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Does dispersal make the heart grow bolder? Avoidance of anthropogenic habitat elements across wolf life history

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Dispersal is a fundamental ecological process that, on an individual level, is associated with intrinsic and fixed personality traits such as 'boldness'. However, it is unknown whether personality traits or behavioural syndromes might change as a consequence of dispersal itself. We analysed 14 GPS-collared grey wolves, *Canis lupus*, in Finland that dispersed from their natal territories and settled in new territories, as well as 22 time-matched nondispersing controls. We used wolf avoidance of low-use forest roads, high-use primary roads and houses as proxies for boldness, and we estimated wolf responses to these features across spatial scales and across dispersal phases. Wolves, which already occupy portions of Finland with low human density, expanded into more human-impacted areas, but with a strong large-scale selection for relatively low human presence. At the finer scale, avoidance of human elements varied as a function of dispersal phase. During dispersal, avoidance of forest roads, primary roads and houses was substantially lower than in natal territories, reflecting the need to take more risks while moving in a small group (alone or with a single mate) in unfamiliar environments. After settling in new territories, the strength of avoidance of those elements continued to be lower than in natal territories, even after controlling for changes in availability. These results suggest that experiences gained across a major life-history transition, such as dispersal, might themselves influence personality traits.

Across animal taxa, dispersal from natal ranges is an essential process for maintaining populations. Dispersal reduces kin competition, alleviates resource scarcity, decreases the likelihood of inbreeding and is the principal mechanism of recolonization and range expansion (Bowler & Benton, 2005; Clobert, Le Galliard, Cote, Meylan, & Massot, 2009; Woodroffe, 2003). While the evolutionary consequences, costs and benefits of dispersal have been extensively studied, the decision-making and behavioural processes that underlie dispersal are complex and poorly understood (Cayuela et al., 2018; Cote, Clobert, Brodin, Fogarty, & Sih, 2010; Matthysen, 2012). Most empirical studies of dispersal behaviour have focused on invertebrates (Belgrad & Griffen, 2018; Dahirel, Vong, Ansart, & Madec, 2017; Johns & Eveleigh, 2013; Ramalho et al., 2014), fish (Le Roy & Seebacher, 2018; Rehage & Sih, 2004), small birds (Dingemanse, Both, van Noordwijk, Rutten, & Drent, 2003) and small mammals (Mabry & Stamps, 2008) that disperse over relatively short distances. Well-replicated studies in which large mammals disperse long distances away from their natal territories are rare.

Behaviourists typically break the process of dispersal into the distinct stages of departure, movement and settlement (Bowler & Benton, 2005; Clobert et al., 2009). Research on the motivations for dispersal often compares personality traits, defined as fixed and repeatable interindividual differences in behaviour (Roche, Careau, & Binning, 2016), between individuals that do disperse and those that do not. Observational or experimental data (e.g. scoring of individual activity or interindividual behavioural interactions) are used to link individuals' personality traits with propensity for and success in dispersal. For example, individuals with aggressive personalities have been observed to 'drive away' other individuals that ultimately disperse to different locations (e.g. house mice, *Mus musculus domesticus*: Pocock, Hauffe, & Searle, 2005). In other

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species (e.g. rhesus macaques, *Macaca mulatta*: Mehlman et al., 1995; mountain bluebirds, *Sialia currucoides*: Duckworth & Badyaev, 2007), behaviourally aggressive individuals are more likely to disperse, presumably because that trait facilitates establishment of new territories. Other personality traits, such as sociability, may also determine individuals' propensity for dispersal. In mosquitofish, *Gambusia affinis*, asocial individuals prefer lower densities and are more likely to disperse (Cote, Clobert et al., 2010; Cote, Fogarty, Weinersmith, Brodin, & Sih, 2010). The boldness personality trait, often quantified in terms of movement activity levels in novel environments, is also linked to dispersal propensity. In both killifish (Fraser, Gilliam, Daley, Le, & Skalski, 2001) and great tits, *Parus major* (Dingemanse et al., 2003), realized dispersal distance is a strong correlate of boldness. Likewise, in roe deer, *Capreolus capreolus*, dispersing individuals were less neophobic and had higher energetic budgets than nondispersers (Debeffe et al., 2014).

Personality traits are often assumed to be fixed. However, personality traits may change over time, such as during an individual's growth towards maturity or as a function of spatial context (Bekoff, 1977; Cote, Clobert et al., 2010). For example, in red squirrels, *Tamiasciurus hudsonicus*, Kelley, Humphries, McAdam, and Boutin (2015) found individuals' activity levels to decrease from juvenile to yearling stages, even as aggression did not change, suggesting that some aspects of personality can change as animals mature. Similarly, Dahirel et al. (2017) demonstrated that subadult land snails (*Cornu aspersum*) were bolder and more dispersive than adults. Likewise, Günther, Finkemeier, and Trillmich (2014) found that exploration behaviour and boldness were ontogenetically plastic personality traits in wild guinea pigs, *Cavia aperea*, suggesting that environmental factors acting upon individuals early in their lives can influence the personalities they ultimately develop. In contrast, Cote and Clobert (2006) found that individual lizards were consistently social or asocial, and this manifested in terms of similar 'social tolerance' of conspecifics both before and after natal dispersal. If animal personality traits are ontogenetically plastic as in the squirrel, snail and guinea pig cases, questions about how experience and context shape those changes naturally follow. However, no studies we are aware of look at how personality traits might be shaped by the process of dispersal itself.

The proliferation of data generated by animal-tracking technology, which provide details on where individuals do and do not go during dispersal, affords a unique opportunity to explore whether and how the process of dispersal might shape animal personality. Resource selection and step selection functions (RSFs and SSFs) are statistical tools commonly used in wildlife studies to compare the environmental attributes of locations where an animal is found against those of points available on a home range scale (RSFs; Johnson, Nielsen, Merrill, Mcdonald, & Boyce, 2006) or while moving through a landscape (SSFs; Thurfjell, Ciuti, & Boyce, 2014). These tools provide selection and avoidance coefficients specific to an environmental variable, which are repeatable, quantitative measures that vary among individuals. As such, we posit that these coefficients can serve as proxies for the personality trait of 'boldness' and that by studying how these coefficients vary across life stages and among individuals, we can indirectly study the way personality traits themselves might change as a consequence of a major life-history process like dispersal.

Grey wolves, *Canis lupus*, are expanding their range throughout Eurasia and North America, almost entirely via natural dispersal (Ciucci, Reggioni, Maiorano, & Boitani, 2009). Although wolf social behaviour can vary, the general pattern of dispersal is that younger, nonbreeding adults leave their natal pack to seek out a mate and establish a new breeding territory elsewhere (Mech & Boitani, 2003). Under idealized circumstances, the majority of wolves eventually disperse, unless they attain breeding status within a pack. Many individual wolf dispersal events have been documented via radiotelemetry (Ballard et al., 1983, 1987; Boyd & Pletscher, 1999; Fritts, 1983; Fritts & Mech, 1981; Fuller, 1989; Gese & Mech, 1991; Mech, 1987; Mech, Fritts, & Wagner, 1995; Peterson, Woolington, & Bailey, 1984; Van Camp & Gluckie, 1979) and GPS tracking (Ciucci et al., 2009; Jimenez et al., 2017; Kojola et al., 2006, 2009; Razen et al., 2016), including exceptional cases of over 1 000 km of linear distance (Wabakken et al., 2007). Broadly, these studies confirm that wolves establish territories to avoid areas occupied by other wolves and to avoid humans. Breeding site selection, in particular, has been shown to be characterized globally by a strong avoidance of human-made structures (Sazatornil et al., 2016). Similarly, attributes of territories selected by wolves indicate areas with fewer houses, roads, agricultural fields and people than in comparably accessible areas (Kaartinen et al., 2005, 2015; Karlsson, Brøseth, Sand, & Andrén, 2007; Mladenoff, Sickley, Haight, & Wydeven, 1995; Sazatornil et al., 2016).

