# Animals in space and time: spatio–temporal movement pattern analysis

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# Summary

Movements of animals are important and highly complex processes which influences the outcome of many large–scale ecological processes. Especially within a changing world understanding the responses of species to environmental change is of fundamental importance for effective management and conservation of biodiversity and hence to maintain ecosystem services for human well–being like access to water or pollination. These changes are affecting the distribution of populations in space and time as well as their resource use. An improved understanding of these processes will contribute to a better ecological understanding and to ensure the survival of populations.

With increasing advances in the technologies of tracking devices and remote sensing applications we are nowadays able to follow animals within their natural habitat and evaluate species–environment relationships.

This thesis investigates different aspects of movement patterns on the individual level of red and roe deer which are equipped with GPS devices within the Bohemian Forest. Studying individuals promotes recognition of between–individual variation in movement patterns and allows for general mechanism to be identified which are directly affecting the population level.

Although the Bohemian Forest, formed by two national parks, the National Park Bavarian Forest on the German side and the Šumava National Park on the Czech side, covers a large area, it does not encompass all occurring processes within this ecosystem. The administration is responsible to institute appropriate arrangements to ensure negative impacts to conventional forestry and agricultural use in the adjoining areas to the borders of the national parks. However this area can only serve as a summer range for red deer and typically deer would migrate to lower elevational regions to stay there during winter time. Due to anthropogenic influences natural migration routes are no longer accessible. Therefore winter enclosures were established in the national parks where red deer are staying during the winter time to prevent possible damage to the adjoining economic forests by e.g. bark stripping.

The processes driving migration patterns of red deer are investigated in a first step. Little is known about the behaviour of red deer after the opening of the winter enclosures. After the forage maturation hypothesis, the animals should follow the phenological gradient of the green–up and hence the emerging food

resources in spring. The investigation shows that for the majority of the animals the emerging food resources only partially shape the movement pattern of red deer after the opening of the winter enclosures and that further factors beside the chosen spatio–temporal information about the environmental conditions need to be considered to explain the movement patters, such as memory effects for resources or threats.

After the release of the winter enclosures deer disperse into the national parks. Mammals do not tend to move at random, they rather restrict their movements to particular areas, so called home ranges. They are generally defined as the spatial expression of all behaviours an animal performs in order to survive and reproduce. As home ranges are the fundamental measure of space use by animals and furthermore link individual movement paths to population dynamics understanding the mechanisms shaping home range size pattern is relevant to understand patterns of space use, habitat preferences and responses to environmental change. The variation of home range sizes in red and roe deer was investigated by taking not only the dominant habitat type into account but also the explicit spatial configuration of habitat types within the home range. The results show that the spatial configuration of the landscape is a dominant factor for the explanation of temporal variation in home range size of red and roe deer. Furthermore the shape of the relationship between home range size and landscape configuration depends on a species' habitat requirements: while roe deer increase their home range size with increasing landscape patchiness, the relationship is hump–shaped for red deer.

A critical point in understanding movement patterns of animals is the definition of resources. While we're gaining increasingly better data by animal tracking devices, the way we define our landscape remains the same. Usually landscapes are defined by the human perception of different land cover types forming categorical classes (e.g. forest or meadows). However, categorical representations of the landscape cannot capture within class variability which might occur within a class, e.g. tree cover variability of small forest gaps within the forest class. A remote sensing approach, fractional cover, is tested and evaluated for the use in habitat selection studies of red deer in the Bohemian Forest. These fractional cover layers provide continuous land cover information per pixel and hence represent a more differentiated landscape. The application of fractional cover in the

context of spatio–temporal animal movement analysis proofed to be valuable by providing information of the within land cover class variability. Home ranges increase with increasing mean values of forest fractional cover and increasing variation of forest fractional cover.

This thesis investigated different aspects of animal movement pattern and especially the importance of spatial patterns of resource patches and their representation for animal movement studies. The combination of these different information sources provide new valuable information for the better understanding of ecological processes and will increase with improving technical advances.

# Zusammenfassung

Bewegungsmuster von Tieren sind hochkomplexe Prozesse, die viele großräumige ökologische Prozesse beeinflussen. Besonders innerhalb einer sich immer schneller verändernden Welt ist das Verständnis, wie bestimmte Tierarten auf Veränderungen reagieren, von grundlegender Bedeutung für den Naturschutz und zur Erhaltung der Biodiversität, sowie für verschiedene Ökosystemleistungen, wie beispielsweise dem Zugang zu Wasser oder der Bestäubung von Pflanzen. Bewegungsmuster von Tieren sind grundlegende Prozesse, welche die Verbreitung von Populationen in Raum und Zeit beschreiben und sind daher ein Schlüsselmechanismus, um zukünftige Veränderungen zu verstehen. Zudem ist das Verständis der zeitlichen und räumlich variierenden Ressourcennutzung von großem Interesse für das bessere Verständnis der Ökosystemfunktionen. Ein besseres Verständnis von Bewegungsmustern ermöglicht ausserdem, Naturschutzstrategien effektiver zu gestalten und so das Überleben von Populationen zu sichern.

Die Entwicklung von GPS–Ortungsgeräten und Fernerkundungsmethoden ermöglicht es heutzutage, Tiere permanent in ihrem natürlichen Habitat zu verfolgen und die Tier–Umwelt–Interaktionen zu analysieren.

In dieser Dissertation werden verschiedene Aspekte der Bewegungsmuster von Hirschen und Rehen im Böhmerwald auf der Individual–Ebene analysiert. Die Tiere sind mit GPS–Ortungsgeräten ausgestattet. Die Untersuchung von individuellen Aspekten innerhalb der Bewegungsmuster fördert das Verständnis über die Variationen innerhalb der Muster. Auf diese Weise können generelle Mechanismen, welche sich direkt auf die Populationen auswirken, identifiziert werden.

Der Böhmerwald wird durch zwei Nationalparks geformt: dem Nationalpark Bayerischer Wald auf deutscher Seite und dem Šumava Nationalpark auf tschechischer Seite. Trotz seiner Größe ist es nicht möglich alle vorkommenden Prozesse innerhalb dieses Ökosystems zu bewahren. Die Verwaltungen der Nationalparks sind daher in der Pflicht, Schutzmaßnahmen zu etablieren, um die angrenzenden ökonomisch genutzten Wälder sowie landwirtschaftlich genutzten Flächen vor Schaden durch z.B. Tiere zu schützen. Der Böhmerwald kann für die Hirsche nur als Sommergebiet dienen. Typischerweise würden die Tiere im Herbst zu ihren Überwinterungsgebieten wandern. Durch anthropogene Einflüsse sind jedoch die ehemaligen Migrationsrouten unterbrochen. Daher wurden innerhalb der Nationalparks Wintergehege errichtet, in denen die Hirsche überwintern. Dadurch

sollen mögliche Schäden, durch z.B. Schälungen an den Bäumen, in angrenzenden Wäldern verhindert werden.

Zunächst werden Prozesse, die die Migrationsmuster der Hirsche nach der Öffnung der Wintergehege beeinflussen, untersucht. Nach der *forage maturation* Hypothese sollten die Tiere dem phänologischen Gradienten der Vegetationsentwicklung und daher den neu entstehenden Futterquellen im Frühling folgen. Die Analysen zeigen, dass für die Mehrheit der Tiere, die zeitlich dynamisch verfügbaren Ressourcen nur teilweise die Bewegungsmuster nach der Öffnung der Wintergehege beeinflussen und dass weitere Faktoren neben der gewählten raum–zeitlichen Information berücksichtigt werden müssen. So ist unter Umständen der Gedächtniseffekt für Ressourcen oder Gefahren ein wichtiger weiterer erklärender Faktor.

Nach der Öffnung der Wintergehege, sollten die Tiere diese verlassen und sich im Park ausbreiten. Säugetiere tendieren nicht dazu, sich zufällig zu bewegen, stattdessen beschränken sie ihre Bewegungsmuster meist auf ein bestimmtes Gebiet, das so genannte Streifgebiet. Faktoren, die die Variationen in den Streifgebietsgrößen von Hirschen und Rehen erklären können, wurden hierbei untersucht. Nicht nur das dominante Habitat innerhalb eines Streifgebietes wurde berücksichtigt, sondern zusätzlich wurde auch die explizite räumliche Konfiguration von Habitattypen innerhalb eines Streifgebietes in die Analysen mit aufgenommen. Die Ergebnisse zeigen, dass die räumliche Konfiguration der Landschaft ein dominanter Faktor ist, der die Variationen der Streifgebietsgröße bei Hirschen und Rehen erklärt. Darüber hinaus ist die Form der Beziehung zwischen Streifgebietsgröße und Landschaftskonfiguration abhängig von den Ansprüchen der Art an ihr Habitat. Während Rehe ihre Streifgebietsgröße bei steigender Klumpung der Habitattypen vergrößern, ist das Verhältnis bei Hirschen unimodal.

Des Weiteren wurde das Potential von Umweltinformationen innerhalb von Landoberflächenklassen zur Erklärung von Bewegungsmustern untersucht. Eine kategoriale Repräsentation der Landschaft liefert keine Informationen über die Variabilität innerhalb einer Klasse, z.B. die Variabilität der Kronendecke oder kleine Lichtungen innerhalb der Klasse Wald. Ein fernerkundlicher Ansatz, *fractional cover*, welcher kontinuierliche Landbedeckungsinformationen liefert, wurde für die Analyse der Habitatselektion von Hirschen verwendet. Die kontinuierlichen Landbedeckungsinformationen zur Quantifizierung der Landoberflächenklassenvariabilität im Kontext von räumlich–zeitlichen Bewegungsmusteranalysen zeigte sich durch die Bereitstellung von Informationen über die Variabilität innerhalb einer Landbedeckungsklasse als nützlich. Die Größe der Streifgebiete nimmt mit steigendem Mittelwert, sowie mit steigender Variation des *fractional cover* Werts von Wald zu.

In dieser Arbeit wurden verschiedene Aspekte der Bewegungsmuster von Tieren analysiert, insbesondere die Bedeutung von räumlichen Mustern in der Landschaft und ihre Repräsentation für Bewegungsmusterstudien. Die Kombination von Tierbewegungsdaten und Fernerkundungsinformationen liefert wichtige neue Erkenntnisse für die ökologische Forschung und wird mit zunehmender Verfügbarkeit weiterer technologischer Fortschritte zunehmend an Bedeutung gewinnen.

# 1

# General introduction

Due to human induced changes we are nowadays confronted to a variety of environmental changes on a global level. This global change is leading besides others to habitat loss and transformation (DeFries *et al.*, 1999; Wessels *et al.*, 2004; Alberti, 2005), resource exploitation (Lambin *et al.*, 2003) and biodiversity loss (Fahrig, 2003; Gaston *et al.*, 2003; Kokko and López-Sepulcre, 2006; Hector and Bagchi, 2007). Furthermore, this trend is likely to continue in the future (IPCC, 2013). The increased trend which human–induced changes are causing, increases the importance of understanding the patterns in biodiversity. Biodiversity influences human well–being through ecosystem services, including access to water, pollination and regulation of climatic conditions (Díaz *et al.*, 2006; Cardinale *et al.*, 2012; Hadley and Betts, 2012). In the context of biodiversity loss and global climate change, understanding the mechanism that shape species richness and composition is crucial for conservation and environmental management (Loreau *et al.*, 2003; Hirzel and Le Lay, 2008).

Protected areas play a key role in preserving biodiversity (Hannah, 2008; Townsend *et al.*, 2009) and ecosystem services (Alcaraz-Segura *et al.*, 2009; Krishnaswamy *et al.*, 2009), still they are restricted by defined borders and are even sometimes too small to preserve animals during their lifespan (Wilcove and Wikelski, 2008; Singh and Milner-Gulland, 2011). Hence, for effective management strategies, knowledge about the distribution of animals and their movements across different spatio–temporal scales is essential.

Animal movement, dispersal and habitat selection are important determinants of the dynamics and distribution of populations in heterogeneous landscapes and form a bridge between animal behaviour, landscape ecology and population dynamics (Lima and Zollner, 1996). The basis of spatio–temporal dynamics of animal distributions is individual movement (Getz and Saltz, 2008; Nathan *et al.*, 2008; Mueller and Fagan, 2008) and the most crucial limit to understand why animals move is to understand what resources they use at a specific time and place and at different spatial scales (Fryxell *et al.*, 2008; Wittemyer, 2008; Beyer *et al.*, 2010; Cagnacci *et al.*, 2010; Gaillard *et al.*, 2010; Morales *et al.*, 2010; Owen-Smith *et al.*, 2010; Smouse *et al.*, 2010)

With technological advances in tracking devices, as well as computational power and analytical techniques, novel application and statistical methods to answer questions related to animal movement and space use are feasible to be addressed, however analysing the factors shaping animal–environmental interaction, especially resource availability remains still difficult (Beyer *et al.*, 2010; Fieberg *et al.*, 2010; Wilson *et al.*, 2012; Warton and Aarts, 2013).

Animal movements are central to population ecology because many spatial processes, like disease spread or metapopulation dynamics, and applications, like the design of protected areas, depend on the movement behaviour of individuals (Morales and Ellner, 2002; Kokko and López-Sepulcre, 2006; Patterson *et al.*, 2008). Recently, the importance of movement ecology has received recognition and advancements have been made in understanding movement processes and building up a general framework for movement ecology (Getz and Saltz, 2008; Nathan *et al.*, 2008; Schick *et al.*, 2008).

The following paragraphs provide a brief overview about the main topics of this thesis followed by a synopsis of the articles of this thesis. Finally, the remaining and future research challenges will be highlighted at the end of this thesis.

## 1.1 Animal movement in space and time

A basic question in ecology is to understand the factors and processes shaping the distribution of species in space and time. The fundamental underlying mechanism is individual movement as it determinates the dynamics and spatial distribution of populations in heterogeneous landscapes (Turchin, 1991; Morales *et al.*, 2010).

Almost all organisms have to move at some point during their lives, either under their own locomotion or transported by physical processes or organic agents. One of the most noted form of animal movements are large scale migration patterns, like the wildebeest migration in the Serengeti where millions of animals follow the rainfall pattern across eastern Tanzania (Bolger *et al.*, 2008; Holdo *et al.*, 2009) or the long–distance migration of birds, such as storks, following seasonal resource availabilities (Higuchi, 2012). However, this is a small snapshot of animal movement or movement pattern. Movements occur on different spatial and temporal scales and are typically categorized into distinct functional groups ranging from small scale foraging movements (Turchin, 1991; Preisler *et al.*, 2004) to frequent large scale migration or dispersal (Sawyer and Kauffman, 2011; Bischof *et al.*, 2012; Middleton *et al.*, 2013; van Moorter *et al.*, 2013). Therefore the term movement encompasses all possible forms of movement and a general unifying framework is still under debate (Nathan *et al.*, 2008).

Technological advances in the remote monitoring of animals due to tracking devices makes it now possible to study animals over long time spans, large areas and with a high frequency of location points (Tomkiewicz *et al.*, 2010). Nowadays we are able to quantify accurately where animals go and this allowed researchers the expansion of the mechanistic approach to the ecology of large animals, with the direct possibility to relate the animals to its environment and to show the interaction of animals with their environment (Cooke *et al.*, 2004; Cagnacci *et al.*, 2010).

Movement is studied by monitoring locations over time. The location points of animals provide the basic unit of movement paths (individual level) which sum up to the effects on the population level. Studying the movement of individuals helps to detect between individual variation in movement patterns, like random effects or effects by sex or age (Holyoak *et al.*, 2008; Revilla and Wiegand, 2008).

With the evolving technology of sensors for studying animals, progress has been made in understanding the relationship between landscape and animal movement (Frair *et al.*, 2005; Mueller *et al.*, 2011; Sawyer and Kauffman, 2011; van Moorter *et al.*, 2013) and the detection of internal behavioural modes (Fryxell *et al.*, 2008; Nathan *et al.*, 2008; Patterson *et al.*, 2008; Gurarie *et al.*, 2009). Furthermore the applicability of theoretical concepts of animals movement patterns can now be investigated (Mueller and Fagan, 2008; Schick *et al.*, 2008;

Pedersen *et al.*, 2011; Moorcroft, 2012).

Despite the progress in technology and the development of statistical methods, comparing animal choices with the availability of resources and to fully understand the movement patterns remains challenging and is still a main focus in ecology and conservation.

## 1.2 The home range concept

Mammals do not tend to move at random, they rather restrict their movements to particular areas, that are much smaller than one might expect from observed levels of mobility, without showing a territorial behaviour. This phenomenon underlies the concept of an animals home range. Home ranges are generally defined as the spatial expression of all behaviours an animal performs in order to survive and reproduce (Burt, 1943). The home range is the fundamental measure of space use by animals. As a result understanding the mechanism shaping home range pattern is crucial to understand patterns of space use, habitat preferences and responses to environmental change.

Understanding why home range size varies between and within species remains a fundamental issue in ecological research (McLoughlin and Ferguson, 2000; Börger *et al.*, 2008; van Beest *et al.*, 2011). The home range size characterizes the interplay between an animal and its environment. Here, the determinants of home range size can be internal or external. Different studies have shown that home range size may e.g. depend on body size (Harestad and Bunnel, 1979; Swihart *et al.*, 1988; Mysterud *et al.*, 2001), forage availability (Tufto *et al.*, 1996) or intra- (Riley and Dood, 1984) and interspecific competition (Loft *et al.*, 1993). The manner in which animals select home ranges and exploit resources within a home range is still not clear, especially the intraspecific variation is not well understood (van Beest *et al.*, 2011).

## 1.3 The role of landscape

Linking movements of animals to the underlying landscape is critical to identify factors shaping animals spatial pattern and behaviour (Lima and Zollner, 1996). Especially the relationship between landscape dynamics and movement is particularly important to large and mobile animals were a high temporal variability of food resources can be critical. Generally the availability and distribution of food resources are recognized as a dominant factor shaping movement pattern. Hence landscape information have to be translated into species specific resource functions which requires a profound understanding of their ecology.

To map habitat over a large area and to gain a realistic representation of the landscape under study is often difficult. With different remote sensing techniques we are nowadays able to map detailed land cover classes which can be related to habitat, biophysical properties (e.g. plant productivity) and natural and human–induced changes within and across landscapes (change detection) (Kerr and Ostrovsky, 2003; Turner *et al.*, 2003).

A common approach in ecology is to use land cover classification of a defined area. Land cover maps are commonly created by classifying remotely sensed imagery, whereas the most general distinction is that of supervised versus unsupervised classifications (Jensen, 1996). The former requires training data from known land cover type, which are used to calibrate a classification algorithm. Unsupervised methods use numerical algorithms to exhaustively cluster the image into spectrally similar groups of pixels (Lu and Weng, 2007). These land cover classifications are commonly used and can be converted to a proxy of habitat cover. The combination of different time–steps allows to retrieve changes in land cover distributions and such land cover change analysis are applied frequently (Townsend *et al.*, 2009). The resulting land cover information can be applied in land cover area estimates for e.g. forest cover and loss as well as for further analysis of the landscape such as spatial attributes of the land cover. Spatial attributes encompasses heterogeneity of a landscape, connectivity or configuration of habitat patches and a variety of different indices exist for characterizing different landscape features (McGarigal *et al.*, 2009). The analysis of the spatial arrangement of land cover patches is important to explain species distribution. The spatial characteristics can influence species abundances (Pearson, 1993) or dispersal routes (Baguette and Dyck, 2007) due to the size or isolation of fragments within the landscape.

Furthermore, temporal environmental information do provide valuable ecological information to explain changes in animal distribution or movement. A variety of remote sensing data sets exist which provide temporal information about the landscape condition. These remote sensing approaches allow to derive phenology through signals of photosynthetic activity of the vegetation, based on vegetation indices. These information have been proven to be valuable for ecological research, due to the fact that seasonal changes in vegetation strongly influences animal distributions and dynamics (Pettorelli *et al.*, 2005).

The amount of remote sensing data sets is steadily increasing as well as the amount of freely available data. Please see table 1.1 for a concise list of remote sensing sensors. New sensors such as the active sensor Sentinel–1 or the multispectral sensor Sentinel–2 will be able to provide ecologically relevant data in the future.

**Table 1.1:** A selection of satellite sensors with applications often used in ecological studies and environmental modelling.

| Sensor | Spatial resolution | Spectral resolution | Ecological variable | Application examples |
|---|---|---|---|---|
| AVHRR | 1 km | V/NIR<br>microwave | land cover,<br>land cover change,<br>phenology,<br>vegetation indices | Box *et al.* (1989),<br>Iverson *et al.* (1994),<br>Shimabukuro *et al.* (1994),<br>DeFries *et al.* (1995),<br>Adams *et al.* (1995),<br>Lambin (1996),<br>Hostert *et al.* (2003),<br>Wessels *et al.* (2004),<br>Mueller *et al.* (2008),<br>Middleton *et al.* (2013) |
| Landsat TM/ETM+ | 30 m | V/NIR<br>SWIR | land cover,<br>land cover change,<br>phenology,<br>vegetation indices | Byrne *et al.* (1980),<br>Boroski *et al.* (1996),<br>Cain *et al.* (1997),<br>Elmore and Mustard (2000),<br>Olthof and Fraser (2007),<br>Forester *et al.* (2007),<br>Schneider *et al.* (2009) |
| MODIS | 250 m - 1 km | V/NIR<br>SWIR, TIR | land cover,<br>phenology,<br>vegetation indices | Friedl *et al.* (2002),<br>Huete *et al.* (2002),<br>Lobell and Asner (2004),<br>Pettorelli *et al.* (2005),<br>Beck *et al.* (2006),<br>Bro-Jø rgensen *et al.* (2008),<br>Sawyer and Kauffman (2011),<br>Hayes *et al.* (2008) |

AVHRR = Advanced Very High-Resolution Radiometer
ETM+ = Landsat Enhanced Thematic Mapper Plus
MODIS = Moderate-resolution Imaging Spectroradiometer
SWIR = short-wave infrared
TIR = thermal infrared
TM = TM Landsat Thematic Mapper
V/NIR = visible/near-infrared.

## 1.4 Focus of my work

This thesis combines different approaches in analysing animal movement pattern and aims to enhance the understanding of the space use of animals. Moreover it aims to include different remote sensing based landscape information for analysing animal movement data.

The studies have been conducted within the National Parks Bavarian Forest (Germany) and Šumava (Czech Republic). Red deer (*Cervus elaphus*) and roe deer (*Capreolus capreolus*) were equipped with GPS–collars. Both species were investigated concerning their movement ecology, whereas the focus lies on the movement pattern of red deer.

This thesis starts by analysing the processes driving migration patterns of red deer (chapter 2), followed by investigating individual levels of movement in relation to the spatial configuration of the landscape (chapter 3). Impacts of within land cover class heterogeneity on animal movement pattern is analysed in chapter 4. Challenges and future perspectives are outlined and discussed in chapter 5.

The research was conducted in the National Park Bavarian Forest, Germany and the adjoining Šumava National Park in the Czech Republic, forming together the Greater Bohemian Forest Ecosystem, the largest protected area in Central Europe. Although the national parks cover a large area, they cannot encompass all occurring processes within this ecosystem. Adjoining to the borders of the national parks are areas with economic interests, like commercial forests or agriculture. Therefore the administration is responsible to institute appropriate arrangements to ensure negative impacts to conventional forestry and agricultural use. Within the borders of the national parks nature is left to its own means and natural processes are allowed to take their course. This is especially visible in the large areas which have been affected by bark beetle outbreaks since the 90s, leaving an area of 5,600 ha converted to regeneration areas with standing and lying dead wood and new young vegetation stands. To ensure the health of the adjoining forest, management in the border regions of the national parks takes place to prevent bark beetle outbreaks in economic forests. Besides the management of “pest species” a major issues is the management of red deer in the national parks. Red deer is known to damage trees by bark stripping in winter when food resources are scarce and the adjoining economic forests need to be prevented from possible damages. The Bohemian Forest can only serve as a summer range for red deer and typically deer would migrate to lower elevational regions to stay there during winter time. Due to anthropogenic influences natural migration routes are no longer accessible. Therefore winter enclosures were established in the national parks were red deer are staying during the winter time.

