Biological Conservation 198 (2016) 9–14

Contents lists available at ScienceDirect

Biological Conservation

journal homepage: www.elsevier.com/locate/bioc

Wolf visitations close to human residences in Finland: The role of age, residence density, and time of day

Ilpo Kojola [a,*], Ville Hallikainen [a], Kari Mikkola [a], Eliezer Gurarie [b], Samuli Heikkinen [c], Salla Kaartinen [c], Ari Nikula [a], Vesa Nivala [a]

[a] Natural Resources Institute Finland (Luke), Box 16, FI 96301 Rovaniemi, Finland
[b] Department of Biology, University of Maryland, College Park, MD 20742, USA
[c] Natural Resources Institute Finland (Luke), Paavo Havaksentie 3, FI 00014, University of Oulu, Finland

ARTICLE INFO

Article history:
Received 25 August 2015
Received in revised form 12 March 2016
Accepted 21 March 2016
Available online xxxx

ABSTRACT

Large carnivorous mammals, such as the gray wolf (*Canis lupus*) have been recently expanding to human-dominated landscapes in many regions. Although wolves tend to avoid human infrastructure, visitations close to human residences might be unavoidable in territories that are highly fragmented by residential areas. House yard visits are of particular concern: according to the Finnish legislation, wolves that repeatedly approach within 150 m from the nearest residential building can legally be killed for human safety. We analyzed the average distance from house yards and probability of house yard visitations by wolves against sex, age class, time of the day, season and house density for 25 territorial GPS-tracked wolves in Finland. Generally, wolves avoid houses — with mean distances higher than from random locations in the territory. This difference became higher with decreasing house density for sub-adults while for adults this difference decreased slightly with decreasing house density. Probability of visitation in house-yards increased with increasing house densities, was far higher at night than in the daytime, a difference that was greater with increasing house density. Sub-adults visited house-yards more often than adult wolves in the first summer after spring dispersal from the natal pack to a territory, but there was no difference in winter. The indication that wolves learn within a season to avoid moving to near residential buildings in human-dominated territories is when the territory becomes more familiar to wolves which is a noteworthy result for the management.

1. Introduction

Large carnivorous mammals were once forced to withdraw from human-dominated landscapes (Woodroffe, 2000) but in many regions they have been recently returning (Okarma, 1993; Swenson et al., 1995; Breitenmoser, 1998; Mech and Boitani, 2003; Bragina et al., 2015). There are, in particular, many recovering populations of gray wolves (*Canis lupus*) in Europe (Chapron et al., 2014). Although the location of wolves' breeding territories indicates that wolves tend to spatially avoid human infrastructure (Mladenoff et al., 1995; Karlsson et al., 2007; Kaartinen et al., 2005, 2015), movements by wolves closer to human residences are probably unavoidable when wolves live in areas of high human activity.

The wolf is an admired while also a feared animal. The fear stems from both legends and a few confirmed incidents where wolves have attacked humans (Løe and Røskaft, 2004; Behdarvand et al., 2014). While occasionally causing livestock depredation in pastures outside villages, wolves may at times intrude into house-yards and attack domestic dogs (Fritts and Paul, 1989; Kojola and Kuittinen, 2002; Kojola et al., 2004). Conflicts related to the range expansion by wolves have aroused campaigns against wolf management policies that are regarded to be too conservation-oriented (Brownlow, 2000; Skogen et al., 2008; Lyon and Graves, 2014).

In Northern Europe human densities are relatively low (Chapron et al., 2014), and wolves generally thrive in human-modified forest areas. For example, in Finland most have learned to use timber roads to facilitate travel and also strongly to avoid paved roads (Gurarie et al., 2011). The number of wolves in Finland started to grow around the mid-1990's after their legal conservation status had improved (Bisi et al., 2007; Kojola et al., 2014). The number of family packs increased from 4 to 25 from 1996 to 2006 (Kojola et al., 2014). The present population estimate is 220–240 wolves and the wolf is classified as a highly endangered species (Rassi et al., 2010). Population size has been mainly limited by poaching and legal hunting (Jansson et al., 2012; Kojola et al., 2014). During the early 2000s the first dispersers from the core eastern range established territories in westernmost Finland, where wolves had been absent for about 100 years (Kojola et al., 2006). In these new

* Corresponding author.
E-mail address: ilpo.kojola@luke.fi (I. Kojola).

http://dx.doi.org/10.1016/j.biocon.2016.03.025

western wolf territories the mean density of humans is many times higher than within their natal territories in the east and the landscape is more fragmented by farms and human infrastructure.

