Movement pattern of wolves

- Impact of intrinsic and extrinsic factors

Julia Björk

Degree project in Biology • 30 credits
Swedish University of Agricultural Sciences, SLU
Faculty of Forest Sciences • Department of Ecology
Master of Science in Biology – Ecology and Conservation
Uppsala 2024

Movement pattern of wolves – Impact of intrinsic and extrinsic factors

Rörelsemönster hos varg - Påverkan av individuella egenskaper och miljövariabler

Julia Björk

Supervisor:	**Camilla Wikenros, Swedish University of Agricultural Sciences, Department of Ecology**
Assistant supervisor:	Håkan Sand, Swedish University of Agricultural Sciences, Department of Ecology
Examiner:	Henrik Andrén, Swedish University of Agricultural Sciences, Department of Ecology

Credits:	30 credits
Level:	Master's level (A2E)
Course title:	Master's thesis in Biology, A2E - Ecology
Course code:	EX0953
Programme/education:	Master of Science in Biology – Ecology and Conservation
Course coordinating dept:	Department of Ecology
Place of publication:	Uppsala
Year of publication:	2024

Keywords:	*Canis lupus*, daily movement distance, habitat suitability coefficient, human activity, inbreeding, intraspecific and interspecific density, prey density, season, social affiliation

Swedish University of Agricultural Sciences
Faculty of Forest Sciences
Department of Ecology
SLU Grimsö Wildlife Research Station

Abstract

The recolonization of large carnivores and the advancements in Global Positioning System (GPS) telemetry technology have presented unique opportunities to study movement in carnivores and how they affect ungulate dominated areas. The aim of the study was to analyse which intrinsic and extrinsic factors that impact on the Scandinavian wolf population's daily movement distance. GPS data from 29 wolves (*Canis lupus*) during the period 2001-2019 was analysed by generalised linear mixed-effects models (GLMMs) to identify relationships between daily movement distance and explanatory variables including, time of the year, human activity, habitat, prey density, brown bear (*Ursus arctos*) density, intraspecific density, inbreeding coefficient and social affiliation. The results showed that the average daily movement distance in the Scandinavia wolf population was 15.4 km. The wolves' daily movement distance was lower during the winter months (December-March) compared to April, and lower in February and March. Daily movement distance was also higher during late spring/early summer (May-June) compared to April. Human activity, measured as night-time lights, had an increasing impact on daily movement distance, while roe deer (*Capreolus capreolus*) density had a decreasing impact on daily movement distance. During summer the daily movement distance increased with increasing brown bear density and inbreeding coefficient. Wolves in scent-marking pairs had a higher daily movement distance compared to wolves in family groups. The study shows that wolf movement patterns are complex and can be affected by several factors. The results have important implications in wolf management and can contribute to less conflicts between humans and wolves since it highlights factors affecting the wolves' movement in relation to human activity.

Keywords: Canis lupus, daily movement distance, habitat suitability coefficient, human activity, inbreeding, intraspecific and interspecific density, prey density, season, social affiliation

Table of contents

List of figures

Abbreviations

DMD	Daily Movement Distance
GPS	Global Positioning System
MCP	Minimum Convex Polygon

1. Introduction

Large carnivores play a crucial ecological role, exerting regulatory and cascading effects on lower trophic levels (Estes et al. 2011). These effects have been diminished due to overexploitation and habitat loss, leading to declines in large carnivore populations (Ordiz et al. 2013; Ripple et al. 2014). In human-dominated landscapes, humans are the primary limiting factor for large carnivore populations, preventing them from reaching ecologically functional levels necessary for density-dependent population regulation (Soulé et al. 2003; Liberg et al. 2011; Kuijper et al. 2016; Nowak & Mysłajek 2016). Consequently, the effect on lower trophic levels in these landscapes is mediated by humans and environmental factors (Gicquel et al. 2020; Ausilio et al. 2021), unlike in protected areas where large carnivores often have a larger impact lower trophic levels (Fortin et al. 2005; Ditmer et al. 2018). However, an increasing trend of large carnivore populations recolonising previously inhabited areas is emerging in Europe (Chapron et al. 2014), presenting unique opportunities for studies on their effects in ungulate dominated areas.

Advancements in Global Positioning System (GPS) telemetry technology have significantly improved the possibilities to study of animal movements and their interactions within ecosystems (Cagnacci et al. 2010). The use of GPS collars provide precise and detailed information on various aspects, including home ranges (Mattisson et al. 2013), habitat selection (Hebblewhite & Haydon 2010), movement (Bryce et al. 2022), and activity patterns (Podolski et al. 2013).

1.1 Movement and activity patterns in large carnivores

The movement of animals is affected by a combination of extrinsic and intrinsic factors (Nathan 2008). Extrinsic factors include, e.g., season (Bryce et al. 2022), human footprint (Carricondo-Sanchez et al. 2020), habitat (Kittle et al. 2016), prey density and distribution (Mattisson et al. 2013), interspecific density (Tallian et al. 2017), and intraspecific density (Mattisson et al. 2013; Fowler et al. 2022). Intrinsic factors, such as inbreeding level (Keller & Waller 2002) and social affiliation (Mech & Boitani 2003), also play a significant role in shaping movement patterns.

1.1.1 Season

Seasons commonly influence the movement patterns of carnivores. African lions (*Panthera leo leo*) adjust their movement patterns based on dry or wet seasons and drought conditions, with daily movement negatively correlated with rainfall (Tuqa et al. 2014). Similarly, the Florida panther (*Puma concolor coryi*) exhibits decreased daily movement during the wet season compared to the dry season (Criffield et al. 2018).

Reproductive seasons also affect movement rates. Female bobcat's (*Lynx rufus*) movement rates increase during the kitten-rearing season, while male movement rates increase during the dispersal season (McNitt et al., 2020). Similar patterns are observed in lynx (*Lynx lynx*), with females moving longer distances during the kitten-rearing season and males during the mating season (Jędrzejewski et al. 2002).

Temperature is another seasonal factor impacting movement. For wolves (*Canis lupus*), higher temperatures during the breeding season increase hourly movement rates due to higher maintenance costs when it is lower temperatures, while movement rates decrease with rising temperatures during the pup-rearing season as they are cold-adapted (Bryce et al. 2022). Increasing snow depth correlates with decreased wolf movement (Bryce et al. 2022) due to higher energetic costs and movement limitations in natural, loose snow (Droghini & Boutin 2018).

1.1.2 Human activity and footprint

Human activity significantly affects the behaviour and activity patterns of carnivores worldwide. For instance, human presence alters the activity patterns of brown bears (*Ursus arctos*), making them more nocturnal to avoid humans (Olson et al. 1998). In the Scandinavian brown bear population, increased human activity have shown to decrease bear activity (Ordiz et al. 2017). Similar adaptations and avoidance behaviour have been observed in other large carnivores, including lions (Lesilau et al. 2021), lynx, wolves, brown bears (Blašković et al. 2022), and amur tigers (*Panthera tigris altaica*) (Yang et al. 2019).

Road density and proximity to roads also influence carnivore movement patterns. A study by Baek et al. (2023) found that male Asiatic black bears (*Ursus thibetanus*) move more slowly near main roads and faster near minor roads. Wolves and grizzly bears (*Ursus arctos horribilis*) exhibit higher movement rates near towns and areas with dense trail networks, likely to minimise human encounters (Whittington et al. 2022). In Scandinavia, wolves avoid areas with high human activity and density (Carricondo-Sanchez et al. 2020). However, in areas with low human activity, wolves use gravel and forest roads to increase travel speed (Zimmermann et al. 2014; Bojarska et al. 2020; Carricondo-Sanchez et al. 2020).

1.1.3 Habitat

Different habitats can also affect movement patterns. Fragmented landscapes, forming mosaics of habitats, facilitate long-distance movements in black bears (*Ursus americanus*) (Tredick et al. 2017). Lions prefer proximity to waterholes, where resources are abundant, and prey is more vulnerable, resulting in slower movement speeds near these areas (Valeix et al. 2010; Kittle et al. 2016). Amur tigers exhibit lower path tortuosity in more suitable habitats compared to less favourable, primarily anthropogenic habitats (Wang et al. 2023).

Wolves select for dense vegetation and avoid human settlements and agricultural land, especially during territory establishment (Sazatornil et al. 2016). However, this is mainly during the denning season. In Scandinavia, the overall selected habitats by wolves are rugged terrain and forests, particularly young forests (Milleret et al. 2018; Ordiz et al. 2020).

1.1.4 Prey density

The composition and grouping of prey influence carnivore abundance differently across species (Gebo et al. 2022). For instance, the abundance of leopards (*Panthera pardus*) and spotted hyenas (*Crocuta crocuta*) show a positive correlation with medium-sized ungulates like Bohor reedbuck (*Redunca redunca*) and common duiker (*Sylvicapra grimmia*). Hyenas also exhibit increased movement speeds in areas with livestock compared to regions without livestock (Green & Holekamp 2019).

In North America, wolves increase their travel distance when making kills when prey density is low (Johnson et al. 2017). In Scandinavia, wolf territory size negatively correlates with roe deer (*Capreolus capreolus*) density, while moose (*Alces alces*) density shows no significant effect (Mattisson et al. 2013).

1.1.5 Individual characteristics

Individual characteristics can potentially influence movement patterns. Wolves are a social species with various social stages, ranging from family groups and scent-marking pairs to solitary individuals (Fuller et al. 2003; Mech & Boitani 2003). There are also indications that larger family group size correlate with smaller home range sizes (Mattisson et al. 2013). Within the home ranges, the distribution of wolves is more uneven and concentrated during summer, especially for wolves with pups (Zimmermann et al. 2019).

The Scandinavian wolf is known to be highly inbred (Liberg et al. 2005), resulting in congenital vertebral defects (Räikkönen et al. 2006), which may affect the dispersal and daily movement distances of some individuals. The scavenging rate of individual wolves in the Scandinavian wolf population also increases with higher levels of inbreeding (Wikenros et al. 2023).

1.2 Inter- and intraspecific density

Inter- and intraspecific density does not appear to affect movement patterns directly. However, the density of brown bears may influence both lynx and wolves in other ways. For example, increasing brown bear densities in Slovenia indirectly impact the endangered lynx through their scavenging behaviours (Krofel & Jerina 2016). However, in Scandinavia, where wolves and brown bears coexist with some differences in habitat preference (May et al. 2008), brown bears may negatively affect wolf territory establishment (Ordiz et al. 2015). Also, the kill rate of wolves decreases in areas where wolf packs are sympatric with brown bears (Tallian et al. 2017). The impact of bear presence varies seasonally: during spring, interference competition occurs between the two species, while in summer, it shifts to exploitation competition (Tallian et al. 2022). Consequently, bear presence causes the intervals between kills to increase in spring and search times to lengthen in summer.

In Scandinavia, home range sizes of lynx decrease with increasing intraspecific density (Aronsson et al. 2016). A similar pattern has been observed in the Scandinavian brown bear population (Dahle & Swenson 2003). For the highly territorial wolf (Mech & Boitani 2003), increasing densities of neighbouring family groups in Montana, USA, negatively impact and restrict wolf territory size (Rich et al. 2012). In Montana, increased wolf pack density also leads to larger pack sizes due to higher spatial competition, which may cause younger wolves to stay longer in the pack (Sells et al. 2022). However, in Scandinavia, population density did not restrict wolf territory size during the initial decades following recolonisation (Mattisson et al. 2013).

2. Objectives

This study aimed to identify intrinsic and extrinsic factors influencing movement patterns, i.e., mean daily movement distance, of Scandinavian wolves. Seven hypotheses (H) and predictions (P) were formulated and tested:

H1: Time of the year will impact on wolf movement patterns.

P1: Daily movement distances are predicted to be lower in winter due to the effects of snow and lower temperatures on energetic costs and movement.

H2: Human activity affects the daily movement distance of wolves.

P2: In areas with higher human activity, an increase in daily movement distances is predicted as wolves tend to avoid areas with higher human activity. In addition, wolves may move longer distance to avoid areas with higher human activity.

H3: Habitat will affect wolf movement patterns.

P3: Daily movement distance is predicted to decrease in preferred habitats compared to less preferred habitats, as wolves will not need to move as extensively in areas they favour.

H4: Prey density affects daily movement distance in wolves.

P4: With increasing prey density, daily movement distance is predicted to decrease because of increased access to prey.

H5: The presence of brown bears will impact wolf movement patterns.

P5: Because presence of brown bears influences wolves' kill rate, the wolves' daily movement distance is predicted to increase when bear density is higher.

H6: Wolves' daily moved distance is influenced by intraspecific density.

P6: Wolves’ highly territorial nature suggests that increased intraspecific density will lead to higher daily movement distances due to the need for more frequent territorial defence.

H7: Social affiliation will impact wolf movement patterns.

P7: Scent-marking pairs are predicted to have longer daily movement distances than wolves in family groups, as family groups tend to be more concentrated in their home ranges during summer when they have pups.

H8: Degree of inbreeding will impact wolf movement patterns.

P8: Wolves with higher inbreeding level are predicted to have shorter daily movement distances due to congenital health issues.

3. Methods

3.1 Study area and population

The study was conducted within the main wolf distribution range in south-central Scandinavia, encompassing parts of Sweden and Norway (Fig. 1). The study area was predominantly characterized by boreal forests, which were primarily composed of coniferous species such as Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), as well as some deciduous species including birch (*Betula* spp.) (Roberge et al. 2024). During the study period, the climate was characterised by continental conditions, with snow cover predominantly present from December to March. The Scandinavian wolf population mainly prey on moose (Sand et al. 2008; Zimmerman et al. 2015), but with higher roe deer densities the wolves kill more roe deer (Sand et al. 2016), which both were present in the study area. In the study area other carnivores like brown bear, Eurasian lynx, and wolverine exists.

The Scandinavian wolf population was hunted to extirpation and considered functionally extinct by the late 1960s (Haglund 1968; Sørensen et al. 1986). In northern Sweden, the first reproduction post-extinction occurred in 1978, and since 1983, successful reproduction has been confirmed annually except for 1986 (Wabakken et al. 2001). Notably, in 1991, two successful reproductions in different locations were recorded for the first time since the 1950s, marking the beginning of the population increase (Wabakken et al. 2001). The Scandinavian wolf population, founded by a few individuals and lacking consistent immigration from the Finnish/Russian population, is severely inbred (Liberg et al. 2005; Åkesson et al. 2016). However, the breeding success and population growth rate increase significantly when an immigrant wolf reproduces with the breeding population (Åkesson et al. 2016). During the 2022/2023 monitoring season, the population was estimated at 510 (range: 403-663) individuals, comprising 49 family groups and 36 scent-marking pairs (Svensson et al. 2023).

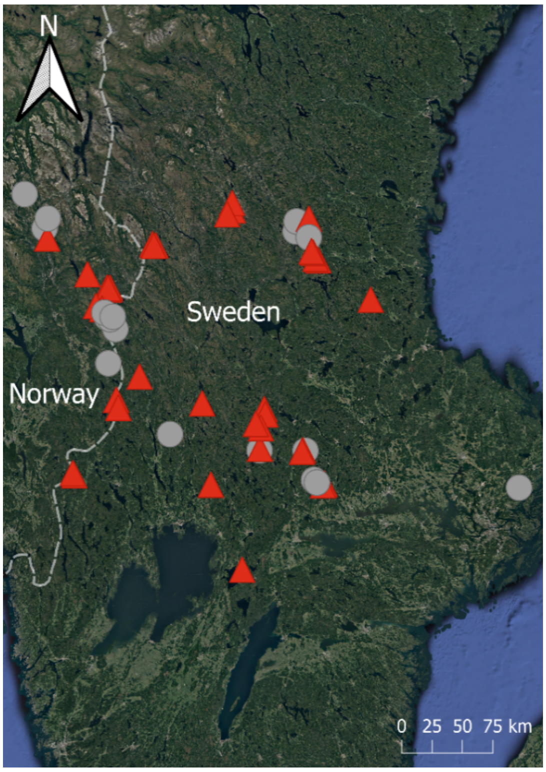


Figure 1. Centroid points from the 100% Minimum Convex Polygons (MCPs) derived from intensive study periods in Scandinavia from 2001-2019. The points represent the distribution of family groups (red triangles) and scent-marking pairs (grey dots) used in this study.

3.2 GPS-dataset

The dataset utilised for analysing the movement patterns of the Scandinavian wolf population contained GPS data with hourly positioning from GPS-collared wolves. As detailed by Sand et al. (2006), the capturing, handling, and collaring of all wolves were conducted in accordance with approvals from the Swedish Animal Welfare Agency and the Norwegian Experimental Animal Ethics Committee. Data collection from 2001 to 2019 comprised 68 intensive predation studies and 63,307 GPS locations (Wikenros et al. 2023). Of these studies, 46 were on family groups (n=23 individuals) and 22 on scent-marking pairs (n=16 individuals). In this study 12 study periods were excluded because there were less than 10 study days within the study period. The analysed data included 29 individuals, with 40 study periods on family groups and 16 study periods on scent-marking pairs (Appendix 1).

3.3 Daily movement distance

The movement patterns of the Scandinavian wolf population were quantified by calculating the daily movement distance (DMD), an estimate of the minimum distance travelled within a 24-hour period. DMD was calculated using the GPS coordinates (RT90) provided by each study. The Euclidean distance between consecutive GPS locations was computed using the dplyr package (Wickham et al. 2023) in R v4.3.3 (R Core Team, 2023). The sum of these distances over a 24-hour period provided the minimum distance travelled. When hourly GPS locations were unavailable, the distance between two consecutive successful positions was used instead.

The number of hourly GPS locations varied significantly across different study periods. To account for days with fewer than 24 GPS locations, calculations were made to estimate the number of positions needed to determine DMD accurately. All days with 24 GPS locations were extracted from the dataset. Using the dplyr package in R, 1-14 positions were randomly removed from each day, resulting in 25 datasets with 10-24 positions per day. DMD was calculated for each dataset as described above. The proportion of DMD, depending on the number of GPS locations, was then compared to the DMD calculated with 24 positions.

