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Finnish wolves avoid roads and settlements

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The avoidance of roads and human settlements by wolves (*Canis lupus*) in a harvested population was studied in boreal woodland landscapes in east-central Finland with a low density of humans (2 km^{-2}) and roads (0.4 km/km^{-2}). The abundance of the primary prey, i.e. moose, is moderate with approximately 50 moose per wolf within wolf pack territories. Twelve alpha wolves in six territories were captured, fitted with radio-collars, and ground-tracked during 1998–2002. The number of wolves has recently been increasing in Finland and they have also expanded their range. This in turn has raised a certain degree of concern among people living in the area, and the wolves are often perceived as a safety threat both to people and domestic animals. We found that wolves tended to avoid human constructions. The avoidance distances were highest for buildings (1000 m) and for roads (250 m). Extrapolating from the avoidance distances to give an estimate for the entire study area revealed that 48% of the study area would potentially be subject to reduced use by the wolf.

Introduction

Wolf populations were exterminated from most of their former European range during the 19th and 20th centuries. However, during the last twenty years wolves have again expanded their range in many countries (Boitani 1995, 2000). The rapid growth of wolf populations together with their adaptability and dispersal ability allows them to increasingly colonize into developed areas (Mech 1995, Mladenoff & Haight 1997, Boitani 2000). Consequently, wolves are living in multiple-use landscapes surrounding human settlements in many parts of Europe (Linnell *et al*. 2001). Within these landscapes there is a high risk of wolves preying on domestic animals (Linnell *et al*. 1999). The conflict with human economies has been the main reason for wolf control, and it is still one of the main causes of wolf mortality (Boitani 2000). Because human tolerance of the wolf depends largely on the behaviour of wolves themselves, landscape features — especially those relating to the impact of humans — can be used to predict suitable wolf habitats (Mladenoff *et al*. 1995, Massolo & Meriggi 1998, Corsi *et al*. 1999). Wolves prefer areas with high forest cover, few roads, and a low human density (Mech *et al*. 1988). Such areas may be the least accessible to humans, and the lack of human presence remains the most important variable predicting wolf viability (Mech 1995).

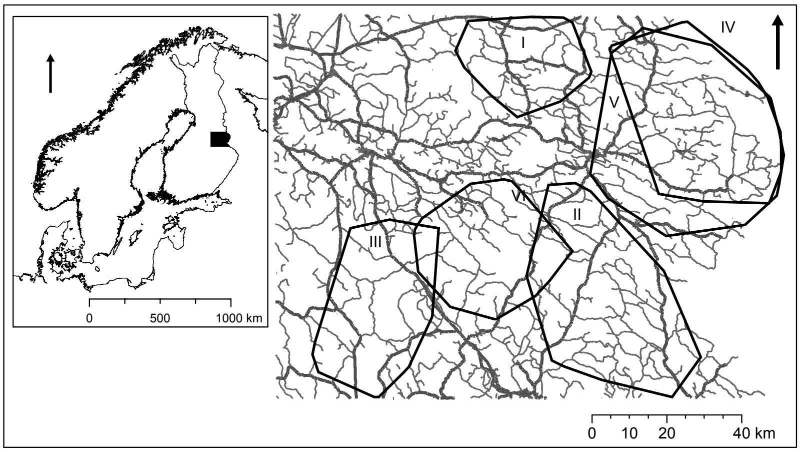

Fig. 1. Study area and wolf territories as MCPs.

Road density has frequently been used as a landscape feature to predict suitable wolf habitats (Mech *et al.* 1988, Mech 1989, Mladenoff *et al.* 1995, Corsi *et al.* 1999). Road systems are essentially transport corridors imposed on the environment by humans to allow the movement of people and the goods required by human society (Bennett 1991). Mladenoff *et al.* (1995) based road densities on paved roads, and improved dirt and gravel roads that appear as solid lines on U.S. Geological Survey (USGS) 1:100 000 quadrangle maps. In our study we used 1:5000–1:10 000 digital maps from the NLS (National Land Survey of Finland) topographic database that also revealed less used forestry access roads.

The wolf population in Finland experienced a major decline during the late 19th century. The distribution shrank to include only the most remote regions in eastern and northern Finland (Pulliainen 1965). The number of wolves has been increasing in Finland recently and they have also expanded their range. This in turn has raised a certain degree of concern among people living in the area, and the wolves are often perceived as a safety threat both to people and domestic animals (I. Kojola *et al.* unpubl. data). No studies exist on the avoidance of human constructions by wolves in northern Europe. Habitats favourable to wolves have been previously assessed in North America (Mladenoff *et al.* 1995, 1999) and southern Europe (Corsi *et al.* 1999). These habitat studies were performed at a landscape level without any detailed examination of the way in which individual wolves avoided human activities.

