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Master thesis

Is there no place like home?

Natal habitat-biased dispersal in the Scandinavian wolf

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Abstract

Natal dispersal is an important mechanism for the viability of populations, as individuals should target the habitat where fitness will be higher. Dispersal theory has suggested that influence of local conditions on individual phenotypes, or experience gained in the natal habitat, could improve future performance if individuals disperse towards a habitat similar to their natal habitat type (i.e, Natal habitat-biased dispersal). Although this phenomenon has been proved for several taxa, little is known about the existence of this effect on large carnivores. In this study, I tested whether the Scandinavian wolf was influenced by the habitat characteristics of its natal territory when choosing a new territory to establish. I used natal and established territories of Scandinavian wolves during the period 1998/1999-2011/2012, and I accounted for potential available habitats for each dispersing individual by simulating dispersing trajectories based on movement behavior characteristics from 13 GPS-collared wolves in Scandinavia. I used several environmental variables to characterize wolf territories. I divided natal, established and available territories with similar habitat charasteristics in clusters by using K-means clustering methods, and tested statistically whether individuals selected the natal habitat type by using conditional logistic regression. Dispersers did not establish in habitats with similar characteristics to those of the natal territory. Groups of territories with similar habitat characteristics were placed in different parts of Scandinavia, so enough habitat heterogeneity was present to expect any type of habitat selection. Although I did not find any clear pattern of habitat selection, wolves avoided areas characterized by high antropogenic disturbance. A combination of wolf intra-species characteristics and its occurrence on the Scandinavian human-dominated landscape could explain the lack of influence of the natal habitat characteristics in the choice of the established territory. Further research on the role the interactions between natal experience, individual heterogeneity and human activities play on dispersal outcomes is needed to understand the mechanisms that drive dispersal choices in large carnivores.

Table of contents

1. Introduction

Natal dispersal influences population dynamics, spatial distribution, genetic structure and social organization of individuals (Ciucci *et al.* 2009; Whitmee & Orme 2013), playing an important role in the viability of natural populations (Palomares *et al.* 2000). Among birds and mammals, it mostly takes place in the immature stage, from the natal area to the site of first potential breeding (Greenwood 1980; Wauters *et al.* 2010). During this process, intraspecific competition, mate choice and habitat quality are determinants for the settlement decision of each individual (Clobert *et al.* 2009). Thus, dispersers rely on both demographic and environmental cues (Lima & Zollner 1996; Matthysen 2005) to target the site where fitness could be maximized (Wauters *et al.* 2010).

An individual may optimize habitat selection by using cues obtained in the natal area to estimate the habitat suitability of the settlement location (Selonen, Hanski & Desrochers 2007). Additionally, local conditions at the birth site might influence the phenotype of dispersers and therefore their subsequent habitat choices (Clobert *et al.* 2009). Hence, individuals originating from a particular type of habitat might perform better if they, for innate or experience-based reasons, disperse to a habitat similar to that where they were born, a phenomenon termed 'natal habitat-biased dispersal' (Haughland & Larsen 2004a; b; Sacks *et al.* 2005; Selonen, Hanski & Desrochers 2007; Wauters *et al.* 2010).

Individuals might disperse towards a habitat similar to their natal habitat for several reasons. Experience gained during the natal phase may improve performance if an individual settles on the same type of habitat, and is likely to encourage phenotypes that are adjusted to these habitat conditions (Stamps & Swaisgood 2007). In addition, cues obtained in the natal site may help dispersers estimating the quality of potential habitats to settle in a short period of time (Davis & Stamps 2004). In any case, habitat heterogeneity and landscape structure play essential roles influencing the dispersal behavior of individuals (Haughland & Larsen 2004a).

The effect of natal experience on habitat preferences (i.e., natal habitat-biased dispersal) has been documented by different terms in taxon-specific literature ('Natal Habitat Preference Induction' and 'Habitat Imprinting' commonly used on vertebrates; Davis & Stamps 2004). Although it has been proved in several studies (Davis 2008), there is a general lack of information about this topic in mammals (Selonen, Hanski & Desrochers 2007), especially in large carnivores.

Factors such as the social structure, extensive space requirements, high mobility and territorial behavior of wolves (*Canis lupus*) make them good candidates for the study of dispersal (Fuller, Mech & Cochrane 2003; Ciucci *et al.* 2009). However, long-range movements by wolves have rarely been studied in detail because of financial and technological reasons (Merrill & Mech 2000b; Wabakken *et al.* 2007), and landscape links are difficult to predict (Fuller, Mech & Cochrane 2003; Ciucci *et al.* 2009). It is important to gain knowledge on this topic for conservation and management purposes, given the slowly re-colonization of wolves across their former ranges throughout Europe (Promberger & Schröder 1993; Ciucci *et al.* 1997) and the world (Ripple *et al.* 2014), spreading back into more human-dominated landscapes (Chapron *et al.* 2014; Ražen *et al.* 2016).

In Scandinavia, wolves exist as a semi-isolated population rooting from 5 founders that originated from a Finnish-Russian population (Vilà *et al.* 2003; Åkesson *et al.* 2014). This population has increased in numbers since 1991, when a wolf pair reproduced in south-central Scandinavia leading to a significant range expansion (Wabakken *et al.* 1994; Liberg & Glöersen 1995; Wabakken *et al.* 2001). However, its expansion has suffered from different constraints, such as illegal poaching and low survival of dispersers that pass through the reindeer management area, which also results in a poor genetic exchange (Wabakken *et al.* 2001). Given the level of inbreeding of this population (Liberg *et al.* 2005), the presence of individuals with contrasting habitat preferences related to different natal origins could be relevant for the maintenance of the genetic variation (Hedrick 1990; Davis 2008).

Although the wolf is a rather generalist species in terms of habitat requirements (Cayuela 2004), some influences of landscape features on its behavior have been documented. For instance, wolves tend to prefer forested and flat areas if available (Ciucci *et al.* 1997), but open areas such as shrub lands are also selected (Huck *et al.* 2011). Besides, prey species availability e.g. moose (*Alces alces*), seem to shape wolf preferences towards the habitat selected by the prey (Walton *et al.* 2001; Lesmerises, Dussault & St-Laurent 2012). Interespecific competition with brown bears (*Ursus arctos*) has also been suggested to affect wolf-pair establishment (Ordiz *et al.* 2015). Wolves usually avoid areas with high anthropogenic influence, such as high cabin densities (e.g., Lesmerises, Dussault & St-Laurent 2012). However, human infrastructure such as secondary roads has also been considered useful (e.g., Lesmerises, Dussault & St-Laurent 2013; Zimmermann *et al.* 2014) or at least non-detrimental (e.g., Ciucci *et al.* 2009; Ražen *et al.* 2016) for wolf movement.

The high number of studies on wolf habitat selection shows large variation in habitat used at different scales. A study in the Canadian Rocky Mountains, showed that the genetic structure of a wolf population was associated with two land cover types, suggesting that habitat affinity or natal habitat-biased dispersal occurred in this population (Cullingham *et al.* 2016). However, to my knowledge, the role of natal experience on a dispersing wolf's territorial choice has never been tested.

The aim of this study is to test whether the Scandinavian wolf is influenced by its natal habitat characteristics when choosing a territory to settle. In other words, I tested whether individuals settled in habitats with similar characteristics to those of the natal territory. Using the re-constructed pedigree of the Scandinavian wolf population (Liberg *et al.* 2005), I considered as natal territory the spatial location of the territory where individuals were born and, as established territory, the location of the territory of the first detected successful pairing. Habitat availability influences the distribution of successful dispersers (Venier & Fahrig 1996). Therefore, I also took into account potential available territories that each individual could have encountered before establishing, by simulating dispersal behavior using characteristics from GPS-collared dispersing wolves in Scandinavia. For natal and established territories, I used the pedigree information and annual locations of scent-marking wolf pairs detected within the winter monitoring program from 1998-2011 (Wabakken *et al.* 2012). I then defined available territories using random locations selected along simulated dispersal trajectories from the natal to the established territory. I studied the similarities between natal, established, and available territories by characterizing their landscape attributes with several environmental variables. I predicted that wolves would be more likely to establish in a territory with habitat characteristics similar to those of the natal territory. Because sex seems to have an influence on dispersal behavior in mammals (Howard 1960; Wabakken *et al.* 2015), I also tested for sex-specific differences.

2. Material and methods

2.1 Study area

The study area was located in south-central Scandinavia within the wolf breeding range, covering approximately 100,000 km^2 (Figure 1). This area is dominated by boreal coniferous forest mixed with bogs and lakes. The main tree species are Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), followed by birch (*Betula pendula* and *B. pubescens*), aspen (*Populus tremula*) and alder (*Alnus incana* and *A. glutinosa*) (Moen 1998; Rydin, Snoeijs & Diekmann 1999). Secondary land cover types are mires, agricultural lands and human settlements. The ground is usually covered by snow between December and March (Dahlström, Raab & Vedin 1995).

