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Wolves at the door? Factors influencing the individual behavior of wolves in relation to anthropogenic features

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ABSTRACT

The recovery of large carnivores in human-dominated landscapes comes with challenges. In general, large carnivores avoid humans and their activities, and human avoidance favors coexistence, but individual variation in large carnivore behavior may occur. The detection of individuals close to human settlements or roads can trigger fear in local communities and in turn demand management actions. Understanding the sources of individual variation in carnivore behavior towards human features is relevant and timely for ecology and conservation. We studied the movement behavior of 52 adult established wolves ((*Canis lupus*), 44 wolf pairs) with GPS-collars over two decades in Scandinavia in relation to settlements, buildings, and roads. We fit fine-scale movement data to individual step selection functions to depict the movement decisions of wolves while travelling, and then used weighted linear mixed models to identify factors associated with potential individual pair deviations from the general behavioral patterns. Wolves consistently avoided human settlements and main roads, with little individual variation. Indeed, after correcting for season, time of the day, and latitude, there was little variability in habitat selection among wolf pairs, demonstrating that all wolf pairs had similar movement pattern and generally avoided human features of the landscape. Wolf avoidance of human features was lower at higher latitudes particularly in winter, likely due to seasonal prey migration. Although occasional sightings of carnivores or their tracks near human features do occur, they do not necessarily require management intervention. Communication of scientific findings on carnivore behavior to the public should suffice in most cases.

1. Introduction

Several populations of large carnivores in Europe and North America are recovering into former ranges (Chapron et al., 2014, Bruskotter and Shelby, 2010), bringing along conservation challenges (Kuijper et al., 2019). Carnivore recovery is good news for conservation, but large carnivores can prey on domestic animals, compete for game species, and induce fear and negative attitudes from people (Treves et al., 2009; Treves and Karanth, 2003).

Range expansions of large carnivore populations, together with an expansion of urbanized areas, result in a higher frequency of interactions between large predators and humans (Treves et al., 2002). These interactions range from the more frequent indirect observations (e.g., signs of presence, remote photographs), to the less frequent direct encounters including predation on livestock and, rarely, fatal attacks on humans (Bombieri et al., 2019). Even though attacks on humans are very rare, the mere risk of a potential encounter with a wolf (*Canis lupus*) or a brown bear (*Ursus arctos*) generates fear, which can be a source of conflict (Linnell et al., 2003; Johansson et al., 2019).

Nevertheless, large carnivores generally avoid interactions with humans. Brown bears and black bears (*Ursus americanus*) seem to adapt their behavior spatiotemporally to decrease the varying risk of interference with humans (Beckmann and Berger, 2003; Ordiz et al., 2011). Likewise, pumas (*Puma concolor*) consistently avoid human neighborhoods (Wilmers et al., 2013). Even when large carnivores coexist spatially with humans, they adjust activity patterns to reduce the risk of encounters. Such is, for instance, the case for tigers (*Panthera tigris*) (Carter et al., 2012), bears (Ordiz et al., 2013), and wolves in Scandinavia (Wam et al., 2014) and elsewhere (e.g., Theuerkauf, 2009). These behavioral changes reveal that large carnivores can perceive risks from

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humans and human activities (Darimont et al., 2015; Sazatornil et al., 2016).

Despite the general avoidance of humans by large carnivores, intraspecific and external factors may influence individual carnivore responses. For example, brown bear attacks on humans are more frequent when encounters involve a specific segment of the population (i.e., females with cubs, Bombieri et al., 2019), and are associated with specific human activities (e.g., hunting, Stoen et al., 2018). Many large carnivores become more nocturnal when inhabiting areas with high human density (e.g., leopards (*Panthera pardus*), Odden et al., 2014 and bears Ordiz et al., 2019). Likewise, individuals may respond differently to humans due to their previous or inherited experience with humans (Milleret et al., 2019; Sanz-Perez et al., 2018), reflecting large individual plasticity (Evans et al., 2019; Greenberg and Holekamp, 2017; Ordiz et al., 2019). Regardless of the underlying mechanisms behind individual variation in the proximity to humans, carnivores using areas close to humans may lead to conflict and ultimately increase carnivore mortality rates (Hebblewhite and Merrill, 2008; Steyaert et al., 2016).

The wolf is regarded as a highly adaptable and cognitive species, with a widespread distribution across very diverse habitat types in the northern hemisphere (Boitani, 2003). In Scandinavia, the wolf population inhabits areas of low human population densities, but the landscape has strong anthropogenic influence, with scattered settlements, an extensive road network, and intensively managed forests and game populations (Ordiz et al., 2015; Wabakken et al., 2001).

Humans are the main cause of mortality of wolves in Scandinavia (Liberg et al., 2012; Milleret et al., 2017), which supports the assumption of humans as a perceived risk for Scandinavian wolves. Indeed, wolf avoidance of human features of the landscape has been documented at different spatial scales. Wolves avoid densely human-populated areas and infrastructures when establishing a territory (Karlsson et al., 2007; Ordiz et al., 2015), and they tend to select areas further from anthropogenic features (Milleret et al., 2019). Nevertheless, they can use secondary roads for travelling during the night (Zimmermann et al., 2014), which has also been described elsewhere (Gurarie et al., 2011; Theuerkauf, 2009; Whittington et al., 2005).

However, individual wolves might respond differently to human features due to specific spatio-temporal factors (Zimmermann et al., 2014), and intrinsic factors, such as sex (Sanz-Perez et al., 2018), or habituation to humans (McNay, 2002). Variation in individual behavior towards human activities or settlements can be more obvious during travelling, because non-travelling time (e.g., time spent at kill sites or breeding locations) is usually spent in less disturbed habitats (Sazatornil et al., 2016, Torretta et al., 2018). The conflict level may increase in winter in areas where snow cover makes it easy to detect tracks from wolves that have passed near houses or settlements (e.g., during nighttime), which may result in individual wolves being perceived as relatively tolerant to people (Wabakken et al., 2019). This may in turn undermine public attitudes and tolerance to wolves (Treves et al., 2013). Such a situation recently occurred in Norway, where concerns arose about a specific wolf pack regarded as conflictive, because wolves and wolf tracks were often reported near human settlements. This situation lead the Norwegian Parliament and the Norwegian Environment Agency to make a call to investigate the behavior of Scandinavian wolves towards human settlement, and our study specifically emerged from that call. Understanding the sources of individual variation in wolf movement relative to human settlement is relevant for a better understating of large carnivore behavior in human-dominated landscapes and, remarkably, for the actual practice of conservation and management.

In this study, we first hypothesized that wolves would generally avoid human features of the landscape while travelling. This kind of behavior has been shown previously for wolves at coarse scales (Milleret et al., 2019; Ordiz et al., 2015) and other large carnivore species (e.g., Ordiz et al., 2011; Beckmann and Berger, 2003; Wilmers et al., 2013), and partially at fine scales in Scandinavian wolves (Zimmermann et al., 2014). Secondly, we hypothesized that if individual behavior deviates from the general pattern, this deviation may be explained by spatial, temporal or intrinsic factors rather than being attributed to a "conflictive" behavior. Given the high seasonality in climatic and daylight conditions in Scandinavia, we expected that wolves would relax the avoidance behavior towards humans in winter and during night, when the risk of interacting with humans is lower (Rio-Maior et al., 2019; Zimmermann et al., 2014). We also expected the wolf response to vary along the latitudinal gradient in our study area given the differences in prey availability (roe deer (*Capreolus capreolus*) towards the south (Mattisson et al., 2013) and moose (*Alces alces*) towards the north (Sand et al., 2016)). We expected this latitudinal variation particularly in winter months due to moose migration to lower altitudes in the snow-rich northern areas (Allen et al., 2016; Singh et al., 2012). Finally, we controlled for pack size and time since territory establishment.

To test these hypotheses, we used a two-phase analytical approach. We first fitted individual step selection functions to fine-scale movement data to depict the movement decisions of individual wolves and the general behavioral pattern towards several human-related variables. Then, we used weighted linear mixed models to test different spatiotemporal and intrinsic factors that could explain potential deviations from the general pattern.

This study illustrates the relevance of applied ecology for the practice of conservation biology. Analyzing large carnivore behavior helps understand the process of large carnivore recovery in human-dominated landscapes, which in turn can aid the management of these species of large conservation interest.