In chapter 2 the behaviour of red deer after the opening of the winter enclosures is investigated. Here, a remotely sensed vegetation index, the Normalized Difference Vegetation Index (NDVI) is used as a proxy for vegetation productivity and phenology to analyse if deer track the spring green–up after the opening of the winter enclosures, as would be expected. Furthermore the management of the opening dates of the winter enclosures can be matched with the start of season of the vegetation period and management strategies can be evaluated.

After the release of the winter enclosures deer distribute in the national parks and the individuals form home ranges. As home ranges link individual movement paths to population dynamics understanding why and how home range sizes vary between and among species is a fundamental issue in ecology. While most studies investigate the variation in home range size with relation to the dominant habitat type, I additionally take the habitat configuration into account, and extent the analyses in home range size variation in chapter 3 by taking the explicit spatial configuration of habitat types within the home range into account. The results show that the spatial configuration of the landscape is the dominant factor explaining variation in home range size of red and roe deer. Furthermore the shape of the relationship between home range size and landscape configuration depends on a species' habitat requirements: while roe deer increase their home range size with increasing landscape patchiness, the relationship is hump–shaped for red deer and the results are robust at all tested spatio–temporal scales.

A critical point in understanding movement patterns of animals is the resource use, the definition of resources respectively. GPS location points provide fine–scale datasets between animals and habitat and the technology of sensors improved over the last years. While we're gaining always better data from animals the way we define our landscape remains the same. Usually landscapes are split into categories defined by the human perception of different land cover types (e.g. forest or meadows). Depending on the system the data was generated we can have a very high spatial resolution. Still a categorical representation of the landscape remains artificial as it cannot capture the spatial variability that usually occurs in the landscape within each category, e.g. tree cover variability or small forest gaps within the forest class. In chapter 4 a remote sensing approach is tested and evaluated for the use in habitat selection studies. These fractional cover provide continuous land cover information per pixel and hence represent a more distinguished landscape. Previous attributes associated with different land cover types (e.g. dense forest) can now be tested and validated. I investigated the use of the fractional cover approach for the analysis of habitat selection of red deer in the Bohemian Forest by analysing the variation of home range sizes with respect to continuous forest fractional cover. In this study, I include the landscape as continuous variable which provides more details for habitat selection regarding fine scale variation.

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# 2

# Migration pattern of red deer in the Bohemian Forest

## Abstract

Resource availability within landscapes varies across space and time. Movements of animals are partly a response to these changes. In temperate regions the seasonal landscape changes lead to migration patterns between summer and winter ranges. The primary mechanism driving migration is here the selection of high–quality foraging areas.

Remote sensing can measure landscapes status and changes over vast areas and across time. The Normalized Difference Vegetation Index (NDVI), provides relevant information on plant phenology and productivity to explain the behavioural response of animals to seasonal patterns.

In this study we investigated the migration pattern of red deer in the Bohemian Forest. Due to anthropogenic landscape modification the natural migration route outside the boundaries of the national park are limited. Therefore, winter enclosures within the national park were established and animals stay there during winter time. We examined the behaviour of red deer after the opening of the winter enclosures related to the phenology and therefore NDVI patterns.

The remotely sensed spatio–temporal landscape attribute provided by the NDVI explains only partially the behavioural pattern of red deer after the opening of the winter enclosures. Further factors beside the chosen spatio–temporal information about environmental conditions need to be considered to explain the movement patterns of red deer such as memory effects for resources or threats.

## 2.1 Introduction

Animal movements are the primary behavioural response to spatio–temporal heterogeneity in resource availability (Boone *et al.*, 2006). Movements can be split into different behavioural responses, e.g. small scale foraging movements or large scale migration movements. Typically ungulates living in temperate regions move between summer and winter ranges, i.e. from lower to higher elevational ranges (Georgii, 1981; Mysterud, 1999). The selection of high–quality forage is thought to be the primary mechanism driving ungulate migration (Fryxell and Sinclair, 1988; Sawyer and Kauffman, 2011) and forage plants are most nutritious to ungulates at the onset of the growing season when they are highly digestible (Albon and Langvatn, 1992; Mysterud *et al.*, 2011; Cagnacci *et al.*, 2011). A variety of studies report that ungulates follow the emerging plant phenology in spring (Hebblewhite *et al.*, 2008; Sawyer and Kauffman, 2011; Fryxell and Avgar, 2012; Christianson *et al.*, 2013). This phenology can be retrieved over large scales through remote sensing. Over the last decades, the remotely sensed Normalized Difference Vegetation Index (NDVI) gained popularity and has frequently and successfully been employed to interpret animal characteristics in relation to vegetation properties (Pettorelli *et al.*, 2005b, 2011). The NDVI provides information on vegetation productivity and phenology over different temporal and spatial scales and has been widely used in recent ecological studies as a proxy for vegetation productivity and phenology (Kerr and Ostrovsky, 2003; Pettorelli *et al.*, 2005b; Boone *et al.*, 2006; Hebblewhite *et al.*, 2008; Hamel *et al.*, 2009). In general, deer did track phenological green–up through parts of the growing season by making adjustment in habitat use. Recently Bischof *et al.* (2012) analysed the behavioural response of migratory red deer to plant phenology and detected different behavioural modes to follow the spring green up, referred to as “surfing” i.e. migrating smoothly along with the leading edge of plant phenology and therefore exploit continuously forage at a high nutritional levels, and “jumping”, i.e. shorter quickly habitat adjustments in order to attempt maximization in access to high forage quality at each range, with all stages in between.

Deer–browse interactions usually cause numerous conflicts between forestry management, deer management and natural conservation. In our study area, the Bohemian Forest, the overall management concept within the National Park is the protection of unaltered natural processes but management is limited to the area of the National Park and forces an arbitrary management in winter months for red deer to prevent impacts in adjoining economic forests. Therefore so called winter enclosures were established within the National Park in the 1970s and 1990s were red deer are fed and stay during winter time. Winter enclosure poses a serious interference with the natural behaviour patterns of red deer as natural migration is stopped as formerly migration routes are interrupted due to settlements and roads. Nevertheless after the opening of the winter enclosures red deer should resume migration behaviour according to the forage maturation hypothesis and select areas with high forage quality (Hebblewhite *et al.*, 2008).

We investigate in this study the migration pattern of red deer in the Greater Bohemian Forest. Furthermore the direct behavioural response of red deer to the opening of the winter enclosures will be analysed and the overall management strategy is evaluated. As a rule of thumb the winter enclosures are opened by the staff of the national park after snow melt when the surrounding of the enclosures show a clear sign of emerging vegetation. So far, there are no studies about the behaviour of red deer after opening and it is assumed that the animals leave the enclosures immediately after opening.

As previous studies showed a clear pattern of deer following the plant phenology (Sawyer and Kauffman, 2011; Bischof *et al.*, 2012; Christianson *et al.*, 2013), we expect red deer in our study area to move to forage rich habitat and follow the green–up immediately after release of the winter enclosures. As the enclosures are opened when vegetation is visible emerging and therefore the vegetation period already started, we hypothesize the animals to "jump along the green wave" (*sensu* Bischof *et al.* (2012)). Furthermore, as the dates of the opening of the enclosures are available we can track the behaviour of the animals in fine steps. We hypothesize that the animals leave the enclosures immediately after the opening. Therefore a strong directionality of the movement steps of the single individuals should be visible, following the green up. In addition to the behavioural responses of deer the management strategy of the timing of the opening of the enclosures is evaluated by using the start of season derived from the NDVI.

Additionally data from three animals not staying in enclosures during winter is available. Although this sample size is rather small, the animals can give insight in the behaviour of the animals during winter time. Unlike the animals within the enclosures, these animals are not fed, therefore we expect a strong behaviour following the green up.

## 2.2 Material and methods

### 2.2.1 Study area

This study was conducted in Central Europe in the Bohemian Forest, an area belonging to two national parks: the Bavarian Forest National Park on the German side of the border (240 km$^2$) and the Šumava National Park on the Czech side of the border (640 km$^2$). These protected areas are embedded within the Bavarian Forest Nature Park (3070 km$^2$) and the Šumava Landscape Protection Area (1000 km$^2$). In its entirety, the area is known as the Bohemian Forest Ecosystem. The area is mountainous, with a variation in elevation between 600 and 1450 m.a.s.l. The mean annual temperature varies between 3°C and 6.5°C along higher elevation and ridges. The mean annual precipitation is between 830 and 2230 mm. Within the park, three major forest types exists: above 1100 m are sub–alpine spruce forests with Norway Spruce (*Picea abies* L.) and some Mountain Ash (*Sorbus aucuparia* L.), on the slopes, between 600 and 1100 m altitude, are mixed montane forests with Norway Spruce, White Fir (*Abies alba* MILL.), European Beech (*Fagus sylvatica* L.), and Sycamore Maple (*Acer pseudoplatanus* L.). In the valley bottoms, spruce forests with Norway Spruce, Mountain Ash, and birches (*Betula pendula* ROTH. and *Betula pubescens* EHRH.) (Fischer *et al.*, 2013). Since the mid–1990s, the forests of the national park have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*). By 2007, this had resulted in the death of mature spruce stands over an area amounting to 5,600 ha (Müller *et al.*, 2008; Lausch *et al.*, 2013).

### 2.2.2 Deer management in the national park

The goal of the Bavarian Forest National Park is to leave nature to its own means and to ensure that natural processes will be allowed to take their course. This includes that wild animal populations should not be affected by human activity. While it is possible to protect animals with small territories within the limits of the national park, large animals with large space requirements cannot be preserved in the National Park alone. This is especially true for animals that undertake seasonal migrations. For red deer the National Parks Bavarian Forest and Šumava can only serve as a summer range. In winter, when snow accumulates up to three meters, animals migrate to lower elevations and outside the park boundaries in areas with private and state forest (Heurich *et al.*, 2011). Forests and agricultural properties that adjoin the National Parks are managed for economic gain and therefore the National Park administration is determined to institute appropriate arrangements to ensure negative impacts to conventional forestry and agricultural use, e.g. by browsing or bark stripping of deer. In order to compensate for the effect that red deer is no longer able to follow its migration route to their natural winter habitat and to prevent damage in the adjoining economic used forests, so called "winter enclosures" encompassing 50–60 ha were established in the 1970s and 1990s (Gerner *et al.*, 2011). A total of 17 enclosures are located within the National Parks, four on the German site and thirteen on the Czech site (figure 2.1). In fall the animals are rounded up into the gates and are kept there and fed until the new vegetation period starts. As a rule of thumb, the gates of the enclosures are opened after snow melt when first leafs in the surrounding of the enclosures are visible. The majority of red deer spend the winter in these enclosures where the animals receive daily supplemental feeding.

### 2.2.3 Deer data and opening dates of winter enclosures

From 2002–2011 red deer were caught during winter, after procedure approved by the national ethical board. Red deer were captured and marked with GPS collars (Vectronic Aerospace, Berlin, Germany) in box traps with side windows after they were lured in with food. No immobilization was necessary. A second approach was to tranquilize deer by dart gun on sides where they were attracted by food (Heurich, 2011).

We collared 79 red deer (39 male, 40 female). Eight individuals were collared two or more times over the single years. Three collared individuals overwintered outside the enclosures in 2006 (two females, one male). The most common sampling design was to mark red deer in late winter and retrieve the collars after a year by collar drop-off or recapturing, allowing the collars to be used on new individuals. Data was screened for position errors beforehand. We classified the samples from the multiple collared animals over the single years as independent.

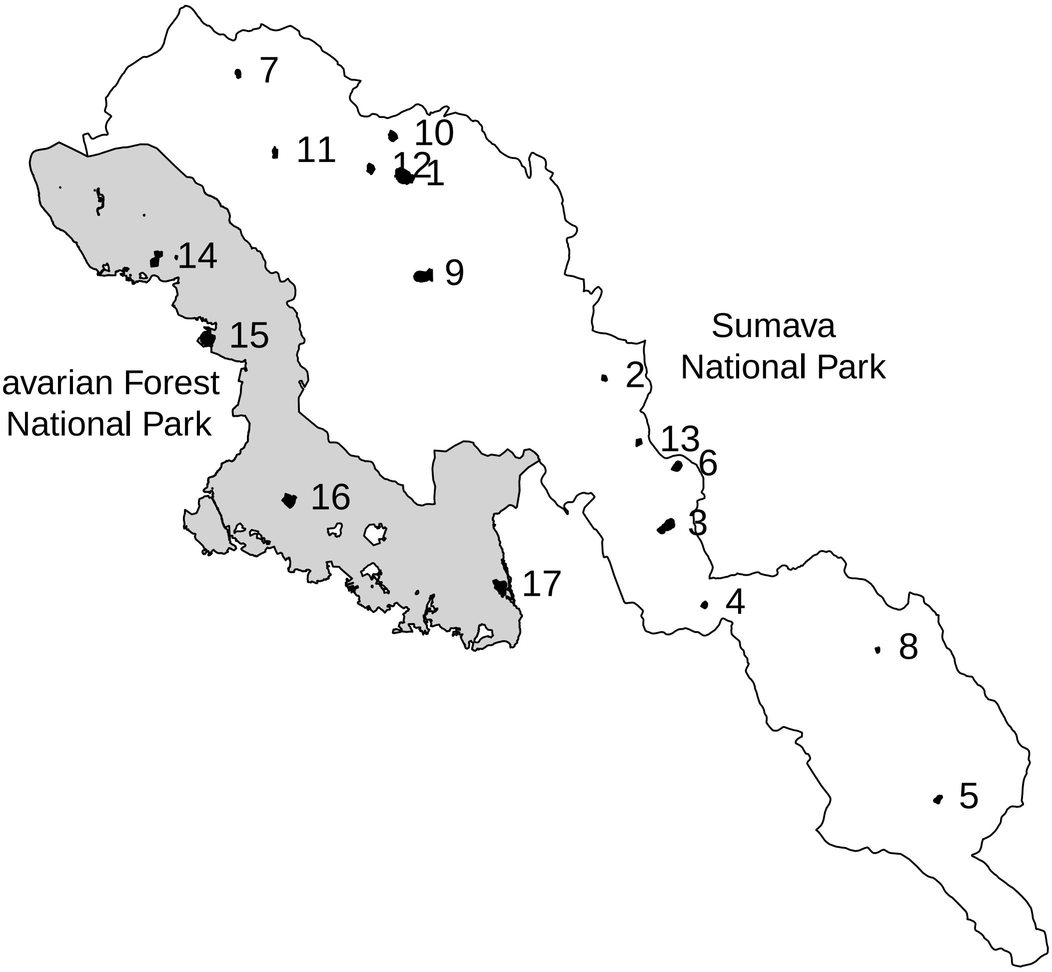

**Figure 2.1:** Location of the winter enclosures (black, indicated with numbers) within the National Parks Bavarian Forest (darkgray) and Šumava (white). White locations withing the National Park Bavarian Forest indicate settlements. Projection: WGS84 UTM Zone 33N. Winter enclosures: (1) Beranky, (2) Frantikov, (3) Kohoutí, (4) Obencníles, (5) U Herciana, (6) Bøezová Lada, (7) Hejhal, (8) Planýrka, (9) Rokyta, (10) Wastl, (11) Zadní Chalupy, (12) Étyøka, (13) Epiéàk, (14) Ahornschachten, (15) Buchenau, (16) Neuhüttenwiese, (17) Riedlhäng.

We took a random sample for animals with sequences of short time intervals (e.g. location point taken every 15 min) to ensure that the locations have a constant interval of one hour. The median spatial accuracy of the GPS locations was 16.5 m (Stache *et al.*, 2012).

For four winter enclosure the exact opening dates over the different years are available (Appendix, table 1). All other enclosures were opened as wel but no opening date was recorded hence these data sets cannot be used to analyse the detailed behaviour of red deer when the gates are opened. All enclosures with known opening dates are located within the National Park Bavarian Forest 2.1. We extracted for the available dates of each enclosure the animals in the respective enclosures and encountered 28 animals (15 male, 13, female) that are tracked and can be related to known opening dates. The behaviour of these individuals can therefore be analysed in detail concerning the impact of greening in relation to the opening of the enclosures.

For the animals within the enclosure with known dates of the opening, the movement paths are analysed to gain fine grained knowledge of the behaviour of red deer after opening of the winter enclosures. It is hypothesized that the animals are leaving the enclosures immediately after the opening and are following the maximum greenness with a directed movement path. Therefore a strong directionality of the turning angels of the movement path should be visible. We calculate the turning angles of the movement path of the individuals and connected them to the green–up to evaluate the direction of the animals and to analyse if these animals follow the maximum greenness.

### 2.2.4 Relating deer movement to plant phenology using NDVI estimates

For retrieving photosynthetic activity we applied the Normalized Difference Vegetation Index (NDVI) which is the most abundantly used and established in ecological research (Pettorelli *et al.*, 2005a, 2011). The NDVI is a spectral index calculated from earth surface reflectance patterns in the red (RED) and near–infrared (NIR) regions of the electromagnetic spectrum (NDVI = (NIR − RED) / (NIR + RED); Reed *et al.* 1994; Myneni *et al.* 1995) and enhances the detection of plant properties (Tucker, 1979). In this study the MODIS NDVI product (MOD13Q1, 250 m spatial resolution, 16–day composites) were acquired for the years 2002 to 2011. TIMESAT (Jönsson and Eklundh, 2002, 2004) was used for the pre–processing of the time series. Temporal smoothing was applied using the Savitzky–Golay filter and the extraction of the phenological parameter Start of Season (SOS). The date of the SOS was estimated for every enclosure separately to capture spatial heterogeneity and therefore variances of phenology within the study area.

Hamel *et al.* (2009) found in their analyses that the steepest part of the annual NDVI curve was positively correlated with the timing of peak faecal crude protein. Therefore herbivores have access to maximum forage quality prior to maximum NDVI (peak green–up) when new vegetation growth steepens the slope of the annual NDVI curve. We calculated the slopes between every composite and extracted the date of the steepest slope and hence the time of maximum forage quality, further referred to as maximum greenness, by extracting the values from each GPS location point. The derived remote sensing time–series data set was then linked to animal movement tracks using corresponding dates. The maximum greenness of the vegetation period of each animal movement location point was calculated in order to test if the animals follow the green–up in the vegetation period. As areas with rocks and bare soil distort the maximum greenness calculation these pixel were removed beforehand.

All analysis are performed in R 2.15.2 (R Development Core Team, 2011).

## 2.3 Results

The behaviour of the animals leaving the enclosures with known opening dates and their response to the green up was analysed in a first step (n = 28). We expected the animals to leave the enclosures immediately but the analyses revealed a different behaviour. After the opening of the enclosures the animals tend to leave the enclosures at the night of the same day or early next morning, but are revisiting the same enclosure the next day and the days after (figure 2.2). There is no time pattern detectable for the revisiting events (e.g. staying during afternoon within the enclosure and leaving during the night) and the distance between revisiting events is variable (figure 2.3). Analysing the directionality, hence a directed movement path, no pattern is visible (figure 2.4), hence these animals are not following the green–up. By analysing the duration of revisiting events, it becomes clear that all animals establish a home range where the enclosures are encompassed. Furthermore 16 (n = 28) animals are staying in the same enclosure the next winter and two animals stay in another enclosure during the next winter. The remaining ten animals are not collared until the next winter.

The whole data set of single individuals within enclosures (n = 89) was analysed concerning a pattern following the green up. The definition of animals leaving the enclosures was defined as at least 20 relocations in a row outside an enclosure (using the date of the first relocation of this sequence). A pattern that individuals follow the green–up was detected in five animals (total n = 89) after the opening of the winter enclosures (figure 2.5). We can split the behavioural response of these 5 individuals in three categories: "surfing the green wave" (n = 1,*sensu* Bischof *et al.* (2012), figure 2.5 A) and "jumping" (n=4, *sensu* Bischof *et al.* (2012)). The response of the "jumping" animals varies between staying in front of the maximum greenness (figure 2.5 B) and staying behind the maximum greenness (figure 2.5 C). All other animals (n = 84) are making no habitat adjustment in order to follow the maximum green-up (figure 2.6).

Furthermore the management of the deer population within the National Parks was evaluated. The enclosures were opened by the staff of the National Park roughly when the area adjacent to the enclosures show a clear sign of emerging vegetation. The analysis shows that for the majority of enclosures the gates where opened after the SOS derived by remote sensing data, hence most of the animals can only leave the enclosures long after the estimated start of season (SOS, figure 2.7). Across all years (2002–2011) only some enclosures where opened before the SOS, which allowed 18 individuals (19.57 %, n = 89) to leave the enclosures prior to the SOS with a range of 72 to 2 days prior to SOS. 74 animals are leaving the enclosures after the start of season in the vegetation period, with 7 individuals within 7 days after SOS (total range: 1–73 days).

Analysing animal movement patterns of individuals not staying inside the enclosure over winter (n = 3) showed contrary to our expectations, no movement pattern following the green–up (figure 2.8).

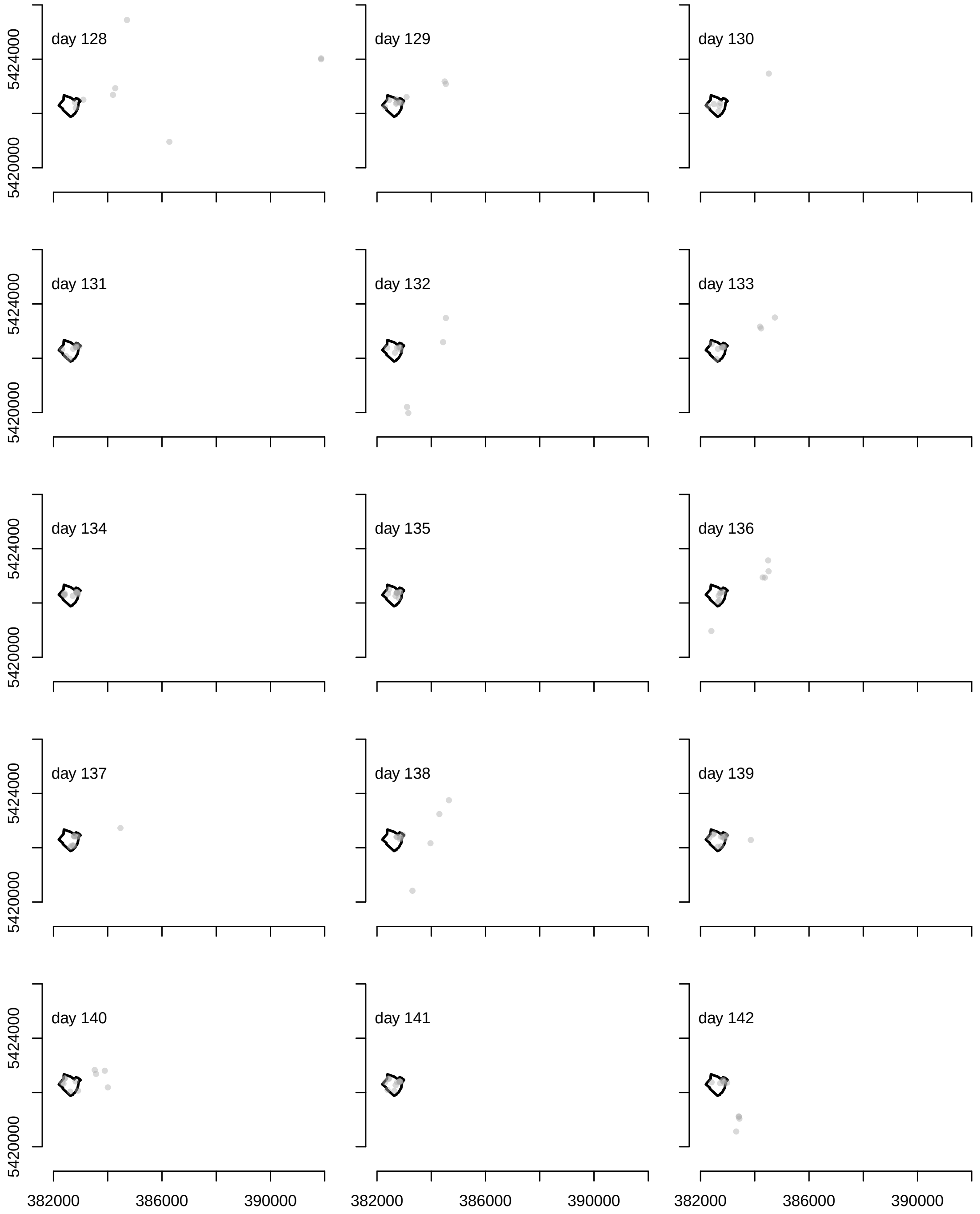

**Figure 2.2:** The daily behaviour of one animal after the opening of the winter enclosure is shown. The sequence of plots starts with the day of the opening of the winter enclosure. Gray circles mark GPS location points, black polygon is the winter enclosure. Days are counted after the day of year (julian date). Projection: WGS84 UTM Zone 33N; animal: ID: 460/229_04, male; winter enclosure "Neuhüttenwiese"; opening date: 2004-05-07 (julian day 128).

