The Influences of Roads on Wolf Movement on the Scandinavian Peninsula in Summer

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Abstract

Over 14,000 GPS wolf positions from 15 wolves (*Canis lupus*) in 9 territories across the Scandinavian Peninsula were used to assess the influences of roads on wolf movement within their territories in the summer. My results show that there was a preference for wolves to travel on roads compared to off roads, and that the preference was highest for forest gravel roads (FGR) as opposed to main roads (MR). The MR density was negatively correlated with presence of wolf traveling positions, but FGR density did not influence wolf movement. Time of day also had an influence on the movement of wolves around MRs. Likelihood of a wolf being closer to a MR during night and early morning hours was higher than that at other times of day. Time of day did not strongly influence wolf travel around FGRs. The distance to a road, independent of road type, did not influence location of kill site. Wolves, in general, preferred to use roads during travel as opposed to resting. These results concur with other research saying that the wolves use the forest roads for ease of travel, hunting for prey, or territory patrolling. Many results on wolf movement in relation to roads vary by region, habitat, type of prey, and availability.

Key Words

Canis lupus, Alces alces, GPS collar, roads, Scandinavia, wolf, wolf movement

Introduction

The building up of our world with advances in transportation, the increasing availability of recreation by road and trail, and the necessity of land and building materials to construct, can all combine together to make the ecology of animals, such as the wolf (*Canis lupus),* and their habitats more difficult. As habitats are being altered or destroyed by human disturbance, new roads and trails are constantly being constructed to meet the demands of transport, forestry, and logging. In Sweden and Norway, due to intense forestry, a high density of forest roads has resulted, thus influencing the movement of the wolf in these countries (Karlsson et al. 2007a, Eriksen et al. 2009, Hamre 2006). The Scandinavian wolf population previously suffered functional extinction in the 1960s, but Finnish-Russian wolves recolonized the area from the 1970s and onward to build a new population which continues today (Wabakken et al. 2001, 2009). The wolf population in this area is not saturated which gives the wolves a lot of choice as to where to settle and travel, which could potentially be important for their degree of adaption and utilization of roads.

Many factors can influence wolf movement, many of which vary by region (Theuerkauf et al. 2003a). Some of these factors are presence or absence of roads, road density, human presence, and prey availability (Theuerkauf et al. 2003a, 2003b, Whittington et al. 2005, Hamre 2006, & Eriksen et al. 2009). The presence or absence of roads has a greater influence on wolves in some regions than others. In Finland, for example, wolves try to establish home ranges in areas where human disturbance is as small as possible and away from human constructions (Kaartinen et al. 2005). In other regions, however, wolves use roads for ease of travel (Theuerkauf et al. 2003a, Whittington et al. 2005, Hebblewhite et al. 2009), accessibility to territory, and depending on prey availability, ease of hunting (Whittington et al. 2005). Within Scandinavia, wolves show a preference for moving on forest gravel roads, suggested for ease of travel, territory patrolling, and searching for prey (Eriksen et al. 2009, Hamre 2006).

The density of roads may also influence habitat suitability for wolves, and the roads may be more used by the wolves when there is limited human use (Theuerkauf et al. 2003a, Whittington et al. 2005). Wolf territories had lower densities of roads, built-up areas, and open land than areas outside the territories in Scandinavia (Karlsson et al. 2007a). In some regions wolves have a greater avoidance of possible human encounter during summer when there is greater human use of forest roads and trails (Whittington et al. 2005). In this same study by Whittington, the two packs of wolves observed had different preferences of road use on different types of road, thus concluding that the type of road or trail has different influences on wolf movement at different seasons throughout the year. Researchers have concluded that wolves prefer using low-use roads and trails, as opposed to high-use roads and trails (Whittington et al. 2004, 2005, Shepherd and Whittington 2006). Many areas of high densities of roads have low survivability of wolves due to illegal killing (Thiel 1985, Mech et al. 1988), but road density alone may not be the only factor affecting survival of wolves, human tolerance also plays a role in wolf habitat suitability and survival (Wabakken et al. 2001, Merrill 2000). Roads have also been connected with direct wolf mortality caused by traffic and illegal hunting and trapping (Wabakken et al. 2001, Person and Russell 2008, Mech et al. 1988).

The time of day also has an influence on wolf road use in some regions. Wolves generally use roads and trails more during the night than day when there is less chance of human encounter (Theuerkauf et al. 2003a, Whittington et al. 2005). Also at night, many large predators move along roads that have low vehicular or human presence (Forman and Alexander 1998). My main objective for this study is to find what the influences of roads are on wolf movement in the

Scandinavian Peninsula in summertime. Based on previous studies including road influences on wolves, I predict:

1. Different types of roads influence wolf movement differently. Correspondingly to Whittington et al. (2004, 2005), we expect the wolves to avoid paved roads and prefer forest gravel roads.
2. Density of roads influences wolf movement. We expect the wolves to prefer areas of intermediate road densities, and to avoid areas of low or high road densities, due to an expected trade-off between ease of movement and human disturbance.
3. Time of day influences road usage by wolves. We expect the wolves to prefer roads during night hours, but to avoid them during daytime, in order to avoid encounters with humans.
4. Presence of roads influences locations of kill sites. We expect the wolves to kill their prey close to roads due to ease of travel during prey search. Alternatively, I expect the wolves to kill their prey far away from roads in order to avoid human disturbance.
5. Time spent on roads is influenced by activity level of wolves. When traveling, not resting, wolves prefer to spend more time on roads.

Methods

Study Area

This study was carried out during the summers of 2002 through 2007 throughout Norway and Sweden, or the Scandinavian Peninsula (55-72°N, 5-25°E). Seventeen time periods were included during the summers in 11 wolf territories (Fig. 1). All territories are located on the Southern halves of Norway and Sweden, some territories lying on the border of the two countries. The area is mainly covered with boreal coniferous forest, which is dominated by Scots pine (*Pinus sylvestris*) and Norway spruce (*Picea abies*), and mixed with some deciduous species, the most abundant species being birch (*Betula pubescens*) and aspen (*Populus tremula*).

The human population density of the Scandinavian Peninsula is 17 humans/km^2, but most of the wolf ranges are under 1 human/km^2 (Sand et al. 2008). Main road (MR) densities within the territories ranged from 0.03 – 0.28 km/km^2 (average ± 2 SE = 0.17 ± 0.04 km/km^2, Appendix 1). A large network of forest gravel roads (FGR) has been created due to extensive commercial logging and forest management practices (Sand et al. 2008, Hamre 2006). The FGR densities in the territories were on average 4.14 times higher than the MR densities and ranged from 0.51 – 1.24 km/km^2 (average ± 2 SE = 0.71 ± 0.10 km/km^2, Appendix 1). The total road density (average ± 2 SE = 0.88 ± 0.09 km/km^2, Appendix 1) did not differ among territories situated in Sweden, Norway, or across the border ($F_{2,13}$ = 2.51, p = 0.319), but there was a higher MR density ($F_{2,13}$ = 8.21, p = 0.005) and lower FGR density ($F_{2,13}$ = 4.04, p = 0.043) in Sweden compared to Norway. Roads were defined as FGRs or MRs by SOSI code in Norway and kategori-kod in Sweden (Appendix 2; Hamre 2006).

