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ABSTRACT

Movement ability and habitat selection of individuals are highly significant in determining the size of a population and impact the range and survival of the entire species. Thus, the conservation and management of animal species requires an understanding of the movement and habitat selection in various environments. Human-modified landscapes often differ from the natural environment of a species and can be highly fragmented. For forest-dwelling species, urbanized areas in particular can pose threats to movement, as forested areas are scarce and separated by roads and buildings.

In this thesis I study how an originally forest-dwelling species, the Eurasian red squirrel (*Sciurus vulgaris*) is accustomed to live in human modified landscapes and move in urban and rural environments. The red squirrel is an arboreal mammal common in the boreal coniferous forests, but recent findings have shown the population declining in Finland. The movements of juvenile red squirrels are followed by radio tracking, and habitat selection, dispersal distance and movement patterns are examined as a response to landscape structures.

The results from the urban environment show that juvenile red squirrels do not avoid roads during their dispersal. In addition, mortality due to vehicles was detected low. Although red squirrels prefer areas with more trees available than in the surrounding urban landscape, they often use sites with only few trees. At the home range scale, the used area did not differ greatly from the habitat composition of the available landscape. Habitat use of juvenile red squirrels differed between the phases of dispersal, including settling in areas with less deciduous land cover type than in the natal area. Thus, red squirrels are well adapted to use urbanized areas and their movements are not inhibited by roads.

I found surprisingly long dispersal distances for juvenile red squirrels in the rural study area, with the maximum being over 16 km. The dispersal distances in the urban area were approximately only a quarter of those observed in the rural area. The landscape structure affected the eventual dispersal paths made by juvenile red squirrels; in the rural landscape, dispersers favored spruce-dominated areas and avoided fields along their dispersal route, although they occasionally crossed even wide fields. In the urban landscape, red squirrels preferred areas with deciduous or coniferous trees. The movement steps made by dispersers were longer in the more hostile landscape compared to forested areas. Despite these effects on movement path, the landscape structure only had a minor effect on straight line dispersal distances moved from the natal nest. Even though the dispersal distances of red squirrels vary greatly, it is obvious that landscape structure plays only a very small role in these differences.

Most of the dispersing individuals compared potential sites for a home range before settling into the one they chose. However, in the rural study area, long-distance dispersing individuals did not compare potential sites and settled in the last site they visited. Landscape characteristics did not explain the number of revisits that individuals made to alternative sites, but the number of revisits declined with a site's distance to the natal nest and the dispersal distance of individuals. The effect of landscape variables on decisions regarding where to settle was small, but surprisingly, in the rural area, juvenile red squirrels settled in sites with more built area compared to sites where juveniles only visited but did not settle in. The decision-making

during natal dispersal seems to be driven mainly by factors other than landscape characteristics and the search strategies vary between individuals and study areas.

In conclusion, juvenile red squirrels are efficient dispersers, and landscape structure has only a small effect on dispersal distances and thus possibly on gene flow of the species. Red squirrels are well-adapted to changing environments; in Finland, their movements are scarcely restricted by roads or unfavorable agricultural areas. The species can utilize urban environments and even exhibits a tendency to settle near human settlement in rural areas. This study has discovered a significant difference in dispersal distances between urban and rural environments, raising questions about the reasons behind extensive dispersal distances in the rural environment.

TIIVISTELMÄ

Eläinten kyky liikkua ja valita elinympäristönsä määrittelee suuresti eläinpopulaatioiden koon ja vaikuttaa koko lajin levinneisyyteen ja selviytymiseen. Täten eläinlajien suojelu ja hoito edellyttävät ymmärrystä siitä miten eläimet liikkuvat ja hyödyntävät erilaisia maisemia. Ihmisen muokkaamat ympäristöt poikkeavat usein lajien luonnollisesta elinympäristöstä ja voivat olla hyvin pirstoutuneita. Erityisesti kaupunkiympäristöt voivat haitata metsälajien liikkumista, sillä niissä puustoiset alueet ovat harvassa ja niitä erottavat tiet ja rakennukset.

Tässä väitöskirjassa tutkin miten alkujaan metsissä elävä orava (*Sciurus vulgaris*) on sopeutunut asuttamaan ihmisen muokkaamia ympäristöjä ja liikkumaan sekä kaupunki- että maalaisympäristössä. Orava on yleinen boreaalisen vyöhykkeen puissa asuva nisäkäs, jonka kanta on uusimpien tutkimusten mukaan Suomessa vähenemässä. Seurasin nuorten oravien liikkeitä radioseurannalla ja selvitin maiseman rakenteen vaikutusta elinympäristön valintaan, dispersaalimatkoihin ja yksilöiden liikkumiseen.

Tulokseni kaupunkiympäristöstä osoittavat, että nuoret oravat eivät välttele teitä dispersaalin aikana. Lisäksi autot eivät olleet merkittävä kuolinsyy turkimuksen nuorille yksilöille. Oravat suosivat kaupungissa puustoisia alueita, mutta käyttivät usein myös harvapuustoisia alueita joilla oli vain muutamia puita. Elinpiirien tasolla tarkasteltuna alueet joita oravat hyödynsivät eivät suuresti eronneet ympäröivästä käytössä olevasta maastosta. Elinympäristön käyttö vaihteli eri dispersaalin vaiheissa nuorten yksilöiden etsiessä omaa elinpiiriään. Nuoret oravat esimerkiksi asettuivat elämään alueille joilla oli vähemmän puustoisia alueita kuin oravien synnyinalueella. Oravat ovatkin hyvin sopeutuneet käyttämään rakennettua kaupunkiympäristöä, eivätkä tiet rajoita niiden liikkeitä.

Havaitsin yllättävän pitkiä dispersaalimatkoja maaseudun nuorille oraville, pisimmän kuljetun matkan ollessa yli 16 kilometriä. Kaupunkiympäristön disperaalimatkat olivat vain noin neljännes maaseudun dispersaalimatkoista. Maiseman rakenne vaikutti siihen miten nuoret oravat liikkuivat dispersaalin aikana. Maalaisympäristössä dispersoivat oravat luonnollisesti suosivat reittiensä varrella kuusivaltaisia metsiä ja välttelivät peltoja, mutta myös toisinaan ylittivät laajojakin peltoalueita. Kaupunkiympäristössä oravat suosivat alueita joilla oli havu- tai lehtipuita. Yksittäisten liikkumishavaintojen välinen etäisyys kasvoi kun epäsuotuisan maaston määrä niiden välillä runsastui, kun taas metsäisten alueiden lisääntyessä etäisyys lyheni. Tämä tarkoittaa että oravat kulkivat nopeammin epäsuotuisten alueiden ylitse, kun taas suotuisassa metsäympäristössä ne kulkivat hitaammin. Huolimatta näistä vaikutuksista dispersaalireittiin, maiseman rakenteella oli vain vähäinen vaikutus oravien dispersaalimatkoihin, eli synnyinpesästä poispäin kuljettuun matkaan linnuntietä pitkin mitattuna. Vaikkakin dispersaalimatkojen pituuksissa oli paljon vaihtelua, ei maiseman rakenteella ollut suurta merkitystä näiden eroissa.

