center of its territory, and so would defend the borders in areas with lower resource availability. Alternatively, territorial defense is strongest in areas with high resource concentrations, and so the territory borders are aligned with resource-rich areas. For example, male common hippopotamus (*Hippopotamus amphibious* L.) defend water resources within their territories from other males to win the right to mate with females (Timbuka 2012), therefore indicating that the shape of territories are strongly correlated with the distribution of water resources.

In some cases, there are habitats that may be inaccessible, which means that landscape features can also influence the shape of a territory. For instance, Peterson and Page(1988) found that the borders of wolf (*Canis lupus*) territories followed the shoreline of an island, suggesting that the sea acted as a barrier for movement. (Peterson and Page 1988). But it was also indicating that wolves grasp the idea of an easily defended shoreline as their territory boundary (Mech and Boitani 2003).

Moreover, breeding pairs of golden eagles (*Aquila chrysaetos*) often defend a territory around their nesting site. In addition to the nesting sites, the territory also secures a hunting range for the breeding pair and their offspring (Chambert et al. 2020; McGrady et al. 2002). In areas with a high density of golden eagles, the boundaries of their territories are squeezed by neighbors, which leads to smaller hunting range and consequently lower productivity (Chambert et al. 2020). On the other hand, the kagu (*Rhynochetos jubatus*) lives in family units and cooperate for breeding and defending the territory (Thuerksuf et al. 2009). The breeding success thus depends on family size and territory size (Thuerksuf et al. 2009).

In addition, population density can affect the existence of territory border. In the endemic migratory Japanese ayu (*Plecoglossus altivelis*), young fish feed on algae that grow on rocks in the riverbed. This creates a boundary in which they defend their territory to protect food resources. When the density of the population becomes too high, territories break down and ayu individuals form a school of fish. Therefore, the energy cost of territory protection can become higher than the benefits of the food resources present (Tanaka et al. 2011).

In this study, we investigated the placement of territory borders of wolves in Scandinavia. The Scandinavian wolves were functionally extinct in the 1960s (Wabakken et al. 2001). However, two wolves dispersed from the Finnish–Russian border in 1980s (Wabakken et al. 2001) and about 40 years later, the population grew up to about 450 individuals in total in 2020 (Wabakken et al. 2020). Wolves live in a pack that most often consists of a pair of breeding adults and their offspring (Mech and Boitani 2003). Scandinavian wolf territories are on average 1,017 km^2 but can vary from a minimum of 259 km^2 to a maximum 1,676 km^2, and those numbers were comparably bigger than its in continental Europe (Mattisson et al. 2013). Those territories are considerably bigger than the size a pair of wolves needs, but they need this range to keep enough prey for raising up their offspring (Peterson et al., 1984). The dominant prey species of Scandinavian wolves is moose (*Alces alces*) (Sand et al. 2008, 2012, 2016; Zimmermann et al. 2015) and it comprises 60 to 100 % of wolf diet (Gervasi et al. 2013). The wolf pups are born in the end of April to mid of May and they spend around 44 days in the den; the movement of the pack increase gradually towards autumn, and reaches maximum in October (Alfredéen 2006). Therefore, abundance of moose is one of the important factors for wolf habitat. In general, wolves select areas with a higher abundance of prey (e. g. Ausilio et al. 2021; Lesmerises, Dussault, and St-Laurent 2012; Oakleaf et al. 2000), but prey are not evenly distributed in space, so that the high prey density areas are in the overlapping zones of wolf territories (Lewis and Murray 1993; Mech 1977; Mech et al. 1980) which is defined as 2 (Peters and Mech 1975) to 6 km width

(Mech 1994).

Habitat selection of wolves has been extensively studied and we expected that those habitat selections can be strongly related to the shape of wolf territories, and it has never been studied so far. To investigate the factors which affect territory borders, we divided wolf territories into center (C) and border (B), and investigated the following hypotheses:

(1) Moose density is higher in the center than the border due to wolves monopolizing areas with higher prey density (BC1), or higher in the border than center as a result of high territorial conflicts at the border of territory (BC2).

(2) Natural barriers (rivers, lakes and ridges) will be predominantly found in the border than the center as a way to reduce energy cost for traveling (BC3).

(3) Anthropogenic features (buildings and main roads) will be predominantly found in the border compared to the center to avoid human encounters (BC4) but forest roads will be found predominantly or in both equally in center than border to use as easy travel routes (BC5).

Additionally, borders of wolf territories can be affected by the presence or absence of neighboring wolf territories. Therefore, we divided the territory borders into two classes: those with neighboring wolf packs (NB) and those with non-neighboring wolf packs (NNB). We then investigated the following hypotheses:

(1) Moose density is higher in border areas with neighboring territories than those with non-neighboring territory, as a result of high territorial conflicts at the neighboring border (NB1).

(2) Natural barriers (rivers, lakes and ridges) will be predominantly found in border areas with non-neighboring territory than those with neighboring territories, as a way to reduce energy cost for traveling (NB2).

(3) Anthropogenic features (houses and main roads) will be predominantly found in border areas with non-neighboring territory compared to those with neighboring territory to avoid human encounters (NB3) but forest roads will be found predominantly in border areas with neighboring territory than those with non-neighboring territory to use as easy travel routes (NB4).

2. Methods

Study area

I carried out this study in the southcentral parts of the Scandinavian peninsula (Sweden and Norway) where the main wolf population of Scandinavia has been located (Fig. 1; 59°–62°N, 11°–19°E). The vegetation is dominated by boreal coniferous forest of mainly Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), but broad-leaved tree species can also occur: birch (*Betula pendula* and B. *pubescens*), aspen (*Populus tremula*), alder (*Alnus incana* and *A. glutinosa*), willow (*Salix* spp.)

and rowan (*Sorbus aucuparia*). Around 60 % of the study area is covered with forest (Table 1) and the tree line is 800-900 m above sea level. The ground vegetation is dominated by lichens, mosses, grasses, herbs, berries and other heather species. The forests are subject to intensive forestry by clearcutting for timber harvest and increasing forest productivity with different silvicultural practices. Because of this, there is a high density of forest roads in the study area (1.01 ± 0.69 km/km^2). The mean number of house density is 19.54 ± 68.07 pr. km^2. The area is covered with snow from November to April (Milleret et al. 2017a; Zimmermann et al. 2015), with an average snow depth of 30–60 cm in mid-winter. The climate is continental with average temperatures of -7 °C in January (Mattisson et al. 2013).

Defining wolf territory border; home range estimation

I used wolf location data collected within the Scandinavian Wolf Research Project (SKANDULV: http:// skandulv.nina.no) since 1999. I analyzed data from 26 wolf territories monitored during one or several winters in the period from 2001 to 2020 (Table 2). Wolves were immobilized using a CO_2-powered dart gun from a helicopter. All captures were approved by the Norwegian Animal Research Authority (FSA), the Norwegian Food Safety Authority, the Norwegian Environmental Agency and the Swedish Committee of Animal Welfare. Both the adult male and female were collared in six pairs of family groups, and only one of the adults in 26 pairs of family groups. Individuals were fitted with a global positioning system (GPS) collar (Simplex TM; Televilt / Followit Positioning AB, Lindesberg, Sweden, or GPS plus; Vectronic Aerospace, Berlin, Germany). Adult wolves of a pair of family group move together most of the time and there are no significant differences in space use between females and males (Mattisson et al. 2013). Thus, I decided to use location data of both female and male per territory but picked one of two animals' simultaneous positions randomly. Ideally, Mattisson et al. (2013) suggested that annual territories of Scandinavian wolf must be estimated with a minimum of 9 months with five or more locations per month. I therefore needed a minimum of 4.5 months with 5 locations per month in our 6 months long study. Thus, I had enough location data to estimate winter wolf territories in Scandinavia.

It is impossible to know where the exact wolf territory borders are. Therefore, I used two methods of home range estimation; minimum convex polygon (MCP) and local convex hull (LoCoH). MCP is an ordinal home range estimation method which shapes the home range by connecting the outer most location points from the animal (Mohr and Stumpf 1966). LoCoH estimates home range with a nonparametric kernel method using a fixed number of nearest neighboring points. This is the most suitable method for GPS data because it can more precisely show the shape of the home range (Getz et al. 2007). MCP is more robust than LoCoH and it can include more places that were never visited by an animal. MCP is comparable with previous studies, therefore using MCP as one of two or more methods of home range calculation is valuable (Harris et al. 1990). I used all of points (100% MCP) to cover all area wolves used. Here, I investigated the factors which shape wolf territories estimated by LoCoH contrasted by MCP. I used the LoCoH-k method a nonparametric kernel method using a fixed number of nearest neighboring points (Getz et al. 2007). I used 95 % of points (95% LoCoH-k) to remove places where wolves did not visit that much often. At the same time, I avoided to have several parts for one territory. All of the estimations of territories were processed in R (Version 4.0.3). Additionally, I generated 1 km and 2.5 km width of buffer on each side of the estimated territory boundaries and defined them as border of territories which means I generated two widths of border; 2 km border and 5 km border (Fig. 4).