The most important prey species for wolves in this area is the moose (*Alces alces*) with a population of approximately 1-2 moose/km^2 in summer. For Scandinavian wolves, moose represent more than 95 percent of their food biomass in summer (Sand et al. 2008). Other ungulate prey for the wolf include roe deer (*Capreolus capreolus*) and in Norway, red deer (*Cervus elaphus*). Other smaller prey are also available for the wolf including beaver (*Castor fiber*), badger (*Meles meles*), capercaillie (*Tetrao urogallus)*, black grouse (*Tetrao tetrix*), and mountain and European hares (*Lepus timidus*, *Lepus europeus*) (Sand et. al 2008). I only included moose in this study as the main prey species.

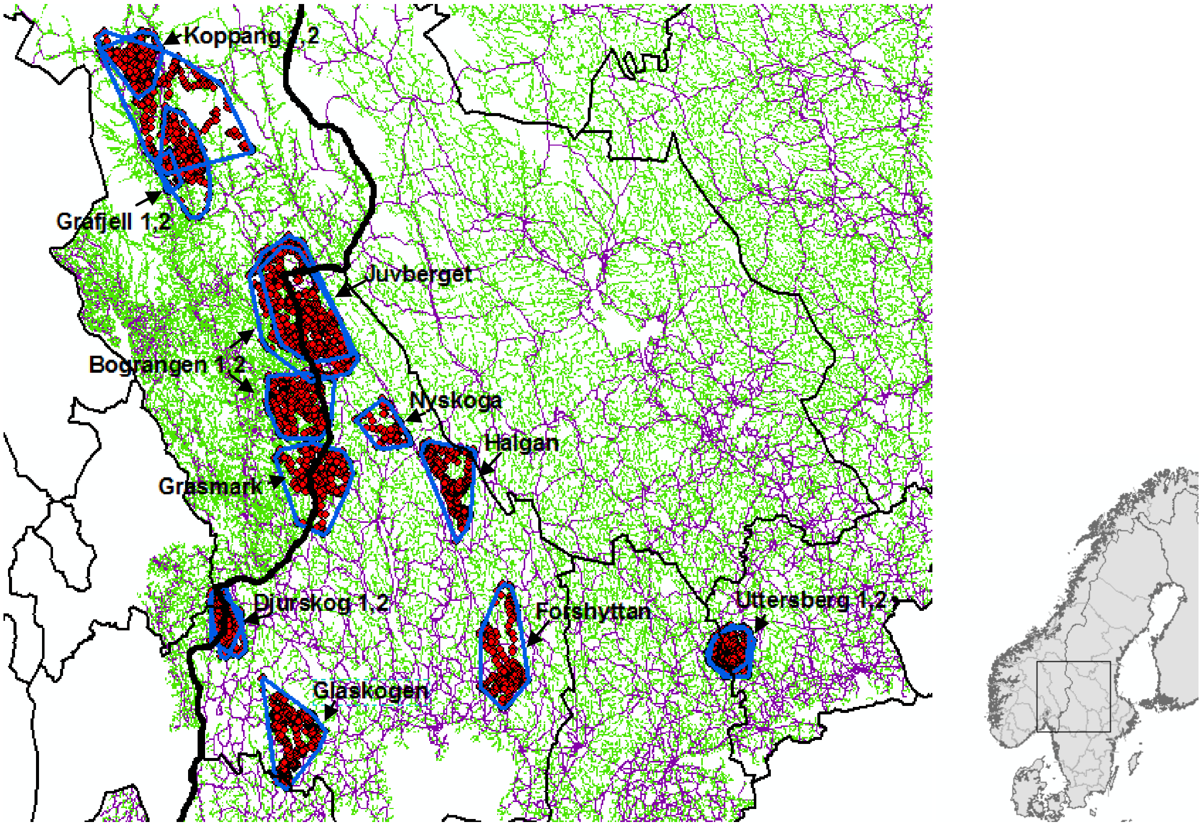

Fig. 1 – Map of wolf GPS positions in 100% MCP home ranges during study periods in the Scandinavian Peninsula. Purple lines are MRs, green lines are FGRs.

Study Animals

As part of the Scandinavian Wolf Research Project (SKANDULV), the data for this study was collected on 15 adult wolves across 11 territories (Appendix 3). The wolves were immobilized from the air from helicopter and equipped with a GPS collar (GPS-Simplex, Web-Direct, or Tellus by Followit, Sweden, or GPS-Plus by Vectronic Aerospace, Germany). The study included 17 time periods during summers between 2002 and 2007, with hourly or half-hourly positioning intervals. GPS wolf position data for this study originated in a study of summer kill rates (Sand et al. 2008), but I included two additional time periods in this study that were not included previously. The study periods ranged between the months of June and September (June 1 – September 29, Appendix 3).

GPS Positions and Cluster Definition

All GPS positions were plotted using ArcGIS 9.3 on regional maps of Norway and Sweden. I used a total of 14,947 hourly or half-hourly GPS positions in this study. Of these positions, 12,271 positions were classified as wolf cluster positions and 2,676 positions were classified as single positions, or further documented in this study as traveling positions. Cluster positions were defined as positions less than 200 m to the closest spatially neighboring position, as opposed to traveling positions. In ArcGIS 9.3, each GPS position was fixed with a 100m radius buffer which was joined with any overlapping buffered positions and defined as a cluster (Zimmermann et al. 2001, 2007, Sand et al. 2005). There were also an additional 194 wolf kill site positions representing where wolves had killed a moose. Kill site positions were taken from the previously mentioned wolf predation study (Sand et al. 2008 and SKANDULV, unpublished data), with the exception of kill site data from the two additional territories included in this study that were not a part of the predation study. The GPS positions and kill sites originally in the Norwegian coordinate system (WGS 1984 UTM Zone 32N or 33N) were converted to the metric Swedish map coordinate system (RT 90 2.5 gon West). I defined home ranges of all territories using the 100% Minimum Convex Polygon method (100% MCP, Mohr 1947, Appendix 3).

Road Maps

To create a map including all home ranges and roads in this study, I joined together digital maps of Norway and Sweden to make a unified regional map. Norwegian (Statens kartverk, 1:50,000) and Swedish (Lantmäteriet, 1:100,000) maps were used (Sand et al. 2008). Roads were categorized as either forest gravel roads (FGR) or main roads (MR). I estimated road densities for FGR and MR in each wolf home range by summing the line lengths of the roads and dividing it by the home range area (Appendix 1, see also Study Area section). I also created a small-scale road density index by using the kernel method. To do so I converted all road lines to points with spacing of 250 m, and used fixed kernel density estimation with bandwidth h = 1000 m. The resulting raster maps indicated FGR and MR densities within home ranges (Fig. 2). I chose this method instead of a buffering method because I expected stronger effects of road intersections or other areas with locally high road densities.