On average 9.5% of the estimated wolf population has been legally harvested in Finland over the last 10 years. During 2000–2004 six out of 20 dead collared wolves were killed illegally and 12 were killed legally (I. Kojola unpubl. data). We examined whether wolves from an exploited wolf population tend to avoid human constructions in boreal forest ecosystems with relatively abundant prey populations and a low density of residences and roads. This type of landscape is characteristic of the home ranges of most wolf packs in northern Europe. In particular, our aim was to assess critical avoidance limits for buildings and roads with different traffic loads and to estimate the proportion of the landscape that can be designed as a habitat that is likely to be avoided based on the avoidance criteria.

Study area

The 13 000 km^2 study area was located in eastern Finland and consisted of parts of the provinces of Kainuu, Pohjois-Karjala and Pohjois-Savo (Fig. 1). This area belongs to the mildly continental part of the mid-boreal coniferous forest zone (Ahti *et al.* 1968). The topography is flat, with elevations (a.s.l.) ranging from 160 to 307 m. Forests cover about 80% of the land area, and lakes and swamps are also common. Commercial forests make up about 93% of the total forested land area and about half of the swamps have been drained. The dominant tree species in the area are the Scots pine (*Pinus sylvestris*) and the Norway spruce (*Picea abies*). Young successional mixed forests are common as a result of extensive logging. Permanent snow usually appears in mid-November and melts in early May. The snow depth usually exceeds 80 cm and peaks in March.

The six wolf packs that occupied the study area were all included in the study. Mean wolf density was 3–3.5 wolves 1000 km^{-2}. For reference the wolf density in Italy and Spain is 2–5 wolves 100 km^{-2} (Boitani 2000). The main species of wolf prey in the study area are moose (*Alces alces*) and wild forest reindeer (*Rangifer tarandus fennicus*). In the dietary analysis the year-round frequency of reindeer and moose remains among all food items was 24.1% and 55.2%, respectively (Kojola *et al*. 2004b). The overall moose density is 540 animals 1000 km^{-2} before the autumn hunting season and approximately 350 animals 1000 km^{-2} in winter (V. Ruusila unpubl. data). The density of the wild reindeer is approximately 200 animals 1000 km^{-2} (K. Heikura unpubl. data). Wild reindeer exist only in the three northernmost wolf territories (Fig. 1).

The mean density of humans in the study area is five people km^{-2}, and 1–2 km^{-2} within wolf territories. Population density is low even by Finnish standards as the mean density of humans in Finland is 17 people km^{-2}. Most people (65%) in the study area live in densely built-up areas near town centres, but many of them maintain a holiday residence in the countryside. The overall density of the year-round residences is 1.09 km^{-2}, and the average (± S.D.) in the wolf territories is 0.38 ± 0.18 km^{-2}. The densities of the holiday residences are 0.46 km^{-2} and 0.22 ± 0.11 km^{-2}, respectively.

The density of primary and secondary roads in the study area is 0.4 km/km^2 (primary roads 0.1 km/km^2 and secondary roads 0.3 km/km^2). In the pack home ranges the mean density of primary roads (± S.D.) is 0.07 ± 0.03 km/km^2 and the density of secondary roads 0.26 ± 0.04 km/km^2. Finland has a high density of forestry roads and in the study area density is 0.76 km/km^2. In the home range areas of the wolf the density of forest roads is just as high and has an average of (± S.D.) 0.73 ± 0.18 km/km^2.

Methods

A total of 36 wolves were captured and fitted with radio-collars during 1998–2002. The wolves were captured using snowmobiles in February–March when the snow was soft and at least 80 cm deep. The snowmobiles were driven alongside the wolves, which were then captured using a neckhold noose attached to a pole. The restrained animals were put in a wooden box strengthened with metal grating on the outside and with doors at both ends. They were kept for 30 min before an anaesthetic was injected intramuscularly. Once the wolf had been collared with a Telonics' radio-collar with MOD-500 transmitter, it was also marked with ear-tags and measured. After this it was placed back in the box. An antagonist was injected and the animal was allowed to recover before it was released (Kojola *et al*. 2004b).

The wolves were not injured during the process. Neck collars rarely affect survivorship, reproduction, behaviour, or condition in medium to large-bodied terrestrial mammals, but definitive tests of transmitter effects are rare (Withey *et al*. 2001). The chief veterinary officer for the province of Oulu granted permission to capture the wolves.

