

Is human infrastructure an acquired taste? Gray wolf habitat use before, during, and after dispersal

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1 Abstract

Natal dispersers are often thought to be “bolder” than their conspecifics. However, little is known about whether the act of dispersing itself influences the behavior of an animal. We analyzed 14 GPS-collared gray wolves (*Canis lupus*) in Finland that dispersed from their natal territories, focusing on their response to habitat features associated with human activity: primary roads, forest roads, and houses. We used resource and step selection analysis to quantify wolf response to these features at the home range scale and more local movement scale. At the home range scale, wolves settled in territories with far lower human presence than in otherwise accessible regions. At the finer scale, results contrasted. Wolves strongly avoided forest roads in their natal territories, but showed a marked increase in forest roads tolerance during dispersal and after settling. The trend in primary road and house selection was similar but muted: wolves became somewhat less sensitive to primary roads and houses as they transitioned into their new territories, but significantly avoided them across all stages of the dispersal process. These results suggest that wolves may acculturate to human habitat elements as they disperse. In particular, forest roads – which are low-use and can provide useful corridors facilitating long distance movement – might be learned in the process of navigating unfamiliar terrain. This study highlights the point that dispersal is not an isolated event, but rather an extended process during which behaviors can change in response to new experiences.

2 Keywords

Canis lupus; behavior; GPS telemetry; step selection; roads; houses

3 Introduction

Dispersal from natal ranges is essential to the survival of many species as it reduces kin competition, alleviates resource scarcity, and decreases the likelihood of inbreeding (Bowler and Benton, 2005; Clobert et al., 2009). Dispersal is also an important mechanism for recolonization and range expansion, and therefore a crucial process to understand in many conservation efforts (Woodroffe, 2003). The decision-making processes that underlie dispersal are complex and poorly understood (Matthysen, 2012). Most empirical studies of dispersal behavior have focused on arthropods and other animals that disperse over short distances (e.g., Doukas and Payne, 2007; Johns and Eveleigh, 2013; Ramalho et al., 2014). The behavioral processes of large dispersing mammals are more difficult to study. The major limitation of GPS telemetry to studies of large animal dispersal is that in most populations relatively few individuals disperse, and tagging efforts have to be sufficiently intense to monitor the movements of the few individuals that do disperse.

The gray wolf (*Canis lupus*) is an excellent model species for the study of dispersal (Ciucci et al., 2009). Although there is considerable variability in wolf social behavior, the general pattern of dispersal is that younger, non-breeding adults leave their natal pack to seek out a mate and establish a new breeding territory elsewhere (Mech and Boitani, 2003). Several studies have investigated wolf dispersal through radiotelemetry (Van Camp and Gluckie, 1979; Fritts and Mech, 1981; Ballard et al., 1983; Fritts, 1983; Peterson et al., 1984; Ballard et al., 1987; Mech, 1987; Fuller, 1989; Gese and Mech, 1991; Mech et al., 1995; Boyd and Pletscher, 1999), and GPS tracking (Kojola et al., 2006; Wabakken et al., 2007; Ciucci et al., 2009; Kojola et al., 2009; Razen et al., 2016; Jimenez et al., 2017). These studies have been essentially descriptive, reporting in detail on the routes of individuals. Broadly, the data confirm that wolves are excellent dispersers, with trajectories routinely hundreds of km in linear distance or, in exceptional cases, more than 1000 km (Wabakken et al., 2007).

Understanding wolf behavior during dispersal is an important goal, particularly in places with a significant human presence. Within a territory, wolves move in a defined area, typically with other adults. In contrast, while dispersing, wolves navigate an unknown environment, usually alone or with a prospective mate, with the sole behavioral imperative of finding a new suitable territory to occupy (Mech and Boitani, 2003). The possibility that dispersing wolves engage in bolder behavior during dispersal, such as approaching houses, crossing roads, depredating livestock, and attacking household pets, is of great interest to managers (Kojola et al., 2016). From a behavioral ecology perspective, contrasting behaviors during the dispersal period and in the natal territory can serve as a natural experiment for inferring

processes of spatial memory (Fagan et al., 2013). We examine wolf dispersal behavior through the lens of wolf response to human infrastructure during dispersal.

Wolf response to human infrastructure is nuanced and largely depends on the spatial scale of selection under consideration (Zimmermann et al., 2014). The *secondary level of selection* refers to selection of a home range within a geographical region, and the *tertiary level of selection* refers to use of available resources at more local movement scale (Johnson, 1980). In the case of wolves, secondary selection refers to the selection of a territory, and tertiary selection refers to the selection of habitat elements within a territory or during dispersal. At the secondary level, wolves prefer territories with few houses, roads, agricultural fields, and people (Mladenoff et al., 1995; Kaartinen et al., 2005; Karlsson et al., 2007; Kaartinen and Antikainen, 2015). Similarly, at the tertiary level, wolves exhibit an aversion toward primary (high-use) roads, houses, and agricultural fields (Kaartinen et al., 2005; Gurarie et al., 2011; Kaartinen et al., 2010). Wolf response toward forest (low-use) roads at the tertiary level is more ambiguous. Some studies (Fritts, 2003; Gurarie et al., 2011) indicate that wolves may use low-use forest roads to facilitate intra-territorial travel, while others studies suggest a general aversion to forest roads as well (Kaartinen et al., 2005).

In this study, we investigate wolf avoidance of roads and houses, comparing behavior across the *movement phases* of natal territory, dispersal, and new territory. We analyze the well-studied Finnish population of GPS-tracked wolves, of which over twenty have dispersed between 2002 and 2013. As with many European and North American wolf populations, wolves in Finland were extirpated in the early twentieth century (Pullianen, 1993). Due to increased legal protection, the population began to rebound in the 1990s (Bisi et al., 2007; Kojola et al., 2014) but has fluctuated in response to different levels of protection and poaching intensity (Jansson et al., 2012). At present, there are about 200 - 235 wolves in Finland (Suutarinen & Kojola, unpublished data). The core of the wolf population resides in eastern Finland near the Russian border. In recent decades dispersing wolves have expanded the population into more densely populated central and southwestern Finland (Kojola et al., 2006, 2009).