Suurin osa dispersoivista yksilöistä vertaili useita eri mahdollisia elinpiirejä ennen kuin ne asettuivat elämään valitsemalleen alueelle. Maalaisympäristössä pitkän matkan dispersoijat eivät kuitenkaan liikkuneet toistuvasti eri vaihtoehtoisten alueiden välillä ja asettuivat elämään viimeiseen kohtaamaansa alueeseen. Maiseman rakenne ei selittänyt nuorten yksilöiden vaihtoehtoisille alueille tekemien uudelleenkäyntien määrää, mutta niiden määrä väheni kun alueen etäisyys synnyinpesästä ja yksilön

dipersaalimatka kasvoivat. Maiseman rakenne ei suuresti vaikuttanut oravien päätöksiin kun ne valitsivat elinaluettaan, mutta yllättäen maalaisympäristössä oravat asettuivat alueille joilla oli enemmän rakennettua ympäristöä kuin vaihtoehtoisilla elinalueilla, joihin oravat tekivät vierailuja mutta eivät asettuneet elämään. Nuorten dispersaalinaikaista päätöksentekoa vaikuttaa ohjaavan muut tekijät kuin maisemalliset muuttujat ja elinalueen etsinnän strategia vaihtelee yksilöittäin ja tutkimusalueiden välillä.

Yhteenvetona voidaan todeta että nuoret oravat ovat tehokkaita liikkumaan ja dispersoimaan, ja maiseman rakenteella on vain vähäinen vaikutus oravan dispersaalimatkaan ja täten lajin geenivirtoihin. Oravat ovat sopeutuneet hyvin muuttuvaan ympäristöön, sillä niiden liikkeitä eivät Suomessa juurikaan rajoita autotiet tai epäsuotuisat maanviljelyalueet. Laji pystyy hyödyntämään kaupunkiympäristöjä ja jopa näyttää suosivat ihmisen lähelle asettumista maalaisympäristössä. Tässä tutkimuksessa löydettiin merkitsevä ero dispersaalimatkojen pituuksien välillä kaupunki- ja maalaisympäristössä, mikä herättää kysymyksiä siitä mitkä tekijät saavat aikaan maalaisympäristön oravien huomattavan pitkät dispersaalimatkat.

Contents

List of original publications

This thesis is based on the following publications and manuscripts, which are referred to in the text by their Roman numerals:

I **Hämäläinen S**, Fey K, Selonen V. (2018) Habitat and nest use during natal dispersal of the urban red squirrel (*Sciurus vulgaris*). *Landscape and Urban Planning* 169: 269–275.

II Fey K, **Hämäläinen S**, Selonen V. (2016) Roads are no barrier for dispersing red squirrels in an urban environment. *Behavioral Ecology* 27: 741–747.

III **Hämäläinen S**, Fey K, Selonen V. (2019) The effect of landscape structure on dispersal distances of the Eurasian red squirrel. *Ecology and Evolution* 9: 1173–1181.

IV **Hämäläinen S**, Fey K, Selonen V. Search strategies in rural and urban environment during natal dispersal of the red squirrel. *Manuscript*.

Articles **I**, **II** and **III** are reprinted with the permission of Elsevier, Oxford University Press, and John Wiley & Sons, respectively.

Author contributions to the original publications:

	I	**II**	**III**	**IV**
Original idea	VS	VS	VS,SH	VS
Data collection	SH, VS, KF	SH, VS, KF	SH, VS, KF	SH, VS, KF
Data handling	SH	KF, VS, SH	SH	SH
Analyses	SH, VS	KF, VS	SH	SH
Writing	SH, VS	KF, VS, SH	SH, VS	SH

SH = Suvi Hämäläinen, VS = Vesa Selonen, KF = Karen Fey.

1. Introduction

1.1 Movement of animals

Movement ability of individuals highly determines the distribution and range of a species and also affects the ability of a population to remain viable. Thus the knowledge about movement of the individuals is important when planning and evaluating the conservation and population dynamics of the species. There are several elements that affect the movements of animals. Both internal and external factors, like an animal's personality trait and the landscape of the area travelled, can affect the movement ability of individuals. Landscape structure can have major impact on animal movement and the distribution of the species (Wiens et al. 1993; Ims 1995; Bowne et al. 1999; Cote et al. 2017), and can sometimes form barriers for movement (Mader 1984; Lodé 2000; Bonte et al. 2012). The responses to these barriers may change with life stages and the age of individuals (Sheperd & Swihart 1995; Debinski & Holt 2000; van Dyck & Baguette 2005; Grilo et al. 2014). Dispersal refers to one-way movement of an animal between the birth place and the first breeding place or between breeding places. For many mammals, the main dispersal period is when a juvenile abandons its natal home range and finds its own territory (Wolff 1994; Clobert et al. 2001). Thus, natal dispersal highly determines the gene flow and invasion potential of several species (Clobert et al. 2001; van Dyck & Baguette 2005: Brommer et al. 2017).

Animals often choose their habitat from several options by using environmental cues to evaluate the quality of the area (Luttbeg 2002; Haughland & Larsen 2004; Mabry & Stamps 2008). Sometimes the uncertainty of the quality of previously visited areas and future options may limit the decision-making process, as may time used for the search and energetic costs (Luttbeg 2002). Environmental cues may also be unreliable, especially in human-modified landscapes (Bonte et al. 2012), and individuals may end up choosing home ranges that are not optimal or beneficial for their future fitness (Schooley et al. 1996; Schlaepfer et al. 2002). While searching for their home range, individuals must make several choices: when to leave, which path to follow, how far to travel and in which of the alternative home ranges to settle in. In order to make an optimal selection, animals need to both assess the quality of the area and balance between the costs of reaching new areas in relation to the uncertainty of the quality of the new encountered areas (Luttbeg 2002; Bonte et al. 2012; Nurmi et al. 2017). The movement choices made by individuals always involve a balance between potential benefits and risks (Larsen & Boutin 1994), and there can be individual differences in the dispersal behavior (Dingemanse et al. 2003). There are different search strategies for selecting a home range from multiple options. Some dispersers compare potential areas by making revisits to the previously visited areas in order to ensure their quality (Luttbeg & Langen 2004; Mabry & Stamps 2008; Selonen & Hanski 2010), whereas other individuals visit each alternative area only once before making a settlement decision (Luttbeg & Langen 2004; Dale et al. 2006).