Human density within the wolf range is low, with less than 1 inhabitant/km^2 (Wabakken *et al.* 2001). Main road density is 0.19 ± 0.02 km/km^2, and due to intensive forest management practices, gravel road density is on average 4.6 times higher (Sand *et al.* 2008; Zimmermann *et al.* 2014).

The main prey species for Scandinavian wolves are moose (*Alces alces*) and to a minor extent, roe deer (*Capreolus capreolus*) (Sand *et al.* 2008; 2012). Sympatric large carnivore species in different parts of the wolf range are brown bear (*Ursus arctos*) (Ordiz *et al.* 2015), Eurasian lynx (*Lynx lynx*) (Liberg & Andrén 2006) and wolverine (*Gulo gulo)* (Wabakken *et al.* 2001).

2.2 Study animals and period

I used data from the long term wolf monitoring program in Scandinavia, which is based on a combination of snow tracking, DNA-analyses and radio telemetry (Wabakken *et al.* 2001; Liberg *et al.* 2011).

Norwegian and Swedish management authorities and research institutions conducted extensive snow tracking every winter, where territorial scent markings and estrus bleeding were recorded to locate and distinguish between different wolf territories (Liberg *et al.* 2011). DNA analyses allowed the reconstruction of a quasi-complete pedigree of the population, based on invasive (tissues from retrieved dead wolves and blood from captured wolves) and non-invasive samples (scats) (Liberg *et al.* 2005; 2011). Additionally, the
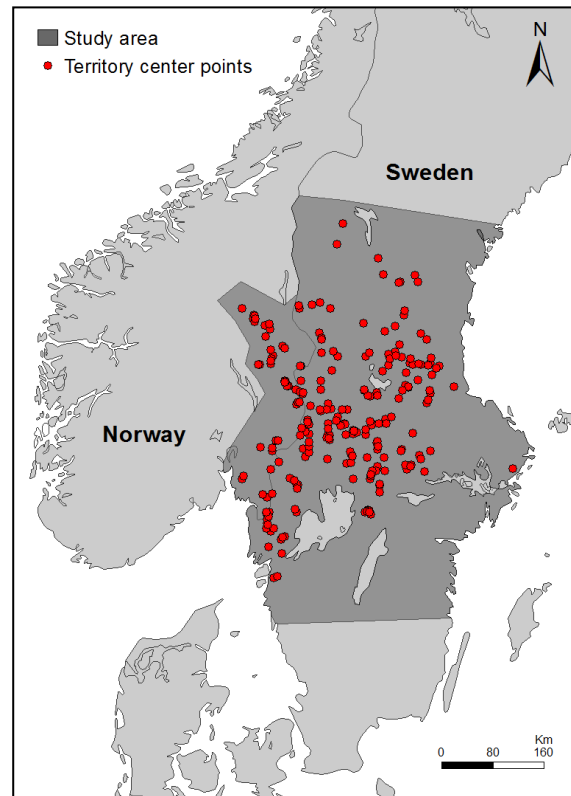
Figure 1. Map of the study area in south-central Scandinavia (the area actually available for wolves is shown in dark gray), showing the center points of all wolf natal and established territories detected from the winter 1998/1999 - 2011/2012

Scandinavian wolf research project (SKANDULV) captured and fit GPS collars on wolves since 1998 (Wabakken *et al.* 2007; Liberg *et al.* 2011; Mattisson *et al.* 2013).

The study period was defined from the winter 1998/1999-2011/2012, when Swedish and Norwegian authorities started to make official annual wolf status reports (Wabakken *et al.* 1999). Genetic identification of new reproductive pairs and territory distribution have been principal goals of the monitoring and research (Liberg *et al.* 2011; Ordiz *et al.* 2015). During this period, the wolf population increased from 70 to 295 wolves on average (Wabakken *et al.* 1999; Wabakken *et al.* 2012).

2.3 Definition of successful dispersal

Wolves are territorial and offspring usually disperse when they are one year old (70 %) or two years old (Chapron *et al.* 2015). I defined natal dispersal as dispersal from the location of the birth (hereafter natal) territory to the site of first detected successful pairing, i.e., a new established (hereafter established) territory. The available genetic pedigree for the

Scandinavian wolf population was used to identify the parents (i.e. the pair) of each individual detected within their first scent marking-pair. For each individual in each pair, the spatial location of the parental pair was defined as the center of the natal territory and the location of the first detected successful pairing was defined as the center of the established territory.

All locations obtained from winter snow tracking and GPS/VHF locations from collared individuals were used to define the location of natal and established territories. Since the accuracy of territory locations varied among pairs and years, I used the centroid of all available locations as the center of the natal territory (i.e., parental pair) and the exact location of the first successful pairing as the center of the established territory. I then applied a 1000 km^2 buffer around each territory center (i.e. the average wolf home range size; Mattisson *et al.* 2013) to define the area occupied by the territory (Ordiz *et al.* 2015). Since birth year was not always known, I assumed that dispersal occurred half year before the detection of the first pairing (i.e. between the winter monitoring period when the individual was first detected in a pair and the previous monitoring period).

2.4 Creation of available territories

In order to account for wolf dispersal behavior when defining available territories, I simulated random dispersal trajectories between the natal and established territories. I used movement characteristics of GPS collared wolves during dispersal (Figure 2). The movement behavior most commonly found by direct observation of animal dispersal trajectories is correlated random walk (CRW), in which the direction of one step is correlated with that of the previous step or steps (Hawkes 2009). Therefore, I created CRW from natal to established territories of each study animal. CRW were simulated from the dispersal movement characteristics of 13 dispersing GPS-collared wolves in Scandinavia (See Appendix 2 for more information of the movement characteristics), using the null model 'NMs.randomCRW' from the R package adehabitatLT (Calenge 2015). Only the GPS locations during dispersal (i.e. from approximate dispersal date to the settling date (Chapron *et al.* 2015)) were used as data to simulate the dispersal trajectory. I used the natal territory of the study animals as a starting point, and the established territory as the ending point of the trajectory. The movement characteristics of each of the 13 wolves during dispersal were used separately to simulate different trajectories and take into account individual variation in dispersal behavior (Hawkes 2009).
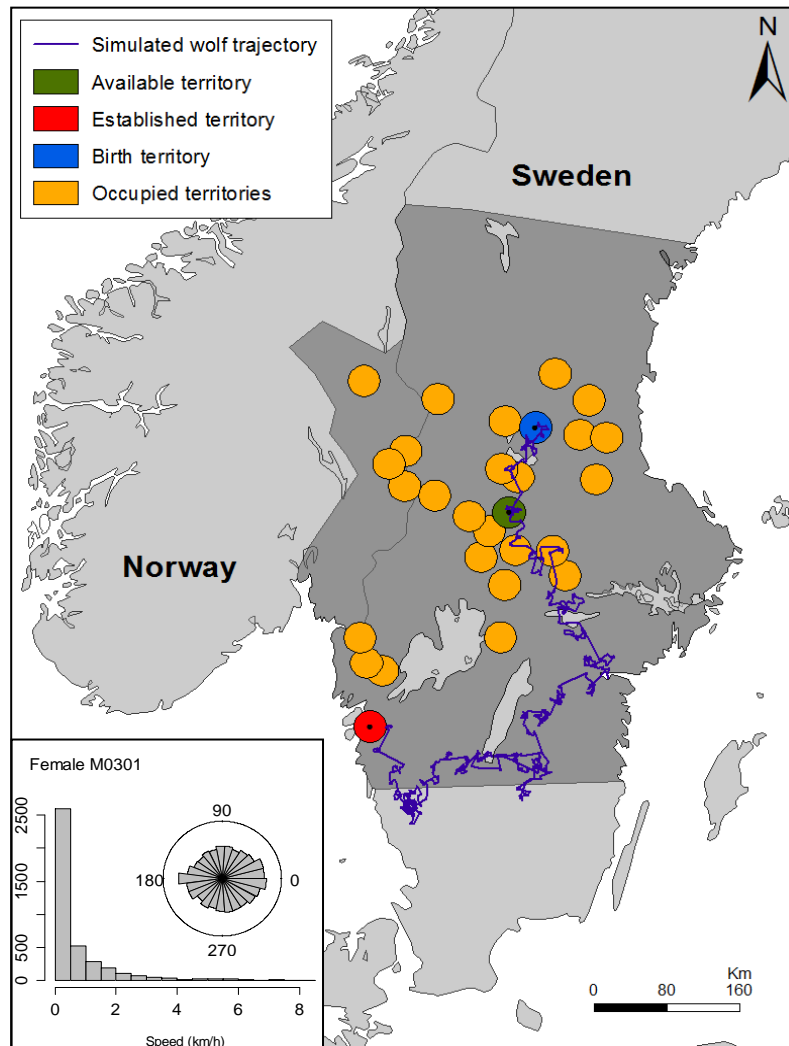
Figure 2. Example of a trajectory (purple line) simulated from the dispersal movement characteristics of the GPS-collared individual M0301 (Down left corner, from Table A. Appendix 2). The simulated trajectory starts from the natal (blue) to the established (red) territory of a male (G 53-10) that dispersed on a long distance. The locations of the territories occupied one year before establishment (t-1) are showed in orange. The territory selected randomly along the simulated dispersal trajectory, created to account for habitat availability, is shown in green. A buffer of 1000 km ^{2} has been applied around the centroid of all territories, from which landscape characteristics were extracted. The study area is shown in dark gray.