Neighboring wolf data

We used data from snow tracking over 2,200–5,600 km each winter (from October 1 to April 30 in 2001 to 2020) by county and national wildlife management agencies, staff from several universities and research institutes as the National wolf population surveys in Sweden and Norway as our neighboring wolf data. At the same time, DNA samples from scat, urine, blood, tissue and hair were also collected, which allowed us to identify wolf individuals and family relationships (Wabakken et al. 2020). During this study period, the number of wolves grew from 23 to 450 individuals (Eriksen et al. 2011; Wabakken et al. 2020). All individual tracks and locations of DNA-samples were used to delineate a minimum range of occurrence with the 100% MCP method. I then calculated centroids of these ranges and buffered them with 20 km to delineate hypothetical wolf territories. The radius of 20 km was chosen because average home range size averaged 1,070 km^2 (Mattisson et al. 2013), corresponding to an average radius of 18 km for a hypothetically round territory. I increased this by an extra 2 km to make sure neighboring ranges would overlap with the territory borders of the studied wolf territories. Then I classified the overlapping parts of the border with the circles of 20 km radius as neighboring border, and other parts of the border as non-neighboring border (see Fig. 5). When I built models, I removed the territories which had a high (< 90 %) or low (> 10 %) rate of neighboring border, because I expected those territories to show none or too little contrast of habitat features between borders with and without neighboring wolves. Therefore 14 territories were removed for the models describing differences between territory borders with and without neighboring wolves (Table 4, 5).

Moose density

Moose density was estimated from moose pellet count surveys. Fecal pellet groups (FPG) were counted after snow melt in spring to estimate moose density inside wolf territories in winter estimated from data of collared wolf with 100% MCP. I used two different sampling regimes: 1) 40 plots aligned at 100 m distance along the border of a 1 km^2 square, or 2) five plots making up the edges and the center point of a square of 50 m side length. The plots were circular and had an area of 100 m^2. The squares were spaced regularly throughout the wolf territory. Winter pellets were identified by comparing the color and the position of the pellet pile in relation to the vegetation. The pellets which were located under the leaves were considered as pellets from before the leaf fall and were therefore not counted. I divided this number of pellets with the defecation rate of moose; 14 times/day (Rönnegård et al. 2008), length of winter and number of sample plots per square to calculate density of moose per square. From there, I scaled the densities up to one km^2. I then interpolated the average moose density (moose/km^2) throughout the wolf territory using inverse distance weighting IDW.

Environmental factors

According to the previous studies, the most common habitat type for moose is forest, especially young forest, as revealed by GPS monitoring and pellet group counts (Månsson et al., 2011), and moose avoid anthropogenic landscape features (Gervasi et al. 2013). Wolves select for rugged, forested areas at lower elevations and avoid human related landscape (May et al. 2008; Ordiz et al. 2020). Therefore, I included the following habitat variables of interest: the density of houses, main roads and forest roads were used as proxy for anthropogenic features, whereas slope, distance to rivers and lakes were selected as natural landscape features. Slope was calculated from digital elevation model (DEM). Land cover was obtained from the Corine Land Cover (2018) and classified into seven categories; anthropogenic land, water, open natural area, young forest, mixed forest, broad-leaved forest and coniferous forest (Table 2).

I also checked the correlation of environmental factors in every territory. I found that elevation had correlations to some other variables (e. g. 9 territories of MCP with 5km buffer got $R^2 > 0.06$). Therefore, elevation data was removed before modeling.

Analysis

I created 1,000 random points for each center and border (2,000 random points per territory). I extracted the values of the habitat variables (moose density, house density, main road density, forest road density, distance to water, slope, elevation, land cover) to each center and border points using Geographic Information System (Q-GIS 3.16). Points that fell outside the area where the moose density was assessed, where excluded from further analysis. This reduced the samples size by 12% for the MCP with 5 km border width and 7.6% for LoCoH with 2 km border width. To examine the effects of environmental factors on the location of center and border (or neighboring border and non-neighboring border), I used generalized linear mixed effect model (GLMM) in package lme4 in R. The category of territory (1 = border, 0 = center and then 1 = neighboring border, 0 = non-neighboring border) was the binary response variable in all models. The fixed variables (moose density, house density, main road density, forest road density, distance to water, slope, elevation, land cover) were assessed for correlation in each territory and scaled to know the strength of contributions. I observed correlation between the distance to water and the elevation (seven territories showed $r > 0.6$ in MCP with 2 km border), and thus removed the elevation from further analyses. For model selection, I tested for different combinations of fixed variables and the inclusion of a quadratic effect for moose density.

Territory ID was added as a random effect in each model. I used Akaike's information criterion (AIC) to find the best model and defined as the model with the lowest AIC value (Table 7, 9).

3. Results

Territory area

I obtained 28 territories from 38 wolves using an average of 718 ± 337 GPS locations per territory (Table 2). The size of territories had large variation in both MCP and LoCoH estimators. They were on average 733 ± 434 km^2 for MCP (maximum 1,799 km^2, minimum 170 km^2) and 512 ± 325 km^2 for LoCoH (maximum 1,356 km^2, minimum 117 km^2), respectively. The difference of area between those two estimators was significant (paired *t*-test; $t = 8.56$, df = 25, $P < 0.0001$) (Fig. 3). The territory borders were longer if estimated with MCP (104 ± 29 km) as compared to LoCoH (97 ± 34 km) (paired *t*-test; $t = 2.81$, df = 25, $P < 0.01$) (Table 3).

I used 14 territory borders to investigate effects of neighboring wolf packs. With 2 km borders, the average center area was larger than border area for both MCP and LoCoH, but vice versa for 5 km borders. The ratio of neighboring to non-neighboring border area was similar for the four combinations of home range estimator and border width (Table 3, 4; Fig. 2).

Habitat differences between territory border and center

- LoCoH with 2 km border

The best models included all variables (Table 8). Distance to water showed the strongest negative effect (Water: $\beta = -0.185$, SE = 0.011, $P < 0.001$) and the strongest positive effect variable was main road density (MR: $\beta = 0.095$, SE = 0.010, $P < 0.001$) (Table 8; Fig. 6). Moose density as quadratic effect showed the second strongest effect in this model with the probability of being a border point decreasing between 0 – 5 scaled moose/km^2, and increasing thereafter (Moose: $\beta = -0.139$, SE = 0.016, $P < 0.001$, $Moose^2$: $\beta = 0.015$, SE = 0.003, $P < 0.001$) (Table 8; Fig. 6). Forest road density had the weakest effect in this model, and it was positive (Slope: $\beta = 0.075$, SE = 0.011, $P < 0.001$) (Table 8; Fig. 6). From the result of land cover, the probability of a point being a border point was highest in broad-leaved forest (Broad-leaved forest: $\beta = 1.267$, SE = 0.271, $P < 0.001$) and lowest in open natural area (Mixed forest: β = - 0.273, SE = 0.081, P < 0.001) (Table 8; Fig. 6).

- LoCoH with 5 km border

The best models included all variables (Table 8). Distance to water showed the strongest negative effect (Water: β = -0.217, SE = 0.012, P < 0.001) and the strongest positive effect variable was main road density (MR: β = 0.111, SE = 0.011, P < 0.001) (Table 8; Fig. 6). Moose density as quadratic effect showed the second strongest effect in this model with the probability of being a border point decreasing between 0 – 5 scaled moose/km^2, and increasing thereafter (Moose: β = -0.187, SE = 0.016, P < 0.001, $Moose^2$: β = 0.026, SE = 0.004, P < 0.001) (Table 8; Fig. 6). Slope had the weakest effect in this model, and it was positive (Slope: β = 0.065, SE = 0.011, P < 0.001) (Table 8; Fig. 6). From the result of land cover, the probability of a point being a border point was highest in broad-leaved forest (Broad-leaved forest: β = 0.780, SE = 0.278, P < 0.005) and lowest in mixed forest (Mixed forest: β = - 0.579, SE = 0.095, P < 0.001) (Table 8; Fig. 6).

- MCP with 2 km border

The best models included all variables (Table 8). Distance to water showed the strongest negative effect (Water: β = -0.251, SE = 0.012, P < 0.001) and the strongest positive effect variable was house density (House: β = 0.147, SE = 0.015, P < 0.001) (Table 8; Fig. 6). Moose density did not have quadratic effect and it showed a weak negative effect in this model (Moose: β = -0.096, SE = 0.012, P < 0.001) (Table 8; Fig. 6). From the result of land cover, the probability of a point being a border point was highest in anthropogenic land (Anthropogenic: β = 0, reference value) and the lowest in water and young forest (Water: β = -0.424, SE = 0.083, P < 0.001; Young forest: β = -0.423, SE = 0.079, P < 0.001) (Table 8; Fig. 6). Broad-leaved forest (P = 0.073) and mixed forest (P = 0.083) were not significant different from anthropogenic land (Table 8; Fig. 6).

- MCP with 5 km border

The best models included all variables (Table 8). Distance to water showed the strongest negative effect (Water: β = -0.268, SE = 0.012, P < 0.001) and the strongest positive effect variable was house density (House: β = 0.157, SE = 0.018, P < 0.001) (Table 8; Fig. 6). Moose density did not have quadratic effect and it showed a weak negative effect in this model (Moose: β = -0.057, SE = 0.012, P < 0.001) (Table 8; Fig. 6). From the result of land cover, the probability of a point being a border point was highest in anthropogenic land (Anthropogenic: β = 0, reference value) and lowest in young forest (Young forest: β = -0.362, SE = 0.081, P < 0.001) (Table 8; Fig. 6). Broad-leaved forest (P = 0.113) and mixed forest (P = 0.549) were not significant different from anthropogenic land (Table 8; Fig. 6).

<u>Habitat differences between borders with and without neighboring wolf territories</u>

- LoCoH with 2 km

The best models included moose density, house density, distance to water, slope and land cover, but excluded main road density and forest road density (Table 9). Moose density showed the strongest effect with quadratic effect (Moose: β = 0.799, SE = 0.050, P < 0.001, $Moose^2$: β = -0.142, SE = 0.015, P < 0.001) and the strongest positive effect variable was distance to water (Water: β = 0.624, SE = 0.030, P < 0.001) (Table 9; Fig. 7). From the result of land cover, the probably of a point being a neighboring border point was highest in water (Water: β = 1.799, SE = 0.286, P < 0.001) and lowest in anthropogenic land (Anthropogenic: β = 0, reference value). Broad-leaved forest (P = 0.240) was not significant different from anthropogenic land (Table 9; Fig. 7).

