

Habitat model for a recolonizing wolf (*Canis lupus*) population in Finland

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Received 26 June, final version received 15 Oct. 2014, accepted 16 Oct. 2014

Kaartinen, S., Antikainen, H. & Kojola, I. 2015: Habitat model for a recolonizing wolf (*Canis lupus*) population in Finland. — *Ann. Zool. Fennici* 52: 77–89.

The wolf (*Canis lupus*) population in Finland is recolonizing its former range after an absence of about 100 years. During its absence, the boreal forest environment has been significantly altered by humans and has become a patchwork of managed forests and human-modified areas. Wolf recolonization has raised a need for information on the potential occurrence of wolf home ranges and habitat requirements. We used a logistic regression to compare a set of habitat features inside 20 known minimum convex polygon (MCP) home ranges of wolves in Finland with the same habitat features in random areas. Wolves tended to show strong avoidance of direct human presence. There did not appear to be a large difference in the occurrence of different forest types between wolf home ranges and random areas. An independent sample of ten wolf home ranges was used to evaluate the probabilities of wolf occurrence predicted by the models. According to our model, 90% of these home ranges had a probability of occurrence greater than 0.50. We also used logistic regression to compare the habitat composition of 50% kernels inside the MCP home ranges. The tendency to avoid human presence was also evident in smaller scale habitat selection.

Introduction

Mobile and elusive animals such as large carnivorous mammals need vast areas with low human disturbance (Woodroffe 2000, Proctor *et al.* 2005, Nellemann *et al.* 2007). Human disturbance is a function of human density, and boreal regions in Europe, for example, might therefore provide the most appropriate area for the successful protection of such animals. On the other hand, productivity of the environment not only affects human density but also the abundance of wildlife. Large predatory mammals compensate

for low prey biomass by increasing mobility and the size of their home range. Therefore, the territories of wolves (*Canis lupus*), for example, are larger in boreal than temperate-vegetation zones (Fuller 1989, Okarma *et al.* 1998).

Protected areas in Europe are small and large carnivores have to extensively share their living space with humans (Linnell *et al.* 2001), which raises the issue of large carnivore–human conflict in the conservation management of large carnivore populations. In Fennoscandia, the primary reason for the presently small number of wolves is presumably wolf–human conflicts, including wolf

predation on semi-domesticated reindeer herds in northern parts of Norway, Sweden and Finland and on sheep flocks especially in Norway, as well as wolf attacks on dogs, a problem that concerns all Nordic countries (Kojola & Kuittinen 2002, Skonhøft 2006, Karlsson *et al.* 2007, Bisi *et al.* 2007, Kojola *et al.* 2009, Tønnesen 2010). The presence of wolves in areas where they have been absent for a hundred years has caused concern among people living in these areas, and the wolf is seen as a foreign invader when it is actually native to the area. Their presence intensifies the feeling that wolves do not belong near human settlements containing families and domestic animals, but in the wilderness, where their activities are of no concern to people (Hiedanpää 2013). A recent survey on the wolf issues in Finland revealed that one of the main concerns among people is the presence of wolves near their homes, and the possibility of wolves habituating to human presence and becoming bold enough to approach human settlements (Suomen Riistakeskus 2014).

The wolf population in Finland fluctuated considerably in the past 15 years. The population increased from an estimated 130–140 wolves in 1995 to approximately 250 by the end of 2006, when it peaked after a 10-year increase and expansion. Thereafter, the wolf population in Finland decreased by 40% by 2011, when the winter census revealed 135–145 animals (Kojola *et al.* 2011). The estimated winter population has since declined even further and was approximately 120–135 wolves in the winter of 2013. There are no biological reasons for the decline, as the roe deer and moose populations are sufficiently dense and there have been no signs of lethal diseases (Kojola *et al.* 2011). Legal removals are concentrated in northern Finland, where wolves cause damage to semi-domesticated reindeer (*Rangifer tarandus*) herds. No formal analysis on the role of poaching has been performed, but as in Scandinavia (Liberg *et al.* 2012), illegal killing has a substantial impact on Finland's wolf population, and might even influence habitat use by wolves and their spatial distribution in the country. Nevertheless, the distribution range of the reproductive wolf population has remained relatively stable, despite the decreasing number of family packs, and the potential for a rapid revival exists.

The goal of the present study was to develop models of territory site selection by wolves using detailed information on the species, human presence, and habitats, and to evaluate the reliability of these models in predicting the occurrence of wolf territories over a broad spatial extent, as well as to model the selection of the highest use areas inside the broad-scale home ranges. We first designed a set of models and compared their fit using radio and GPS-GSM tracking data and landscape information for the breeding wolf population in Finland outside the reindeer management area. The model predictions were then spatially extrapolated and the predictive accuracy of the models was evaluated using an additional dataset.

Material and methods

Study area

The study area (ca. 210 000 km²) comprised southern and central Finland outside the reindeer management area (MRA), and excluding the Åland archipelago. Almost all of the study area belongs to the mildly continental part of the mid-boreal coniferous forest zone, and only the southernmost areas of Finland are an intermediate between boreal forests and the temperate forests of central Europe (Ahti *et al.* 1968). Forests cover about 80% of the land area and commercial forests make up about 93% of the total forested land area. Lakes and mires are common, but about half of the nine million ha of peatland have been drained for forestry purposes (Finnish Forest Research Institute 2005). As a result of extensive logging, young successional mixed forests are common (Finnish Forest Research Institute 2005). Approximately 65% of forests in Finland are dominated by pine (*Pinus sylvestris*), 23% by spruce (*Picea abies*) and 9% by birch (*Betula* spp.) (Kaartinen 2011).

Territory data

We used data on 25 radio-collared (Televilt Tellus GPS 2 D, Followit AB, Lindesberg, Sweden or Vectronic GPS Plus 2, Vectronic

Aerospace GmbH, Berlin, Germany) wolves (10 females and 15 males) marked in 2000–2012. The collaring procedure is described in detail elsewhere (Kojola *et al.* 2004). Five of the study wolves were breeding with another marked individual and their positions were plotted together. We based our analysis on the packs that had had at least one litter, and the data therefore consisted of 20 territories in total (Fig. 1). Home range areas were determined both as 100% minimum convex polygons (MCP, Mohr 1947) and 50% kernels (fixed smoothing factor 5000, output cell size 50 m) (Worton 1989, Kernohan *et al.* 2001). We used 100% to represent the whole possible home range area as we also wanted to include extra-territorial movements and unused matrix inside the home range into the evaluated area. The 50% kernel represented the areas of high use by wolves (Ripple *et al.* 2001). The mean home range size (MCP) was 1750 km² (range 621–3868 km²) and the mean 50% kernel home range size was 128 km² (range 63–425 km²). The number of positionings used in the territory size estimation ranged from 416 to 5415 per individual, with 44 002 positionings in total. The majority of home ranges overlapped spatially, but not temporally, with another home range, as the wolf population in Finland has clustered in the east-central part of the country.