However, it was not possible to define an arrival point when creating random walks. I therefore simulated random walks until one of them crossed the established territory, i.e. the random walk fell inside the $1000km^2$ buffer created around the center of the established territory. Simulated trajectories from GPS collared individuals with short dispersal distances had movement characteristics that did not allow the trajectory to reach the established territory for individuals having long dispersal distances. I therefore used GPS-collared wolves with long, medium and short dispersing distances to simulate long (> 200 km), medium (40 - 200 km) and short (< 40 km) dispersal trajectories between natal and

established territories, respectively. I considered short dispersal distance (< 40km) which is about twice the radius size of a wolf territory (i.e. 20 km is the radius of an average home range size of 1000 km^2). Therefore, short dispersal category characterized individuals that established their territory contiguously from their natal territory. The trajectories from natal to established territories of short dispersing individuals were simulated with the movement characteristics of 2 of the 13 GPS-collared wolves, i.e. the GPS-collared wolves with shortest dispersal distances (Figure B, Appendix 2). These simulated trajectories had an exploratory pattern due to the short dispersal distance. Therefore, I did not stop the CRW when it reached the established territory (i.e. fell inside the 1000 km^2 buffer around the established territory) in order to obtain an exploratory dispersal pattern around the natal and established territory. The threshold between the medium and long category (200 km), was chosen based on computing limitations. Indeed, only movement characteristics of the GPS-collared that performed long dispersal could be used to simulate CRW for long observed distances (>200 km) between natal and established territories (i.e. in order that the simulated trajectory reached the established territory). I used the other 11 of the 13 GPS-collared wolves, i.e. the ones with longer dispersal distances (Figure A, Appendix 2), to simulate the trajectories with medium distances between natal and established territories. From these 11 GPS-collared wolves, I chose the 3 GPS-collared wolves with the longest dispersal distances to simulate the trajectories where distances between natal and established were the longest (Figure A, Appendix 2).

I then sampled one random point in each simulated walk, constraining the creation of the points by: (1) the management regime limits the wolf population to south-central Scandinavia (Figure 1), due to reindeer husbandry in the north, open land sheep husbandry in the west and high human densities in the south (Liberg *et al.* 2011). Since wolves that establish outside of this area get most likely killed, I prevented random points from falling outside the area. (2) Availability changed annually, as territory occupancy is dynamic and wolf pairs cannot settle in territories that are already occupied by another pair. Therefore, I also prevented random points from occurring in territories that were occupied on the year before establishment (*t-1*), which also represented the situation of the year of establishment (*t*). However, if a turn-over or the death of the individual composing the territory was observed between *t-1* and *t*, the location of the random point within this territory was made possible.

For each wolf, I obtained 11 random points extracted from 11 different walks. I chose 11 because it is a commonly used design in case-control study (Zimmermann *et al.* 2014; Ordiz *et al.* 2015). In addition, I was limited to use 11 GPS trajectories for the medium and long dispersing individuals, because the two other GPS-collared individuals had dispersal distances that were too short to be used in this simulation.

2.5 Landscape-related variables

In order to characterize the landscape characteristics of natal, established and available territories, I applied a 1000 km^2 buffer around each territory center, (i.e. the average wolf home range size; Mattisson *et al.* 2013; Ordiz *et al.* 2015) and extracted all variables described below. Variables were stored in a raster with a grid size of 1km x 1km. For a more detailed information of the variables and sources of information see Appendix 1.

Interspecific variables

For moose in Scandinavia, harvest density is related to variation in moose density with a one year delay (temporal variation in harvest density is better explained by moose density in year t-1 than in year t; Ueno *et al.* 2014). Therefore, I used moose harvest density (number of moose harvested/km^2) at the municipality and management unit level in Scandinavia with a one-year time lag (Milleret; unpublished manuscript; Ordiz *et al.* 2015).

Bear density and distribution is well reflected by hunting reports (Swenson, Sandegren & SO-Derberg 1998; Kindberg, Ericsson & Swenson 2009; Ordiz *et al.* 2015). Thus, I used an index of bear density ranging between 0 and 1, low and high density respectively, based on records of shot bears during 22 years (see Ordiz *et al.* 2015).

Human-related variables

I obtained human density (inhabitants/km^2) at the municipality level. I also used building density (buildings/km^2), density of main and gravel roads (km/km^2) and an index of remoteness and accessibility of the landscape based on combined building and road densities (number of building along km of road stretches) (Milleret; unpublished manuscript; Ordiz *et al.* 2015).

Land-cover variables

I used a vegetation map (Table A, Appendix 1) and simplified the classification to keep the following land cover categories: forest, mires, mountains, water, agricultural areas and other human-dominated areas. I analyzed vegetation at a 200 m grid size by calculating the

proportion of each cell in relation to the surrounding cells, and then resized the resolution to 1000 m for computing limitations. I merged the Digital Elevation Model of Sweden and Norway to obtain the altitude (m above sea level). I also computed the slope (degrees) and roughness at a 25 m resolution by using the 'terrain' command (R package raster; Hijmans *et al.* 2015) from the DEM layer. In order to analyze slope and roughness at a 25 m grid size, I calculated the average of each cell with the surrounding cells, and I created a moving window with a matrix size of 5 x 5 cells.

2.6 Statistical analyses

2.6.1 Multivariate analyses

I performed a Principal Component Analysis (PCA) on the resulting matrix containing the environmental variables characterizing the natal, established and available territories. Since wolf density had increased continuously during the study period, I also included Year as a continuous variable to control for an eventual year effect. I standardized all variables to remove the differences caused by distinct units. I retained the first 5 principal components based on the Kaiser method, which suggests keeping only components with eigenvalues > 1 (Table 1).

2.6.2 Cluster selection analyses

In order to determine whether wolves established in similar or different habitats than that of the natal territory, I used a K-means cluster analysis over the 5 Principal Components of the PCA analysis to group territories with similar habitat characteristics (each cluster contained natal, established and available territories). In order to select the appropriate clustering method and number of clusters, I used cluster validation measures with the function 'clValid' (R package clValid; Brock *et al.* 2011). This recommended a K-means cluster analysis with a 5-cluster division. K-means divides the data points into k groups, such that the sum of squares from points to the assigned cluster centers is minimized. Preliminary analyses showed that a biological interpretation of the clusters was difficult when 5 groups were used. The within-group sum of squares dropped after 5 to 8 clusters (Figure 3), so I used 6 different clusters to group similar natal, established and available territories. Each one of the natal, established and available territories was assigned to one of the 6 clusters.

I then statistically tested whether individuals established in territories with similar habitat characteristics (i.e., same cluster) than their natal territories. I regrouped individuals sharing the same natal cluster, and I used a case-control design matching established with available territories for each of them. I used one conditional logistic regression with the binary response established (1) and available (0) for individuals with the same natal cluster using the clogit function (R package survival; Therneau 2013). I repeated the same procedure for each sex in order to test for sex differences. I included the variable Cluster (1-6) as a categorical explanatory variable. The 11 available territories were paired with the established territory (1:11) of each individual as a "stratum" (Fortin *et al.* 2005). Using the cluster analyzed as the reference category in the conditional logistic regression, I checked whether individuals significantly selected or avoided other clusters using p-values and 0.05 as a threshold. All analyses were conducted in R 3.1.1 (R Core Team 2014).
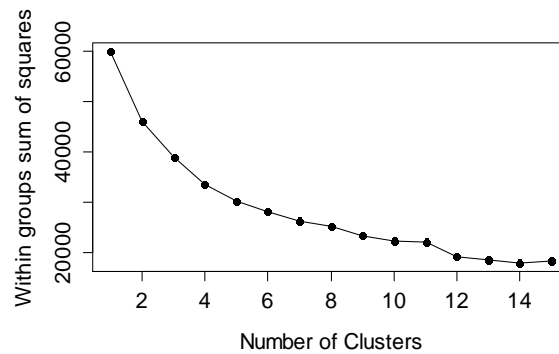

Figure 3. Plot of the within group sum of squares versus the clusters extracted. The drop between the 5 to 7 clusters suggests that a 6-cluster division is valid.