2. Material and methods

2.1. Study area

The study area is situated in south-central Scandinavia, including parts of Sweden and Norway, encompassing the breeding range of Scandinavian wolves (Fig. 1). The landscape is dominated by coniferous forest, mainly composed of Norway spruce (*Picea abies*) and Scots pine (*Pinus silvestris*), and a minor proportion of deciduous tree species like birch (*Betula pendula* and *B. pubescens*), aspen (*Populous tremula*), and alder (*Alnus incata* and *A. glutinosa*). The forests are extensively managed and therefore, a dense network of forest roads exists throughout the study area. The proportion of land dedicated to agriculture increases towards the south (Mattisson et al., 2013). Human population density averages 17 persons per km^2, although most of the population is concentrated in settlements (www.scb.se, Sweden; www.ssb.no, Norway). Vast parts of the study area have less than one person per km^2 (Wabakken et al., 2001).

Moose and roe deer are the staple prey of the Scandinavian wolves (Sand et al., 2016), and are distributed throughout the study area. However, roe deer densities decrease to the north (Mattisson et al., 2013).

2.2. GPS locations

We used high frequency GPS data (30-min and one-hour intervals, n = 41,358 locations) from 52 territorial wolves (scent marking adults) in 44 different packs. In eight packs, both male and female of the reproductive pair were collared. The wolves were captured between 2001 and 2017 (see Table S4) and equipped with neck collars (GPS-Simplex or Tellus, TVP Positioning, Lindesberg, Sweden or GPS-Plus VECTRONIC Aerospace GmbH, Berlin, Germany) following the ethically-approved procedures described in Arnemo and Evans (2017). The location data were collected into the Wireless Remote Animal Monitoring database system for data validation and management (Dettki et al., 2013).

Because we were interested in the behavior of wolves during travelling, we identified and excluded stationary locations (mainly

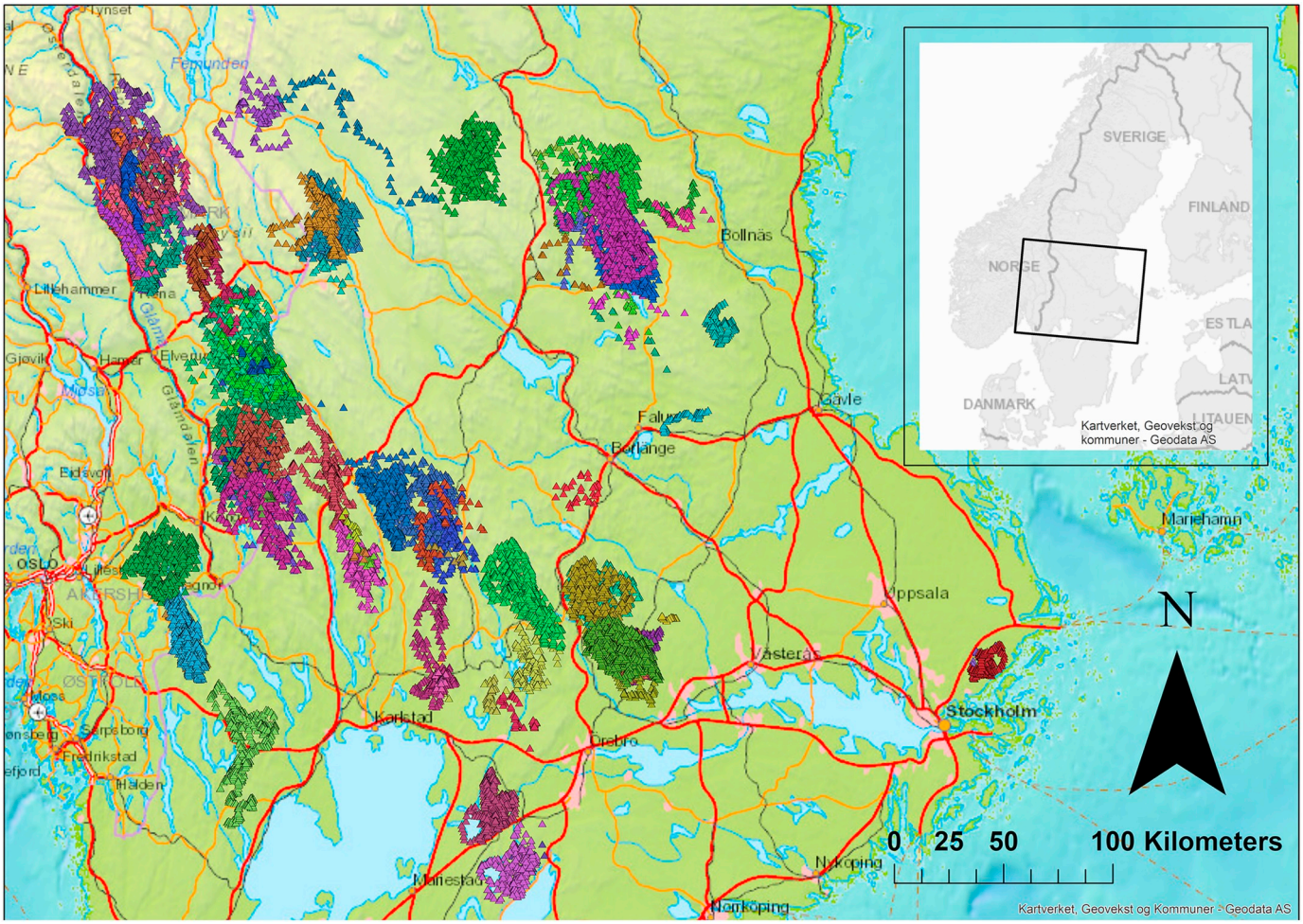

Fig. 1. Study area in south-central Scandinavia (map in the upper right corner) where the movement decision of adult territorial wolves (n = 52) were studied in relation to anthropogenic features. Triangles represent the actual GPS locations (n = 41,358) of wolves and the different colors represent different individuals. Red and orange lines represent main roads. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

resting-, kill-, rendezvous- or den-sites) by creating buffers of 100 m around each location, and then removing GPS locations from overlapping consecutive buffers. We defined clusters following conservative distances from previous studies in this wolf population (Sand et al., 2005).

2.3. Individual variation in fine-scale habitat selection

2.3.1. Random locations

For each of the observed locations, we simulated five random steps, where the endpoint of each step represented an available location. We first computed frequency distributions of the step lengths and turning angles from the observed half-hourly locations (mean step length: 1116 ± 6.8 m; mean angle: 1.4 ± 0.6 degrees) and hourly locations (mean step length: 1766 ± 9.8 m; mean angle: 0.8 ± 0.5 degrees). We then used the correspondent empirical distribution (computed separately for half-hourly and hourly locations) to generate five random steps using each observed location as a starting point, using the "movement.ssfsamples" function from the Geospatial Modelling Environment (Beyer, 2015).

2.3.2. Covariates

For each observed and random location, we calculated the (i) distance to the closest human settlement and the (ii) distance to the closest forest edge (with positive values for locations outside and negative values for locations inside the forest), using the Vegetation Map of Norway (Johansen, 2009) and the Corine land cover map in Sweden, both with a resolution of 200 m. We also calculated the distance to the closest (iii) main road and (iv) forest road (1:100000, Lantmäteriet, Sweden; N50 kartdata, Statens kartverk, Norway). The (v) density of buildings (i.e., houses, cabins, isolated farms, and other buildings) was obtained by estimating the kernel densities, with a bandwidth of one kilometer, of the point layers representing the buildings in Norway and Sweden obtained from the cadaster data from each country (www.lantmateriet.se, Sweden; www.kartkatalog.geonorge.no, Norway). All the data was extracted using R (R Core Team, 2018) and ArcGis v.10.3 (ESRI, 2009).

Additionally, we computed the 95% Minimum Convex Polygon (hereafter, MCP) for each wolf home range and calculated the centroid point. We extracted the latitude value of each MCP centroid and used it as a latitude covariate of each home range. We also calculated an average light index in each MCP extracted from the calibrated night-time lights layer with a resolution of 1 km (Venter et al., 2016). This index takes values from zero to ten, representing an increasing continuum of night-light pressure per pixel. We used the light index as a proxy for population density within each territory. For each wolf, we also used the size of the pack to which it belonged and the number of years since territory establishment using data from the annual wolf monitoring during winter.

2.3.3. Step selection functions

We used conditional logistic regressions in a Bayesian framework to fit the same full model to each wolf for each season (summer, 1st of May to the 30th of September; winter, 1st of October to 30th of April), and time of day (day, 08:00–19:59; night, 20:00–07:59; Zimmermann et al., 2014). In our boreal study area, this classification does not reflect daylight and darkness, but it is a proxy for the periods with outdoors human activity (Zimmermann et al., 2014). The binary response variable was actual location (GPS-locations = 1) or available location (random locations = 0) for a given wolf, time of day, and season. The full model included distance to human settlement, density of buildings, distance to main road, and distance to forest road as potential explanatory variables. Wolves are more exposed outside forest patches, where human settlements and agricultural areas are (Person and Russell, 2008). Therefore, we also included distance to forest edge in the models. These spatial variables are susceptible to vary between observed and available locations. After subsetting by individual wolf, season, and time of day, data sets that did not include >50 observed locations (i.e., at least ten observations per exploratory variable) were discarded from the analyses.