In this study we ask four questions: (i) Are new territories more human-impacted than natal territories? (ii) Does average movement speed differ between movement phases? (iii) Does selection of a new territory reflect an avoidance of human presence? (iv) How does avoidance of human habitat features change as a wolf transitions from its natal territory via dispersal to a new territory? In all cases, we use primary roads, forest roads, and houses as proxies for human presence and impact.

4 Materials and methods

4.1 Study Area

The study area (210,000 km²) consisted of all of mainland Finland excluding the reindeer management area (RMA), within which wolves have no legal protection and can not establish territories (Figure 1). Most of the study area belongs to the boreal forest zone, while the southernmost areas are an intermediate between the boreal forest and temperate forest zones. The dominant tree species are Scots pine (*Pinus sylvestris*), spruce (*Picea abies*), and birch (genus *Betula*), which constitute 65%, 23%, and 9% of forest cover, respectively (Kaartinen and Antikainen, 2015). Lakes and other water bodies are common and make up approximately 12% of the land cover. Moose (*Alces alces*), which are present at low densities throughout Finland, is the primary species of wolf prey in the study area. The core range of the Finnish wolf population is in the central eastern part of Finland mainly in the administrative regions of Kainuu, Karelia and Northern Savonia. The mean density of humans in the core range is (5 people km⁻²) is less than the mean density of humans in Finland (17 people km⁻²) (Kaartinen et al., 2005).

4.2 Movement data

A total of 58 wolves were captured and collared in late winter or early spring from 2002 to 2013. Individuals were looped from a snowmobile or darted from a helicopter. Details of the capture and immobilization procedure are given elsewhere (see, e.g., Kojola et al., 2006). The wolves were equipped with collars that contained global positioning system receivers (GPS Plus 2, Vectronic Aerospace GmbH, Berlin, Germany) and Very High Frequency (VHF) radio beacon transmitters (Televilt, Lindesberg, Sweden). The collars transmitted locations every two or four hours, with a few exceptions at higher frequencies.

4.3 Ancillary data

4.3.1 Digiroad

Road data were obtained from the Digiroad database provided by the Finnish Transportation Agency (version 02/2016). Digiroad contains the geometry and attribute data of the streets, paths, and trails of Finland. Roads are classified into one of following eight functional classes, listed in decreasing order of importance to traffic: Class I Main Road, Class II Main Road, Regional Road, Connecting Road, Class I Private Road, Class II Private Road, Forest Road,

and Pedestrian Path. We pooled the first five classes and defined them as *primary roads*, and we pooled the sixth and seventh classes and defined them as *forest roads*. Pedestrian Paths were not used because they are fairly uncommon and unimportant to the population under study. This pooling procedure was based on visual inspection of the Digiroad data and is consistent with the scheme used by Gurarie et al. (2011).

4.3.2 CORINE 2006

House and water data were obtained from the European Environmental Agency’s CORINE 2006 land cover database (CLC 2006). The CORINE database categorizes European land cover on the basis of automated interpretation of satellite images. The data on Finland were delivered in raster format at a resolution of 25 m², with each cell classified into one of 44 different land classes (LC). Five land classes constituted more than 70% of the 100% MCP of all wolf locations: complex cultivation patterns (LC 2.4.2; 29.1%), estuaries (LC 5.2.2; 12.8%), land principally occupied by agriculture, with significant areas of natural vegetation (LC 2.4.3; 11.7%), broad-leaved forest (LC 3.1.1; 8.8%), and transitional woodland-shrub (LC 3.2.4; 7.9%). We defined continuous urban fabric, discontinuous urban fabric, and industrial or commercial units (LC 1.2.1 - 1.2.3) as *houses*, and we defined watercourses, water bodies, coastal lagoons, estuaries, seas and oceans (LC 5.1.1, 5.1.2, 5.2.1 - 5.2.3) as *water*.

4.4 Processing

4.4.1 Selection of Wolves

A *territory* was defined as a set of tortuous, encamped movements, and a *dispersal event* was defined as a set of migratory, directed movements between territories. A supervised, continuous-time stochastic process algorithm helped identify all territories and dispersal events present in the data (see Appendix). Among the 58 wolves that were captured and collared, not all dispersed. Moreover, among the wolves that dispersed, not all were tracked for the entirety of the dispersal process. Only wolves with data available across all three movement phases (natal territory, dispersal, new territory) were selected for use in the analysis. In total, 44 wolves were excluded due to one of the following reasons: no observed natal territory, no observed dispersal, no observed new territory, unclear distinction between territory and dispersal, excessive points in Russia, or missing data. The final dataset contained 14 separate natal territories, 23 separate dispersal events, and 22 separate new territories. (See Appendix for plots of relevant movement tracks color-coded by movement phase.)

4.4.2 Filtering of Data

We passed the location data through three distinct, increasingly refined filters. First, we eliminated all locations outside Finland because road and house data were not available outside Finland. This resulted in the exclusion of 7.6% of all locations.

Second, we removed clustered locations under the assumption that remaining locations would correspond to traveling movements (Gurarie et al., 2011; Killeen et al., 2014; Dickie et al., 2017). Step speeds (defined as distance between consecutive locations divided by elapsed time) were calculated for each wolf, pooled, and then log-transformed. Kernel density estimation was used to approximate the underlying distribution of the log-transformed speeds, and a clear bimodal distribution resulted (default bandwidth of 0.268 m/h used). The local minimum corresponded to a critical speed of 35.9 m/h, which we took to be the threshold of active movement. We removed all displacements below this threshold, amounting to 37.5% of all observations.