A tight network of small roads resulting from intensive forestry and the scattered distribution of human settlements enabled comprehensive radio tracking from the ground. All the radio-collared wolves were ground-tracked regularly throughout the year by triangulation of at least two directional bearings recorded at known remote locations. We used vehicles with car-top dipole antenna systems to locate the positions where VHF signals could be heard. After that, location estimates were obtained using a Telonics H-Adcock hand-held RA-2AK antenna with Telonics TR2 and TR5 receivers. Each wolf was located 2–5 times every week.

The location data on wolves in a pack were not independent; in the analysis each breeding pair was treated as a statistical unit (Aebischer *et al*. 1993). This was justifiable as young members usually constitute only a temporary portion of packs, and the only long-term members are the breeding pair (Mech 1999). This means that the 12 alpha wolves in the six packs were included in the analysis.

Digital geographic data on human constructions in the study area were bought from the National Land Survey of Finland (NLS). Road information in the NLS database is updated annually and data on buildings every 3–10 years. Vehicle traffic data were obtained from The Finnish Road Administration.

Proximity functions of operations are among the most common spatial analysis tools and buffering is one of the most commonly used proximity functions. A buffer is a region that is less than or equal to a specified distance from one or more features. They may be determined for point, line, or area features, and for raster or vector data. Buffers typically identify areas that are outside a given threshold distance *vs.* those inside the threshold distance. Nested buffering, also called multi-ring buffering, can be used to identify zones that are at a given distance from a feature (Bolstad 2003). We generated a series of distance-from-construction buffers for each type of human construction that created zones around features at a given distance: A (0–100 m), B (100–250 m), C (250–500 m), D (500–1000 m) and E (> 1000 m).

We separated the roads into three classes according to their size and amount of traffic. The first class consists of primary roads. These are paved or improved gravel that are over five meters wide with two or more lanes. The second class consists of secondary roads. These are improved gravel or paved roads that are 3–5 meters wide with one lane. The third class comprises forestry roads that are less than three metres wide gravel forestry access roads. Buildings were separated into two classes: houses inhabited all year round and holiday residences that are mostly used during the summer.

We generated minimum convex polygon (MCP) home ranges (Mohr 1947) for each wolf pack for the time period. The choice of MCP as the home range estimate was based on its widespread use (Harris *et al.* 1990). We calculated the total area of each buffer zone around all the constructions in each MCP home range and the proportion of wolf locations that fell within each buffer zone around constructions.

We used log-ratio analysis of compositions i.e. compositional analysis (Aebischer *et al.* 1993) to analyse the selection by wolves of different construction buffers. This is a MANOVA-based technique that is used to analyse the statistical significance of differences and the rank order of differences between two sets of data in which variables are presented as proportions. Compositional analysis uses proportions of data such as habitat and use adding up to one, by using a log-ratio transformation (Aebischer *et al.* 1993). This renders the data independent (Aitchinson 1986). The technique compares the set of proportions relating to habitat use with the set of proportions corresponding to habitat availability under the null hypothesis of random use.

Compositional analysis deals with different habitat types simultaneously, which reduces the likelihood of Type I errors that are associated with multiple applications of the same statistical test (Aebischer & Robertson 1992). The Bonferroni corrections are not only unnecessary but would increase the risk of Type II error. The overall test using Wilk's lambda provides the protection that is needed against Type I error (N. J. Aebischer pers. comm.).

All analyses were carried out using a Compositional Analysis 4.0 Add-In for the Microsoft Excel spreadsheet program (Smith 2003). Where buffer zones were completely unused, we replaced the zero proportion by a proportion that was an order of magnitude smaller than the smallest non-zero proportion in this study and ranged from from 0.01 to 0.001. Monte Carlo randomization was used to determine the significance of Wilk's λ and t values to overcome the problems arising when the distribution of log-ratio differences is not multivariate normal (Smith 2003).

We analysed the habitat selection data at two scales: territory *vs.* total study area, and proportional habitat use based on radio-locations *vs.* home range composition. These correspond to second and third orders of habitat selection. First-order selection is the selection of physical or geographical range of a species. Second-order selection determines the home range of an individual or social group within that range. Third-order selection pertains to the usage made of various habitat components within the home range (Johnson 1980). Second-order selection was estimated by comparing the proportion of buffer zones within the home ranges with the proportion of buffer zones available across the study area. We estimated the third-order selection by comparing the proportion of buffer zones in location data with the proportion of buffer zones available across the home ranges.

We calculated the area that is potentially avoided by wolves as a result of avoiding each type of human construction by creating the ArcInfo coverage of the maximum significant avoidance distance that has been demonstrated for each construction type using the log-ratio analysis of compositions (Aebischer *et al*. 1993) as in Dyer *et al*. (2001). The cumulative effect of the reduced use was calculated by combining the ArcInfo coverage for all the human construction classes. The potential area affected by this reduced use was presented as a percentage of the total study area.