We ran Pearson correlation tests to all pairs of explanatory variables. The highest correlation value was 0.338 for the correlation between the distance to settlement and the distance to main roads. Therefore, we kept all the covariates in the models. We standardized all continuous variables by $(x_i - \overline{X})/(2 \times SD)$ (Gelman and Hill, 2007) except distance to forest edge, which scale was comparable to the standardized variables (range from −2.193 to 2.141 km). We wrote the models in JAGS (Appendix A1) and fit them by using the package 'rjags' (Plummer, 2018) in R 3.5.1 (R Core Team, 2018). We used normal distributions ($\mu = 0$, sd = 5) as weakly informative priors for the explanatory variables and run three chains of 30,000 iterations, discarding 10,000 in each of them as burn-in. We checked for the convergence of the models using the Gelman and Rubin's converge diagnosis and visually inspecting the mixing of the chains (Gelman and Rubin, 1992).

2.3.4. Weighted linear mixed regressions

For each wolf (*i*), season (*k*), and time of day (*t*), we obtained the selection coefficients of each variable (β_{ijkt}, where j represents each variable) by extracting the mean posterior estimates from the posterior distributions obtained from the conditional logistic models. In order to investigate the causes of variation in individual selection, we modelled each set of selection coefficients of the covariates included in the step selection functions (distance to human settlement, density of buildings, distance to main roads, distance to forest roads, and distance to forest edge) using weighted linear mixed regressions in a Bayesian framework. In order to account for the β_{ijkt} uncertainty, we used the inverse Bayesian standard error of each β_{ijkt} as model weight (Evans et al., 2019). We used season and time of day as temporal covariates, the standardized latitude of the centroid of each 95% MCP, and the average night-light index of each 95% MCP (proxy for human density) as spatial covariates, and pack size and years since establishment as intrinsic covariates, such as:

$$\beta_{ijkt} \sim \text{Temporal} + \text{Spatial} + \text{Intrinsic}$$

From this full model, we created a list of thirteen candidate models by using different combination of these covariates and interactions between them (Table S1). To select the best random structure, we fit null models to all β_{ijkt} first by using individual wolf id as a random effect and then by using pair id (i.e., one or two wolves of the reproductive pair) as random effect. All models using pair id as a random effect showed a better fit than those using individual id according to their widely applicable information criterion (WAIC) value (Table S2). Therefore, we included pair id as a random effect in all models.

We performed model selection among candidate models calculating the WAIC (Vehtari et al., 2016) for each model. Therefore, we conducted five model selection processes, one for each β_j estimated in the previous phase. From the best-ranked model and for each of the selection processes we calculated the repeatability value by:

$$R = \frac{\sigma_\alpha^2}{\sigma_\alpha^2 + \sigma_\varepsilon^2}$$

where $\sigma_\alpha{}^2$ is the among-group variance and $\sigma_\varepsilon{}^2$ is the within-group variance (Nakagawa and Schielzeth, 2010). The repeatability value represents the proportion of the total variance that can be explained by variation among groups (Nakagawa and Schielzeth, 2010). It can be interpreted as the amount of consistent individual (or pair, in this case) variation. In other words, r = 1 indicates that individuals (or pairs) behave differently from each other, and no repeatability (r = 0) indicates that individuals behave similarly within the population.

Additionally, we studied whether the sex had an influence on the selection coefficients by restricting the analysis to the wolf pairs in which both the reproductive male and female were collared (n = 8 pairs). We evaluated the fit of six candidate models (Table S3) that included the direct relationship between the coefficients with sex, and the interactions between sex, season and time of the day.

3. Results

3.1. Step selection functions

To investigate the individual behavior during travelling towards each infrastructure for each wolf, season, and time of the day, we ran 157 models with an average sample size of 250.7 locations (±16.1 SE) for 52 different wolves. Of the 208 possible combinations, 51 were removed due to a small sample size. All models converged. Wolves consistently avoided human settlements (Fig. 2). However, 89% of the 95% credible intervals of the posterior distributions for this coefficient overlapped zero. Only three wolves selected areas significantly closer than expected by random to human settlements, two during winter nights and one during summer nights (Table S4). No wolf selected for areas with high density of buildings at any season and time of the day (Fig. 2, Table S4). Most wolves tended to move further away from main roads (Fig. 2, Table S4). However, wolves selected shorter distances to forest roads than expected by random (Fig. 2). Wolves selected for short distances to forest roads in 33% of all combinations of wolf, season, and time of day, mainly during the night (Table S4). Along a gradient from the center to outside of a forest patch, most wolves (57%) preferred to travel closer to the center rather than towards outside (Fig. 2).

3.2. Weighted linear mixed regressions

To test whether the deviation of individual behaviors from the general behavioral pattern can be explained by spatial, temporal, or intrinsic factors, we modelled the variation in the selection coefficients of the wolves (as estimated in the previous section). The best models for all behaviors improved the respective null models (ΔWAIC >2) except for the distance to settlements (ΔWAIC = 1.3) (Table 1).

All models showed a low measure of repeatability (Fig. 3). This indicated that little variation in wolf behavior was explained by differences in habitat selection among wolf pairs during travelling, and it was mainly explained by our fixed variables. We found the highest repeatability values for the distance to settlements and the density of buildings, i.e., pairs behaved somewhat differently after correcting for the fixed variables (Fig. 3). However, wolves consistently avoided both features (note the positive coefficients for the distance to settlements and negative coefficients for the density of buildings; Fig. 3). Of the included covariates, temporal covariates, especially season, explained most variation in wolf behavior in all the best models, except for distance to settlement, which was best explained by spatial differences,

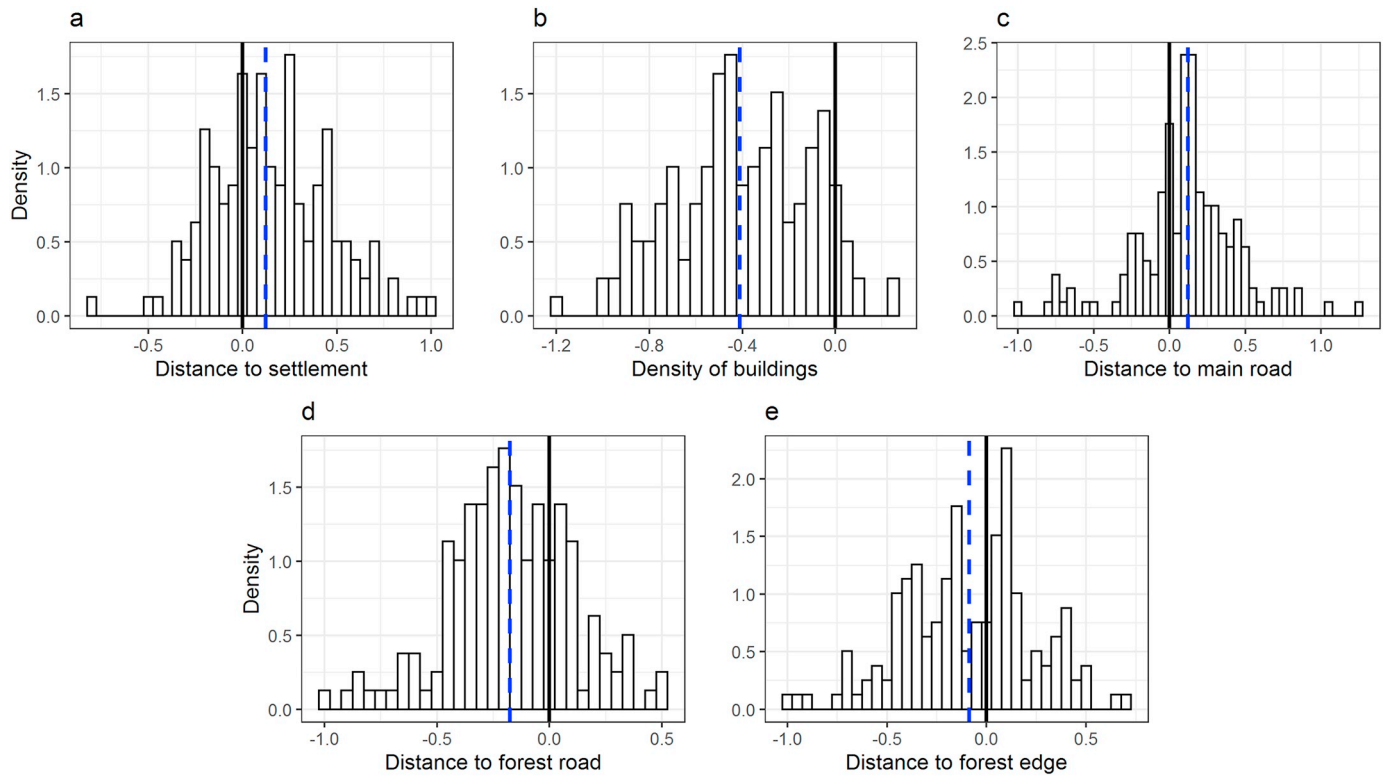

Fig. 2. Distribution of the mean posterior beta coefficients obtained from each individual conditional logistic model studying the behavior of Scandinavian wolves to anthropogenic features from 2001 until 2017. Black line represents the zero value, and dashed blue line is the median of all the mean estimates. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

especially by latitude (Tables 1 and 2).