Within a territory, wolf response to human elements is more nuanced. Forest roads, for example, are avoided in some populations (Kaartinen et al., 2005), although wolves may preferentially use low-use forest roads specifically to facilitate intraterritorial travel (Dickie, Serrouya, McNay, & Boutin, 2017; Fritts, 2003; Gurarie, Suutarinen, Kojola, & Ovaskainen, 2011). These differences in preference are likely highly behaviourally specific. For example, Gurarie et al. (2011) identified wolves' general avoidance of forest roads while hunting or resting but a preference when returning to the den after a kill, where forest roads served as a useful corridor facilitating mobility. This observation was made on two closely studied and well-established wolf packs but did not appear to hold more generally across the summer movements of wolves, which generally avoided forest roads, although with considerable individual variation (Gurarie et al., 2011).

In this study we analyse a population of GPS-tracked wolves in Finland. As with many European and North American wolf populations, wolves in Finland were extirpated in the early 20th century (Pulliainen, 1993). The population began to rebound in the 1990s under legal protection from Finland and the European Union (Bisi, Kurki, Svensberg, & Liukkonen, 2007; Kojola et al., 2014) but has fluctuated between 100 and 300 animals with changing levels of protection and poaching intensity (Jansson, Ruokonen, Kojola, & Aspi, 2012; Suutarinen & Kojola, 2017). The core of the wolf population resides in eastern Finland near the Russian border, but the dispersing wolves have expanded the population into more densely populated central and southwestern Finland (Kojola et al., 2006, 2009). Wolves in Finland have been intensely studied, with over 130 individuals tracked with VHF or GPS collars since 1998 (Suutarinen & Kojola, 2017), including over 20 individuals that clearly dispersed from their natal territory.

Unlike most behavioural investigations of the link between personality and dispersal, our data set is unique in that it provides a rare portrait of individuals' experiences during all three stages of dispersal (predispersal, dispersal, settlement). Our goal is to leverage this data set to understand how the process of dispersal itself might shape wolf responses to human landscape features. In particular, we seek to understand how wolves' experiences during the process of dispersal shape the personality and preferences they exhibit after settlement. For example, if wolves disperse through habitats with buildings or roads, do they settle in landscapes with similar features? Or do they preferentially settle in areas lacking such features? How, if at all, does their avoidance of human elements change throughout the dispersal process? If boldness is acquired – i.e. if wolves learn to successfully navigate environments with higher human densities – we would predict lower levels of avoidance in new territories. On the other hand, the stresses of dispersal may, on the contrary, lead to heightened shyness in new territories. By comparing dispersers against a baseline of non-dispersing wolves and comparing across the three phases of dispersal (natal territories, dispersal movements, new territories), our data set allows us to fully characterize these behavioural responses and the ultimate outcomes of dispersal.

METHODS

Study Area

The study area consisted of all mainland Finland excluding the Reindeer Management Area (RMA), a large area encompassing the northern third of Finland within which wolves have no legal protection and have never established territories (Fig. 1). Most of the study area belongs to the boreal forest zone, while the southernmost areas are intermediate temperate forest zones, with 80% of the area covered by forests. Because commercial forests make up 93% of the forested area, young successional mixed forest areas are common. Bogs and peatlands are also common, although about half have been drained for forestry purposes (Finnish Forest Resource Institute, 2005). The dominant tree species are Scots pine, *Pinus sylvestris*, Norway spruce, *Picea abies*, and birch (genus *Betula*), which constitute 65%, 23% and 9% of forest cover, respectively (Kaartinen et al., 2015). Finland is generally flat and lacking in topography and the main geographical barriers to movement are lakes, which are common and make up approximately 10% of the land cover. In winter, however, most freeze over and are easily traversed.

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 (5 people/km^2) is low relative to the mean density of humans in Finland (17 people/km^2) (Kaartinen et al., 2005). The main human population centres are located in the south and west of Finland (Fig. 1). Moose, *Alces alces*, are present at relatively high densities throughout Finland and are the primary prey of wolves. Wolves also hunt Finnish forest reindeer, *Rangifer tarandus fennicus* (Gurarie et al., 2011), in the core range and introduced white-tailed deer, *Odocoileus virginianus*, in the southwest.

Wolf Data

A total of 58 wolves were captured and collared in late winter or early spring during 2002–2013. 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; Wabakken et al., 2007). 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 2–4 h, with a few exceptions at higher frequencies. We refer to the wolves by name to facilitate cross-referencing with other studies.

Ethical Note

After being captured, wolves were kept in a wooden box for at least 30 min. Wolves were injected in the hindleg with a mixture of medetomin and ketamin to reduce stress. The box in which wolves were kept was big enough for wolves to turn around in and stand on all four feet. Human capturers maintained a distance from the box and stayed silent until wolves recovered. Capturers followed the wolves' re-activation from a distance. Capture, handling and anaesthetizing 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).

Environmental Covariates

Road data were obtained from the Digiroad database provided by the Finnish Transportation Agency (version 02/2016, https://vayla.fi/web/en/open-data/digiroad). Digiroad contains the geometry and attribute data of the streets, paths and trails of Finland. Roads are classified into one of eight 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’. This pooling procedure was consistent with the scheme used by Gurarie et al. (2011).

House and water data were obtained from the European Environmental Agency's CORINE 2006 land cover database (https://www.eea.europa.eu/publications/COR0-landcover). The CORINE database partitions European land cover into 25 × 25 m grid cells and classifies each cell into one of 44 different land classes. Of these, five land classes constitute more than 80% of the land cover of Finland: coniferous forest (Scots pine forestry operations; 40.1%), transitional woodland shrub (recovering clear cuts; 13.1%), mixed forest (mixture of broad-leaved trees and coniferous trees; 11.6%), water bodies (9.5%) and peat bogs (8.1%). We pooled the continuous urban fabric, discontinuous urban fabric and industrial or commercial units into a generic ‘house’ category and the freshwater, seas and ocean categories into a generic ‘water’ category.