It was determined that a loss of 1.5% in DMD for most individuals (>25th quartile) was acceptable. Figure 2 shows the proportion of the decrease in DMD relative to the number of GPS locations, and it was concluded that a minimum of 22 positions per day was required for an accurate DMD estimate. Only study periods with at least 10 days having 22, 23, or 24 GPS locations were included. After excluding days with fewer than 22 GPS locations and study periods with fewer than ten days, the dataset comprised 1,955 study days.

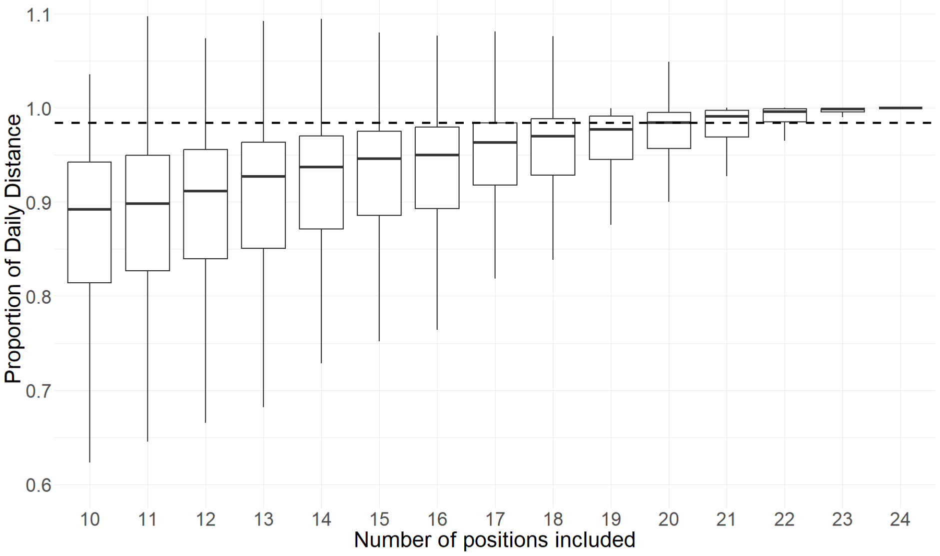


Figure 2. The proportion of daily movement distance in relation to the number of GPS locations included in the estimation, based on resampling 68 intensive study periods with 24 GPS locations per day (mean = 21.5, range: 1-61 days study period^{-1} with 24 positions day^{-1}). Daily movement distance above the dashed line decreased by less than 1.5% compared to days with 24 positions.

3.4 Explanatory variables

3.4.1 Human activity and footprint

To account for human activity and footprint, the average night-time light index and the density of paved and gravel roads were calculated within 100% minimum convex polygons (MCPs) representing the areas used during the study periods. The night-time light index was sourced from the dataset by Venter et al. (2016), which provides an index ranging from zero to ten, with each pixel assigned a different light index. The dataset has a resolution of 1 km and includes data from 1993 and 2009; for this study, the 2009 data was used. The night-time light values were extracted from the MCPs, and the average value within each MCP was calculated.

For each MCP, the density of paved and gravel roads was estimated using data from Topografi 100 (Lantmäteriet, Sweden) and N50 kartdata (Statens kartverk Norway). The road density (km/km^2) was extracted and calculated in QGIS 3.34.0 by dividing the total length (km) of paved or gravel roads within each MCP by the area (km^2) of the MCP.

3.4.2 Seasons

Months were set as an explanatory variable to evaluate how DMD changes over the year. April was set as the reference month. The dataset was also divided into annual, winter, and summer datasets since brown bears hibernate during winter and moose and roe deer densities are estimated through pellet counts representing the winter period. The months included in the summer dataset were May-October and in the winter dataset November-April

Brown bear, roe deer, and moose density

Data from Wikenros et al. (2023) was used to include the variable brown bear density in the analysis. This dataset provided a relative index of brown bear density (per km2) derived from official statistics on the annual harvest numbers and their geographical distribution. The pre-calculated brown bear density was incorporated directly into the summer dataset analysis without any modifications.

When received for the analysis, data on roe deer and moose density had already been calculated as described by Sand et al. (2016). The dataset contained the winter density of moose and roe deer (individual/km) within the wolf territories, derived from pellet counts within the territories. The pre-calculated densities were incorporated directly into the winter dataset analysis without any modifications.

3.4.3 Habitat suitability coefficient

A habitat suitability coefficient was calculated to determine whether habitat suitability in the MCPs affected DMD. Land cover data was sourced from Corine

Land Cover (CLC) 2018, with the 44 CLC classes consolidated into 6 classes (Appendix 2). These classes were assigned different habitat selection values calculated similarly to the method described by Onotaro et al. (2011). This involved calculating the distance between the GPS locations of individuals within a study period and the habitat classes (i.e., habitat use) and comparing it with the distance between random points generated within the MCPs and each habitat class (i.e., habitat availability). For each MCP study period, random points equal to 10 times the number of GPS locations were generated. The tool "Shortest Line between Features" in QGIS 3.34 was used to calculate the distances.

For each study period, the mean distance from the GPS locations to each habitat class was divided by the mean distance from the random points to each habitat class to obtain the distance ratio. A ratio >1 indicates avoidance of the habitat class, as the mean distance between the wolf and the habitat class is greater than that between the random points and the habitat class. Conversely, a ratio <1 indicates selection for the habitat, as the mean distance from the wolf to the habitat class is shorter than that from the random points.

The method by Criffield et al. (2018) was used to further calculate a habitat suitability coefficient. The proportion of each habitat class within each MCP was calculated for the study periods. This proportion was then multiplied by the corresponding habitat selection value. The products from each study period were averaged to obtain a habitat suitability coefficient for each individual within each study period. A habitat suitability coefficient <1 indicates a suitable habitat, while a coefficient >1 indicates an unsuitable habitat.

3.4.4 Individual characteristics

Monitoring the Scandinavian wolf population primarily relies on snow-tracking and DNA analyses conducted between 1 October and 31 March (Liberg et al. 2012; Svensson et al. 2023). These methods collected information regarding social affiliation (family group, scent-marking pair, or single) and territory belonging. The number of neighbouring territories was already calculated as the number of neighbouring territories within an 18 km radius buffer on the territory centroid. Since the reestablishment of the Scandinavian wolf population, an annual pedigree of the entire population has been constructed and annually updated (Åkesson et al. 2023), from which the inbreeding coefficient was obtained.

Adult scent-marking pairs generally move together, except during the pup-rearing season (Zimmermann et al. 2015). The study used the highest inbreeding coefficient of the pair in the family group or in the scent-marking pair, as this individual is likely to limit the daily movement distance of the pair.

3.5 Statistical analyses

All statistical analyses were conducted in R v4.3.3 (R Core Team, 2023). To estimate the effect of different explanatory variables on DMD, generalised linear mixed-effects models (GLMMs) with a gamma-distributed error structure and log link function were employed using the glmmTMB package (Mollie et al. 2017). The response variable was DMD in kilometres. Wolf ID was included as a random factor. Spearman's correlation coefficient was used to account for any collinearity between the explanatory variables, with variables having a correlation coefficient (rho) >0.4 not included in the same model.

Due to the seasonal specificity of some variables, the analyses were divided into three parts. The first analyses were conducted on the annual dataset, using month, social affiliation (scent-marking pair, $n_{studyperiods/individuals}=18/12$, or family group, $n_{study\ periods/individuals}=39/21$), number of neighbouring territories (wolf density, range: 0-5), night-time lights (range: 0-0.63), habitat suitability coefficient (range: 0.10-0.18), inbreeding coefficient (range: 0.13-0.32), and paved road density (range: 0.05-0.41km/km^2). Gravel road density was excluded due to its correlation with the habitat suitability coefficient. Two additional analyses were conducted to include moose density (range: 0.46-3.38/km^2), roe deer density (range: 0.00-5.14/km^2), and brown bear density (range: 0.00-0.59/km^2), one for summer and one for winter.

In the winter analysis, moose and roe deer densities were added to the model, as these species are monitored each winter. Gravel road density was excluded due to its correlation with the habitat suitability coefficient, and paved road density was excluded due to its correlation with roe deer density.

In the summer analysis, brown bear density was added, as brown bears hibernate during the winter. Gravel road density was excluded due to its correlation with the habitat suitability and inbreeding coefficients. Paved road density was excluded due to its correlation with brown bear density, and the night-time lights index was excluded due to its correlation with the habitat suitability coefficient.

Given the number of variables, the dredge function from the MuMIn package (Bartón, 2023) was used during the model selection procedure for the three datasets. AIC corrected for small sample sizes (AICc) was calculated to identify the highest-ranked model in the three analyses. Models within ΔAICc ≤ 2 were considered the highest-ranked models. Nakagawa's R2 (Lüdecke et al., 2021) was used to assess model fit.

4. Results

4.1 Annual movement pattern

The average daily movement distance (DMD) for the annual dataset ($n_{studydays}$=1955) was 15.4 km (95% CI: 14.9-15.8 km). The distribution of DMD is presented in Appendix 6.1.

The model analysis identified three models with an ΔAICc ≤ 2. The highest-ranked model included month, night-time lights and habitat suitability coefficient; these variables were also present in the two other models (Table 1). Increasing night-time light had a significant positive impact on DMD, while an increasing habitat suitability coefficient had a significant decreasing impact on DMD (Fig. 3). Results show significantly higher DMD during May, June, and October compared to April (the reference month) and significantly lower DMD during February and March compared to April (Table 2, Fig. 3). Other months had non-significant impacts on DMD (95% CI overlapped zero, Table 2). The second highest-ranked model included paved road density, which had a non-significant decreasing impact on DMD (Table 2; Appendix 3.1). The inbreeding coefficient was included in the third highest-ranked model, showing a non-significant decreasing impact on DMD (Table 2; Appendix 3.2).

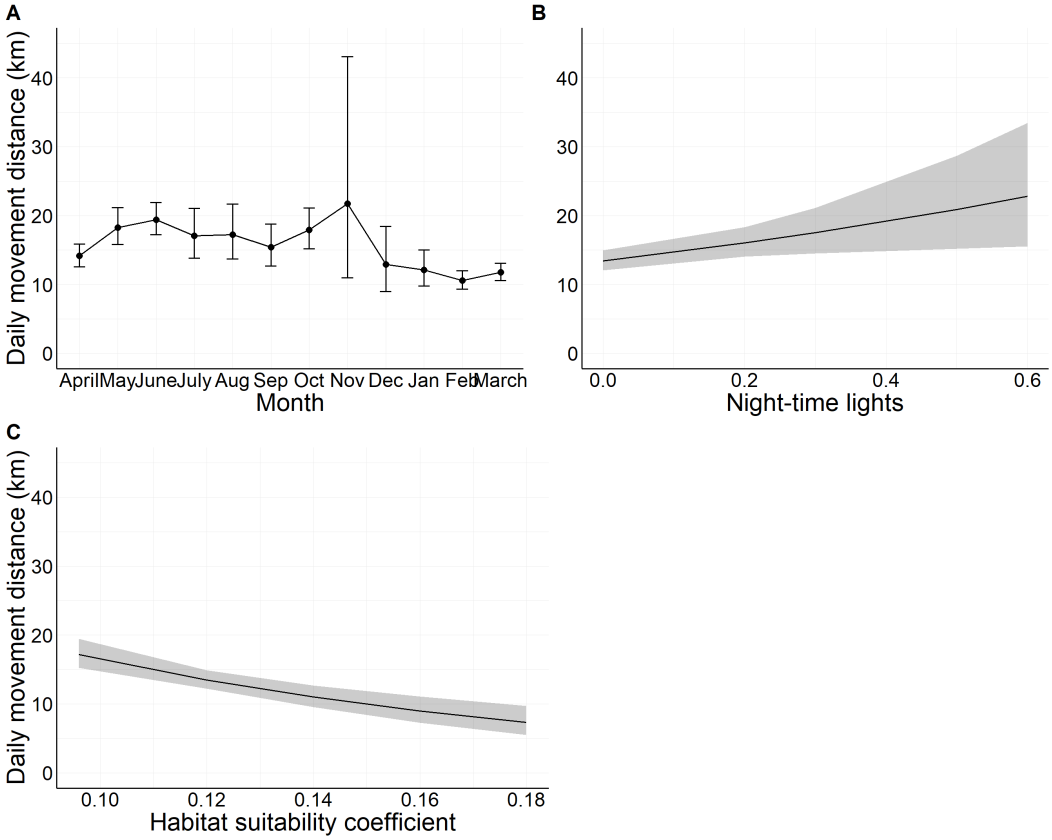


Figure 3. The impact of A) months, B) night-time lights, and C) habitat suitability coefficient on daily movement distance with 95% CI by wolves (n=29) in the Scandinavian wolf population during 2001-2019 from the highest-ranked model in the annual analysis.

4.2 Movement pattern during winter

The average DMD for the winter dataset ($n_{studydays}$=1243) was 13.9 km (95% CI: 13.4-14.4 km). The distribution of DMD during winter is represented in Appendix 6.2. The model analysis revealed five models with an ΔAICc ≤ 2 (Table 1). The highest-ranked model included night-time light, roe deer density and habitat suitability coefficient; these variables were also present in the other four models (Table 1). Night-time light had a significantly increasing impact on DMD, while increasing roe deer density and habitat suitability coefficient had a significantly decreasing impact on DMD (Table 2; Fig. 4).

The second highest-ranked model included wolf density, which had a non-significant increasing impact on DMD (Table 2; Appendix 4.1). In the third highest-ranked model, when social affiliation was added, night-time lights had a non-significant increasing impact on DMD (Table 2; Appendix 4.2). Wolves in scent-marking pairs had lower DMD than those in family groups, though this impact was non-significant (Table 2; Appendix 4.2). When wolf density and social affiliation were included in the fourth highest-ranked model, night-time light had a significantly increasing impact on DMD again (Table 2; Appendix 4.3). Wolf density had a non-significant increasing impact on DMD, and wolves in scent-marking pairs had a lower DMD than wolves in family groups, but the evidence was non-significant. Moose density was included in the fifth highest-ranked model, showing a non-significant increasing impact on DMD (Table 2; Appendix 4.4).

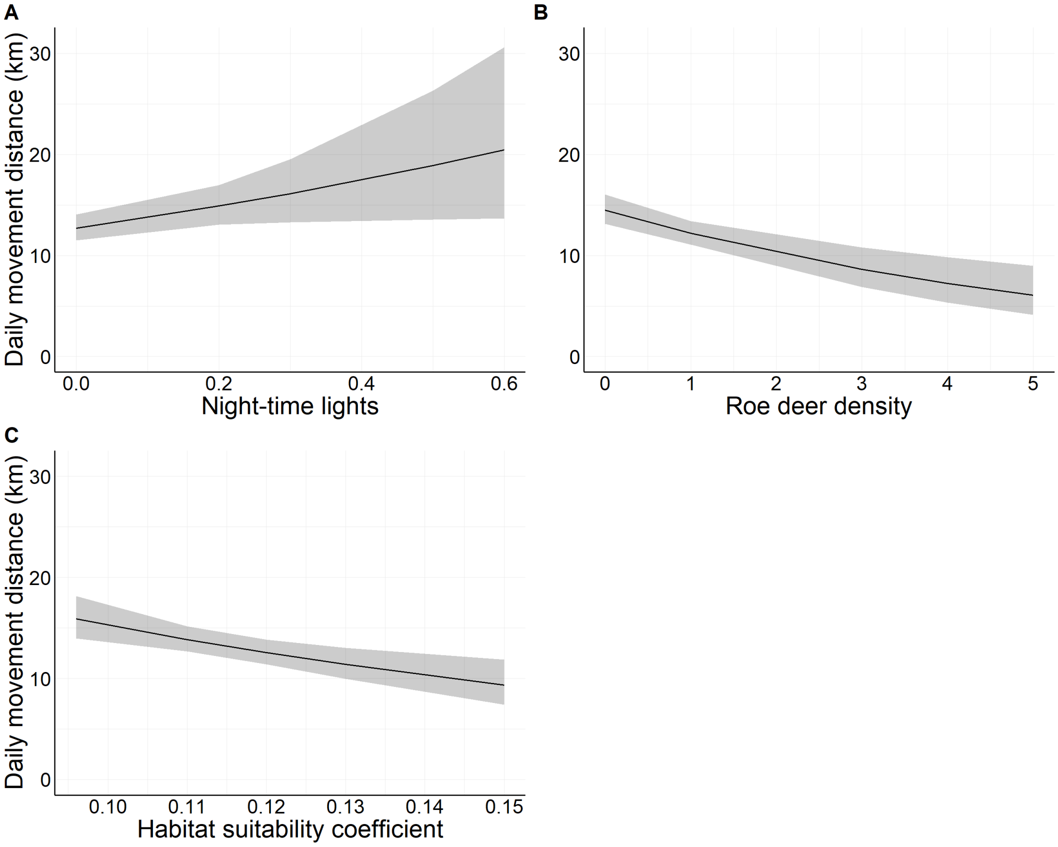


Figure 4. The impact of A) night-time lights, B) roe deer density, and C) habitat suitability coefficient on daily movement distance with 95% CI by wolves (n=25) in the Scandinavian wolf population during 2001-2019 from the highest-ranked model in the winter dataset.

4.3 Movement pattern during summer

The average DMD for the summer dataset ($n_{studydays}$=606) was 19.3 km (95% CI: 18.6-20.0 km). The distribution of DMD during summer is presented in Appendix 6.3. The model analysis identified five models with an ΔAICc ≤ 2 (Table 1). The highest-ranked model included brown bear density, inbreeding coefficient and social affiliation (Table 1). All five top models included brown bear density and inbreeding coefficient, while social affiliation was included in four. Higher brown bear density and inbreeding coefficient were associated with significantly increased DMD. Wolves in scent-marking pairs had significantly higher DMD than wolves in family groups (Table 2; Fig. 5).

