Norwegian University of Life Sciences
Faculty of Environmental Sciences
and Natural Resource Management

Philosophiae Doctor (PhD)
Thesis 2021:94

Large carnivore responses to human activity and infrastructure at multiple scales in Scandinavia

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Neri Horntvedt Thorsen

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Abstract

Large carnivores have been recovering throughout Europe following local and regional extinction. However, the landscape they are returning to is not the same that they left, as human impacts have changed it drastically. If Europe is to maintain viable populations of large carnivores, their conservation must occur in today's human-dominated landscape, as there are few remote wilderness areas left. The objective of my thesis has been to explore how large carnivores respond to human activity and infrastructure in the human-dominated landscape of Scandinavia. Understanding these responses is important for management of large carnivores in the future, where human impact is predicted to be even higher than today. In this thesis, I have used data from GPS collared individuals of brown bear (*Ursus arctos*), wolf (*Canis lupus*) and Eurasian lynx (*Lynx lynx*) to study their responses to human activity and infrastructure, together with data from physiological implants (biologgers), crowd-sourced recreational data and proximity telemetry. My thesis includes one experimental and three observational studies. I have studied physiological, behavioural, space-use and temporal responses at several different spatial scales.

Article I described an experiment that tests how hunting dogs and human approaches influence the behaviour and physiology of female brown bears. We found that dogs during simulated hunts have a larger physiological and behavioural impact on female brown bears than humans approaching on foot, and that longer hunts increased the time the bear spent resting after a hunt. For humans approaching on foot, we only detected a behavioural response (displacement), and no response in the physiological parameters we measured. **Article II** focused on how human recreationists affect habitat selection by lynx at two spatial scales and explored the temporal aspect of habitat use of areas associated with human recreationists. We found that lynx only avoided human recreationists at a local scale, and not at a larger scale, and that lynx temporally adjusted their habitat use in a manner that likely reduced the risk of encountering humans. These local scale and temporal responses may be important for ensuring large-scale coexistence of lynx and humans. **Article III** explored factors contributing to a wolf pack in Norway being repeatedly observed close to houses. Our results suggest that wolves spent more time close to houses due to the high prey density found in the same area. Winter-ploughed roads likely channelized the movement of wolves close to houses, and sometimes through house-yards. Visits to house-yards happened almost exclusively at night. Indicating that wolves, like lynx, use temporal adjustment in their habitat

use to reduce the risk of encountering people. **Article IV** investigated how human infrastructure affects movement and habitat selection at two different spatial scales during two different life stages ("dispersing" and "resident") for male brown bears. We found that dispersing bears were more tolerant toward human infrastructure than resident males at the landscape scale (which part of the landscape they selected), while the difference was not as large at the local scale. This implies that landscape connectivity estimates based on resident males underestimate the connectivity experienced by a dispersing male.

These studies indicate that large carnivores are able to adjust to the human-dominated landscape in a manner that facilitates coexistence. How far we can push land-sharing in the human-dominated landscape will likely be limited more by human social tolerance than the ecological tolerance of large carnivores.

Sammendrag

Bestandene av de store rovdyra har økt i Europa etter at de har vært utryddet lokalt og regionalt. Landskapet de vender tilbake til er ikke det samme som de forlot. Den menneskelige påvirkningen på landskapet har endret seg drastisk og det finnes få villmarkspregede områder igjen. Hvis Europa skal opprettholde levedyktige bestander av store rovdyr må dette derfor skje i flerbrukslandskapet. Hensikten med denne doktorgraden har vært å utforske hvordan store rovdyr responderer til menneskelig aktivitet og infrastruktur i det skandinaviske flerbrukslandskapet. Det er viktig for rovdyrforvaltningen å forstå disse responsene siden menneskets påvirkning trolig vil øke i framtiden. I denne doktorgraden har jeg brukt data fra GPS-merkede individer av brunbjørn (*Ursus arctos*), ulv (*Canis lupus*) og gaupe (*Lynx lynx*) til å studere deres responser menneskelig aktivitet og infrastruktur, sammen med data fra fysiologiske implantat, aktivitetsdata på mennesker fra en mobiltelefon app og nærhetsteknologi. Doktorgraden min inkluderer ett eksperiment og tre observasjonsstudier. Jeg har studert fysiologi, adferd, områdebruk og temporære responser på flere romlige skalaer.

I **artikkel I** utførte vi et eksperiment for å teste om jakthunder og mennesker som passerte nær bjørnen påvirket adferden og fysiologien til hunnbjørner. Vi fant at jakthunder, under simulerte jakter (som en vanlig jakt, men der bjørnen ikke ble skutt), hadde en større fysiologisk og adferdsmessig påvirkning på hunnbjørner enn mennesker som gikk forbi bjørnen. Simulerte jakter som varte lengre førte til at bjørnen hvilte mer den påfølgende dagen. For mennesker som passerte nærme bjørnen så vi bare en adferdsrespons, der bjørnen beveget seg hurtigere enn den vanligvis ville gjort, og ingen fysiologisk respons i de fysiologiske parameterne vi undersøkte. **Artikkel II** fokuserte på hvordan turgåere påvirker habitatvalg hos gaupe på to romlige skalaer og undersøkte om gaupa endret bruken av områder assosiert med turgåere utfra tiden på døgnet. Vi fant at gaupa bare unngikk turgåere på lokal skala (dvs. 1 – 2 km), men ikke på en større skala (innenfor reviret), og at gaupa brukte områder assosiert med turbruk mer på natten enn om dagen. Denne adferden reduserer antageligvis risikoen for å treffe på mennesker. Denne lokale responsen til turgåere og endring i områdebruk med tid på døgnet, er antagelig viktig for sameksistens av gaupe og mennesker. **Artikkel III** utforsket faktorer som førte til at en ulveflokk (Slettåsflokken) gjentatte ganger beveget seg i nærheten av hus. Våre resultater foreslår at ulvene brukte mye tid nær hus grunnet høyere byttedyrtetthet i disse områdene. Brøytede veier kanaliserte videre

trolig ulvenes bevegelse mot hus og noen ganger gjennom gårdstun. Slike passeringer nærme hus skjedde nesten utelukkende på nattestid. Dette indikerer at Slettåsulvene, i likhet med gaupa, endrer habitatbruken gjennom dagen på en slik måte at de reduserer risikoen for å møte folk. **Artikkel IV** undersøkte hvordan menneskelig infrastruktur påvirker bevegelse og habitatvalg hos hannbjørner for to forskjellige livsstadier (som ‘spreder’ og som ‘bosatt i et hjemmeområde’) og for to forskjellige skalaer. Vi fant at spredere var mer tolerante mot menneskelig infrastruktur enn hannbjørner som hadde slått seg ned i et hjemmeområde på en landskapsskala (hvilken del av landskapet velger bjørnene å være i), mens forskjellene ikke var like store på den lokale, romlige skalaen. Dette indikerer at når bjørner som har slått seg ned i et hjemmeområde brukes til å estimere landskapets egnethet for bevegelse, så vil denne bli underestimert for spredere.

Disse studiene indikerer at store rovdyr klarer å tilpasse seg flerbrukslandskapet på en måte som muliggjør sameksistens. Hvor langt vi skal gå i å dele landskapet med store rovdyr vil trolig være mer begrenset av menneskers toleranse til store rovdyr enn store rovdyrs toleranse til mennesker.

List of articles

Article I

Le Grand, L., Thorsen, N. H., Fuchs, B., Evans, A. L., Laske, T. G., Arnemo, J. M., Sæbø, S. & Støen, O. G. (2019) Behavioral and physiological responses of Scandinavian brown bears (*Ursus arctos*) to dog hunts and human encounters. *Frontiers in Ecology and Evolution*. doi: 10.3389/fevo.2019.00134

Article II

Thorsen, N. H., Bischof, R., Mattisson, J., Hofmeester, T. R., Linnell, J. D.C. & Odden, J. Smartphone app helps reveal local, but not home range scale avoidance of human recreationists by Eurasian lynx (*Lynx lynx*). Under review in Scientific Reports.

Article III

Thorsen, N. H., Bischof, R., Zimmermann, B., Linnell, J. D.C., Støen, O. G, Rauset, G. R., Frank, J., Wabakken, P. & Odden, J. The distribution of prey and roads facilitate wolf pack visits to houses by in Norway. Manuscript.

Article IV

Thorsen, N. H., Hansen, J. E., Støen, O.-G., Kindberg, J., Zedrosser, A. & Frank, S.C. Human infrastructure influence life stage-dependent movement and habitat selection in a large carnivore. Manuscript.

Synopsis

Large carnivores in the human-dominated landscape

As top predators large carnivores are naturally rare and have generally large space requirements (Linnell et al. 2021). Large carnivores have a tendency to come into conflict with humans, through e.g. livestock depredation (Baker et al. 2008, Inskip and Zimmermann 2009), competition for prey (Melis et al. 2009, Gervasi et al. 2012) and a range of social conflicts, including fear (Røskaft et al. 2003). This has motivated the persecution of large carnivores during recent centuries and caused major range contractions and fragmentation in Europe (Wolf and Ripple 2017). After a long period of persecution, the remaining large carnivore populations in Europe persisted in remote areas with low human densities (Woodroffe 2000), where the human-related mortality was low. During the 20th century, extermination policies came to an end and several large carnivore species became protected under legislation from indiscriminate and unregulated hunting (Linnell et al. 2001). These legislative instruments have proved successful as many large carnivore populations in Europe have now recovered and are still recovering (Chapron et al. 2014). However, the landscape they are returning to is different from the one they left. Human impact has changed the landscape drastically. The global human population has more than tripled between 1920 and 2020 (United Nations 2019), cities have expanded and new ones have emerged, new roads and railways connect the growing cities, and forestry and agriculture have intensified to fulfil the growing need for natural resources. Large carnivores are recolonizing a landscape dominated by humans. At the same time, human pressure has also relaxed, with the move away from extermination policies.

Large carnivores have successfully adjusted and adapted to Europe's human dominated landscape, and at present they occupy areas of high human density, especially wolves (*Canis lupus*) (Chapron et al. 2014, Cretois et al. 2021). Sharing the human dominated landscape appears to be the only option for conserving large carnivores in Europe, as the remote wilderness has more or less disappeared, and its few remnants are not large enough to maintain viable populations of large carnivores. Even in Scandinavia, where human density is generally lower than farther south in Europe, conserving large carnivores only in remote wilderness areas is practically impossible. There are few remote areas without human disturbance (Venter et al. 2016), and most of the landscape is heavily impacted by humans. Forestry and forestry roads (roads used for forestry) have made remote forest areas more accessible. Furthermore, there is high hunting pressure on mammals throughout most of

Scandinavia, and free-ranging sheep and semi-domestic reindeer occupy the vast majority of the landscape.

The most obvious effect of humans on large carnivores is human-caused mortality. Human-caused mortality (e.g. hunting, vehicle collisions, poaching) is also the most common cause of death in large carnivores in Scandinavia (wolf: Liberg et al. (2012), lynx (*Lynx lynx*): Andren et al. (2006), wolverine (*Gulo gulo*): Persson et al. (2009), brown bear (*Ursus arctos*): Bischof et al. (2009)). Human-related mortality can have direct impacts on the population demographics, as manifested through previous declines and extinctions. In Scandinavia, human-related mortality, i.e., hunting and culling, is used to regulate population sizes. As humans adopt the role of a super-predator by severely limiting large carnivore populations, humans have more or less taken over the ecological function of large carnivores as apex predators on wild herbivores (Estes et al. 2011). Furthermore, large carnivores have effectively become a "prey" species with respect to humans (Ordiz et al. 2013, Ordiz et al. 2021). As all predators, humans impose both lethal (predation) and non-lethal effects on their prey (Lima 1998). The non-lethal effects include for instance physiological (Stoen et al. 2015), behavioural and space-use responses, e.g. reduced feeding time due to more time spent being vigilant or abandoning prey earlier (Smith et al. 2017). Non-lethal effects have the potential to affect growth rates of prey (Turner 2004) and population dynamics through fitness reduction (Tablado and Jenni 2017). Predation risk is not evenly distributed in time or space - often referred to as the "landscape of fear" (Laundré et al. 2010). As the main predator of large carnivores, humans create a landscape of fear where large carnivores need to navigate and adjust their behaviour in ways that reduce their risk of being disturbed or killed.

Humans not only induce responses in large carnivores through acting as their main predator, humans also induce responses by modifying habitat and the landscape. There are a range of responses to, and effects of, human infrastructure (Kuijper et al. 2016, Tucker et al. 2018). Habitat alterations can induce physiological (Stoen et al. 2015) and behavioural responses (Trombulak and Frissell 2000), as well as affect population structure and dynamics (Gould et al. 2021). Some responses towards human infrastructure and human-caused habitat changes may not necessary be directly adverse. For instance, human-made linear features such as roads or pipelines facilitate movement (Zimmermann et al. 2014, Dickie et al. 2019). Such habitat changes can alter the ecological conditions for both large carnivores and their prey. In some cases human-made habitat changes and infrastructure can make prey more susceptible to predation (Whittington et al. 2011) or increase the prey density or food availability (Ciucci et al. 2020). However, the effects of human-made habitat changes and human infrastructure are often considered negative. Fenced highways, high traffic-volume roads, and urban and sub-urban development are often avoided (Trombulak and Frissell 2000, Northrup et al. 2012), and can reduce the connectivity in the landscape (i.e., the movement of individuals) (McClure et al. 2017, Tucker et al. 2018). Habitat loss and reduced connectivity can create fragmented populations (Andren 1994, Crooks et al. 2011), associated with reduced gene flow. When populations become isolated, low genetic variation may threaten the long-term survival of the population, as is the case for the Scandinavian wolf population (Åkesson et al. 2016).

Understanding large carnivore responses to human activity and human infrastructure is critical for their population management and land-use planning. Human settlement patterns are predicted to change with more people settling in cities, i.e., urbanization (Seto et al. 2012). The growing need for resources will likely cause further habitat transformation and more infrastructure. Additionally, new border fences are under construction or have already been built (Linnell et al. 2016), and human presence through recreation is also increasing globally (Balmford et al. 2009). Navigating this landscape may be challenging for large carnivores, hence, understanding the responses of large carnivores to human activity and infrastructure may help management implement a strategy to enhance coexistence of wildlife and humans in the future. In this PhD thesis, I have explored large carnivore responses to human activity and human infrastructure for three large carnivore species in Scandinavia.

The responses studied in this PhD, include physiology, behaviour, habitat use and habitat selection, as well as temporal patterns in these responses over multiple spatial scales. First, we explored how female brown bears physiologically and behaviourally respond to approaching humans and simulated hunts with dogs (**article I**). Second, we investigated the responses in habitat use and selection at two spatial scales by lynx towards outdoor recreation (**article II**). Third, we explored how a wolf pack in Norway responded to human infrastructure at multiple spatial scales during winter (**article III**). Finally, we studied how human infrastructure affected habitat selection and movement of male brown bears at two spatial scales and during two different life history stages (**article IV**). In this synopsis I will briefly present the methods and results, and end with a discussion about large carnivore responses to human activity and human infrastructure, while focusing on the implications for sharing the human dominated landscape with large carnivores.

General methods

Study species

In Scandinavia, there are four mammals considered to be part of the large carnivore functional guild; grey wolf, Eurasian lynx, brown bear and wolverine. In this PhD project, I have studied wolves, bears and lynx. Wolves and lynx are obligate carnivores, i.e. animals that depend on meat in their diet, while the brown bear is an omnivore which preys upon wild herbivores like moose (*Alces alces,* especially calves), but also includes grass, herbs and berries in its diet (Stenset et al. 2016). The main prey for lynx in our study area is roe deer (*Capreolus capreolus*), but lynx also prey on free-ranging sheep (*Ovis aries*), red deer (*Cervus elaphus*) and small game species (Odden et al. 2006). Wolves prey primarily on moose, supplemented by roe deer (Sand et al. 2016). The carnivore species typically range in body weight from 15-25 kg for lynx, through 30-45 kg for wolves and to 100-200 kg for bears. Brown bears hibernate during winter (Krofel et al. 2017), while wolves and lynx do not.

Study areas

The data from the study species have been collected in Norway (lynx and wolf) and Sweden (brown bear) (Figure 1). The study area for wolves and brown bears consists mainly of boreal forests dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), and some birch (*Betula sp.*). The topography in these areas consist of gently rolling hills, and while the human densities are low there is an extensive network of forestry roads which are kept open in winter to varying degrees. The climate is continental with stable winters. These areas are sparsely populated by humans. The study area for the lynx is located in south-eastern Norway, where the topography is hilly with some steep slopes, and deep valley systems. The area also has a higher human density, and more agricultural land, although this is generally constrained to either valley floors or lower elevations around the Oslo fjord. The northern part of the lynx study area is quite continental while the southern area is generally more oceanic and receives less snow during winter. The lynx study area also contains a much higher density of human, with a total population size of approximately 2 million.

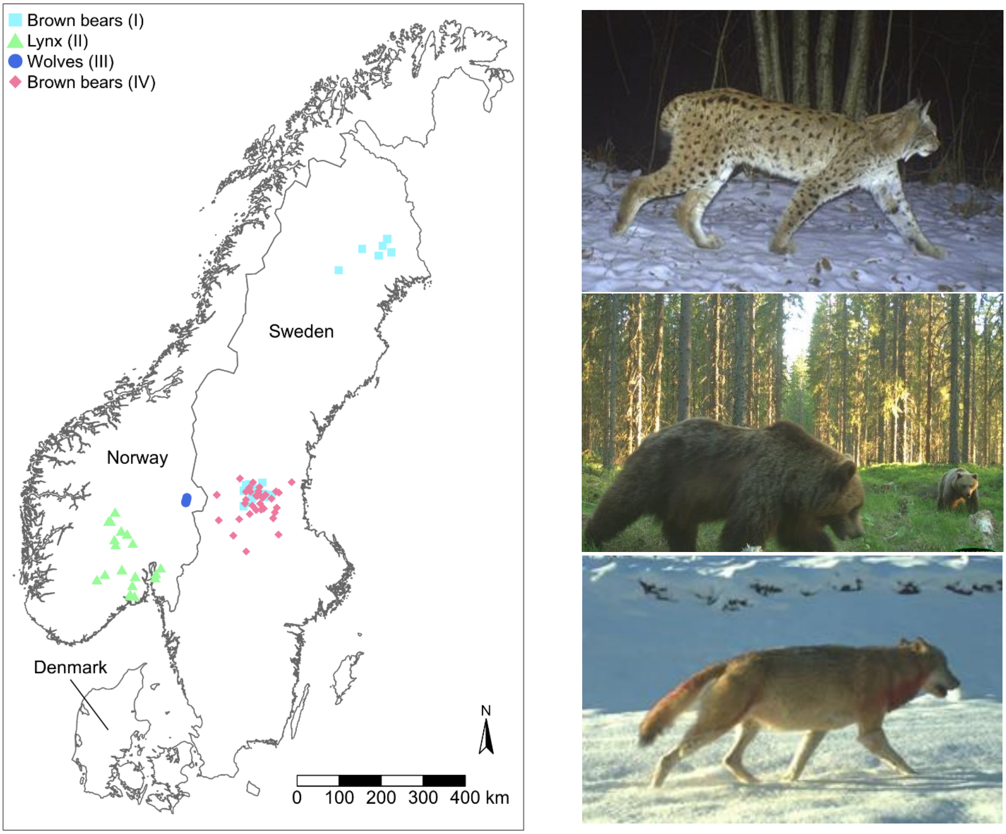

Figure 1. Centroid locations for each individual used in this PhD project (to the left). The Roman numerals behind species names indicate the number of the corresponding article. The borders delineate the Scandinavian countries Norway, Sweden and Denmark. To the right, images of the study species, Eurasian lynx, brown bear, and wolf (from top to bottom, © www.viltkamera.nina.no).

GPS collars and biologgers

All four studies in this PhD project relied on GPS collared animals (Table 1). The animals were captured with different techniques depending on the species. Lynx were captured in wooden walk-through box traps or foot snares placed at kill sites, while wolves and bears were immobilized from helicopters. In addition to GPS collars, brown bears in the first study were surgically implanted with biologgers that monitored body temperature and heart rate. Biologger data was retrieved after recapturing each individual.

Habitat use and habitat selection at different scales

From GPS collared animals we can measure a wide range of parameters. We can investigate temporal activity patterns, movement extent or where the animals have established their home range (sensu Burt 1943). I used the GPS collar data to infer habitat use, habitat selection, and movement. Ecologists refer to habitat use as the habitat the animal uses and spends time in, e.g. the percentage of GPS locations from a lynx in the agricultural land can be interpreted as the lynx' habitat use of this particular habitat type. Habitat use should not be confused with habitat selection. Habitat selection refers to the process whereby the animal selects which habitat to use relative to what it has available (Johnson 1980). E.g., a lynx selects for agricultural land when the habitat use of agricultural land is disproportionally larger than the availability of this habitat type, and it avoids agricultural land when the habitat use is disproportionality smaller than the availability.

Habitat selection can be examined on multiple scales (Johnson 1980), depending on how availability is defined. First an animal must decide where to locate its home range, i.e., where to live, this is often referred to as 2nd order habitat selection. For this scale it is common practice to use the study area as the availability definition, or at least an area much larger than the study species' home range size. In this thesis I will refer to this scale as the *landscape scale*, as the individual selects home range location in the wider landscape. After an animal establishes a home range it will use some habitat features within the home range more, or less, than the availability inside the home range. This is referred to as 3rd order of habitat selection. In this thesis I will refer to the 3rd order of habitat selection as the *home range scale*, as the home range is used as the availability definition. At even finer scales, the individual selects one patch or specific location over another, e.g., a brown bear will select one patch of blueberries over another. This is called 4th order of habitat selection. For this scale the availability definition is constrained to a much smaller area than the home range, as the 4th order habitat selection is taking place over small scales, e.g. over the distance the bear is able to walk during an hour. I will refer to this as the habitat selection at the *local scale*.

To estimate habitat selection at these different scales (or orders) I have used both resource selection functions (Manly et al. 2002) and step selection functions (Avgar et al. 2016). I used resource selection functions to estimate habitat selection on the landscape (c.f. 2nd order) and home range scale (c.f. 3rd order) and step selection functions to estimate local scale habitat selection (c.f. 4th order). The functions were fit with logistic regression (and conditional logistic regression) where the response variable is coded 1 for used locations of the animal and 0 for locations that have been randomly sampled inside the availability definition. Resource selection functions can obtain the relative selection probability, but not the absolute selection probability. This means that we are not able to calculate the probability of lynx selecting agricultural land (absolute), but we will be able to calculate the probability of lynx selecting agricultural land over another habitat type (relative).

Animal movement

Additionally, I have also investigated movement on local scales. Through an approach called integrated step selection analysis, it is possible to investigate in which habitats the collared individual moved faster or slower (Avgar et al. 2016). The logic behind these functions is to make steps out of two consecutive GPS locations. Based on how the animal moved we can create available steps that the animal could have used, but did not. By comparing the endpoints of used and available steps we can interpret habitat selection at local scales. The spatial scale at which habitat selection is interpreted increases as the time between consecutive GPS locations (step duration) increase, although it will generally be interpreted at the *local scale*. To be able to interpret and calculate speed we need to use the start point in each step and include the step length, then we can see if the step lengths are longer in certain habitats (higher speed) and derive the average speed from when the animal started a step in that habitat.

Human infrastructure and scale

To explore the responses of large carnivores towards human infrastructure I also used spatial data on human infrastructure. In this thesis I have used spatial data on buildings, houses, roads, land use type (e.g. urban, built-up, forest) and human density. I obtained this data from national maps of Norway (www.geonorge.no) and Sweden (www.lantmateriet.se), which are mostly freely available. I also obtained data on non-human variables from the same sources. When interpreting the effect of a covariate, it is important to consider the scale at which these covariates may act upon the ecological process of interest. For instance, for houses we can calculate the density at different spatial scales. The density of houses within 0.1 km or within 10 km would have quite different meaning and interpretation, since the scale has drastically changed (the area increased from 0.03 km^2 for 0.1 km radius to 314 km^2 for 10 km). Furthermore, we can also calculate other spatial metrics, e.g. distance to houses. It is important to keep in mind how the spatial covariate is calculated when interpreting its effect.

In this thesis, I have used spatial covariates which have been calculated as density in buffers with a radius of 50 m to 1 km, and distance to ‘feature’.

Human activity

For **article I**, which describes an experimental study, personnel intentionally disturbed the study animals. The advantage of this approach is that we have control over the human activity or disturbance and can directly study how the animals respond. These kinds of studies are possible to conduct on small spatial scales, where the point of interest is the encounter with the given individuals. Obtaining data on human activity on larger spatial scales, however, is a challenge. One can estimate where people are hiking or running through trail counters, questionnaire surveys, GPS loggers or aerial surveys, but these approaches require huge amounts of resources. In **article II**, we used a smartphone app (Strava), to obtain a proxy (a variable that exhibits high correlation with the variable of interest) for recreation. Almost 5 % of Norway’s population are Strava users. The activity data on humans from the Strava app is aligned to linear features in the landscape. We used this data generated by this app to create a map that was static in time, but where we could infer where people actually were active, e.g. running, hiking and walking. We only included activities from users that were walking, running or hiking.

Methods for each study

Article I – Female brown bear encounters and simulated hunts

This study was an experiment that explored the behavioural and physiological responses of brown bear females towards humans approaching on foot and towards simulated hunts. The personnel conducting the experiment passed the bear at a distance of approximately 50 m with the wind blowing from the personnel towards the bear. The simulated hunts were conducted by releasing pursuing and/or baying dogs after the bears. The pursuing dogs are barking while chasing the bear, but also when the bear does not move, while the baying dogs are only barking when the bear does not move (Figure 2). The baying dogs are generally better able to prompt the bear stand still than the pursuing dogs. Bears that were part of this study were equipped with biologgers monitoring the heart rate and body temperature. We used heartrate and the body temperature during the day of the hunt or the day of the approach as two physiological measures. In addition, we also used the speed of the bear and distance travelled as behavioural measures. We compared the experiments with 3-day control periods prior to the treatment (approach/simulated hunt).

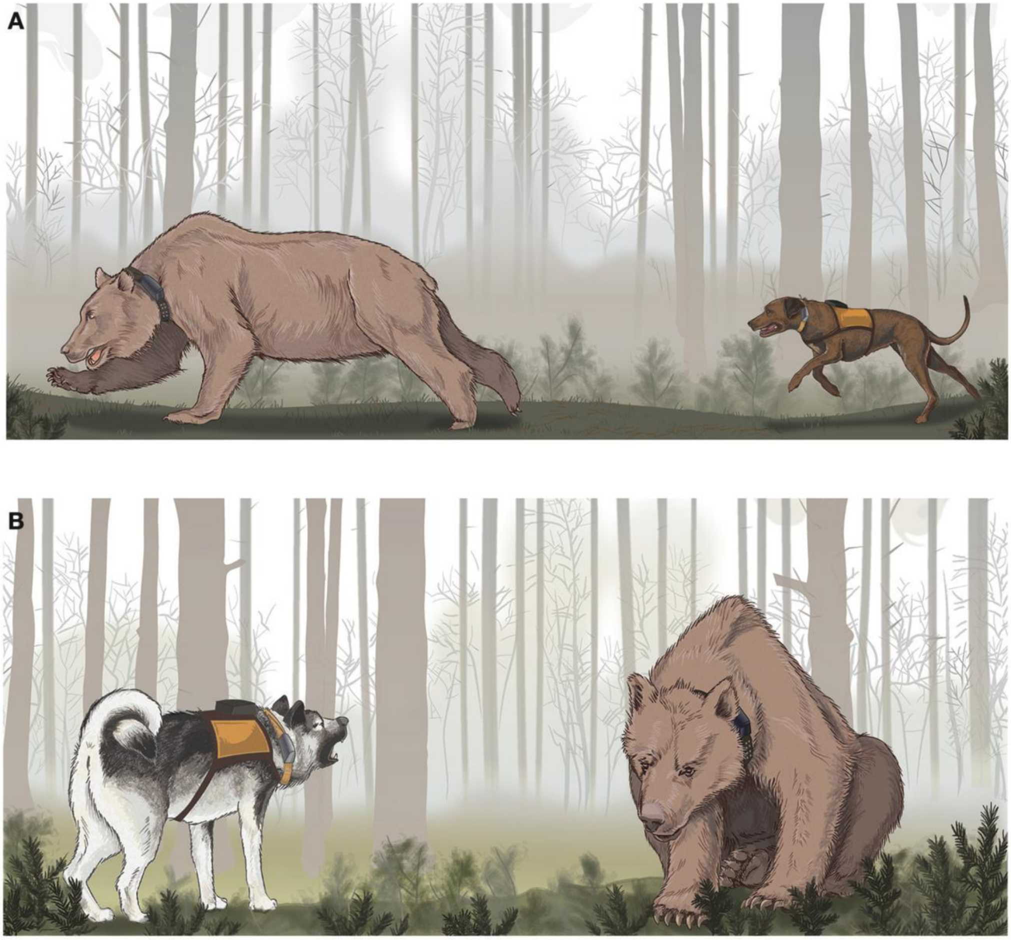

Figure 2. (A) ‘Pursuing dog’ (Plott hound) pursuing a bear during a simulated hunt. (B) Elkhound baying a bear during a simulated hunt. Illustration reproduced from **Article I**.

Article II – Lynx and recreation

We used resource selection functions to explore lynx habitat selection at a local scale (1-2 km) and at the home range scale in relation to recreation. We accounted for relevant covariates and included two proxies for human recreation; one proxy represented by the density of hiking paths and the other by the data collected from the Strava smartphone app. For the local scale analysis, we also included an interaction with time of day (night vs. day) to test if the habitat selection at the local scale was dependent on time of day. The covariates were prepared differently for the two scales. At the home range scale, we mainly used large spatial scale covariates, measured at the density inside 1 km radius, while at the local scale we either used distance to "feature" or density over a small spatial scale, approximately 100 m. Additionally, we explored if the lynx' habitat use of areas associated with recreationists was influenced by the time of day. We included the following human-related covariates: houses, forestry roads, public roads and agricultural land.

Article III – The Slettås wolf pack and infrastructure

This study was conducted on a wolf pack perceived as conflictful, i.e., viewed as being "bold" or "not shy". This perception arose due to repeated observation of wolves near houses. This created a conflict on whether or not to cull the pack. Six of at least nine wolves in the pack were collared with GPS collars with a proximity function. Proximity transmitters were placed close to houses that had been approached by wolves before the study. GPS collars on the wolves were programmed to trigger a rapid *burst* of position fixes (10 GPS locations with 1 minute intervals) if the GPS detected a signal from a proximity transmitter. During the same study period clusters of GPS locations were visited in the field to search for kill and bed sites. Moose pellet density was estimated through field surveys in the subsequent spring. We combined these data and studied the habitat selection of the wolves inside their territory, i.e. at the home range scale, while controlling for relevant covariates. We also studied the movement and habitat selection during periods with bursts, i.e. while the wolves were close to houses, using step selection functions (local scale). Additionally, we defined visits to houses as GPS locations from wolves less than 100 m from a house. We investigated which habitat the wolves selected during visits, with path selection analysis (similar to previously mentioned step selection functions). We included the following human-related covariates in our analysis for all scales: houses, roads (all roads) and agricultural land.

Article VI – Life history dependent responses to infrastructure by male brown bears

Consecutive GPS locations of male brown bears were classified as resident GPS tracks or dispersing GPS tracks by visual inspection, and the start and end point of the dispersal track were identified. We excluded data from the bears while resting, as our focus was on movement. We used resource selection functions to study habitat selection at the landscape scale, and step selection functions to study movement and habitat selection at a local scale. We ran individual models per bear-year and investigated if and how the resident and dispersing males differed in their responses towards human infrastructure and other covariates. We included the following human-related covariates: buildings, forestry roads, public roads and clearcuts. In this study we used the same spatial covariates at both the local and landscape scale.

Table 1. Overview of articles, their data sources, methods, spatial scale, and the responses they explore.

Article	**Study species**	**Data sources**	**Methods**	**Spatial scale**	**Response**
I	Brown bear	GPS collars Biologgers	Experiment Human approaches and simulated hunts	Local	Physiological Behavioural
II	Lynx	GPS collars Human crowdsourced mobility data	Observational Habitat selection over two spatial scales and habitat use	Home range Local	Habitat selection Temporal habitat use
III	Wolf	GPS collars with proximity function	Observational Habitat selection and movement over multiple spatial scales	Home range Local	Habitat selection Movement Temporal habitat use
IV	Brown bear	GPS collars	Observational Habitat selection and movement at two spatial scale and two life stages	Landscape Local	Habitat selection Movement

Main results

Article I – Female brown bear encounters and simulated hunts

Female brown bears demonstrated the strongest responses to dogs during simulated hunts. On days with a simulated hunt the bears had higher maximum heartrates and body temperatures than on days when humans approached them on foot. The bears also ran longer and faster on days with simulated hunts than on days with human approaches. The day following a simulated hunt, bears rested more than during the corresponding control period, and the time bears spent resting the day after a simulated hunt increased with the duration of the simulated hunt. On days with a human approach, bears did not have higher maximum heartrate or body temperature, and they did not walk longer than on days during the control periods. However, while adults moved faster on days with human approaches than during the control period, subadults did not. Bears did not rest more on the day after a human approach than during the control period. We detected only minor differences in the behavioural response of adult and subadult bears.

Article II – Lynx and recreation

The Strava smartphone app revealed high human recreational use of linear features other than hiking trails. In fact, most of the recreational activity occurred on roads and in urban settings. We detected local scale avoidance of areas receiving more recreation, but lack of avoidance on the home range scale. In addition, we detected a temporal adjustment in use of areas associated with recreation: lynx were more likely to use areas that were associated with recreation during the night, and less likely to use these areas during daytime. The hiking path proxy for recreation did not emerge as significant in any of our models. Of the human infrastructure variables included, lynx avoided areas of high house density and selected for higher agricultural land density and forestry road density at the home range scale. At the local scale, they avoided public roads during daytime and selected for forestry roads at night and were indifferent to houses and public roads at night and forestry roads during the day.

Article III – The Slettås wolf pack and infrastructure

Inside the wolf territory in Slettås the field surveys for the prey density revealed that there were few areas far from houses with a high density of moose. Hence, hunting close to houses was the only option if the wolves were to hunt in areas with the highest prey density. The wolves selected areas with low moose density when they were far from houses, and they selected for high moose density when they were close to houses at the home range scale. During the day wolves used areas farther away from houses, while at night they spent more time closer to houses. This was also reflected in kill and bed site locations. Bed sites used by the wolf pack were on average more than twice as far from houses as sites where wolves killed moose. The analysis of the proximity GPS data (bursts) revealed the importance of roads for wolf movement; they selected roads on a local scale and increased the speed of movement. The path analysis of the visits approaching houses and entering yards revealed that adult wolves selected for roads during visits, while juveniles did not share the strong selection for roads. See Figure 3 for some example bursts that visited houses.

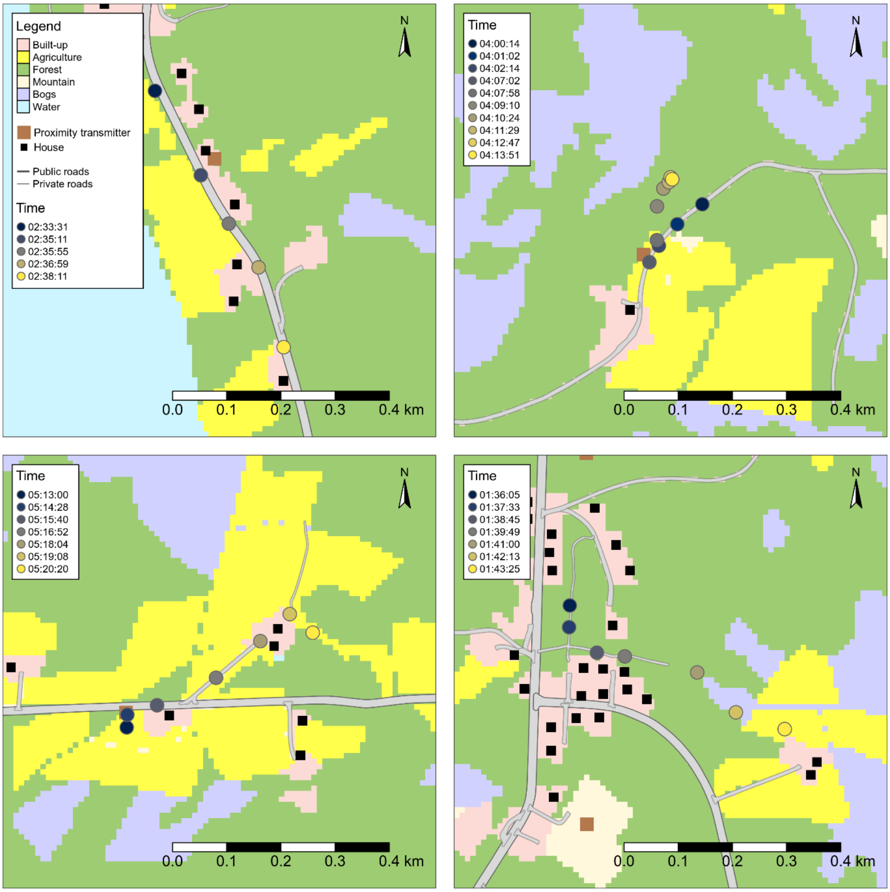

Figure 3. Example bursts that visited a house (less than 100 m from the wolf to the house) from wolves in the Slettås pack. Black squares are houses and the circular dots represent the wolf locations. The colour on the dots indicate the time of the wolf location.

Article VI – Life history dependent responses to infrastructure by male brown bears

Resident brown bear males (i.e., adult males with an established home range) avoided buildings and public roads at the landscape scale and at the local scale, while they selected distances closer to forestry roads at both scales. Resident male brown bear also increased their speed closer to forestry roads and public roads. Selection for forestry roads and increased speed in relation to forestry roads are indicative of movement facilitation. Dispersing males on the other hand, were mostly indifferent to human infrastructure, except that they avoided buildings at the local scale and moved faster when closer to buildings. Additionally, dispersing males also increased their speed closer to forestry roads and public roads. Interestingly, we only detected evidence of avoidance by dispersing males, but not attraction to landscape features we tested in this study.