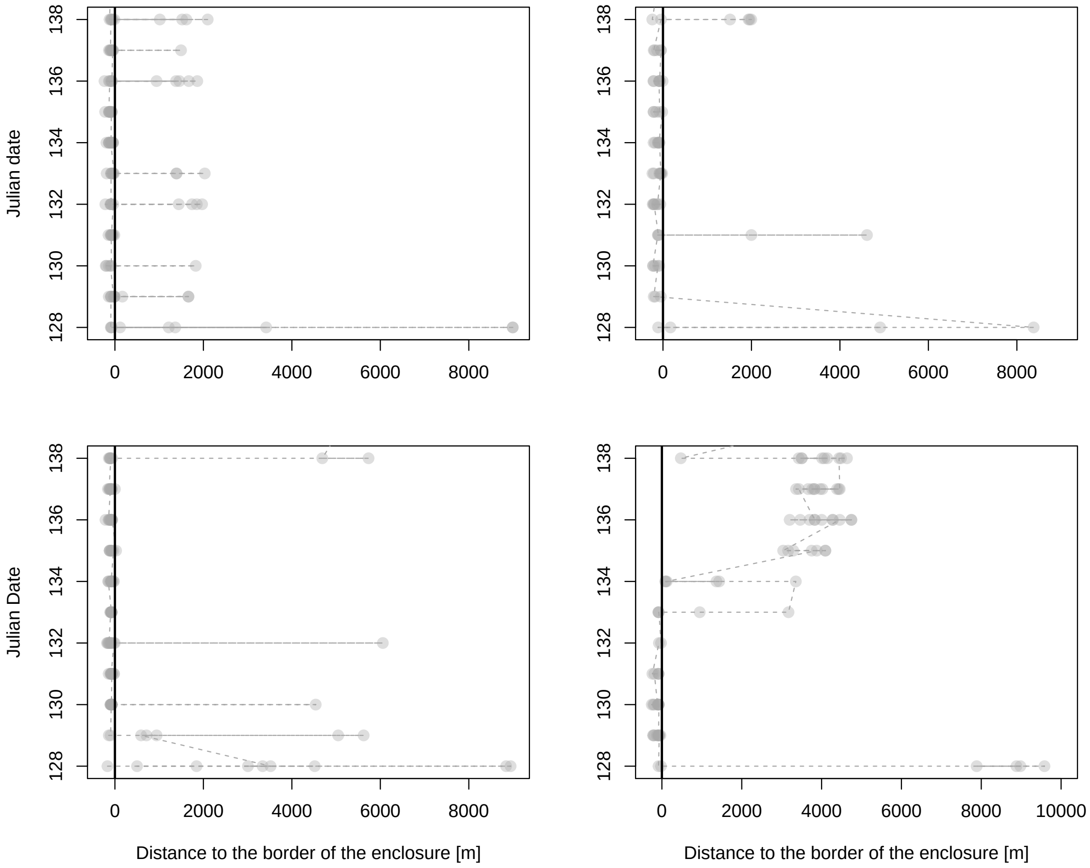

**Figure 2.3:** Overview of the behaviour of four exemplary red deer leaving the same winter enclosure, shown for 10 consecutive days after the opening date of the enclosure (winter enclosure "Neuhüttenwiese"; opening date: 2004-05-07 (julian day 128)). Animal locations points are drawn in gray. Darker shades of gray indicate 2 or more overlapping location points. The points are drawn with their distance to the border of the enclosure, whereas the black vertical line marks the border. Hence location points left of the vertical black line are location points within the enclosure, right handed location points are locations point were animals are outside the enclosure, drawn with their distance to to the border of the enclosure. The dashed line connects the points with their temporal stamp (top left: animal ID: 460/229_04, male; top right: animal ID: 494/294_04, male; bottom left: animal ID:624/_04, female; bottom right: animal ID: 411/211_04, female). Please note the different x-axis in the bottom right plot.

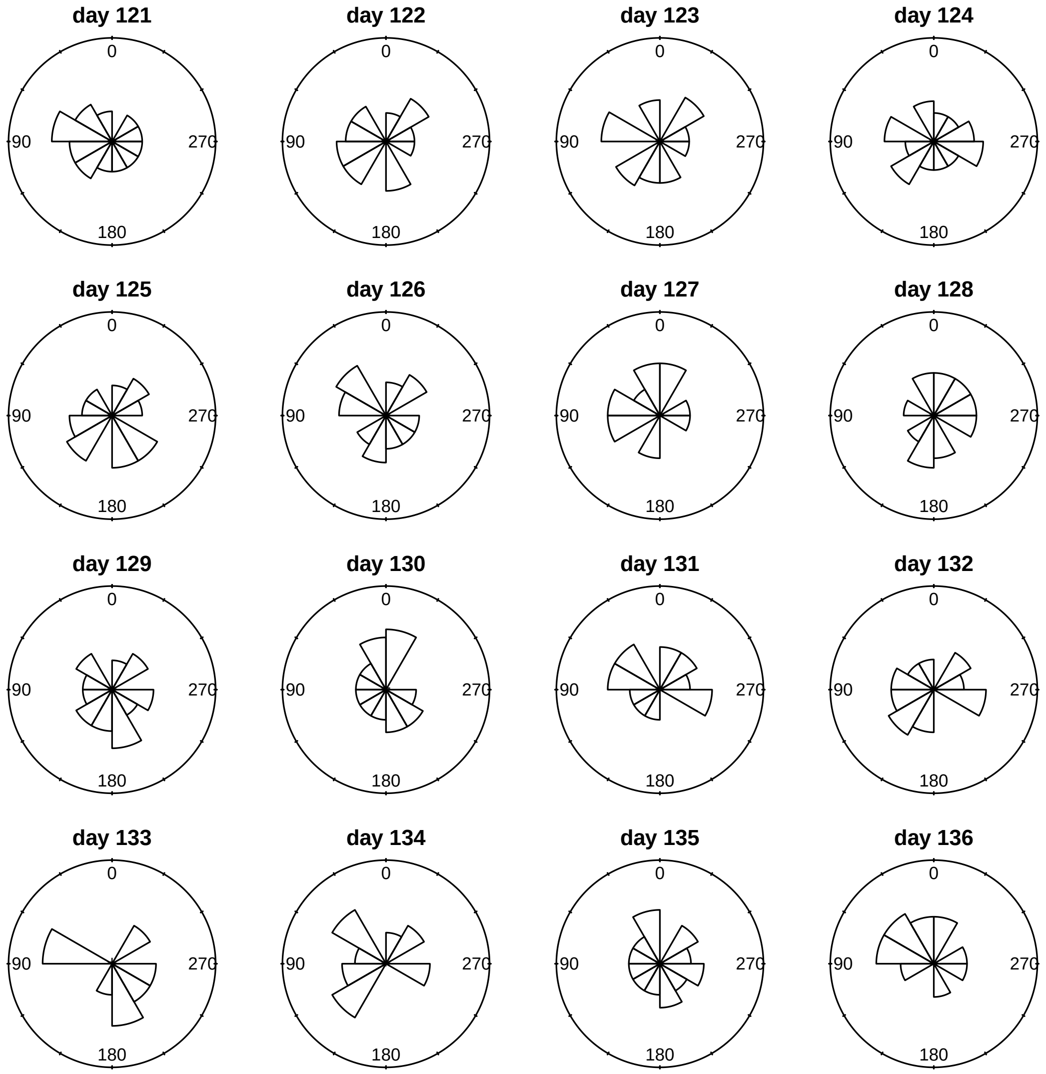

**Figure 2.4:** Rose diagram of circular frequency of the turning angles (in degrees) of one animal leaving the winter enclosure shown for consecutive days (julian date), beginning with the day of the opening of the winter enclosure (animal ID: 08-6_08, female; winter enclosure "Riedeläng"; opening date: 2008-04-30). Within the analysis no directionality was detectable, resulting in no clear trend of the turning angles .

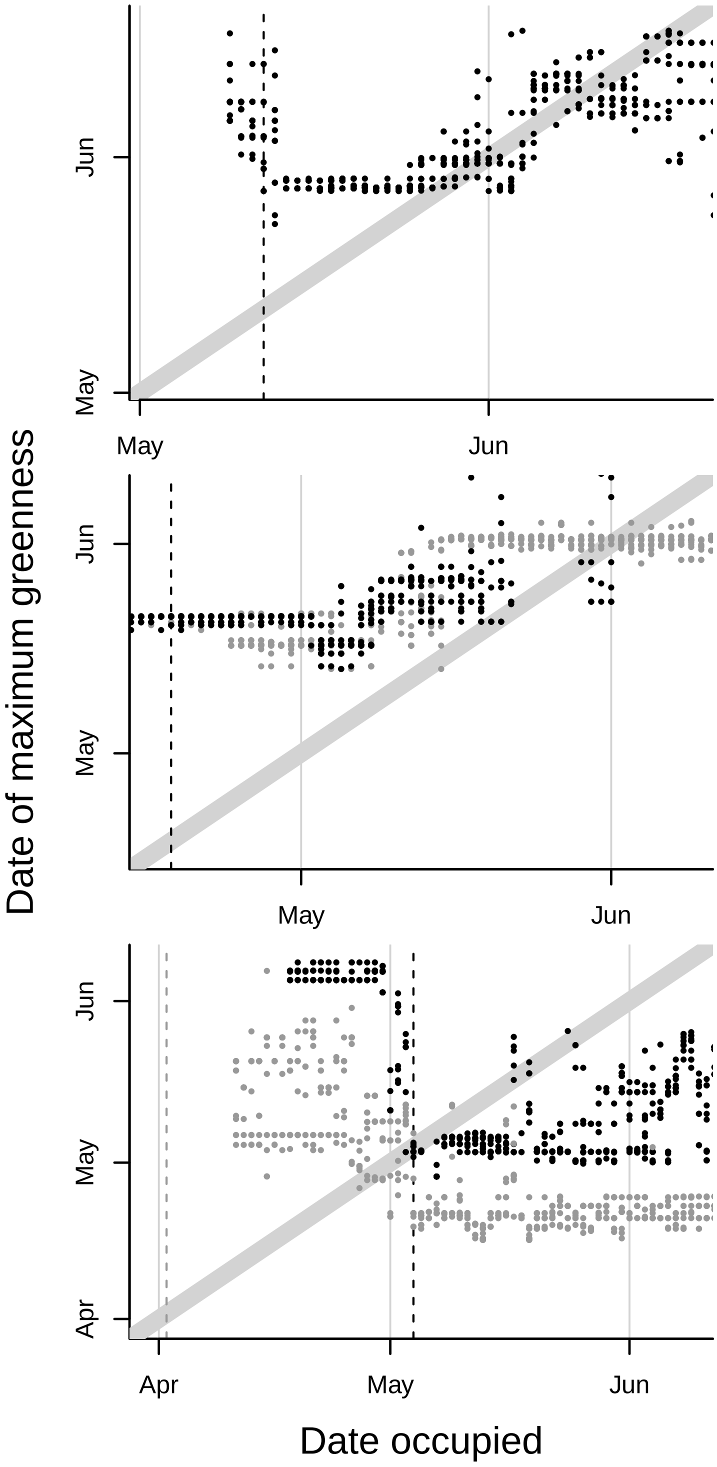

**Figure 2.5:** Migration pattern of maximum greenness experienced by five red deer after opening of winter enclosures. Plots show the relationship between the date of maximum greenness at a given location and the date at which that location was occupied during migration (black and dark grey points). The thick grey line marks the maximum greenness and points on that line correspond to locations at the time of the maximum greenness. Dashed lines mark the start of season (SOS). (A) an animal tracking the green–up from late May until late June (ID = 08-6_08; female; n = 2649, leaving enclosure 3 days prior to SOS). (B) and (C) are showing animals tracking the green–up by rapid adjustment whereas in (B) the animals are staying ahead of the maximum greenness (black: ID = 06-7_06; female; n = 3581; leaving enclosure 28 days prior to SOS; grey: ID = 06-8_06; female; n = 3366; leaving enclosure 19 days prior to SOS; both animals have the same SOS), and the animals in (C) are tracking the maximum greenness by staying behind the green–up (black: ID = 05-8_05; male; n=1948; leaving enclosure 58 days prior to SOS; grey: ID = 307/307_07; male; n = 1426; leaving enclosure 9 days after SOS)

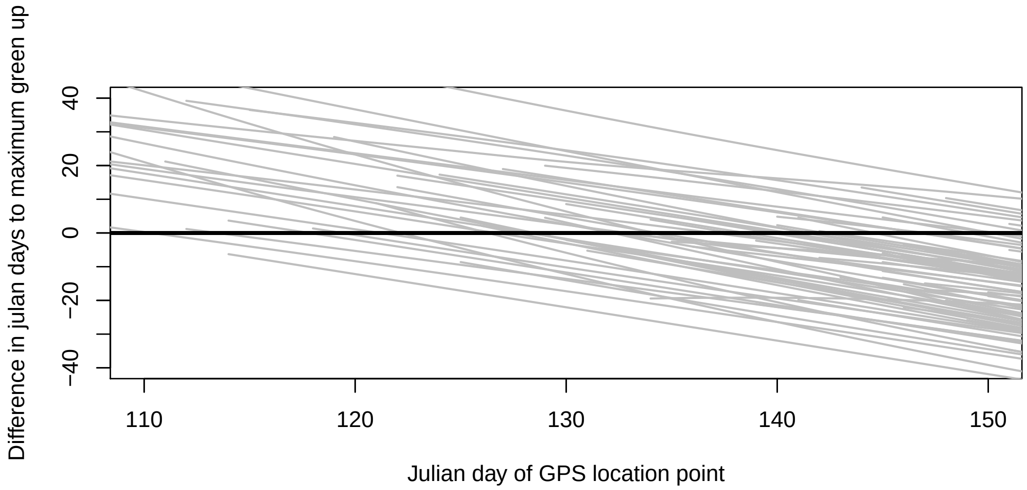

**Figure 2.6:** In order to evaluate the movement behaviour of red deer after the release of the winter enclosures the GPS locations were related to the maximum green up in a buffer around of 2000 m around the GPS location point and the difference in days to the maximum green up was calculated. For graphical display, location points of individual red deer were smoothed with a loess function and represented with a gray line (n=84) in relation to the distance to the maximum greenness calculated as the differences in days (black line). If animals track the phenology their location points (translated in julian days) should accompany the maximum greenness, here the black horizontal line.

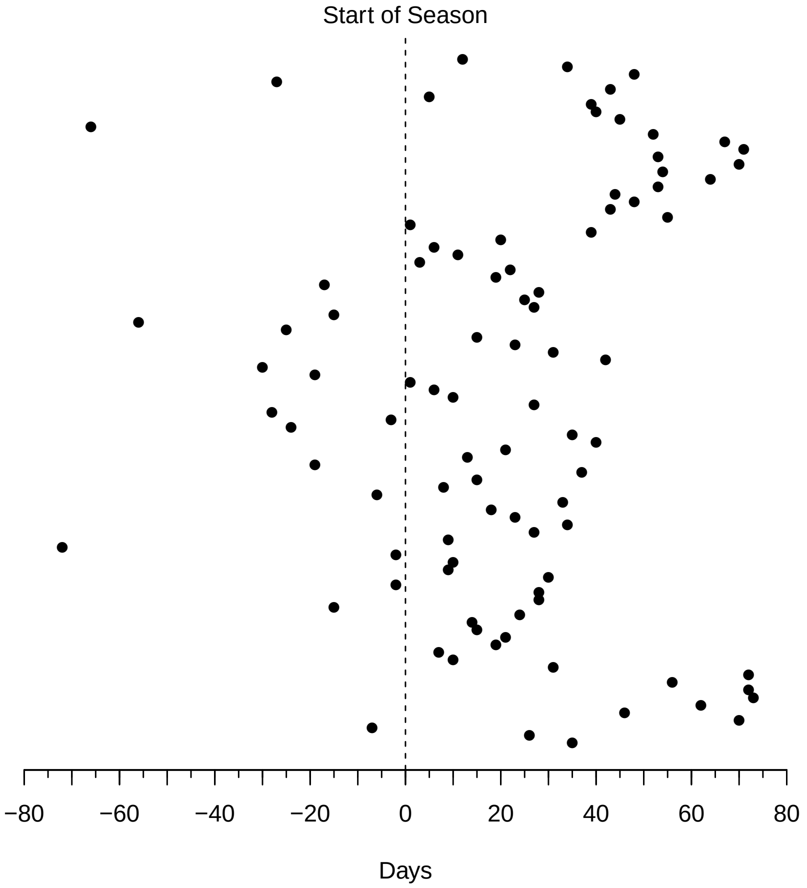

**Figure 2.7:** Overview of the release dates of red deer out of the winter enclosure within the study area. For each year of the study period the Start of Season of the vegetation period for the single enclosures was detected using MODIS NDVI time–series. Enclosures are opened by the staff of the National Park when the adjacent area shows a clear sign of emerging vegetation. The Start of season is here set to day zero (dashed line). The difference in days when an animal leaves the winter enclosures is shown here whereas every black point marks an individual (n = 89).

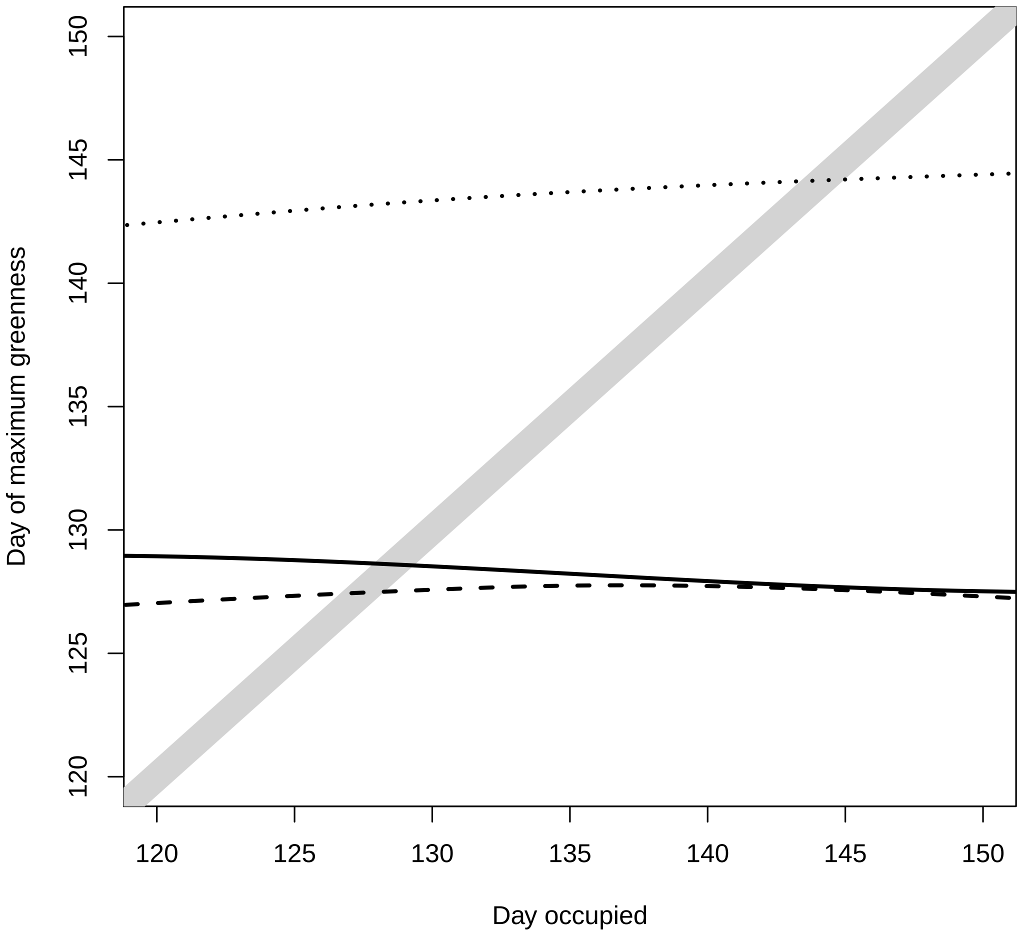

**Figure 2.8:** Overview of the relationship between the date (in julian days) of maximum greenness (gray) at a given location and the date at which that location was occupied by three free ranging red deer that did not stay in enclosures during winter time (dashed: ID: 14/14_06, female, n=5253; dotted: ID: 05-2_06, male, n=1783; solid: ID: 15/15_06, female, n=5602). For a clearer graphical representation the location points of the animals are represented with a loess function and points are not drawn. If animals follow the maximum green up, their location points should be near to the slope, representing the maximum greenness

## 2.4 Discussion

This study examines the behaviour of red deer after the opening of winter enclosures as well as the timing of the opening. Typically ungulates living in temperate regions move between summer and winter ranges (Georgii, 1981; Mysterud, 1999). The National Park Bohemian Forest can only serve as a summer range for red deer. It is surrounded by economic forests and natural migration routes are interrupted by settlements. To prevent damage to the adjoining forest, winter enclosures are established were red deer stay during winter time. Nevertheless, as forage plants are most nutritious to ungulates at the onset of the growing season (Albon and Langvatn, 1992; Mysterud *et al.*, 2011; Cagnacci *et al.*, 2011), deer should respond to the green–up after release. Furthermore a variety of studies report that ungulates follow the emerging plant phenology in spring (Hebblewhite *et al.*, 2008; Sawyer and Kauffman, 2011; Fryxell and Avgar, 2012; Christianson *et al.*, 2013). So far, there are no studies about the behaviour of red deer after opening.