3. Results

3.1 PCA and cluster interpretation

The first 5 axes retained from the PCA explain 79.80 % of the variance (Table 1). The first axes (PC1) describes the difference between the variables bear, mires, building density versus moose, main roads, slope and roughness , located at opposite sides of the axes (Figure 4). The second axes separates variables related to human disturbance versus variables related with terrain characteristics (mires, altitude, forest, mountain, slope and roughness). The third, fourth and fifth axes were retained to create the clusters because it explained a cumulative proportion of the variance (Table 1), but did not show a clear separation of the relevant variables

Table 1. Variance and cumulative variance explained by the 5 first principal components retained from the PCA. Principal components were retained according to the Kaiser method (eigenvalues > 1).

	Principal component number				
	1	2	3	4	5
Eigenvalue	6.34	2.66	2.31	1.21	1.04
Proportion of variance explained	37.30	15.67	13.59	7.13	6.09
Cumulative variance explained (%)	37.30	52.98	66.58	73.72	79.81

The output of the PCA and K-means results showed 6 different clusters. Each cluster contained natal, established and available territories characterized by similar landscape variables (Figure 4). Consistent with their habitat characteristics, each cluster presented a different location on the study area (Figure 5). Cluster 1 (Bear-Mires), was represented by high bear densities and mires, with some influence of altitude and located north of the study area; In contrast, Cluster 2 (Intermediate human) was mainly characterized by intermediate levels of the human-related variables human density, agricultural fields and main roads, with some effect of year and water. It was located at the center of the study area; Cluster 3 (Building) was highly influenced by building density, with some effect of year, and human variables such as secondary roads, remoteness and human-dominated areas, located on the east part of the study area; Cluster 4 (Rough terrain) was represented by high levels of mires, altitude, forest, mountains, slope and roughness, and located at the north-west part of the study area; Cluster 5 (High human) represented high influence of all the human-related variables and was located south of the study area. Both clusters 4 and 5 were distributed
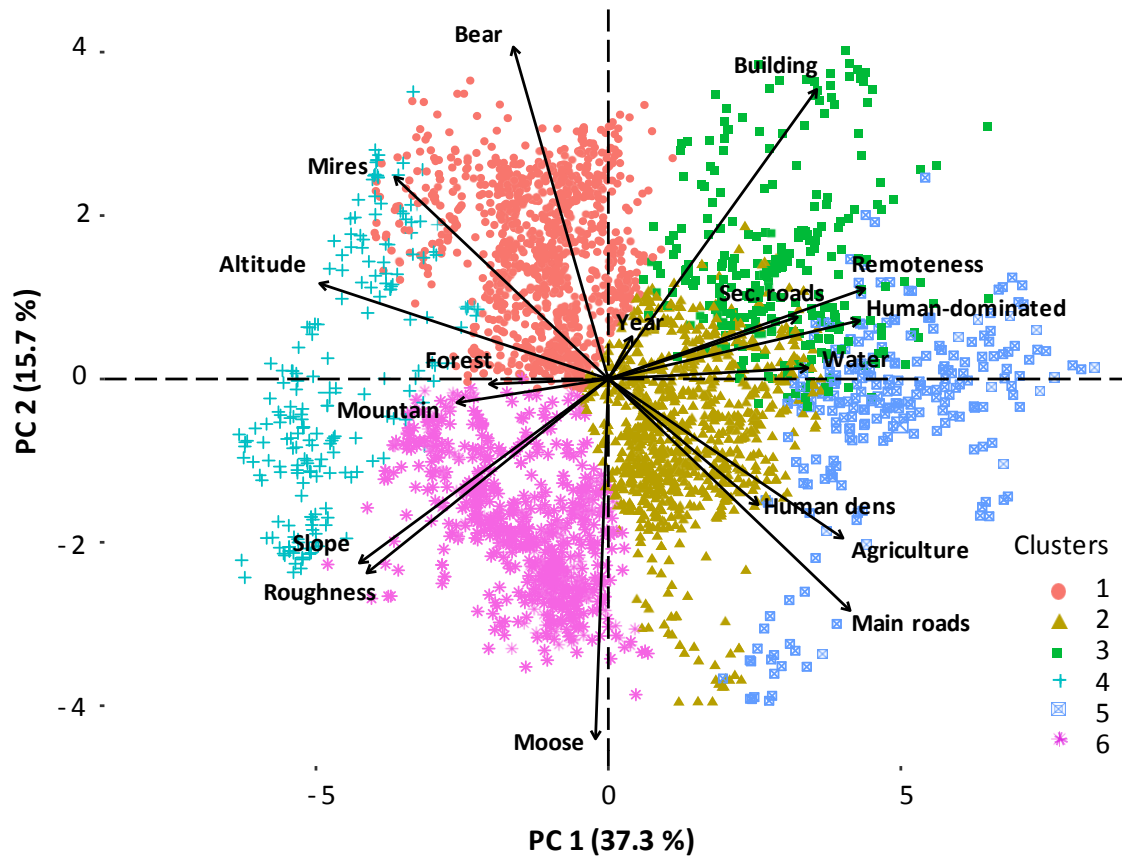
Figure 4. Principal component analysis (PCA) for natal, established and available territories showing the two first principal components and their proportion of variance explained (%). Variables are represented by arrows with contribution to the PCA related to the length of the arrow. Landscape variables showed are: bear, mires, altitude, forest, mountain, slope, roughness, moose, main roads, human density, agriculture, water, human-dominated landscape, remoteness, secondary roads, year and building density. The 6 clusters obtained by K-means are represented by different colors and shapes. Each cluster contains natal, established and random available territories with similar habitat characteristics.

continuously along the PC 2 in opposite directions; Cluster 6 (Moose) was mainly characterized by intermediate-high moose density, mountain, forest, slope and roughness, with location west of the study area.

3.2 Habitat influence on natal dispersal

The number of natal and established territories varied among clusters (Table 2). Since I did not detect any natal territory in Cluster 3 (Building), I could not use it for further analyses. I only obtained significant results on the conditional logistic regression of individuals born in Bear-mires (Cluster 1), Intermediate human (Cluster 2) and Moose (Cluster 6) (Table 3). The 95 % CI around the estimates (β) with significant p-values did not overlap with 0, indicating either avoidance or selection for other clusters.
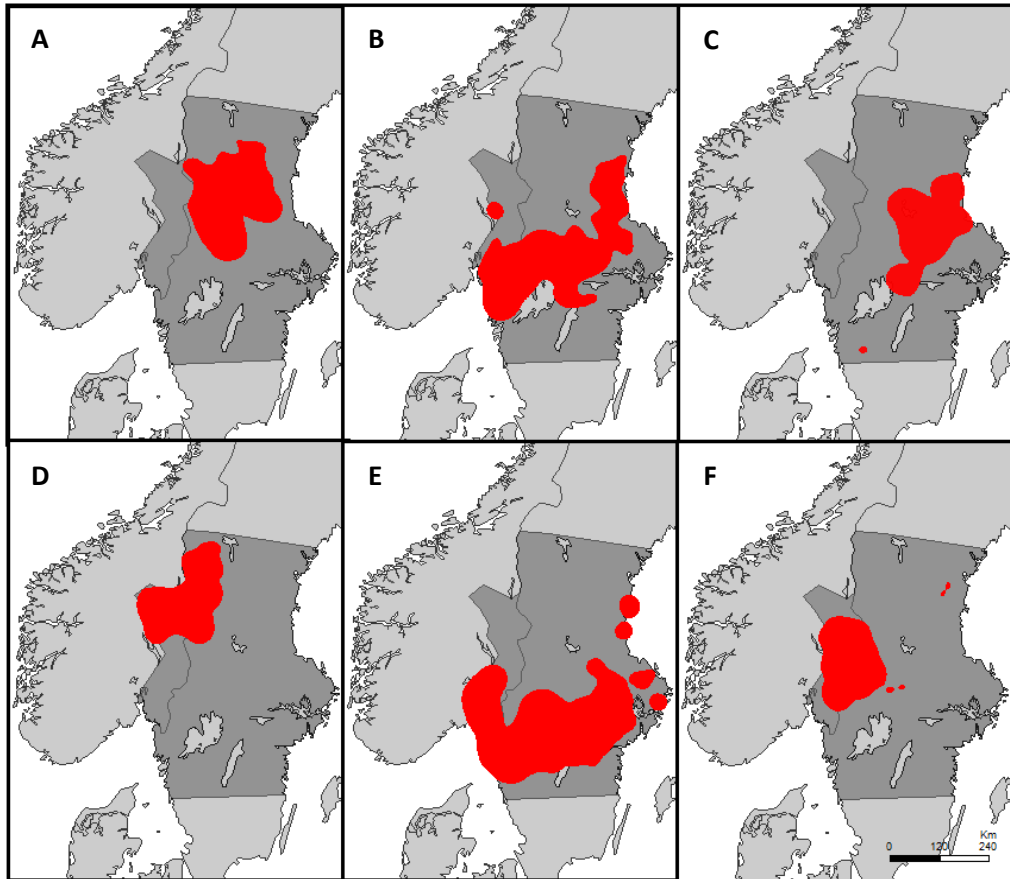
Figure 5. Spatial location of the clusters identified by K-means clustering analysis. The red areas represent the location of wolf territories (natal/established/available) with similar habitat characteristics in south-central Scandinavia from 1998-2012. A 95% kernel contour was applied to locations of territories for each cluster: Cluster 1-Bear mires (A), Cluster 2-Intermediate human (B), Cluster 3-Building (C), Cluster 4-Rough terrain (D), Cluster 5-High human (E), Cluster 6-Moose (F).