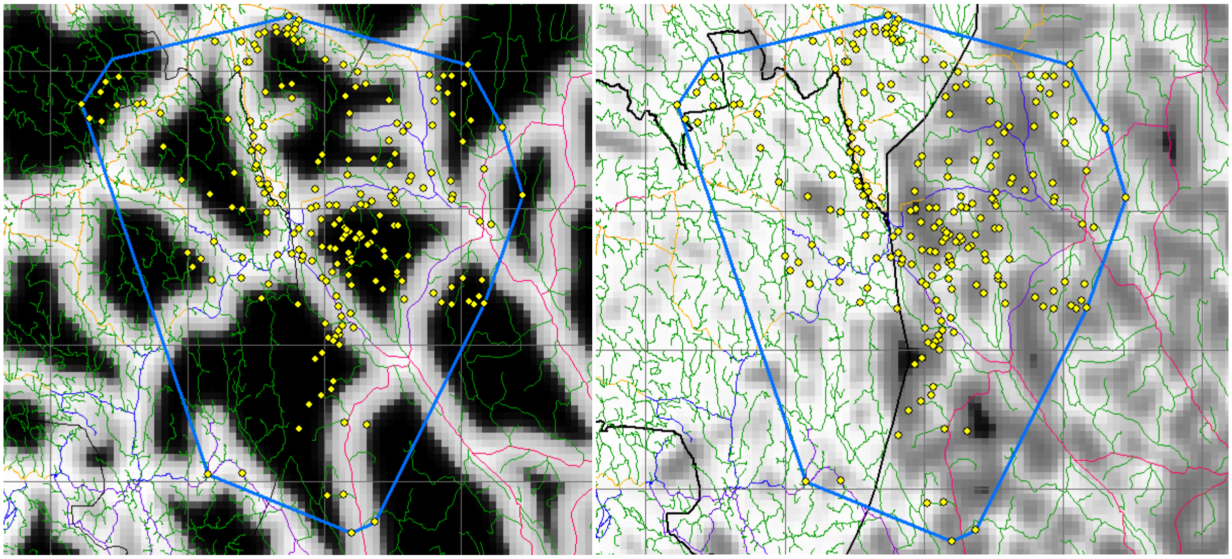

Fig. 2. Example of a road density map. Maps of Gräsmark territory for MR (left) and FGR (right), as obtained by fixed kernel estimation of equally spaced points along the roads. Yellow points are wolf positions. Gräsmark territory covers parts of Norway and Sweden. The country boarder runs in the center of the territory and is seen vertically in the FGR estimate map (right). Lower road densities are darker color.

Data Analysis

Resource selection functions (RSF, Many et al. 2002) in form of mixed model linear and logistic regression models in SAS (SAS 9.2, Glimmix), were used to analyze data. I included home range as a random factor in all analyses and used a nested design to correct for biases in sample size. The response variable in the logistic models was the binary variable indicating presence (1) or absence (0) of wolf positions or kill sites. Absence was simulated by 500 randomly generated points per home range.

To investigate the influence of road type on wolf movement, I used ArcGIS 9.3 to measure the distance from wolf traveling positions and random points to the closest MR and FGR. For each road type, I performed a RSF model with the distance variable as the only fixed effect. I also categorized the wolf traveling positions and random points into being on or off the road and used this as another explanatory variable. If a point was located either on or within 25 m from a road, it was categorized in the analysis as being on the road. All other points were considered off the road. The distance of 25 m corresponds to the slight inaccuracy of GPS positions (Bowman et al. 2000, Rodgers 2001).

To investigate if wolves preferred areas of high, low, or intermediate road densities, mixed models were used to see if road density had an influence on wolf movement. I extracted the road kernel density index from the underlying raster map to each wolf traveling position and random point. For each road type, I performed a RSF model and entered the road density index as a fixed effect. In order to test the hypothesis that wolves may prefer intermediate road densities, I also performed non-linear models with FGR and MR road densities entered as quadratic terms.

To test if wolves used roads at varying degrees depending on time of day, I split the day into six time periods: Night, Early Morning, Morning, Mid-day, Afternoon, and Evening. I assigned these periods randomly to the random points. For this analysis the RSF models for MR and FGR included the interaction between the distance to the closest road and the time of day.

To analyze the preference of wolves to kill prey either close to or far from roads, I used distance of kill sites and random points to FGR and to MR as explanatory variables in the RSF models. I also compared wolf traveling positions with kill sites in relation to distances to roads with a linear mixed model. Here I used distance to road as a response and position type (traveling position or kill site) as an explanatory variable.

To test the probability of a wolf being on a road either while traveling or resting, I defined the first position on each cluster as a resting position, and contrasted those to the traveling positions. Traveling vs. resting positions was used as an explanatory variable, as well as time of day. The presence of a wolf on (within 25 m) or off the road was used as a response in the mixed model logistic regression. Time of day was included as a covariate. Another model was done to see if the distance to the road had an influence on whether the wolf was in a traveling or resting position. I used distance to road as a response with cluster vs. single position as an explanatory variable. Distance to FGR and MR were square root transformed to normalize data prior to running the models in SAS.

Results

Wolf preference of road type

Traveling positions constituted 18% of all wolf positions. In other words, wolves across territories spent 18% of their time traveling and 82% in a cluster. Of the traveling positions, 15% were on FGRs, 1% on MRs, and 84% off roads. In contrast, 3%, 0.8%, and 96% of the random points were on FGRs, MRs, and off roads, respectively. The RSF model contrasting wolf traveling positions to random points proved highly significant ($F_{2,46}$ = 22.96, P = <0.001). Back-transformed least square means indicated that the probably of a wolf traveling on a road was higher than off roads, and that the probability of a wolf traveling on FGRs was 1.83 times higher compared to MRs, and 0.66 times higher compared to areas greater than 25 m from a road (off road) (Fig. 3).

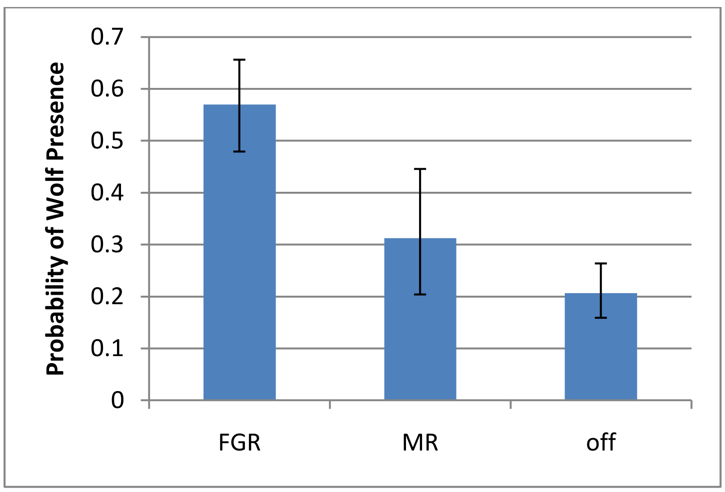

Fig. 3. Probability of wolf presence on FGRs, MRs, or off roads (>25 m from the closest road).