- LoCoH with 5 km

The best models included moose density, house density, forest road density, distance to water and land cover, but excluded main road density and slope (Table 9). Moose density showed the strongest effect with quadratic effect (Moose: β = 0.769, SE = 0.049, P < 0.001, $Moose^2$: β = -0.099, SE = 0.012, P < 0.001) and the strongest positive effect variable was distance to water (Water: β = 0.577, SE = 0.030, P < 0.001) (Table 9; Fig. 7). From the result of land cover, the probably of a point being a neighboring border point was highest in water (Water: β = 2.405, SE = 0.307, P < 0.001) and lowest in anthropogenic land (Anthropogenic: β = 0, reference value). Broad-leaved forest (P = 0.210) was not significant different from anthropogenic land (Table 9; Fig. 7).

- MCP with 2 km

The best models included all variables except forest road density and slope (Table 9). Moose density showed the strongest effect with quadratic effect (Moose: β = 0.794, SE = 0.052, P < 0.001, $Moose^2$: β = -0.121, SE = 0.031, P < 0.001) and the strongest positive effect variable was distance to water (Water: β = 0.748, SE = 0.031, P < 0.001) (Table 9; Fig. 7). From the result of land cover, probability of neighboring border was the highest in open natural area (Open natural area: β = 1.565, SE = 0.264, P < 0.001) and the lowest in anthropogenic land (Anthropogenic: β = 0, reference value). Broad-leaved forest (P = 0.734) was not significant different from anthropogenic land (Table 9; Fig. 7).

- MCP with 5 km

The best models included all variables except slope (Table 9). The strongest positive effect variable was distance to water (Water: β = 0.668, SE = 0.032, P < 0.001) and moose density showed the second strongest effect with quadratic effect (Moose: β = 0.482, SE = 0.053, P < 0.001, $Moose^2$: β = 0.069, SE = 0.029, P = 0.016) and from the result of land cover, probability of neighboring border was the highest in water (Water: β = 1.860, SE = 0.271, P < 0.001) and the lowest in anthropogenic land (Anthropogenic: β = 0, reference value). Broad-leaved forest (P = 0.130) was not significant different from anthropogenic land (Table 9; Fig. 7).

4. Discussion

Habitat differences between territory border and center

Both methods of MCP and LoCoH showed that the borders of wolf territories were located where the density of anthropogenic features was high, and it was located near water. Only the effect of moose density was different between home range estimators. For the MCP method, I found that territory borders in general had lower moose densities than the territory centers. This result supports hypothesis BC1, indicating that wolves monopolize areas of prey concentrations and place territory borders in areas of lower prey densities. For the LoCoH method that more accurately describes the shape of the wolf territory by excluding areas that were not used by wolves, border areas had on average either lower or higher moose densities than the centers. This partly supports the alternative hypothesis BC2, stating that territory borders are shaped by intra-specific competition for areas with high resource concentrations. In a study on wolves in Minnesota, the United States (Fritts and Mech 1981), wolf predation changed from core areas to the edge of the territory during a period of prey decline. No documented intraspecific fights have been observed in Scandinavia (Liberg et al. 2020; Mattisson et al. 2013), and so far Scandinavian moose have not responded to the presence of wolves by changing their behavior (Ausilio et al. 2021; Eriksen et al. 2011; Gervasi et al. 2013; Gicquel et al. 2020; Nicholson et al. 2014; Northrup et al. 2013; Sand et al. 2006; Wikenros et al. 2016). Therefore, it has been considered that moose densities in Scandinavia might be affected more strongly by human-driven bottom-up processes than top-down regulation by wolves (Ausilio et al. 2021). Clearcutting and enhanced productivity in forestry and agriculture lead to a patchy distribution of forage availability for moose, with important browse species being associated with valley bottoms close to settlements, rivers and roads. In winter, moose distribution and habitat selection therefore overlap with that of humans. In our study, wolf territory borders defined by LoCoH were closer to anthropogenic areas and at higher moose densities than the center of wolf territory.

I found support for the third hypothesis (BC3), since natural barriers (rivers, lakes and ridges with steep slopes) were more common in the border than in the center of the wolf territories in all our models. There are several studies suggesting large rivers can act as barriers for wolves. Paquet et al. (1996) reported for wolves in Alberta, Canada, that large rivers might represent barriers to wolf travel in summer, and that wolves walked parallel to the shoreline until finding a convenient point of crossing, and they occasionally crossed by swimming. However, when the rivers were frozen, it turned to be an easy travel route for wolves (Paquet et al., 1996). Especially when river and lakes together with anthropogenic features, it became barriers for wolves (Blanco, Cortés, and Virgós 2005; Carmichael et al. 2001). In our study area, there was no significant correlation between distance to water and density of anthropogenic features (density of house and main road), but it was quite common to see houses and roads along rivers (or lakes). Therefore, it is possible that wolf territories were synergistically shaped by those rivers (or lakes), roads and houses.

The territory borders had on average steeper slopes than the centres. In generally, wolves select flat area as their home range (Singleton 1995; Ciucci et al., 2003; Lesmerises et al., 2012) either as their travel routes (Ciucci et al. 2003; Singleton 1995; Whittington, St. Clair, and Mercer 2005) and as predation site (Kauffman et al. 2007). However, steep slopes are mostly combined with the topography of valley bottoms, where borders occur along rivers and lakes, and therefore include the declining valley slopes. I hypothesize that the effect of slope is therefore more an effect of the topography than the steepness in itself for limiting the extent of a wolf territory.

The density of forest and main roads was higher at the border compared to the center of wolf territories, providing support for our fourth hypothesis (BC4). Wolves avoid areas of high anthropogenic activity, which often include main roads, high-ways and houses (Lesmerises et al. 2012; Mancinelli and Ciucci 2018; May et al. 2008; Zimmermann et al. 2014). Main roads may therefore have a barrier effect. Although, forest roads can be useful to travel long distances, wolf territories were located in low forest road density area in Scandinavia included (Ciucci et al. 2003; Zimmermann et al. 2014). Furthermore, forest roads can be used as scent marking spots (Bojarska et al. 2020). Normally the center of wolf territories included denning sites (Ciucci and Mech 1992), this might explain why we found lower density of forest road in the center than border of wolf territories.

Habitat differences between borders with and without neighboring wolf territories

I only found support for the first hypothesis (NB1) that moose density would be higher in neighboring border than non-neighboring border in MCP models with 5 km border. There was a possibility that 5 km border of MCP included border of neighboring wolf territory border which had high moose density area, but more data is needed to investigate this relationship. Contrasted to this, other models than MCP with 5 km border showed that when the moose density was low to middle, the probability of a point being in neighboring border became higher. This was indicating that borders that were not shared by neighboring wolf packs had either a lower or higher moose density than borders that were shared by neighbors. According to the previous studies in North America, wolves avoided territory border to avoid encounters with neighboring wolves (Carbyn 1983; Mech 1977, 1994; Mech and Harper 2002), and the density of prey in the border of territory became higher than at the center of territory because prey used the wolf territory border as refuges (Lewis and Murray 1993; Mech 1977; Mech et al. 1980). However, Carbyn (1983) did not observed a similar response for prey species of wolves in Manitoba, Canada, and concluded that this difference might be due to differences in prey density and the high human-caused mortality. In Scandinavia, the density of moose is higher than other places where moose is a main prey species of wolves and also hunting success rate is also high (Sand et al. 2006). Additionally, the human-caused mortality is high among Scandinavian wolves (Liberg et al. 2020). Those two factors may make the same situation with the wolves in Mountain National Park, Manitoba.

I found support for the hypothesis (NB2), since natural barriers were predominantly found in non-neighboring rather than neighboring borders. This was indicating that neighboring borders were further from water than non-neighboring borders. This may be explained that the territories overlapped because of absence of river or lakes, meaning that the water makes wolves easier to defend their territory (Mech and Boitani 2003). The slope was significant in only LoCoH with 2 km border and it showed that the probability of a point being in neighboring border was higher when it was flatter. This may be explained as water that steeps are acting like barrier between wolf territories.

I did not found support for the third hypothesis (NB3), since house density was high in neighboring border compare to non-neighboring border in all models. The main road density showed a similar effect but only models of MCP included the variables. Additionally, since forest road density also showed a similar effect with house and main road density, the fourth hypothesis (NB4) was supported in model of LoCoH with 2 km border and MCP with 2 km border. Those were indicating that the density of all three anthropogenic features were higher in neighboring border than non-neighboring border. Considering of neighboring border had fewer natural barriers than non-neighboring border, it might be explained as neighboring border were located human activity area. However, the result of landcover was not similar to those result that water cover or open natural area showed the highest probability of a point being in neighboring border and anthropogenic land showed the lowest. At least, I can say that those environmental factors in neighboring border were not moose preference neither wolf preference factors. Thus, there is a possibility that wolf territories are overlapping where the wolves do not prefer to use.