The second highest-ranked model included wolf density, which had a non-significant decreasing impact on DMD (Table 2; Appendix 5.1). In the third highest-ranked model, only brown bear density and inbreeding coefficient were included, both increasing DMD significantly (Table 2; Appendix 5.2). When the habitat suitability coefficient and again social affiliation were added in the fourth highest-ranked model, there was non-significant evidence for higher DMD in wolves in scent-marking pairs compared to family groups (Table 2; Appendix 5.3). The habitat suitability coefficient had a non-significant increasing impact on DMD. In the fifth highest-ranked model, wolf density was added with a non-significant decreasing impact on DMD (Table 2; Appendix 5.4). However, wolves in scent-marking pairs again had significantly higher DMD than those in family groups, and the habitat suitability coefficient had a non-significant increasing impact on DMD.

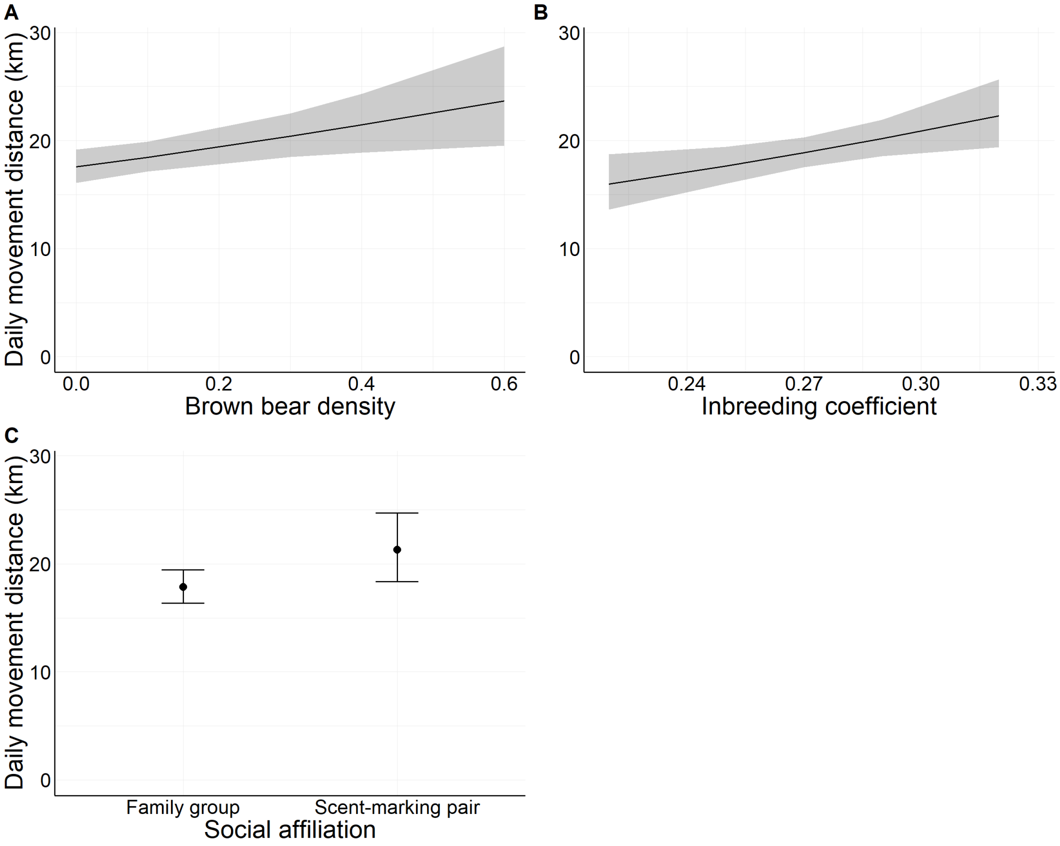


Figure 5. The impact of A) brown bear density, B) inbreeding coefficient, and C) social affiliation on daily movement distance with 95% CI by wolves (n=18) in the Scandinavian wolf population during 2001-2019 from the highest-ranked model in the summer dataset

Table 1. Generalised linear mixed models to assess the effect of months, social affiliation (scent-marking pair, family group), wolf density (neighbouring territories), night-time lights, habitat selection coefficient, inbreeding coefficient from the adult wolf with the highest coefficient within a scent-marking pair/family group ($Fi_{highest}$), paved road density, bear density, moose density, and roe deer density, on daily movement distance by wolves in Scandinavia between 2001-2019. Explanatory variables are denoted as follows: a '+' sign indicates an increasing effect on DMD, a '-' sign indicates a decreasing effect on DMD, 'NA' signifies that the variable was not included in the model, and 'x' denotes that the variable was not included in the analysis.

Dataset	**No.**	**Intercept**	**Month**	**Social affiliation**	**Wolf density**	**Night lights**	**Habitat**	**$Fi_{highest}$**	**Paved road**	**Bear**	**Moose**	**Roe deer**	**df**	**ΔAICc**	**LogLik**	**$R2_c$**	**$R2_m$**
Annual	1	+	+	NA	NA	+	-	NA	NA	x	x	x	16	0.00	-6773.5	0.30	0.18
n=1955	2	+	+	NA	NA	+	-	NA	-	x	x	x	17	1.60	-6773.3	0.28	0.18
	3	+	+	NA	NA	+	-	-	NA	x	x	x	17	1.90	-6773.4	0.30	0.18
Winter	1	+	x	NA	NA	+	-	NA	x	x	NA	-	6	0.00	-4272.8	0.16	0.08
n=979	2	+	x	NA	+	+	-	NA	x	x	NA	-	7	0.47	-4272.1	0.17	0.09
	3	+	x	+	NA	+	-	NA	x	x	NA	-	7	1.32	-4272.5	0.17	0.08
	4	+	x	+	+	+	-	NA	x	x	NA	-	8	1.40	-4271.5	0.17	0.09
	5	+	x	NA	NA	+	-	NA	x	x	NA	-	7	1.91	-4272.8	0.16	0.08
Summer	1	+	x	+	NA	x	NA	+	x	+	x	x	6	0.00	-2162.8	0.15	0.09
n=606	2	+	x	+	-	x	NA	+	x	+	x	x	7	1.08	-2162.3	0.16	0.10
	3	+	x	NA	NA	x	NA	+	x	+	x	x	5	1.51	-2164.6	0.15	0.07
	4	+	x	x	NA	x	+	+	x	+	x	x	7	1.53	-2162.6	0.15	0.09
	5	+	x	x	-	x	+	+	x	+	x	x	8	1.85	-2161.7	0.16	0.10

Table 2. Conditional model parameter estimates (β), with standard error (SE) and 95% confidence interval (CI) for each explanatory variable in the models within ΔAICc ≤ 2 (Table 1). Explanatory variables shown in bold are not overlapping zero. The reference for months is April, and the reference for social affiliation is family group.

Dataset	No.	Explanatory variable	Beta	SE	95% CI
Annual	1	Intercept	3.78	0.24	3.30, 4.26
n=1955		**Month: May**	0.26	0.06	0.13, 0.38
		Month: June	0.32	0.05	0.22, 0.41
		Month: July	0.19	0.10	-0.01, 0.39
		Month: August	0.20	0.12	-0.03, 0.43
		Month: September	0.09	0.09	-0.09, 0.27
		Month: October	0.24	0.07	0.09, 0.38
		Month: November	0.43	0.35	-0.25, 1.11
		Month: December	-0.09	0.18	-0.45, 0.27
		Month: January	-0.15	0.11	-0.37, 0.06
		Month: February	-0.29	0.06	-0.41, -0.18
		Month: March	-0.18	0.04	-0.26, 0.10
		Night lights	0.88	0.36	0.18, 1.58
		Habitat	-10.14	2.06	-14.19, -6.10
	2	Intercept	3.86	0.27	3.34, 4.38
		Month: May	0.25	0.06	0.13, 0.38
		Month: June	0.32	0.05	0.22, 0.42
		Month: July	0.19	0.10	-0.01, 0.39
		Month: August	0.21	0.12	-0.02, 0.44
		Month: September	0.09	0.09	-0.09, 0.28
		Month: October	0.25	0.07	0.10, 0.39
		Month: November	0.44	0.35	-0.24, 1.12
		Month: December	-0.10	0.18	-0.46, 0.26
		Month: January	-0.16	0.11	-0.37, 0.06
		Month: February	-0.29	0.06	-0.41, -0.18
		Month: March	-0.18	0.04	-0.26, -0.10
		Night lights	0.89	0.34	0.22, 1.55
		Paved road	-0.50	0.70	-1.87, 0.88
		Habitat	-10.27	2.01	-14.21, -6.33
	3	Intercept	3.89	0.39	3.13, 4.65
		$\mathrm{Fi}_{\mathrm{highest}}$	-0.33	0.88	-2.06, 1.40
		Month: May	0.26	0.06	0.13, 0.38
		Month: June	0.32	0.05	0.22, 0.41
		Month: July	0.18	0.10	-0.02, 0.43
		Month: August	0.20	0.12	-0.03, 0.43
		Month: September	0.08	0.09	-0.10, 0.26
		Month: October	0.23	0.07	0.09, 0.38
		Month: November	0.43	0.35	-0.25, 1.11
		Month: December	-0.09	0.18	-0.45, 0.27
		Month: January	-0.15	0.11	-0.37, 0.06

		Month: February	-0.29	0.06	-0.41, -0.18
		Month: March	-0.18	0.04	-0.26, -0.10
		Night lights	0.89	0.36	0.19, 1.59
		Habitat	-10.34	2.14	-14.52, -6.15
Winter *n*=1243	1	Intercept	3.74	0.34	3.07, 4.41
		Night lights	0.79	0.38	0.05, 1.53
		Roe deer	-0.17	0.04	-0.26, -0.09
		Habitat	-9.81	3.00	-15.70, -3.93
	2	Intercept	3.77	0.34	3.10, 4.44
		Wolf density	0.04	0.03	-0.02, 0.10
		Night lights	0.86	0.38	0.12, 1.61
		Roe deer	-0.17	0.04	-0.26, -0.09
		Habitat	-10.50	3.07	-16.51, -4.49
	3	Intercept	3.83	0.37	3.11, 4.55
		Night lights	0.73	0.39	-0.04, 1.49
		Roe deer	-0.17	0.04	-0.26, -0.08
		Habitat	-10.40	3.13	-16.53, -4.26
		Social affiliation: Pair	-0.06	0.07	-0.20, 0.08
	4	Intercept	3.89	0.37	3.16, 4.62
		Wolf density	0.04	0.03	-0.02, 0.11
		Night lights	0.79	0.39	0.02, 1.56
		Roe deer	-0.17	0.04	-0.25, -0.08
		Habitat	-11.38	3.26	-17.77, -4.99
		Social affiliation: Pair	-0.08	0.07	-0.22, 0.07
	5	Intercept	3.68	0.39	2.92, 4.43
		Moose density	0.03	0.08	-0.12, 0.17
		Night lights	0.78	0.38	0.05, 1.52
		Roe deer	-0.17	0.04	-0.26, -0.09
		Habitat	-9.52	3.09	-15.57, -3.47
Summer *n*=606	1	Intercept	1.91	0.37	1.19, 2.63
		Bear	0.50	0.19	0.12, 0.87
		$\mathrm{Fi}_{\mathrm{highest}}$	3.34	1.34	0.72, 5.97
		Social affiliation: Pair	0.18	0.09	0.001, 0.35
	2	Intercept	1.89	0.38	1.15, 2.62
		Bear	0.47	0.20	0.08, 0.85
		$\mathrm{Fi}_{\mathrm{highest}}$	3.56	1.38	0.85, 6.27
		Wolf density	-0.02	0.02	-0.07, 0.02
		Social affiliation: Pair	0.20	0.10	0.02, 0.39
	3	Intercept	2.01	0.40	1.23, 2.79
		Bear	0.38	0.20	-0.01, 0.78
		$\mathrm{Fi}_{\mathrm{highest}}$	3.22	1.47	0.34, 6.09
	4	Intercept	1.70	0.48	0.76, 2.64
		Bear	0.50	0.19	0.13, 0.88
		$\mathrm{Fi}_{\mathrm{highest}}$	3.43	1.35	0.78, 6.07
		Habitat	1.68	2.37	-2.96, 6.32
		Social affiliation: Pair	0.17	0.09	-0.002, 0.35

5	Intercept	1.51	0.51	0.51, 2.52
	Bear	0.46	0.20	0.07, 0.85
	$Fi_{highest}$	3.78	1.40	1.03, 6.53
	Wolf density	-0.03	0.02	-0.08, 0.02
	Habitat	2.87	2.58	-2.18, 7.92
	Social affiliation: Pair	0.21	0.21	0.02, 0.40

5. Discussion

When analysing the annual movement patterns of south-central Scandinavian wolf populations' daily movement distances (DMD), the most important variables were months, night-time lights, and the habitat suitability coefficient. The mean DMD was 15.4 km. However, variables affecting DMD differs between winter and summer. During winter, night-time light and habitat suitability still were the most essential variables describing the changes in DMD, but also roe deer density, and there was a decrease in mean DMD (13.9 km) compared to year-round. The analysis of the movement pattern during summer revealed that brown bear density, inbreeding coefficient, and social affiliation were the most important variables and there is an increase in mean DMD during this time of year (19.3km) compared to year-round.

5.1 Time of year matters

As predicted, DMD was lower during the winter months (December, January, February, and March) compared to April, with a substantial decrease observed in February and March. These months are characterised by lower temperatures and frequent snowfall, likely contributing to the reduced DMD. Ungulates are often in poorer condition during late winter and early spring, leading to easier kills for wolves (Metz et al. 2012). Additionally, increased snow depth reduces chasing distances due to wolves' lower foot-load advantage (Wikenros et al. 2009). This combination of factors likely results in shorter DMD during these months.

Another factor could be the preservation of carcasses during colder months, which would allow wolves to use them for more extended periods and reduce the need for more frequent kills (Selva et al. 2003). Furthermore, the increased basal metabolic rate required for thermoregulation in colder temperatures may limit the energy available for longer movements (Careau et al. 2007).

As predicted, DMD was higher during late spring and summer, particularly in May and June, when wolves have pups and primarily feed on newborn moose calves. A study by Bryce et al. (2022) also found that DMD was higher during the pup-rearing season, which generally occurs in May-July. Potentially, this could lead to a higher DMD since they have to search and chase enough ungulates to be able to feed the whole family group. During this time, the wolves' primary prey is juvenile moose, and the kill rate is higher than during winter (Sand et al. 2008). The need to provide for the entire family group and the higher kill rate of juvenile moose with less biomass during this time likely contribute to the increased DMD.

5.2 Assessing the impact of human activity

The explanatory variable night-time lights was included to indicate human activity and footprint, as an increasing night-time light index suggests a higher human presence. This variable was excluded from the summer dataset model due to its correlation with the habitat selection coefficient but was included in both the annual and winter models. As predicted, increasing night-time lights were associated with increased DMD. Several studies indicate that wolves avoid areas with higher human activity (Zimmermann et al., 2014; Milleret et al., 2019; Carricondo-Sanchez et al., 2020). The night-time light, derived from artificial light sources such as houses, farms, and streetlamps, i.e., human activity, likely causes wolves to take detours to avoid these areas, explaining the higher DMD with increasing night-time light.

Paved road density, included only in the annual dataset models, also indicates human activity. Contrary to the prediction, the results revealed weak evidence for a decrease in DMD with increasing paved road density. Zimmermann et al. (2014) found that Scandinavian wolves prefer gravel roads for travel and avoid paved roads. Since wolves prefer to use gravel roads rather than paved roads for travel, that could explain why there were indications of decreasing DMD with increasing paved road density.

5.3 Evaluating the influence of habitat suitability

The habitat suitability coefficient was used to assess how habitat affects DMD, with a lower coefficient indicating a more suitable habitat. Contrary to the prediction, DMD was higher in the suitable habitats. A study on the Florida panther by Criffield et al. (2018) found lower DMD in more selected habitats. However, wolves and panthers are different species, so direct comparisons are limited. The habitat suitability coefficient in this study was relatively low and never exceeded 1, indicating that all habitats within the study were generally suitable for wolves. Wolves in Scandinavia are known to select rugged terrain and young forests (Milleret et al., 2018; Ordiz et al., 2020), and a lot of the area in south-central Scandinavia, where the study takes place, consists of these landscapes. With not many disturbances, the possibility is that they can move more freely within their territories and do not have to consider the not-as-suitable attributes as perhaps the Florida panther must.

5.4 Densities of different prey species matter

This study tested how moose and roe deer density affected DMD during winter. As predicted, there was clear evidence for decreasing DMD with increasing roe deer density. A slight increase in DMD with increasing moose density was observed, but the evidence was weak. Although moose are the primary prey for most wolf family groups in Scandinavia, roe deer also constitute a part of their diet (Sand et al. 2005; 2008; 2016). Wolves are opportunistic predators (Peterson & Ciucci 2003) and can switch between prey based on availability. With higher roe deer densities, the prey availability is higher, and they do not need to move as much as they would if the prey availability was lower, to find food. Wolves in Scandinavia select roe deer instead of moose when roe deer density increases (Sand et al. 2016). With higher densities of roe deer, there will likely be more favourable opportunities for the wolves to kill roe deer, which in turn results in the wolves not needing to cover as long distances during the predation as they would in areas with lower prey density. This could explain the observed decrease in DMD with increasing roe deer density. Conversely, the lack of significant results for moose density may be due to the wolves' ability to adapt their diet and hunting strategies based on prey availability.