In Finland the wolf population is controlled through quota-based management hunting or special licenses. Wolves' movements near human residences have been one of the most important criteria for a license to kill a wolf (e.g. Ministry of Agriculture and Forestry, decision 277/13/2012). Therefore we examined data from remotely tracked wolves throughout Finland to explore factors that could account for the variation in the frequency of wolves' visits near residences. Our first order predictions were that (1) wolves approach houses more often at night than during the day, because European wolves are mostly nocturnal (Ciucci et al., 1997; Kusak et al., 2005; Theuerkauf et al., 2007) and that (2) overall density of residences might influence the probability at which visits occur because the selection of a given resource may vary as a function of its availability (Mysterud and Ims, 1998; Benson et al., 2015). Visitations have been shown to be more frequent with higher human density in cougars (*Puma concolor*; Knopff et al., 2014) and wolves in the Canadian Rockies (Hebblewhite and Merrill, 2008). We also expected, based on the "naivety hypothesis" (see review by Elfström et al., 2012), that (3) sub-adult wolves might approach house-yards more than adult individuals. Finally, sexual selection that favors differential personality traits and boldness is probably of higher significance for male than female fitness (Smith and Blumstein, 2008). Based also on the finding that in domestic dog males are usually bolder than females (Kubinyi and Miklosi, 2009; Starling et al., 2013), we expected that (4) male wolves might move close to residential buildings more often than female wolves.

2. Material and methods

2.1. Data

Our 25 wolf territories were located in southern and eastern Finland (Fig 1.). Each territory was represented by one wolf. We captured and collared them with Global Positioning System (GPS) — Global System with Mobile (GSM) transmitters that provided wolf positions at 4 h intervals. Wolves were captured during 2003–2012 by looping them from a snowmobile or darting from the helicopter. Details for the capture and immobilization procedure are given elsewhere (Kojola et al., 2006; Wabakken et al., 2007). None of the study wolves had a collar in the end of 2014 because they had dropped the collar (drop off was set to take place 2 years after collaring) or were legally or illegally killed. When we had data for more than one wolf in a given territory, we selected the individual that provided the largest number of locations. The number of locations per wolf averaged 1269 ($\pm$590 SD, range 447–2789) and the duration of study period 270 days ($\pm$98 SD, range 126–607 days). We did not measure telemetry error but according to a literature review mean location error in GPS collars is 9.7 m (Cain et al., 2005).

We divided our study wolves by sex (10 females, 15 males) and by reproductive status. The *adult* category ($n = 18$) consisted of mated wolves, while *sub-adults* ($n = 7$), were animals that had dispersed from their natal territory and established new territories during the spring (see Kojola et al., 2006; Kojola et al., 2009). Sub-adults were therefore necessarily naive with respect to their habitat, in particular during the first summer. We defined territory boundaries as 100% minimum convex polygons (MCPs, Fig. 1). We chose 100% MCP precisely because it is a generous measure of wolf space use that includes rarely visited outlying areas and the focus of our study is on rare events such as visits close to residences. Geographic locations of residential buildings (mostly referred to as house thereafter) were obtained from official registries that provide the location of houses at the accuracy of $\pm$5 m. To test the effect of house density, we calculated distances between random location and the nearest house for each wolf position within the given territory using the program ESRI ArcGIS for Desktop 10.2.1.

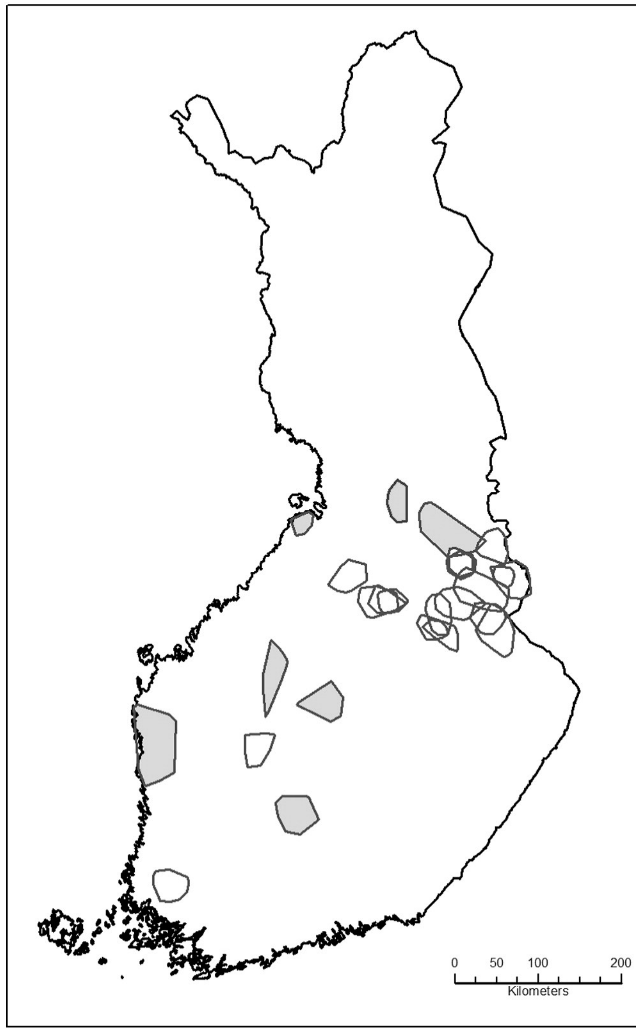

Fig 1. Wolf territories of the study ($n = 25$, territory boundaries as 100% minimum convex polygons) in Finland. Each territory is represented by a single GPS-collared wolf. Gray color indicates sub-adult wolves.