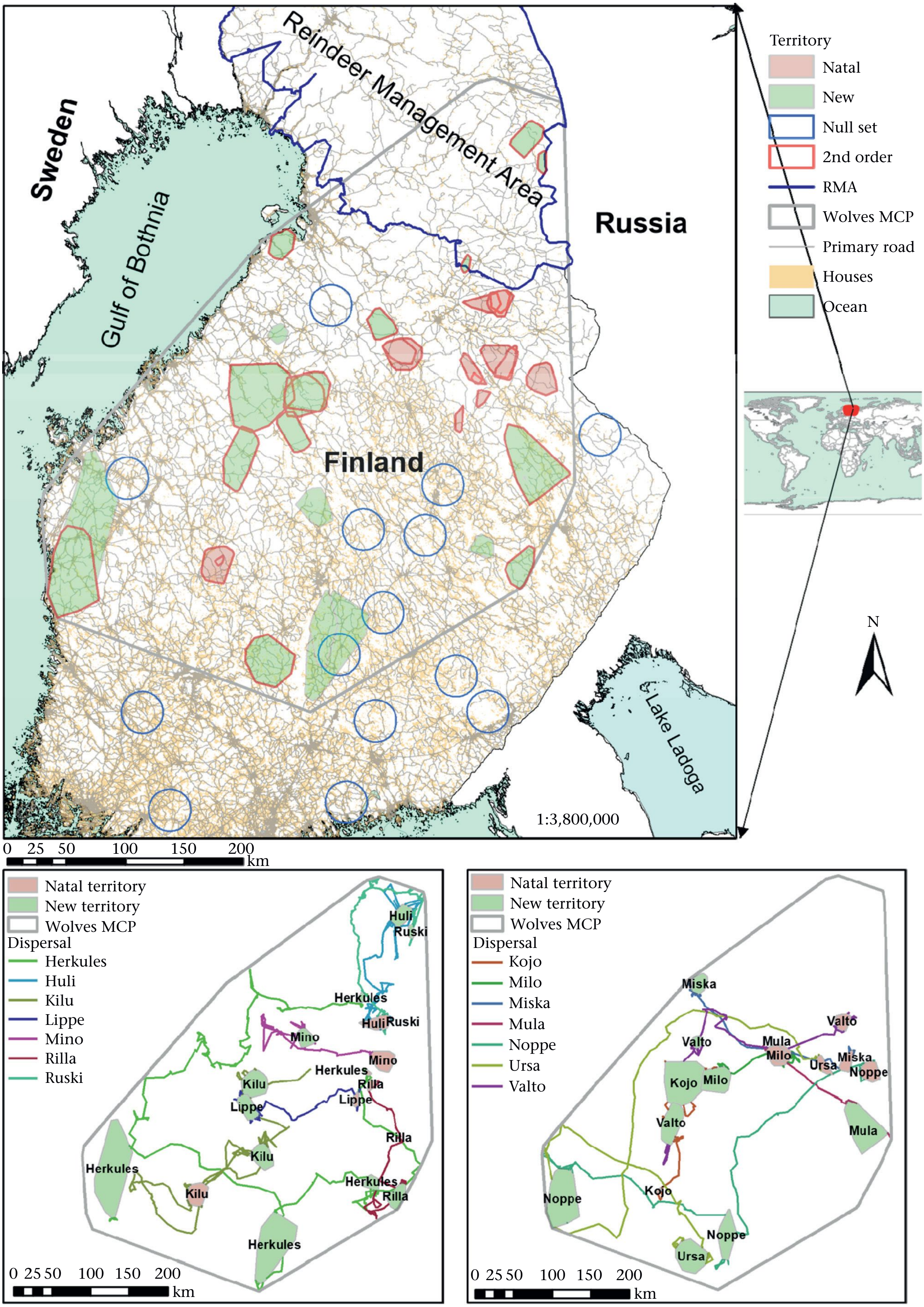
Statistical Methods

Wolf behaviour

We distinguished territorial from nonterritorial movements by testing for the presence of a central attractor to the motion. We defined a ‘territory’ as a set of tortuous movements with a central attractor that persisted for 5 days or longer. In contrast, a ‘dispersal event’ was defined as a set of transient, unconstrained movements that linked territories (Fig. 2). To identify when dispersal events began and ended, we used a likelihood-based change point algorithm (Gurarie, Andrews, & Laidre, 2009) that searched for the times when movements transitioned from being spatially constrained with a central attractor (i.e. a spatial Ornstein-Uhlenbeck or OUF process sensu Calabrese, Fleming, & Gurarie, 2016; Fleming et al., 2014a, b) to being spatially unconstrained (i.e. a correlated velocity movement sensu Gurarie et al., 2017). Speed was not a criterion for distinguishing territorial from dispersing phases of movement. For more details, including R code, see Supplementary material 1.

Among the 58 wolves that were captured and collared, 27 were clear dispersers. We excluded from our analysis dispersers that did not have data available across all three movement phases (natal territory, dispersal, new territory). We further excluded wolves that dispersed into Russia, where land cover data were unavailable. In the end our data included 14 dispersing wolves with 14 unique natal territories, 23 separate dispersal events and 22 new territories (Fig. 1). The number of dispersal events and new territories exceeded the number of natal territories because some wolves dispersed multiple times (see e.g. Fig. 2).

We also used in our analysis a set of wolves that did not disperse from their territories during the period of tracking. These wolves served as controls against which we compared the behaviour of the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Gulf of Bothnia
Russia
Finland
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km
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Territory
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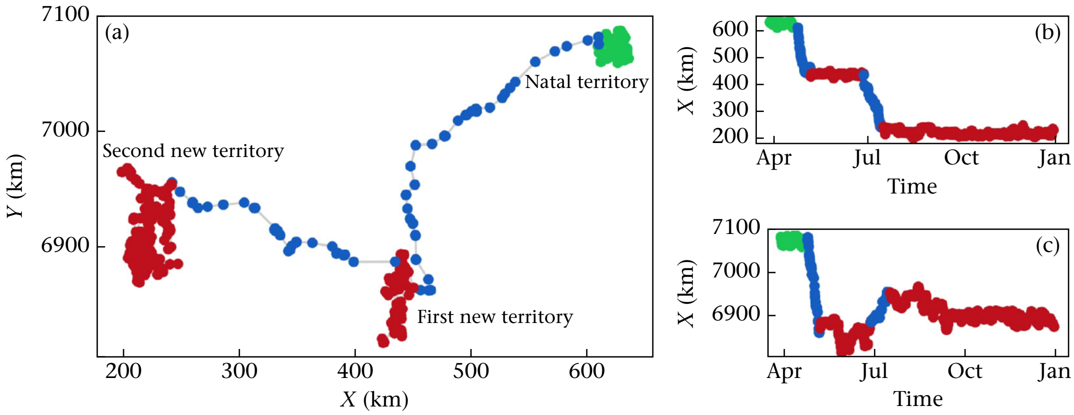

Figure 2. The trajectory of a dispersing wolf (Noppe). Points correspond to observed locations and are colour-coded by movement phase (green for natal territory, blue for dispersal, red for new territory). Movement phases were identified using a likelihood-based change point algorithm. (a) Vertical displacement versus horizontal displacement; (b) horizontal displacement versus time; (c) vertical displacement versus time.

dispersing wolves. We required all control wolves to have a single, clearly defined territory and no extraterritorial excursions or forays. The final control data set contained 22 distinct wolves and 22 corresponding control territories (Fig. 3). The territories of control wolves, which we call 'control territories', should not be confused with 'natal' territories, which were the initial territories of dispersing wolves. Our total sample size across dispersing and control wolves was 36 wolves.

We filtered away all locations that corresponded to resting or denning (Dickie et al., 2017; Gurarie et al., 2011; Killeen et al., 2014). We did this by fitting a kernel density estimate to the log-transformed step speeds (distance between consecutive locations divided by elapsed time), resulting in a bimodal distribution. The minimum between the two modes occurred at 35.9 m/h, which we took to be the threshold separating resting from active movement behaviours. We classified all observations with speeds below this threshold (37.5% of observations) as resting locations, and removed them from subsequent analyses. Additionally, we manually removed all forays from the location data, where 'forays' were identified as short, exploratory, extraterritorial trips taken by a wolf before actually dispersing (Mech & Boitani, 2003). In total we removed four forays, the longest of which occurred over a period of 13 days.

Large-scale habitat selection

To obtain a baseline for human impact across the largest scale of territorial selection, we compared the new territories to the natal territories and to the available range of habitats in central and southern Finland more broadly. We constructed a null set of non-territory areas by generating a set of 'potential displacement vectors' by connecting the centroid of each natal territory to the centroid of the corresponding new territory (in the case of animals with multiple new territories, the final such territory was used). We randomly paired dispersal distances and angles to generate a set of 'pseudo-displacements' and added a random sampling of these vectors to the centroids of randomly selected natal territories. We centered circles of area 986 km^2 (the mean area of new territories) at the resultant points, thereby generating a set of 'null territories'. In total, we generated 14 null territories that did not overlap with each other, with observed territories, or with the Reindeer Management Area (Fig. 1). Our approach is similar to that used by (Kaartinen et al., 2015) in an analysis of territory site selection across Finland, although slightly more conservative due to using only empirically derived dispersal distances.

We then compared primary road, forest road and house densities across the three territory types (natal, null, new). 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^2/km^2). Given that 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). For wolves with multiple new territories, only road and house densities obtained from the final such territory were used in this analysis. To compare natal territories to new territories, we used paired t tests. To compare new territories to null territories, we fitted a logistic regression model wherein the response variable was territory type (i.e. new versus null) and the predictor variables were primary road, forest road and house density. We fitted all univariate ($N = 3$) and bivariate ($N = 3$) models and ranked them according to Akaike's information criterion corrected for small samples (AIC_c).