Third, we removed all “forays” from the location data. A *foray* is a “trial” dispersal, or a short, exploratory, extraterritorial trip taken by a wolf before actually dispersing (Mech and Boitani, 2003). Forays were identified manually. Although behaviorally interesting, the forays of four wolves (Huli, Milo, Mino, and Rilla) were eliminated to more clearly separate territorial and dispersive behaviors.

4.4.3 Territory Null Set

We constructed a null set of non-territory areas from central and southern Finland to assess secondary selection of new territories. We determined dispersal distance (defined as the distance between the centroids of natal territories and new territories), direction, and starting location for each wolf. For those wolves with multiple new territories ($n = 5$), the final such territory was used. We randomly drew one value from each of the observed datasets for dispersal distance, direction, and starting location to obtain a set of quantities that represented a pseudo-dispersal event. We then centered a circle with area 986 km² (mean area of new territories) at the endpoint of the pseudo-dispersal event to create a null territory. We repeated this process until we obtained 14 null territories outside the reindeer management area that did not overlap with each other or with observed territories (Figure 1). In the end, this procedure led to a set of null territories similar to that used by Kaartinen and Antikainen (2015), who randomly sampled circles from all of Finland south of the reindeer management area. However, our approach has the advantage of being grounded in the empirical data on dispersal distance, direction, and starting location.

4.4.4 Movement Null Set

We generated a null set of pseudo-absences to compare selection of roads and houses at the tertiary level of selection across areas of variable road and house density. For each observed location, we generated 30 potential movement steps (where a step was defined as the vector connecting consecutive locations) by first drawing randomly from a distribution of vectors that actually occurred over a four hour time period, and then adding these sampled vectors to the observed location (similar to, e.g., [Gurarie et al., 2011](#); [Killeen et al., 2014](#)). Points in water and outside Finland were excluded from the null set because wolves typically cannot traverse water ([Kojola et al., 2009](#)) and human infrastructure data were unavailable outside Finland. Pseudo-absences reflect where a wolf *could* have moved given its previous position. The null set allows for the analysis of habitat use via the step selection function. Figure 2 displays the null set constructed for the dispersal event of a wolf.

4.5 Statistical methods

Our statistical analyses separately addressed four distinct questions.

4.5.1 Question 1: Are new territories more human-impacted than natal territories?

We conducted three separate paired t-tests to compare primary road, forest road, and house density across natal and new territories. For wolves with multiple new territories, only road and house densities obtained from the final such territory were used in the t-test.

Road density for a given territory was defined as total road length divided by territory area (km/km^2). House density was defined as the total surface area of raster pixels corresponding to “houses” in the CORINE database divided by territory area (m/km^2). Given the resolution of the CORINE raster was 25 m^2 and the average floor area of a Finnish dwelling in 2008 was 79 m^2 , roughly 3-4 pixels represent a single house ([Statistics Finland, 2008](#)).

4.5.2 Question 2: Do wolves move faster during dispersal than in their natal and new territories?

Movement speed was calculated by computing the distance between two consecutive locations and then dividing by the time elapsed between those locations (m/h). To assess the effect of movement phase (i.e., natal territory, dispersal period, new territory) on movement speed, we constructed a mixed effects linear model wherein movement speed was the response,

movement phase was a fixed effect, and individual wolf was a random intercept. The *natal territory* movement phase was set as the reference category in the model. We assessed whether movement phases differed significantly by examining the 95% CI of mean movement speed for each phase: movement phases whose 95% CIs did *not* overlap were considered to differ significantly, while movement phases whose 95% CIs did overlap were *not* considered to differ significantly (at the $\alpha = 0.05$ level).

4.5.3 Question 3: Does selection of a new territory reflect an avoidance of human presence?

To determine whether wolves avoided human infrastructure when settling in a new territory, we compared new territories to null territories using logistic regression. For wolves with multiple new territories, only road and house densities obtained from the final such territory were used in this analysis. Null territories ($n = 14$) were constructed in accordance with the section “Territory null sets” (4.4.3). The predictor variables used in the logistic regression model were primary road, forest road, and house density (defined as above), and the binary response variable was territory presence or absence. All possible univariate ($n = 3$) and bivariate ($n = 3$) models were fitted and analyzed.

4.5.4 Question 4: Does avoidance of human habitat features change as a wolf transitions from its natal territory via dispersal to a new territory?

We used step selection functions (SSFs) to analyze wolf habitat use at the tertiary level of selection (Thurfjell et al., 2014). Historically, researchers have used the resource selection function (RSF) to quantify animal habitat use. RSFs contrast observed (or “used”) locations to random (or “available”) locations, allowing for the inference of habitat use from movement data. Typically, available locations are drawn randomly from some subset of the study area, such as an animal’s home range. RSFs are generally fitted using unconditional (or classical) logistic regression (Duchesne et al., 2010). More recently, researchers have used SSFs to quantify habitat use. An SSF is an RSF wherein each used location is matched with a set of random locations that represent where an animal *could* have traveled given its previous position. SSFs better model the habitat use of moving animals (Thurfjell et al., 2014), and allow for the analysis of habitat use by animals that do not have clearly defined home ranges (e.g., dispersers) (Duchesne et al., 2010). SSFs can be estimated using conditional logistic regression.

We used a standard step selection function of the form

$$w(\mathbf{x}) = \exp \left(\sum_{i=1}^n \beta_i x_i \right),$$

where $\mathbf{x} = (x_1, x_2, \dots, x_n)^T$ is a vector of habitat covariates, $\beta_1, \beta_2, \dots, \beta_n$ are coefficients to be estimated using conditional logistic regression, and w is an SSF score related to the odds that an animal will take the given step (Fortin et al., 2005). Because wolves exhibit variability in habitat use (Kojola et al., 2016), it was necessary for us to account for individual-level variation. To this end, we fitted a mixed conditional logistic regression model to the data, using individual wolf as a random factor. Mixed conditional logistic regression models can be challenging to estimate. To fit our model, we used a two step procedure. First, we fitted (fixed) conditional logistic regression models to each animal separately. Then, we used the EM algorithm in conjunction with restricted maximum likelihood estimation obtain population-level estimates of the parameters in the model by pooling together the individual-level estimates. This procedure produces consistent and stable estimates of the model parameters when the number of observed locations is large (as was the case with our data) (Craiu et al., 2011), and accounts for within-individual correlation (Fieberg et al., 2010). We used version 1.2.5 of the R package `TwoStepCLogit` to carry out this analysis (Craiu et al., 2011).

