1 Corresponding author: Ilpo Kojola, e-mail: ilpo.kojola@luke.fi, phone +358400292098

2

3 **Wolf visitations close to human residences in Finland: the role of age, residence density, and**
 4 **time of day**

5

6 Ilpo Kojola¹, Ville Hallikainen¹, Kari Mikkola¹, Eliezer Gurarie², Samuli Heikkinen³, Salla
 7 Kaartinen³, Ari Nikula¹, Vesa Nivala¹

8

9 ¹ Natural Resources Institute Finland (Luke), Box 16, FI-96301 Rovaniemi, Finland

10 ² Department of Biology, University of Maryland, College Park, MD 20742, USA

11 ³ Natural Resources Institute Finland (Luke), Paavo Havaksentie 3, FI-00014 University of Oulu,
 12 Finland

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

27 winter. The indication that wolves learn within a season to avoid moving near residential buildings
 28 in human-dominated territories when the territory becomes more familiar to wolves is a noteworthy
 29 result for management.

30 **Introduction**

31 Large carnivorous mammals were once forced to withdraw from human-dominated landscapes
 32 (Woodroffe, 2000) but in many regions they have been recently returning (Okarma, 1993; Swenson
 33 et al., 1995; Breitenmoser, 1998; Mech, 1999; Bragina et al., 2015). There are, in particular, many
 34 recovering populations of gray wolves (*Canis lupus*) in Europe (Chapron et al., 2014). Although the
 35 location of wolves' breeding territories indicate that wolves tend to spatially avoid human
 36 infrastructure (Mladenoff et al., 1995; Karlsson et al., 2004; Kaartinen et al., 2005; 2015),
 37 movements by wolves closer to human residences are probably unavoidable when wolves live in
 38 areas of high human activity.

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

46 In Northern Europe human densities are relatively low (Chapron et al., 2014), and wolves
 47 generally thrive in human-modified forest areas. For example, in Finland most have learned to use
 48 timber roads to facilitate travel while also strongly avoiding paved roads (Gurarie et al., 2011). The
 49 number of wolves in Finland started to grow around the mid-1990's after their legal conservation
 50 status improved (Bisi et al., 2007; Kojola et al., 2014). The number of family packs increased from
 51 4 to 25 from 1996 through 2006 (Kojola et al., 2014). The present population estimate is 220-240
 52 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 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 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 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 dogs males are usually bolder than females (Kubinyi et al., 2009; Starling et al., 2013), we expected that (4) male wolves might move close residential buildings more often than female wolves.

79 **Material and methods**

80 *Data.* Our 25 wolf territories were located in southern and eastern Finland (Fig 1.). Each territory
 81 was represented by one wolf. We captured and collared them with Global Positioning System
 82 (GPS) – Global System with Mobile (GSM) transmitters that provided wolf positions at 4 hour
 83 intervals. Wolves were captured during 2003 – 2012 by looping them from a snowmobile or darting
 84 from the helicopter. Details for the capture and immobilization procedure are given elsewhere
 85 (Kojola et al., 2006; Wabakken et al., 2007). None of the study wolves had a collar in the end of
 86 2014 because they had dropped the collar (drop off was set to take place 2 years after collaring) or
 87 were legally or illegally killed. When we had data for more than one wolf in a given territory, we
 88 selected the individual that provided the largest number of locations. The number of locations per
 89 wolf averaged 1 269 (+/- 590 SD, range 447 - 2 789) and the duration of study period 270 days (+/-
 90 98 SD, range 126-607 days). We did not measure telemetry error but according to a literature
 91 review mean location error in GPS collars is 9.7 m (Cain et al. 2005).

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

distances did not depend on the sample size (range 447 - 2 789, 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/km². The time of 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).

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):

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

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_{rk} is the distance from the random locations and d_{ol} 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 near houses, we focused on locations within 150 m from the nearest residential building, conforming with the legal definition of house-yards

130 according to the Finnish hunting law (Metsästyslaki 615/1993/25§). Repeated visitations may lead
 131 to a license to kill a wolf for human safety. We modeled visits in house-yards with a binary logistic
 132 autoregressive model. To control spatial autocorrelation between consecutive GPS locations, we
 133 selected positions that were located ≤ 1000 m from the nearest house (7 011 of 31 658 locations).
 134 The resultant mean correlation between consecutive locations was 0.25 (Fig. 1).