Coefficient of variation (CV) in random distances did not depend on the sample size (range 447–2789, Pearson $r = 0.335$, $P = 0.102$, $n = 25$). We chose this variable instead of simple houses/area variable as it more accurately reflects the human footprint in a territory by accounting for spatial clustering or non-clustering of houses. Mean house densities among territories ranged between 0.2–3.2 houses/km^2. The time of the day was classified into night and day according to sunset and sunrise times (http://www.moisio.fi/taivas/aurinko.php) in various locations in Finland. To estimate season effect the calendar year was divided into summer (May–September) and winter (October–April).

2.2. Statistical analysis

First we constructed a linear model to study how the of wolves' distances to the nearest house deviated from the distances of the random locations to the nearest house (1):

$$D_i = \left(\frac{1}{n_{ri}}\sum_{k=1}^{n_{ri}} d_{ri}\right) - \left(\frac{1}{n_{oi}}\sum_{l=1}^{n_{oi}} d_{oi.}\right)$$

where D_i is the difference between the distances for wolf *i*, n_{ri} denotes the number of random locations for the wolf *i* that equals the number of locations for the wolf *i* (n_{oi}), d_{ri} is the distance from the random

Table 1
Mean deviation of wolves' locations to the nearest house from the distance of random locations to the nearest house in Finland. The adjusted R^2 of the model is 0.22, $F_{3,21} = 3.29$ and $P = 0.041$.

Variable	Estimate	SD	t-value	*P*
Intercept	685.85	363.50	1.89	0.073
Wolf' status (subadult vs adult)	−750.77	492.80	−1.52	0.143
Distance from the nearest house	−0.18	0.16	−1.10	0.285
Wolf's status * distance from the nearest house	0.58	0.23	2.48	0.022

locations and d_{oi} is the distance from the wolf i to the nearest house, respectively.

Negative values of D_i indicate that mean distances to the nearest house were shorter than the random distances, i.e. attraction to houses, while positive values indicate avoidance of homes (Table 1). The linear model was defined as (2):

$$D_i = X_i\beta + \varepsilon_i, \varepsilon_i \sim (0, \sigma^2)$$

where X_i is a vector of covariates in the linear model, β is the parameter vector of the linear model and ε_i represents a normally distributed error term with the mean 0 and variance σ^2. Independent variables in this model were wolves' reproductive status (adult, subadult) and the distance between the random location and the nearest house.

To study more specifically when wolves move to near houses, we focused on locations within 150 m from the nearest residential building, conforming with the legal definition of house-yards according to the Finnish hunting law (Metsästyslaki 615/1993/25§). Repeated visitations may lead to a license to kill a wolf for human safety. We modeled visits in house-yards with a binary logistic autoregressive model. To control spatial autocorrelation between consecutive GPS locations, we selected positions that were located ≤1000 m from the nearest house (7011 of 31,658 locations). The resultant mean correlation between consecutive locations was 0.25 (Fig. 1).

The binary autoregressive logistic model can be described as follows. Suppose that $Y_{ij} \sim \text{Bernoulli}(p_{ij})$ where $p_{ij} = P(Y_{ij} = 1)$. Then, a binary autoregressive logistic model with lag 1, will be defined as (3):

$$logitP(Y_{ij} = 1 \vee Y_{ij-1}, U_i, X_{ij}) = log\frac{P(Y_{ij} = 1 \vee Y_{ij-1}, U_i, X_{ij})}{1-P(Y_{ij} = 1 \vee Y_{ij-1}, U_i, X_{ij})}$$
$$= \alpha + X_{ij}\beta + U_i + \gamma_1 Y_{ij-1}$$

where X_{ij} is a vector of covariates for the i'th wolf at the jth time point, β is the associated parameter vector, α is and the intercept parameter. U_i is a random effect of the wolves (random intercept). Y_{ij-1} is the past response of the i'th wolf at the 1'th lag, and $\gamma_1$is the associated correlation parameter for lag 1 (see Hansen et al., 2015 for more details).

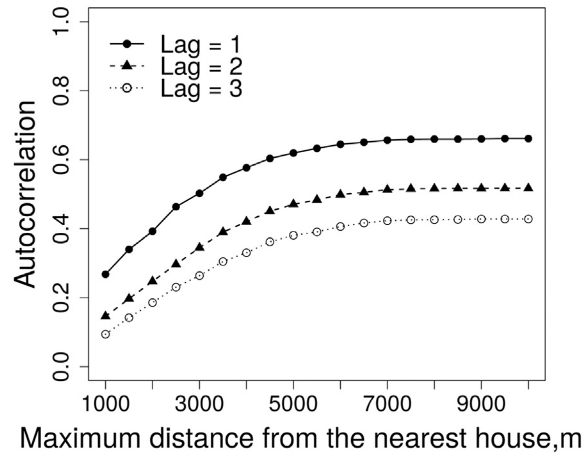

Fig. 2. Mean autocorrelation coefficients in different categories of wolves' maximum distances to the nearest house in Finland.