Discussion

Large carnivore encounters

Many wildlife species respond to humans like they do to natural predators (Frid and Dill 2002). Based on previous studies, large carnivores in Scandinavia have two main alternative strategies to avoid close encounters with approaching humans; they can remain still at their location or they can flee (Moen et al. 2012). Large carnivores can also exhibit threatening behaviour (Sweanor et al. 2005), however this behaviour has not been reported for any of the approach studies on large carnivores in Scandinavia (Sunde et al. 1998, Karlsson et al. 2007, Wam et al. 2014, Sahlén et al. 2015, Moen et al. 2019, Ordiz et al. 2019). Which strategy an individual decides to use will likely depend on the situation, the species, the experience and the age of the animal. For instance, in Sweden bears fled 80 % of the times in response to human approaches and older individuals were less likely to flee (Moen et al. 2012). Brown bears and lynx usually flee from humans when the distance to the human (flight initiation distance) is around 50-150 (Sunde et al. 1998, Moen et al. 2019). Flight initiation distance is somewhat longer for wolves (Karlsson et al. 2007, Wam et al. 2014). Flight initiation distances tend to decrease with the degree of forest cover (Moen et al. 2012). Detectability of humans also influences the flight initiation distances, as wolves fled at shorter distances when the wind speed was higher and it was likely harder to hear the approaching humans (Karlsson et al. 2007), and bears had a tendency to flee at longer distances when more humans were approaching (Moen et al. 2012). The activity the large carnivore is engaged in during an approach can also influence their flight initiation distance, as active bears tended to flee at longer distances than resting bears (Moen et al. 2012).

In **Article I** we demonstrate that for female brown bear dogs in simulated hunts induce larger physiological and behavioural responses than approaching humans. This is not surprising as simulated hunts with dogs either involved being chased by dogs or standing still at the same location with a dog, or dogs, barking close to the bear. Further, the duration of a simulated hunt was also much larger than the duration of an approaching human. We also found evidence that the simulated hunts had lasting effects on female brown bear, as they spent more time resting the day following more intensive simulated hunts. Lasting effects have also been found after human approaches (Ordiz et al. 2019), where brown bears responded by being more active at night during days following an approach by humans. In our study we did not detect any physiological responses to human approaches. The physiological parameters maximum heart rate and body temperature might be too coarse for detecting a response to humans approaching on foot. For instance, brown bears in the same study area have been shown to be more stressed closer to human settlements and during the berry and hunting season (Stoen et al. 2015). This may indicate that bears likely have some kind of physiological response towards human approaching on foot as well.

In the Swedish bear population close to 10 % of the population is shot every year (Frank et al. 2017), and the hunt is very intensive as the quotas tend to be filled few days into the hunting season. The short hunting period and high efficiency of hunting may suggest that there are not many bears that are subject to repeated hunts and still are able to flee. Unless there is extensive illegal training of hunting dogs outside the hunting season, or bears are accidentally chased during other kinds of hunting (e.g. moose hunting), the non-lethal effects from this type of "hunt" are likely to have minor impacts on the population demographics. Although, human approaches induced a much smaller response than simulated hunts, human approaches are likely much more common and may have a higher cumulated impact. There is scarce information about how the other large carnivores in Scandinavia are affected by approaching humans and simulated hunts compared to brown bears. In particular, it could be interesting to investigate how lynx, as an ambush predator with relatively low endurance, respond to hunts with dogs both behaviourally and physiologically.

Human activity/recreation

The responses induced by humans approaching a large carnivore, or during a simulated hunt, comes with an energetical cost (**article I**). Hence, large carnivores should opt to avoid these encounters with humans or hunting dogs. Human activity can be predictable in space, as humans tend to follow linear features in the landscape, e.g. humans tend to hike on forestry roads and hiking paths, and cycle and drive cars on roads. In such cases large carnivores can avoid space that humans are likely to be active in (Ladle et al. 2019, Corradini et al. 2021). However, sometimes human activity may be harder to predict in space, but easier to predict in time, such as the berry picking season or the diurnal activity of humans. For instance, bears select more concealed bed sites (Ordiz et al. 2011) and are more active at night time during the berry and hunting season than earlier in the year(Ordiz et al. 2012). As berry picking and hunting may be harder to predict in space (but see Steyaert et al. 2016), avoidance in time might be a more suitable approach to avoid humans. Large carnivores can also use the same space as humans, at times when humans are not active (**article II**). Illustrating that avoidance of human recreationists can be achieved at local spatial scale and through temporal adjustments of habitat use.

One challenge when studying the response of large carnivores to human activity or outdoor recreation is to obtain a reliable proxy for recreation, over the large areas in which they roam. In **article II** we used a widely distributed smartphone app to obtain a proxy of recreation when studying the response of lynx towards recreation. Lynx avoided areas receiving more human recreationists at a local scale, but not larger areas receiving more human recreationists at the home range scale, and used habitat associated with recreationists to a larger degree during night. This mechanism likely reduced the probability of encountering humans, and probably enabled the lynx to use larger areas of their home ranges which received higher numbers of human recreationists. Instead of avoiding an area with generally high levels of human recreationists completely, lynx used this area and rather avoided the immediate surrounding of the linear features associated with higher levels of recreation within the wider area. Such local scale and behavioural adjustments by large carnivores may be important for coexistence of large carnivores and humans in general (Oriol-Cotterill et al. 2015).

Avoidance of different types of recreation have been reported by other species of large carnivores, e.g. Canada lynx (*Lynx canadensis*) (Squires et al. 2019), brown bears (Ladle et al.

2019, Corradini et al. 2021), wolves (Anton et al. 2020) and wolverines (Heinemeyer et al. 2019). There are many different types of recreation, and the different species of large carnivores will most likely respond differently to different types of recreation. For instance brown bears will likely not respond to skiing along linear features at all, since they are hibernating during the winter (Krofel et al. 2017), while dispersed (i.e. away from linear features) skiing might affect them (Linnell et al. 2000). High levels of dispersed recreation are likely the recreation type which is hardest to avoid for large carnivores, hence they might need to avoid the areas in which dispersed recreation occur at high levels or use them at night. E.g. these off-trail / off-road disturbance appear to be more avoided by wolverines than recreation along predictable linear features (Heinemeyer et al. 2019). There may also exists threshold to how much human activity or human recreationists large carnivores are able to tolerate. However, studies on this will be challenging to conduct in Scandinavia because the levels of human disturbance are quite low compared to farther south in Europe (our lynx study was conducted in the most intensively used recreation area in Norway). Another, important aspect of human recreation is that the impact of human activity and recreation will likely be less in landscapes with low human-related mortality.

Infrastructure

Large carnivores do not only respond to human activity associated with linear features, they also respond to the linear features themselves (Trombulak and Frissell 2000). These responses can occur over multiple spatial scales. On the landscape scale, brown bears appears to avoid public roads (**article IV**) and they appear to locate their home ranges in ways that reduce contact with large public roads (Bischof et al. 2017). Traffic volume is important as roads receiving higher number of cars are more strongly avoided and can impede movement (Northrup et al. 2012). In **article IV** we also reported avoidance of public roads on a local scale, indicating that roads with high traffic volumes are avoided at most scales of habitat selection by brown bears. However, smaller roads with less human activity/traffic volume can be selected and used by large carnivores. On a local scale minor roads with less traffic, e.g. forestry roads (gravel roads), may facilitate movement (**article III-IV,** Dickie et al. (2019)). These roads are likely favourable due to their firm surface, which can reduce the energy cost of movement, and their relatively low human activity. Although, minor roads can facilitate movement of large carnivores it should be noted that they can be associated with increased predation risk, as large carnivores appear to have an increased risk of getting shot closer to forestry roads (Basille et al. 2013, Leclerc et al. 2019).

Other sources of human infrastructure are often avoided by large carnivores, such as houses, buildings, towns or other kinds of human settlement (Nellemann et al. 2007). In **article III**, however, it was a perception of lack of avoidance that made one wolf pack in Norway infamous on a national level. These wolves were known to walk through house-yards (Wabakken et al. 2019), and were perceived as conflictful. When large carnivores occupy a human-dominated landscape, human-large carnivore encounters will likely occur, illustrated by examples from Europe (Huber et al. 2016). In the Slettås case it appeared likely that wolves occurred close to houses due to high prey densities in these areas during winter. Furthermore, ploughed roads facilitated the local scale movement of wolves which likely led them to move through the house-yards. Similar to what likely drives visits to house-yards in Finland (Kojola et al. 2016). Although the wolves were moving through house-yards we do not know if this wolf-pack in particular were moving more often through house-yards than others. The wolves visited houses almost exclusively during the night, which likely explains the lack of direct observations of the wolves (Wabakken et al. 2019), as most of the observations were track left on the snow. This case study, illustrates again how adaptable large carnivores are to living in human-dominated landscapes, and in this case where the prey is generally close to houses.

From a wildlife conservation perspective, a common topic is the importance of connectivity in the landscape, i.e. the ease of movement for animals between patches of suitable habitat or between populations (Moilanen and Nieminen 2002). Moving in the landscape may become harder, as the human-dominated landscape is becoming increasingly built-up and fragmented by infrastructure (Zeller et al. 2017, Tucker et al. 2018). Connectivity is commonly inferred from habitat selection and movement parameters (Zeller et al. 2012). Several studies have shown that habitat selection and movement may differ, depending on the life-stage (Elliot et al. 2014, Barry et al. 2020, Hemmingmoore et al. 2020), i.e. as a dispersing individual looking for a home range or as a resident which already have settled in a home range. As connectivity is often referred to in a genetic diversity context (Zeller et al. 2012), it is important to cautiously interpret the consequences of human infrastructure on genetic connectivity when the connectivity models are inferred from data obtained from resident individuals (Elliot et al. 2014).

In **article IV**, we revealed that residents brown bear males have stronger responses to human infrastructure than dispersing males. Dispersing male brown bears generally did not respond towards most human infrastructure, the only human infrastructure they avoided was buildings on a local scale. This is likely due to the landscape being novel to dispersers and they do not know where they will find preferred features. Furthermore, the dispersers where even more tolerant towards human infrastructure on the landscape scale. This raises the question for which spatial scale should be used when creating connectivity models, as based on our results it appears that one would obtain lower connectivity if habitat selection on the local scale had been used to inform the connectivity models. Nonetheless, the lack of responses of dispersers toward human infrastructure is good news for connectivity as this indicates that connectivity models based on data from resident males may underestimate the true connectivity and be a conservative estimate of connectivity (Elliot et al. 2014).

Coexistence

The long term viability of large carnivore populations requires that they share space with humans (Boitani and Linnell 2015, Carter et al. 2016). As long as humans pose a substantial mortality risk towards large carnivores, large carnivores have to avoid humans to reduce their predation risk. For coexistence to be possible over large spatial scales, local scale adjustments in habitat selection and temporal adjustment of habitat are likely necessary (e.g. **article II-IV**). For some large carnivores, i.e. those that avoid human infrastructure at large spatial scales (e.g. landscape scale), coexistence will be more challenging than for species that are able to tolerate high human impact through human activity and infrastructure at the local scale. Previous studies and this PhD project suggest that large carnivores are able to adjust and occupy human-dominated landscapes (e.g. Chapron et al. 2014, Bouyer et al. 2015, Cretois et al. 2021). However, there is another, and crucial prerequisite for coexistence; the willingness and acceptance of people to live side by side with large carnivores (Carter et al. 2016, Cretois et al. 2021). As long as people tolerate the presence of large carnivore close to humans, and there is a will by the public to maintain viable populations of large carnivores, the opportunities for large carnivores to persist in the human-dominated landscape appear to be present.

Concluding remarks

This PhD project has demonstrated that large carnivores respond to simulated hunts with dogs both physiologically and behaviourally, and to human encounters behaviourally. The impact of the simulated hunts appeared to be stronger when the duration of the hunt increased. Future studies investigating the physiology of large carnivores towards simulated hunts, and especially human approaches, should explore other physiological parameters than the one we used. Furthermore, studying these effects on other large carnivores, in particular for ambush predators with low endurance, could reveal new insights as to how human approaches and hunts with dogs affect large carnivores. The lynx study documented that spatial avoidance of human recreationists at a local scale and temporal adjustments of habitat use, are likely important for lynx to utilize the human-dominated landscape. Future studies could attempt to relate the response towards human activity to human-caused mortality, which could provide useful information in a conservational perspective. The wolf study revealed how a wolf pack perceived as conflictful moved and selected habitat. This case study produced detailed information about this single wolf pack and aimed to provide some answers to behaviour being perceived as conflictful. Studying how wolves in general move and use space close to houses with GPS collars with high fix rates could provide important information for management and the public, as it may help to explain what the wolves do close to houses. Lastly the life stage-dependent response to human infrastructure for brown bear males, provide more evidence for the importance of life stage in relation to movement in the human-dominated landscape. Future studies should explore how this actually translates into connectivity, and how habitat selection estimated at different spatial scales and from different life stages affect connectivity estimates.

The overall conclusion from this PhD project, is that large carnivores appears to be able to occupy human-dominated landscape based on temporal adjustments of habitat and local scale spatial avoidance of space where humans will likely be active. I believe large carnivores will be able to occupy human-dominated landscapes, as long as this is tolerated by the public with which they must share space.

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Behavioral and Physiological Responses of Scandinavian Brown Bears (*Ursus arctos*) to Dog Hunts and Human Encounters

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Innovations in biologging have offered new possibilities to better understand animals in their natural environment. Biologgers can be used by researchers to measure the impact of human disturbances on wildlife and guide conservation decisions. In this study, the behavioral and physiological responses of brown bears (*Ursus arctos*) to hunts using dogs (*Canis lupus familiaris*) and human encounters were assessed to better understand the impact of human outdoor activities on brown bears. In Scandinavia, brown bear hunting and the use of dogs during hunts is increasing in popularity. Nonetheless, not every hunt leads to a killed bear. This means that for each bear that is shot, multiple bears may be chased but not killed. In addition, bears can also be disturbed when encountering non-hunting humans. Heart rates, body temperatures, GPS coordinates and dual-axis activity data were collected from 52 simulated hunts (a simulated hunt using dogs with the bear allowed to flee at the end) and 70 human encounters (humans intentionally approaching the bear) that were carried out on 28 free-ranging female brown bears in two study areas in Sweden. The results showed that: (1) simulated hunts had a greater impact and induced a greater energy cost than human encounters; (2) the amount of time bears rested the day after the simulated hunts increased linearly with the duration of the simulated hunts, implying a lasting behavioral impact relative to the intensity of the disturbance. Although not tested in this study, brown bears that are repeatedly disturbed by dog hunts and human encounters may be unable to compensate the disturbances' energy cost, and their fitness may, therefore, be altered. If it is the case, this effect should be accounted for by managers.

Keywords: activity, body temperature, carnivore, heart rate, human disturbance, hunting dog

INTRODUCTION

Innovations in biologging have increasingly been used in the past few decades to better understand animals in their natural environment (Wilmers et al., 2015). The use of biologgers can also allow researchers to measure human disturbances and guide conservation decisions (Wilson et al., 2015). Hunting practices raise ethical questions and have spurred research on the physiology and behavior of pursued animals (for example: foxes (*Vulpes vulpes*) (Kreeger et al., 1989), pumas (*Puma concolor*) (Bryce et al., 2017) or red deer (*Cervus elaphus*) (Jarnemo and Wikenros, 2014). Several variables may be used to measure how human outdoor activities disturb wild animals and to determine if the disturbances may incur extra energy costs. Longer traveled distances (Rode et al., 2007), higher heart rates (Kreeger et al., 1989; Ditmer et al., 2015) or higher body temperature (Evans et al., 2016) have, for example, been considered as indicators of disturbances that lead to extra energy costs. In addition, animals may run to flee, with the higher speeds demanding more energy (Pagano et al., 2018). They may also need to recover and rest after a disturbance, preventing their compensation of the lost energy.

Brown bears (*Ursus actos*) have been a game species in Sweden since 1943 (Swenson et al., 2017) with a hunting season starting on August 21st and ending when the quotas set by the county board are filled, or at the latest on October 15th. Family groups (adult females with dependent cubs) are protected but there are no age or sex specifications applied to the hunting quotas (Bischof et al., 2008). In Sweden, legal hunting by humans represents the primary cause of mortality for adult brown bears (Bischof et al., 2017), with the most common hunting method being based on the use of trained hunting dogs (*Canis lupus familiaris*) (Bischof et al., 2008). Dogs are released to pursue the bears with the hunters following and attempting to shoot the bear (hereafter dog hunts). Bear hunting is increasing in popularity with the number of hunters specialized in bear hunting rising (Swenson et al., 2017). There are no statistics known for Sweden, but when hunting black bears (*Ursus americanus*) in a similar way in Virginia (USA), the recorded success is generally low [20%, Vaughan and Inman (2002)]. This means that for each bear that is shot, multiple bears may be chased but not killed.

Hunting is not the only human outdoor activity that affects bears in Sweden. Bears flee when encountered by humans (Moen et al., 2012) and change their movement patterns for at least 2 days following the event (Ordiz et al., 2013b). In areas with higher road densities, bears adopt movement patterns that are more nocturnal and less diurnal, to avoid human activity (Ordiz et al., 2014). Bears avoid denning near roads (Elfström et al., 2008) and select more concealed denning sites near humans (Sahlén et al., 2011). Brown bears have a general anti-predator behavior toward humans. A behavior that is not only affected by hunting activities, but also by the year-round presence of humans. It is therefore important to understand the impacts of both dog hunts and human encounters on brown bears.

To better understand how human outdoor activities influence brown bears in Scandinavia, simulated hunts using dogs with the bear allowed to flee at the end (hereafter simulated hunts) and human encounters (humans intentionally approaching the bear) were conducted on GPS-collared female brown bears. For each experiment, five variables were measured: (1) the distance traveled by the bears, (2) their speed, (3) their heart rate, (4) their body temperature, and (5) their resting behavior. This was done within three different time periods: (1) during a control period (3 days prior to an experiment), (2) during the day of the experiment and (3) during the 2 days following the experiment. The following hypotheses were tested by comparing the five variables at the different time periods: [H1] Dog hunts and human encounters are a source of physiological and behavioral disturbance for brown bears. [H2] The physiological and behavioral impacts of dog hunts on brown bears are greater than the impact of human encounters. [H3] Dog hunts that last longer in time have greater physiological and behavioral impacts on brown bears. [H4] Dog hunts and human encounters have lasting physiological and behavioral effects on brown bears.

MATERIALS AND METHODS

Study Area

In Sweden, brown bears are distributed into three main populations (Norman, 2016). This study was carried out from 2014 to 2016 in two different areas covering the southernmost and northernmost bear subpopulations (61.50°N; 15.06°E & 66.76°N; 21.02°E). In both areas, the landscape is hilly and mostly covered by managed productive forest, mainly composed of Scots pine (*Pinus sylvestris*), Norway spruce (*Picea abies*) and birch (*Betula* spp.).

Data Collection

Human encounters and simulated hunts were conducted on 28 free-ranging female brown bears. The bears were equipped with a VHF transmitter implant (M1255B, Advanced Telemetry Systems, Isanti, USA); a GPS-Plus collar with GSM modems or Iridium modems with an included VHF transmitter and a dual-axis motion sensor (Vectronic Aerospace GmBh, Berlin, Germany); cardiac biologgers (Reveal XT, Medtronic, Minneapolis, USA) implemented with modified software (BearWare, Medtronic, Minneapolis, USA); and temperature biologgers (DST Centi-T, Star-Oddi, Gardabaer, Iceland). The biologgers were surgically implanted in the bears with the cardiac biologgers subcutaneous to the left of the sternum and the temperature biologgers in the abdomen of the bear (Arnemo and Evans, 2017). The cardiac biologgers continuously recorded the bears' inter-beat intervals (R-R, in milli seconds), based on electrocardiogram (ECG) measurements. Every 2 min the mean R-R interval was converted into a heart rate in beats per minute (bpm). The body temperatures of the bears were measured every 4 min with an accuracy of ± 0.01°C. The activity of the bear was measured as the true acceleration in two orthogonal directions at a frequency of six to eight times per second. The average of the activity values over 5 min for each orthogonal direction was then recorded in the GPS collar with its associated date and time (Friebe et al., 2014).

GPS coordinates of the bears were recorded by default every 30 min or every hour. During the human encounters and the simulated hunts, a GPS location was recorded every minute for 3 or 4 h. During some of the simulated hunts, the dogs were equipped with Ultra High Frequency (UHF) transmitters (Vectronic Aerospace GmbH, Berlin, Germany) that emitted a signal every second, triggering the recording of GPS coordinates every 70 s in the bears' GPS collars at ≤ 500 m. The GPS collars on the brown bears scanned for UHF signals for 1.5 s every 8 s, and the recording ended automatically 60 min after the last detection of a dog collar. Humans (hereafter observers) were equipped with hand-held Garmin GPSMAP 60CSx or Astro 320 and the dogs were equipped with T 5 or DC40 Dog Devices, with all types of equipment being set to record a GPS coordinate every second (Garmin Ltd., Olathe, USA).

For more details on how the bears were captured and immobilized, please refer to Arnemo and Evans (2017). All captures were approved by the Swedish Ethical Committee on Animal Research (application numbers C7/12 and C18/15) and the Swedish Environmental Protection Agency (application numbers NV-00741-18 and NV-01758-14).

Experimental Design

Following the same methods presented by Moen et al. (2012), the human encounters were started between 8:30 and 14:30 local time (GMT+2). The observers walked toward the bear, intending to pass the bear at an approximate distance of 50 m, whilst talking to each other or to themselves if alone, simulating hikers. When the bear had been passed or when the bear ran away, they returned to the car and made sure not to encounter the bear a second time. The 70 human encounters were carried out in 2014 (1st June−7th August; $n = 17$), in 2015 (8th June−28th July; $n = 24$) and in 2016 (2nd June−20th August; $n = 29$). The minimum distance recorded between the observers and the bear was on average 55 ± 27 m (median 51 m, minimum 18 m, maximum 137 m; $n = 70$). In total, 25 female bears were used, with five subadults, 16 adults and four that were used when they were both subadults and adults.

Simulated hunts were started between 8:00 and 17:00. The observers with hunting dogs kept on a leash walked toward the bear until a dog showed interest in the scent of the bear, either in the wind or from its tracks, before the dogs were released and allowed to pursue the bear (**Figure 1**). The simulated hunt was stopped when the dogs came back to the observers or by the observers calling in or intercepting the path of the dogs. The simulated hunts were intended to last about 2 h but ended both earlier and later due to practicalities. During the same simulated hunt, one to six different dogs were used. However, only a maximum of two dogs were let loose simultaneously to hunt the bear. Bears were considered to be disturbed by both types of experiments if the minimum distance recorded between the bear and the observers or dogs at any time was < 200 m.

The 52 simulated hunts were carried out in 2014 (9th August−15th August; $n = 4$), in 2015 (11th June−2nd October; $n = 19$) and in 2016 (18th June−7th October; $n = 29$). The minimum distance recorded between the observers and / or the dogs and the bear was on average 20 ± 34 m (median 5 m, minimum 0 m, maximum 168 m; $n = 52$). The duration of a simulated hunt was defined as the time between when the observers and dogs started heading from the car toward the bear until when they were back at the car. Simulated hunts lasted on average 229 ± 104 min (median 198 min, minimum 67 min, maximum 508 min; $n = 52$). In total, 17 female bears were used, with two subadults, 14 adults and one that was used when it was both a subadult and an adult.

Some bears were used in multiple human encounters and / or simulated hunts during the same year. No research activities that could have affected the bears were carried out for at least 5 days before and 2 days after the experiments.

Data Processing and Statistical Analyses

All the data analyses and data processing were carried out using the statistical programming language and environment, R 3.4.2 (R Core Team, 2017). All data (GPS, activity, heart rate and body temperature) was stored in the WRAM database (Wireless Remote Animal Monitoring, Dettki et al., 2014).

Response Variables

The distance traveled by the bear was measured as the variable TRAVEL, which is the sum of all hourly displacements for each day. In this way, days with GPS coordinates taken with a different frequency were directly comparable. The distances (shortest distance between two points on the WGS84 ellipsoid) between the hourly positions were measured using the distGeo function from the geosphere package, version 1.5-7 (Hijmans, 2017). The maximum speed of the bear was measured as the variable MAXSPEED, which is the highest speed recorded of the day based on all hourly displacements within the 24 h. The heart rate of the bear was measured as the variable HEARTRATE30, which is the highest value measured by a rolling mean ran over all the measured heart rates of the day, with a window of 30 min and a constant forward shift of 2 min. When processing the heart rate data, a constant mismatch between the heart rate and the corresponding time was observed for some bears. The mismatch was corrected through using the correlation between the activity of the bear and its heart rate. Heart rate data was not used in the analysis if the activity data was not available or if the method led to a suggested time shift that was not consistent throughout the data. The body temperature of the bear was measured as the variable T_bAREA, which is the area under the curve of the measured body temperature values and above the median body temperature of the bear over a 24-h period. The median body temperature was based on data from 1st June to 30th September for each bear-year. Days when the bears were involved in research activities (human encounters, simulated hunts or captures) were not included in this data set. The area was calculated using a trapezoidal approximation (all points are connected by a direct line forming multiple trapezoids) using the AUC function from the DescTools package, version 0.99.23 (Signorell, 2017). The resting behavior of the bear was measured as the variable REST, which is the amount of time the bear was resting in minutes during a day. The two values for each orthogonal, measured by the dual-axis motion sensor, were summed resulting in a variable ranging from 0 to 510. A value lower than 23 was considered resting behavior (Gervasi et al., 2006).

Explanatory Variables

Human encounters and simulated hunts were considered as two different treatments in a binary variable, hereafter named TYPE. The variable PERIOD consisted of four unique levels. The 1st level represents the control period defined as the mean values recorded during the 3 days prior to the human encounter day or simulated hunt day. The 2nd level represents the day of the experiment. The 3rd and 4th levels represent the following and

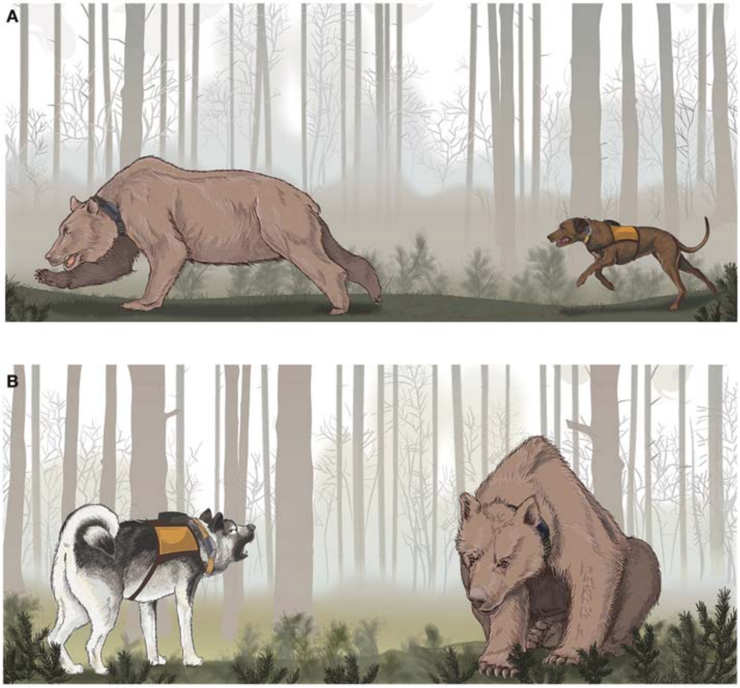

FIGURE 1 | While being hunted, a brown bear can run in order to escape hunting dog(s) and sometimes end up lying on the ground with the dog(s) barking and running around it (baying). When the dog(s) is/are baying the bear, the hunter is typically sneaking in and shooting the bear. **(A)** Plott hound pursuing a bear during a simulated hunt. The dog is equipped with a collar (DC40 Dog Device) used to collect GPS coordinates, as well as a dog harness equipped with a UHF transmitter that triggers the recording of coordinates every 70 s in the GPS-Plus collar fitted on the bear. **(B)** Elkhound baying a bear during a simulated hunt. The same equipment as in **(A)** is illustrated. Scientific Illustration by Juliana D. Spahr, SciVisuals.com (reproduced with permission).

second day after the experiment, respectively. The age of the bears was considered in the binary variable AGE with subadult bears $<$ 4 years old. The duration of the simulated hunts was also used as an explanatory variable.

Model Construction

Linear mixed effect models (LME) were fitted using TRAVEL, MAXSPEED, HEARTRATE30, T_bAREA and REST as response variables, and TYPE, PERIOD, AGE and the interactions as explanatory variables. The experiments' ID nested in the bears' ID were added as random factors. The normality of the residuals was improved by a square root transformation of the response in the TRAVEL, MAXSPEED, HEARTRATE30 and the T_bAREA models. The models were created using the lmer function from the lme4 package, version 1.1-14 (Bates et al., 2014) and fitted using the restricted maximum likelihood (REML) method, as the models were composed of small sample sizes. The final model was obtained by following the backward selection method. The significance of the variables and the interaction were computed using the Anova function from the car package, version 2.1-6 (Fox and Weisberg, 2011), with the type-III method. A pairwise analysis of the estimated marginal means (EMMs) was then performed to interpret the final models using the emmeans package, version 1.1. (Lenth, 2018). This method was used as the models had an unbalanced number of human encounters and simulated hunts (**Table 1**). The EMMs were based on a 0.95 confidence level with the Tukey correction method. Some of the 70 human encounters and 52 simulated hunts did not have data for all the response variables. For this reason, n varied between the different LME models (**Table 1**).

When only considering the simulated hunts data, the variables TRAVEL, MAXSPEED, HEARTRATE30, T_bAREA, and REST were used as response variables in LME models, with the duration of the simulated hunts, the variable AGE and the interaction as explanatory variables. In these models, the variables TRAVEL, MAXSPEED and T_bAREA were square root transformed to improve the normality of the residuals. The models were created following the same method as the method presented for the previous LME models but were created using the lme function from the nlme package, version 3.1-131 (Pinheiro et al., 2017). The model included the ID of the bears as a random factor, as some simulated hunts were carried out on the same bears (**Table 1**).

TABLE 1 | Number of human encounters and simulated hunts with complete data sets.

Variable:	N human encounters (N bears: Subadult, Adult, Both)	N simulated hunts (N bears: Subadult, Adult, Both)
TRAVEL	70 (5, 16, 4)	50 (2, 13, 1)
MAXSPEED	70 (5, 16, 4)	50 (2, 13, 1)
HEARTRATE30	21 (1, 8, 0)	26 (2, 9, 0)
T_bAREA	35 (5, 9, 2)	35 (3, 10, 0)
REST	60 (4, 15, 4)	46 (2, 13, 1)

The number of bears that were used when being subadult, adult or both are also indicated in brackets.

In the models HEARTRATE30 and REST with PERIOD, TYPE, AGE and the interactions as explanatory variables, the variable AGE and the corresponding interactions were not kept in the models after using the backward selection method. However, the interaction between PERIOD and TYPE was significant (all $P < 0.0001$). Both the PERIOD and TYPE variables were thus used in the pairwise analysis of the EMMs. In the models TRAVEL, MAXSPEED, and T_bAREA, the variables AGE, PERIOD and TYPE were kept in the models after using the backward selection method. All three explanatory variables were therefore used in the pairwise analysis of the EMMs.

RESULTS

The distances traveled by both adult and subadult bears were longer during the day of the simulated hunts than during the corresponding control periods (*post hoc* test: estimated difference: both adult and subadult: 755 ± 15 m, $P < 0.0001$, both 10% longer, range measured difference: Adult: −3 to 22 km, Subadult: −1 to 12 km) and longer than during the day of the human encounters (*post hoc* test: estimated difference both adult and subadult: = 527 ± 22 m, $P < 0.0001$, Adult: 3 %, Subadult: 4% longer). Adult and subadult bears did not travel longer distances on the day of the human encounters than during the corresponding control periods (both $P = 0.13$).

Both adult and subadult bears ran faster during the day of the simulated hunts than during the corresponding control periods (*post hoc* test: estimated difference: Adult: 679 ± 61 m h^{-1}, $P < 0.0001$, 31% faster, range measured difference: −280 to 6360 m h^{-1}, Subadult: 455 ± 94 m h^{-1}, $P = 0.0002$, 17% faster, range measured difference:−680 to 3580 m h^{-1}) and ran faster than during the day of the human encounters (*post hoc* test: estimated difference: both: 450 ± 62 m h^{-1}, $P < 0.0001$, Adult 10 % faster, Subadult: 16 % faster). Adult bears also ran faster the day of the human encounters than during the corresponding control periods (*post hoc* test: estimated difference: Adult: 216 ± 53 m h^{-1}, $P = 0.005$, 3% faster, range measured difference: −1470 −8850 m h^{-1}). Subadults, however, did not run faster on the day of the human encounters than during the corresponding control periods ($P > 0.90$).

The maximum heart rates were higher during the day of the simulated hunts than during the corresponding control periods (*post hoc* test: estimated difference = 7 ± 0.06 bpm, $P < 0.0001$, 7% higher, range measured difference: 4–106 bpm) and higher than during the day of the human encounters (*post hoc* test: estimated difference = 3 ± 0.12 bpm, $P < 0.0001$, 3% higher). Bears did not have a different maximum heart rate the day of the human encounters than during the corresponding control periods ($P = 0.18$, maximum measured difference: −50–106 bpm).

The body temperature areas of the adult bears were greater during the day of the simulated hunts than during the corresponding control periods (*post hoc* test: estimated difference = 1553 ± 59 T_bAREA, $P < 0.0001$, 12% greater) but not for subadult bears ($P = 0.15$). The body temperature areas of the bears were not greater during the day of the simulated hunts than during the day of the human encounters (Adult: $P = 0.64$, Subadult: $P = 0.57$). The body temperature areas of both adult and subadult bears were not different on the day of the human encounters compared to during the corresponding control periods (both $P > 0.90$).

The day after the simulated hunts, bears rested more than during the corresponding control periods (*post hoc* test: estimated difference = 68 ± 19 min, $P = 0.008$, 1% more, range measured difference: −4 h 15 min−5 h 15 min) but not more than during the day after the human encounters ($P = 0.62$). The day after the human encounters, bears did not rest more than during the corresponding control periods ($P > 0.90$). The amount of time bears rested the day after the simulated hunts increased linearly with the duration of the simulated hunts (**Figure 2**). Bears did not rest less during the day of the human encounters or the simulated hunts than during the corresponding control periods (both $P > 0.90$). Bears did not rest less during the day of the simulated hunts than the day of the human encounters ($P = 0.18$).

There was no difference between the control periods of the human encounters and the control periods of the simulated hunts (adults or subadults) for the distance traveled, the maximum speed, the maximum heart rate, the body temperature area or how long the bear rested (**Table 2**, all $P > 0.13$). There was no difference between the first and second days following the human encounters or the simulated hunts, compared to the corresponding control periods, for the distance traveled, the maximum speed, the maximum heart rate or the body temperature areas of the bears (all $P > 0.09$). The duration of the simulated hunts had no effect on the distance traveled, maximum speed, maximum heart rate, body temperature area or how long the bear rested the day of the simulated hunt (all $P > 0.15$).

DISCUSSION

During human encounters, adult bears ran faster than during the corresponding control periods, but did not have higher heart rates, higher body temperatures or travel longer distances. There were no significant differences between the day of the human encounters and the corresponding control periods in any of these variables for subadults. These results provide support for the hypothesis that human encounters are a behavioral disturbance

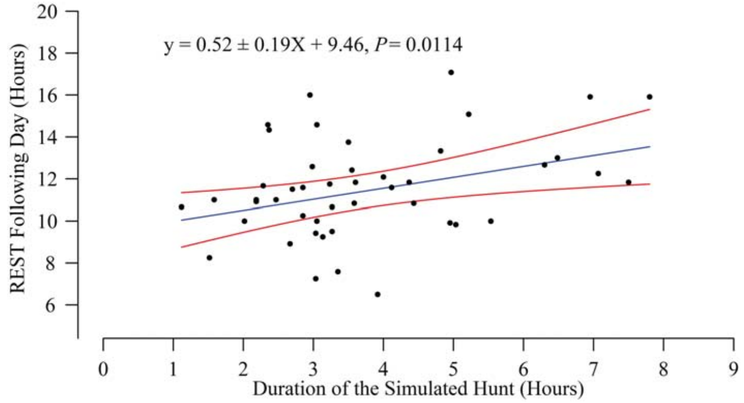

FIGURE 2 | The day after the simulated hunts, female bears rested more if the simulated hunts were longer ($P = 0.0114$). The 46 simulated hunts are represented by the black dots with the regression line, as well as the lower and upper 95% confidence interval. The model REST ∼ Duration of the simulated hunt*AGE was fitted with the Bear ID as a random factor. The variable AGE was not kept after using the backward selection method (Interaction: $P = 0.34$, AGE: $P = 0.29$).

TABLE 2 | Estimated marginal means (EMM) for the control periods of the human encounters and the control periods of the simulated hunts.

Control Period	EMM Human Encounters		EMM Simulated Hunts	
	Subadult	Adult	Subadult	Adult
TRAVEL $_{(m)}$	5836 ± 26	7945 ± 13	5744 ± 33	7838 ± 17
MAXSPEED $_{(mh-1)}$	1115 ± 77	1231 ± 48	1101 ± 85	1217 ± 55
HEARTRATE30 $_{(bpm)}$	109 ± 0.07		104 ± 0.06	
T_bAREA	9165 ± 132	13358 ± 60	8899 ± 167	10271 ± 63
REST $_{(h:min \pm min)}$	10:49 ± 20		10:10 ± 22	

No differences between the control period values were found when carrying out all the possible pairwise comparisons (HumanAdult-HumanSubadult, HumanAdult-HuntAdult, HumanAdult-HuntSubadult, HumanSubadult-HuntSubadult, HuntAdult-HuntSubadult, HuntAdult-HumanSubadult; all P > 0.13).

for brown bears [H1] but do not support the hypothesis that human encounters are a physiological disturbance for brown bears.

Contrary to human encounters, simulated hunts led to a clear disturbance with longer traveled distances, higher speeds and higher heart rates than during the corresponding control periods or the human encounters. Adult female bears also had greater body temperatures compared with the control periods. These results support the hypothesis that dog hunts represent both a behavioral and physiological disturbance [H1]. The results also support the hypothesis that dog hunts have a greater impact on brown bears than human encounters [H2].