Randomization of non-pack areas

Geographic information system (GIS) data management and mapping was performed with ArcGIS 10.1 (ESRI, Redlands, California). Twenty non-pack areas were sampled in mainland Finland outside RMA using Geospatial Modelling Environment 0.7.2.1.RC2 (Beyer 2012) (Fig. 1). Sampling was carried out without replacement but allowing overlap with study home ranges. These non-pack areas were round-shaped areas of 1750 km², i.e. the mean home range size of the MCP estimation. Overlap with study home ranges was allowed to maintain the trend of wolf territories being clustered in east-central Finland and therefore also to preserve the geographical distribution of landscape characteristics in the study. This might result in bias and incorrect logistic regression coeffi-

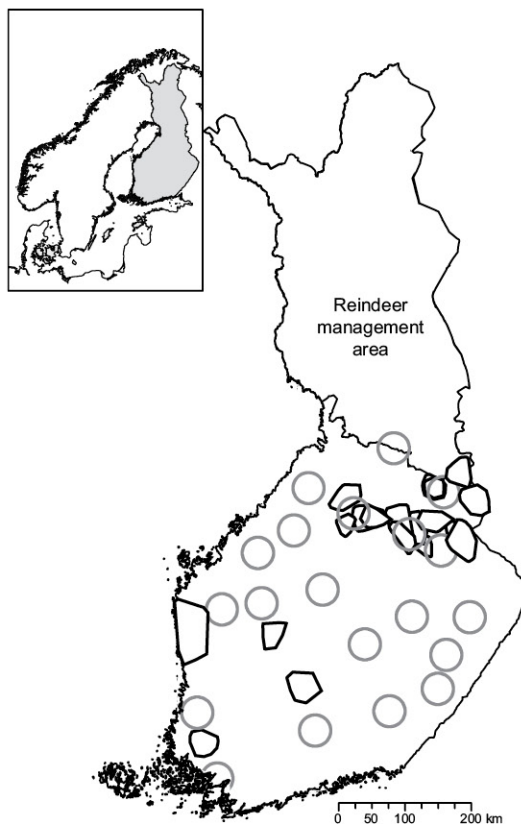


Fig. 1. Location of wolf home ranges (MCPs, black polygons) and random locations (grey circles) used in the modelling.

cients (*see* Johnson *et al.* 2006). Nevertheless, as wolves are highly capable of dispersing over very long distances, the whole study area (i.e. Finland, except for the RMA) can be assumed to have been available for each of the marked individuals to occupy as their home range. Therefore, the pattern of home ranges being biased in east-central Finland can be assumed to also have ecological significance.

Human inhabitant data and habitat categories

Landscape variables were selected to represent both human habitation and the main habitat types in Finland (Table 1). The principal units employed here to represent human habitation (variable 'people') were the 250 × 250 m grid

cells defined in the data produced by Statistics Finland (Statistics Finland 2013). The cells contain register-based information on the population, independent of any administrative units (Rusanen *et al.* 2003). For the purposes of this study, the cells were classified into two classes: cells with and without people living inside them.

Habitat data were based on the CORINE Land Cover 2006 database provided by the Finnish Environment Institute (SYKE) as part of the European CORINE2006 Land Cover project, and Multi-source National Forest Inventory data (MS-NFI) from the Finnish Forest Research Institute (Metla), combining field data, satellite imagery and other data sources. The 25 × 25 m resolution CORINE data used in this study comprised five classes of land cover: (1) human-influenced land, (2) deciduous and mixed forests > 30 years old, (3) coniferous forests > 30 years old (4) open, and (5) water (Table 1). Human-influenced land comprises all the built-up land including roads, settlement areas and agricultural land. The Open variable includes open woodlands and mires (Table 1). The database covers the whole country and has a minimum mapping unit of 25 ha. It is based on the automated interpretation of satellite images and data integration with existing digital map data. The accuracy of the database is rather good (for details, see SYKE 2009). The age class of the < 30-year-old forest stands was derived from the MS-NFI data. We used NFI9 data from 2009 and NFI11 data from 2011, so that we obtained the correct categories for different age groups for the home

ranges in different years. We used three forest age classes in this study for young forest stands and cut blocks: (a) cut blocks ≤ 5 years old, (b) cut blocks 5–15 years old, and (c) forest stands 15–30 years old (Table 1).

Statistical analysis and modelling process

Our habitat selection analysis was based on information-theoretic (IT) methods, in which hypotheses are first specified and mathematically formulated and these hypotheses are then ranked according to their parsimony (Johnson & Omland 2004, Rushton *et al.* 2004, Greaves *et al.* 2006, Klar *et al.* 2008). We designed a set of candidate models of the occurrence of wolf territories based on the following general hypotheses: (1) wolves avoid areas where human presence is continuous (Mladenoff *et al.* 1995, 1999, Theuerkauf *et al.* 2003, Karlsson *et al.* 2007); (2) wolves seek areas where there is sufficient forest cover (Mladenoff *et al.* 1995, 1999, Massolo & Meriggi 1998, Theuerkauf *et al.* 2003, Karlsson *et al.* 2007); and (3) densities of moose (*Alces alces*), the primary prey, are highest in areas dominated by mixed forests and young successional forests (Nikula *et al.* 2004, Edenius *et al.* 2002). Road density was taken as indicative of human presence in the area in many wolf habitat studies and wolves generally avoid areas with high road densities (Mladenoff *et al.* 1995, 1999, Wydeven *et al.* 2001, Gurarie *et al.* 2011). In this study, roads

Table 1. Description and availability of habitat categories in the study area (southern part of Finland, excluding the reindeer management area) and in wolf MCP home ranges.

