Understanding animal movement behaviour in dynamic agricultural landscapes

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Content

Abstract

The movement of organisms has formed our planet like few other processes. Movements shape populations, communities, and entire ecosystems. They also guarantee fundamental ecosystem functions and services, like seed dispersal and pollination. Yet, global, regional and local anthropogenic impacts change the movements of organisms across ecosystems all around the world. In particular, land-use modifications, like habitat loss and fragmentation can disrupt animal movements. This disruption has profound consequences for ecosystems, reaching from the decline of species richness and abundance to increased disease transmissions. However, neither the influence of anthropogenic change on animal movement processes nor the resulting effects on ecosystems are well understood. Therefore, we need a coherent understanding of the causes and consequences of altered organismal movements and advocate suitable land-use management options to mitigate potential impacts on ecosystem functions.

In this thesis I aim at understanding the influence of anthropogenically caused land-use change on animal movement processes and their underlying mechanisms. In particular, I am interested in the synergistic influence of changes in large-scale landscape structure and fine-scale habitat features on basic-level movement behaviours (e.g. the daily amount of time spend running, foraging, and resting) and their emerging higher-level movements (e.g. home range formation). Based on my findings, I identify likely consequences of altered animal movements and recommend conservation measures for land-use management.

The study system of my thesis are European brown hares (*Lepus europaeus*) in agricultural landscapes. Hares are well-suited to study animal movements in agricultural landscapes, as they are hermerophiles and prefer open habitats. They have historically thrived in agricultural landscapes, but their numbers are in decline. The main reasons for this decline are changes in land-use patterns and agricultural intensification. Agricultural areas are severely impacted by land-use change and are the largest land-use class, covering 38% of the world’s terrestrial surface. To study the influence of land-use change on hare movement behaviour, I selected two differently structured agricultural landscapes: a complex landscape in Southern Germany with small fields and many landscape elements

(e.g. hedges and tree stands), and a simple landscape in Northern Germany with large fields and few landscape elements.

Hares were tracked with GPS devices (hourly fixes) and internal high-resolution accelerometers (4 min samples). Accelerometers provide an almost continuous observation of the animals' behaviours via acceleration analyses. The spatial and the behavioural information can be used to derive movement processes and mechanisms, which in combination with remote sensing data (normalized difference vegetation index, or NDVI, a proxy for resource availability) generate an almost complete idea of what the animal was doing when, why and where. Apart from landscape structure (represented by the two differently structured study areas), I specifically tested whether the following fine-scale habitat features influence animal movement behaviour: resource variability, agricultural management, habitat diversity, and habitat structure.

My results show that, irrespective of the movement process or mechanism and the type of fine-scale habitat features, landscape structure was the overarching variable influencing hare movement behaviour. High resource variability compels hares to enlarge their home ranges, but only in the simple and not in the complex landscape. Agricultural management events result in home range shifts in both landscapes, but hares additionally increase their home ranges in the simple landscape. Further, habitat selection for areas with low vegetation and against high vegetation was stronger in the simple landscape. High and dense standing crops restrict hare movements to very local and small habitat remnants. Hence, crop fields temporarily pose insuperable barriers and separate habitat patches that were previously connected by mobile links, disrupting the transport of nutrients and genetic material. This mechanism is also working on a global scale as human induced changes, from habitat loss and fragmentation to expanding monocultures, cause a reduction in animal movements worldwide.

The movement mechanisms behind those findings show that higher-level movements, like increasing home ranges, emerge from underlying basic-level movements, like daily behavioural modes (i.e. time spend running, foraging, resting). Increasing landscape simplicity first acts on the behavioural modes, i.e. hares run and forage more, but have less time to rest. Hence, the observed larger home ranges in the simple landscapes are based on an increased proportion of time running and foraging, largely due to longer travelling times between distant habitats and scarce resource items in the landscape. The relationship between behavioural modes and landscape structure was especially strong during the reproductive phase, demonstrating the importance of high-quality habitat for reproduction and the need to keep up self-maintenance first in low quality areas. These changes in movement behaviour may release a cascade of processes, starting with more time being allocated to running and foraging, which results into higher energy expenditure and lower individual fitness. Decreased individual fitness and reproductive output will ultimately affect population viability leading to local extinctions.

In conclusion, I show that landscape structure is one of the most important parameters affecting hare movement behaviour. Synergistic effects of landscape structure, and fine-scale habitat features, first affect and modify basic-level movement behaviours, which can scale up to alter higher-level movements and may even lead to the decline of species richness and abundances, thereby disrupting ecosystem functions. With regard to the paramount importance of landscape structure, I strongly recommend to decrease the size of agricultural fields and increase crop diversity. Conservation policies should also assure the year-round provision of areas with low vegetation and high-quality forage. This could be done by generating wildflower strips and additional (semi-) natural habitat patches. Implementing these measures will not only help to increase the populations of European brown hares and other farmland species, but also ensure and protect the continuity of mobile links and their intrinsic value for sustaining important ecosystem functions and services.

Zusammenfassung

Wenige biologische Prozesse haben unseren Planeten so stark geprägt wie die Bewegungen von Organismen. Individuelle Tierbewegungen haben weitreichende Auswirkungen auf ganze Populationen, Artengemeinschaften und Ökosysteme. Tierbewegungen sind außerdem verantwortlich für fundamentale Ökosystemfunktionen und –leistungen, wie z.B. die Verbreitung von Samen und die Bestäubung von Wild- und Nutzpflanzen. Doch globale, regionale und lokale Einflüsse durch den Menschen verändern die ursprünglichen Bewegungsmuster von Organismen. Insbesondere Landnutzungsänderungen stören die Tierbewegungen durch Habitatverlust und –fragmentierung. Dies kann schwerwiegende Folgen für Ökosystemfunktionen und –leistungen nach sich ziehen. Eine erhöhte Wahrscheinlichkeit der Krankheitsübertragung, der drastische Rückgang der Artenvielfalt und der damit einhergehende Verlust von Bestäubern sind nur einige der möglichen Folgen. Dennoch sind weder die Auswirkungen von Landnutzungsänderungen auf die Bewegungsabläufe von Tieren, noch deren Einfluss auf die Ökosysteme bis heute gut verstanden. Folglich benötigen wir ein ganzheitliches Verständnis der organismischen Bewegungsprozesse um die Auswirkungen veränderter Tierbewegungen analysieren und entsprechende Landnutzungsstrategien entwickeln zu können.

In meiner Doktorarbeit befasse ich mich daher mit dem Einfluss anthropogener Landnutzungsänderungen auf die Bewegungsprozesse und -mechanismen von Wildtieren. Im Speziellen untersuche ich die synergetischen Effekte großflächiger Landschaftsstrukturen und kleinflächiger Habitatmerkmale auf Bewegungsprozesse, wie z.B. die Entstehung von Streifgebieten, und auf die zugrundeliegenden täglichen Verhaltensweisen wie das Laufen, die Nahrungssuche und das Schlafen. Die hierbei gewonnen Erkenntnisse ermöglichen es mir, die voraussichtlichen Folgen veränderter Tierbewegungen auf Ökosysteme abzuleiten und Anregungen für nachhaltigere Landnutzungsstrategien zu empfehlen.

Als Modelsystem für meine Doktorarbeit benutze ich Feldhasen (*Lepus europaeus*) in Agrarlandschaften. Feldhasen eignen sich besonders gut zur Untersuchung von Tierbewegungen in landwirtschaftlich genutzten Gebieten, da sie Kulturfolger sind und offene Lebensräume, wie Agrarlandschaften und Steppen bevorzugen. Seit den 1960er

Jahren sind die Bestände in vielen europäischen Ländern jedoch stark zurückgegangen. Intensiven Landnutzungsänderungen in Agrarlandschaften stellen oft einen Grund für diesen Rückgang darstellen. Aufgrund des steigenden Nahrungsmittelbedarfs und der sich schnell entwickelnden Agrartechnologien stellen Agrarflächen mittlerweile das weltweit flächenmäßig größte Landnutzungssystem dar und bedecken 38% der Erdoberfläche. Um die Auswirkungen von Landnutzungsänderungen auf die Bewegungsprozesse von Feldhasen zu untersuchen, habe ich zwei unterschiedlich strukturierte Agrarlandschaften ausgewählt: eine relativ einfach strukturierte Landschaft in Norddeutschland, die sich v.a. durch große Feldern und wenige Landschaftselementen (z.B. Hecken und kleinere Baumbestände) auszeichnet und eine komplexere Landschaft in Süddeutschland, die durch kleinere Felder und vielen dieser Landschaftselementen charakterisiert ist.

Mit Hilfe von GPS-Halsbändern, die mit internen hochauflösenden Beschleunigungssensoren ausgestattet sind, wurden die Bewegungen der Feldhasen aufgezeichnet. Die Beschleunigungssensoren liefern nahezu kontinuierliche Daten, die mit Hilfe von statistischen Klassifikationsverfahren das Verhalten der Tiere wiedergeben können. Aus den räumlichen GPS-Daten und der Informationen über die Verhaltensweisen der Tiere lassen sich Bewegungsprozesse und –mechanismen ableiten, die ich dann im Zusammenhang mit der Landschaftsstruktur (dargestellt durch die beiden unterschiedlich strukturierten Untersuchungsgebiete) und den folgenden kleinflächigen Habitatmerkmale betrachte: raumzeitliche Variabilität in der Ressourcenverfügbarkeit, landwirtschaftliche Managementmaßnahmen, Habitatdiversität und Habitatstruktur.

Die Ergebnisse meiner Forschungsarbeit zeigen, dass unabhängig vom Bewegungsprozess oder -mechanismus und der Art der Habitatmerkmale, die Landschaftsstruktur die Bewegungen der Feldhasen am stärksten beeinflusst. Eine hohe Ressourcenvariabilität bringt die Feldhasen dazu, ihre Streifgebiete zu vergrößern, jedoch nur in der einfachen und nicht in der komplexen Landschaft. Landwirtschaftliche Managementmaßnahmen führen zu einer Verschiebung der Streifgebiete in beiden Landschaftstypen. In der einfachen Landschaft jedoch, vergrößern die Tiere zusätzlich ihre Streifgebiete. Feldhasen bevorzugen niedrige und vermeiden hohe Vegetation. Im Vergleich zur komplexen Landschaft ist diese Art der Habitatselektion stärker in der einfachen Landschaft ausgeprägt. Hohe und dichte Feldfrüchte, wie z.B. Raps oder Weizen, beschränken die Bewegungen der Feldhasen vorübergehend auf kleinere, lokale Gebiete. So werden Felder zu unüberwindbaren

Barrieren und trennen Habitate voneinander, die vorher durch sogenannte „mobile links“ miteinander verbunden waren. „Mobile links“ transportieren z.B. Nährstoffe oder genetisches Material zwischen entfernten Habitaten. Durch die Trennung, wird dieser Transport vorübergehend unterbrochen und stört somit die Funktionstüchtigkeit des Ökosystems. Diese Reduktion von „mobile links“, durch anthropogen verursachte Landnutzungsänderungen und die damit einhergehenden Einschränkungen von Tierbewegungen, ist weltweit vorzufinden.

Die Resultate meiner Untersuchungen zeigen zudem, dass Bewegungsprozesse, wie z.B. die Vergrößerung der Streifgebiete, durch die zugrundeliegenden Verhaltensweisen ausgelöst werden. Eine zunehmende Vereinfachung von Landschaftsstrukturen wirkt sich zunächst auf die täglichen Verhaltensweisen aus, d.h. Feldhasen haben weniger Ruhezeit, da sie mehr laufen und sich häufiger auf die Suche nach Nahrung und anderen Ressourcen begeben. Dies führt zur Vergrößerung der Streifgebiete in einfach strukturierten Landschaften. Zusätzlich zeigen meine Untersuchungen, dass die Beziehung zwischen den Verhaltensweisen und der Landschaftsstruktur während der Fortpflanzungsphase besonders stark ausgeprägt ist. Ein qualitativ hochwertiger Lebensraum ist also während der Fortpflanzungsphase besonders wichtig, da Tiere in Gebieten mit geringer Habitatqualität sich erst um das eigene tägliche Überleben kümmern müssen und somit weniger Zeit in die Fortpflanzung investieren können. Ein erhöhter Anteil an Laufen und Futtersuche, bedeutet gleichzeitig eine Steigerung des Energieaufwands. Wenn Tiere viel Energie aufwenden müssen, um das eigene tägliche Überleben zu sichern, kann dies einen Rückgang ihrer individuellen Fitness bedeuten. Die Abnahme der Fitness und der Reproduktionsleistung wird sich letztendlich auf die Überlebensfähigkeit der Population auswirken und kann zum lokalen Aussterben führen.

Die Struktur der Agrarlandschaft stellt eine der wichtigsten Einflussgrößen für das Bewegungsverhalten von Feldhasen dar. Die synergistischen Effekte der großflächigen Landschaftsstruktur und der kleinflächigen Habitatmerkmale beeinflussen und modifizieren zunächst die täglichen Verhaltensweisen, die dann wiederum zu veränderten Bewegungsprozessen führen und damit zu Störungen der Ökosystemfunktionen und zum Rückgang der biologischen Vielfalt beitragen. Daher empfehle ich dringend die Größe der landwirtschaftlichen Felder zu verringern und die Vielfalt der Anbaukulturen zu erhöhen. Zusätzliche kleinräumige Naturerhaltungsmaßnahmen können ganzjährig Habitate mit geringer Vegetationshöhe und hochwertigem Futter bereitstellen. Dies kann durch den Anbau von Blühstreifen und der Schaffung bzw. dem Erhalt von (halb-)natürlicher Lebensräume erreicht werden. Diese Maßnahmen werden nicht nur dazu beitragen, die Populationen der Feldhasen und anderer Kulturfolger zu vergrößern, sondern helfen auch dabei das Fortbestehen der „mobile links“ und der damit verbundenen Ökosystemfunktionen und –leistungen zu gewährleisten und zu schützen.

General Introduction

Motivation and background

Movement is an elementary characteristic of life. That means it is present in all living organisms, from the smallest microbes over plants to the largest mammals (Nathan et al. 2008). Many bacteria have flagella which they use to actively move with. Plants move via seed dispersal or are passively transported by wind, water or other organisms. Animals however, have the broadest motion spectrum. The most impressive movements are probably long distant migrations of large wildebeest herds or thousands of birds that cross the entire globe. On smaller, daily scales, animals disperse, search for resources or mates or move to avoid predators. The famous example by Ripple and Beschta (2004) demonstrates the strong impact of daily animal movements on an entire ecosystem, as elk, in the presence of wolves, stop feeding in open habitats, which eventually results in natural restoration of wetlands and streams. Thus movement shapes populations, communities and ecosystems (Swingland and Greenwood 1983, Ripple et al. 2001), and it is a driver for biodiversity and evolution (Levey et al. 2002, Jeltsch et al. 2013). For example, the coevolution of flowering plants and pollinators is completely based on movement – no movement no pollination (Proctor et al. 1996), as is the evolutionary arms race in predator-prey systems (Hilborn et al. 2012). Also, biodiversity is affected/ maintained by organismal movements that connect isolated habitats and inherently transport new genetic material and resources. The mobile link concept by (Lundberg and Moberg 2003) distinguishes such movements into resource links, genetic links and process links. While resource linkers mainly transport nutrients and genetic linkers transport new genetic material, process linkers like grazers or ecosystem engineers influence local communities by their actions and then wander off to new grounds which are being influenced by them. Movements also play a crucial role in coexistence theory when e.g. intra- and interspecific interactions, where weaker competitors actively avoid stronger competitors, may enhance species coexistence (sensu Chesson 2000). The two main movement concepts in coexistence theory are stabilizing and equalizing mechanisms, where stabilizing mechanisms increase negative intraspecific interactions as compared to interspecific interactions and equalizing mechanisms reduce fitness differences between different species (Chesson 2000).

The observed and predicted anthropogenic impacts significantly change movements of organisms worldwide. The increased human footprint, for example, decreases animal movements by about half of what they would be in pristine areas (Tucker et al. 2018). Often, movements are not only decreased but even impeded, for example under habitat loss and fragmentation (e.g. Bonte et al. 2006, Sawyer et al. 2013). Restricted or impeded animal movements disrupt ecosystem functions, like dispersal, food networks, metapopulations and diseases dynamics (Kremen et al. 2007, Bauer and Hoye 2014, Tucker et al. 2018). We are just beginning to understand the consequences of disrupted ecosystem functions, but they can be severe for all organisms – including human beings (Allan et al. 2003). One key challenge of ecologists is to improve our understanding of how anthropogenic global change impacts movement processes, their underlying mechanisms and what these changes mean at ecosystem level. Only then, we can assure suitable conservation management, appropriate restoration measures as well as disease and pest control (Nathan et al. 2008).

Studying movement processes and their underlying mechanisms, requires to obtain information about the organisms' location, the environment they strive in at any given time and specific methods and concepts to unify the obtained information. Recent advances in biotelemetry and remote sensing make it possible to access unprecedented spatiotemporal information about the animals' locations and the environment at the time of relocation (Pettorelli et al. 2014, Kays et al. 2015).

Technological progress in **biotelemetry** over the last two decades has helped to a great extent to shed light on the processes and mechanisms of organismal movement, which historically have been difficult to observe, because of small sizes, elusiveness or speed of many animals (Kays et al. 2015). Current GPS tracking devices and data logger are powered by solar panels or ever smaller batteries with a longer life-time, which allows for tracking even very small animals and insects (Bridge et al. 2011, Kissling et al. 2014). Smart reverse GPS technology makes it even possible to track animals in real-time and at very high frequencies, e.g. 1 Hz (Minerva Center for Movement Ecology 2014). Many of these new technologies enable simultaneous tracking of various individuals, of the same or of multiple species, at the same time in the same area. These new tracking technologies generate unique and big data sets that allow for a whole new set of insights into animal coexistence and movement ecology (Kays et al. 2015). Furthermore, biologging devices like animal mounted cameras, heartbeat sensors and tri-axial accelerometers provide a new set of detailed information about the animal’s surroundings, state and movements respectively (Rutz and Hays 2009). The tri-axial accelerometers are especially useful to study animal movement, as they continuously sample information about the animals motions which can then be translated into the actual behaviour the animal conducts and the energy it spends during each behaviour (Nathan et al. 2012, Scharf et al. 2016). The next step is to associate the animals’ behaviour and emergent spatiotemporal movement patterns like home ranges and habitat selection to underlying environmental information.

Satellite based **remote sensing** technologies can be used to gain global, long-term data sets to monitor biodiversity and anthropogenic impacts, which then can be correlated to animal movements (Handcock et al. 2009, Ewald et al. 2014, Duncan et al. 2015). Global land cover maps produced by satellites, such as Landsat or Sentinel provide almost complete small scale spatial information on environmental variables (Strand 2007, Pettorelli et al. 2014). Also the bi-weekly temporal resolution of these maps allows to relate fine scale movements at home range scale but also long-term animal migration patterns to spatiotemporal changes in environmental properties (Mueller et al. 2011, van Moorter et al. 2013, Teitelbaum et al. 2015). The predominantly used satellite derived environmental information is the normalized difference vegetation index (NDVI). The NDVI measures the greenness of the vegetation, which can function as a proxy for resource availability and plant phenology (Pettorelli et al. 2005) and thus be used to study, e.g. habitat selection, home range size and breeding phenology (Herfindal et al. 2005, Loe et al. 2005, Hansen et al. 2009).

Obtaining biotelemetry and remote sensing is becoming more sophisticated with technological advancement and the spatial and temporal scales are becoming smaller and smaller. New methods for analysing these data are currently being developed (e.g. Fleming et al. 2015, Kranstauber et al. 2017). However, obtaining and analysing the data are just the first steps, setting the findings into a coherent picture is the subsequent task, which can be accomplished by using the concepts and frameworks in the newly emerging research field of movement ecology (Nathan et al. 2008).

The movement ecology framework

The movement ecology framework describes how external factors act on the fundamental movement mechanisms, which are translated into movement processes and subsequent ecological consequences (Nathan et al. 2008). External factors are all kinds of influences from outside the organism that cause movement. These can be biotic, e.g. the approach of a conspecific or a predator, or abiotic, e.g. changing weather conditions or anthropogenic influences like land-use change. The external factors then act on the fundamental movement components: the internal state (Why to move?), the navigation capacity (Where to move?) and the motion capacity (How to move?) resulting in the movement path (Fig. I1). A simple example can be made by looking at frugivorous birds reacting to the fragmentation of forest remnants (Howe and Miriti 2004). The external factor in this case is the sudden fragmentation and removal of the bird's habitat, which causes a change in the bird's internal state – the animal is disturbed and moves away from the disturbance and the potential threat it poses. The navigation capacity results in moving towards a new habitat that can substitute the loss of the old habitat. The motion capacity would be translated into a fast flight towards a new, less fragmented forest. The resulting movement path is just a small part in the bird's lifetime track from birth to death. The different spatiotemporal scales of movement – a snapshot of fleeing from a threat versus long-term location data – are the link between movement mechanisms and processes. The smallest spatial and temporal scales show behavioural modes that are conducted by the

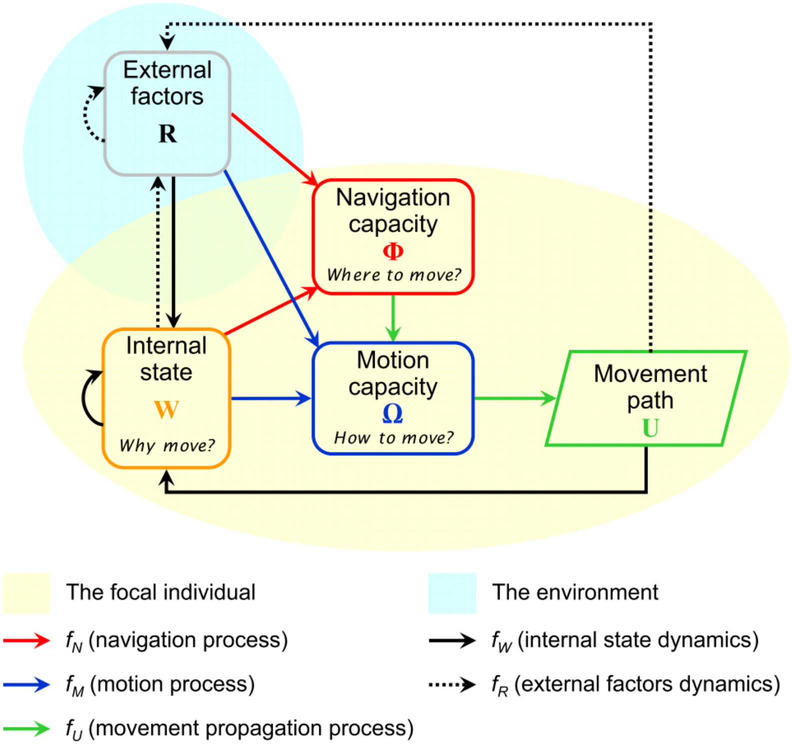

Figure I1: The basic components of the movement ecology framework consist of the internal state, the navigation capacity and the motion capacity of the focal individual, as well as of external factors situated in the environment. Those four basic components lead to the emergent movement path of the animal. This graph was taken from the original paper by Nathan et al. (2008).

animals at a given moment in time, e.g. resting, grooming, foraging and flying or running – these are the basic-level movements. On slightly larger spatiotemporal scales, a conjunction of subsequent behavioural modes, lead to movement phases, like the entire movement of fleeing from a threat or searching for new habitat. Putting together subsequent movement phases results in spatiotemporal movement patters, which are analysable as e.g. dispersal distance, habitat selection, home range size or home range shift. These spatiotemporal movement patterns are higher-level movement processes, as they have emerged from the basic-level movement behaviours. External factors operate first on the basic-level movements, like habitat fragmentation might increase the amount of flying (Bruun and Smith 2003) and then scales up to higher-level movement processes like an increased home range size. The higher-level movement processes might then determine whether species persist or perish in the altered environment, as increased home range sizes in low diverse habitats (Schai-Braun and Hackländer 2014, Ullmann et al. 2018) can increase energy expenditure (Mace and Harvey 1983) and subsequently result in local extinction (Daan et al. 1996). Local extinctions have been frequently observed in strongly human-dominated habitats like agricultural landscapes, where they are the usual consequence of agricultural intensification and habitat loss (Benton et al. 2003, Reidsma et al. 2006). Therefore, agricultural landscapes provide the ideal setting to study the influence of anthropogenically changed external factors on the movement behaviour of animals.

Agricultural landscapes

Until today 38% of Earth's surface has been converted into agricultural landscapes. The future demand for food of the rising human population will further increase the area needed for crop production (Foley et al. 2011). In Europe, agricultural landscapes already pose with 45%, the largest land-use class, resulting in one of the most intensively used agricultural regions worldwide (Ramankutty et al. 2008). Because they are so widely spread, most wildlife in Europe is forced to move across or use agricultural landscapes. Animals are then confronted with spatially and temporally variable habitats and matrix areas with an ever-increasing degree of agricultural intensification. Agricultural intensification usually leads to decreased landscape diversity due to habitat loss and the homogenization of the agricultural matrix. Both of these features (spatiotemporal dynamics and changes in landscape diversity) are the two crucial external factors influencing animal movement behaviour in dynamic agricultural landscapes.

The **spatiotemporal dynamics** of agricultural landscapes emerge from the spatial distribution (configuration and composition) of crop fields in the landscape and from temporally occurring agricultural management. Management activities can be distinguished into two different types: 1) management events creating a sudden change of resources after harvesting and mowing, and 2) management events without the change of resources (e.g. ploughing or the application of fertilizers). Within an agricultural year, management events with resource changes cause the sudden, unforeseeable and often synchronous removal of food and cover across multiple crop fields. Between years, the entire landscape mosaic changes due to the crop rotation system. However, as crop diversity declines and more fields harbour the same crop type, harvests happen more and more in sync and often over the time span of only a few hours. These temporal dynamics in agricultural landscapes have largely been neglected in landscape ecology (Vasseur et al. 2013), as well as in animal ecology (Mueller et al. 2011). Further, agricultural management events *per se* can directly influence animal movement behaviour, as agricultural machinery might scare animals. Indeed, approaching tractors for example increased roe deer displacement (Padié et al. 2015), and home ranges were shifted away from ploughed fields (Cimino and Lovari 2003). Whether animals find new resources after management events with resource change or shelter when fleeing from agricultural machinery depends largely on the landscape diversity and therewith the different kinds of habitats the landscape has to offer.

Landscape diversity is the second external factor influencing animal movement behaviour in agricultural landscape. Existing agricultural landscapes have been subject to significant intensification over the past decades, often entailing habitat fragmentation, increasing field sizes, and reductions in crop diversity. This leads to an overall decrease in landscape diversity (Tscharntke et al. 2005). The loss of agricultural landscape diversity commonly leads to a decline in species richness and abundance (Pimm and Raven 2000, Benton et al. 2003). The extent to which species are lost depends on the remaining decgree of landscape diversity and on the landscape structure (Dauber et al. 2003, Batáry et al. 2017). Simply structured landscapes, with large crop fields and a small number of landscape elements (fallow land, hedge rows, tree stands) result in few and distance habitat remnants surrounded by a vast agricultural matrix. These simple landscapes harbour fewer species than more complex agricultural landscapes with small crop fields and a larger number of landscape elements.

The model system: Hares in Agricultural landscapes

European hares are typical representatives of agricultural landscapes. They pose the perfect model organisms to study animal movement behaviour in dynamic agricultural landscapes. Hares prefer an open and structured habitat with diverse crops (Tapper and Barnes 1986, Lewandoski and Nowakowski 1993). Hare populations have been in decline throughout Europe over the last 5 decades, despite the large quantity of agricultural landscapes in Europe (Smith et al. 2005). In some areas they are close to local extinction and thus are listed as “near threatened” or “threatened” in the Red List of Threatened Species in a number of European countries (Reichlin et al. 2006). In Germany European hares are classified as “vulnerable” in the Red List (Bundesamt für Naturschutz 2009). Agricultural intensification and the correlated decrease in landscape diversity are most likely the main reasons for the population decline (Smith et al. 2005).

European hares are diurnal, foraging at night and rest during the daylight hours. They live exclusively above ground and hence have to look for suitable resting sites and spend more energy in thermoregulation, growth and parental care compared to mammals with dens or nesting sites (Schai-Braun et al. 2015). The breeding season starts as early as January, peaks between April and June and ends around September (Frylestam 1980). The social behaviour during the breeding season is characterized by males competing for oestrous females, by chasing weaker competitors away from the female (Holley 1986, Alves et al. 2008). Females visit their well-hidden offspring once per day for lactation (Broekhuizen and Maaskamp 1980).

For my thesis I selected two contrasting agricultural landscapes in Germany that differed considerably in landscape structure. The study area in northwest Germany is characterized by large monocultures (hereafter referred to as simple landscape), while the area in south German is dominated by small crop fields and thus represents a complex landscape structure (Fig. I2). I chose these two study areas to represent land-use change from finely structured to simple landscapes. Increased economic efficiency for farmers fosters this type of land-use change in many areas (Chartin et al. 2013, Batáry et al. 2017). In the simple landscape animals have to cross large agricultural matrix areas to reach distant – but important – habitat patches. The differences in field sizes and agricultural matrix areas are demonstrated in Figure I2, which shows satellite images of the two study areas. The same figure (Fig. I2) occures in the material and methods part of chapter 1-3, it will be only displayed here – and not again in the chapters themselves – to avoid repetitions.