5.5 The impact of brown bear density

Brown bear density was included only in the summer dataset due to their hibernation during winter. The results showed that increasing brown bear density increased DMD, aligning with the prediction. In Scandinavia, wolves and bears experience interference competition during spring, shifting to exploitation competition in summer (Tallian et al. 2022). This conclusion is based on the increased search time for wolves when they are sympatric with bears. Additionally, the presence of brown bears leads to a lower kill rate for wolves (Tallian et al. 2017), likely due to the increased search time required in the presence of bears. However, in this study, May is included in the summer analysis, but the majority of the summer analysis includes the summer months. So consequently, the competition between wolves and bears results in increased DMD for wolves as they need to cover greater distances when searching for prey.

5.6 The weak impact of wolf density

The annual and winter datasets showed non-significant increasing impacts of wolf density on DMD, aligning with the prediction that higher intraspecific density increases DMD. However, in the summer dataset, wolf density had non-significant decreasing impact on DMD, contradicting the prediction.

Wolf density does not appear to be an important predictor of DMD. However, there are some indications of increasing impacts on DMD with increasing wolf density, which could be explained by the fact that wolves are highly territorial (Mech & Boitani 2003). Increasing wolf density implies more threats to their territories, necessitating increased patrolling and marking activities.

The non-significant decreasing impact of wolf density on DMD in the summer dataset requires further investigation. One possible explanation could be seasonal variations in territorial behaviour or resource availability, which might reduce the need for extensive patrolling during summer. For example, the Scandinavian wolf population uses more concentrated parts of their territories during summer (Zimmermann et al. 2019). This could explain the decreasing impact of wolf density on DMD during summer.

5.7 Individual characteristics can matter

The highest inbreeding coefficient of the adult pair and social affiliation were used to examine the effects of individual characteristics. The inbreeding coefficient only had a significant impact in the summer. During the winter, it was not included in the highest-ranked model. In the annual analysis, it was only included in one model, showing non-significant decreasing impacts on DMD. The prediction was that DMD would decrease with higher inbreeding due to the high levels of inbreeding and low genetic variation in the Scandinavian wolf population (Åkesson et al. 2016; 2022). Vertebral defects associated with higher inbreeding (Räikkönen et al. 2006) could limit DMD. However, the annual analysis showed only weak decreasing impacts, suggesting that these defects do not significantly restrict DMD. Conversely, the summer dataset revealed that increasing inbreeding substantially increased DMD. Highly inbred wolves in Scandinavia have been observed to scavenge more than less inbred wolves (Wikenros et al. 2023), potentially indicating a lower success rate in killing prey. This could lead to more frequent but unsuccessful hunting attempts, resulting in higher DMD.

Social affiliation was analysed to determine differences in DMD between scent-marking pairs and family groups. This variable was included in all three datasets but not in any top models for the annual dataset. The winter analysis included it in two models, showing weak evidence for lower DMD in scent-marking pairs compared to family groups. The summer analysis included it in four top models, showing that scent-marking pairs had higher DMD than family groups. As mentioned above, wolves tend to use a more clumped area of their territories during summer, and family groups with pups' usage of the territory are even more clumped compared to scent-marking pairs (Zimmermann et al. 2019). Since family groups use an even smaller area of the home range than scent-marking pairs during summer, this may decrease DMD.

5.8 Weaknesses of the study

This study utilised a comprehensive dataset of GPS locations from the Scandinavian wolf population spanning 2001 to 2019. However, significant data were discarded due to missing daily GPS locations during various study periods. Despite advancements in GPS technology, limitations persist, such as the inability to record hourly locations. Factors like canopy cover can affect GPS accuracy (Frair et al. 2004), and given that wolves prefer forests, this can explain the loss in GPS locations. Although the dataset remained substantial post-cleaning, additional data could have improved accuracy. The dataset provided only hourly GPS locations, likely underestimating wolves' daily movement distances (DMD). Shorter intervals between GPS recordings yield more precise and extended DMD estimates (McCann et al. 2021), suggesting that more frequent GPS data collection would have yielded more accurate results in this study.

There are also limitations concerning the explanatory variables in this study. The dataset providing night-time light data was from 2009, which does not accurately represent the entire study period from 2001 to 2019. The availability of datasets for additional years would have enhanced the accuracy of the estimates beyond those centred around 2009. Similarly, the habitat suitability coefficient is limited by the 2018 land cover dataset, which may not reflect changes between 2001 and 2019, such as tree growth, clear-cutting, and construction. More land cover datasets from earlier years would have provided better accuracy for different study periods, enhancing the habitat suitability coefficient's precision.

There are inherent limitations in estimating the densities of bears, moose, and roe deer, for example, due to human factors. For bear density, which is based on harvest data, the estimates can be influenced by varying hunting pressures over time. This variability can lead to inconsistencies in the data. Similarly, the densities of moose and roe deer, derived from pellet counts, are subject to observer bias. Differences in the experience and skills of field technicians can affect the accuracy of the counts. Additionally, recording errors may further compromise the reliability of these estimates. These factors can impact the density estimates, potentially affecting the overall results of this study.

This study did not account for sex differences, which is a source of error since the sex of the wolves may have different impacts on them, especially during summer when they may have pups. During this time, the sexes exhibit behavioural differences, which can have large impacts on their movements. It would also have been favourable to include whether family groups and scent-marking pairs were reproductive or non-reproductive since that also could have influenced the results of their daily movement distances. The inbreeding coefficient for both males and females would have been beneficial to analyse, as it is unclear if the individual with the highest inbreeding coefficient limits the DMD of the scent-marking pair or family group.

The dredge function was employed for analysis to manage the large number of variables. While this function identifies the best-fitted models, it also explores numerous potential models, increasing the risk of overfitting. Consequently, some selected models may be statistically robust but lack biological significance, necessitating cautious interpretation. Nonetheless, the results appear biologically relevant, particularly in the context of wolf movement patterns and the influence of variables on DMD. This study's conditional and marginal R^2 values were relatively low (Table 1), indicating the limited explanatory power of both the fixed and random effects. This suggests that much of the variation in DMD remains unexplained, likely due to other influential factors not accounted for in this analysis. Despite these limitations, the study provides valuable insights into the factors that may influence DMD in the Scandinavian wolf population.

5.9 Future implications and studies

Wolves are known to travel extensive distances daily, and the availability of suitable habitats significantly enhances their ability to cover longer distances. This understanding is crucial for conservation planning, as identifying and protecting key habitats that support extended DMD can ensure wolves have the necessary space and resources for survival. While the study found that paved roads had a weak effect on wolf movement, it still underscores the importance of planning wildlife corridors to facilitate safe passage between habitats, potentially reducing mortality from vehicle collisions. The knowledge of how wolves react and move in relation to human activity can be important when planning buildings and infrastructure. More knowledge about how different factors, e.g., prey density, interspecific density, and inbreeding, affect the wolf's behaviour can be used to make informed decisions accounting for wolf ecology and behaviour.

The study also indicates that wolves tend to avoid areas with high human activity, travelling longer distances in such regions. This behaviour presents an opportunity to educate the public about wolves. Increased knowledge and education have been shown to foster more positive attitudes towards wolves (Ericsson & Heberlein 2003). By leveraging this study, we can enhance public understanding and potentially improve the societal status of wolves, thereby minimising human-wildlife conflict.

As there was relatively low explanatory power, other variables can have more profound effects on wolves' DMD. Does the size of wolves' home ranges affect their DMD, or could the percentage of different habitats within their home ranges affect their movement patterns? One could also examine in depth how inbreeding affects wolves' movement patterns. For example, if one examines the differences in inbreeding coefficients between the pair, the results could differ. Since this study did not consider sex differences, future studies should do that. An interesting question that could be answered is whether there is a difference between daily movement distances between males and females, especially during the pup-rearing season, and whether this changes over the year. It would also be interesting to see how wolves change their movement patterns in different habitats. Both in daily movement distance and their speed (m/h).

Future studies should also consider more detailed GPS data. Since the GPS locations were one hour apart, a lot of movement was missed. Having GPS locations taken at shorter intervals would increase the accuracy of their daily movement distance.

6. Conclusion

In conclusion, the average daily movement distance in the Scandinavian wolf population was 15.4 km. The study identified several factors with significant effects on daily movement distance, including time of year, human activity, habitat, prey and bear density, inbreeding coefficient and social affiliation. This shows that wolves adapt their behaviours and that their movement patterns are a result between needs, such as finding resources, avoid risks, and individual characteristics. This knowledge is important when developing effective management strategies for wolves in Scandinavia.

References

Aronsson, M., Low, M., López-Bao, J.V., Persson, J., Odden, J., Linnell, J.D.C. & Andrén, H. (2016). Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. Ecology and Evolution, 6 (9), 2957–2967. https://doi.org/10.1002/ece3.2032

Ausilio, G., Sand, H., Månsson, J., Mathisen, K.M. & Wikenros, C. (2021). Ecological Effects of Wolves in Anthropogenic Landscapes: The Potential for Trophic Cascades Is Context-Dependent. Frontiers in Ecology and Evolution, 8. https://doi.org/10.3389/fevo.2020.577963

Baek, S.-Y., Shimazaki, A., Zedrosser, A., Naganuma, T., Yamazaki, K. & Koike, S. (2023). Response to human-modified landscape of an apex consumer: Sex- and season-related variations in road selection and movement pattern. Global Ecology and Conservation, 46, e02603. https://doi.org/10.1016/j.gecco.2023.e02603

Bartoń K (2023). _MuMIn: Multi-Model Inference_. R package version 1.47.5, <https://CRAN.R-project.org/package=MuMIn>.

Blanco, J.C. & Cortés, Y. (2007). Dispersal patterns, social structure and mortality of wolves living in agricultural habitats in Spain. Journal of Zoology, 273 (1), 114–124. https://doi.org/10.1111/j.1469-7998.2007.00305.x

Blašković, S., Gomerčić, T., Topličanec, I. & Sindičić, M. (2022). Temporal overlap of human and apex predator activity on wildlife trails and forest roads. Journal of Vertebrate Biology, 71 (22029), 22029.1–9. https://doi.org/10.25225/jvb.22029

Bojarska, K., Sulich, J., Bachmann, S., Okarma, H., Theuerkauf, J. & Gula, R. (2020). Opportunity and peril: how wolves use a dense network of forest roads. Mammalian Biology, 100 (2), 203–211. https://doi.org/10.1007/s42991-020-00014-0

Bryce, C.M., Dunford, C.E., Pagano, A.M., Wang, Y., Borg, B.L., Arthur, S.M. & Williams, T.M. (2022). Environmental correlates of activity and energetics in a wide-ranging social carnivore. Animal Biotelemetry, 10 (1), 1. https://doi.org/10.1186/s40317-021-00272-w

Cagnacci, F., Boitani, L., Powell, R.A. & Boyce, M.S. (2010). Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. Philosophical Transactions of the Royal Society B: Biological Sciences, 365 (1550), 2157–2162. https://doi.org/10.1098/rstb.2010.0107

Carricondo-Sanchez, D., Zimmermann, B., Wabakken, P., Eriksen, A., Milleret, C., Ordiz, A., Sanz-Pérez, A. & Wikenros, C. (2020). Wolves at the door? Factors influencing the individual behavior of wolves in relation to anthropogenic features. Biological Conservation, 244, 108514. https://doi.org/10.1016/j.biocon.2020.108514

Careau, V., Morand-Ferron, J. & Thomas, D. (2007). Basal Metabolic Rate of Canidae from Hot Deserts to Cold Arctic Climates. Journal of Mammalogy, 88 (2), 394–400. https://doi.org/10.1644/06-MAMM-A-111R1.1

Chapron, G., Kaczensky, P., Linnell, J.D.C., von Arx, M., Huber, D., Andrén, H., López-Bao, J.V., Adamec, M., Álvares, F., Anders, O., Balčiauskas, L., Balys, V., Bedő, P., Bego, F., Blanco, J.C., Breitenmoser, U., Brøseth, H., Bufka, L., Bunikyte, R., Ciucci, P., Dutsov, A., Engleder, T., Fuxjäger, C., Groff, C., Holmala, K., Hoxha, B., Iliopoulos, Y., Ionescu, O., Jeremić, J., Jerina, K., Kluth, G., Knauer, F., Kojola, I., Kos, I., Krofel, M., Kubala, J., Kunovac, S., Kusak, J., Kutal, M., Liberg, O., Majić, A., Männil, P., Manz, R., Marboutin, E., Marucco, F., Melovski, D., Mersini, K., Mertzanis, Y., Mysłajek, R.W., Nowak, S., Odden, J., Ozolins, J., Palomero, G., Paunović, M., Persson, J., Potočnik, H., Quenette, P.-Y., Rauer, G., Reinhardt, I., Rigg, R., Ryser, A., Salvatori, V., Skrbinšek, T., Stojanov, A., Swenson, J.E., Szemethy, L., Trajçe, A., Tsingarska-Sedefcheva, E., Váňa, M., Veeroja, R., Wabakken, P., Wölfl, M., Wölfl, S., Zimmermann, F., Zlatanova, D. & Boitani, L. (2014). Recovery of large carnivores in Europe's modern human-dominated landscapes. Science, 346 (6216), 1517–1519

Criffield, M., van de Kerk, M., Leone, E., Cunningham, M.W., Lotz, M., Oli, M.K. & Onorato, D.P. (2018). Assessing impacts of intrinsic and extrinsic factors on Florida panther movements. Journal of Mammalogy, 99 (3), 702–712

Dahle, B. & Swenson, J.E. (2003). Home ranges in adult Scandinavian brown bears (Ursus arctos): effect of mass, sex, reproductive category, population density and habitat type. Journal of Zoology, 260 (4), 329–335. https://doi.org/10.1017/S0952836903003753

Ditmer, M.A., Fieberg, J.R., Moen, R.A., Windels, S.K., Stapleton, S.P. & Harris, T.R. (2018). Moose movement rates are altered by wolf presence in two ecosystems. Ecology and Evolution, 8 (17), 9017–9033. https://doi.org/10.1002/ece3.4402

Droghini, A. & Boutin, S. (2018). Snow conditions influence grey wolf (*Canis lupus*) travel paths: the effect of human-created linear features. Canadian Journal of Zoology, 96 (1), 39–47. https://doi.org/10.1139/cjz-2017-0041

Ericsson, G. & Heberlein, T.A. (2003). Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. Biological Conservation, 111 (2), 149–159. https://doi.org/10.1016/S0006-3207(02)00258-6

Estes, J.A., Terborgh, J., Brashares, J.S., Power, M.E., Berger, J., Bond, W.J., Carpenter, S.R., Essington, T.E., Holt, R.D., Jackson, J.B.C., Marquis, R.J., Oksanen, L., Oksanen, T., Paine, R.T., Pikitch, E.K., Ripple, W.J., Sandin, S.A., Scheffer, M., Schoener, T.W., Shurin, J.B., Sinclair, A.R.E., Soulé, M.E., Virtanen, R. & Wardle, D.A. (2011). Trophic Downgrading of Planet Earth. Science, 333 (6040), 301–306. https://doi.org/10.1126/science.1205106

Fortin, D., Beyer, H.L., Boyce, M.S., Smith, D.W., Duchesne, T. & Mao, J.S. (2005). Wolves Influence Elk Movements: Behavior Shapes a Trophic Cascade in

Yellowstone National Park. Ecology, 86 (5), 1320–1330. https://doi.org/10.1890/04-0953

Fowler, N. L., Petroelje, T. R., Kautz, T. M., Svoboda, N. J., Duquette, J. F., Kellner, K. F., Beyer, D. E., & Belant, J. L. (2022). Variable effects of wolves on niche breadth and density of intraguild competitors. Ecology and Evolution, 12 (2), e8542-n/a. https://doi.org/10.1002/ece3.8542

Frair, J.L., Nielsen, S.E., Merrill, E.H., Lele, S.R., Boyce, M.S., Munro, R.H.M., Stenhouse, G.B. & Beyer, H.L. (2004). Removing GPS Collar Bias in Habitat Selection Studies. Journal of Applied Ecology, 41 (2), 201–212.

Fuller, T.K., Mech, L.D. & Cochrane, J.F. (2003). Wolf population dynamics. Wolves: Behavior, Ecology, and Conservation (eds L.D. Mech & L. Boitani). University of Chicago Press.

Gebo, B., Takele, S. & Shibru, S. (2022). Effects of prey abundance on carnivore populations in the Faragosa-Fura landscape of the Southern Rift Valley, Ethiopia. Global Ecology and Conservation, 34, e02029. https://doi.org/10.1016/j.gecco.2022.e02029

Gicquel, M., Sand, H., Månsson, J., Wallgren, M. & Wikenros, C. (2020). Does recolonization of wolves affect moose browsing damage on young Scots pine? Forest Ecology and Management, 473, 118298. https://doi.org/10.1016/j.foreco.2020.118298

Green, D.S. & Holekamp, K.E. (2019). Pastoralist activities affect the movement patterns of a large African carnivore, the spotted hyena (*Crocuta crocuta*). Journal of Mammalogy, 100 (6), 1941–1953. https://doi.org/10.1093/jmammal/gyz135

Haglund, B. (1968). De stora rovdjurens vintervanor II. Viltrevy 5 (5): 213-361.