I also tested the wolves' movement behavior in relation to distance to roads. Wolf traveling positions were on average 539m away from FGRs (strongly right-skewed distribution of distances, median = 374 m, maximum = 4238 m) and 2653m away from MRs (slightly right-skewed, median = 2237 m, maximum = 11672 m), whereas random points were on average 578 m from FGRs (strongly right-skewed distribution of distances, median = 454 m, maximum = 5754 m) and 2385 m from MRs (slightly right-skewed distribution, median = 2019 m, maximum = 14055 m). The distance to the FGR tested significant for traveling positions of wolves ($F_{1,15}$ = 7.11, P = 0.018, slope b = -0.882 ,Fig. 4), but distance to MR did not ($F_{1,15}$ = 0.31, P = 0.587,). As the distance to FGR increased, the likelihood for a traveling position to be present decreased (Fig. 4). RSF estimates were back-transformed to obtain probabilities between 0 and 1.

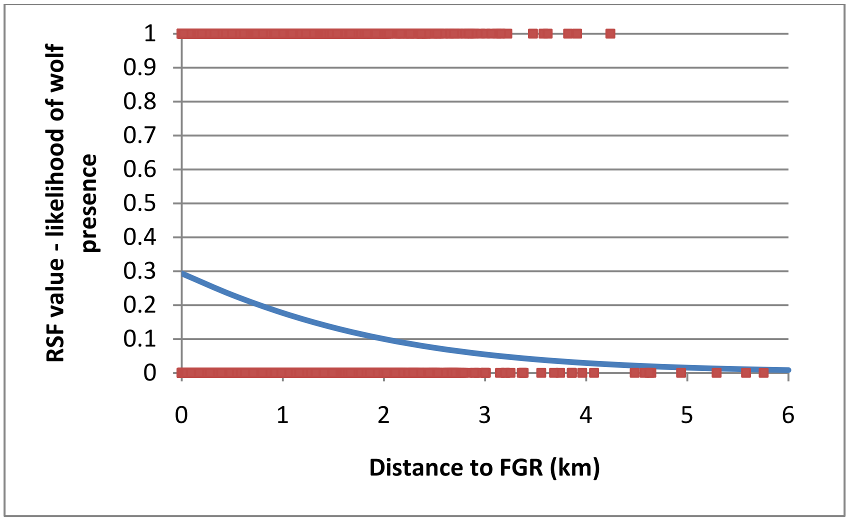

Fig. 4. Likelihood of wolf traveling positions as distance to FGR increases. The blue line represents the RSF, and the red dots are the observed wolf traveling positions (1) and random points (0).

Density of roads

The density of FGRs in relation to a wolf presence (or in a traveling position) was not significant, nor was the model significant that was entered with quadratic terms, representing the intermediate FGR density ($F_{1,15}$ = 2.29, P = 0.151; $F_{1,15}$ = 0.30, P=0.595). The model that represented intermediate MR density was also not significant ($F_{1,15}$ = 0.61, P = 0.448). However, the MR density was significant in relation to wolf presence, showing that the MR density had an influence on the MR usage by wolves ($F_{1,15}$ = 7.92, P = 0.013). RSF estimates were back-transformed to plot the likelihood of wolf presence with increasing MR density (Fig. 5). As MR density grew, the likelihood of wolf presence decreased. This model was run again excluding the four outlying random points with densities higher than 0.6 (ref. Figure 5) and was still significant ($F_{1,15}$ = 7.75, P=0.014). Wolves preferred to travel in areas of low MR density, but density of FGR had no influence on wolf presence.

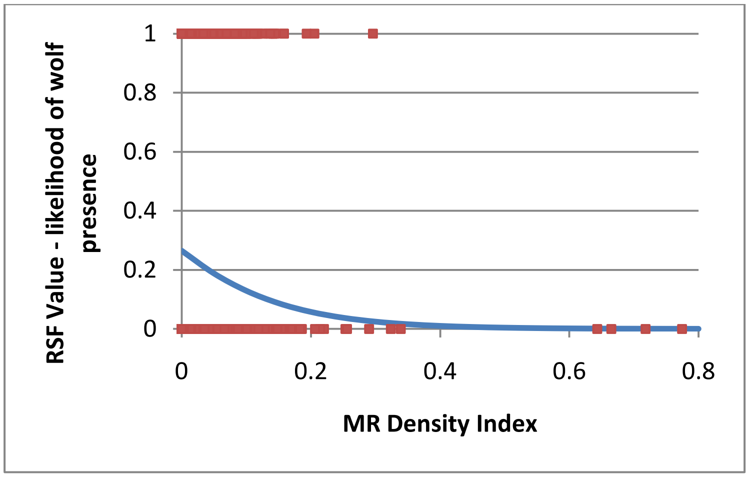

Fig. 5. Likelihood of wolf traveling positions as MR density increases. The blue line represents the RSF, and the red dots are the observed wolf traveling positions (1) and random points (0).

Time of Day

The relationship between time of day and wolf being in a traveling position (wolf presence) was highly significant ($F_{5,1E4}$ = 61.98, P < 0.001), as was the interaction between time of day, distance to MR, and wolf presence ($F_{5,91}$ = 3.56, P = 0.006) (Fig. 6). The likelihood of a wolf being closer or farther from a MR was influenced by time of day. During night and early morning, wolves were more likely to be closer to a main road, but at other times of the day, the wolves were more likely to be further from the road. However, the interaction between time of day, distance to FGR, and wolf presence was not significant, nor was the interaction between time of day and the wolf being on or off the road ($F_{5,90}$ = 0.95, P = 0.454; $F_{10,225}$ = 1.38, P = 0.192). Thus, distance to FGR did not influence wolf presence during certain times of day as distance to MR did, and time of day did not influence whether the wolf was on or off the road. Separate statistical tests were not run for FGRs and MRs and whether the wolf was on or off the road. The classification of being on a road covered both MRs and FGRs. Raw data counts of wolf traveling positions on FGRs during the night and evening were greater than that of other times of day, but this was not statistically significant. Wolves, while traveling, spent the most time on FGRs during the night and evening, 5.7% and 4.6% respectively (Table 1). Time spent on MRs was much less.