We constructed a separate SSF model for each movement phase (i.e., natal territory, dispersal period, new territory). Response variables were “use” (coded by 1) and “available” (coded by 0); “available” locations were obtained in accordance with section 4.4.4 (“Movement null set”). The predictor variables were distance to primary roads, distance to forest roads, and distance to houses, all of which were log-transformed and then multiplied by -1. We log-transformed distances to model the likely attenuation in space of a wolf’s response to human habitat elements, and to reduce the effect of large tails. We multiplied by -1 so that positive regression coefficients would reflect preference, and negative regression coefficients would reflect avoidance. (Note that multiplication by -1 changes the sign, but not magnitude, of a regression coefficient.) Additionally, we normalized each variable by subtracting the mean value and dividing by standard deviation to facilitate comparisons between variables. Due to a high correlation between houses and forest roads, ($r = 0.65$), we fitted univariate models only. A regression coefficient was considered to differ significantly from 0 if it deviated from 0 by more than two standard errors.

We refer to the coefficients of the mixed conditional logistic regression model as “selection coefficients” because they reflect the extent to which wolves selected different habitat elements. Moreover, we say the wolves “avoided” a habitat element if the corresponding selection coefficient was significantly less than 0; “preferred” a habitat element if the corre-

sponding selection coefficient was significantly greater than 0; and were “neutral” toward a habitat element if the corresponding selection coefficient did not significantly differ from 0.

4.6 Software

All programming was done in the language R (R Core Team, 2016). Packages used for statistics were `stats`, `lme4`, `TwoStepCLogit` (R Core Team, 2016; Bates et al., 2015; Craiu et al., 2011). The packages `spatstat`, `rgeos`, `rgdal`, `sp`, `splancs`, `adehabitatHR`, `maptools`, and `raster` were used in data processing (Baddeley et al., 2015; Bivand and Rundel, 2016; Bivand et al., 2016; Pebesma and Bivand, 2005; Bivand et al., 2015; Calenge, 2006; Bivand and Lewin-Koh, 2016; Hijmans, 2015).

5 Results

5.1 Summary statistics

The number (and type) of movement phases observed for each wolf differed due to variations in behavior and tracking duration. Every wolf (by design) had an observed natal territory, dispersal event, and new territory. Several wolves had more than one observed new territory, and one wolf (Herkules) had four observed new territories. Eleven (78.6%) wolves were male and three (21.4%) were female. The mean number of observed territories and dispersals per wolf was 2.6 and 1.6, respectively. Mean dispersal departure date was May 17 (min = March 17, median = May 4, max = October 31), mean dispersal distance averaged across each wolf was 162.4 km (median = 147.0 km, IQR = 71.5 km, sd = 63.8 km), and mean dispersal duration averaged across each wolf was 23.5 days (median = 19.5 days, IQR = 26.0 days, sd = 17.5 days). Descriptive statistics are summarized in table 1.

5.2 Answer to question 1: Are new territories more human-impacted than natal territories?

Primary road density and house density differed significantly between natal ($\bar{x} = 0.077$, sd = 0.071; $\bar{x} = 101.8$, sd = 131.1) and new ($\bar{x} = 0.21$, sd = 0.11; $\bar{x} = 378.3$, sd = 276.1) territories ($t_{13} = 4.92$, $P = 0.0003$; $t_{13} = 3.57$, $P = 0.0034$). Forest road density, on the other hand, did not significantly differ between natal ($\bar{x} = 1.46$, sd = 0.30) and new ($\bar{x} = 1.54$, sd = 0.48) territories ($t_{13} = 0.53$, $P = 0.607$). These results suggest that, overall, wolves moved

into more human-impacted areas as they transitioned from natal to new territories (figure 3).

5.3 Answer to question 2: Do wolves move faster during dispersal than in their natal and new territories?

Mean movement speed was greatest during the dispersal period ($\bar{x} = 941$, CI lower bound = 849, CI upper bound = 1,032), second greatest in the new territory ($\bar{x} = 673$; CI lower bound = 589, CI upper bound = 757), and least in the natal territory ($\bar{x} = 423$; CI lower bound = 336, CI upper bound = 510). All movement phases differed significantly from one another pairwise (figure 4).

5.4 Answer to question 3: Does selection of a new territory reflect an avoidance of human presence?

Primary road, forest road, and house densities were higher in null ($\bar{x} = 0.42$, sd = 0.21; $\bar{x} = 2.10$, sd = 0.42; $\bar{x} = 989.4$, sd = 594.4) territories than in new ($\bar{x} = 0.21$, sd = 0.11; $\bar{x} = 1.54$, sd = 0.49; $\bar{x} = 378.3$, sd = 276.1) territories (figure 3). House density was the best single-variable predictor for territory presence or absence, followed by primary road density and forest road density (table 2). The Pearson correlation coefficients between primary road and forest road density, primary road and house density, and forest road and house density were $r = 0.65$, $r = 0.98$, and $r = 0.65$, respectively. In general, the bivariate models were inferior to the univariate models in predicting territory presence or absence (as quantified by AIC_c). This was due to multicollinearity among the predictor variables. These results suggest that wolves avoided human infrastructure when selecting a new territory.

5.5 Answer to question 4: Does avoidance of human habitat features change as a wolf transitions from its natal territory via dispersal to a new territory?

The selection coefficient corresponding to primary roads increased from natal territory ($\beta = -0.56$) to dispersal ($\beta = -0.41$) to new territory ($\beta = -0.29$), reflecting an increase in tolerance for primary roads over time. Despite this trend, wolves avoided primary roads across all movement phases.