135

136 The binary autoregressive logistic model can be described as follows. Suppose that $Y_{ij} \sim$
 137 $Bernoulli(p_{ij})$ where $p_{ij} = P(Y_{ij} = 1)$. Then, a binary autoregressive logistic model with lag 1, will be
 138 defined as (3):

139

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

140

141 where X_{ij} is a vector of covariates for the i 'th wolf at the j th time point, β is the associated parameter
 142 vector, and α is the intercept parameter. U_i is a random effect of the wolves (random intercept). Y_{ij-1}
 143 is the past response of the i 'th wolf at the l 'th lag, and γ_1 is the associated correlation parameter for
 144 lag 1 (see Hansen et al. 2015 for more details).

145

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

147

$$\text{logit}P(Y_{ij} = 1) = \alpha + X_{ij}\beta$$

148 Due to autocorrelation between consecutive locations, entire data (31 658 positions) were used only
 149 for the rough point estimates for the probabilities of the visits near houses. The proportion of wolf
 150 locations within house-yards (< 150 m) was 0.009 out of all locations in the data and 0.043 for
 151 locations filtered to within 1 000 m from the nearest house. In these binary models independent
 152 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 characteristics (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.

We performed all analyses using the R statistical environment (R Core Team 2013), using the `glmmPQL` function in the MASS-package (Venables and Ripley, 2002) for fitting the autoregressive logistic models, the effects 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.

Results

Mean distance from the wolf's location to the nearest house was 2 362 m (range 13 - 9 489 m) compared to 1 713 m (range 2 - 9 043 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 < 1 000 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 < 1 000 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

179 coefficients and standard errors (Table 2). The t-values and probabilities were the same as in models
 180 where original distances were used.

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

189 In the model analyzing the trimmed data, the predicted mean probability for the fixed part was
 190 0.039 and 0.042 using both fixed and random parts of the model. The observed mean probability
 191 was also 0.042. In the model using all locations, mean probability was 0.007 using fixed part and
 192 0.009 using both fixed and random parts, with a corresponding observed probability of 0.009. Thus
 193 both models predicted mean proportions very good. Our model predicted the observed probabilities
 194 well for 22 of 25 wolves (Fig. 6).

195 **Discussion**

196 Although wolves avoid human settlements (Karlsson et al., 2007; Kaartinen et al., 2014; this study),
 197 our results provided evidence that wolves' expansion to human-dominated landscapes has led to an
 198 increase in nightly visits within residential areas. The two-way interaction between random distance
 199 to the nearest house and time of the day agrees with an earlier study where Hebblewhite and Merrill
 200 (2008) showed that with increasing human activity, wolves in the Canadian Rockies displayed
 201 spatio-temporal avoidance of human activity during daylight. Wolf nocturnal activity might
 202 principally be an adaptation to the primarily diurnal human activity and therefore be reflected most
 203 strongly in wolves living in human-dominated landscapes. Greater nocturnal activity allows wolves
 204 with territories in areas with high human activity to better exploit food resources that are available

205 near human settlements with reduced risk of conflict and greater freedom of movement. In Finland
 206 a major prey species in southern wolf territories where human densities are highest is non-native
 207 white-tailed deer (*Odocoileus virginianus*) (Ruusila and Kojola 2010), which is relatively well-
 208 adapted to living near human settlements.

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

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

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

228 The two-way interaction between season and wolf's status might principally support the naivety
 229 hypothesis because all sub-adults in our study were yearlings who had just settled down in a new
 230 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.

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 near residences when the territory becomes more familiar to them is noteworthy for management. It emphasizes patience in decision making, despite strong political and public pressure 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 area where they have been absent for a long time people who live in the area are not used defensive pens for dogs or take their dogs indoors before night which are 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.

Acknowledgements

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 is acknowledged for funding this study. EG was partially funded by US National Science Foundation grants ABI-1062411 and ABI-1458748.