Movement patterns during dispersal

We performed several analyses of movement behaviour because habitat use itself can be linked with behaviours (e.g. higher use of linear elements might be related to facilitated travel). Thus, we compared movement speed and proportion of time spent resting across movement phases. Movement speed was defined as the distance between consecutive locations divided by the time elapsed. To assess shifts in movement speed across phases, we fitted a mixed-effects linear model with log-transformed movement speed as the response, movement phase as a fixed effect and individual wolf as a random intercept. We defined the proportion of time spent resting as the fraction of steps classified as 'resting' (movement speed <35.9 m/h; see Wolf data above for justification). We assessed shifts in the proportion of time spent resting by fitting a mixed-effects logistic regression model. The binary response was step type (i.e. 'resting' or 'active movement'), and the fixed and random effects were the same as before. We computed 95%

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 study wolf territory selection. The grey 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 dispersing wolves.

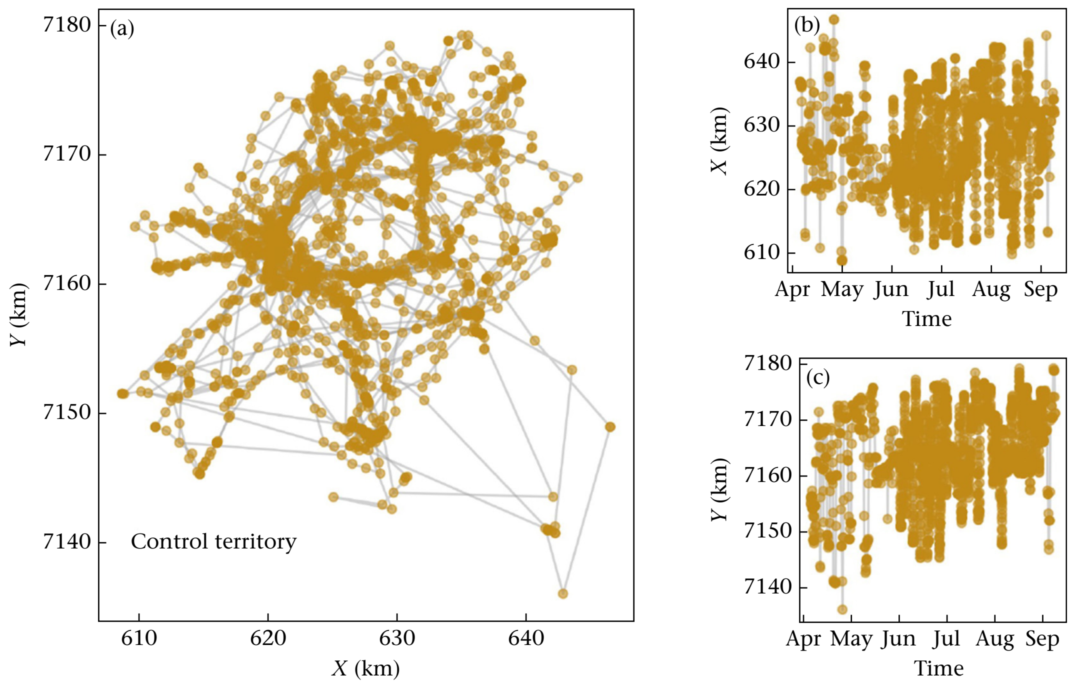

Figure 3. The trajectory of a control wolf (Niki). (a) Vertical displacement versus horizontal displacement; (b) horizontal displacement versus time; (c) vertical displacement versus time.

confidence intervals for mean speed and proportion of time spent resting in each movement phase.

Fine-scale responses to human elements

We analysed wolf avoidance of human habitat elements at the more local movement scale using a standard step selection analysis, which contrasts observed locations against a localized availability null set that is matched to each respective location (Thurfjell et al., 2014). To obtain the availability null set, we first generated a large pool of potential displacement vectors by identifying and aggregating all displacements that actually occurred over a 4 h time interval. For each observed location, we randomly sampled 30 displacement vectors from the respective wolf's movements and added these vectors to the observed location. Points in water were excluded from the null set because wolves typically do not traverse water, particularly in the late spring and summer when most of the dispersal events occurred (Kojola et al., 2009). Similarly, points outside Finland were excluded because human infrastructure data were unavailable outside Finland. This design is 'matched' in the sense that each observed location is associated with a specific set of 30 null locations (Duchesne, Fortin, & Courbin, 2010; Fortin et al., 2005).

After constructing the null set, we prepared the habitat covariates for statistical modelling. Rather than use linear distance or some linear transformation (e.g. log or square root) to a given habitat element, as a covariate, we analysed the distance in terms of a discrete threshold, i.e. the covariate was set to 0 if it was within a specific distance threshold of a given habitat element and 1 otherwise. The thresholds we selected were chosen by finding the value at which the likelihood of a logistic model was maximized after sweeping across distance thresholds from 25 m to 2 km (see details in Supplementary material 2), leading to us to use a threshold distance of 200 m from forest roads and 600 m for primary roads and houses. This approach satisfied two important criteria for our purposes. First, it allowed us to identify a limit for the zone of influence of each variable type. Second, it provided us with a discrete contingency table (of used–available versus near–far locations) to summarize the strength of avoidance for a given element across time (see equation (1) below).

To explore fine-scale avoidance of human habitat elements over time and across movement phases, we performed two separate, complementary statistical analyses. The goal of the first analysis was to understand annual seasonal patterns of avoidance and to compare control animals against dispersers in natal and new territories. For a given movement phase p (in natal, new, control), we included a given day of the year in the analysis if at least three distinct wolves in phase p had data available on that day. We coarsened the data by pooling together days that occurred within the same week, forming a set W_p of distinct, nonoverlapping, 7-day periods (or weeks). For a given week i in W_p, and for a given habitat element h (forest roads, primary roads, houses), we defined the 'avoidance' $a^{(i)}_{p,h}$ of habitat h in phase p during period i by

$$a^{(i)}_{p,h} = \log\left(\frac{(of)^{(i)}_{p,h} \Big/ (nf)^{(i)}_{p,h}}{(oc)^{(i)}_{p,h} \Big/ (nc)^{(i)}_{p,h}}\right) \quad (1)$$

Here, $(of)^{(i)}_{p,h}$ is the number of observed points in phase p and period i that are far from element h; $(oc)^{(i)}_{p,h}$ is the number of observed points in phase p and period i that are close to element h; $(nf)^{(i)}_{p,h}$ is the number of null points in phase p and period i that are far from element h; and finally $(nc)^{(i)}_{p,h}$ is the number of null points in phase p and period i that are close to element h. We identified points as being either close or far using the thresholds described previously (i.e. 200 m for forest roads and 600 m for primary roads and houses).

The metric in equation (1) is similar to the metric introduced by Aebischer, Robertson, and Kenward (1993) to measure relative selection and avoidance of discrete habitat types. It quantifies avoidance of an element by dividing the ratio of observed to null points that are far from the element by the ratio of observed to null points that are close to the element. Values greater than 0 indicate avoidance, with bigger values corresponding to more extreme avoidance. For example, if over a week-long period, 80 out of 100 observations are greater than 600 m from the nearest house, whereas in the corresponding null set only 600 out of 3 000 observations (there are 30 null observations for each actual location) are further than 600 m from the nearest house, the score is $\log((80/100)/(600/3000)) = \log(4) = 1.39$, a strong positive indicator of avoidance.

For movement phase p and element h, we regressed the $a^{(i)}_{p,h}$ values against a spline of day of year to obtain an estimate of the avoidance of element h over time. The control group spline was wrapped around 31 December − 1 January, while the natal and new territories were limited to data ranges that fitted our criteria for minimal number of observations (early March − early June for dispersal, early May − 31 December for the new territories). Finally, for all movement phases and elements we plotted the splined regression prediction, which we refer to as an 'Aebischer avoidance index' and its associated pointwise standard error. We did not calculate avoidance during the dispersal period because dispersal events were short and did not sufficiently overlap in time to make population level inferences about avoidance.