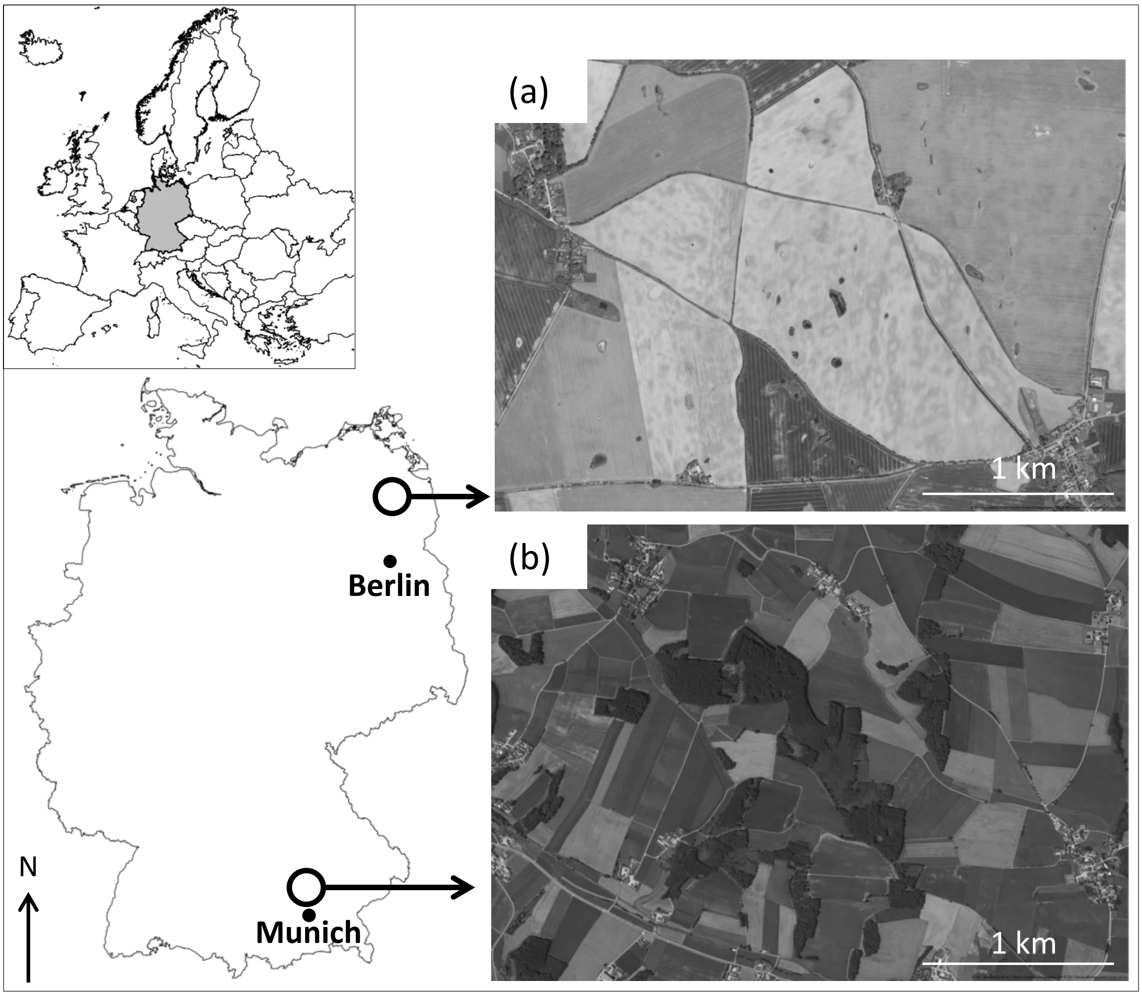

Figure I2. The map depicts the location of Germany in Europe (upper left panel) and the study areas in northeast Germany and south Germany (GADM http://gadm.org/). The satellite images (Google maps 2017) show representative extracts of (a) the simple landscape in North-east Germany and (b) the complex landscape in South Germany. Both landscape representations have the same scale (1:12000).

Objectives

In an increasingly human-dominated world animals have to adapt to substantial environmental changes within their habitats. Movement is the key process they can apply in order to deal with these changes. An understanding of how movement processes and their underlying mechanisms are used to interact with the environmental changes contributes to the mechanistic comprehension of biodiversity research, gives a notion of a specie's probability to persist in a given landscape diversity and will help to improve conservation strategies. My approach to gain a mechanistic understanding of how environmental changes influence movement behaviour is two-fold. First, in accordance with the movement ecology framework (Nathan et al. 2008) I aim at understanding the emergence of higher-level movement behaviour like home range formation from underlying basic-level behavioural modes. Second, I investigate those different movement levels at different spatial scales. The largest scale would be the landscape structure, followed by the medium scale habitat diversity, and the small scale of vegetation type and height, which eventually results into specific patterns of resource variability caused by the smallest dynamic scale: agricultural management, with differences of when and what is harvested, ploughed and fertilized.

Structure of the thesis

External factors affect animal movement behaviour on multiple levels, eventually leading to local persistence or extinctions. The most basic level constitutes of behavioural modes like resting, running and foraging. Behavioural modes result into higher-level movement behaviour like home range size and shift, energy expenditure or habitat selection. In this thesis I investigate the influence of external factors (i.e. different landscape features: landscape structure, spatiotemporal resource variability, agricultural management and landscape diversity) on the different levels of movement behaviour.

The thesis is structured into four chapters that are independently readable research papers written in the first-person plural as they are co-authored. Therefore, I will use the first-person plural to describe which part of the thesis is covered by each of the chapters. I am the lead author in chapter 1 to 3 and was predominantly responsible for the study design, the field work, the data collection, the analyses and the writing. In chapter 4 I am a co-author and collected a large proportion of the data set and helped to edit the paper.

In **chapter 1** we analyse the influence of spatiotemporal resource variability on higher-level movement behaviour – home range size. We especially focus on whether the movement reaction depends on the underlying landscape structure (simple versus complex). We assumed that the higher the resource variability the more unpredictable a landscape becomes. This can be a problem in simple landscapes, as the animal has to search for new foraging grounds leading to increased home ranges, while complex landscapes might pose enough alternative resource-rich habitat patches to overcome the unpredictability problem. Hence, we hypothesize that animals in structurally simple landscapes will have to increase their home range size with increasing resource variability. To test this hypothesis, we combine GPS tracking information and satellite derived environmental information on vegetation greenness (NDVI) as a proxy for resource variability.

In **chapter 2** we aim at understanding the underlying causes for the observed spatiotemporal resource variability identified in chapter one and investigate the influence of agricultural management events on higher-level movement behaviours. We explicitly considered the two different types of agricultural management events 1) with the sudden change of resources (harvest and mowing) and 2) without resource changes (e.g. the application of fertilizers or pesticides). In the first type of management events, the quick harvest of crop fields suddenly changes the availability of formerly known resources in large parts of an animal's home range, which are predominantly responsible for the observed resource variability in chapter one. In chapter 2, we looked at short-term changes in higher-level movement behaviours and record home range shift, home range size and energy expenditure for 4 days before and after both types of management events. For management events with resource changes, we predict an increase in home range size or shift to incorporate the recently harvested fields, which are used to forage for fallen grains or corn stalks. For management events without resource changes, we predict that hares flee from agricultural machinery and exclude fields that are recently disturbed. Additionally, we test whether the movement reaction to agricultural management events differed between simple and complex landscapes, as we expected to find a larger set of movement reactions in the simple landscape as was shown in chapter one.

In **chapter 3** we investigate whether the changes in higher-level movement behaviours identified in chapter 1 and 2 (i.e. home range size, home range shift and energy expenditure) emerge from specific basic-level movement behaviours (i.e. running, resting and foraging). In chapter 1 and 2 we show that simple landscapes promote larger home range sizes. In chapter 3 we test how landscape diversity first affects basic-level movement behaviours, which then scales up to higher-level movement behaviours. Using tri-axial accelerometers to continuously sample information about the hares' movement behaviours and applying random forests allows us to classify the corresponding behaviours into five categories (resting, foraging, moving, grooming and standing upright). We predict that habitats of low diversity will force hares to run and forage more, while they have less time to rest in comparison to animals in diverse habitats. The larger amount of running and foraging is likely be caused by longer travelling distances between habitat patches and scarce resources, respectively, in low diverse habitats. We suggest that these behaviours translate into larger home ranges, as seen in chapter 1 and 2.

In **chapter 4** that I co-authored, we focus on the effect of small-scale landscape features (vegetation height, vegetation type and field size) on higher-level movement behaviour (i.e. habitat selection). Looking at field size from a habitat selection point of view completes the picture we gain on home range formation and field size in chapter one. In chapter 4 we aim at demonstrating the importance of synergistic effects between fine-scale habitat features and field size as a surrogate for landscape structure. We hypothesize that hares select their habitat according to vegetation height and vegetation type, and that the importance of those two variables depends on field size.

In the **general discussion** I synthesize the findings of the four chapters to bring them into a general context and explain how they contribute to the scientific progress in movement ecology. I will also provide recommendations for conservation measures to increase hare and other farmlands animal populations. Further, I highlight future perspectives for and consequences of changes in animal movements, focussing on the importance of animal movements for ecosystem functions and therefore explain the integration of movement ecology and biodiversity research, which would help to assure ecosystem functioning. Finally, I will provide an outlook on the generation of deeper ecological insights through technological advancements in telemetry and remote sensing.

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Chapter 1

Spatiotemporal variability in resources affect herbivore home range formation in structurally contrasting and unpredictable agricultural landscapes[1]

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Abstract

Context Movement is one of the key mechanisms for animals to deal with changes within their habitats. Therefore, resource variability can impact animals' home range formation, especially in spatially and temporally highly dynamic landscapes, such as farmland. However, the movement response to resource variability might depend on the underlying landscape structure.

Objectives We investigated whether a given landscape structure affects the level of home range size adaptation in response to resource variability. We tested whether increasing resource variability forces herbivorous mammals to increase their home ranges.

Methods In 2014 and 2015 we collared 40 European brown hares (*Lepus europaeus*) with GPS-tags to record hare movements in two regions in Germany with differing landscape structures. We examined hare home range sizes in relation to resource availability and variability by using the normalized difference vegetation index (NDVI) as a proxy.

Results Hares in simple landscapes showed increasing home range sizes with increasing resource variability, whereas hares in complex landscapes did not enlarge their home range.

Conclusions Animals in complex landscapes have the possibility to include various landscape elements within their home ranges and are more resilient against resource variability. But animals in simple landscapes with few elements experience shortcomings when resource variability becomes high. The increase in home range size, the movement related increase in energy expenditure, and a decrease in hare abundances can have severe implications for conservation of mammals in anthropogenic landscapes. Hence, conservation management could benefit from a better knowledge about fine-scaled effects of resource variability on movement behaviour.

Introduction

Movement is one of the main processes for organisms to deal with spatiotemporal changes in the availability of key resources, such as food, shelter or nest sites. The spatiotemporal availability of resources (hereafter: resource variability) includes the given spatial variability of resources in a landscape (determined by spatial heterogeneity and landscape structure) and the temporal variability of resources within a landscape (see below for details). From an animal's perspective the predictability of where and when resources are available adds a third level affecting movement behaviour. Large scale movement types might have evolved as a result of underlying resource variability and unpredictability, where low spatial variability favours a sedentary life style, while seasonal variability results in migration, and unpredictable habitats tend to foster nomadism (Mueller and Fagan 2008; Mueller et al. 2011). Hence, resource variability on large spatiotemporal scales affects long-distance movements, but fast and short-term environmental changes result in short movements on a small spatial scale (van Moorter et al. 2013). For example, during foraging, animal movements are influenced by the spatial and temporal availability of resources and their predictability in space and time. However, it remains largely unclear, if and how resource availability and particularly its spatiotemporal variability influence animal movements at scales relevant for daily movement decisions within home ranges and whether that influence persists in differently structured landscapes with unpredictable resource availability. This is particularly important given the large extent of unpredictable landscapes such as agricultural landscapes, where resources availability changes abruptly and unforeseeably in short time periods. Therefore, we studied combined effects of resource availability and variability on herbivore home range size in two differently structured agricultural landscapes.

In a spatial context high habitat heterogeneity and with that high resource availability leads to smaller home range sizes (Smith et al. 2004; Anderson et al. 2005; Saïd and Servanty 2005), and higher individual abundances (Johnson et al. 2002; Smith et al. 2005; Fischer and Schröder 2014). In addition to different types of habitat, the spatial distribution and availability of specific resources affect animals' space use. The resource dispersion hypothesis (RDH) states that home ranges are smaller when food resources are locally abundant, such as in complex landscapes, and larger when resources are spatially dispersed, such as in simple landscapes (MacDonald 1983). This hypothesis was found true for carnivore species, omnivore species, ungulates and ground birds (e.g. Johnson et al. 2002, Relyea et al. 2000, Mortelliti and Boitani 2008; Hansen et al. 2009, Marable et al. 2012). The more different kinds of key resources such as food and shelter are available in a small space and the more abundant those resources are, the less an animal has to travel to cover its requirements and thus saves energy that can be used e.g. for reproduction (Harestad and Bunnel 1979; Swihart 1986; Saïd et al. 2009). Therefore, home ranges should be smaller in complex landscapes as the possibility of finding all requirements satiated in a small space is higher than in simple landscapes.

In a temporal context, animal movements may vary over seasons in concert with seasonal changes in resource availability. Home ranges increase in low productive habitats with high seasonality, e.g. during resource poor conditions like in winter, home ranges are often larger than in summer (Smith et al. 2004, Saïd et al. 2009). Assuming that a large proportion of habitat becomes suddenly unsuitable (e.g. in agricultural landscapes during the synchronous harvest of various fields) the remaining habitat patches might not provide enough resources to satiate the inhabitant (Johnson et al. 2002). Hence, given that spatiotemporal resource variability is high, animals move larger distances or switch more frequently between patches (Mcloughlin et al. 2000; Mueller and Fagan 2008). Furthermore, the predictability of resources in space and time can have an influence on home range size as well (Mueller and Fagan 2008; Jonzén et al. 2011). In brown bears and many carnivore species home range sizes increase with higher degrees of unpredictability in resource availability (Mcloughlin et al. 2000; Duncan et al. 2015).

Agricultural landscapes provide an excellent model system to investigate the effects of resource variability and predictability on animal home range behaviour, as they are highly dynamic at small spatial and short temporal scales. The distribution of arable fields with different crops and other landscape elements results in spatially heterogeneous landscape mosaics consisting of a variety of crop fields, (semi-)natural areas, settlements and infrastructure. The temporal dynamics in agricultural landscapes arise from changes in resource availability caused by vegetation growth, crop rotation and agricultural management, such as sowing, weed control, and harvesting. The temporal aspect of underlying crop and vegetation dynamics has often been neglected in landscape ecology (Vasseur et al. 2013), as well as in animal ecology (Mueller et al. 2011). The habitat within agricultural landscapes changes rapidly over the course of a year as well as between years. These sudden changes in resources can occur within a few hours on a spatial scale of hundreds of hectares, due to modern highly efficient agricultural machinery creating an unpredictable and highly variable environment for animals. This unpredictability in agricultural landscapes, which includes the sudden removal of large proportions of biomass is particularly challenging compared to (semi-)natural landscapes, where resource availability and distribution follow the natural changes from growing to ripe plant material, senescence and withered standing plants until the next vegetation period begins.

The degree to which resource variability and unpredictability might be important for home range formation may also depend on the landscape structure, where complex landscapes might provide better habitats and more resources than simple landscapes. A complex landscape has many different elements and supplies a variety of resources for animals. In consequence, unpredictability and variability seem less important for animals in those complex landscapes as individuals can easily switch between habitat patches. In a structurally simple landscape that consists of few landscape elements, animals might have to cross longer distances to find shelter, forage or mating partners.

Longer movement distances or larger home ranges might force animals to allocate energy first into self-maintenance and just secondarily into reproduction, which in the long run will lead to lower individual fitness (Daan et al. 1996). A persisting decrease in individual fitness and reproductive output will first affect population size and might eventually lead to local extinction. An example of affected population sizes can be found in Germany, where European brown hare (*Lepus europaeus*) populations are very small and decreasing in North-east Germany, while population sizes are large and stable in the rest of the country (Strauß et al. 2008). North-east Germany consists of large crop fields and a structurally simple landscape, while South Germany is comprised of small fields and a more complex landscape structure including many different landscape elements.

To study the impact of landscape complexity and the spatiotemporal availability and variability of key resources on space use of an herbivorous mammal, we selected the European brown hare in agricultural landscapes as model system. Hares were studied in a simple landscape with large fields in North-east Germany and a complex landscape with small fields in South Germany. Hares were collared with high resolution GPS tags (hourly GPS fixes) to calculate 10-day home range sizes. For each home range, the mean and standard deviation of the normalized difference vegetation index (NDVI) was calculated as proxies for resource availability and variability respectively. The NDVI measures within each home range were calculated repeatedly over time. This allowed us to estimate resource variability as the spatial distribution of resources in each home range and also as the temporal change of the spatial distribution in time.

We hypothesize that increasing resource variability and unpredictability forces European brown hares as a characteristic herbivorous mammal to increase their home range size. We predict that hares in simple landscapes would have to increase their home ranges when environmental variability was high, while hares in complex landscapes do not need to adjust home range size to resource variability.

Material and Methods

Study area

We selected two study areas which strongly differed in landscape structure (Fig. I2). The study area representing the complex landscape is located in South Germany, Bavaria, around 50 km north of Munich (centred at 48° 48′ N; 11° 86′ E). The 256 km² study area is characterized by small-scale agriculture with an average field size of 2.9 ± 0.04 ha (mean ± SE; calculated based on maps provided by the Bayerische Vermessungsverwaltung 2014) and a high amount of field edges (Batáry et al. 2017). The complex landscape includes a variety of landscape elements like hedgerows, tree stands and fallow land. Arable land covers 66% of the study area and the main land use types are maize, cereals and grassland (Bayerisches Landesamt für Statistik und Datenverarbeitung 2016). The study area representing the simple landscape is located in North-east Germany, Brandenburg, around 100 km north of Berlin (centred at 53° 35′ N; 13° 68′ E) within the catchment of the river "Quillow" and the long-term research platform *AgroScapeLab Quillow* (Agricultural Landscape Laboratory Quillow) of the Leibniz Centre for Agricultural Landscape Research (ZALF) and the Biomove research training group www.biomove.org/about-biomove/study_area/). The 213 km² area is characterized by large-scale agriculture with an average field size 27.5 ± 1.1 ha (mean ± SE; calculated based on maps provided by the Landesvermessung und Geobasisinformation Brandenburg (InVeKoS 2014)) and a low amount of field edges (Batáry et al. 2017). In North-east Germany the landscape includes only few (semi-) natural landscape elements. The area is covered up to 62% by arable land which mainly consists of cereals, maize and oil seed rape (Landesvermessung und Geobasisinformation Brandenburg (InVeKoS 2014)).

Model organism and GPS tracking

European brown hares (*Lepus europaeus*) present the ideal model organism to test whether home range sizes increase with increasing resource variability in agricultural landscapes. Hares are adapted to open areas and spend a large portion of their life on agricultural fields (Tapper and Barnes 1986; Lewandoski and Nowakowski 1993; Smith et al. 2005). They are therefore frequently in contact with the highly dynamic resource changes of agricultural landscapes. We equipped 40 adult hares with GPS collars in spring 2014 and 2015 simultaneously in both study areas (for detailed information and deployment times see appendix A1).

Hares were driven into woollen nets, then weighed, sexed and collared according to Rühe and Hohmann (2004). The 69 g collars (Model A1, e-obs GmbH, Munich – Germany, www.e-obs.de) consisted of a GPS unit and an acceleration sensor, which provides the possibility to use acceleration informed GPS duty cycles. During active periods GPS fixes were taken every full hour, during inactive periods GPS fixes were recorded every four hours. Inactivity was determined automatically by the acceleration sensor when three consecutive acceleration samples did not surpass a variance threshold of 700 (e-obs raw values without unit). All tracking data were stored at www.movebank.org (Wikelski and Kays 2016).

Home Range Size

Home ranges were calculated after accounting for locations that were produced by the acceleration informed duty cycle. Those locations where assumed to be the same as the last recorded location. The R package *adehabitatHR* (Calenge 2006) was used to calculate 10-day home ranges based on kernel utilization distributions (Worton 1989). The bandwidth was estimated with the h_{ref} optimization method by using the default settings for kernel density estimation. The time span of 10 days was used to track the reaction of hare space use behaviour to changes in resource availability, to be able to compare home ranges across individuals and time and to correct for differences in sample size. The 95% kernel utilization distributions were calculated to receive an estimate of the animals' space use excluding long distant excursions that would cover areas that were not actually used by the animal in its daily movement patterns (Burt 1943).

Resource variability

We used the spatial and the temporal variability of resource availability to account for resource variability, where the spatial variability of resources was measured repeatedly over time to explicitly consider the temporal aspect of resource variability. We used variables derived from the normalized difference vegetation index (NDVI) to approximate for potential resource availability and variability in space and time. The NDVI is a measurement for vegetation greenness and represents chlorophyll concentration, i.e. plant productivity (Pettorelli et al. 2005, 2011). It has been shown that NDVI can be used to predict resource availability for mammals and to account for resource predictability (Handcock et al. 2009, Mueller et al. 2011; Pettorelli et al. 2011; Requena-Mullor et al. 2014). Vegetation indices have also been shown to account for a large part of intra-specific home range variation (Naidoo et al. 2012). However, it is important to keep in mind, that NDVI reflects the green vegetation per se, that means all the existing vegetation and not only the resources that are used by the study animal. Hence, NDVImn is a proxy for the potential but not the actual resource availability. Surface reflectance imagery with cloud cover masks were obtained in a bimonthly temporal resolution and a 30 x 30 m spatial resolution from Landsat 8 OLI TIRS for the two study years 2014 and 2015 (US Geological Survey Earth Resources Observation and Science Center (EROS) with the Processing Architecture (ESPA) at https://espa.cr.usgs.gov/). Cloud cover masks were used on the surface reflectance imagery to mask invalid values (Wegmann et al. 2016). Band 4 (visible red light: RED) and 5 (near infrared light: NIR) of the resulting image were used to calculate the NDVI via the formula: NDVI = (NIR – RED)/(RED + NIR) (Rouse Jr 1974). NDVI values range between -1.0 and 1.0 and are unit less. Negative values usually indicate water, values around zero represent bare ground and high values stand for high photosynthetic activity (Wegmann et al. 2016). All imagery preparation and raster calculation were performed in R (R Core Team 2016) using the packages *RStoolbox* (Leutner and Horning 2016), *rgdal* (Bivand et al. 2014) and *raster* (Hijmans and Van Etten 2014).

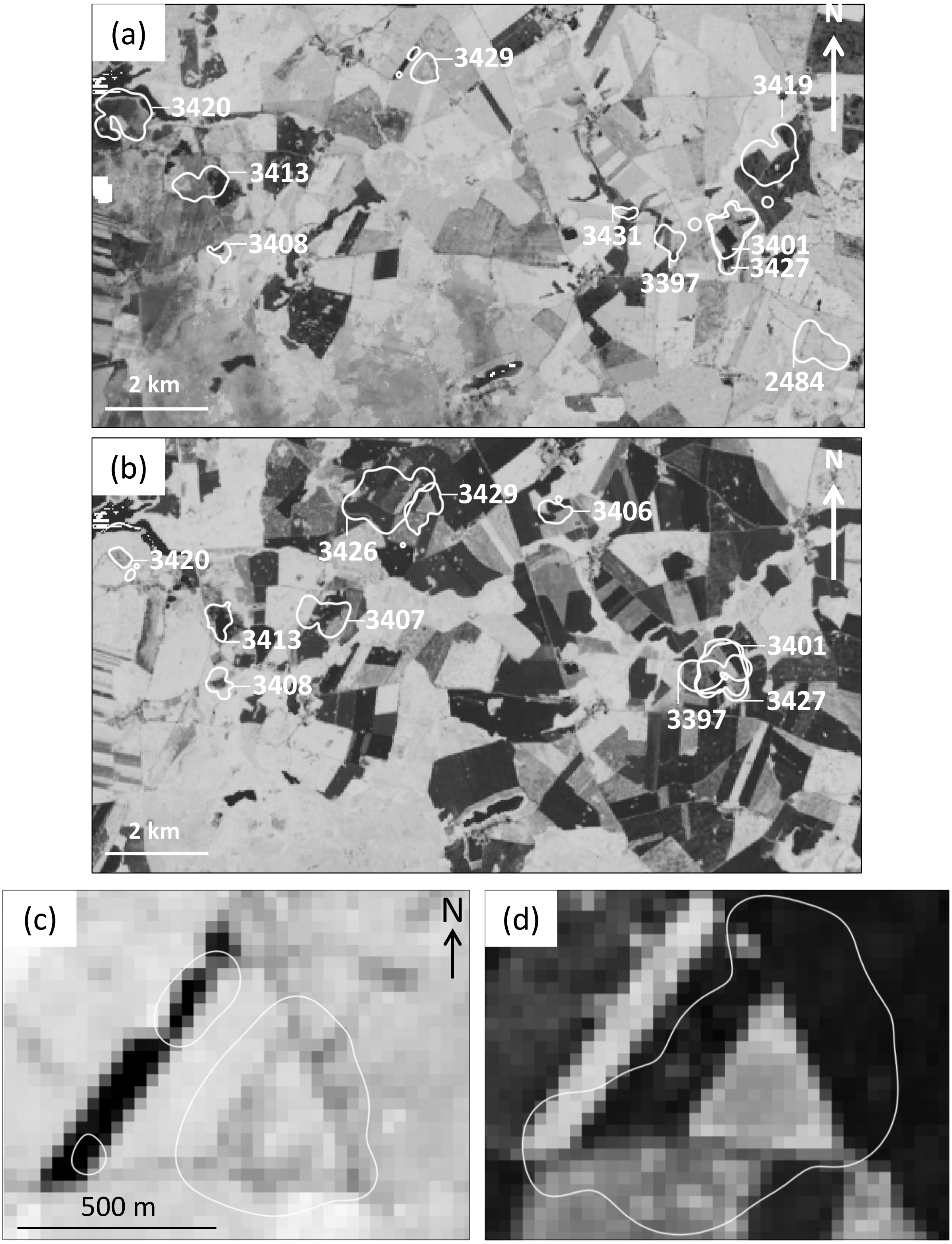

Figure 2: NDVI raster image acquired on 10.06.2014 (a and c) and 13.08.2014 (b and d) with the corresponding 10-day home ranges. The images show the differences in NDVI within home ranges and between different seasons (June and August 2014). The home ranges are labelled with the hare's tag id. The red squares show the home ranges of hare 3429 which are extracted and presented in panel c and d. Panel c) shows the NDVI raster image acquired on the 10.06.2014 with the 10-day home range (24.66 ha) of hare 3429 calculated for the time from 05.06.2014 – 14.06.2014. The NDVI

measures were NDVImn = 0.75, NDVIsd = 0.11. Panel d) shows the NDVI image acquired on the 13.08.2014 with the 10-day home range (39.79 ha) of hare 3429 calculated for the time from 08.08.2014 – 17.08.2014. The NDVI measures were NDVImn = 0.44, NDVIsd = 0.17. The darker the cells the less green light was reflected. Black cells represent bare ground, whereas light grey cells represent green vegetation. Each pixel has a spatial resolution of 30 x 30 m.

The NDVI raster file time series was used to extract and calculate the mean (hereafter NDVImn) as proxy for potential resource availability and the standard deviation of the NDVI (hereafter NDVIsd) as proxy for resource variability in time within each 10-day home range (Fig. 2 c, d). The 10-day home ranges were assigned to NDVI images for a period of 5 days before the image was taken to 4 days after the image acquisition date. Individual hares contributed repeatedly with 10-day home ranges to extract and calculate NDVImn and NDVIsd (see A2 for the data table containing the animals' ID, the date of the raster image, the home range size and the two NDVI measures). The analysis only contains home ranges with less than 30% cloud cover (for a complete listing of remote sensing images see appendix A3). Suitable NDVI images were available between Julian Day 145 and 305 for both study years. We pooled the study years and used Julian day to account for the time of the year in which the image was taken and the respective home ranges were calculated. Thus, we received NDVI images from different dates throughout 2014 and 2015. To each of these NDVI images we added the 10-day hare home ranges that correspond to that particular NDVI acquisition date (Fig. 2). We then extracted the NDVImn and NDVIsd for each hares' home range on that image and also calculated each home range size.

Statistical analysis

We first tested whether home range size, NDVImn and NDVIsd differed between the simple and complex landscape to assure that a comparison between the different study areas was feasible. For the comparison we used ANOVA with hare ID as random error term:

1) Home range size ~ Landscape Structure

2) NDVImn ~ Landscape Structure and

3) NDVIsd ~ Landscape Structure.

We tested the effect of sex on home range size by using ANOVA with hare ID as random error term but did not include this variable into our analysis as it was insignificant ($F_{1,40} = 1.52$, $P = 0.23$). For all analyses home ranges sizes were log transformed to assure normality and homoscedasticity which were diagnosed visually. Linearity was checked and approved by using GAMs from the package *mgcv* (Wood 2001). We used Linear mixed effects models (R package *nlme* (Pinheiro et al. 2014)) to test whether home range size is affected by NDVIsd, NDVImn, landscape structure (simple vs. complex) and season (Julian day):

$$\text{10-Day Home Range Size} \sim \text{NDVIsd} * \text{Landscape Structure} + \text{NDVImn} + \text{Day} + \text{Day}^2$$

Covariates were tested for collinearity first (Zuur et al. 2009). An interaction term was used for NDVIsd and landscape structure to test for different relationships between home range size and resource variability in the two landscape structures. NDVImn was included as a confounding variable, as we expected home range size to decrease with resource availability (Mcloughlin et al. 2000; Hansen et al. 2009; Duncan et al. 2015). The confounding variable Julian day was added to check for temporal effects of resource variability on home range size. We used a second-order polynomial for Julian day because we expected a quadratic relationship between home range size and Julian day (Smith et al. 2004). Thus, home ranges were thought to be large in spring, decrease during summer and increase after harvest again. Hare ID was used as a random term. Model selection was based on the backwards stepwise method using the lowest Akaike Information Criterion (AIC; based on the methods stated by Burnham and Anderson (2002)) with the stepAIC() function from the *MASS* R package (Venables and Ripley 2002). We followed Maximum likelihoods (ML) were used for the selection process, while the final model was reported using restricted maximum likelihood (REML). All analyses were executed in R version 3.3.2 (R Core Team 2016). In the text and figures mean values and standard deviations are given.

Results

Mean and standard deviation of NDVI ranged around similar values within the home ranges in both landscape structures (NDVImn: complex landscape = 0.56 ± 0.13, simple landscape = 0.59 ± 0.12, $F_{1,40} = 0.27$, $P = 0.61$, Fig. 3a and NDVIsd: complex landscape = 0.17 ± 0.05, simple landscape = 0.18 ± 0.05, $F_{1,40} = 0.29$, $P = 0.59$, Fig. 3b). However, the mean 10-day home range size in the complex landscape with 18.5 ± 13.7 ha was significantly smaller than those in simple landscapes with 55.41 ± 34.56 ha ($F_{1,40} = 38.7$, $P < 0.001$, Fig. 3c).

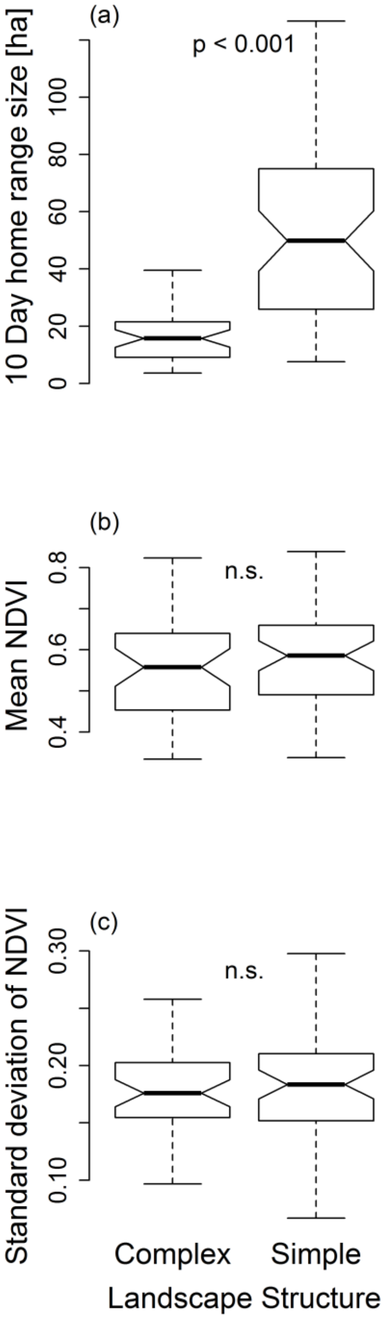

Figure 3: Impacts of landscape structure on (a) 10-day home range size and on the proxies for (b) resource availability (mean NDVI) and (c) spatiotemporal variability in resources (standard deviation of NDVI).