257 **References**

- 258 Ballard, W. B., Ayres, L. A., Gardner, C. L., Foster, J. W. 1991. Den site activity patterns of gray
259 wolves, *Canis lupus*, in south-central Alaska. *Canadian Field Naturalist* 105, 497-504.
- 260 Ballard, W. B., Whitman, J. S., Gardner, C. L., 1987. Ecology of an Exploited Wolf Population in
261 South-Central Alaska. *Wildlife Monographs* 98, 3-54.
- 262 Bates, D., Maechler, M., 2014. Matrix: Sparse and Dense Matrix Classes and Methods. R
263 package version 1.1-4.
- 264 Benson, J. F., Mahoney, P. J., Patterson, B. R. 2015. Spatiotemporal variation in selection of roads
265 influences for mortality risk for canids in unprotected landscape. *Oikos* 124, 1664-1673.
- 266 Behdarvand, N., Kaboli, M., Ahmadi, M., Nourani, E., Mahini, A. S., Aghbolaghi, M. A., 2014.
267 Spatial risk model and mitigation implications for wolf–human conflict in a highly modified
268 agroecosystem in western Iran. *Biological Conservation* 177, 156-164.
- 269 Bisi, J., Kurki, S., Svensberg, M., Liukkonen, T., 2007. Human dimensions of wolf (*Canis lupus*)
270 conflicts in Finland. *European Journal of Wildlife Research* 53, 304–314.
- 271 Bragina, E.V., A. R. Ives, A.R, Pidgeon, A. M., Baskin, L. M., Gubar, Y. P., Piquer-Rodrigues, M,
272 Keuler, N. S., Petrosyan, V. G, Radeloff, V. C., 2015. Rapid declines of large mammal
273 populations after the collapse of the Soviet Union. *Conservation Biology* 29, 844-853.
- 274 Breitenmoser, U. 1998. Large predators in the Alps: the fall and rise of man's competitors.
275 *Biological Conservation* 83, 279–289.
- 276 Brownlow, A. 2000: A wolf in the garden: ideology and change in the Adirondack landscape. In:
277 Philo, C., Wilbert, C. (Eds), *Animal spaces, beastly places*. Taylor & Francis, New York. NY,
278 pp. 143-160.
- 279 Cain, J. W., Krausman, P. R., Jansen B. D. & Morgart, J. R. (2005) Influence of topography and
280 GPS fix interval on GPS collar performance. *Wildlife Society Bulletin* 33, 926-934.
- 281 Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andren, H, Lopez-Bao, J.V.,
282 Adamec, M., Alvares, F., Anders, O., Balciauskas, L., Balys, V., Bedo, P., Bego, F., Blanco,

- 283 J.C., Breitenmoser, U., Broseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder,
 284 T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremic, J.,
 285 Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak,
 286 J., Kutal, M., Liberg, O., Majic, A., Männil, P., Manz, R., Marboutin, E., Marcuccio, F.,
 287 Melovski, D., Mersini, K., Mertzanis, Y., Myslajek, R.W., Nowak, S., Odden, J., Ozolins, J.,
 288 Palomero, G., Paunovic, M., Persson, J., Potocnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I.,
 289 Rigg, R., Ryser, A., Salvatori, V., Skrbinsek, T., Stojanov, A., Swenson, J. E., Szemethy, L.,
 290 Trajce, A., Tsingarska-Sedefcheva, E., Vana, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl,
 291 S., Zimmermann, F., Zlatanova, D., Boitani, L., 2014. Recovery of large carnivores in Europe's
 292 modern human-dominated landscapes. *Science* 19, 1517-1519.
- 293 Ciucci, P., Boitani, L., Francisci, F., Andreoli, G., 1997. Home range, activity and movements of a
 294 wolf pack in central Italy. *Journal of Zoology* 243, 803–819.
- 295 Elfström, M., Zedrosser, A., Støen, O.-G., Swenson, J. E. 2012. Ultimate and proximate
 296 mechanisms underlying the occurrence of bears close to human settlements: review and
 297 management implications. *Mammal Review* 44, 5–18.
- 298 Fox J., 2003. Effect displays in R for generalized linear models. *Journal of Statistical Software* 8, 1–
 299 27.
- 300 Fritts, S. H., Mech, L. D., 1981. Dynamics, movements, and feeding ecology of a newly protected
 301 wolf population in Northwestern Minnesota. *Wildlife Monographs* 80, 3-79.
- 302 Fritts, S. H., Paul, W. J., 1989. Interactions of wolves and dogs in Minnesota. *Wildlife Society*
 303 *Bulletin* 17, 121-123.
- 304 Fuller, T. K., 1989. Population Dynamics of Wolves in North-Central Minnesota. *Wildlife*
 305 *Monographs* 105, 3-41.
- 306 Hansen AM, Jeske, D, Kirsch, W., 2015. A chi-square goodness-of-fit test for autoregressive
 307 logistic regression models with applications to patient screening. *Journal of*