5. Conclusion

In this study, I found that wolf territories in Scandinavia can be shaped by both natural (e.g., large rivers, large lakes, and ridges as natural barriers) and anthropogenic (houses and roads) features. Wolves normally avoid anthropogenic features meaning that it looked as if wolf territories were forced to be there by those features. However, assuming the high moose density area were beside of anthropogenic features, wolves may be tolerant to live in this human dominated landscape. Additionally, I found that wolf territories are overlapping in where wolves are not interested in. This may indicate that wolves have still enough space to live. In methodologically, I found that much more differences between home range estimators (MCP and LoCoH) than between widths of borders (2 km and 5 km). I consider that MCP may be better when we explain in terms of the resource distribution of basement of wolf territories. In contrast, when we explain the structure of actual wolf territories, LoCoH can be better estimator. The width of border should not be a big problem since I got similar result when compared the habitat within center and border of territories. However, since I got very different result from MCP with 5 km border, I need to investigate which width of border is better to see the habitat of neighboring border and non-neighboring border. Looking into the structure of habitat within the wolf territories might be important to understand what they need and do not need.

6. Management implications

In Scandinavia, human-carnivore conflicts have become long history like many other countries. Since low productivity of agriculture due to the high latitude, livestock productivity has been important industry (Strand et al. 2019). Number of sheep killed by wolf has been increased after the wolf started recolonizing in 1980s, but it is decreasing in those few years, due to the arraignment of Carnivore Management Zone (CMZ) by Ministry of Environment. CMZ covers 55 % of land of Norway and only 10 % of the CMZ is wolf management zone (Hansen et al. 2019). The annual wolf quota is four litters by reproducing groups in Norway and two litters in Sweden inside of wolf management zone (Strand et al. 2019). The CMZ is not a sanctuary and people can live, but livestock farming needs to be protected to avoid conflicts with carnivores (Strand et al. 2019). Due to the main cause of wolf mortality is by humans in Scandinavia (Liberg et al. 2020; Milleret et al. 2017b; Recio et al. 2018), wolves choose low human activity area when they settle their territories (Ordiz et al. 2015). However, observation of footprints on snow by human settlement make residents to understand like the wolves became tolerance to human and can be fear for the residents. Hence, Carricondo-Sanchez et al. (2020) investigated the movement and habitat use of wolves and concluded that wolves consistently avoided human settlements and main roads, and observed the avoidance became lower at higher latitudes particularly in winter. They considered this was because of the wintering areas of wolf prey (Carricondo-Sanchez et al. 2020). It can be also explained from my study that the wolf territory borders were located near anthropogenic features and high moose density area at the same time. Therefore, observation of wolf or wolf tracks near human settlements in winter is not because of wolf tolerance to people neither utility of anthropogenic land by wolves, but it is because of the moose wintering area may became closer to human activity area. This result will be useful together with summer data to design the wolf management zone in future.

Acknowledgements

Firstly, I would like to thank **Koji Yamazaki**-sensei who let me join the Japanese Asian black bear research project and then let me go to Inland Norway University and send me heartwarming messages from Japan during the COVID-19 pandemic situation. I could not be there without your help. Next, I would like to thank **Petter Wabbakken** and **Barbara Zimmermann** for accepting me as part of the great wolf project, SKANDULV. I was even afraid to use all of the data collected by many people across many years. I cannot imagine how hard building those systems was. I also appreciate **Boris Fuchs**, **Alina Evans**, **Erling Maartmann** and **Kristoffer Nordli** for taking us wolf capturing and collaring. It has been my long-term dream so I was very happy. I would like to acknowledge **Giorgia Ausilio** and **Laura Nicolai** for always supporting me during my thesis and I could not have made it without you. Also, **Hijiri Shimojima** taught me how to use GIS in very first step, and **Yui Nemto** helped analyzing data in the last moments, I appreciate your strong support from Japan. In addition, I want to thank **Ruben Leroy**, **Malena Diaz Gomez**, **Irene Garcia Noa**, **Sara Skybak** and **Isabelle Demange** and all other students from Evenstad who helped our huge area of moose pellet counting. I spent wonderful moments with you. I want to thank the friendly students from Tokyo University of Agriculture, especially **Yu Hirano**, **Kazuma Aoiki** and **Ayaka Hasegawa**, they supported me at all times, even when we could not see each other!

Lastly, I appreciate this amazing animal, the wolf, and the beautiful nature in Norway and Sweden. It is hard to compare nature in Japan and Scandinavia, but what I loved most in Scandinavian is that they have nature in their lifestyle, which was very different from what we have in Japan. Moreover, the most different part was the number of species of large carnivore. We lost two sub-species of wolves, Japanese wolf (*Canis lupus hodophilax*) and Ezo wolf (*Canis lupus hattai*), for more than hundred years ago. Then we have only Japanese black bear (*Ursus thibetanus japonicus*) and Ezo brown bear (*Ursus arctos yesoensis*) as large carnivores. I consider human’s final goal is to coexist with large carnivores and then, our life becomes a sustainable life. I really hope people and wolf will live along together in Norway and Sweden.

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Tables

Table 1 Summary of land cover in study area.

Land Cover	Area (km²)	Ratio (%)
Coniferous forest	67042	58.54
Anthropogenic	13741	12.00
Water	11349	9.91
Open natural area	8629	7.53
Young forest	8017	7.00
Mixed forest	4818	4.21
Broad-leaved forest	923	0.81

Table 2 names of environmental factors, used code in model and units.

Variable	Variable code	Units
Natural factors		
Moose density	Moose	moose/km²
Distance to water	Water	km
Slope	Slope	degrees
Anthropogenic factors		
House density	House	pr. km²
Main road density	MR	km/km²
Forest road density	FGR	km/km²
Land cover	LC	
Coniferous forest	Coniferous forest	count
Broad-leaved forest	Broad-leaved forest	count
Mixed forest	Mixed forest	count
Young forest	Young forest	count
Open natural area	Open natural area	count
Water	Water	count
Anthropogenic land	Anthropogenic	count

Table 3 Summary of GPS collared wolf data including 38 individuals within 26 territories.

Wolf ID	Sex	Territory ID	Territory Year	GPS positions	MCP100% (km^2)	LoCoH95% (km^2)	Perimeter of MCP (km)	Perimeter of LoCoH (km)
M0109 M0110	M F	Gråfjell	2002	1027	1418.06	946.77	152.63	174.75
M0204	F	Tyngsjö	2002	557	1178.16	849.06	129.17	133.28
M0009	M	Bograngen	2003	439	858.36	636.58	119.73	104.03
M0105	M	Hasselfors	2003	383	436.02	324.55	84.75	75.53
M0209 M0306	F M	Djurskog	2004	821	340.68	252.62	87.22	81.67
M0404 M0405	M F	Jangen	2004	436	430.33	274.03	90.55	74.20
M0506 M0601	M F	Uttersberg	2006	786	381.88	225.05	74.90	63.30
M0610 M0611	F M	Gräsmark	2007	1184	1799.47	1355.86	162.75	139.96
M0602	F	Ulriksberg	2007	604	880.83	661.97	123.59	117.27
M0507	F	Kloten	2008	402	522.27	372.41	85.38	80.92
M0904 M0906	M F	Fulufjället	2009	843	517.48	367.36	90.41	97.64
M0901 M1003	M F	Riala	2010	851	221.94	149.29	58.14	50.39
M1001 M1002	F M	Tenskog	2010	488	730.84	675.92	99.60	102.71
M0909 M1103	F M	Tandsjön	2012	843	1074.32	741.77	125.45	116.67
M1301 M1302	F M	Kukumäki	2014	686	882.33	636.66	116.46	123.24
M1501 M1502	F M	Aspafallet	2015	415	636.74	434.68	96.16	106.64
M1503 M1714	M F	Slettås	2017	645	582.61	282.66	111.05	85.12
M1812 M1813	M F	Juvberget	2018	406	553.06	232.73	103.73	62.58
M1814	M	Norrsjön	2018 2019	316 1258	742.12 1606.42	510.34 1205.44	105.88 160.19	89.96 168.38
M1708 M1817	M F	Varåa	2018 2019 2020	309 1254 1119	169.99 399.64 470.80	116.96 297.16 336.23	55.18 78.93 87.02	41.37 76.20 84.43
M1813 M1902	F M	Juvberget	2020	1249	660.20	434.50	95.39	88.23
M1901 M1904	F M	Bograngen	2020	1152	1322.26	832.89	139.83	116.99
M2002	F	Ulvåa	2020	204	232.81	170.10	66.34	54.26
				Mean	732.68	512.45	103.86	96.53
				SD	434.38	324.82	29.24	33.53

Table 4 Area of center (C), border (B), neighboring border (NB) and non-neighboring border (NNB) of wolf territories estimated with 95 % LoCoH with 2 km and 5 km border. NB (%) shows ratio of NB within B. There were 14 territories which have ratio of NB was < 10 % or > 90 % were removed from analysis of modeling NB and NNB (*).