The model selection procedure showed that resource availability (NDVImean) and Julian Day had no effect on the respective 10-day hare home range sizes in both landscapes. In contrast, increasing spatiotemporal variability of the resources (NDVIsd) in the structurally simple landscape led to an increase in home range sizes whereas hares did not respond with any change of home range size in the complex landscape (Fig. 4). According to the lowest AIC value, the reduced model contained an interaction term between NDVI standard deviation and landscape structure, as well as both of those variables as main terms, which resulted into two different regression lines for the two landscape structures (Table 1). The intercept for the complex landscape was 2.86 ha and for the simple landscape 2.93 ha, while estimates for the slopes were -0.97 and 5.94 respectively (before back transformation, Table 1).

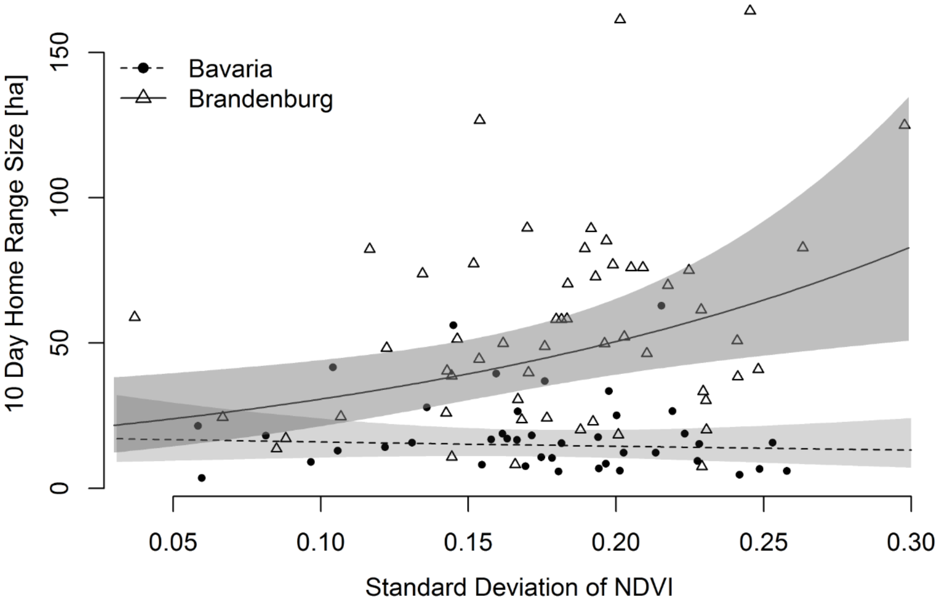

Figure 4: Impact of resource variability (NDVIsd) on 10-day home range sizes in the complex landscape (filled circles and dashed regression line) and in the simple landscape (open triangles and solid regression line). Regression parameters were taken from the reduced linear mixed effects model and were back transformed to fit the original data. Shaded areas represent 95% confidence intervals.

Table 1: LMM output – degrees of freedom, coefficients and standard errors (df, β ± SE) for explanatory variables retained in the most parsimonious model predicting home range sizes of European brown hares. The reference category is the complex landscape.

	df	β	SE
Intercept (complex landscape)	54	2.86	0.38
NDVI_sd (complex landscape)	54	-0.97	2.06
Landscape Structure (simple landscape)	38	0.06	0.51
NDVI_sd * Landscape Structure (simple landscape)	54	5.94	2.71

Number of observations: 96. Number of groups (random effect: Hare Id): 40. AIC = 190.9, BIC = 206, LogLik = -89.4

Discussion

We tested if resource availability and variability in agricultural landscapes affect home range sizes of a herbivorous mammal. Resource availability was defined as the average amount of resources (mean of NDVI grid cells within each home range) in an animal's home range and resource variability as spatial variability (standard deviation of NDVI grid cells within each home range) of resources in that home range. Since both variables were measured repeatedly over time, they had a spatial and a temporal aspect. To our knowledge this is the first study analysing resource-triggered changes in animal home range behaviour at small spatial and fine temporal scales. We hypothesized that home ranges increase with increasing resource variability and were particularly interested whether the spatial configuration of an agricultural landscape affects the relevance of resource availability and variability for hare space use. Therefore, we tested our hypothesis in a structurally complex landscape with small agricultural fields and many landscape elements such as (semi-) natural areas versus a structurally simple landscape with large agricultural fields and few landscape elements.

Despite a similar amount of resources (NDVImn) and resource variability (NDVIsd) in simple and complex agricultural landscapes, hare's home range sizes were significantly larger in the simple landscape with large field sizes compared to the complex landscape (a pattern also found by Tapper and Barnes 1986, Frylestam 1992, Rühe and Hohmann 2004, Smith et al. 2004, Schai-Braun and Hackländer 2014). Although we expected a clear relationship between resource availability and home range size within each landscape (as found by MacNab 1963, Mcloughlin et al. 2000, Marable et al. 2012), surprisingly, no such pattern was found here. In contrast, our analyses show that resource variability (SD of NDVI) was of higher importance for home range size than the potential resource availability (mean NDVI) per se. The lack of a relationship between home range size and mean NDVI might be caused by disparities between the parts of the vegetation that are actually used by hares and the parts that are reflected by the NDVI images. The mean NDVI cannot show e.g. single plant palatability but the change in NDVI also mirrors the change in potential resource availability. Hence, it might be easier to detect an effect of resource changes on hare movement behaviour. The effect of increasing resource variability was particularly strong in the simple landscape where hare home range sizes increased with resource variability. Animals in the spatially complex landscape did not show a response in home range size.

Applying our approach to a gradient of landscape complexity would help to better differentiate between landscape structure and different geographical regions.

The increase in home range size in the simple landscape can be explained by the synergistic effects of landscape structure and short-term changes in resource availability. From a hare’s perspective in a structurally simple landscape, agricultural practices e.g. mowing and harvesting increase the variability in resource availability and create an unpredictable resource landscape. Home ranges may then increase in structurally simple landscapes because hares need to switch to distant alternative habitat patches when areas within their home ranges become temporarily unsuitable. This leads to longer travelling distances to reach the desired resource patch, which was used for foraging, shelter or in search of mates within a home range. The larger the agricultural matrix between those resource patches the longer the animals have to spend travelling. Additionally, such an increase in the time spent for travelling reduces the time for energy intake (Daan et al. 1996) and may lead to lower individual fitness, reproductive output and can even cause local extinctions (Boersma and Rebstock 2009; Morales et al. 2010). Many studies have shown that agricultural intensification (due to habitat loss and lower heterogeneity) can lead to a decrease in animal abundance and species diversity on a global scale (Benton et al. 2003; Tscharntke et al. 2005; Kleijn et al. 2006). Intensive, conventional agriculture is often accompanied by changes in crop diversity and the consolidation of fields to increase management efficiency resulting in a decline from complex to simple landscapes with large crop fields. However, hares are a highly mobile species and therefore might have the ability to deal with simple landscapes. Indeed, Marboutin and Aebischer (1996) showed that hare abundances can be high (20 – 27 hares per km^2) in simply structured and intensively used agricultural landscapes, with average field sizes of 20 ha. This shows that other factors (e.g. changes in management, juvenile mortality, wet winters, high predation pressure and diseases) might be even more important for the overall decline in hare populations (Edwards et al. 2000, Schmidt et al. 2004). For smaller animals, which are less mobile (Blaum et al. 2012) or have higher energy requirements (Daan et al. 1996) such a fitness decline might be even more obvious than for the mobile hares. Still our observed increase in home ranges size in the simple landscape could contribute to a decline in individual fitness. Revisiting the study area of Marboutin and Aebischer (1996) for example to recount and compare the population size of European hares to the 1996 data may help to improve our understanding of how increased travel distances mirrored by lager home range sizes affect fitness over time.

Their high mobility allows hares to quickly adapt their home range size to sudden resource changes occurring in agricultural landscapes. Schai-Braun *et al.* (2014) showed that hares increased their home ranges after harvest in complex agricultural landscapes (average size of crop fields was 3.1 ha as in our study) and conclude that hares might switch to alternative habitats outside their usual home range for a short time after harvest. In contrast, home range sizes of our GPS-tagged hares in the spatially complex landscape showed no response to resource variability. We believe that there was no need to increase the home range during times of high resource variability, because hare home ranges already included multiple different landscape elements that already provided a large and sufficient variety of food resources. However, the bimonthly characteristic of the NDVI data we used was not suitable to show direct responses to sudden resource changes (mowing and harvest).

The relationship between increased home range sizes and variation in resource variability might be a global phenomenon. In mainly natural landscapes this was shown for carnivores, omnivores and ungulates (Mcloughlin et al. 2000; Eide et al. 2004; Hansen et al. 2009; Nilsen et al. 2009; McLoughlin et al. 2010; Mueller et al. 2011; van Moorter et al. 2013; Duncan et al. 2015). For example, brown bear home ranges are larger when seasonality is high, but animals in stable environments acquire enough energy already in small home ranges (Mcloughlin et al. 2000). Similarly, home range sizes of Arctic foxes are small when prey is spatially accumulated and predictable in space and time (Eide et al. 2004). Van Moorter et al. (2013) showed that ungulates exhibit short-distance movements when the underlying resource pattern were stable in space and time. These studies showed the effect of resource variability on home range size in mainly natural settings. Our study highlights that this effect persists also in human-modified agricultural landscapes with high resource variability indicating that the synergistic effects of landscape structure and anthropogenically caused resource variability play a key role in home range dynamics.

Research so far focused on large scale (tens to hundreds of kilometres) animal movements in relation to long term (annual) natural vegetation dynamics and at large spatial scales (e.g. Nilsen et al. 2009; Mueller et al. 2011; Naidoo et al. 2012). For example, Mueller *et al.* (2011) showed that ungulates exhibit relatively short annual movements in landscapes of rather stable annual vegetation patterns, while animals in intra- and inter-annually variable environments show long-distance movements. In our study we combined high resolution GPS data to calculate 10-day home ranges with the corresponding NDVI image. This enabled us to focus on both, short term changes in animal movement as well as resource availability. Shorter spatial and temporal scales were investigated by very few studies (Mcloughlin et al. 2000; Marable et al. 2012; McClintic et al. 2014). In these studies, environmental variability was calculated either on the basis of monthly means of evapotranspiration or on very few NDVI images instead of a time series. Environmental variability was then related to home range sizes calculated over a period of one year. In our approach, we used all suitable different NDVI images to increase our temporal resolution of environmental variability. By applying the corresponding 10-day home ranges to each of the NDVI images, instead of using an annual home range and averaging over the NDVI images, enabled us to analyse a much finer temporal scale to get a better understanding of the underlying movement mechanisms causing home range size adjustments in agricultural landscapes.

To conclude, hares in spatiotemporal highly dynamic but simple agricultural landscapes showed larger home ranges with increasing resource variability compared to complex landscapes. Alternatives within home ranges must exist to be able to evade unsuitable areas and to switch to suitable habitat patches. Yet, in simple landscapes (semi-) natural habitat patches are distant, scarce and surrounded by a large, often inhospitable matrix, which in combination with high environmental variability can cause even greater difficulties for less mobile animals (e.g. rodents) (Blaum et al. 2012). Smaller animals have a lower movement capacity and an increase in home range size might not be enough to deal with those challenges. Fischer et al. (2011) showed that agri-environmental measures had a stronger effect on small mammal diversity and abundance in simple landscapes than in complex landscapes. Habitat diversity therefore seems a necessary feature to improve simple landscapes, in which animals have to travel far distances to cover all their requirements (Fahrig et al. 2015). The observed increase in hare home range size and decrease in their abundances can have severe implications for conservation in anthropogenic landscapes. Our results suggest that conservation management could benefit strongly from a better knowledge about fine-scaled effects of resource variability on movement behaviour.

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Chapter 2

How do agricultural management events affect movement behaviour of wildlife?[2]

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Abstract

Agricultural landscapes cover significant areas across ecosystems worldwide. These spatially and temporally dynamic areas force wildlife to interact with agricultural machinery, and with sudden changes in resource availability during harvests and mowing events. Animals may avoid agricultural machinery and the changed habitat after management events to search for undisturbed habitat. Whether this search is successful depends on the landscape structure, which can influence the animals' movement behaviour. Here we study how agricultural management events affect animal movement behaviour in two contrastingly structured agricultural landscapes.

In 2014 and 2015 we collared 36 European brown hares (*Lepus europaeus*) with GPS-tags and accelerometers in a simple (large fields, few landscape elements) and a complex (small fields, many landscape elements) landscape in Germany. We recorded hares' movement behaviour for 4 days before and after agricultural management events with (harvest and mowing) and without resource changes (e.g. application of fertilizer). We used four proxies for movement behaviour: the number of GPS points on the focal field, utilization range shift, utilization range size, and energy expenditure (measured as overall dynamic body acceleration).

The results show that hares adjust their behaviour in relation to crop type, management type and landscape structure. We found more GPS locations on the focal field after the harvest of maize, rape seed and wheat, but not on grasslands. Hares showed longer utilization range shifts after management with and without resource changes. Utilization range size was only affected in wheat fields in the simple landscape. It increased after harvest and decreased after agricultural management without resource changes. Energy expenditure was unaffected by agricultural management.

Hares profit from harvested fields, as they find food in form of fallen grains and improve their predator detection probability. The reaction to agricultural management events without resource change might depend on the precise type of management, as inorganic fertilizer can foster different movement reactions than liquid manure. Landscape structure

plays an important role as utilization range sizes increase due to the necessity to reach distant alternative habitats. The provision of high crop diversity and set-asides with high quality forage throughout the year will help to increase hare and other farmland animal populations.

Introduction

Agricultural landscapes cover about 38 % of the earth's terrestrial surface and approximately 45 % of Europe (FAO 2014). Animals in these dynamic landscapes are confronted with a variety of challenges, such as habitat degradation due to field consolidation (Frylestam 1992, Haddad et al. 2003), frequent disturbances by agricultural machinery (Báldi and Faragó 2007, Padié et al. 2015), and abrupt spatiotemporal changes due to the synchronous harvest of multiple crops fields (Vasseur et al. 2013, Schai-Braun et al. 2014). However, there is a lack of understanding how animals may respond or adapt to these often-interlinked challenges in human-dominated dynamic systems.

Movement is the key process for animals to adjust to the degradation of agricultural landscapes and to specific agricultural management events like harvests. One prominent aspect of landscape degradation is the consolidation of fields, which leads to a large and homogeneous agricultural matrix with greater distances between (semi-) natural habitat patches and a reduced number of landscape elements such as hedgerows and tree stands. In such simple landscapes, animals have to travel longer distances between e.g. resting sites and foraging patches, increasing their utilization ranges (Schai-Braun and Hackländer 2014, Ullmann et al. 2018). This increase in movement can lead to higher energy expenditure (Harestad and Bunnel 1979, Daan et al. 1996) and a reduction in reproductive output (Doherty and Driscoll 2018) in comparison to complex landscapes where foraging comes at energetically lower costs.

Possible negative effects of landscape degradation on animals may be exacerbated by different agricultural management events. In particular, animals can experience two different types of management events: 1) management events with resource changes, such as harvesting and mowing, and 2) management events without resource changes, such as the application of fertilizer and plant protection products. Harvesting and mowing may cause multi-layer habitat changes that are important to wildlife as they simultaneously remove cover and physical barriers (Vercauteren and Hygnstrom 1998, Rühe 1999).Harvests also eliminate possible forage for animals, but concurrently provide space for freshly sprouting plants (Späth 1989, Cimino and Lovari 2003). Roe deer (*Capreolus capreolus*) for example shift their home ranges away from corn fields after harvesting, supposedly to find new foraging grounds and cover possibilities (Vercauteren and Hygnstrom 1998, Cimino and Lovari 2003). In contrast, European brown hares (*Lepus europaeus*) may show no change in utilization range shift, but an increase in utilization range size after cereal harvest to allot alternative foraging habitats to their utilization ranges (Schai-Braun et al. 2014, but see Reitz and Léonard 1994, Marboutin and Aebischer 1996, Rühe and Hohmann 2004). These findings point towards a usage of harvested fields and a release from spatially restricted space use for European brown hares (Rühe 1999), but a loss of shelter resources for roe deer.

While we have a notion of how crop harvests shapes animal movements, there are few studies investigating the direct effect of agricultural management events without resource changes. Cimino and Lovari (2003) showed that roe deer shifted their home range away from recently ploughed field, but did not change their home range size. Roe deer were also observed to flee from agricultural machinery (Mrlik 1990, Stankowich 2008, Padié et al. 2015). However, these experiments were conducted by running a tractor through a forest and cannot directly be linked to agricultural management events on the crop fields (e.g. application of fertilizer).

How animals react to agricultural management events – irrespective of resource changes – can vary considerably (Vercauteren and Hygnstrom 1998, Drygala and Zoller 2013, Schai-Braun et al. 2014). Animals might apply a whole variety of movement processes to deal with changes in their habitats (Nathan et al. 2008). Increasing the utilization range, for example, would benefit the animal by incorporating alternative habitat. However, animals can also shift their utilization range centre to incorporate new habitats or to avoid agricultural machinery and fields that have recently been managed. Other movement processes, like the daily movement distance or the type and speed of movements (resting, foraging, foraging, slow and/or fast movements), could also change after management events. These reactions may be accompanied by changes in energy expenditure (Harestad and Bunnel 1979), which has often been stated (Rühe and Hohmann 2004, Schai-Braun et al. 2014) but could not be measured to date.

Another level of complexity in how animals adjust their movement behaviour in response to different management events is added by different types of crops in agricultural landscapes. Previous studies considered only cereal fields because they were the main crop type in the respective study areas (Marboutin and Aebischer 1996, Schai-Braun et al. 2014).

However, maize and rape seed have become more numerous over the last decades and by now cover substantial parts of agricultural landscapes (MEL Bundesministerium für Ernährung und Landwirtschaft 2014, Sauerbrei et al. 2014).

In this study, we investigated adjustments in movement behaviour and energy expenditure of European brown hares to agricultural management events with and without resource changes and set a special focus on landscape structure and the different crop types. Hares are especially well-suited to study movement reactions to agricultural disturbances, as they mainly live in open areas like agricultural fields (Tapper and Barnes 1986, Lewandoski and Nowakowski 1993). We collared hares with GPS tags and internal accelerometers in a simple landscape with few landscape elements and large fields in northeast Germany and in a complex landscape with many landscape elements and small fields in south Germany. Acceleration bursts (recorded for 3 seconds every 4 minutes) were used to calculate the overall dynamic body acceleration (ODBA) as a proxy for energy expenditure (Scharf et al. 2016). Local farmers were interviewed to correlate dates, sites and types of agricultural management events (on the focal fields) to possible changes in movement behaviour before and after each of those management events. We used the number of GPS fixes on the focal field, the utilization range shift, the change in utilization range size and the change in energy expenditure as movement parameters. As far as we know neither the impact of the two different types of management events (with and without resource changes) have been disentangled, nor have more specific adjustments in movement behaviour been analysed.

We hypothesize that hares react differently to the two types of agricultural management events. After events without resource changes we expect hares to exclude the disturbed fields from their space use. We predict that utilization ranges and energy expenditure will increase and hares will shift away from the focal field to avoid the agricultural machinery. In contrast, after management events with resource changes, we expect hares to incorporate the harvested fields into their utilization ranges. Here, we predict an increase in utilization range size and energy expenditure, as hares incorporate and explore the newly gained habitat. Hares might also shift their entire utilization range towards the harvested field. We furthermore hypothesize that hare movement reactions are stronger in simple landscapes than in complex landscapes, as fewer alternative habitats, cover and new food resources are available.

Methods

Study area

We selected two study areas which differed in landscape structure (Fig. I2). The study area in the complex landscape is located in South Germany, Bavaria 50 km north of Munich (centred at 48° 48′ N; 11° 86′ E). The 256°km² area is characterized by small-scale agriculture with an average field size of 2.9 ± 0.04 ha (mean ± SE; calculated based on maps provided by the Bayerische Vermessungsverwaltung 2014) and a high amount of field edges, hedgerows, tree stands and fallow land. Arable land covers 66% of the study area and the main land use types are wheat, maize and grassland (Bayerisches Landesamt für Statistik und Datenverarbeitung 2016). The study area in the simple landscape is located in North-east Germany, Brandenburg, around 100 km north of Berlin (centred at 53° 35′ N; 13° 68′ E) and used as the long-term research platform AgroScapeLab Quillow (Agricultural Landscape Laboratory Quillow) of the Leibniz Centre for Agricultural Landscape Research (ZALF) and the Biomove research training group (www.biomove.org/about-biomove/study_area/). The 213 km² area is characterized by large-scale agriculture with an average field size of 27.5 ± 1.1 ha (mean ± SE; calculated based on maps provided by the Landesvermessung und Geobasisinformation Brandenburg (InVeKoS 2014)) and a low amount of field edges and only few (semi-) natural landscape elements (Batáry et al. 2017). The area is covered up to 62% by arable land which consists mainly of wheat, maize and rape seed (Landesvermessung und Geobasisinformation Brandenburg (InVeKoS 2014)).

Management assessment

We recorded hare movement parameters for two management types and a control: (i) management events with resource change, (ii) events without resource change, and (iii) for periods without management at all (hereafter referred to as baseline). We included the baseline into our analysis to account for possible changes in movement parameters that might occur naturally during an 8-day period, irrespective of a management action. Movement parameters for the baseline were calculated for 4 days before and after a day without a management event. Movement parameters for the two management types where calculated for 4 days before and after each management event. Furthermore, we recorded the crop type of each managed field (Table 1).

Local famers were asked for information about the agricultural management measures within each hares' utilization range. We gained information for 73% of all fields and only those were included in the analysis. We excluded samples in which hares displayed less than three GPS fixes on the focal field during the 4 days before or after the management event.

Table 1: The number of agricultural management events with and without resource changes and the baseline (no management as a control) used for statistical analyses. The numbers given for wheat, grassland, maize, rape seed and other crops (barley, spelt, mustard, oats, peas, radish, rye, sugar beet, potatoes and triticale) include management types with and without resource changes. In contrast, the numbers given for the baseline only include samples without any kind of management. The samples are further distinguished between the simple and the complex landscape structure.

Landscape type	Baseline	Wheat	Grassland	Maize	Rape seed	Other crops
Simple	84	40	4	19	18	32
Complex	61	34	15	17	9	16
Total	145	74	19	36	27	48

Animal tracking

We equipped 36 adult hares with GPS collars in spring 2014 and 2015 simultaneously in both study areas (for detailed information and deployment times see supplementary material SD1). Hares were driven into woollen nets, weighed, sexed and collared according to Rühe and Hohmann (2004). The 69 g collars (Model A1, e-obs GmbH, Munich – Germany, www.e-obs.de) consisted of a GPS unit and a tri-axial acceleration sensor, which provides the possibility to use acceleration informed GPS duty cycles. During active periods GPS fixes were taken every full hour, during inactive periods GPS fixes were recorded every four hours. Inactivity was determined automatically by the acceleration sensor when three consecutive acceleration samples did not surpass a variance threshold of 700 (e-obs raw values without unit). The acceleration sensor was programmed to record a movement burst every 4 minutes. Each burst was recorded at 33 Hz for 3.27-seconds, receiving 110 samples per burst per axis. All tracking and acceleration data are stored at www.movebank.org (Wikelski and Kays 2015).

Movement parameters

We used four different movement parameters (the number of GPS fixes on the focal field, utilization range shift, utilization range size and energy expenditure (ODBA)) to describe hare movement behaviour 4 days before and 4 days after agricultural management events and the baseline:

The number of GPS points on the focal field was extracted by overlaying the topological shape files (Bayerische Vermessungsverwaltung 2014, InVeKoS 2014) with the GPS fixes using the R packages *rgdal* (Bivand et al. 2014), *rgeos* (Bivand and Rundel 2016) and *raster* (Hijmans and Van Etten 2014).

Utilization ranges were calculated using the R package *adehabitatHR* (Calenge 2006). We used 95% minimum convex polygons (MCP) to calculate the 4-day utilization ranges before and after each management event. We only included utilization ranges that were based on at least 15 GPS fixes per day (> 60% of the data). The distance between the centres of the "before" and "after" utilization ranges was used to calculate the utilization range shift, using the R package *rgeos* (Bivand and Rundel 2016). The area of each 4-day utilization range was used to measure utilization range size.

Energy expenditure was measured as overall dynamic body acceleration (ODBA), which was calculated as described by Scharf et al. (2016). We originally calculated ODBA for each single day of the 4-day time period. Subsequently, the mean was used to gain one ODBA value for each 4-day time period. We only calculated the ODBA for the time from 22:00 to 02:00 at night as hares are active during night time, and as hares shift their activity time with advancing sunset/sunrise (Schai-Braun et al. 2012). We avoided the daylight shift by using only hours that were always set in the dark period within the study areas and over the course of the study period. ODBA values have no units.

In utilization range size as well as in energy expenditure we accounted for seasonality and temperature effects by subtracting the values of each "before" movement parameter from the corresponding "after" movement parameter and thus received "delta values". Otherwise our data might have been biased towards management events that occur early in the year, as hare utilization range sizes are larger in spring and early summer (Smith et al. 2004).

Statistical analyses

We used (Generalized) Linear mixed effects models (R package lme4 (Bates et al. 2014)) to test the effect of agricultural management events with and without resource changes on the four movement parameters. Animal ID was the random effect for all models. We analysed the number of GPS fixes on the focal field with a negative binomial model including the following fixed effects: the event status (before and after management events), the management event (baseline, with or without resource change), the landscape structure (simple versus complex), the study year (2014 and 2015) and the date of the management event (Julian date). For this model we used an interaction between the event status and the management type. For the utilization range shift, the delta utilization range size and the delta energy expenditure we used linear mixed effects models with the same fixed effects, except for the event status, as this one was not applicable. For these models we added an interaction term between management type and landscape structure, as we expected stronger reactions of movement parameters to agricultural management events in the simple landscape than in the complex one. For all four movement parameters we first analysed a general model irrespective of the crop type. To reduce the level of complex interactions, we then repeated the same analysis for each of the four main crop types (wheat, grassland, maize, and rape seed) separately. In all models we tested covariates for collinearity (Zuur et al. 2009), which could be safely dismissed. We then checked the relationship between the response variables and the single explanatory variables by using generalized additive models (GAMs) from the *mgcv* package (Wood 2001). The fixed effect Julian date was included as a quadratic term, as hares might react differently to management events in different seasons (Smith et al. 2004). There was no need to apply transformations to the other explanatory variables. We assessed linearity visually by simulating scaled residuals with the R package *DHARMa* (Hartig 2017). The study year (2014 and 2015), as well as the Julian date were included as confounding variables to avoid overparameterization. Utilization range shift was log-transformed to assure normality and homoscedasticity. Julian date was standardized to a zero mean and 0.5 SD to avoid estimates of very different scales between explanatory variables (Grueber et al. 2011). Model selection was done by constructing a set of all possible submodels from the global models (Dochtermann and Jenkins 2011). Subsequently we applied an information theoretic approach and selected the models with the lowest AICc value. The R package *MUMIn* (Barton 2013) was used for the model selection process. However, all models within delta AIC < 2 (Burnham and Anderson 2003) can be found in the supplementary material ST2.

Results

Number of GPS fixes on the focal field

On average, we received 82±8 GPS fixes for each 4-day time period before and after a management event (in comparison to a maximum of 96 possible fixes). This was our reference number of fixes for comparison of hare's reactions towards management events.

Irrespective of the crop type, we found that the GPS fixes increased from 7.7±1.1 to 17.9±1.2 on the focal field after harvesting or mowing, whereas the number of GPS fixes slightly decreased from 17.6±1.1 to 14.2±1.1 GPS fixes after management events without resource change (Fig. 2A, see supplementary material ST1 for summary tables).

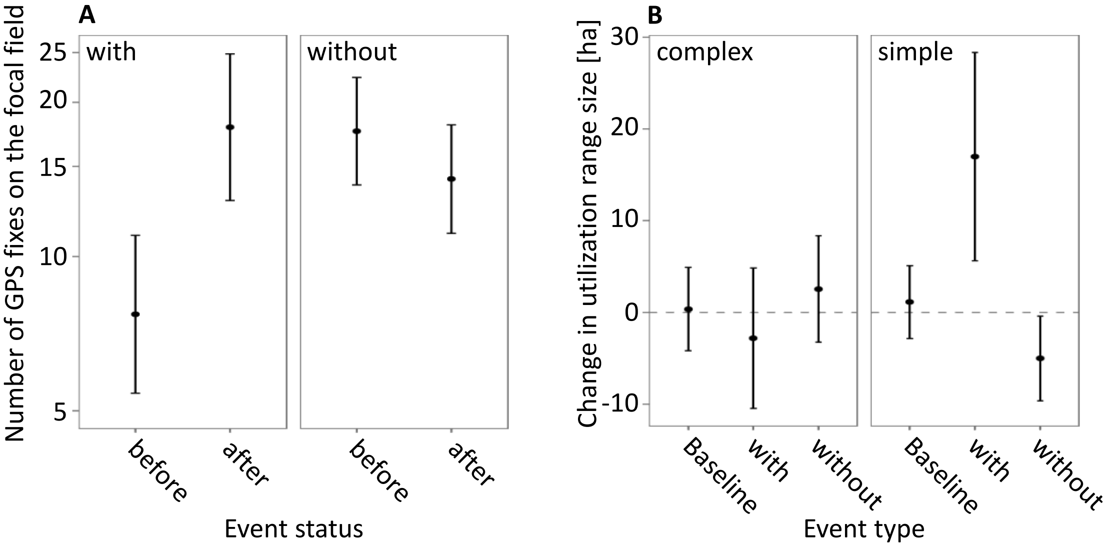

Figure 2: The response of movement parameters to different variables of agricultural management events. Graph 2A shows the number of GPS points (± 95% confidence intervals) on the focal field (irrespective of the crop type) before and after agricultural management events with (left panel) and without (right panel) a change of resources. Mind the logarithmic y-axis. Graph 2B shows the change in utilization range sizes (± 95% confidence intervals) on wheat fields from before to after the two management events (with resource change and without resource change) and the baseline (no management event).

Hares increased the number of GPS fixes on the focal field after the harvest of wheat fields by almost double from 8.5±1.4 GPS fixes to 15.4±1.4. There was no influence of mowing on the number of GPS fixes on grasslands. On maize fields hares increased the amount of GPS points after both types of agricultural management events from 11.5±1.2 to 18.6±1.2 and on rape seed fields the increase was even fivefold from 2.1±1.5 to 10.3±1.4

GPS fixes. In contrast, only on wheat fields did hares react to management events without resource change by decreasing the time they spent on the focal field from 9.9±1.3 to 6.2±1.3 GPS fixes. All model summary tables, models within delta AIC < 2 and further effects plots see supplementary material ST1, ST2 and SA1 respectively.

Utilization range shift

Utilization range shifts were on average longer in the simple landscape (110±7 m) than in the complex landscape (72±6 m). Overall, the shifts were shorter in winter than in early summer and autumn. Utilization range shifts increased from 71±5 m (baseline) to 117±14 m after management with resource change and to 109±8 m after management events without resource change (Fig. 3).