Results

Location data

The six wolf packs yielded 6468 locations over the data collection period, of which 1785 locations were recorded between 18:00 and 6:00 that we considered to be night. These night locations constitute 27.2% of the location data. The number of locations varied with the pack (Table 1). The mean size of the six wolf MCP home ranges was 1372 km^2.

Selection of buffers around forestry roads

Wolves differ significantly from one another in their use of buffer zones around constructions when they select a home range in the study area ($\lambda = 0.0974$, $\chi^2_4 = 13.97$, $P = 0.0074$). The log ration analysis of compositions indicated that wolves used buffer zone E (areas > 1000 metres from secondary roads) significantly more than buffer zone D (500–1000 m; Table 3). There was no significant difference between the use of the other buffer zones.

There was a detectable difference in the use of zones defined by buffer lines within MCP ranges ($\lambda = 0.0613$, $\chi^2_4 = 16.75$, $P = 0.0022$). The 0–100 m buffer zone (A) was used significantly less than buffer zones B (100–250 m), C (250–500 m) and D (500–1000 m). The most favoured was buffer zone D (500–1000 m). Use of buffer zone E (> 1000 metres from forestry roads) was not significantly different from the use of other buffer zones (Table 2).

Selection of buffers around secondary roads

Wolves differ significantly from one another in their use of buffer zones around constructions in relation to secondary roads when they select a home range in the study area ($\lambda = 0.0937$, $\chi^2_4 = 14.21$, $P = 0.0067$). The log ratio analysis of compositions indicated that wolves used buffer zone E (> 1000 metres from secondary roads) significantly more than buffer zone D (500–1000 m; Table 3). There was no significant difference between other buffer zones.

There was also a detectable difference in the use of zones defined by buffer lines within MCP ranges ($\lambda = 0.0086$, $\chi^2_4 = 28.56$, $P < 0.0001$). Wolves used buffer zones situated closer than 250 metres from secondary roads (i.e. buffer

Table 1. The home range (MCP) area and number of locations for six breeding pairs between April 1998 and December 2002.

Pack	Home range area (km^2)	Daytime locations (*n*)	Nighttime locations (*n*)
I	688.68	1028	946
II	1660.56	822	300
III	1136.92	346	46
IV	1552.87	436	92
V	2137.42	723	95
VI	1057.78	1295	306
Mean ± S.D.	1372.37 ± 514.35	775.5 ± 357.29	297.5 ± 336.78

Table 2. Mean pairwise log-ratio differences in radio-locations *vs*. home-range composition comparing buffer classes in which significant avoidance effects were detected. (d.f. = 5). Rand *p* values were determined with Monte Carlo randomization tests.

Construction class	Numerator	Denominator	Mean log-ratio (S.E.)	*t*	*p*	Rand *p*
Forestry road	0–100	100–250	–0.303 (0.0802)	–3.78	0.0129	0.029
	0–100	250–500	–0.5218 (0.1327)	–3.93	0.011	0.029
	0–100	500–1000	–0.7791 (0.1192)	–6.54	0.0013	0.029
	100–250	250–500	–0.2187 (0.0617)	–3.54	0.0165	0.029
	100–250	500–1000	–0.4761 (0.0676)	–7.05	0.0009	0.029
	250–500	500–1000	–0.2574 (0.0521)	–4.94	0.0043	0.029
Secondary road	0–100	250–500	–1.347 (0.3113)	–4.33	0.0075	0.035
	0–100	500–1000	–1.1701 (0.2733)	–4.28	0.0078	0.035
	0–100	< 1000	–1.6265 (0.3227)	–5.04	0.004	0.035
	100–250	250–500	–1.1275 (0.3141)	–3.59	0.0157	0.035
	100–250	500–1000	–0.9506 (0.127)	–7.49	0.0007	0.035
	100–250	> 1000	–1.407 (0.1485)	–9.48	0.0002	0.035
	500–1000	> 1000	–0.4564 (0.0954)	–4.78	0.005	0.035
Primary road	0–100	> 1000	–4.4382 (1.229)	–3.61	0.0154	0.03
	100–250	500–1000	–2.4745 (0.8715)	–2.84	0.0363	0.03
	100–250	> 1000	–3.9865 (1.1629)	–3.43	0.0187	0.03
	250–500	> 1000	–1.67 (0.3562)	–4.69	0.0054	0.03
House	0–100	250–500	–2.2266 (0.5294)	–4.21	0.0084	0.03
	0–100	500–1000	–2.3912 (0.3836)	–6.23	0.0016	0.032
	0–100	> 1000	–3.2993 (0.4185)	–7.88	0.0005	0.032
	100–250	500–1000	–1.4098 (0.5279)	–2.67	0.0443	0.032
	100–250	> 1000	–2.3178 (0.576)	–4.02	0.0101	0.032
	250–500	> 1000	–1.0727 (0.1982)	–5.41	0.0029	0.032
	500–1000	> 1000	–0.9081 (0.0997)	–9.11	0.0003	0.032
Holiday residence	0–100	250–500	–2.155 (0.5495)	–3.92	0.0112	0.025
	0–100	500–1000	–2.3438 (0.4402)	–5.32	0.0031	0.025
	0–100	> 1000	–3.2551 (0.4559)	–7.14	0.0008	0.025
	100–250	500–1000	–1.4688 (0.498)	–2.95	0.0319	0.025
	100–250	> 1000	–2.3801 (0.5566)	–4.28	0.0079	0.025
	250–500	> 1000	–1.1001(0.1878)	–5.86	0.0021	0.025
	500–1000	> 1000	–0.9113(0.0993)	–9.17	0.0003	0.025