Territory ID		LoCoH/2km					LoCoH/5km					
		C (km^2)	B (km^2)	NB (km^2)	NNB (km^2)	NB (%)	C (km^2)	B (km^2)	NB (km^2)	NNB (km^2)	NB (%)	
Gråfjell	2002	776.43	279.62	82.58	197.04	29.53	537.97	697.80	203.94	493.87	29.23	
Tyngsjö	2002	719.36	265.80	0.00	265.80	0.00	538.32	661.61	0.00	661.61	0.00	*
Bograngen	2003	536.41	207.28	46.72	160.56	22.54	400.64	515.30	115.40	399.90	22.39	
Hasselfors	2003	252.90	150.24	0.00	150.24	0.00	160.09	372.43	0.00	372.43	0.00	*
Djurskog	2004	175.02	161.33	1.90	159.43	1.18	76.78	394.55	10.37	384.18	2.63	*
Jangen	2004	204.05	147.13	0.00	147.13	0.00	116.23	361.76	0.00	361.76	0.00	*
Uttersberg	2006	165.70	125.55	0.00	125.55	0.00	92.10	309.29	0.00	309.29	0.00	*
Gräsmark	2007	1219.26	346.83	43.51	303.32	12.55	1027.11	853.06	107.37	745.69	12.59	
Ulriksberg	2007	548.35	233.78	38.03	195.75	16.27	391.70	581.57	94.29	487.29	16.21	
Kloten	2008	295.07	161.27	0.00	161.27	0.00	192.95	400.41	2.35	398.06	0.59	*
Fulufjället	2009	274.86	190.81	0.00	190.81	0.00	157.36	456.99	0.00	456.99	0.00	*
Riala	2010	102.59	100.04	0.00	100.04	0.00	48.91	244.73	0.00	244.73	0.00	*
Tenskog	2010	576.63	204.78	0.00	204.78	0.00	440.48	509.55	0.00	509.55	0.00	*
Tandsjön	2012	629.26	231.95	0.00	231.95	0.00	476.07	574.68	0.00	574.68	0.00	*
Kukumäki	2014	517.18	245.64	0.00	245.64	0.00	353.00	609.72	0.00	609.72	0.00	*
Aspafallet	2015	331.92	209.76	197.66	12.10	94.23	200.41	506.06	474.80	31.26	93.82	*
Slettås	2017	202.12	168.07	36.97	131.10	22.00	97.94	411.02	89.48	321.54	21.77	
Juvberget	2018	174.40	123.82	123.82	0.00	100.00	103.03	304.51	304.51	0.00	100.00	*
Norrsjön	2018	424.13	179.21	62.49	116.72	34.87	308.88	445.36	155.41	289.95	34.90	
Norrsjön	2019	1040.65	335.15	88.20	246.95	26.32	806.99	833.38	217.66	615.71	26.12	
Varåa	2018	79.08	82.34	52.96	29.38	64.32	35.63	204.09	134.00	70.09	65.66	
Varåa	2019	225.24	151.03	102.28	48.75	67.72	133.60	372.27	252.53	119.74	67.83	
Varåa	2020	255.35	167.99	67.06	100.93	39.92	149.55	409.02	169.76	239.26	41.50	
Juvberget	2020	350.39	175.14	110.28	64.86	62.97	241.07	431.42	274.24	157.18	63.57	
Bograngen	2020	720.24	232.28	110.45	121.83	47.55	567.60	574.81	271.61	303.20	47.25	
Ulvåa	2020	119.24	108.21	106.73	1.48	98.63	57.49	267.53	265.39	2.15	99.20	*
Mean		419.84	191.73	48.91	142.82	28.48	296.61	473.19	120.89	352.30	28.66	
SD		294.44	66.82	53.34	83.31	33.62	249.47	166.42	130.10	206.92	33.67	

Table 5 Area of center (C), border (B), neighboring border (NB) and non-neighboring border (NNB) of wolf territories estimated with 100 % MCP with 2 km and 5 km border. NB (%) shows ratio of NB within B. There were 14 territories which have ratio of NB was < 10 % or > 90 % were removed from analysis of modeling NB and NNB (*).

Territory ID		MCP/2km					MCP/5km					
		C (km^2)	B (km^2)	NB (km^2)	NNB (km^2)	NB (%)	C (km^2)	B (km^2)	NB (km^2)	NNB (km^2)	NB (%)	
Gråfjell	2002	1269.01	325.22	84.25	240.97	25.91	1058.87	812.10	218.13	593.97	26.86	
Tyngsjö	2002	1052.33	258.09	0.00	258.09	0.00	876.14	644.28	0.00	644.28	0.00	*
Bograngen	2003	742.30	238.88	59.89	178.98	25.07	581.96	595.03	149.31	445.71	25.09	
Hasselfors	2003	354.70	169.16	0.00	169.16	0.00	245.70	421.53	0.00	421.53	0.00	*
Djurskog	2004	256.93	174.07	19.38	154.69	11.13	144.36	433.71	47.38	386.32	10.93	*
Jangen	2004	343.81	180.16	0.00	180.16	0.00	229.33	446.69	0.00	446.69	0.00	*
Uttersberg	2006	310.45	149.41	0.00	149.41	0.00	216.67	371.72	0.00	371.72	0.00	*
Gräsmark	2007	1640.09	304.77	46.99	257.78	15.42	1413.57	760.05	115.29	644.77	15.17	
Ulriksberg	2007	760.65	246.86	38.03	208.84	15.41	593.32	615.84	94.29	521.55	15.31	
Kloten	2008	440.27	170.47	0.38	170.09	0.22	329.98	425.06	10.68	414.38	2.51	*
Fulufjället	2009	430.45	180.53	15.06	165.47	8.34	312.55	450.24	36.77	413.47	8.17	*
Riala	2010	167.46	115.70	0.00	115.70	0.00	99.60	286.97	0.00	286.97	0.00	*
Tenskog	2010	634.53	199.01	0.00	199.01	0.00	502.32	496.86	0.00	496.86	0.00	*
Tandsjön	2012	952.33	250.53	0.00	250.53	0.00	782.31	624.93	0.00	624.93	0.00	*
Kukumäki	2014	769.22	232.66	0.00	232.66	0.00	612.15	580.64	0.00	580.64	0.00	*
Aspafallet	2015	544.05	191.93	174.85	17.08	91.10	417.99	478.42	434.15	44.27	90.75	*
Slettås	2017	474.96	221.79	119.73	102.06	53.99	327.10	552.48	296.74	255.74	53.71	
Juvberget	2018	453.27	206.61	200.58	6.04	97.08	318.43	513.29	497.38	15.91	96.90	*
Norrsjön	2018	639.80	211.28	62.49	148.79	29.58	499.66	526.44	155.41	371.03	29.52	
Norrsjön	2019	1449.47	320.24	93.39	226.85	29.16	1226.18	800.07	230.82	569.25	28.85	
Varåa	2018	118.37	109.88	60.40	49.48	54.97	54.94	272.34	157.10	115.25	57.68	
Varåa	2019	324.08	157.58	107.51	50.06	68.23	223.68	392.59	269.49	123.10	68.64	
Varåa	2020	387.20	173.71	84.35	89.36	48.56	275.34	432.27	211.69	220.58	48.97	
Juvberget	2020	568.08	190.59	131.02	59.57	68.74	442.14	475.79	326.05	149.75	68.53	
Bograngen	2020	1185.89	279.28	189.06	90.21	67.70	994.30	696.75	462.48	234.27	66.38	
Ulvåa	2020	170.01	132.24	130.76	1.48	98.88	91.18	326.80	324.65	2.15	99.34	*
Mean		632.30	207.33	62.24	145.10	31.13	494.99	516.65	155.30	361.35	31.28	
SD		406.03	58.53	64.60	80.47	33.62	363.38	146.69	159.72	200.73	33.58	

Table 6 Mean number of fixed variables (a) and count number and rate of land cover (b) inside of wolf territories center and border estimated with 100 % MCP.

(a)

Variable	Units	C (n = 25,349)		B (n = 17,848)	
		Mean	SD	Mean	SD
Moose density	moose/km²	1.23	0.97	1.22	0.96
House density	pr. km²	3.78	10.63	5.67	15.75
Main road density	km/km²	0.20	10.63	0.25	0.37
Forest road density	km/km²	0.87	0.52	0.92	0.55
Distance to water	km	4.44	3.16	3.79	3.19
Slope	degree	1.89	1.66	2.09	1.70

(b)

Land cover	C (n = 25,349)		B (n = 17,848)	
	Count	%	Count	%
Coniferous forest	17,383	68.57	11,918	66.77
Open natural area	3,252	12.83	2,304	12.91
Young forest	2,462	9.71	1,560	8.74
Water	1,212	4.78	944	5.29
Mixed forest	564	2.22	529	2.96
Anthropogenic land	449	1.77	565	3.17
Broad-leaved forest	27	0.11	28	0.16

Table 7 Selecting models for comparing B (= 1) and C (= 0). All four models included all seven variables.

Method	Model	k	AICc	ΔAICc	AICcWt	Cum.Wt	LL
LoCoH/2km							
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + Slope + LC	15	65341	0.00	1.00	1.00	-32655
	Moose + House + MR + FGR + Water + Slope + LC	14	65359	18.01	0.00	1.00	-32665
LoCoH/5km							
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + Slope + LC	15	63078	0.00	1.00	1.00	-31524
	Moose + House + MR + FGR + Water + Slope + LC	14	63128	50.07	0.00	1.00	-31550
MCP/2km							
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + Slope + LC	15	63078	0.00	1.00	1.00	-31524
	Moose + House + MR + FGR + Water + Slope + LC	14	63128	50.07	0.00	1.00	-31550
MCP/5km							
	Moose + House + MR + FGR + Water + Slope + LC	14	56592	0.00	0.73	0.73	-28282
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + Slope + LC	15	56594	1.96	0.27	1.00	-28282

Table 8 Summary of all four models for explaining B (= 1) and C (= 0).