The selection coefficient corresponding to forest roads was greatest in the new territory

($\beta = -0.004$), second greatest during the dispersal period ($\beta = -0.047$), and least in the natal territory ($\beta = -0.27$). Wolves avoided forest roads in the natal territory, and were neutral to forest roads during the dispersal period and in the new territory.

The selection coefficient corresponding to houses was greatest during the dispersal period ($\beta = -0.33$) and new territory ($\beta = -0.32$), and was least in the natal territory ($\beta = -0.49$). As with primary roads, wolves avoided houses across all movement phases. Results of this analysis are displayed in figure 5.

6 Discussion

Wolves are broadly sympatric with humans and must necessarily navigate the near ubiquitous influence of humans on their habitat. This is particularly true as wolf populations increase and expand in parts of their range in Europe and North America. Generally, wolves avoid humans due to historical and current persecution as well as large-scale anthropogenic habitat loss (Gangaas et al., 2013; Ripple et al., 2014; Sazatornil et al., 2016). Notably, wolves exhibit a fairly consistent aversion to roads and houses, key proxies of human presence (Person and Russell, 2008; Kojola et al., 2016). On the other hand, certain human landscape elements can appeal to wolves. For example, low-use roads facilitate travel by serving as linear corridors (Musiani et al., 1998; Zimmermann et al., 2014; Dickie et al., 2017) and can augment kill rates by increasing the frequency of encounters with prey (James and Stuart-Smith, 2000; Whittington et al., 2011). Human settlements are sometimes associated with the presence of livestock and dogs which are occasional targets of wolf depredation (Kaartinen et al., 2009; Kojola et al., 2016).

Earlier analyses suggest that time of day, season, spatial scale, infrastructure type (e.g., primary road, forest road, trail, house), breeding status, and age influence the probability of Fennoscandian wolves interacting with human habitat elements (Gurarie et al., 2011; Zimmermann et al., 2014; Kojola et al., 2016). Our study provides several new insights by exploring wolf response to human habitat elements specifically in the context of dispersal and settlement. This is, to the best of our knowledge, the second study to analyze the time-evolution of habitat use by a dispersing mammal using GPS telemetry (the first being Killeen et al., 2014), and the first to do so with a carnivore.

6.1 Characteristics of new territories (secondary selection)

As they dispersed from their core range in eastern Finland into central and southern Finland, wolves established territories in more human-impacted areas. Northward dispersal is limited by liberal hunting license policies in the reindeer management area (RMA), while eastward dispersal into Russia, which also occurs (Kojola et al., 2006), was outside of our study area. This general trend of movement into more human-impacted areas mirrors that observed elsewhere in Europe and in North America, where wolves are currently expanding their populations.

We distinguished wolf habitat use at the secondary level (i.e. selection of a new territory out of the available range in southern Finland) and the tertiary level (i.e. selection of habitat components within a territory or while dispersing). At the secondary level, wolves avoided all human habitat elements when settling in new territories, demonstrating a particularly strong preference for territorial areas with lower house densities than expected by randomness. In general, new territories were established far from population centers, with the exception of one territory (belonging to the wolf Ursa), which was established within 65 km of the city of Tampere. A cluster of new territories was located in the Suomenselkä region of Finland, a drainage divide parallel to the Gulf of Bothnia coast with relatively low human densities and disturbance. Two others were in the eastern portion of Finland somewhat south of the core range. The core lake area of Finland is not preferred by wolves, but many navigated it during dispersal before settling down elsewhere.

Wolves were largely successful at finding suitable locations within the available area of Finland, at least with respect to human densities. This successful large-scale selection occurred despite the relatively small area “sampled” by the wolf during dispersal. An exploration of the cognitive mechanisms that lead to a successful dispersal (such as spatial memory, acquisition of non-local information, and a giving-up strategy) is a topic of future work.

Wolf avoidance of humans and human activity at the secondary level of selection is well-established (Mladenoff et al., 1995; Kaartinen et al., 2005; Karlsson et al., 2007; Jędrzejewski et al., 2008; Kaartinen and Antikainen, 2015). Our results, however, strengthen these conclusions by focusing on the mechanism by which individual wolves actually select their new territories. It should be noted that, in generating random null territories, we excluded locations in the mostly rural reindeer management area. Wolves cannot establish and maintain long-term territories in the RMA because they are not legally protected in this region (Kaartinen et al., 2005). Three observed, new territories overlapped at least partially with the RMA, and so the null set may not have completely captured areas that are available

for settlement. We ran a second analysis in which randomized, null territories were not restricted to the RMA; the results were very similar, though slightly weaker.

6.2 Patterns of avoidance of human habitat elements (tertiary selection)

In addition to analyzing habitat selection at the secondary scale, we investigated habitat selection at the finer tertiary scale. The patterns in forest road use were the most striking of the three variables we explored. Wolves clearly used forest roads much less than expected based on availability while in the natal territory. This probably reflects the general tendency of wolves to avoid encounters with humans and human habitat impacts (Kaartinen et al., 2005). Forest road use, however, increased markedly from natal territory to dispersal: while wolves avoided forest roads in the natal territory, they exhibited neutrality toward forest roads during dispersal. This shift in preference is a result of the increased importance of travel efficiency during dispersal. By exploiting forest roads, wolves were able to move their landscape rapidly (Dickie et al., 2017) and quickly find a new territory. The wolves in our study traveled about twice as fast, on average, during the dispersal period than in the natal territory.

Surprisingly, wolves continued to use forest roads at a heightened level in the new territory. In fact, the selection coefficient corresponding to forest road use was slightly greater in the new territory than it was during dispersal. One possible explanation for this result is that wolves learned to use forest roads while navigating an unfamiliar terrain during dispersal, and then subsequently used forest at a heightened level after settling. If this is the case, forest roads can be thought of as an “acquired taste” in the sense that they reflect the spatial memories wolves gained as they dispersed (Fagan et al., 2013). Another possibility is that wolves used forest roads to hasten the process of establishing a new territory. Wolf movement speeds in the new territory, while lower than those during dispersal, were greater than those in the natal territory. Regardless of the exact cause of the observed increase in forest road selection, these results highlight the fact that habitat preferences are not static, but rather dynamic and responsive to new experiences.