We expected red deer to follow green–up immediately after release of the winter enclosures. For 28 animals the exact opening dates of the winter enclosures are available and their behaviour was analysed in detail. Contrary to our expectation, deer did not leave the enclosures immediately, they rather stayed within the enclosures until nightfall or next morning. This could be due to recognition time of the gates being open (and stopped feeding) and due to the activity behaviour of deer in the study area, using open areas for feeding during the night and resting in forests during the day (Stache *et al.*, 2012). Therefore with dawn, with rising forage activity, deer move out of the enclosures. Unexpectedly, deer revisited the enclosures the following days and weeks, whereby no time pattern (e.g. only during day or night) and no relationship to the green–up was detected. Furthermore, the animals established home ranges encompassing the enclosure they stayed during winter and return to the same enclosure the next winter.

For the overall data set a pattern following the maximum greenness after the release of the winter enclosures was detected in n 5 of 89 animals. Here both events occurred – leaving the enclosure before and after the start of season. Animals benefit from pursuing the maximum greenness as they have access to younger rapidly growing plants, rather than older plants which have indigestible ingredients, such as secondary compounds (Langvatn and Hanley, 1993). Still we detected a pattern only in a minority of the animals. The study area is characterised by long winters. Snow cover lasts or 7–8 months at the higher elevations and for 5–6 months in the valleys. After snow melt we see a rapid rise in the NDVI values in our study area and thus a fast emergence of vegetation. Winters with extended periods of snow cover often result in later springs with more rapid green–up (Dye and Tucker, 2003; Christianson *et al.*, 2013). As a result, after the release of the enclosures, animals have quickly access to good forage, as the vegetation develops fast. This is suppressing migration behaviour on a scale we can detect.

Therefore the spatial scale of MODIS might be an issue even though it has been successfully used in other studies investigating the migration pattern along a phenological gradient (Bischof *et al.*, 2012; Christianson *et al.*, 2013; van Moorter *et al.*, 2013), but these study areas encompass serveral 100 $km^2$ and are far larger than the Greater Bohemian Forest. Using a time–series with a higher spatial resolution might especially be valuable for heterogeneous areas e.g. using RapidEye (Franke and Menz, 2007), Landsat 8 (Lulla *et al.*, 2013) or the forthcoming Sentinel (Berger *et al.*, 2012) and might result in more ecological meaningful results for this study region. However all mentioned sensors will have problems to provide continuous time–series for deriving ecological relevant phenological measurements (Bradley *et al.*, 2007). Nevertheless a combination of different sources with comparable data sets might provide a meaningful phenological time–series on a ecological more appropriate spatial scale for this study area.

Additionally, the importance of memory has recently been recognized (Van Moorter *et al.*, 2009; Gautestad and Mysterud, 2010; Gautestad *et al.*, 2013). Mammals have the capacity to utilize spatial information in a cognitive map and are able to revisit sites even after a long period (Wolf *et al.*, 2009; Gautestad, 2011). The cognitive map provides a capacity for short and long term memory (Gautestad, 2011). We can see from animals which are collared over two or more years that these animals move back to previously established home ranges after the release of the enclosures. The behaviour is memory related and the green-up plays here a secondary role. A study by Fickel *et al.* (2012) analysing the behaviour of red deer, after the border between Germany and former Czechoslovakia was removed, showed that deer did not cross the border immediately. Red deer live in matrilinear systems and the behaviour of migration routes and feedings sites is passed on (Guinness *et al.*, 1979; Mysterud *et al.*, 2004). The genotypic panmixis was re-established 20 years (roughly three generations in red deer) after the removal of the iron curtain (Coulson *et al.*, 1998) and gene flow was predominantly realised by stag dispersal, while does showed stronger philopatry (Fickel *et al.*, 2012). Additionally to this long term memory, it is likely that deer are conditioned to the winter enclosure sites over the last decades as deer are migrating into the enclosures without any force. It is likely that deer have learned to migrate to the enclosures and that this has lead to a behavioural change, as deer can expect there save supplementary feeding.

We expected to find a clear pattern in following the maximum greenness within the three animals not staying within the winter enclosures as winter condition can be very harsh and food is limited. Surprisingly we did not detect a behavioural pattern in the free ranging animals regarding the maximum greenness. Two animals established home ranges near the border of the National Parks and are overlapping with adjoining forests. It is likely that these animals receive supplemental feeding during winter from hunters in areas adjoining the National Park. Eventually, this supplemental feeding is suppressing typical migration patterns as food is not the primary limiting resource.

Although national parks can cover a large area, they are still restricted by boundaries. If they cannot function as a complete annual habitat for, e.g. migrating large ungulates, the park administration has to initiate arrangements to prevent negative impacts in adjoining areas. Therefore seventeen winter enclosures were established in the Bohemian Forest to hinder deer migration in winter time outside of the National Park and to prevent damage to adjoining economic forestry. As the enclosures pose a serious interference with the natural behaviour patterns of red deer the park administration discussed the closing of the enclosures with affected stakeholders within an decision–making–process, but the communication process failed (for a detailed discussion see Gerner *et al.* (2011)). In addition to the complete closing of the enclosures a more appropriate management can be designed with small steps within these restrictions. We related the opening dates of the winter enclosures to the estimated start of season of the vegetation period. Through all years, most of the animals can leave the enclosures far after the start of season of the vegetation period. Opening the enclosures much earlier would ensure that the animals can leave with the start of the vegetation period. Furthermore, the data shows that not all animals are leaving immediately and are revisiting or are staying nearby the enclosures in the first days. In order to avoid human-wildlife conflicts an alternative approach would be to leave the enclosures open but still feed the animals at the feeding sites within the enclosures to keep the animals within the borders of the National Park.

## 2.5 Conclusion

In this study we used the NDVI Index to evaluate the management strategies in the Greater Bohemian Forest and investigated the behaviour of red deer after opening of the winter enclosures. While the future of the management in the National Parks is a highly debated issue and the positions are hardened, the NDVI shows nevertheless that within the strict guidelines it is possible to modify the management strategies more naturally by open the enclosures far earlier to let the animals follow the emerging vegetation period and to led them move to their previously established home range sizes. Furthermore due to the geographic region and hence the climatic conditions the vegetation period emerges very fast leading to only a short phase where possible behavioural adaption can be detected. Overall the majority of deer did not show a migration pattern and we see a more important role of memory, leading the animals to previous established home ranges, than of limited food resource.

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# Appendix

## Opening dates of winter enclosures

TABLE 1: Table of winter enclosures with known opening and closing dates. All four listed winter enclosures are located within the National Park Bavarian Forest.

| enclsoure | opening date | closing date |
|---|---|---|
| Ahornschachten | 2003-05-07 | 2002-12-19 |
| | 2004-05-03 | 2003-12-18 |
| | 2005-05-13 | 2004-12-20 |
| | 2006-05-15 | 2005-11-23 |
| | 2007-04-30 | 2007-01-03 |
| | 2008-04-21 | 2007-11-15 |
| | 2010-05-17 | 2009-12-15 |
| Buchenau | 2003-05-06 | 2002-12-03 |
| | 2005-05-12 | 2004-11-09 |
| | 2006-05-15 | 2005-11-14 |
| | 2007-04-18 | 2006-12-29 |
| | 2008-04-23 | 2007-11-12 |
| Neuhüttenwiese | 2003-05-07 | 2002-10-13 |
| | 2004-05-07 | 2003-10-07 |
| | 2005-05-05 | NA |
| | 2006-05-12 | 2005-11-14 |
| | 2007-04-20 | 2006-11-03 |
| | 2008-04-28 | 2007-10-22 |
| | 2009-04-26 | 2008-11-17 |
| | 2010-04-27 | 2009-10-15 |
| Riedlhäng | 2003-05-10 | 2002-12-09 |
| | 2004-05-12 | 2003-12-07 |
| | 2005-05-03 | 2004-12-14 |
| | 2007-04-17 | 2006-12-11 |
| | 2008-04-30 | 2007-11-01 |
| | 2009-04-28 | 2008-11-24 |
| | 2010-04-29 | 2009-10-16 |

# 3

# Landscape configuration is a major determinant of home range size variation

## Abstract

Most animals restrain their movement activities to familiar areas. Although understanding both establishment and shifts of such home ranges is highly relevant for basic science and conservation, pinpointing the factors that shape the dynamics of home ranges remains a challenge. Evidently home ranges are influenced by the underlying landscape. Landscape composition, i.e. the fraction of different land cover types, has recently been shown to affect home range size. Yet, the explicit spatial configuration of the landscape, a factor which is known to be of central importance in spatial ecology, is not taken into account by most studies. We quantify the effect of landscape configuration on summer home range sizes across multiple spatio-temporal scales using GPS data from two behaviourally distinct ungulate species, red (*Cervus elaphus*) and roe deer (*Capreolus capreolus*), in the Bavarian Forest National Park, Germany. We show that the spatial configuration of the landscape is the dominant factor explaining home range size. Furthermore, we find that the shape of the relationship between home range size and landscape configuration depends on a species' habitat requirements: while roe deer decrease their home range size with increasing landscape patchiness, the relationship is hump-shaped for red deer. Our results are robust at all tested spatio-temporal scales.

## 3.1 Introduction

With increasing human wildlife conflicts it is necessary to understand and predict the changes of wildlife behaviour in general and specifically of animal movement patterns (Wilcove and Wikelski, 2008). Such conflicts can be due to the growing human populations or to changing landscapes as a consequence of anthropogenic land use like agriculture or natural changes like fires or bark beetles. A correct interpretation of the causes of animal movement and dispersal is pivotal for understanding habitat selection and more generally the diversity and distribution of species (Chave *et al.*, 2002). Most animals do not move randomly through a landscape (Nathan *et al.*, 2008; Gautestad and Mysterud, 2010; Fronhofer *et al.*, 2013) and restrain their movement activities to familiar areas. While central place foragers, such as bees or ants, return to their nest after a foraging bout (Wakefield *et al.*, 2014) and territorial animals, such as some felids, defend well defined landscape stretches (Valeix *et al.*, 2012), a large majority of animals use familiar areas without defending them (Burt, 1943). The latter behaviour leads to the establishment of home ranges, which are generally defined as the spatial expression of all behaviours an animal performs in order to survive and reproduce (Burt, 1943). As home ranges link individual movement paths to dispersal and (meta-)population dynamics (Hanski and Gilpin, 1998; Fronhofer *et al.*, 2012)understanding why and how home range sizes vary between and among species is a fundamental issue in ecology. While theory still struggles to explain the emergence of home ranges (Börger *et al.*, 2008) the availability of large movement data sets allows us to formulate some testable hypotheses. Progress in GPS-sensor technology and satellite techniques makes it possible to track animals over long time spans with high temporal and spatial resolution and to analyse their habitat requirements and movement paths (Tomkiewicz *et al.*, 2010; Thiebault and Tremblay, 2013). Early analyses have shown that home range size depends on different variables. Generally home range size was shown to decrease with decreasing body size (Swihart *et al.*, 1988) and forage availability (Tufto *et al.*, 1996). Also increasing intraspecific competition leads to smaller home range sizes (Riley and Dood, 1984) while interspecific competition leads to increasing home range sizes (Loft *et al.*, 1993) see van van Beest *et al.* (2011) for a more complete list). Besides these factors it is well known that the spatial arrangement of different habitat types can influence the distribution of large mammals (Clutton-Brock *et al.*, 1987) as this will influence movement trajectories. Previous studies focused only on large spatio-temporal scales like, landscape scale as spatial scale and seasonal scale as temporal scale (Kie *et al.*, 2002; Saïd *et al.*, 2005; Walter *et al.*, 2009; Quinn *et al.*, 2013), yet smaller scales might also be relevant, depending on the degree and scale of landscape heterogeneity. In addition, mechanisms that affect variation in home range size may differ depending on the temporal and spatial scale under investigation (van Beest *et al.*, 2011). Animals move in order to find resources such as food, shelter or mating partners. In a spatially structured landscape one single habitat patch regularly not always satisfies all these needs at the same time. Typically for ungulates in temperate regions a forage-rich habitats providing high quality food are more exposed, while closed habitats provide cover resulting in a trade-off in habitat choice (Godvik *et al.*, 2009). A large number of studies have shown that the landscape is an essential determinant of home range size and dynamics in ungulates. Yet, these studies typically only took the dominant habitat type within a home range into account. For example, the landscape composition was included only as the fraction of meadow or forest within the home range (Frair *et al.*, 2005; Börger *et al.*, 2006b; Rivrud *et al.*, 2010). However, natural landscapes are heterogeneous in the spatial arrangement of resources, as these are often autocorrelated and form resource clusters or patches of varying size and density (see figure 1). We illustrate the extent to which the appearance of a landscape may differ depending on the arrangement of habitats by two artificial landscapes, derived from our true natural landscape. In both cases the fraction of land cover types is kept constant but arranged randomly in space (figure 1B) or ordered (figure 1C). These different landscape configurations will likely affect home range size. Specifically, home ranges in a randomized landscape may be expected to become much smaller, as a large number of different land cover types can be found on a much smaller scale. On the other hand, an artificially ordered landscape would lead to longer movement paths, e.g. when an animal needs to reach the land cover type “meadow” after having been in “deciduous forest”, for example, and therefore needs to cross a block of “mixed forest”. It is only recently that the explicit spatial configuration of habitat types, the arrangement of all land cover types within the home range, and the size of these patches is taken into account in the study of home range sizes (e.g. (Moorcroft *et al.*, 2006; Moorcroft, 2012). We here analyse the relationship between the spatially explicit landscape configuration and home range size for two sympatric ungulates, red and roe deer. Since the explicit spatial configuration of land cover types will affect the movement path of an animal searching for food or shelter we hypothesized that the spatial configuration is a central determinant of home range size. More specifically we expected larger home ranges in aggregated landscapes, because larger distances have to be covered regularly in order to utilize resources (food, shelter, etc.) that can be found in different land cover types. Red and roe deer differ in their habitat requirements and behaviour. Red deer are widely roaming animals with a broad spectrum of possible food sources (Gebert and Verheyden-Tixier, 2001). They rely on open habitats for food supply as well as on covered areas for refuge (Hebblewhite *et al.*, 2008). As the habitat demands a variety of different resource patches and furthermore red deer easily moves across wide areas we expect a high impact of the landscape configuration. Roe deer on the other hand are smaller, with typically smaller home ranges (Radeloff *et al.*, 1999) and with very selective foraging preferences. As they rely more on highly digestible food items, such as fruits, seeds or sprouting shoots (Demment and Van Soest, 1985), the effect of the land cover types should be more pronounced than for red deer. Nevertheless the spatial configuration should play an important role, as it determines the spatial arrangement of the patches.

## 3.2 Materials and methods

### 3.2.1 Study area

The study was conducted in the Bavarian Forest National Park which is situated in south-eastern Germany along the border to the Czech Republic ($49^\circ\,3'\,19''$ N, $13^\circ\,12'\,9''$ E). The National Park covers an area of 240 km$^2$. Adjacent to the park, on the Czech side of the border, lies the Šumava National Park with an area of 640 km$^2$. These protected areas are embedded within the Bavarian Forest Nature Park (3070 km$^2$) and the Šumava Landscape Protection Area (1000 km$^2$). In its entirety, the area is known as the Bohemian Forest Ecosystem. The area is mountainous, with a variation in elevation between 600 and 1450 m.a.s.l. The mean annual temperature varies between 3°C and 6.5°C along higher elevation and

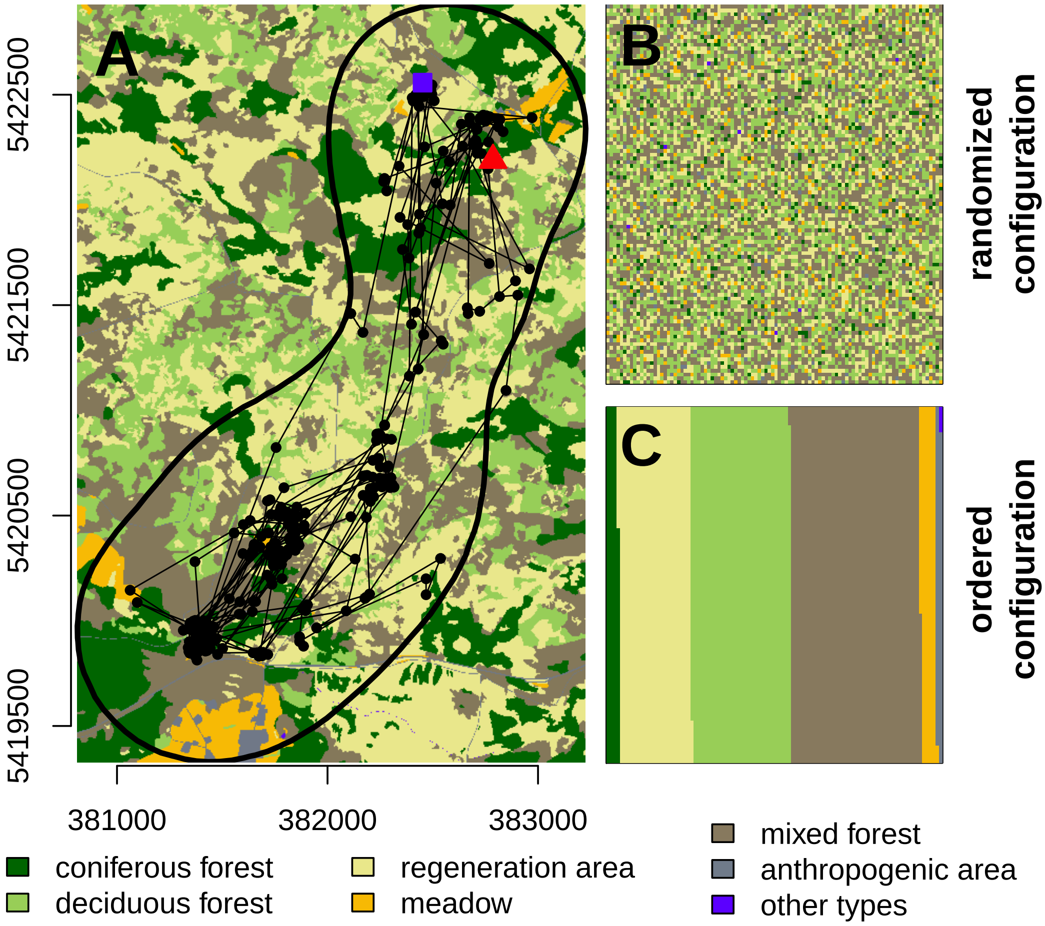

**Figure 3.1:** (A) Example of a home range shown with the trajectory (connected points, red triangle refers to the start of the trajectory and the blue square to the end) of a red deer (individual 668_668_07, female, calculated with the fixed kernel method (90% isopleth) on 286 location points in the month September, projection: WGS84 UTM Zone 33N) in the Bavarian Forest National Park. A land cover map with seven categories is shown in the background. "Regeneration area" are land stretches that have suffered from massive bark beetle outbreaks during the 90s, "anthropogenic areas" comprise cities, roads, railways and "other types" refers to water and peat bogs. (B) The same landscape with a randomized spatial configuration but the same fraction of land cover types. (C) The same landscape with a blocked spatial configuration but the same fraction of land cover types. These two artificial landscapes illustrate strongly spatial configuration of a landscape can vary for the same composition.

ridges. The mean annual precipitation is between 830 and 2230 mm. Within the park, three major forest types exists: above 1100 m are sub-alpine spruce forests with Norway Spruce (*Picea abies* L.) and some Mountain Ash (*Sorbus aucuparia* L.), on the slopes, between 600 and 1100 m altitude, are mixed montane forests with Norway Spruce, White Fir (*Abies alba* MILL.), European Beech (*Fagus sylvatica* L.), and Sycamore Maple (*Acer pseudoplatanus* L.). In the valley bottoms, spruce forests with Norway Spruce, Mountain Ash, and birches (*Betula pendula* ROTH. and *Betula pubescens* EHRH.) (Fischer *et al.*, 2013). Since the mid-1990s, the forests of the national park have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*). By 2007, this had resulted in the death of mature spruce stands over an area amounting to 5,600 ha (Lausch *et al.*, 2013), leading to areas which regenerate naturally and go through different successional phases. Today these areas are characterized by shrubby vegetation of spruce and mountain ash.

### 3.2.2 Deer data

Red deer were caught during winter in the years 2002-2009. Animals were captured and marked with GPS collars (Vectronic Aerospace, Berlin, Germany) in box traps with side windows after they were lured in with food. Here no immobilization was necessary. A second approach was to tranquillize deer by dart gun on sites where they were attracted by food. We collared 14 male and 18 red deer individuals. Four individuals were collared two or more times over the duration of the study. Roe deer were captured during the winter months (October to March) in the years 2005-2010 using wooden box traps. A total of 40 roe deer (24 male, 16 female) were collared, with five animals collared two or more times over the years of the study. The most common sampling design was to mark roe and red deer in late winter and retrieve the collars after a year by collar drop–off or recapturing, allowing the collars to be used on new individuals.Animal handling was performed in compliance with German laws and regulations. We restrict our analysis for both species to summer home ranges only. We checked the data before the statistical analysis and removed spatial and temporal outliers. Temporal outliers were locations points which were less than sixty apart and spatial outliers were removed by visual inspection of the data. This leads to a removal of 19% of the raw data for red deer and 16% for roe deer. We used only the summer months

(May-October; red deer stay in enclosures during winter time) for the analysis and only if the calculated home ranges had at least 95% overlap with the land cover map. Further, we classified the samples from the multiple collared animals over the single years as independent. We took a random sample for animals with sequences of short time intervals (e.g. location point taken every 15 min) to ensure that the locations have an interval of one hour. The elapsed time between locations for each animal averaged 157.57 min for red deer and 365.77 min for roe deer with an overall position acquisition rate of 72.8% and a median accuracy of 16.5 m (Stache *et al.*, 2012).

### 3.2.3 Home range estimation

Home ranges were estimated with a commonly used approach, the fixed kernel method (Worton, 1989) using the reference method for the smoothing factor h (Kernohan et al., 2001). We used three different home range isopleths (50 %, 70 %, 90 %) to spatial behaviour at different scales. In addition, all home ranges were estimated on three temporal scales: weekly, biweekly and monthly. We only estimated home ranges for individuals with at least six relocations for the temporal scale under study and restricted our analyses to summer months.

### 3.2.4 Land cover types and environmental data

To characterise the landscape in our study area we considered five land cover types: “coniferous forest”, “deciduous forest”, “mixed forest”, “meadow” and “regeneration areas”, i.e. areas containing mature trees killed by bark beetles and showing now regrowing vegetation, characterized by a shrubby appearance. Anthropogenic areas (e.g. roads) and water bodies were not taken into account as they cover only a negligible area within the study area. The land cover classification was derived through digitalization from aerial images from the year 2008. In order to take into account the rapid forest dynamics due to bark beetle outbreaks, we update the land cover classification for every year of the study. As a measure of the landscape’s spatial configuration we calculated different landscape indices within a given home range (McGarigal et al., 2002). As the calculation of the landscape indices require a raster, we converted the land cover classification into grid with a resolution of 5 m. We quantify the landscape configuration as the percentage of like adjacencies (PLADJ) as this index could be shown to be most scale-independent (see Supplementary Material for details). In the following we will refer to this index as configuration index. Furthermore, we estimated the mean elevation of the home ranges using ASTER GDEM (resolution: 30 m; http://asterweb.jpl.nasa.gov/gdem.asp).