Variables		LoCoH/2km			LoCoH/5km			MCP/2km			MCP/5km		
		β	SE	P	β	SE	P	β	SE	P	β	SE	P
	(Intercept)	0.169	0.083	0.041	0.271	0.089	0.002	0.056	0.099	0.575	-0.123	0.104	0.240
	Moose	-0.139	0.016	< 0.001	-0.187	0.016	< 0.001	-0.096	0.012	< 0.001	-0.057	0.012	< 0.001
	$Moose^2$	0.015	0.003	< 0.001	0.026	0.004	< 0.001	-	-	-	-	-	-
	House	0.078	0.013	< 0.001	0.089	0.013	< 0.001	0.147	0.015	< 0.001	0.157	0.018	< 0.001
	MR	0.095	0.010	< 0.001	0.111	0.011	< 0.001	0.066	0.011	< 0.001	0.075	0.012	< 0.001
	FGR	0.076	0.011	< 0.001	0.085	0.011	< 0.001	0.114	0.012	< 0.001	0.115	0.012	< 0.001
	Water	-0.185	0.011	< 0.001	-0.217	0.012	< 0.001	-0.251	0.012	< 0.001	-0.268	0.012	< 0.001
	Slope	0.093	0.011	< 0.001	0.065	0.011	< 0.001	0.082	0.011	< 0.001	0.047	0.012	< 0.001
LC	Broad-leaved forest	1.267	0.271	< 0.001	0.780	0.278	0.005	0.397	0.221	0.073	0.454	0.287	0.113
	Coniferous forest	-0.335	0.075	< 0.001	-0.553	0.076	< 0.001	-0.351	0.072	< 0.001	-0.288	0.074	< 0.001
	Mixed forest	-0.317	0.093	< 0.001	-0.579	0.095	< 0.001	-0.160	0.092	0.083	-0.057	0.095	0.549
	Open natural area	-0.273	0.081	< 0.001	-0.436	0.083	< 0.001	-0.280	0.079	< 0.001	-0.248	0.081	0.002
	Water	-0.283	0.084	< 0.001	-0.508	0.086	< 0.001	-0.424	0.083	< 0.001	-0.234	0.085	0.006
	Young forest	-0.423	0.081	< 0.001	-0.545	0.082	< 0.001	-0.423	0.079	< 0.001	-0.362	0.081	< 0.001

Table 9 Selecting models for comparing NB (= 1) and NNB (= 0). All four models included all seven variables.

Method	Model	*k*	AICc	ΔAICc	AICcWt	Cum.Wt	LL
LoCoH/2km							
	Moose + $(\text{Moose})^2$ + House + Water + Slope + LC	13	9357	0.00	0.37	0.37	-4666
	Moose + $(\text{Moose})^2$ + House + FGR + Water + Slope + LC	14	9357	0.25	0.33	0.70	-4665
	Moose + $(\text{Moose})^2$ + House + MR + Water + Slope + LC	14	9359	1.68	0.16	0.86	-4665
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + Slope + LC	15	9359	1.92	0.14	1.00	-4664
	Moose + House + MR + FGR + Water + Slope + LC	14	9492	134.76	0.00	1.00	-4732
LoCoH/5km							
	Moose + $(\text{Moose})^2$ + House + FGR + Water + LC	13	8864	0.00	0.43	0.43	-4419
	Moose + $(\text{Moose})^2$ + House + FGR + Water + Slope + LC	14	8865	1.04	0.25	0.68	-4418
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + LC	14	8865	1.47	0.20	0.88	-4419
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + Slope + LC	15	8867	2.59	0.12	1.00	-4418
	Moose + House + MR + FGR + Water + Slope + LC	14	8944	79.57	0.00	1.00	-4458
MCP/2km							
	Moose + $(\text{Moose})^2$ + House + MR + Water + LC	13	8593	0.00	0.36	0.36	-4283
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + LC	14	8593	0.33	0.31	0.67	-4282
	Moose + $(\text{Moose})^2$ + House + MR + Water + Slope + LC	14	8594	1.45	0.17	0.84	-4283
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + Slope + LC	15	8594	1.64	0.16	1.00	-4282
	Moose + House + MR + FGR + Water + Slope + LC	14	8607	14.25	0.00	1.00	-4289
MCP/5km							
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + LC	14	8321	0.00	0.69	0.69	-4146
	Moose + $(\text{Moose})^2$ + House + MR + FGR + Water + Slope + LC	15	8322	1.91	0.27	0.95	-4146
	Moose + House + MR + FGR + Water + Slope + LC	14	8326	5.39	0.05	1.00	-4149

Table 10 Summary of all four models for explaining NB (= 1) and NNB (= 0).

Variables		LoCoH/2km			LoCoH/5km			MCP/2km			MCP/5km		
		β	SE	P	β	SE	P	β	SE	P	β	SE	P
	(Intercept)	-2.709	0.946	0.004	-3.387	0.964	< 0.001	-2.678	0.986	0.007	-3.150	1.084	0.004
	Moose	0.799	0.050	< 0.001	0.769	0.049	< 0.001	0.794	0.052	< 0.001	0.482	0.053	< 0.001
	$Moose^2$	-0.142	0.015	< 0.001	-0.099	0.012	< 0.001	-0.121	0.031	< 0.001	0.069	0.029	0.016
	House	0.438	0.038	< 0.001	0.434	0.042	< 0.001	0.415	0.043	< 0.001	0.345	0.044	< 0.001
	MR	-	-	-	-	-	-	-0.162	0.030	< 0.001	-0.078	0.031	0.011
	FGR	-	-	-	-0.176	0.033	< 0.001	-	-	-	-0.114	0.032	< 0.001
	Water	0.624	0.030	< 0.001	0.577	0.030	< 0.001	0.748	0.031	< 0.001	0.668	0.032	< 0.001
	Slope	-0.112	0.031	< 0.001	-	-	-	-	-	-	-	-	-
LC	Broad-leaved forest	0.957	0.814	0.240	0.866	0.692	0.210	0.437	1.284	0.734	3.897	2.577	0.130
	Coniferous forest	0.965	0.269	< 0.001	1.590	0.288	< 0.001	1.212	0.253	< 0.001	1.384	0.252	< 0.001
	Mixed forest	1.062	0.311	< 0.001	1.884	0.327	< 0.001	0.915	0.294	0.002	1.539	0.295	< 0.001
	Open natural area	0.920	0.279	< 0.001	1.532	0.298	< 0.001	1.565	0.264	< 0.001	1.749	0.264	< 0.001
	Water	1.799	0.286	< 0.001	2.405	0.307	< 0.001	1.537	0.273	< 0.001	1.860	0.271	< 0.001
	Young forest	0.964	0.284	< 0.001	1.864	0.301	< 0.001	1.222	0.269	< 0.001	1.491	0.269	< 0.001

Figures

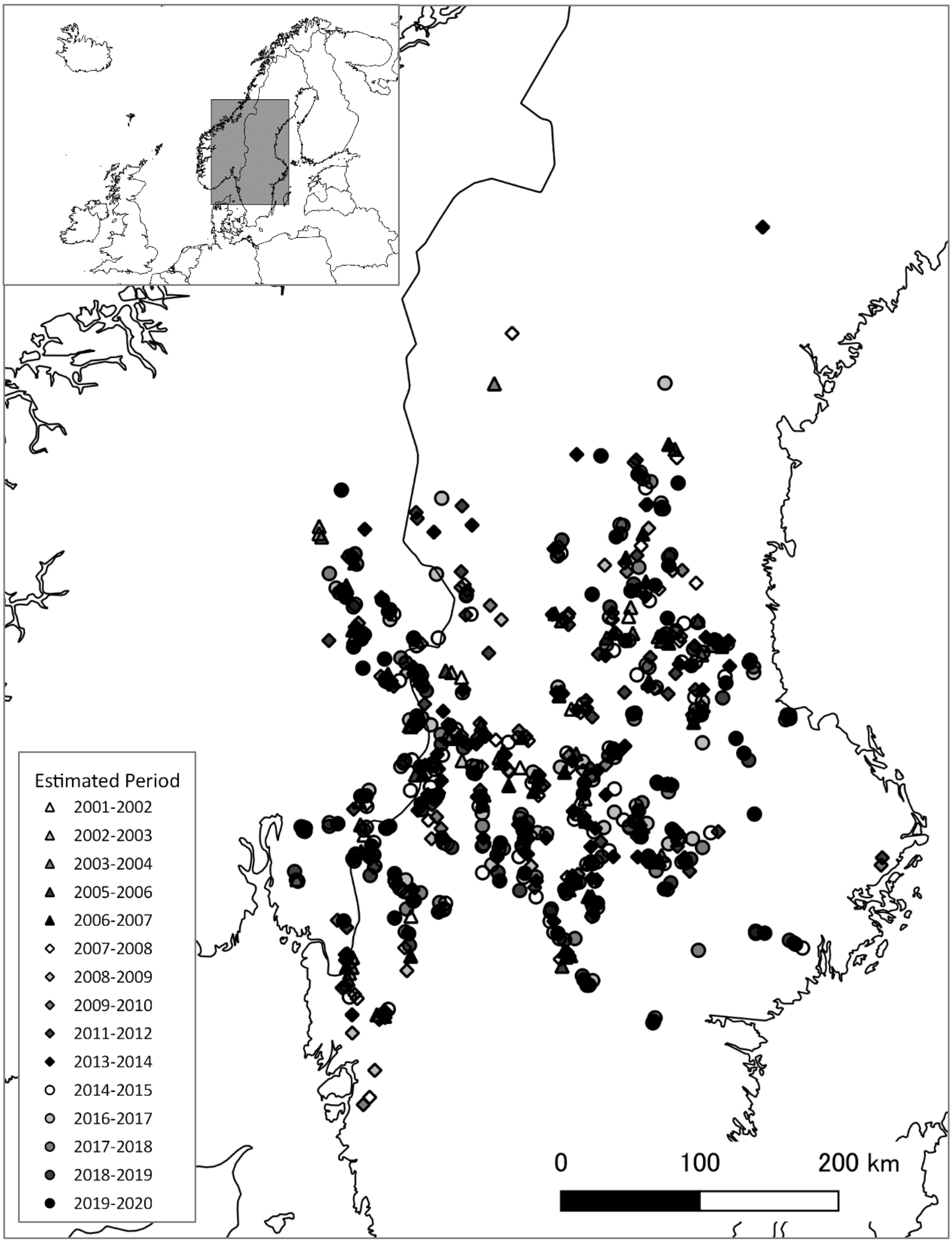

Fig. 1 Location of study area and centroids of all wolf territories which I used in analysis.