1.2 Effect of anthropogenic actions on movement ability

Human actions dramatically alter landscapes by processing land for agriculture, residential areas and industry (Collinge 1996; Farina 2000). Urbanized environments generally differ from the natural environment of a species, by being extremely fragmented with semi-natural areas divided by roads and buildings (Saunders et al. 1991; Magris & Gurnell 2002), and for some species by lacking natural nest sites (Verbeylen et al. 2003; Rytwinski & Fahrig, 2012). Roads can cause significant mortality in urban mammals (Lowry et al. 2013) and also have a deterrent effect on animal movements. In addition to replacing natural forest environment in urbanized areas, both roads and buildings can form barriers to movement, and inhibit the colonization of remaining isolated habitat patches (Lodé 2000; Rondinini & Doncaster 2002; Verbeylen et al. 2003; Bonte et al. 2012). The conservation and management of species requires an understanding of the effects of habitat loss and fragmentation on animal populations (Dooley & Bowers 1998; Nupp & Swihart 2000). In addition to negative effects through habitat loss and fragmentation, human presence and infrastructure can affect behavior and movement patterns of animals (Latham et al. 2011). Individuals can show behavioral responses to urban environments and human disturbance through spatial and temporal variation in foraging and movement in order to avoid high human activity (Dowding et al. 2010; Lowry et al. 2013).

There are, however, species that can benefit from urbanization and even have higher population densities in urban areas than in their natural habitats (Bateman & Fleming 2012). Species adapted to urban areas are often generalists and more accustomed to human-induced disturbance (Baker & Harris 2007; McCleery 2010). Usually the beneficial effect of urbanization is related to a lower density of natural predators and more abundant and versatile resources (Baker & Harris 2007; Adams 2016). Forest stands in urban areas usually differ greatly from those in natural environments. In the boreal areas, for example, the diversity of tree species is higher in urban areas, providing alternative food supplies.

Humans also influence animals in rural areas. For example, forest management and agriculture decrease the amount of suitable habitat for forest species and create isolated habitat patches. As a result of clear-cutting and agricultural practices, wide-open areas are established and these may inhibit the movement of forest species (Mader 1984; Bonte et al. 2012) either through indirect or direct effects, like for example through increased predation risk (Bonte et al. 2012; Cote et al. 2017). Whether the species can move in fragmented environments depends on the gap-crossing willingness of individuals (Bakker & van Vuren 2004; Selonen & Hanski 2004; Mäkeläinen et al. 2016), which may vary highly between species. It has been observed that dispersing individuals are sometimes more willing to cross gaps than non-dispersing individuals (van Dyck & Baquette 2005; Selonen & Hanski 2006).

1.3 Aims of the thesis

In this thesis my aim is to understand how an originally forest-dwelling species is able to live in human-modified landscapes and move in urban and rural environments. In Chapter **I**, I inspect the habitat use of urban red squirrels at a scale of movement locations and home ranges. I also look into the possible differences in habitat use between different dispersal phases of juvenile individuals. In Chapter **II**, I look into the responses of dispersing urban red squirrels to roads. I aim to find out if red squirrels avoid roads when moving in the city area, and if squirrels are reluctant to cross roads.

Landscape structure can have major effects on gene flow by inhibiting movements of individuals. For arboreal species, open areas in particular are believed to act as barriers for movement. In Chapter **III**, I examine the effect of urban structures such as roads and buildings, and rural open areas like fields, on dispersal distances of juvenile red squirrels. I also look into the movements dispersing individuals make during their dispersal, and find out if these are affected by landscape structures.

Decisions made during natal dispersal highly influence the future fitness of an animal (Bowler & Benton 2005). The selection of future home range affects, for example, the food supply and mating success of the individual. In Chapter **IV**, I study how juvenile individuals choose their future home range from many alternative settlement areas, and if the landscape characteristics of the area affect this decision-making. Juvenile dispersers are good model organisms to study search strategies, because we can be sure that they are visiting different sites for the first time in their lives, and the decisions are not affected by former experience (Mabry & Stamps 2008).

The work presented in this thesis addresses the following questions:

1) What kind of habitat do arboreal species use in an urban landscape? Are there differences in habitat use between different dispersal phases of juvenile red squirrels? (Chapter **I**)

2) Do roads prevent movements of red squirrels in an urban area? (Chapter **II**)

3) Does landscape structure affect dispersal distances of juvenile red squirrels? (Chapter **III**)

4) Which search strategy do juvenile red squirrels use when they are searching for their home range? Is the selection of a home range affected by landscape characteristics? (Chapter **IV**)

For Chapter **I**, I predicted that red squirrels would favor their natural forest habitat and avoid roads and buildings. In Chapter **II**, I predicted that red squirrels would avoid close proximity to roads and crossing them, as roads are a mortality threat for squirrels. In Chapter **III**, I expected the landscape to explain at least part of the differences in dispersal distances, as resistance for movement differs between habitats. Finally, for the study questions of the last Chapter **IV**, I predicted that juvenile individuals would compare different potential future home ranges. I also anticipated the landscape characteristics to affect the final selection of an area as a home range.

2. Materials and methods

2.1 Study species

The red squirrel (*Sciurus vulgaris*) (Fig. 1) is a diurnal, arboreal mammal inhabiting forested areas throughout Eurasia (Lurz et al. 2005). There is a variety of forest types along their extensive range, from broad-leaved temperate forests in the south to the boreal coniferous forests in the north. In the boreal region, red squirrels prefer the coniferous forest as their habitat (Andrén & Delin 1994). In Finland, coniferous forests mainly consist of Norway spruce (*Picea abies*) and Scots pine (*Pinus sylvestris*). Red squirrels are flexible in their habitat requirement (Lurz et al. 2005), and are also observed in parks and urban areas (e.g. Verbeylen et al. 2003; Haigh et al. 2017). The first sightings of the species in city areas of Finland were made in the 1930's (Haapanen 1999) and one possible reason enabling the spread of the species in the urban areas was winter bird feeding starting at the same time (Adams 2016).