Our second analysis used step selection methods to similarly quantify avoidance, including during the dispersal period, but did not account for seasonal changes in avoidance. We fitted a mixed-effects conditional logistic regression model (Duchesne et al., 2010) to the observed versus null observations for the (1) control, (2) disperser in natal territory, (3) disperser while dispersing and (4) disperser in new territory (including transient territories) categories. Thresholded proximity to each element was the explanatory covariate. Each individual had its own set of random coefficients for each of the three habitat elements. We followed the two-step strategy of fitting the model as recommended by Craiu, Duchesne, Fortin, and Baillargeon (2011). We refer to the estimated fixed coefficients as 'avoidance coefficients' because they reflect the extent to which wolves avoided the habitat elements in the model.

The two fine-scale human element avoidance analyses we performed had distinct strengths and weaknesses. In the first analysis we defined avoidance directly, which allowed us to easily and explicitly model avoidance as a function of time of year with some necessary minimal amount of data pooling at a 1-week interval. This allowed us to control for typical seasonal variation when comparing the avoidance signature of various dispersers. We compared the pattern of avoidance exhibited by dispersers and time-matched controls, thus enabling us to tease apart the effect of time of year and dispersal status on habitat preference. In the second analysis we indirectly measured avoidance by fitting a mixed-effects conditional logistic regression model for each movement phase. The logistic regression framework allowed us to straightforwardly account for the stratified and hierarchical nature of the data (by conditioning on the number of cases per time step and incorporating random coefficients into the likelihood, respectively). Moreover, we were able to estimate avoidance during the dispersal period itself, as the logistic regression set-up did not require dispersal events to overlap in time. Together, these analyses paint a comprehensive picture of local human element avoidance in the context of dispersal and settlement.

Programming and data processing

We did all programming in the language R (R Core Team, 2017). We conducted statistical analyses using the 'stats', 'lme4', 'TwoStepCLogit', 'mgcv' and 'emmeans' packages (Bates, Mächler, Bolker, & Walker, 2015; Craiu et al., 2011; Lenth, 2019; R Core Team, 2017; Wood, 2011). We carried out spatial processing using the 'spatstat', 'rgeos', 'rgdal', 'sp', 'splancs', 'adehabitatHR', 'maptools' and 'raster' packages (Baddeley, Rubak, & Turner, 2015; Bivand et al., 2015, 2016; Bivand & Lewin-Koh, 2016; Bivand & Rundel, 2016; Calenge, 2006; Hijmans, 2015; Pebesma & Bivand, 2005).

RESULTS

By design each of the 14 dispersing wolves had an observed natal territory, one or more dispersal events, and one or more new territories (Table 1). 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. Median dispersal departure date was 4 May (range 17 March − 31 October); median dispersal distance averaged across each wolf was 147.0 km (interquartile range = [126.1, 199.8] km); median dispersal duration averaged across each wolf was 16.1 days (interquartile range = [9.1, 33.5] days); and median territory area averaged across each wolf was 554 km^2 (interquartile range = [360, 1 096] km^2). We also tracked a set of 22 control (i.e. nondispersing) wolves. The control wolves were tracked for a median of 279.9 days (interquartile range = [186.1, 1 343.2] days).

Some wolves dispersed from the same natal territory. In particular, Herkules, Lippe and Ursa dispersed from one territory; Huli and Ruski dispersed from a second territory; Milo and Mula dispersed from a third territory; and Mino and Miska dispersed from a fourth territory. Wolves that dispersed from the same

Table 1
Summary statistics on dispersing wolves

Wolf	Sex	No. of observed		Dispersal start date	Mean dispersal		Mean territory	
		Dispersals	Territories		Distance (km)	Duration (day)	Duration (day)	Area (km^2)
Herkules	M	4	5	18 Apr 2005	227.2	26.4	41.3	1395
Huli	M	1	2	15 Apr 2002	149.2	53.7	85.7	400
Kilu	M	4	4	30 May 2012	152.0	16.5	144.0	560
Kojo	M	1	2	24 Apr 2013	144.9	35.8	287.5	1282
Lippe	F	1	2	17 Mar 2005	140.5	11.8	72.5	331
Milo	M	1	2	31 Oct 2012	87.9	3.5	142.4	872
Mino	M	1	2	14 Jun 2005	106.4	45.2	104.8	547
Miska	M	1	2	15 May 2003	215.6	9.0	80.4	346
Mula	M	1	2	22 Jun 2012	144.0	2.5	71.0	1170
Noppe	M	2	3	24 Apr 2003	251.6	15.6	81.2	1295
Rilla	F	2	3	28 Mar 2005	77.5	7.2	36.3	218
Ruski	M	1	2	28 May 2012	121.4	26.6	75.5	176
Ursa	F	1	2	06 Apr 2004	301.2	38.0	158.7	778
Valto	M	2	3	19 May 2005	152.2	9.6	132.9	520

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. Territory duration and area were averaged across each distinct territory.

territory dispersed in different years (Table 1) with two exceptions: Herkules and Lippe dispersed (1 month apart from one another) in 2005, and Milo and Mula dispersed (5 months apart from one another) in 2012.

New Territories are More Human-impacted Than Natal Territories

Forest road density did not significantly differ between natal ($\bar{x} \pm SD = 1.47 \pm 0.30$) and new ($1.54 \pm 0.48$) territories ($t_{13} = 0.44$, $P = 0.66$). Primary road density and house density, on the other hand, differed significantly between natal and new territories ($\bar{x} \pm SD$: primary road density: natal: 0.076 ± 0.071; new: 0.21 ± 0.11; $t_{13} = 4.95$, $P = 0.0003$; house density: natal: 4.02 ± 5.25; new: 15.1 ± 11.0; $t_{13} = 3.59$, $P = 0.0033$). These results suggest that, overall, wolves moved into more human-impacted areas as they transitioned from natal to new territories (Fig. 4).

Wolves Move Faster, But Do Not Rest More, During Dispersal

Mean movement speed was greatest during the dispersal period ($\bar{x} = 5.0$ km/h; CI = [4.5, 5.6] km/h), second greatest in the new territory ($\bar{x} = 4.1$ km/h; CI = [3.7, 4.5] km/h) and least in the natal territory ($\bar{x} = 2.9$ km/h; CI = [2.6, 3.2] km/h) (Fig. 5). Movement speed during dispersal and in the new territory significantly exceeded movement speed in the natal territory. Proportion of time spent resting, in contrast, did not differ significantly between natal territory ($\bar{x} = 0.72$; CI = [0.68, 0.75]), dispersal ($\bar{x} = 0.73$; CI = [0.69, 0.76]) or new territory ($\bar{x} = 0.71$; CI = [0.67, 0.75]).

Wolves Avoid Human Presence When Settling in a New Territory

Forest road, primary road and house densities were higher in null territories ($\bar{x} \pm SD$: 1.87 ± 0.42, 0.34 ± 0.14 and 29.6 ± 17.5, respectively) than in new territories (1.54 ± 0.48, 0.21 ± 0.11 and 15.1 ± 11.0, respectively) (Fig. 4). Primary road density and house density were the best single-variable predictors of territory presence or absence (Table 2). The Pearson correlation coefficients between forest road and primary road density, between primary road and house density and between forest road and house density were $r = 0.80$, $r = 0.95$ and $r = 0.77$, respectively. In general, the bivariate models were inferior to the univariate models in predicting territory presence or absence (as quantified by AIC_c), possibly due to multicollinearity among the predictor variables.