Primary roads typically have higher levels of traffic and human density than forest roads (Whittington et al., 2005; Gurarie et al., 2011) and may serve as barriers to dispersal (Beyer et al., 2016), so it is unsurprising that wolves strongly avoided primary roads across all movement phases. That said, tolerance for primary roads did gradually increase from natal territory to dispersal to new territory. This is likely explained by the relative difficulty of

avoiding large roads and highways during dispersal, when, among other constraints, wolves are naive about their habitats. The strong primary road avoidance that is learned in the natal territory may be diluted by the experience of a successful dispersal, leading individuals to be less road-wary in the new territory.

Wolves in Finland display a strong aversion houses and other human settlements (Kaartinen et al., 2005; Kojola et al., 2016). Our results confirm that wolves avoid houses across all movement phases of the dispersal process. Interestingly, wolves displayed a somewhat greater tolerance for houses during the dispersal period and in the new territory than in the natal territory. This is likely a result of the fact that houses correlate strongly with primary roads in Finland.

6.3 Implications for recovery and management

As wolf populations recover and expand into areas in which humans have increased their footprint, wolf-human interactions necessarily become more common. Surveys indicate that public attitudes in Europe toward wolves have become less positive over the past 40 years (Dressel et al., 2015). Wolf-human conflicts, such as wolf attacks on livestock and household dogs, are most likely responsible for such changes (Kaartinen et al., 2009; Dressel et al., 2015; Kojola et al., 2016). An important question is whether individual wolves become less-risk averse as they disperse into more populous areas. Dispersers undergo a significant perturbation to the customary territorial patterns of predation and patrolling in a well-defined and well-known area. Because dispersing wolves are typically younger, always naive to their new environment, and often travel alone or with a single other companion, their behaviors during and after dispersal may be more daring.

Our results indicate that wolf avoidance of human habitat features, especially forest roads, dulled in response to dispersal. This, combined with the higher baseline density of human habitat elements in new territories, implies wolf-human interactions will be more frequent in new territories than in natal territories. That said, wolf aversion toward primary roads and houses – the habitat elements most closely associated with human presence among those that we investigated – remained fairly strong in the new territory. All wolves except one maintained a distance farther away from houses and primary roads than expected by randomness after settling. Thus, while wolves may be somewhat “desensitized” after dispersing, they are still basically human-shy.

6.4 Conclusion

Dispersal is a crucial event in the life of an individual, and of fundamental importance to the persistence of species in changing, fragmented environments (Woodroffe, 2003; Clobert et al., 2009). The detailed processes at play during dispersal are not well understood, especially among large mammals. Our results suggest that wolves generally avoid human infrastructure across the various stages of dispersal and spatial scales of selection. However, wolves appear to exhibit an especially high tolerance for forest roads during dispersal and in their post-dispersal territories. These results highlight the fact that dispersal is not simply a “one-off” event in an animal’s life, but rather a complex process that can influence subsequent behaviors. We believe that future research into the decision-making processes of dispersing wolves, as well as other carnivores, is warranted.

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8 Compliance with ethical standards

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8.2 Conflict of interest

The authors declare that they have no conflict of interest.

8.3 Ethical approval

Capture, handling, and anesthetizing of the wolves met the guidelines issued by the Animal Care and Use Committee at the University of Oulu and permits provided by the provincial government of Oulu (OLH-01951/Ym-23).

9 Supplementary material

The supplementary material consists of a single appendix. The authors will supply the data required to replicate these analyses upon acceptance of the manuscript.

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10 Figures and figure legends