Bear-mires (Cluster 1)

Females and males that originated from this cluster selected the Moose cluster for establishment significantly more than expected (Females: $\beta \pm SE = 1.74 \pm 0.49$; $p<0.001$, Males: $\beta \pm SE = 1.48 \pm 0.44$; $p<0.001$; Figure 6A). Additionally, males selected the Intermediate human and Rough terrain clusters to establish more than expected (C2: $\beta \pm SE = 0.95 \pm 0.42$; $p<0.05$, C4: $\beta \pm SE = 1.65 \pm 0.66$; $p<0.05$; Figure 6B).

Intermediate human (Cluster 2)

Females born in this cluster avoided settling in the High human cluster ($\beta \pm SE = -1.35 \pm 0.26$; $p<0.05$). Moreover, males that originated from this cluster selected the Bear-mires and Moose clusters for establishment (C1: $\beta \pm SE = 1.35 \pm 0.54$; $p<0.05$, C6: $\beta \pm SE = 1.48 \pm 0.53$; $p<0.05$).

Rough terrain (Cluster 4) and High human (Cluster 5)

Individuals born in these clusters did not show any significant pattern when selecting or avoiding other clusters for establishment (Table 3)

Moose (Cluster 6)

Males born in this cluster selected Bear-mires, Intermediate human and Rough terrain clusters to establish more than expected (C1: $\beta \pm SE = 1.47 \pm 0.54$; $p<0.05$, C2: $\beta \pm SE = 2.12 \pm 0.55$; $p<0.05$, C4: $\beta \pm SE = 1.68 \pm 0.76$; $p<0.05$).

3.3 Human influence on wolf cluster selection

The results of the PCA and K-means clustering presented three groups of territories characterized by human-influencing variables: Intermediate human (Cluster 2), Building (Cluster 3) and High human (Cluster 5). The Building and High human clusters were the only ones not selected by individuals, independently from their natal cluster (Figure 6; Table 3). Additionally, High human was significantly avoided by females born in Intermediate human (Table 3). In addition, males from Bear-mires and Moose selected significantly the Intermediate human cluster to settle.

Table 2. Number of natal (N) and Established (E) wolf territories in south-central Scandinavia from 1998-2012 in each cluster.

Cluster		Females	Males	Total
Bear-mires	N	52	57	109
(1)	E	39	41	80
Intermediate human	N	38	36	74
(2)	E	43	45	88
Buildings	N	0	0	0
(3)	E	8	8	16
Rough terrain	N	6	7	13
(4)	E	8	11	19
High human	N	1	1	2
(5)	E	4	5	9
Moose	N	34	39	73
(6)	E	29	30	59

The clusters that included higher occurrence of natal and established territories were Bear-mires, Intermediate human and Moose. I did not detect any natal territories in the Buildings cluster, although 16 individuals settled on it. I also found more established than natal territories in the Intermediate human, Rough terrain and High human clusters (Table 2

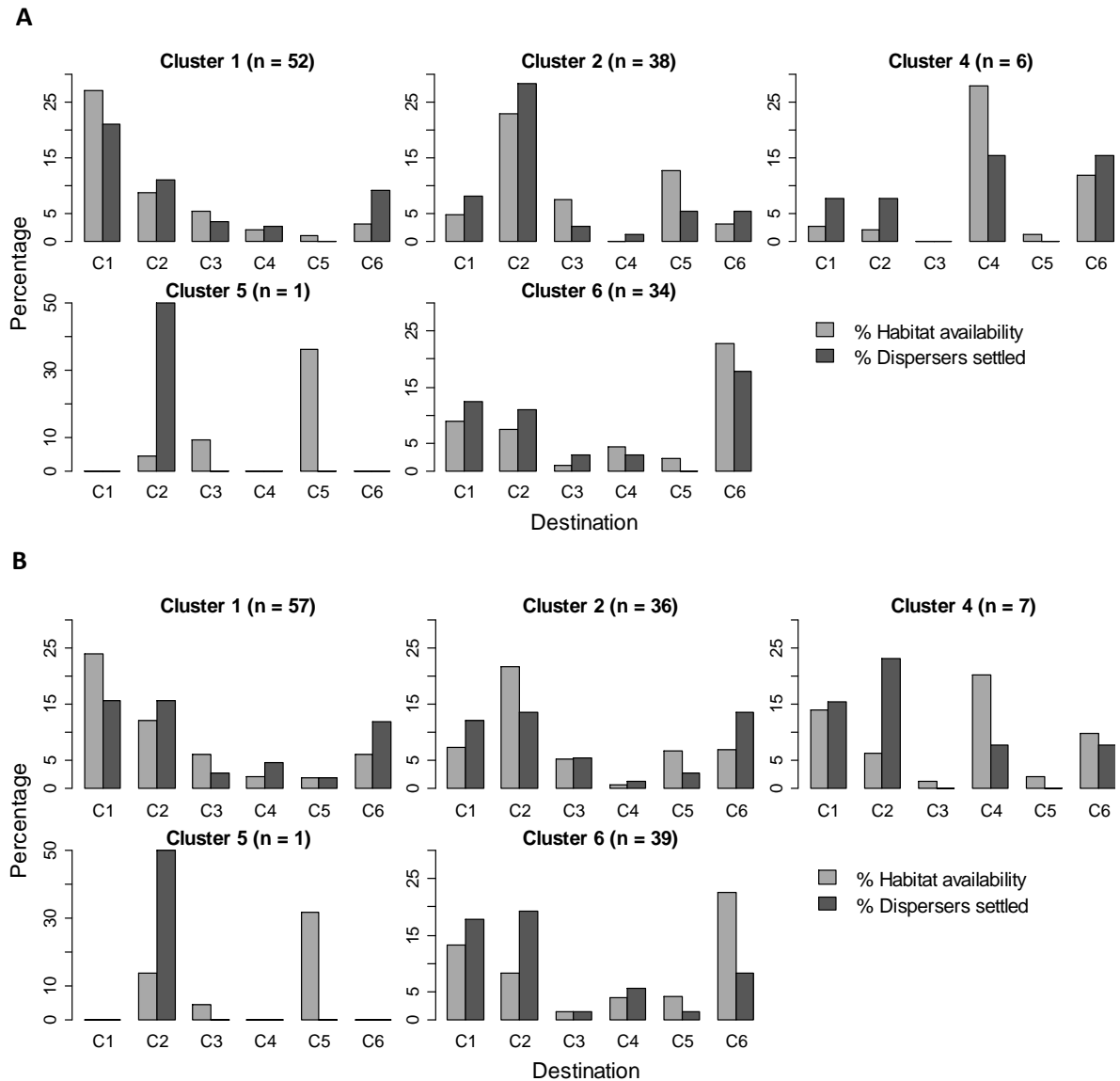**Figure 6.** Wolf establishment in the different habitat clusters in Scandinavia (C1-Bear-mires, C2-Intermediate human, C4-Rough terrain, C5-High human, C6-Moose) for individuals born on each natal habitat presented by Females (A) and Males (B) during the period 1998-2012. Cluster 3 (Building) is missing due to the absence of natal territories. Proportion of habitat available is taken into account for each cluster (light gray).

Table 3. Coefficients (β) and 95 % confidence intervals (CI) of natal cluster selection in south-central Scandinavia (1998-2012). Parameters are estimated from each of the 10 conditional logistic regressions made for individuals born in each cluster (i.e., the natal territories belonging to each cluster) and for each sex. Cluster where individuals established (E) represents the categorical variable "Cluster". Wald test scores and p-values are included for each category. For each regression, the natal cluster is used as the reference category to estimate beta coefficient of the conditional logistic regression.