During simulated hunts, bears were pursued by dogs and may have been forced to flee in a more dramatic way than when moving away from encountered humans, which is most likely the reason why simulated hunts had a greater impact. Simulated hunts were also characterized by smaller minimum distances as dogs were able to come closer to the bears than observers were during the human encounters. Because running faster can be associated with higher energy costs (Pagano et al., 2018), human encounters and dog hunts can be considered a direct energy cost for adult female brown bears, with dog hunts having the highest impact. Simulated hunts also led to longer traveled distances, higher heart rates and, for adult females, greater body temperature areas, giving further support to the idea that dog hunts represent an important energy cost. The fact that bears use more energy while running than other quadrupedal mammals (Pagano et al., 2018) suggests that human encounters and dog hunts may represent relatively large energy costs in bears.

If an adult female bear is frequently disturbed by human encounters and dog hunts, its body condition may be affected by the energy cost of these disturbances. Females do not always reach their energetic needs, e.g., poor berry seasons affect the reproductive success of lightweight female bears in Sweden (Hertel et al., 2018). Adult females give birth during the denning period and depend on their fat reserves for the gestation and lactation of their cubs (Robbins et al., 2012; Lopez-Alfaro et al., 2013). Even if observed mating, captive adult female brown bears having a body fat content lower than 20% do not give birth (Robbins et al., 2012). Lopez-Alfaro et al. (2013), using an energy consumption model, estimated that with a body fat content below 19%, a female would not be able to reproduce during a hibernation period that lasts over 120 days. In Sweden, adult females spend on average 181 days in winter dens (Friebe et al., 2001). Energy costs due to human encounters and dog hunts may thus affect the body condition of adult female bears and ultimately affect their fitness by altering the reproductive success.

Higgins (1997) compared the body condition of 13 adult female black bears from non-hunted populations with 20 adult female black bears from a hunted population and found an indication that black bears from the hunted population may be lighter and in worse physical condition ($P = 0.09$). However, Massopust and Anderson (1984) carried out eight dog hunts on five black bears with a maximum of two dog hunts per individual and observed no injuries or abnormal weights on the bears when captured at their den. It is possible that more than two dog hunts are needed to affect the weight of the bears. Tourism (bear viewing), experimentally simulated for one summer in an undisturbed bear area in Alaska, did not lead to losses in weights, nor any changes in body condition (Rode et al., 2007). However, the studied bear population could feed on salmon (*Oncorhynchus kisutch* and *Oncorhynchus nerk*), a more nutrient-rich alimentation than the berries eaten by the Scandinavian brown bears (Welch et al., 1997), giving the bears a better opportunity to maintain their body condition.

Human encounters and dog hunts do not seem to have a profound lasting impact on bears, because there was no difference in distances traveled, maximum speeds, maximum heart rates, and body temperature areas between the control periods and the 2 days after the experiments. This may seem surprising as brown bears change their movement patterns for at least 2 days after human encounters (Ordiz et al., 2013b). Our study was based on hourly displacements and may underestimate the real movement pattern of the bears and thus the behavioral disturbance. The effects found in our study may also have been underestimated, because the bears could have been disturbed during the control periods, making the differences smaller between the experimental days and the control periods. All the human encounters in the project were conducted in the summer and many during the berry picking season, making it likely that the bears also encountered other humans during the control periods. Simulated hunts were not carried out during the bear hunting season, but a few simulated hunts were conducted during the moose hunting season. Dogs used for hunting moose (*Alces alces*) may also chase bears (Bischof et al., 2008).

Bears rested more the day after a simulated hunt compared with the control period and if the simulated hunt was longer. These results support the hypothesis that longer dog hunts may have a greater impact [H3], and that dog hunts may have a lasting behavioral effect on brown bears [H4]. The longer rest after simulated hunts suggests that bears may be fatigued by dog hunts. Longer dog hunts on deer (*Cervus elaphus*) increased the disturbance impact and were associated with a higher concentration in enzymes related to muscle breakdown (Bateson and Bradshaw, 1997). Deer that are shot after a long hunt present physiological signs of extreme exhaustion (Bateson and Bradshaw, 1997). Bears may suffer from similar physiological impacts, and may have to increase their rest to recover from it. Bateson and Bradshaw (1997) concluded that red deer were not well-adapted to fleeing dogs. Bears may be even less adapted to dog hunts than red deer as they are energetically less efficient when running compared to other quadrupedal mammals (Pagano et al., 2018). After prolonged exercise, extra energy consumption can be measured during the recovery time (Børsheim and Bahr, 2003). This may also represent an extra post-disturbance energy cost.

Brown bear hunting in Sweden has known impacts beyond the initial offtake of direct mortality, such as altering life history traits (Bischof et al., 2017; Frank et al., 2017) or inducing an increase in sexually-selected infanticide through an increased male turnover (Swenson et al., 1997). Furthermore, adult bears that would naturally face low mortality rates (Bischof and Zedrosser, 2009; Bischof et al., 2009, 2017) adopt antipredator behaviors in response to human hunting pressure (Ordiz et al., 2013a). For example, when the hunting season starts, bears decrease their foraging activity during the time of the day with the highest risk of being shot, forcing them to forage less efficiently and in areas with poorer berry quality (Hertel et al., 2016). This antipredator behavior, combined with the direct energy costs of human encounters and dog hunts may lead to a lower fitness if it prevents adult females from reaching the required body condition threshold for successful breeding.

CONCLUSION

Dog hunts represent a greater physiological and behavioral source of disturbance for female brown bears than human encounters. Adult female bears were behaviorally disturbed by human encounters but did not travel longer distances or have different heart rates and body temperatures. Simulated hunts had lasting behavioral effects on bears by inducing longer resting periods the day following the actual experiment. Longer resting periods found after longer simulated hunts suggested that the impact of dog hunts increases with their duration. By representing an energy cost, human encounters and dog hunts could lower the fitness of adult female bears if experienced frequently. Further research is needed to assess if bears that are repeatedly disturbed by dog hunts and human encounters are unable to compensate the disturbances' energy cost and if this affects their fitness. Nonetheless, if it is the case, this effect should be accounted for by managers. Human encounters have a lower impact than dog hunts on the bears but are not restricted in time like dog hunts. Thus, they may have a lower impact *per se* but may still have an important impact due to their higher frequency. Distance traveled, speeds, hearts rates, body temperature and resting behavior are universal variables that can be used on other animals to assess the impact of human activities. Looking at behavioral and physiological variables within the same study helps to have a better understanding of the disturbance.

ETHICS STATEMENT

All captures were approved by the Swedish Ethical Committee on Animal Research (application numbers C7/12 and C18/15) and the Swedish Environmental Protection Agency (application numbers NV-00741-18 and NV-01758-14).

AUTHOR CONTRIBUTIONS

LG, JA, and O-GS conceived the ideas and designed the methodology. AE, JA, and O-GS instrumented the bears and recovered devices in the field with input from TL. Pre-database, data-management and submission to WRAM (wireless remote animal monitoring, SLU) was conducted by BF. All authors contributed to the data analyses. LG led the writing of the manuscript. All authors reviewed the drafts and gave final approval for publication.

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Conflict of Interest Statement: TL is an employee of Medtronic, Inc. and all cardiac biologgers were donated by Medtronic.

The remaining authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

Paper II

Smartphone app helps reveal local, but not home range-scale avoidance of human recreationists by Eurasian lynx (*Lynx lynx*).

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Abstract

Outdoor recreation is increasing and affects habitat use and selection by wildlife. These effects are challenging to study, especially for elusive species with large spatial requirements, as it is hard to obtain reliable proxies of recreational intensity over extensive areas. Commonly used proxies, such as the density of, or distance to, hiking paths, ignore outdoor recreation occurring on other linear feature types. Here we utilized crowdsourced data from the Strava training app to obtain a large scale proxy for pedestrian outdoor recreation intensity in southeast Norway. We used the proxy and GPS-tracking data from collared Eurasian lynx (*Lynx lynx*) to investigate how recreation affects habitat selection at the home range-scale and local-scale by lynx during summer. We fitted resource selection functions at the two scales using conditional logistic regression. Our analysis revealed that lynx avoided areas of recreational activity at the local-scale, but not at home range-scale. Nonetheless, lynx frequently used areas associated with recreation, and to a greater degree at night than during the day. Our results suggest that local-scale avoidance of recreation and temporal adjustments of habitat use by lynx mitigate the need for a home range-scale response towards recreation. Scale-dependent responses and temporal adjustments in habitat use may facilitate coexistence between humans and large carnivores.

Introduction

Large carnivores living in human-dominated landscapes face widespread land-use changes, infrastructure, and the presence of humans. The ability of large carnivores to share the landscape with humans will be increasingly challenged, as the human population is growing [1]. Land-use changes and human infrastructure impact the behaviour, habitat use, and habitat selection of large carnivores [2]. Although less conspicuous, outdoor recreation constitutes another disturbance pressure on wildlife in the human-dominated landscape. Despite being more benign than, for example, hunting and habitat conversion, recreation also affects behaviour, habitat use, and habitat selection [3]. For some wildlife species the negative impact from recreation is even considered an important conservation issue [4]. Hence, understanding the effects of recreation on wildlife is crucial for mitigating its potential negative impacts at present and in the future.

The vast extent and intensity of outdoor recreation is illustrated by an estimate of 8 billion visits solely to protected areas per year globally and 4 billion visits per year in Europe alone [5]. Outdoor recreation is rising [6] and, in combination with increasing urbanisation [7,8], the patterns will likely change in the future, with growing levels of outdoor recreation especially around urban areas. These changes will have implications for wildlife. The effects of recreation on wildlife have received increased research attention throughout recent decades [9] and a wide range of effects of recreation on wildlife have been documented [3]. Generally, animals tend to respond to humans in the same way they respond to a predator [10]. The detection of a human is usually followed by a behavioural and/or physiological response [11,12]. These responses might in turn influence energy budgets, habitat use and fitness, hence, recreation can in the worst case influence population trends and the distribution of animals [3].

Habitat selection, i.e. the disproportional use of a habitat type relative to its availability, can be inferred at multiple scales based on how availability is defined[13]. In this article we refer to habitat selection inside the home range (c.f. 3rd order of habitat selection) as habitat selection at the home range-scale. Habitat selection over small scales which the animals are able to traverse in a short amount of time (e.g. hours) will be referred to as habitat selection at the local-scale (c.f. 4th order of habitat selection). Animals may respond to the same habitat feature differently based on the scale of habitat selection [14]. For instance animals may locally avoid linear features associated with recreation[15,16], or they may avoid large patches of habitat that contain many linear features or receive high levels of recreation at the home range-scale [17]. The scale at which animals respond to recreation is important for coexistence of humans and wildlife, as the ability to respond to recreation at the local scale [18] may mitigate disturbance effects at the home range-scale.

Large carnivores are now recovering in Europe from past persecution and returning to a human-dominated landscape [19]. Despite large carnivores being apex predators, humans influence their behaviour [20] and ecosystem function [21]. Numerous studies have shown behavioural and physiological responses in large carnivores when humans directly approach on foot (e.g. brown bears (*Ursus arctos*)[12,22], black bears (*Ursus americanus*) [23], wolf (*Canis lupus*) [24] and puma (*Puma concolor*) [25]), but less attention has been paid to how habitat selection and habitat use by large carnivores are affected by human recreational activity and not only the infrastructure associated with recreation. Recreation can reduce habitat quality [26] and spatial avoidance of suitable habitat due to recreation can be functionally equivalent to habitat loss [17,27]. Large scale segregation due to recreation has been documented for group-living herbivores in open landscapes [28] and indirect habitat loss reported for wolverines (*Gulo gulo*) in mountain areas [17]. However, it is unclear how large carnivores, with large space requirements, respond to outdoor recreation over different scales in forested habitats.

The paucity of studies on the effect of recreation on habitat selection by large carnivores so far is likely in part due to the lack of measures of human activity or recreation for the large areas in which these species live. Path density or distance to paths have been commonly used as proxies for human recreation [9,29]. These proxies ignore the fact that different path segments are associated with different levels of recreation and that other linear features than paths are also associated with recreation, such as forest roads and public roads. Estimating the level of recreation along linear features with, for example, human counters [30] or camera traps requires vast resources if it is to be done at a scale relevant for large carnivores. Today, ubiquitous smartphones and smartwatches with built-in GPS-loggers have opened up new possibilities to obtain proxies for human activity at large spatial scales [31]. Users of certain software applications (apps), like the training app Strava (www.strava.com), agree to share their spatial locations with the company. For apps with large userbases, such data can provide relative proxies for the spatial distribution of recreational activity [32,33]. Here we utilize data from the Strava app as a proxy for pedestrian outdoor activity (walking, running, or hiking) during summer in southeast Norway and investigate how habitat selection and habitat use by Eurasian lynx (*Lynx lynx*) are influenced by recreation.

The Scandinavian lynx population has recovered after being hunted to the edge of extirpation in the mid-20th century [34]. The population continues to be exposed to legal hunting, and human-caused sources of mortality (mainly hunting, some poaching and vehicle collisions) are high [35]. Hence, there should be potential for strong selection for avoidance of humans in this population. We studied the effect of summer recreation on habitat selection by lynx with resource selection functions (RSF[36]) at two spatial scales with different availability definitions; within the home range (hereafter referred to as home range-scale, cf. 3rd order of habitat selection[13]) and within a buffer of 1-2 km around locations used by the lynx (hereafter referred to as local-scale, cf. 4th order of habitat selection[13]). We also investigated if and how local-scale habitat selection was influenced by the time of day. Lastly, we explored how lynx use of areas associated with recreation changed throughout the day.

Methods

Study area

The study area (approximately 43 000 km^2) is located in southeast Norway (centroid coordinate: N 59.96982, E 9.693853), in Innlandet, Vestfold og Telemark, Oslo, and Viken counties (Figure 1). The study area includes the most heavily populated areas in Norway, and has an overall human population of 2 million inhabitants (www.ssb.no). In the southeast part of the study area, the landscape consists of forest fragmented with agricultural land and settlements, and a rolling topography. In the northwest, the topography is characterized by steep slopes, valley systems and some agricultural land along the valley floors. Most of the forests are heavily exploited by commercial forest industry and associated clearcut practices. The main tree species are Norway spruce (*Picea abies*), Scots pine (*Pinus sylvestris*) and birch (*Betula* sp.). Roe deer (*Capreolus capreolus*), free-ranging domestic sheep (*Ovis aries*), red deer (*Cervus elaphus*), and small prey species such as mountain hare (*Lepus timidus*), tetraonids and other birds comprise the diet of the lynx in the area [37,38].

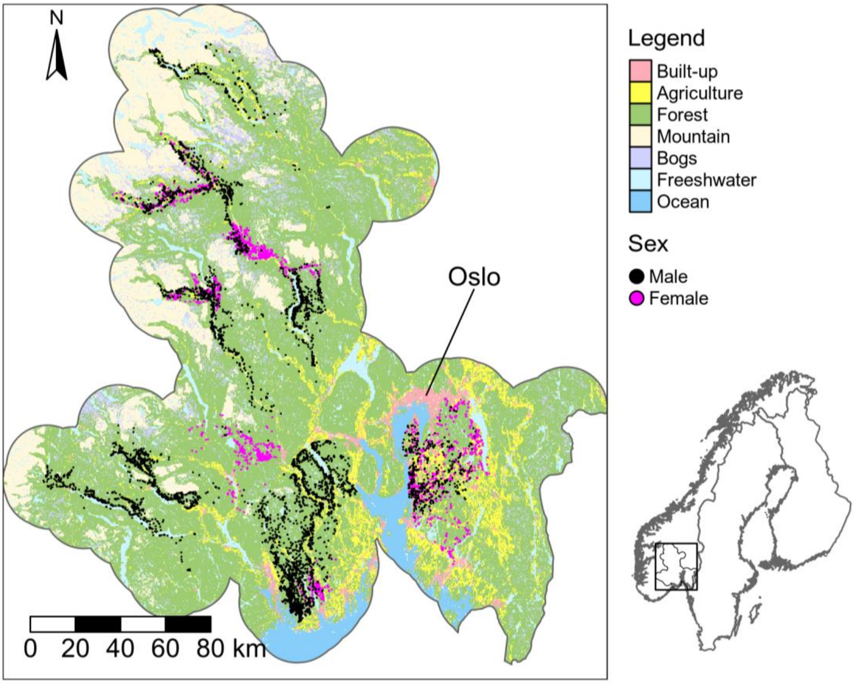

Figure 1. Study area (coloured region) and GPS-locations of lynx (dots). The study area was delineated by drawing an 18-km buffer around all original lynx GPS-location.

Animal capture and GPS-data

From 2008 to 2014, 25 lynx (11 females and 14 males) were captured in foot snares or wooden box traps and equipped with GPS-collars following a pre-established protocol [39]. All capture and handling procedures were approved by the Norwegian Experimental Animal Ethics Committee (permit numbers 2012/206992, 2010/161554, 2010/161563, 08/127430, 07/81885, 07/7883). This study was conducted in compliance with the ARRIVE guidelines, and all our methods were performed in accordance with relevant guidelines and regulations. In this study, we only analysed data from adult lynx in years where they were settled in a home range. GPS-collars were programmed to take between 1-19 GPS-locations per day. Fix schedules varied across individuals and alternated between intensive predation study periods and less intensive monitoring periods [38]. As the aim of this study was to explore how recreation affects habitat selection by lynx during the snow-free period, we included observations from 1st May to 31st October for all the years. To increase the robustness of the analyses, we only included combinations of lynx individuals and years (lynx-years) with 200 or more GPS-locations. This resulted in a final dataset of 13 611 GPS-locations for 22 lynx-years (10 females and 12 males) from 20 individual lynx (8 females and 12 males).

Recreation

We used two different proxies for recreation, crowdsourced human mobility data from Strava and hiking path density. We used the latter, traditional method to facilitate comparison with the Strava data. Strava is an app for smartphones and smartwatches, used primarily to record and upload georeferenced human training activities (hereafter referred to as "activity event"). Activity events can also be uploaded directly to the Strava webpage. Strava stores this data and processed version of it can be purchased from Strava Metro. To maintain anonymity and conform with privacy regulations, access is limited to data processed by Strava through removal of personal identifiers and spatial and/temporal aggregation (see Figure 2). The processing involves linking individual activity events to nearby linear features (paths, roads etc) in OpenStreetMap (OSM, www.openstreetmap.org). Hence, in the absence of OSM linear features close to an activity event (or parts of it), that event (or parts of it) is not included in the aggregated version of the dataset (see Figure 2). Further, to conform with privacy legislations, linear features with less than three unique users are removed and the number of activity events are rounded up to the nearest multiple of five. We used yearly Strava data, i.e., data where the timespan for at least three unique users was a year, to maximise the spatial coverage. We included Strava data from 2016 to 2019 and summed this over all years to result in a single static covariate. We only used Strava activities left by pedestrians (walking, running, hiking etc.). A more detailed description of how we processed the Strava data can be found in Supplementary material S1.

We obtained data on hiking paths from the OSM (key=highway and value=track and path) using the *osmdata* package [40] in R (version 4.0.3[41]). To derive our proxies for recreation, we divided our study area into a grid of 50 x 50 m (a compromise of computational time and high resolution). For hiking paths, we calculated the line lengths of hiking paths inside each grid cell. For the Strava data, we summed up all the pedestrian activity happening inside each grid cell. We refer to this covariate as the Strava index. The value of this index in a given grid cell can be viewed as the total number of activity events taking place on all linear features within that grid cell during the entire period when the Strava data were collected. The Strava index accounts for different levels of human activity associated with all types of linear features (not only hiking paths) inside a grid cell, while the hiking path density is only a measure of the length of the hiking path inside a grid cell and does not account for the level of associated human activity.

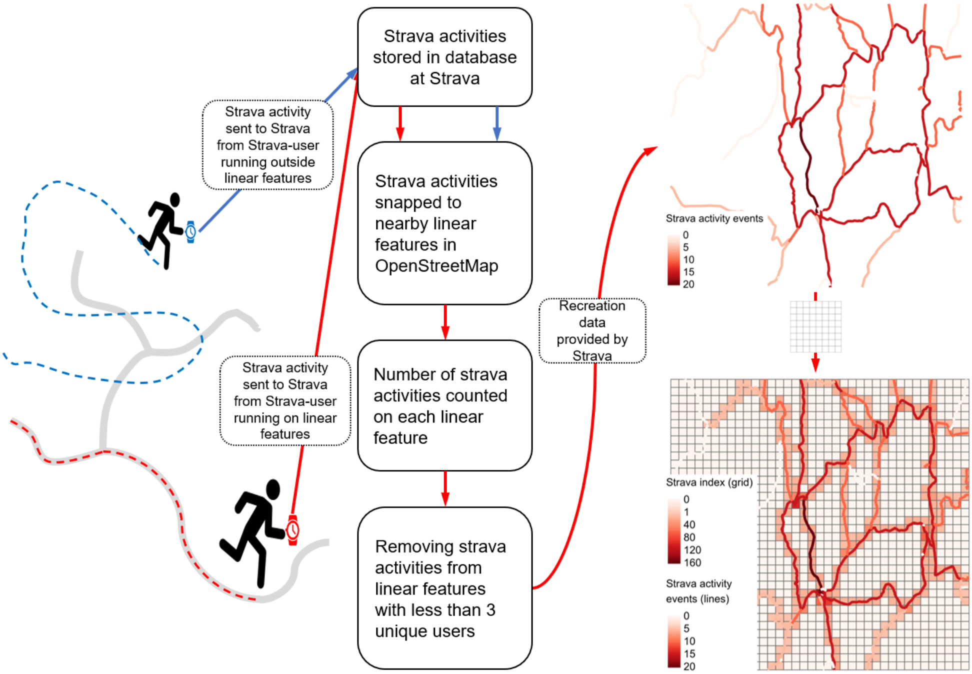

Figure 2. Schematic presentation of the recreation data provided by Strava. The grey linear features to the left represent the linear features in the OpenStreetMap (OSM). The dotted lines represent the track left by two Strava-users, where the blue is from a user running outside linear features and the red is from a user running on linear features. The activity event from the blue user is not possible to snap to linear features in OSM and is removed during the processing. The map to the top right represents a network of linear features and associated Strava activity events. The legend shows how many activity are associated with the different paths (note that they are rounded to nearest multiple of 5). The map in the bottom right represents the same network after the number of Strava activity events for every linear feature in each grid cell have been counted.

Resource selection functions at two scales

We used resource selection functions (RSF[36]) to estimate habitat selection by lynx. RSF depends upon a use-available design, where locations used by GPS-collared lynx are compared to locations not used but considered as available ("null model"). For each used GPS-location, we randomly sampled 30 available locations (excluding open water). We had two different availability definitions (Figure 3). For the home range-scale habitat selection we sampled available locations inside the home range. Home ranges were estimated with the Brownian bridge kernel method [42] with the *kernelbb* function in the *adehabitathr* package [43] in R. We used the 95 % isopleths. For the local-scale we sampled available locations inside a buffer with the mean step lengths (distance between two consecutive GPS-locations) of the individual as radius from the used GPS-location (Table S1). We then fitted conditional logistic regression to obtain the RSFs by using the *coxph* function in the *survival* package [44] in R. The response was whether a location was used (1) or available (0). Conditional logistic regression relies on a matched design, where groups of observations are matched with given grouping IDs. For the home range-scale we matched used and available locations by including the lynx-year ID as strata (not to be confused with the Strava index) and for the local-scale we used an unique identifier for the buffer as the strata. This ensured that used locations in a home range were only compared to available locations sampled from the same home range, and also that the used location in a buffer was only compared to the available locations in the same buffer. Furthermore, we included the lynx-year ID as a cluster variable in the models to obtain robust standard error estimates for the coefficients [45,46]. We interpreted robust confidence intervals overlapping 0 as a lack of evidence for either avoidance or selection.

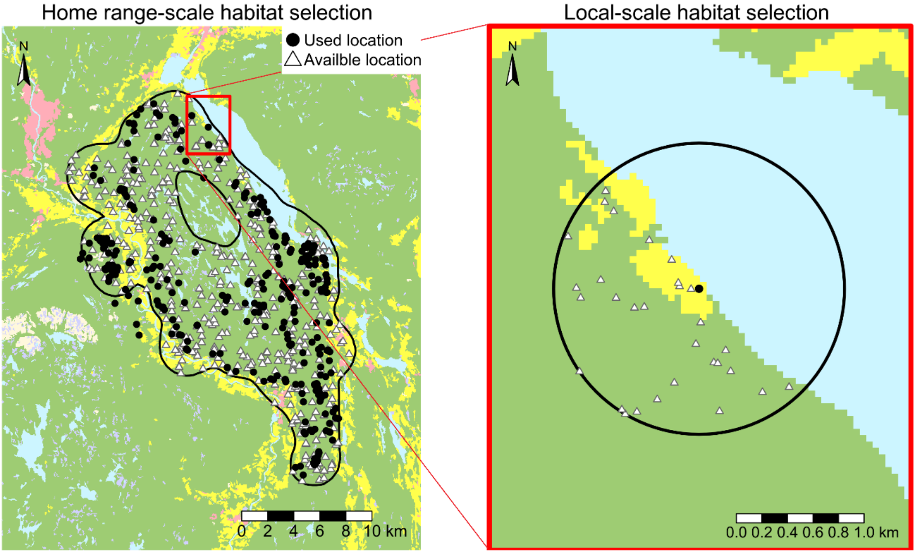

Figure 3. Illustration of the different scales and availability definitions. For the home range-scale analysis (left map) we sampled 30 available locations per used location inside the home range of the lynx (for illustration purposes we used a ratio of 1:1 in the left map). While for the local-scale analysis (right map) we sampled 30 available locations inside a buffer with the radius equal to the mean step length (distance between two consecutive locations) of the lynx (for illustration purposes we removed two buffers and their corresponding points in the right map).

Covariates

Based on findings previously reported for lynx [29,47-49], we considered the following covariates: slope, agricultural land (hereafter referred to as fields), forest, forest roads, public roads, and houses. In addition, we also considered the Strava index and hiking path density as proxies for recreation. Spatial data on fields and forest were obtained from an open access land cover map (AR50[50], 1:50 000); and vector data on public roads, forest roads and houses from the Norwegian Mapping Authority (www.geonorge.no). We defined a house as a building used for or approved as a residential building for the entire year. This excludes summer houses and recreational cabins, which is associated with a variable degree of human activity. Slope was calculated with the *terrain* function (based on the 8 nearest neighbouring raster cells) in the *raster* package in R [51], based on a digital elevation model with 50 m resolution from the Norwegian Mapping Authority (www.geonorge.no). All covariates were rasterized to a 50 x 50 m resolution (see Table S2 for simple summary of the covariates).

We prepared the covariates differently for the home range- and local-scale (see Table S2), to account for the different definitions of available habitat. For the home range-scale analysis we calculated the density of houses, forest roads and public roads, the proportion of forest, and the proportion of fields in a buffer of 1 km radius around each cell (50 x 50 m). For hiking path density we calculated the sum of all cells in a buffer of 1 km radius around the focal cell, while for the Strava index and slope we used the mean. We denote the hiking path density, Strava index, and slope with the subscript 1000 (e.g., Strava index_{1000}) to separate them from the covariates with similar names used for the local-scale. For the local-scale analysis we used distance to house, distance to forest road, distance to public road and distance to field, instead of density or proportion metrics. We included forest as a binary variable (1=forest and 0=not forest). For the Strava index and hiking path density we calculated the mean (Strava index) or sum (hiking path) of the covariate in the four closest neighbouring cells and the focal cell. This ensured that the hiking path density and Strava index extended at least 50 m outside the linear feature they were associated with. For slope on the local-scale we used the original calculation as previously described. We denote the Strava index, hiking path density and slope used for the local-scale analysis with the subscript 50 (e.g., Strava index_{50}) to separate them from the covariates used in the home range-scale analysis. In addition, we also considered day vs. night as a covariate in models at the local-scale. Night was defined as the time between sunset and sunrise, obtained by the sunriset function in maptools [52]. We standardized all the continuous covariates by subtracting the mean and dividing by the standard deviation of all used and available locations prior to fitting the models. The distance "to feature" covariates were log-transformed, to make the effect of the covariate decrease with the distance from the feature (we added 1 m to all distances prior to log-transformation).

Candidate models and model selection

We considered four different candidate models for the home range-scale and eight different models for the local-scale analysis (see Table 1). The simplest model ("core model") contained parameters that have previously been shown to be important for habitat selection by lynx. For both scales, we tested whether including recreation covariates improved our core model by adding the density of hiking paths ("path model"), the Strava index ("Strava model") or both the density of hiking paths and the Strava index ("full model"). In the core model for the home range-scale we included the quadratic term of the proportion of forest as the results of Bouyer, et al. [49] suggested selection for an optimum less than 100 % forest cover. In addition, we tested if local-scale habitat selection was influenced by time of day by including an interaction with night (true/false) for slope and forest as Filla, et al. [29] showed that lynx select gentler slopes and spend more time in open habitats during the night. Given the diurnal activity of humans, we also included an interaction with night for the following human related covariates: distance to public and forest roads, density of hiking paths, and the Strava index. We did not include a main effect of night in the model as this variable was constant for any given stratum (single used location and associated sample of available locations) and could therefore not be meaningfully evaluated. We used Akaike's Information Criterion (AIC[53]) to rank models with the strongest support, and based inferences on models within 2 delta AIC of the top ranked model [54]. We interpreted that including recreational activity improved our models when either the full-, Strava-, or path model ranked highest or ≤ 2 delta AIC off the top-ranked model. We conducted sensitivity analysis [55] and based on this analysis the choice of 30 available locations per used appeared satisfactory (see Figure S3-S4).

Table 1. Candidate models for home range-scale and local-scale habitat selection. Refer to table S2 and S3 to see how the covariates were prepared for the different scales. The night interaction was only considered at the local-scale.

Model	Model specification home range-scale	Model specification local-scale
Core	Slope$_{1000}$ + forest cover + (forest cover)^2 + field cover + forest road density + public road density + house density	Slope$_{50}$ + forest (dummy variable) + distance to fields + distance to house + distance to forest road + distance to public road
Path	Core + hiking path density$_{1000}$	Core + hiking path density$_{50}$
Strava	Core + Strava index$_{1000}$	Core + Strava index$_{50}$
Full	Core + hiking path density$_{1000}$ + Strava index$_{1000}$	Core + hiking path density$_{50}$ + Strava index$_{50}$
Core_ night		Distance to fields + distance to house + slope$_{50}$: night + forest : night + distance to forest road : night + distance to public roads : night
Path_night		Core_night + hiking path density$_{50}$: night
Strava_night		Core_night + Strava index$_{50}$: night
Full_night		Core_night + hiking path density$_{50}$: night Strava index$_{50}$: night

Time dependent habitat use of areas associated with Strava use

In addition to habitat selection, we explored how the habitat use of areas associated with the Strava index$_{50}$ changed throughout the day. This was done by fitting a generalized additive mixed model (GAMM[56]) to only the GPS locations used by the lynx. As response, we used the GPS-locations of the lynx and coded them as 1 if the location had Strava activity (Strava index$_{50} > 0$) and 0 if not. We used a binomial distribution with a logit link to model the response. The predictors included hour of the day with a cyclic spline as a smoothing term and lynx ID as a random intercept. We used the *gamm* function in *mgcv* package [57] in R to fit the model. The time of day was corrected for differences in day length using two anchors (one at sunrise and one at sunset) and the average method [58] in the *activity* package [59] in R.

Results

Mean human density within lynx home ranges was 26 km^{-2} (range: 4.8-166 km^{-2}). On average, 12 % (range: 0.8 – 31 %) of the used GPS-locations per lynx, and 16 % (range: 5.7 – 37 %) of lynx home range areas, were located in grid cells with Strava index$_{50} > 0$. Corresponding values for Strava index$_{1000} > 0$ were 82 % (range: 40 – 99.5 %) of the used GPS-locations per lynx and 79 % (46 – 98 %) of their home range area.

Of the Strava activity events inside the lynx home ranges, 58 % were located in forest, 24 % occurred in built-up areas (urban, sub-urban, small towns etc.), 11 % on fields, and 5 %

in alpine areas (open areas above the forest). Inside the lynx home ranges, roads were the linear features that had the highest levels of activity events, with hiking paths receiving fewer activity events (Figure S2).

Home range-scale habitat selection

The four candidate models differed only moderately from each other in terms of AIC (Table S4). The model including hiking paths ranked highest, but the full model was within 2 ΔAIC. We therefore present the results from the full model. In addition, the direction of effects (when included) was similar in both models.

We did not detect evidence that hiking path$_{1000}$ or Strava index$_{1000}$ significantly influenced habitat selection at the home range-scale (Figure 4, P value 0.502 and 0.483, respectively). Lynx selection increased with steeper slope (slope$_{1000}$, P value $< 2*10^{-16}$), higher proportion of fields (P value $2.56*10^{-4}$), higher forest road density (P value $3.74*10^{-4}$), lower house density (P value $3.96*10^{-4}$) and they selected forest cover with an optimum around 77 % forest (see Figure 6A, P value 0.458 and $4.86*10^{-6}$ for first and second order term, respectively). We did not find evidence that public road density significantly influenced habitat selection by lynx at the home range-scale (P value 0.153).

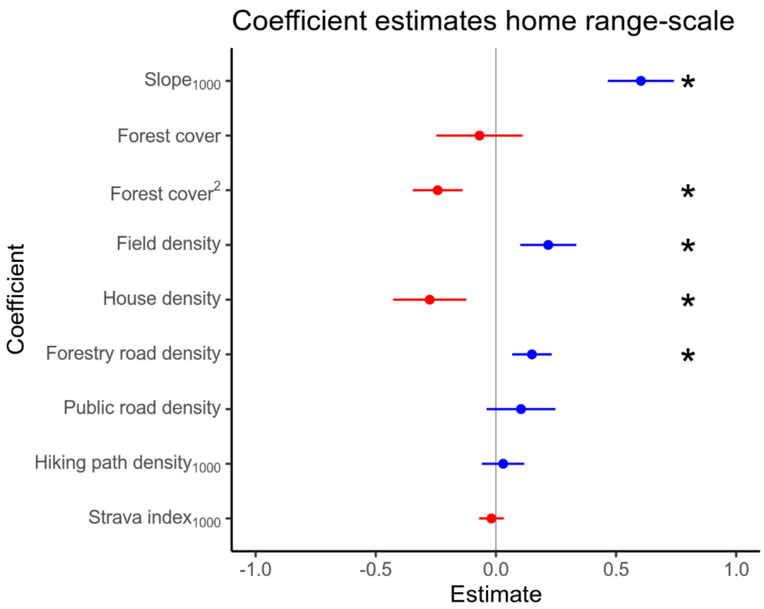

Figure 4. Selection coefficients for home range-scale habitat selection. Point estimates and 95 % confidence intervals based on the robust standard errors for the home range-scale RSF models. Red colours indicate negative value of the estimate (i.e. avoidance) and blue colours indicate positive values of the estimate (i.e. selection). Stars indicate significant estimates at the alpha level of 0.05.

Local-scale habitat selection

The full model including interaction with time of day emerged as the top model for local-scale habitat selection (Table S4) and was clearly the most supported model. Models including "night" and/or the Strava index performed better than those without. Lynx avoidance increased with higher Strava index$_{50}$ during both day (P value $9.51*10^{-4}$) and night (P value 0.017, Figure 5). The effect of hiking path density$_{50}$ was not significant (P value 0.079 and 0.920 for day and night, respectively), regardless of the time of day, although there was a trend towards avoidance during the day.

Lynx selection decreased with distance to fields (Figure 6B, P value 0.001). We did not detect an effect of distance to house on local-scale habitat selection (P value 0.063). Lynx selection increased with steeper slope (P value day $< 2*10^{-16}$ and night $< 2*10^{-16}$) and in forest (P value day: $1.63*10^{-6}$ and night: $3.61*10^{-4}$), but this effect was weaker during the night. During the day, lynx selection increased with distance from public roads (avoidance, P value $3.95*10^{-4}$) but showed no response to forest roads (P value 0.195), whereas at night, lynx selection decreased with distance to forest roads (selection for, P value $1.17*10^{-4}$) but showed no response to public roads (P value 0.318).

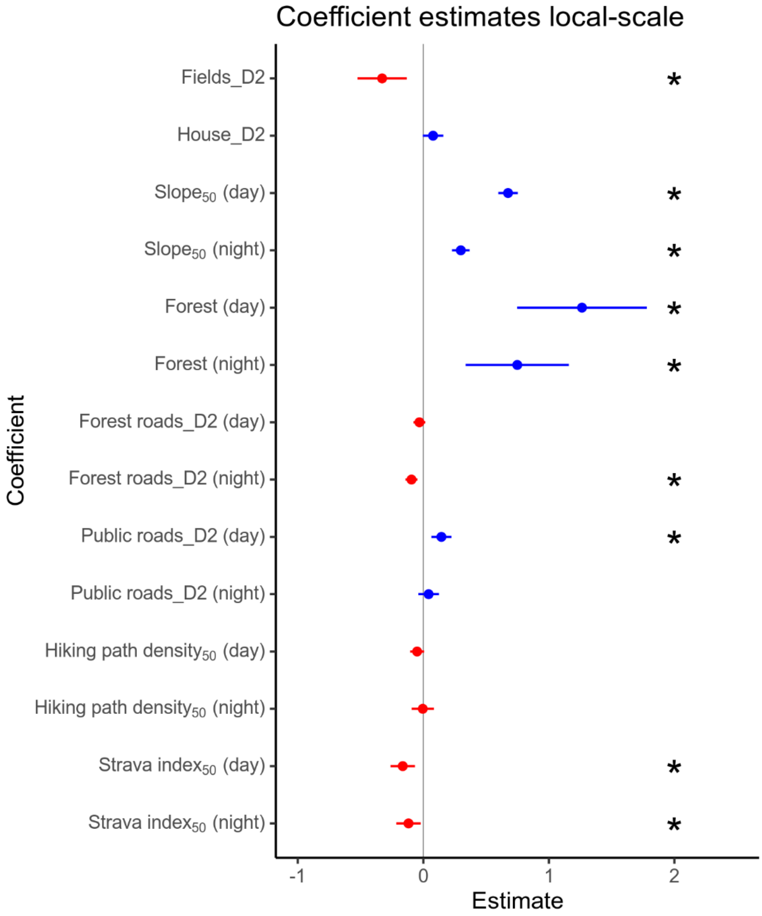

Figure 5. Selection coefficients for local-scale habitat selection. The point estimates and 95 % confidence intervals based on the robust standard errors for the local-scale RSF models. Red colours indicate negative value of the estimate and blue colours indicate positive values of the estimate. D2 is an abbreviation for "distance to", all "distance to" features have been log-transformed to make the effect decrease with large distances. Note that a positive estimate for distance to feature indicates avoidance (selecting for areas farther away for the feature). Stars indicate significant estimates at the alpha level of 0.05.