Habitat type (variable)	Description	Availability (%) study area ¹	Availability (%) MCP ¹
People	Human inhabited grid cells	9	3
0–5	Recent cuts ≤ 5 years old	2	4
5–15	Regenerating cuts 5–15 years old	4	4
15–30	Forest stands 15–30 years old	8	8
Human influence	Human-use lands (built-up areas, agricultural land)	15	7
Conifer	Coniferous trees ≥ 30 years old	36	47
Deciduous-mixed	Mixed forest stands ≥ 30 years old	11	13
Open	Open woodland (tree canopy closure < 30%, wetlands)	8	11
Water	Lakes, rivers	12	6

¹ The sums of the variables are > 100% as cell sizes of these variables differ.

were included into the ‘human influence’ variable through the CORINE data. We did not consider road density directly, as we used the variable ‘people’, which represents human presence. Preliminary assessment of the data showed that road density is highly correlated with the ‘people’ variable.

To identify any multi-collinearities between variables, we conducted Spearman’s pairwise correlation analysis and calculated the variance inflation factor (VIF) values for the full model before modelling (Zuur *et al.* 2010). First, we dropped any variable with a strong correlation ($|r| > 0.6$) (Green 1979, Fielding & Haworth 1995, Sawyer *et al.* 2006, Klar *et al.* 2008), and after this we calculated VIF values and sequentially dropped the covariate with the highest VIF. VIFs were then recalculated, and this process was repeated until all VIFs were smaller than a threshold value (Zuur *et al.* 2010). In this study, we used a VIF threshold value of 2 to avoid non-significant parameter estimates (Zuur *et al.* 2010).

Logistic regression together with Akaike’s Information Criterion (Akaike 1973) corrected for small sample sizes [AIC_c (Hurvich & Tsai 1989)] was used to model the important habitats for wolf packs when selecting their territory in the study area. We based the selection of the best approximating models on the ΔAIC_c values, which were calculated as the differences between the current and minimum observed values of AIC_c (Burnham & Anderson 2002, 2004). Models with $\Delta AIC_c > 2$ were considered not to fit the data (Burnham & Anderson 2002, Grueber *et al.* 2011). Akaike weights (w_i) and evidence ratios (w_1/w_i , where w_1 is the Akaike weight of the best-fitting model) for all models were also calculated. We used the IT model averaging approach, a method suggested by Burnham and Anderson (2002) to quantify the evidence for the importance of each variable, because there was considerable model selection uncertainty in our data. The IT approach accounts for this uncertainty to obtain robust parameter estimates or predictions (Grueber *et al.* 2011). Akaike weights across all the models where individual variables occurred were summed to obtain the relative importance of the variables (Grueber *et al.* 2011). We used model averaging to produce the best model, including aspects of a

number of models (Greaves *et al.* 2006). Parameter estimates, their standard errors and confidence intervals in the set of best approximating models were examined to assess the reliability of each variable as a predictor of the occurrence of a wolf territory. Statistical analyses were carried out using R 3.0.2 (R Development Core Team 2014) with the package *MuMIn* (Bartoń 2009).

We performed the modeling in two parts. First, we included 20 MCP home ranges and 20 random areas to model the probability of occurrence of a breeding territory in Finland outside the RMA. Second, we modeled the differences in habitat composition between 50% kernel and 100% MCP home ranges for all 20 packs.

Model evaluation

We evaluated the accuracy of habitat predictions using an independent sample of ten home ranges not used for model fitting for an MCP home-range selection model.

We also used the MCP home-range selection model to build predictive maps of wolf territory locations in the study area. We calculated the predicted probabilities for the existence of a wolf territory in 10×10 km squares to determine all the possible wolf territory locations, regardless of the size of the area.

Results

Model selection

MCP home-range selection

Strong positive and negative correlations were found between several study variables (Fig. 2). As the variables ‘people’ and ‘human influence’ were highly correlated, we decided not to use ‘human influence’ in modeling, as the variable ‘people’ was considered more relevant for the study in question. The variable ‘open’ was also removed from the studied variable list at this point, as other variables were more relevant. The deciduous and mixed forests variable (deciduous and mixed forests > 30 years old, or ‘dec_mix’) was removed from the global model, as it had