Natal cluster	E	Female β	Female 95% CI	Female Z score	Female p-value	Male β	Male 95% CI	Male Z score	Male p-value
Bear-Mires (1)	2	0.68	[-0.15 - 1.51]	1.61	0.19	0.95	[0.13 - 1.78]	2.27	**0.02**
	3	-0.19	[-1.31 - 0.93]	-0.34	0.74	-0.43	[-1.74 - 0.87]	-0.65	0.52
	4	0.72	[-0.79 - 2.24]	0.93	0.35	1.65	[0.36 - 2.94]	2.51	**0.01**
	5	-16.83	[-10598.48 - 10564.83]	-0.003	0.99	0.81	[-0.85 - 2.49]	0.96	0.34
	6	1.74	[0.77 - 2.70]	3.52	**<0.001**	1.48	[0.61 - 2.36]	3.34	**<0.001**
Intermediate human (2)	1	0.36	[-0.79 - 1.6]	0.64	0.52	1.35	[0.28 - 2.42]	2.45	**0.01**
	3	-1.48	[-3.06 - 0.12]	-1.81	0.07	0.65	[-0.65 - 1.96]	0.98	0.33
	4	0.19	[-11875.80 - 11915.49]	0.003	0.99	2.28	[-0.42 - 4.99]	1.65	0.09
	5	-1.35	[-2.54 - (-0.16)]	-2.22	**0.02**	-0.62	[-2.23 - 0.97]	-0.77	0.44
	6	0.49	[-0.69 - 1.69]	0.82	0.41	1.48	[0.44 - 2.52]	2.72	**0.005**
Rough terrain (4)	1	3.12	[-0.56 - 6.79]	1.66	0.09	0.96	[-1.49 - 3.42]	0.77	0.44
	2	22.09	[-30716.03 - 30757.22]	0.001	0.99	21.96	[-29824.94 - 29868.87]	0.001	0.99
	3	-	-	-	-	-17.61	[-68153.34 - 68118.12]	-0.001	1.00
	5	1.87	[-74728.87 - 74732.61]	0	1.00	-17.39	[-55247.47 - 55212.69]	-0.001	1.00
	6	1.79	[-0.96 - 4.54]	1.28	0.20	1.43	[-1.58 - 4.45]	0.93	0.35
High human (5)	1	-	-	-	-	-	-	-	-
	2	24.02	[-161035.9 - 161084.0]	0	1.00	22.15	[-95658.64 - 95702.94]	0	1.00
	3	8.67e-07	[-360140.6 - 360140.6]	0	1.00	-5.15e-08	[-270626.16 - 270626.16]	0	1.00
	4	-	-	-	-	-	-	-	-
	6	-	-	-	-	-	-	-	-
Moose (6)	1	0.72	[-0.26 - 1.69]	1.44	0.15	1.47	[0.41 - 2.52]	2.72	**0.006**
	2	0.82	[-0.34 - 1.71]	1.30	0.19	2.12	[1.04 - 3.19]	3.84	**<0.001**
	3	1.45	[-0.31 - 3.22]	1.61	0.11	1.37	[-0.89 - 3.63]	1.19	0.23
	4	-0.24	[-1.87 - 1.38]	-0.29	0.77	1.68	[0.18 - 3.17]	2.20	**0.02**
	5	-0.72	[-14537.83 - 14501.89]	-0.002	0.99	0.32	[-1.93 - 2.57]	0.28	0.78

4. Discussion

There is evidence that dispersing individuals do not move randomly, but that selection of post-dispersal habitat could rely upon information about their natal and future breeding environments (Clobert *et al.* 2009). However, this study suggests that the Scandinavian wolf is not influenced by its natal habitat when choosing a new territory to settle. Individuals born in habitats with specific characteristics did not select habitats with similar characteristics to establish, i.e., natal and established territories belonged to different clusters. However, wolves did not seem to select territories randomly, but they tended to avoid habitats characterized by strong anthropogenic activities.

The lack of influence of natal experience on habitat preferences in this large carnivore, is opposed to what has been described in different species of insects, amphibians, birds (Davis & Stamps 2004) or small mammals (Haughland & Larsen 2004a; 2004b; Selonen, Hanski & Desrochers 2007; Wauters *et al.* 2010). Although little is known about dispersal in large carnivores, some studies have shown different factors affecting habitat selection patterns such as differentiation of habitat preferences among species (May *et al.* 2008), human-risk avoidance (Ordiz *et al.* 2011) or prey distribution (Oakleaf *et al.* 2006). To my knowledge, this is the first study of habitat biased natal dispersal in a large carnivore.

Wolves live in packs and long association with the parental pair could increase offspring opportunity to learn the components of hunting behavior that are not innate (Mech & Boitani 2010). According to Stamps and Swaisgood (2007), habitat-biased natal dispersal should be especially intense when ability to handle, capture or process food is improved by experience in the natal habitat, and when the members of that species evolved in different landscapes containing different sets of food items. The main wolf preys in Scandinavia (i.e., moose and roe deer; Wabakken *et al.* 2001) have been shown to differ in their anti-predator behavior due to variation in size and vigilance capacity (Wikenros *et al.* 2009). Furthermore, hunting moose compared to roe deer might not involve the same strategy. Indeed, it might be riskier for wolves to hunt moose compared to roe deer (Gervasi *et al.* 2013). Therefore, experience gained in hunting strategies for one type of prey in the natal habitat should confer an advantage if that prey is present in the new settled territory. Since moose and roe deer are associated with different habitat types (Torres *et al.* 2011), hunting performance might also be habitat-specific and therefore benefit individuals that disperse towards a similar habitat as the natal habitat type.

Moreover, prey and habitat specialization has been shown on wolves before, in a population where two genetic clusters were associated with two different types of habitat (Cullingham *et al.* 2016). Although this could be a sign of habitat-biased natal dispersal, it is unclear whether this mechanism is responsible of the population structure in that study.

Wolves are site-faithful after establishment, and therefore the initial choice of the settlement territory has a strong impact on lifetime reproductive success (Davis & Stamps 2004). Despite experience gained in a similar habitat as where they establish could be helpful for a better performance after establishment, there are some factors and intra-species characteristics indicating that this mechanism may not be essential in wolves. Experience may play a secondary role in highly plastic species, able to cope with different types of environments in a short time span. Thus, individuals may not be benefit from preferring the natal habitat type if they can undergo phenotypic changes when settling in a non-natal habitat (Davis 2008). This might be the case for wolves, since they are considered as generalist predators ranging from arctic (Mech & Cluff 2011) to arid extreme environments (Hefner & Geffen 1999). Therefore, they have the capacity to adjust their phenotypes to a broad range of conditions and could explain the lack of biased natal habitat selection.

If experience in the natal habitat is not driving wolf behavior when deciding a new territory to settle, other type of stimuli must be interacting with the settlement choice. Dispersing wolves tend to maximize breeding opportunities rather than resource acquisition (Boyd *et al.* 1995; Ciucci *et al.* 2009) and, in Scandinavia, dispersal might be ultimately affected by the probability of finding a mate (Wabakken *et al.* 2001; 2007). Moreover, dispersers can be influenced to leave their natal pack by the presence of potential mates around their area (Fritts & Mech 1981; Mech & Boitani 2010). Thus, there might be positive fitness consequences if wolves optimize mating opportunities rather than choosing the natal habitat type.

Individuals with difficulties estimating the quality of unfamiliar habitats may benefit by dispersing towards an habitat similar to the natal habitat type. Indeed, cues obtained in the natal habitat reduce the time invested on exploring new environments (Stamps & Swaisgood 2007). Therefore, a high mobility and exploratory capacity could enable individuals to estimate habitat quality without the use of cues from the natal habitat. The physical body condition and territorial behavior of wolves make them highly mobile species, able to cover the distance of a wolf territory in less than a day (Mech & Boitani 2010). Additionally, benefits of delayed dispersal on adult performance have been shown for the red wolf (*Canis*

rufus) (Sparkman *et al.* 2010), as this mechanism could provide them with a robust body condition and energy reserves before leaving the natal area. These physical advantages together with the high exploratory capacity could explain why wolves are able to estimate efficiently the quality of new territories and may not need to rely on cues from the natal habitat.

Besides the apparent fact that the Scandinavian wolf is not influenced by its natal habitat type while choosing the established territory, I did not detect any clear pattern of habitat selection. Individuals from both sexes did not select one cluster to a greater extent than others (Figure 6). Moreover, males from the Moose cluster selected the Bear-mires cluster and vice versa. This contradictory result could be explained by the negative NHPI theory, referring to situations in which experience in a low quality natal habitat reduces attractiveness for cues associated with that type of habitats (Stamps & Davis 2006), and this would result in individuals avoiding the natal habitat type. However, given the negative influence of bear density on wolf occurrence in Scandinavia (Ordiz *et al.* 2015), and the positive effect of prey availability on wolf habitat preferences (Walton *et al.* 2001; Lesmerises, Dussault & St-Laurent 2012), it seems unlikely that negative NHPI is the mechanism underlying wolf behavior of the Moose cluster. This could mean that relevant landscape features characterizing those clusters have not been detected or, alternatively, support the theory that other factors than habitat structure drive wolf settlement choices (e.g., find a mate) (Wabakken *et al.* 2007).