Hebblewhite, M. & Haydon, D.T. (2010). Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. Philosophical Transactions of the Royal Society B: Biological Sciences, 365 (1550), 2303–2312. https://doi.org/10.1098/rstb.2010.0087

Jędrzejewski, W., Schmidt, K., Okarma, H. & Kowalczyk, R. (2002). Movement pattern and home range use by the Eurasian lynx in Białowieża Primeval Forest (Poland). Annales Zoologici Fennici, 39 (1), 29–41

Johnson, I., Brinkman, T., Lake, B. & Brown, C. (2017). Winter hunting behavior and habitat selection of wolves in a low-density prey system. Wildlife Biology, 2017 (1), wlb.00290. https://doi.org/10.2981/wlb.00290

Keller, L.F. & Waller, D.M. (2002). Inbreeding effects in wild populations. Trends in Ecology & Evolution, 17 (5), 230–241. https://doi.org/10.1016/S0169-5347(02)02489-8

Kittle, A.M., Bukombe, J.K., Sinclair, A.R.E., Mduma, S.A.R. & Fryxell, J.M. (2016). Landscape-level movement patterns by lions in western Serengeti: comparing the influence of inter-specific competitors, habitat attributes and prey availability. Movement Ecology, 4, 17. https://doi.org/10.1186/s40462-016-0082-9

Krofel, M. & Jerina, K. (2016). Mind the cat: Conservation management of a protected dominant scavenger indirectly affects an endangered apex predator. Biological Conservation, 197, 40–46. https://doi.org/10.1016/j.biocon.2016.02.019

Kuijper, D.P.J., Sahlén, E., Elmhagen, B., Chamaillé-Jammes, S., Sand, H., Lone, K. & Cromsigt, J.P.G.M. (2016). Paws without claws? Ecological effects of large carnivores in anthropogenic landscapes. Proceedings of the Royal Society B: Biological Sciences, 283 (1841), 20161625. https://doi.org/10.1098/rspb.2016.1625

Lesilau, F., Verschueren, S., Zelfde, M. van't, Musters, K.C.J.M., Snoo, G.R. de & Iongh, H.H. de (2021). Spatial ecology of lions in a small, semi-fenced park surrounded by dense human populations: the case study of Nairobi National Park, Kenya. Mammalia, 85 (3), 198–207. https://doi.org/10.1515/mammalia-2020-0116

Liberg, O., Andrén, H., Pedersen, H.-C., Sand, H., Sejberg, D., Wabakken, P., Åkesson, M. & Bensch, S. (2005). Severe inbreeding depression in a wild wolf Canis lupus population. Biology Letters, 1 (1), 17–20. https://doi.org/10.1098/rsbl.2004.0266

Liberg, O., Aronson, Å., Sand, H., Wabakken, P., Maartmann, E., Svensson, L. & Åkesson, M. (2012). Monitoring of wolves in Scandinavia. Hystrix, the Italian Journal of Mammalogy, 23 (1). https://doi.org/10.4404/hystrix-23.1-4670

Liberg, O., Sand, H., Wabakken, P. & Chapron, G. (2011). Illegal killing of wolves in Scandinavia 1998-2011: variation in space and time. A report to World Wide Fund for Nature, WWF, (Sweden). Grimsö Wildlife Research Statio, SLU. 24 p.

Lüdecke, D., Ben-Shachar, M., Patil, I., Waggoner, P., & Makowski, D. (2021). Performance: An R package for assessment, comparison and testing of statistical models. Journal of Open Source Software, 6, 3139.

Mattisson, J., Sand, H., Wabakken, P., Gervasi, V., Liberg, O., Linnell, J.D.C., Rauset, G.R. & Pedersen, H.C. (2013). Home range size variation in a recovering wolf population: evaluating the effect of environmental, demographic, and social factors. Oecologia, 173 (3), 813–825. https://doi.org/10.1007/s00442-013-2668-x

May, R., Van Dijk, J., Wabakken, P., Swenson, J.E., Linnell, J.D.C., Zimmermann, B., Odden, J., Pedersen, H.C., Andersen, R. & Landa, A. (2008). Habitat differentiation within the large-carnivore community of Norway's multiple-use landscapes. Journal of Applied Ecology, 45 (5), 1382–1391. https://doi.org/10.1111/j.1365-2664.2008.01527.x

McCann, R., Bracken, A.M., Christensen, C., Fürtbauer, I. & King, A.J. (2021). The Relationship Between GPS Sampling Interval and Estimated Daily Travel Distances in Chacma Baboons (Papio ursinus). International Journal of Primatology, 42 (4), 589–599. https://doi.org/10.1007/s10764-021-00220-8

McNitt, D.C., Alonso, R.S., Cherry, M.J., Fies, M.L. & Kelly, M.J. (2020). Sex-specific effects of reproductive season on bobcat space use, movement, and resource selection in the Appalachian Mountains of Virginia. PLoS ONE, 15 (8), e0225355. https://doi.org/10.1371/journal.pone.0225355

Mech, L.D. & Boitani, L. (2003). Wolf social ecology. Wolves: Behavior, Ecology, and Conservation (eds L.D. Mech & L. Boitani). University of Chicago Press.

Metz, M. C., Smith, D. W., Vucetich, J. A., Stahler, D. R., & Peterson, R. O. (2012). Seasonal patterns of predation for gray wolves in the multi-prey system of

Yellowstone National Park. The Journal of Animal Ecology, 81(3), 553–563. https://doi.org/10.1111/j.1365-2656.2011.01945.x

Milleret, C., Ordiz, A., Chapron, G., Andreassen, H.P., Kindberg, J., Månsson, J., Tallian, A., Wabakken, P., Wikenros, C., Zimmermann, B., Swenson, J.E. & Sand, H. (2018). Habitat segregation between brown bears and gray wolves in a human-dominated landscape. Ecology and Evolution, 8 (23), 11450–11466. https://doi.org/10.1002/ece3.4572

Milleret, C., Ordiz, A., Sanz-Pérez, A., Uzal, A., Carricondo-Sanchez, D., Eriksen, A., Sand, H., Wabakken, P., Wikenros, C., Åkesson, M. & Zimmermann, B. (2019). Testing the influence of habitat experienced during the natal phase on habitat selection later in life in Scandinavian wolves. Scientific Reports, 9 (1), 6526. https://doi.org/10.1038/s41598-019-42835-1

Mollie E. Brooks, Kasper Kristensen, Koen J. van Benthem, Arni Magnusson, Casper W. Berg, Anders Nielsen, Hans J. Skaug, Martin Maechler and Benjamin M. Bolker (2017). glmmTMB Balances Speed and Flexibility Among Packages for Zero-inflated Generalized Linear Mixed Modeling. The R Journal, 9(2), 378-400. doi: 10.32614/RJ-2017-066.

Nathan, R. (2008). An emerging movement ecology paradigm. Proceedings of the National Academy of Sciences, 105 (49), 19050–19051. https://doi.org/10.1073/pnas.0808918105

Nowak, S. & Mysłajek, R.W. (2016). Wolf recovery and population dynamics in Western Poland, 2001–2012. Mammal Research, 61 (2), 83–98. https://doi.org/10.1007/s13364-016-0263-3

Olson, T.L., Squibb, R.C. & Gilbert, B.K. (1998). Brown Bear Diurnal Activity and Human Use: A Comparison of Two Salmon Streams. Ursus, 10, 547–555

Onorato, D.P., Criffield, M., Lotz, M., Cunningham, M., McBride, R., Leone, E.H., Bass Jr, O.L. & Hellgren, E.C. (2011). Habitat selection by critically endangered Florida panthers across the diel period: implications for land management and conservation. Animal Conservation, 14 (2), 196–205. https://doi.org/10.1111/j.1469-1795.2010.00415.x

Ordiz, A., Bischof, R. & Swenson, J.E. (2013). Saving large carnivores, but losing the apex predator? Biological Conservation, 168, 128–133. https://doi.org/10.1016/j.biocon.2013.09.024

Ordiz, A., Milleret, C., Kindberg, J., Månsson, J., Wabakken, P., Swenson, J.E. & Sand, H. (2015). Wolves, people, and brown bears influence the expansion of the recolonizing wolf population in Scandinavia. Ecosphere, 6 (12), 1–14. https://doi.org/10.1890/ES15-00243.1

Ordiz, A., Sæbø, S., Kindberg, J., Swenson, J.E. & Støen, O.-G. (2017). Seasonality and human disturbance alter brown bear activity patterns: implications for circumpolar carnivore conservation? Animal Conservation, 20 (1), 51–60. https://doi.org/10.1111/acv.12284

Ordiz, A., Uzal, A., Milleret, C., Sanz-Pérez, A., Zimmermann, B., Wikenros, C., Wabakken, P., Kindberg, J., Swenson, J.E. & Sand, H. (2020). Wolf habitat selection when sympatric or allopatric with brown bears in Scandinavia. Scientific Reports, 10 (1), 9941. https://doi.org/10.1038/s41598-020-66626-1

Pereira, L. M., Owen-Smith, N., & Moleón, M. (2014). Facultative predation and scavenging by mammalian carnivores: seasonal, regional and intra-guild comparisons. Mammal Review, 44(1), 44–55. https://doi.org/10.1111/mam.12005

Peterson, R.O. & Ciucci, P. (2003). The wolf as a carnivore. Wolves: behaviour, ecology and conservation (eds L.D. Mech & L. Boitani). University of Chicago Press, Chicago and London

Podolski, I., Belotti, E., Bufka, L., Reulen, H. & Heurich, M. (2013). Seasonal and daily activity patterns of free-living Eurasian lynx Lynx lynx in relation to availability of kills. Wildlife Biology, 19 (1), 69–77. https://doi.org/10.2981/12-049

R Core Team. (2023). R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria. <https://www.R-project.org/>.

Rich, L.N., Mitchell, M.S., Gude, J.A., Sime, C.A. & Van Vuren, D.H. (2012). Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. Journal of Mammalogy, 93 (3), 722–731

Ripple, W.J., Estes, J.A., Beschta, R.L., Wilmers, C.C., Ritchie, E.G., Hebblewhite, M., Berger, J., Elmhagen, B., Letnic, M., Nelson, M.P., Schmitz, O.J., Smith, D.W., Wallach, A.D. & Wirsing, A.J. (2014). Status and Ecological Effects of the World's Largest Carnivores. Science, 343 (6167), 1241484. https://doi.org/10.1126/science.1241484

Roberge, C., Dahlgren, J., Nilsson, P., Wikberg, P. & Fridman, J. (2024). Forest statistics 2024. Department of Forest Resource Management, Swedish University of Agricultural Sciences Umeå.

Räikkönen, J., Bignert, A., Mortensen, P. & Fernholm, B. (2006). Congenital defects in a highly inbred wild wolf population (Canis lupus). Mammalian Biology, 71 (2), 65–73. https://doi.org/10.1016/j.mambio.2005.12.002

Räikkönen, J., Vucetich, J.A., Vucetich, L.M., Peterson, R.O. & Nelson, M.P. (2013). What the Inbred Scandinavian Wolf Population Tells Us about the Nature of Conservation. PLoS ONE, 8 (6), e67218. https://doi.org/10.1371/journal.pone.0067218

Sand, H., Eklund, A., Zimmermann, B., Wikenros, C. & Wabakken, P. (2016). Prey Selection of Scandinavian Wolves: Single Large or Several Small? PLOS ONE, 11 (12), e0168062. https://doi.org/10.1371/journal.pone.0168062

Sand, H., Wabakken, P., Zimmermann, B., Johansson, Ö., Pedersen, H. C., & Liberg, O. (2008). Summer kill rates and predation pattern in a wolf-moose system: can we rely on winter estimates. Oecologia, 156 (1), 53–64. https://doi.org/10.1007/s00442-008-0969-2

Sand, H., Wikenros, C., Wabakken, P. & Liberg, O. (2006). Effects of hunting group size, snow depth and age on the success of wolves hunting moose. Animal Behaviour, 72 (4), 781–789. https://doi.org/10.1016/j.anbehav.2005.11.030

Sand, H., Zimmermann, B., Wabakken, P., Andrèn, H. & Pedersen, H.C. (2005). Using GPS Technology and GIS Cluster Analyses to Estimate Kill Rates in Wolf-Ungulate Ecosystems. Wildlife Society Bulletin (1973-2006), 33 (3), 914–925

Sazatornil, V., Rodríguez, A., Klaczek, M., Ahmadi, M., Álvares, F., Arthur, S., Blanco, J.C., Borg, B.L., Cluff, D., Cortés, Y., García, E.J., Geffen, E., Habib, B., Iliopoulos, Y., Kaboli, M., Krofel, M., Llaneza, L., Marucco, F., Oakleaf, J.K., Person, D.K., Potočnik, H., Ražen, N., Rio-Maior, H., Sand, H., Unger, D., Wabakken, P. & López-Bao, J.V. (2016). The role of human-related risk in breeding site selection by wolves. Biological Conservation, 201, 103–110. https://doi.org/10.1016/j.biocon.2016.06.022

Sells, S.N., Mitchell, M.S., Podruzny, K.M., Ausband, D.E., Emlen, D.J., Gude, J.A., Smucker, T.D., Boyd, D.K. & Loonam, K.E. (2022). Competition, prey, and mortalities influence gray wolf group size. The Journal of Wildlife Management, 86 (3), e22193. https://doi.org/10.1002/jwmg.22193

Selva, N., Jedrzejewska, B., Jedrzejewski, W., & Wajrak, A. (2003). Scavenging on European bison carcasses in Bialowieza Primeval Forest (eastern Poland). Écoscience (Sainte-Foy), 10(3), 303–311. https://doi.org/10.1080/11956860.2003.11682778

Soulé, M.E., Estes, J.A., Berger, J. & Del Rio, C.M. (2003). Ecological Effectiveness: Conservation Goals for Interactive Species. Conservation Biology, 17 (5), 1238–1250. https://doi.org/10.1046/j.1523-1739.2003.01599.x

Svensson, L., Wabakken, P., Maartmann, E., Nordli, K., Flagstad, Ø., Danielsson, A., Hensel, H., Pöchhacker, K. & Åkesson, M. (2023). Inventering av varg vintern 2022-2023. Bestandsovervåking av ulv vinteren 2022-2023. Bestandsstatus for store rovdyr i Skandinavia. Beståndsstatus för stora rovdjur i Skandinavien 1-2023. 65s.

Sørensen, O.J., Kvam, T., Wabakken, P. & Landa, A. (1986). Ulven (Canis lupus l.) i Norge 1948-84. Viltrapport 33, 1-94.

Tallian, A., Ordiz, A., Metz, M.C., Milleret, C., Wikenros, C., Smith, D.W., Stahler, D.R., Kindberg, J., MacNulty, D.R., Wabakken, P., Swenson, J.E. & Sand, H. (2017). Competition between apex predators? Brown bears decrease wolf kill rate on two continents. Proceedings of the Royal Society B: Biological Sciences, 284 (1848), 20162368. https://doi.org/10.1098/rspb.2016.2368

Tallian, A., Ordiz, A., Metz, M.C., Zimmermann, B., Wikenros, C., Smith, D.W., Stahler, D.R., Wabakken, P., Swenson, J.E., Sand, H. & Kindberg, J. (2022). Of wolves and bears: Seasonal drivers of interference and exploitation competition between apex predators. Ecological Monographs, 92 (2), e1498. https://doi.org/10.1002/ecm.1498

The Swedish Environmental Protection Agency. (N.Da). Jakt på kronhjort. https://www.naturvardsverket.se/amnesomraden/jakt-och-vilt/jakt-pa-klovvilt/kronhjort/ [2024-08-16]

The Swedish Environmental Protection Agency. (N.Db). Jakt på rådjur, dovhjort, vildsvin och mufflonfår. https://www.naturvardsverket.se/amnesomraden/jakt-och-vilt/jakt-pa-klovvilt/radjur-dovhjort-vildsvin-och-mufflonfar/ [2024-08-16]

Tredick, C.A., Stauffer, D.F., Kelly, M.J. & Vaughan, M.R. (2017). Landscape-level habitat use and movement patterns of black bears in northeastern Arizona. The Southwestern Naturalist, 62 (1), 85–91. https://doi.org/10.1894/0038-4909-62.1.85

Tuqa, J.H., Funston, P., Musyoki, C., Ojwang, G.O., Gichuki, N.N., Bauer, H., Tamis, W., Dolrenry, S., Van‘t Zelfde, M., de Snoo, G.R. & de Iongh, H.H. (2014). Impact of severe climate variability on lion home range and movement patterns in the Amboseli ecosystem, Kenya. Global Ecology and Conservation, 2, 1–10. https://doi.org/10.1016/j.gecco.2014.07.006

Valeix, M., Loveridge, A.J., Davidson, Z., Madzikanda, H., Fritz, H. & Macdonald, D.W. (2010). How key habitat features influence large terrestrial carnivore movements: waterholes and African lions in a semi-arid savanna of north-western Zimbabwe. Landscape Ecology, 25 (3), 337–351. https://doi.org/10.1007/s10980-009-9425-x

Venter, O., Sanderson, E.W., Magrach, A., Allan, J.R., Beher, J., Jones, K.R., Possingham, H.P., Laurance, W.F., Wood, P., Fekete, B.M., Levy, M.A. & Watson, J.E.M. (2016). Data from: Global terrestrial Human Footprint maps for 1993 and 2009 [Lights 2009]. Dryad. https://doi.org/10.5061/dryad.052q5

Wabakken, P., Sand, H., Liberg, O. & Bjärvall, A. (2001). The recovery, distribution, and population dynamics of wolves on the Scandinavian peninsula, 1978-1998. Canadian Journal of Zoology, 79 (4), 710–725. https://doi.org/10.1139/z01-029

Wang, Y., Cheng, W., Guan, Y., Qi, J., Roberts, N.J., Wen, D., Cheng, Z., Shan, F., Zhao, Y. & Gu, J. (2023). The fine-scale movement pattern of Amur tiger (Panthera tigris altaica) responds to winter habitat permeability. Wildlife Letters, 1 (3), 119–130. https://doi.org/10.1002/wll2.12020

Whittington, J., Hebblewhite, M., Baron, R.W., Ford, A.T. & Paczkowski, J. (2022). Towns and trails drive carnivore movement behaviour, resource selection, and connectivity. Movement Ecology, 10, 17. https://doi.org/10.1186/s40462-022-00318-5

Wickham, H., François, R., Müller, K. & Vaughn, D. (2023). dplyr: A Grammar of Data Manipulation. R package version 1.1.4, <https://CRAN.R-project.org/package=dplyr>.