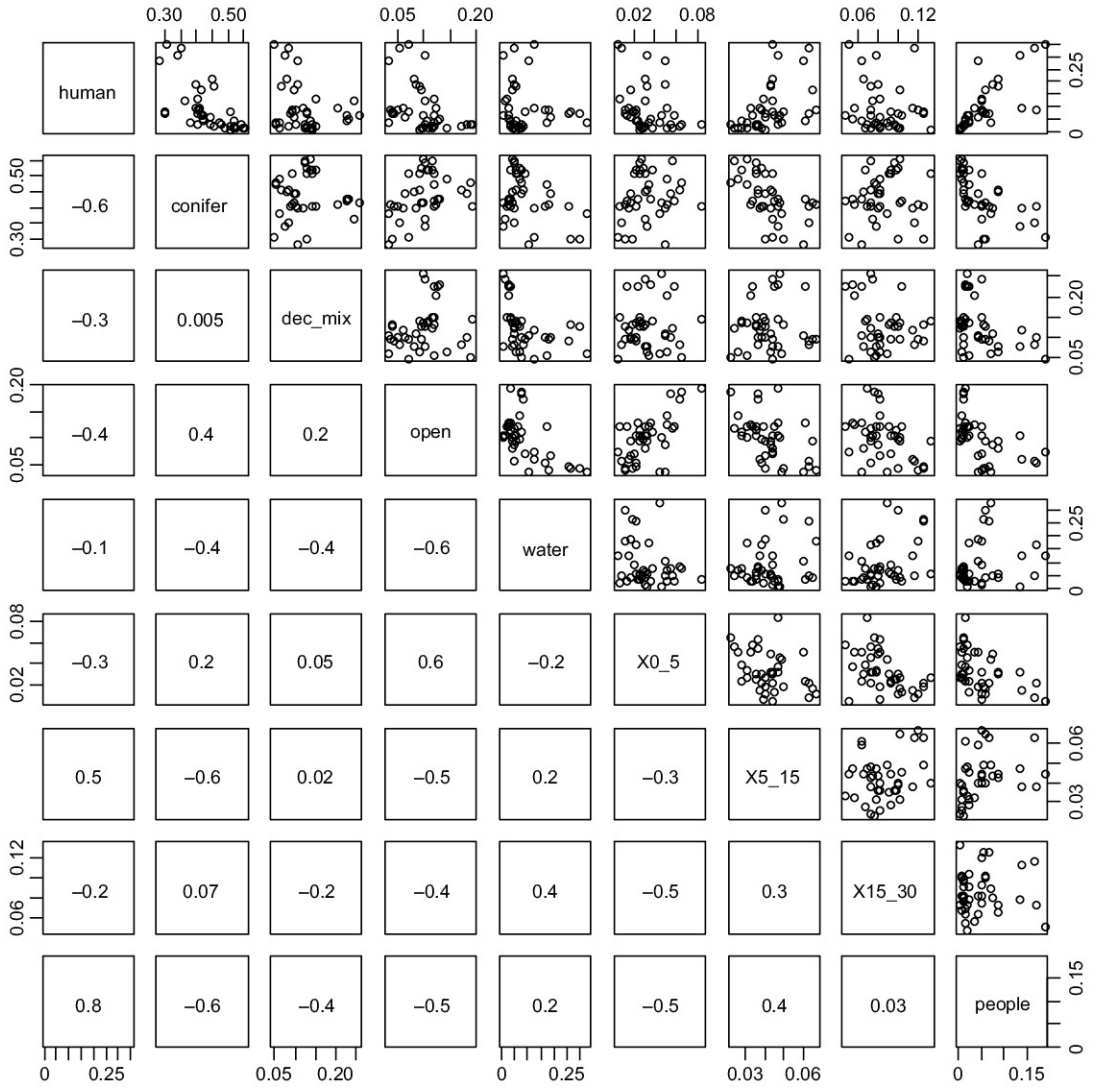


Fig. 2. Multi-panel scatterplot of model variables for MCPs *versus* random areas. The upper/right panels are scatterplots for variable pairs, and the lower/left panel contains Pearson's correlation coefficients. Abbreviations: human = human-influenced land, conifer = coniferous forests > 30 years old, dec_mix = deciduous and mixed forests > 30 years old, X0_5 = forests 0–5 years old, X5_15 = forests 5–15 years old, X15_30 = forests 15–30 years old.

a very high VIF value (Table 2). At the second stage of VIF calculation, we removed the forest age class variable '15–30'. Removal of the 'dec_mix' and '15–30' variables reduced all the other VIFs to a tolerable level (Table 2).

There were two plausible models ($\Delta AIC < 2$), and as reflected by the Akaike weights, there was uncertainty in model selection (Table 3). Nevertheless, the following general patterns are worth noting. The model that included people

and water was ranked as the best model to approximate variation in the occurrence of wolf territories in the data. The variable 'people' was included in both of the best models, whereas the models that did not include this variable all had $\Delta AIC > 7$ (Table 3), and were not therefore supported by the data. As the proportion of the human-occupied grid cells was included in the top models, it is unlikely that any of the models not including the variable 'people' would be the

best model. Model-averaged parameter values revealed that the probability of occurrence of a wolf territory decreased with an increasing proportion of human habitation and water. The forest age variables were not included in the top two models ($\Delta AIC < 2$). The model-averaged slopes (β values) of the variables, their standard errors and confidence intervals are presented in Table 4. Notably, the 95% confidence intervals of the variable 'water' include zero, so there is little evidence that variables other than 'people' affect wolf home-range selection.

Kernel home-range selection

Strong positive and negative correlations were found between several study variables (Fig. 3). Due to the high correlation between the variables 'people' and 'human influence', we decided to use the variable 'people' only, which was considered to be more relevant than 'human influence'. We also did not use the variable 'open',

as it correlated with the variable '0–5', and this forest age variable was more relevant. The forest age variable '0–5' was removed from the global model, as it had a very high VIF value (Table 5). Removing this variable reduced all the other VIFs to a tolerable level (Table 5).

There were four plausible models ($\Delta AIC < 2$), and as reflected by the Akaike weights, there was uncertainty in model selection (Table 6). The variable 'people' was included in all four top-ranking models. Again, all the

Table 2. MCP model variance inflation factor (VIF) values for the full and reduced models.

Variable	Full model	Reduced model 1	Reduced model 2
People	1.79	1.30	1.30
Water	1.80	1.42	1.05
0–5	1.82	1.72	1.21
5–15	1.48	1.33	1.28
15–0	2.01	2.04	
Deciduous-mixed	2.28		

Table 3. Generalized linear model (GLM) for the occurrence of MCP wolf home ranges using a binomial distribution and the logit link function. The models are ranked according to the AIC_c values.

Rank	Model	AIC_c	ΔAIC_c	w	K
1	people + water	45.5	0	0.32	3
2	people	45.9	0.4	0.26	2
3	people + water + 0–5	48.0	2.4	0.10	4
4	people + water + 5–15	48.0	2.4	0.09	4
5	people + 5–15	48.2	2.6	0.09	3
6	people + 0–5	48.3	3.7	0.08	3
7	people + water + 0–5 + 5–15	50.5	5.0	0.03	5
8	people + 0–5 + 5–15	50.6	5.1	0.03	4
9	water + 5–15	53.3	7.7	0.01	3
10	water	53.4	7.8	0.01	2
11	water + 0–5	54.4	8.9	0	3
12	water + 0–5 + 5–15	55.3	9.8	0	4
13	5–15	56.2	10.7	0	2
14	0–5	56.9	11.4	0	2
15	0–5 + 5–15	57.3	11.7	0	3
16	"null model"	57.6	12.2	0	1

Table 4. Summary results after model averaging: effects of each parameter on MCP home-range selection.

Parameter	Estimate	Unconditional SE	95% confidence interval	Relative importance
(intercept)	1.85	0.75	(0.38, 3.33)	
People	–35.03	14.95	(–64.33, –5.74)	1.00
Water	–9.14	6.47	(–21.82, 3.54)	0.55