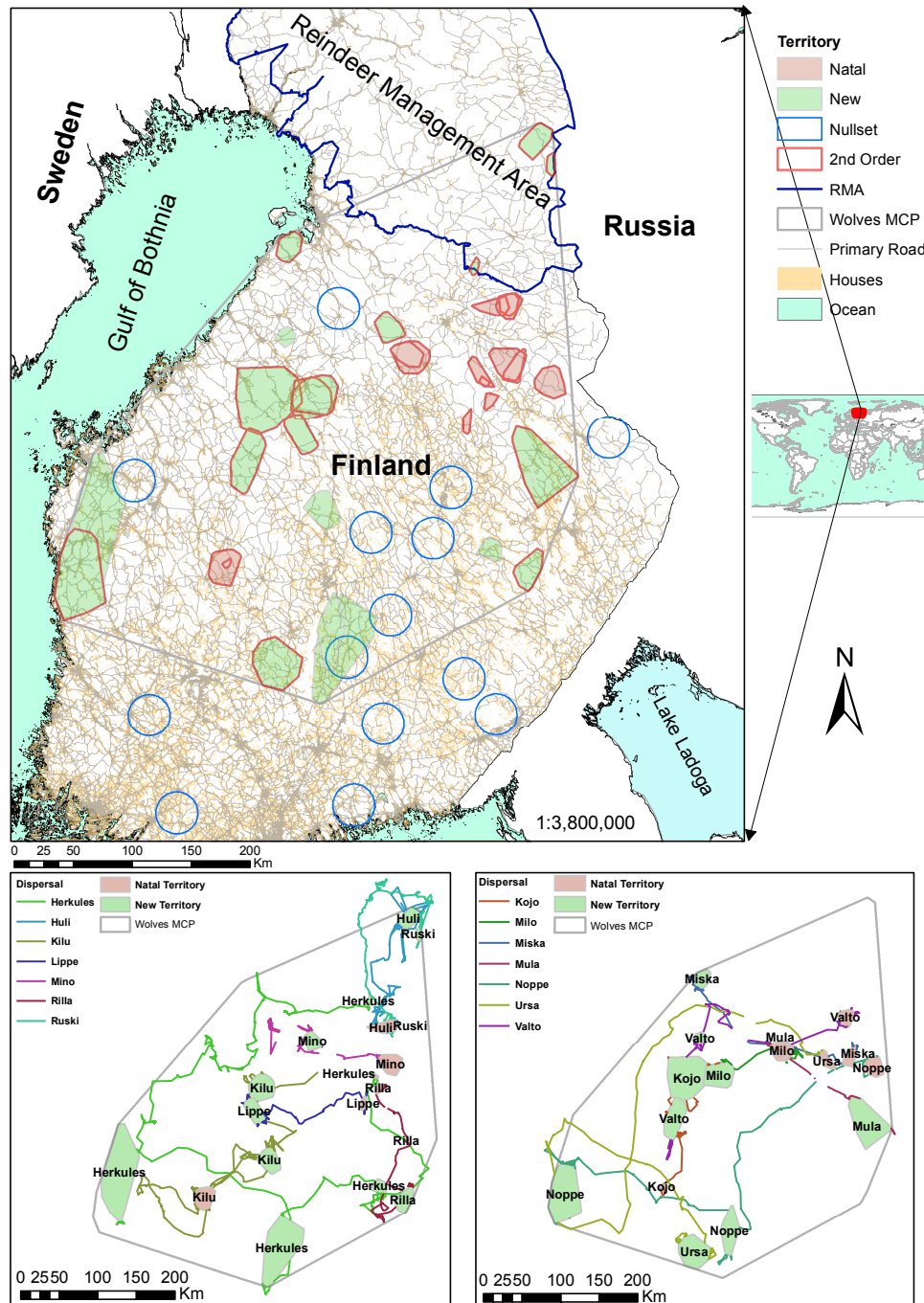


Figure 1: Top: Natal territories, new territories, null territories, primary roads, and houses plotted over a map of Finland. Territories marked “2nd Order” were used to answer questions 1 and 3 as described in the “Statistical methods” section. The gray polygon denoted “Wolves MCP” is the 100% minimum convex polygon (MCP) of all wolf locations. Forest roads are not depicted because forest roads were extremely dense throughout the study area. Bottom: Natal territories, dispersal trajectories, and new territories of all wolves. The gray polygon is the 100% MCP of all wolf locations.

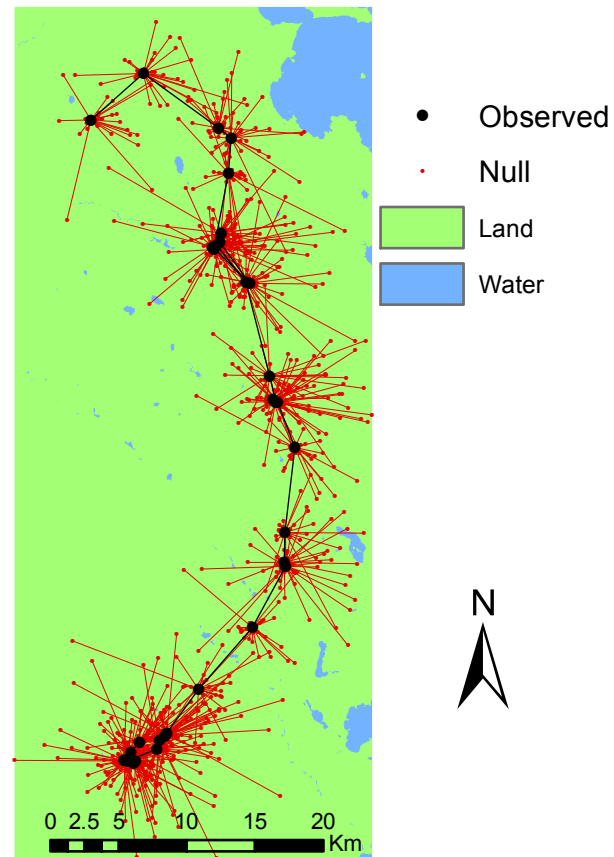


Figure 2: The null set constructed for the dispersal event of an individual wolf. The null set was created by adding 30 randomly-drawn steps to every observed location.

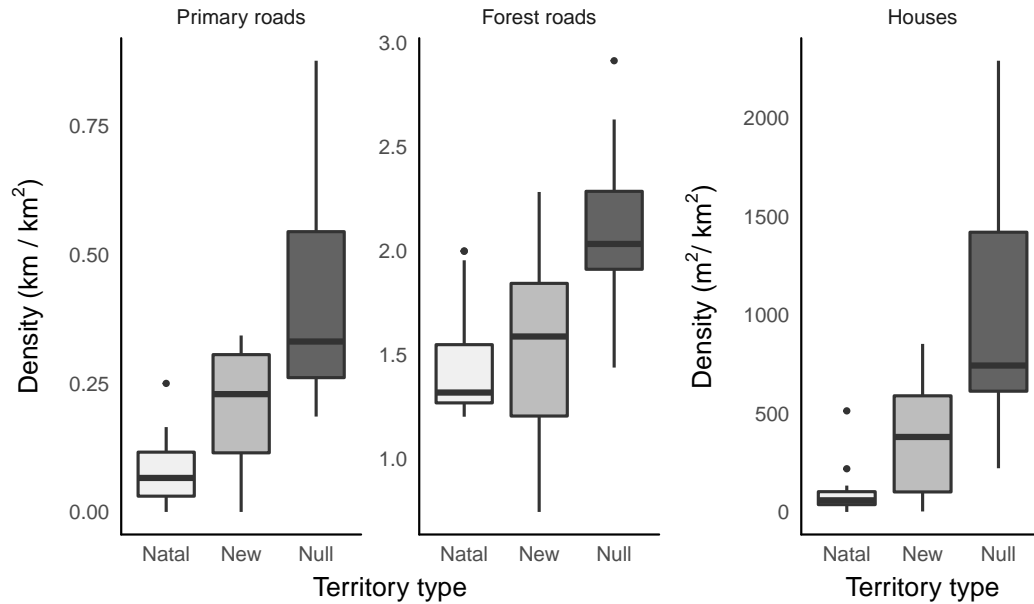


Figure 3: Density of primary roads, forest roads, and houses in natal, new, and null territories. The median density of each habitat element was greatest in the null territories, second greatest in the new territories, and least in the natal territories. For wolves with multiple new territories, the final such territory was used to create this plot.