Figure 3: Hare utilization range shifts (± 95% confidence intervals) after management events with and without resource changes compared to baseline events (no management event). The values and confidence intervals were taken from the models irrespective of crop type (= All crops) and for the main crop types. Y-axis was log transformed.

The longer utilization range shifts after both type of management events compared to the baseline were observed for most of the main crop types (Fig. 3). On wheat fields hares' utilization range shifts were similar after both type of management events (after harvest: 106±28 m and 108±15 m after management events without resource change) but longer compared to the baseline (69±8 m). Grasslands were an exception, as there were only longer utilization range shifts after mowing (128±34 m) but after management events without resource changes (109±65 m) the utilization range centre did not shift more than in the baseline (66±8 m). On maize fields hares shifted their utilization ranges by 73±9 m in the baseline treatment, but increased the displacement after management events with (114±30 m) and without (146±27 m) resource changes. On rape seed fields the shifts were 76±8 m long in the baseline, but increased after both management events (with: 187±83 m, without: 111±27 m).

Utilization range size

There was also no effect of management events on delta utilization range size for the model irrespective of crop type. When focusing on the single crop types there was only an effect of agricultural management events on wheat fields in the simple landscape (Fig. 2B). Here, hares did not change their utilization range size in the baseline treatment (1±2 ha), but increased their utilization ranges by 17±6 ha after harvest, and decreased the utilization ranges by 5±2 ha smaller after management events without resource change (Fig. 2B).

Energy expenditure

There was no apparent effects of management and crop type on energy expenditure (ODBA).

Results summary

We found that management activities affect hare movement and space use. The models including all crop types showed a higher number of GPS fixes on the focal field after harvesting events and a lower number of GPS fixes on the focal field after management events without resource changes. Furthermore, utilization range shifts were larger after both management types. Utilization range size and energy expenditure on the other hand were not affected by agricultural management (Table 2 – All Crops).

Focusing on the four most common crop types, we found that hare movement behaviour depended on the crop type and the landscape structure. The number of GPS fixes on the focal field increased after harvesting events on wheat, maize and rape seed fields, and decreased after management events without resource changes on wheat fields (Table 2). There was no effect of mowing grasslands on the number of GPS fixes. Utilization range shifts increased after all management events and on all crop types (except for management events without resource changes on grasslands). Utilization range size was only affected by management events on wheat fields in the simple landscape and increased after harvest, but decreased after management events without resource changes. Energy expenditure was not affected by agricultural management type (Table 2).

Visual inspection of the utilization ranges, their size and shift, showed how variable the movement responses of individual hares are to agricultural management events (Fig. 4).

Table 2: Impacts of management event type and crop species on hare movement reactions. Arrows and grey shading indicate the direction of change of movement reactions (increasing = arrow up, dark grey; decreasing = arrow down, light grey; and no change = arrow pointing to the right, white cells), based on the relevance of the variable contribution (see supplementary material ST1). Cells that include the letter "s" show effects only for the simple landscape, but not for the complex landscape (interaction: management event * landscape structure).

Movement reaction	All Crops		Wheat		Grassland		Maize		Oilseed Rape	
	with	without	with	without	with	without	with	without	with	without
Nb. of GPS fixes	↑	↓	↑	↓	→	→	↑	↑	↑	→
Utilization range shift	↑	↑	↑	↑	↑	→	↑	↑	↑	↑
Utilization range size	→	→	↑s	↓s	→	→	→	→	→	→
Energy expenditure	→	→	→	→	→	→	→	→	→	→

Discussion

We investigated the movement behaviour of European brown hares in two contrasting landscapes (simple versus complex) for four major crop types and two types of agricultural management events: 1) with resource changes (harvests and mowing), and 2) without resource changes (e.g. application of fertilizer). Our results show that hares respond context specific and adjust their movement behaviour and space use differently in relation to management type, crop species and depending on landscape structure. The number of GPS points was higher than expected on harvested crops, but not on mown grasslands. Hares also spent less time on wheat fields after management events without resource changes. Utilization range shifts were longer after both management types and in most crop types. However, utilization range size increased only after the harvest of wheat fields in the simple landscape. Remarkably, we did not find any effect of agricultural management on energy expenditure.

Figure 4: Hares showed individually different reactions to management events. Here we show the movement reactions of four hares to the harvests of different crop types. While hares showed generally long utilization range shifts after harvests (panels A and B), we also observed individuals showing small utilization range shifts after harvests (panels C and D). Examples for these individual differences are: A) large utilization range shift and large change in utilization range size, B) large utilization range shift and small change in utilization range size, C) small utilization range shift and large change in utilization range size and D) small utilization range shift and small change in utilization range size. The name of the crop overlays the harvested field. The "before" utilization ranges and GPS points are depicted in blue, while the "after" utilization ranges are in red. The squares show the utilization range centre, whereas the white line shows the utilization range shift. The simple landscape is represented in panels A) and C), while the complex landscape is shown in panels B) and D). All panels show the same scale (1:9000).

Management events with resource changes

European brown hares shifted their utilization ranges towards the focal field and spent more time on that field after harvest. This might have two non-exclusive reasons. First, hares forage on the harvested field for fallen grains, corn stalks and freshly sprouted weeds (Späth 1989). Second, they incorporate the newly gained habitat into their utilization range because they favour areas with low vegetation height, most likely to improve vigilance and to spend less energy to move through neighbouring dense and high crop fields (Marboutin and Aebischer 1996, Smith et al. 2004, Godt et al. 2010, Mayer et al. 2018). Standing crops are too high for hares, which prefer open habitat to easily perceive predators (Tapper and Barnes 1986, Rühe 1999). However, as soon as the fields are harvested hares can approach a new and easily accessible part of their surrounding habitat (Rühe and Hohmann 2004).

Schai-Braun et al. (2014) showed that hares in a complex agricultural landscape did not shift, but increased their utilization ranges after cereal harvest. The authors argue that hares increased their utilization range size to incorporate alternative habitat, as the harvested fields could no longer be used e.g. for cover. This stands in contrast to our findings, showing no effect on utilization range size, but substantially increased utilization range shifts. However, both movement parameters (i.e. increased utilization range size and shift) can be used to incorporate alternative habitats.

In our study we show the importance of sudden resource changes for the movement behaviour of European hares, which are attracted by harvested crop fields. However, sudden resource changes also influences the movement behaviour of other farmland species, like deer, but also smaller animals such as rodents. For example, white-tailed deer (Odocoileus virginianus) and roe deer were found to shift their utilization ranges away from crop fields after harvest due to a loss of cover possibilities (Vercauteren and Hygnstrom 1998, Cimino and Lovari 2003). They simultaneously increased their utilization range size to find new foraging grounds and perennial cover sites (Vercauteren and Hygnstrom 1998). Furthermore, Cavia et al. (2005), showed that the rodent *Akodon azarae* moved from corn and wheat fields to the weedy field margins after harvests, likely due to increased predation risk. Especially young and inexperienced animals suffer the loss of cover availabilities and increased predation risk after crop harvests (Tew and Macdonald 1993, Vercauteren and Hygnstrom 1998, Van Deelen and Gosselink 2006, Gosselink et al. 2010). Predators, like the red fox (*Vulpes vulpes*), on the other hand showed no change in utilization ranges and habitat use patterns after resource changes (Drygala and Zoller 2013). In general, these results show that most animals are affected by sudden resource changes, but differ in their responses.

Management events without resource changes

Hares movement reaction to agricultural management without resource changes depends on the crop type. Hares avoided wheat fields and shifted their utilization range accordingly to less disturbed areas. In the simple landscape hares additionally decreased their utilization range sizes on wheat fields, probably looking for safe places and abstaining from large excursions to decrease the risk of being overrun. Cimino and Lovari (2003) showed similar effects on the movement behaviour of roe deer, which shift their utilization ranges away from ploughed fields. These findings point towards a general avoidance of recently managed fields. However, there was no change in the number of GPS points on grasslands, and rape seed, and for maize the number of GPS points even increased. These results are in line with the findings from Rühe (2002), who showed that hares do not avoid fields after the application of plant protection products. Hence, the actual movement reaction of hares to management events without resource changes might depend even on a more specific practice of the management event without resource changes, which was not considered in this study. For example, while plant protections products might not be a problem for hares, organic fertilizer might pose a barrier to them, as the liquid manure clogs the fur and is difficult to be cleaned off. Future studies should incorporate the impact of the different management types without resource changes on animal movement behaviour.

Landscape structure effects

Agricultural management affected utilization range size only in the simple landscape and only on wheat fields. This confirms our hypothesis that hares in simple landscapes show more or stronger movement reactions to management events. Animal movements—especially utilization range size—in human-modified areas depend on landscape structure (Mortelliti and Boitani 2008, McClintic et al. 2014, Ullmann et al. 2018). Complex landscapes, with many different kinds of landscape elements, provide more alternatives to forage and to find cover in case of resource changes (Beasley et al. 2007). Animals in simple landscapes with large fields would have to move longer distances to reach adequate landscape elements, which often translates into larger home ranges (Smith et al. 2004, 2005). Despite the increase in home range size, fields can be so large as to not be crossable when crops are high. This barrier function temporarily disrupts animal movements between habitats – especially, in simple landscapes where it is infeasible to circumvent large fields with high and dense standing crops – and thus may inhibit mobile linkers to fulfil their function in the ecosystem (Lundberg and Moberg 2003). For hares standing crops are difficult to pass through (Rühe 1999) and thus are not used as long as the corps are high and dense. During this time hares cannot connect habitat patches that are separated by the standing crop barrier. The temporally disconnected habitats might therefore experience a lack of fresh genetic material – which would be detrimental for organisms that need to exchange genetic material during the time of high standing crops – or resources such as nutrients (Lundberg and Moberg 2003). In the case of hares, harvests or mowing events can therefore provide the opportunity to reconnect those previously separated habitats so that hares could once again function as genetic, process and resource linkers.

Energy expenditure

Animals that are disturbed by human activity often suffer a net loss in their energy budget resulting in poor body conditions (Bechet et al. 2004, Hertel et al. 2016) and reduced reproductive output (French et al. 2011, Strasser and Heath 2013). Surprisingly, we could find no evidence of increased energy expenditure after agricultural management events. Hence, in our case it seems that hares follow Blumstein's (2016) theory of not fleeing but being more vigilant. However, if the animal runs away from agricultural machinery only once or twice per day during the management event, the measured energy expenditure (ODBA) might not be significantly increased. The ODBA values are very similar for a day where a hare runs 4 times versus a day the animal runs 6 times (see supplementary material SA3). However, we expected that at least an increase in utilization range size (as was shown for wheat fields in the simple landscape) would produce an increase in energy expenditure (Harestad and Bunnel 1979, Daan et al. 1996). Yet, there is variation in the relationship between energy expenditure and utilization range size. Some of the animals that contribute to the sample of wheat fields in the simple landscape increased their utilization range after harvest, but their ODBA stayed almost the same (supplementary material SA3). There was only one hare that increased its utilization range as well as its energy expenditure. Thus, inter-individual differences might account for the discrepancy between energy expenditure and utilization range size in our sample. Moreover, hares might also compensate for increased utilization range sizes by executing different fractions of behavioural categories, like resting, foraging, running, feeding. They might move more to explore but also find more food in a newly gained patch and thus compensate with smaller foraging movements that do not require much energy.

Human-Wildlife coexistence

Heavy agricultural machinery poses a direct threat to farmland wildlife. The machines are becoming wider and faster and easily overrun even adult animals, but more often kill the young (Steen et al. 2012). Disturbances by agricultural machinery might also cause short term escape movements of just a few minutes, which we could not detect with our hourly GPS duty cycle. Similar to hares, roe deer live in highly human dominated landscapes, but still flee approaching tractors, even if the machine is still 100 m away (Padié et al. 2015). However, Reimoser (2012) on the other hand showed that roe deer and red deer increased their activity level only slightly after being disturbed by tractors. Whether to flee or to stay may depend on the energetic costs associated with the behaviour. Some animals flee early to avoid monitoring costs, while for others it is less expensive to stay and be vigilant (Blumstein 2016). Furthermore, Báldi and Faragó (2007) showed that hare abundances significantly decreased in agricultural landscapes with increased numbers of tractors, which might also be due to a correlation with intensified agriculture.

Conclusion

To our knowledge this is the first study that disentangles how an entire set of animal movement parameters is affected by different crop types and the synergistic effects of agricultural machinery and sudden resource changes due to harvest and mowing. We show that both types of agricultural management events (with and without resource change) affect animals’ movement behaviour. After management events without resource changes hares avoid cereal—but not grassland, maize, and rape seed —fields and shift their utilization range. On the other hand, they profit from harvested fields, spending more time on them and incorporating them into their utilization range. Hence, in comparison to other species, such as white-tailed deer and red foxes, hares benefit from crop harvests (Brinkman et al. 2005, Drygala and Zoller 2013). However, ensuing studies should further disentangle the effects of the different agricultural management events without resource changes. Animals might show different movement behaviours after the application of mineral fertilizer versus organic fertilizer, as organic material stays longer on the field and is difficult to be cleaned off. Furthermore, the effects of the different chemical plant protection products on animal well-being and reproductive success are still largely unknown (Rühe 2002).

We also showed that a simple landscape structure increases utilization range sizes. Consolidated fields—very frequent in simple landscapes—are one consequence of intensified agriculture, leading to a strong reduction in biodiversity on all trophic levels (Benton et al. 2003, Meichtry-Stier et al. 2014, Lee and Goodale 2018). We recommend to provide high crop diversity and sufficient alternative habitat patches with high quality forage throughout the year. This would help to (i) increase hare population numbers, (ii) stabilize and improve other farmland wildlife populations and (iii) assure the continuous connectivity between habitat patches by mobile linkers.

Animals in highly dynamic agricultural landscapes might cope with and adjust to human impact—to a certain extent. Our study contributes to disentangling the severity of agricultural management events with and without resource changes and can help to improve human-wildlife coexistence.

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Chapter 3

The secret life of wild animals revealed by accelerometer data: How landscape diversity and seasonality influence the behaviour of European hares[3]

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Abstract

Movement is one key process for animals to deal with alterations in their habitat, and research has shown that animal movement behaviour, such as home range formation, is related to changes in landscape diversity. However, the underlying behavioural mechanisms for this relationship have remained largely unexplored, because it is nearly impossible to observe free ranging animals continuously. Biologging devices, like tri-axial accelerometers can overcome this gap and provide the opportunity to record data on animals' energy expenditure and behaviour at very high temporal resolutions (e.g. every 5 mins).

We investigated the hidden behaviours of animals in agricultural landscapes and related daily movement behaviours to landscape diversity. We want to shed light on the behavioural mechanisms shaping home range formation and show how the relationship between landscape diversity and animal behaviours is influenced by life-history dependent seasonality.

We used accelerometer data from 32 European hares to classify animal behaviours into five categories: resting, foraging, moving, grooming and standing upright (=vigilance) and tested whether the amount of conducted behaviours in each behavioural category differed with landscape diversity and whether it changed over the course of the year. We conducted the study in two structurally contrasting landscapes (a simple versus a complex landscape).

Hares in diverse landscapes rested more, moved less and spend less time searching for resources. This effect was especially pronounced during the peak breeding season from April to July. Furthermore, the behaviour of male hares was strongly influenced by the reproductive cycle. They move significantly more during mating, and when their testes are largest, than in the non-mating season, when their testes are smallest.

For animals in agricultural landscapes, high landscape diversity is important, especially during the breeding season. As only then, animals can allocate their energy into reproduction and guarantee species persistence in human altered habitats. Our study highlights that accelerometers are excellent tools to detect underlying behavioural adaptations of wild life to ongoing changes in landscape diversity caused by increasing land use pressure.

Introduction

It is crucial to understand the relationship between biodiversity and landscape diversity in an increasingly crowded world, as human population growth further stresses ecosystems through its demand for increased food prodution (Firbank et al. 2008, Rockström et al. 2009). In particular, agricultural landscapes—the largest land-use class in Europe (Ramankutty et al. 2008)—have been subject to significant anthropogenic stress over the past decades, often entailing habitat fragmentation, increased field sizes, and reductions in crop diversity. This has led to a decline in landscape diversity and reduction in the abundance and richness of species across taxonomic groups (Pimm and Raven 2000, Benton et al. 2003, Reidsma et al. 2006). Animals living in agricultural landscapes must not only contend with a degraded habitat, but also with human-caused disturbances (e.g. the application of fertilizers and pesticides) and the sudden removal of biomass during harvest. To adjust to the consequences of intensifaction of these agricultural practices, movement is one of the few options animals have.

Animal movement, a key life-history trait translating into survival and fitness, is influenced by landscape diversity (Turner et al. 2001, Bennett et al. 2006). Examples of this effect are numerous throughout the literature. Researchers found that increasing habitat fragmentation results in a smaller proportion of dispersing animals (Bonte et al. 2006). It was also shown that the agricultural matrix functions as a barrier and thus influences habitat choice (Smith et al. 2004, Dolný et al. 2014). Furthermore, home range sizes and travel distances increase with increasing homogenization and habitat fragmentation (Diffendorfer et al. 1995, Schai-Braun and Hackländer 2014, Ullmann et al. 2018). However, the mechanisms underlying these changes in movement behaviour remain largely unexplored. One promising avenue to investigating the underlying processes is through the animals' daily behavioral patterns. Although researchers have recently begun to explore the daily behaviours of free ranging animals (Wilson et al. 2006, Grünewälder et al. 2012, Lush et al. 2016), they have not yet accounted for the influence of landscape diversity on those behaviours.

The main reason daily behaviours have not been subject to closer inspection arises from difficulties in quantifying the behaviours of free ranging animals. For a long time it was impossible to constantly observe wildlife, especially over longer time periods and during night. Modern GPS telemetry with integrated biologging devices, like tri-axial accelerometers, provide a novel opportunity to continously observe the hidden behaviour of animals and even gain insight into their energy expenditure (Shepard et al. 2008, Wilson et al. 2008, 2016, Scharf et al. 2016). For example, accelerometers are used with livestock to remotely monitor the animals' health status (Martiskainen et al. 2009, Rutten et al. 2013). With free ranging animals, the applications vary widely. Accelerometer data have been used to quantify the vigilance behaviour in European hares in relation to day length (Lush et al. 2016), vultures' flight behaviour in relation to seasonal wind conditions (Nathan et al. 2012), and the activity of caribou in relation to vegetation abundance (Mosser et al. 2014). In these studies the researchers often use machine learning to classify the animals' behaviour into several behavioural modes such as resting, moving/flying, foraging, and grooming. The most imporant advantage of acceleration sensors is that movement information can be sampled on a regular basis (supplying almost continous observations of the animals' activities) and can be directly linked—via GPS locations—to the specific location of an animal in the landscape. Weterings (2018) made use of this and relate forage quality to the time spend foraging. Another study, by Shamoun-Baranes et al. (2012), with a similar focus, demonstrated that the time allocation of certain behavioural modes differs between habitats.

In our study we aim to go a step further and investigate whether changes in behavioural modes are caused by changes in landscape diversity. Areas of low agricultural landscape diversity often force animals to travel long distances or to stay in a patch when encountering barriers, e.g. the agricultural matrix (Dolný et al. 2014, Schai-Braun and Hackländer 2014). In contrast, areas of high landscape diversity provide all necessary resources (e.g. food and cover) to satisfy the animals requirements within a small spatial scale (Anderson et al. 2005, Saïd and Servanty 2005). Differences in landscape diversity would therefore lead to changes in the animals' behavioural modes, with animals in low diversity areas having less time for resting because they need to move more often across matrix areas in search of food and shelter in distant habitat patches. Such an increase in movement and corresponding decrease in resting would lead to higher energy expenditure, and ultimately to a decline in body conditions and individual fitness (Daan et al. 1996).

We used GPS telemetry with internal tri-axial accelerometers to quantify the influence of agricultural landscape diversity on the behavioural responses of a typical open-habitat species, the European hare (*Lepus europaeus*). Since the 1960s, hare populations have declined strongly throughout Europe, primarily due to agricultural intensification and an associated decline in landscape diversity (Smith et al. 2005). In the 1980s it was already shown that hares in diverse landscapes are more abundant, have a higher survival rate, are heavier, and have larger litters (Frylestam 1980, Tapper and Barnes 1986). But when landscape diversity declines and the size of agricultural crop fields increases, hares increase their home range sizes and subsequentely spend more energy (Mace and Harvey 1983, Tapper and Barnes 1986, Schai-Braun and Hackländer 2014, Ullmann et al. 2018). While these findings indicate the sensitivity of hares to within their habitat, we were particularly interested in identifying how the animals' underlying behavioural modes change with landscape diversity. We used two spatial components to derive a proxy for landscape diversity. First, we set the landscape scale by choosing two study areas in differently sturctured landscapes: a structurally simple landscape with large fields in northeast Germany and a structurally complex landscape with small fields in Southern Germany. Second, for both landscape structures we used each hare's monthly utilization range to calculated the underlying habitat's diversity. We calculated habitat diversity by using the Shannon-Wiener diversity index on the landscape elements within the utilization range. We then related landscape structure and habitat diversity to the hares' behavioural modes. Further, we focused on the relevance of seasonal changes in landscape diversity for sex-specific behavioural responses within certain life-history stages (e.g. mating during the spring and summer, versus reproductive pause in late autumn and winter).

Specifically, we hypothesize that:

1. Hares in diverse habitats will have more time to rest, while those in habitats with low diversity will have to move more frequently, as they must spend more time searching for food and travelling longer distances.
2. This same effect—described in hypothesis 1—will scale to the landscape, resulting in hares spending more time moving in simple landscapes than in complex landscapes.
3. The behavioural modes of males and females will change seasonally following important life-history events like reproduction, resulting in increased moving behaviour during mating and more extended resting periods in the non-reproductive period.

We discuss our findings in the light of the opportunities that behavioral mode analysis from accelerometers provides for a mechanistic view on animal's life-history, and the implications of our findings for human-wildlife coexistence in agricultural landscapes.

Material and Methods

Study area

The study was carried out in two structurally contrasting agricultural landscapes in Germany (Fig. I2). The simple landscape is situated in Northeast Germany, Brandenburg, roughly 100 km north of Berlin (centred at 53° 35′ N; 13° 68′ E). This study area is located in the "Quillow" catchment, within the research platform AgroScapeLab*Quillow* (Agricultural Landscape Laboratory Quillow) of the Leibniz Centre for Agricultural Landscape Research (ZALF) and the BioMove research training group (www.biomove.org/about-biomove/study_area/). The main land-use type is large-scale agriculture with an average field size of 27.5 ± 1.1 ha (mean ± SE; calculated based on maps provided by the Landesvermessung und Geobasisinformation Brandenburg (InVeKoS 2014)) and a low amount of field edges and only few (semi-) natural landscape elements (Batáry et al. 2017). The 213 km² area is up to 62% arable land consisting mainly of wheat, maize, and oilseed rape (Landesvermessung und Geobasisinformation Brandenburg (InVeKoS 2014)). The complex landscape is situated in Southern Germany, Bavaria, 50 km north of Munich (centred at 48° 48′ N; 11° 86′ E). The 256 km² study area is characterized by small-scale agriculture with an average field size of 2.9 ± 0.04 ha (mean ± SE; calculated based on maps provided by the Bayerische Vermessungsverwaltung 2014). Further, the amount of field edges is higher than in North-east Germany (Batáry et al. 2017). The study area in Southern Germany is covered to 66% by arable land. The main crop types are wheat, maize, and grassland (Bayerisches Landesamt für Statistik und Datenverarbeitung 2016). Hare densities were counted by conducting spotlight counts in both study areas during spring and autumn 2014 and 2015. There was no difference in hare abundance (5 hares per km²) in the two differently structured study areas.

Both study areas were classified into 11 different landscape elements: arable land, forest, grassland, loose woods (like hedge rows, avenues and small tree stands), parks, quarries, streets, urban areas, water (usually small streams), field paths, and wetlands (kettle holes). For each landscape element “arable land,” we also recorded the monthly tillage state and/or crop type for both study areas during the entire study period.

Animal tracking

In the spring and summer of 2014 and 2015, hares were caught by driving them into woollen nets (Rühe and Hohmann 2004). During the capture, we weighed the hares, determined their sex, and collared them. We equipped 32 adult hares with GPS collars in both study areas simultaneously (for detailed information and deployment times see Supplement SD). We used collars with a weight of 69 g (Model A1, e-obs GmbH, Munich – Germany, www.e-obs.de) which included a tri-axis acceleration sensor (ACC sensor) besides the GPS device. The ACC sensor allowed us to set an acceleration informed GPS duty cycle, i.e. during inactive periods (variance threshold: 700) no GPS fixes were taken. During times when hares were active, one GPS fix was taken every full hour. Acceleration samples were taken every 4 min, regardless of the hares’ activity state. All tracking and acceleration data were stored at www.movebank.org (Wikelski and Kays 2015).

Behaviour classification

Preceding the behaviour classification we conducted direct observations of three different hares to match the performed behaviour with the corresponding accelerometer output. We observed one hare in an enclosure and two free ranging hares, collecting 3777 acceleration samples (“ bursts”). Those samples were used to calculate predictors which were then employed to train a random forest (R package *randomforest* by Breiman (2001)). The predictors were the same for all three axes and were comprised of the following: standard deviation, mean, range (maximum value minus minimum value) and the mean of the burst before the current burst.

The ACC sensor was set to sample at 33 Hz. Each burst lasted for 3.27 seconds, resulting in 110 samples per burst per axis. Within 3.27 seconds, hares can easily conduct more than one or two different behaviours, so we cut each burst into 1-second intervals and classified the behaviour of each of these 1-second intervals. We took one ACC burst every 4 min, which resulted in 15 samples per hour and thus 360 samples per day or correspondingly 11 160 samples per month (31 days). As each of these samples had three 1-second intervals, our dataset contained 3*360 = 1 080 classified behavioural modes per day or 3*11 160 = 33 480 classified behavioural modes per month. We display the data in two ways. First, we present the number of hours per month and second, we show the percent of each behavioural mode. A full month is represented by 744 hours and 33 480 samples. We used the accelerometer data to determine five different behavioural modes: resting, foraging, moving, grooming and vigilance behaviour (Fig. 2). The cross validation showed an overall error rate of 10.5 % with the following classification error rates: Resting = 0.05, Foraging = 0.22, Moving = 0.08, Grooming = 0.27 and Vigilance behaviour = 0.38. Foraging was most often confused with resting. Grooming was equally often confused with foraging, moving, and resting. The vigilance behaviour was most often confused with resting, as it also is a rather static behavior (see Supplement ST for more details on the classification and variable importance).

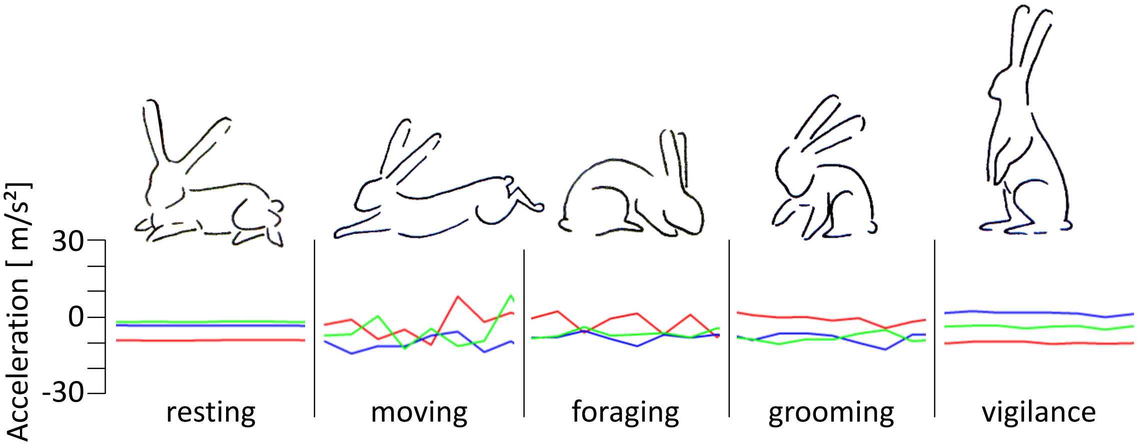

Figure 2. The accelerometer output of the five different behavioural modes. The x-axis is shown in red, the y-axis in blue and the z-axis in green. Resting shows the normal position of the three axis. During a bout of moving (= running) the hare executes strong movements and shows a wide variation of acceleration. When the hare forages, the head is turned to the ground, therefore the x-axis is located about the other two axes. Grooming shows a simlar pattern. During vigiliance behaviour the hare stands upright on its hindlegs, therfore the y-axis is located above the z-axis (as opposed to resting).

We defined resting behaviour as all kinds of sitting positions that did not include any further movements. That involves the head being positioned low to the ground up to sitting up right. Foraging behaviour was defined as slowly moving forward and swaying with the head from side to side or up and down. The actual feeding behaviour, however, is part of the behavioural mode "resting", as hares usually fed in a sitting position while chewing their food. Hence, in our study we use the behavioural mode "foraging" in the sense of searching for resources. We defined moving behaviour as all kinds of displacement, like running or hopping from one location to another, without further behaviours like searching or stopping or resting. Grooming was classified when the animals where licking, scratching, or stretching themselves. Vigilance behaviour in our study was defined as standing up on the hind legs to get a better overview of the surroundings. However, we disregarded behavioural modes for the analysis when the classification error was higher than 0.2 and the behavioural mode occurred less than 5%. Thus, we analysed resting, moving, and foraging behaviours, but did not take into account grooming and vigilance behaviour in the manuscript. For interested readers the results can be found in the Supplement SG.

Determination of habitat diversity

We calculated habitat diversity by using the Shannon-Wiener habitat diversity index on land-use shapefiles containing data on field and landscape element properties (Turner 1990). We used each hares' monthly utilization ranges to determine the area for which the Shannon-Wiener diversity index should be calculated, and from these areas, we extracted information about the underlying habitat. We calculated the monthly utilization ranges by using 100 % minimal convex polygon (MCP) from the *adehabitatHR* package (Calenge 2006), and additionally buffered the MCP polygons with a 50 m buffer (package *rgeos*, Bivand and Movedel (2016)). This was done to consider the animals' perceptual range as well as possible movements that occurred just before or after a GPS fix was taken. We then used each monthly utilization range and the land-use shapefiles to acquire the type and the size of all landscape elements for the corresponding month (package *raster*, Hijmans and Van Etten (2014)). For each landscape element "arable land", we added the information on the field's current crop type or tillage state. We then calculated the Shannon-Wiener habitat diversity for each monthly utilization range. Further, we counted the number of each behavioural mode per month to account for shifts in hare behaviour over the course of the year. We added the information on monthly behavioural modes to the respective hare's monthly utilization range and habitat diversity. We received data from collared hares from April to January for both study years (2014 and 2015) and thus added January as month 13 to the data set (month 4 to 13) for illustration purposes and easier interpretation of the results.

Statistics

We used linear mixed effects models (R package *lme4*, Bates et al. (2014)) to test for the influence of landscape diversity and seasonality on the count of monthly behavioural modes (resting, moving, and foraging). We ran the analyses for each behavioural mode separately to assure normally distributed residuals, as assumption of normality could not be met when the values for resting behaviour are normally distributed around 70% but for foraging behaviour around 20%.