Wikenros, C., Di Bernardi, C., Zimmermann, B., Åkesson, M., Demski, M., Flagstad, Ø., Mattisson, J., Tallian, A., Wabakken, P. & Sand, H. (2023). Scavenging patterns of an inbred wolf population in a landscape with a pulse of human-provided carrion. Ecology and Evolution, 13 (7), e10236. https://doi.org/10.1002/ece3.10236

Wikenros, C., Sand, H., Ahlqvist, P., & Liberg, O. (2013). Biomass flow and scavengers use of carcasses after re-colonization of an apex predator. PloS One, 8(10), e77373–e77373. https://doi.org/10.1371/journal.pone.0077373

Wikenros, C., Sand, H., Wabakken, P. et al. (2009). Wolf predation on moose and roe deer: chase distances and outcome of encounters. Acta Theriol 54, 207–218. https://doi.org/10.4098/j.at.0001-7051.082.2008

Yang, H., Han, S., Xie, B., Mou, P., Kou, X., Wang, T., Ge, J. & Feng, L. (2019). Do prey availability, human disturbance and habitat structure drive the daily activity patterns of Amur tigers (Panthera tigris altaica)? Journal of Zoology, 307 (2), 131–140. https://doi.org/10.1111/jzo.12622

Zimmermann, B., Nelson, L., Wabakken, P., Sand, H. & Liberg, O. (2014). Behavioral responses of wolves to roads: scale-dependent ambivalence. Behavioral Ecology, 25 (6), 1353–1364. https://doi.org/10.1093/beheco/aru134

Zimmermann, B., Sand, H., Wabakken, P., Liberg, O. & Andreassen, H.P. (2015). Predator-dependent functional response in wolves: from food limitation to surplus killing. Journal of Animal Ecology, 84 (1), 102–112

Zimmermann, B., Wikenros, C., Sand, H., Eriksen, A., & Wabakken, P. (2019). Elg i ulverevir: predasjon og elgjakt. Skriftserien nr 23 – 2019, Høgskolen i Innlandet, Elverum. 50 s.

Åkesson, M., Danielsson, A., Flagstad, Ö. & Svensson, L. (2023). Sammanställning av släktträdet över den skandinaviska vargpopulationen fram till 2022. Rapport från SLU Viltskadecenter 2023-5.

Åkesson, M., Flagstad, Ø., Aspi, J., Kojola, I., Liberg, O., Wabakken, P. & Sand, H. (2022). Genetic signature of immigrants and their effect on genetic diversity in the recently established Scandinavian wolf population. Conservation Genetics, 23 (2), 359–373. https://doi.org/10.1007/s10592-021-01423-5

Åkesson, M., Liberg, O., Sand, H., Wabakken, P., Bensch, S. & Flagstad, Ø. (2016). Genetic rescue in a severely inbred wolf population. Molecular Ecology, 25 (19), 4745–4756. https://doi.org/10.1111/mec.13797

Popular science summary

The return of large carnivores, like the wolf, and the advancements in GPS technology have opened up new ways to study how these animals move, and impact areas dominated by prey species, like the roe deer. The aim of this study was to understand what factors influence the daily travel distance of the Scandinavian wolf population. By analysing GPS data collected between 2001 and 2019 from 29 Scandinavian wolves, statistical models were used to explore how different variables, such as time of year, human activity, prey and bear densities, inbreeding level, if the wolf was in a scent-marking pair or a family, and wolf density, affect wolf movement.

The findings revealed that, on average, the Scandinavian wolf population travel about 15.4 km each day. They have shorter travel distances during the winter months (December to March), especially in February and March, compared to April. Conversely, their travel distance is longer in late spring and early summer (May and June). Human activity, which was indicated by night-time lights, tends to increase their daily travel distance, while higher roe deer densities decrease the daily distance. During summer, increased bear density and inbreeding also lead to longer daily travel distances. Additionally, the daily travel distances of wolves who live in scent-marking pairs is higher than those who live in family groups.

These insights into wolf movement patterns are important for wolf management and it can help reduce conflicts between humans and wolves by highlighting the factors that influence their movement.

Acknowledgements

I would like to start thanking my main supervisor, Camilla Wikenros, for the opportunity to once again write a thesis under your guidance. I am very grateful for your support throughout this process and for all the help and input you have provided. It has been really fun to work with you onsite instead of Zoom, and I appreciate the opportunities you have given me. I would also like to thank my assistant supervisor Håkan Sand for your valuable thoughts and guidance during the writing process. I will always remember the mechanisms during the writing process from now on. Of course, a big thank you to my bunker girls – it has been amazing to have you both by my side throughout the entire course of the thesis! And thank you to my family and friends for always supporting me and listening to me talk endlessly about the wolves. Thank you!

Appendix 1

Appendix 1, table 1. Monitoring data of the Scandinavian wolves (n=29) used in the study. Including original study length, used study days (fulfilled the criteria), season of the study, sex of the wolves, social affiliation, territory, neighbouring territories, and inbreeding coefficient of the male and female of the adult pair (Fi).

Wolf ID	Year	Study length (days)	Used (days)	Season	Sex	Social affiliation	Territory	Neighbouring territories	Fi_{male}	$\text{Fi}_{\text{female}}$
M0007	2004	33	30	Winter	Male	Pack	Nyskoga	1	0.125	0.2344
M0009	2003	43	26	Summer	Male	Pack	Bograngen	1	0.125	0.2481
	2003	63	61	Winter	Male	Pair	Bograngen	1	0.125	0.375
	2004	21	13	Summer	Male	Pair	Rotna	2	0.125	0.2695
M0105	2003	55	21	Winter	Male	Pack	Hasselfors	0	0.125	0.3047
M0109	2001	70	50	Winter	Male	Pair	Grafjell	1	0.125	0.2344
	2003	43	17	Summer	Male	Pack	Grafjell	1	0.125	0.2344
M0204	2002	84	52	Winter	Female	Pack	Tyngsjö	0	0.1875	0.125
M0306	2004	57	45	Winter	Male	Pack	Djurskog	0	0.1875	0.2344
	2004	22	10	Summer	Male	Pack	Djurskog	1	0.1875	0.2344
M0402	2004a	22	19	Summer	Male	Pair	Koppang	0	0.2344	0.2695
	2004b	19	14	Summer	Male	Pair	Koppang	0	0.2344	0.2695
M0404	2004	60	16	Winter	Male	Pair	Jangen	1	0.2695	0.2812
M0505	2005	18	11	Summer	Male	Pack	Forshyttan	0	0.2969	0.2812
M0506	2005a	22	15	Summer	Male	Pack	Uttersberg	0	0.2969	0.2695
	2005b	22	15	Summer	Male	Pack	Uttersberg	0	0.2969	0.2695
	2006	62	33	Winter	Male	Pack	Uttersberg	0	0.2969	0.2695
M0507	2008	50	43	Winter	Female	Pair	Kloten	1	0.2998	0.3022
M0601	2006	35	11	Winter	Female	Pack	Uttersberg	0	0.2969	0.2695
M0602	2006	57	40	Winter	Female	Pair	Ulriksberg	0	0.1875	0.2388
	2007	51	38	Winter	Female	Pack	Ulriksberg	0	0.1875	0.2388
M0611	2006	29	12	Summer	Male	Pack	Gräsmark	1	0.1875	0.2969
	2007	51	13	Winter	Male	Pack	Gräsmark	0	0.1875	0.2969
M0904	2009	53	46	Winter	Male	Pack	Fulufjället	1	0.2905	0.2676
	2010	43	40	Summer	Male	Pack	Fulufjället	1	0.2905	0.2676
	2010	62	56	Winter	Male	Pack	Fulufjället	1	0.2905	0.2676
M0910	2009	34	30	Winter	Male	Pack	Åmot/Ockelbo	1	0.2344	0.2197
M0918	2009	29	28	Summer	Male	Pack	Kloten	1	0.2998	0.3022
	2011	50	23	Winter	Male	Pack	Kloten	4	0.2998	0.3022

M1001	2010	58	56	Winter	Female	Pair	Tenskog	0	0.2607	0.293
M1002	2011	28	26	Summer	Male	Pack	Tenskog	1	0.2607	0.293
	2011	64	62	Winter	Male	Pair	Tenskog	1	0.2607	0.293
M1003	2010	42	40	Winter	Female	Pair	Riala	0	0	0.2671
M1103	2012	85	81	Winter	Male	Pack	Tandsjön	0	0.2671	0.262
	2014	34	24	Summer	Male	Pack	Tandsjön	0	0.2671	0.262
	2014	38	19	Winter	Male	Pack	Tandsjön	0	0.2671	0.262
M1301	2015	43	40	Summer	Male	Pack	Kukumaki	1	0.2478	0.297
	2015	42	39	Winter	Male	Pack	Kukumaki	1	0.2478	0.297
M1302	2013	63	62	Winter	Male	Pair	Kukumaki	1	0.2478	0.297
	2014	35	25	Summer	Male	Pack	Kukumaki	0	0.2478	0.297
	2014	54	38	Winter	Male	Pack	Kukumaki	0	0.2478	0.297
M1502	2015	43	40	Summer	Male	Pair	Aspafallet	5	0.2974	0.2925
	2015	43	41	Winter	Male	Pair	Aspafallet	5	0.2974	0.2925
M1503	2017	74	61	Winter	Male	Pack	Slettås	2	0.139	0.2761
M1708	2018	50	37	Winter	Male	Pack	Varåa	4	0.2292	0.238
	2019	42	39	Fall	Male	Pack	Varåa	4	0.2292	0.238
	2019	29	23	Summer	Male	Pack	Varåa	2	0.2292	0.238
	2019	42	38	Winter	Male	Pack	Varåa	2	0.2292	0.238
M1812	2018	28	27	Summer	Male	Pack	Juvberget	5	0.3171	0.2339
	2018	50	41	Winter	Male	Pack	Juvberget	5	0.3171	0.2339
M1814	2018	28	27	Summer	Male	Pack	Norrsjön	1	0.2246	0.1655
	2018	43	42	Winter	Male	Pack	Norrsjön	1	0.2246	0.1655
	2019	43	42	Fall	Male	Pack	Norrsjön	1	0.2246	0.2246
	2019	44	42	Winter	Male	Pack	Norrsjön	1	0.2246	0.1655
M1902	2019	42	41	Fall	Male	Pair	Juvberget	4	0.2432	0.2339
	2019	29	28	Summer	Male	Pair	Juvberget	3	0.2432	0.2339
	2019	42	39	Winter	Male	Pair	Juvberget	3	0.2432	0.2339

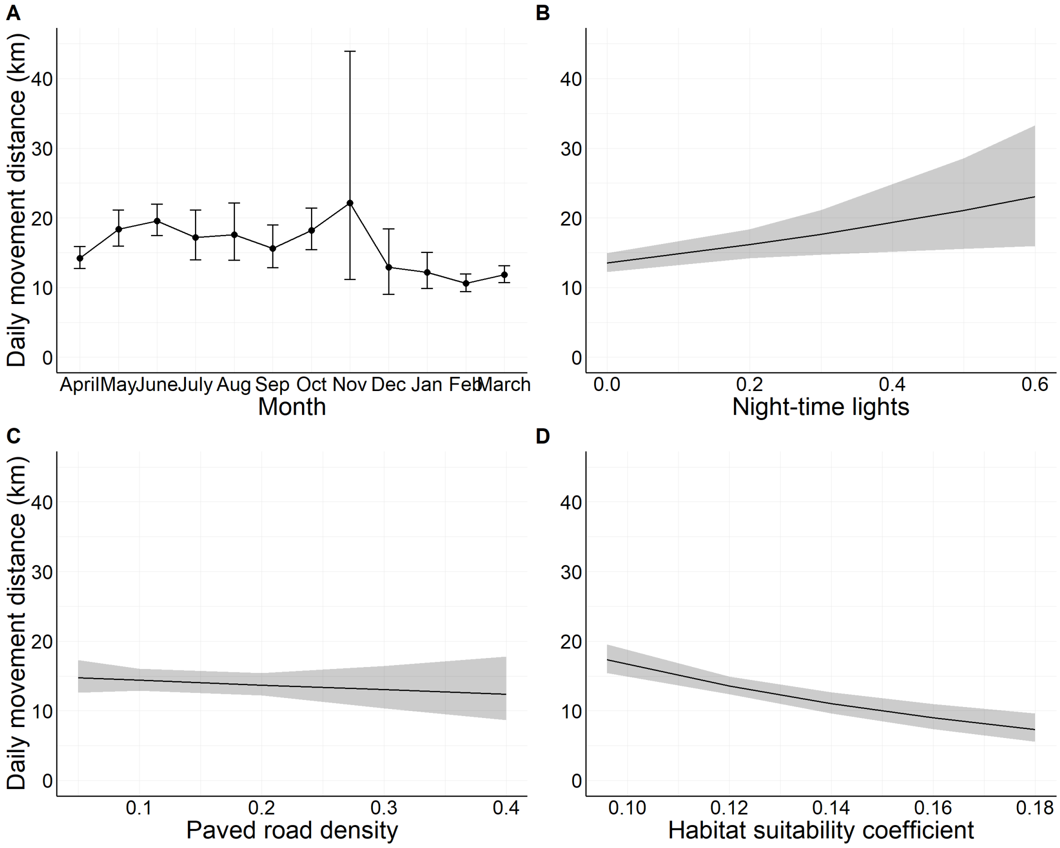
Appendix 2

Appendix 2, Table 1. The habitats assigned to the land cover classes in CLC18 during the process of calculating the habitat suitability coefficient.

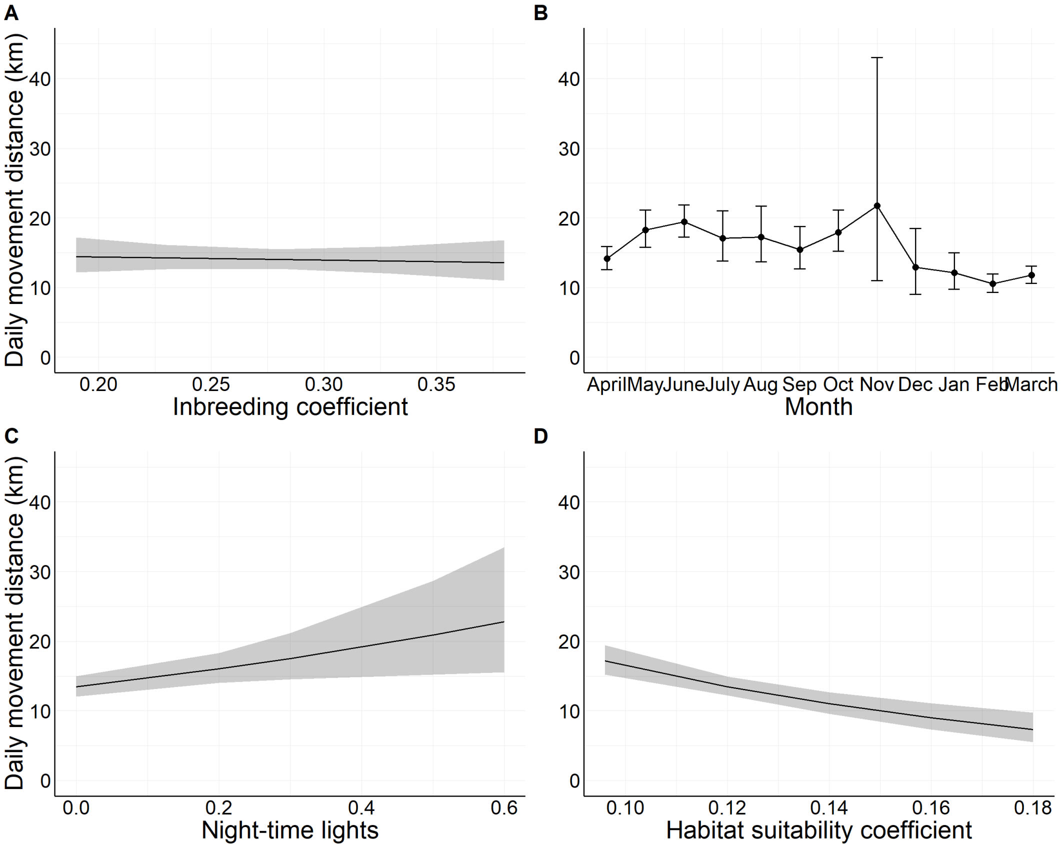
Habitat	Code in CLC18	Land cover class in CLC18
Urban area	111	Continuous urban fabric
	112	Discontinuous urban fabric
	121	Industrial or commercial units
	122	Road and rail networks and associated land
	123	Port areas
	124	Airports
	131	Mineral extraction sites
	132	Dump sites
	133	Construction sites
	141	Green urban areas
	142	Sport and leisure facilities
Agricultural land	211	Non-irrigated arable land
	212	Permanently irrigated land
	213	Rice fields
	221	Vineyards
	222	Fruit trees and berry plantations
	223	Olive groves
	231	Pastures
	241	Annual crops associated with permanent crops
	242	Complex cultivation patterns
	243	Land principally occupied by agriculture, with significant areas of natural vegetation
	244	Agro-forestry areas
Forest	311	Broad-leaved forest
	312	Coniferous forest
	313	Mixed forest

Open land	321	Natural grassland
	322	Moors and heathland
	323	Sclerophyllous vegetation
	324	Transitional woodland/shrub
	331	Beaches, dunes, sands
	332	Bare rock
	333	Sparsely vegetated areas
	334	Burnt areas
	335	Glaciers and perpetual snow
Wetland	411	Inland marshes
	412	Peatbogs
	421	Salt marshes
	422	Salines
	423	Intertidal flats
Water	511	Water courses
	512	Water bodies
	521	Coastal lagoons
	522	Estuaries
	523	Sea and ocean