The combined effect of season and time of day was for instance evident for distance to roads: wolves avoided main roads, although road avoidance decreased during the winter and during nights (Fig. 5). Wolves also moved closer to forest roads especially during the winter nights (Fig. 5). Along a gradient from the center to outside of a forest patch, wolves generally preferred to travel closer to the center, except during winter nights, where we observed the opposite pattern (Fig. 6). Latitude was an important factor explaining the variation in the movement decisions of wolves in relation to anthropogenic features (Tables 1 and 2). With increasing latitude, the strength of the avoidance behavior of wolves in relation to the distance to settlements decreased, as did the density of buildings and the distance to main roads (Table 2, Fig. 4). This relationship was more pronounced during the winter months for the density of buildings and the distance to main roads (Table 2, Fig. 4). Nevertheless, the light index showed no relationship with any of the responses except for a positive relationship with the behavior towards density of buildings during the winter (i.e., wolves in territories with high light index tended to move to areas of higher densities of buildings in the winter; Table 2). None of the intrinsic variables (pack size and years since establishment) explained variation in wolf behavior during travelling (Table 2). Sex did not explain variation in wolf behavior during travelling (Table S5). The model using only sex as a fixed variable showed a better fit than the null model for the distance to forest roads and distance to forest edge (Table S5). However, the association with sex was weak, with 95% CRI including zero and therefore preventing clear conclusions about any behavioral sex differences (coefficient for the distance to forest road: 0.011 95% CRI (−0.167, 0.181); coefficient for the distance to forest edge: 0.133 95% CRI (−0.083, 0.347)).

4. Discussion

Wolves consistently avoided anthropogenic features in the landscape when travelling at a fine, step decision scale, with low individual variation in this general pattern. Indeed, after correcting for season, time of the day, and latitude (proxy for distribution of the staple wolf prey), little variation was regarded as genuine departure from the general pattern. Therefore, our hypotheses that wolves would generally avoid human features of the landscape while traveling and that individual deviations from this pattern may be explained by spatial, temporal or intrinsic factors, are supported by the results. Wolf elusive behavior at a fine scale is in accordance with other studies at different spatial scales (Lesmerises et al., 2012; Zimmermann et al., 2014) and with results reported for other large carnivores, such as black and brown bears (Evans et al., 2019; Frackowiak et al., 2014). Reaffirming that wolf avoidance of human features in the landscape is a consistent behavioral pattern is essential for wolf-human coexistence now that wolf and other large carnivore populations are recovering in Scandinavia (e.g., Ordiz et al., 2015) and elsewhere (Chapron et al., 2014).

However, we identified some factors that might influence this general pattern. For example, wolves tended to move closer to forest roads, where human activity is generally low, especially during night when they likely travel and patrol their territory (Zimmermann et al., 2014). Moreover, wolves moved closer to forest roads particularly in winter, when wolf avoidance of densely human populated areas was at its weakest and wolves moved closer to the forest edge or even outside forest patches. Likewise, wolves moved closer to main roads in the same periods. This behavior has also been observed in wolves in Finland (Kojola et al., 2016) and Italy (Ciucci et al., 1997). Becoming nocturnal is a typical wildlife response when exposed to human activity (Gaynor

Table 1
Models that best explained the observed variation in individual selection coefficients for wolves in Scandinavia. ΔWAIC is the model ranking in relation to the top model. The null model only included the random factor pair id. Temporal represents Season and Time of the Day variables, Spatial represents Latitude and Luminosity variables, and Intrinsic represent Pack size and Years since establishment variables. Seasonal represent the indicated variables interacting with Season.

Model	Model structure	ΔWAIC
Distance to settlement		
Model 6	Spatial + Intrinsic	0
Model 3	Spatial	0
Model 7	Temporal + Spatial + Intrinsic	−0.124
Model 2	Intrinsic	−0.706
Model 5	Temporal + Spatial	−0.722
Model 4	Temporal + Intrinsic	−0.832
Model 9	Temporal + Intrinsic + Intrinsic seasonal	−0.98
Model 0	NULL	−1.265
Model 12	Temporal + Intrinsic + Intrinsic seasonal	−1.789
Model 1	Temporal	−1.936
Density of buildings		
Model 13	Temporal + Spatial + Intrinsic + Temporal seasonal + Spatial seasonal + Intrinsic Seasonal	0
Model 10	Temporal + Spatial + Temporal seasonal + Spatial seasonal	−1.554
Model 0	NULL	−31.363
Distance to main road		
Model 9	Temporal + Intrinsic + Intrinsic seasonal	0
Model 10	Temporal + Spatial + Temporal seasonal + Spatial seasonal	−1.762
Model 7	Temporal + Spatial + Intrinsic	−1.972
Model 0	NULL	−23.18
Distance to forest road		
Model 5	Temporal + Spatial	0
Model 8	Temporal + Temporal seasonal	−0.105
Model 10	Temporal + Spatial + Temporal seasonal + Spatial seasonal	−0.375
Model 1	Temporal	−0.601
Model 9	Temporal + Intrinsic + Intrinsic seasonal	−0.866
Model 7	Temporal + Spatial + Intrinsic	−0.943
Model 12	Temporal + Intrinsic + Intrinsic seasonal	−1.424
Model 11	Temporal + Intrinsic + Temporal seasonal + Intrinsic seasonal	−1.458
Model 4	Temporal + Intrinsic	−1.759
Model 13	Temporal + Spatial + Intrinsic + Temporal seasonal + Spatial seasonal + Intrinsic Seasonal	−1.811
Model 0	NULL	−44.671
Distance to forest edge		
Model 8	Temporal + Temporal seasonal	0
Model 11	Temporal + Intrinsic + Temporal seasonal + Intrinsic seasonal	−1.113
Model 10	Temporal + Spatial + Temporal seasonal + Spatial seasonal	−1.176
Model 13	Temporal + Spatial + Intrinsic + Temporal seasonal + Spatial seasonal + Intrinsic Seasonal	−1.706

et al., 2018), and it has been reported for several large carnivore species; e.g., brown bear (Ordiz et al., 2013), common leopard (Odden et al., 2014), and Eurasian lynx (*Lynx lynx*) (Filla et al., 2017).

The avoidance pattern of Scandinavian wolves to human features was lower at higher latitudes. Wolves in the northern part of our study area did not select nor avoid human settlements as clearly as in the south, and they even selected for main roads in winter. This pattern may be explained by differences in landscape productivity and snow conditions, which influence prey distribution. In our study area, productivity decreases towards the north, where agricultural land is scarce and forest cover dominates the landscape (Mattisson et al., 2013). Roe deer prefers agriculture areas, and their abundance decreases towards the north (Mattisson et al., 2013). At high densities of roe deer, wolves prefer this prey over moose, which are the staple prey at higher latitudes (Sand et al., 2016). Moose inhabiting the northern part of our study area migrate to areas of lower elevation during winter, generally to valleys where food availability is higher and snow conditions (lower snow depth) are more favorable (Allen et al., 2016; Singh et al., 2012). Those are the valleys where human settlements and main roads are concentrated, which leads to an overlap between moose and humans (Wabakken et al., 2019). Consequently, wolves in this area may use areas closer to human features during winter because they select for areas with a higher density of moose. To test this hypothesis, we would need moose density data at the fine scale of our wolf movement data.