The marginal predictions were calculated from the following equation (4):

$$logitP(Y_{ij} = 1) = \alpha + X_{ij}\beta.$$

Due to the autocorrelation between consecutive locations, entire data (31,658 positions) were used only for the rough point estimates for the probabilities of the visits near houses. The proportion of wolf locations within house-yards (<150 m) was 0.009 out of all locations in the data and 0.043 for locations filtered to within 1000 m from the nearest house. In these binary models independent variables were the wolf, season (summer, winter), time of the day (day, night), wolf's sex and status (adult, sub-adult) and the distance from the random location to the nearest house. Two models were conducted. In the first model distances were as original and the second model as standardized, centered values. Standardization changed the intercept, coefficients and standard errors. They are given in parentheses in Table 2. Individual wolves were treated as a random effect. The curve of receiver operation characteristic (ROC) analysis (Sing et al., 2005) was used in the evaluation of the model. The predicted probabilities were plotted against the observed probabilities at which wolves visited house-yards.

Table 2
The coefficients and the analysis of deviance table (type III tests) in autoregressive logistic model for the probability of wolves' visitations closer than 150 m to the nearest house in Finland. A random distance in the distance from random location to the nearest house within wolf's territory. The intercept, coefficients and standard errors from models with standardized distances are given in parenthesis.

Variable/category	Coefficient	Standard error	Df	t/chi-square	*P*
Fixed effects					
Intercept	-5.471 (-4.936)				
Random distance (RD)	$3.48 * 10^{-4}$ (0.261)	$2.95 * 10^{-4}$ (0.222)	22	1.177	0.252
Wolf's status (ref. adult)			1	11.143	0.001
– Sub-adult	1.055	0.316	22	3.336	0.003
Time of day (ref. day)			1	67.484	<0.001
– Night	3.767	0.459	6978	8.211	<0.001
Season (ref. summer)			1	3.270	0.071
– Winter	−0.376	0.208	6978	−1.807	0.071
Time of day * RD			1	16.111	<0.001
– Night * RD	$1.106 * 10^{-3}$ (-0.832)	$2.757 * 10^{-4}$ (0.207)	6978	−4.012	<0.001
Wolf's status * Season			1	7.757	0.005
– Sub-adult * winter	−0.791	0.284	6978	−2.784	0.005

Variable/category	Variance	Phi
Random effects		
Wolf (intercept)	0.149	
Residual	0.962	0.051

We performed all analyses using the R statistical environment (Core Team, 2013), using the glmmPQL function in the MASS-package (Venables and Ripley, 2002) for fitting the autoregressive logistic models, the effect package (Fox, 2003) for visualizing model results. The lsmeans package (Lenth, 2013) for tests of coefficients, and the Matrix package (Bates and Maechler, 2014) for working with the distance matrix (Fig. 2).

3. Results

Mean distance from the wolf's location to the nearest house was 2362 m (range 13–9489 m) compared to 1713 m (range 2–9043 m) for random points in all 25 territories. The linear model which related wolves' distances to the random distances from the nearest house provided evidence of avoidance, with an average avoidance index of −0.18. The difference between sub-adult and adult wolves increased with decreasing house density (Table 1, Fig. 3).

Mean proportion of locations <1000 m from the nearest house was 0.22 ($n = 25$ wolves), ranging between 0.02 and 0.77 across individuals (Fig. 4). Relative differences between observed probabilities with which wolves and random locations were <1000 m from the nearest house were highest at low probability of the random locations (Fig. 4). In the analysis of house-yard entering probability (<150 m from the nearest house) four variables were significant: (1) time of the day, (2) the distance from the random location to the nearest house, (3) the interaction between house density and time of the day, and (4) the interaction between wolf's status and season (Table 2). We run an additional model by using standardized, centered distances which resulted in different coefficients and standard errors (Table 2). The t-values and probabilities were the same as in models where original distances were used.

In summer sub-adult wolves visited house yards about three times more often than the adults but this difference did not exist in winter (Fig 5a). The probabilities in the trimmed and untrimmed data were 0.06 vs 0.02 and 0.007 vs 0.002, respectively. Time of the day has a strong effect and this variable interacted with a random distance on the probability of wolf's visits in house-yards (Fig 5b). The probability of daytime visits was extremely low and not influenced by the house density in wolf's territory (Fig 5b). The figures yielded in ROC analysis showed good classification efficiency for the model: ROC for the fixed component was 0.80, and 0.81 for the combination of the fixed and random components.