### 3.2.5 Statistical Methods

To investigate the influence of different land cover types and the landscape configuration on home range sizes, we used linear mixed models (R version 3.0.2, (R Development Core Team, 2013), package “nlme”, (Pinheiro *et al.*, 2013) on the log transformed home range areas (km$^2$) and included spatio-temporal autocorrelation structures following the framework proposed by Börger *et al.* (2006b).We used the year of measurement nested in individuals (ID) as a random effect, as individuals were sampled repeatedly in subsequent years. After inspection for colinearity we removed the variables “mixed forest” and “elevation” for the red deer data set as both variables showed a Pearson correlation index $> 0.7$ with “regeneration area” and “configuration index”. For the roe deer data we only removed “mixed forest” as it showed a correlation with elevation (Pearson correlation index $> 0.7$). We first selected the best autocorrelation structure using AIC on the full models and subsequently simplified our models using ANOVA as described in Crawley (2013). To evaluate the importance of landscape configuration for the model fit, we compared the best models and analogous models without the landscape configuration using an R$^2$ measure calculated as $1–\exp(-(2/N * \delta L))$ with N as the sample size and $\delta L$ as the difference between the log–likelihood of the model of interest and the log-likelihood of the null model. We repeated the analysis steps for the three definitions of home range size and for the three definitions of temporal scale.

## 3.3 Results

### 3.3.1 The role of landscape configuration

Home range sizes varied across all spatio–temporal scales, especially for red deer (table 1, Appendix). The fixed effects of the most parsimonious models explained between 0.19–0.37 $R^2$ (table 3.1) for red deer and 0.12-0.15 $R^2$ (3.2) for roe deer across scales. Landscape configuration was the key determinant of home range sizes for both species. Especially for red deer the variance explained through the configuration index was high across all scales (0.13-0.21 $\Delta$ $R^2$, table 3.1). In the roe deer data set the configuration index played a major role but its impact varied across scales (0.02-0.10 $\Delta$ $R^2$) and was highest at the 50 % kernel weekly scale (table 3.2). Especially at the monthly scale the configuration index was exceed by the land cover type “meadow”.

**Table 3.1:** The $\Delta$ $R^2$ values are shown retained from the mixed model with the best correlation structure calculated for all temporal (monthly, biweekly and weekly) and all spatial scales (90 %, 70 % and 50 % isopleths) for red deer with ID and nested year as random structure. The variable configuration was fitted as quadratic term.

| Time-scale | Kernel size | correlation | variables | relation-ship | t–value | p–value | $\Delta$ $R^2$ |
|---|---|---|---|---|---|---|---|
| **monthly** | 50 | temporal | coniferous | positive | 3.47 | <0.001 | 0.05 |
| | | | deciduous | positive | 4.63 | <0.001 | 0.08 |
| | | | configuration | linear | 5.29 | <0.001 | 0.13 |
| | | | configuration | quadratic | -4.23 | <0.001 | |
| | 70 | spatial | coniferous | positive | 4.42 | <0.001 | 0.07 |
| | | | deciduous | positive | 5.86 | <0.001 | 0.12 |
| | | | configuration | linear | 6.82 | <0.001 | 0.18 |
| | | | configuration | quadratic | -5.48 | <0.001 | |
| | 90 | none | coniferous | positive | 5.71 | <0.001 | 0.10 |
| | | | deciduous | positive | 5.33 | <0.001 | 0.09 |
| | | | configuration | linear | 7.28 | <0.001 | 0.17 |
| | | | configuration | quadratic | -5.98 | <0.001 | |

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| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **biweekly** | 50 | temporal | deciduous | positive | 1.93 | 0.05 | 0.01 |
| | | | meadows | negative | -2.16 | 0.03 | 0.01 |
| | | | regeneration | negative | -3.93 | 0.001 | 0.03 |
| | | | configuration | linear | 7.89 | <0.001 | 0.16 |
| | | | configuration | quadratic | -6.22 | <0.001 | |
| | 70 | temporal | deciduous | positive | 4.46 | 0.05 | 0.01 |
| | | | meadows | negative | -2.16 | 0.003 | 0.02 |
| | | | regeneration | negative | -3.93 | <0.001 | 0.04 |
| | | | configuration | linear | 9.55 | <0.001 | 0.19 |
| | | | configuration | quadratic | -8.38 | <0.001 | |
| | 90 | spatial | meadows | negative | -2.16 | 0.03 | 0.01 |
| | | | regeneration | negative | -5.10 | <0.001 | 0.05 |
| | | | configuration | linear | 10.42 | <0.001 | 0.21 |
| | | | configuration | quadratic | -9.01 | <0.001 | |
| **weekly** | 50 | temporal | deciduous | positive | 2.28 | 0.005 | 0.01 |
| | | | meadows | negative | -2.39 | 0.02 | 0.01 |
| | | | regeneration | negative | -5.85 | <0.001 | 0.04 |
| | | | configuration | linear | 8.44 | <0.001 | 0.13 |
| | | | configuration | quadratic | -6.46 | <0.001 | |
| | 70 | temporal | deciduous | positive | 3.06 | 0.002 | 0.01 |
| | | | meadows | negative | -3.37 | <0.001 | 0.01 |
| | | | regeneration | negative | -6.05 | <0.001 | 0.04 |
| | | | configuration | linear | 11.80 | <0.001 | 0.16 |
| | | | configuration | quadratic | -9.84 | <0.001 | |
| | 90 | temporal | meadows | negative | -4.45 | <0.001 | 0.02 |
| | | | regeneration | negative | -8.66 | <0.001 | 0.07 |
| | | | configuration | linear | 12.05 | <0.001 | 0.15 |
| | | | configuration | quadratic | -10.32 | <0.001 | |

**Table 3.2:** The $\Delta\ R^2$ values are shown retained from the mixed model with the best correlation structure calculated for all temporal (monthly, biweekly and weekly) and all spatial scales (90 %, 70 % and 50 % isopleths) for roe deer with ID and nested year as random structure.

| **Time-scale** | **Kernel size** | **correlation** | **variables** | **relation-ship** | **t–value** | **p–value** | $\Delta\ R^2$ |
|---|---|---|---|---|---|---|---|
| **monthly** | 50 | temporal | meadows | negative | -3.91 | <0.001 | 0.06 |
| | | | configuration | positive | 3.00 | 0.004 | 0.04 |
| | | | sex | male > female | 2.82 | 0.008 | 0.03 |
| | 70 | spatial | coniferous | positive | 2.55 | 0.01 | 0.02 |
| | | | deciduous | positive | 2.62 | 0.01 | 0.03 |
| | | | meadows | negative | -2.96 | 0.003 | 0.03 |
| | | | configuration | positive | 2.33 | 0.02 | 0.02 |
| | | | sex | male > female | 2.71 | 0.01 | 0.02 |
| | 90 | spatial | coniferous | positive | 3.36 | 0.001 | 0.04 |
| | | | deciduous | positive | 2.01 | 0.05 | 0.01 |
| | | | meadows | negative | -4.05 | <0.001 | 0.05 |
| | | | sex | male > female | 2.39 | 0.02 | 0.02 |
| **biweekly** | 50 | temporal | meadows | negative | -5.93 | <0.001 | 0.05 |
| | | | regeneration | negative | -2.40 | 0.02 | 0.01 |
| | | | configuration | positive | 6.58 | <0.001 | 0.07 |
| | | | elevation | positive | 2.37 | 0.02 | 0.01 |
| | | | sex | male > female | 3.18 | 0.003 | 0.01 |
| | 70 | spatial | coniferous | positive | 2.23 | 0.02 | 0.01 |
| | | | deciduous | positive | 2.91 | 0.004 | 0.01 |
| | | | meadows | negative | -3.84 | <0.001 | 0.02 |
| | | | configuration | positive | 6.89 | <0.001 | 0.07 |
| | | | sex | male > female | 2.82 | 0.007 | 0.01 |
| | 90 | spatial | deciduous | positive | 2.03 | 0.04 | 0.01 |
| | | | meadows | negative | -4.86 | <0.001 | 0.03 |
| | | | configuration | positive | 7.32 | <0.001 | 0.08 |
| | | | sex | male > female | 2.56 | 0.01 | 0.01 |

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| | | | | | | | |
|---|---|---|---|---|---|---|---|
| **weekly** | 50 | temporal | coniferous | positive | 3.72 | <0.001 | 0.01 |
| | | | deciduous | positive | 3.85 | <0.001 | 0.01 |
| | | | meadows | negative | -5.41 | <0.001 | 0.02 |
| | | | configuration | positive | 11.29 | <0.001 | 0.10 |
| | | | elevation | positive | 3.60 | <0.001 | 0.01 |
| | | | sex | male > female | 2.78 | 0.009 | 0.005 |
| | 70 | temporal | coniferous | positive | 4.10 | <0.001 | 0.01 |
| | | | deciduous | positive | 4.48 | <0.001 | 0.02 |
| | | | meadows | negative | -5.85 | <0.001 | 0.03 |
| | | | configuration | positive | 10.46 | <0.001 | 0.08 |
| | | | elevation | positive | 2.95 | 0.003 | 0.01 |
| | | | sex | male > female | 2.40 | 0.02 | 0.004 |
| | 90 | spatial | coniferous | positive | 3.41 | <0.001 | 0.01 |
| | | | deciduous | positive | 3.14 | 0.002 | 0.01 |
| | | | meadows | negative | -8.74 | <0.001 | 0.08 |
| | | | configuration | positive | 2.93 | 0.003 | 0.01 |
| | | | sex | male > female | 2.88 | 0.007 | 0.01 |

### 3.3.2 Landscape configuration explains home range size

The configuration index showed a high explanatory value for the variation in home range size of both study species. In red deer, the relationship was hump-shaped with largest home range sizes at intermediate patch aggregation, while roe deer continuously increased their home range size as patches became more aggregated (figure 2).

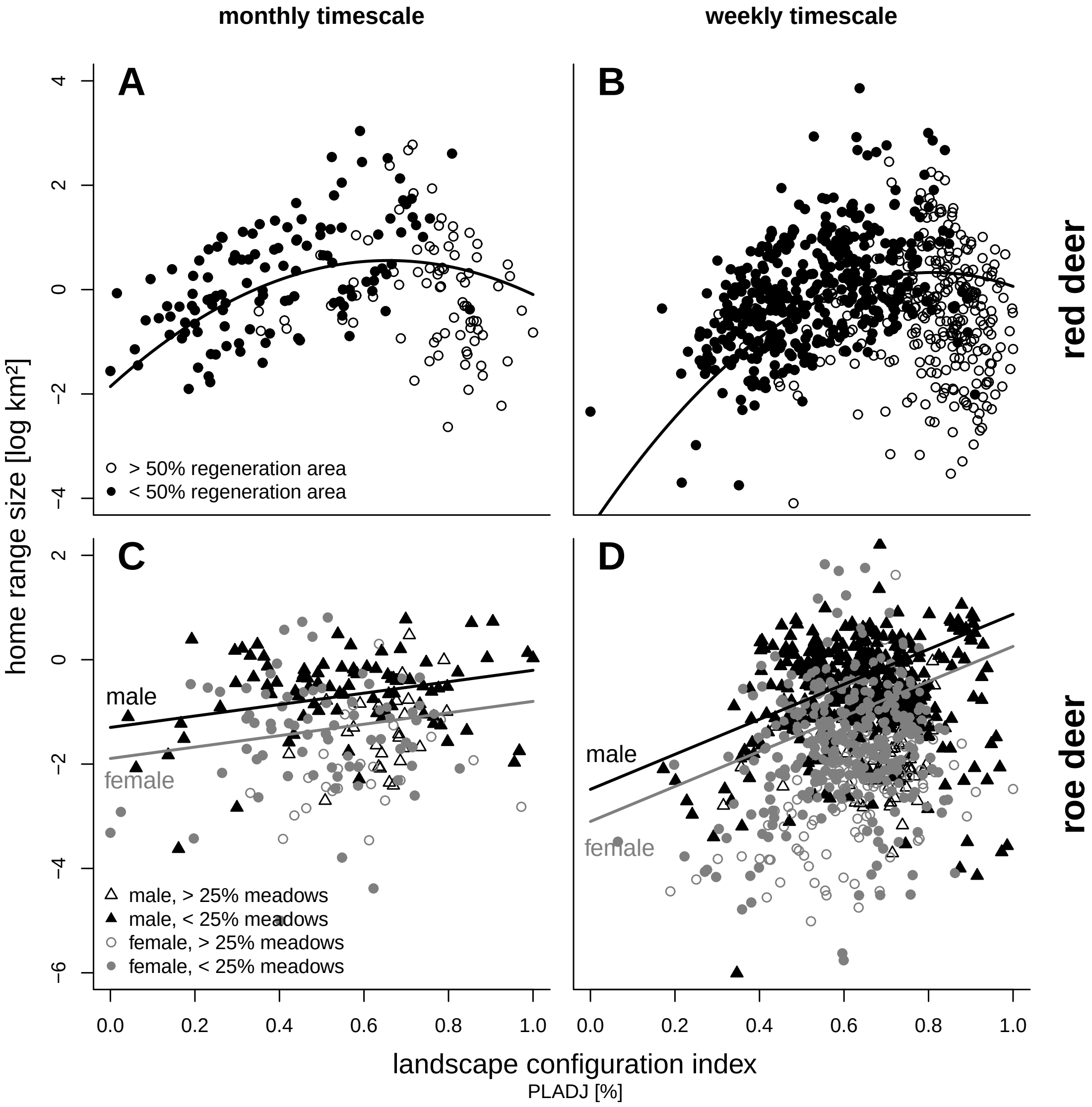

**Figure 3.2:** Home range size (log $\mathrm{km}^2$) for red deer (A, B) and roe deer (C, D) as a function of patch aggregation. Home ranges are calculated on 50 % monthly scale and 50 % weekly scale on each individual home range. The models revealed a different effect of the sexes, therefore the male (black, triangle) and female (grey, points) are presented separately. In red deer, filled points show home ranges with less than 50 % land cover type "regeneration area" within the home range and unfilled points show home ranges with 50 % and more than 50 % "regeneration areas" within the home range. In roe deer, filled triangles show male home ranges sizes with less than 25 % land cover type "meadow" within the home range and unfilled triangles show home ranges with 25 % or more land cover type "meadow" within the home range. The same holds for females, the symbols here are coded as points. Lines show model fit and points true values. Red deer: monthly: n = 210, weekly: n = 753; male roe deer: monthly: n = 112, weekly: n = 483; female roe deer: monthly: n = 99, weekly: n = 448.

### 3.3.3 Land cover type

In red deer the land cover types "regeneration area" and "meadow" played a secondary role at the biweekly and weekly scale, while "coniferous forest" and "deciduous forest" were more important at the monthly scale. Generally, "regeneration area" and "meadow" lead to smaller home ranges, while "coniferous forest" and "deciduous forest" lead to larger home ranges. In roe deer "meadow" had an impact across scales and lead to smaller home ranges. The land cover types "coniferous forest" and "deciduous forest" showed a positive effect across scales but without clear pattern.

## 3.4 Discussion

Most empirical studies on home range dynamics and size, especially within ungulates, take into account vegetation, i.e. the fraction of land cover types but not the explicit spatial configuration of a landscape (Börger *et al.*, 2006a; Rivrud *et al.*, 2010; van Beest *et al.*, 2011). So far, studies which include landscape heterogeneity are analysing the impact on large scales. For example Kie *et al.* (2002) analysed female mule deer in North America at the landscape scale with a multiple regression model, using buffers around home ranges centres and seasonal 95 % adaptive kernels on a landscape resolution of 50 x 50 cell grid. At the largest spatial scale the landscape analysis extended the home range scale. They found similar results at these scales (larger home ranges in aggregated landscapes) but restricted their analysis to landscape indices only. Similarly Quinn *et al.* (2013) analysed home range sizes of white-tailed deer in North America on an annual and seasonal temporal scale using different landscape metrics and linear regressions and found similar results, decreasing home range size with increasing patchiness of the landscape. The present study shows the effect of the landscape's spatial configuration on individual variation in home range sizes on different spatio-temporal scales for two sympatric ungulate species, red deer and roe deer including individual variation with the use of mixed effect models. The temporal scales range from monthly to weekly and the spatial scale from 90 % to 50 % kernel isopleths and compare therefore a wide range of behavioural habitat selections of the animals. Moreover, we see different responses within the two species and our results are constant over the different spatio–temporal scales. Furthermore we quantify the effect of the landscape configuration but are including also further parameters. We demonstrate that by including landscape configuration, predictions of home range size can be significantly improved (table 1, table 2). This finding can be explained by comparing the artificially ordered landscape in figure 1 C with the random landscape in figure 1 B: if we consider an animal located in a patch of "deciduous forest" that aims to reach a "meadow" patch in order to forage, it needs to cross a large block of "mixed forest" to reach its goal. The same animal will reach its goal with a much shorter movement path in a very fine grained landscape (figure 1 B). Real landscapes contain a mixture of patches differing in size and habitat type and an animal will establish a home range according to its needs in the context of the underlying landscape. Hence the home range will contain patches that provide resources according to the needs of the animal (e.g. food or shelter) as well as patches it needs to traverse when switching between different activity modes. As a consequence, home range size is heavily influenced by the spatial configuration of a landscape.

### 3.4.1 The role of landscape configuration

The results of our study are consistent with this short verbal model. As patch aggregation increases home range size generally increases as well because animals typically have two contrasting needs: (1) to find forage resources and (2) to find shelter. As described above these needs are often connected to different habitats which may even change over time forcing an animal to move between different resource patches. Yet, the differences in habitat preference of our study organisms lead to different relationships for the two species. While roe deer show a positive linear relationship with patch aggregation, this relationship is hump-shaped for red deer. Red and roe deer differ in their habitat requirements and behaviour: red deer are widely roaming animals and intermediate feeders that consume both, high and poor-quality food (Hofmann, 1989; Clauss *et al.*, 2009). In our study area very large patches are typically "regeneration areas", i.e. land stretches that have suffered from massive bark beetle outbreaks during the 90s. These outbreaks affected an area of approximately 5,600 ha especially in the subalpine regions, leading to sunny openings (Lausch *et al.*, 2011). After a first succession phase the characteristics of these areas provide exceptionally good habitat for red deer, as these areas show high grass cover and with lying dead wood and regrowing vegetation the food supply is diverse and furthermore at the same time these vegetation characteristics provide next to abundant food supply good shelter for the animals and furthermore both are occurring at small spatial scales. This leads to shorter movement paths and smaller home ranges, an effect that is highly visible in our study and responsible for the hump-shaped relationship depicted in figure 2. Roe deer, on the contrary, show characteristically smaller movement radii, are very selective feeders and only consume highly digestible forage (Barančeková *et al.*, 2009; Mueller *et al.*, 2013). As a consequence the fraction of habitat types containing valuable food resources for roe deer (e.g. "meadow") increases the quality of our model. As shown in figure 2 larger amounts of valuable resources within the landscape ("regeneration areas" for red deer, "meadow" for roe deer) significantly decrease the size of a home range. While for red deer such valuable resources occur especially in large "regeneration areas", which leads to the hump-shaped relationship shown in figure 2, meadows can be found all along the patch aggregation axis (open symbols in figure 2 C and D). Roe deer that have a high amount of "meadow" in their home range typically have smaller home ranges, as open symbols in figure 2 occur especially in the lower parts of the graph. We chose to use the most common estimator for home range size calculation to have a basis for comparison to other studies. While the best home range estimate is under discussion and new methods are continuously proposed (Hemson *et al.*, 2005; Kie *et al.*, 2010; Kranstauber *et al.*, 2012), we expect our results to be robust against the choice of a particular estimator of home range size, since we focused on core areas of home range activity.

## 3.5 Concluding remarks

Although home ranges have been studied extensively for quite some time, it is only recently that the importance of the underlying landscape configuration has been recognized (Kie *et al.*, 2002; Moorcroft *et al.*, 2006; Walter *et al.*, 2009; Moorcroft, 2012; Quinn *et al.*, 2013). An increasing number of studies could show that the fraction of different habitats present in a landscape at least partially explain home range size (Frair *et al.*, 2005; Börger *et al.*, 2006b; Rivrud *et al.*, 2010). Yet, it is intuitively clear that the spatial configuration of land cover types should determine home range size too, as these external conditions define the actual distances animals have to cover in order to satisfy different needs. Here, we have shown that the spatial configuration of the landscape is one the most important factors explaining home range size for two exemplary deer species. Our results were robust at all tested spatio-temporal scales.

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# Appendix

## Area dependencies of landscape indices

Buffers around 90 % kernel home range centres (monthly scale, n = 214) from the red deer data set were drawn from 500 m to 7000 m in 500 m steps. We then calculated six landscape indices for each buffer circle (area–weighted mean patch area (AREA_AM), contagion (CONTAG), percentage of like adjacencies (PLADJ), landscape division index (DIVISION), effective mesh size (MESH), aggregation index (AI)). Afterwards we ran a mixed model to check for size dependencies of the indices. In total 13.42 % of calculated buffers were excluded from further analyses as they contained more than 5 % missing values in land cover data.

The analysis of the area–dependency of the landscape indices revealed a high size–dependency of the metrics AREA_AM, DIVISION and MESH, hence these indices were excluded from further analyses. Additionally the indices CONTAG, PLADJ and AI were highly correlated with each other (Pearson's correlation Index $> 0.8$). The PLADJ index accounts not only for patch size but also on patch shape (McGarigal et al., 2002), and furthermore shows the least dependency on area (figure 3.3), so we choose this index for all further analysis. Note that the indices AI and CONTAG show essentially the same results. The software tools R version 3.0.2 (R Development Core Team, 2013), GRASS 6.4.1 (Grass Development Team, 2012) and FRAGSTATS v3 (McGarigal et al., 2002) were used for the analyses.

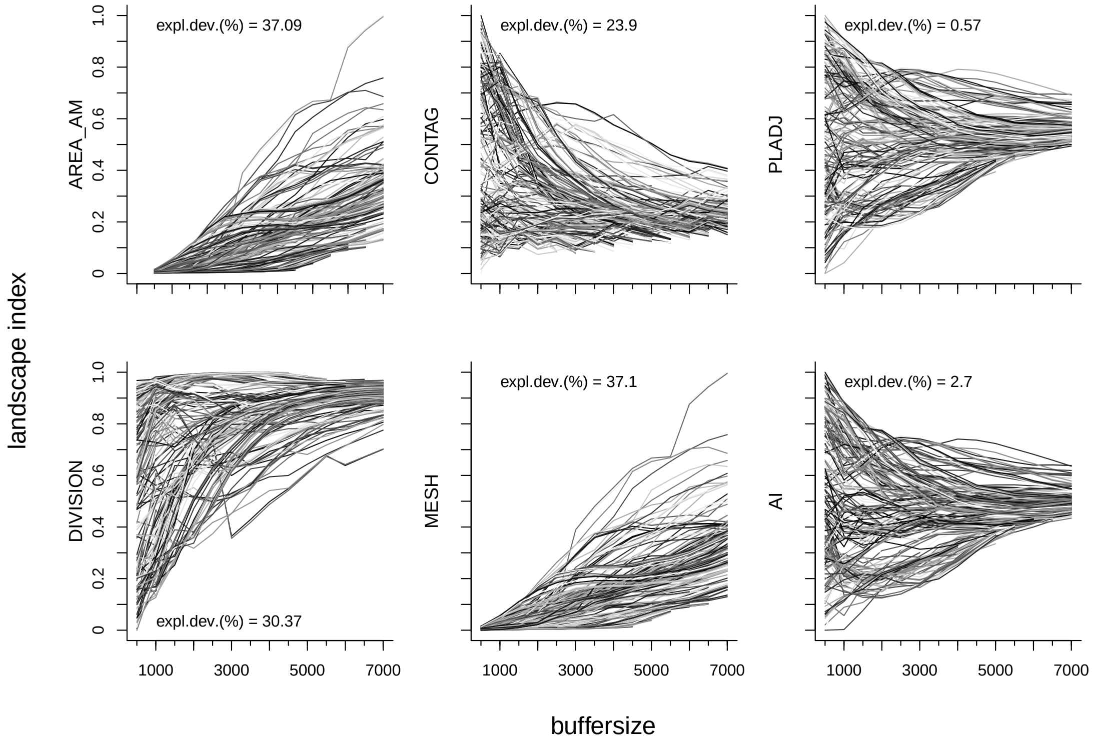

**Figure 3.3:** Overview of the size dependencies of six calculated landscape metrics analysed with a mixed model. Buffer index values belonging to the same home range centre point are connected with a line. The explanatory value (expl.dev( %)) of the size dependency for each landscape index is drawn within the plot.