The small within-group variation (wolf pair variation) might be due to actual differences in personality, which might be defined in the early years of life (Milleret et al., 2019) or inherited genetically (Saetre et al., 2006). Future research investigating the relationship between behavioral variability and genetic relatedness might reveal interesting results. Moreover, other intrinsic factors might prove important in future studies. The range of years since wolf establishment is small in our data, as wolves were mainly captured soon (1.08 years (SD 1.5)) after establishment. This might have kept us from detecting an effect of this variable on inter-individual variation in wolf behavior towards human features. Furthermore, because wolves were often captured soon after establishment, the median pack size in our data is just four wolves, which may explain the lack of an effect of pack size in our study. Additionally, mortality and turnover rates are very high in Scandinavian wolves (Liberg et al., 2012; Milleret et al., 2017), which might hinder potential effects of these factors. Reproductive wolf pairs often travel together (Mech and Boitani, 2003) and therefore their movement relative to human features is not independent of each other, as illustrated by the overall consistent pattern of human avoidance. Our models showed a better fit using the wolf pair than the individual in the random structure for all the behaviors (Table S2). Moreover, our sex analyses did not reveal different behavior between male and female within the pack, even though the reproductive pair often travels separately during the lactating period. This is consistent with previous studies in the Scandinavian population (Milleret et al., 2017) and supports the notion that wolf pairs are the actual wolf social unit, rather than the individual per se (Mech and Boitani, 2003). Indeed, the loss of one of the breeders can affect the dynamic of the pack by lowering pup survival, leaving the territory, or dissolving the pack (Brainerd et al., 2008). This, in turn, may have counter-expected management consequences, such as increasing the number of packs in a given area (e.g., Fernández-Gil et al., 2016). This illustrates the crucial importance of targeting the right social unit when trying to disentangle the role of individual or group (pair, in our case) variation in solitary and group-living species, respectively.

Our study also illustrates how advanced ecological knowledge can inform conservation decisions. Seeing wolves or their tracks closer to human settlements in winter might be explained, for instance, by seasonal prey redistribution, but may be interpreted as the wolves losing their shyness or actively seeking human settlements. Therefore, possible measures to avoid this phenomenon could include the management of the prey (e.g., "hunting for fear") (Cromsigt et al., 2013), which in turn means managing the behavior of the wolf (Kuijper et al., 2019). Yet, to avoid conflict and help the conservation of the population, monitoring by responsible management agencies is advisable to be able to detect wildlife behaviors that depart from normality. The analytical approach used in this study provides a potential tool for such monitoring.

In this study, we attempted to identify and explain behavior of individual large carnivores that may depart from a general behavioral pattern, i.e., consistent avoidance of human features by wolves. Although external factors explained most of the individual (wolf pair) variation, our study focused on the behavior of established wolf pairs during travelling. Other patterns may emerge for dispersers, pups, or floating individuals. We suggest that discerning between circumstantial and actual "conflictive" behavior is important in order to prevent intrusive management actions such as lethal control of individuals that are perceived as "conflictive" because they, their tracks or other signs,

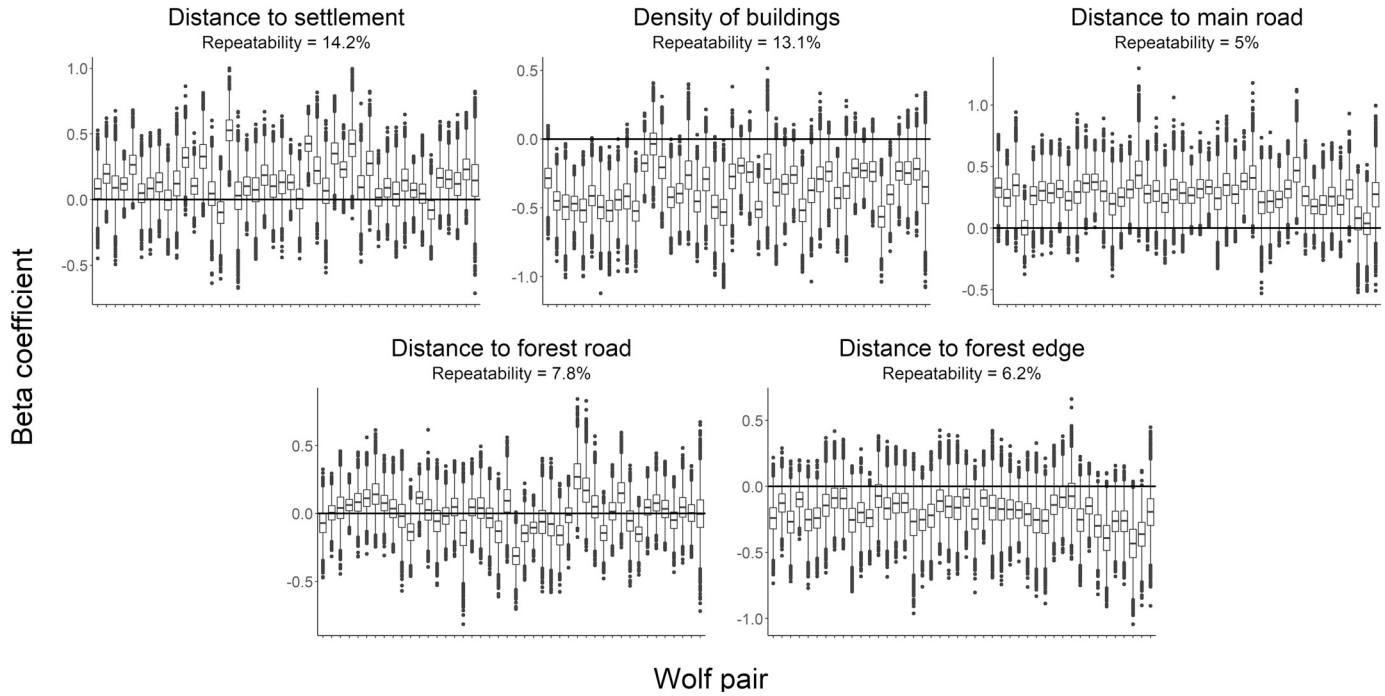

Fig. 3. Variation in the random intercepts and repeatability values after controlling for the fixed effect of each best model for the different selection coefficients explaining the variation of behavior in relation to anthropogenic features of the different wolf pairs in south-central Scandinavia (n = 44) from 2001 to 2017.

are occasionally seen near houses or settlements. Such actions might hamper conservation goals without being neither necessary nor successful at preventing the repetition of the same phenomenon. In this regard, scientific communication should help inform human attitudes and favor human coexistence with wildlife in general and with large carnivores in particular (Dressel et al., 2015; Treves et al., 2013). Reporting that wolves consistently avoided human features of the landscape at the fine scale of our study is a reassuring message for management agencies and the general public, particularly now that several large carnivores are recolonizing former ranges (Chapron et al., 2014).

CRediT authorship contribution statement

David Carricondo-Sanchez: Data curation, Formal analysis, Visualization, Writing - original draft, Writing - review & editing. **Barbara Zimmermann:** Conceptualization, Funding acquisition, Writing - review & editing. **Petter Wabakken:** Conceptualization, Funding acquisition, Writing - review & editing. **Ane Eriksen:** Conceptualization, Funding acquisition, Writing - review & editing. **Cyril Milleret:** Writing - review & editing. **Andrés Ordiz:** Writing - review & editing. **Ana Sanz-Perez:** Writing - review & editing. **Camilla Wikenros:** Conceptualization, Funding acquisition, Writing - review & editing.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Table 2
The mean posterior model coefficients and 95% credible intervals for the best ranking models according their WAIC explaining the variation in the selection coefficients of the different wolf pairs in south-central Scandinavia (n = 44) from 2001 to 2017. In brackets is the reference value of the factor variables.