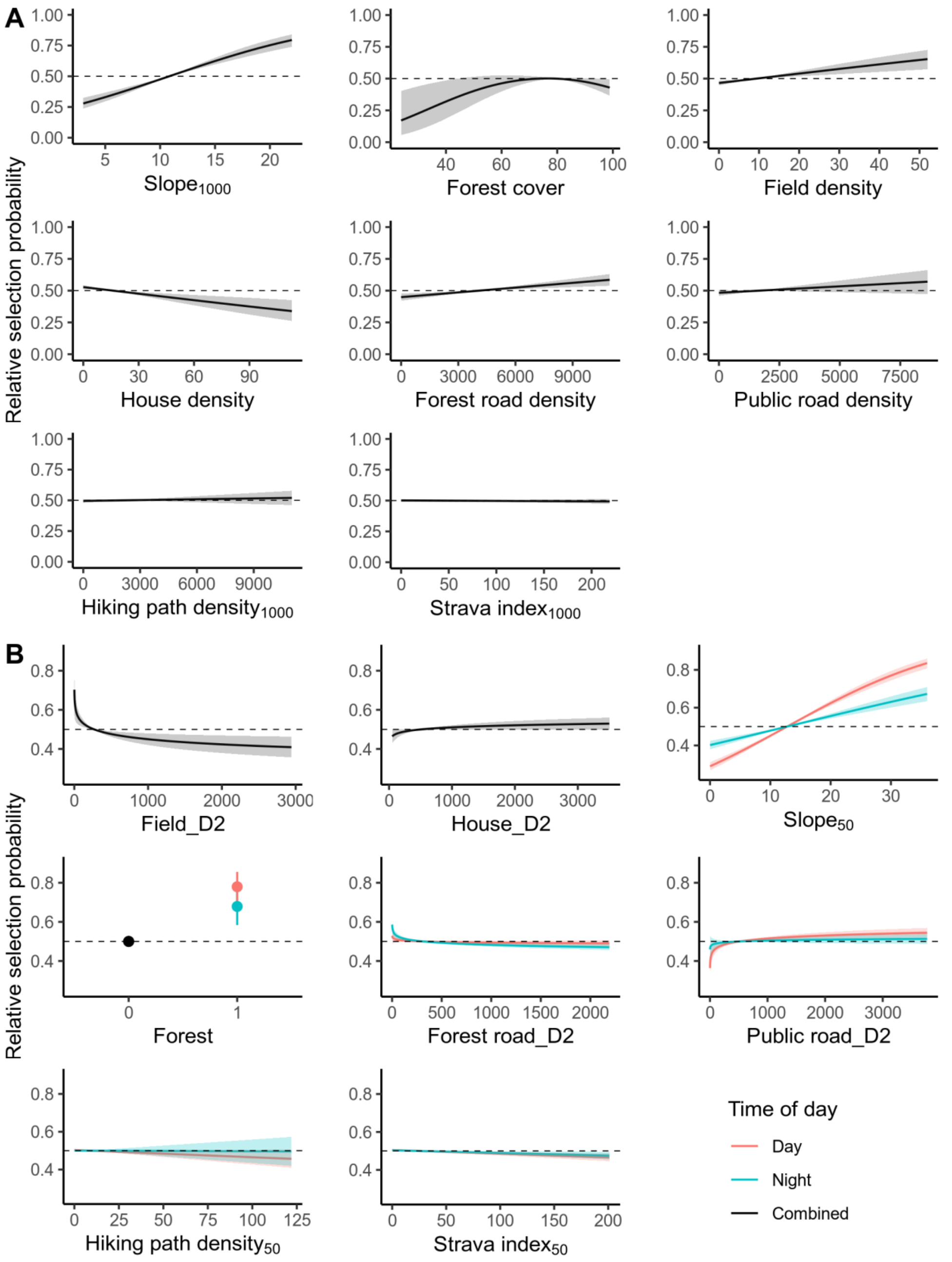

Figure 6. Predicted relative selection probability for each covariate for the home range-scale (A) and local-scale (B) habitat selection. The range of covariates is their 2.5 and 97.5 % percentiles. Probabilities over the dashed horizontal line indicate selection and probabilities below indicate avoidance, relative to the "reference cell". The reference cell, which all probabilities are relative to, is a cell where all the covariates are at their mean (due to the standardization prior to model fitting), and is not the same for home range-scale and local-scale habitat selection.

Time dependent habitat use of areas associated with the Strava index$_{50}$

Despite lynx selection decreasing with the Strava index$_{50}$ at the local-scale both during day and night, lynx still used areas with a Strava index$_{50}$ > 0. The GAMM revealed a time-dependent use of these areas (Figure 7). The proportion of lynx locations having a Strava index$_{50}$ higher than 0 was lowest during the day, from around 08:00 to 16:00 when predicted proportion was in the range of 0.06 to 0.07. From 16:00 to 00:00 the proportion increased and reached a peak of 0.14 around 01:00, after the peak the proportion declined until 08:00.

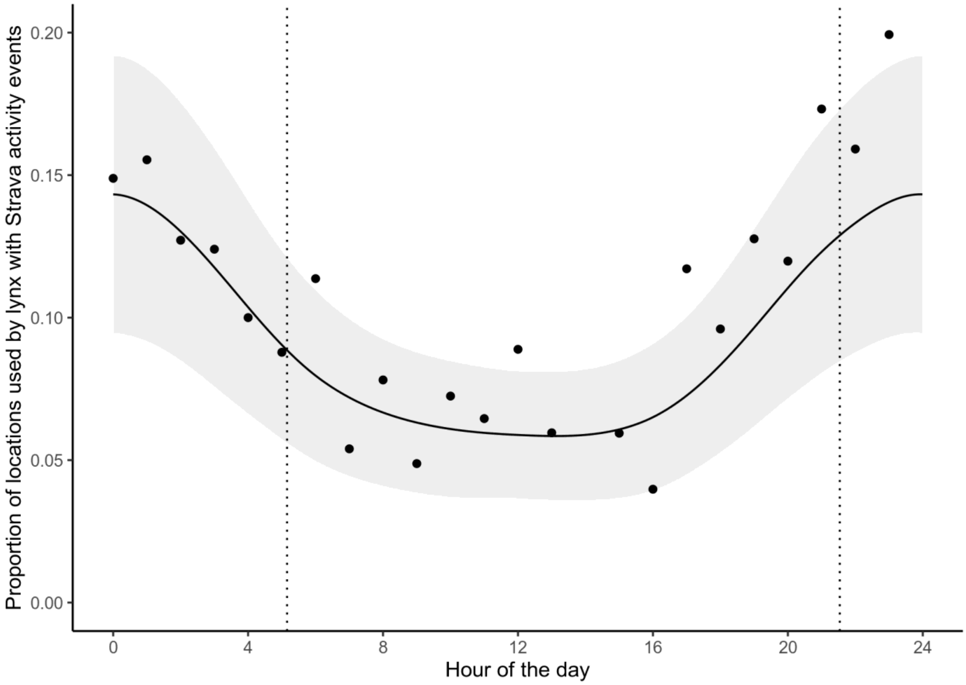

Figure 7. Prediction (black line) from the generalized additive mixed model (GAMM) with GPS-locations as a response, coded 1 if they were located in a grid cell with Strava index$_{50}$>0 and 0 if not. The y-axis shows the proportion of locations used by lynx that were associated with recreation. Hour of the day was included as a explanatory variable and lynxID as a random effect on the intercept. The shaded area represent the 95 % confidence interval around the prediction. Black dots indicate the proportion of GPS-locations in grid cells with Strava index$_{50}$>0 during a given hour; only hours with more than 100 GPS-locations are shown. All times have been corrected for differences in day lengths with two anchors (sunrise and sunset). Sunrise and sunset are shown as vertical dotted lines.

Discussion

Our study revealed that lynx exhibit local-scale avoidance of areas with high levels of recreation in summer. Interestingly, while this effect was pronounced at the local-scale habitat selection, we did not detect any effect of recreation on home range-scale habitat selection. These results suggest that lynx are capable of adjusting their habitat selection and temporally adjusting their habitat use to recreation in a way that allows them to occupy human-dominated landscapes. This study also illustrates the added value presented by crowdsourced human mobility data as a reliable proxy for human activity in ecological studies, and the importance of accounting for the level of recreation associated with linear features of all types.

Accounting for the intensity of recreational use is important when studying the impact of recreation on wildlife, as the level of recreation can affect the animals' responses [15]. The high level of recreational activity observed on other linear features than hiking paths suggests that using hiking paths as proxies for summer recreation fails to cover the entire spectrum of recreation. The inclusion of the crowdsourced human mobility data in our study revealed new details about the habitat selection and habitat use of lynx, similar to a recent study on brown bears (*Ursus arctos*) in Italy [32]. Lynx appeared to be relatively tolerant towards recreation, as we detected comparatively high use of the areas associated with the Strava $index_{50}$ (11 % of the used locations had values higher than 0). Due to the lack of avoidance at the home range-scale, lynx do not seem reluctant to occupy the same areas that humans use for recreation, but they do avoid the immediate surroundings of linear features associated with high levels of recreation (local-scale avoidance).

Previous studies have investigated the effect of recreation on home range-scale habitat selection and habitat use of large carnivores. These studies have reported selection for areas with nonmotorized winter recreation by Canada lynx (*Lynx canadensis*) [60,61], avoidance of areas with higher intensity of winter recreation (both motorized and non-motorized) by wolverines [17], avoidance of areas with higher recreational intensity by brown bears [32] and daybed selection for areas assumed to receive less recreational activity by lynx [62]. In this study, we did not detect any spatial avoidance of hiking path density nor Strava $index_{1000}$ (in a 1 km buffer) by lynx at the home range-scale habitat selection. Lynx have been reported to have relatively short flight initiation distances in forests, with a median distance at 50 m [63]. Hence, a substantial reduction in the need to initiate a flight response is likely achieved by local-scale avoidance of areas with high recreation levels at local-scale habitat selection. This local-scale avoidance might mitigate the need to exhibit larger scale avoidance; instead of avoiding a large forest area associated with high levels of recreation, lynx can still use it and can reduce the risk of encountering humans by local-scale avoidance of recreationists and temporal adjustments of habitat use.

During the day, local-scale avoidance of recreation likely reflects a selection of resting sites away from areas with high recreational use, which has also been reported for lynx in southern-Europe [62]. We found that lynx avoidance of areas with higher Strava index_{50} persisted throughout the night, at times when lynx are most active [64] and humans are not. A lack of temporal adjustment in habitat selection towards areas associated with recreation (non-motorized and motorized recreation during winter) has also been reported for Canada lynx [60]. However, our results show that lynx, despite locally avoiding areas associated with higher levels of recreation, used areas associated with recreation quite often. Especially at night, when habitat use of Strava index_{50} was twice as high during the day, showing some temporal adaptations towards recreation. Higher habitat use of areas associated with the Strava index_{50} could be explained by cost-effective transportation, as linear features have been shown to facilitate movement for other carnivores [14,65].

Lynx in our study area occupy a human-dominated landscape and are thus capable of adjusting to human infrastructure [66] and, as our results suggest, also recreation. The level of recreation in our study area might not be high enough to force lynx to adjust their habitat selection at larger scales. Nonetheless, our study area contains one of the most heavily used recreational areas in the immediate proximity of the capital of Norway (Oslo), and lynx still used this area. Additionally, the Scandinavian lynx population has been, and still is, subject to strong selection pressure to avoid humans due to hunting and poaching [34,35]. In this context, a lack of avoidance at the home range-scale habitat selection suggests that an area needs to receive substantially high levels of recreation before lynx start to avoid it at large scale, and that the other spatial and behavioural adaptations are sufficient. Our study area is forested, with abundant hiding cover and widespread access to rugged terrain and/or boulders. Dense horizontal cover has been shown to reduce the flight initiation distance for lynx [63] and other large carnivores [11]. Hence, the effect of recreation might be less pronounced in forested landscapes with access to cover.

Strava data have proven useful in previous studies, and high correlations with ground truth data have been reported from cities in Norway [67], the UK [68], the USA [69] and Australia [70] as well as in rural areas in Austria [33] and in Italy [32]. As our Strava index is an index of pedestrian recreation and the app is not used by everyone engaging in recreational activities in a defined area, true recreational activity is bound to be higher. For example, Venter, et al. [67] found the ratio between the Strava data and human counters to range between 1:30 and 1:40 in Oslo, Norway, meaning that for each person using the Strava app there are an additional 30 to 40 people on the same track or road during the same time period. However, as long as Strava users are not using different areas than non-Strava users, this proxy for human activity should reliably represent relative recreational activity in our study area. We believe spatially crowdsourced data on human mobility or activity can open a range of new possibilities for wildlife research and inform management in the future. In cases like ours, with a study area of approximately 43 000 km^2, crowdsourced data is currently the most feasible, and maybe the only, option for deriving a proxy for human activity across the whole area.

Conclusions

This study gives an example of the added-value from the application of crowdsourced human mobility data for ecological studies. Our results suggest that lynx reduce their direct interaction with pedestrian recreationists through local-scale avoidance and temporal adjustments in habitat use. The consequences of recreation for lynx in Norway are therefore likely minor as the impact of recreation appears to be spatially restricted to the immediate surroundings of linear features in which the recreation occurs. We believe the levels of recreation in our study area are not high enough to impede lynx from sharing the landscape with humans. Instead, spatial avoidance at local-scales and temporal adjustments in habitat use may facilitate coexistence between humans and large carnivores.

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Supplementary material

Supplementary material S1 – Description of strava data

When the Strava app is in use (e.g., during a running or cycling trip) it records the user's GPS-tracks during their activity (hereafter referred to as an activity event) and provides the user with activity results such as distance, speed, and a route summary for the given activity event. Activity events can also be uploaded to Strava`s webpage after the activity have been recorded by for instance a smartwatch. An activity type (e.g., pedestrian or cyclist) is assigned to each activity event. Every activity event is stored by Strava and aggregated forms of the data can be purchased from Strava Metro. To maintain anonymity and conform with privacy regulations, access is limited to data processed by Strava after removal of personal identifiers and aggregating the data. The processing includes linking individual activity events to nearby linear features (paths, roads etc) in OpenStreetMap (OSM, www.openstreetmap.org). Hence, in the absence of OSM linear features close to the entire activity event (or parts of it), the activity event (or parts of it) is not included in the aggregated version of the dataset (see Figure 2). A linear feature is defined by lines, or a set of lines, connecting two intersections (where two or more linear features intersect), or the start- or endpoint of a line (e.g., the start of path from a parking place to the first path intersection). For each linear feature the number of activity events and the number of unique users for the given activity type are grouped by activity type and counted. For illustration, if five unique users walk or run on the same linear feature five times during a year this will be counted as 25 activity events and 5 users for that linear feature. The timespan for which the number of activity events and number of unique Strava users are counted range from hourly to yearly. Furthermore, to protect user privacy, only linear features with more than 3 unique users are reported and all counts are rounded up to the nearest multiple of 5.

We chose to use Strava data on a yearly temporal scale in our analyses to avoid losing too much of the spatial resolution, i.e., to maximise the spatial cover of the Strava data (the time period to record at least 3 unique users). Furthermore, we decided to use the total number of pedestrian activity events, which excludes biking and the main winter activity of cross-country skiing. We also explored in which land cover classes and what kind of linear features the Strava activities were located (see Figure S2).We used yearly Strava data from 2016 to 2019 and assumed that the spatial patterns of recreation had not changed during the time the lynx had operational collars (2008-2014) and the time the Strava data was collected. In 2020, 9.5 million activity events labelled as pedestrians (running, hiking, or walking) were collected by close to 280 000 unique users in Norway (approximately 5 % of the Norwegian population). The userbase of Strava in Norway has increased since the service commenced. To determine whether patterns of activity events had changed drastically across years we inspected the correlations between the years. The correlation was high (0.97-0.99) for all the combinations of years (see Figure S1), suggesting no conspicuous change in spatial patterns in activity over years.

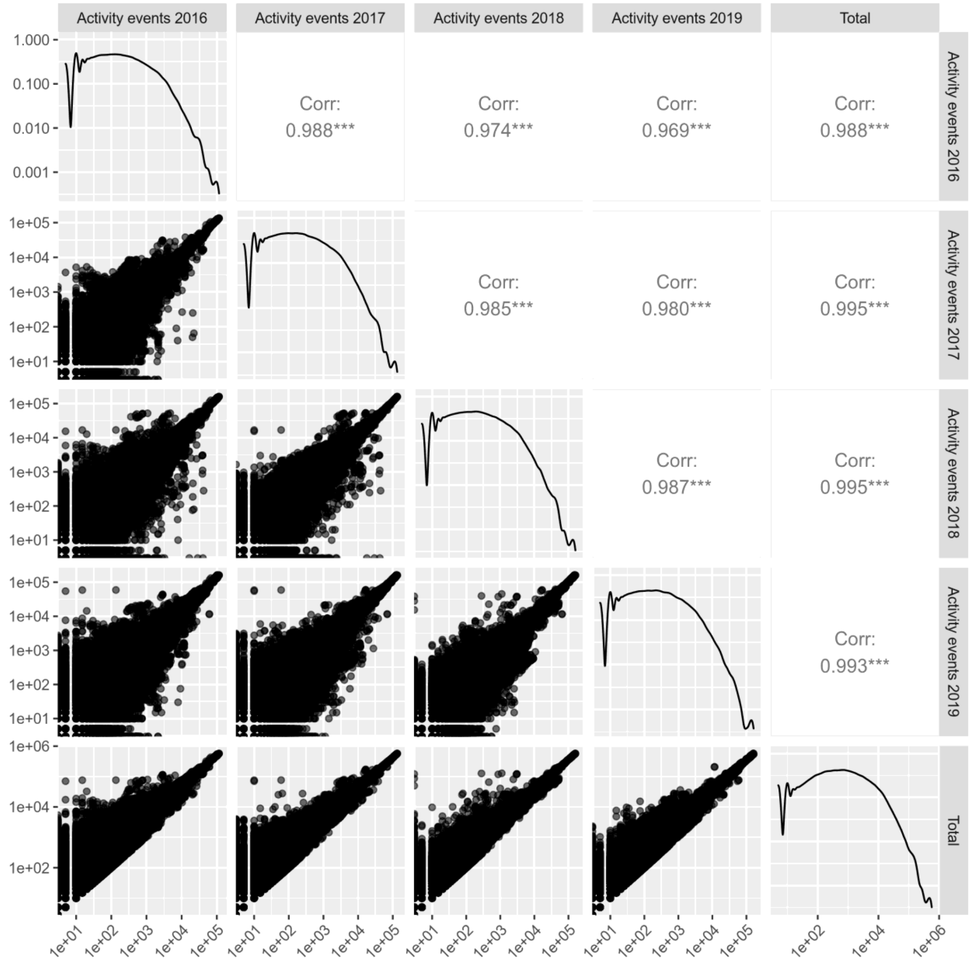

Figure S1. Correlation between the number of Strava activity events on linear features in the OpenStreetMap between years. The diagonal panels (from left top to right bottom) are the density distribution for each year and all years combined ("Total"). Values in the panels above the diagonal indicate the correlation between the different combinations of years. In the panels below the diagonal each dot represents a linear feature in the OpenStreetMap. The x-axis in all plots shows the number of activity events. The y-axis for the density distributions show the probability density function, while the y-axis for the panels below the diagonal show the number of activity events. For all panels both axes are given on a log10 scale.

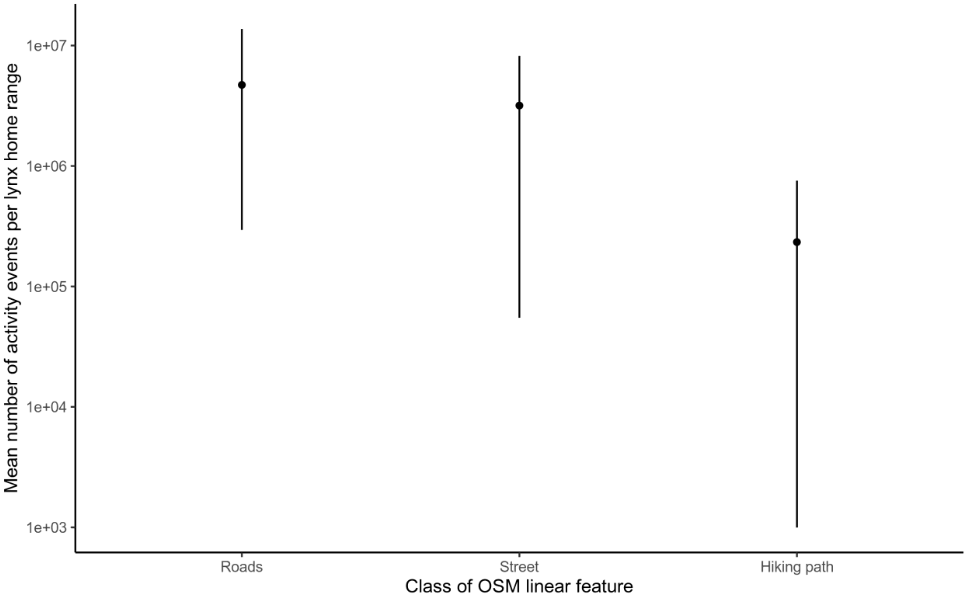

Figure S2. Mean number of pedestrian activity events inside the lynx home ranges associated with three different classes of linear features in OpenStreetMap (OSM). The black dot is the mean for all home ranges and the lines represent the 10 % and 90 % percentiles. The OSM classes were derived according to the list below. The class "roads" represent all types of roads where cars are able to drive, "hiking path" represent paths and trails that are typically used during hiking (mainly outside urban areas), and "street" represents linear features that are built for pedestrian or cycling activity in urban settings (e.g. sidewalks). The y-axis is shown on log10-scale.

Roads contains the following OSM values: Highway.motorway, Highway.motorway_link, Highway.trunk, Highway.trunk_link, Highway.primary, Highway.primary_link, Highway.secondary, Highway.secondary_link, Highway.tertiary, Highway.residential, Highway.unclassified and Highway.service.

Street contains the following OSM values: Highway.pedestrian, Highway.living_street, Highway.cycleway, Highway.footway and Highway.steps

Hiking path contains the following OSM values: Highway.track and Highway.path.

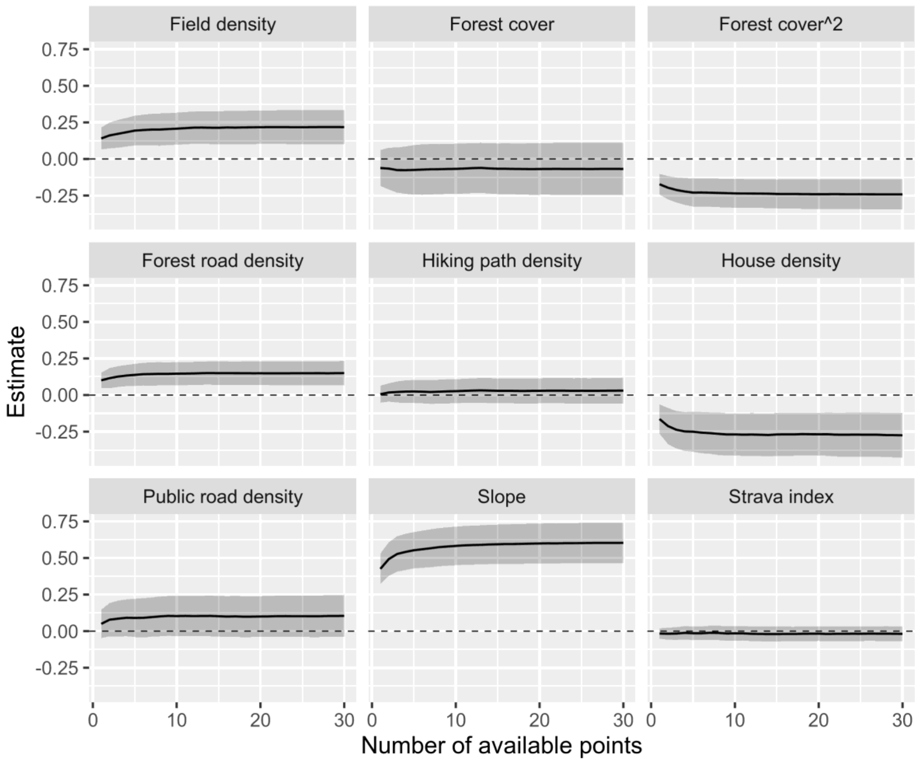

Figure S3. Sensitivity analysis for habitat selection at the home range scale. We fitted the model with 1 to 30 available locations. The shaded area is the 95 % confidence interval for the coefficient estimate for the given number of available locations.

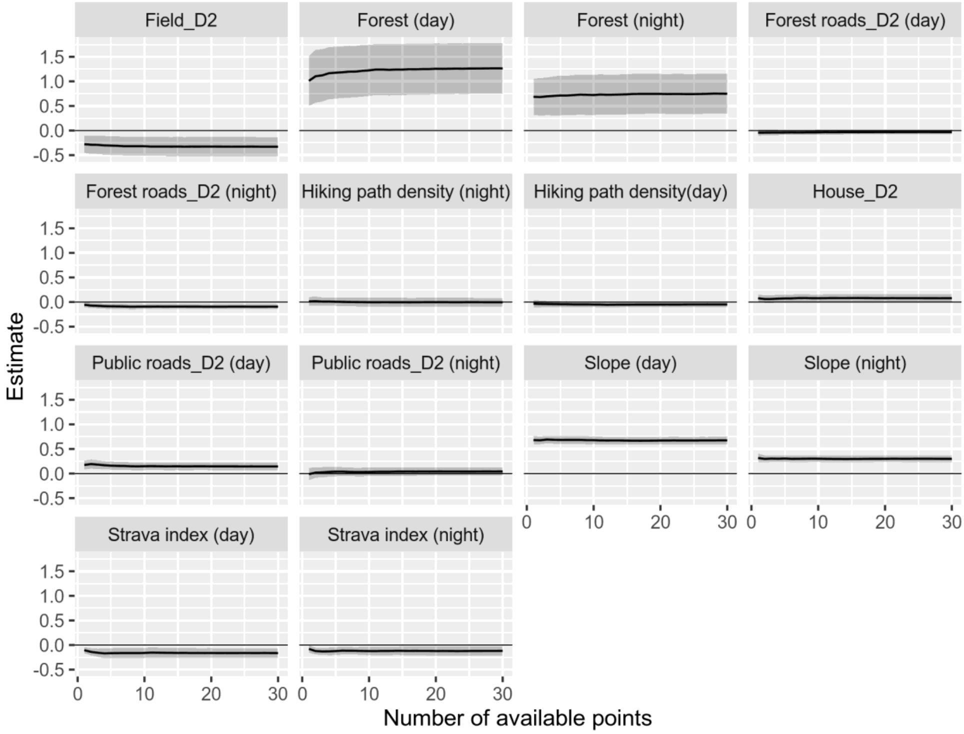

Figure S4. Sensitivity analysis for habitat selection at the local scale. We fitted the model with 1 to 30 available locations. The shaded area is the 95 % confidence interval for the coefficient estimate for the given number of available locations.

Table S1. Summary of the step lengths and step duration for the individual lynx used in the analysis.

Individual	Mean step length (m)	Median step length (m)	Standard deviation step length	Mean step duration in hours	Median step duration in hours
F218	727	228	1165	6,4	4
F228	1058	682	1272	8,4	6
F229	1246	565	1898	7,3	7
F237	1816	671	2797	7,1	4
F264	446	111	858	4,3	2
F293	839	358	1170	12,8	8
F305	825	365	1252	7	6
F306	1615	736	2215	7,3	6
M250	1139	357	2208	4,8	1
M251	1055	240	1895	6,8	2
M255	2029	724	3431	7,8	2
M256	1233	519	2102	5,2	1
M263	1949	452	4603	6,2	1
M271	1311	300	3209	5,1	1
M272	1210	424	2828	5,1	1
M273	1221	282	3088	5,2	1
M275	1343	270	3062	5	1
M294	1545	528	3501	5,8	1
M314	1605	758	2039	6,3	6
M323	1138	572	1696	5,4	6

Table S2. Covariates used for home range-scale habitat selection. The used and available values reported are prior to standardization.

Covariate	Description	Used values (mean and range)	Available values (mean and range)
Slope_{1000}	Mean of the slope_{50} (see also Table S3) in 1 km radius from focal cell.	12.4 (0.74 – 28.7)	10.8 (0 – 35.4)
Forest cover	Proportion grid cells with forest in 1 km radius.	82 % (8.4 – 100)	79 (0 – 100)
Field density	Percent grid cells with fields in 1 km radius.	9.9 % (0 – 86)	9.3 % (0 – 98)
Forest road density	Sum of forest road length in 1 km radius (km / 3.14 km^2).	4.37 (0 – 24.2)	4.10 (0 – 29.6)
Public road density	Sum of forest road length in 1 km radius (km).	1.77 (0 – 23.8)	1.68 (0 – 45.2)
Hiking path density_{1000}	Sum hiking path length per grid cells in 1 km radius (km).	2.11 (0 – 58.6)	2.10 (0 – 62.6)
$\text{Strava-index}_{1000}$	Mean number of Strava activities in 1 km radius.	22.1 ($0 – 4.40*10^3$)	27.0 ($0 – 6.24*10^3$)

Table S3. Covariates used for the local-scale habitat selection. The used and available values reported are prior to any transformations.

Covariate	Description	Day		Night	
		Used values (mean and range)	Available values (mean and range)	Used values (mean and range)	Available values (mean and range)
Slope$_{50}$	Calculated as defined by Horn (1981).	18.1 (0.03 – 57.6)	12.8 (0 – 68.4)	14.3 (0 – 57.4)	12.3 (0 – 68)
Forest	Categorical raster where 1 indicates forest.	0.94 (0 – 1)	0.85 (0 – 1)	0.87 (0 – 1)	0.83 (0 – 1)
Distance to field	Euclidean distance to closest fields (km).	0.70 (0 – 5.81)	0.74 (0 – 6.10)	0.67 (0 – 5.7)	0.72 (0 – 6.34)
Distance to forest road	Euclidean distance to closest forest road (km).	0.61 (0 – 12.8)	0.63 (0 – 13.4)	0.67 (0 – 12.1)	0.69 (0 – 13.0)
Distance to public road	Euclidean distance to closest public road (km).	0.98 (0 – 8.21)	1.02 (0 – 9.30)	0.96 (0 – 7.48)	1.01 (0 – 7.62)
Distance to house	Euclidean distance to closest house (km).	0.85 (0 – 7.15)	0.89 (0 – 8.31)	0.84 (0 – 6.11)	0.89 (0 – 7.34)
Density of hiking paths$_{50}$	Sum hiking path length inside the focal grid cell and its fours closest neighbours (m).	6.33 (0 – 361)	8.32 (0 – 626)	8.52 (0 – 478)	9.13 (0 – 536)
Strava index$_{50}$	Mean of Strava activities inside the focal grid cell and its fours closest neighbours.	9.13 (0 – $4.77*10^3$)	21.5 (0 – $2.02*10^4$)	14.8 (0 – $4.62*10^3$)	28.4 (0 – $2.23*10^4$)

Table S4. Model selection for the home range-scale and local-scale habitat selection.

Model	ΔAIC	
	Home range-scale	Local-scale
Core	2.47	521
Path	**0**	503
Strava	4.46	468
Full	0.08	460
Core_ night		64.2
Path_night		43.3
Strava_night		9.17
Full_night		**0**

References for supplementary material

Horn, B. K. 1981. Hill shading and the reflectance map. Proceedings of the IEEE **69**:14-47.

Paper III

The distribution of prey and roads facilitate wolf pack visits to houses by in Norway

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Abstract

Occasionally a single wolf or wolf pack living close to people are perceived as conflictful if they adopt behaviour that is viewed as being “bold” or “not shy”. Such cases tend to capture the attention of the public media and are challenging for wildlife management. Norway recently experienced such a case with the Slettås-pack. This pack created national debate about the presence of wolves close to houses. The Norwegian government decided to capture the wolves and equip them with GPS collars with a proximity-function. Once these GPS collars received signal from a “proximity-transmitter”, the GPS collars collected GPS locations with high temporal resolution. The proximity-transmitters were placed close to houses to collect detailed information about wolf movement in these areas. We used the GPS data in combination with data on prey density, resting sites and kill sites to explore wolf behaviour in detail. We used resource selection functions, integrated step selection analysis, and path selection and aimed to answer what brought the wolves close to houses, how they moved and selected habitat close to houses, and which features they selected during visits to houses (< 100 m from a house). Moose density was high close to houses, and wolf bed sites were located more than twice as far from houses as kill sites. Wolves selected habitats close to houses when prey density was high, and selected habitats far for from houses when prey density was low. Roads facilitated movement close to houses and were selected for during visits to houses. Visits to houses occurred almost exclusively at night. We argue that wolves in Slettås used space close to houses because of high moose density, and that winter-ploughed roads channelled the wolves into house-yards. This study shows how detailed information from multiple sources may help answer questions about wolf behaviour, which can be beneficial for large carnivore management when individuals are perceived as conflictful.

Introduction

Large carnivores in Europe almost exclusively live in a multi-use landscape dominated by humans. Wolves (*Canis lupus*) in particular, have successfully adapted to this landscape and can include areas of high human density in their home ranges (Chapron et al., 2014). When wolves and humans share the same landscape, the presence of wolves close to human settlements or houses is almost inevitable. Despite wolf attacks on humans being extremely rare (Linnell et al., 2003, Linnell et al., 2021), the presence of wolves close to people induces fear in many humans (Roskaft et al., 2003). As such, cases of wolves approaching humans or human settlements tend to capture the media`s attention and the public's interest. There is a widespread discourse among the public that such wolves are displaying an excessive degree of boldness and that this is associated with an increased risk of attacks (Linnell and Alleau, 2016). However, there is a paucity of detailed information about wolf behaviour in such contexts. Filling this knowledge gap may reduce some of the social conflicts associated with wolf conservation (Skogen et al., 2017).

On broad scales human settlements are generally avoided by wolves in Europe (Ordiz et al., 2020, Kaartinen et al., 2005, Carricondo-Sanchez et al., 2020), and North-America (Mladenoff et al., 1995). Nonetheless, wolves sometimes cross agricultural fields, or visit human settlements or house-yards and gardens (Kojola and Kuittinen, 2002, Kojola et al., 2004, Fritts and Paul, 1989, Kojola et al., 2016). Several explanations as to what brings wolves close to houses or human settlements have been suggested. Wolves may search for anthropogenic food sources (Ciucci et al., 1997, Mohammadi et al., 2019), be interested in dogs as either potential mates (Lescureux and Linnell, 2014) or targets of intraguild predation/killing (Butler et al., 2014), higher density of wild prey may occur close to human settlements (Lescureux and Linnell, 2014), or it may be convenient to travel along linear infrastructure (e.g. smaller roads and trails) that passes close to human settlements when travelling (Kojola et al., 2016).

Despite many suggestions as to what brings wolves close to houses and how they approach, few studies have been able to investigate this topic in detail. This might be due to the challenge of collecting the data needed to be able to answer these questions. Even if wolves often live close to human settlements they spend little time close to them, which means that these very close approaches are relatively rare events (Kojola et al., 2016) that are difficult to detect and thus study. This is even the case when wolves are equipped with GPS collars. Such events are best captured with GPS collars with fix schedules with very high frequency (e.g. Bischof et al., 2019). However, battery capacity, and therefore the potential for position acquisition frequency, is limited. In recent years, proximity technology has been used to investigate interactions between animals (Triguero-Ocaña et al., 2019). The same technology can be used to make a GPS collar intensify data collection when an instrumented animal approaches a transmitter placed at a point of interest. This opens the potential to intensify fix location frequency when an animal approaches an area of interest equipped with a proximity transmitter (e.g. human settlement), and at the same time maintain low frequency outside the area of interest. In this study we report the use of this technology to study the behaviour of a wolf pack that was perceived as conflictful, i.e. viewed as being "bold" or "not shy", in Norway.

The Slettås wolf pack, in Norway, became famous for its space-use close to human settlements and for walking through house-yards. The Slettås wolf pack used a territory containing small villages and dispersed houses in the valley bottoms. The area had been without a wolf territory for more than 100 years (Wabakken et al., 2001) before a wolf pack settled there in 2009. From 2009 to 2017 close to 1 000 media articles were written about this wolf pack or the fear of wolves in the local community (Wabakken et al., 2019). All the attention the pack gained by media made it a political concern and even the Minister of Climate and Environment visited Slettås in 2017. Several applications to kill the wolf pack were submitted, but none of them were approved by the authorities. In 2017, the Norwegian Parliament instructed the Norwegian Environment Agency to GPS collar the pack members to investigate their behaviour. The wolves were equipped with proximity-collars and in cooperation with local people, proximity transmitters were installed close to houses where the wolves had been observed earlier, to collect bursts of high temporal resolution GPS locations when instrumented wolves were close to settlements. In addition to the proximity-collars, we estimated relative moose density, and identified kill sites and resting sites made by the wolves by visiting the GPS locations on site. Together, these data offer a unique opportunity to study in detail a wolf pack repeatedly observed close to houses and perceived as conflictful by locals.

Here we present the results from our investigation of the Slettås wolf pack, where we explored the following questions: (1) What brought the wolves close to houses? (2) Which habitat did the wolves select for and how did they move when close to houses (less than 1.5

km from a house)? (3) Which habitat did the wolves select for during visits to houses (less than 100 m from a house)?