Balance between the costs and benefits of dispersal depends on the factor driving the evolution of this behavior (e.g., reproductive success), but also on the internal state of each individual (Clobert *et al.* 2009). Individual traits such as body size or age at sexual maturity may vary widely among individuals of the same species, and this could result in an unclear pattern of the dispersal outcome. According to Mech and Boitani (2010) wolf temperaments may change due to each individual's mood state (e.g., the activity of neuroendrocine systems) and social experience (e.g., the interactions within a family) (McLeod *et al.* 1996; Sands & Creel 2004), showing as well high individual variation in learning ability in captivity (Cheney 1982). Additionally, the presence of certain behaviors (e.g. boldness or agressiveness) have been shown to reduce the costs of dispersal (Duckworth 2006; Clobert *et al.* 2009). If individual heterogeneity is influencing wolf choices during the different stages of dispersal, a clear pattern of habitat selection should not be expected unless intra-population variation is taken into account.

Several studies prove the negative human influence on wolf occurrence in Scandinavia (Karlsson *et al.* 2007; May *et al.* 2008; Ordiz *et al.* 2015), being the principal cause of mortality since the beginning of the population recovery (Wabakken *et al.* 2001). This study provides evidence of anthropogenic avoidance, since the clusters representing high levels of human disturbance (i.e., High human and Building clusters, Figure 4) were the only ones not selected by individuals that originated from any of the natal clusters. In addition, both clusters presented the lowest number of natal and established territories throughout all the study period (Table 2). These clusters presented considerably more established than natal territories, being this more accused for the Building cluster, with total absence of natal territories and 16 individuals establishing in it. Although this would deserve further analysis, it could be the sign of an ecological trap (Battin 2004). Indeed, wolves might be attracted by this kind of habitat but would not be able to persist long enough to reproduce or produce successful offspring, resulting in the absence of natal territories in those clusters.

Although human avoidance has been reported in other studies in Europe (e.g., Ciucci *et al.* 1997; Huck *et al.* 2011), the ability of wolves to cross areas previously known as barriers such as agricultural fields, developed areas or linear infrastructures has been confirmed (Merrill & Mech 2000a; Blanco, Cortés & Virgós 2005; Ciucci *et al.* 2009; Ražen *et al.* 2016). This supports the idea that the wolf's responses are primarily driven by the level of human activity rather than by the presence of the infrastructure itself (Lesmerises, Dussault & St-Laurent 2013). Despite the fact that the High human and Building clusters were avoided in this study, the Intermediate human cluster was selected by males born in two of the five clusters analyzed. This cluster was characterized by intermediate levels of human density, agricultural fields and roads (Figure 4), indicating that wolves may tolerate moderate levels of human activity and presence of infrastructures when settling territories.

Increased environmental variation, e.g. human caused, has been shown to alter or even eliminate the cues animals use to select habitats during dispersal (Remeš 2000; Schlaepfer, Runge & Sherman 2002; Wauters *et al.* 2010). Altered cues in the natal habitat may mask its overall quality and therefore reduce the level of preference for those specific cues. In this study, 3 out of the 6 clusters that represented different types of habitats in Scandinavia were related to human variables, supporting the idea that the Scandinavian wolf population coexists and expands in a human-dominated landscape (Karlsson *et al.* 2007). The high impact that human activities (i.e., poaching and low survival outside the breeding range) have on Scandinavian wolves (Wabakken *et al.* 2001), could alter the cues of their natal

habitats and therefore mask any pattern of natal habitat-biased dispersal in this population. Moreover, this study is restricted to the wolf breeding range, because wolves in Scandinavia are not allowed to establish outside. Therefore, the results of this study are biased towards habitats and territories that occur inside this range and any dispersal pattern outside of it could have been undetected.

Habitat-biased natal dispersal has been validated for small mammals in studies including very contrasted habitats (Haughland & Larsen 2004b; Selonen, Hanski & Desrochers 2007). Indeed, spatial heterogeneity in the landscape and resource distribution is essential for habitat selection to occur (Gaillard *et al.* 2010). Although the Scandinavian landscape might be perceived as relatively homogenous, the cluster analysis highlighted 6 different kinds of habitats related to their spatial location within Scandinavia (Figure 5). Therefore, habitat heterogeneity should be sufficient to expect natal habitat-biased dispersal.

Dispersal distances of Scandinavian wolves are unusually long, probably because of the low wolf density and probability of finding mates (Wabakken *et al.* 2001; 2015). High level of similarity between natal and established territories has been previously related to short dispersal distances, as availability of the natal habitat type increases closer to the natal territory (Wiggett, Boag & Wiggett 1989; Haughland & Larsen 2004b). In this study, I accounted for habitat availability by drawing correlated random walks from natal to established wolf territories, so I considered the habitat available for each individual in relation to its dispersal distance. Since the clusters with different habitat characteristics were placed in different parts of Scandinavia (Figure 5), it is most likely that the availability of the natal habitat type for long-dispersing individuals was low, and this decreased the probability of establishing in this habitat type.

The high human influence on the Scandinavian wolf population together with intra-species characteristics such as plasticity, high mobility or maximization of breeding opportunities could act together explaining why natal habitat-biased dispersal was not detected on this study. Future research on the influence of the natal habitat type in relation to dispersal distances or the role of individual heterogeneity on dispersal decisions would provide a better insight into the reasons of the unclear pattern obtained this study. Moreover, the study of natal habitat-biased dispersal on other wolf populations would be essential to determine whether this mechanism could be used by this species.

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Appendix 1

Table A. Summary of the landscape variables used to characterize the wolf territories and sources of information. All layers were converted to 1km x 1km grid cells.

| Landscape variables	Description	Source
Interspecific		
Bear density	Kernel density estimator based on records of shot bears	Scandinavian brown bear project, Ordiz *et al.* (2015)
Moose density	Annual harvest density at municipality/management unit	www.viltadata.se, Sweden; www.ssb.no, Norway
Human		
Human density	N° inhabitants per km^2	www.scb.se, Sweden; www.ssb.no, Norway
Building density	N° buildings per km^2	www.scb.se, Sweden; Generated for Norway, Milleret (2011); unpublished manuscript, 200 x 200 m
Main road density	km of main roads per km^2	1:100 000 Lantmäteriet, Sweden; N50 kartdata, Staten-skartverk, Norway
Secondary road density	km of gravel roads per km^2	1:100 000 Lantmäteriet, Sweden; N50 kartdata, Staten-skartverk, Norway
Remoteness and accessibility	Combination of building and road densities per km^2	(Milleret; unpublished manuscript; Ordiz *et al.* (2015)), 200 x 200 m
Land cover		
Vegetation	Percentage of Forest, Mires, Mountains, Human-dominated areas, Water and Agricultural areas.	Mattisson *et al.* (2013); Swedish Corine land cover map Lantmäteriet, Sweden, 25 x 25 m merged with Northern Research Institute's vegetation map, Norway, 30 x 30 m into a 25 x 25 m raster
Altitude	Altitude in meters above sea level	
Slope	Slope in degrees	DEM 25 x 25 m; Geographical Data Sweden, Lantmäteriet; Norge digital, Statens kartverk, Norway
Roughness	Difference in m between the maximum and the minimum value of a cell and its 8 surrounding cells	