## Home range size of red and roe deer across spatio–temporal scales

TABLE 1: Summary statistics of male and female red (A) and roe deer (B) home range sizes (km$^2$) across spatio–temporal scales (N = Number of samples included in home range estimation). Home ranges were estimated with the fixed kernel method using the reference method for the smoothing factor h (Worton, 1989; Kernohan et al., 2001). The software R version 3.0.2 using the package "adehabitatHR" was used for the analysis (R Development Core Team, 2013; Calenge, 2006).

| **A** | **Red deer (*Cervus elaphus*) – males** | | Number of animals = 14 | |
|---|---|---|---|---|
| | | **Kernelsize** | | |
| **Timescale** | | **90 %** | **70 %** | **50 %** |
| **monthly** | Number of GPS–location: mean = 218, range = 70–403 | | | |
| | Mean (range) | 11.05 (0.58–89.62) | 5.60 (0.32–37.47) | 3.00 (0.17–20-91) |
| | N | 93 | 94 | 95 |
| **biweekly** | Number of GPS–location: mean = 58, range = 6–165 | | | |
| | Mean (range) | 7.73 (0.43–103.98) | 4.15 (0.16–51.25) | 2.28 (0.08–26.53) |
| | N | 179 | 181 | 183 |
| **weekly** | Number of GPS–location: mean = 58, range = 6–165 | | | |
| | Mean (range) | 6.75 (0.07–190.85) | 3.51 (0.03–93.34) | 1.91 (0.02–47.40) |
| | N | 338 | 340 | 342 |

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**Red deer (*Cervus elaphus*) – females** Number of animals = 18

| | | Kernelsize | | |
|---|---|---|---|---|
| **Timescale** | | **90 %** | **70 %** | **50 %** |
| **monthly** | Number of GPS–location for home range estimation: mean = 233, range = 82–383 | | | |
| | Mean (range) | 4.14 (0.27–15.22) | 2.04 (0.14–8.62) | 1.11 (0.07–5.26) |
| | N | 115 | 115 | 115 |
| **biweekly** | Number of GPS–location for home range estimation: mean = 54, range = 11–136 | | | |
| | Mean (range) | 4.06 (0.07–32.81) | 1.99 (0.04–13.33) | 1.07 (0.02–7.00) |
| | N | 221 | 221 | 221 |
| **weekly** | Number of GPS–location for home range estimation: mean = 54, range = 11–136 | | | |
| | Mean (range) | 3.84 (0.07–67.08) | 1.94 (0.04–34.90) | 1.07 (0.02–18.81) |
| | N | 411 | 411 | 411 |

**B** **Roe deer (*Capreolus capreolus*) – males** Number of animals = 24

| | | Kernelsize | | |
|---|---|---|---|---|
| **Timescale** | | **90 %** | **70 %** | **50 %** |
| **monthly** | Number of GPS–location for home range estimation: mean = 146, range = 67–366 | | | |
| | Mean (range) | 1.96 (0.18–8.94) | 1.07 (0.05–4.30) | 0.61 (0.03–2.17) |
| | N | 108 | 111 | 112 |
| **biweekly** | Number of GPS–location for home range estimation: mean = 93, range = 34–250 | | | |
| | Mean (range) | 1.99 (0.005–11.37) | 1.10 (0.002–6.35) | 0.64 (0.001–3.68) |
| | N | 247 | 253 | 258 |
| **weekly** | Number of GPS–location for home range estimation: mean = 70, range = 17–195 | | | |
| | Mean (range) | 2.10 (0.005–40.21) | 1.16 (0.002–17.05) | 0.67 (0.001–9.09) |
| | N | 465 | 473 | 483 |

**Roe deer (*Capreolus capreolus*) – females** Number of animals = 16

| | | Kernelsize | | |
|---|---|---|---|---|
| **Timescale** | | **90 %** | **70 %** | **50 %** |
| **monthly** | Number of GPS–location for home range estimation: mean = 199, range = 77–565 | | | |
| | Mean (range) | 1.30 (0.03–11.19) | 0.62 (0.01–4.11) | 0.34 (0.01–2.24) |
| | N | 97 | 99 | 99 |
| **biweekly** | Number of GPS–location for home range estimation: mean = 102, range = 35–261 | | | |
| | Mean (range) | 1.15 (0.01–13.44) | 0.58 (0.01–6.81) | 0.32 (0.004–3.69) |
| | N | 225 | 228 | 228 |
| **biweekly** | Number of GPS–location for home range estimation: mean = 62, range = 15–135 | | | |
| | Mean (range) | 1.04 (0.01–22.09) | 0.56 (0.006–11.56) | 0.32 (0.003–6.23) |
| | N | 441 | 451 | 448 |

## Table of random effects for mixed models on all spatio–temporal scales for red and roe deer

TABLE 2: Table of random effects and standard deviation (SD) of the linear mixed models for all spatio–temporal scales for both species, red (A) and roe deer (B). All models were fitted with ID as random effect. Additionally as the data samples are taken over different years, the models were additionally fitted with year as a nested variable within ID.

| **A** | **Red deer (*Cervus elaphus*)** | | | |
|---|---|---|---|---|
| | | **Kernel size** | | |
| **Timescale** | | **90 %** | **70 %** | **50 %** |
| **monthly** | | | | |
| | random effect | 0.37 | 0.31 | 0.27 |
| | SD | 0.61 | 0.56 | 0.52 |
| **biweekly** | | | | |
| | random effect | 0.28 | 0.17 | 0.16 |
| | SD | 0.53 | 0.41 | 0.40 |
| **weekly** | | | | |
| | random effect | 0.34 | 0.27 | 0.22 |
| | SD | 0.69 | 0.59 | 0.56 |

| **B** | **Roe deer (*Capreolus capreolus*)** | | | |
|---|---|---|---|---|
| | | **Kernel size** | | |
| **Timescale** | | **90 %** | **70 %** | **50 %** |
| **monthly** | | | | |
| | random effect | 0.21 | 0.24 | 0.21 |
| | SD | 0.45 | 0.57 | 0.52 |
| **biweekly** | | | | |
| | random effect | 0.25 | 0.28 | 0.27 |
| | SD | 0.62 | 0.71 | 0.70 |
| **weekly** | | | | |
| | random effect | 0.24 | 0.53 | 0.47 |
| | SD | 0.67 | 0.99 | 0.88 |

## Tables of the mixed models with different correlation structure for all spatio–temporal scales for red and roe deer

We checked for spatial and temporal correlation structure using the full model. Following the approach of **?** we specified the spatial correlation structure with the geographic coordinates of the home range centres and used a vector for the temporal autocorrelation specifying the time variable. Afterwards we compared the models using the Akaike Information Criterion (AIC) to obtain the best model.

TABLE 3: Table of the reddeer data set fitted with a mixed effect model with different correlation structure. The best models are indiciated in bold format.

| **Timescale** | **Kernel size** | **correlation structure** | **AIC** |
|---|---|---|---|
| **monthly** | 50 | none | 522.66 |
| | | spatial | 524.59 |
| | | **temporal** | **521.67** |
| | 70 | none | 495.07 |
| | | **spatial** | **494.17** |
| | | temporal | 495.43 |
| | 90 | **none** | **475.20** |
| | | spatial | 477.20 |
| | | temporal | 475.57 |
| **biweekly** | 50 | none | 1026.01 |
| | | spatial | 1015.45 |
| | | **temporal** | **990.48** |
| | 70 | none | 996.59 |
| | | spatial | 975.01 |
| | | **temporal** | **953.66** |
| | 90 | none | 990.69 |
| | | **spatial** | **939.42** |
| | | temporal | 945.14 |

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| | | | |
|---|---|---|---:|
| **weekly** | 50 | none | 1845.95 |
| | | spatial | 1827.49 |
| | | **temporal** | **1769.49** |
| | 70 | none | 1775.74 |
| | | spatial | 1758.22 |
| | | **temporal** | **1698.13** |
| | 90 | none | 1743.23 |
| | | spatial | 1669.97 |
| | | **temporal** | **1655.84** |

TABLE 4: Table of the roedeer data set fitted with a mixed effect model with different correlation structure. The best models are indiciated in bold format.

| **Timescale** | **Kernel size** | **correlation structure** | **AIC** |
|---|---|---|---:|
| **monthly** | 50 | none | 546.09 |
| | | spatial | 543.32 |
| | | **temporal** | **540.08** |
| | 70 | none | 528.94 |
| | | **spatial** | **521.09** |
| | | temporal | 522.88 |
| | 90 | none | 490.06 |
| | | **spatial** | **455.61** |
| | | temporal | 482.55 |
| **biweekly** | 50 | none | 1204.29 |
| | | spatial | 1205.73 |
| | | **temporal** | **1185.11** |
| | 70 | none | 1188.40 |
| | | **spatial** | **1138.01** |
| | | temporal | 1158.22 |
| | 90 | none | 1133.32 |
| | | **spatial** | **1057.91** |
| | | temporal | 1103.70 |

Continued on next page

| | | | |
|---|---|---|---|
| **weekly** | 50 | none | 2394.76 |
| | | spatial | 2375.51 |
| | | **temporal** | **2324.86** |
| | 70 | none | 2260.48 |
| | | spatial | 2262.48 |
| | | **temporal** | **2177.32** |
| | 90 | none | 1950.43 |
| | | **spatial** | **1882.14** |
| | | temporal | 1913.11 |

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# 4

# Adding structure to land cover – using fractional cover to study animal habitat use

## Abstract

Linking animal movements to landscape features is critical to identify factors that shape the spatial behaviour of animals. Habitat selection is led by behavioural decisions and is shaped by the environment, therefore the landscape is crucial for the analysis. Land cover classification based on ground survey and remote sensing data sets are an established approach to define landscapes for habitat selection analysis.

We investigate an approach for analysing habitat use using continuous land cover information and spatial metrics. This approach uses a continuous representation of the landscape using percentage cover of a chosen land cover type instead of discrete classes. This approach, fractional cover, captures spatial heterogeneity within classes and is therefore capable to provide a more distinct representation of the landscape. The variation in home range sizes is analysed using fractional cover and spatial metrics in conjunction with mixed effect models on red deer position data in the Bohemian Forest, compared over multiple spatio–temporal scales.

We analysed forest fractional cover and a texture metric within each home range showing that variance of fractional cover values and texture explain much of variation in home range sizes. The results show a hump–shaped relationship, leading to smaller home ranges when forest fractional cover is very homogeneous or highly heterogeneous, while intermediate stages lead to larger home ranges.

The application of continuous land cover information in conjunction with spatial metrics proved to be valuable for the explanation of home–range sizes of red deer.

## 4.1 Introduction

Habitat use of animals is assumed to be mainly driven by forage availability and is a complex hierarchical process of behavioural responses and choices (Gaillard *et al.*, 2010). Individuals choose habitat that maximizes resources (e.g. food or shelter) and conditions necessary for survival and reproduction (Richard *et al.*, 2011), whereas these resources are influenced by temporal and spatial variations of the landscape (Gustafson, 1998). Habitat selection is led by behavioural decisions and is shaped by the environment, leading to the observed habitat use (Johnson, 1980).

A large majority of animals use certain areas without showing a territorial behaviour, referred to as home range. In contrast to territories, a home range has no defended borders (Burt, 1943). Home ranges are generally defined as the spatial expression of all behaviours an animal performs in order to survive and reproduce (Burt, 1943). Since home ranges link individual movement paths to dispersal and population dynamics, understanding why and how home range sizes vary between and among species is a fundamental issue in ecology. The current and prospective availability of large movement data sets and remotely sensed environmental information will allow further detailed analysis (Wikelski *et al.*, 2007). Progress in GPS–sensor receiver technology and satellite telemetry makes it possible to track animals over long time spans with high temporal and spatial resolution and to analyse their habitat requirements and movement paths (Tomkiewicz *et al.*, 2010).

By studying variation in home range size and identifying the factors involved in such variation, we can identify how habitat influence individual's habitat use (Richard *et al.*, 2011) and therefore the variation in home ranges. A number of factors have been addressed for shaping variation in home range sizes, these include the environmental productivity and the heterogeneity of the landscape (Boyce *et al.*, 2003; Nilsen *et al.*, 2005; Saïd *et al.*, 2009). Especially the availability of forage is a main driver shaping home range sizes (Tufto *et al.*, 1996). A common trade–off often faced by many large mammals takes places when open habitats provide the best forage, while closed habitats provide shelter against predators and this may vary with different spatio–temporal scales (Godvik *et al.*, 2009).

Typically in habitat use studies the landscape is represented with a categorical habitat map usually derived from a classification (Torres *et al.*, 2012; Massé and Côté, 2012), while in other studies the landscape is represented only by the dominant habitat type (Börger *et al.*, 2006b; Rivrud *et al.*, 2010). A variety of land cover classifications are routinely produced using remotely sensed data such as MODIS and AVHRR (Friedl *et al.*, 2002).

However, the way the landscape is defined is crucial for the analysis of habitat use. In many studies the landscape is defined in land cover categories, containing classes such as “meadows”, “forest” and “agriculture” (Börger *et al.*, 2006b; Torres *et al.*, 2012) and it is common sense that different needs of an animal corresponds to different land cover types, for example “forest” as areas for shelter and therefore resting or hiding sites, and “meadows” as areas for forage sites (Godvik *et al.*, 2009).

However, landscapes rarely contain sharp borders between cover types although that is how they are portrayed using a classical land cover classification approach. Moreover information about spatial variation within a *a–priori* defined land cover class is not provided when using a classification. A forest might vary spatially due to different age classes of the trees or small tree fall gaps which increase spatial heterogeneity. This within land cover variation is not captured by categorical maps.

Therefore we use a continuous land cover approach such as fractional cover for the inclusion of spatial variation within classes for our analyses. Fractional cover is a multiscale analysis combined with spatial prediction. This method is related to spectral unmixing methods (Asner and Heidebrecht, 2002). The fractional cover image are typically created using a higher resolution land cover classification image to calculate fractional cover training data for lower resolution imagery. For each pixel of the coarse resolution image the percentage coverage for each land cover class within the high resolution is calculated and used for a spatial prediction of the land cover percentages. The percentage cover for the chosen land cover types per pixel of the coarse resolution image is provided as result.

With this approach a continuous land cover classification can be derived which captures the spatial structure in a fine scale manner and this provides a more realistic and more ecologically meaningful representation of the landscape. Global maps with similar approaches of percentage coverage already exist such as MODIS or AVHRR (DeFries *et al.*, 2000; DiMiceli *et al.*, 2011) however only at a coarse spatial resolution and not validated in the study area.

Furthermore in many habitat use studies forests have structural attributes like “dense forest” or “light forest” with corresponding functional effects, such as light forest with plentiful food resources due to an established understory as enough sunlight can reach the forest floor. However, these structural attributes are often not validated and instead they are implicitly assumed (Debeljak *et al.*, 2001). With the fractional cover approach these structural attributes can be addressed clearly.

In this study, we investigate the potential of continuous land cover information for habitat use of red deer in the Bohemian Forest. As habitat use leads to differing home range sizes, we investigate the potential of continuous land cover information and its spatial representation for the explanation of their variation in size. We hypothesize larger home ranges with increasing forest cover due to lower density of food resources. We test our hypothesis on different spatial (90 %, 70 % and 50 % isopleths) and temporal scales (monthly, biweekly and weekly) to account for temporal and spatial differences.

## 4.2 Materials and Methods

### 4.2.1 Study area

The study area is located in Central Europe in the Bohemian Forest, an area belonging to two national parks: the Bavarian Forest National Park on the German side of the border (240 $\mathrm{km}^2$) and the Šumava National Park on the Czech Republic side of the border (640 $\mathrm{km}^2$). These protected areas are embedded within the Bavarian Forest Nature Park (3070 $\mathrm{km}^2$) and the Šumava Landscape Protection Area (1000 $\mathrm{km}^2$). In its entirety, the area is known as the Bohemian Forest Ecosystem. The area is mountainous, with a variation in elevation between 600 and 1450 m.a.s.l.. The mean annual temperature varies between 3°C and 6.5°C along higher elevation and ridges. The mean annual precipitation is between 830 and 2230 mm. Within the park, three major forest types exists: above 1100 m: sub–alpine spruce forests with Norway Spruce (*Picea abies* L.) and some Mountain Ash (*Sorbus aucuparia* L.), on the slopes, between 600 and 1100 m elevation, are mixed montane forests with Norway Spruce, White Fir (*Abies alba* MILL.), European Beech (*Fagus sylvatica* L.), and Sycamore Maple (*Acer pseudoplatanus* L.). In the valley bottoms, spruce forests with Norway Spruce, Mountain Ash, and birches (*Betula pendula* ROTH. and *Betula pubescens* EHRH.) (Fischer *et al.*, 2013). Since the mid–1990s, the forests of the national park have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*). By 2007, this had resulted in the death of mature spruce stands over an area amounting to 5,600 ha (Müller *et al.*, 2008; Lausch *et al.*, 2013).

### 4.2.2 Red deer data

From 2002–2011 red deer were caught during winter, using a procedure approved by the Government of Upper Bavaria, Germany. Red deer were captured and fitted with GPS collars (Vectronic Aerospace, Berlin, Germany) in box traps with side windows after they were lured in with food. Here no immobilization was necessary. A second approach was to tranquillize deer by dart gun where they were attracted by food (Heurich, 2011).

We collared 80 deer (39 male, 41 female). Ten individuals were collared two or more times. As animals spend the winter in enclosures, we restricted the analysis temporally from May to the end of September. The most common protocol was to mark red deer in late winter and retrieve the collars after a year by collar drop–off or recapturing, allowing the collars to be used on new individuals. We removed spatial and temporal false fixes (i.e. locations taken only a few seconds apart) beforehand. We defined the samples from the multiple collared animals over the single year as independent. As the schedule of the collars are adjusted to take a location every 15 min for one day of the week we took a random sample of animals with sequences of short time intervals to ensure that all locations have a minimum interval of one hour. The median accuracy of the GPS locations was 16.5 m (Stache *et al.*, 2012).

### 4.2.3 Home range estimation

Home ranges were estimated with a commonly used approach, the fixed kernel method (Worton, 1989; Calenge, 2006) using the reference method for the smoothing factor h (Kernohan *et al.*, 2001). We used three different home range definitions to include a spatial scale and to investigate the effect on the core area (50 % kernel) and a wider range (70 % kernel, 90 % kernel). In addition, all home range definitions were estimated on three temporal scales: monthly, biweekly and weekly. We only estimated home ranges for individuals with at least ten locations for a given temporal scale, after removing spatial and temporal outliers (Börger *et al.*, 2006a).

### 4.2.4 Representation of the landscape

For the calculation of fractional cover a high resolution classified image was derived from aerial images and was used for training. The classified image contained 26 categories (different forest types such as coniferous, deciduous and mixed forest, and age classes such as mature, medium, young). Due to used spatial and spectral resolution we grouped those classes to three major categories in order to be able to discriminate them appropriately: forest (containing all forest types and age classes), open areas (e.g. meadows, regeneration areas, clear cut areas) and others (e.g. water, rocks, roads). To create our training data the fractional cover of each class within 30 m Landsat pixels was calculated. The resulting percent cover values for a particular class were used as response variables to train a random forest (RF) regression model (Breiman, 2001). Random forest uses an ensemble of decision trees (in our case regression trees) to model non-linear relations among response variables (Hansen *et al.*, 2002, 2003; Hayes *et al.*, 2008). The resulting RF model was then used to predict percent cover for the cover type being modelled on a Landsat image using pixel spectral values as predictor variables. The number of regression trees used in the random forest model was 1000, the number of predictors tried on each split was set to the algorithm's default value (number of Landsat image bands/3). An unbiased accuracy assessment is provided by RF using "Out Of Bag" statistics calculated from a random selection of 1/3 of the training data (Breiman, 2001). Three cloud free Landsat 5 scenes (path 192, row 26) with bands 1–5 from 2006 (July 15th, October 19th) and 2009 (September 9th) were used for the fractional cover analysis. The three predicted vegetation layers complement each other and sum up to 100 %. The class "others" contains only small values in our study area, therefore the major part of the values are split between "forest" and "grassland". Since both layers complement each other we included only the class "forest" in our analysis. Figure 4.1 shows the categorical map and the fractional cover layers "forest" and "grassland" for the whole study area (upper panels). An enlarged display of a section shows how the formerly categorical representation of the landscape is now split up in continuous values (middle panels). The lower panels show the representation of the categorical values within the fractional cover values in a histogram. The discrete classes are represented by very high cover values within the study area (appendix, figure 3 for a figure of the observed vs. predicted values of the regression model).

We extracted all fractional cover values of the forest class within the home ranges and calculated mean, standard deviation and variance. In addition to fractional cover we chose to also calculate texture measures for each home range. Texture metrics were developed by Haralick *et al.* (1973) and capture habitat structure which can be quantified using the variability of pixel values in a given area. Second–order texture measures are calculated from the gray–level co–occurrence matrix (GLCM) and account for spatial arrangement of pixel values. Haralick *et al.* (1973) presented a variety of different texture metrics, however he states that these metrics are highly correlated and can be difficult to interpret. To ensure that the chosen texture metric is not size dependent we calculated buffers from 500 to 7000 m in 500 m steps around the home range centres of the 90 % kernel isopleths and analysed all texture metrics with regard to their size dependency. We calculated texture measures using all pixel values within the home range. A moving window was used to calculate the texture metric for every pixel relative to its direct neighbours (eight pixels around a centre pixel). We then averaged the resulting texture values to obtain one value for the home range to fit into the mixed model design. We chose to use the texture metric "contrast", as it shows the least size dependency (see appendix, figure 1) and is easy to interpret as a measure of local variation in the image and therefore an indicator of landscape heterogeneity. Throughout the remaining text we will refer to the contrast metric as a texture metric or simply as texture.

We choose to use standard deviation of the forest fractional cover calculated within a home range as a measure for variability and the mean forest fractional cover as an estimate of overall forest fractional cover within each home range. Since variables standard deviation and variance show high collinearity (Dormann *et al.*, 2013), variance is not considered in the analysis. For simplicity we will refer to the standard deviation as variation of fractional cover values.

Furthermore we estimated the mean elevation of the home ranges using the 30 m ASTER Global Digital Elevation Map (GDEM) (http://asterweb.jpl.nasa.gov/gdem.asp).

The chosen variables showed no correlation with each other (Pearson's correlation with the threshold as set to 0.7, - 0.7 respectively).