Table 3. Mean pairwise log-ratio differences in home-range *vs*. study area comparing buffer zones in which significant avoidance effects were detected. (d.f. = 5). Rand *p* values were determined with Monte Carlo randomization tests.

Construction class	Numerator	Denominator	Mean log-ratio (S.E.)	*t*	*p*	Rand *p*
Primary road	0–100	250–500	–0.0395 (0.0099)	–3.98	0.0105	0.028
	100–250	250–500	–0.0257 (0.0059)	–4.34	0.0074	0.028
Secondary road	500–1000	> 1000	–0.1609 (0.0712)	–2.26	0.0735	0.03
House	0–100	100–250	–0.2647 (0.0178)	–14.87	0.0	0.03
	0–100	250–500	–0.4397 (0.0493)	–8.92	0.0003	0.03
	0–100	500–1000	–0.8154 (0.1021)	–7.99	0.0005	0.03
	0–100	> 1000	–1.6077 (0.2262)	–7.11	0.0009	0.03
	100–250	> 1000	–0.175 (0.0352)	–4.97	0.0042	0.03
	100–250	250–500	–0.5508 (0.0905)	–6.08	0.0017	0.03
	100–250	500–1000	–1.343 (0.2151)	–6.24	0.0015	0.03
	250–500	> 1000	–0.3758 (0.0558)	–6.73	0.0011	0.03
	250–500	500–1000	–1.1681 (0.181)	–6.45	0.0013	0.03
	500–1000	> 1000	–0.7923 (0.1291)	–6.14	0.0017	0.03
Holiday residence	0–100	100–250	–0.1216 (0.0196)	–6.20	0.0016	0.038
	0–100	250–500	–0.25 (0.0065)	–4.49	0.0065	0.038

zones A and B) significantly less than buffers further than 250 metres away (buffer zones C, D and E). Buffer zones 250–500 m and over 1000 metres from secondary roads were used significantly more than other buffer zones (Table 2).

Selection of buffers around primary roads

Wolves differ significantly from one another in their use of buffer zones around constructions in relation to primary roads when they select a home range in the study area (λ = 0.14, χ^2_4 = 11.79, P = 0.0189). The log-ratio analysis of compositions indicated that wolves used buffer zones C (250–500 metres from primary roads) significantly more than buffers zones A (0–100 m) and B (100–250 m). There were no significant differences between buffer zones A and B or between zones C, D and E (Table 3).

There was also a detectable difference in the use of zones defined by buffer lines within MCP ranges (λ = 0.1269, χ^2_4 = 12.38, P = 0.0147). Wolves use buffer zones A and B (areas < 250–500 metres from primary roads) less than buffer zones C, D and E (areas > 250–500 metres from primary roads; Table 2). The most frequently used buffer zones were D and E (areas situated 500–1000 m and over 1000 metres from primary roads, respectively).

Selection of buffers around houses

The log-ratio analysis of compositions indicated that the wolves differ significantly from one another in use of buffer zones around houses when they select a home range in the study area (λ = 0.0001, χ^2_4 = 57.62, P < 0.0001). Wolves used buffer zone E (> 1000 metres from buildings) significantly more than any other buffer zones. The least used buffer zone was A (0–100 metres from houses; Table 3).

There was also a detectable difference in the use of zones defined by buffer lines within MCP ranges (λ = 0.0193, χ^2_4 = 23.67, P = 0.0001). Wolves use areas over 1000 metres from houses (buffer zone E) significantly more than other areas. Buffer zones A and B (0–100 and 100–250 metres from houses respectively) were used significantly less (Table 2).