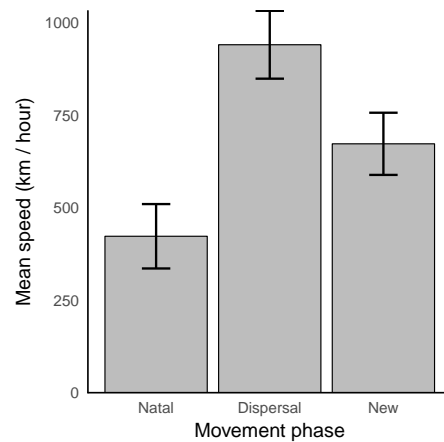


Figure 4: Mean movement speed (with associated 95% CI) for each movement phase. Wolves moved fastest during the dispersal period, second fastest in the new territory, and slowest in the natal territory.

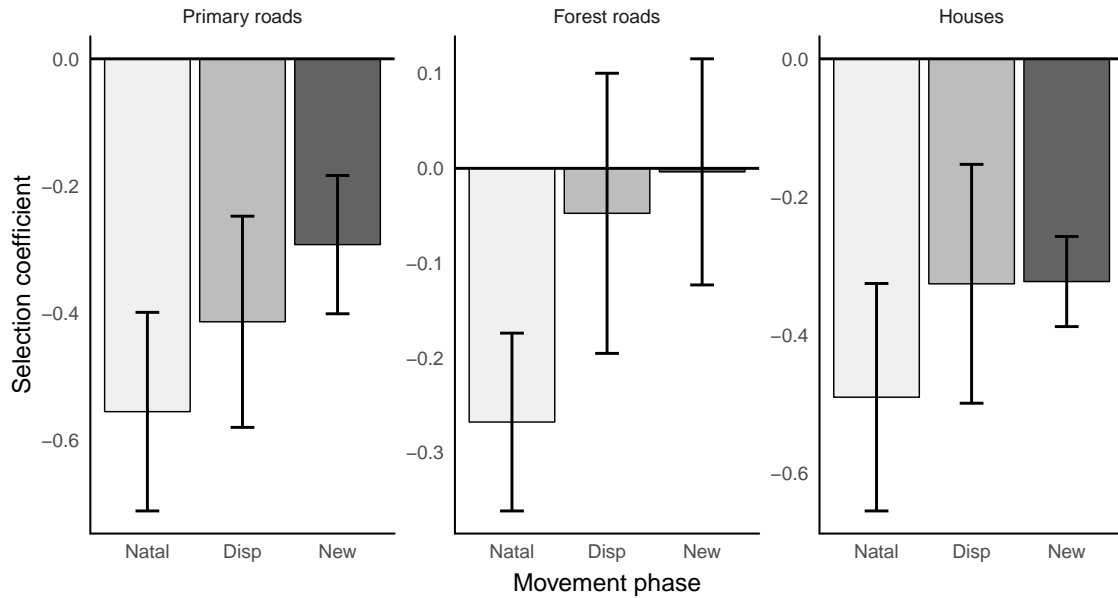


Figure 5: The selection coefficient for primary roads, forest roads, and houses in each of the different movement phases. Error bars represent ± 2 se. Wolves avoided primary roads and houses in all movement phases. Wolves avoided forest roads in the natal territory, but not in the dispersal period or in the new territory.

11 Tables and table legends

Wolf ID	Sex	N obs. disps.	N obs. ters.	Initial disp. start date	Mean disp. distance (km)	Mean disp. duration (day)
Herkules	M	4	5	04-18-2005	227.21	27.17
Huli	M	1	2	04-15-2002	149.10	56.50
Kilu	M	4	4	05-30-2012	151.99	22.37
Kojo	M	1	2	04-24-2013	144.88	37.83
Lippe	F	1	2	03-17-2005	140.51	12.33
Milo	M	1	2	10-31-2012	87.87	3.83
Mino	M	1	2	06-14-2005	106.44	51.83
Miska	M	1	2	05-15-2003	215.61	10.00
Mula	M	1	2	06-22-2012	144.03	3.33
Noppe	M	2	3	04-24-2003	250.55	16.53
Rilla	F	2	3	03-28-2005	77.72	7.58
Ruski	M	1	2	05-28-2012	124.26	30.92
Ursa	F	1	2	04-06-2004	301.13	38.34
Valto	M	2	3	05-19-2005	152.26	10.25

Table 1: Summary statistics on dispersing wolves. Dispersal start date refers to the date on which the wolf departed from its natal territory. Dispersal distance and duration were averaged across each distinct dispersal event and recorded in the mean distance and duration columns, respectively. Column abbreviations: obs. – observed, ter. – territory, disp. – dispersal.

Model no.	Predictor variables	AIC _c	Δ AIC _c	Log lik.	Estimate	SE	Partial P
1	Houses	31.1	0.00	−13.30	−0.004	0.002	0.021
2	Primary	31.8	0.76	−13.68	−11.263	5.119	0.028
3	Forest + Houses	32.7	1.65	−12.86	−1.367	1.495	0.360
4	Primary + Forest	33.1	2.05	−13.07	−7.6944	5.504	0.162
5	Primary + Houses	33.6	2.52	−13.30	0.203	13.993	0.988
6	Forest	33.9	2.78	−14.69	−2.919	1.200	0.015

Table 2: Performance of univariate and bivariate logistic regression models in distinguishing between new wolf territories and null territories. The models are listed in decreasing order of performance, as quantified by AIC_c. House density was the best predictor of wolf territory presence or absence.