In the model analyzing the trimmed data, the predicted mean probability for the fixed part was 0.039 and 0.042 using both fixed and random parts of the model. The observed mean probability was also 0.042. In the model using all locations, mean probability was 0.007 using fixed

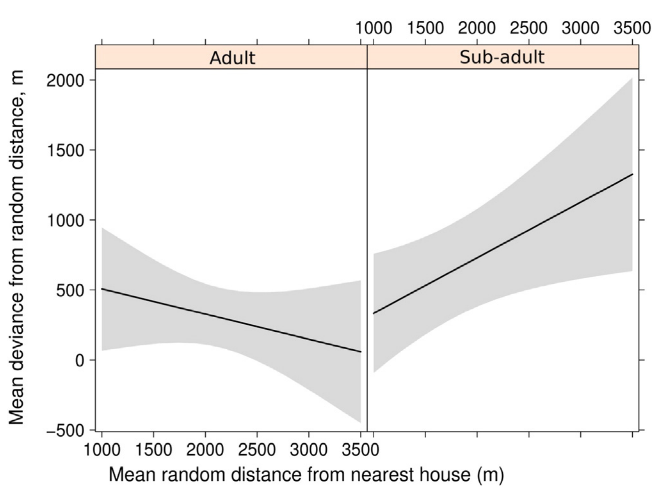

Fig. 3. Deviance of adult and sub-adult wolves' mean distance to the nearest house from a random distance to the nearest house with increasing random distances in Finland.

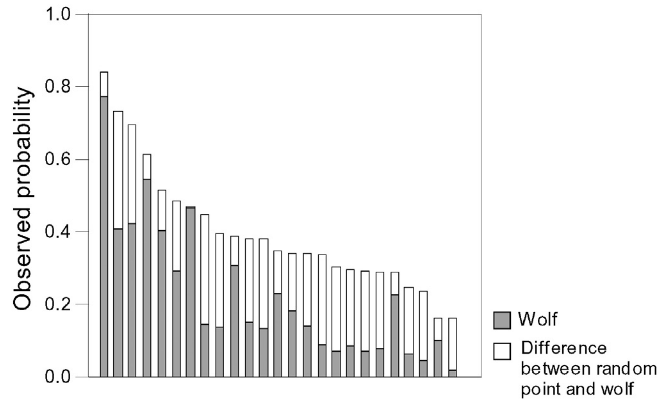

Fig. 4. The observed probability at which the wolf was <1000 m from the nearest house in relation to the probability at which random distances (RDs) were <1000 m from the nearest house within the 25 study territories in Finland.

part and 0.009 using both fixed and random parts, with a corresponding observed probability of 0.009. Thus both models predicted mean proportions very good. Our model predicted the observed probabilities well for 22 out of 25 wolves (Fig. 6).

4. Discussion

Although wolves avoid human settlements (Karlsson et al., 2007; Kaartinen et al., 2015; this study), our results provided evidence that wolves' expansion to human-dominated landscapes has led to an

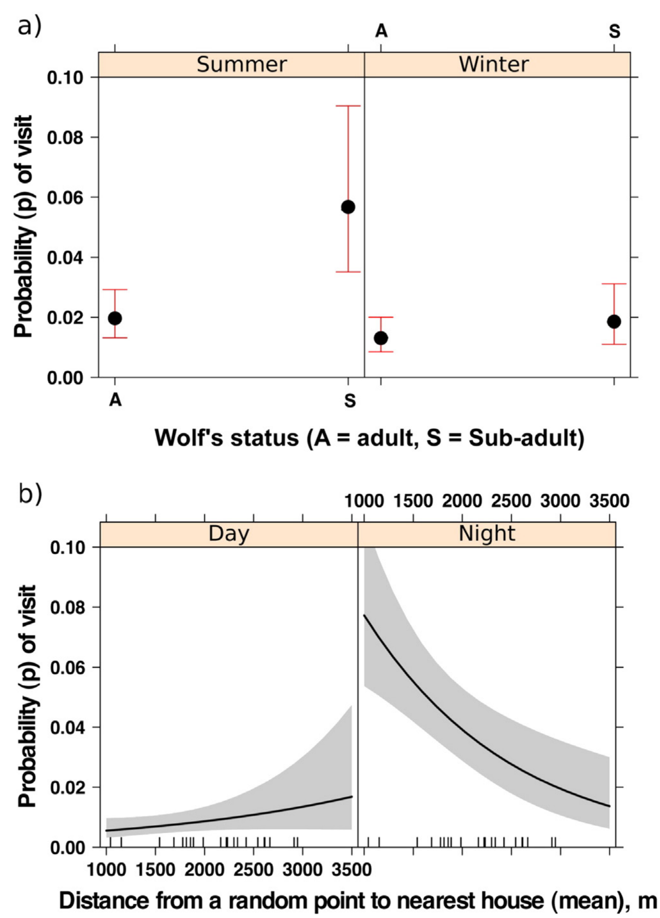

Fig. 5. Interaction between wolf's status and season (a), and between time of the day and a random distance from the nearest house (b), on the probability at which wolves visit <150 m to a house in Finland.