The response variable for the linear mixed effects models was the monthly count of the behavioural mode (resulting in 3 linear mixed models). The animals' sex (female or male), landscape structure (simple vs. complex), month, and habitat diversity (Shannon-Wiener diversity index) were used as fixed factors, while animal ID was the random term. We included two-way interactions between all explanatory variables. We then used each global model as well as all its nested submodels for model selection (Dochtermann and Jenkins 2011). As the study spans almost an entire yearly cycle the best model to conduct the analyses with was to use the third polynomial for month. The fixed factors were tested for collinearity (Zuur et al. 2009) and for non-linear relationships by using generalized additive models (GAMs – package *mgcv*, Wood (2001)). Scaled residuals (R package *DHARMa*, Hartig (2017)) were used to test linearity and temporal autocorrelation. We used an information theoretic approach build into the R package *MUMIn* (Barton 2013) to select models based on the lowest AIC score. In the Supplement SA we indicate the summary output of the chosen model as well as all other models within delta AIC < 2 (Burnham and Anderson 2003).

Results

Resting – The resting activity for female hares was almost stable throughout the year, but for males, resting was with 58% (420 h) lowest in January and with 71% (527 h) highest in October (Fig. 3A). Habitat diversity had a strong influence on resting behaviour in the complex landscape, but not in the simple landscape (Fig. 4). While hares in the complex landscape rested about 65% (486 h) of their time in areas of low habitat diversity, they rested 74% (555 h) in areas of high habitat diversity (Fig. 4). An increase in resting behaviour with increasing habitat diversity was most prominent in April, May, June, and July, while for the rest of the year resting was not affected by habitat diversity (Fig. 5).

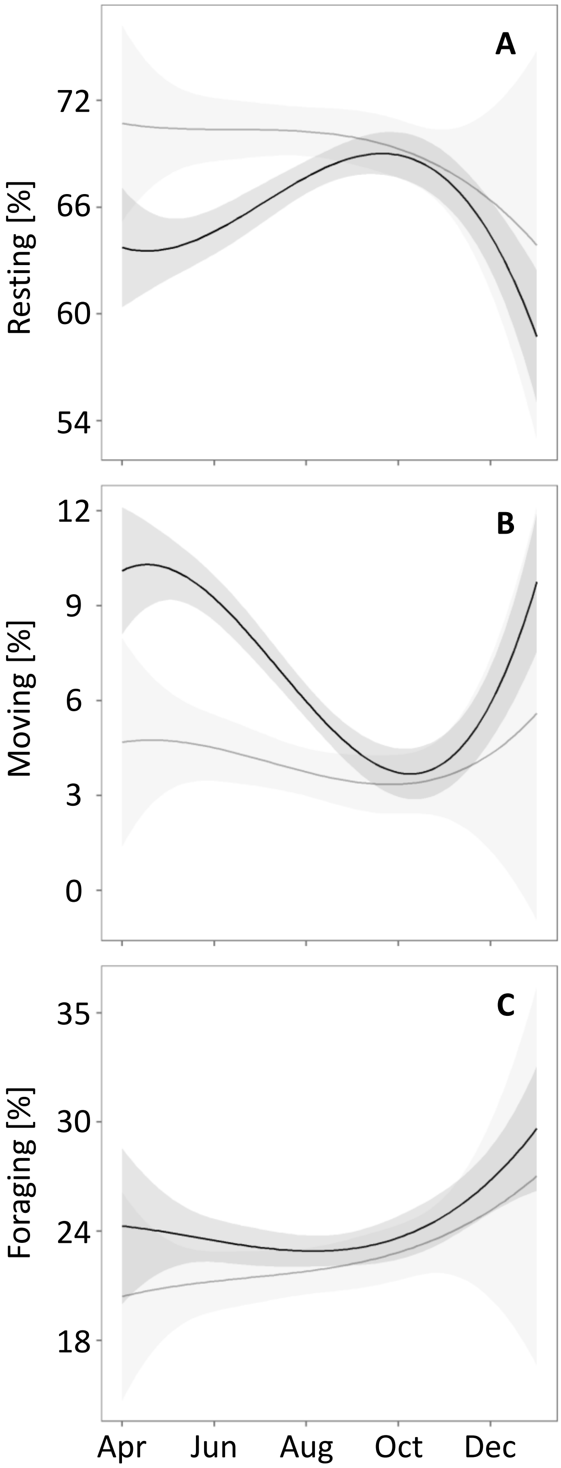

Figure 3: The monthly percentages of the behavioural modes resting (A), moving (B) and foraging (C) over the course of the year and for the two sexes. Black lines = males; grey lines = females.

Moving – Female hares moved most from December to June—5.5% (41 h) per month— while they moved only 3% (24 h) in October (Fig 3B). Male hares showed a similar pattern time wise, but it was more pronounced than for female hares. In April and May male hares spent 10% (75 h) of their time moving, while they only spent 4% (28 h) moving in October (Fig. 3B). Hares moved 6% (44 h) of their time in the simple landscape and 4% (30 h) in the complex landscape (Fig. 6A). They also moved less with increasing habitat diversity during April and May, for the rest of the year however there was no relationship between moving and habitat diversity (Fig. 5). In April, for example, hares moved 17% (126 h) per month in areas of low habitat diversity, while they moved only 2% (16 h) per month in areas of high habitat diversity (Fig. 5).

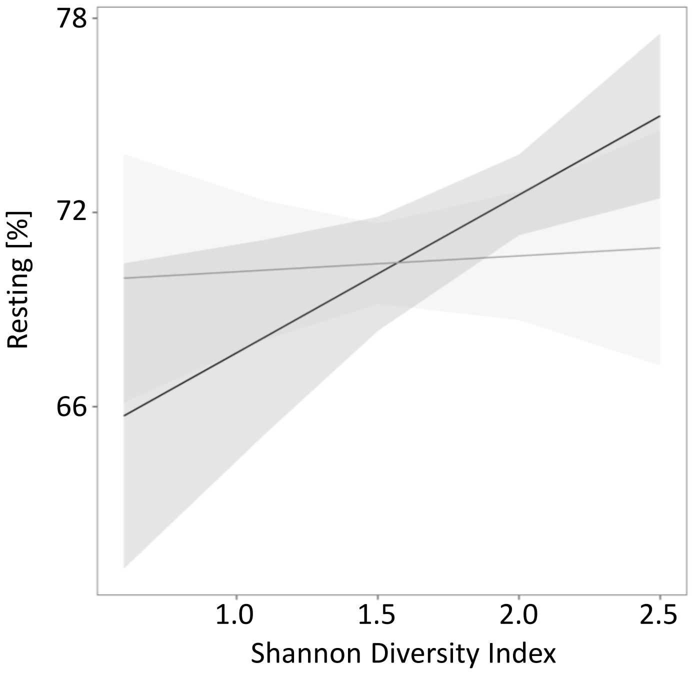

Figure 4: Impact of habitat diversity on the monthly percentage of resting behaviour in two contrasting agricultural landscapes in Germany. Black line = complex landscape; grey line = simple landscape.

Foraging – Female hares spent about 18% (140 h) per month of their time searching for food (Fig. 6B). Male hares on the other hand foraged substantially more often – they used 21% (156 h) of their time to forage (Fig. 6B). Hares of both sexes foraged less with increasing habitat diversity, but mainly in June and July – the rest of the year habitat diversity had a minor influence on foraging behaviour (Fig. 5). In June, for example hares searched for food for about 24% (179 h) in areas of low habitat diversity and 18% (132 h) in areas of high habitat diversity (Fig. 5). We could not detect a relationship between animal sex and season for foraging behaviour (Fig. 3C).

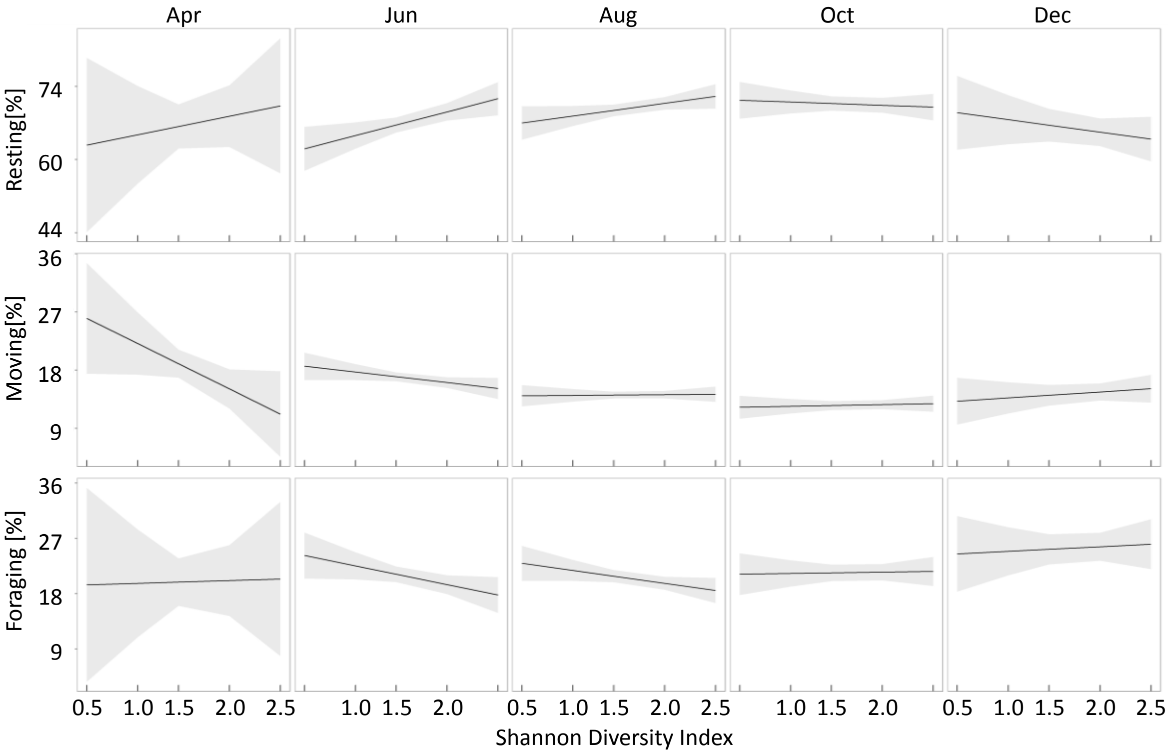

Figure 5: Monthly percentages of resting, moving and foraging behaviours in relation to habitat diversity. The different panels show the months: April, June, August, November and December. Both animal sexes (males and females) and both landscapes (simple and complex) are pooled together in this graph.

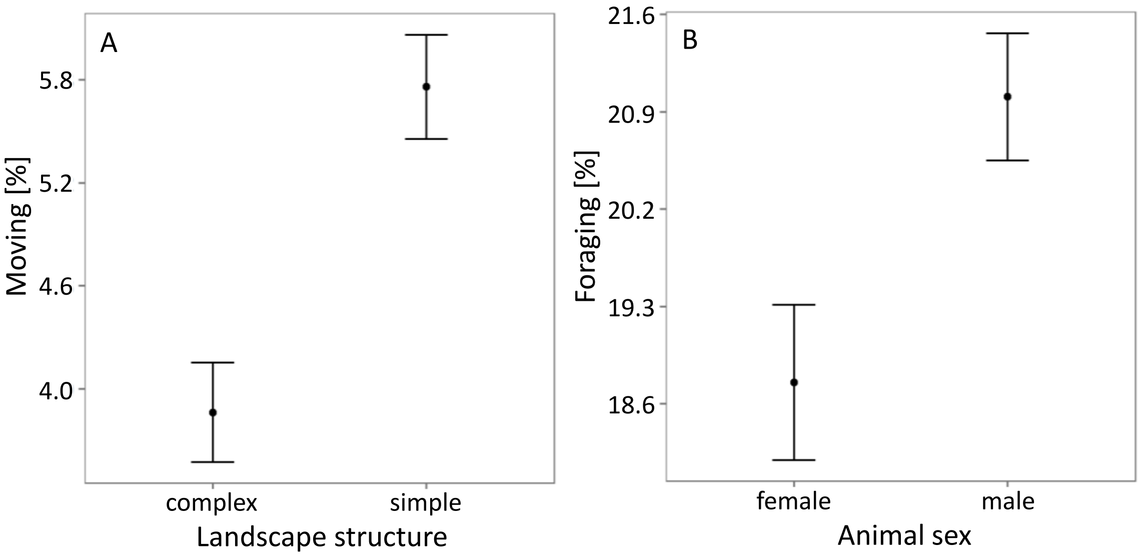

Figure 6: The monthly percentage of hare moving behaviour in the simple and in the complex landscape (A) and the monthly percentage of foraging behaviour for female and male hares (B).

Discussion

Agricultural areas cover large parts of Europe and wild life comes into regular contact with them. They display significant differences in their underlying landscape diversity, and provide varying degrees of habitat quality to hares and other animal species. In our study we show that changes in hare movement behaviour is connected to landscape diversity. We combined information on habitat diversity and the GPS locations of hares with an analysis of accelerometer data, providing new—mechanistic—insights into hare behaviours. Three of the five classified behavioural modes (resting, moving, and foraging) proved to be sensitive to seasonal changes in habitat diversity. We found that hares in areas of low habitat diversity—where resources were scarce and spatially distant—were resting less, moving more, and spending more time searching for food than animals in diverse habitats. We also showed that hares in simple landscapes generally moved more than hares in complex landscapes. The diversity effects on the three behavioural modes were especially pronounced during the peak breeding season from April to June, indicating a strong necessity for high quality habitats during reproduction. This influence was particularly striking in the males' behaviour, which showed significantly higher movement activity during the reproductive period.

Movement is one of the key features that help animals to deal with environmental variability, such as seasonal changes in habitat quality or landscape diversity. At a broader spatiotemporal scale, this may be reflected in changes in home range size (Lucherini and Lovari 1996, Saïd et al. 2009, Lovari et al. 2013, Schai-Braun and Hackländer 2014). By focusing on accelerometer data of a high temporal resolution (every 4 minutes), we were able to explain these changes in the hares' higher-level movement behaviour (i.e. home range formation) through extracting their underlying, minute-by-minute, movement behaviour.

Hares in simple landscapes with large fields moved more than hares in complex landscapes with small fields. This increase in the behavioural mode "moving" explains the increase in their home range size from complex to simple landscapes (Ullmann et al. 2018), and thereby may also be the underlying reason for the observed enlargement of their home range size with increasing crop field size shown by Schai-Braun and Hackländer (2014). Home range sizes may also be influenced by animal densities (Finlayson and Moseby 2004), but due to similar hare abundances in both of our two study areas, we can dismiss this. In addition, hare home ranges usually overlap strongly, where dominants and subordinates share the same space, showing no spatial territoriality (Monaghan and Metcalfe 1985, Holley 1986, Marboutin and Aebischer 1996). Hence, we assume that the change in animal behaviour is indeed due to changes in the underlying habitat diversity.

Clearly, landscape diversity is strongly linked to habitat quality (Turner 1989, Dunning et al. 1992) and affects movement behaviour (Turner et al. 2001). For example, Klein et al. (2004) show that some hymenoptera spend less time foraging in high quality habitat. When resources are abundantly available they are easily found and the time saved from searching for them can be allocated into other activities like resting or playing (Li and Rogers 2004). This is in line with our results showing that hares in diverse habitats are resting more and spend less time moving and searching for resources. Furthermore, habitat diversity had the largest effects on behavioural patterns between April and June, i.e. the peak of reproduction in hares (Frylestam 1980). Such high importance of habitat quality during the breeding season was also found in roe deer (McLoughlin et al. 2007). Choosing a home range within high quality habitat plays an important role for individual fitness, as it subsequently results into favourable proportions of resting vs. moving and foraging behaviour. This is crucial during the breeding period as animals are able to allocate more energy into reproduction when other requirements (e.g. food and shelter) are easily available (Trivers 1972, Tieleman et al. 2008).

We found that the behaviours of male hares were especially impacted by the annual reproductive cycle. They moved most during May and least during October, coincident to the peak and end (September/October) of reproduction (Flux 1965, Frylestam 1980, Hansen 1992). The social behaviour during the breeding season is characterized by males competing for oestrous females, mainly by boxing or chasing competitors far away from the female, but also by fights between males and unreceptive females (Holley 1986, Alves et al. 2008). These behaviours relate to an increased amount of moving during the breeding season, as we found in our study. The seasonal changes in male movement activity are probably related to the position and structure of their testes. We recorded the lowest movement activity of male hares in October, when testes usually move from the scrotum to the inner part of the abdomen, and highest activity in January at the beginning of the reproduction time, when testes are returned to the scrotum (Simeunovič et al. 2000). A very similar isochronic pattern can be observed for the weight of the testes (Simeunovič et al. 2000, Alves et al. 2002).

Our observed changes in the behavioural modes of hares relative to agricultural landscape diversity will likely apply to other mobile species as well. Hares, as well as other species—such as roe deer, red fox, wild turkey, and lynx—react to environmental changes by altering their home range size (Lucherini and Lovari 1996, Herfindal et al. 2005, Saïd and Servanty 2005, McLoughlin et al. 2007, Marable et al. 2012, Lovari et al. 2013, Morellet et al. 2013). These home range size adjustments are caused by changes in the proportion of behavioural modes, driven by changes in habitat quality and diversity. For animals in agricultural landscapes, land-use intensification decreases habitat quality (Chamberlain et al. 2000, Burel et al. 2004). Eventually, low habitat diversity forces animals to move more and search longer for food, allocating less energy into reproduction, which can result in a decline in fitness and, over the long term, may lead to the local extinctions frequently observed in intensified agricultural landscapes (Benton et al. 2003, Tscharntke et al. 2005).

Through our research, we have shown that the underlying cause of shifts in home range size arises from changes in the animals' behaviour, especially during reproduction. High landscape diversity assures that the individuals' strength is allocated to reproduction rather than self-maintenance. Landscape diversity has to be increased to assure the survival of wild life in agricultural areas. This aim may be reached by planting wild flower strips (Meichtry-Stier et al. 2014), increasing the proportion of ecological farming (Winqvist et al. 2011), decreasing field size (Tapper and Barnes 1986, Schai-Braun and Hackländer 2014, Fahrig et al. 2015, Batáry et al. 2017) and implementing agri-environmental schemes (Fischer et al. 2011).

Lastly, our study provides further a proof-of-concept in the strength of biologging technologies to illuminate some of the most prescient questions in ecology. Combining GPS positions, synchronous accelerometer data, and information about the underlying landscape gives researchers a remarkable opportunity to follow the secret life of wild animals, mechanistically linking changes in their behavioural patterns to their precise environment. This advancement holds great promise to improve predictions of animals' movement behaviour and energy expenditure.

Data accessibility

The GPS and accelerometer data is deposited in Movebank (study name: “AgroScapeLabs”).

Acknowledgments

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Chapter 4

Habitat selection by the European hare in arable landscapes: The importance of small-scale habitat structure for conservation[4]

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Abstract

Agricultural land-use practices have intensified over the last decades, leading to population declines of various farmland species, including the European hare (*Lepus europaeus*). In many European countries, arable fields dominate agricultural landscapes. Compared to pastures, arable land is highly variable, resulting in a large spatial variation of food and cover for wildlife over the course of the year, which potentially affects habitat selection by hares. Here, we investigated within-home-range habitat selection by hares in arable areas in Denmark and Germany to identify habitat requirements for their conservation. We hypothesized that hare habitat selection would depend on local habitat structure, i.e., vegetation height, but also on agricultural field size, vegetation type, and proximity to field edges. Active hares generally selected for short vegetation (1-25 cm) and avoided higher vegetation and bare ground, especially when fields were comparatively larger. Vegetation >50 cm potentially restricts hares from entering parts of their home range and does not provide good forage, the latter also being the case on bare ground. The vegetation type was important for habitat selection by inactive hares, with fabaceae, fallow and maize being selected for, potentially providing both cover and forage. Our results indicate that patches of shorter vegetation could improve the forage quality and habitat accessibility for hares, especially in areas with large monocultures. Thus, policymakers should aim to increase areas with short vegetation throughout the year. Further, permanent set-asides, like fallow and wildflower areas would provide year-round cover for inactive hares. Finally, the reduction of field sizes would increase the density of field margins, and farming different crop types within small areas could improve the habitat for hares and other farmland species.

Introduction

Agricultural landscapes dominate in large parts of the world, with 38% of the Earth's ice-free surface being covered by cropland and pasture (Foley *et al.* 2011). In Europe, pastures (permanent grassland and meadow) cover 14.4% of the land area and arable land (cropland used under a system of crop rotation) accounts for 26.5% of the area, making Europe one of the most intensely used agricultural areas (Ramankutty *et al.* 2008). Accordingly, agricultural areas are important habitats for a wide range of Europe's biodiversity, including birds and mammals of which some have adapted to these culturally influenced habitats. Since the beginning of the 20th century, agriculture intensified steadily in Europe, leading to increased yields due to larger field sizes, the use of agro-chemicals and the improved efficiency of machinery (O'Brien & De La Escosura 1992; Marshall & Moonen 2002; Smith *et al.* 2004). This intensification ultimately led to a decreased habitat heterogeneity (Benton, Vickery & Wilson 2003), causing a steep decline in biodiversity (Reidsma *et al.* 2006), for example, abundance and species richness of plant species (Storkey *et al.* 2011) and farmland birds (Donald, Green & Heath 2001; Heldbjerg, Sunde & Fox 2017; Bowler *et al.* 2018).

Agricultural land is the main habitat of the European hare (*Lepus europaeus*, hereafter hare, Fig. 1) (Frylestam 1980; Vaughan *et al.* 2003). Hares have declined throughout Europe since 1960 (Smith, Jennings & Harris 2005) and are classified as "near threatened" or "threatened" on the Red List of Threatened Species in several countries, for example Austria, Germany, Norway and Switzerland (Boye 1996; Reichlin, Klansek & Hackländer 2006). There is an increasing body of literature suggesting that agricultural intensification is the ultimate reason for the decline of hare populations (Smith, Jennings & Harris 2005 and references therein), although predation, disease, hunting, and a changing climate may also be population limiting factors (Lindström *et al.* 1994; Edwards, Fletcher & Berny 2000; Hackländer, Arnold & Ruf 2002). Hence, in order to implement effective conservation measures, it is important to investigate the elements affecting hare habitat use in intensively used agricultural landscapes.

Figure 1: Our study species, the European hare (Lepus europaeus) in a barley field in Denmark.

Home range sizes of hares increase with agricultural field size, and hares generally select for proximity to field edges (Petrovan, Ward & Wheeler 2013; Schai-Braun & Hackländer 2013) and avoid roads (Roedenbeck & Voser 2008). Moreover, it was shown that hares utilize different habitats when being active (typically during nighttime) for foraging compared to when resting (typically during daytime) (Tapper & Barnes 1986; Neumann *et al.* 2012). However, little is known about how habitat and vegetation structure affect within-home-range habitat selection in arable landscapes (but see Tapper & Barnes 1986). Smith *et al.* (2004) investigated how vegetation height affected habitat selection by hares in pastural landscapes in Britain. They argued that there is a greater potential to increase hare numbers in pastural landscapes compared to arable land, because in pastural landscapes hare densities are comparatively lower and hares are in poorer body condition. In the United Kingdom, 63% of the agricultural land is pastural, and 37% is arable land. However, in most western (apart from Great Britain), central and northern European countries, arable land makes up the majority of the agricultural landscape (Table 1). For example, arable land accounts for 71% of the agricultural used land in Germany and for 92% in Denmark (Table 1). Thus, for large parts of Europe, arable land is highly important for hares simply because it makes up such a large proportion of its habitat.

Table 1: The percentage of land use type in selected European countries in 2013 (Source: http://ec.europa.eu/eurostat/statistics-explained/index.php/Farm_structure_statistics#Agricultural_land_use).

	Land use type		
Country	Arable land	Pastural land	Other
Denmark	**91.5**	**7.5**	**1.02**
Sweden	85.1	14.8	0.16
Hungary	81.6	15.1	3.29
Poland	74.7	22.3	3.08
Slovakia	71.7	27.3	1.04
Czech Republic	71.4	27.5	1.13
Germany	**71.1**	**27.7**	**1.21**
Bulgaria	70.5	27.3	2.16
France	66.6	29.7	3.72
Belgium	61.1	37.2	1.67
Netherlands	56.2	41.8	1.98
Croatia	55.9	39.3	4.75
Austria	50.0	47.5	2.45
Luxembourg	47.8	51.1	1.18
United Kingdom	**36.7**	**63.1**	**0.21**
Slovenia	35.6	58.6	5.82
Ireland	21.0	79.0	0.03
European Union	**59.8**	**34.2**	**6.1**

In this study, we investigated within-home-range habitat selection by hares in agricultural landscapes dominated by arable land in Denmark and Germany using GPS technology. Arable crops greatly change both within and between the vegetative seasons, providing cover and food during parts of the year, but not during others when high crops potentially represent a barrier and decrease forage quality, and ploughed fields restrict cover and forage. Further, the size of agricultural fields should be important, because areas with larger fields are more homogenous, providing less cover and foraging opportunities (Petrovan, Ward & Wheeler 2013; Schai-Braun & Hackländer 2013), resulting in increased home range sizes (Ullmann *et al.* 2018). Thus, we hypothesized that both vegetation height and field size would be more important in explaining habitat selection by hares than the vegetation type itself. This is important, because using a measure of vegetation height and field size rather than crop types would facilitate the identification of vital habitat requirements for hares and other threatened farmland species, in turn providing simple guidelines to increase the habitat quality. We calculated hare home range sizes to investigate the influence of field size, vegetation height, and vegetation type on hare habitat selection. Specifically, we predicted that hares would select for comparatively shorter vegetation when being active as this provides better forage and allows the detection of predators, and for comparatively higher vegetation when inactive (providing cover). Similarly, we predicted that active hares would select for vegetation types that provide good forage (e.g. fallow, pasture, young cereals) and inactive hares select for vegetation types that provide good cover (e.g. fabaceae, maize). Further, we predicted that hares would generally select for smaller fields, because they constitute a more heterogeneous landscape, and more so with increasing vegetation height, because high vegetation potentially represents a barrier to enter further into (larger) fields. Finally, we predicted that hares would select for proximity to field edges, because they increase habitat heterogeneity (Petrovan, Ward & Wheeler 2013) providing both cover and food, and more so with increasing vegetation height, because high vegetation might represent a physical barrier.

Materials and methods

Study Area

We conducted fieldwork in three study areas that were located in 1) Syddjurs community, Midtjylland region, Denmark (hereafter Denmark), 2) Uckermark, Brandenburg, Germany (hereafter Northern Germany), and 3) Freising, Bavaria, Germany (hereafter Southern Germany) (Fig. 2). The landscape was dominated by arable land in all three study areas. The Danish study area mostly consisted of arable fields (94%) tilled with wheat (*Triticum aestivum*), barley (*Hordeum vulgare*), rapeseed (*Brassica napus*), beans (*Vicia* *faba*), and oats (*Avena sativa*). The rest of the area consisted of meadow, game fields, and fallow.

The study area in Northern Germany primarily consisted of large arable fields (90%) interspersed with some forest patches, pastures, urban areas and water (InVeKoS 2014). Wheat, barley, rapeseed, and maize (*Zea mays*) were the dominant crop types, but sugar beet (*Beta vulgaris*), charlock mustard (*Sinapis arvensis*) and triticale were also present. The study area in Southern Germany mostly consisted of smaller arable fields (83%) interspersed with forest patches, pastures, water and urban areas (Vermessungsverwaltung 2014). Wheat, maize, barley, rapeseed and charlock mustard were the most common crop types, but hops (*Humulus lupulus*), pastures, sugar beet, rye (*Secale cereale*), triticale, clover (*Trifolium* spp.), oats, peas (*Pisum sativum*) and potatoes (*Solanum tuberosum*) were also cultivated. Hare density in both German areas was approximately 5 hares per km^2, but fox density was higher in Northern Germany (ca. 0.8 per km^2) than in Southern Germany (ca. 0.2 per km^2; Wiebke Ullmann, unpublished results). We did not obtain data on hare and fox densities in Denmark.

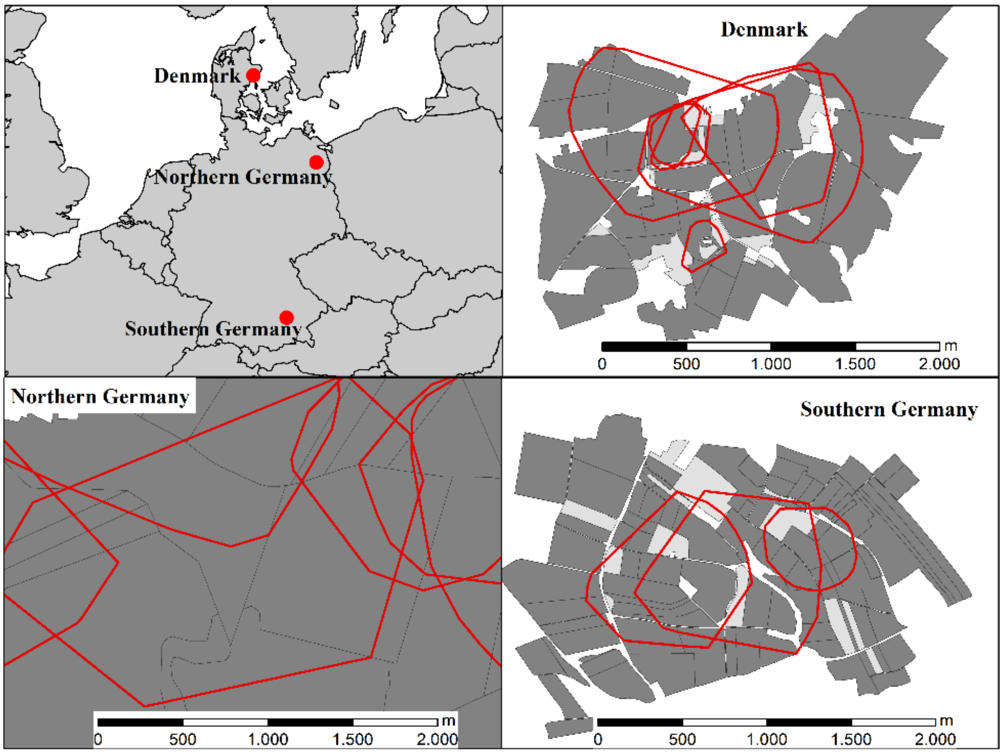

Figure 2: Map showing the location of the three study areas (red dots, top left), and exemplary European hare (*Lepus europaeus*) home ranges (red lines) from Denmark (top right), Northern Germany (bottom left), and Southern Germany (bottom right). Arable fields are shown in dark grey, pastures in light grey. Hare GPS data were obtained in 2014-2015.