	Distance to settlement	Density of buildings	Distance to main road	Distance to forest road	Distance to forest edge
Intercept	0.144 (0.073, 0.213)	−0.353 (−0.457, −0.252)	0.273 (0.174, 0.372)	−0.002 (−0.082, 0.077)	−0.196 (−0.314, −0.072)
Season (winter)		−0.17 (−0.28, −0.058)	−0.173 (−0.266,-0.081)	−0.099 (−0.167, −0.030)	0.029 (−0.105, 0.164)
Time (night)		0.033 (−0.072, 0.139)	−0.121 (−0.207,-0.038)	−0.194 (−0.255, −0.132)	−0.031 (−0.172, 0.107)
Latitude	−0.124 (−0.182, −0.066)	−0.02 (−0.102, 0.064)	−0.051 (−0.142, 0.041)	−0.030 (−0.078, 0.019)	
Luminosity	0.033 (−0.024, 0.091)	0.09 (−0.02, 0.2)	0.066 (−0.054, 0.185)	0.006 (−0.038, 0.053)	
Pack size	0.052 (−0.011, 0.116)	−0.08 (−0.165, 0.003)			
Years since establishment	−0.007 (−0.064, 0.049)	0.042 (−0.044, 0.127)			
Season ∗ time		0.117 (0.035, 0.195)			0.309 (0.132, 0.484)
Season ∗ latitude		−0.027 (−0.14, 0.083)	−0.081 (−0.179, 0.016)		
Season ∗ luminosity		0.146 (0.011, 0.278)	−0.134 (−0.261, −0.006)		
Season ∗ pack size		0.04 (−0.041, 0.123)			
Season ∗ years since establishment		0.016 (−0.071, 0.104)			

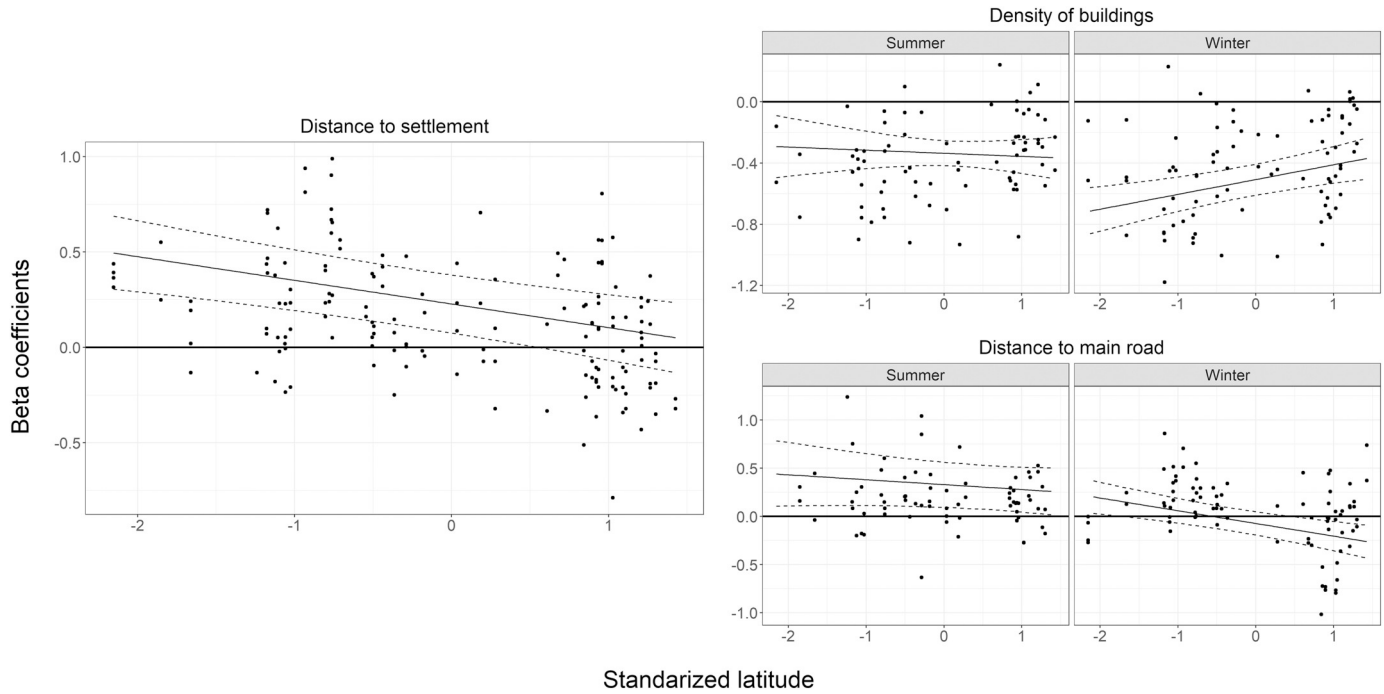

Fig. 4. Relationship with latitude in the models explaining the variation in the selection coefficients of the different wolf pairs in south-central Scandinavia (n = 44) from 2001 to 2017. Dots represent the different selection coefficients, thin solid lines show the mean posterior, dashed lines are 95% credible intervals, and the thick solid line represent the zero (no selection nor avoidance) coefficient. Positive latitude values indicate latitudes north from the average latitude in the study area and vice versa.

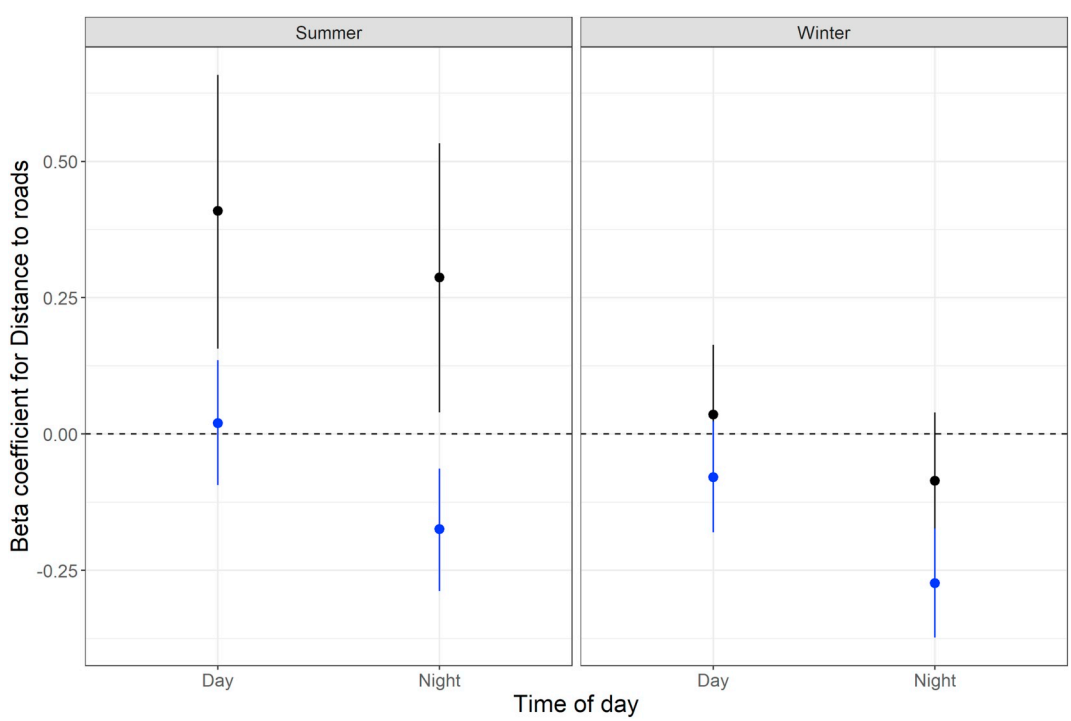

Fig. 5. Variation in the selection coefficients of wolf pairs (n = 44) in Scandinavia from 2001 to 2017 for distance to roads as a function of season, time of day and sex. Dots represent the mean posterior; lines are the range of the 95% credible intervals. Blue represent the coefficients for forest roads and black those for main roads. Note that positive values show avoidance (i.e., increasing distance to the road) whereas negative values show selection. (For interpretation of the references to color in this figure legend, the reader is referred to the web version of this article.)