The weight of an adult red squirrel varies between 240–400 g (Wauters et al. 2007). The main food item of red squirrels in the boreal region is spruce seeds (Andrén & Lemnell 1992; Gurnell & Wauters 1999; Selonen et al. 2015), the abundance of which can vary dramatically between years from mast to zero crops (Jokimäki et al. 2017). Other food items used by red squirrels are pine seeds, buds, mushrooms, berries, insects and bird eggs (Rajala & Lampio 1962; Lurz et al. 2005). The red squirrel nests usually in twig dreys, but can also utilize cavities, nest boxes and buildings (Shuttleworth 1999;

Figure 1. Juvenile red squirrel equipped with radio transmitter. Photograph by Suvi Hämäläinen.

Lurz et al. 2005). Red squirrels can produce two litters in a year; first litter is born in March–April and the second litter from May onwards (Lurz et al. 2005). The litter size is 3–6 offspring, and juveniles are weaned at the age of 8–10 weeks, after which juvenile individuals move to their future home ranges (Lurz et al. 2005). Home range size of red squirrels varies with habitat and season, being 2–30 ha, and males tend to have larger home ranges than females (Wauters & Dhondt 1992; Andrén & Delin 1994; Lurz et al. 2005).

2.2 Study areas

The data used in Chapters **I** and **II** was gathered from the urban area of the city of Turku (with 180 000 inhabitants) in southern Finland. In Chapters **III** and **IV**, in addition to the urban study area, data was collected also from the rural area of Kauhava, Lapua and Lappajärvi in southern Ostrobothnia, western Finland (hereafter called "Kauhava area"). The landscape composition differs greatly between the study areas. In the urban Turku area, the landscape consists of heavily built grid plan areas with multi-storey buildings, public park areas and private gardens. The main tree species in the city area are elm (*Ulmus glabra*) and lime tree (*Tilia sp.*), but isolated patches of coniferous trees, such as Scots pine and Norway spruce grow in park areas as well. In the rural study area, the landscape is a mosaic of mainly managed boreal forests separated by large agricultural areas, the dominant tree species being Norway spruce and Scots pine. The rural area is fairly sparsely populated and the settlement consists mainly of detached houses.

2.3 Data collection

In order to study the movements and dispersal of juvenile red squirrels, I followed radio-tracked individuals (Fig. 2) both in the urban areas of Turku and in the rural areas of Kauhava. Juvenile red squirrels were captured either from the ground by using live traps, or by using a net to catch them from a nest box or cavity. The red squirrels were collared at the approximate age of 1.5–2 months (178 ± 48 g in Turku, and 133 ± 44 g in the Kauhava area) with Biotrack radio collars weighing 5 or 8 g (model PIP3SM, battery life ~10 months). Collars were fitted to a tightness that allowed the neck of a juvenile individual to grow without being too loose and fall off. After collaring, individuals were immediately released at the place of capture. Individuals were located approximately five times per week from early June to late

September resulting in an average of 63 ± 7 locations per individual in the Turku area, and 33 ± 22 in the Kauhava area. These numbers differ from the expected amount of locations based on tracking frequency due to the deaths and occasional disappearances of the study individuals. During the active dispersal period, the individuals were tracked more frequently. Red squirrel locations were collected by determining either a single tree or a group of trees where the animal was located. In some occasions, when the landscape was difficult to enter (e.g. the red squirrel was located on a private yard), we used triangulation to determine the location of the animal. We continued the tracking in the Turku study area throughout the following winter, with tracking intervals of one to two weeks, and in the Kauhava area until the end of the year with 1 to 3 week intervals. Red squirrel locations were made both in daytime and after dusk to gather both movement locations and nest locations. In total, I collared and monitored 59 juvenile red squirrels during 2012–2015, of which 32 were in the urban area of Turku and 27 in the rural area of Kauhava.

Figure 2. Radio tracking in progress. Photograph by Joonas Kinnunen.

2.3.1 Landscape variables

In order to study the habitat use of juvenile red squirrels and how landscape affects the movements and dispersal distances of individuals, I calculated different landscape variables for both study areas. A separate landscape map was created for both study areas. In order to study the habitat selection and movement responses in the urban Turku study area (**I, III**, **IV**), a landscape map was made by manually digitizing different land use classes from an aerial orthophotograph (provided by: National Land Survey of Finland, 2008, ETRS-TM35FIN, terrain resolution: 0.5 m) into a map at a scale of 1:800, with a minimum mapping unit of 1 m. I divided the landscape into six different land use classes: deciduous trees, coniferous trees, shrub or grass, waterway, building, and asphalt, gravel or sand (hereafter called “asphalt”). I also calculated the edge density to represent the relationship of woodlot size to the amount of habitat edge. This was accomplished by merging the landscape classes into two different land use types: wooded areas and other areas.

In the Kauhava study area, the landscape was stratified into the following seven land use classes: young forest (including clear-cuts), birch-dominated forest, pine-dominated forest, spruce-dominated forest, built landscape (including buildings and roads), field, and water. Clear-cuts were included in the young forest category, because they remain small in size in our study area, red squirrels occasionally move within clear-cuts in the few trees left to the area (personal observation), and both areas yield very few seeds. I also calculated the edge density for the rural study area. The land use classification was carried out with an existing land use map (on a 25 × 25 m pixel grid) based on the SLICE dataset, Landsat Images, and two forest classifications from 1997 and 2009. For a detailed description of land use map construction, see Morosinotto et al. (2017). This landscape map was used to study the effect of landscape on dispersal distances and search strategies in the rural area during natal dispersal (**III**, **IV**).

I studied the habitat use of the species in the urban area (**I**) using two scales: squirrel location and scale of home ranges. For scale of red squirrel location, I created a buffer with a 10 m radius around each red squirrel observation, and the landscape inside this buffer was considered as the used landscape of the individual. The landscape around squirrel observation was compared to available area, which was considered to be within a 100 m radius around the squirrel location (based on the average movement distance of the study individuals). To sample the landscape of available area, I created 100 random points inside each available area and created a 10 m buffer around each random point. From the buffers around random points I calculated the average values for each landscape variables, which represents the available landscape around squirrel location. With the scale of squirrel locations, I also studied whether the habitat use of juvenile squirrels differs between the different dispersal phases. For this approach the location points of juvenile individuals were divided into movements within the natal area, movements during exploration or dispersal, and movements within the settlement area (following Wauters, Matthysen et al. 1994 and Selonen & Hanski 2010).