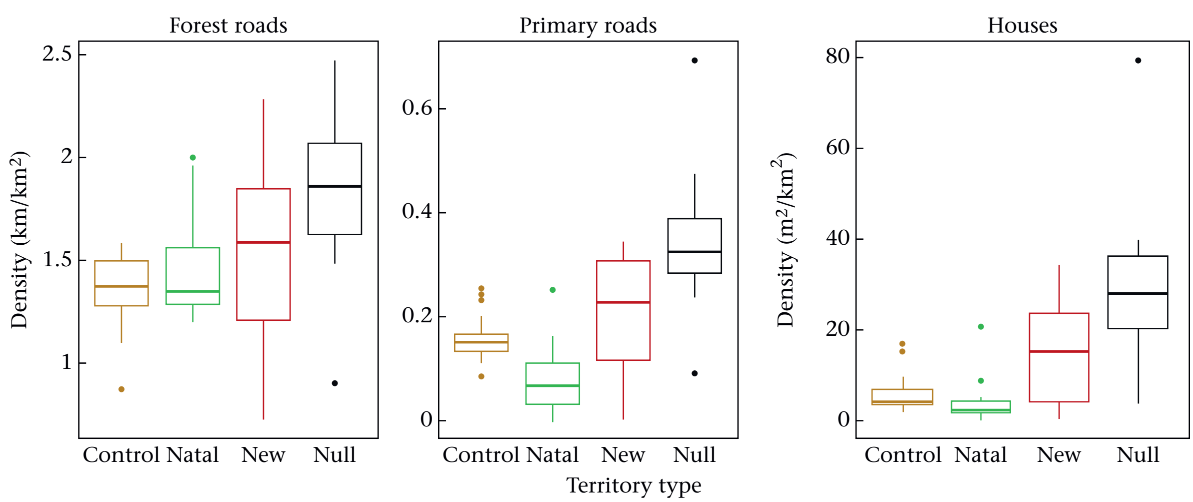

Figure 4. Median density of forest roads, primary roads and houses in natal, new and null territories. Box lengths represent interquartile range. For wolves with multiple new territories, the final such territory was used to create this plot.

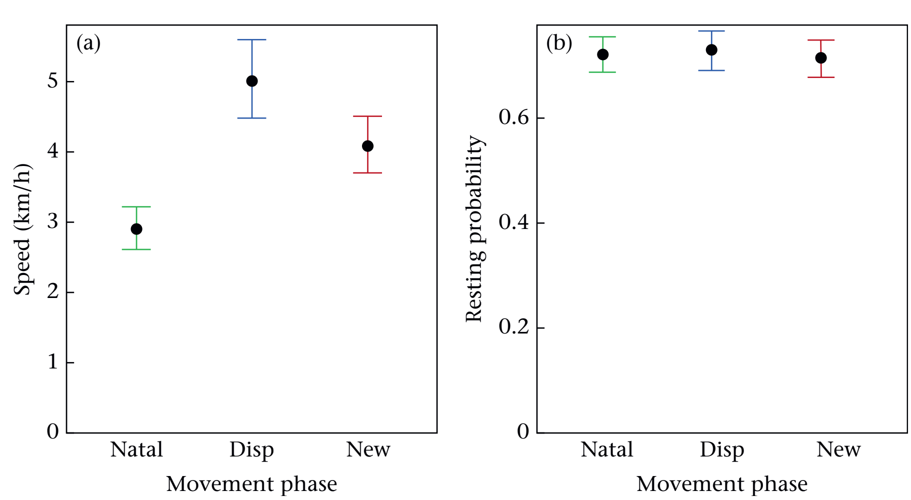

Figure 5. (a) Mean movement speed (with associated 95% CI) for each movement phase (natal territory, dispersal, new territory). (b) Proportion of time spent resting (with associated 95% CI) for each movement phase.

Table 2
Performance of univariate and bivariate logistic regression models in distinguishing between new wolf territories and null territories

Model no.	Predictor variables	AIC_c	ΔAIC_c	AIC	Log lik.	Estimate	SE	Partial *P*
1	Primary	35.26	0.00	34.8	−15.39	−10.66	4.83	0.03
2	Houses	35.84	0.58	35.4	−15.68	−0.09	0.04	0.03
3	Primary +	37.29	2.03	36.3	−15.15	−14.75	8.05	0.07
	Forest	37.29	2.03		−15.15	1.19	1.74	0.50
4	Houses +	37.75	2.49	36.7	−15.37	−0.02	0.10	0.86
	Primary	37.75	2.49		−15.37	−8.83	11.49	0.44
5	Houses +	37.96	2.71	37.0	−15.48	−0.13	0.07	0.08
	Forest	37.96	2.71		−15.48	1.08	1.75	0.54
6	Forest	39.64	4.39	39.2	−17.58	-1.69	0.96	0.08

The models are listed in decreasing order of performance, as quantified by AIC_c.

Wolves Avoid Human Elements Less during Dispersal and in the New Territory Than in the Natal Territory

According to both the nonparametric regression and conditional logistic regression analyses, dispersing wolves and control wolves alike avoided all human elements across all phases of dispersal. The nonparametric regression analysis revealed that avoidance was highest for primary roads ($\bar{x} \pm$ SE: control fit = 0.85 ± 0.072; natal fit = 1.37 ± 0.24; new fit = 0.601 ± 0.10), second highest for houses (control fit = 0.67 ± 0.13; natal fit = 0.66 ± 0.12; new fit = 0.38 ± 0.044) and least for forest roads (control fit = 0.34 ± 0.041; natal fit = 0.48 ± 0.08; new fit = 0.265 ± 0.050). This measure is based on a much lower spatial threshold for forest roads (200 m) than for primary roads and houses (600 m), such that a higher avoidance effect acts on a greater distance for the latter two elements. The baseline nonparametric regression for control wolves revealed notable annual seasonal structure. In particular, avoidance of human elements (especially houses) was highest in April, i.e. the den-up season, and lower in the middle of summer (Fig. 6 – yellow bands). Among dispersers, avoidance of human elements was lower in the new territory than in the natal territory (Fig. 6 – red and green bands). Notably, dispersers in the new territory displayed less avoidance of human elements than time-matched controls. Curiously, dispersing wolves in natal territories showed a distinct drop within the relatively narrow predispersal window in avoidance of primary roads and houses.

The results of the conditional logistic regression analysis largely agreed with those of the nonparametric regression analysis. Dispersers avoided all habitat elements across all movement phases. However, avoidance decreased by a factor of roughly 2 from natal territory ($\bar{x} \pm 2$ SE avoidance: forest roads = 0.23 ± 0.072; primary roads = 0.35 ± 0.11; houses = 0.21 ± 0.052) to dispersal (forest roads = 0.15 ± 0.108; primary roads = 0.19 ± 0.074; houses = 0.11 ± 0.086) and remained low in the new territory (forest roads = 0.11 ± 0.064; primary roads = 0.17 ± 0.056; houses = 0.17 ± 0.060), especially for forest roads and houses (Fig. 7). Control wolves displayed greater avoidance of human elements (forest roads = 0.14 ± 0.050; primary roads = 0.27 ± 0.060; houses = 0.23 ± 0.068) than dispersers in the new territory.

DISCUSSION

The relationship between boldness and dispersal links individual behaviour to a fundamental ecological processes and therefore points to an essential aspect of behavioural ecology (Cote, Clobert et al., 2010). In studies where relationships between the two have been demonstrated (Belgrad & Griffen, 2018; Chapman et al., 2011; Debeffe et al., 2014; Dingemanse, Both, Drent, van Oers, & van Noordwijk, 2002; Rehage & Sih, 2004), boldness was generally assumed to be an immutable – and even inherited – trait, sometimes referred to as a ‘dispersal syndrome’ that predicts the probability of an individual dispersing. In our study we looked at the inverse question: How might the act of dispersing affect an individual's boldness? We leveraged a detailed telemetry data set of dispersing and nondispersing free-ranging animals, finding evidence that behavioural traits, in particular propensity for boldness, might change as a result of dispersal.