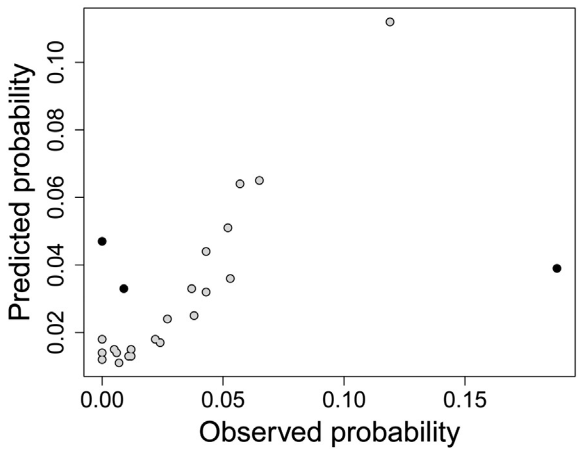

Fig. 6. Observed and predicted probabilities with which wolves visit <150 m to houses in Finland. Predicted probabilities were yielded from autoregressive logistic model using GPS-locations ≤1000 m to the nearest house. The model treated the wolf as random variable, wolf's sex, status (adult, sub-adult), season, time of the day and a random distance to the nearest house as fixed variables. Black symbols are outliers.

increase in nightly visits within residential areas. The two-way interaction between a random distance to the nearest house and time of the day agrees with an earlier study where Hebblewhite and Merrill (2008) showed that with increasing human activity, wolves in the Canadian Rockies displayed spatio-temporal avoidance of human activity during daylight. Wolf nocturnal activity might principally be an adaptation to the primarily diurnal human activity and therefore be reflected most strongly in wolves living in human-dominated landscapes. Greater nocturnal activity allows wolves with territories in areas with high human activity to better exploit food resources that are available near human settlements with reduced risk of conflict and greater freedom of movement. In Finland a major prey species in southern wolf territories where human densities are highest is non-native white-tailed deer (*Odocoileus virginianus*) (Ruusila and Kojola, 2010), which is relatively well-adapted to living near human settlements.

Even in territories where house density was higher, moving across the territory does not necessarily compel visits within house-yards as they may become increasingly familiar landscape elements. Adult wolves moved slightly closer to houses than recently settled yearlings but they showed clearer avoidance in territories where house densities were high. This could be a consequence of increased confidence and consistency based on prior experience and learning.

Small gravel roads that wolves commonly use when moving through their territories (Gurarie et al., 2011) connect farms and small villages and may act as a route to house-yards. Thus, many house-yard visits are possibly an ancillary consequence of displacement along forest roads. However, in some cases the ultimate motivation may be prey searching near houses. Domestic dogs are sometimes attacked by wolves within house-yards (Fritts and Paul, 1989; Kojola et al., 2004) and might attract wolves. In Finland, 40–60 dogs annually are killed by wolves, and almost half of these incidences take place within house-yards (I. Kojola, unpublished data). It is important to note that the attacks are not the only a possible interaction, as wolves may also occasionally pair and breed with dogs (Vila et al., 2003; Lescureux and Linnell, 2014).

The probability with which wolves enter house-yards did not differ between females and males, despite the fact that domestic dog males tend to be bolder than females (Kubinyi and Miklosi, 2009; Starling et al., 2013). Visits in house-yards function as a more valid measure of personality in summer than in winter when mates tend to move together more (Ballard et al., 1991; Mech and Boitani, 2003).

The two-way interaction between season and wolf's status might principally support the naivety hypothesis because all sub-adults in our study were yearlings who had just settled down in a new area after dispersal that usually takes place with a unimodal seasonal peak in spring (Fritts and Mech, 1981; Ballard et al., 1987; Fuller, 1989; Kojola et al., 2006). In winter, yearlings were more experienced with their new territory. Movements of adult wolves slightly closer to residences might be a consequence of increased confidence that is based on prior experience and learning.

5. Conservation implications

When a wolf establishes its territory in human-dominated landscape, the risk of getting killed via legal process is increased because the rate of visits near residences is influenced by residence density. The major justification according to which authorities approve special permits to kill wolves that visit house-yard areas is human safety. It is unclear whether these nighttime visitations are linkable to concrete human safety risk. However, wolf tracks or sightings near human settlements lead municipality councils in Finland to organize taxi transportation for schoolchildren, a major added cost of wolf conservation. The indication that wolves might learn to avoid moving to near residences is when the territory becomes more familiar to them which is noteworthy for the management. It emphasizes patience in decision making, despite strong political and public pressures for killing a wolf that has been spotted near residential areas.

Some wolves appear to be motivated by a chance to prey on domestic dogs within house-yards (Kojola et al., 2004). When wolves established a territory in an area where they have been absent for a long time the people who live in the area used defensive pens for dogs or take their dogs indoors before night which are the routines in regions where wolves have been constantly present (Bisi et al., 2007). One way to mitigate this conflict is a public and face-to-face informing local people for the presence of wolves and ways to protect their dogs from attacks by wolves.