To study the habitat choice on a home range scale, I compared the habitat within the natal and settlement area to the habitat available within our study area. To define the available area, I calculated 400 m radius buffers around each red squirrel location and then merged all the buffers into one polygon. A 400 m radius was selected to describe the average dispersal distance of the studied red squirrels. The available landscape was calculated by creating 1.000 random points with 110 m radius buffers within this available area. A 110 m radius buffer formed an area equivalent to the average size of red squirrels' natal and settlement areas (3.9 ha) calculated by using 100% minimum convex polygon (MCP) for observations of that dispersal phase. For both of the scales, I compared the landscape of used and available areas to find out the possible preference for certain landscape characteristics by the urban red squirrels.

The effect of roads on the movement of the species in the urban area (**II**) was examined by using a map of the roads in Turku, provided by the Finnish Transport Agency (Digiroad, www.digiroad.fi). Roads are categorized in the map according to their size and type as highways, trunk roads, regional roads, connecting roads, and local roads. Bicycle paths and other light traffic roads were excluded from the map. From red squirrel tracking history, the amounts of road crossings were calculated for following movement types; routine movement, exploring movement, and dispersal movement (see Chapter **II** for a more detailed description of movement types). We also compared the amount of road crossings performed by juvenile individuals to the expected amount of crossings. The expected number of road crossings was calculated for each individual by generating a random walk path inside the convex polygon surrounding all individuals' tracking locations and calculating the road crossings of that path. To determine if the urban red squirrels avoid roads, we studied whether the distance of the squirrel from the road was greater than expected based on randomly generated locations. We generated as many random points as there were tracking locations for each individual and placed them inside a convex polygon outlining the area of all tracking locations. For each tracking location and random location, the distance to the nearest road was calculated and these distances were compared with each other.

The effect of landscape on dispersal distances and movements during dispersal in both urban and rural area was studied by creating buffers of 25 m around movement paths of individuals (the buffer size was determined by the pixel size of the rural landscape map) (**III**). Inside these buffers, I calculated the landscape characteristics and examined their relation to the overall dispersal distance, step length and dispersal route length of the individual. To study dispersal distances, I combined the data of the two study areas and grouped their landscape classes to be identical (detailed description in Chapter **III**).

I also examined whether red squirrels avoid or favor certain landscape characteristics along their dispersal routes (**III**). In order to do this, a special tool was created for ArcMap and 100 random dispersal paths for each individual were generated. From these random paths, I calculated the available landscape through which the squirrels could have dispersed and compared that to the landscape of the original dispersal routes. The random walk paths were generated separately for each individual by using the original squirrel step lengths (distance between two consecutive observations) and randomizing the direction of movement for each step. Random paths started from the place of capture of the squirrel and ended at the distance of the squirrel's dispersal distance ±10 %. Landscape characteristics were calculated inside 25 m buffers for both squirrel routes and random routes.

The decision-making of juvenile red squirrels was examined in both study areas by calculating the average landscape for each site an individual squirrel visited during its dispersal process (see definition of visited sites in Chapter **IV**). This was accomplished by creating buffers of 25 m around squirrel locations and calculating average landscape composition for each site by using the location points within that site. I also calculated the Euclidean distance to the natal nest from the center of each visited site. I examined the landscape of visited sites in relation to the amount of revisits made into the site, and also if the landscape affected the selection of a site as a home range. Additionally, the effect of dispersal distance on the total amount of revisits made by an individual during its dispersal period was examined.

2.4 Statistical analyses

In Chapter **I**, I used conditional logistic regression analysis to investigate the habitat selection in the urban area at the scale of red squirrel locations. The conditional structure of the model linked each squirrel location to the habitat available around this particular location (Boyce 2006). For home range scale, the logistic regression (not conditional) was used to compare the landscape of areas used by squirrels and available areas. A generalized linear mixed model was used to study whether the habitat use differed between dispersal phases. In order to avoid multicollinearity, I analyzed the effect of deciduous trees or coniferous trees, depending on the analysis, in a separate model to achieve a variance inflation factor (VIF) less than 4.

In Chapter **II**, general linear mixed models were used to compare the distance of red squirrel observations from roads to the distance of random points from roads, and similarly to study if the amount of observed road crossings differed from the expected based on random paths. A generalized linear mixed model was also used to calculate the likelihood that an individual was observed crossing a road in relation to movement type and if the size of the road affects this likelihood.

In Chapter **III**, I tested if the dispersal distance or dispersal route length differed between the two study areas, or between sexes, by performing an analysis of variance.

In order to test whether the landscape along dispersal routes differed from that of random routes, a logistic regression was performed separately for the Kauhava and Turku study areas with individual ID as a repeated factor. To avoid strong collinearities between explanatory variables and a high VIF, I created a separate model for the land use category field in the Kauhava study area, whereas in the Turku area, I included asphalt in a separate model. A generalized linear mixed model was performed to study the effect of landscape variables on the step length of dispersing individuals. To study the effect of landscape characteristics on dispersal distance and route length, linear mixed models were created, having separate models for open areas to achieve VIF values under four.

In the last chapter (**IV**), a logistic regression model with the event/trial response was performed in order to investigate the relationship between dispersal distance and amount of revisits performed during dispersal. I made a logistic regression to study if selection of an area is related to the landscape composition and the number of revisits made into the area. Due to collinearities, I performed separate models for open areas in the Kauhava area and deciduous in the Turku study area, and thus attained VIF values under four for each variable. In order to study how landscape composition affects the amount of revisits that juvenile red squirrels made to an area, I performed models separately for the Turku and Kauhava study areas with individual as the repeated measure. I conducted a separate model for asphalt in the Turku area to attain VIF under four. For Kauhava area, a logistic regression was performed to study if land use categories and distance from the natal nest explained whether revisits were made for visited areas. The response variable was binomial: the area being revisited or not, which was due to the low number of revisits within this study area.

In order to take into account the individual variation and repeated measurements, I used individual as a random variable whenever needed in the above-mentioned analyses. The analyses of this study were mainly performed with SAS statistical software, by using the GLIMMIX procedure (Stroup 2013), but for example the conditional logistic regressions were made by using R (R Core Team 2016).