### 4.2.5 Statistical analysis

To investigate the influence of forest fractional cover and texture on home range sizes, we used linear mixed models (Bates *et al.*, 2011) on the log transformed home range areas ($km^2$). Afterwards we ran a backfit on the t–values to derive the essential variables (Tremblay and Ransijn, 2011). Preliminary analysis showed that the variables texture and elevation have a hump–shaped relationship with home range size in the red deer data and we therefore used a quadratic fit in the models.

Following the framework of Zuur *et al.* (2009) for mixed effect models, we first identified the best structure for the random effect term. We fitted random intercepts for each individual (ID), different sexes and the year the locations were sampled, using the full model with respect to fixed effects terms and using the REML criterion for fitting. We started with the full random term and then simplified the model. Afterwards we compared the models with an ANOVA and the best model was evaluated with the Akaike Information Criterion (AIC). For variable selection, models were fitted with a maximum likelihood criterion. We considered as fixed effects the mean value of the fractional cover layer forest within a home range, the standard deviation of fractional cover values within a home range, the texture metric contrast and elevation. The final models where fitted using the REML criterion. We derived minimal adequate models by backward stepwise selection using a t–value of 2 as a threshold for inclusion (Tremblay and Ransijn, 2011). We repeated the analysis for the three definitions of home range size and for the three definitions of temporal scale.

We used the software tool R version 3.0.1 (R Development Core Team, 2013) for all

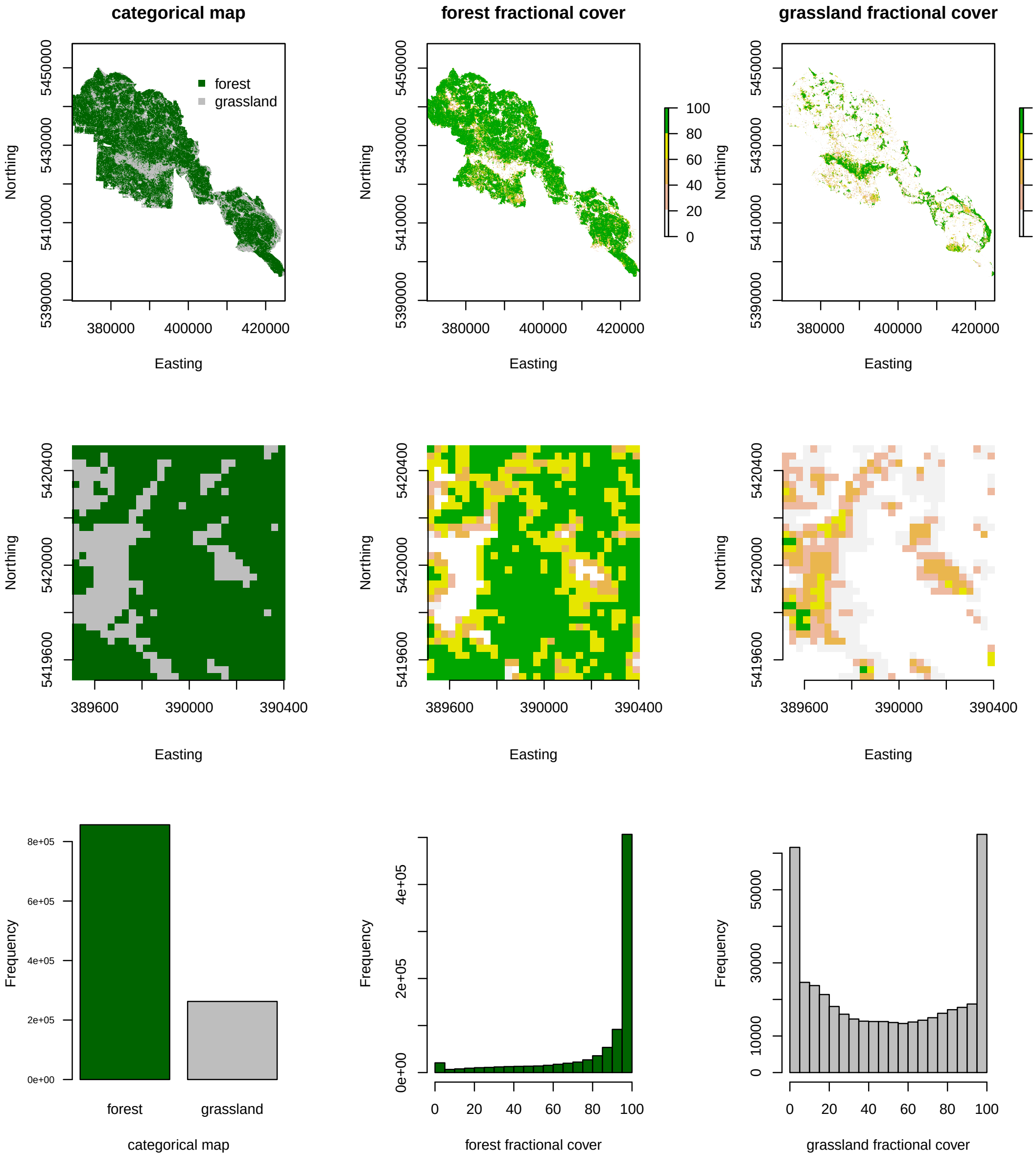

**Figure 4.1:** Overview of the landcover and fractional cover values within the study area. The upper panels show the distribution of the categorical (left hand side) and continuous fractional cover values (middel and right hand panel). The second row shows a zoom–in for better representation and the last row shows the distribution of the values for the whole study area.

analysis. The package "adehabitatHR" (Calenge, 2006) was used for the kernel calculations, "raster" (Hijmans, 2013), "EBImage" (Pau *et al.*, 2013) and "randomForest" (Liaw and Wiener, 2002) for creation of the environmental variables and "lmer" (Bates *et al.*, 2011) and "LMERConvenienceFunctions" (Tremblay and Ransijn, 2011) were used for the statistical analyses.

## 4.3 Results

The fractional cover approach allows a differentiation of variations within land cover types, compared to categorical classes. The spatial heterogeneity of within class variation is captured by this approach. The fit of the random forest regression model for the forest layer was 70.15%. The diversity of fractional cover values within the home range level can be seen in figure 4.2. As outlined in figure 4.1, the corresponding categorical values are represented by the very high percentage values within the fractional Cover approach.

Home ranges of red deer show a high variation in size in our study area (appendix, table 1). We analysed the variation of home range sizes with a mixed model, using mean and standard deviation of the forest fractional cover, as well as the variable elevation and a texture metric. The main random effect in all models was the individual effect (variable ID) with an explained deviance of 0.26–0.38 % (appendix, table 3). The fixed effects of the most parsimonious models explained between 26.88 % and 30.88 % of the observed variation in home range size for red deer across the different spatio–temporal scales (appendix, table 2).

In all models the texture metric showed the highest explained deviance (7.98 %–14.72 %) across scales and was the dominant variable explaining variation in home range size with a hump–shaped relationship (figure 4.3, appendix, table 2). However, this hump–shaped relationship was only pronounced at the monthly time scale, whereas in the biweekly and weekly time scale this relationship changed to a negative linear relationship. The texture metric can be interpreted as an index for spatial heterogeneity in a given area. Hence, at larger temporal scales very homogeneous and very heterogeneous landscapes are leading to small home ranges, while at smaller temporal scales only very heterogeneous landscapes lead to small home ranges.

Furthermore the variation of forest fractional cover (the standard variation) within a home range contributes significantly with an explained deviance of 7.22–11.59 % and a positive relationship, leading to larger home ranges where the variation of forest fractional cover values is higher (figure 4.3).

Additionally the mean showed a positive effect (5.48–7.12 % explained deviance), with no effect on the monthly time scale kernel 50 % isopleth (appendix, figure 2 A).

Elevation had a hump–shaped effect on home range size and showed a low explanatory value of 0.35 %–6.02 % (appendix, figure 2 B).

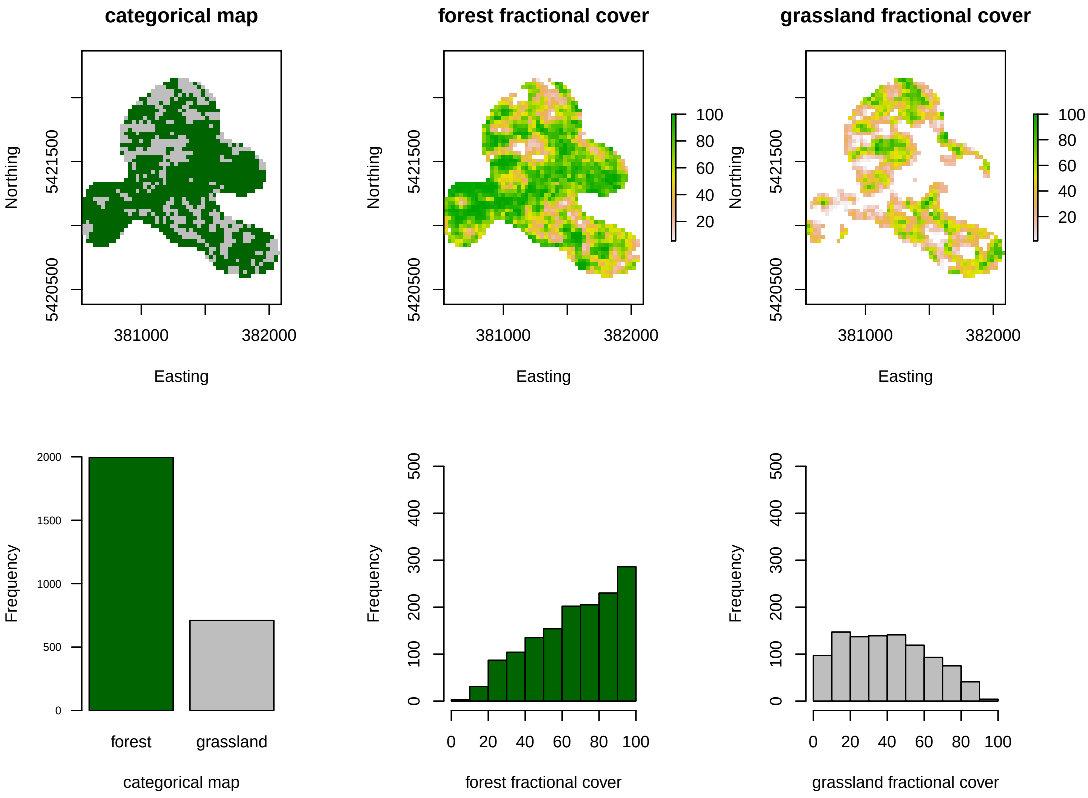

**Figure 4.2:** Representation of the landscape for one home range with both approaches, the categorical and the continuous fractional cover. The lower panels show the distribution of the values within the home range for each approach.

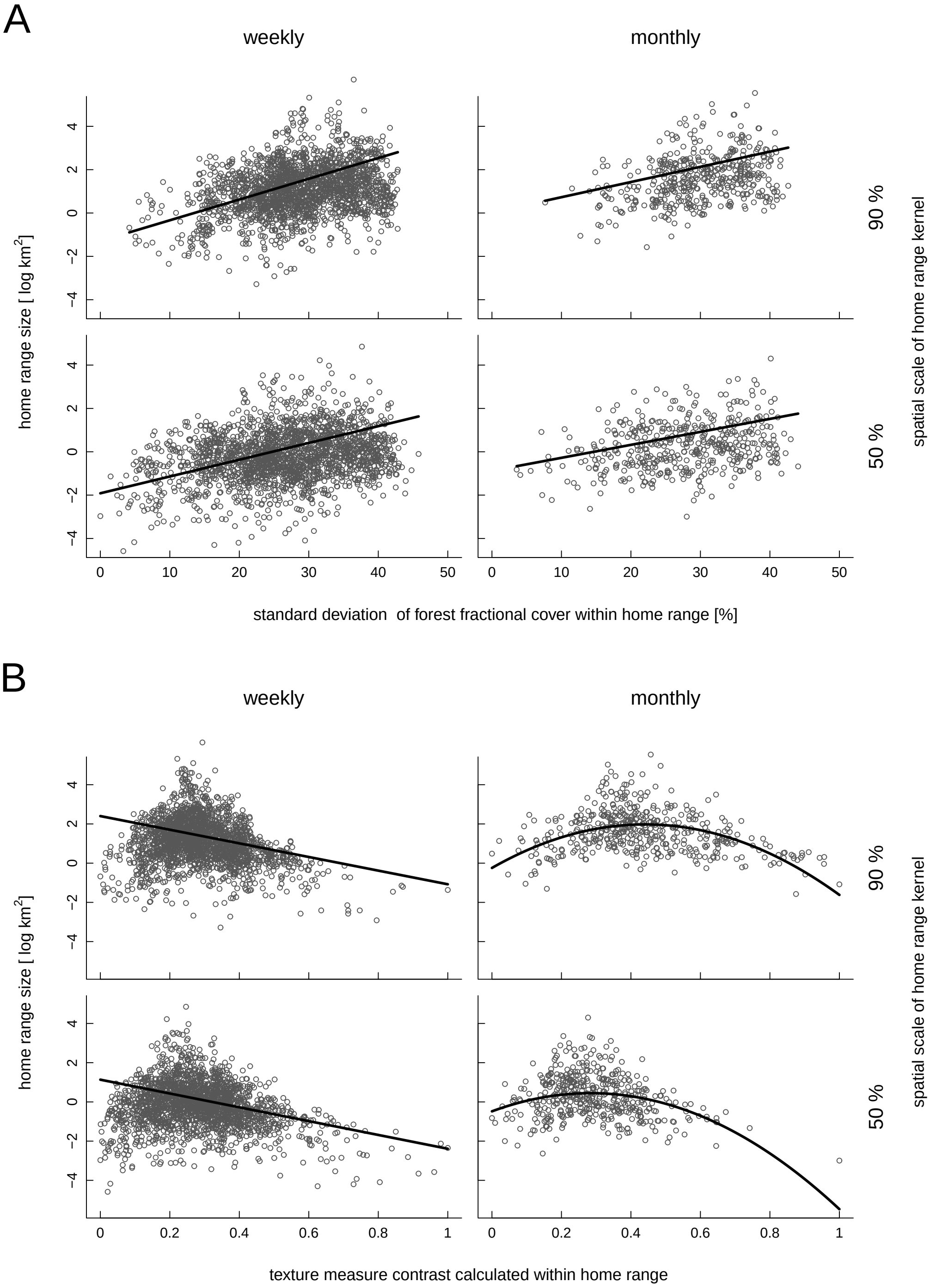

**Figure 4.3:** Plot of log–transformed home range sizes (km$^2$) for red deer in relation to (A) the standard deviation of the forest fractional cover values within each home range and (B) the texture measure calculated within each home range. Home ranges were calculated with the kernel method and the smoothing factor h. Estimates are given for the 90 % and 50 % kernels and the weekly and monthly time scale. Lines show predicted values and points raw residuals.

## 4.4 Discussion

Many studies of habitat use and home range variation consider the landscape as a categorical map with defined and clearly separated patches (Torres *et al.*, 2012; Massé and Côté, 2012). This study investigates the use of continuous land cover information, fractional cover, to analyse the within land cover class variation of home ranges over different spatial and temporal scales for red deer in the Bohemian Forest. We demonstrate that small scale variations represented by continuous landscape data provide important information for modelling habitat use.

Red deer as a mixed feeder (Albon and Langvatn, 1992) has the ability to digest a broad spectrum of food items and benefits from forest edges and from the food supply of younger forest stands which show a low forest canopy cover and therefore have a pronounced understory, as sunlight can reach the ground. Mean forest fractional cover shows a positive relationship with home range size meaning that a higher proportion of dense forest will lead to larger home ranges. Whereas in forest patches with less crown cover and therefore more heterogeneous structure, food resources are more abundant which leads to smaller home ranges. This result is in support with other studies (Owen-Smith *et al.*, 2010; van Beest *et al.*, 2011; Massé and Côté, 2012). Mean forest fractional cover is a rather unsuitable derivative, as it averages all pixels within the home range. Nevertheless it shows a significant explanatory value and gives an overview of the overall forest structure within the home range.

The standard deviation of forest fractional cover values captures the variability of values within a home range. High values indicate a wide spectrum of forest fractional cover and therefore a more heterogeneous landscape while small values indicate a more homogeneous landscape within the home range. Tufto *et al.* (1996) have shown, that female roe deer adjust the size of their home range in response to food supply. In accordance to this study red deer home range sizes increase in our study area with increasing standard deviation and therefore with more heterogeneous forest fractional cover, leading to a higher amount of unfavourable forest habitat within the home range.

The explanatory deviance is largest for the texture metric and also consistent over all spatio–temporal scales with a hump–shaped relationship at larger time scales. Low values of the texture metric correspond to high heterogeneity within the home range, while high values of the texture metric correspond to landscapes which have large aggregated patches. This relationship was detected in a previous study (Bevanda *et al.*, 2014) and can be explained by the characteristics of the National Parks. Bark beetle outbreaks in the 90ies affected an area of approximately 5,600 ha especially in the subalpine regions, leading to sunny openings and large regeneration areas characterized by high grass cover, lying dead wood and regrowing vegetation (Müller *et al.*, 2008). These areas appear very homogeneous when calculated with a texture metric but offer good habitat for deer, as different resources are provided in a small area, leading to small home ranges, as both requirements, food and cover, are fulfilled at the same spot. Furthermore a heterogeneous landscape, providing many different resources, leads to small home ranges as all the resources needed can be reached within a small distance. The hump–shaped effect flattens in the biweekly and weekly time scale and can only be described with a negative linear trend. However, a pattern towards hump–shaped distribution can be seen (figure 3 B). This result shows that the temporal scale needs to be accounted for when analysing home ranges as they are likely to change not based on ecological patterns only but on the time scale of the study. The time period of the study is restricted to the summer months, therefore the resource cover can be regarded as static, i.e. not highly changing over the time, while the resource food is dynamic and depleting. Therefore food supply is the main force shaping home range size during summer. When large patches of dense forest occur within the home range, the texture value will increase. These areas provide shelter against predators, but provide only little food resources. Therefore, as food resources are regarded to be a main force shaping home range size, home ranges will increase in size with the inclusion of large patches of dense forest (intermediate values of texture). Furthermore, these regeneration areas are located at higher altitude and are therefore explaining the effect of elevation, reflecting the importance of bark beetle areas in this study. Like the regeneration areas, elevation shows a hump–shaped fit leading to smaller home ranges where important resources are abundant (Anderson *et al.*, 2005).

It is known that other factors, like body mass, age, reproductive status or climatic parameters like temperature or rainfall have an effect on home range size (please see van Beest *et al.* (2011) for a more complete list) and it is likely, that by including these parameters, the explanatory value of the models could be increased. However, the best method to estimate home ranges is under debate. While we used at least 10 relocation points (Börger *et al.*, 2006a) to estimate our home ranges other studies suggest at least 20 relocation points (Kernohan *et al.*, 2001).

The choice of environmental parameters is important for habitat use modelling. Using classified land cover requires clear definitions of the land cover types but definitions often vary between different maps making them difficult to compare (Herold *et al.*, 2008). Moreover do these classes need to reflect the ecological requirements. An increased discrimination of different land cover types is often helpful to better describe a landscape but an increase in the number of land cover classes often results in lower per–class accuracy. Using alternative information such as continuous cover can help to improve how a landscape is represented in a model. Applying remote sensing time–series data can be valuable to further discriminate land cover types and hence allow more fractional cover classes if distinct temporal signature exist for the different targeted land cover types. Applying continuous land cover information for environmental analysis provides detailed information about ecotones and within land cover variation. This research illustrates that fractional cover mapping has potential benefits for ecological research by avoiding categorical values or sharp, most often artificial, boundaries in the landscape. However, the fractional cover approach requires more analytical steps including spatial prediction models and might therefore be potentially biased by the model used.

## 4.5 Conclusion

The study demonstrates that continuous land cover information can provide valuable information about spatial within class variation as well as gradual vegetation changes, a feature that is not available when using discrete classes. This is especially relevant in movement ecology where a continuous representation of the landscape might be more ecological appropriate. However, to evaluate the added value of the fractional cover approach with regard to land cover classification or biophysical parameter further analysis are needed. Fractional cover mapping of different land cover types adds information, critical to ecological studies, beyond what traditional land cover categorical mapping can offer. As the synergy between remote sensing and ecology increases improved processing and analysis methods will continue to be developed which will have a positive impact on ecological research. These benefits will be especially important with the growing interest in spatio–temporal movement pattern.

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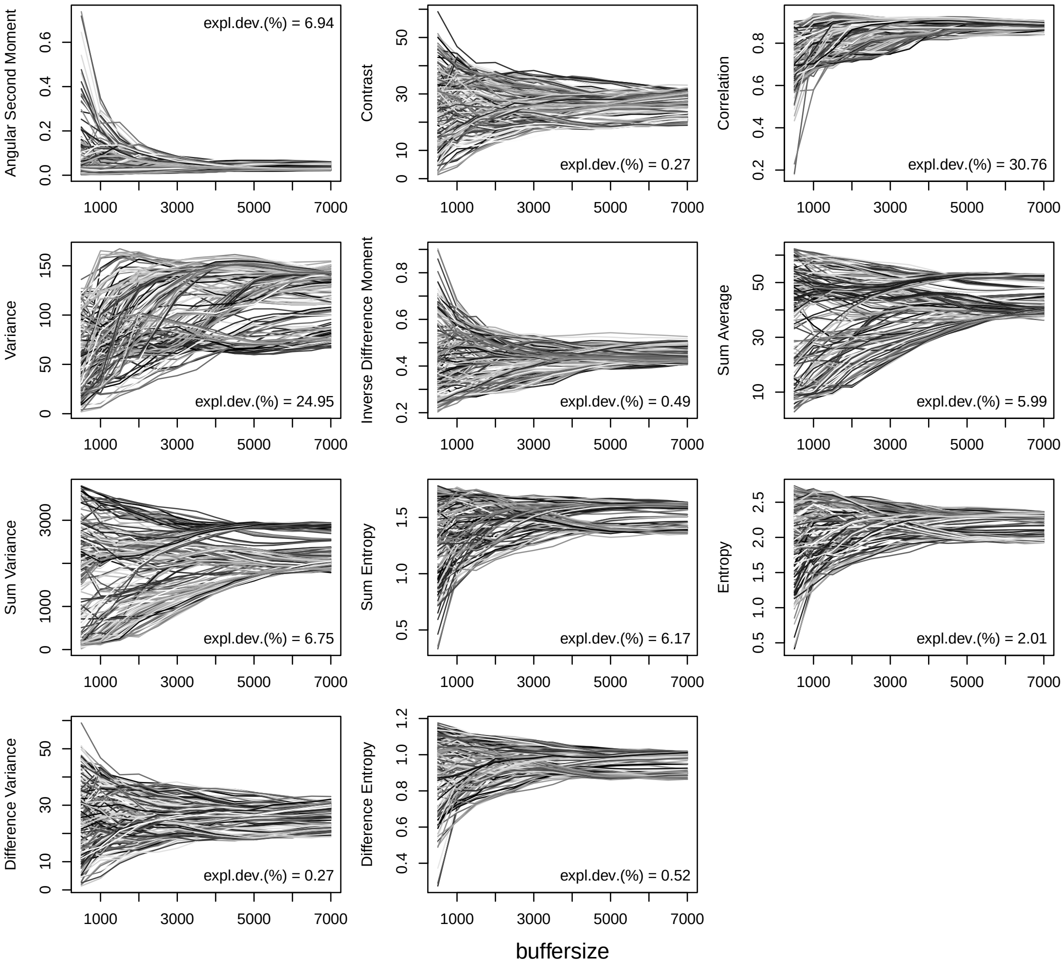
# Appendix

## Overview of size dependency of the texture metrics

FIGURE 1: Overview of the sizes dependencies of the texture metrics established by Haralick *et al.* (1973) analysed with a mixed model Zuur *et al.* (2009); R Development Core Team (2013); Bates *et al.* (2011); Tremblay and Ransijn (2011). Buffers around 90 % kernel home range centres (monthly scale) were drawn from 500 m to 7000 m in 500 m steps around the home range centre for the red deer data set. Buffer index values belonging to the same home range centre point are connected with a line. The explanatory value (expl.dev(%)) of the size dependency for each landscape index is drawn within the plot.