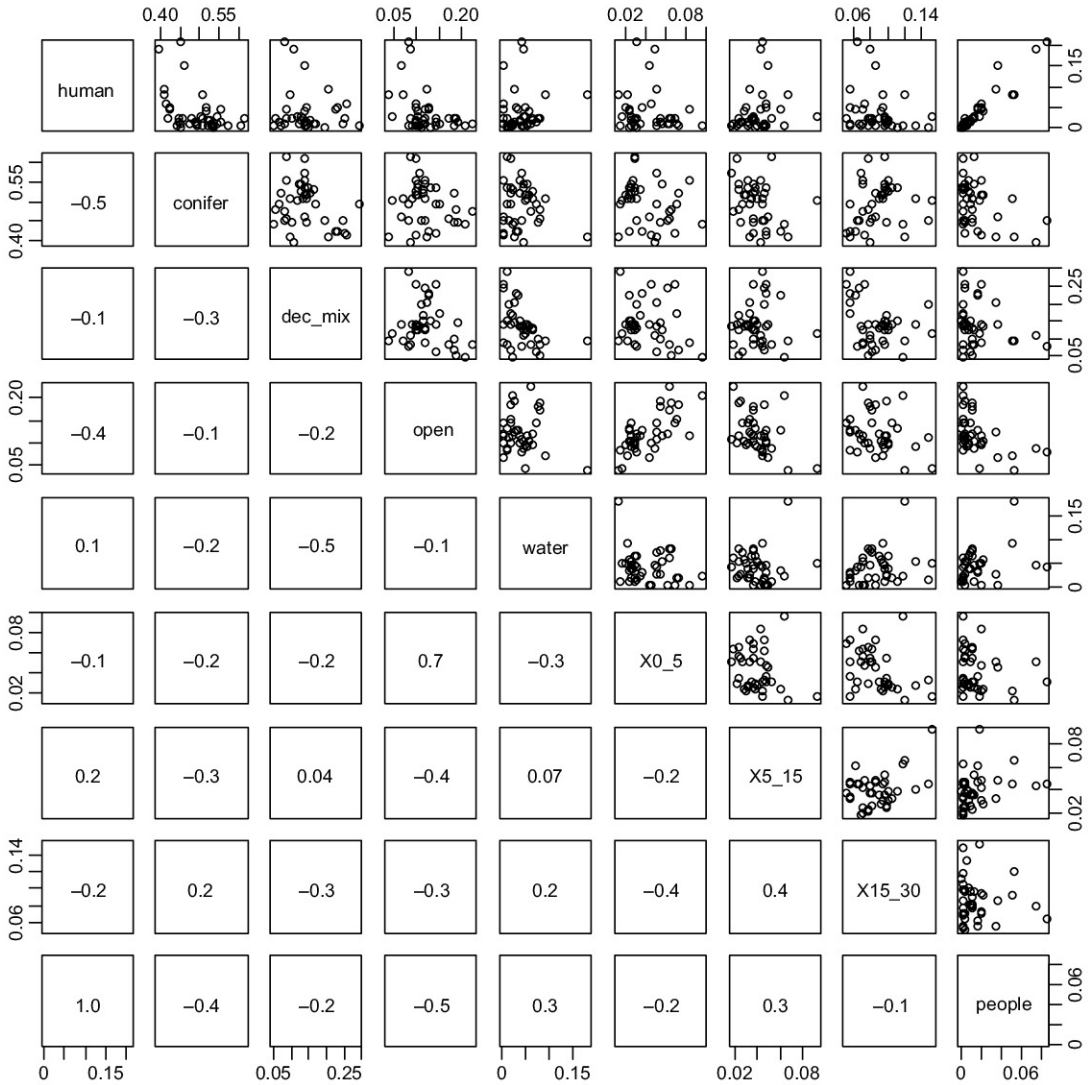


Fig. 3. Multi-panel scatterplot of model variables for 50% kernels *versus* MCPs. The upper/right panels are scatterplots for variable pairs, and the lower/left panel contains Pearson's correlation coefficients. For abbreviations, see Fig. 2.

Table 5. 50% kernel model variance inflation factor (VIF) values for the full and reduced model.

Variable	Full model	Reduced model 1
People	1.62	1.21
Conifer	2.76	1.36
Deciduous-mixed	3.01	1.34
0-5	3.32	
5-15	1.70	1.55
15-30	2.43	1.41

models that did not include the variable 'people' had $\Delta AIC > 6$ (Table 6) and were not supported by the data. The other two variables in the top-ranking models were 'conifer' and 'forest age group 5-15'. The model-averaged slopes (β values) of the variables and their standard errors for core area models are presented in Table 7. Notably, the 95% confidence intervals of the variables 'conifer' and 'forest age group 5-15' include 0, so there is little evidence that variables other than 'people' affect the selection of core areas inside the wolf home ranges (Table 7).

Model evaluation and predictions

An independent sample of ten wolf home ranges was used to evaluate the probabilities predicted by the models. The mean probabilities (\pm SE) of these home ranges ranged between 0.46 ± 0.22 and 0.81 ± 0.09 . Most of these home ranges had

a probability of occurrence greater than 0.60 (Table 8).

Mapping of the predictions for wolf home ranges, when home range sizes were not taken into account, indicated that 33% of the study area had a predicted value of over 0.5 for the occurrence of a wolf home range (Fig. 4).

Table 6. Generalized linear model (GLM) for the occurrence of 50% kernel wolf home ranges using a binomial distribution and the logit link function. The models are ranked according to the AIC_c values.

Rank	Model	AIC_c	ΔAIC_c	w	K
1	people	49.4	0	0.19	2
2	people + 5–15	49.5	0.05	0.18	3
3	people + 5–15 + conifer	50.7	1.29	0.10	4
4	people + conifer	51.2	1.73	0.08	3
5	people + 15–30	51.6	2.15	0.07	3
6	people + dec_mix	51.6	2.21	0.06	3
7	people + 5–15 + 15–30	51.9	2.49	0.06	4
8	people + dec_mix + 5–15	52.0	2.52	0.05	4
9	people + conifer + dec_mix + 5–15	53.0	3.57	0.03	5
10	people + conifer + 5–15 + 15–30	53.0	3.57	0.03	5
11	people + conifer + dec_mix	53.1	3.66	0.03	4
12	people + conifer + 15–30	53.6	4.12	0.02	4
13	people + dec_mix + 15–30	53.8	4.32	0.02	4
14	people + dec_mix + 5–15 + 15–30	54.6	5.11	0.02	5
15	people + conifer + dec_mix + 15–30	55.5	6.03	0.01	5
16	people + conifer + dec_mix + 5–15 + 15–30	55.6	6.17	0.01	6
17	conifer	56.3	6.85	0.01	2
18	conifer + dec_mix	56.8	7.31	0.01	3
19	“null model”	57.6	8.11	0	1
20	conifer + 5–15	57.7	8.24	0	3
21	conifer + dec_mix + 5–15	58.2	8.74	0	4
22	conifer + 15 – 30	58.5	9.10	0	3
23	conifer + dec_mix + 15–30	58.7	9.30	0	4
24	dec_mix	59.2	9.77	0	2
25	15–30	59.4	9.93	0	2
26	5–15	59.7	10.24	0	2
27	conifer + 5–15 + 15–30	60.1	10.68	0	4
28	dec_mix + 15 – 30	60.7	11.25	0	3
29	conifer + dec_mix + 5–15 + 15–30	60.7	11.31	0	5
30	dec_mix + 5–15	61.5	12.04	0	3
31	5–15 + 15–30	61.7	12.27	0	3
32	dec_mix + 5–15 + 15–30	63.1	13.71	0	4

Table 7. Summary results after model averaging: effects of each parameter on kernel home-range selection inside the MCP home range.