Methods

Study area

The Slettås wolf territory (411 km^2, as defined by the 100 % minimum convex polygon (MCP) of all wolf GPS locations), was located in the eastern part of Innlandet county, Norway (Figure 1). The elevation ranges from 430 to 1060 meter above sea level, and the topography is characterized by gently rolling hills. The area is covered by boreal forest, dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*), which are intensively harvested through clearcut forestry practices. The wolf territory consisted of 68 % forest, 19 % bogs, 8.5 % water, 2.1 % mountain, 1.9 % agricultural land and 0.3 % built-up area. The snow depth during this study was at least 50 cm across the entire wolf territory (www.met.no). The main prey of wolf in the area is moose (Alces alces; Sand et al., 2016). Roe deer (*Capreolus capreolus*) occur at low densities and some red deer (*Cervus elaphus*) also occupy the area (detected by faecal pellet surveys). The area is sparsely inhabited with approximately 670 humans (1.63 humans/km^2) living within the pack territory. Most people live in three small villages (100-300 people in each) and along the shores of the Osensjøen lake, but there are also a few isolated inhabited houses.

GPS data and field surveys

Routine population monitoring (snow-tracking and DNA) during the 2016-2017 winter indicated that the Slettås wolf pack consisted of 9-10 individuals (Svensson et al., 2017). Rangers from the Norwegian Nature Inspectorate (SNO) organised the capture and collaring of six of these wolves on the 13th and 14th of January, and 24th February 2017 by darting from helicopters and following the standard protocol for wolf captures and handling in Scandinavia (Arnemo and Evans, 2017). These wolves included one adult female, one adult male and four juveniles less than one year old. Hence, there were likely an additional 3-4 wolves in the pack that were not collared. The collared wolves were equipped with GPS collars with a proximity function (hereafter referred to as proximity-collars). The proximity-collars were programmed to collect one GPS location each hour (hourly GPS locations) as a standard baseline. In addition, these collars had an ultra-high frequency (UHF) receiver that searched for a specific UHF signal for 1.5 seconds every 60th second. An UHF signal was sent from the proximity-transmitters every second. When the proximity-collars detected a UHF-signal they were programmed to collect one GPS location every minute for as long the GPS collar received the proximity-signal or for a minimum of the next 10 minutes. We refer to this sequences of high temporal resolution GPS data triggered by the proximity transmitters as “bursts” (see Figure 2) and the GPS locations taken every hour as “hourly GPS locations”. We defined a single burst (with its own burstID) as all GPS locations in consecutive steps with a step duration of less than 5 minutes. Bursts with less than two steps (three GPS locations) due to poor fix acquisition were removed.

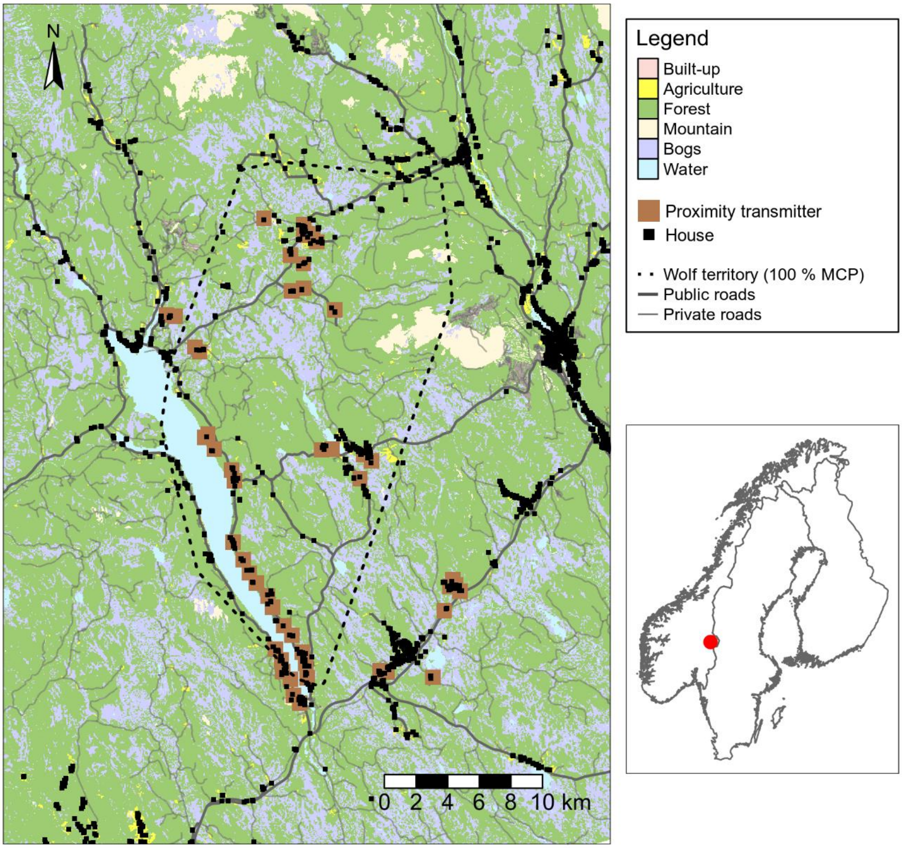

Figure 1. Study area with the wolf territory. The depicted wolf territory is based on the minimum convex polygon (100 %) of all wolves for the study period.

Local people from the Norwegian Hunters' and Fishermen's Association deployed 49 proximity-transmitters close to houses in the wolf territory from 11.02.2017 to 25.02.2017, where they previously had seen wolves or wolf tracks close to houses. The proximity function in the proximity collars was turned on from 15.02.2017 (05.03.2017 for the adult female) and turned off on 28.03.2017, this period defines our study period. One of the juveniles (M_17_03) dispersed on 26.02.2017 and was therefore removed from the study.

During the study period every cluster of GPS locations left by the wolves were visited on-site in the field. A cluster was defined as at least two hourly GPS locations located less than 200 m apart, following established protocols (Sand et al., 2005). On every cluster, signs of wolves were used to differentiate between kill sites and other sites. When a carcass of a prey was detected, the species, age, sex, possible time of death and probable cause of death were recorded (Sand et al., 2005).

To estimate the relative density of moose within the pack territory during winter we carried out faecal pellet count after the snow had melted, from 26.05.2017 to 07.06.2017. The pellet counts were conducted on 635 sample plots. Each sample plot was circular and had an area of 100 m^2 (5.64 m in radius). The sample plots were organised in quadrats of 50 x 50 m, with a plot in each corner and one plot in the centre of the quadrat, for a total of five sample plots per quadrat. Inside the full-year home range of the wolves, 74 quadrats were regularly distributed at a distance of 3.5 km. In addition, 53 quadrats were placed out every 500 m along four different transect lines (Figure S1). All moose pellet groups after last leaf fall were counted, and the date of leaf fall was set to 10.10.2016. For each quadrat we calculated the number of pellets group per day, as the sum of the pellets groups for the five sample surfaces in each quadrat divided by the number of days since leaf fall. As each quadrat has a sample area of 500 m^2, (5 x 100 m^2), we multiplied the mean number of pellet group per day by 2000 (1 000 000 m^2/5 00 m^2) to get the density of pellet groups per day per km^2 (pellets groups x day^{-1} x km^{-2}).

The relative moose pellet density for the whole study area was extrapolated from the pellet counts. We used ordinary and universal kriging models (Zimmerman et al., 1999) using the package gstat (Pebesma, 2004) in R (version, R Core Team (2020)). We used 10-fold cross validation (Stone, 1974) and identified the model that best predicted the pellet density based on the root mean square error and the bias (see Table S1 for models). We fitted this model to the full dataset and extrapolated for the complete study area and rasterized the result to a raster with 200 m resolution. Finally, we divided the density of pellet groups by 14, as a moose deposits approximately 14 pellet groups per day (Ronnegard et al., 2008), and obtained an estimate of relative moose density. For the purposes of this study our focus is on the variation in the relative density of moose within the pack territory rather than the absolute density. The moose density is estimated for the whole winter period, hence, we assumed that this density also represent the moose density during our study period.

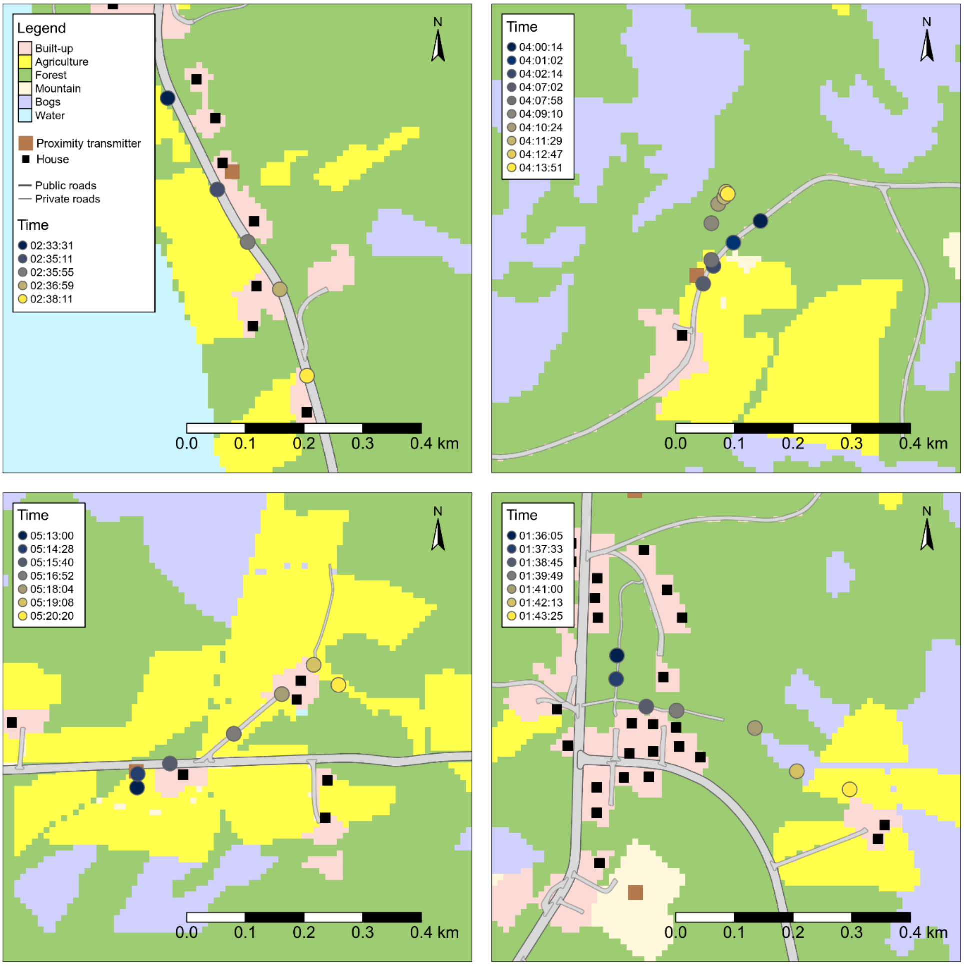

Figure 2. Example maps for illustration of bursts visiting houses. Top left shows M_17_02 (juvenile female) moving on the public road, close to houses. Top right shows the same individual walking towards a house, turn an walk in the opposite direction. Bottom left shows the same individual coming into the public road close to a house, following the road for a few meters before changing to a private road and into a new house-yard. Bottom right shows M_17_04 (juvenile female) moving through the middle of Slettås.

Covariates

We used the following covariates in this study: elevation, terrain ruggedness index, land cover, snow depth, distance to roads, houses and water, and moose pellet density. Elevation was obtained from the Norwegian Mapping Authority (www.geonorge.no) and the terrain ruggedness index was calculated with the terrain function in the raster (Hijmans, 2020) package in R. Forest, water and agricultural land (binary variables indicating presence or absence of forest or water, respectively) were obtained from national maps (AR5) (www.geonorge.no). Daily snow depth for 1 x 1 km grid cells was obtained from The Norwegian Meteorological Institute (www.met.no). Based on the daily snow depths we calculated a mean snow depth for the whole study area for the whole study period, as the snow depth was quite stable throughout the study period. This study was conducted during winter when the lakes and rivers were covered by ice. Roads and buildings were obtained from national maps (FKB) (www.geonorge.no). We calculated the shortest Euclidean distance to water, roads and houses using the proximity function in GRASS (GRASS Development Team, 2020) run from R using rgrass7 (Bivand, 2020). Previous studies have found that wolves at this latitude in Scandinavia have similar responses to public and private roads (Carricondo-Sanchez et al., 2020), hence, we used a composite category called roads. Registered houses in the FKB-data might not always be inhabited. Hence, we intersected the buildings registered as houses with human density data from Statistics Norway (www.ssb.no) and assumed that all houses inside a 250 by 250 m grid registered with at least one person were inhabited. We also explored the temporal aspect of the GPS data, with night (vs. day) defined as the time between sunset and sunrise. Sunrise and sunset were extracted using the sunriset function in the R package maptools (Bivand and Lewin-Koh, 2021). All spatial covariates, except the snow depth data and relative moose density, were rasterized to a 10 x10 m resolution.

Data analysis

Home range scale habitat selection

To investigate what brought the wolves close to houses we used GPS data, the moose density data, and the field data collected at the clusters. We used resource selection functions (RSF, Manly et al., 2002), to evaluate home range scale habitat selection (3rd order of habitat selection, c.f. Johnson (1980)), i.e. habitat selection within the home-range. We used the same availability definition (the pack territory) for all wolves, and defined it as the 100 % MCP of all the wolves' hourly GPS locations (see Figure 3). For each hourly GPS location obtained from the wolves we sampled 30 random locations inside the 100 % MCP and refer to these locations as the available locations. Then, we fitted logistic regression models with the used GPS locations (1), and available locations (0), as the response variable using the glm function in the stats package in R. We fitted one model for each individual and used the same available locations for all individuals. We included the following covariates as explanatory variables in our RSF models: mean snow depth, terrain ruggedness index, forest, distance to road, distance to house and moose density, as these covariates have been previously shown to influence home range scale habitat selection of wolves (Zimmermann et al., 2014, Milleret et al., 2018, Ordiz et al., 2020). We included an interaction between the density of moose pellets and distance to a house, as we observed that moose density was higher closer to houses. Furthermore, we included a second order polynomial of distance to house and density of moose to allow for non-linear responses in our model. We interpreted the results from this model based on the parameter estimates and their 95 % confidence intervals.

Local scale habitat selection and movement close to houses

To investigate what the wolves selected for and how they moved when close to houses, we used integrated step selection analysis (iSSA) (Avgar et al., 2016) on the bursts (see Figure 3). The iSSA simultaneously investigates local scale habitat selection and movement. iSSA is a form of step selection function where a step is defined as two consecutive GPS locations of an animal, and the turning angle is the degree of change in direction between two steps in radians. The iSSA assumes a probability distribution for the step lengths and a probability distribution for the turning angles, which are fitted based on the data. Prior to fitting the step length distribution, we removed step lengths shorter than 5 m to make sure that we did not include stationary individuals. We assumed and fitted a gamma distribution for the step lengths and a Von Mises distribution for the turning angles. From these probability distributions, we randomly drew step lengths and turning angles and joined them together as steps. We refer to random steps as the available steps and the step actually used by the animal as the used step. For each used step we drew 30 available steps, and a unique step ID was assigned to the used step and corresponding 30 available steps.

We fitted the iSSA through a conditional logistic regression using the coxph function in the survival package (Therneau, 2020) in R. The response variable was used (1) vs. available steps (0), and the step ID was included as a stratum. The stratum matched the used step and the available steps to make sure that only used steps and available steps from the same step ID are compared. We ran individual models and excluded wolf M_17_04 (juvenile female) from this analysis, due to too few bursts. In the iSSA, habitat selection is inferred from covariates included at the end of each step (did the wolf select an endpoint far from a house or close to a house). We included the following covariates at the end of the steps: distance to house, on/off road, on/off water (i.e. ice) and forest (on/off defined as being on the feature if less than 20 meter from the feature). We also chose to include water in the iSSA model as we wanted to control for wolves potentially using the ice-covered water for movement. To make the interpretation easier we calculated log relative selection strength (log RSS) (Avgar et al., 2017). This expresses the relative risk of selecting location x_1 over x_2. In the iSSA, covariates included at the start point of a step and in an interaction with the step length or the logarithm of the step length, can be used to update the initial parameters of step length distribution (step length updates scale parameter and logarithm of the step length update the shape parameter of the gamma distribution) and thereby to estimate speed in different habitats. We included the following covariates at the start of each step in an interaction with the logarithm of the step length: distance to house, on/off road, and on/off water. Additionally, we included 'cos(turning angle)' and an interaction between 'cos(turning angle)' and 'log(step length)', to account for directional movements generally having longer steps, and an interaction between step length and step duration, to account for steps with longer duration generally being longer. Finally, we estimated the movement speed in different habitats by updating the scale and shape parameter with the estimated coefficient (Avgar et al., 2016).

Path selection for the visits to houses

We defined a visit to a house as a GPS location (both for hourly GPS location and for the burst) closer than 100 m from a house (see Figure 3). To explore what the wolves selected during visits to houses we used path selection analysis on the bursts (e.g. Elliot et al., 2014). We included only bursts containing a visit and at least thre GPS locations, and intersected them with a buffer of 150 m from all houses. We refer to the bursts that met these criteria as paths, as they contain three or more GPS locations. By definition all paths had a maximum distance from a house of 150 m or less and with a minimum distance from a house less than

100 m. For each of these paths we created available paths from the start point to the endpoint of the used path. The available paths were simulated as the realization of a Brownian bridge which moved in a sequential manner from the start point to the end point (Horne et al., 2007). To have the same criteria for the available paths as for the used paths, we subsampled the available paths and included only available paths that did not go beyond 150 m from a house and that had a minimum distance of less than 100 from a house. Three complex used paths were excluded as it was not possible to create available paths fulfilling these criteria (paths starting and ending almost at the same location, see Figure S2). After subsampling, we ensured that each used path was associated with 30 available paths, and assigned each used path and its corresponding 30 available paths a path ID. We used the available (coded as 0) and used paths (coded as 1) as a response in a conditional logistic regression and included the path ID as a strata. We considered the following covariates: proportion of path on agricultural land, proportion of path on roads (the path was assumed to be on a road if it was less than 20 m from a road), and the mean distance to a house for the raster cells that were intersected by the path. We only considered this full model and interpret the results based on the parameter estimates and their confidence intervals. Due to a low number of used paths for each individual (adult male: 7, adult female 12, juveniles: 3, 6 and 8) we fitted one model for adults and one for juveniles.

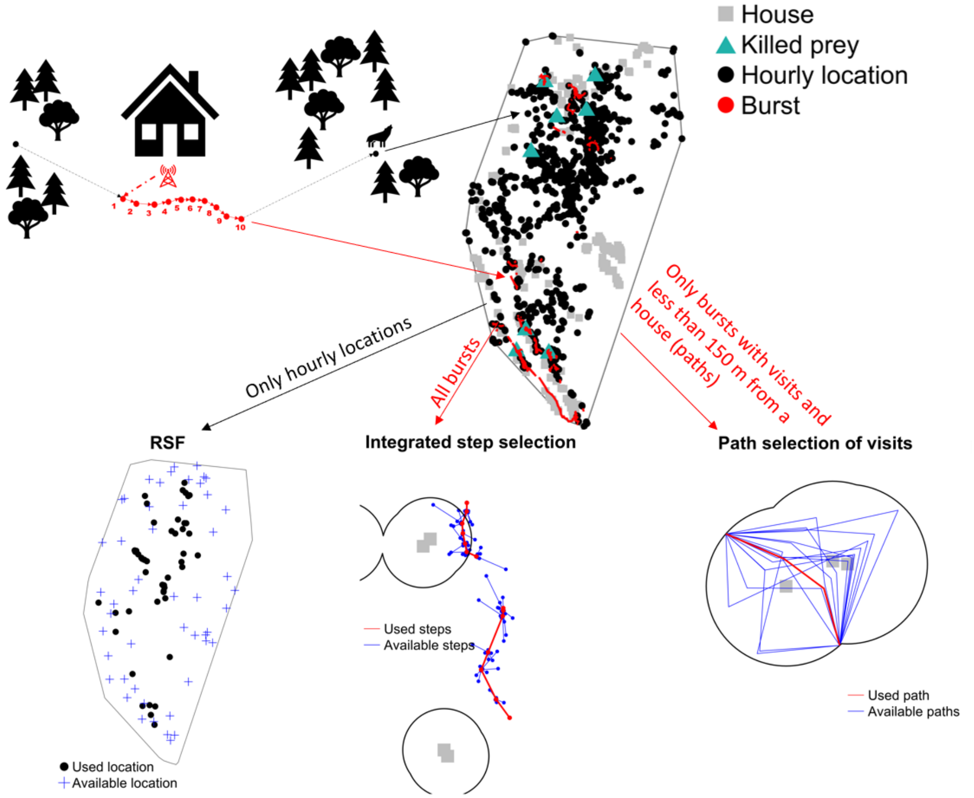

Figure 3. Schematic illustration of the study design and analysis. Top left corner illustrates a wolf with proximity collar walking from the forest and passes a house with a proximity transmitter. The proximity collar is triggered and takes a burst of 10 locations before the wolf walk into the forest again. The polygon on the top right is the 100 % MCP of all wolf locations. The three illustrations on the bottom illustrates our three analysis. The buffer around the houses is 150 m and illustrates the area for which we intersected the bursts to create paths. All paths was within 100 m from a house at least once.

Results

Moose data, kill sites and resting sites

Inside the wolf territory the mean density of moose was approximately 0.78 moose/km^2. The density of moose was generally higher closer to houses (Figure 4A). From 15.02.2017 to 28.03.2017, 80 locations (single GPS locations and clusters) were visited in the field. During this fieldwork, 9 kill sites and 25 locations including at least one wolf bed site were detected. The kill sites included 8 moose and 1 roe deer. Kill sites were located significantly closer to houses than bed sites, the mean distance to a house from a kill site was 0.64 km (range: 0.12 – 2.1 km, only one kill was farther than 1 km from a house), while for bed sites it was 1.5 km (range: 0.26 – 3.7 km, Welch Two Sample t-test: p-value=0.009).

Table 1. Summary of hourly GPS-locations and bursts. 'N locations' represent the number of GPS-locations for the given temporal resolution, 'N visits' the number of GPS-locations 100 m from a house or closer, 'N bursts' the number of bursts from the given wolf and 'N bursts visits' the number of bursts with at least one visiting location. The number of days each wolf had the proximity function working is shown in the column 'N days with proximity'. M_17_03 dispersed in the beginning of the study period and were excluded from the study.

	Hourly			**Bursts**				
Wolf_ID	**Age and sex**	**N locations**	**N visits**	**N locations**	**N visit**	**N bursts**	**N bursts visits**	**N days with proximity**
M_15_03	Adult male	973	1	1472	33	125	8	41
M_17_14	Adult female	745	3	1995	41	148	10	41
M_17_01	Juvenile male	862	0	502	32	66	10	41
M_17_02	Juvenile female	730	3	253	24	39	7	41
M_17_04	Juvenile female	983	4	74	16	19	5	23
Total		4293	11	4296	146	397	40	187

Home range scale habitat selection

The individuals spent from 10 to 40 % of the time in a location that was not associated with any other GPS-collared individuals (Table S2). For the hourly GPS locations wolves were significantly closer to houses at night (mean distance 1.78 ± 1.32 km) compared to day (mean distance 1.92 ± 1.23 km, Welch Two Sample t-test: p-value< 0.001). The home range scale habitat selection revealed a selection for distance to houses and moose density that followed a similar pattern for all individuals, albeit with slight variation among individuals in terms of the coefficients that emerged as significant (Figure 5). Nonetheless, all wolves had a significant negative interaction between distance to a house and moose pellet density (Figure 4, Figure 5), i.e. wolves selected for areas with high moose pellet density in proximity to houses and low moose pellet density far from houses (Figure 4). One juvenile exhibited selection that increased with distance from roads, while the rest of the individuals had a coefficient estimate with 95% confidence intervals that overlapped zero (Figure 5). The adults selected landscape patches with low mean snow depth, while two of the juveniles selected for landscape patches with high snow depth and the last juvenile had a confidence interval overlapping zero. The adults and one juvenile selected for higher terrain ruggedness index, one juvenile selected for lower terrain ruggedness index while the last juvenile had a confidence interval overlapping zero. All individuals selected forest (Figure 5).

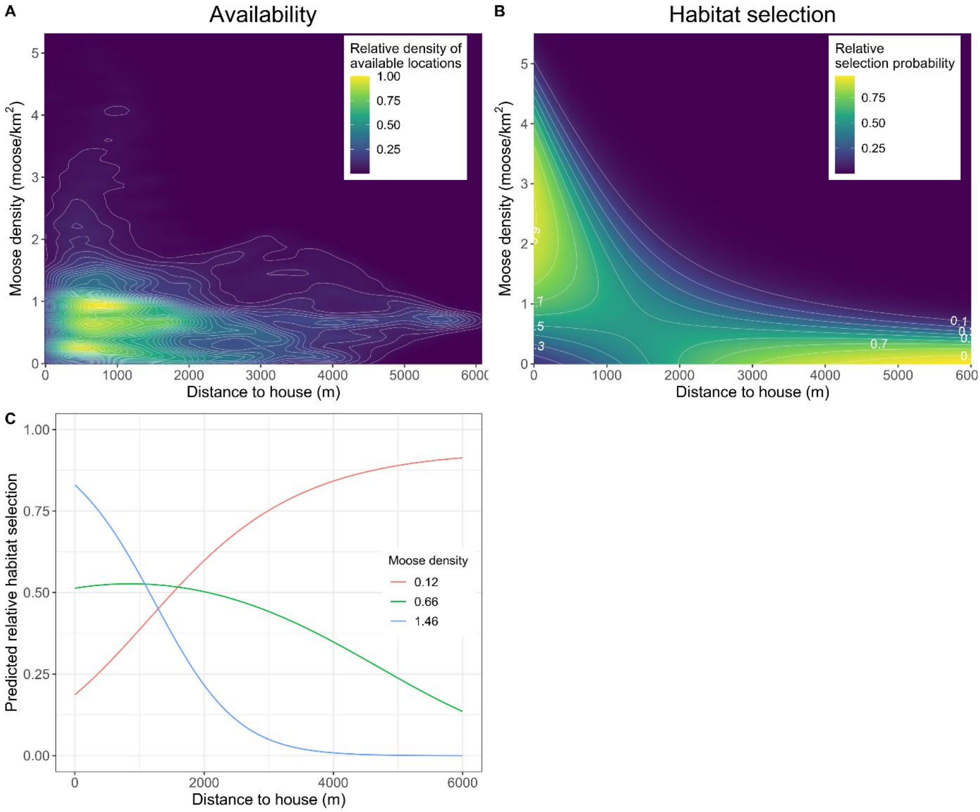

Figure 4. A) Relative density of available locations (scaled between 0 and 1) distance to house and density of moose piles. This illustrate the area the wolves had available inside their territory. White dots represent kill sites. B) Predicted relative selection probability from the resource selection model for the adult male, illustrating the interaction between distance to house and density of moose. C) Predicated relative habitat selection in relation to distance to house for three different levels of moose density (10, 50 and 90 % percentiles for the available locations) for the adult male. In B) and C) the intercept have been removed prior to the predictions as this is not informative (it reflect the ratio of used to available locations).

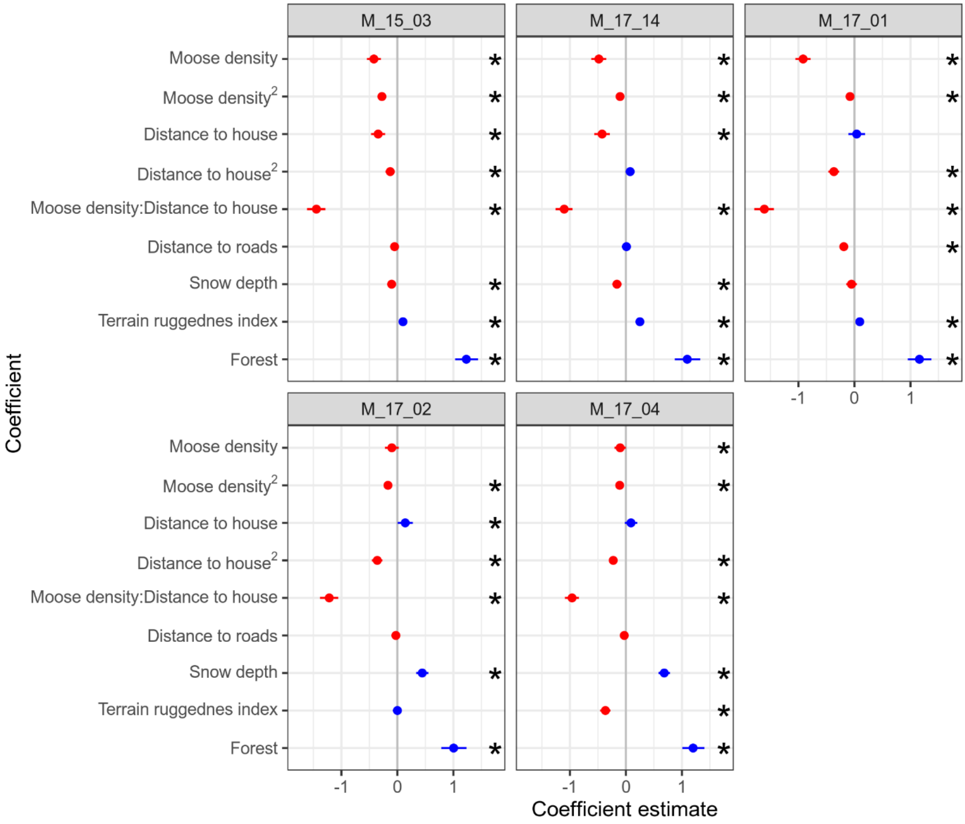

Figure 5. Coefficient estimates from resource selection functions for the home range scale. The different facets represents different individuals. The intercept is omitted from the output, as this coefficient is not informative. Stars denote significant coefficient estimates and the colour indicate the direction (red for negative and blue for positive).

Local scale habitat selection and movement close to houses

During bursts, the mean distance to a house was significantly closer at night (mean: 348 m) than during the day (mean 387 m, Welch Two Sample t-test: p-value < 0.001). The mean step length for the bursts was 41 m (25 % and 75 % quantiles: 9 and 48 m) and mean step duration was 106 seconds (range: 23 – 300 seconds). The results from the iSSA need to be interpreted in the context of the local availability being constrained by the step length distribution fitted to these steps. The iSSA revealed a highly consistent response to roads. All wolves selected for roads and increased their speed when on a road (Figure 6 and Figure 7). All juveniles selected areas farther away from houses, while the adults did not display a selection pattern for distance to house (Figure 6). The log relative selection strength derived from the iSSA indicated that the selection for roads were stronger than the avoidance of houses (Figure 7A). As the wolves were more likely to select steps that ended farther from houses when they were off a road (red line Figure 7A). However, if the step rather ended on a road, the wolves were more likely to move closer to the house than continue to stay off the road (Figure 7A: all blue lines have positive values). The movement response in relation towards houses differed between individuals, the adult male increased its speed closer to houses, while the two juveniles decreased their speed and the adult female did not show a significant response. One of the juveniles did not spend any time on water (presumably frozen), hence, this parameter was removed for this individual. The three remaining wolves showed the same response to water; they did not select for it but increased their speed when moving on water.

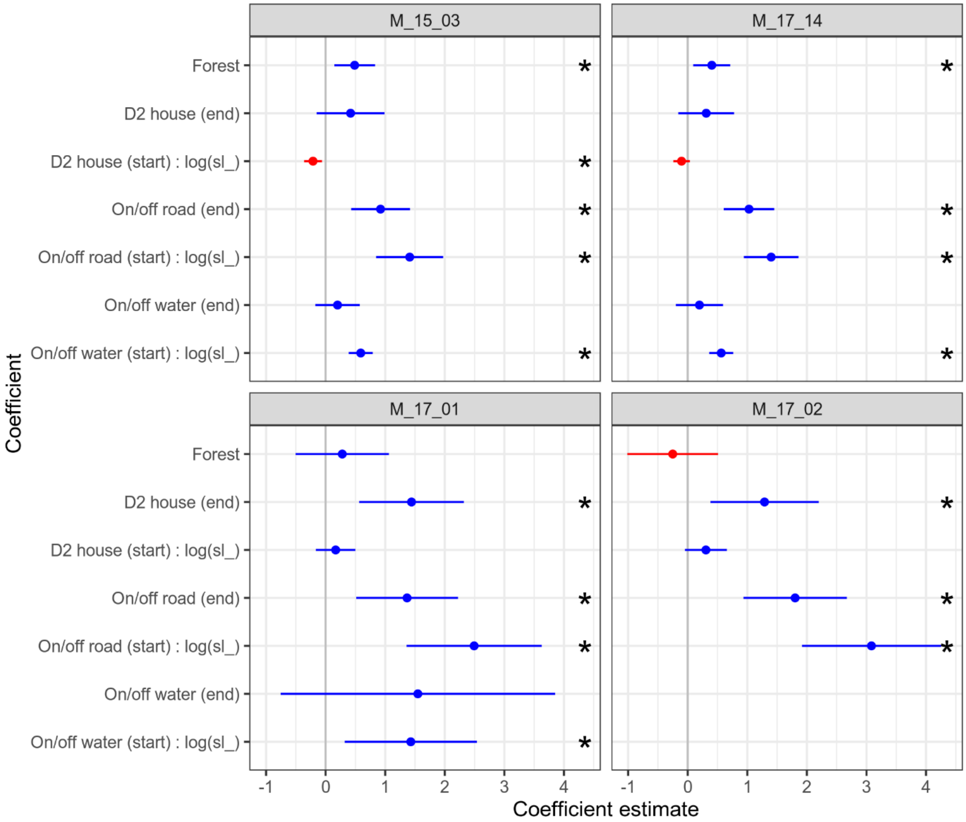

Figure 6. Coefficient estimates from the integrated step selection analysis (iSSA). D2 is an abbreviation for "Distance to" and "On/off" refers to being "on the feature"(coded as 1) or being "off the feature" (coded as 0). All distance to features have been log transformed. Coefficients denoted with "(end)" refers to covariates extracted at the end points of a step, hence they can be interpreted in terms of habitat selection (e.g. M_15_03 selected steps ending closer to roads). Coefficients denoted with "(start)" refers to covariates extracted at the starting points of a step. Since they are included in an interaction with step length they are interpreted as movement (e.g. M_15_03 moved faster when the individual started on a road). Stars indicate significant coefficients and the colour indicate the direction (red for negative and blue for positive).

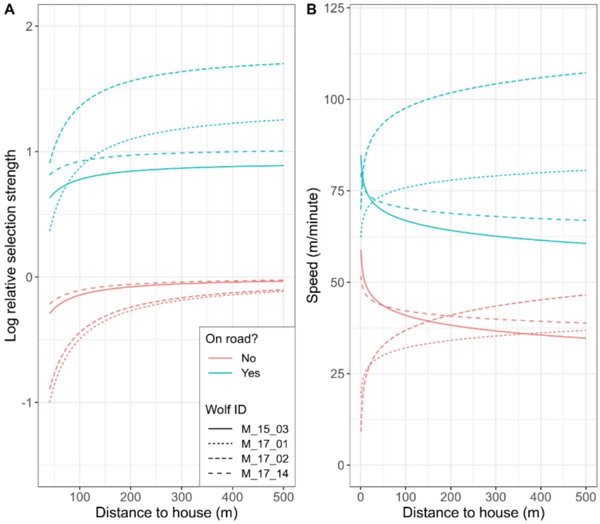

Figure 7. Log relative selection strength (A) and movement rates (B) calculated from the four individuals with enough data to run iSSA for. A) shows the relative selection strength of taking a step that ends 41 meter (mean step length) closer to a house when the step ends on a road (blue) or off road (red), compared to a reference location. The reference location is a habitat with the same distance from house (i.e. not moving 41 meter closer) and off a road. Positive values indicate that the wolf are more likely to move 41 m closer to the house compared to select the reference location, while negative values shows that the wolf are more likely to select the reference location. B) shows the movement speed for wolves at different distances to a house and whether the wolf was on a road or not. The speed in B are illustrated for wolves walking in a straight line, with step duration of 60 seconds and not on a ice-covered lake.

Path selection for the visits to houses

Based on the hourly GPS locations, each wolf had from 0 to 4 visits to houses (less than 100 m from a house) (Table 1), corresponding to less than 0.5 % of the hourly GPS locations for each wolf. Based on the bursts, each wolf had from 16 to 41 GPS locations defined as visits, which belonged to between 5 and 10 different bursts per wolf (Table 1). For the adult female this corresponded to around one visit every other day (Table 1), but these visits were not spaced evenly in time (Figure S3).

From the 40 bursts that included a visit to a house, 98 % were made during the night (only one made during the day). This proportion was significantly higher than for the bursts that did not include a visit to a house; 68 % were recorded during the night (p-value < 0.001, two sample Z test of proportions). The path selection revealed a selection for roads for adults, while the coefficient for juveniles was not significant (p-value=0.080, Table 2). Juveniles avoided agricultural land during the visits, while the effect of agricultural land for adults was marginally non-significant (p-value=0.063, Table 2). The mean distance to a house was not significant for any of the age classes.

Table 2. Model output from conditional logistic regression where used path (1) vs. available paths (0) was the response. We divided the individual into two different models, adults and juveniles.

Coefficient	**Age**	**Estimate**	**SE**	**Z-value**	**P-value**
Proportion of road	Adults	0.103	0.021	4.959	< 0.001
Mean distance to house		0.020	0.025	0.791	0.429
Proportion agricultural land		-0.060	0.032	-1.858	0.063
Proportion of road	Juveniles	0.0312	0.018	1.752	0.080
Mean distance to house		-0.007	0.031	-0.228	0.820
Proportion agricultural land		-0.080	0.036	-2.253	0.024

Discussion

What brought the wolf pack close to houses?

Wolves generally avoid houses (Ordiz et al., 2020, Kaartinen et al., 2005, Mladenoff et al., 1995) and are also more likely to occupy habitat with high prey density (Roder et al., 2020). In the Slettås-territory the estimates of relative moose density revealed that the wolves faced a trade-off: select high prey densities vs avoid space close to houses, as areas far from houses had a low density of moose and the highest moose densities were associated with areas close to houses. The wolves` solution to this trade-off appeared to be selecting for high prey density when close to houses and for low prey densities when far from houses, and venturing closer to houses at night than during the day. This was also evident for the resting sites, which were located far from houses and more than twice as far from houses as the kill sites. The area close to houses likely offered good hunting grounds, as 8 of 9 kill sites were closer than 1 km from a house. Together, high moose density close to houses, short distance from kill sites to houses, long distances from bed sites to houses and selection for areas close to houses only at high moose density, strongly indicate that wolves used areas close to houses because of the high prey densities. Alternative explanations could be anthropogenic food sources (Ciucci et al., 1997) like baits used for fox hunting, or dogs as attractants. However, we do not find this likely as we should have detected fox baits on the clusters or detected multiple visits to the same houses for the bursts if the wolves were attracted by dogs or fox baits.