Selection of buffers around holiday residences

The log-ratio analysis of compositions indicated that the wolves differ significantly from one another in use of buffer zones around holiday residences when they select a home range in the study area (λ = 0.0056, χ^2_4 = 31.09, P < 0.0001). Wolves used buffer zone A (0–100 metres from holiday residences) significantly less than other buffer zones (Table 3).

There was also a detectable difference in the use of zones defined by buffer lines within MCP ranges (λ = 0.0062, χ^2_4 = 30.47, P = 0.0000). Wolves use areas over 1000 metres from holiday residences (buffer zone E) significantly more than other areas (Table 2).

Cumulative area avoided

The cumulative effect of the avoidance of different construction classes was calculated by combining the ArcInfo coverages of significant avoidance effects. When the avoidance distances determined by this study were used, the effect of human constructions on the selection of territory was considerable. About 50% of the study area would potentially be used less than expected by wolves (Table 4).

Table 4. Maximum significant avoidance distance (m) and area potentially affected (km^2). Total potentially avoided area is smaller than the sum of avoidance of different construction classes due to the overlap in avoidance effects. The area potentially affected as a percentage of the total study area appears in parentheses.

Construction class	Avoidance distance (m)	Area potentially avoided (km^2)
Secondary road	250	1835.55 (14.1)
Primary road	250	627.34 (4.8)
Roads together		2319.16 (17.8)
House	1000	5771.87 (44.4)
Holiday residence	100	141.09 (1.1)
Buildings together		5797.65 (44.6)
All together		6582.42 (50.6)

Discussion

Our results provided evidence that wolves avoided human settlements and roads in our study area. There are several potential explanations as to why wolves did not use residential areas. Livestock, especially sheep farms could attract wolves, but there were only a few in the study area. At the same time, the abundance of the primary prey, i.e. moose, is moderate. Using the observed moose density (0.35 moose km^{-2}; V. Ruusila's unpubl. data based on helicopter surveys in March 2003 and 2004), the mean maximum pack size in midwinter (7.0, range from 3 to 12; I. Kojola *et al.* unpubl. data) and mean territory size, the mean numerical ratio was approximately 50 moose per one wolf within wolf pack territories. This figure is fairly close to the similarly high prey density area in Quebec, Canada (calculated from Messier 1985). The moderate number of pups (on average 4–5 pups born per pack) produced every year indicates that the amount of nutrition acquired is adequate (I. Kojola unpubl. data).

During the study there were 21 wolf attacks on domestic dogs (*Canis familiaris*) within wolf territories. Most confirmed attacks (76%) were made in one territory and 70% of these attacks took place in house yards. It seems that some wolves do actively look for dogs (Kojola *et al.* 2004a). Although these wolf attacks on dogs happened during our study period, the radio-tracking data suggest that wolves still avoided human residential areas and did not spend time near human settlements.

The density of primary and secondary roads together in our study area at 0.4 km/km^2 is substantially lower than the threshold value in North American forests which was assessed at 0.6 km/km^2 (Wydeven *et al.* 2001). Although road density did not critically affect the viability of the wolf population in our study area, wolves did avoid both primary and secondary roads. Roads are likely to be avoided for two potential reasons; the risk of traffic accidents and being shot by humans using the road. In areas where public access is restricted, road density is not a good indicator of wolf presence (Merrill 2000), suggesting that wolves may avoid people rather than roads (Musiani & Paquet 2004). Roads have been found to increase mortality among grizzly bears (*Ursus arctos*) by providing easier access to the bears for hunters and poachers (McLellan & Shackelton 1998). Studies indicate that wolves may use roads and other linear corridors as easy travel routes in areas with limited human activity (Thurber *et al.* 1994). Linear corridors may allow wolves to travel more quickly through their environment (James & Stuart-Smith 2000).

On average, 9.5% of the estimated wolf population has been legally harvested in Finland during the last 10 years (I. Kojola unpubl. data). Fladders are regularly used in wolf hunting. The method uses a tether, which is several kilometres long and has flags stitched to it at regular distances. Wolves are driven into the loop, made out of the fladders, where gunmen are waiting. Since the fladders retain a human scent for several days, wolves tend to stay within the encircled area. Fladders are usually put near small forest roads (M. Suominen pers. comm.). Moving on roads, especially during daytime, increases the risk of being shot illegally, and this may also shape the behaviour of wolves.