Parameter	Estimate	Unconditional SE	95% confidence interval	Relative importance
(intercept)	–0.88	3.29	(–7.33, 5.58)	
People	–100.36	48.67	(–195.77, –4.96)	1.00
5–15	44.40	32.25	(–18.82, 107.61)	0.51
Conifer	7.20	7.95	(–8.40, 22.79)	0.32

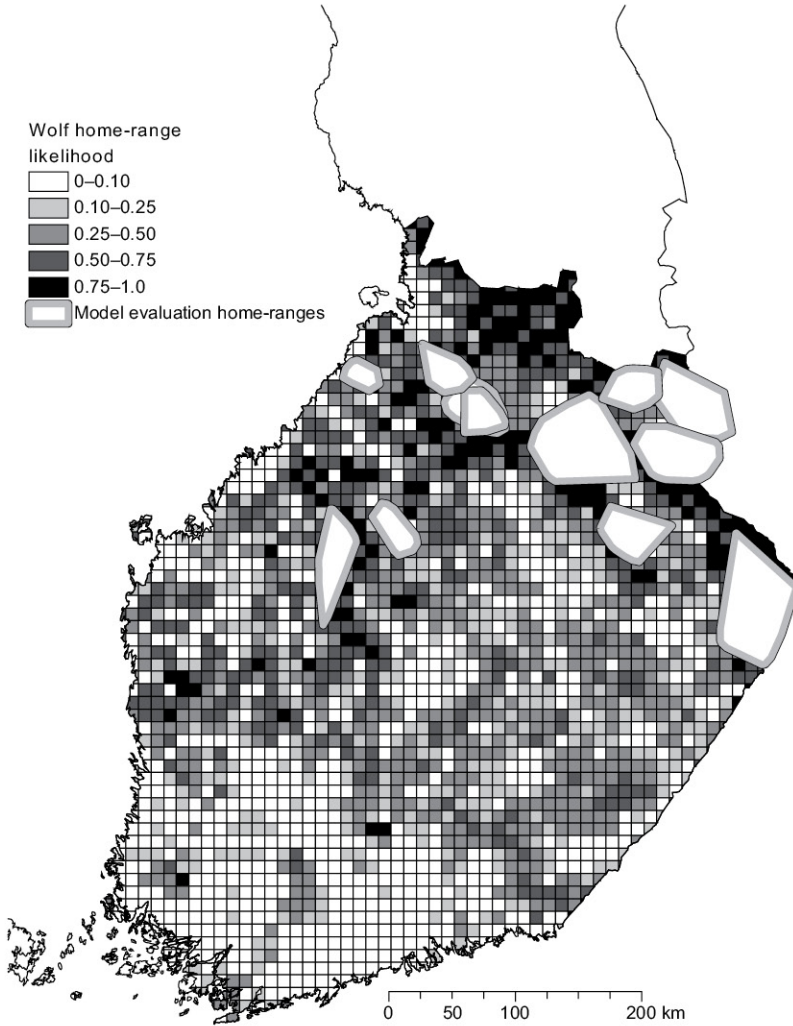


Fig. 4. Predicted probability of wolf home range occurrence in four probability classes calculated for 10×10 km squares and the evaluation set of wolf home ranges.

Table 8. Predicted values and standard errors for the evaluation set of home ranges.

Home range	Predicted probability	SE
1	0.60	0.10
2	0.46	0.22
3	0.80	0.09
4	0.80	0.10
5	0.60	0.12
6	0.81	0.09
7	0.72	0.10
8	0.81	0.10
9	0.64	0.12
10	0.75	0.09

Discussion

Our model fitting approach revealed that the single most important factor influencing wolf home-range selection was the lack of human occurrence in the area. The same was apparent at both levels of selection, i.e. MCP home ranges vs. random locations and 50% kernel home ranges vs. MCP home ranges. We did not calculate threshold values for human occurrence as other factors likely do affect wolf home-range selection and we did not evaluate all the interactions between model variables.

We found no preference for a particular forest type in this study. This may reflect the preference

for any forest type over the areas dominated by the presence of humans, and closer inspection of the data excluding human influence might have revealed a pattern of forest preference. In a previous study, a pattern of preference and avoidance was found among closely-tracked Finnish wolves at the scale of the summer territory and local movements, as almost all the wolves showed preference for open-woodland habitats and avoided coniferous forests (Gurarie *et al.* 2011). These preference patterns are probably reflections of prey preferences and habitat use (Gurarie *et al.* 2011). The primary prey of the wolf in Finland is the moose (Gade-Jørgensen & Stagegaard 2000, Kojola *et al.* 2004). Differences in prey population sizes around the study area is useful for determining the average size of wolf territories and density of wolves in areas occupied by wolves but ungulate density does not do well in predicting the presence of wolves (Fuller 1989, Fuller *et al.* 2003). We did not model the effects of moose population densities on this selection, since moose densities averaged from 0.22 to 0.45 km⁻², and were thus higher than the density of prey to which wolves respond numerically (Fuller 1989, Messier 1994, Perterson *et al.* 1998). In Scandinavia, where moose densities are also high, moose density does not significantly affect the probability of wolf occurrence (Karlsson *et al.* 2007).

We carried out the modeling in two parts. This study revealed the same clear pattern of avoidance of areas where human disturbance is greatest as in previous studies (Kaarinen *et al.* 2005, Gurarie *et al.* 2011). Poaching has only recently been investigated in Finland, but as in Scandinavia (Liberg *et al.* 2012), it may have a substantial impact on the wolf population in Finland. It may also be one of the underlying influences on habitat use by wolves. The whole study area (i.e. Finland, excluding the reindeer management area) can be assumed to be available as territory for wolves to occupy, since they are highly capable of dispersing over very long distances (van Camp & Gluckie 1979, Fritts & Mech 1981, Ballard *et al.* 1983, Messier 1985, Merrill & Mech 2000, Wabakken *et al.* 2001, Kojola *et al.* 2006, 2009). Therefore, the pattern of home ranges being biased in the population core area in east-central Finland is likely to have

ecological significance. The area predicted to be best for wolf occupation is larger in east-central Finland, whereas in southern and western Finland there are smaller patches that are not connected to each other, and habitable sites are often smaller than the average size of wolf home ranges.