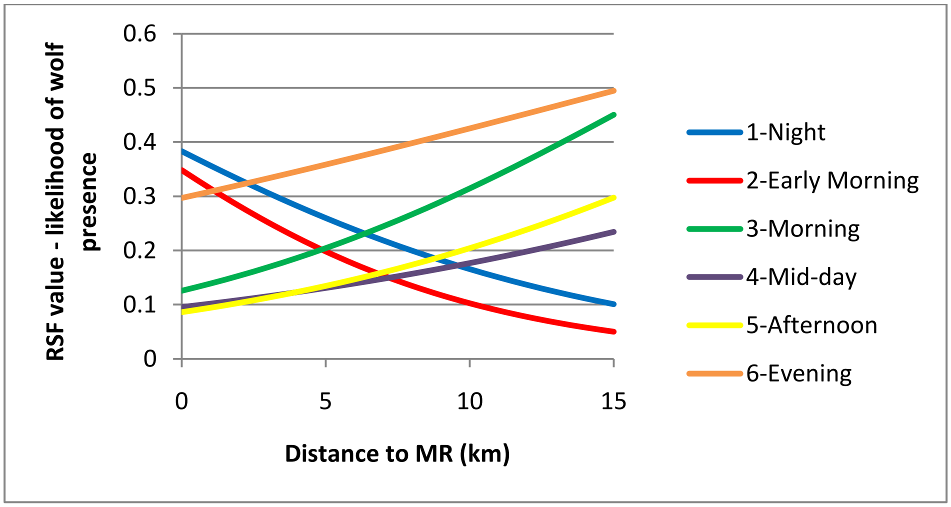

Fig. 6. Likelihood of wolf presence at increasing distance to MR during different time of the day.

Table 1. Percentages of time wolves spent on roads at different times of day. Total number of wolf single/traveling positions is 2676.

Time of Day Category	Time of Day (4 hour interval)	Number of traveling positions on MR	Number of traveling positions on FGR	% of traveling positions on MR	% of traveling positions on FGR
1-Night	23:00 – 02:59	15	153	0.56	5.72
2-Early Morning	03:00 – 06:59	8	64	0.30	2.39
3-Morning	07:00 – 10:59	2	25	0.07	0.93
4-Mid-day	11:00 – 14:59	1	16	0.04	0.60
5-Afternoon	15:00 – 18:59	0	21	0.00	0.78
6-Evening	19:00 – 22:59	5	122	0.19	4.56
Total		31	401		

Presence of roads and kill sites

RSF models describing the distance of kill sites to roads (FGR and MR) were not significant (FGR – $F_{1,17}$ = 0.3, P = 0.592; MR – $F_{1,17}$ = 0.78, P = 0.390). Roads did not have influence on location of kill sites, or in other words, wolves did not have a preference for killing prey near to or far from the road.

Traveling vs. Resting positions

The wolves had 2.43 times higher probability of being on a road if it was traveling rather than resting ($F_{1,30}$ = 16.49, P<0.001) (Fig. 7).

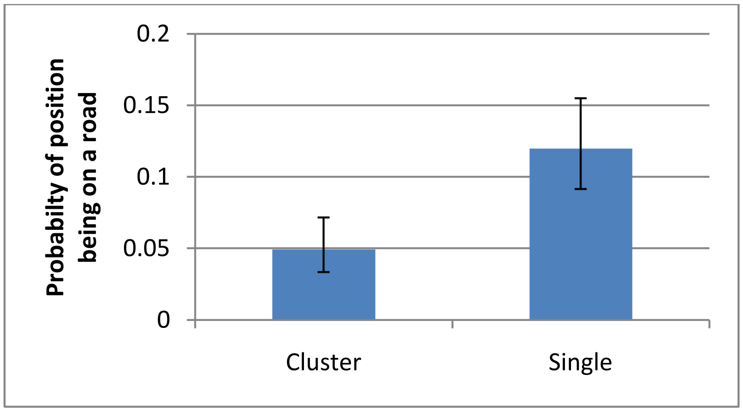

Figure 7. Probability of a wolf being on a road while in a cluster (resting) or single (traveling) position.

Distance to FGR and MR also had an influence on whether the wolf was traveling or resting ($F_{1,15}$ = 22.96, P < 0.001, $F_{1,15}$ = 12.14, P = 0.003) (Fig. 8). The wolves traveled closer to both MRs and FGRs. While resting, they were farther from roads.

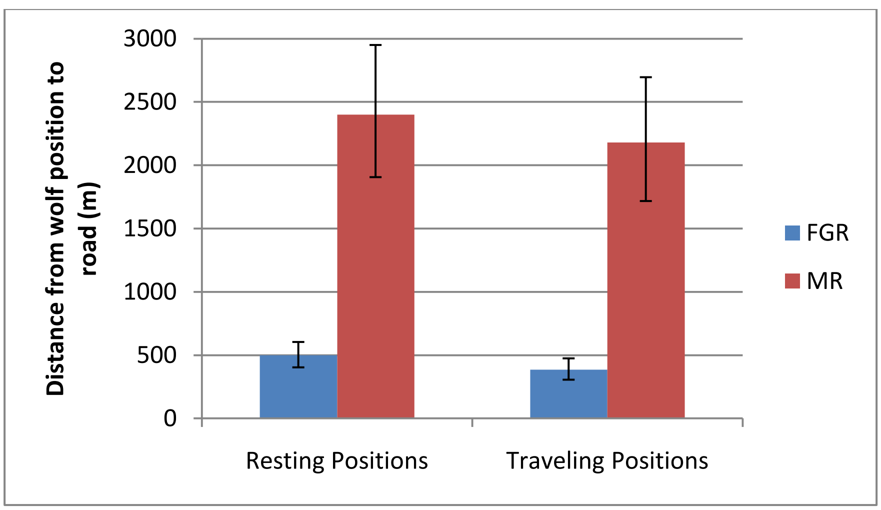

Figure 8. Distances from resting and traveling positions to FGRs and MRs.

Discussion

In this study, I found that wolf movement is influenced differently by different types of roads. In agreement with several other studies and my hypothesis, wolves preferred to travel on FGRs (Whittington et al. 2004, 2005; Jedrzejewski et al. 2004; Gehring and Potter 2005; Hamre 2006; Musiani et al. 1998; Thurber et al. 1994; Theuerkauf et al. 2003a & Eriksen et al. 2009). The wolves were perhaps using the FGRs for ease and speed of travel through or around home ranges, territory patrolling, scent-marking, and searching for prey faster. Since the distance to MRs was not significant for wolf presence, I cannot assume the wolves were avoiding MRs. This did not agree with my hypothesis that the wolves would avoid MRs, but given the proportions of wolf positions on MRs compared to the proportions of positions on FGRs, the wolves were simply traveling on the FGRs more. Considering the small amount of road available per territory, it was significant that the wolves preferred to use a MR over being off the road, and in turn, the FGRs were preferred over MRs and being off the roads, for travel. A study done by Whittington et al. (2004) had similar results with FGR usage in Canada. The wolves in that study traveled on roads, trails, and railway lines 16% of the time and in through forests, rivers, and meadows 84% of time, the same percentages as in my study (16% on roads, 84% off). This is in support of my hypothesis that wolves prefer to use FGRs over MRs. The wolves in Whittington et al. (2004) study, however, were tracked in winter months with snow tracking. In a barrier crossing study done in Canada, linear features, such as roads, seismic lines, and railroads, were crossed by wolves regularly when the feature was of low-use by humans. The wolves were more likely to cross low-use features than high-use features, suggesting that wolves avoid the hazards associated with people rather than the feature used by people (Whittington et al. 2004; Thiel 1985, Mech et al. 1988; & Mladenoff et al. 1995). By not using MRs, there is less human disturbance to the wolves and less of a chance for mortality associated with vehicles and hunting (Gehring and Potter 2005; Person and Russell 2008; Jedrzejewski et al. 2004; Wabakken et al. 2001), which can explain why the wolves were using FGRs more than MRs.