Which habitat did the wolves select for and how did they move when close to houses?

Linear features and roads have previously been shown to facilitate wolf movement (Whittington et al., 2004, Latham et al., 2011), including the Scandinavian population (Zimmermann et al., 2014). Our integrated step selection analysis reported similar results for the Slettås-pack, but with higher temporal resolution data. When in proximity to houses the wolves in the Slettås-pack used roads for locomotion, as all wolves selected for roads and increased their speed on roads. The speed of the wolves on roads (approximately 80 m/minute) is similar to that reported for GPS data with 5-min intervals in North-America (Dickie et al., 2017). The roads in the Slettås-territory likely offer favourable conditions for travelling, as shown previously (Zimmermann et al., 2014, Gurarie et al., 2011), especially since many roads are ploughed in winter. Although these wolves had been perceived as a source of conflict, the juveniles selected steps that ended farther away from houses (local scale avoidance) and both adults had a trend of doing the same for the bursts. This is in line with the general pattern observed in Scandinavia with lower intensity data (Carricondo-Sanchez et al., 2020). The ploughed roads possibly facilitated these visits to house-yards, since selecting roads appeared more important than avoiding houses (Figure 7A). As noted by Kojola et al. (2016), the road network connects small villages, farms and houses, and possibly act as channelising routes to house-yards. Despite the indication of the Slettås pack locally avoiding houses, they did sometimes visit them. This may be explained by the distinction between habitat selection and habitat use. On average, wolves *selected* steps that ended farther from houses, however this does not imply that they never *used* a step that ended close to a house. Since the wolves selected for high prey density close to houses at the home range scale, they likely had many opportunities to visit houses, and sometimes they did walk through the house-yards.

Which habitat did the wolves select for during visits to houses?

The path selection also revealed that the adults showed quite strong selection for roads during the visits (< 100 m from a house), while the juveniles did not exhibit a significant estimate. This illustrates that roads were not only facilitating movement when close to houses, but also during the actual visits to houses. As illustrated by the examples of bursts, wolves sometimes followed the road straight through the house-yard, sometimes they turned and returned to where they came from, and sometimes they jumped out of the road and walked around the house instead. The ease of transportation on roads is likely a greater benefit than the perceived cost associated with failing or ignoring to avoid a house. Especially, when considering every visit except one happened at night. Similar results have been reported in Finland, where the probability of visit to house (here it was defined as less than 150 m from a house) increased during night time (Kojola et al., 2016). Actually, most wolf observations in the Slettås-territory consisted of tracks left in the snow and few were direct sightings (Wabakken et al., 2019), which suggests that the wolves were quite successful in not encountering humans despite using habitat close to houses. Based on our results, we consider the visits to houses in the Slettås-pack as a result of the wolves selecting high prey density close to houses in combination with an intensive use of roads for transportation.

The role of new technology in providing novel insights

By combining data on moose density, kill and resting sites, hourly GPS locations and the bursts we could study the behaviour of one wolf pack in great detail. The use of proximity-collars allowed us to pinpoint the area of interest and to collect GPS data of high temporal resolution on relatively rare events (only 0.5 % of the hourly locations were closer than 100 m from a house). The disadvantage of proximity-collars is the lack of a clearly defined detection range. The proximity-transmitter in some cases triggered the GPS collar at distances of more than 1 km when there was clear view between the GPS collar and a proximity-transmitter (e.g. over lakes), while in other cases the proximity-transmitter only triggered the GPS collar at short range. On the other hand, the use of geofence (or virtual fences) is not suitable as it requires a GPS location inside the virtual fence before the GPS can increase the acquisition frequency (Wall et al., 2014), hence geofence-technology would not have been able to detect the visits we report here. We analysed both the bursts and the hourly location data with individual models. This approach should reduce the chance of falsely reporting too small standard errors, as might have happened if all individuals where included in the same model (Millar and Anderson, 2004). However, the decisions made by one individual is likely dependent on the decisions made by another, e.g. the adult pair tended to spend time together (supplementary text S1). Such dependence should not be of importance for this study as our aim was to explore how this pack behaved, and not the variation between wolves in the pack.

Management implications

The Slettås-pack represent a classic example of a wolf pack perceived as being “bold” or “not shy”, and thereby receive huge attention from media and requiring substantial resources from the wildlife management agencies. The public and media narratives that follow such cases often make it challenging for wildlife management, as their decisions will be questioned regardless of whatever they decide. We find similar cases across Europe (Huber et al., 2016), but to our knowledge few, if any, have been investigated in such a detail as the Slettås-pack. Understanding the behaviour of wolves being perceived as conflictful, and in which contexts this behaviour arises, can form a common understanding of what brings certain wolf packs close to houses. This might reduce fear in the public, as knowledge tends to reduce the fear of large carnivores (Johansson et al., 2019). In this case, managers have a possible answer to the mechanisms that brought wolves close to houses—it was likely because of moose density and travel corridors. This case study illustrates how detailed information gathered from one wolf pack considered as conflictful, can give new insight and offer potential explanations of the behaviour of a conflictful pack in similar contexts. Future studies concerning conflictful wolf packs can reveal if the patterns reported here are general, and further studies are clearly needed to understand the processes of habituation and degrees of boldness in wolves.

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Supplementary material

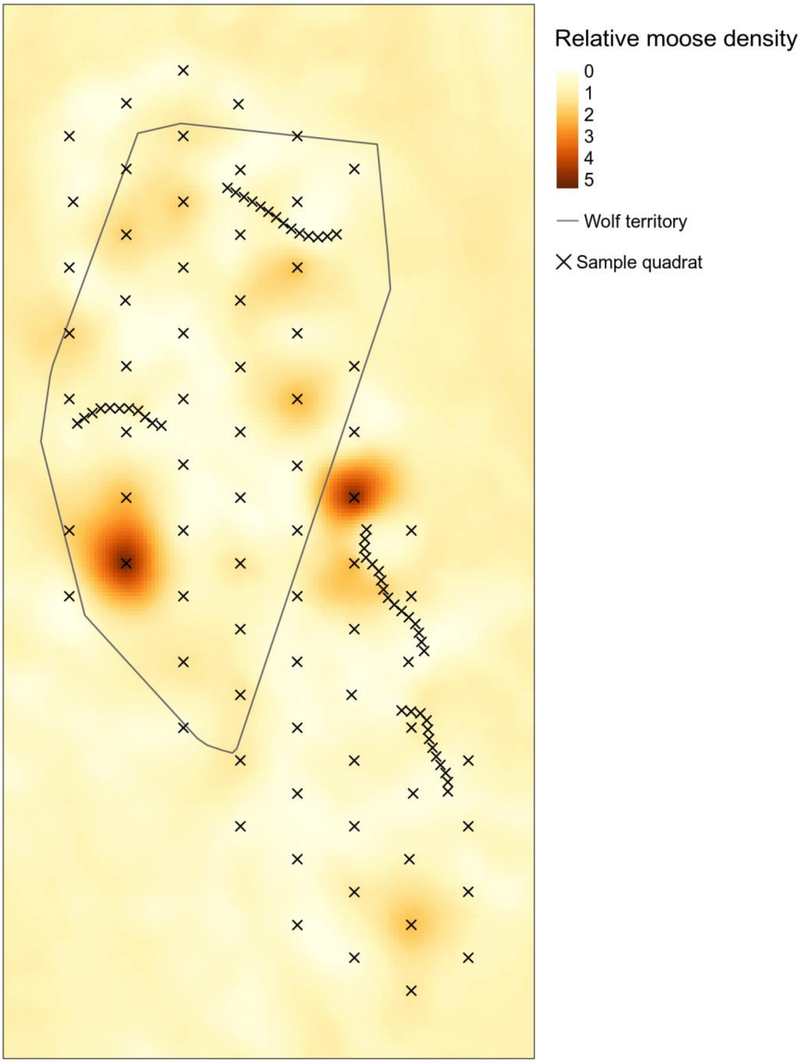

Figure S1. Map of the sample plots for the moose pellet survey. The wolf territory for this study is depicted as a solid line. The relative moose density is used a background map.

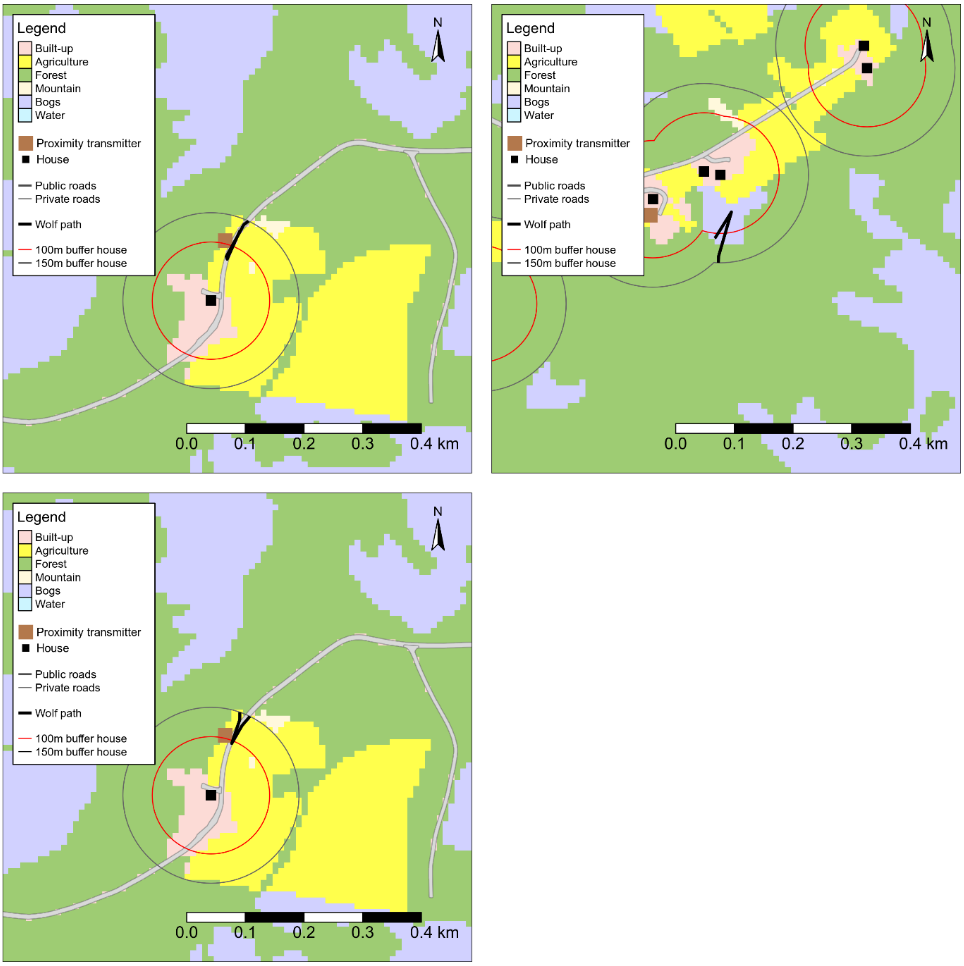

Figure S2. The three complex used paths our method were not able to create available paths for. All of these three paths started and ended close to each other, and in addition quite far from the 100 m buffer for the houses, which caused the available paths not cross the 100 m buffer. Crossing the 100 m buffer was a criteria for the available paths to be included. Adult female (M_15_03) on the top left, juvenile male (M_17_01) on the top right and juvenile female (M_17_02) on the bottom left.

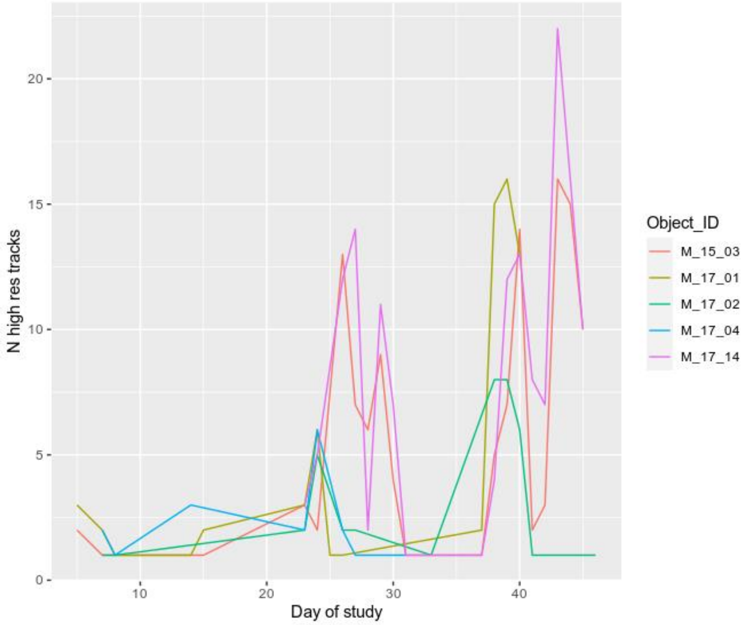

Figure S3. Number of bursts created for the different individuals throughout the study period. The y-axis present the number of burst per day.

Table S1. Spatial interpolation models for the moose pellet density. The columns RMSE and MAE are abbreviations for root-mean square error and mean absolute error. The intercept model is fitted through ordinary kriging while universal kriging are used for the rest. Snow depth and roads are the same as defined in the main text. The bogs variable was binary (1 for bog, 0 if not bog), Bogs1000, pine1000 and spruce1000 is the proportion of bogs, pine and spruce in 1000 m radius.

Model	RMSE	MAE	Bias
Bogs1000+Pine1000	**13,26488**	**9,494036**	**0,224716**
Bogs1000+Spruce1000	13,41565	9,523354	0,322865
Bogs1000 + Spruce1000 + Pine1000	13,44984	9,502213	0,240185
Bogs1000	13,57525	9,641277	0,459603
Forestry roads (distance to)	13,7255	9,827063	0,428477
Pine1000	13,75695	9,840699	0,557587
Intercept	13,78159	9,855995	0,575159
Bogs	13,78672	9,719855	0,513529
Spruce1000	13,82905	9,843729	0,544942
Snow depth	13,86617	9,91579	0,578548
Spruce1000 + Pine1000	13,86981	9,819113	0,541943
Elevation	13,87063	9,906048	0,578835
Roads (distance to)	13,89301	10,00221	0,599058
Public roads (distance to)	13,90224	9,946639	0,659157
House (distance to)	13,94105	10,00053	0,706946

Supplementary text S1

Based on the hourly GPS-locations, adults spent 77 % of their time together, and juveniles spent more than 40 % of their time with at least one of the adults (Table S2). Juveniles spent more time without other GPS-collared wolves (33-41 % of the time “alone”, Table S2) than the adults (10 and 13 % of the time “alone”, Table S2). Of the 373 bursts 46 % were left by single wolves (i.e., no bursts from another wolf closer than 500 m within 15 minutes), 35 % of the bursts were left by two wolves (two different wolves created two different bursts closer than 500 m within 15 minutes), 8.0 % were by three wolves together and 9.7 % were by four wolves together. For those cases where the wolf was accompanied by another GPS-collared wolf, one of the adults was included in the group in 70 % of the cases.

Table S2. Time spent together in pairs for the hourly GPS locations. The columns and rows represent the individuals. The value in each cell represent to percent of time a pair of individuals were less than 200 m apart around each complete hour. The diagonal from top left to bottom right shows the amount of time the individuals spent without any other GPS collared individual.

	M_17_01	**M_17_02**	**M_17_04**	**M_17_14**	**M_15_03**
M_17_01	39,3	33	40,6	39,6	53,3
M_17_02	33	40,6	27,9	38,2	34
M_17_04	40,6	27,9	32,9	41,3	49,9
M_17_14	39,6	38,2	41,3	10,1	76,8
M_15_03	53,3	34	49,9	76,8	13,1

Paper IV

Human infrastructure influence life stage-dependent movement and habitat selection in a large carnivore

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Abstract

The movement extent of mammals is greatly reduced in human-modified areas which can affect population demographics. Understanding how human infrastructure influences movement at different life stages is important for wildlife management. This is true especially for large carnivores, due to their substantial space-requirements and potential for conflict with humans. We investigated human impact on life stage-dependent movement and habitat selection by GPS-collared male brown bears (*Ursus arctos*) in two life stages (residents and dispersers) in central Sweden. We identified dispersers visually based on their GPS locations and used hidden Markov models to define the timing of the dispersal events, i.e. when they were classified as dispersers. We used integrated step selection analysis (iSSA) to infer movement and habitat selection at a local scale (availability defined by hourly relocations), and resource selection functions (RSFs) to infer habitat selection at a landscape scale (availability defined by the study area extent). Movement of residents on a local scale was facilitated by small forestry roads as they moved faster and selected areas closer to forestry roads, and they avoided areas closer to larger public roads and buildings on both scales. Dispersers were more ambivalent in their response to human infrastructure. Dispersers increased their speed closer to both small forestry roads and larger public roads, did not exhibit significant selection for or against any road class and avoided areas with higher closer to buildings only at local scale. Dispersers did not select for any features on the landscape, which is likely explained by the novelty of the landscape and their naivety towards it. Our results show that movement in male brown bears is life stage-dependent and indicate that dispersers may have better landscape connectivity than residents. This suggests that data from dispersing animals provide more realistic models for population reconnecting than if data were derived from resident animals alone.

Introduction

Human activity and infrastructure have reduced the movement extent of wildlife globally (Tucker et al. 2018). Animals are generally sensitive to human infrastructure (Wilmers et al. 2013), especially to the creation of linear structures (Trombulak and Frissell 2000), which in turn is commonly reflected in their movement patterns. Maintaining connectivity, i.e. the ease of movement between suitable habitat patches or between populations, within a human-dominated landscape is important to avoid fragmentation of populations and to ensure gene flow (Zeller et al. 2012). As dispersal contributes to population connectivity and genetic diversity (Clobert 2012), it is crucial to understand how dispersing individuals ("dispersers") respond to human infrastructure and if they respond differently compared to individuals settled within a home range ("residents"). Connectivity is often derived from habitat selection estimates (e.g. Zeller et al. 2012). Habitat selection can vary across life stages (e.g. Elliot et al. 2014, Barry et al. 2020), i.e. dispersers compared to residents. Thus, connectivity estimates may differ based on which life stage the habitat selection estimates are obtained from (Elliot et al. 2014).

Life stage-dependent movement decisions are important for the conservation of species, e.g., for defining potential connectivity and conservation corridors within and between populations (Abrahms et al. 2017). Dispersal is risky and energetically costly, as it often exposes individuals to unknown environments, especially in human-modified landscapes (Bonte et al. 2012, Gaynor et al. 2018, Gaynor et al. 2019) where the mortality risk can be higher (Johnson et al. 2009). This implies that dispersers are either unable to perceive and/or fail to adjust habitat use or movement in response to human risk due to their naivety (e.g. Thurfjell et al. 2017) or they might be more 'tolerant' or 'bold' and traverse risky habitats (Ciuti et al. 2012). In contrast, the home range is familiar to a resident, and risk encountered during movement may be mitigated through spatiotemporal shifts or altered habitat selection based on prior experience (e.g. Thurfjell et al. 2014, Hertel et al. 2016b). This strategy might not be available to naïve dispersers facing unexpected or less predictable, risky features on the human-dominated landscape (Fahrig 2007).

Habitat selection, i.e. the disproportionate use of a habitat feature in relation to its availability (Johnson 1980), can be estimated at different spatial scales depending on how availability is defined. Throughout this article we refer to habitat selection on the "landscape scale" when the availability is defined for an area many times the size of an animal's home range, e.g. an entire study area. We refer to habitat selection at the "local scale" when the availability is defined over smaller areas or shorter distances (e.g. for step selection functions) that an animal is able to traverse between successive (e.g. hourly) locations. Animals may respond differently to the same covariate depending on the scale of availability (Ciarniello et al. 2007). This also applies to human infrastructure, e.g. wolves (*Canis lupus*) avoid gravel roads within their home range but select gravel roads on a local scale (Zimmermann et al. 2014). Spatial scale can also be of importance for life stage-dependent movement and habitat selection, since dispersers navigating a novel landscape will likely only know what is in its immediate surroundings and have less knowledge at a landscape scale.

Here we use the brown bear (*Ursus arctos*) as a model species within a human-modified landscape in Sweden and study the impact of human infrastructure on life stage-dependent movement and habitat selection at the landscape and local scale. Like other large carnivores, brown bears have large home ranges (McLoughlin et al. 2000) and can travel long distances (Bartoń et al. 2019). There is ample scientific evidence that humans influence brown bear behaviour (e.g. Skuban et al. 2018, Le Grand et al. 2019, Lodberg-Holm et al. 2019), but it is unknown how dispersers navigate human-modified environments compared with residents. In this study, we focus on male brown bears in two life stages, dispersers and residents. We study life stage-dependent habitat selection and movement, and whether the effect of human infrastructure differs between the life stages. Further, we investigate the effect of infrastructure over two spatial scales of habitat selection, on the landscape scale and the local scale.

We hypothesize (H1) that human infrastructure is important for explaining movement of dispersers and residents male brown bears. In support of (H1), we predict (P1) that the most parsimonious model explaining movement and habitat selection for both dispersers and residents will include human infrastructure covariates. We hypothesize (H2) that dispersers will be more naïve and/or risk-tolerant compared to residents. In support of H2, we predict (P2) that dispersers will show less avoidance and be closer to human infrastructure (roads and buildings) than residents. Alternative to H2, we hypothesize (H3) that the dispersers sensitivity to human infrastructure will resemble the pattern of residents. Thus, in support of H3, we predict (P3) that there will be no difference in selection or avoidance for human infrastructure between the two life stages. We hypothesize (H4) that bears of both life stages will be more sensitive to human infrastructure at the local scale than the landscape scale. In support of H4, we predict (P4) that bears in each life stage will exhibit more avoidance of human infrastructure at the local compared to landscape scale.

Methods

Study area and study species

The study area is located in southcentral Sweden (approximately 61° N, 15° E), primarily within Gävleborg and Dalarna counties, spanning ~50,000 km² (Figure 1a). The landscape consists of boreal forest, bogs, lakes, and sparse agricultural land. The intensively managed forest is dominated by Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*) (Martin et al. 2010). There is an extensive road network, dominated by forestry gravel roads used for logging. Rolling hills comprise the general topography, with steeper and more rugged terrain in the western part of the study area (elevation range 0-997 m a.s.l.). Human settlement in the area is sparse, with an average of 8.64 inhabitants/km^2 and people tend to live in small villages (Statistics Sweden 2019). Current brown bear density in the study area ranges from ca 20 to 60 bears per 1000 km² (Bischof et al. 2020). Scandinavian brown bears generally avoid humans and their settlements (Steyaert et al. 2016). Male brown bears have large home ranges, on average 800 km^2 (Dahle and Swenson 2003), that can overlap several female ranges. We focused on males because dispersal is primarily male-biased (94%) (Zedrosser et al. 2007).

Telemetry data

Brown bears were captured, collared, and monitored from 2007 to 2017 as part of a long-term research project (www.bearproject.info). See Arnemo and Evans (2017) for a more detailed description of capture and handling procedures. Bears were fitted with GPS collars (GPS Plus, Vectronic Aerospace GmbH) with different programming schedules, but all were scheduled to take at least one GPS location each hour. All GPS locations were resampled to one location every hour (± 3 min tolerance). We retained only GPS locations with a dilution of precision (DOP) of less than 10 to minimize bias introduced by measurement errors (Frair et al. 2010). As our focus was on movement and habitat selection in relation to human infrastructure, we removed resting sites (day and night beds) (Ordiz et al. 2011). To identify bed sites in our data set, we used an algorithm based on movement criteria corresponding to the number of GPS locations and duration of such locations at visited and verified bear beds, yielding a validated success rate of 98.7% in bed detection (Steyaert et al. unpublished data).

Defining dispersing and resident bear-years

We focused only on natal dispersal, i.e. the permanent movement from birth site to first breeding, and will hereafter refer to it as dispersal. We visually looked through the GPS tracks of every bear-year, i.e. the unique combination of bear ID and year, to identify bear-years with dispersal events (Fig 1b). We performed 'path segmentation' (Edelhoff et al. 2016) on movement tracks of bear-years identified with a dispersal event and used hidden Markov models (HMM), a form of state-space modeling (Langrock et al. 2012), to define the transient period of dispersal. Hence, this method identified the onset and end of the dispersal event. For each track, we fit seven HMMs that varied in the number of states and the initial parameters (see supplement S1 for more details on model fitting and structures). We selected the most parsimonious (hereafter 'best') model using Akaike's Information Criterion (Akaike 1974) and used the Viterbi algorithm (Zucchini et al. 2016) to classify behaviors from the best model. Based on the classified behaviors we defined the onset and end for the dispersal period for the bear-years identified as dispersing. Only one dispersal period was defined for each of the bear-years identified as dispersing, and only data from this period for each bear-year was used in the further analysis for dispersers. We used the R package 'moveHMM' (Michelot et al. 2016) for fitting HMMs, model selection, and behavioral classification.

We defined resident bear-years as all years that a GPS-collared bear had been solitary for at least three years (Figure 1b), and no dispersal event had been detected. Males separate from their mother at 1 or 2 years of age (Dahle et al. 2003) and Støen et al. (2006) showed that 100% of male bears (N = 67) had dispersed by four years of age in the study area. Hence, based on our definition of a resident bear-year, we avoided the inclusion of solitary pre-dispersing males, i.e. young males that had left their mother but not dispersed yet, as resident bear-years. We only included data from residents with GPS locations in at least 70% of the days during the study period each year in the further analysis. The study period was defined as the period between 25 April and 20 August which is the active period after den emergence and prior to the hunting season for brown bears in Sweden.

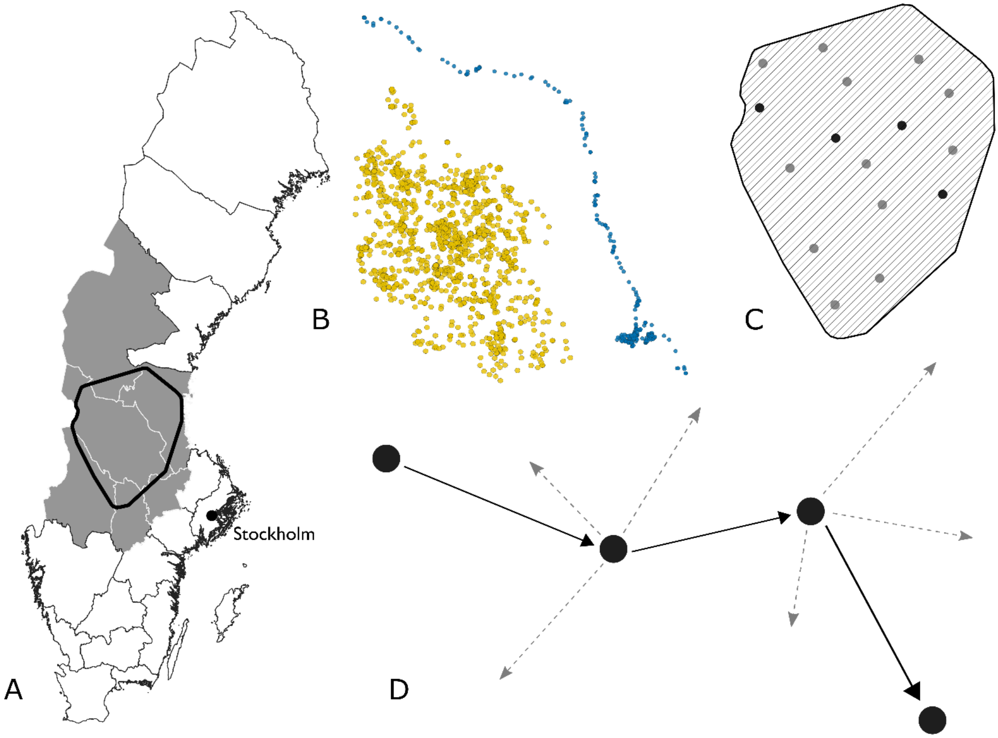

Figure 1. Diagram shows (A) study area within Sweden. (B) Differences between GPS locations of resident (gold) and dispersing (blue) male brown bears. (C) Availability space and sampling design for landscape scale for resource selection function (RSF) where grey dots represent available location and black points represent used. (D) Availability and sampling design for local scale for integrated step selection analysis (iSSA), where grey arrows represent available steps and black arrows represent used steps.

Covariates

We included the following 'core' covariates reported to influence brown bear habitat selection and movement in our analysis: terrain ruggedness index (TRI) (Nellemann et al. 2007), clearcuts (Nielsen et al. 2004), bogs (Leclerc et al. 2016), and distance to water (Steyaert et al. 2011, Steyaert et al. 2013). We calculated TRI from a digital elevation model (25 m resolution) with the R package spatialEco (Evans 2021) using a 3 × 3 cell moving window. We obtained data on landcover, roads and buildings from the Swedish Mapping, Cadastral and Land Registration Authority (https://www.lantmateriet.se/, "Fastighetskartan"). In Sweden, forestry practitioners must report timber harvesting activities, and we used the data for defining clearcuts, as logged areas from first cutting up to 10 years (Hertel et al. 2016a). We created a clearcut raster (presence = 1, absence = 0) for each year of the study.

We divided our road data into forestry and public roads. Forestry roads represent the majority of the road network in the study area (mean 1.27± 1.07 km/km^2) which are mainly small gravel roads built for forestry and usually open for the public. Public roads are larger and mostly paved and associated with higher traffic volume (0.18 km/km^2, SD=0.45). We included all buildings, the majority of which were houses or cabins (mean density 10.7± 39.4 buildings/km^2). We rasterized all covariates to a resolution of 25 m. We calculated the Euclidean distance from all cells in the raster to the nearest forestry road, public road and building, for each feature separately. All distance to covariates were log transformed prior to the analysis to attenuate covariate effects at longer distances.

Habitat selection and movement analyses

We used resource selection functions (RSF) to estimate habitat selection at the landscape scale (availability defined by the study area extent) (Manly et al. 2002), and integrated step selection analysis (iSSA) to estimate habitat selection and movement parameters at the local scale (availability defined by hourly relocations) (Avgar et al. 2016). RSF and iSSA models were fitted on the bear-year level, i.e. one model for each bear-year. The estimates from each model on the bear-year level were later averaged to obtain one population estimate for dispersing individuals and one for resident individuals. All GPS locations found in water, for both the RSF and the iSSA, were removed prior to analyses.

For the RSF, the availability space was defined as the 100% minimum convex polygon of all observed GPS locations for all bears-years buffered by the radius of a circular mean male home range size (r = ~18 km). For each bear-year, we randomly sampled available GPS locations from the availability space with a ratio of 20:1 available-to-use (Figure 1c). The RSF was obtained by fitting a generalized linear model with the glm function in R. The GPS locations were used as the response variable and coded 1 for used and 0 for available.

iSSA is a form of step selection functions that simultaneously estimate habitat selection and movement parameters (Avgar et al. 2016). We created "steps" by combining two consecutive GPS locations. Every step had a duration of 1 hour. An iSSA uses 'local scale availability', i.e. locations to which an animal could possibly have moved to in a given step. Based on the used steps, we calculated step lengths and fitted a gamma probability density function based on maximum likelihood estimation for both life stages combined. We drew 20 step lengths from the fitted gamma distribution for each used step (20:1 available-to-use ratio) and combined them with turning angles drawn from a uniform distribution to generate 'available' steps (Figure 1d). We assigned a unique stepID to each used step and its 20 associated available steps. The available steps represent what was locally available to bears at the starting point of every step. The iSSA was modelled using conditional logistic regression with used (coded as 1) and available steps (coded as 0) as the response variable, and the stepID as the stratum (for matching the used and available steps). Covariates for used and available steps were extracted at the start- and endpoints of the step. See Avgar et al. (2016) for a detailed description of iSSA.

Candidate models and model selection

For each RSF and iSSA, we developed candidate models for all dispersers and residents. Each candidate model set contained a model including a set of 'core covariates', i.e. habitat covariates that had been shown to be important for bear habitat selection. This core model was extended with additional covariates representing specific human infrastructure attributes to form competing candidate models. We also included a 'full' model containing all covariates into the analysis (Table 1). RSF and iSSA candidate model formulae were identical, except iSSA models included movement-related covariates (Table 1). For iSSA, we included step lengths (SL) and the natural logarithm of step lengths (lnSL) in all models to capture movement differences between life stages.

Table 1. Candidate models used to test the relative importance of forestry roads, public roads and buildings and local scale habitat selection and movement in male brown bears.

Model	Explanatory covariates
Resource Selection Function (landscape availability)	
Core	clearcut + bog + TRI + D2.Water
Forestry roads	Core + D2.ForestryRoads
Public roads	Core + D2.PublicRoads
Buildings	Core + D2.Building
Forestry and public roads	Core + D2.ForestryRoads + D2.PublicRoads
Forestry roads and buildings	Core + D2.ForestryRoads + D2.Building
Public roads and buildings	Core + D2.PublicRoads + D2.Building
Full	Core + D2.ForestryRoads + D2.PublicRoads + D2.Building
Integrated Step Selection Analysis (local availability)	
Core	SL[a] + log(SL) + cos(TA[b]) + clearcut_end[c] + bog_end + TRI_end + D2.Water_end[d] + log(SL):clearcut_start
Forestry roads	Core + D2.ForestryRoads_end + log(SL):D2.ForestryRoads_start
Public roads	Core + D2.PublicRoads_end + log(SL):D2.PublicRoads_start
Buildings	Core + D2.Building_end + log(SL):BuildlingDensity_start
Forestry and public roads	Core + D2.ForestryRoads_end + log(SL):D2.ForestryRoads_start + D2.PublicRoads_end + log(SL):D2.PublicRoads_start
Forestry roads and buildings	Core + D2.ForestryRoads_end + log(SL):D2.ForestryRoads_start + D2.Building_end + log(SL):BuildlingDensity_start
Public roads and buildings	Core + Public roads + log(SL):D2.PublicRoads_start + D2.Building_end + log(SL):BuildlingDensity_start
Full	Core + D2.ForestryRoads_end + log(SL):D2.ForestryRoads_start + D2.PublicRoads_end + log(SL):D2.PublicRoads_start + D2.Building_end + log(SL):BuildlingDensity_start

[a] Step length

[b] Turning angle

[c] "_end" and "_start" denote if the covariate was extracted from the start or the end point.

[d] "D2" is an abbreviation for "distance-to", and the distance to features were log transformed.

We performed model selection for each bear-year for both the RSF and iSSA models. We calculated AIC for all models for each bear-year and calculated the delta AIC from the best model for all candidate models within bear-years. We summed the delta AIC for all the candidate models and considered the model with the lowest mean AIC for each life stage as the best model for that life stage. Note that this may cause the best model to have a mean delta AIC > 0, because that model structure might not be 'best' across all bear-years for a given life stage and scale.

Population level effects

To infer habitat selection and movement responses at the population level, i.e. for dispersers and residents, we used inverse variance-weighted linear modelling (Murtaugh 2007), following the approach by Dickie et al. (2019). We fitted inverse-variance linear regression models separately for residents and dispersers and for each RSF and iSSA model set. We used either RSF or iSSA coefficients as response variables and included the mean availability of each variable as an explanatory variable for a given bear-year We used the inverse of the estimated variance for the coefficients as weights. The availability used in the inverse variance-weighted linear regression models was centered (x - mean of x), to aid in interpretation. The population-level coefficients can be interpreted as the mean coefficient at the mean availability for the males in the population (each for dispersers and residents and for the RSF and iSSA). We interpreted coefficients with 95% CIs overlapping with zero as 'indifferent' and non-overlapping 95% CIs as significant avoidance or selection, or as an effect of the covariate on movement rate (Dickie et al. 2019). We also recorded the direction of the coefficients for all individual bear-year models and reported the proportion of bear-year models that followed the same direction as the mean of all bear-years in a given life stage. This measure reflects the consistency of individual responses to covariates for each life stage between the local and the landscape scale for the population.

In iSSA, the estimated coefficients for SL, lnSL, and their interactions function as modifiers for the initial estimates of the scale and shape parameters, respectively, in the fitted gamma distribution (used for sampling the available step lengths) on step lengths (Avgar et al. 2016). For each bear-year, we adjusted the shape and scale parameters of the fitted gamma distribution. We calculated movement rates at the bear-year level by multiplying the adjusted shape and adjusted scale parameters from the gamma distribution. To illustrate changes in movement rates, we calculated movement rates at several levels for each of the focal covariates and kept all other interacting covariates (with lnSL) constant at their mean observed step value. Movement rates at the population level were obtained by calculating the mean of individual bear-year movement rates across the different levels of a given focal variable and for each life stages separately (iSSA only).

For both RSF and iSSA results, we calculated the relative selection strength (RSS) following Avgar et al. (2017) for all covariates in each analysis. The RSS was calculated based on the population-averaged estimates from the inverse-variance weighted linear models (one for each life stage and availability scale). For step selection functions (iSSA), the ln RSS is a relative measure of how likely the individual is to select a step that ends at location x_1 in relation to a step that ends at location x_2 (the reference location). For "distance to feature" covariates, we calculated the RSS moving one mean step length closer to the feature compared to staying at the same location, and for the other covariates we calculated the RSS of selecting a given feature over the mean of the covariate.

All spatial density and distance calculations were performed in GRASS 7.2 (GRASS Development Team 2017). We used the 'amt' package (Signer et al. 2019) for iSSA and R 3.6.0 all other statistical analyses (R Core Team 2021).

Results

Dispersal phases lasted from 21 to 65 days (mean: 43 ± 15) for the 15 males (15 bear-years) defined as dispersing. During their dispersal events, these bears ranged in age from 2 to 4 years old (mean 2.7 years, n=15). We identified 20 males spanning 46 bear-years that met our resident criteria. The resident bear-years ranged in age from 4 to 21 years old (mean 9.7 years, n=45, one with unknown age).

The bed removal procedure removed 28% of the GPS-locations, leaving 75 212 GPS-locations for statistical analysis. Mean step lengths were 729 m for dispersers and 586 m for residents. Used locations rarely (<0.5%) occurred in bogs and clearcuts (Table 2), and the mean distance to water was 694 m for dispersers and 692 m for residents. There were large differences between dispersers and residents in the mean values of their used locations for human covariates. Used locations of dispersers and residents occurred on average 787 and

1188 m from buildings, 3032 and 5156 m from public roads, and 253 and 291 m from forestry roads, respectively.