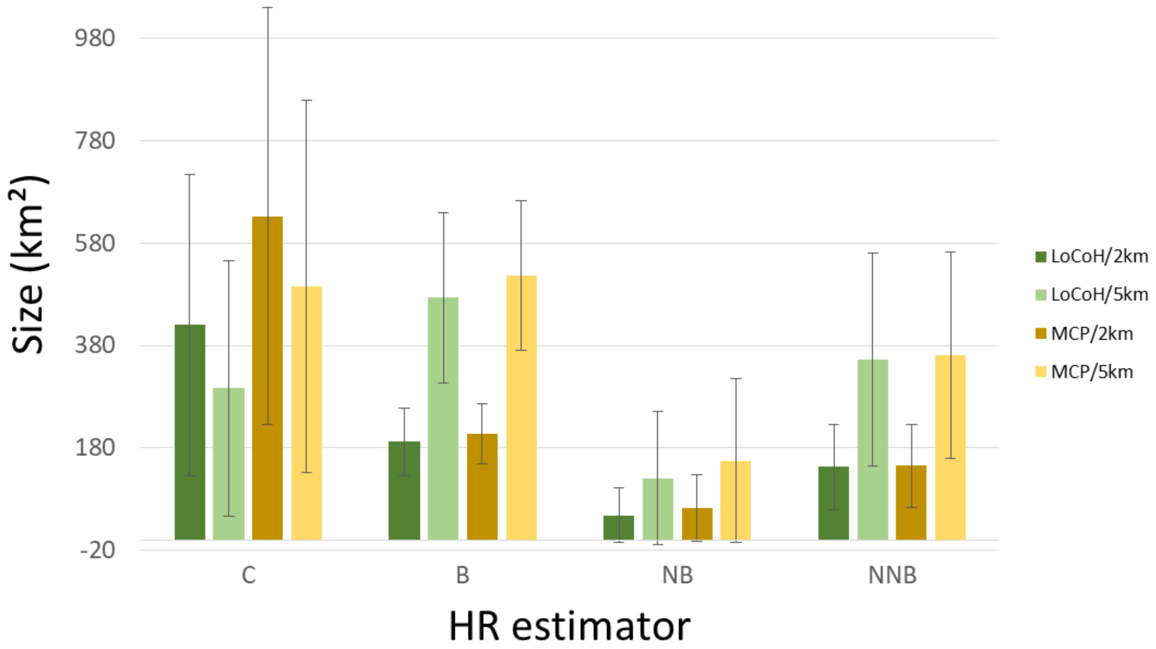

Fig. 2 Comparing area of each HR estimator with each polygon.

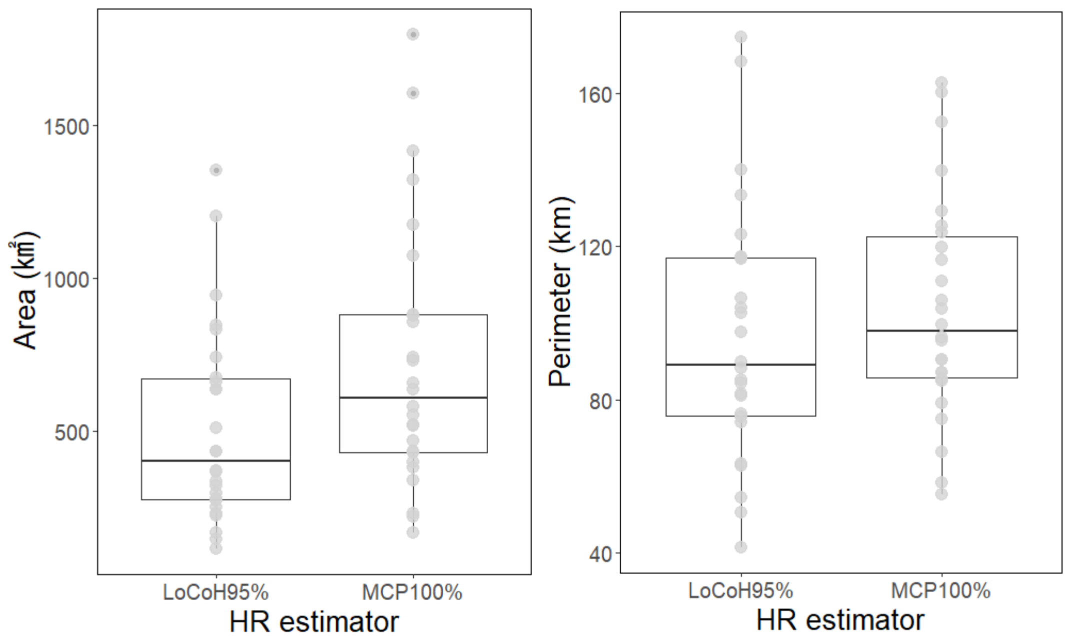

Fig. 3 Comparing areas and perimeters of each HR estimator.

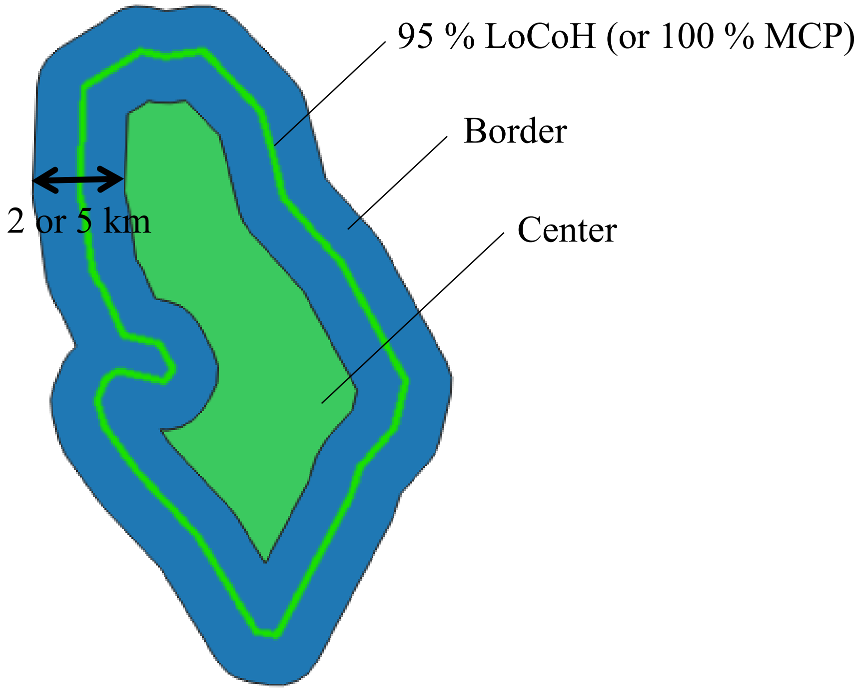

Fig. 4 Defining wolf territory border

An example of wolf territory estimated from GPS location (green line). I generated a buffer width of 2 or 5 km along the estimated territory (using 95 % LoCoH or 100 % MCP) and defined as border of territory (blue). The rest of part defined as center of territory (green).

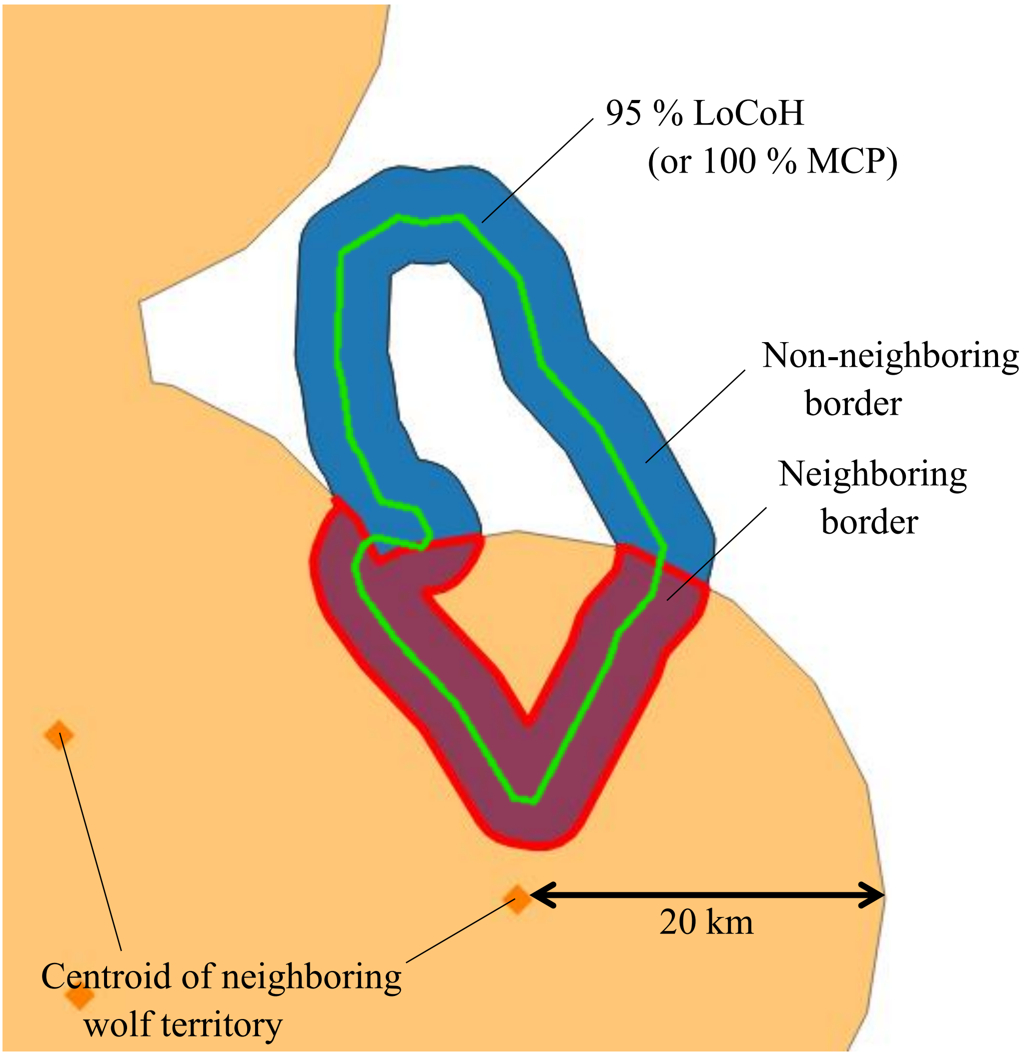

Fig. 5 Defining neighboring border and non-neighboring border

I generated 20 km radius from centroids (orange) of neighboring wolf territories which were estimated from winter snow tracking. The overlapping part of neighboring circles and border defined as neighboring border (red). the rest of part of border was defined as non-neighboring border (blue).