Appendix 2
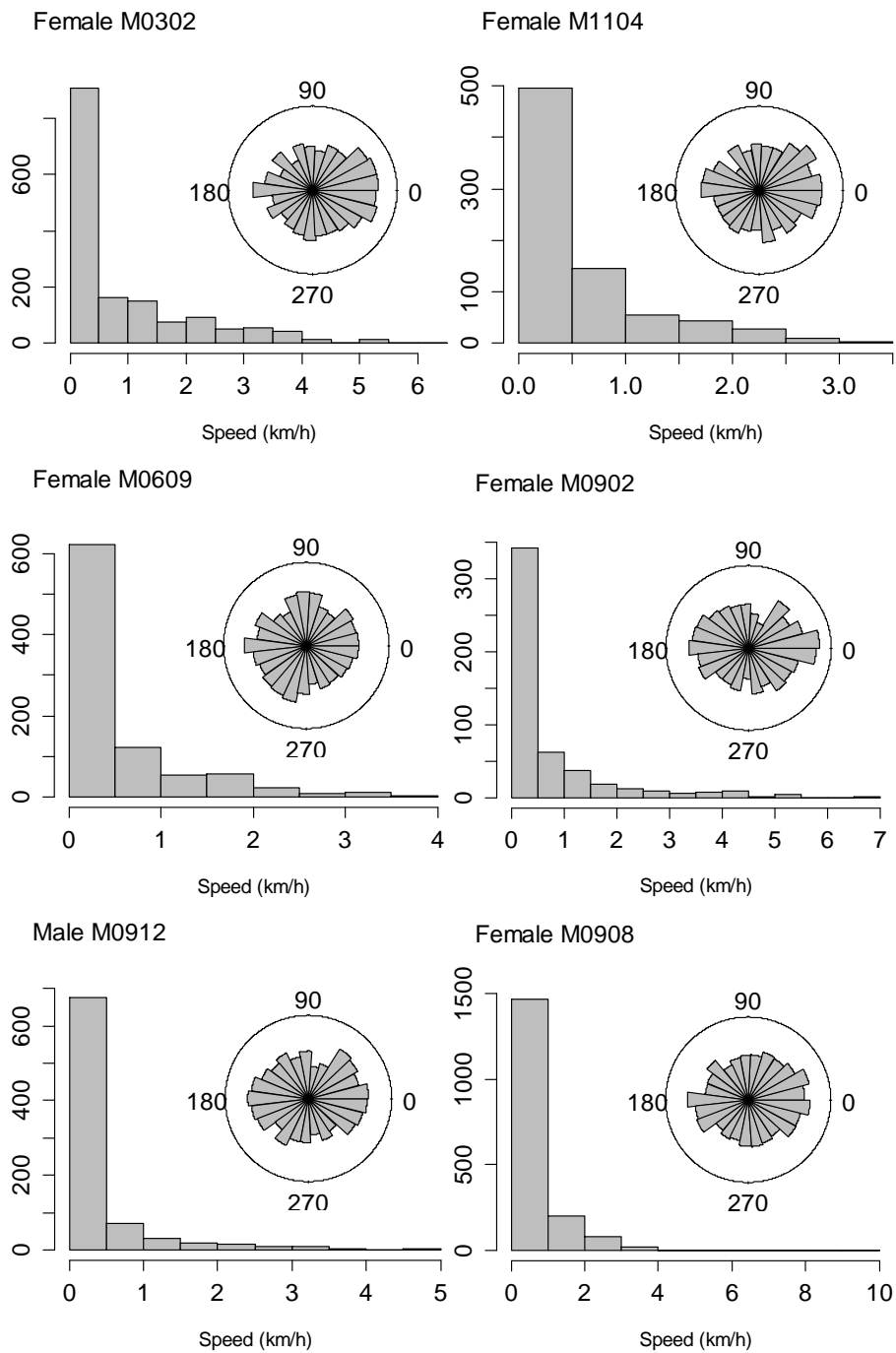
Figure A (I). Distribution of the dispersal movement characteristics of the medium and long dispersing GPS-collared wolves in Scandinavia used to simulate trajectories from natal to established territories. The long trajectories were simulated from the individuals M1408, M1105 and M0301. The movement characteristics are Speed (km/h) on the vertical histogram and Turning angles (Degrees) on the circular histogram.
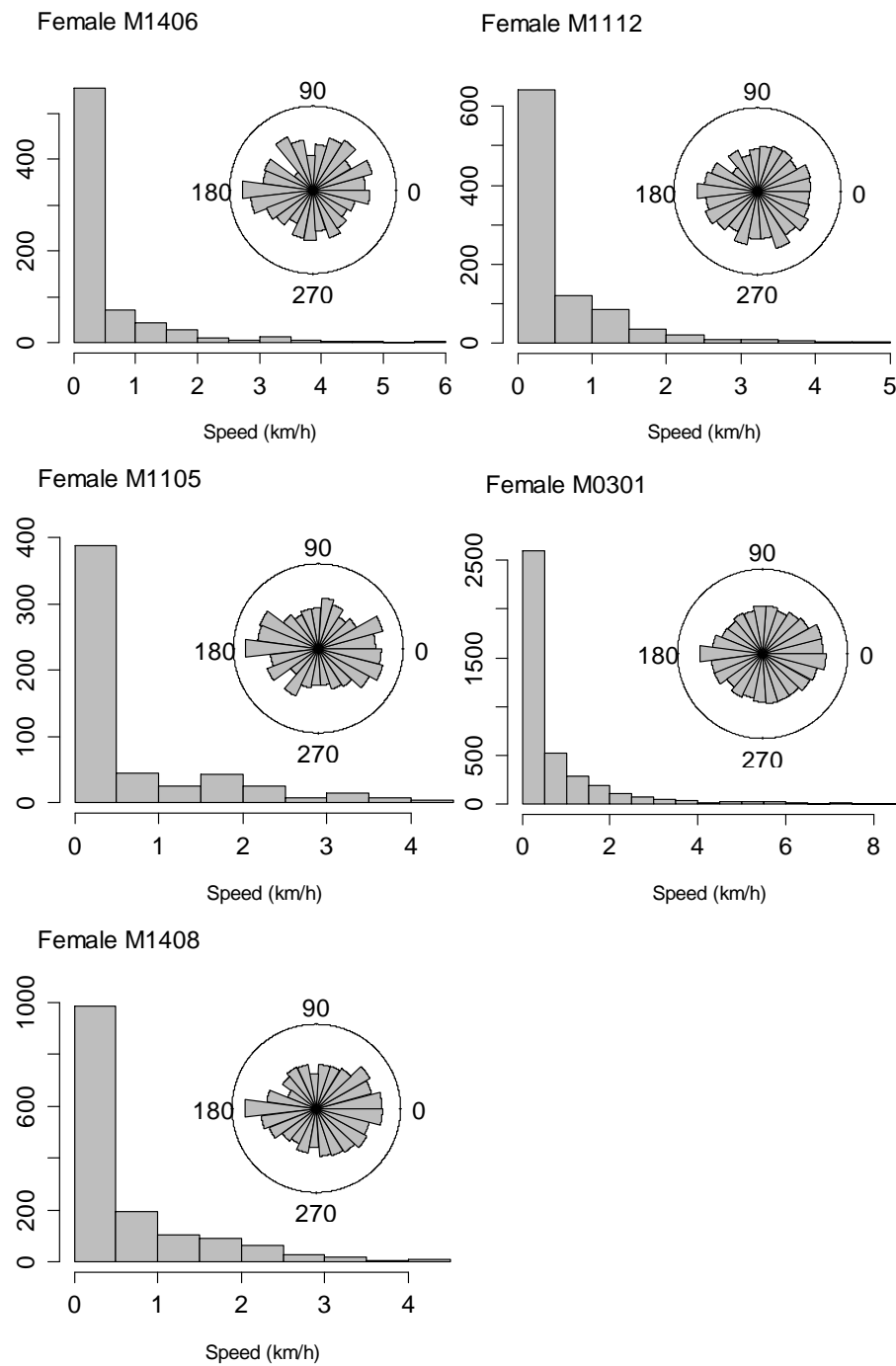
Figure A (II). Distribution of the dispersal movement characteristics of the medium and long dispersing GPS-collared wolves in Scandinavia used to simulate trajectories from natal to established territories. The long trajectories were simulated from the individuals M1408, M1105 and M0301. The movement characteristics are Speed (km/h) on the vertical histogram and Turning angles (Degrees) on the circular histogram.
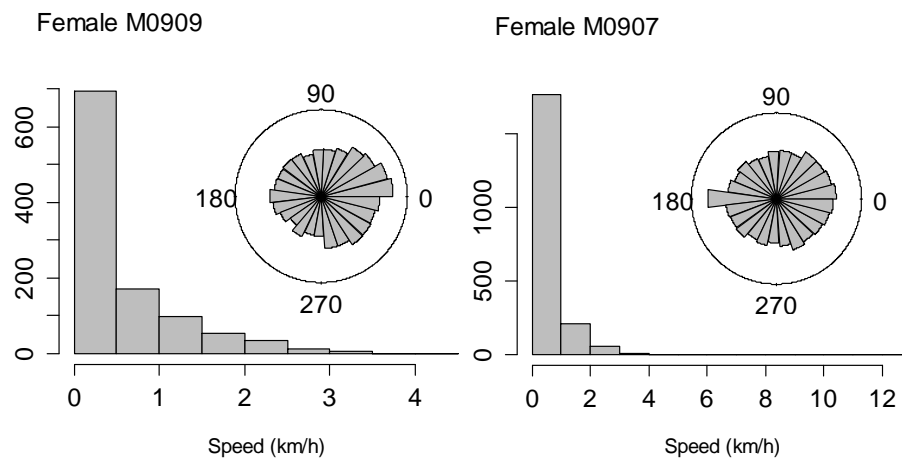
Figure B. Distribution of the dispersal movement characteristics of short dispersing GPS-collared wolves in Scandinavia used to simulate trajectories from natal to established territories. The movement characteristics are Speed (km/h) on the vertical histogram and Turning angles (Degrees) on the circular histogram.