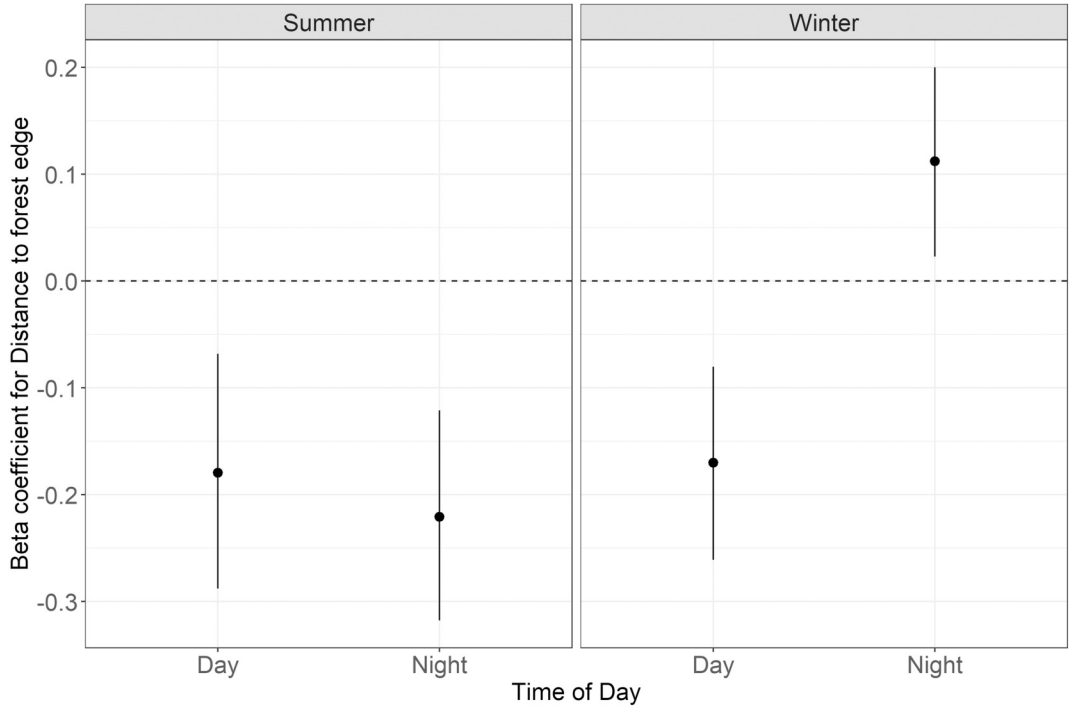

Fig. 6. Variation in the selection coefficients of wolf pairs (n = 44) in Scandinavia from 2001 to 2017 for distance to forest edge as a function of season and time of day. Dots represent the mean posterior and lines are the range of the 95% credible intervals. Note that positive values show movements towards the outside of forest patches, whereas negative values represent movements towards the inside of these patches.

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Data accessibility

Data is accessible via DataverseNO at https://doi.org/10.18710/QL1CTR.

Appendix A. Supplementary data

Supplementary data to this article can be found online at https://doi.org/10.1016/j.biocon.2020.108514.

References

Allen, A.M., Mansson, J., Sand, H., Malmsten, J., Ericsson, G., Singh, N.J., 2016. Scaling up movements: from individual space use to population patterns. Ecosphere 7.
Arnemo, J.M., Evans, A.L., 2017. In: Sciences, I. N. U. O. A. (Ed.), Biomedical Protocols for Free-ranging Brown Bears, Wolves, Wolverines and Lynx. Inland Norway University of Applied Sciences.
Beckmann, J.P., Berger, J., 2003. Rapid ecological and behavioural changes in carnivores: the responses of black bears (Ursus americanus) to altered food. J. Zool. 261, 207–212.
Beyer, H.L., 2015. Geospatial Modelling Environment (Version 0.7.4.0). URL: http://www.spatialecology.com/gme.
Boitani, L., 2003. Wolf conservation and recovery. In: Mech, D., Boitani, L. (Eds.), Wolves: Behaviour, Ecology and Conservation. The University of Chicago Press, United States of America, pp. 317–340.
Bombieri, G., Naves, J., Penteriani, V., Selvas, N., Fernandez-Gil, A., Lopez-Bao, J.V., ... Delgado, M.M., 2019. Brown bear attacks on humans: a worldwide perspective. Scientific Reports 9.
Brainerd, S.M., Andrén, H., Bangs, E.E., Bradley, E.H., Fontaine, J.A., Hall, W., ... Wydeven, A.P, 2008. The Effects of Breeder Loss on Wolves. The Journal of Wildlife Management 72 (1), 89–98. https://doi.org/10.2193/2006-305.
Bruskotter T, Jeremy, Shelby B, Lori, 2010. Human Dimensions of Large Carnivore Conservation and Management: Introduction to the Special Issue. Human Dimensions of Wildlife 15 (5), 311–314. https://doi.org/10.1080/10871209.2010.508068.
Carter, N.H., Shrestha, B.K., Karki, J.B., Pradhan, N.M.B., Liu, J.G., 2012. Coexistence between wildlife and humans at fine spatial scales. Proc. Natl. Acad. Sci. U. S. A. 109, 15360–15365.
Chapron, G., Kaczensky, P., Linnell, J.D.C., Von Arx, M., Huber, D., Andren, H., ... Boitani, L., 2014. Recovery of large carnivores in Europe's modern human-dominated landscapes. Science 346, 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.
Cromsigt, J.P.G.M., Kuijper, D.P.J., Adam, M., Beschta, R.L., Churski, M., Eycott, A., ... West, K., 2013. Hunting for fear: innovating management of human–wildlife conflicts. Journal of Applied Ecology 50 (3), 544–549. https://doi.org/10.1111/1365-2664.12076.
Darimont, C.T., Fox, C.H., Bryan, H.M., Reimchen, T.E., 2015. The unique ecology of human predators. Science 349 (6250), 858–860. https://doi.org/10.1126/science.aac4249.
Dettki, H., Ericsson, G., Giles, T., Norrsken-Ericsson, M., 2013. Wireless Remote Animal Monitoring (WRAM) — a new international database e-infrastructure for telemetry sensor data from fish and wildlife. In: The European Society Of Telemetry (Ed.), Proceedings Etc 2012: Convention for Telemetry, Test Instrumentation and Telecontrol. Books on Demand, pp. 247–256.
Dressel, S., Sandstrom, C., Ericsson, G., 2015. A meta-analysis of studies on attitudes toward bears and wolves across Europe 1976–2012. Conserv. Biol. 29, 565–574.
ESRI, 2009. ARCGIS Desktop. Environmental Systems Research Institute, Redland.
Evans, M.J., Hawley, J.E., Rego, P.W., Rittenhouse, T.A.G., 2019. Hourly movement decisions indicate how a large carnivore inhabits developed landscapes. Oecologia 190, 11–23.
Fernández-Gil, A., Naves, J., Ordiz, A., Quevedo, M., Revilla, E., Delibes, M., 2016. Conflict misleads large carnivore management and conservation: brown bears and wolves in Spain. PLoS One 11 (3), e0151541. https://doi.org/10.1371/journal.pone.0151541.
Filla, M., Premier, J., Magg, N., Dupke, C., Khorozyan, I., Waltert, M., Bufka, L., Heurich, M., 2017. Habitat selection by Eurasian lynx (Lynx lynx) is primarily driven by avoidance of human activity during day and prey availability during night. Ecol. Evol. 7, 6367–6381.
Frackowiak, W., Theuerkauf, J., Pirga, B., Gula, R., 2014. Brown bear habitat selection in relation to anthropogenic structures in the Bieszczady Mountains, Poland. Biologia 69, 926–930.
Gaynor, K.M., Hojnowski, C.E., Carter, N.H., Brashares, J.S., 2018. The influence of human disturbance on wildlife nocturnality. Science 360https://doi.org/10.1126/science.aar7121. (1232–+).