Acknowledgements

We wish to express our sincere thanks to L. Korhonen, R. Ovaskainen, S. Ronkainen and M. Suominen for their invaluable work in capturing wolves. We also thank two anonymous referees for useful comments on the manuscript.

References

- Ahti, T., Hämet-Ahti, L. & Jalas, J. 1968: Vegetation zones and their sections in northwestern Europe. — *Annales Botanici Fennici* 5: 169–211.
- Akaike, H. 1973: Information theory and an extension of the maximum likelihood principle. — In: Petrov, B. N. & Csaki, F. (eds.), *Proceedings of the 2nd International Symposium on Information Theory*: 267–281. Akademiai Kiado, Budapest.
- Ballard, W. B., Farnell, R. & Stephenson, R. O. 1983: Long distance movement by grey wolves (*Canis lupus*). — *Canadian Field-Naturalist* 97: 333.
- Bartoń, K. 2009: *MuMIn: multi-model inference*. — Available at <http://cran.r-project.org/web/packages/MuMIn/index.html>
- Beyer, H. L. 2012: *Geostatistical modelling environment* — Available at <http://www.spatialecology.com/gme/index.htm>.
- Bisi, J., Kurki, S., Svensberg, M. & Liukkonen, T. 2007: Human dimension of wolf (*Canis lupus*) conflicts in Finland. — *European Journal of Wildlife Research* 53: 304–314.
- Burnham, K. P. & Anderson, D. R. 2002: *Model selection and multimodel inference. A practical information-theoretic approach*, 2nd ed. — Springer, New York.
- Burnham, K. P. & Anderson, D. R. 2004: Multimodel inference: Understanding AIC and BIC in model selection. — *Sociological Methods & Research* 33: 261–304.
- Edenius, L., Bergman, M., Ericsson, G. & Danell, K. 2002: The role of moose as a disturbance factor in managed boreal forests. — *Silva Fennica* 36: 57–67.
- Fielding, A. H. & Haworth, P. F. 1995: Testing the generality of bird-habitat models. — *Conservation Biology* 9: 1466–1481.
- Finnish Forest Research Institute 2005: *Finnish Statistical Yearbook of Forestry 2005*. — The Finnish Forest Research Institute.
- Fritts, S. H. & Mech, L. D. 1981: Dynamics, movements, and feeding ecology of a newly protected wolf population in

- northwestern Minnesota. — *Wildlife Monographs* 80: 1–79.
- Fuller, T. K. 1989: Population dynamics of wolves in north-central Minnesota. — *Wildlife Monographs* 105: 1–43.
- Fuller, T. K., Mech, L. D. & Cochrane, J. F. 2003: Wolf population dynamics. — In: Boitani, L. & Mech, L. D. (eds.), *Wolves, Behavior, Ecology and Conservation*: 161–191. University of Chicago Press, Chicago, Illinois, USA.
- Gade-Jørgensen, I. & Stægaard, R. 2000: Diet composition of wolves *Canis lupus* in east-central Finland. — *Acta Theriologica* 45: 537–547.
- Greaves, R. K., Sanderson, R. A. & Rushton, S. P. 2006: Predicting species occurrence using information-theoretic approaches and significance testing: an example of dormouse distribution in Cumbria, UK. — *Biological Conservation* 130: 239–250.
- Green, R. H. 1979: *Sampling design and statistical methods for environmental biologists*. — John Wiley & Sons, New York.
- Grueber, C. E., Nakagawa, S., Laws, R. J. & Jamieson, I. G. 2011: Multimodel inference in ecology and evolution: challenges and solutions. — *Journal of Evolutionary Biology* 24: 699–711.
- Gurarie, E., Suutarinen, J., Kojola, I. & Ovaskainen, O. 2011: Summer movements, predation and habitat use of wolves in human modified boreal forests. — *Oecologia* 165: 891–903.
- Hiedanpää, J. 2013: Institutional misfits: Law and habits in Finnish wolf policy. — *Ecology and Society* 18: 24, doi:10.5751/ES-05302-180124.
- Hurvich, C. M. & Tsai, C.-L. 1989: Regression and time series model selection in small samples. — *Biometrika* 76: 297–307.
- Johnson, C. J., Nielsen, S. E., Merrill, E. H., McDonald, T. L. & Boyce, M. S. 2006: Resource selection functions based on use-availability data: theoretical motivation and evaluation methods. — *Journal of Wildlife Management* 70: 347–357.
- Johnson, J. B. & Omland, K. S. 2004: Model selection in ecology and evolution. — *Trends in Ecology and Evolution* 19: 101–108.
- Kartinen, S. 2011: Space use and habitat selection of the wolf (*Canis lupus*) in human altered environment in Finland. — *Acta Universitatis Ouluensis A570*: 13–51.
- Kartinen, S., Kojola, I. & Coelpart, A. 2005: Finnish wolves avoid roads and settlements. — *Annales Zoologici Fennici* 42: 523–532.
- Karlsson, J., Brøseth, H., Sand, H. & Andrén, H. 2007: Predicting occurrence of wolf territories in Scandinavia. — *Journal of Zoology* 272: 276–283.
- Kernohan, B. J., Gitzen, R. A. & Millsbaugh, J. J. 2001: Analysis of animal space use and movements. — In: Millsbaugh, J. J. & Marzluf, J. M. (eds.), *Radio tracking and animal populations*: 125–166. Academic Press, San Diego, California, USA.
- Klar, N., Fernández, N., Kramer-Schadt, S., Herrman, M., Trinzen, M., Büttner, I. & Niemitz, C. 2008: Habitat selection models for European wildcat conservation. — *Biological Conservation* 141: 308–319.
- Kojola, I. & Kuittinen, J. 2002: Wolf attacks on dogs. — *Wildlife Society Bulletin* 30: 498–501.
- Kojola, I., Helle, P. & Heikkinen, S. 2011: Susikannan viimeaikaiset muutokset Suomessa eri aineistojen valossa [Recent changes in wolf population in Finland based on various data sets]. — *Suomen Riista* 57: 55–62. [In Finnish with English summary].
- Kojola, I., Kartinen, S., Hakala, A., Heikkinen, S. & Voipio, H.-M. 2009: Dispersal behavior and the connectivity between wolf populations in northern Europe. — *Journal of Wildlife Management* 73: 309–313.
- Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C. & Ronkainen, S. 2006: Dispersal in an expanding wolf population in Finland. — *Journal of Mammalogy* 87: 281–286.
- Kojola, I., Huitu, O., Toppinen, K., Heikkinen, S., Heikura, K. & Ronkainen, S. 2004: Predation by wolves (*Canis lupus*) on European wild forest reindeer in east-central Finland. — *Journal of Zoology* 263: 219–228.
- Liberg, O., Chapron, G., Wabakken, P., Pedersen, H. C., Hobbs, N. T. & Sand, H. 2012: Shoot, shovel and shut up: cryptic poaching slows restoration of a large carnivore in Europe. — *Proceedings of the Royal Society B* 279: 910–915.
- Linnell, J. D. C., Swenson, J. E. & Andersen, R. 2001: Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. — *Animal Conservation* 4: 345–349.
- Massolo, A. & Meriggi, A. 1998: Factors affecting habitat occupancy by wolves in northern Apennines: a model of habitat suitability. — *Ecography* 21: 97–102.
- Merrill, S. B. & Mech, L. D. 2000: Details of extensive movements by Minnesota wolves (*Canis lupus*). — *American Midland Naturalist* 144: 428–433.
- Messier, F. 1985: Solitary living and extra-territorial movements of wolves in relation to social status and prey abundance. — *Canadian Journal of Zoology* 63: 239–245.
- Messier, F. 1994: Ungulate population models with predation: a case study with the North American moose. — *Ecology* 75: 478–488.
- Mladenoff, D., Sickley, T. A., Haight, F. G. & Wydeven, A. 1995: A regional landscape analysis and prediction of favourable gray wolf habitat in the Northern Great lakes region. — *Conservation Biology* 9: 279–294.
- Mladenoff, D., Sickley, T. A. & Wydeven, A. 1999: Predicting grey wolf landscape recolonization: logistic regression models vs. new field data. — *Ecological Applications* 9: 37–44.
- Mohr, C. O. 1947: Table of equivalent populations of North American small mammals. — *American Midland Naturalist* 37: 223–249.
- Nellemann, C., Støen, O.-G., Kindberg, J., Swenson, J. E., Vistnes, I., Ericsson, G., Katajisto, J., Kaltenborn, B. P., Martin, J. & Ordiz, A. 2007: Terrain use by an expanding brown bear population in relation to age, recreational resorts and human settlements. — *Biological Conservation* 138: 157–165.
- Nikula, A., Heikkinen, S. & Helle, E. 2004: Habitat selection of adult moose *Alces alces* at two spatial scales in central Finland. — *Wildlife Biology* 10: 121–135.