High MR density was the only level of density that influenced wolf movement in this study. As MR density increased, the likelihood of a wolf position near the MR decreased significantly. Intermediate MR and FGR densities, as well as low FGR densities, didn’t influence the distances to roads that the wolves were located. This did not agree with my prediction, but agrees with other studies saying that wolves prefer low road density habitats, and high MR density habitats are avoided (James and Stuart-Smith 2000; Thurber et al. 1994; & Forman and Alexander 1998). My results do agree, however, with the Whittington et al. (2005) study in Canada where it says that individual roads and trails had little negative effect on wolf movement, but wolves avoided the cumulative effect of high road and trail density. A possible reason for this is suggested that it is not the roads that are avoided, but the positive correlations between road density and chance of mortality by hunters or collisions with vehicles (Whittington et al. 2005; Thiel 1985; Mech et al. 1988; Mladenoff et al. 1995). In addition to this positive correlation, high human disturbance, in general, may be another reason for only MR density influencing wolf movement. Also since many studies differ in what road density wolves can survive in, Merrell (2000) suggests that road density is an index of vehicles and human attitude and there are situations when road density alone is not an accurate index of wolf habitat suitability. Mech (1989) concludes that small areas of high road densities can sustain wolves so long as suitable roadless areas are also available for use. Another possible explanation for my results is that present Scandinavian wolves that originated from the Finnish-Russian wolf population with low road utilization may have increased road tolerance and use of roads (Hamre 2006).

Wolf positions varied at different times of day in relation to distance to road. In the night and early morning hours, the likelihood decreased of a wolf being farther from an MR as the distance to an MR increased, whereas during other times of the day, as the distance to an MR increased, the likelihood of a wolf traveling closer to the MR decreased. In other words, it was more likely to see a traveling wolf closer to a main road during the night and early morning hours than it is during the other hours in the day. This relationship was not significant for FGRs, meaning it was not significant compared to random positions that wolves were traveling close to, on, or off roads at certain times of the day. However, the time of day did have an influence on wolf position itself when compared to random positions. Based on raw data of traveling positions, there were more positions recorded on roads during night and evening hours, and fewer positions during other hours of the day (Table 1). These results support my hypothesis of wolves traveling during the night hours, but the only result that was significant for avoiding the roads during the day was when the wolves traveled on MRs. I cannot assume the wolves were avoiding traveling on or close to FGRs during the day; this relationship did not yield significant results. Theuerkauf et al. (2003b) reports many different activity levels of wolves depending on human presence and region or country and suggests that humans and wolves are spatio-temporally separated and do not change their movement patterns because of human influence, but they avoid being in the same place at the same time. They also suggest that some wolves, such as those in Poland, have daily activity patterns shaped around hunting prey. However, the wolves in Poland avoided larger roads and trails during the day and not at night, and avoided tertiary roads the least during the day without avoidance at night, but still avoided larger roads at night (Theuerkauf et al. 2003a). Based on results of this and other studies, I suggest that wolves adapt their movement behavior during daylight hours according to amount of human presence, spatio-temporal prey patterns, and time of day.

Presence of road did not influence location of kill site, as was predicted. It appears that, in this study, wolves didn't prefer areas either close to or far from roads when killing their prey. This may have many explanations. The wolves may not prefer to hunt on roads (Hamre 2006), or that the wolves might have experience already where to locate prey (Hamre 2006; Mech and Boitini 2003; & Frame et al. 2004). A study done in Scandinavia discusses that moose clearly avoided moving on roads while wolves preferred using FGRs possibly as a means to find where the moose crossed the road and then deviate from the road to track the moose (Eriksen et al. 2009). There are many studies that discuss moose avoidance to road to avoid predation (Eriksen et al. 2009; Laurian et al. 2008; Hamre 2006; James and Stuart-Smith 2000; Kunkel and Pletscher 2000), which could have an influence on where the wolves kill prey. In Bergman et al. (2006), wolves preferred certain types of forest edge for greater predation of elk. An elk was more vulnerable to predation along hard edges because the switch in terrain around the edge would pose a handicap on the elk in escaping from wolves. The delay in escape would allow the wolves to narrow a chase. Wolves usually take advantage of areas that allow them so stalk and chase prey over short distances (Kunkel and Pletscher 2001; Farmer et al. 2006). Most studies widely vary by region on this subject and more research will need to be done in Scandinavia to either support or explain my data.

When traveling, wolves clearly preferred to use or stay close to roads more than when resting. The probability was higher for the wolf being on a road when it was traveling, as opposed to it being fairly low while the wolf was in a cluster or resting. Distance to FGR had an influence on whether the wolf was resting or traveling. Based on previous results in this study, the wolves preferred to use FGRs while traveling, so I infer that as the wolf is closer to the FGR, the likelihood of the wolf traveling instead of resting is greater. These results agree with the prediction that the wolves prefer to spend more time on the roads when traveling. There have not been very many studies comparing single positions to cluster positions. A cluster position can be a den, rendezvous, kill, or resting site, and according to a study done in Poland, the den and rendezvous sites were selected farther from roads than random sites (Theuerkauf et al. 2003c). This is in accordance with my results, but Theuerkauf does not compare traveling positions to clusters. Other studies include much information on predation and are mainly associated with my previous kill site hypothesis.

Wolf movement may also be influenced by wind speed and wind direction when traveling on roads. This is one explanation for variation, but was not included in this study. Karlsson et al. (2007b) reported that wolves moved away from approaching humans when the wind was blowing toward them. This might then suggest that wind direction and speed can have an influence on the wolf if it is using the road for hunting or territory patrolling. Whittington et al. (2004) also reports that people with their organic scent can be a strong deterrent to wolf movement on road. Another explanation for variation in this study could be the season in which the data was gathered. Since this study was done in the summer season and most studies are done in the winter with snow tracking of the wolves, my results could differ from previous studies. Much of the kill rate data is gathered during the winter, when it is easier to detect the kill site through tracking. Sand et al. (2008) suggest that summer predation is underestimated due to undetected kills. Also in spring-summer, wolf movements concentrated around breeding den and rendezvous sites in a Polish study, with movements in the fall-winter being much more mobile throughout the territory (Jedrzejewski et al. 2001). Wolves may also limit their daylight movement in the summer to avoid overheating (Theuerkauf et al. 2007b). This could have influence on the time of day results when compared to winter data. Wolf movement may be much different during the winter when many FGRs in Scandinavia and other areas are closed due to snow and human access being limited (Thurber et al. 1994). The availability of GPS collars in future studies should shed more light on summer data as well as influences of time of day.