3. Results and discussion

Traditionally dispersal has been studied through its starting and ending point, and not as a whole process including the transition phase (but see e.g. Merrick & Koprowski 2017a). However, there are many obstacles along the transition phase of dispersal which can be reflected on individual fitness, and thus gene flow and population dynamics as well. For this reason, in this thesis, I examine the whole process of dispersal that leads to the selection of a certain site as a home range. The study focuses on the effects of landscape characteristics on dispersal movements and habitat selection in both a highly urbanized area, and in rural area with high degree of agriculture and forestry.

3.1 Red squirrel in urban landscape

3.1.1 Habitat use

My results from the urban area (Chapter **I**) show that even though red squirrels in Finland naturally inhabit large conifer dominated forests, they are also able to utilize urban landscapes. In addition, previous studies have shown a similar preference for forested areas by different squirrel species in urban areas (gray squirrel, *Sciurus carolinensis*, Bonnington et al. 2014; fox squirrel, *Sciurus niger*, McCleery et al. 2007). Expectedly, at the scale of location points, red squirrels preferred areas with more trees available than in the surrounding urban landscape and avoided buildings and roads. Despite these findings, red squirrels were also often encountered in heavily built sites with only a few trees. At the home range scale, considering natal and settlement areas of juvenile individuals, red squirrels favored areas with deciduous trees, but there was no preference or avoidance found for other landscape structures. For adult red squirrels, I found no difference in habitat composition between home ranges and available landscape, indicating that the squirrels used different habitats in relation to their availability. Red squirrels are found to be flexible in their habitat use in different parts of their wide distribution range (Lurz et al. 2005) and my results strongly support this, red squirrels being able to utilize very small patches of trees and also single trees surrounded by buildings. Thus, at some level my study contradicts earlier studies indicating that red squirrels need forest patches of several hectares (Wauters, Casale et al. 1994, for a review see Selonen & Hanski 2015). Food availability, for example, is one major factor, in addition to patch size, determining where an animal can prosper.

I found that the habitat use of juvenile red squirrels differs between the phases of natal dispersal. Dispersing red squirrels settled in areas with fewer deciduous trees and more buildings than in the natal area. Juvenile individuals also used less deciduous trees during explorative and dispersal movements than during movements in the natal area. In contrast, the use of asphalt and other hard flat surfaces increased during exploration and dispersal movement. In general, the study individuals were born in urban park areas, but they dispersed through and settled in sites outside the parks, with larger proportion of built environment, like roads and buildings, compared to their natal sites.

3.1.2 The effect of roads on movement of red squirrels

Animals' reactions to roads have been previously studied by observing only adult individuals, but not young dispersing individuals, whose movements highly determine the gene flow of many mammalian species. In Chapter **II**, I found juvenile red squirrels to not avoid roads or crossing them during their dispersal movements, meaning that roads do not inhibit the dispersal of red squirrels in urbanized areas. Adult females avoided roads during movements in the urban area, and also the juvenile individuals avoided roads and crossing them during movements in the natal or settlement areas, but the behavior changed during explorative and dispersal movements (Fig. 3). Juvenile individuals were found not to avoid crossing roads during the transition from their mother's home range to their new settlement site. During the routine movements of adult individuals and juvenile movements in natal and settlement sites, red squirrels crossed big roads only rarely. However, during exploration and dispersal, red squirrels crossed all sizes of roads. In addition to the deterrent effect of roads being insignificant for dispersal of juvenile red squirrels, straight mortality caused by vehicles among dispersing individuals was also detected to be low in the urban area. The main cause of death of urban juvenile individuals was observed to be predation, presumably by domestic cats and urban foxes.

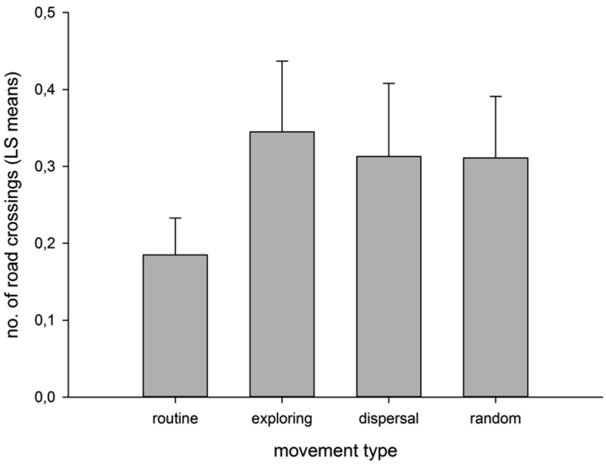

Figure 3. Estimated means (± SE) from generalized linear mixed model of red squirrels' road crossings in the city of Turku between subsequent tracking locations according to the individual's movement type and accounting for step length.

3.2 Dispersal distances

In **Chapter III,** I found surprisingly long natal dispersal distances in the rural Kauhava study area. The longest observed dispersed distance by juvenile red squirrel was over 16 km. The observed dispersal distances in the urban study area were significantly shorter, only a third of those in the rural area (Fig. 4). The observed dispersal distances in the rural area (mean distance: 3.6 km) are longer than those of previous studies, where the distances vary between 250–1.000 meters depending on forest type (Wauters & Dhondt 1993; Wauters et al. 2010). The dispersal distances observed in this study in the urban area (mean distance: 430 m) better correspond to the distances observed in the rural areas of Belgium (250–1.000 m, Wauters & Dhondt 1993; Wauters et al. 2010). In accordance to previous findings, I found no sex bias in dispersal distances of juvenile red squirrels (Wauters et al. 2011). The efficiency of dispersal ability has also been detected on other arboreal squirrel species. The high movement potential is addressed in invasive squirrel species, such as *Callosciurus* and gray squirrel (see Selonen & Mäkeläinen 2017 for a review), and the Siberian flying squirrel is also known to be an effective disperser (Selonen & Hanski 2004, 2012). The results of my thesis can help to estimate movements and spread of the species and may also contribute more generally to the protection of arboreal squirrels. For example, in the British isles, where the native red squirrel is threatened by an invasive squirrel species, the gray squirrel (*Sciurus carolinensis*), the knowledge of dispersal ability and habitat selection of the red squirrel may promote the protection of the species. Also in Finland, where the red squirrel populations

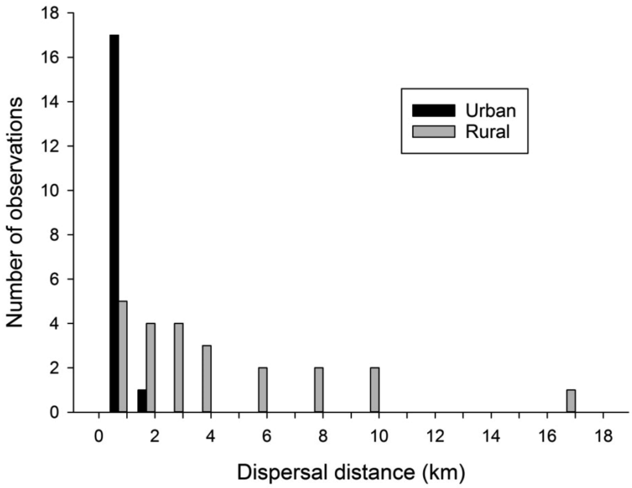

Figure 4. The distribution of natal dispersal distances of the red squirrel in the rural (gray bars) and urban (black bars) study areas (in km).

are declining, it is beneficial to know the movement potential of the species when evaluating the factors threatening the squirrel populations.