As with any observational study on a large and wide-ranging mammal, we had no control over environmental factors and no opportunity to experimentally manipulate the animals (e.g. to independently determine boldness). To make inferences we therefore relied on a modelling framework that took into account

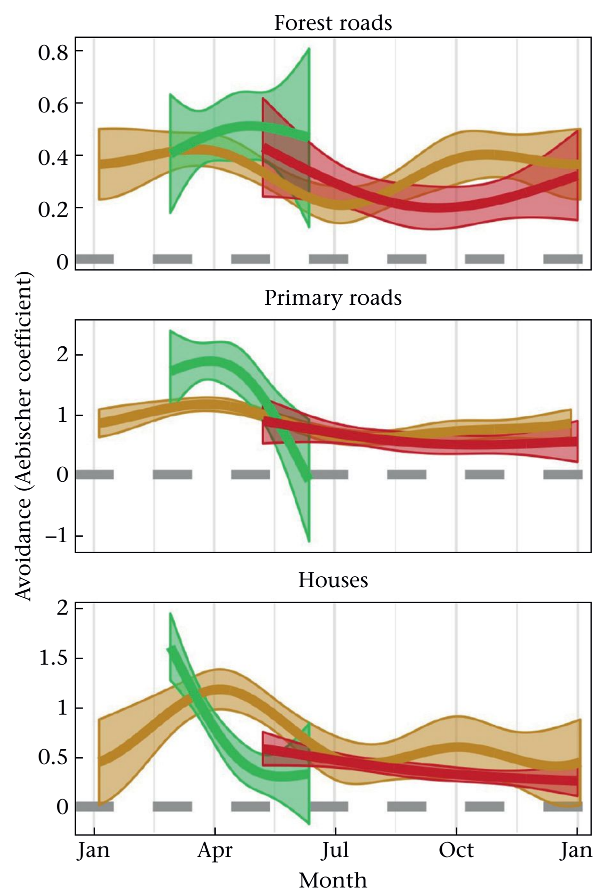

Figure 6. Aebischer avoidance of forest roads, primary roads and houses as a function of time of year, computed as the log of the ratio of locations near and far using a threshold distance of 200 m from forest roads and 600 m from primary roads and houses for used and null data sets. Curves are coloured by wolf subgroup and disperser movement phase (yellow for control animals, green for dispersers in natal territories, red for dispersers in new territories). Bands indicate ± 2 SE pointwise. Note difference in *Y*-axis scales.

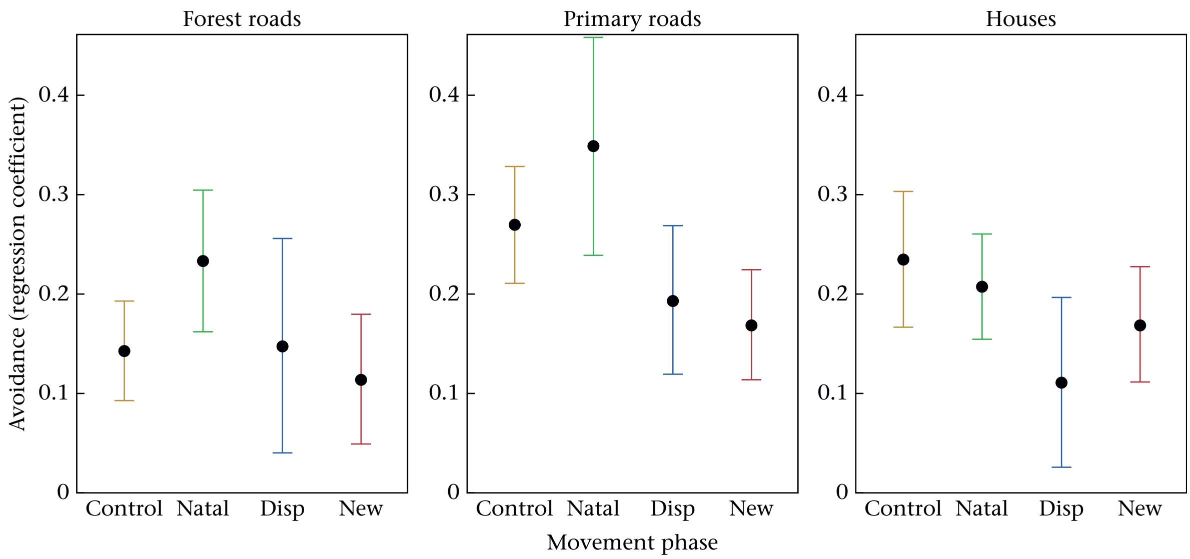

Figure 7. Avoidance coefficients for each movement phase (control, natal territory, dispersal, new territory) based on conditional logistic step selection analysis for forest roads, primary roads and houses using discrete thresholds of 200, 600 and 600 m, respectively. Error bars show ± 2 SE.

environmental, social and seasonal structure in wolf behaviours, and selected what we considered indexes of boldness based on well-understood aspects of wolf behaviour. The observational nature of our study also required a contextualization of wolf dispersal in general, and in Finland in particular.

Large-scale Avoidance

Due to historic and current persecution, as well as large-scale anthropogenic habitat loss (Ripple et al., 2014; Sazatornil et al., 2016; Suutarinen & Kojola, 2017), wolves are highly human-averse and avoid roads and settlements throughout their global range (Kojola et al., 2016; Person & Russell, 2008; Sazatornil et al., 2016). In Finland, wolves are more or less compelled to disperse to more human-impacted areas from a less densely human-populated core range, as northward dispersal is limited by strict predator control in the Reindeer Management Area while eastward dispersal is limited by the presence of established and largely saturated wolf populations in Russia (Kojola et al., 2006).

Wolves were successful in establishing territories with relatively low house and road densities (Fig. 4), and new territories were established far from population centres. While this large-scale selection for less-impacted areas is well established (Jędrzejewski et al., 2008; Kaartinen et al., 2005, 2015; Karlsson et al., 2007; Mladenoff et al., 1995; Sazatornil et al., 2016), previous studies did not constrain the set of available territories by taking into account the dispersal process itself. By focusing on the dispersal process, we found that wolves had a striking ability to find sites with low human impact despite the relatively small immediate area 'sampled' during dispersal. Wolves likely make inferences about an area based on indirect indicators, including presence of human-built elements, which may correlate with less human impact. The cognitive mechanism (i.e. the combination of spatial memory, exploration and giving-up strategy) by which wolves select new territory, resulting in their identification and establishment in areas with reduced human impact, remains a mystery and a topic of future work. We noted in our data that most territories were settled immediately after a hair-pin backtrack in the dispersal track, suggesting the wolf determined a particular portion of its dispersal trajectory was suitable for an attempted settlement. In moving through an environment with which they are not familiar and needing to make a basis for selecting the new territory, it is likely that a certain amount of exploratory boldness was necessary for dispersing wolves.

Intrinsic Boldness

It is difficult to make inferences about the intrinsic boldness of wolves that eventually dispersed. Animals that eventually dispersed showed, if anything, somewhat stronger avoidance of human elements in the months before dispersing than control animals that never dispersed, which superficially contradicts an expected link between boldness and a dispersal syndrome. This, however, likely reflects the fact that the nondispersing control group did not disperse during the period they were collared, but many of those wolves had likely dispersed earlier in their lives. There may have even been a bias in our results in that dispersing wolves typically leave packs that are well established with relatively high annual recruitment of pups, which may be correlated with natal territories more concentrated in the less human impacted core range of wolves in Finland. This reflects the difficulty of selecting appropriate control groups for explorations of personality traits in a wild population.

Another reason dispersing wolves did not appear to show any intrinsically higher boldness is that the movements of an individual while in an established pack is largely social (Mech & Boitani, 2003), such that the movements of one collared wolf are often used as proxies for the movements of an entire pack (Gurarie et al., 2011). The lone, dispersing individual does so in an entirely different social context. Typical dispersers – male or female – are sexually mature younger animals leaving their family group to find a mate. Under neutral conditions with high food availability, the majority of wolves eventually disperse, and individual boldness may play a smaller role in that decision. In fact, those animals that successfully attain reproductive status within their own pack may, in fact, be the more aggressive animals. In Finland, illegal hunting of wolves is relatively common (Suutarinen & Kojola, 2017), and when animals are killed, this can be an exogenous trigger for an animal to disperse. The behaviour of an animal prior to dispersal is therefore a poor proxy for its individual boldness. We did, however, observe a decrease in avoidance of primary roads and houses directly preceding the onset of dispersal (Fig. 6), an intriguing signal that might be explained be an innate expression of boldness immediately preceding dispersal.