Traffic noise is apparently more important than visual disturbance (Forman & Alexander 1998). This could explain why primary roads that are the most heavily used had the largest impact on wolf avoidance. On the other hand, it is possible that the avoidance is caused by the absence of prey from areas near roads. Various large mammals tend to have lower population densities within 100–200 m of roads. These road-effect zones generally exhibit lower breeding densities and reduced numbers of species compared with control sites (Forman & Alexander 1998). There are no studies on moose avoidance of roads in Finland. Rolley and Keith (1980) found that moose in North America tended to avoid agricultural clearings. The avoidance of disturbances such as roads and settlements was dependent on the time of the year and mean distance from dwellings, roads, and clearings, and decreased as moose moved to winter ranges (Rolley & Keith 1980). In Sweden damage to pine trees in winter caused by moose browsing is heaviest within 3 km of roads. Roads may act as a partial barrier for moose and make their migration more difficult, which increases their density near roads. Moose may also be attracted by road salt (Ball & Dahlberg 2002). Wolf avoidance patterns in this study may be influenced by the impact of the behaviour of prey, but little can be inferred before more information is collected about the behaviour of prey in relation to human constructions.

Wolves can adapt to living close to human activities as long as they are not disturbed (Boitani 2000). The survival tactics of wolves in areas where the environment has been altered by human activity may involve a process of finely-tuned adaptation to local conditions. The home-range location and configuration, habitat use, activity and movements are highly integrated to make the best functional compromise between the necessity to exploit the main food resources available and the need to avoid any direct form of disturbance by humans (Ciucci *et al*. 1997).

As the number of wolves increases, the conflicts between humans and wolves become more frequent. Often these conflicts lead to extermination of some of the wolves and in many cases these measures are justified, though this is not always so. Our study indicates that in general, wolves tend to avoid human settlements and roads. They try to establish home ranges in the areas where the human disturbance is as small as possible and inside these home ranges they tend to choose areas away from human constructions.

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References

Aebischer, N. J. & Robertson, P. A. 1992: Practical aspects of compositional analysis as applied to pheasant habitat utilization. — In: Priede, I. G. & Swift, S. M. (eds.), *Wildlife telemetry: Remote monitoring and tracking of animals*: 285–293. Ellis Horwood, Chichester.

Aebischer, N. J., Robertson, P. A. & Kenward, R. E. 1993: Compositional analysis of habitat use from animal radio-tracking data. — *Ecology* 74: 1313–1325.

Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Ann. Bot. Fennici* 5: 169–211.

Aitchison, J. 1986: *The statistical analysis of compositional data*. — Chapman and Hall, London, England.

Ball, J. P. & Dahlberg, J. 2002: Browsing damage on pine (*Pinus sylvestris* and *P. contorta*) by migrating moose (*Alces alces*) population in winter: Relation to habitat composition and road barriers. — *Scand. J. Forest Res*. 17: 427–435.

Bennet, A. F. 1991: Roads, roadsides and wildlife conservation: a review. — In: Saunders, D. A. & Hobbs, R. J. (eds.), *Nature conservation 2: the role of corridors*: 99–117. Surrey Beatty & Sons PTY Limited, Chipping Norton, Australia.

Boitani, L. 1995: Ecological and cultural diversities in the evolution of wolf–human relationships. — In: Carbyn, L. N., Fritts, S. H. & Seip, D. R. (eds.), *Ecology and conservation of wolves in a changing world*: 3–11. Canadian Circumpolar Institute, Edmonton, Canada.

Boitani, L. 2000: *Action plan for the conservation of the wolves (Canis lupus) in Europe*. — Convention on the conservation of European wildlife and natural habitats.

Bolstad, P. 2003: *GIS fundamentals: A first text on geographic information systems*. — Eider Press, Minnesota, USA.

Ciucci, P., Boitani, L., Francisci, F. & Andreoli, G. 1997: Home range, activity and movements of a wolf pack in central Italy. — *J. Zool., Lond*. 243: 803–819.

Corsi, F., Duprè, E. & Boitani, L. 1999: A large-scale model of wolf distribution in Italy for conservation planning. — *Conserv. Biol*. 13: 150–159.

Dyer, S. J., O'Neill, J. P., Wasel, S. M. & Boutin, S. 2001: Avoidance of industrial development by woodland caribou. — *J. Wildl. Manage*. 65: 531–542.

Forman, R. T. T. & Alexander, L. E. 1998: Roads and their major ecological effects. — *Annu. Rev. Ecol. Syst*. 29: 207–231.

Harris, S., Cresswell, W. J., Forde, P. G., Trewhalla, W. J., Woollard, T. & Wray, S. 1990: Home range analysis using radio-tracking data — a review of problems and techniques particularly as applied to the study of mammals. — *Mamm. Rev*. 20: 97–123.

James, A. R. C. & Stuart-Smith, A. K. 2000: Distribution of caribou and wolves in relation to linear corridors. — *J. Wildl. Manage*. 64: 154–159.