Hare Captures

In Denmark, we captured hares in 2014 using box traps that were set up in pairs along the edges of agricultural fields. In Germany, we captured hares in 2014 and 2015 by driving them into nets (Rühe & Hohmann 2004). We transferred captured hares into a canvas cone (Denmark) or a wooden box (Germany), where they could be handled without anesthesia. Hares were sexed and fitted with a GPS collar (e-obs A1, e-obs GmbH, Gruenwald, Germany). GPSs in Denmark were set to take one-hourly GPS positions. In the two German areas, GPSs were set to take one-hourly positions while hares were active (defined by an acceleration threshold), and to take four-hourly positions when hares were inactive. We obtained GPS data from May until December in Denmark, from May until January (the following year) in Southern Germany, and from all months in Northern Germany.

Data Preparation

Habitat data

We categorized the different crop species in the variable ‘vegetation type’, consisting of 11 categories based on biological knowledge (Table 2). Other landscape elements (e.g. forest, permanent plantations, and water banks) were excluded, because they made up a negligible proportion of individual hare home ranges (<1%). The variable ‘vegetation height’ was grouped into five categories: no vegetation (bare ground), 1-25 cm, >25-50 cm, >50-100 cm, and >100 cm. We used this categorization, because vegetation height was measured too infrequently (monthly or bi-monthly depending study area and year), and because crops grow very fast during the vegetative season, not allowing for a precise continuous variable. In Denmark the height category ‘>100 cm’ was absent, because crops did not grow over 100 cm in height. We calculated the size of agricultural fields (in ha) in ArcMap 10.4.1 (Esri, Redlands, CA, USA), defined as the continuous variable ‘field size’. Further, we calculated the Euclidean distance of GPS positions to field edges as a measure of proximity to field edges in ArcMap, defined as the continuous variable ‘edge distance’.

GPS data

We removed individuals, where the GPS failed after a short time period (<100 GPS positions; 12 of 64 individuals). Further, we removed the first day from the analysis to avoid possible effects of capture and handling. We then calculated the home range size of

Table 2: Showing the crop species and agricultural treatments that we categorized into the 12 different vegetation types; and the number of random and used GPS positions. Percentages of random and used GPS positions are given in parentheses.

Vegetation type	Crop species/agricultural treatment	random GPS positions	used GPS positions
Beet	Sugar beet (*Beta vulgaris*)	1860 (43.6)	2409 (56.4)
Brassicaceae	Charlock mustard (*Sinapis arvensis*), rapeseed (*Brassica napus*), winterrape	6794 (57)	5118 (43)
Cereal	Barley (*Hordeum vulgare*), oats (*Avena sativa*), rye (*Secale cereale*), triticale, wheat (*Triticum aestivum*), winterbarley, winterwheat	25600 (54.2)	21612 (45.8)
Fabaceae	Beans (*Vicia faba*), peas (*Pisum sativum*)	2113 (38.3)	3408 (61.7)
Fallow	Fallow and game fields consisting of various plant species	2035 (41.9)	2822 (58.1)
Fodder	Agricultural grass, clover (*Trifolium* spp.)	1021 (53.1)	901 (46.9)
Hops	Hops (*Humulus lupulus*)	381 (50.3)	377 (49.7)
Maize	Maize (*Zea mays*)	12529 (49.2)	12957 (50.8)
No vegetation (bare ground)	Harrowed, ploughed, raked, and freshly sown ground	10246 (45.5)	12261 (54.5)
Pasture	Meadow and pasture	11233 (42.5)	15222 (57.5)
Stubbles	Harvested cereal, maize, and rape	5529 (46.2)	6446 (53.8)

individual hares based on 95% minimum convex polygons (MCP) during each individuals' sampling period (mean ± SD: 1607 ± 1157 individual GPS positions) in R 3.2.5 (R Core Team 2013) using the *adehabitatHR* package (Calenge 2006). We used MCPs instead of Kernel density estimation, because the latter potentially excludes available but unused areas, which could bias the analysis. To get a measure of resource availability, we created the same number of random GPS positions than we had obtained from each hare within each individual hare home range. We then assigned each random and used (hare) GPS position to the vegetation type, vegetation height, field size, and the edge distance using the 'join' tool in ArcMap. We removed all GPS positions (both used and random) that could not be assigned to a vegetation type or height (14% of the data). To obtain a proxy of activity, we calculated the straight-line distance between consecutive (that is, hourly) hare GPS positions (Schai-Braun, Rödel & Hackländer 2012). We then plotted the average distance moved per hour against the time of the day separately for long (>12 hours daylight) and short (<12 hours daylight) days, because hares shift their activity with changing daylight length (Schai-Braun, Rödel & Hackländer 2012). Further, we plotted them separately for the three study areas, because hare home range sizes differed significantly between areas (see results), leading to different hourly movement distances (Fig. S1). Finally, we calculated the overall average distance moved (separately for the three areas), and set the threshold for activity as 75% of the overall average distance moved, that is, we categorized hares as 'active' if hourly distance moved was >75% of the average distance moved, and 'inactive' if it was <75% of the average distance moved (Fig. S1).

Statistical Analysis

We used resource selection functions (Manly *et al.* 2007) to investigate within-home-range habitat selection by hares separately for active and inactive GPS positions due to different habitat requirement for foraging and resting (Neumann *et al.* 2012). We built generalized linear mixed models (GLMM) with a Bernoulli distribution and a logit link as dependent variable (1 = used (hare) GPS position versus 0 = available (random) GPS position). To investigate the relative importance of field and vegetation features for habitat selection, we created four candidate models, including one fixed effect per model: 1) vegetation type, 2) vegetation height, 3) field size, and 4) the quadratic function of edge distance (fitted better than the linear function based on Akaike's Information Criterion corrected for small sample size (AIC_c) (Burnham, Anderson & Huyvaert 2011). The vegetation type 'cereal' and the vegetation height '26-50 cm' were used as reference, because they were present and largely available in all study areas. The hare ID, area and month nested within year (to control for seasonal and annual effects) were included as random intercept.

We then investigated finer-scale habitat selection using GLMMs (1 = used, 0 = available) separately for active and inactive GPS positions. Fixed effects were the vegetation type, vegetation height, field size, and the quadratic function of the edge distance. We included two interactions: 1) vegetation height x edge distance to test if hares would select for proximity to field edges with increasing vegetation height, 2) vegetation height x field size to investigate if higher vegetation was a greater barrier in larger fields. For this analysis, we merged vegetation heights '>50-100 cm' and '>100 cm', because vegetation >50 cm was generally avoided (see results). Hare ID, area and month nested within year were included as random intercept to control for annual/seasonal variation and multiple observations. After initially checking for sex differences in habitat selection, we did not include this variable in our main analyses, because we found no differences between females and males. We used a set of 20 candidate models including different combinations of the fixed effects and the above-described interactions (Table S1).

Field size and edge distance were log-transformed to normalize residuals of the statistical models. We found no collinearity among fixed effects ($r < 0.6$ in all cases), and variance inflation factors were < 3 (Zuur, Ieno & Elphick 2010). Model selection was based on AIC_c and AIC weights (Burnham, Anderson & Huyvaert 2011), and was carried out using the R package *MuMIn* (Barton 2013). If ΔAIC_c was < 10 in two or more of the most parsimonious models, we performed model averaging (Anderson 2008; Bolker *et al.* 2009). Parameters that included zero within their 95% CI were considered uninformative (Arnold 2010). We validated the most parsimonious models by plotting the model residuals versus the fitted values (Zuur *et al.* 2009). All statistical analyses were carried out in R 3.2.5 (R Core Team 2013).

Results

Home range sizes and agricultural field sizes

We obtained data of 52 individuals (28 in Northern Germany, 18 in Southern Germany, and 6 in Denmark), 22 females and 30 males, from which we got 1607 ± 1157 (mean ± SD) individual GPS positions, resulting in a total of 83.533 GPS positions (61.746 active and 21.787 inactive positions) that we could assign to different habitat parameters. Individual home range sizes varied between 4 and 150 ha. After controlling for different GPS sampling durations (by including the number of individual GPS locations), home ranges were significantly larger in Northern Germany (77 ± 43 ha) compared to Denmark (44 ± 41 ha) and Southern Germany (30 ± 19 ha, linear regression: $p < 0.01$). Home range sizes in Denmark did not differ significantly from Southern Germany ($p = 0.54$). Further, agricultural fields in Northern Germany were significantly larger compared to Southern Germany and Denmark (t-test: $t > 6$, $df > 78$, $p < 0.001$), and Danish fields were significantly larger compared to Southern Germany ($t = 2.31$, $df = 48.1$, $p = 0.03$).

Table 3: The model selection result for the candidate models investigating the relative importance of habitat type and habitat structure for habitat selection by European hares (*Lepus europaeus*) based on data collected in Denmark and Germany (2014-2015). Hare ID, area and month were included as random effects. Models were ranked based on AIC_c.

Model	df	logLik	AIC_c	delta AIC_c	AIC_c weight
Active GPS positions					
Vegetation height	9	-82128	164275	0	1
Vegetation type	15	-82619	165268	993	0
log (Field size)	6	-83096	166205	1930	0
log (Edge distance) + log (Edge distance)^2	7	-83165	166344	2069	0
Inactive GPS positions					
Vegetation type	15	-28554	57139	0	1
Vegetation height	9	-28831	57681	542	0
log (Field size)	6	-29143	58298	1159	0
log (Edge distance) + log (Edge distance)^2	7	-29160	58335	1196	0

Habitat selection

Relative importance of habitat type and structure

When evaluating the relative importance of habitat type and structure for habitat selection by hares, the model including the vegetation height was by far the best (AIC weight = 1) for active GPS positions, followed by vegetation type, field size, and edge distance (Table 3). When investigating inactive GPS positions, the model including vegetation type was the best (AIC weight = 1), followed by vegetation height, field size, and edge distance (Table 3).

Table 4: Effect size (β), standard error (SE), lower (LCI) and upper (UCI) 95% confidence interval of explanatory variables for the analyses of habitat selection by European hares in Denmark, Southern and Northern Germany (2014-2015) separately for active and inactive GPS positions. Informative parameters are given in bold. Positive β values indicate a higher relative probability of use (selection), whereas negative values indicate a lower relative probability of use (avoidance).

	Active GPS positions				*Inactive GPS positions*			
Variable	β	SE	LCI	UCI	β	SE	LCI	UCI
(Intercept)	0.11	0.11	-0.11	0.32	0.26	0.14	-0.01	0.54
Vegetation type No vegetation	**0.82**	**0.07**	**0.69**	**0.95**	**0.39**	**0.11**	**0.17**	**0.61**
Vegetation type Fabaceae	**0.20**	**0.05**	**0.10**	**0.31**	**1.37**	**0.06**	**1.26**	**1.49**
Vegetation type Beet	**0.35**	**0.05**	**0.26**	**0.44**	**-0.21**	**0.08**	**-0.37**	**-0.05**
Vegetation type Brassicaceae	**-0.11**	**0.03**	**-0.17**	**-0.06**	**0.19**	**0.05**	**0.10**	**0.28**
Vegetation type Fallow	**0.34**	**0.04**	**0.27**	**0.42**	**0.73**	**0.07**	**0.60**	**0.86**
Vegetation type Fodder	-0.06	0.06	-0.17	0.05	**-0.55**	**0.11**	**-0.76**	**-0.33**
Vegetation type Hops	0.04	0.09	-0.13	0.21	-0.08	0.17	-0.42	0.25
Vegetation type Maize	**0.49**	**0.02**	**0.45**	**0.53**	**0.82**	**0.04**	**0.75**	**0.90**
Vegetation type Pasture	**0.24**	**0.02**	**0.20**	**0.29**	**0.27**	**0.04**	**0.19**	**0.35**
Vegetation type Stubbles	-0.01	0.03	-0.06	0.05	**0.21**	**0.05**	**0.12**	**0.30**
Vegetation height No vegetation	**-0.76**	**0.10**	**-0.96**	**-0.57**	**-0.55**	**0.18**	**-0.90**	**-0.20**
Vegetation height 1-25 cm	**-0.36**	**0.07**	**-0.49**	**-0.23**	**-0.66**	**0.11**	**-0.88**	**-0.44**
Vegetation height >50 cm	-0.07	0.07	-0.21	0.07	**-0.56**	**0.12**	**-0.80**	**-0.32**
log (Edge distance)	**0.12**	**0.03**	**0.07**	**0.18**	**-0.24**	**0.05**	**-0.34**	**-0.14**
log (Edge distance)^2	**-0.04**	**0.00**	**-0.05**	**-0.04**	0.01	0.01	-0.01	0.02
log (Field size)	**-0.07**	**0.02**	**-0.10**	**-0.03**	**0.08**	**0.03**	**0.02**	**0.14**

Vegetation height No vegetation x log (Field size)	**-0.05**	**0.02**	**-0.09**	**-0.01**	**-0.12**	**0.04**	**-0.20**	**-0.04**
Vegetation height 1-25 cm x log (Field size)	0.03	0.02	-0.01	0.06	**-0.16**	**0.03**	**-0.23**	**-0.09**
Vegetation height >50 cm x log (Field size)	**-0.17**	**0.02**	**-0.21**	**-0.13**	**-0.20**	**0.03**	**-0.27**	**-0.13**
Vegetation height No vegetation x log (Edge distance)	**0.12**	**0.02**	**0.08**	**0.17**	**0.23**	**0.04**	**0.15**	**0.31**
Vegetation height 1-25 cm x log (Edge distance)	**0.17**	**0.02**	**0.14**	**0.21**	**0.33**	**0.03**	**0.26**	**0.39**
Vegetation height >50 cm x log (Edge distance)	-0.02	0.02	-0.06	0.01	**0.15**	**0.03**	**0.08**	**0.22**

Active GPS positions

When investigating finer-scale habitat selection, the full model performed best in explaining habitat selection by active hares (Table 4 and S1). With >25-50 cm high vegetation as reference, active hares had a higher relative probability (hereafter referred to as ‘selection’) to use short vegetation (1-25 cm) and a lower relative probability (hereafter referred to as ‘avoidance’) to use higher vegetation (>50 cm) and bare ground (Table 4, Fig. 3). There was no apparent selection for or against >25-50 cm high vegetation (Fig. 3). Concerning the vegetation type and with cereals as reference, active hares selected for bare ground, fabaceae, sugar beet, fallow, maize and pasture, and avoided brassicaceae (Table 4).

There was no apparent selection for or against fodder, hops and stubbles. Relative to random locations, we found that active hares generally selected for bare ground and maize, avoided brassicaceae, cereal, fodder, and stubbles, and showed no apparent selection for or against sugar beet, fabaceae, fallow, hops and pasture (Fig. 3). Further, the interaction between vegetation height and field size showed that active hares generally selected for shorter vegetation (1-50 cm), and avoided vegetation >50 cm and bare ground with increasing field sizes (Fig. 4). When field sizes were smaller (in Southern Germany), there was no apparent selection for or against a specific vegetation height (CIs overlapped; Fig. 4). The interaction between vegetation height and edge distance revealed that active hares selected for proximity to field edges when vegetation height was >25 cm, but selected for intermediate distances from field edges in short vegetation (1-25 cm) and on bare ground (Fig. 4).

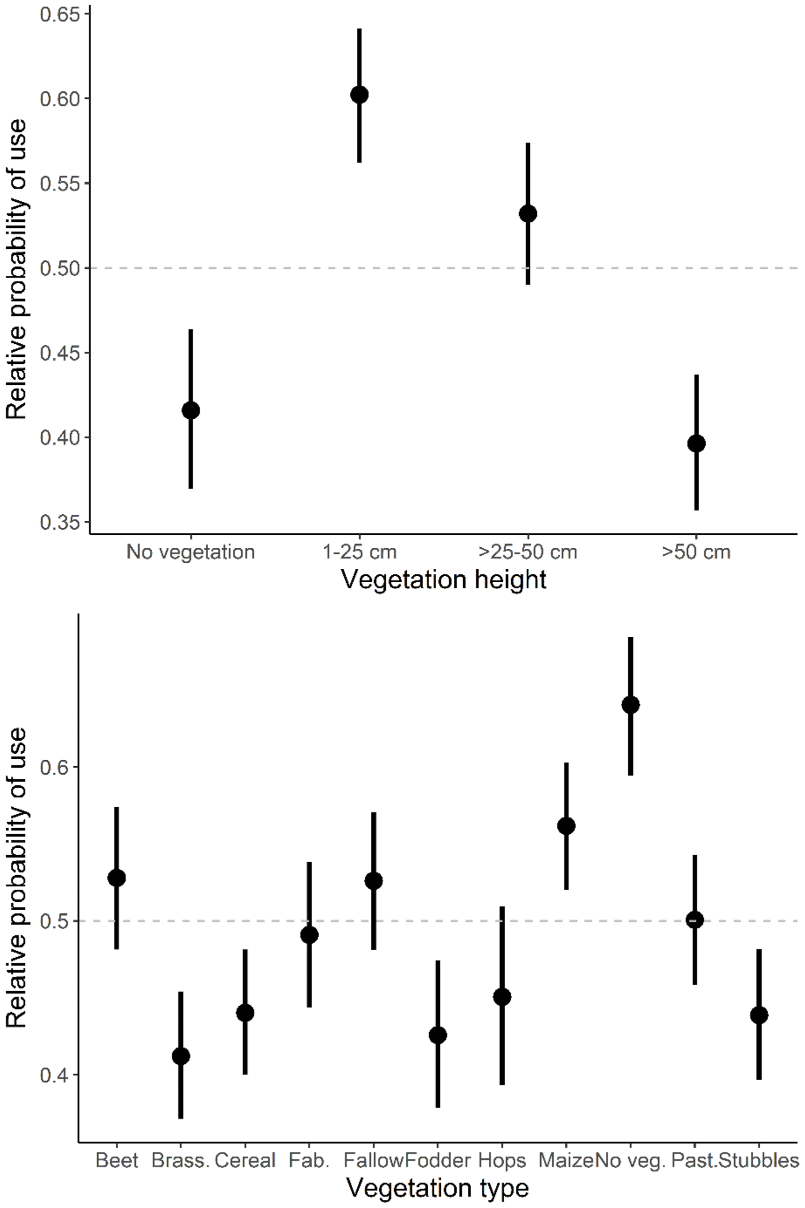

Figure 3: The effect of vegetation height (top) and vegetation type (bottom) on the relative probability of use by active European hares (*Lepus europaeus*). Values >0.5 indicate selection, whereas values <0.5 indicate avoidance. The 95% confidence intervals are given as bars. Data were obtained from 52 GPS-collared hares in Denmark and Germany (2014-2015). Brass. = Brassicaceae, Fab. = Fabaceae, No veg = No vegetation, Past. = Pasture.

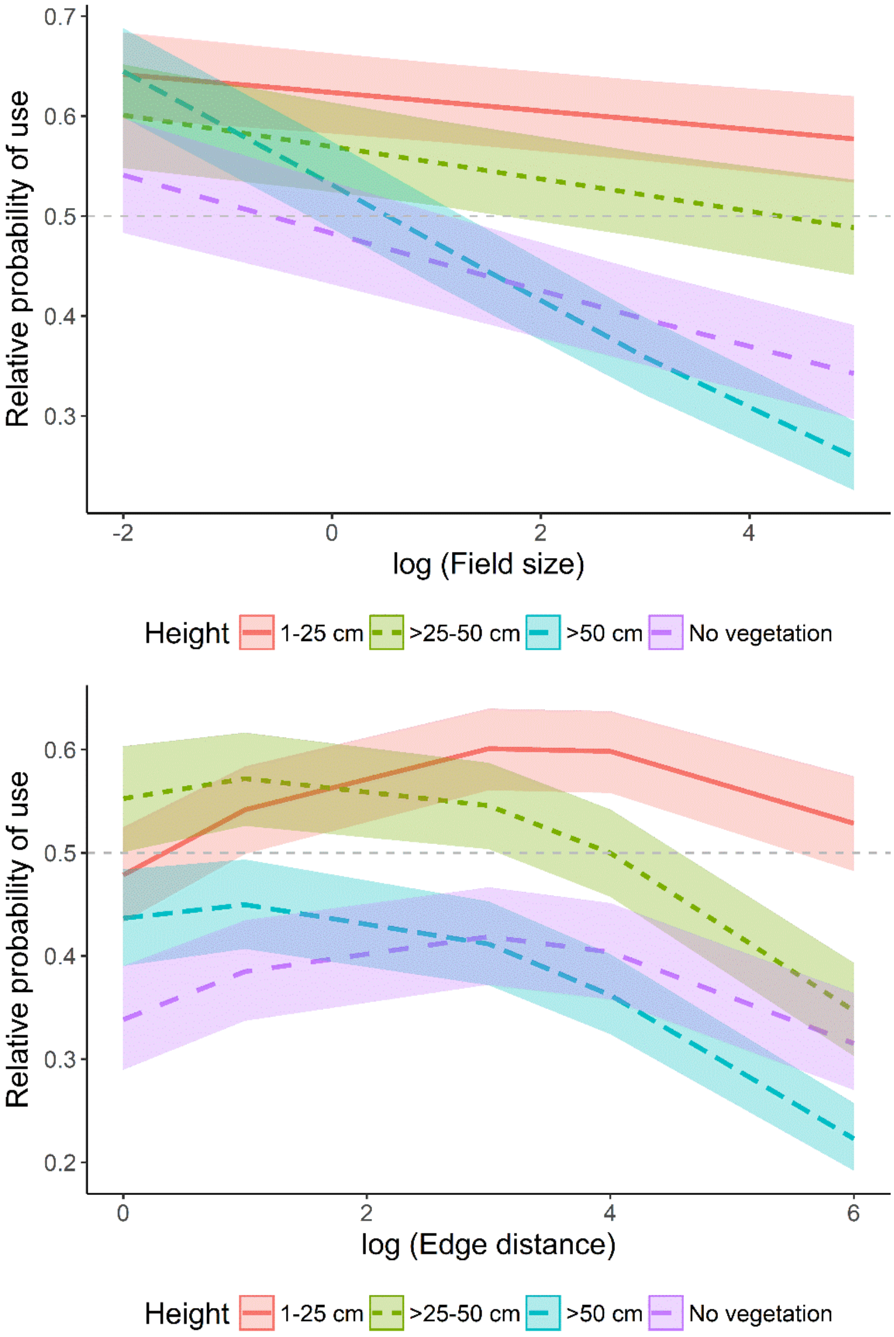

Figure 4: Effect plots showing the effect of the interaction between vegetation height and field size (log-transformed; top), and between vegetation height and edge distance (log-transformed; bottom) on the relative probability of use by active European hares (*Lepus europaeus*). Values >0.5 indicate selection, whereas values <0.5 indicate avoidance. The 95% confidence intervals are given as shading. Data were obtained from 52 GPS-collared hares in Denmark and Germany (2014-2015).

Inactive GPS positions

Habitat selection analyzed for inactive hare GPS positions was also best explained by the full model (Table 4 and S1). With >25-50 cm high vegetation as reference, inactive hares also selected for short vegetation (1-25 cm) and avoided vegetation >50 cm (Table 4, Fig. 5).

There was no apparent selection for or against >25-50 cm high vegetation and bare ground (Fig. 5). Concerning the vegetation type and with cereals as reference, inactive hares selected for bare ground, fabaceae, brassicaceae, fallow, maize pasture and stubbles, and avoided sugar beet and fodder (Table 4). There was no apparent selection for or against hops. Relative to random locations, we found that hares generally selected for fabaceae, fallow and maize, and avoided brassicaceae, cereal, fodder, hops, stubbles and sugar beet, and showed no apparent selection for or against bare ground and pasture (Fig. 5).

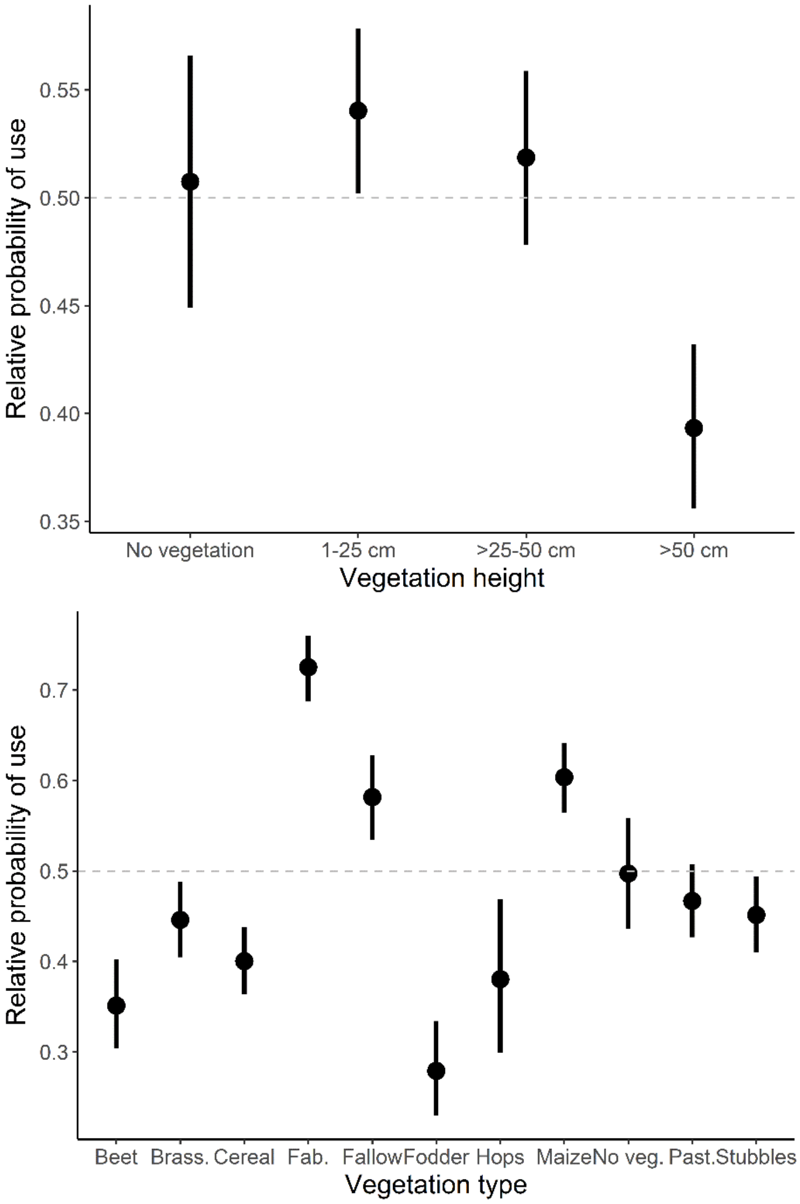

Figure 5: The effect of vegetation height (top) and vegetation type (bottom) on the relative probability of use by inactive European hares (*Lepus europaeus*). Values >0.5 indicate selection, whereas values <0.5 indicate avoidance. The 95% confidence intervals are given as bars. Data were obtained from 52 GPS-collared hares in Denmark and Germany (2014-2015).

The interaction between vegetation height and field size indicated that with increasing field size inactive hares selected for >25-50 cm high vegetation and avoided lower and higher vegetation including areas without vegetation (Fig. 6). Finally, the interaction vegetation height and edge distance revealed that inactive hares selected for proximity to field edges when vegetation was >25-50 cm high (and to a lesser degree >50 cm), and remained further from field edges in short vegetation (<25 cm) and to a lesser degree on bare ground (Fig. 6).

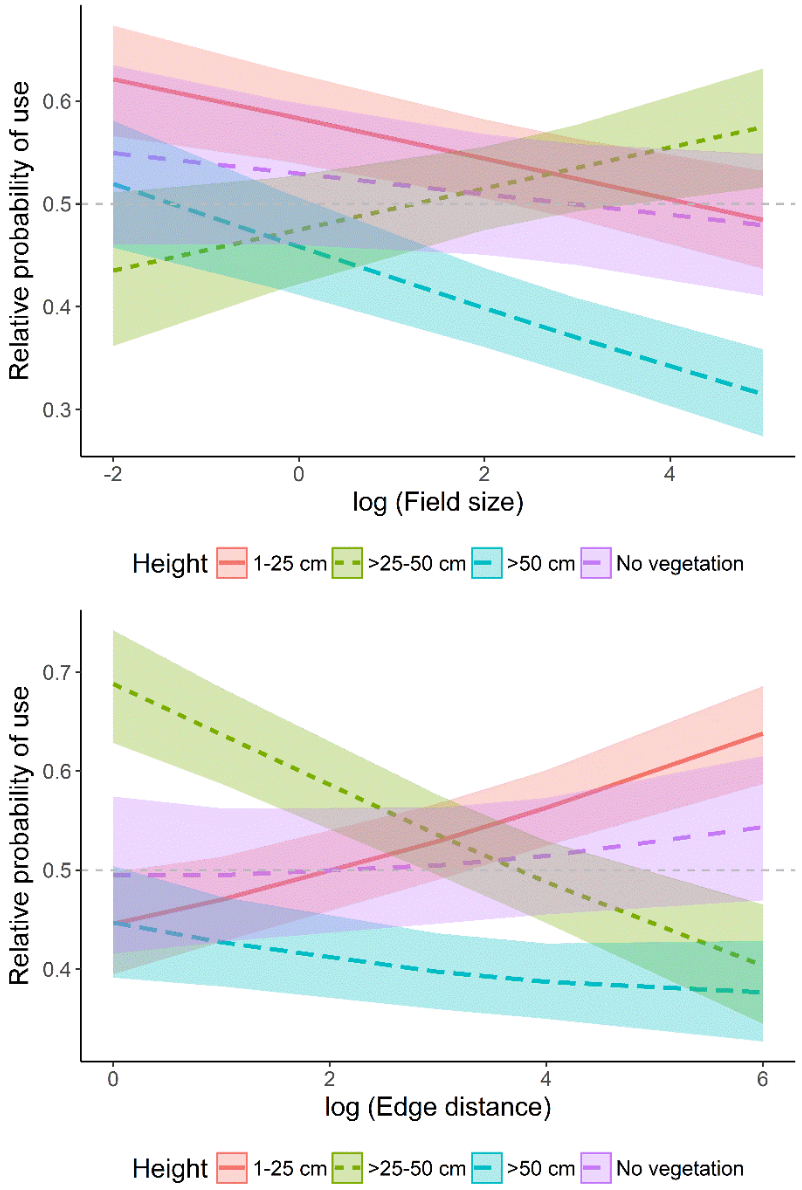

Figure 6: Effect plots showing the effect of the interaction between vegetation height and field size (log-transformed; top), and between vegetation height and edge distance (log-transformed; bottom) on the relative probability of use by inactive European hares (*Lepus europaeus*). Values >0.5 indicate selection, whereas values <0.5 indicate avoidance. The 95% confidence intervals are given as shading. Data were obtained from 52 GPS-collared hares in Denmark and Germany (2014-2015).

Discussion

Vegetation height and type, field size and proximity to field edges all were important in explaining within-home-range habitat selection by hares, emphasizing the importance of small-scale habitat structure in highly variable arable landscapes. Vegetation height was most important for habitat selection of active hares, with short vegetation (1-25 cm) being preferred, possibly for reasons of food quality and predator detection/avoidance. Vegetation type was most important for habitat selection by inactive hares, with fabaceae, fallow and maize being preferred, potentially providing cover from predators and forage at the same time. Our results also emphasize that differences in field sizes ultimately affect habitat selection by hares.