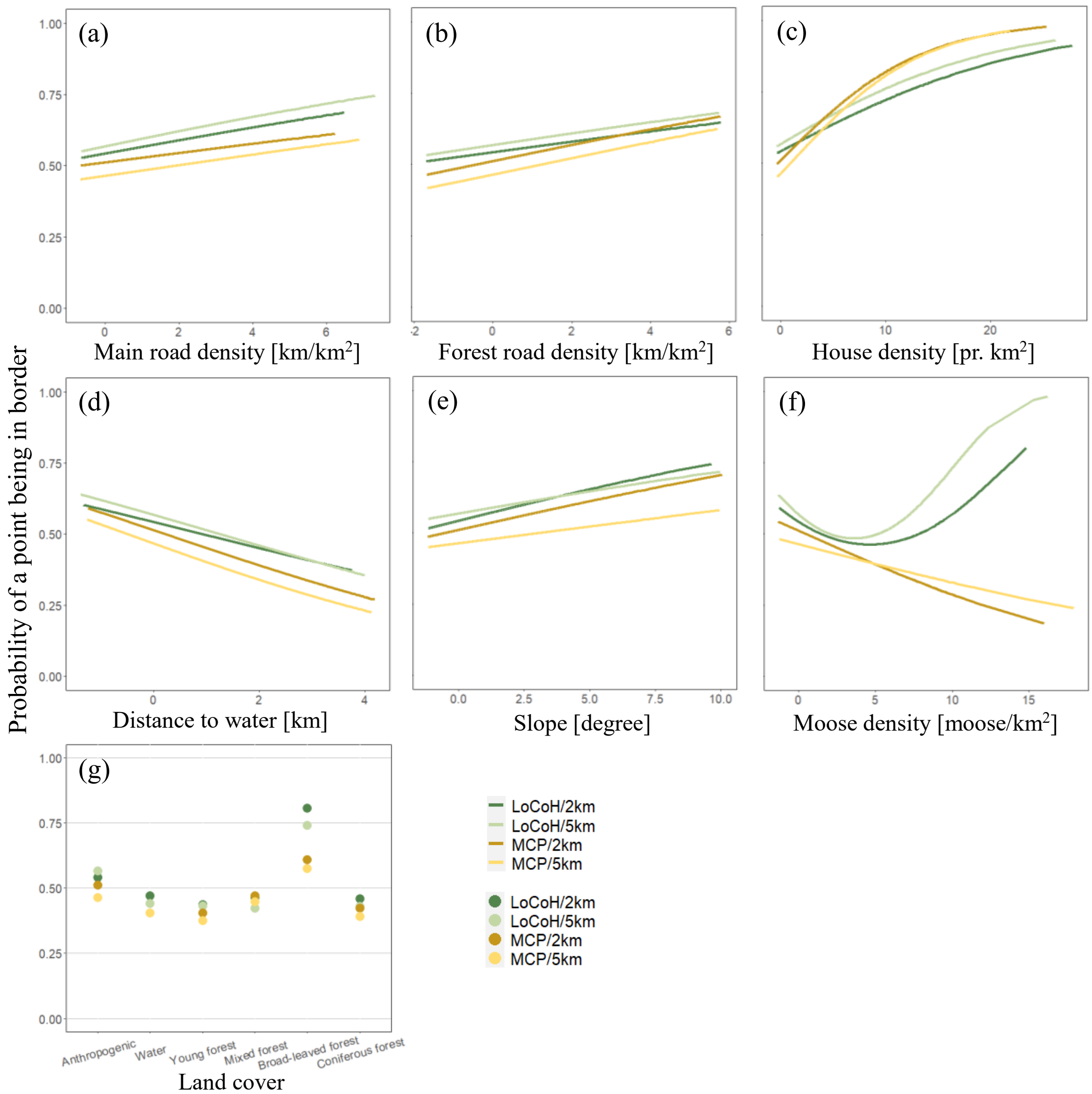

Fig. 6 Regression lines of models for explaining border (= 1) and center (= 0) with variables of main road density (a), forest road density (b), house density (c), distance to water (d), slope (e), moose density (f) and land cover (g). Four models (LoCoH with 2 or 5 km border and MCP with 2 or 5 km border) are included in one graph.

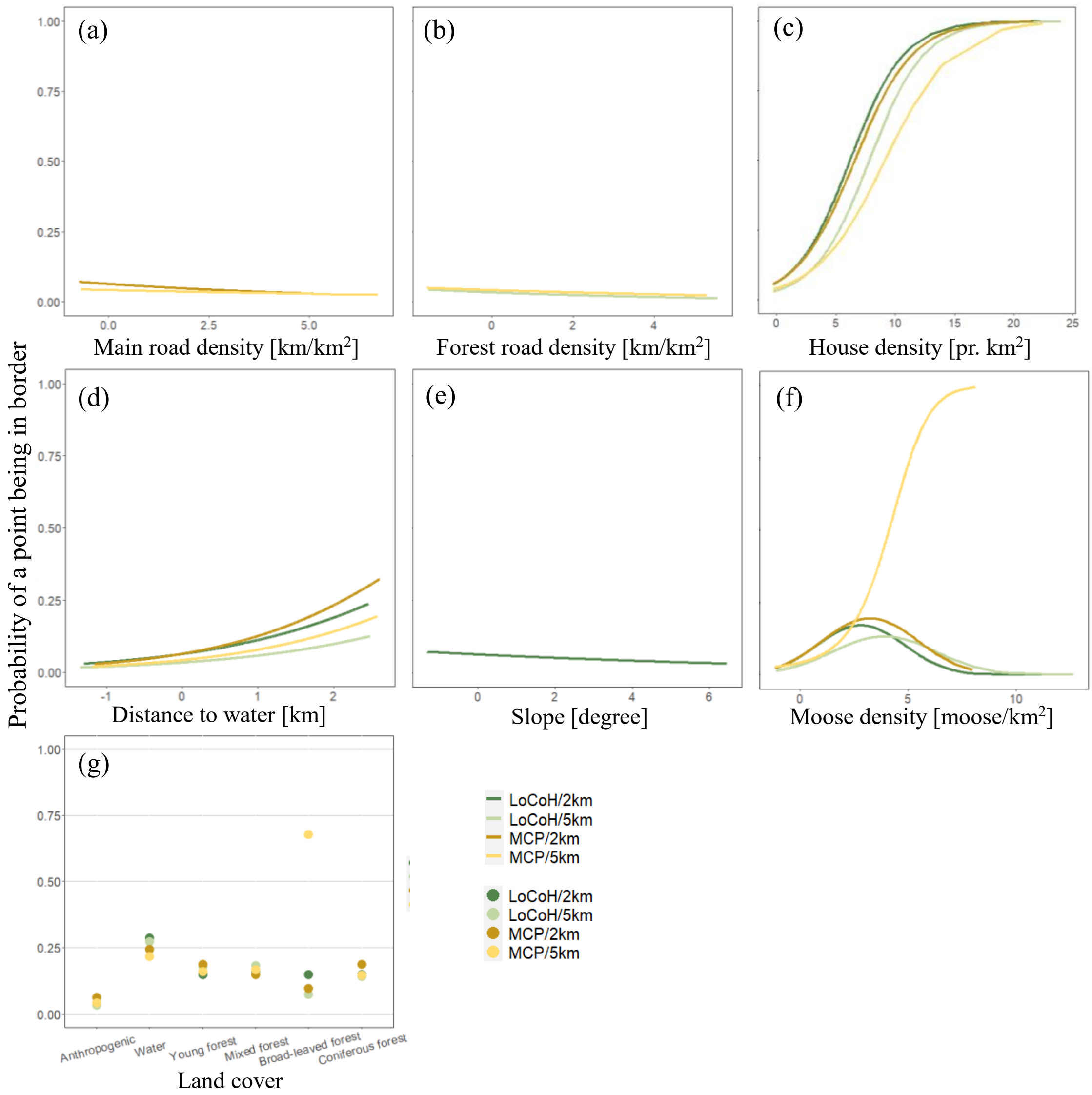

Fig. 7 Regression lines of models for explaining neighboring border (= 1) and non-neighboring border (= 0) with variables of main road density (a), forest road density (b), house density (c), distance to water (d), slope (e), moose density (f) and land cover (g). Four models (LoCoH with 2 or 5 km border and MCP with 2 or 5 km border) are included in one graph.