- Okarma, H., Jedrzejewski, W., Schmidt, K., Sniezko, S., Bunevich, A. N. & Jedrzejewska, B. 1998: Home ranges of wolves in Bialowieza Forest, Poland, compared with other Eurasian populations. — *Journal of Mammalogy* 79: 842–852.
- Peterson, R. O., Thomas, N. J., Thuber, J. M., Vucetich, J. A. & Waite, T. A. 1998: Population limitation and the wolves of Isle Royale. — *Journal of Mammalogy* 79: 828–841.
- Proctor, M. F., McLellan, B. N., Strobeck, C. & Barclay, M. R. 2005: Genetic analysis reveals demographic fragmentation of grizzly bears yielding vulnerably small populations. — *Proceedings of the Royal Society B* 272: 2409–2416.
- R Development Core Team. 2014: *R: A language and environment for statistical computing*. — R Foundation for Statistical Computing, Vienna, Austria.
- Ripple, J. W., Larsen, E. J., Renkin, R. A. & Smith, D. W. 2001: Trophic cascades among wolves, elk and aspen on Yellowstone National Park's northern range. — *Biological Conservation* 102: 227–234.
- Rusanen, J., Muilu, T., Colpaert, A. & Naukkarinen, A. 2003: Georeferenced data as a tool for monitoring the concentration of population in Finland in 1970–1998. — *Fennia* 181: 129–144.
- Rushton, S. P., Ormerod, S. J. & Kerby, G. 2004: New paradigms modelling species distribution. — *Journal of Applied Ecology* 41: 193–200.
- Sawyer, H., Nielson, R. M., Lindzey, F. & McDonald, L. L. 2006: Winter habitat selection of mule deer before and during development of a natural gas field. — *Journal of Wildlife Management* 70: 396–403.
- Skonhofs, A. 2006: The costs and benefits of animal predation: An analysis of Scandinavian wolf re-colonization. — *Ecological Economics* 58: 830–841.
- Statistics Finland 2013: *Grid database* — Available at http://www.stat.fi/tup/ruututietokanta/index_en.html.
- Suomen Riistakeskus 2014: *Suden ongelmallisuuteen liittyvän keskustelun yhteenveto* — Available at <http://riista.fi/riistatalous/riistakannat/hoitosuunnitelmat/susikanta/>.
- SYKE 2009: *CLC2006-Finland. Final Report*. — Finnish Environment Institute, Helsinki.
- Theuerkauf, J., Jedrzejewski, W., Schmidt, K. & Gula, R. 2003: Spatiotemporal segregation of wolves from humans in the Bialowieza forest (Poland) — *Journal of Wildlife Management* 67: 706–716.
- Tønnesen, M. 2010: Wolf Land. — *Biosemiotics* 3: 289–297.
- van Camp, J. & Gluckie, R. 1979: A record long-distance move by a wolf (*Canis lupus*). — *Journal of Mammalogy* 60: 236.
- Wabakken, P., Sand, H., Liberg, O. & Björvall, A. 2001: The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. — *Canadian Journal of Zoology* 79: 710–725.
- Woodroffe, R. 2000: Predator and people: using human densities to interpret declines of large carnivores. — *Animal Conservation* 3: 165–173.
- Worton, B. J. 1989: Kernel methods for estimating the utilization distribution in home-range studies. — *Ecology* 70: 164–168.
- 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 Lake region. — *Endangered Species UPDATE* 18: 110–119.
- Zuur, A. F., Ieno, E. N. & Elphick, C. S. 2010: A protocol for data exploration to avoid common statistical problems. — *Methods in Ecology and Evolution* 1: 3–14.