The role of vegetation height

Both active and inactive hares generally selected for short vegetation (1-25 cm) and avoided vegetation >50 cm. However, selection for specific vegetation height was related to agricultural field sizes and proximity to field edges. Hares avoided higher vegetation, likely because it did not provide good forage, acted as a physical barrier (Rühe 1999), and impeded their ability to detect predators (Hewson 1977).

Vegetation height and forage quality

Although hares select for wild weeds during spring and summer, the majority of their diet consists of agricultural crops, because crops dominate the available plant species in arable landscapes throughout the year (Reichlin, Klansek & Hackländer 2006; Schai-Braun *et al.* 2015); a pattern that is increasing with the increasing use of pesticides and fertilizers (Storkey *et al.* 2011). The amount of standing dead plant biomass increases with increasing height of the standing crop (van de Koppel *et al.* 1996), leading to a higher proportion of fiber and subsequently to a lower forage quality (Wilmshurst, Fryxell & Hudsonb 1995). Thus, it is plausible that active hares avoided higher crops for reasons of decreased forage quality (Tapper & Barnes 1986) and due to increasingly dense vegetation that could not be accessed (van de Koppel *et al.* 1996). In addition, active hares avoided areas without any vegetation, likely because bare ground does not provide forage.

Vegetation height and agricultural field size can act as a barrier

Active hares generally selected for short (1-25 cm) vegetation independent of the agricultural field size. Conversely, bare ground and >50 cm high vegetation were increasingly avoided with increasing field size. Similarly, inactive hares avoided >50 cm high vegetation with increasing field size, and both active and inactive hares stayed close to field edges when vegetation was >25 cm high, but not in lower/no vegetation. Combined, the results indicate that larger fields with high and dense vegetation (e.g. brassicaceae, cereals, and maize) potentially presented a physical barrier inhibiting hares from entering farther into them (Hewson 1977). In smaller fields there was no clear selection for a specific vegetation height by both active and inactive hares, suggesting that vegetation height plays a minor role when field sizes are generally small, and therefore more heterogeneous (Benton, Vickery & Wilson 2003).

Hare home ranges were smallest in Southern Germany (generally small fields) and largest in Northern Germany (generally large fields), indicating that home range size is affected by field sizes (Ullmann *et al.* 2018). Hares that are potentially excluded from larger fields when vegetation is higher and therefore denser (Robel *et al.* 1970), only gain access to high-quality forage by increasing their home range. This suggests that hares increase their home range size when field sizes are increasing, a finding reported in numerous other studies (Tapper & Barnes 1986; Rühe & Hohmann 2004; Smith *et al.* 2004; Schai-Braun & Hackländer 2013). It was suggested that smaller agricultural fields result in a more heterogeneous landscape (Benton, Vickery & Wilson 2003), leading to decreased hare home range sizes (Schai-Braun & Hackländer 2013), in turn potentially sustaining higher population densities compared to homogenous habitat with large fields as shown in Poland (Panek & Kamieniarz 1999).

Vegetation height, proximity to field edges and predation risk

Apart from restricting spatial movements, high vegetation can also reduce the perceptual range of animals. For example, the perceptual ranges of two neotropical marsupials (*Philander frenatus* and *Didelphis aurita*) were markedly larger in mowed pastures compared to abandoned pastures and manioc (*Manihot esculenta*) plantations (Prevedello, Forero-Medina & Vieira 2011). Higher vegetation potentially decreases the probability of detecting predators, but might at the same time decrease the predation probability (Goheen *et al.* 2003). In hares, it was shown that individuals show stronger reactive movements towards simulated predators in short vegetation (Weterings *et al.*

2016), suggesting that they have an increased risk of being detected by predators. However, the greater visibility in open landscapes might also increase the probability of detecting a predator, and the chances of escape. It was previously reported that hares generally select for proximity to field edges (Petrovan, Ward & Wheeler 2013; Schai-Braun & Hackländer 2013). Here, we argue that this pattern depends on vegetation height. Both active and inactive hares stayed further from field edges when vegetation was low (<25 cm), possibly to increase the probability to detect and outrun predators. Conversely, they stayed close to field edges in >25 cm high vegetation. Predators generally use field edges more frequently than field centers (for example in wildflower strips: (Hummel *et al.* 2017)), which could lead to an increased predation risk close to field edges. Thus, when vegetation is short, both active and inactive hares might remain further from field edges to avoid detection by predators. When vegetation is higher, this might be unnecessary, because predator detection probability is decreased in higher vegetation (Goheen *et al.* 2003). Additionally, as mentioned above, high vegetation could act as a physical barrier and decrease forage quality. Consequently, as vegetation height increases, hares might remain closer to field edges where they have access to better quality forage (wild herbs and weeds) (Meichtry-Stier *et al.* 2014).

The role of vegetation type

Cultivated crops dominate food availability and use by hares in arable landscapes (Reichlin, Klansek & Hackländer 2006; Schai-Braun *et al.* 2015). Overall, active hares selected most vegetation types (bare ground, fabaceae, sugar beet, fallow, maize and pasture) over cereals, the most common crop type, which was avoided. This indicates that more heterogeneous vegetation types are favorable for hares. Similarly, Tapper and Barnes (1986) reported that hares in England selected areas with various vegetation types and that autumn hare density was positively related to landscape diversity, and an agent-based modelling approach revealed that hare density increased with habitat heterogeneity (Topping, Høye & Olesen 2010).

Concerning inactive hares, we found that fabaceae, fallow and maize were selected as resting places, the latter two also reported by Bertolino, Montezemolo and Perrone (2011). Especially fabaceae and fallow probably provided both cover and forage for inactive hares. Conversely to our prediction, inactive hares avoided higher (>50 cm) vegetation, which is also in contrast to other studies (Tapper & Barnes 1986; Neumann *et al.* 2012). However, the vegetation types included in our study were exclusively agricultural, often brassicaceae and cereals, and did not include forest or woodland as in other studies (Tapper & Barnes 1986; Neumann *et al.* 2012; Petrovan, Ward & Wheeler 2013), which was likely the reason for these different findings. In structurally simple areas with large fields (like Northern Germany), hares presumably are not able to include wooded patches in their home range, and thus, select for resting spots in short vegetation away from field edges, allowing them to detect predators from greater distances.

Conclusion

Arable fields dominate agricultural land in many European countries, thereby forming the main habitat of hares. We could show that vegetation height is a useful parameter to describe within-home-range habitat selection in highly variable landscapes. Hares avoided higher vegetation (> 50 cm) probably, because it does not provide high quality forage and restricts their spatial movements. Within-home-range habitat selection also depended on differences in field sizes and potentially the number of cultivated crops among the three study areas. Both active and inactive hares avoided large fields when vegetation was >50 cm high, leading to larger individual home ranges in these areas. Generally, agricultural intensification has led to increased field sizes and a reduction of field margins (non-cropped farmland, such as vegetated paths, shrub land and wildflower strips) throughout Europe, which likely is the ultimate cause for declining hare and farmland bird populations (Benton, Vickery & Wilson 2003; Meichtry-Stier *et al.* 2014). Field margins play an important role to preserve biodiversity in agricultural landscapes, because they provide high quality forage and shelter throughout the year (Marshall & Moonen 2002; Petrovan, Ward & Wheeler 2013; Meichtry-Stier *et al.* 2014). Thus, in order to increase hare numbers in arable landscapes, managers should focus on the improvement of forage quality throughout the year and the reduction of homogenous landscapes. This could be achieved by increasing ecological compensation areas with high structural diversity, like wildflower fields (Meichtry-Stier *et al.* 2014). Between 1992 and 2007, the Common Agricultural Policy by the EU made it compulsory for large arable farmers to transform 10% of the agriculturally used land as set-aside, leading to a partial increase in insect, bird and mammal numbers (Oppermann, Neumann & Huber 2008). We argue that the re-introduction of mandatory permanent set-asides as suggested by Langhammer *et al.* (2017), the reduction of field sizes, e.g. via subsidizing small-scale agriculture, and the farming of various cultivated crop types on a local scale could improve the habitat for hares and other farmland species, halting their decline.

Authors' Contributions

MM, WU, CF, PS and NB developed the design of the work, WU, and CF contributed to the data collection, MM and WU prepared the data for the analyses, MM performed the statistical analyses and wrote the manuscript, and WU, CF, PS, and NB commented and improved the manuscript. The authors declare no competing financial interests.

Data accessibility

GPS data is deposited in Movebank (http://www.movebank.org/panel_embedded_movebank_webapp?gwt_fragment=page=studies,path=study4048590).

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General Discussion

The movement of organisms is fundamental for the functioning of ecosystems and the maintenance of individuals, populations, and communities (Nathan et al. 2008). Without the daily search for food an individual would starve. Without moving to look for mates a population would perish. Without fleeing – sometimes successfully and sometimes not – no predator-prey community could persist. And without wolves hunting for elk, wetland ecosystems may even turn into pasture (Ripple and Beschta 2004). From seed dispersal and pollination, via the exchange of genetic material, over nutrient transportation to the prevention of disease – organismal movements provide ecosystem services and assure ecosystem functions (Swingland and Greenwood 1983). Yet, animal movements are changing in our rapidly changing world. Human modifications, especially in the realm of land-use change, strongly affect animal movements and species persistence (Tscharntke et al. 2005, Fahrig 2007, Jeltsch et al. 2013, Tucker et al. 2018), but the consequences of altered organism movements for our ecosystems and ourselves are largely unknown (Tucker et al. 2018). To better predict ecosystem changes and the likely repercussions for plants, animals and human beings, it is important to understand animal movement processes and their underlying mechanisms (Nathan et al. 2008). In this thesis I investigated the effect of anthropogenically caused external factors on movement processes and movement mechanisms in agricultural landscapes, the probably most expansive human dominated landscape. I was particularly interested, how human-modified changes in resource variability, landscape structure and landscape diversity affect basic and higher-level animal movements, and set a special focus on different landscape scales – from small-scale habitat features like vegetation height and agricultural management to large-scale landscape characteristics, i.e. landscape structure.

Following, I will synthesize the findings from the chapter 1-4 and explain the achieved scientific advancements in the research field of movement ecology. I will first discuss the relation between external factors, basic-level movements and their emerging higher-level movement behaviours. Second, I will focus on the effect of land-use change – of different spatial scales – on higher-level movement behaviour, pointing out the overarching importance of landscape structure and its synergistic effect with smaller spatial scales. Third, I will give recommendations on how to improve landscape structure for conservation measures, with the aim to increase hare and other farmland species population sizes. Fourth, I will discuss future perspectives for and consequences of changes in movement ecology. I will focus on the importance of animal movements for ecosystem functions and therefore explain the integration of movement ecology and biodiversity research, as biodiversity is crucial for the maintenance of ecosystems and their functions. Finally, I will provide an outlook on the generation of deeper ecological insights through technological advancements in telemetry and remote sensing.

The anthropogenic impact on processes and mechanisms of animal movement behaviour

One of the most prominent examples of anthropogenic influence on animal movement processes are changes in migration patterns. These anthropogenic influences occur on a global scale through climate change, and on a local scale through land-use change. Increasing global temperatures, for example, force many bird species to start their spring migration earlier in order to diminish the phenological mismatch between breeding-ground temperatures and arrival times (Hüppop 2003). Land-use change, like the expansion of agricultural areas, severely inhibit ungulate migration routes (Ottichilo et al. 2001, Bolger et al. 2008). The effect of agriculture on movement processes and mechanisms are many-fold and depend on the animal species and its individual requirements, as well as on landscape structure and diversity (Frylestam 1992, Fahrig 2007, Dolný et al. 2014, Schai-Braun and Hackländer 2014, Ullmann et al. 2018). Whereas, agricultural areas pose impassable barriers for some species and thus restrict their movements to small natural habitat patches (Ottichilo et al. 2001, Dolný et al. 2014), other animals pass through and even use the agricultural matrix (Fahrig et al. 2011). Regardless of the actual use of agricultural landscapes by certain species, all animals in contact with (or avoidance of) agricultural areas are affected by the landscape structure and intrinsically by its diversity (e.g. Saïd and Servanty, 2005; Taylor et al., 1993; Turner et al., 2001; White et al., 2018). The ultimate effect of decreased landscape structure and diversity is the decline of species, i.e. local extinctions (Foley et al. 2005). Besides the direct loss of species due to a lack of resources and habitats, the decline in landscape structure and diversity leads indirectly to the loss of species, based on a cascade of preceding impacts on animal movements.

In a first step landscape diversity influences basic-level movement behaviours, as was shown in chapter 3, where low habitat diversity leads to an increase of running and foraging behaviour. In a second step, this scales up to higher-level movement processes, like increased home range sizes. Chapter 1 and 2 show that hares in simply structured landscapes have larger home ranges, which are emergent properties from an increase in running and foraging behaviours (chapter 3). And in a third step, changes in movement behaviours have implications for the animals' well-being and the population viability (Boyce 1992, Daan et al. 1996). These three steps are discussed in the following three sections.

The effect of external landscape factors on basic-level movement behaviour and their emerging higher-level movements

The emergence of higher-level movement behaviours, like home range formation, from underlying basic-level movements, was historically difficult to study, because it is almost impossible to directly observe movement behaviour of shy, cryptic and nocturnal animals. With the help of high-resolution accelerometers (3.27 sec bursts every 4 minutes), chapter 3 explains higher-level movement behaviours through extracting their underlying, minute-by-minute, behavioural modes (e.g. resting, running, foraging). Hares in simple landscapes run and forage more, but rest less than hares in complex landscapes. This simultaneously connects to higher-level movements by showing significantly larger hare home ranges in the simple landscapes (chapter 1). The phenomenon that different proportions of behavioural modes are the basic property for home range formation might also be the underlying reason for increased home ranges in other studies and other mammal species. Schai-Braun and Hackländer, (2014) for example, showed that hare home ranges increase with decreasing landscape structure, which is in line with our findings. In a general aspect one could imagine an increase in home range size with decreasing amount of (semi-) natural landscape elements would produce the same movement processes (enlargement of home ranges), because of the same underlying mechanisms (an increased amount of running and foraging behaviour). Next to European hares this holds true for example for red foxes and porcupines as well (Lucherini and Lovari 1996, Lovari et al. 2013).

Using accelerometer derived behavioural modes to explain movement processes is still a novel opportunity and should be used more often in future studies. It would not only shed light on movement processes and how they function in a changing world, but could also be helpful to improve decision-making in biological conservation. With the inclusion of animal behaviour, conservation measures can be more directly targeted, for example by improving wildlife corridor identification based on the actual behaviour conducted in the supposed corridors (LaPoint et al. 2013). In combination with modelling studies (e.g. Langhammer et al., 2017), one could even find the ideal landscape configuration and crop composition to decrease the amount of unnecessary fast movements (e.g. running long distances) and long searches for resources. Furthermore, the incorporation of physiological biologging devices that help to correlate behavioural modes with e.g. parasitic infestation or heart rate as a stress response, could help to understand the mechanisms producing animal movements. On theses grounds, we would vastly improve our understanding of animal movement behaviour by including information about the underlying minute-by-minute behaviours and physiological aspects.

The effects of different scales of human-modified landscape structure on higher-level movements

Landscape and habitat diversity not only affect species richness and abundance (e.g. Benton et al., 2003; Fahrig et al., 2015; Smith et al., 2004; Tscharntke et al., 2005), they also influence higher-level movement behaviour like home range formation or home range shifts (Saïd and Servanty 2005, Said et al. 2009, Schai-Braun and Hackländer 2014). The spatial scale often plays an important role in determining the effects of land-use change on animal movement (Kie et al. 2002, Tscharntke et al. 2005, Fischer et al. 2011). Chapter 1-4 of my thesis clearly show the strong, synergistically additive impact of landscape structure (simple versus complex landscapes) on higher-level animal movements. Although resource variability (chapter 1) and fine-scale habitat features (vegetation height, crop type, agricultural management events – chapter 2 and 4) affect higher-level movement behaviours, the synergistic effects of landscape structure and these variables best explained animal movement behaviour. Chapter 1 demonstrates the synergistic effect between resource variability and landscape structure by showing that home range sizes increased with increasing resource variability only in the simple landscape. Chapter 2 shows that agricultural management affects home range size, but this effect was observed only in the simple landscape. Chapter 4 indicates that hares select more rigorously for vegetation height – in the simple landscape. Additionally, hares also moved and foraged more – in the simple landscape (chapter 3). A similar overarching role of landscape structure for higher-level movement behaviours might also be true for other animal species. For example, home ranges of roe deer are significantly smaller in complex landscapes (Saïd and Servanty 2005) and landscape connectivity is a more important driver of home range formation in white-tailed deer than typical habitat conditions like the distance to forests or urban settlements (Walter et al. 2009).

The study design of my thesis includes landscape structure as a two-level category (simple and complex), and all of the chapters (1- 4) showed that the simple landscape has a stronger effect on animal movements than the complex landscape. However, the degradation from a complex to a simple landscape happens continuously. Accordingly, there might also be a continuous slow increase in e.g. home range size, home range shift or other higher-level movement behaviours, with decreasing landscape diversity. On the other hand, there might be one or more species specific thresholds for movement processes linked to landscape structure. Below the threshold movement processes function well, but above a certain landscape simplicity, movements are disrupted and home ranges become very large, with a possible third threshold leading to non-viable levels of landscape structure (With and Crist 1995). Future studies should therefore implement a gradient of landscape structure to investigate the effect of land-use on animal movements.

After accounting for large-scale landscape structure, there are still strong effects of spatiotemporal dynamics, landscape diversity, and fine-scale habitat features on movement behaviour. The spatiotemporal dynamics arise from the agricultural landscape's configuration and composition (chapter 1) and agricultural management events (chapter 2). Those dynamics lead to high resource variability in agricultural landscapes, especially as plant biomass is suddenly and unforeseeably removed during harvest and mowing events. In my PhD thesis, I was able to look at different spatial and temporal scales simultaneously. Hence, I could investigate short-term behavioural adjustments, by testing the synergistic effects of large-scale landscape structure and short-term resource variability in chapter 1, and the underlying agricultural management in chapter 2. In the past, research has mainly concentrated on the effect of long term vegetation dynamics and large scales animal movement (Nilsen et al. 2009, Mueller et al. 2011, Naidoo et al. 2012), showing for example that large scale movement types, like nomadism are the result of the underlying vegetation dynamics, where low spatial and temporal variability of resources lead to sedentariness, seasonal variation in resource availability favours migration and unpredictable spatiotemporal variability of resources fosters nomadism (Mueller and Fagan 2008, Mueller et al. 2011). Chapter 1 and 2 show similar effects acting on small scales and short time periods, the larger the resource variability in a hare's home range the larger the home range becomes. Hence, the common species response to increased resource variability in natural systems (Mcloughlin et al. 2000, Eide et al. 2004, Hansen et al. 2009, Duncan et al. 2015) also exists in human impacted agricultural landscapes.

Fine-scale habitat features can also affect basic- and higher-level movement behaviours (Fortin et al. 2005, Killeen et al. 2014). Chapter 2, shows that harvests increase hare home range shift and home range size, while chapter 4 points out that vegetation height is an important variable for hare habitat selection. It becomes clear, in both cases, that hares prefer low vegetation height – as much in the general sense as after harvest and mowing when vegetation height abruptly changes from high to low. This preference is based on i) increased forage quality (fallen grains and freshly sprouted crops (Späth 1989) in the case of harvests and lower fiber contents in the case of young crops (Wilmshurst et al. 1995)), ii) a higher predator detection probability (Prevedello et al. 2011, Weterings 2018), and iii) high vegetation acts as a physical barrier (Rühe 1999). When parts of the agricultural matrix act as a barrier for hares or other animal species, animal movements are restricted (Smith et al. 2004).

The restriction of animal movements inhibits mobile links, i.e. the biological connection between distant habitat patches (Jeltsch et al. 2013, Tucker et al. 2018). During the disruption no exchange of resources, like nutrient, and genetic materials can happen between these habitats (Zeigler and Fagan 2014). The reticence of mobile linkers can have profound implications for the functioning of ecosystems (Lundberg and Moberg 2003). A more detailed description of the importance of mobile link is given below in the "Future perspectives" section. The effects of disrupted mobile links might scale up to ecosystem level, changes in movement behaviour can also affect the animal directly – e.g. by lowering its fitness – scaling up to effects on the animals' population.

Changes in movement behaviour affect populations

Changes in movement behaviour can have severe implications for individuals and may scale up to the level of populations and communities. Increased home range sizes, and with that increased running and foraging behaviour, implies that more time is allocated to moving and there is less time for the actual energy intake (Daan et al. 1996). Simultaneously, larger home ranges and an increased amount of moving behaviour increases energy expenditure (Mace and Harvey 1983). This in turn, results in lower individual fitness and reproductive output (Boersma and Rebstock 2009; Morales et al. 2010). In chapter 3 I show, that the effect of landscape diversity on basic-level movement behaviour is especially important during the reproductive phase. Animals in areas of low habitat diversity have to assign more time to their self-maintenance, which might hamper their reproductive output. How important habitat quality is, especially during reproduction, was also shown for other animals (Trivers 1972, McLoughlin et al. 2007, Tieleman et al. 2008). When the numbers of animals are diminished, e.g. through decreased reproductive output, the population viability decreases and can result in local extinctions (Boyce 1992). These cascading effects, from changes in landscape structure to changes in movement behaviour, increased energy expenditure and decreased individual fitness and reproductive output, may be even more important for less mobile species than European hare. Smaller animals have a lower movement capacity and an increase in home range size might not be enough to deal with structural landscape changes. Fischer et al., (2011) showed that agri-environmental measures had a stronger effect on small mammal diversity and abundance in simple landscapes than in complex landscapes

Conservation aspects

Species maintenance in anthropogenically influenced systems can only be assured when the basic requirements for those species are met. Although hares are inhabitants of agricultural landscapes, they need well-structured landscapes and habitats, i.e. small crop fields with many field margins as shown in chapter 1 and 4, providing them with areas of low vegetation cover as shown in chapter 4 and a variety of food items (Schai-Braun et al. 2015). Following, I recommend measures to improve large- and small-scale landscape structures to counteract further hare population decline. European hares are classified as “near threatened” or “threatened” on the Red List of Threatened Species in several European countries (Reichlin et al. 2006). However, improved landscape diversity will not only benefit hare populations but also increase the numbers of other animal species in agricultural landscapes. The most striking landscape effect in my thesis was the large-scale landscape structure. Although fine-scale habitat features are of importance too, I think that the overall landscape structure should be a complex one, with small fields and a large variety of crop types. Given this, many of the fine-scale features emerge intrinsically. Therefore, the first step should be to decrease the size of crop fields and increase crop diversity. This would be basically accompanied by a larger amount of margins and higher habitat heterogeneity, these measures have been shown to help animal movements and increase animal abundance and species richness (Smith et al. 2004, Fahrig et al. 2015). On the smaller scale, one could ensure the provision of a year-round varied diet by planting wildflower strips and generating additional (semi-) natural habitat patches. These measures do not only increase hare populations (Meichtry-Stier et al. 2014), but also many other animal populations (e.g. Jönsson et al., 2015; Vickery et al., 2002). I also argue for the re-introduction of law enforced agri-environment measures, like the 10% minimum of set-asides implemented by the EU Common Agricultural Policy, as an important additional measure next to private biodiversity enhancements (Doremus 2003, Langhammer et al. 2017). All these measures have one overarching aim: the maintenance of biodiversity, which in turn assures the functioning of ecosystems.

Future perspectives

The concept of movement ecology provides an incredibly helpful base upon which we can now build useful extensions to deepen our understanding animal movements. One aspect that urgently needs to be investigated is the link between animal movements and biodiversity. Allan et al., (2003), for example, showed that forest fragmentation restricts the movements of various mammal species, i.e. these species will move to larger forests and avoid the small forest remnants. Subsequently, certain rodents thrive in the small forests, benefiting from the release of interspecific competition. These rodents happen to be hosts for the lyme bacterium, carrier of the lyme disease. The infection probability for humans is therefore significantly higher in the small forest fragments. In another example we set the scene to tropical forest fragments, where herbivorous mammals are excluded from small forest fragments too (Howe and Miriti 2004). By feeding on saplings they usually keep the plant diversity at a high level. When these ground feeding herbivores are missing in the small fragments the entire plant community changes. Frugivorous birds might then function as the only link between fragments – carrying seeds that might slow down the change in community composition (Mueller et al. 2014). These examples show that animal movements strongly influence species richness and abundance, fostering important ecosystem functions (Jeltsch et al. 2013). In the following sections I will focus on the possible extensions of the movement ecology framework and also provide an outlook of advances in technology that are helpful to study animal movements.

Extensions of the movement ecology paradigm

The original movement ecology framework by Nathan et al., (2008) shows that the movement path of an individual is explained by the relationship of external factors affecting the internal state of the individual, it's navigation capacity and it's motion capacity. Recently, this framework has been extended by Jeltsch et al. (2013) to integrate movement ecology with biodiversity research (Fig. D1). This extension is based on the inherent linkage between organismal movements and two major coexistence concepts: the mobile link concept (Chesson 2000, Lundberg and Moberg 2003) and the concept of stabilizing and equalizing mechanisms (Chesson, 2000). Mobile links connect distant and otherwise separated habitats by transporting resources or genetic material (Sommer et al. 2013) or by performing certain actions, like the grazing example above, where herbivores change plant species composition. Changes in mobile link functions and movements related to intra- and interspecific interactions are the base for stabilizing and equalling mechanisms, which influence community composition (Chesson 2000). Hence, movement is not only one of the key features for animals to deal with environmental change, but also a necessary component for biodiversity maintenance, especially in regions of strong habitat fragmentation, where animal movements provide the solely connection between distant habitat patches (Mueller et al. 2014).

Future research should investigate the effect of animal movements – and the disruptions of those movements by anthropogenic intervention – on biodiversity and the corresponding feedback cycles, i.e. from patterns to processes and from processes to patterns. The framework by Jeltsch et al., (2013) helps to coherently study the consequences of animal movements on biodiversity and its feedbacks. A specific example, based on my thesis would be to study the impacts of the temporarily disconnected habitats in agricultural landscapes, when hares perceive the matrix as a barrier. A set of research questions could help to understand changes in movement processes and their consequences: Does the severity of disconnectedness depend on the time of disconnectedness? Are there other animal species, e.g. roe deer that can still connect the separate habitats and substitute the missing mobile link, while hare movements are restricted?

The movement ecology paradigm can also be extended by a framework of personality-dependent spatial ecology (Spiegel et al. 2017). Investigating dispersal linked to animal personality, can facilitate the understanding of specific animals' internal states and thus predict where to, how, and how successfully these specific behavioural types disperse. Space use also depends on personality types. For example, certain animal personality types accumulate less parasites, because they prefer to evade contact with conspecifics (Sih et al. 2018). Including individual variation to the movement ecology paradigm seems therefore an important issue, especially to avoid confusion between causation and correlation in studies investigating the effect of external factors on movement processes, while changes in movement processes might also stem from personality types or resulting physiological conditions.

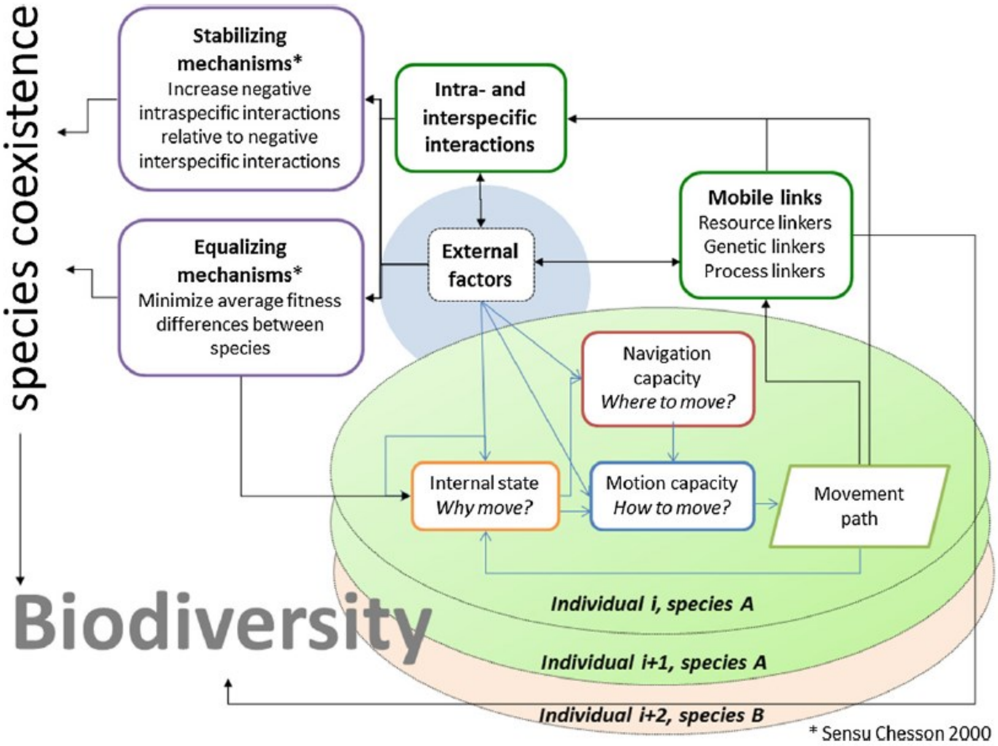

Figure D1: Framework for the integration of movement ecology and biodiversity research (Jeltsch et al. 2013) with adoptions from the movement ecology framework (Nathan et al. 2008), the mobile link concept (Lundberg and Moberg 2003) and equalizing/stabilizing mechanisms for species coexistence (Chesson 2000).

Telemetry and remote sensing technology

The rapid development of telemetry technologies allows the simultaneous and almost continuous tracking of various animal species of different sizes ("Minerva Center for Movement Ecology" 2014). A multi-species approach could provide new insights into animal movements and coexistence theories by studying e.g. changes in intra- and interspecific niche partitioning and predator-prey interactions under global change.

In my thesis I used GPS tags to track hare movements. The tags had a weight of 69 g and included an accelerometer. The inclusion of this biologging device is crucial to learn more about the underlying mechanisms of movement processes. Machine learning algorithms like random forest or neural networks are easily implemented and freely available (Resheff et al. 2014). The accuracy with which they classify animal movement behaviours depends on the complexity of the behaviour, but is already at a high level (Nathan et al. 2012, Alvarenga et al. 2016, Wijers et al. 2018). Acceleration sensors also come with the benefit of being very light. The main part of the 69 g collar weight is held by the battery, followed by the GPS device and the outer mantle. Therefore, I would recommend the inclusion of accelerometers in future animal tracking studies.

Gaining access to the behavioural modes via acceleration data provides the opportunity to even go a step deeper and study the physiological mechanisms that produce behaviours. Parasite infestation, for example, can change animals' habitat choice (Poulin 1994), but how does it translate into the actual behavioural modes? Furthermore, accelerometers in combination with biologging devices that sample heart rate can strongly improve the measure for energy expenditure (Clark et al. 2010), but may also be used to infer the effect of stress on behavioural modes (Thayer et al. 2012).

The combination of high-resolution tracking data, biologging data and additional information about the environment (remote sensing data) can offer a holistic picture about an animal's doings. In this thesis I used bi-monthly NDVI data from the Landsat 8 satellite to calculate a proxy for resource variability. This method worked out just fine, but could nowadays be improved by using e.g. Sentinel data with higher (5 days) temporal and (10 m) spatial resolutions (Pettorelli et al. 2014).