According to my results, there is a preference for certain landscape features along the dispersal routes of juvenile red squirrels. In the urban study area, red squirrel paths included more deciduous and coniferous trees and buildings than what would be expected at random. The preference for close proximity to buildings during dispersal movements was unexpected, but this can be explained by the supplementary feeding provided by humans (Jokimäki et al. 2017). A few study individuals in the urban area also had nests in buildings. In the rural area, red squirrels expectedly favored spruce-dominated forests and avoided fields. Surprisingly, squirrels also favored young forests with limited cone production along their dispersal routes. In the rural area, red squirrel paths also contained more forest edges than the random paths.

The landscape affected not only where juvenile individuals move during dispersal, but also the length of movement steps made by dispersers. Movement steps were found to be shorter in the forested areas and longer in the more hostile areas, like fields and asphalt. This suggests that squirrels moved faster with longer movement steps when moving over open areas compared to forested areas. This result is in accordance with previous findings on small mammals. For example, Vásquez et al. (2002) found degus (*Octodon degus*) to move faster with longer movement bursts in the open area compared to the more sheltered shrub habitat.

Although the landscape affected the movements of dispersing individuals, I found it to explain only a small part of the differences in final dispersal distances. In the rural area, the increasing amount of forest edge along the dispersal path seemed to shorten the dispersal distances of juvenile red squirrels. As I also found a preference for forest edges during movements of dispersal, it is not obvious that the shorter dispersal distances in high edge density environment would mean that edges prevented individuals dispersing. There are earlier studies showing a tendency of red squirrels towards forest edges (Dylewski et al. 2016; Turkia et al. 2018), suggesting that edges are a preferred environment for red squirrels, possibly due to their higher cone production compared to the more inner parts of forests (Dylewski et al. 2016). It is also possible that the individuals moved along edges when searching for their home range (e.g. Latham et al. 2011), and used edges in order to orientate themselves in the landscape. It is likely that the shorter dispersal distances in edge habitat are caused by a preference for forest edges, rather than inhibition of movement ability or unwillingness to cross an edge. Contrary to my hypotheses the amount of open areas or roads and buildings did not decrease the dispersal distances of juvenile red squirrels. Some of the study individuals in the rural area crossed very large field areas with no trees to cover when dispersing to their settlement sites. The widest crossing of an open field was approximately 3 km at its narrowest point, with also a river that had to be crossed to get to another wood lot and no circuitous route available. Indeed, it has been studied that the gap-crossing willingness of adult squirrels is not affected by the gap size or crossing distance (Bowman & Fahrig 2002; Bakker & Van Vuren 2004) and red squirrels have been observed to be able to cross large open areas (Verbeylen et al. 2003; Selonen & Hanski 2015). In addition, previous study by Wauters et al. (2010) showed that habitat fragmentation does not inhibit dispersal of the species. However, there are also studies showing that fragmentation caused by agriculture can inhibit movements of other squirrel species, like the fox squirrel (Sheperd & Swihart 1995).

According to my findings, it seems that factors other than landscape structure determine the natal dispersal distances of the red squirrel. A possible explanation for the observed differences in dispersal distances between rural and urban environments is different settlement decisions that are based on resource availability and population density (Selonen & Hanski 2012; Merrick & Koprowski 2017a). For red squirrels, these variables are found to be potentially higher in urban areas compared to rural areas (Haigh et al. 2017; Jokimäki et al. 2017) mainly due to the supplementary feeding provided by humans and more versatile tree stands of urbanized areas. In rural areas, red squirrels are dependent on conifer seed crops that fluctuate heavily from year to year (Jokimäki et al. 2017). This may lead to larger home ranges of adult individuals and thus longer dispersal distances of juvenile individuals in order to leave their mother's home range. In general, home range sizes are smaller in urban areas compared to the rural equivalents (Šálek et al. 2015). It has also been found that urban eastern chipmunks (*Tamias striatus*) have reduced locomotion compared to the rural representatives of the species (Lyons et al. 2017), which is in line with our findings of shorter dispersal distances in the urban area.

3.3 Decision-making during natal dispersal

The results of **Chapter IV** show that the majority of the study individuals perform revisits to the alternative settlement areas during their natal dispersal before choosing their home range (Fig. 5). This indicates that individuals actively collect information about the alternative home ranges and compare them before making a decision to settle. Similar results have also been made, for example for dispersing brush mice (*Peromyscus boylii*) (Mabry & Stamps 2008). In the urban study area, all studied individuals performed revisits, but in the rural area also threshold decision-making was used, meaning that the squirrel stopped searching home ranges when it found a site of good enough quality to settle. This could mean that there is a quality threshold to be met before the settlement decision is to be made (Luttbeg & Langen 2004; Mabry & Stamps 2008). The dispersal distance affected the total amount of revisits individuals performed during their dispersal, with long-distance dispersers performing less revisits than short-distance dispersers, which is in line with previous studies of other squirrel species (Selonen & Hanski 2010). Red squirrels performed significantly more revisits in the urban area than in the rural area. During natal dispersal, male squirrels performed more revisits than females. In both study areas, habitat type of visited areas did not affect the amount of revisits made per area , but the juvenile red squirrels performed more revisits to the areas that they choose to settle in.