## Overiew of red deer home range sizes across spatio–temporal scales

TABLE 1: Summary statistics of red deer home range sizes (km$^2$) across spatio–temporal scales. N = Number of samples included in home range estimation.

| **Red deer (*Cervus elaphus*)** | | | | |
|---|---|---|---|---|
| | | **Kernelsize** | | |
| **Timescale** | | **90 %** | **70 %** | **50 %** |
| **monthly** | | | | |
| | Mean (range) | 9.14 (0.21–142.90) | 4.87 (0.10–130.55) | 2.60 (0.05–73.76) |
| | N | 456 | 458 | 458 |
| **biweekly** | | | | |
| | Mean (range) | 7.15 (0.05–133.41) | 3.77 (0.02–90.50) | 2.06 (0.01–42.29) |
| | N | 1063 | 1065 | 1065 |
| **weekly** | | | | |
| | Mean (range) | 5.78 (0.03–122.84) | 3.07 (0.01–115.26) | 1.76 (0.01–128.03) |
| | N | 2009 | 2011 | 2012 |

## Overview of fixed effects across spatio–temporal scales

TABLE 2: F-values and explained deviance (%) are shown retained from the mixed model calculated for all temporal (monthly, biweekly and weekly) and all spatial scales (90 %, 70 % and 50 % isopleths) with ID as random structure. The variables variance, texture and elevation were fitted as quadratic term.

| **Time-scale** | **Kernel-size** | **Variables** | **Estimate** | **Std. Error** | **p–value** | **F–value** | **relation- ship** | **expl.dev. (%)** |
|---|---|---|---|---|---|---|---|---|
| weekly | 50 | mean value | 0.008 | 0.001 | $< 0.001$ | 215.49 | positive | 5.48 |
| | 50 | standard deviation | 0.077 | 0.003 | $< 0.001$ | 283.61 | positive | 7.22 |
| | 50 | texture metric | -3.52 | 0.64 | $< 0.001$ | 546.8 | negative | 13.91 |
| | 50 | texture metric | -1.69 | 0.76 | 0.03 | 5.99 | quadratic | 0.15 |
| | 50 | elevation | $< 0.001$ | $< 0.001$ | $< 0.001$ | 25.38 | quadratic | 0.65 |
| | 70 | mean value | 0.01 | 0.001 | $< 0.001$ | 262.67 | positive | 6.46 |
| | 70 | standard deviation | 0.09 | 0.004 | $< 0.001$ | 308.65 | positive | 7.59 |
| | 70 | texture metric | -5.49 | 0.24 | $< 0.001$ | 585.17 | negative | 14.38 |
| | 70 | elevation | $< 0.001$ | $< 0.001$ | $< 0.001$ | 14.35 | quadratic | 0.35 |
| | 90 | mean value | 0.01 | 0.002 | $< 0.001$ | 298.05 | positive | 7.00 |
| | 90 | standard deviation | 0.10 | 0.004 | $< 0.001$ | 417.16 | positive | 9.8 |
| | 90 | texture metric | -3.39 | 0.79 | $< 0.001$ | 565.87 | negative | 13.3 |
| | 90 | texture metric | -3.09 | 0.98 | $< 0.001$ | 8.95 | quadratic | 0.21 |
| | 90 | elevation | 0.01 | 0.002 | $< 0.001$ | 2.25 | positive | 0.05 |
| | 90 | elevation | $< 0.001$ | $< 0.001$ | $< 0.001$ | 12.7 | quadratic | 0.3 |

Continued on next page

| Time-scale | Kernel-size | Variables | Estimate | Std. Error | p–value | F–value | relation- ship | expl.dev. (%) |
|---|---|---|---|---|---|---|---|---|
| biweekly | 50 | mean value | 0.008 | 0l002 | $< 0.001$ | 135.95 | positive | 6.37 |
| | 50 | standard deviation | 0.07 | 0.004 | $< 0.001$ | 108.88 | positive | 5.1 |
| | 50 | texture metric | -5.23 | 0.32 | $< 0.001$ | 314.09 | negative | 14.72 |
| | 50 | elevation | 0.017 | 0.003 | $< 0.001$ | 0.13 | positive | 0.01 |
| | 50 | elevation | $< 0.001$ | $< 0.001$ | $< 0.001$ | 23.83 | quadratic | 1.12 |
| | 70 | mean value | 0.016 | 0.002 | $< 0.001$ | 154.99 | positive | 7.13 |
| | 70 | standard deviation | 0.08 | 0.005 | $< 0.001$ | 117.81 | positive | 5.42 |
| | 70 | texture metric | -2.99 | 0.95 | $< 0.001$ | 317.24 | negative | 14.58 |
| | 70 | texture metric | -2.31 | 1.06 | $< 0.001$ | 4.81 | quadratic | 0.22 |
| | 70 | elevation | | $< 0.001$ | $< 0.001$ | 14.46 | quadratic | 0.66 |
| | 90 | mean value | 0.02 | 0.002 | $< 0.001$ | 155.44 | positive | 6.76 |
| | 90 | standard deviation | 0.09 | 0.006 | $< 0.001$ | 194.15 | positive | 8.44 |
| | 90 | texture metric | -1.96 | 0.98 | $< 0.001$ | 314.23 | negative | 13.66 |
| | 90 | texture metric | -3.61 | 1.11 | $< 0.001$ | 10.75 | quadratic | 0.47 |
| | 90 | elevation | $< 0.001$ | $< 0.001$ | $< 0.001$ | 12.32 | quadratic | 0.54 |

Continued on next page

| Time- scale | Kernel- size | Variables | Estimate | Std. Error | p–value | F–value | relation- ship | expl.dev. (%) |
|---|---|---|---|---|---|---|---|---|
| monthly | 50 | standard deviation | 0.07 | 0.006 | $< 0.001$ | 74.18 | positive | 7.66 |
| | 50 | texture metric | -4.38 | 0.46 | $< 0.001$ | 117.77 | quadratic | 12.16 |
| | 50 | elevation | 0.03 | 0.004 | $< 0.001$ | 10.05 | positive | 1.04 |
| | 50 | elevation | $< 0.001$ | $< 0.001$ | $< 0.001$ | 58.29 | quadratic | 6.02 |
| | 70 | mean value | 0.009 | 0.003 | 0.02 | 55.84 | positive | 5.75 |
| | 70 | standard deviation | 0.06 | 0.008 | $< 0.001$ | 86.64 | positive | 8.92 |
| | 70 | texture metric | -3.84 | 1.41 | $< 0.01$ | 101.42 | negative | 10.44 |
| | 70 | texture metric | 0.13 | 1.30 | 0.9 | 7.99 | quadratic | 0.82 |
| | 70 | elevation | 0.02 | 0.006 | $< 0.001$ | 2.31 | positive | 0.24 |
| | 70 | elevation | $< 0.001$ | $< 0.001$ | $< 0.001$ | 12.76 | quadratic | 1.31 |
| | 90 | mean value | 0.01 | 0.004 | $< 0.01$ 0 | 67.33 | positive | 6.52 |
| | 90 | standard deviation | 0.07 | 0.009 | $< 0.001$ | 119.7 | positive | 11.59 |
| | 90 | texture metric | 2.04 | 1.22 | 0.09 | 82.4 | negative | 7.98 |
| | 90 | texture metric | -4.43 | 1.17 | $< 0.001$ | 18.22 | quadratic | 1.76 |
| | 90 | elevation | 0.02 | 0.005 | $< 0.001$ | 2.2 | positive | 0.21 |
| | 90 | elevation | $< 0.001$ | $< 0.001$ | $< 0.001$ | 9.38 | quadratic | 0.91 |

## Overview of random effect values

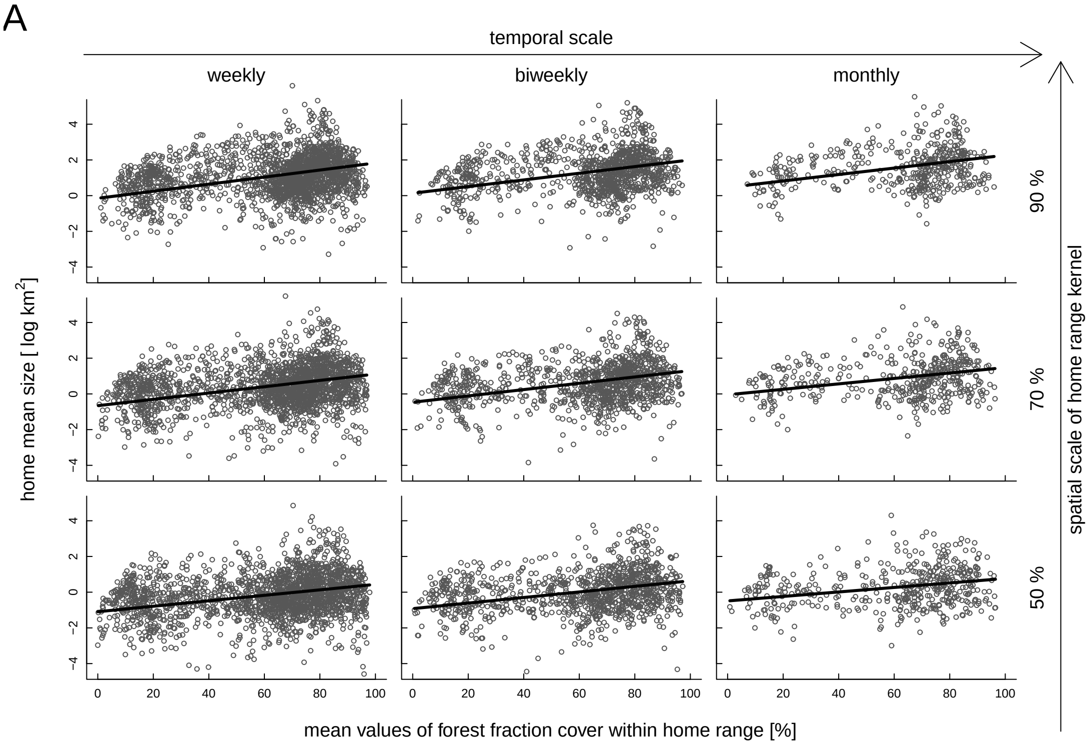
TABLE 3: Table of random effects and standard deviation (SD) of linear mixed models for all spatio–temporal scales for the red deer data set.

**Red deer (*Cervus elaphus*)**

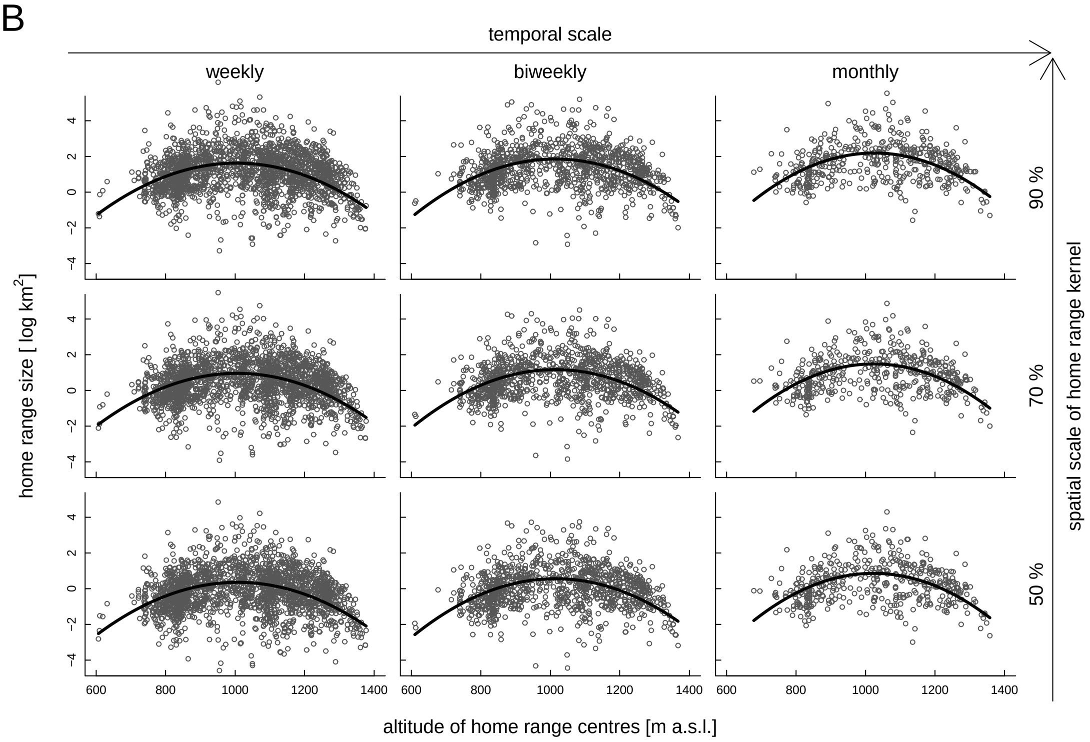
| | | **Kernel size** | | |
|---|---|---|---|---|
| **Timescale** | | **90 %** | **70 %** | **50 %** |
| **monthly** | | | | |
| | random effect | 0.28 | 0.26 | 0.28 |
| | SD | 0.52 | 0.51 | 0.53 |
| **biweekly** | | | | |
| | random effect | 0.32 | 0.28 | 0.38 |
| | SD | 0.57 | 0.54 | 0.53 |
| **weekly** | | | | |
| | random effect | 0.38 | 0.34 | 0.30 |
| | SD | 0.61 | 0.58 | 0.55 |

## Plot of elevation and mean forest fractional cover values within home ranges across spatio–temporal scales

FIGURE 2: Plot of log–transformed home range sizes (km$^2$) for red deer in relation to (A) the mean values of the forest fractional cover values within each home range and (B) the altitude of the home range centres. Home ranges were calculated with the kernel method and the smoothing factor h. Estimates are given for the 90 %, 70 % and 50 % kernels and the weekly, biweekly and monthly time scale. Lines show predicted values and points raw residuals.

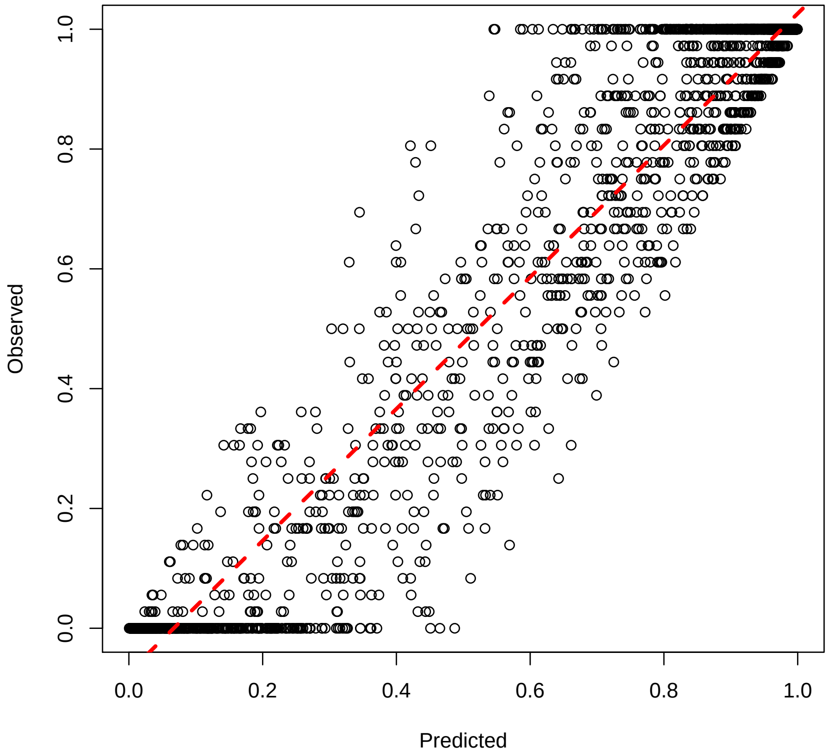


B


temporal scale
weekly
biweekly
monthly
90 %
70 %
50 %
spatial scale of home range kernel
home range size [ log km$^2$]
altitude of home range centres [m a.s.l.]
4
2
0
−2
−4
600
800
1000
1200
1400

## Plot of observed and predicted values of the forest fractional cover regression model

FIGURE 3: This plot shows the fit of the observed vs. predicted values of the forest fractional cover regression model.



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Tremblay, A. and J. Ransijn (2011). LMERConvenienceFunctions: A suite of functions to back-fit fixed effects and forward-fit random effects, as well as other miscellaneous functions. *R package version 1.6.8.3*.

Zuur, A., E. N. Ieno, N. J. Walker, A. A. Saveliev and G. M. Smith (2009). *Mixed effects models and extensions in ecology with R*. Springer, New York, United States, 596 pp.

# 5

# Challenges and perspective

The topic of animal movement is a fast developing discipline, not at least because of the recent progress in technology of GPS and remote sensing techniques. Based on these recent developments, advances in movement ecology could been observed. The application of remote sensing data for ecological research is well established and lead to new findings. The combination of actual spatio–temporal information of animal movement and the linkages to the corresponding environmental attributes allows new insights into ecological patterns. However an unifying framework how to combine and implement these new information into ecological and conservation research has yet to be established.

New opportunities which arise through these new technical opportunities are enormous. Constant improvements of the weight of the devices are made, allowing to collar smaller animals, such as small songbirds (Bridge *et al.*, 2011). In combination with an improved battery consumption, which is so far one limiting factor to track animals across their whole life, it will be possible to analyse the spatio–temporal movement of animals across different development stages. Different behavioural patterns and hence movement and species–environment interaction will then be possible to be analysed in more detail. Moreover physiological parameters, like body temperature, and activity data, will be collected for a wide range of species, which will give more insight into the behaviour of animals (Löttker *et al.*, 2009; Durner *et al.*, 2011). Hence these technical developments will allow to map the entire life of an animal and will give crucial insights into their ecology.

Parallel to these emerging technologies also the computational development advanced and new statistical methods are developed. These new methods are now, with respect to home range size analysis, not only addressing the spatial arrangement of points but also allow to take the time sequence into account, thus characterizing a home range more accurately (Benhamou, 2011; Kranstauber *et al.*, 2012).

To analyse the behaviour of animals a representation of the landscape is essential. Remote sensing is already and will become even more an invaluable tool for ecological research. Free data access is increasingly available and is not hampering its scientific use any more. Large areas can now be mapped with a higher spatial and temporal resolution and in combination with field data it is providing valuable environmental information. Moreover a variety of spatial and temporal resolution are available allowing to address spatial scaling issues or mapping single trees (Wu, 2004; Hirschmugl *et al.*, 2007). Also near–real time land cover monitoring will increasingly be available, such as disturbance monitoring (Verbesselt *et al.*, 2012). Moreover new remote sensing developments such as hyperspectral and LiDAR data might be available globally and open new avenues to analyse land cover attributes, such a vertical vegetation structure (Müller and Brandl, 2009; Bässler *et al.*, 2010; Mücher *et al.*, 2013). Remote sensing data is successfully applied in a variety of ecological research, such as the analysis of species-environment interaction (Naidoo *et al.*, 2012) or modelling species distribution (Wilson *et al.*, 2013; Rocchini, 2013).

However with these new technologies which are advancing continuously also new challenges for ecological application need to be addressed. Tracking devices sample at pre–defined intervals which is just an approximation of the actual animal movement. Even though these devices are developed to allow increasingly shorter intervals which might lead to a higher accuracy it also comes with disadvantages of larger data sets and an emerging need to rethink the ecological accuracy of animal tracking devices in conjunction with remote sensing data. Both data come with an intrinsic error margin, both with a spatial inaccuracy as well as a spectral approximation of the land surface conditions by remote sensing data. The ecological application of these new techniques will soon lead to a needed discussion of ecological relevance. However the enormous added value of these new techniques are without question, however the ecological adequate application needs to be addressed.

Environmental information are commonly extracted from land cover classifications. However these classifications are not primarily created with respect to ecological requirements but based on a human perception of the landscape. For instance forest definitions vary between land cover classifications such as GlobCover, IGBP or Corine and various authors aimed to combine these global classification legends (Herold *et al.*, 2008). Additionally the validation of these data sets are still a challenge (Defourny *et al.*, 2007) and are also partly politically important (see FAO forest report, (FAO, 2012)). These commonly used land cover classes are rarely providing an ecological adequate representation of the respective habitat for the studied species. However ecologists are using the available remote sensing data developed for generic purposes for ecological research. Moreover indices such as Vegetation Indices or biophysical parameters such as LAI or fPAR are highly relevant for ecological research as well, but all data sets are just an approximation of the condition on the ground. Remote sensing data are impacted by a variety of factors such as the atmosphere as well as technical limits or the comparability between sensors. These challenges need to be understood by ecologists in order to be able to interpret the provided data adequately.

Despite these remaining challenges and obstacles remote sensing has already proven to be valuable and is and will provide future opportunities for ecological research In order to ensure a sound implementation of these increasingly used techniques in ecological research several interdisciplinary developments are needed.

Within the field of animal movement the role of a cognitive map and the role of memory is highly relevant to increase our understanding of movement paths and hence the emergence of home ranges (Van Moorter *et al.*, 2009; Spencer, 2012). The implementation of such factors will play a key role in further development of techniques analysing animal movement data. Also the development of new remote sensing data sets as well as sensors specifically designed to meet ecological needs is crucial for a sustainable use of these techniques. Moreover an active participation of ecologists in the improvement of data sets such as tracking devices is highly needed to ensure its adequacy. The tracking interval is an important factor and should not only be defined by technical possibilities but also by ecological needs.

Interdisciplinary discussions and joint projects will lead to an improved application and future development of these new techniques in ecology and conservation.

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# Appendix – R-Code

The R–code for the different analysing steps can be accessed on the supplied CD.

# List of manuscripts and of own contribution

**Manuscript 1**

| | |
|---|---|
| Authors | Bevanda, M., Zeidler, J., Heurich, M., Šustr, P., Reineking, B. and J. Müller, |
| Title | Migration pattern of red deer in the Bohemian Forest |
| Status | in preparation |
| Own contributions | 70 %: idea, data analysis and interpretation , manuscript writing, corresponding author |

**Manuscript 2**

| | |
|---|---|
| Authors | Bevanda, M., Fronhofer, E. A., Heurich, M., Mueller, J. and B. Reineking |
| Title | Landscape configuration is a major determinant of home range size variation |
| Status | published in Ecosphere Volume 6, Issue 10, Pages 1-12 |
| Own contributions | 90 %: idea, data analysis and interpretation, manuscript writing, corresponding author |

**Manuscript 3**

| | |
|---|---|
| Authors | Bevanda, M., Horning, N., Reineking, B., Heurich, M., Wegmann, M. and J. Mueller |
| Title | Adding structure to land cover – using fractional cover to study animal habitat use |
| Status | published in Movement Ecology Volume 2, Issue 26, Pages 1-10 |
| Own contributions | 90 %: idea, data analysis and interpretation, manuscript writing, corresponding author |

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