Johnson, D. H. 1980: The comparison of usage and availability measurements for evaluating resource preference. — *Ecology* 61: 65–71.

Kojola, I., Ronkainen, S., Hakala, A., Heikkinen, S. & Kokko, S. 2004a: Interactions between wolves *Canis lupus* and dogs *C. familiaris* in Finland. — *Wildlife Biol*. 10: 101–106.

Kojola, I., Huitu, O., Toppinen, K., Heikkinen, S., Heikura K. & Ronkainen, S. 2004b: Predation by wolves (*Canis lupus*) on European wild forest reindeer in east-central Finland. — *J. Zool., Lond*. 263: 219–228.

Linnel, J. D, Swenson, J. & Andersen, R. 2001: Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. — *Anim. Conserv*. 4: 345–350.

Linnell, J. D., Odden, J., Smith, M. E., Aanes, R. & Swenson, J. E. 1999: Large carnivores that kill livestock: do "problem individuals" really exist? — *Wildl. Soc. Bull.* 27: 698–705.

Massolo, A. & Meriggi, A. 1998: Factors affecting habitat occupancy by wolves in northern Apennines (northern Italy): a model of habitat suitability. — *Ecography* 21: 97–107.

McLellan, B. N. & Shackleton, D. M. 1988: Grizzly bears and resource-extraction industries: effects of roads on behaviour, habitat use and demography. — *J. Appl. Ecol.* 25: 451–460.

Mech, L. D. 1989: Wolf population survival in an area of high road density. — *Am. Midl. Nat.* 121: 387–389.

Mech, L. D. 1995: The challenge and opportunity of recovering wolf populations. — *Conserv. Biol.* 9: 270–278.

Mech, L. D. 1999: Alpha status, dominance, and division of labor in wolf packs. — *Can. J. Zool.* 77: 1196–1203.

Mech, L. D., Fritts, S. H., Radde, G. L. & Paul, W. J. 1988: Wolf distribution and road densities in Minnesota. — *Wildl. Soc. Bull.* 16: 85–87.

Merrill, S. B. 2000: Road densities and gray wolf, *Canis lupus*, habitat suitability: an exception. — *Can. Field-Nat.* 114: 312–313.

Messier, F. 1985: Solitary living and extraterritorial movements of wolves in relation to social status and prey abundance. — *Can. J. Zool.* 63: 239–245.

Mladenoff, D. J. & Haight, R. G. 1997: Causes and implications of species restoration in altered ecosystems. — *Bioscience* 47: 21–32.

Mladenoff, D. J., Sickley, T. A., Haight, R. G. & Wydeven, A. P. 1995: A Regional landscape analysis and prediction of favorable habitat in the northern Great Lakes region. — *Conserv. Biol.* 9: 279–294.

Mladenoff, D. J., Sickley, T. A., Haight, R. G. & Wydeven, A. P. 1999: Predicting gray wolf landscape recolonization: logistic regression models *vs.* new field data. — *Ecol. Appl.* 9: 37–44.

Mohr, C. O. 1947: Table of equivalent populations of North American small mammals. — *Am. Midl. Nat* 37: 223–249.

Musiani, M. & Paquet, P. C. 2004: The practices of wolf persecution, protection, and restoration in Canada and United States. — *Bioscience* 54: 51–60.

Pulliainen, E. 1965: Studies on the wolf (*Canis lupus* L.) in Finland. — *Ann. Zool. Fennici* 2: 215–314.

Rolley, R. E. & Keith, L. B. 1980: Moose population dynamics and winter habitat use at Rochester, Alberta, 1965–1979. — *Can. Field-Nat.* 94: 9–18.

Smith, P. G. 2003: Compositional Analysis Excel tool user's guide, ver. 4.0. Available from the author (e-mail: pgsmith@aber1.fsnet.co.uk), Bettws Cottage, Bettws, Abergavenny, Monmouthshire, NP7 7LG, Wales, UK.

Thurber, J. M., Peterson, R. O., Drummer, T. D. & Thomasma, S. A. 1994: Gray wolf response to refuge boundaries and roads in Alaska. — *Wildl. Soc. Bull.* 22: 61–68.

Withey, J. C., Bloxton, T. D. & Marzluff, J. M. 2001: Effects of tagging and location error in wildlife radiotelemetry studies. — In: Millspaugh, J. J. & Marzluff, J. M. (eds.), *Radio tracking and animal populations*: 43–75. Academic Press, USA.

Wydeven, A. P., Mladenoff, D. J., Sickley, T. A., Kohn, B. E., Thiel, R. P. & Hansen, J. L. 2001: Road density as a factor in habitat selection by wolves and other carnivores in the Great Lakes region. — *Endangered Species UPDATE* 18: 110–114.