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References

Bergman, E. J., R. A. Garrott, S. Creel, J. J. Borkowski, R. Jaffe, & F. G. R. Watson. 2006. Assessment of prey vulnerability through analysis of wolf movements and kill sites. *Ecological Applications*. 16(1):273-284.

Bowman, J. L., C. O. Kochanny, S. Demarais, & B. D. Leopold. 2000. Evaluation of a GPS collar for white-tailed deer. *Wildlife Society Bulletin*. 28: 141-145.

Eriksen, A., P. Wabakken, B. Zimmermann, H. P. Andreassen, J. M. Arnemo, H. Gundersen, J. Milner, O. Liberg, J. D. C. Linnell, H. C. Pedersen, H. Sand, E. J. Solberg, & T. Storaas. 2009. Encounter frequencies between GPS-collared wolves and moose (*Alces alces*) in a Scandinavian wolf territory. *Ecological Research.* 24:547-557.

Gehring, T.H., & B. A. Potter. 2005. Wolf habitat analysis in Michigan: an example of the need for proactive land management for carnivore species. *Wildlife Society Bulletin*. 33(4):1237-1244.

Farmer, C.J., D. K. Person, & R. T. Bowyer. 2006. Risk factors and mortality of black-tailed deer in a managed forest landscape. *Journal of Wildlife Management*. 70(5):1403-1415.

Forman, R.T.T, & L. E. Alexander. 1998. Roads and their major ecological effects. *Annual Review of Ecology and Systematics*. 29:207-231.

Frame, P.F., D. S. Hik, H. D. Cluff, & P. C. Paquet. 2004. Long foraging movement of a denning tundra wolf. *Arctic*. 57:196-203.

Hamre, Ø. 2006. Spatial and temporal use of forest roads by wolves in Scandinavia during summer. MSc Thesis. Faculty of Science, Department of Biology, University of Tromsø, Norway.

Hebblewhite, M., R. H. Munro, & E. H. Merrill. 2009. Trophic consequences of postfire logging in a wolf-ungulate system. *Forest Ecology and Management.* 257:1053-1062.

James, A.R.C. & A. K. Stuart-Smith. 2000. Distribution of caribou and wolves in relation to linear corridors. *Journal of Wildlife Management*. 64:154-159.

Jedrzejewski, W., M. Niedzialkowska, S. Nowak, & B. Jedrzejewska. 2004. Habitat variables associated with wolf (*Canis lupus*) distribution and abundance in northern Poland. *Diversity and Distributions*. 10:225-233.

Jedrzejewski, W., K. Schmidt, J. Theuerkauf, B. Jedrzejewska, & H. Okarma. 2001. Daily movements and territory use by radio-collared wolves (Canis lupus) in Bialowieza Primeval Forest in Poland. *Canadian Journal of Zoology*. 79:1993-2004.

Kaartinen, S., I. Kojola, & A. Colpaert. 2005. Finnish wolves avoid roads and settlements. *Ann. Zool. Fennici.* 42:523-532.

Karlsson, J., H. Brøseth, H. Sand, & H. Andrén. 2007a. Predicting occurrence of wolf territories in Scandinavia. *Journal of Zoology*. 272:276-283.

Karlsson, J., M. Eriksson, & O. Liberg. 2007b. At what distance do wolves move away from an approaching human? *Canadian Journal of Zoology*. 85:1193-1197.

Kunkel, K.E. & D. H. Pletscher, D.H. 2000. Habitat factors affecting vulnerability of moose to predation by wolves in southeastern British Columbia. *Canadian Journal of Zoology*. 78:150-157.

Kunkel, K.E. & D. H. Pletscher. 2001. Winter hunting patterns of wolves in and near Glacier National Park, Montana. *Journal of Wildlife Management*. 65(5):520-530.

Laurian, C., C. Dussault, J. Ouellet, R. Courtois, M. Poulin, & L. Breton. 2008. Behavior of moose relative to a road network. *Journal of Wildlife Management*. 72(7):1550-1557.

Manly, B. F., L. McDonald, D. L. Thomas, T. L. McDonald, & W. P Eriksen. 2002. Resource selection by animals: statistical design and analysis for field studies. Kluwer Academic Publishers, Norwell, Massachusetts, USA.

Mech, L.D. 1989. Wolf population survival in an area of high road density. *American Midland Naturalist*. 121:387-389.

Mech, L.D. & L. Boitini. 2003. Wolves: Behavior, Ecology, and Conservation. The University of Chicago Press 60637, Chicago.

Mech, L.D., S. H. Fritts, G. L. Radde, & W. J. Paul. 1988. Wolf distribution and road density in Minnesota. *Wildlife Society Bulletin.* 16:85-87.

Merrill, S.B. 2000. Road densities and gray wolf, *Canis lupus*, habitat suitability: an exception. *The Canadian Field-Naturalist*. 114(2):312-313.

Mladenoff, D.J., T. A. Sickley, R. G. Haight, & A. P. Wydeven. 1995. A regional landscape analysis and prediction of favorable gray wolf habitat in the northern Great Lakes region. *Conservation Biology*. 9:279-294.

Mohr, C. O. 1947. Table of equivalent populations of North American small mammals. *American Midland Naturalist*. 37:223-249.

Musiani, M., H. Okarma, & W. Jedrzejewski. 1998. Speed and actual distances travelled by radiocollared wolves in Bialowieza Forest (Poland). Acta Theriologica. 43(4):409-416.

Person, D.K. & A. L. Russell. 2008. Correlates of mortality in an exploited wolf population. *Journal of Wildlife Management*. 72(2):1540-1549.

Rodgers, A. R. 2001. Tracking animals with GPS: the first ten years. Pages 1-10 in A. M. Sibbald & I. J. Gordon, editors. Tracking Animals with GPS. GPS-conference, Aberdeen, Scotland.

Sand, H., B. Zimmermann, P. Wabakken, H Andrn, & H. C. Pedersen. 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf-ungulate ecosystems. *Wildlife Society Bulletin*. 33(3):914-925.

Sand, H., P. Wabakken, B. Zimmermann, Ö Johansson, H. C. Pedersen, & O. Liberg. 2008. Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates? *Oecologia.* 156: 53-64.

Shepherd, B. & J. Whittington. 2006. Response of wolves to corridor restoration and human use management. *Ecology and Society.* 11(2):1.

Theuerkauf, J., W. Jedrzejewski, K. Schmidt, & R. Gula. 2003a. Spatiotemporal segregation of wolves from humans in the Bialowieza Forest (Poland). *Journal of Wildlife Management*. 67:706-716.

Theuerkauf, J., W. Jedrzejewski, K. Schmidt, H. Okarma, I. Ruczynski, S. Sniezko, & R. Gula. 2003b. Daily patterns and duration of wolf activity in the Bialowieza Forest, Poland. *Journal of Mammalogy*. 84(1): 243-253.