Acknowledgments

We wish to thank Antero Hakala, Leo Korhonen, Reima Ovaskainen, Seppo Ronkainen and Markus Suominen for capturing and collaring the study wolves. Ministry of Agriculture and Forestry (1562/324/2012) is acknowledged for funding this study. EG was partially funded by the US National Science Foundation grants ABI-1062411 and ABI-1458748.

References

Ballard, W.B., Whitman, J.S., Gardner, C.L., 1987. Ecology of an exploited wolf population in south-central Alaska. Wildl. Monogr. 98, 3–54.
Ballard, W.B., Ayres, L.A., Gardner, C.L., Foster, J.W., 1991. Den site activity patterns of gray wolves, *Canis lupus*, in south-central Alaska. Canadian Field Naturalist 105, 497–504.
Bates, D., Maechler, M., 2014. Matrix: sparse and dense matrix classes and methods. R package version 1, 1–4.
Behdarvand, N., Kaboli, M., Ahmadi, M., Nourani, E., Mahini, A.S., Aghbolaghi, M.A., 2014. Spatial risk model and mitigation implications for wolf–human conflict in a highly modified agroecosystem in western Iran. Biol. Conserv. 177, 156–164.
Benson, J.F., Mahoney, P.J., Patterson, B.R., 2015. Spatiotemporal variation in selection of roads influences for mortality risk for canids in unprotected landscape. Oikos 124, 1664–1673.
Bisi, J., Kurki, S., Svensberg, M., Liukkonen, T., 2007. Human dimensions of wolf (*Canis lupus*) conflicts in Finland. Eur. J. Wildl. Res. 53, 304–314.
Bragina, E.V., Ives, A.R., Pidgeon, A.M., Baskin, L.M., Gubar, Y.P., Piquer-Rodrigues, M., Keuler, N.S., Petrosyan, V.G., Radeloff, V.C., 2015. Rapid declines of large mammal populations after the collapse of the Soviet Union. Conserv. Biol. 29, 844–853.
Breitenmoser, U., 1998. Large predators in the Alps: the fall and rise of man's competitors. Biol. Conserv. 83, 279–289.
Brownlow, A., 2000. A wolf in the garden: ideology and change in the Adirondack landscape. In: Philo, C., Wilbert, C. (Eds.), Animal Spaces, Beasty Places. Taylor & Francis, New York. NY, pp. 143–160.
Cain, J.W., Krausman, P.R., Jansen, B.D., Morgart, J.R., 2005. Influence of topography and GPS fix interval on GPS collar performance. Wildl. Soc. Bull. 33, 926–934.
Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andren, H., Lopez-Bao, J.V., Adamec, M., Alvares, F., Anders, O., Balciauskas, L., Balys, V., Bedo, P., Bego, F., Blanco, J.C., Breitenmoser, U., Broseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremic, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majic, A., Männil, P., Manz, R., Marboutin,

E., Marcucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Myslajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunovic, M., Persson, J., Potocnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinsek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajce, A., Tsingarska-Sedefcheva, E., Vana, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 19, 1517–1519.

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

Core Team, R., 2013. R: a language and environment for statistical computing. R Foundation for Statistical Computing. Austria. URL, Vienna. http://www.R-project.org.

Elfström, M., Zedrosser, A., Støen, O.-G., Swenson, J.E., 2012. Ultimate and proximate mechanisms underlying the occurrence of bears close to human settlements: review and management implications. Mammal Rev. 44, 5–18.

Fox, J., 2003. Effect displays in R for generalized linear models. J. Stat. Softw. 8, 1–27.

Fritts, S.H., Mech, L.D., 1981. Dynamics, movements, and feeding ecology of a newly protected wolf population in Northwestern Minnesota. Wildl. Monogr. 80, 3–79.

Fritts, S.H., Paul, W.J., 1989. Interactions of wolves and dogs in Minnesota. Wildl. Soc. Bull. 17, 121–123.

Fuller, T.K., 1989. Population dynamics of wolves in north-central Minnesota. Wildl. Monogr. 105, 3–41.

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.

Hansen, A.M., Jeske, D., Kirsch, W., 2015. A chi-square goodness-of-fit test for autoregressive logistic regression models with applications to patient screening. J. Biopharm. Stat. 25, 89–108.

Hebblewhite, M., Merrill, E., 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. J. Appl. Ecol. 45, 834–844.

Jansson, E., Ruokonen, M., Kojola, I., Aspi, J., 2012. Rise and fall of a wolf population: Genetic diversity and structure during recovery, rapid expansion, and drastic decline. Mol. Ecol. 21, 5178–5193.

Kaartinen S., Kojola, I., Colpaert, A., 2005. Finnish wolves avoid roads and settlements. Ann. Zool. Fenn. 42, 423–432.

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

Karlsson, J., Brøseth, H., Sand, H., Andren, H., 2007. Predicting occurrence of wolf territories in Scandinavia. J. Zool. 272, 276–283.

Knopff, A.A., Knopff, K.H., Boyce, M.S., StClair, C.C., 2014. Flexible habitat selection by cougars in response to anthropogenic environment. Biol. Cons. 178, 136–145.