- 308 Biopharmaceutical Statistics 25, 89-108.
- 309 Huber, D., Kusak, J., Frković, A., Gužvica, G., Gomerčić, T., 2002. Causes of wolf mortality in
310 Croatia during 1986-2001. Veterinarski arhiv. 72, 131-139.
- 311 Gurarie, E., Suutarinen, J., Kojola, I. & Ovaskainen, O., 2011. Summer movements, predation and
312 habitat use of wolves in human modified boreal forests. Oecologia 165, 891-903.
- 313 Hansen, A.M. 2012. Goodness-of-fit tests for autoregressive logistic regression models and
314 generalized linear mixed models. UC Riverside Electronic Thesis and Dissertations.
315 Escholarship. University of California. 96 p. <http://escholarship.org/uc/item/53t2g6g3>.
- 316 Hebblewhite, M., Merrill, E. 2008. Modelling wildlife-human relationships for social species with
317 mixed-effects resource selection models. - Journal of Applied Ecology 45: 834-844.
- 318 Kaartinen S., Kojola, I., Colpaert, A., 2005. Finnish wolves avoid roads and settlements. Annales
319 Zoologici Fennici 42, 423 - 432.
- 320 Kaartinen, S., Antikainen, H., Kojola I., 2015. Habitat model for a recolonizing wolf (*Canis*
321 *lupus*) population in Finland. Annales Zoologici Fennici 52, 77-89.
- 322 Karlsson, J., Sjöström, M., 2007. Human attitudes towards wolves, a matter of distance.
323 Biological Conservation 137, 610 –616.
- 324 Kojola I., Kuittinen, J., 2002. Wolf attacks on dogs in Finland. Wildlife Society Bulletin 30, 498 -
325 501.
- 326 Kojola, I., Ronkainen, S., Hakala, A., Heikkinen, S., Kokko, S., 2004. Interactions between wolves
327 *Canis lupus* and dogs *C. familiaris* in Finland. Wildlife Biology 10, 101-107.
- 328 Kojola, I., Aspi, J., Hakala, A., Heikkinen, S., Ilmoni, C., Ronkainen, S., 2006. Dispersal in an
329 expanding wolf population in Finland. Journal of Mammalogy 87, 281–286.
- 330 Kojola I., Helle P., Heikkinen S., Linden, H., Paasivaara, A., Wikman, M., 2014. Tracks in snow
331 and population size estimation: wolf in Finland. Wildlife Biology 20, 279-284.
- 332 Kubinyi, E., Turcsan, B., Miklosi, A., 2009. Dog and owner demographic characteristics and dog

- 333 personality trait associations. *Behavioural Processes* 81, 392–401.
- 334 Kusak, J., Skrbinsek, A. M., Huber, D., 2005. Home ranges, movements, and activity of wolves
335 (*Canis lupus*) in the Dalmatian part of Dinarids, Croatia. *European Journal of Wildlife*
336 *Research* 51, 254–262.
- 337 Lenth, R.V., 2013. Lsmeans: Least-Squares Means. R package version 2.11. [http://](http://CRAN.R-project.org/package=lsmeans)
338 CRAN.R-project.org/package=lsmeans.
- 339 Lescureux, N., Linnell, J.D.C., 2014. Warring brothers: The complex interactions between
340 wolves (*Canis lupus*) and dogs (*Canis familiaris*) in a conservation context. *Biological*
341 *Conservation* 171, 232–245.
- 342 Løe J., Røskift, E., 2004. Large carnivores and human safety: a review. *Ambio* 33, 283-288.
- 343 Lyon, T. B., Graves, W. N., 2014. The real wolf: The science, politics, and economics of co-
344 existing with wolves in modern times. 343 p. ISBN 10 1-59112-122-X.
- 345 Mech, L. D. & Boitani, L. 2003. Wolf social ecology. In: Mech, L. D., Boitani, L. (Eds.), *Wolves.*
346 *Behavior, Ecology and Conservation*. The University of Chicago Press, pp. 1-35.
- 347 Mysterud, A., Ims, R. A. 1998. Functional responses in habitat use: availability influence relative
348 use in trade-off situations. - *Ecology* 79: 1435-1441.
- 349 Okarma H., 1993. Status and management of the wolf in Poland. *Biological Conservation* 66,153-
350 158.
- 351 R Core Team 2013., R: A language and environment for statistical computing. R Foundation for
352 Statistical Computing, Vienna, Austria. URL <http://www.R-project.org/>.
- 353 Rassi, P., Hyvärinen, E., Juslen, A., Mannerkoski, I. 2010. The 2010 Red List of Finnish species.
354 685 p. Ministry of the Environment. Finnish Environmental Institute.
- 355 Ruusila, V., Kojola, I. 2010. Ungulates and their management in Finland. In: Apollonio, M.,
356 Andersen, R., Putman, R. (Eds.), *European ungulates and their management in the 21st century.*
357 Cambridge University Press, pp. 86 - 102.
- 358 Sing, T., Sander, O., Beerenwinkel, N., Lengauer, T., 2005. ROCR: visualizing classifier