Acquired Boldness

Our ultimate proxy for acquired boldness was in the comparison of wolf avoidance of human elements before, during and after dispersal. As predicted under the hypothesis of boldness acquisition, avoidance of human elements generally decreased across the phases of dispersal, with some persistence of the lower level of avoidance in the newly settled phase.

Unpaved forest roads are nearly ubiquitous in rural Finland, and, although rarely used by humans and providing potentially useful movement corridors, wolves generally avoid them. Wolf use of unpaved forest roads increased markedly during dispersal. This shift is probably a result of the increased importance of travel efficiency during dispersal and a lack of familiarity with other useful corridors such as creek beds and forest edges – both also used by wolves to facilitate movement (Gurarie et al., 2011). Wolves in our study moved, on average, twice as fast during the dispersal period than in the natal territory, consistent with the increases in speed observed by wolves using seismic lines (two-fold increase) and forest roads (three-fold increase) in Alberta, Canada (Dickie et al., 2017).

Wolves continued to use forest roads at a higher level in the new territory – even to a slightly greater extent in the new territory than during dispersal. Because forest road density is approximately constant across natal and new territories, the observed change in forest road selection reflects a true shift in behaviour and not an artefact of forest road availability – which was in any case controlled for in both our fine-scale selection analyses. Wolf movement speeds in the new territory, while lower than those during dispersal, were greater than those in the natal territory, which is again possibly linked to increased forest road use. A close analysis of kill sites for two packs in the core wolf range in Finland indicated that prey species also avoid forest roads (Gurarie et al., 2011), suggesting that it is improved mobility through a landscape rather than hunting that motivates road use.

Wolves strongly avoided houses and primary roads across all movement phases. Although the coefficients of avoidance were comparable to those of forest roads, the distance threshold of avoidance was much greater – around 600 m for houses and primary roads, compared to 200 m for forest roads. Paved primary roads have higher levels of traffic and human density than forest roads (Whittington, St Clair, & Mercer, 2005), serve as barriers to dispersal (Beyer et al., 2016) and were shown to be strongly avoided by wolves throughout Finland. Similarly, houses are the most direct indicators of human presence and activity (Kojola et al., 2016). As with forest roads, during dispersal itself, the strength of avoidance weakened considerably and remained low for primary roads, again suggesting that the wolves may have learned to fear them less having survived the dispersal without consequences. Avoidance of houses, however, rebounded to near predispersal levels, perhaps suggesting a stronger, more deeply seated aversion for direct and constant human presence once settled.

In an analysis of house and yard visits among Finnish wolves, Kojola et al. (2016) reported that the movements of adult wolves tended to skirt somewhat closer to houses than did the movements of younger recent dispersers, but adult wolves showed clearer avoidance in territories where house densities were high. The authors suggested that this could be a consequence of increased confidence based on prior experience and learning. Specifically, they suggested that this reflects not merely acquired boldness but increasingly intelligent boldness, as older wolves in more human-impacted areas modify their activity to become familiar with their surroundings and, as happens in more human-impacted areas, to be more active at night (Hebblewhite & Merrill, 2008). This observation, which explicitly points to a change of responses over an extended period of ageing for a wolf, underscores the complexity of the dispersal process and the difficulty of demonstrating acquired boldness unequivocally. Our argument relies on the assumption that a reduction in avoidance of certain human landscape elements is a reliable indicator of the boldness personality trait, whereas the actual avoidance of habitat elements may be determined in part by constraints imposed by the act of dispersal itself. In natal territories, dispersing wolves are generally junior members of an established pack, often moving jointly with other adults and targeting larger prey. In contrast, in newly settled territories, dispersing wolves are solitary or consist of a single breeding pair, possibly leading the animals to have a higher tolerance for risk. Furthermore, our sample size – while large for a dispersal study on a large carnivore – is still somewhat limited, and our confidence intervals, derived from intentionally conservative statistical analyses, are rather wide, reflecting the considerable variation among the individual dispersal events, as is to be expected from a complex and individually idiosyncratic species like the wolf.

To strengthen our conclusions regarding the persistence of a new behavioural trait, it would be necessary to follow the habitat use and preferences of newly settled wolves as they age and accrue experiences and as their packs grow. Ideally, an animal would be tracked as long as its newly established pack is similar in size and composition to the natal pack it abandoned, with sufficiently large sample sizes to make strong inferences. Monitoring efforts of wolves are ongoing in Finland, although high levels of illegal killing (Suutarinen & Kojola, 2017) make longer-term studies of wolves a challenge.

Consequences of Boldness

For many species, boldness leads to higher risk and higher reward scenarios (Cote, Clobert et al., 2010), the costs and benefits of which are highly context dependent. For example, bolder swift foxes, *Vulpes velox,* reared in captivity showed lower survival in a reintroduction programme (Bremner-Harrison, Prodohl, & Elwood, 2004), whereas bolder geckos showed higher foraging success in urban environments (Short & Petren, 2008). Speed of invasions for non-native fish (Myles-Gonzalez, Burness, Yavno, Rooke, & Fox, 2015; Rehage & Sih, 2004) and birds (Duckworth & Badyaev, 2007) are accelerated by a 'front' of bold dispersers. For wolves, the potential increase in boldness as a direct consequence of dispersing into areas with a greater human footprint suggests that wolf–human interactions may become even more frequent than might be expected with baseline (i.e. predispersal) behaviours, in a dynamic comparable to the 'invasion acceleration' phenomenon. This dynamic is of potential concern, because direct wolf–human conflicts (e.g. livestock depredation and attacks on household dogs), however rare, are responsible for a worsening public attitude towards wolves in Europe over the past 40 years (Dressel, Sandström, & Ericsson, 2015; Kaartinen, Luoto, & Kojola, 2009; Kojola et al., 2016) . However, wolf aversion towards primary roads and houses remained consistent throughout the dispersal and settlement process. The effect of this conflict inflation is therefore likely minimal in Finland, where overall mean human densities are among the lowest in Europe and wolves' diets are almost entirely wild, with very low levels of livestock depredation (Kaartinen et al., 2009), almost no direct diet supplementation and a population heavily regulated by legal and illegal killing (Suutarinen & Kojola, 2017). In other, more densely populated areas, especially in Europe, however, acquired boldness may lead to higher levels of wolf–human conflict.

Conclusion

The wide and ever-increasing application of animal telemetry, with ever-higher spatial and temporal resolution and ever-greater device longevity, is providing novel opportunities to study fundamental relationships between personality traits, such as boldness, and large-scale processes, such as dispersal, in wild populations (Debeffe et al., 2014). To leverage these data, analysis frameworks are required that can (1) identify large-scale behavioural modes, (2) identify measures of boldness and (3) control for social, temporal and environmental dynamics. Resource selection and step selection modelling frameworks provide a consistent way to quantify behavioural responses to environmental 'stimuli' – responses that vary among individuals and, as we have shown, across life stages. Despite the complexity of observational studies on large mammals in uncontrolled environments, these coefficients more or less satisfy these criteria (measurable, behavioural, variable, interpretable). Even taking the context-specific caveats into account, we conclude that wolves do acquire an elevated tolerance for some human elements during dispersal, a tolerance which persists in a new territory, indicating that an empirical measure of 'boldness' may be acquired through experiences gained in the very act of dispersal.

Data Availability

The data required to replicate the analyses are available at Mendeley https://doi.org/10.17632/9722chrknz.1.

Conflict of Interest

We declare that we have no conflict of interest.

Acknowledgments

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Supplementary Material

Supplementary material associated with this article is available, in the online version, at doi https://doi.org/10.1016/j.anbehav.2020.06.015.

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