Appendix 3

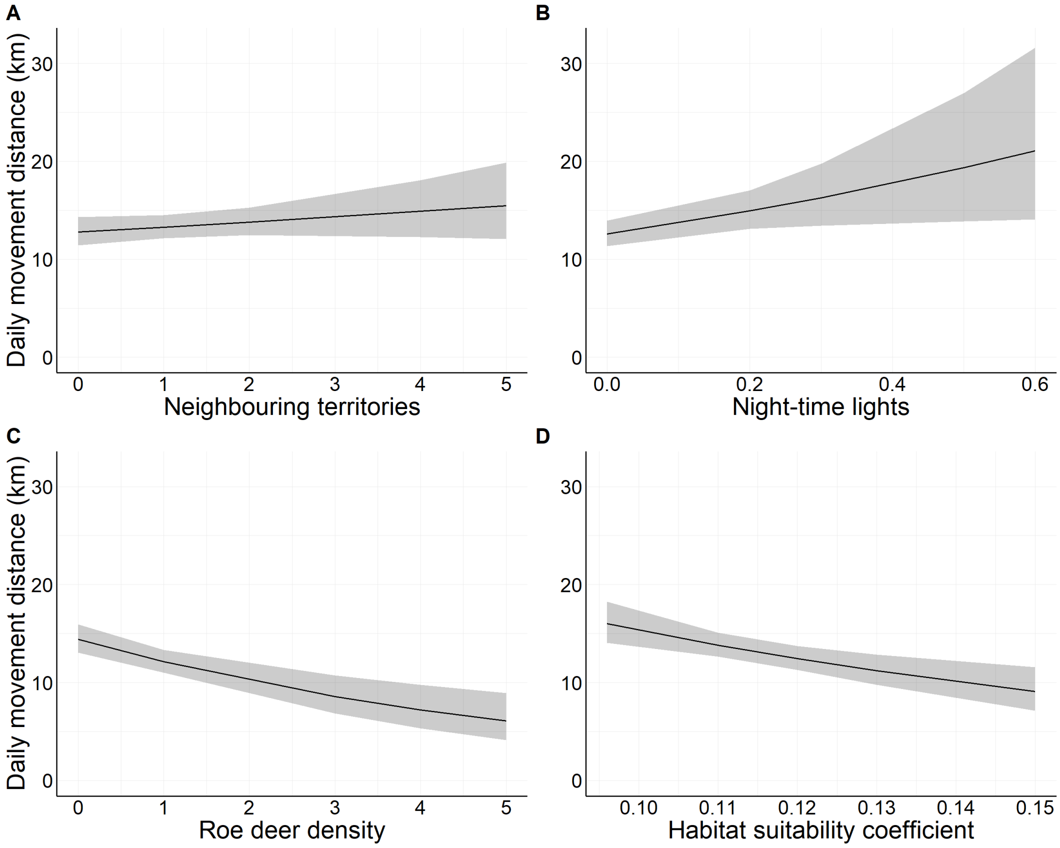


Appendix 3.1, Figure 1. The impact of A) months, B) night-time lights, C) paved road density, and D) habitat selection coefficient on daily movement distance by wolves (n = 29) in the Scandinavian wolf population during 2001-2019 from the second highest-ranked model in the annual dataset.

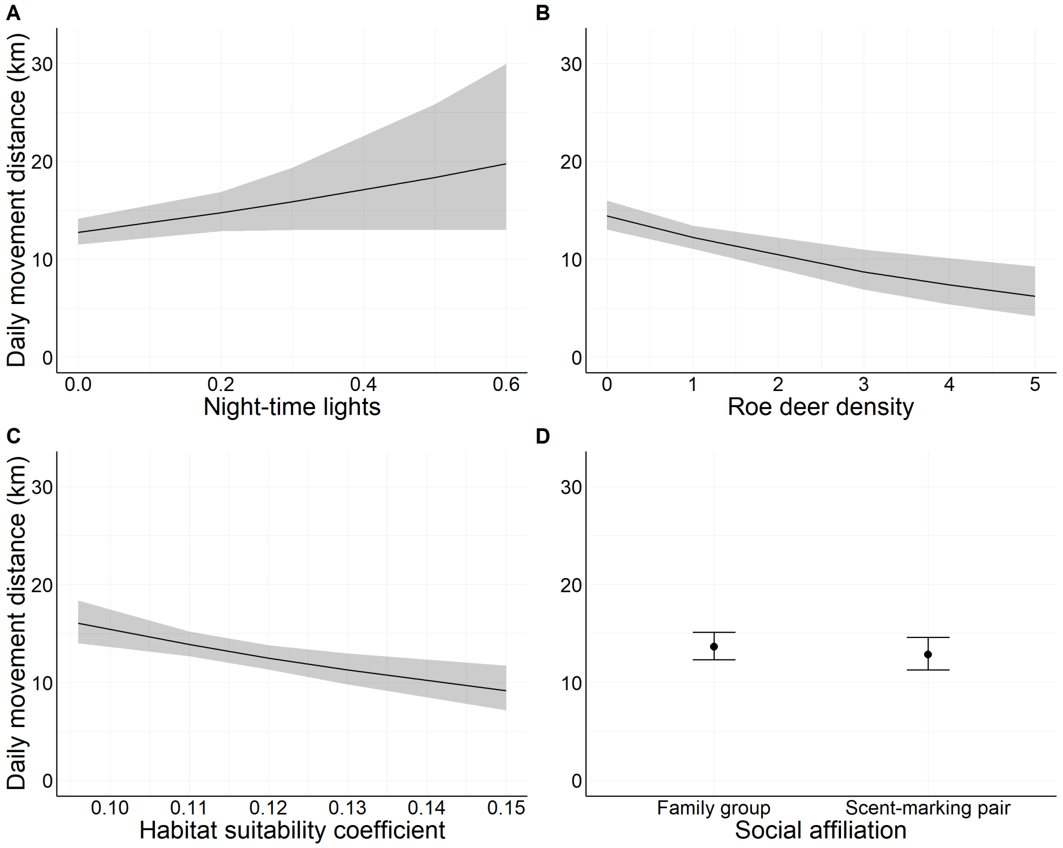


Appendix 3.2, Figure 2. The impact of A) inbreeding coefficient, B) month, C) night-time lights, and D) habitat selection coefficient on daily movement distance by wolves (n = 29) in the Scandinavian wolf population during 2001-2019 from the third highest-ranked model in the annual dataset.

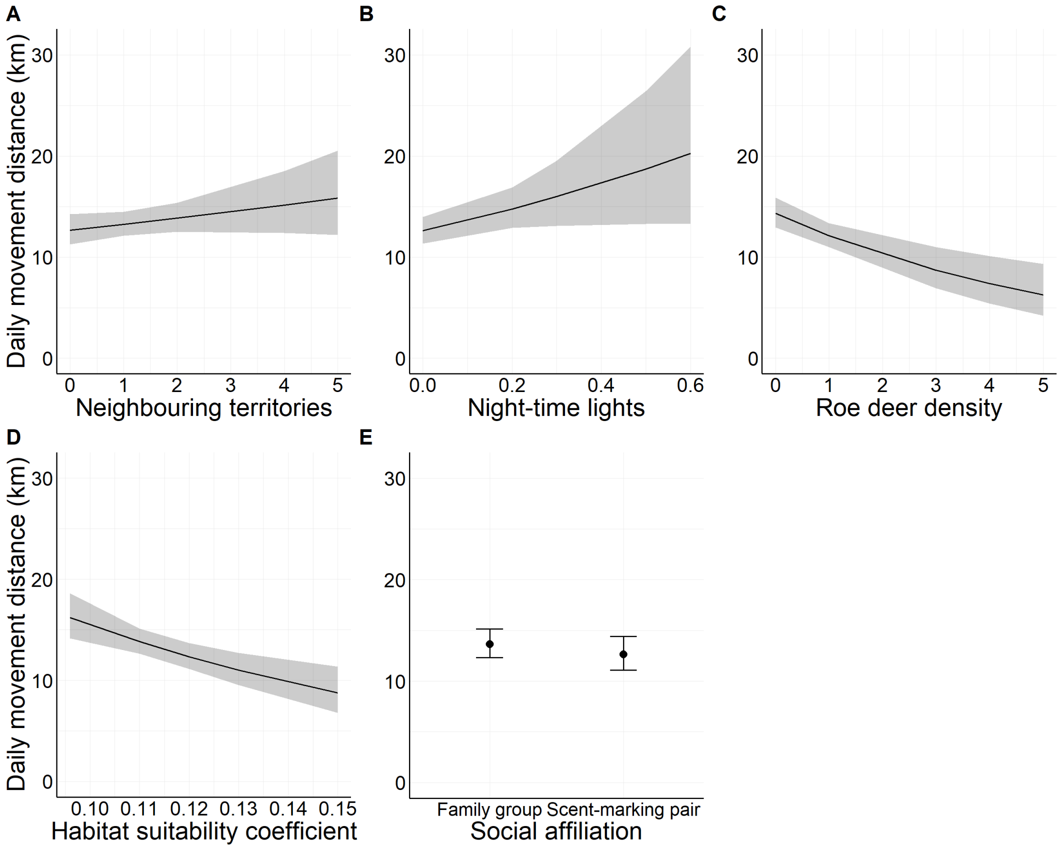
Appendix 4



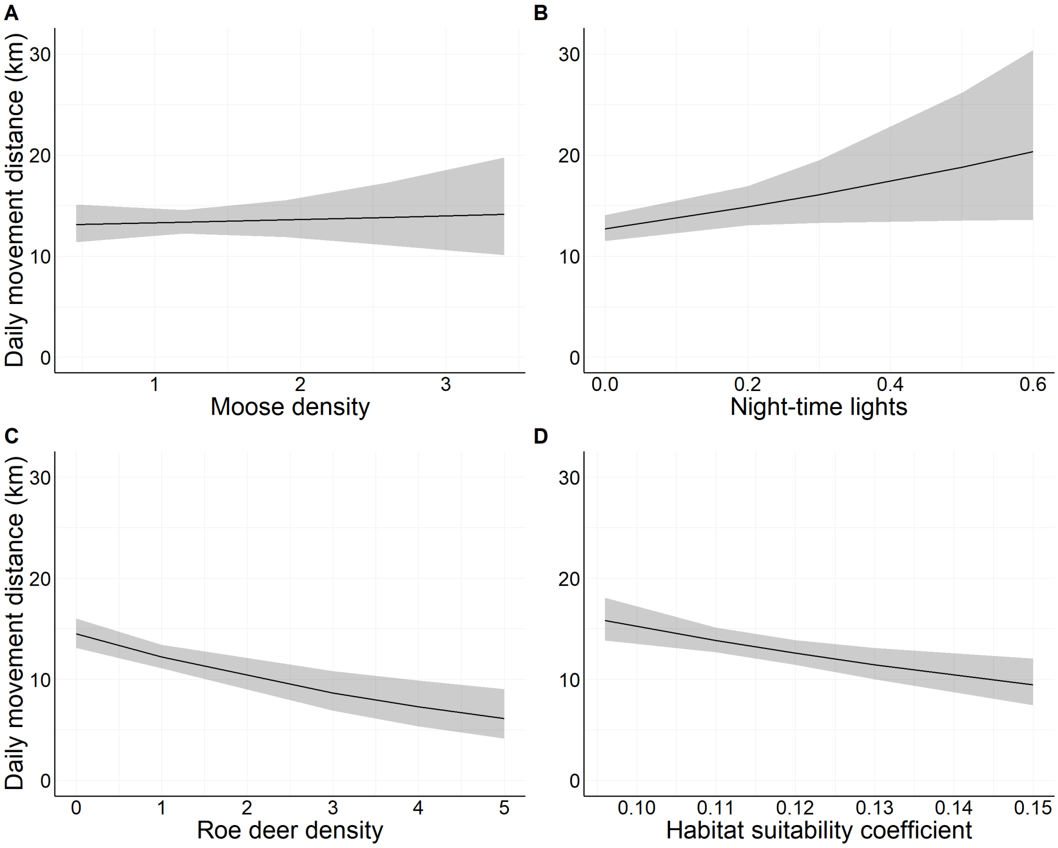
Appendix 4.1, Figure 1. The impact of A) neighbouring territories (wolf density), B) night-time lights, C) roe deer density, and D) habitat selection coefficient on daily movement distance by wolves (n = 25) in the Scandinavian wolf population during 2001-2019 from the second highest-ranked model in the winter dataset.



Appendix 4.2, Figure 2. The impact of A) night-time lights, B) roe deer density, C) habitat selection coefficient, and D) social affiliation on daily movement distance by wolves (n = 25) in the Scandinavian wolf population during 2001-2019 from the third highest-ranked model in the winter dataset.

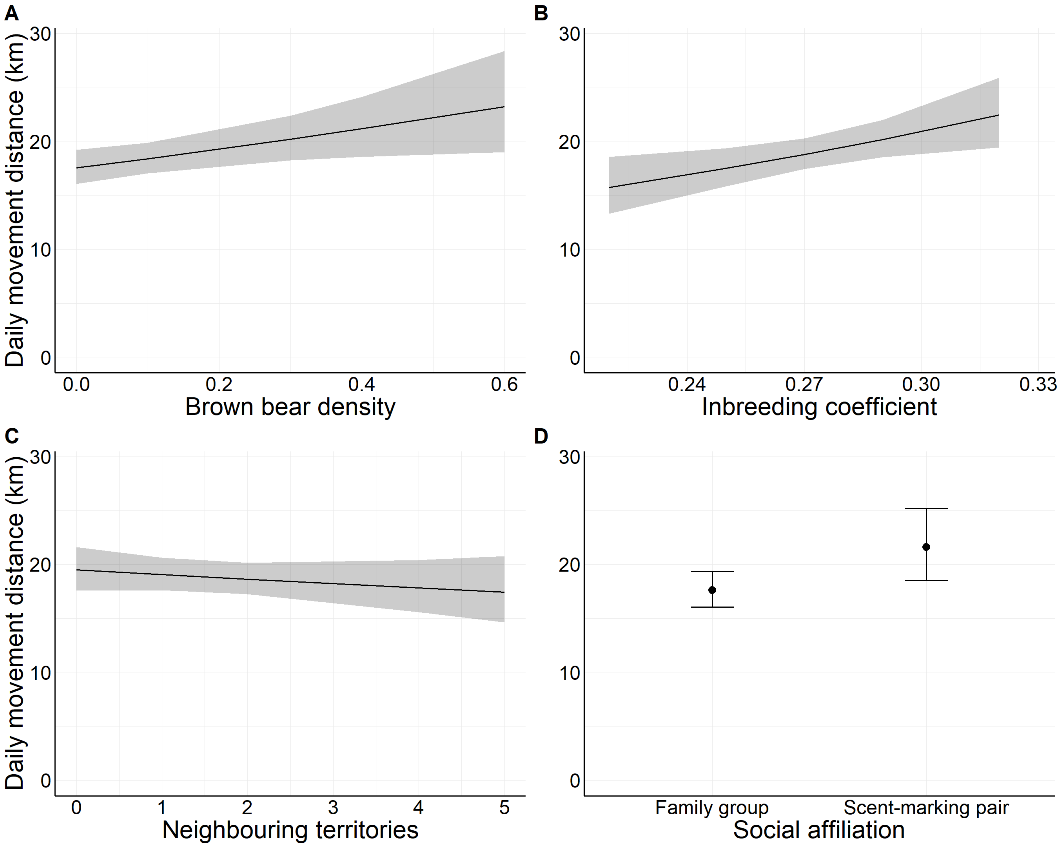


Appendix 4.3, Figure 3. The impact of A) neighbouring territories (wolf density), B) night-time lights, C) roe deer density, D) habitat selection coefficient, and E) social affiliation on daily movement distance by wolves (n = 25) in the Scandinavian wolf population during 2001-2019 from the fourth highest-ranked model in the winter dataset.

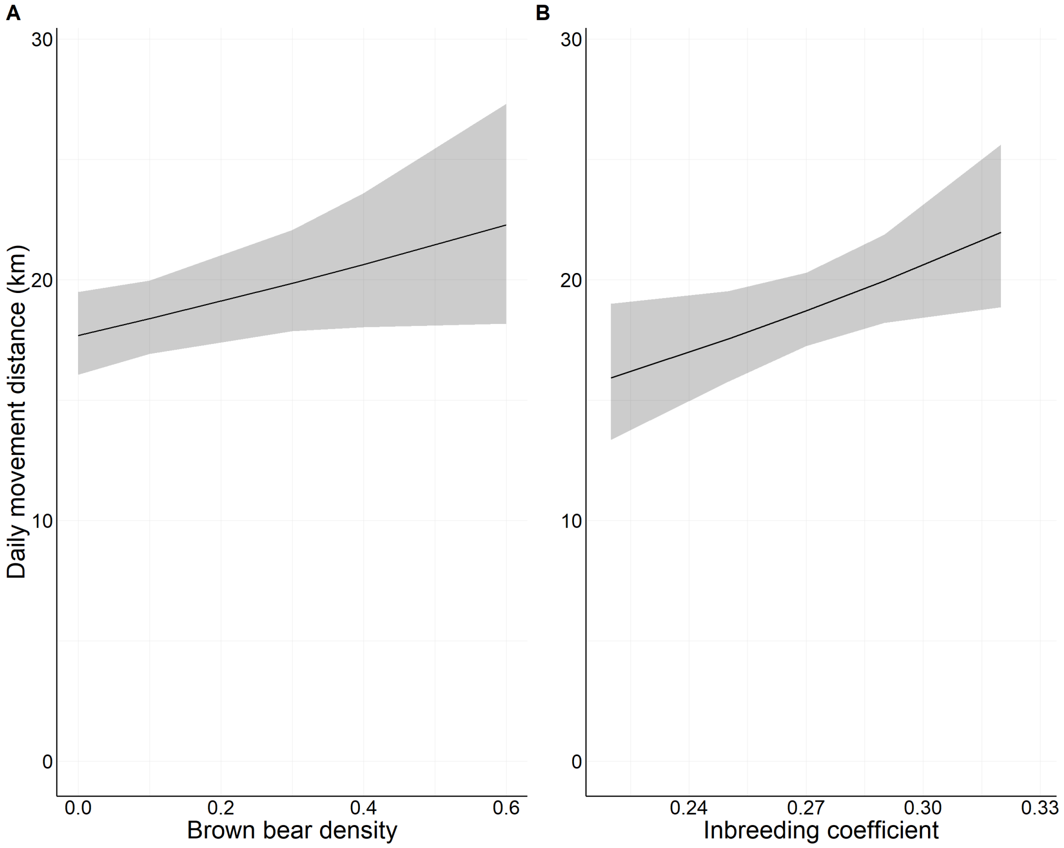


Appendix 4.4, Figure 4. The impact of A) moose density, B) night-time lights, C) roe deer density, and D) habitat selection coefficient on daily movement distance by wolves (n = 25) in the Scandinavian wolf population during 2001-2019 from the fifth highest-ranked model in the winter dataset.