Gelman, A., Hill, J., 2007. Data Analysis Using Regression and Multilevel/Hierarchical Models. Cambridge University Press, Cambridge.
Gelman, A., Rubin, D., 1992. Inference from iterative simulation using multiple sequences. Stat. Sci. 7 (4), 457–472.
Greenberg, J.R., Holekamp, K.E., 2017. Human disturbance affects personality development in a wild carnivore. Anim. Behav. 132, 303–312.
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.
Hebblewhite, M., Merrill, E., 2008. Modelling wildlife-human relationships for social species with mixed-effects resource selection models. J. Appl. Ecol. 45, 834–844.
Johansen, B., 2009. Vegetasjonskart for Norge basert på Landsat TM/ETM+ data. Norut-Tromsø Rapport 4/2009 86 s.
Johansson, M., Flykt, A., Frank, J., Stoen, O.G., 2019. Controlled exposure reduces fear of brown bears. Hum. Dimens. Wildl. 24, 363–379.
Karlsson, J., Broseth, H., Sand, H., Andren, H., 2007. Predicting occurrence of wolf territories in Scandinavia. J. Zool. 272, 276–283.
Kojola, I., Hallikainen, V., Mikkola, K., Gurarie, E., Heikkinen, S., Kaartinen, S., Nikula, A., Nivala, V., 2016. Wolf visitations close to human residences in Finland: the role of age, residence density, and time of day. Biol. Conserv. 198, 9–14.
Kuijper, D.P.J., Churski, M., Trouwborst, A., Heurich, M., Smit, C., Kerley, G.I.H., Cromsigt, J., 2019. Keep the wolf from the door: how to conserve wolves in Europe's human-dominated landscapes? Biol. Conserv. 235, 102–111. https://doi.org/10.1016/j.biocon.2019.04.004.
Lesmerises, F., Dussault, C., St-Laurent, M.H., 2012. Wolf habitat selection is shaped by human activities in a highly managed boreal forest. For. Ecol. Manag. 276, 125–131.
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. Proc. R. Soc. B Biol. Sci. 279, 910–915.
Linnell, J.D., Solberg, E.J., Brainerd, S., Liberg, O., Sand, H., Wabakken, P., Kojola, I., 2003. Is the fear of wolves justified? A Fennoscandian perspective. Acta Zool. Litu. 13, 27–33.
Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R., Pedersen, H.C., 2013. Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia 173, 813–825.
McNay, M.E., 2002. Wolf-human interactions in Alaska and Canada: a review of the case history. Wildl. Soc. Bull. 30 (3), 831–843.
Mech, D., Boitani, L., 2003. Wolf social ecology. In: Mech, D., Boitani, L. (Eds.), Wolf: Behaviour, Ecology, and Conservation. The Chicago University Press, United States of America, pp. 1–34.
Milleret, C., Wabakken, P., Liberg, O., Akesson, M., Flagstad, O., Andreassen, H.P., Sand, H., 2017. Let's stay together? Intrinsic and extrinsic factors involved in pair bond dissolution in a recolonizing wolf population. J. Anim. Ecol. 86, 43–54.
Milleret, C., Ordiz, A., Sanz-Perez, A., Uzal, A., Carricondo-Sanchez, D., Eriksen, A., Sand, H., ... Zimmermann, B., 2019. Testing the influence of habitat experienced during the natal phase on habitat selection later in life in Scandinavian wolves. Scientific Reports 9.
Nakagawa, S., Schielzeth, H., 2010. Repeatability for Gaussian and non-Gaussian data: a practical guide for biologists. Biol. Rev. 85, 935–956.
Odden, M., Athreya, V., Rattan, S., Linnell, J.D., 2014. Adaptable neighbours: movement patterns of GPS-collared leopards in human dominated landscapes in India. PLoS One 9, e112044.
Ordiz, A., Stoen, O.G., Delibes, M., Swenson, J.E., 2011. Predators or prey? Spatio-temporal discrimination of human-derived risk by brown bears. Oecologia 166, 59–67.
Ordiz, A., Stoen, O.G., Saebo, S., Sahlen, V., Pedersen, B.E., Kindberg, J., Swenson, J.E., 2013. Lasting behavioural responses of brown bears to experimental encounters with humans. J. Appl. Ecol. 50, 306–314.
Ordiz, A., Milleret, C., Kindberg, J., Mansson, J., Wabakken, P., Swenson, J.E., Sand, H., 2015. Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. Ecosphere 6.
Ordiz, A., Moen, G.K., Saebo, S., Stenset, N., Swenson, J.E., Stoen, O.G., 2019. Habituation, sensitization, or consistent behavioral responses? Brown bear responses after repeated approaches by humans on foot. Biol. Conserv. 232, 228–237.
Person, D.K., Russell, A.L., 2008. Correlates of mortality in an exploited wolf population. J. Wildl. Manag. 72 (7), 1540–1549. https://doi.org/10.2193/2007-520.
Plummer, M., 2018. rjags: Bayesian graphical models using MCMC. R package version 4.8. https://CRAN.R-project.org/package=rjags.
R Core Team, 2018. R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria Retrieved from. https://www.R-proje. ct.org.
Rio-Maior, H., Nakamura, M., Alvares, F., Beja, P., 2019. Designing the landscape of coexistence: integrating risk avoidance, habitat selection and functional connectivity to inform large carnivore conservation. Biol. Conserv. 235, 178–188. https://doi.org/10.1016/j.biocon.2019.04.021.
Saetre, P., Strandberg, E., Sundgren, P.-E., Pettersson, U., Jazin, E., Bergström, T.F., 2006. The genetic contribution to canine personality. Genes Brain Behav. 5 (3), 240–248. https://doi.org/10.1111/j.1601-183X.2005.00155.x.
Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H., Pedersen, H.C., 2005. Using GPS technology and GIS cluster analyses to estimate kill rates in wolf—ungulate ecosystems. Wildl. Soc. Bull. 33 (3), 914–925. https://doi.org/10.2193/0091-7648(2005)33[914:ugtagc]2.0.co;2.
Sand, H., Eklund, A., Zimmermann, B., Wikenros, C., Wabakken, P., 2016. Prey selection of Scandinavian wolves: single large or several small? PLoS One 11, 17.
Sanz-Perez, A., Ordiz, A., Sand, H., Swenson, J.E., Wabakken, P., Wikenros, C., ... Milleret, C., 2018. No place like home? A test of the natal habitat-biased dispersal hypothesis in Scandinavian wolves. Royal Society Open Science 5.
Sazatornil, V., Rodriguez, A., Klaczek, M., Ahmadi, M., Alvares, F., Arthur, S., ... Lopez-Bao, J.V., 2016. The role of human-related risk in breeding site selection by wolves. Biological Conservation 201, 103–110. https://doi.org/10.1016/j.biocon.2016.06.022.
Singh, N.J., Borger, L., Dettki, H., Bunnefeld, N., Ericsson, G., 2012. From migration to nomadism: movement variability in a northern ungulate across its latitudinal range. Ecol. Appl. 22, 2007–2020.
Steyaert, S., Zedrosser, A., Elfstrom, M., Ordiz, A., Leclerc, M., Frank, S.C., Swenson, J.E., 2016. Ecological implications from spatial patterns in human-caused brown bear mortality. Wildl. Biol. 22 (4), 144–152. https://doi.org/10.2981/wlb.00165.
Stoen, O.G., Ordiz, A., Sahlen, V., Arnemo, J.M., Saebo, S., Mattsing, G., ... Swenson, J.E., 2018. Brown bear (Ursus arctos) attacks resulting in human casualties in Scandinavia 1977–2016; management implications and recommendations. Plos One 13 (5). https://doi.org/10.1371/journal.pone.0196876.
Theuerkauf, J., 2009. What drives wolves: fear or hunger? Humans, diet, climate and wolf activity patterns. Ethology 115, 649–657.
Torretta, E., Caviglia, L., Serafini, M., Meriggi, A., 2018. Wolf predation on wild ungulates: how slope and habitat cover influence the localization of kill sites. Curr. Zool. 64 (3), 271–275. https://doi.org/10.1093/cz/zox031.
Treves, A., Karanth, K.U., 2003. Human-carnivore conflict and perspectives on carnivore management worldwide. Conserv. Biol. 17, 1491–1499.
Treves, A., Jurewicz, R.R., Naughton-Treves, L., 2002. Wolf depredation on domestic animals in Wisconsin, 1976–2000. Wildl. Soc. Bull. 30, 231–241.
Treves, A., Wallace, R.B., White, S., 2009. Participatory planning of interventions to mitigate human-wildlife conflicts. Conserv. Biol. 23, 1577–1587.
Treves, A., Naughton-Treves, L., Shelley, V., 2013. Longitudinal analysis of attitudes toward wolves. Conserv. Biol. 27, 315–323.
Vehtari, A., Gelman, A., Gabry, J., 2016. Practical Bayesian Model Evaluation Using Leave-one-out Cross-validation and WAIC. arXiv:150704544v5 [statCO].
Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., ... Watson, J.E.M, 2016. Global terrestrial Human Footprint maps for 1993 and 2009. Sci. Data 3 (1), 160067. https://doi.org/10.1038/sdata.2016.67.
Wabakken, P., Sand, H., Liberg, O., Bjarvall, A., 2001. The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978–1998. Can. J. Zool. 79, 710–725.
Wabakken, P., Zimmermann, B., Eriksen, A., Maartmann, E., Nordli, K., Carricondo-Sanchez, D., Sand, H., Wikenros, C., 2019. Seasonal Conflicts Between Humans and Wolves in Areas With Snow and Seasonal Migrations of Moose: Wolves Within the Slettås Territory, 2009–2018 (in Norwegian). Skriftserien Inland Norway University, Elverum.
Wam, H.K., Eldegard, K., Hjeljord, O., 2014. Minor habituation to repeated experimental approaches in Scandinavian wolves. Eur. J. Wildl. Res. 60, 839–842.
Whittington, J., St Clair, C.C., Mercer, G., 2005. Spatial responses of wolves to roads and trails in mountain valleys. Ecol. Appl. 15, 543–553.
Wilmers, C.C., Wang, Y.W., Nickel, B., Houghtaling, P., Shakeri, Y., Allen, M.L., Kermish-Wells, J., Yovovich, V., Williams, T., 2013. Scale dependent behavioral responses to human development by a large predator, the Puma. PLoS One 8, 11.
Zimmermann, B., Nelson, L., Wabakken, P., Sand, H., Liberg, O., 2014. Behavioral responses of wolves to roads: scale-dependent ambivalence. Behav. Ecol. 25, 1353–1364.