Table 2. The mean and standard deviation (in parentheses) for all used and available points in each resource selection function (RSF) and integrated step-selection analyses (iSSA), i.e. landscape and local availabilities, respectively, for each dispersing and resident male brown bears. Local availability was summarized using the end points of steps. Values for clearcut and bog are the proportion of all (end)points that were located in a clearcut or bog, respectively.

	Resident		Dispersal	
Covariate*	Used	Available	Used	Available
Landscape scale (RSF)				
bog	0.06 (0.23)	0.10 (0.30)	0.04 (0.19)	0.10 (0.30)
clearcut	0.06 (0.23)	0.06 (0.24)	0.06 (0.24)	0.06 (0.24)
D2.Water	692 (513)	639 (492)	694 (502)	639 (493)
TRI	6.09 (4.83)	5.08 (4.19)	5.48 (4.44)	5.08 (4.18)
D2.Building	$1.19*10^{3}$ (667)	872 (657)	787 (555)	874 (659)
D2.PublicRoads	$5.16*10^{3}$ ($3.84*10^{3}$)	$3.09*10^{3}$ ($3.07*10^{3}$)	$3.03*10^{3}$ ($2.89*10^{3}$)	$3.11*10^{3}$ ($3.08*10^{3}$)
D2.ForestryRoads	291 (251)	318 (489)	253 (205)	320 (498)
Local scale (iSSA)				
bog	0.06 (0.23)	0.09 (0.29)	0.04 (0.19)	0.06 (0.24)
clearcut	0.06 (0.23)	0.07(0.25)	0.06 (0.24)	0.07 (0.25)
D2.Water	692 (513)	671 (519)	694 (502)	692 (509)
TRI	6.09 (4.83)	5.65 (4.47)	5.48 (4.44)	5.29 (4.35)
D2.Building	$1.19*10^{3}$ (667)	$1.18*10^{3}$ (671)	787 (555)	788 (571)
D2.PublicRoads	$5.16*10^{3}$ ($3.84x10^{3}$)	$5.14*10^{3}$ ($3.86*10^{3}$)	$3.03*10^{3}$ ($2.89*10^{3}$)	$3.03*10^{3}$ ($2.90*10^{3}$)
D2.ForestryRoads	291 (251)	290 (261)	253 (205)	248 (205)

* D2 is an abbreviation for 'distance-to' and is in meters. 'bog', 'clearcut', and 'TRI' for local availability are endpoints of steps.

The full models had the lowest mean delta AIC at both spatial scales for dispersers (landscape scale ΔAIC = 0.82, local scale ΔAIC = 2.06) as well as residents (landscape scale ΔAIC = 0.32, local scale ΔAIC = 0.96). The full model scored the lowest AIC for 40% and 20% of the bear-years for the dispersers at the landscape scale and local scale, respectively (Table 3). The full model scored the lowest AIC for 78% and 63% of the bear-years for the residents at the landscape scale and local scale, respectively (Table 3). The four best RSF (landscape scale) models for both life stages contained the covariate public roads, while the four best iSSA models (local scale) for both life stages contained the covariate forestry roads.

Table 3. Model selection for dispersing and resident male brown bears of model sets fit using resource selection functions (RSFs) and integrated step selection analysis (iSSA). Mean ΔAIC is the mean ΔAIC for all bear-years during the given life stage (n = 15 for dispersing males and n = 46 for resident males). Minimum AIC tally is the number of times that a given model had the lowest AIC among candidate models within a bear-year and the proportion of the model-specific tally for model sets is given in parentheses.

	Resident		Dispersal	
Model	Mean ΔAIC	Minimum AIC tally	Mean ΔAIC	Minimum AIC tally
Landscape scale (RSF)				
Full	**0.32**	**36 (0.78)**	**0.82**	**6 (0.40)**
Public roads and buildings	21.11	6 (0.13)	6.24	6 (0.40)
Forestry roads and public roads	189.84	0 (0)	20.88	1 (0.07)
Public roads	204.26	0 (0)	26.67	0 (0)
Forestry roads and buildings	536.49	4 (0.09)	33.84	0 (0)
Buildings	556.54	0 (0)	39.46	1 (0.07)
Forestry roads	1019.13	0 (0)	74.65	1 (0.07)
Core	1035.81	0 (0)	81.20	0 (0)
Local scale (iSSA)				
Full	**0.96**	**29 (0.63)**	**2.06**	**3 (0.2)**
Forestry roads and public roads	11.38	7 (0.15)	3.62	3 (0.2)
Forestry roads and buildings	11.47	5 (0.11)	6.74	4 (0.27)
Forestry roads	22.82	2 (0.04)	9.88	2 (0.13)
Public roads and buildings	40.22	2 (0.04)	15.07	0 (0)
Public roads	49.80	0 (0)	17.42	2 (0.13)
Buildings	50.68	1 (0.02)	19.95	0 (0)
Core	61.24	0 (0)	24.57	1 (0.07)

Core covariates

At the population level, both dispersers and residents avoided bogs at both spatial scales, showing the same pattern for >91% of the bear-years in each model (Table 4, Figure S1). Both dispersers and residents avoided clearcuts locally, but were indifferent to them on the landscape scale (Table 4, Figure 2). Dispersers and residents were indifferent to distance to water on the landscape scale, but residents selected for distances farther from water at the local scale (Table 4, Figure 2). Dispersers were indifferent to TRI at either scale, however, residents selected for higher TRI at both scales (Table 4). In general, dispersers showed more individual variation and less consistency in their habitat selection towards the core covariates, i.e. a lower proportion of all bear-year estimates conformed to the same direction as the population mean effect, for dispersers compared to residents (Table 4; dispersers: mean of all proportions = 0.59, range = 0.333 – 0.933; residents: mean of all proportions = 0.79, range = 0.391 – 0.957). Only residents moved faster when their step started in a clearcut.

Human infrastructure

At the population level and across scales, dispersers were indifferent to human infrastructure, except for buildings which they avoided at the local scale. Residents avoided buildings and public roads, and selected forestry roads at both local and landscape scale. Residents did not alter their movement rate closer to buildings, while dispersers moved faster closer to buildings (Table 4, Figure S1). Both dispersers and residents increased their movement rate closer to forestry roads and closer to public roads (Table 4).

Dispersers and residents moved 551 m/h and 599 m/h, respectively, faster when their step started on a forestry road compared to the movement rate when starting 500 m away from a forestry road (Figure 3a). Similarly, dispersers and residents moved 141 m/h and 169 m/h, respectively, faster when their step started on a public road compared to the movement rate at 500 m away from a public road (Fig 3b). In other words, the change in the movement speed for dispersers and residents was 3.26 and 3.54 times higher, respectively, on forestry roads compared to public roads.

Table 4. Average habitat selection and movement rate coefficients for dispersers and residents at the landscape (RSF) and local scale (iSSA). Each bear-year was modelled separately before inverse-variance weighted linear models were run for both dispersers and residents. The proportion columns ('prop') give the proportion of the bear-years that had coefficient estimates in the same direction as the averaged coefficient (n =15 for dispersers and n= 46 for residents). Bolded values indicate that the 95% confidence interval of the coefficients do not overlap zero.

		Resident					Dispersal				
category	coefficient name	estimate	CI lower	CI upper	prop	direction	estimate	CI lower	CI upper	prop	direction
Landscape scale (RSF)											
habitat selection	Bog	**-0.638**	**-0.801**	**-0.476**	0.913	avoided	**-0.934**	**-1.318**	**-0.549**	0.933	avoided
habitat selection	Clearcut	0.001	-0.132	0.134	0.391	indifferent	0.023	-0.263	0.310	0.333	indifferent
habitat selection	TRI	**0.049**	**0.032**	**0.066**	0.783	selected	0.020	-0.011	0.051	0.533	indifferent
habitat selection	D2.Water	0.044	-0.056	0.143	0.478	indifferent	0.063	-0.094	0.220	0.533	indifferent
habitat selection	D2.buildings	**0.324**	**0.219**	**0.430**	0.913	avoided	-0.028	-0.114	0.059	0.400	indifferent
habitat selection	D2.ForestryRoads	**-0.042**	**-0.051**	**-0.032**	0.783	selected	-0.008	-0.035	0.019	0.400	indifferent
habitat selection	D2.PublicRoads	**0.295**	**0.146**	**0.443**	0.870	avoided	0.002	-0.084	0.088	0.533	indifferent
Local scale (iSSA)											
habitat selection	Bog_end	**-0.653**	**-0.727**	**-0.580**	0.935	avoided	**-0.959**	**-1.198**	**-0.719**	0.933	avoided
habitat selection	Clearcut_end	**-0.423**	**-0.520**	**-0.326**	0.717	avoided	**-0.375**	**-0.660**	**-0.090**	0.600	avoided
habitat selection	TRI_end	**0.022**	**0.017**	**0.026**	0.913	selected	0.005	-0.007	0.016	0.600	indifferent
habitat selection	D2.Water_end	**0.119**	**0.096**	**0.142**	0.957	avoided	-0.020	-0.099	0.059	0.333	indifferent
habitat selection	D2.buildings_end	**0.060**	**0.021**	**0.100**	0.761	avoided	**0.111**	**0.016**	**0.205**	0.800	avoided
habitat selection	D2.ForestryRoads_end	**-0.059**	**-0.075**	**-0.043**	0.804	selected	-0.008	-0.054	0.038	0.467	indifferent
habitat selection	D2.PublicRoads_end	**0.093**	**0.052**	**0.133**	0.826	avoided	0.022	-0.074	0.118	0.800	indifferent
movement	SL	0.000	0.000	0.000	0.674	indifferent	**0.000**	**-0.001**	**0.000**	0.867	faster
movement	log(SL)	-0.010	-0.215	0.195	0.109	indifferent	0.070	-0.277	0.416	0.867	indifferent
movement	log(SL)*clearcut_start	**0.120**	**0.076**	**0.163**	0.826	faster	0.091	-0.033	0.215	0.867	indifferent
movement	log(SL)*D2.buildings_start	0.008	-0.016	0.033	0.543	indifferent	**-0.032**	**-0.058**	**-0.007**	0.467	faster
movement	log(SL)*D2.ForestryRoads_start	**-0.071**	**-0.082**	**-0.061**	0.978	faster	**-0.070**	**-0.106**	**-0.033**	0.800	faster
movement	log(SL)*D2.PublicRoads_start	**-0.022**	**-0.036**	**-0.008**	0.717	faster	**-0.052**	**-0.090**	**-0.014**	0.667	faster

* D2 is an abbreviation for "distance to"

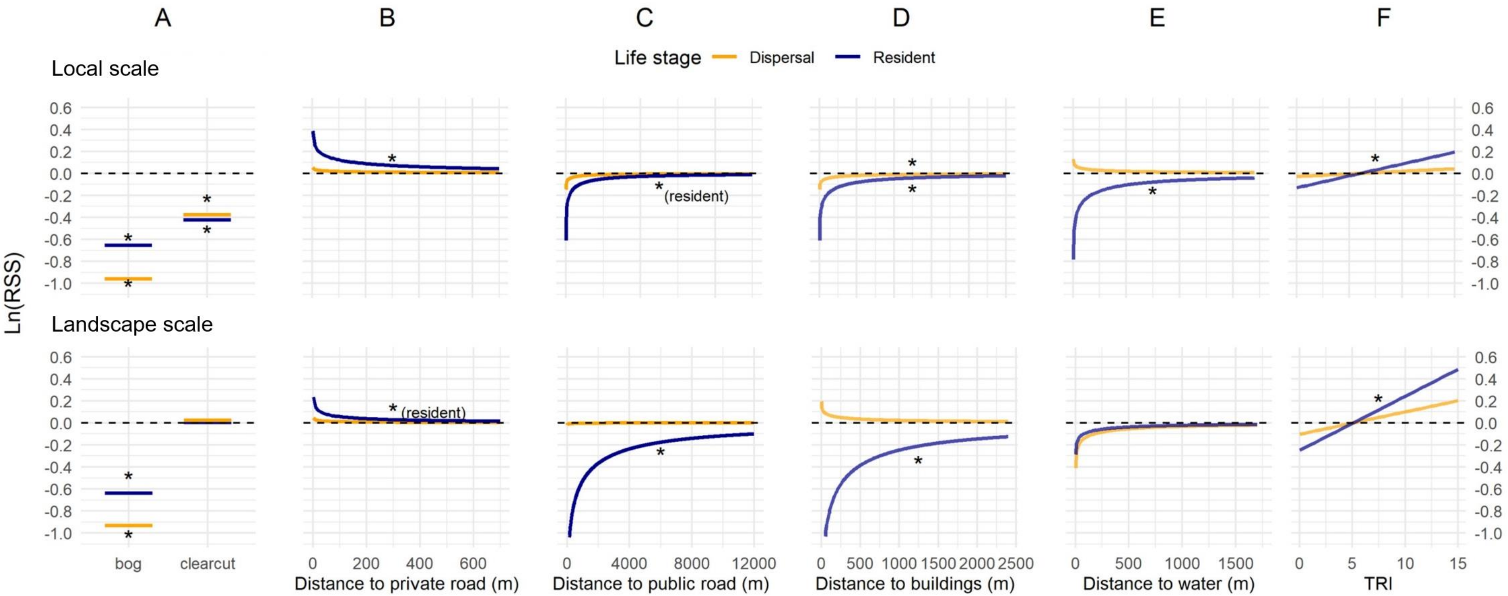

Figure 2. Relative selection strength (RSS) for dispersing and resident male brown bears from the inverse-variance weighted linear model. Column (A) is the RSS of staying in the habitat reference category (i.e. not bogs or clearcuts) compared to selecting for either bogs or clearcuts. Columns (B), (C), (D), and E) show the RSS of moving closer towards the features (leftward) vs staying at the same distance across a range of starting distances (x-axis). Column (F) illustrates the RSS of selecting a given TRI value (x-axis) over the mean value (4.19).
* indicates covariate was significant for respective ‘Resident’ and ‘Dispersal’ models (95% CIs did not overlap zero) for the curve that it is nearest. In cases where placement could be unclear, clarification is given in parenthesis.

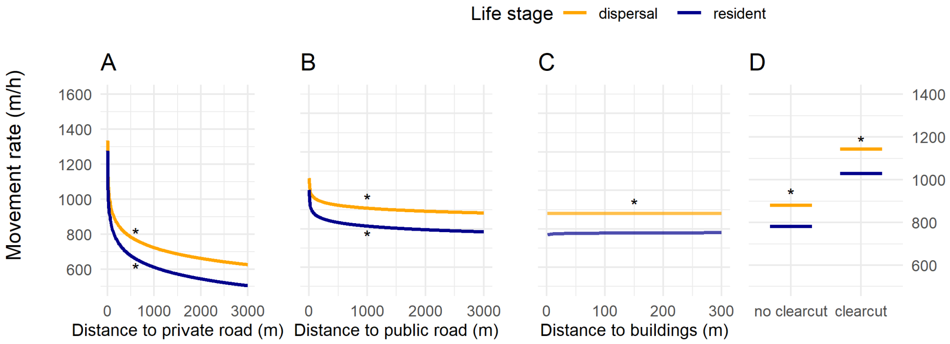

Figure 3. Mean movement rates (in meters/hour) for dispersing and resident male brown bears in relation to (A) distance to forestry roads, (B) distance to public roads with the same range as for forestry roads, (C) distance to buildings, (D) and whether or not the bear started in a clearcut. The focal variable has been varied while all other variables have been kept constant the mean of all used starting points and outside a clearcut for (A), (B), and (C). The asterisks * near 'Resident' and 'Dispersal' curves indicate that respective model estimates were significant (95% CIs did not overlap zero).

Discussion

We found evidence that human infrastructure is important for describing habitat selection and movement (P1 in support of H1) regardless of life stage at both the local and landscape scale, as models containing human infrastructure performed best. However, at the landscape scale, dispersers appeared indifferent towards most landscape features, including human infrastructure (Table 4 and Figure S1). Dispersers were more often indifferent towards human infrastructure on both scales (P2 in support of H2), and did not share the same avoidance patterns of human infrastructure as residents (no support of H3). Dispersers were less sensitive towards human infrastructure on the landscape scale than local scale, this did not apply to residents (P4 partial support of H4).

Human infrastructure appears important for both dispersers and resident at the local scale and the landscape scale (H1). At the local scale, dispersers as well as residents avoided buildings, but dispersers moved faster closer to buildings suggesting they are perceived as risky habitat. Both dispersers and residents moved faster closer to public and forestry roads. Residents appeared to treat public roads as risky habitat (avoiding and moving faster) whereas they used forestry roads for travel (selecting and moving faster). Movement facilitation in relation to linear features, such as roads, have also been observed in other areas (Dickie et al. 2019). Dispersers were indifferent in terms of habitat selection for either road type and traveled faster near them, indicating that each public and forestry roads may potentially serve as both risky features (Proctor et al. 2019) and/or as facilitators of movement (Roever et al. 2010) during dispersal. The actual risk along forestry roads during our study period was assumed to be relatively low, as traffic accidents do not account for a large proportion of mortality (<2%; Bischof et al. 2009) and our study ended before the onset of the hunting season, after which roads have an additive effect on hunting success (Bischof et al. 2017). However, bears are sensitive to human-derived risk and likely attempt to avoid human contact throughout the year (Ordiz et al. 2014).

Although the best models at the landscape scale contained human infrastructure for both life stages (support of H1), dispersers were mainly indifferent to all human infrastructure. They also used habitat closer to human infrastructure compared to residents. This is in support of H2 that dispersers were either naïve and/or risk-tolerant to human infrastructure, which in turn indicates no support for the alternative H3. This was also evident at the local scale, where dispersers avoided only buildings. In contrast, residents were sensitive to human infrastructure and avoided both public roads and buildings at both availability scales. Hence, we suggest that naivety and/or risk-tolerance plays a prominent role in the behavior of dispersers when navigating novel landscapes outside of the natal range, i.e., dispersers increase their exposure to human-derived risks on the landscape. Dispersal is often considered risky due to movement through novel landscapes (Long et al. 2021), and human-derived risks can have an additive effect beyond what is ‘normally expected’ by animals when weighing the decision to disperse and where to go (Johnson et al. 2009). In contrast, the assumption that residents are more familiar with their home ranges than dispersers are on novel terrain, is supported by the residents avoidance of potential human-derived risk at both local and landscape scales.

Alternatively, areas with lower human mortality risk might not be preferred by dispersers, due to increased intraspecific mortality risk originating from larger, adult males (Swenson et al. 2001, Elfstrom et al. 2014), which would effectively sandwich dispersing males between two sources of mortality risk (sensu Lone et al. 2014), i.e. humans and conspecifics. This is consistent with our core covariate findings, i.e., residents selected for rugged terrain, while dispersers did not, maybe partially related to the avoidance of larger adult males (Nellemann et al. 2007). Similarly, clearcuts and bogs are open habitat types in which bears have less cover from human detection (Sahlén et al. 2015). Such habitats were avoided by both dispersers and residents at the local scale, indicating a similar avoidance of potential human-derived risk in these open or semi-open habitat types. Dispersing males in other large carnivores, such as African lions (*Panthera leo*), depict a similar pattern with weaker avoidance or no avoidance of human infrastructure (Elliot et al. 2014). Lack of avoidance of human infrastructure may be explained by avoidance of larger males. However, it can also be explained by the inability of the dispersing individuals to detect these features at relevant distances. Similarly, the lack of selection for landscape features preferred by older males may also be explained by the dispersing males not knowing where to find these features when moving through the landscape, e.g. the lack of selection for rugged terrain by dispersers in this study. This is supported by the dispersers not selecting for any features at all on any of the scales.

We found partial support of H4, that the scale of availability influenced how sensitive bears were towards human infrastructure, as only dispersers were more selective at the local scale compared to landscape scale (P4). Furthermore, dispersers more often treated human infrastructure indifferently in habitat selection and movement rates (Table 4). In this study area, bears are intensively hunted annually (upwards of 10% of the population; Frank et al. 2017), putting them into contact with human-derived risk virtually everywhere in the study area, and bears modify their behavior to minimize human predation risk (Ordiz et al. 2012, Hertel et al. 2016b, Leclerc et al. 2017). Hence, resident bears likely select areas where human impact is low (Nellemann et al. 2007) and further reduce potential encounter rates with humans through behavioral changes on local spatial scales and temporally (Ordiz et al. 2011, Ordiz et al. 2012). As dispersers were more exposed to human infrastructure, they also potentially exposed themselves to higher human predation risk. Indeed, survival probability of males is lower than females at the onset of dispersal in this bear population (Bischof et al. 2017, Frank et al. 2020), which could partially be due to male-biased dispersal (Støen et al. 2006), increased risk-taking or tolerance during dispersal, and/or the inability of dispersing males to adequately recognize and adjust to novel human-derived mortality risk.

Our study highlights that life stage can influence how individuals respond to human landscape features across scales. Other studies that separated life stages and analyzed habitat selection patterns of large carnivores have shown higher tolerance of dispersers towards human infrastructure. For example, dispersing African wild dogs (*Lycaon pictus*) in Kenya occurred closer to higher human population densities (O'Neill et al. 2020) and dispersing gray wolves (*Canis lupus*) showed lower avoidance of human infrastructure compared to residents (Barry et al. 2020). Given the substantial space-requirements of large carnivores, their conservation has focused on how populations can become or remain connected in human-dominated landscapes (e.g. Wolf and Ripple 2018). The key to attaining reliable connectivity models is the recognition that animal dispersal decisions and movement patterns are life stage-dependent. Our findings suggest that risk-tolerant and/or naïve dispersers might use movement pathways that more risk-averse or habitat-familiar residents would avoid. As a result, landscape resistance or connectivity maps derived from dispersal movement data may provide more numerous as well as more realistic pathways than those derived from resident movement data alone (Killeen et al. 2014, Vasudev et al. 2015, Blazquez-Cabrera et al. 2016). The differences in scale-specific decisions between dispersers and residents provide the foundation for understanding functional connectivity of a population, in which animals disperse and establish a home range for subsequent reproduction (Zeller et al. 2020). Attaining individual-based dispersal data on large carnivores is costly but informative, particularly in human-dominated systems where coexistence has been touted as not only possible, but imperative on some level for large carnivore persistence (Chapron et al. 2014, Oriol-Cotterill et al. 2015, Lamb et al. 2020).

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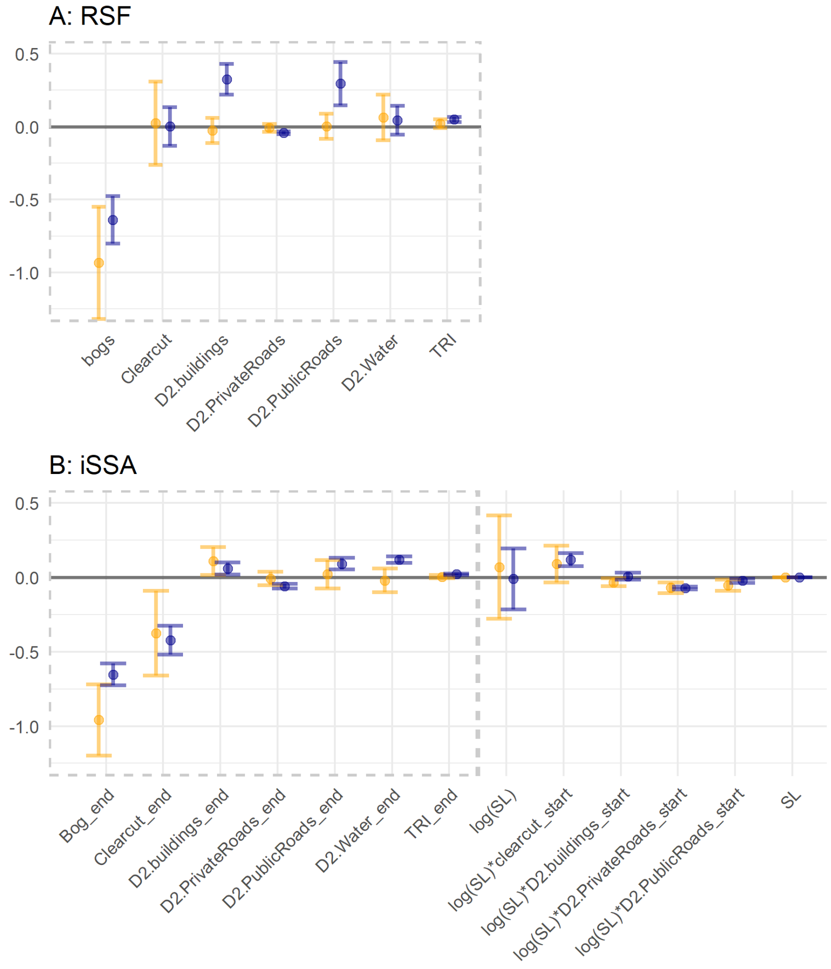
Supplementary material


A: RSF

B: iSSA

Figure S1. Coefficient plots from resource selection functions (A) and the integrated step selection analysis (B). Yellow color indicate dispersing males and blue color indicate resident males.

Table S1. The mean availability coefficient for the weighted linear models calculating the population estimates. Significant coefficients are indicated in bold and indicate a functional response, i.e. that the effect of the covariate variates with the availability.

		Resident			Dispersal		
			95% Confidence interval			95% Confidence interval	
category	coefficient (response)	mean availability (coefficient)	low	high	mean availability (coefficient)	low	high
Integrated Step Selection Analysis (local availability)							
habitat selection	Bog_end	-0.729	-2.932	1.475	0.214	-5.224	5.652
habitat selection	Clearcut_end	**8.221**	**4.026**	**12.416**	**19.160**	**8.428**	**29.891**
habitat selection	D2.buildings_end	0.021	-0.137	0.179	0.099	-0.061	0.260
habitat selection	D2.PrivateRoads_end	0.062	-0.016	0.139	-0.002	-0.208	0.205
habitat selection	D2.PublicRoads_end	**0.168**	**0.080**	**0.256**	-0.083	-0.215	0.049
habitat selection	D2.Water_end	0.067	-0.018	0.152	0.298	-0.123	0.719
habitat selection	TRI_end	-0.001	-0.005	0.003	**0.013**	**0.003**	**0.022**
movement	log(SL)	-0.024	-0.048	0.001	0.009	-0.005	0.022
movement	log(SL)*clearcut_start	-0.621	-2.150	0.908	1.193	-1.437	3.824
movement	log(SL)*D2.buildings_start	**-0.121**	**-0.215**	**-0.027**	**-0.074**	**-0.121**	**-0.027**
movement	log(SL)*D2.PrivateRoads_start	0.034	-0.015	0.083	-0.010	-0.173	0.154
movement	log(SL)*D2.PublicRoads_start	-0.007	-0.034	0.021	**-0.057**	**-0.110**	**-0.004**
movement	SL	0.000	0.000	0.000	0.000	0.000	0.000

Supplement S1

Human impact on life stage dependent movement in male brown bear (*Ursus arctos*) Thorsen et al. 202

Step-by-step documentation for hidden Markov model (HMM) fitting procedure in moveHMM v1.7

In this supplement, we go step-by-step through the fitting procedure of hidden Markov models (HMMs) for an individual male bear, W0612, and the selection of dates for the dispersal process.

Load required packages:

```r
library(moveHMM)
library(doBy)
library(plyr)
library(ggplot2)
library(plotly)
```

Importing and prepping the data

Import geolocations* from one male bear (W0612)

```r
W0612 <- readRDS("W0612_anon.rds")

# subset to active season, 01 April - 01 October

W0612 <- subset(W0612, format(GMT.date,'%m%d')>='04-01' & format(GMT.date, '%m%d')
                <= '10-02')
```

Create a ‘move’ object from geolocations. This will calculate distance traveled between each step as well as turning angles of movement.

```r
W0612Move <- prepData(W0612, type = "UTM", coordNames = c("x", "y"))
```

We keep only steps that are separated by an hour. This prevents unrealistic step lengths and turning angles from being included in the modeling procedure.

```r
# copy to a new object called "W0612Reg"

W0612Reg <- W0612Move

# get time differences between each step
```

```
W0612Reg$diffHour <- difftime(W0612Move$GMT.date[1:length(W0612Move$GMT.date)] ,
                              W0612Move$GMT.date[2:length(W0612Move$GMT.date)])

# keep only times that are separated by an hour

W0612Reg <- W0612Reg[W0612Reg$diffHour >= -1 & W0612Reg$diffHour < 2, ]
```

Fitting HMMs for 2- and 3-states

In the following section, we first fit three models with two behavioral states, representing short and long movement patterns. Later, we fit four models with three behavioral states.

Fitting a hidden Markov model to movement data requires four starting parameters specified for n behavioral states. The first parameter is mean step length distance, mu. The second is the standard deviation for each step-length mean, sigma. The third parameter is the mean turning angle, angleMean. The final parameter is kappa, concentration of the turning angle.

Each set of initial parameters are different, which increases the chance of finding the global maximum (Michelot et al. 2016). The first set of initial parameters were chosen by looking at summaries of the step lengths and turning angles, histograms and density plots. The second set of initial parameters were "wider" (smaller/larger) values than the first set. The initial parameters for the third model were the estimated parameters from the previous model.

There is no exact science behind the selection of initial parameters, but practical guidance is available. One should always try at least a few different starting parameters and check that the global maximum has been successfully estimated.

Model specification is as follows:

fitHMM(move_object, number of behavior states, initial parameters, theoretical distribution for step lengths, theoretical distribution for turning angles)

We selected the gamma distribution for the step lengths and the vonMises distribution for the turning angles.

```
# first set of initial parameters

mu2a <- c(10, 1000)
sigma2a <- c(20, 2000)
angleMean2a <- c(pi, 0.005)
kappa2a <- c(0.2, 2)
stepPar2a <- c(mu2a, sigma2a)
anglePar2a <- c(angleMean2a, kappa2a)

# fit the first 2-state HMM

W0612_2a <- fitHMM(W0612Reg, nbStates = 2, stepPar0 = stepPar2a, anglePar0 = anglePar2a,
                   stepDist = "gamma", angleDist = "vm")
W0612_2a
```

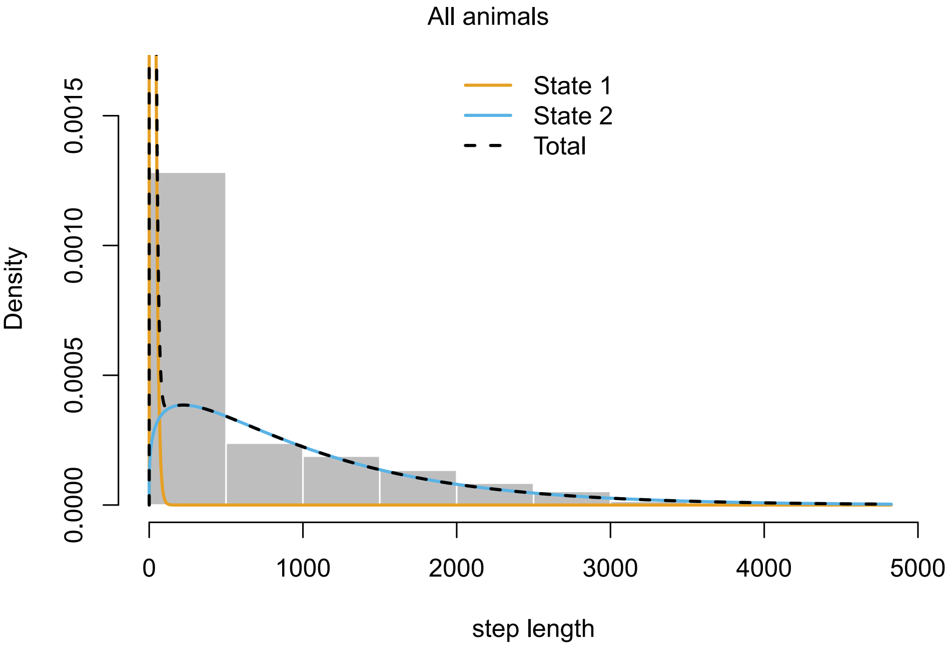
```
## Value of the maximum log-likelihood: -26234.64
##
## Step length parameters:
## ----------------------
##       state 1   state 2
## mean 17.00918 1042.0373
```

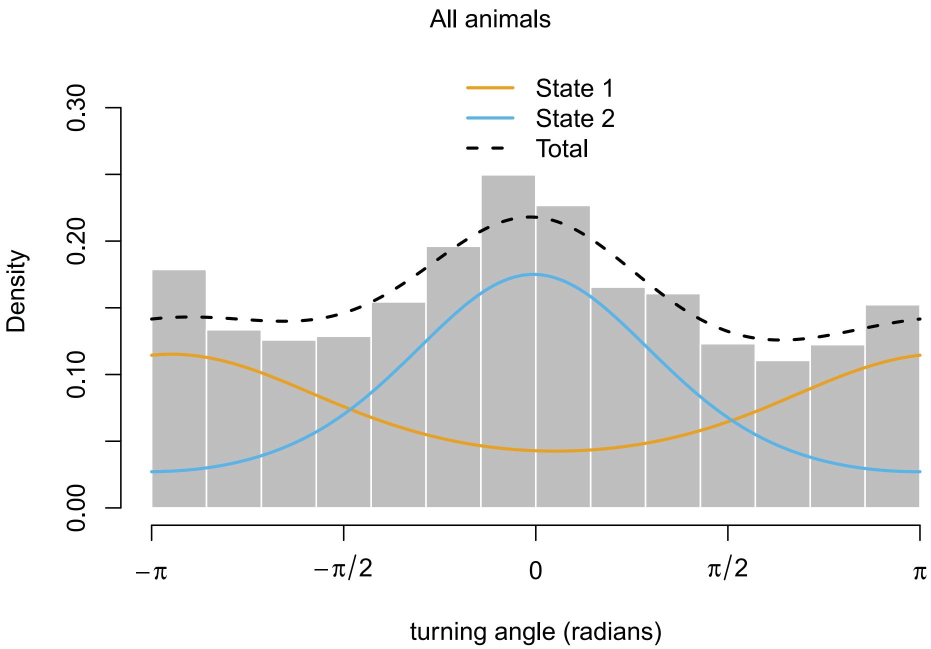
```
## sd   14.02674  924.3737
##
## Turning angle parameters:
## ------------------------
##                   state 1     state 2
## mean           -2.9787585 -0.01945528
## concentration  0.4975304  0.93201121
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##              1 -> 2    2 -> 1
## intercept -1.281184 -1.476296
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]
## [1,] 0.7826513 0.2173487
## [2,] 0.1859875 0.8140125
##
## Initial distribution:
## --------------------
## [1] 1.154684e-06 9.999988e-01
```

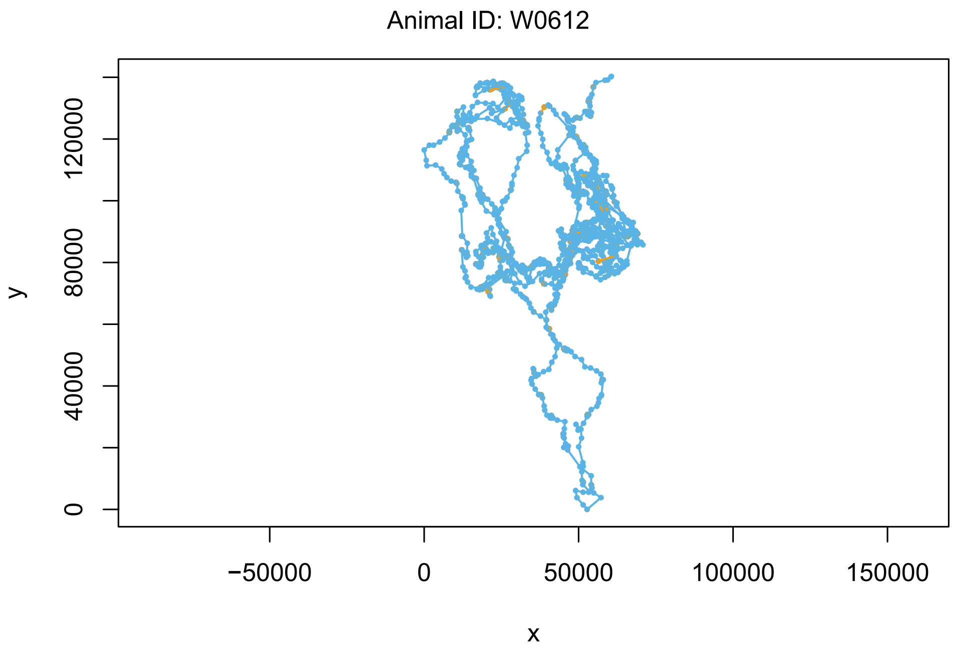
Plotting the fitted model gives three outputs: histograms of the step lengths and turning angles classified for each state overlaid by the estimated density function and a trajectory that has been color-coded by classified state.

```
# plot the fitted model results

plot(W0612_2a)
```

```
## Decoding states sequence... DONE
```


All animals
State 1
State 2
Total
Density
0.0000
0.0005
0.0010
0.0015
0
1000
2000
3000
4000
5000
step length


All animals
State 1
State 2
Total
Density
0.00
0.10
0.20
0.30
$-\pi$
$-\pi/2$
0
$\pi/2$
π
turning angle (radians)