Kojola, I., Kaartinen, S., Hakala, A., Heikkinen, S., Voipio, H.-M., 2009. Dispersal behavior and the connectivity between wolf populations in Northern Europe. J. Wildl. Manage. 73, 309–313.

Kojola I., Kuittinen, J., 2002. Wolf attacks on dogs in Finland. Wildl. Soc. Bull. 30, 498–501.

Kojola, I., Ronkainen, S., Hakala, A., Heikkinen, S., Kokko, S., 2004. Interactions between wolves *Canis lupus* and dogs *C. familiaris* in Finland. Wildl. Biol. 10, 101–107.

Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C., Ronkainen, S., 2006. Dispersal in an expanding wolf population in Finland. J. Mammal. 87, 281–286.

Kojola, I., Helle, P., Heikkinen, S., Linden, H., Paasivaara, A., Wikman, M., 2014. Tracks in snow and population size estimation: wolf in Finland. Wildl. Biol. 20, 279–284.

Kubinyi, E.,Turcsan,B., Miklosi, A., 2009. Dog and owner demographic characteristics and dog personality trait associations. Behav. Process. 81, 392–401.

Kusak, J., Skrbinsek, A.M., Huber, D., 2005. Home ranges, movements, and activity of wolves (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. Eur. J. Wildl. Res. 51, 254–262.

Lenth, R.V., 2013. Lsmeans: least-squares means. R package version 2, 11. http://CRAN.R-project.org/package=lsmeans.

Lescureux, N., Linnell, J.D.C., 2014. Warring brothers: the complex interactions between wolves (*Canis lupus*) and dogs (*Canis familiaris*) in a conservation context. Biol. Conserv. 171, 232–245.

Løe, J., Røskaft, E., 2004. Large carnivores and human safety: a review. Ambio 33, 283–288.

Lyon, T.B., Graves, W.N., 2014. The Real Wolf: the Science, Politics, and Economics of Co-existing With Wolves in Modern Times. p. 343 p. (ISBN 10 1-59112-122-X).

Mech, L.D., Boitani, L., 2003. Wolf social ecology. In: Mech, L.D., Boitani, L. (Eds.), Wolves. Ecology and Conservation. The University of Chicago Press, Behavior, pp. 1–35.

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

Mysterud, A., Ims, R.A., 1998. Functional responses in habitat use: availability influence relative use in trade-off situations. Ecology 79, 1435–1441.

Okarma, H., 1993. Status and management of the wolf in Poland. Biol. Conserv. 66, 153–158.

Rassi, P., Hyvärinen, E., Juslen, A., Mannerkoski, I., 2010. The 2010 Red List of Finnish Species. Ministry of the EnvironmentFinnish Environmental Institute, p. 685 p.

Ruusila, V., Kojola, I., 2010. Ungulates and their management in Finland. In: Apollonio, M., Andersen, R., Putman, R. (Eds.), European Ungulates and Their Management in the 21st Century. Cambridge University Press, pp. 86–102.

Sing, T., Sander, O., Beerenwinkel, N., Lengauer, T., 2005. ROCR: visualizing classifier performance in R. Bioinformatics 21, 3940–3941.

Skogen, K., Mauz, I., Krange, O., 2008. Cry wolf!: narratives of wolf recovery in France and Norway. Rural. Sociol. 73, 105–133.

Smith, B.R., Blumstein, D.T., 2008. Fitness consequences of personality: a meta-analysis. Behav. Ecol. 19, 448–455.

Starling, M.J., Branson, N., Thomson, P.C., McGreevy, P.D., 2013. Age, sex and reproductive status affect boldness in dogs. Vet. J. 197, 868–872.

Swenson, J.E., Wabakken, P., Sandegren, F., Bjärvall A., Franzén R., Söderberg, A., 1995. The near extinction and recovery of brown bears in Scandinavia in relation to the bear management policies of Norway and Sweden. Wildl. Biol. 1, 11–25.

Theuerkauf, J., Gula, R., Pirga, B., Tsunoda, H., Eggermann, J., Brzezowska, B., Rouys, S., Radler, S., 2007. Human impact on wolf activity in the Bieszczady Mountains, SE Poland. Ann. Zool. Fenn. 44, 225–231.

Venables, W.N., Ripley, B.D., 2002. Modern Applied Statistics. Springer, New York, NY.

Vila, C., Walker, C., Sundqvist, A.-K., Flagstad, Ø., Andersone, Z., Casulli, A., Kojola, I., Valdmann, H., Halverson, J., Ellegren, H., 2003. Combined use of maternal, paternal and bi-parental genetic markers for the identification of wolf–dog hybrids. Heredity 90, 17–24.

Wabakken, P., Sand, H., Kojola, I., Zimmermann, B., Arnemo, J.M., Pedersen, H.C., Liberg O., 2007. Multi-stage, long-stage natal dispersal by a GPS-collared Scandinavian wolf. J. Wildl. Manag. 71, 1631–1634.

Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large carnivores. Anim. Conserv. 3, 165–173.