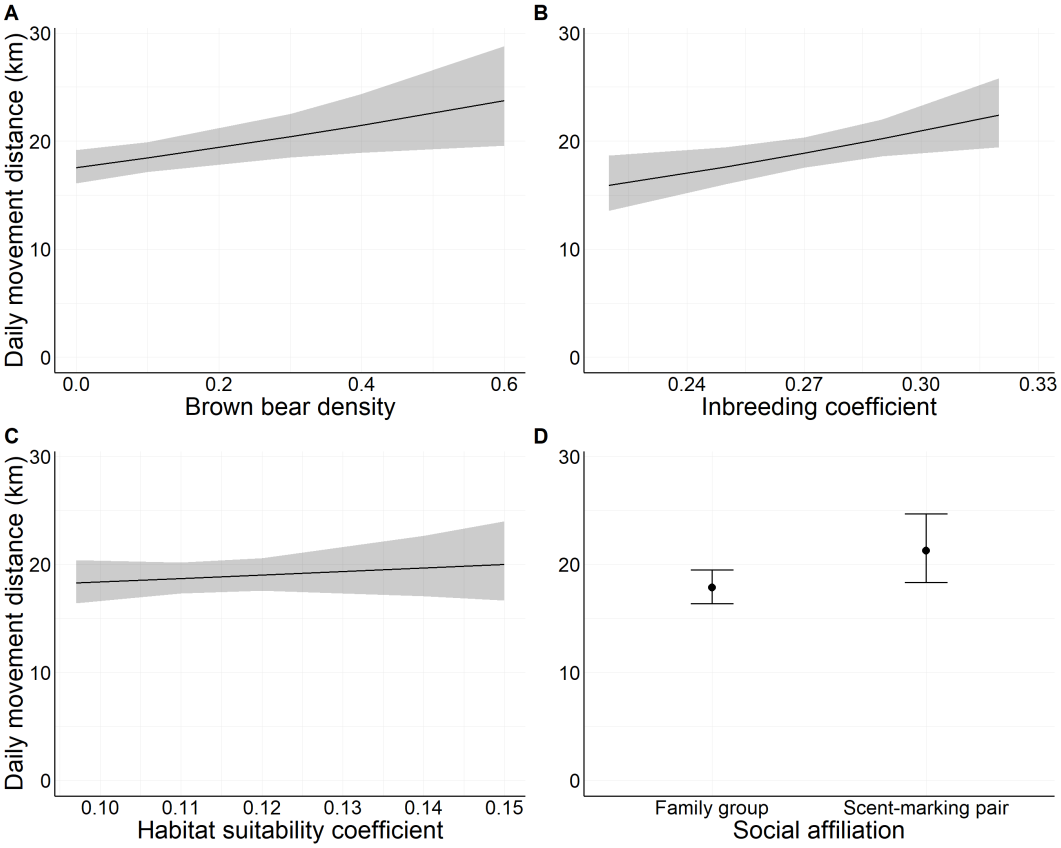
Appendix 5



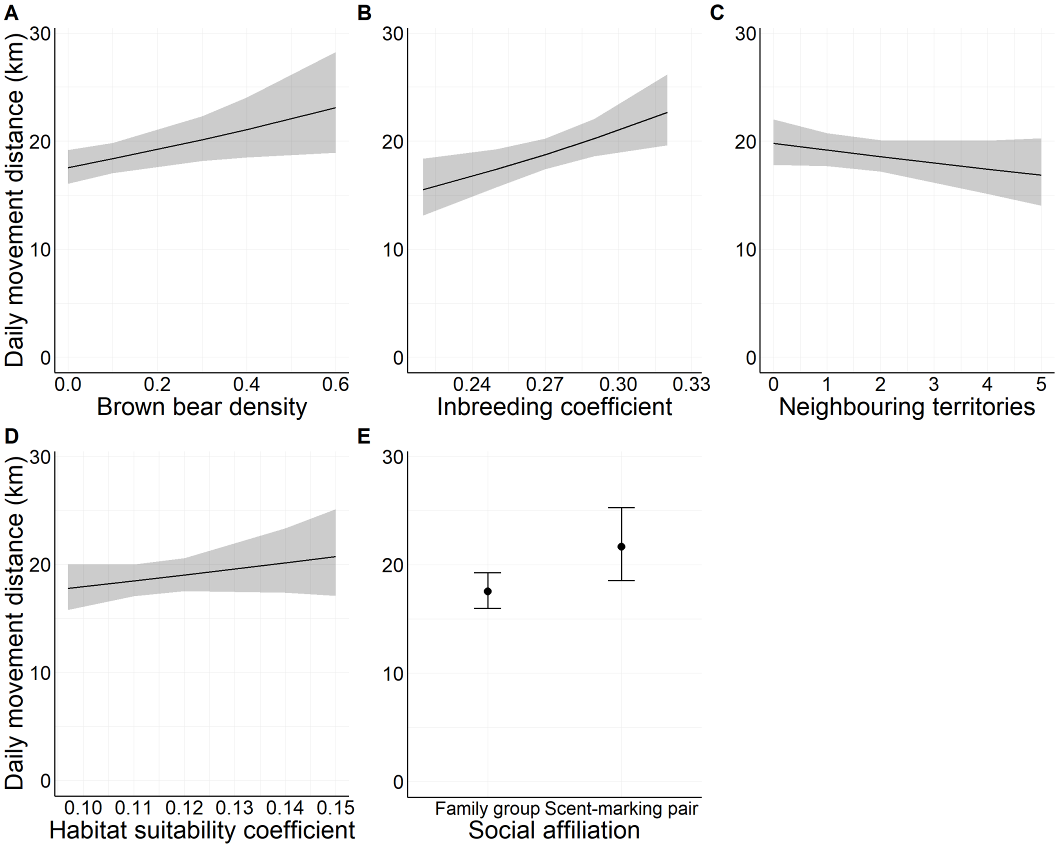
Appendix 5.1, Figure 1. The impact of A) bear density, B) inbreeding coefficient, C) neighbouring territories (wolf density), and D) social affiliation on daily movement distance by wolves (n = 18) in the Scandinavian wolf population during 2001-2019 from the second highest-ranked model in the summer dataset.



Appendix 5.2, Figure 2. The impact of A) bear density and B) inbreeding coefficient on daily movement distance by wolves (n = 18) in the Scandinavian wolf population during 2001-2019 from the third highest-ranked model in the summer dataset.

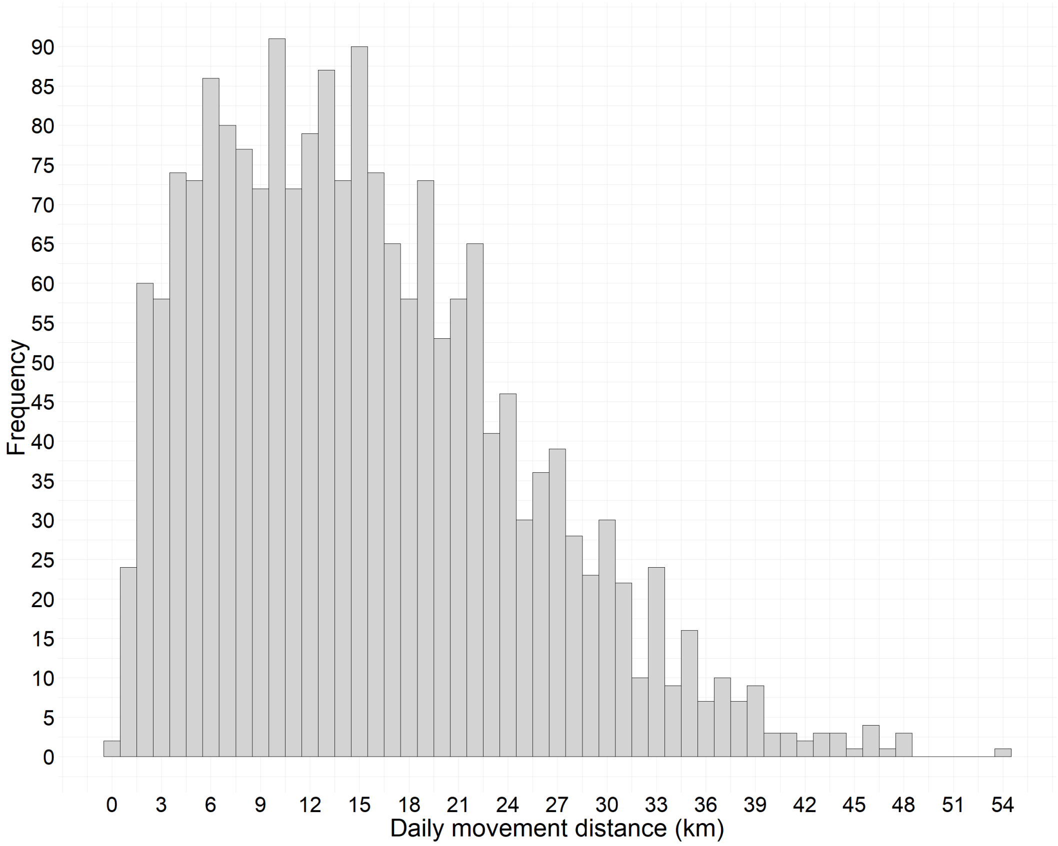


Appendix 5.3, Figure 3. The impact of A) bear density, B) inbreeding coefficient, C) habitat selection coefficient, and D) social affiliation on daily movement distance by wolves (n = 18) in the Scandinavian wolf population during 2001-2019 from the fourth highest-ranked model in the summer dataset.

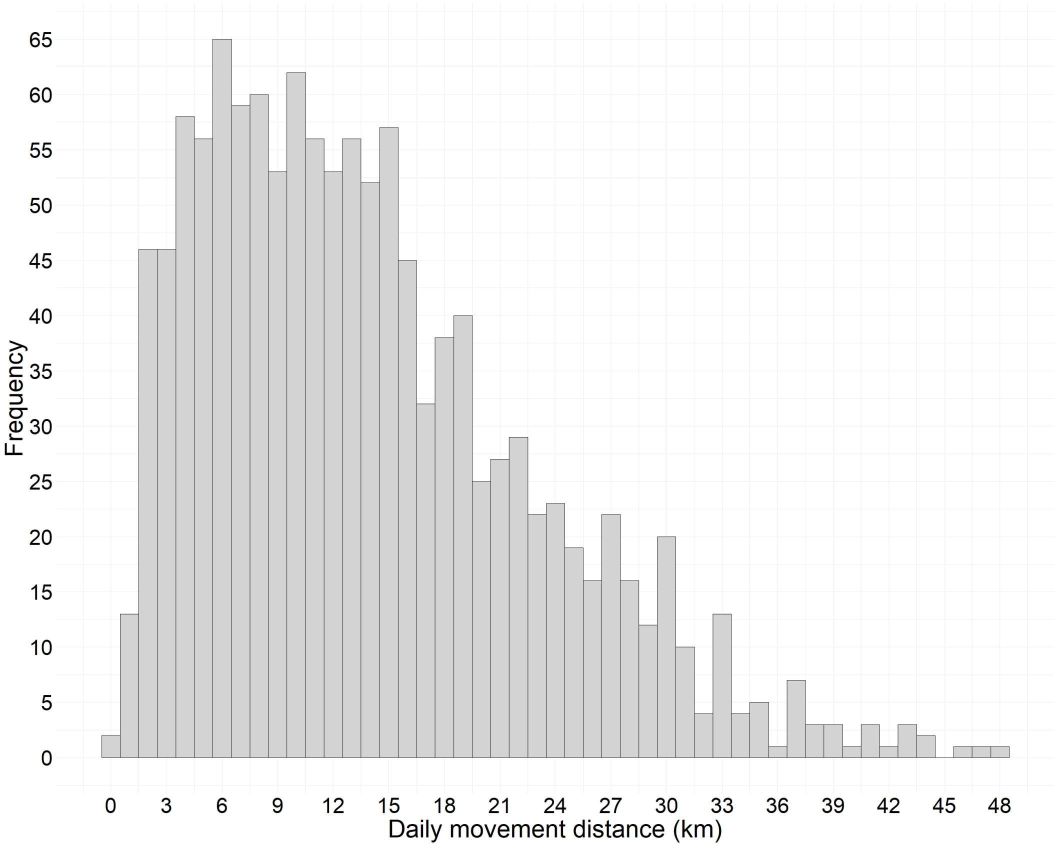


Appendix 5.4, Figure 4. The impact of A) bear density, B) inbreeding coefficient, C) neighbouring territories (wolf density), D) habitat selection coefficient, and E) social affiliation on daily movement distance by wolves (n = 18) in the Scandinavian wolf population during 2001-2019 from the fifth highest-ranked model in the summer dataset.

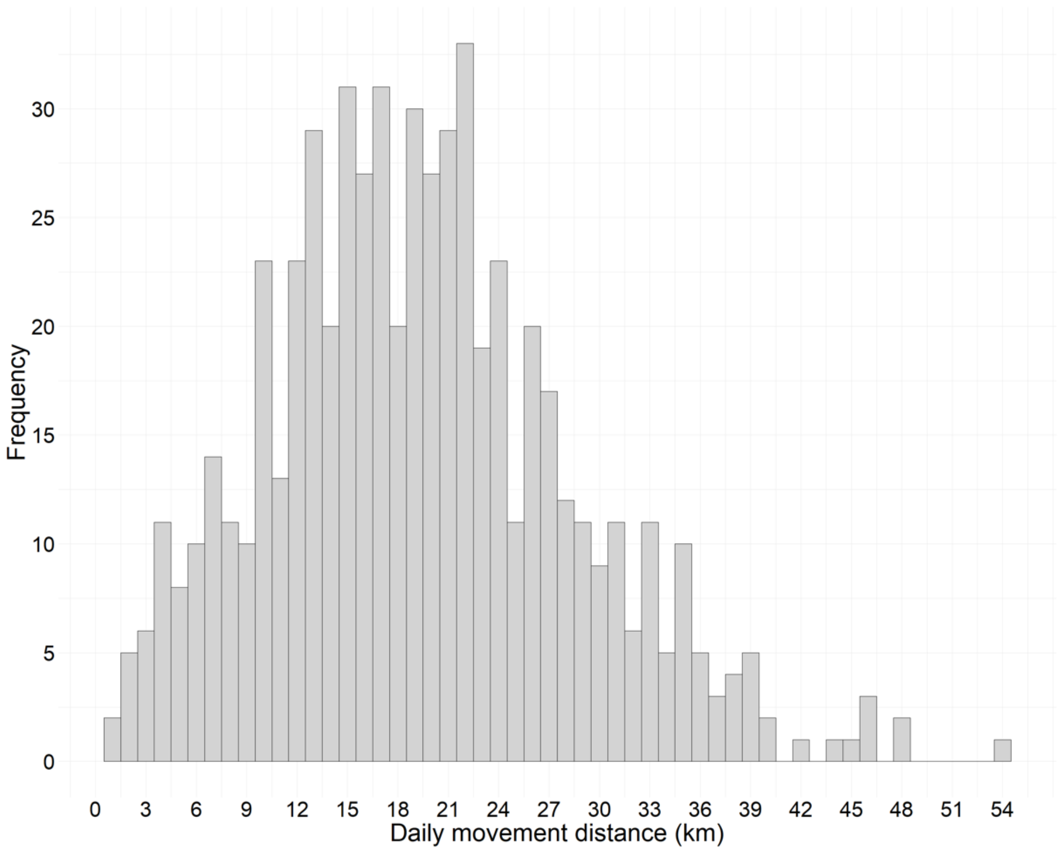
Appendix 6



Appendix 6.1, Figure 1. The histogram illustrates the distribution of daily movement distances (km) over the entire year (1955 study days). The x-axis represents the distance intervals, while the y-axis shows the frequency, i.e., the number of observations within each interval.



Appendix 6.2, Figure 2. The histogram illustrates the distribution of daily movement distances (km) over the winter (1243 study days). The x-axis represents the distance intervals, while the y-axis shows the frequency, i.e., the number of observations within each interval.



Appendix 6.3, Figure 3. The histogram illustrates the distribution of daily movement distances (km) over the summer (606 study days). The x-axis represents the distance intervals, while the y-axis shows the frequency, i.e., the number of observations within each interval.

Publishing and archiving

Approved students' theses at SLU are published electronically. As a student, you have the copyright to your own work and need to approve the electronic publishing. If you check the box for **YES**, the full text (pdf file) and metadata will be visible and searchable online. If you check the box for **NO**, only the metadata and the abstract will be visible and searchable online. Nevertheless, when the document is uploaded it will still be archived as a digital file. If you are more than one author, the checked box will be applied to all authors. You will find a link to SLU's publishing agreement here:

- https://libanswers.slu.se/en/faq/228318.

☒ YES, I/we hereby give permission to publish the present thesis in accordance with the SLU agreement regarding the transfer of the right to publish a work.

☐ NO, I/we do not give permission to publish the present work. The work will still be archived and its metadata and abstract will be visible and searchable.