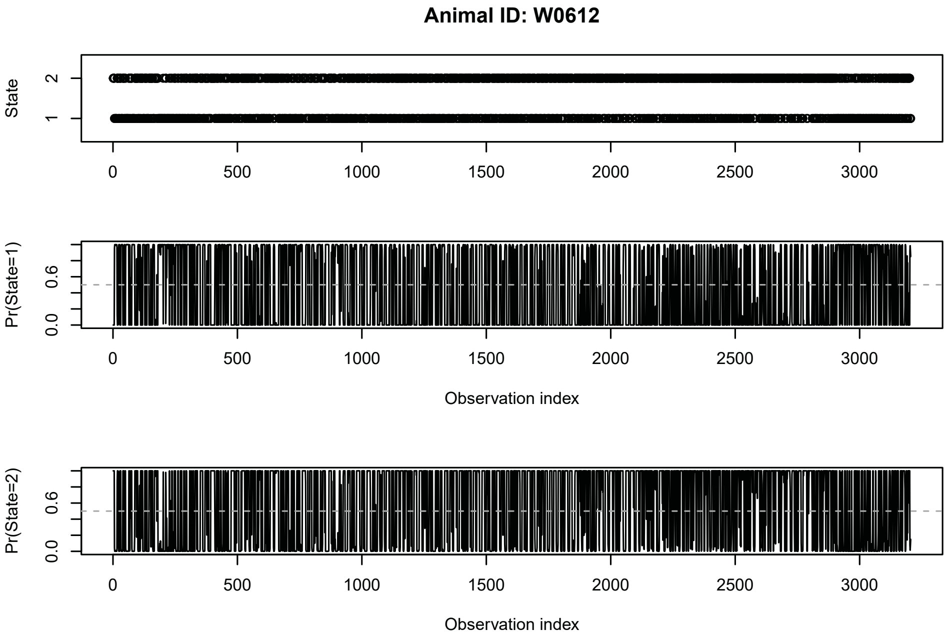
The Viterbi algorithm (Zucchini and MacDonald 2009) assigns probable behavioral states to each step. We show the first 20 assigned states for the first model. The plotStates function returns a plow showing the probability of being in a particular state at each observation index location (step).

```
head(viterbi(W0612_2a), n = 20)
```

```
##  [1] 2 2 2 2 2 1 1 1 1 1 1 1 1 1 1 1 2 2 2 2
```

```
plotStates(W0612_2a)
```

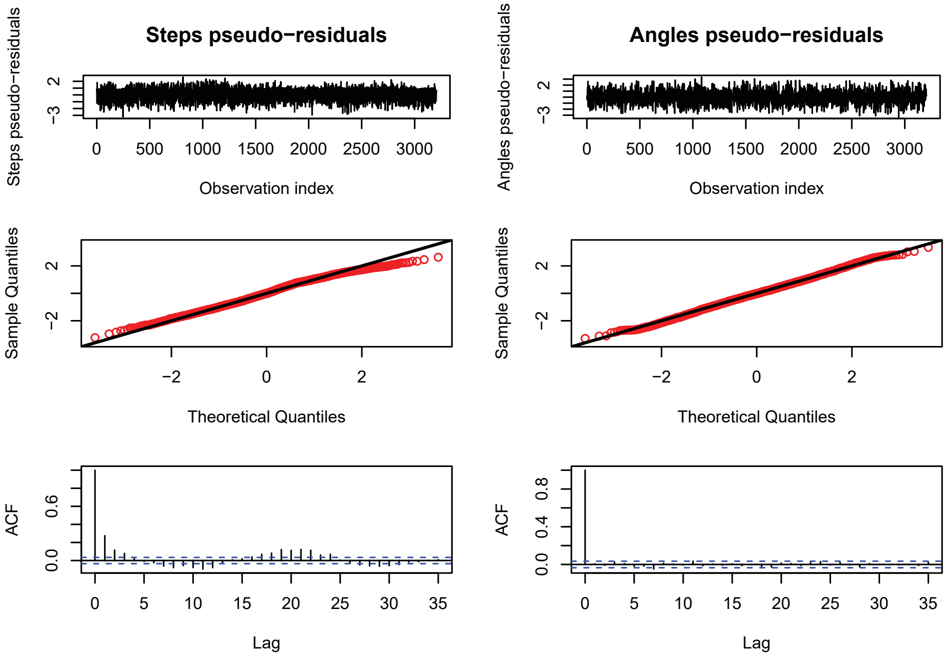
```
## Decoding states sequence... DONE
## Computing states probabilities... DONE
```



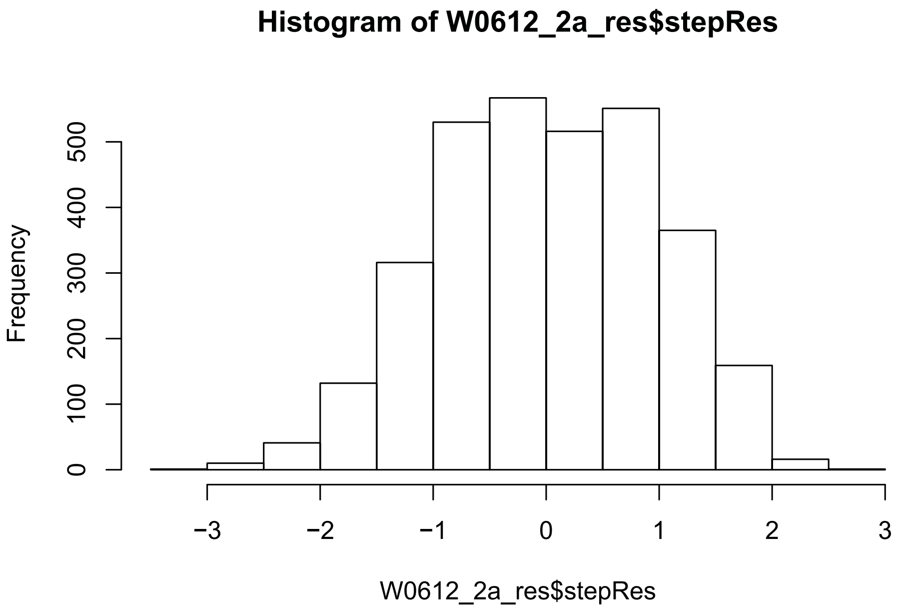
The final step of the HMM fitting process is to look at the pseudo-residuals to check the fit of the model to the data. Plotting the model object directly will show the time series, qq-plots, and sample ACF functions of the pseudo-residuals for steps and turning angles. We also produced histograms of the pseudo-residuals for step lengths and turning angles.

```r
plotPR(W0612_2a)
```

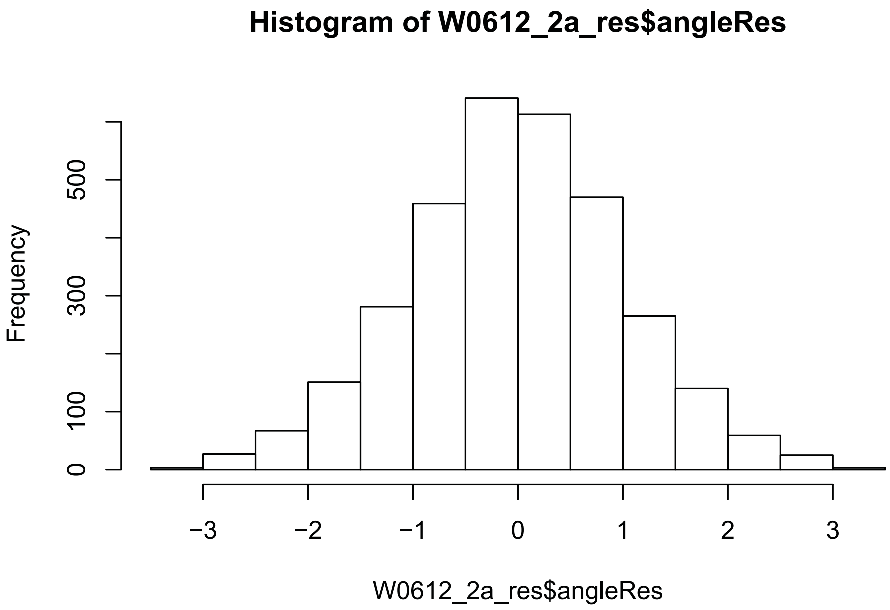
```
## Computing pseudo-residuals... DONE
```



```r
W0612_2a_res <- pseudoRes(W0612_2a)
hist(W0612_2a_res$stepRes)
```



```
hist(W0612_2a_res$angleRes)
```



We fit the remaining two models with different initial parameters. (An abbreviated process is shown to reduce redundancy.)

```
# second set of parameters (wider values)

mu2b <- c(5, 2000)
sigma2b <- c(8, 1000)
angleMean2b <- c(pi, -0.005)
kappa2b <- c(0.1, 1)
stepPar2b <- c(mu2b, sigma2b)
anglePar2b <- c(angleMean2b, kappa2b)


# fit the second 2-state HMM

W0612_2b <- fitHMM(W0612Reg, nbStates = 2, stepPar0 = stepPar2b, anglePar0 = anglePar2b,
                   stepDist = "gamma", angleDist = "vm")
W0612_2b
```

```
## Value of the maximum log-likelihood: -26234.64
##
## Step length parameters:
## ----------------------
##        state 1   state 2
## mean 17.00917 1042.0356
## sd   14.02674  924.3724
```

```
##
## Turning angle parameters:
## -------------------------
##                   state 1     state 2
## mean           -2.9787801 -0.01945568
## concentration  0.4975309  0.93201136
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##              1 -> 2    2 -> 1
## intercept -1.281185 -1.476297
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]
## [1,] 0.7826515 0.2173485
## [2,] 0.1859874 0.8140126
##
## Initial distribution:
## ---------------------
## [1] 4.445916e-07 9.999996e-01
```

```
# third set of parameters (estimated parameters from previous model)

mu2c <- c(17, 1042)
sigma2c <- c(14, 924)
angleMean2c <- c(-2.98, -0.02)
kappa2c <- c(0.5, 0.93)
stepPar2c <- c(mu2c, sigma2c)
anglePar2c <- c(angleMean2c, kappa2c)


# fit the third 2-state HMM

W0612_2c <- fitHMM(W0612Reg, nbStates = 2, stepPar0 = stepPar2c, anglePar0 = anglePar2c,
                   stepDist = "gamma", angleDist = "vm")
W0612_2c
```

```
## Value of the maximum log-likelihood: -26234.64
##
## Step length parameters:
## ----------------------
##       state 1   state 2
## mean 17.00917 1042.0380
## sd   14.02674  924.3724
##
## Turning angle parameters:
## -------------------------
##                  state 1    state 2
## mean           -2.978775 -0.0194565
## concentration  0.497498  0.9320255
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
```

```
##              1 -> 2    2 -> 1
## intercept -1.281186 -1.476288
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]
## [1,] 0.7826515 0.2173485
## [2,] 0.1859887 0.8140113
##
## Initial distribution:
## --------------------
## [1] 8.609635e-06 9.999914e-01
```

Results of the 2-state modeling indicate a poor fit of step lengths in the model. We continue with fitting a 3-state model with the following behavior states: resting, foraging/short-distance movement, and directed, long-distance traveling.

Fitting of the 3-state HMM is the same as for a 2-state except that we have three values for each parameter that represent the behavioral states. Initial parameter values for the 3-state HMMs were chosen as follows:

1. Educated guess based on step length and turning angle summaries.
2. Creating three equal bins for the distributions.
3. From a combination histogram-density plot in ggplot2.
4. The estimated parameters from the previous model.

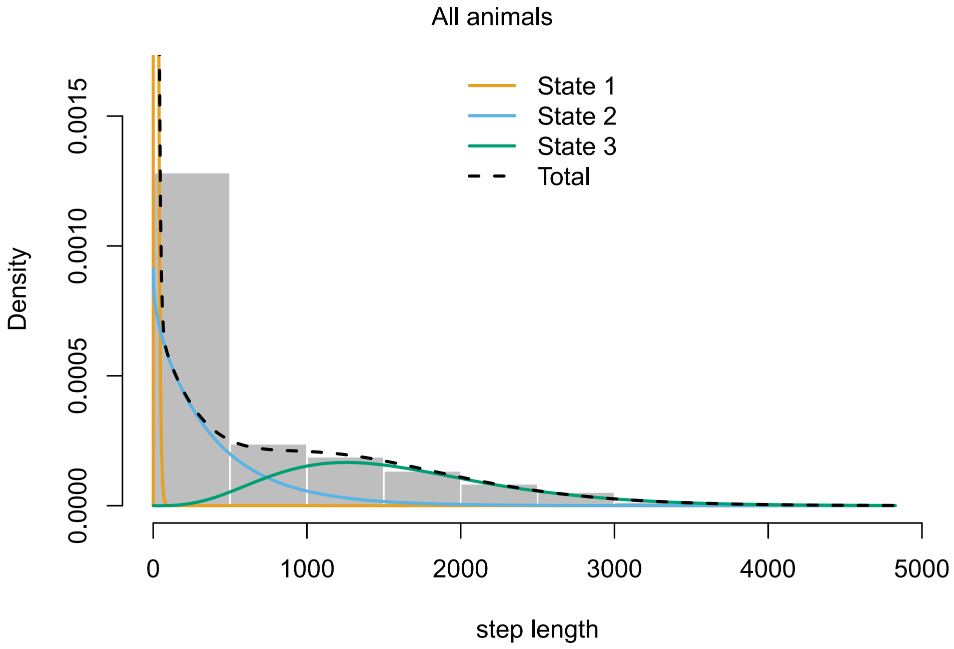
```r
# initial parameters for 3-state model

mu3a <- c(4, 200, 3500)
sigma3a <- c(5, 300, 1500)
angleMean3a <- c(pi, 0.005, 0.05)
kappa3a <- c(0.1, 0.5, 1)
stepPar3a <- c(mu3a, sigma3a)
anglePar3a <- c(angleMean3a, kappa3a)


# fit the first 3-state HMM

W0612_3a <- fitHMM(W0612Reg, nbStates = 3, stepPar0 = stepPar3a, anglePar0 = anglePar3a,
                   stepDist = "gamma", angleDist = "vm")
W0612_3a
```

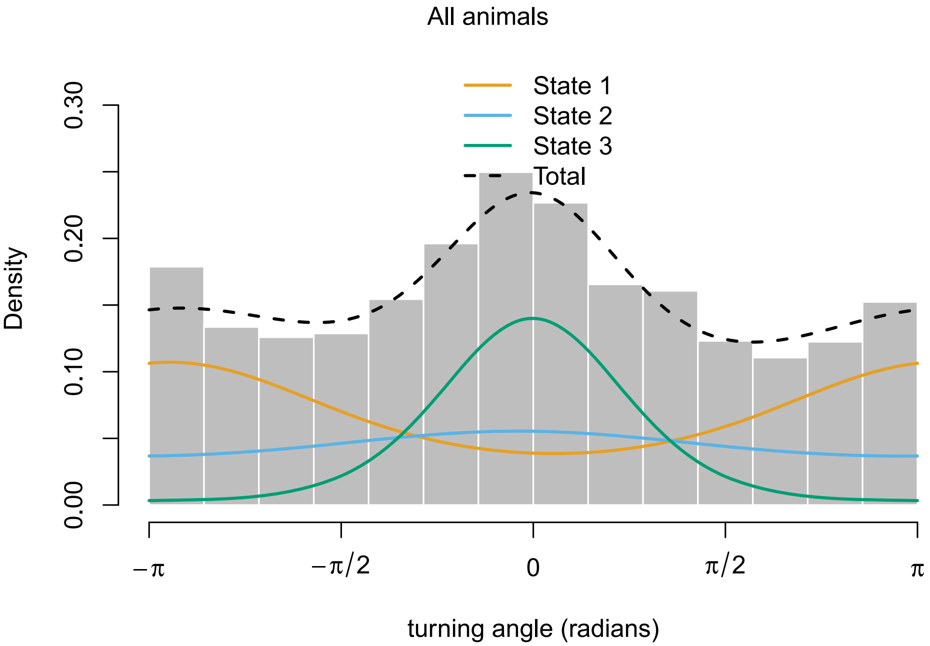
```
## Value of the maximum log-likelihood: -25864.43
##
## Step length parameters:
## ----------------------
##       state 1  state 2   state 3
## mean 13.87421 388.2844 1604.8023
## sd   10.06471 396.6112  749.0172
##
## Turning angle parameters:
## ------------------------
##                 state 1    state 2      state 3
## mean          -2.9698675 -0.1243276 -0.005814789
```

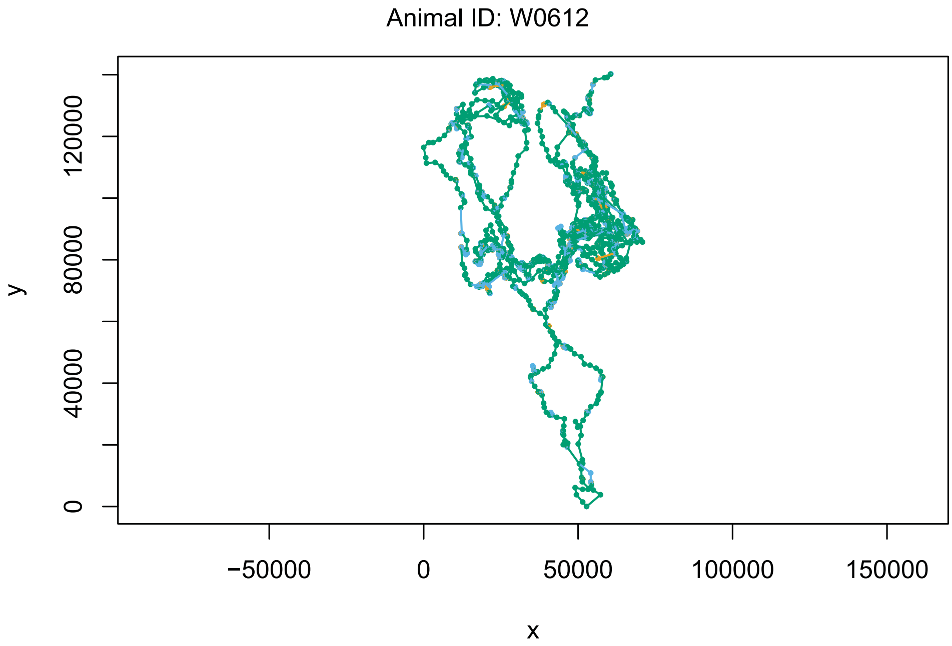
```
## concentration  0.5097004  0.2057111  1.868910436
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##              1 -> 2    1 -> 3     2 -> 1     2 -> 3    3 -> 1    3 -> 2
## intercept -1.289126 -3.098643 -0.6737897 -0.9160029 -2.426462 -1.161481
##
## Transition probability matrix:
## -----------------------------
##            [,1]      [,2]       [,3]
## [1,] 0.75721904 0.2086225 0.03415843
## [2,] 0.26691251 0.5235909 0.20949663
## [3,] 0.06304459 0.2233685 0.71358691
##
## Initial distribution:
## --------------------
## [1] 1.873944e-06 9.999981e-01 3.746110e-09
```

```
# plot the fitted model results

plot(W0612_3a)
```

```
## Decoding states sequence... DONE
```




All animals
State 1
State 2
State 3
Total
Density
0.00
0.10
0.20
0.30
$-\pi$
$-\pi/2$
0
$\pi/2$
π
turning angle (radians)



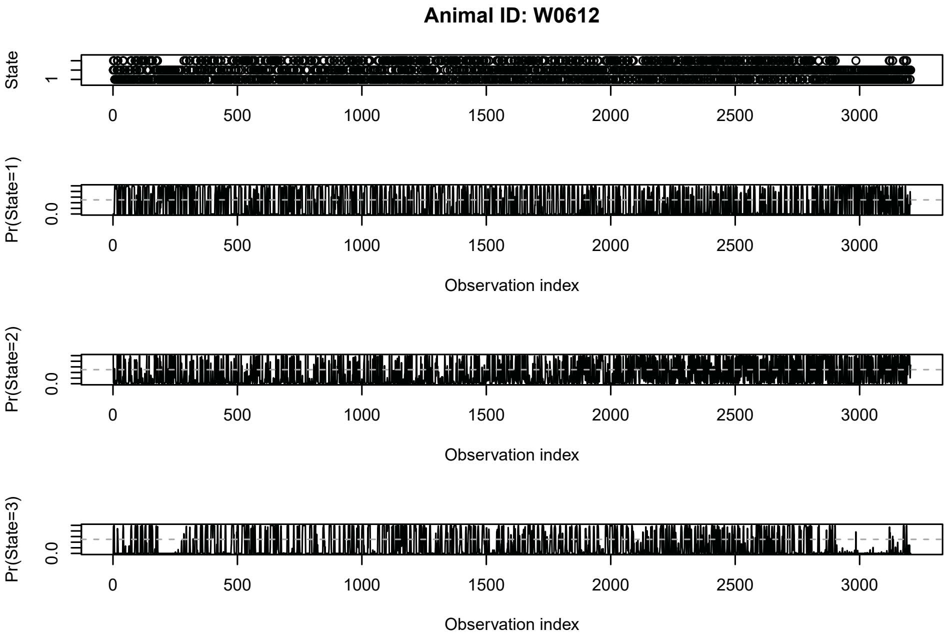
As before, we show the classified states from the Viterbi algorithm for the first 20 steps. We plot the fitted model object to look at the probability of each state in the observation index.

```
head(viterbi(W0612_3a), n = 20)
```

```
##  [1] 2 3 3 3 3 2 1 1 1 1 1 1 1 1 1 1 2 3 3 3
```

```
plotStates(W0612_3a)
```

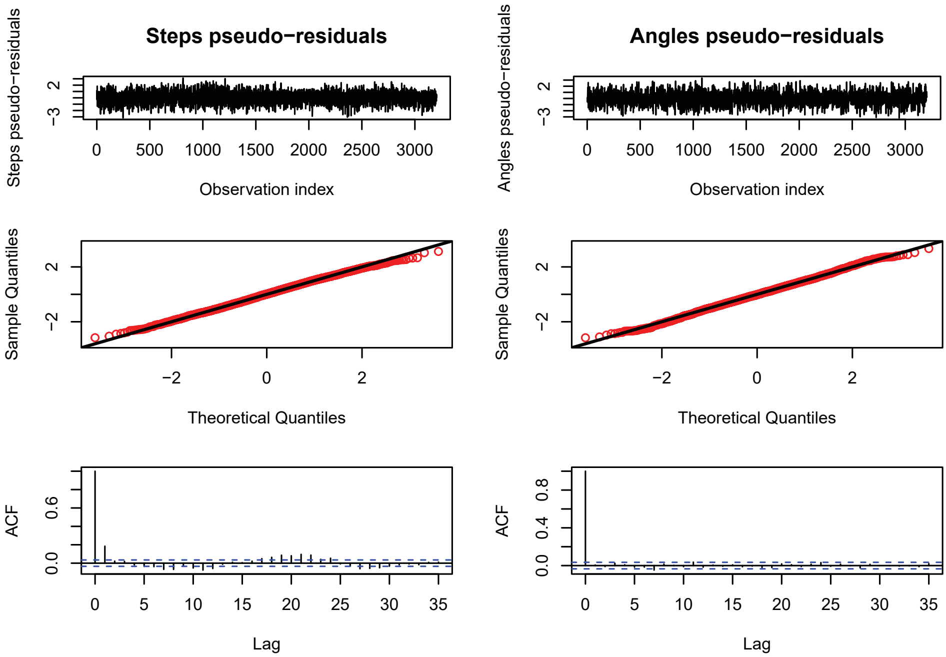
```
## Decoding states sequence... DONE
## Computing states probabilities... DONE
```



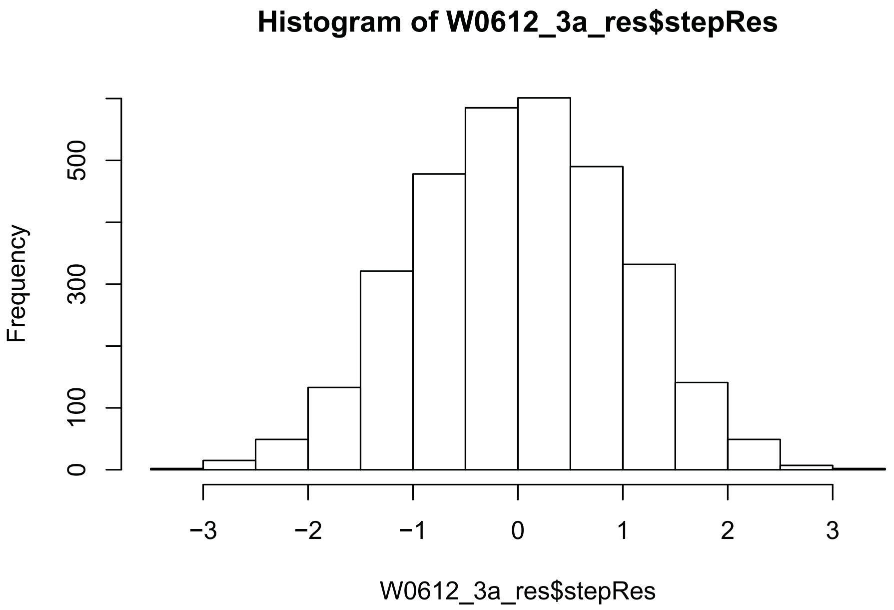
We inspect the pseudo-residuals for model fit.

```r
plotPR(W0612_3a)
```

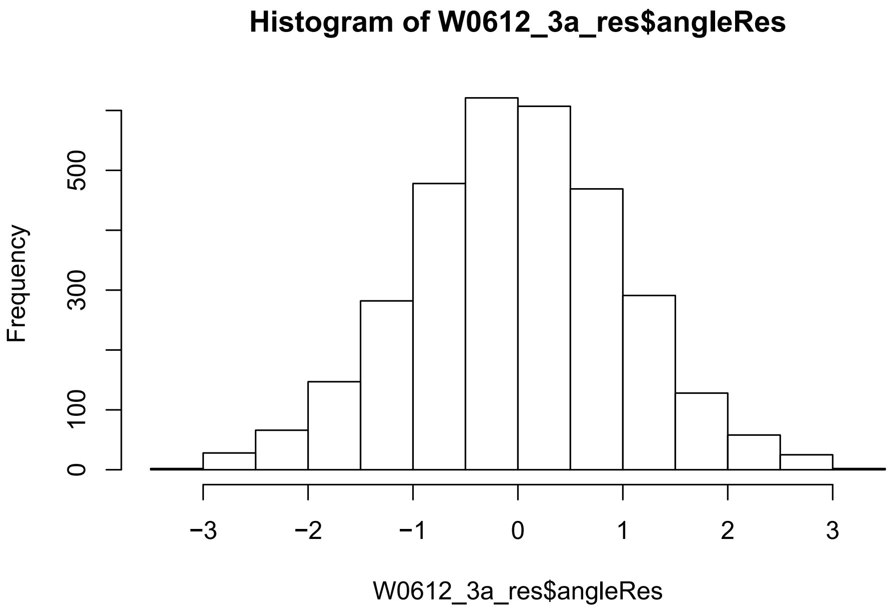
```
## Computing pseudo-residuals... DONE
```



```
W0612_3a_res <- pseudoRes(W0612_3a)
hist(W0612_3a_res$stepRes)
```



```
hist(W0612_3a_res$angleRes)
```



We continue to fit the next three 3-state HMMs. (We again show an abbreviated process to reduce redundancy.)

```
# second set of parameters (from equal binning)

mu3b <- c(10, 300, 2000)
sigma3b <- c(5, 150, 750)
angleMean3b <- c(pi,-0.005974, 1.57)
kappa3b <- c(1, 1, 1)
stepPar3b <- c(mu3b, sigma3b)
anglePar3b <- c(angleMean3b, kappa3b)

# fit the second 3-state HMM

W0612_3b <- fitHMM(W0612Reg, nbStates = 3, stepPar0 = stepPar3b, anglePar0 = anglePar3b,
                   stepDist = "gamma", angleDist = "vm")
W0612_3b
```

```
## Value of the maximum log-likelihood: -25864.43
##
## Step length parameters:
## ----------------------
##        state 1  state 2  state 3
## mean 13.87423 388.2872 1604.803
## sd   10.06474 396.6137  749.017
##
```

```
## Turning angle parameters:
## ------------------------
##                  state 1    state 2      state 3
## mean           -2.969865 -0.1243188 -0.005815661
## concentration  0.509698  0.2057129  1.868911138
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##              1 -> 2    1 -> 3     2 -> 1     2 -> 3    3 -> 1    3 -> 2
## intercept -1.28913 -3.098652 -0.6737915 -0.9160046 -2.426423 -1.161484
##
## Transition probability matrix:
## -----------------------------
##           [,1]      [,2]       [,3]
## [1,] 0.7572199 0.2086219 0.03415817
## [2,] 0.2669122 0.5235913 0.20949646
## [3,] 0.0630469 0.2233675 0.71358556
##
## Initial distribution:
## --------------------
## [1] 5.665121e-07 9.999994e-01 6.391494e-10
```

```r
# third set of parameters (from histogram-density plot in ggplot2)

mu3c <- c(25, 500, 1500)
sigma3c <- c(30, 300, 750)
angleMean3c <- c(pi,-0.005974, 1.57)
kappa3c <- c(0.5, 0.75, 1)
stepPar3c <- c(mu3c, sigma3c)
anglePar3c <- c(angleMean3c, kappa3c)

# fit the third 3-state HMM

W0612_3c <- fitHMM(W0612Reg, nbStates = 3, stepPar0 = stepPar3c, anglePar0 = anglePar3c,
                   stepDist = "gamma", angleDist = "vm")
W0612_3c
```

```
## Value of the maximum log-likelihood: -25864.43
##
## Step length parameters:
## ----------------------
##       state 1  state 2   state 3
## mean 13.87423 388.2859 1604.8017
## sd   10.06474 396.6122  749.0182
##
## Turning angle parameters:
## ------------------------
##                  state 1    state 2      state 3
## mean           -2.9698641 -0.1243471 -0.005813025
## concentration  0.5096999  0.2057083  1.868919615
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##               1 -> 2    1 -> 3     2 -> 1     2 -> 3    3 -> 1    3 -> 2
```

```
## intercept -1.289134 -3.098638 -0.6737932 -0.9159935 -2.426424 -1.161486
##
## Transition probability matrix:
## -----------------------------
##             [,1]      [,2]       [,3]
## [1,] 0.75722019 0.2086212 0.03415866
## [2,] 0.26691128 0.5235903 0.20949839
## [3,] 0.06304689 0.2233671 0.71358598
##
## Initial distribution:
## --------------------
## [1] 1.291640e-05 9.999870e-01 6.550713e-08
```

```r
# fourth set of parameters (the estimated parameters of the previous model)

mu3d <- c(14, 388, 1605)
sigma3d <- c(10, 397, 749)
angleMean3d <- c(-2.97,-0.124, -0.006)
kappa3d <- c(0.51, 0.21, 1.87)
stepPar3d <- c(mu3d, sigma3d)
anglePar3d <- c(angleMean3d, kappa3d)

# fit the fourth 3-state HMM

W0612_3d <- fitHMM(W0612Reg, nbStates = 3, stepPar0 = stepPar3d, anglePar0 = anglePar3d,
                   stepDist = "gamma", angleDist = "vm")
W0612_3d
```

```
## Value of the maximum log-likelihood: -25864.43
##
## Step length parameters:
## ----------------------
##       state 1  state 2   state 3
## mean 13.87421 388.2857 1604.8032
## sd   10.06471 396.6125  749.0181
##
## Turning angle parameters:
## ------------------------
##                  state 1    state 2      state 3
## mean          -2.9698623 -0.1243197 -0.005814957
## concentration  0.5096991  0.2057115  1.868915061
##
## Regression coeffs for the transition probabilities:
## --------------------------------------------------
##               1 -> 2    1 -> 3     2 -> 1     2 -> 3    3 -> 1   3 -> 2
## intercept -1.289122 -3.098663 -0.6737882 -0.9159975 -2.426431 -1.16148
##
## Transition probability matrix:
## -----------------------------
##            [,1]      [,2]       [,3]
## [1,] 0.7572189 0.2086233 0.03415775
## [2,] 0.2669125 0.5235901 0.20949745
## [3,] 0.0630464 0.2233683 0.71358529
##
```

```
## Initial distribution:
## --------------------
## [1] 2.255205e-06 9.999977e-01 4.853313e-09
```

Model selection and assigning behavioral states to steps

We use Akaike's Information Criterion (AIC) to determine which model has the best fit to the data.

```
AIC(W0612_2a, W0612_2b, W0612_2c, W0612_3a, W0612_3b, W0612_3c, W0612_3d)
```

```
##      Model      AIC
## 1 W0612_3b 51768.86
## 2 W0612_3a 51768.86
## 3 W0612_3d 51768.86
## 4 W0612_3c 51768.86
## 5 W0612_2b 52491.27
## 6 W0612_2a 52491.27
## 7 W0612_2c 52491.27
```

All 3-state models have an equally good fit, so we arbitrarily select the final model as the "best" model.

```
# store behavioral states in new data column for best model

W0612Reg$state <- viterbi(W0612_3d)

# extract date from GMT.date into individual date column

W0612Reg$date <- as.Date(W0612Reg$GMT.date)

# get step length and turning angle means for each behavior state

bxStepMeans <- aggregate(step ~ state, W0612Reg, mean)
bxStepMeans
```

```
##   state       step
## 1     1   13.69453
## 2     2  371.89280
## 3     3 1618.44929
```

```
bxTurnMeans <- aggregate(angle ~ state, W0612Reg, mean)
bxTurnMeans
```

```
##   state       angle
## 1     1 -0.16628247
## 2     2 -0.01961102
## 3     3  0.01435323
```

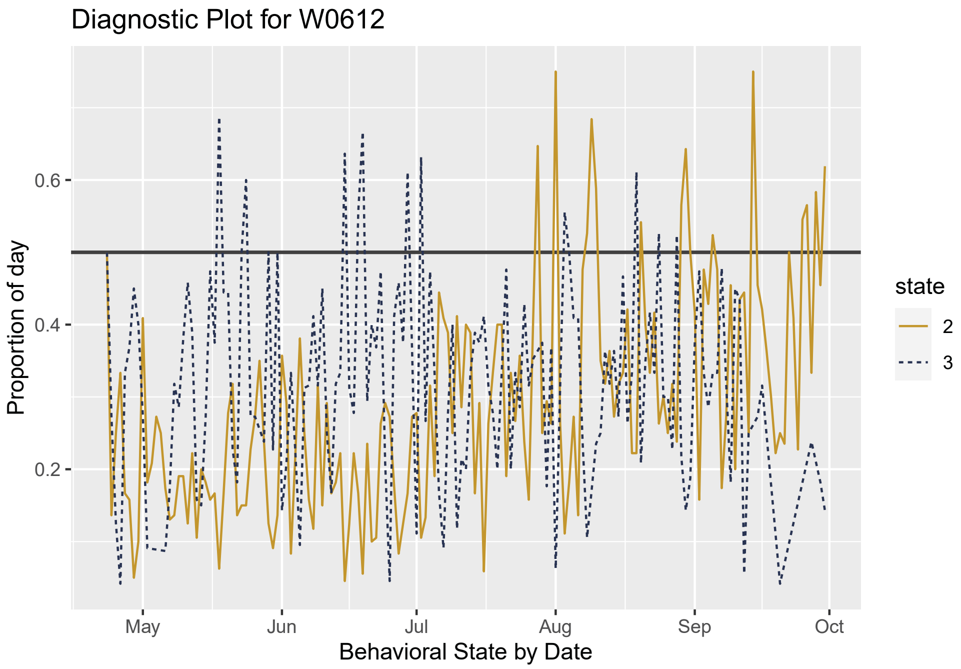
Diagnostic plotting of behavioral states

We construct a dataframe that summarizes the states per date before plotting.

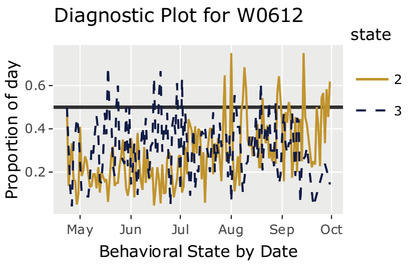
```
allBx <- summaryBy(state ~ date + state + ID, FUN=length, data = W0612Reg)

prop <- function(x) x/sum(x)

allBx <- ddply(allBx, "date", transform, share = prop(state.length))

allBx$state <- as.factor(allBx$state)
```

We plot the data in ggplot to look at how the proportion of the day in each state changes over time. We look only at the second and third behavioral states, as resting is not important in determining whether or not dispersal is occurring.

```
bxPlot <- ggplot(allBx, aes(x=date, y=share, group=state, colour=state)) +
  geom_hline(yintercept = 0.5, linetype = "solid", color = "grey25", size = .8) +
  geom_line(aes(linetype = state), subset(allBx, state != "1")) +
  scale_color_manual(values = c("#C4961A", "#293352")) +
  xlab("Behavioral State by Date") +
  ylab("Proportion of day") +
  ggtitle("Diagnostic Plot for W0612")

bxPlot
```



```
# interactive plot in plotly

ggplotly(bxPlot)
```



We find the dates where the individual spends at least half of the day in the third behavior, representing a dispersal state.

```
dates <- allBx[allBx$state == "3" & allBx$share >= 0.5, ]
dates
```

```
##            date state    ID state.length     share
## 2   2009-04-23     3 W0612            1 0.5000000
## 74  2009-05-18     3 W0612           11 0.6875000
## 89  2009-05-23     3 W0612           10 0.5000000
## 92  2009-05-24     3 W0612           12 0.6000000
## 106 2009-05-29     3 W0612           12 0.5000000
## 112 2009-05-31     3 W0612           11 0.5000000
## 157 2009-06-15     3 W0612           14 0.6363636
## 166 2009-06-18     3 W0612           10 0.5555556
## 169 2009-06-19     3 W0612           12 0.6666667
## 199 2009-06-29     3 W0612           11 0.6111111
## 208 2009-07-02     3 W0612           12 0.6315789
## 302 2009-08-03     3 W0612           10 0.5555556
## 305 2009-08-04     3 W0612           11 0.5000000
## 349 2009-08-19     3 W0612           11 0.6111111
## 364 2009-08-24     3 W0612           10 0.5263158
## 376 2009-08-28     3 W0612           11 0.5238095
```

The final step was completed in the geographic information system (GIS) software, QGIS. We looked at a shapefile of the geolocations classified by behavior states. Based on the plots, date summaries, and inspection in QGIS, we selected 29 April - 02 July as the dates the individual was dispersing.

```r
W0612Dispersal <- subset(W0612, GMT.date >= "2009-04-29 00:00:00" &
                            GMT.date <= "2009-07-02 23:00:00")

saveRDS(W0612Dispersal, "W0612Dispersal.rds")
```

---

* geolocations have been anonymized; their spatial relationships remain unchanged

References

Michelot, T., Langrock, R. and Patterson, T.A. 2016. moveHMM: an R package for the statistical modelling of animal movement data using hidden Markov models. Methods in Ecology and Evolution 7: 1308-1315. doi:10.1111/2041-210X.12578

Zucchini, W. and MacDonald, I.L. 2009. Hidden Markov Models for Time Series: An Introduction Using R. Chapman & Hall (London).

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