Theuerkauf, J., S. Rouys, & W. Jedrzejewski. 2003c. Selection of den, rendezvous, and resting sites by wolves in the Bialoweiza Forest, Poland. *Canadian Journal of Zoology*. 81:163-167.

Thiel, R. P. 1985. Relationship between road densities and wolf habitat suitability in Wisconsin. *American Midland Naturalist*. 113:404-407.

Thurber, J.M., R. O. Peterson, T. D. Drummer, & S. A. Thomasma. 1994. Gray wolf response to refuge boundaries and roads in Alaska. *Wildlife Society Bulletin*. 22:61-68.

Wabakken, P., H. Sand, O. Liberg, & A. Bjärvall. 2001. The recovery, distribution and population dynamics of wolves on the Scandinavian Peninsula, 1978-1998. *Canadian Journal of Zoology. 79*: 710-725.

Wabakken, P., Å. Aronson, H. Sand, H. Rønning, & I. Kojola. 2004. Ulv i Skandinavia: Statusrapport for vinteren 2002-2003. Oppdragsrapport nr. 2 - 2004. Høgskolen i Hedmark.

Wabakken, P., Å. Aronson, T. H. Strømseth, H. Sand, & I. Kojola. 2005. Ulv i skandinavia: Statusrapport for vinteren 2004-2005. Oppdragsrapport nr. 6-2005. Høgskolen i Hedmark.

Wabakken, P., Å. Aronson, T. H. Strømseth, H. Sand, E. Maartmann, L. Svensson, & I Kojola. 2009. Ulv i Skandinavia: Statusrapport for vinteren 2008-2009. Oppdragsrapport nr. 6 - 2009. Høgskolen i Hedmark.

Whittington, J., C. C. St Clair, & G. Mercer. 2004. Path tortuosity and the permeability of roads and trails to wolf movement. *Ecology and Society.* 9(1):4.

Whittington, J., C. C. St Clair, & G. Mercer. 2005. Spatial response of wolves to roads and trails in mountain valleys. *Biological Applications.* 15:543-553.

Zimmermann, B., T. Storaas, P. Wabakken, K. Nicolaysen, O. K. Steinset, M. Dötterer, H. Gundersen, & H. P. Andreassen. 2001. GPS collars with remote download facilities, for studying the economics of moose hunting and moose-wolf interactions. Pages 33-38 in A. M. Sibbald & I. J. Gordon, editors. Tracking Animals with GPS. GPS-conference, Aberdeen, Scotland, 12-13 March 2001.

Zimmermann, B. T., P. Wabakken, H. Sand, H. C. Pedersen, & O. Liberg. 2007. Wolf movement patterns: a key to estimation of kill rate? *Journal of Wildlife Management. 71: 1177-1182.*

Appendices

Appendix 1. Road Densities per Territory. The territory size (or home range) is the 100% MCP estimate of all positions, both traveling and resting positions, within each study period.

	Territory	100% MCP Estimate (km²)	Road Density (km road/km²)	MR Density (km road/km²)	FGR Density (km road/km²)	Avg Density (km road/km²)
Territories covering parts of Norway and Sweden[1]	Bograngen1	1596.88	0.88	0.14	0.74	**0.86**
	Djurskog 1	219.82	0.85	0.14	0.71	
	Djurskog 2	264.96	0.80	0.11	0.69	
	Gräsmark	819.72	1.08	0.23	0.85	
	Juvberget	1039.77	0.77	0.13	0.64	
Swedish Territories	Forshyttan	698.23	0.82	0.30	0.52	**0.80**
	Glaskogen	637.08	0.70	0.20	0.51	
	Halgån	545.35	0.73	0.21	0.52	
	Nyskoga	261.32	0.80	0.17	0.63	
	Uttersberg1	295.44	0.90	0.28	0.62	
	Uttersberg2	246.51	0.85	0.26	0.59	
Norwegian Territories	Koppang1	403.89	0.74	0.17	0.57	**0.99**
	Koppang2	2003.41	0.70	0.13	0.56	
	Gråfjell1	632.61	1.01	0.07	0.94	
	Gråfjell2	102.37	0.99	0.03	0.97	
	Bograngen2[1]	639.70	1.39	0.16	1.24	
Average per territory		650.44	0.88	0.17	0.71	

[1]Bograngen 2 covers parts of Sweden, but only 13% (83.5 km²) of the 100% MCP home range was in Sweden. Bograngen 2 was therefore classified as a Norwegian territory (14 traveling positions out of 238 total traveling positions were in Sweden).

Appendix 2. Road types of Norwegian and Swedish national map data and the classification used in this study.

	Road Type	Explanation	Classification
Sweden	Almäna vägar (av)	Main Road	MR
	Enskilda vägar (ev)	Forest Road	FGR
Norway	F – Fylkesvei	County Road	MR
	K – Komunavei	Municipal Road	MR
	R – Riksvei	Highway	MR
	P – Privatvei	Privately owned road	FGR

Appendix 3. Individual adult, scent-marking wolves in this study. Territory names, study periods, GPS intervals, and type of GPS are also given.

Individual	Sex	Territory[1]	Study Period	GPS Interval	GPS Collar Type
03-06	M	Djurskog 1,2	06/21/04 - 07/15/04, 08/02/04 - 08/22/04	30 minute	Simplex
05-05	M	Forshyttan	08/08/05 - 08/29/05	30 minute	
02-13	M	Glaskogen	06/24/02 - 09/08/02	30 minute	Simplex
01-10	F	Gråfjell 1	06/02/03 - 07/13/03	hourly	Simplex
01-09	M	Gråfjell 1	06/02/03 - 07/13/03		Simplex
01-09	M	Gråfjell 2	06/14/04 - 07/04/04	hourly	Simplex
00-09	M	Bograngen 1	06/02/03 - 07/13/03	30 minute	Simplex
00-09	M	Bograngen	06/14/04 - 07/04/04	30 minute	Simplex
04-02	M	Koppang 1,2	06/14/04 - 07/04/04, 08/19/04 - 09/05/04	30 minute	Simplex
04-03	F	Koppang 1,2	06/14/04 - 07/04/04, 08/19/04 - 09/05/04	30 minute	Simplex
06-10	F	Gräsmark	06/10/06 - 07/07/06	Hourly	Vectronics
06-11	M	Gräsmark	06/10/06 - 07/07/06	Hourly	Vectronics
02-06	F	Halgån	06/21/03 - 08/21/03	30 minute	
06-06	M	Juvberget	06/04/07 - 07/01/07	30 minute	Simplex
05-10	F	Juvberget	06/14/07 - 06/26/07		Tellus
00-07	F	Nyskoga	06/01/03 - 06/10/03		Web-direct
05-06	M	Uttersberg 1,2	08/01/05 - 08/22/05, 09/12/05 - 09/29/05	30 minute	Vectronics

[1]Geographical distribution and other details of each territory are given by Wabakken et al. (2003, 2005).