In the rural study area, I found a preference of juvenile red squirrels for settling near built areas, that is buildings and roads. This was observed when the landscape of selected areas was compared to the areas only visited. This is an interesting result, because it has been recently discovered that the abundance of red squirrels is increasing in cities and near human settlement (Jokimäki et al. 2017), whereas the populations of red squirrels have been found to be declining in many rural regions in Finland and northwest Russia (Turkia et al. 2018). These findings may be related to more stable food resources and fewer natural predators present in urban areas and in close proximity to human settlement in rural areas. The natural predators of the red squirrel, the goshawk (*Accipiter gentilis*) and the pine marten (*Martes martes*), occur in low densities in urban areas, and do not pose a major threat to the species (Jokimäki et al. 2017). However, feral cats (*Felis catus*) and foxes (*Vulpes vulpes*) are more abundant in some cities than in the rural environment (Baker & Harris 2007) and may pose a threat especially to juvenile red squirrels. Indeed, feral cats and foxes seemed to be the biggest single cause of mortality for our juvenile study individuals radio-tracked in the urban area (Chapter **II**). I found no difference in landscape composition between selected areas and only visited areas in the urban area, indicating that red squirrels select urban landscape structures as their home range in relation to their availability, and are not dependent on large forest areas. Possible determinants for settlement decisions for arboreal squirrels, instead of landscape structure, can be the site occupancy of conspecifics (Boutin et al. 1993; Lurz et al. 1997; Wauters et al. 2001; Wauters et al. 2010) but unfortunately we did not have the data of densities or occupancies within our study areas. Red squirrels have been observed to settle in forest patches where the same-sex density is lower than in alternative patches (Wauters et al. 2010). Previous studies have also shown that forest structure and canopy cover affect the habitat selection of squirrels (Selonen & Hanski 2012; Merrick & Koprowski 2017b).

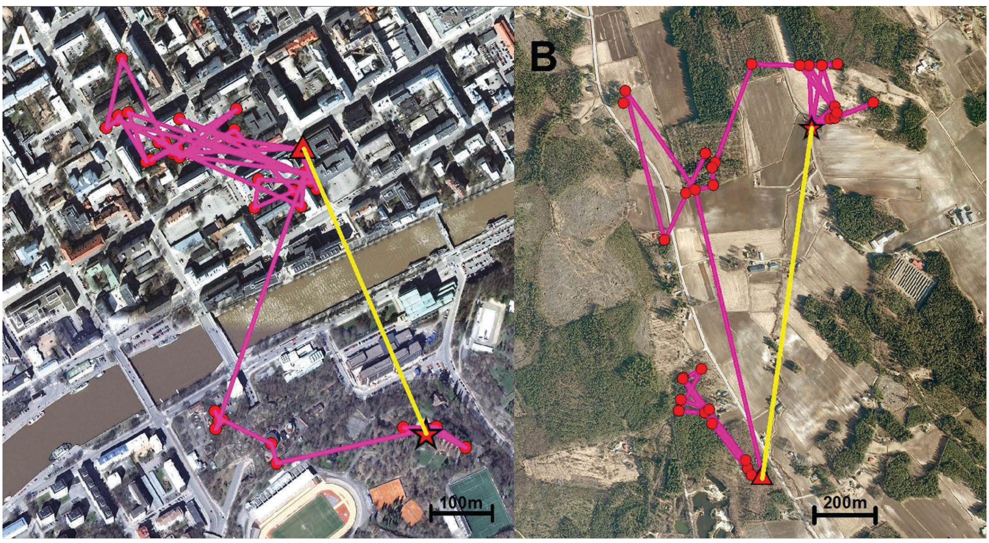

Figure 5. Examples of two individuals' dispersal route (purple) both in the urban (a) and in the rural (b) study area. Original squirrel locations are marked with red dots. The stars refer to the starting places of dispersal, and the triangles refer to the settlement places of dispersal. The yellow line between these locations is the straight line distance, that is, the dispersal distance.

4. Conclusions

In my thesis, I have studied the effect of landscape on movements and habitat selection of the red squirrel. The studies presented in this thesis show how both movement and habitat selection are connected with landscape structure, and how these variables differ between urbanized and rural areas that are both affected by anthropogenic forces.

Chapter **I** of my thesis showed that the red squirrel is well-adapted to live in human-altered landscapes. According to my results, red squirrels even prefer living in close proximity to humans and human-modified areas compared to more forested areas in the intensively managed Finnish forest landscape (Chapter **III**). The success of red squirrels in urban landscapes and in close proximity to humans is probably due to the generalist nature of the species and the more stable and diverse food supply near human settlement.

According to the results of Chapter **II** and **III**, red squirrels are effective dispersers and their movements are not restricted by unfavorable habitats. Red squirrels are very capable of utilizing urban structures and areas with only few trees. These findings support the hypothesis that urban animals tend to behave differently than individuals of the same species in more natural environments (Lowry et al. 2013; Sol et al. 2013). I discovered that in the urban area roads do not prevent dispersal of juvenile individuals, or even affect their movements during dispersal. In Chapter **III**, I found the movements of red squirrels to be affected by landscape structure; squirrels moved faster with long movement steps in unfavorable environments, like fields, and slower with shorter movement steps in spruce-dominated forest and other favorable environments. Although the dispersing individuals altered their movements in different landscapes, I found that in both urban and rural environments landscape structure had only a limited effect on dispersal distances of individuals, and squirrels crossed large fields and roads while searching for their new home range. Red squirrels performed surprisingly long dispersal distances in relation to the size of the animal in order to find their home range in the rural area, while dispersal distances remained short in the urban study area. Since the landscape structure, such as the amount of open areas crossed during dispersal, did not explain the differences in dispersal distances, it remains somewhat unclear what it is that drives rural dispersers to move such long distances.

According to the results of Chapter **IV**, the strategy to find a new home range altered between the study individuals of rural and urban areas. The landscape had only a small effect on dispersing individuals' decisions regarding how to visit alternative home ranges and in which place to settle. Although in the rural area juveniles chose to settle in close proximity to human settlements, the majority of decision-making in search for a home range during the natal dispersal is mainly determined by factors other than landscape structure. The results of my thesis provide tools to estimate species distribution and spread in a changing environment. The knowledge of arboreal squirrel movements and habitat selection in relation to landscape features has implications for both protecting threatened species and inhibiting the spread of invasive species.

To conclude, the results of this thesis show that the red squirrel is well adapted to live in human-modified landscapes and can utilize heavily built environments with only small fragments of natural forest environment. In addition, the dispersal distances of red squirrels are not affected by unfavorable landscapes, such as fields or roads, but individuals are able to disperse significantly long distances regardless of the landscape they encounter when moving to their new home range. The species seems to be well-accustomed to human disturbance and will probably not suffer from ongoing urbanization. Thus, the landscape structure in the study areas does not create a threat for movement and dispersal of the red squirrel populations.

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