- 359 performance in R. *Bioinformatics* 21, 3940 - 3941.
- 360 Skogen, K., Mauz, I., Krange, O., 2008. Cry Wolf!: Narratives of Wolf Recovery in France and
361 Norway. *Rural Sociology* 73,105–133.
- 362 Smith, B.R., Blumstein, D. T., 2008. Fitness consequences of personality: a meta-analysis.
363 *Behavioral Ecology* 19, 448-455.
- 364 Starling, M. J., Branson N.,Thomson, P. C., McGreevy, P. D., 2013. Age, sex and reproductive
365 status affect boldness in dogs. *Veterinary Journal* 197, 868–872.
- 366 Swenson, J.E., Wabakken, P., Sandegren, F., Bjärvall A., Franzén R., Söderberg, A., 1995. The
367 near extinction and recovery of brown bears in Scandinavia in relation to the bear
368 management policies of Norway and Sweden. *Wildlife Biology* 1, 11 - 25.
- 369 Theuerkauf, J., Gula, R., Pirga, B., Tsunoda, H., Eggermann, J., Brzezowska, B., Rouys, S., Radler,
370 S., 2007. Human impact on wolf activity in the Bieszczady Mountains, SE Poland. *Annales*
371 *Zoologici Fennici* 44, 225-231.
- 372 Venables, W.N., Ripley, B.D., 2002. *Modern Applied Statistics*. Springer, New York, NY
- 373 Vila, C.,Walker, C.,Sundqvist, A.-K., Flagstad, Ø., Andersone, Z., Casulli, A., Kojola, I., Valdmann,
374 H., Halverson, J., Ellegren, H., 2003. Combined use of maternal, paternal and bi-parental
375 genetic markers for the identification of wolf–dog hybrids. *Heredity* 90, 17–24.
- 376 Wabakken, P., Sand, H., Kojola, I., Zimmermann, B., Arnemo, J.M., Pedersen, H.C., Liberg O.,
377 2007. Multi-stage, long-stage natal dispersal by a GPS-collared Scandinavian wolf. *Journal of*
378 *Wildlife Management* 71, 1631 - 1634.
- 379 Weiß, C.H., Kim, H.-Y., 2013. Parameter estimation for binomial AR(1) models with applications
380 in finance and industry. *Statistical Papers* 54, 563 – 590.
- 381 Woodroffe, R. 2000. Predators and people: using human densities to interpret declines of large
382 carnivores. *Animal Conservation* 3, 165 - 173.
- 383
- 384

385 Table 1. Mean deviation of wolves' locations to the nearest house from the distance of random
 386 locations to the nearest house in Finland. The adjusted R^2 of the model is 0.22, $F_{3,21} = 3.29$ and $P =$
 387 0.041.

388

389

Variable	Estimate	SD	t-value	<i>P</i>
Intercept	685.85	363.50	1.89	0.073
Wolf's 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

390

391

392

393

394

395

396

397

398

399

400

401

402

403

404 Table 2. The coefficients and the analysis of deviance table (type III tests) in autoregressive logistic
 405 model for the probability of wolves' visitations closer than 150 m to the nearest house in Finland.
 406 Random distance in the distance from random location to the nearest house within wolf's territory.
 407 The intercept, coefficients and standard errors from models with standardized distances are given in
 408 parenthesis.
 409
 410

Variable / category	Coefficient	Standard error	Df	t / chi-square	<i>P</i>
Fixed effects					
Intercept	-5.471 (-4.936)				
Random distance (RD)	$3.48 \cdot 10^{-4}$ (0.261)	$2.95 \cdot 10^{-4}$ (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	$1.106 \cdot 10^{-3}$ (-0.832)	$2.757 \cdot 10^{-4}$ (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
Random effects					
	Variance	Phi			
Wolf (Intercept)	0.149				
Residual	0.962	0.051			

412 **Figure legends**

413

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

417

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

420

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

423

424 Fig. 4. The observed probability at which the wolf was < 1 000 m from the nearest house in relation
425 to the probability at which random distances (RD) were < 1 000 m from the nearest house within
426 the 25 study territories in Finland.

427

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

431

432 Fig. 6. Observed and predicted probabilities with which wolves visit < 150 m to houses in Finland.
433 Predicted probabilities were yielded from autoregressive logistic model using GPS-locations $\leq$
434 1 000 m to the nearest house. The model treated the wolf as random variable, wolf's sex, status
435 (adult, sub-adult), season, time of the day and random distance to the nearest house as fixed
436 variables. Black symbols are outliers.

437

438

439 Fig 1.

440
441
442

Fig 2

Fig 3

Fig 4.

532 Fig 5.
533

534
535
536
537
538
539

540
541
542 Fig 6.
543

544
545