Concluding remarks

There is an immense body of literature showing that a decline in landscape diversity reduces species richness and abundance (e.g. Benton et al., 2003; Fahrig et al., 2015, 2011; Smith et al., 2004; Tews et al., 2004; Tscharntke et al., 2005). In my PhD thesis I point out some of the underlying movement-related reasons for this species decline. I show that synergistic changes in large- and small-scale landscape diversity act on basic-level movement behaviours and their emergent higher-level movements. Changes in movement processes in turn affect the animals' individual fitness and their reproductive output, eventually leading to diminished species abundances and local extinctions. The decline in species richness *per se*, as well as changes in movement behaviour, can have severe consequences for ecosystems and for human kind in general. Therefore, it seems inevitable to manage agricultural landscapes in such a way that species persistence and animal movements, and with that ecosystem functioning, are assured. We humans have the power to shape our environment to our convenience, but that power comes along with the responsibility to use it wisely. The knowledge about the negative relationship between landscape heterogeneity and species richness is not new (Wiens et al. 1993, Barbault 1995), yet the augmentation of monocultures and field consolidation are still in progress (Deutscher Bauernverband 2012) and most agricultural landscapes are managed for fast profit, not for sustainability. Especially here in Germany, where I conducted my thesis, we are now at great conditions, with a budget surplus and unemployment rates below 4%. It is time, now, to move and maintain populations, communities, ecosystem functions and species diversity in our agricultural landscapes. Therefore, we should be courageous enough to actually increase landscape diversity, especially in simply structured landscapes.

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Appendix – Chapter 1

A1: Information on individual hares including their tag number, the location in which they were caught, sex, weight in kg (on the day of collar deployment), deployment date, date of last movement, the amount of days the collar recorded GPS fixes and the total number of valid GPS fixes.

Tag ID	Study area	Sex	Weight [kg]	Deployment Date	Date of last Movement	Deployment Days	Valid GPS fixes
1647	North Germany	m	4.3	02.07.2015	28.12.2015	179	2123
2484	North Germany	m	4	24.03.2014	17.06.2014	85	1533
3397	North Germany	f	4.45	02.06.2014	05.12.2014	186	3080
3398	North Germany	m	3.95	27.07.2014	08.02.2015	196	3426
3400	North Germany	f	4.2	22.05.2015	27.07.2015	66	1156
3401	North Germany	m	4.2	01.06.2014	07.12.2014	189	2888
3406	North Germany	f	4.9	23.06.2014	21.09.2014	90	1500
3407	North Germany	m	3.75	16.06.2014	17.01.2015	215	3805
3408	North Germany	f	3.95	09.03.2014	10.08.2014	154	2529
3409	North Germany	f	5.1	22.06.2014	19.11.2014	150	2813
3411	North Germany	m	3.9	22.05.2015	21.11.2015	183	3319
3413	North Germany	m	3.75	04.05.2014	27.10.2014	176	3355
3414	North Germany	m	4.4	28.05.2015	19.06.2015	22	434
3415	North Germany	m	3.75	17.05.2014	16.07.2014	60	1180
3418	North Germany	m	3.6	31.05.2014	13.06.2014	13	169
3419	North Germany	f	5.1	28.05.2015	31.08.2015	95	1757
3420	North Germany	f	4.05	05.05.2014	01.11.2014	180	3124
3426	North Germany	m	3.7	08.06.2014	12.09.2014	96	1651
3427	North Germany	m	4	31.03.2014	22.10.2014	205	4013
3429	North Germany	m	4.35	25.03.2014	11.10.2014	200	3556
3431	North Germany	f	4.25	02.06.2014	15.06.2014	13	212
3432	North Germany	m	3.95	29.05.2015	28.09.2015	122	2282
3433	North Germany	m	4.3	15.06.2014	27.07.2014	42	772
4067	North Germany	m	4.35	19.06.2015	24.12.2015	188	3246
4461	North Germany	f	5	06.06.2015	13.01.2016	221	3778
3399	South Germany	f	4.6	14.05.2014	30.11.2014	200	3479
3402	South Germany	m	3.85	13.05.2014	28.11.2014	199	3738
3403	South Germany	f	4.4	15.05.2014	11.11.2014	180	3274
3404	South Germany	f	3.35	15.05.2014	10.12.2014	209	3757
3410	South Germany	f	4.4	13.05.2015	05.06.2015	23	258
3412	South Germany	m	4	14.05.2015	31.07.2015	78	1449
3421	South Germany	m	4.1	11.07.2014	31.01.2015	204	3724
3422	South Germany	f	3.6	13.07.2014	12.01.2015	183	3288
3424	South Germany	m	3.95	05.06.2014	25.12.2014	203	3628
3425	South Germany	m	3.6	03.05.2015	06.11.2015	187	3533
3428	South Germany	m	4	15.05.2015	28.10.2015	166	3122
3430	South Germany	m	3.5	01.05.2015	22.10.2015	174	3210

3435	South Germany	m	3.5	08.05.2015	18.11.2015	194	3762
Tag ID	**Study area**	**Sex**	**Weight [kg]**	**Deployment Date**	**Date of last Movement**	**Deployment Days**	**Valid GPS fixes**
3436	South Germany	f	3.4	05.05.2015	19.09.2015	137	2378
3437	South Germany	f	4.55	15.07.2014	22.12.2014	160	4772

A2: Data used for the analysis including the hares' ID, the study area, the NDVI acquisition date, the corresponding date of the year (Julian day) and the extracted NDVI measures (mean and standard deviation) as well as the size of the corresponding 10-day home range.

Tag ID	Study Area	Image Date	Julian Day	NDVIsd	NDVImn	Home Range Size [ha]
2484	North Germany	10.06.2014	161	0.04	0.84	62.94
3397	North Germany	10.06.2014	161	0.14	0.69	19.88
3397	North Germany	21.07.2014	202	0.15	0.35	26.88
3397	North Germany	13.08.2014	225	0.09	0.40	16.61
3397	North Germany	07.09.2014	250	0.17	0.49	46.06
3398	North Germany	13.08.2014	225	0.09	0.81	18.49
3401	North Germany	10.06.2014	161	0.18	0.63	63.94
3401	North Germany	21.07.2014	202	0.13	0.34	53.02
3401	North Germany	13.08.2014	225	0.20	0.48	82.51
3401	North Germany	07.09.2014	250	0.15	0.57	41.11
3406	North Germany	13.08.2014	225	0.25	0.54	43.87
3406	North Germany	07.09.2014	250	0.17	0.66	30.77
3407	North Germany	13.08.2014	225	0.24	0.58	55.60
3408	North Germany	10.06.2014	161	0.16	0.73	6.82
3409	North Germany	13.08.2014	225	0.15	0.72	55.21
3413	North Germany	10.06.2014	161	0.15	0.55	47.30
3413	North Germany	13.08.2014	225	0.17	0.30	20.03
3415	North Germany	10.06.2014	161	0.19	0.70	86.95
3418	North Germany	10.06.2014	161	0.19	0.56	76.97
3420	North Germany	10.06.2014	161	0.13	0.50	70.59
3420	North Germany	13.08.2014	225	0.09	0.77	17.66
3426	North Germany	10.06.2014	161	0.15	0.73	53.53
3426	North Germany	13.08.2014	225	0.15	0.37	116.44
3427	North Germany	10.06.2014	161	0.18	0.68	93.53
3427	North Germany	21.07.2014	202	0.20	0.41	87.37
3427	North Germany	13.08.2014	225	0.20	0.50	86.37
3427	North Germany	07.09.2014	250	0.15	0.53	75.53
3429	North Germany	10.06.2014	161	0.11	0.75	24.78
3429	North Germany	13.08.2014	225	0.18	0.42	49.21
3431	North Germany	10.06.2014	161	0.23	0.65	6.10
3433	North Germany	21.07.2014	202	0.18	0.61	59.83
1647	North Germany	01.09.2015	244	0.12	0.42	49.93
1647	North Germany	03.10.2015	276	0.22	0.63	39.60
3400	North Germany	13.06.2015	164	0.23	0.71	87.56

3400	North Germany	29.06.2015	180	0.12	0.56	14.76
Tag ID	**Study Area**	**Image Date**	**Julian Day**	**NDVIsd**	**NDVImn**	**Home Range Size [ha]**
3411	North Germany	13.06.2015	164	0.23	0.48	109.41
3411	North Germany	29.06.2015	180	0.17	0.60	69.96
3411	North Germany	03.10.2015	276	0.30	0.48	150.64
3414	North Germany	13.06.2015	164	0.25	0.62	164.27
3419	North Germany	13.06.2015	164	0.26	0.66	38.68
3419	North Germany	29.06.2015	180	0.19	0.71	59.20
3432	North Germany	13.06.2015	164	0.18	0.55	19.99
3432	North Germany	01.09.2015	244	0.23	0.45	57.51
4067	North Germany	29.06.2015	180	0.11	0.62	73.67
4067	North Germany	16.08.2015	228	0.20	0.61	56.53
4067	North Germany	01.09.2015	244	0.07	0.64	24.36
4067	North Germany	03.10.2015	276	0.12	0.79	76.23
4461	North Germany	09.08.2015	221	0.17	0.73	13.21
4461	North Germany	16.08.2015	228	0.20	0.59	31.77
4461	North Germany	01.09.2015	244	0.25	0.49	44.03
4461	North Germany	10.09.2015	253	0.23	0.51	34.56
4461	North Germany	26.09.2015	269	0.21	0.42	84.87
4461	North Germany	12.10.2015	285	0.23	0.47	42.73
3399	South Germany	25.05.2014	145	0.19	0.62	6.51
3399	South Germany	10.06.2014	161	0.19	0.57	5.93
3399	South Germany	26.06.2014	177	0.23	0.57	4.42
3399	South Germany	01.11.2014	305	0.17	0.63	9.33
3402	South Germany	25.05.2014	145	0.20	0.74	54.69
3402	South Germany	10.06.2014	161	0.22	0.71	65.40
3402	South Germany	01.11.2014	305	0.20	0.63	28.35
3403	South Germany	25.05.2014	145	0.08	0.82	11.99
3403	South Germany	10.06.2014	161	0.11	0.78	12.97
3403	South Germany	26.06.2014	177	0.13	0.67	9.18
3404	South Germany	25.05.2014	145	0.18	0.75	38.06
3404	South Germany	10.06.2014	161	0.22	0.63	26.59
3404	South Germany	26.06.2014	177	0.15	0.56	13.60
3421	South Germany	01.11.2014	305	0.12	0.59	25.63
3422	South Germany	01.11.2014	305	0.17	0.59	29.26
3424	South Germany	10.06.2014	161	0.19	0.69	9.10
3424	South Germany	26.06.2014	177	0.08	0.79	15.68
3424	South Germany	01.11.2014	305	0.09	0.77	14.31
3437	South Germany	01.11.2014	305	0.16	0.49	6.97
3410	South Germany	28.05.2015	148	0.06	0.64	21.49
3412	South Germany	31.07.2015	212	0.25	0.59	8.47
3425	South Germany	28.05.2015	148	0.16	0.55	19.11
3425	South Germany	31.07.2015	212	0.21	0.63	12.12
3425	South Germany	01.09.2015	244	0.17	0.44	17.36
3425	South Germany	17.09.2015	260	0.16	0.49	17.25

3425	South Germany	03.10.2015	276	0.17	0.67	9.47

Tag ID	Study Area	Image Date	Julian Day	NDVIsd	NDVImn	Home Range Size [ha]
3428	South Germany	28.05.2015	148	0.15	0.59	55.69
3428	South Germany	31.07.2015	212	0.22	0.44	18.81
3428	South Germany	01.09.2015	244	0.17	0.45	28.81
3428	South Germany	17.09.2015	260	0.20	0.54	31.80
3428	South Germany	03.10.2015	276	0.19	0.50	29.11
3430	South Germany	28.05.2015	148	0.13	0.53	17.02
3430	South Germany	31.07.2015	212	0.20	0.40	16.08
3430	South Germany	01.09.2015	244	0.18	0.33	18.14
3430	South Germany	03.10.2015	276	0.17	0.45	7.70
3435	South Germany	31.07.2015	212	0.24	0.51	18.49
3435	South Germany	01.09.2015	244	0.21	0.44	12.30
3435	South Germany	17.09.2015	260	0.23	0.36	5.64
3435	South Germany	03.10.2015	276	0.18	0.45	10.11
3436	South Germany	01.09.2015	244	0.20	0.47	21.83
3436	South Germany	17.09.2015	260	0.20	0.46	6.72

A3: Remote sensing NDVI images used for the analysis, including the Landsat 8 Scene ID and the acquisition date of the image.

Scene ID	Image Date	Path	Row	Study Area
LC81930232014161LGN00	10.06.2014	193	23	North-east Germany
LC81920232014202LGN00	21.07.2014	192	23	North-east Germany
LC81930232014225LGN00	13.08.2014	193	23	North-east Germany
LC81920232014250LGN00	07.09.2014	192	23	North-east Germany
LC81930232015164LGN00	13.06.2015	193	23	North-east Germany
LC81930232015180LGN00	29.06.2015	193	23	North-east Germany
LC81920232015221LGN00	09.08.2015	192	23	North-east Germany
LC81930232015228LGN00	16.08.2015	193	23	North-east Germany
LC81930232015244LGN00	01.09.2015	193	23	North-east Germany
LC81920232015253LGN00	10.09.2015	192	23	North-east Germany
LC81920232015269LGN00	26.09.2015	192	23	North-east Germany
LC81930232015276LGN00	03.10.2015	193	23	North-east Germany
LC81920232015285LGN00	12.10.2015	192	23	North-east Germany
LC81930262014145LGN00	25.05.2014	193	26	South Germany
LC81930262014161LGN00	10.06.2014	193	26	South Germany
LC81930262014177LGN00	26.06.2014	193	26	South Germany
LC81930262014305LGN00	01.11.2014	193	26	South Germany
LC81930262015148LGN00	28.05.2015	193	26	South Germany
LC81930262015180LGN00	29.06.2015	193	26	South Germany
LC81930262015212LGN00	31.07.2015	193	26	South Germany
LC81930262015244LGN00	01.09.2015	193	26	South Germany
LC81930262015260LGN00	17.09.2015	193	26	South Germany
LC81930262015276LGN00	03.10.2015	193	26	South Germany

Appendix – Chapter 2

Supplementary material SA1 – Effects plots

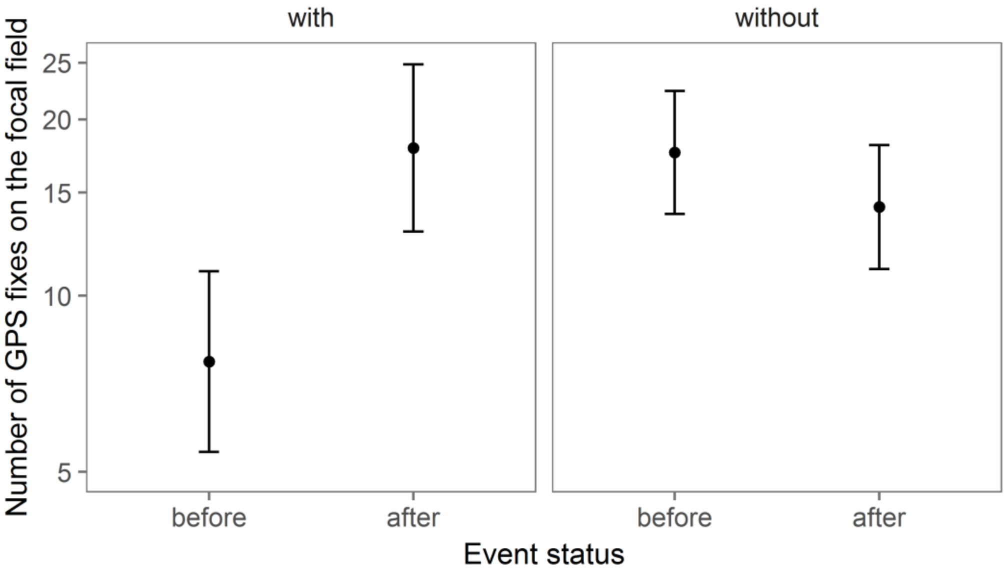


Figure SA2.1a: The number of GPS points (± 95% confidence intervals), disregarding the crop type, on the focal field before and after agricultural management events with (left panel) and without (right panel) a change of resources. The y-axis was log-transformed.

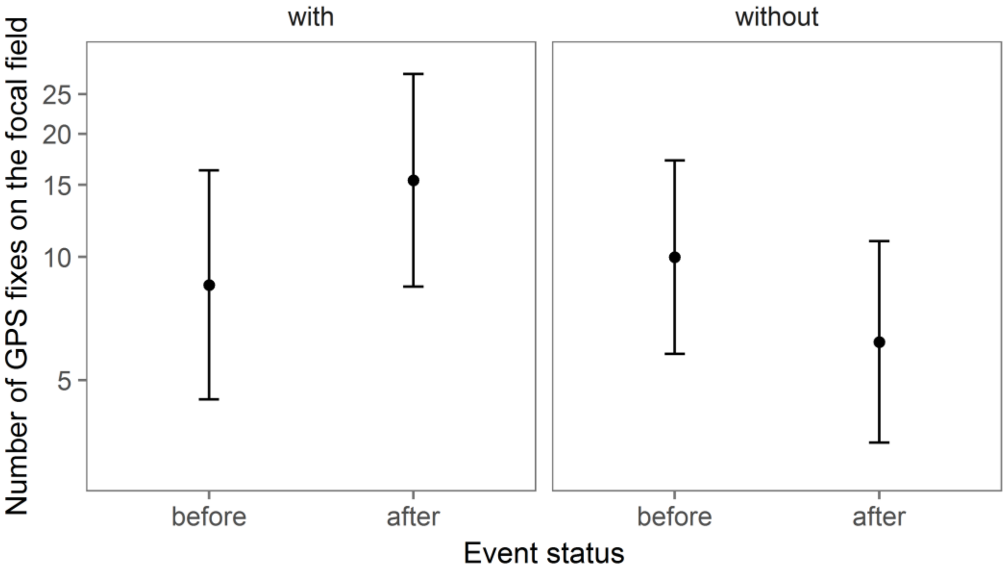


Figure SA2.1b: The number of GPS points (± 95% confidence intervals) on the wheat fields before and after agricultural management events with (left panel) and without (right panel) a change of resources. The y-axis was log-transformed.

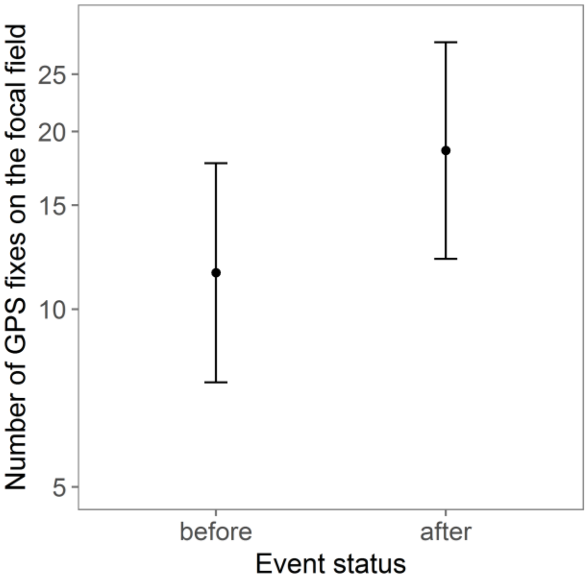


Figure SA2.1c: The number of GPS points (± 95% confidence intervals) on maize fields before and after both types of agricultural management. The y-axis was log-transformed.

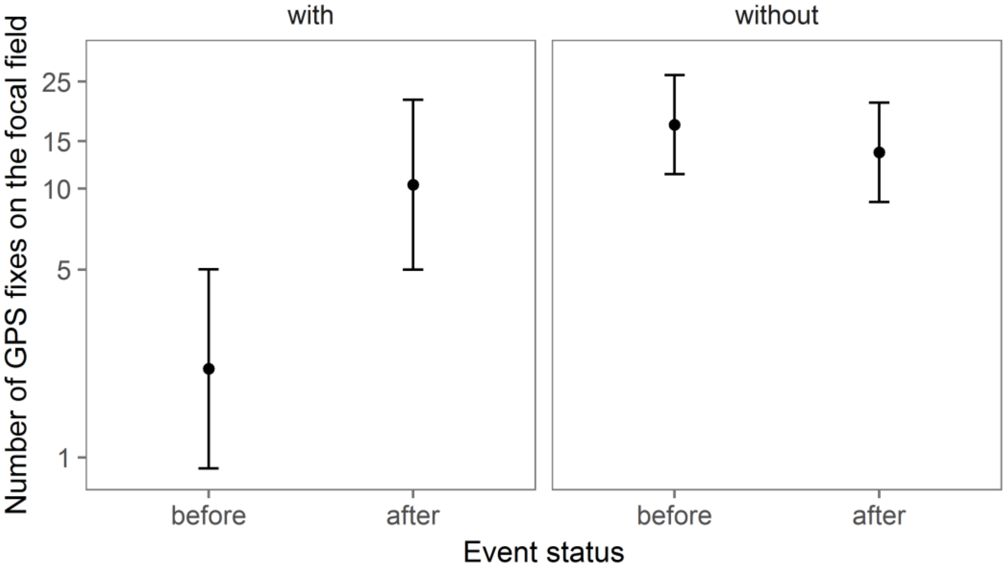


Figure SA2.1d: The number of GPS points (± 95% confidence intervals) on rape seed fields before and after agricultural management events with (left panel) and without (right panel) a change of resources. The y-axis was log-transformed.

Figure SA2.2a: Hare utilization range shifts (± 95% confidence intervals) after management events with and without resource changes compared to baseline events (no management event). The values and confidence intervals were taken from the models irrespective of crop type (= All crops) and for the main crop types. Y-axis was log transformed.

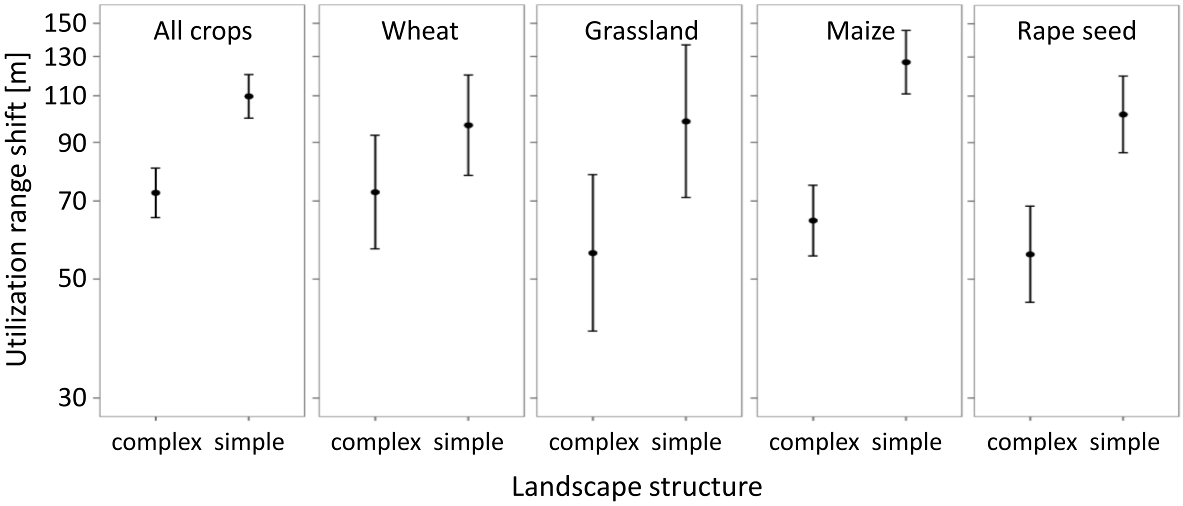


Figure SA2.2b: Hare utilization range shifts (± 95% confidence intervals) in the complex and in the simple landscape. The values and confidence intervals were taken from the models irrespective of crop type (= All crops) and for the four main crop types. Y-axis was log transformed.

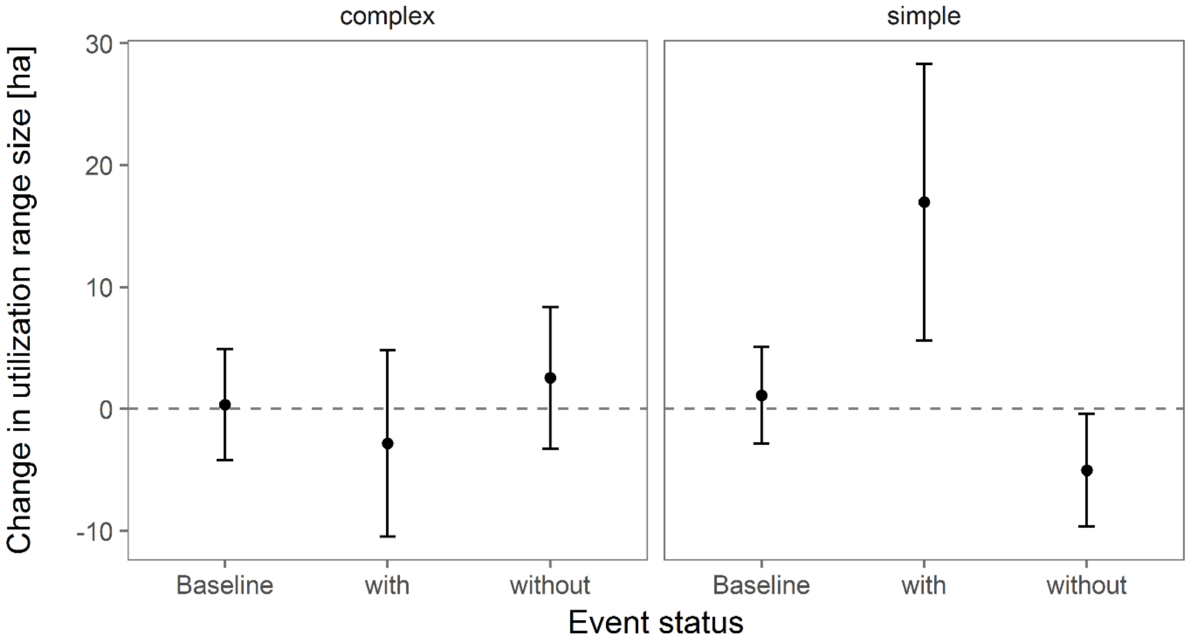
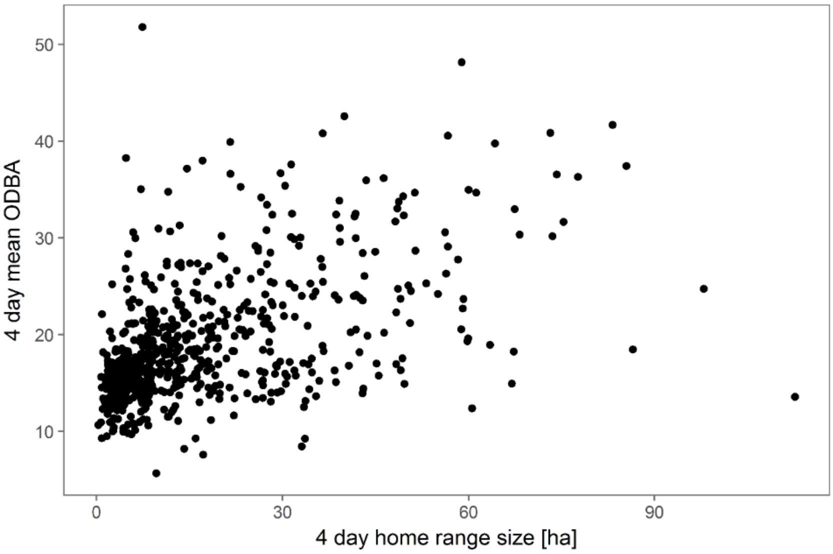


Figure SA2.3: The change in utilization range sizes (± 95% confidence intervals) on wheat fields from before to after the two management events (with resource change and without resource change) and the baseline.

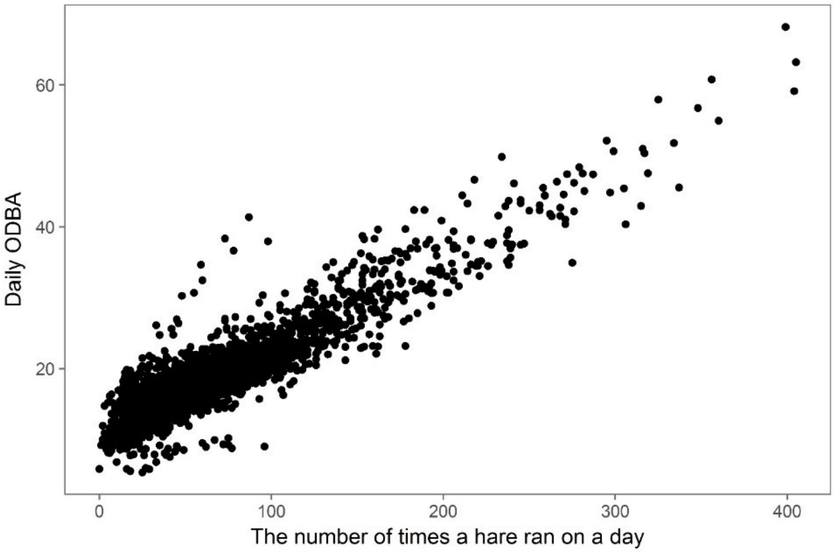
Supplementary material SA2 – ODBA and Home Range Size



SA3.1: The 4-day utilization range [ha] plotted against the 4 day mean ODBA value.

SA3.2: Examples of some hares which increased their utilization range size after management events but kept their energy expenditure similar to the time period before the management event (3429 and 3406), of hares that did not change their utilization range size nor their energy expenditure (3407 and 3409) and a hare that increased the utilization range size as well as the energy expenditure (3426).

Tag ID	Date of management event	Event State	HR Size [ha]	Mean ODBA
3429	27.07.2014	before	23.28	20.51
3429	27.07.2014	after	48.34	22.30
3406	27.07.2014	before	3.48	14.61
3406	27.07.2014	after	12.94	16.20
3407	22.08.2014	before	15.86	17.80
3407	22.08.2014	after	13.29	16.36
3409	25.08.2014	before	13.13	17.29
3409	25.08.2014	after	16.78	17.37
3426	27.07.2014	before	6.88	16.01
3426	27.07.2014	after	56.21	30.60



SA3.3: The frequency of running behaviour per day plotted against the daily ODBA of the corresponding animal.

Supplementary Material SD1 – Hare Data Information

SD1: Information on individual hares including their tag number, the study area in which they were caught, sex, weight in kg (on the day of collar deployment), deployment date, date of last movement, the amount of days the collar recorded GPS fixes and the total number of valid GPS fixes.

Tag ID	Study area	Sex	Weight [kg]	Deployment Date	Date of last Movement	Deployment Days	Valid GPS fixes
1647	North Germany	m	4.3	02.07.2015	28.12.2015	179	2123
2484	North Germany	m	4	24.03.2014	17.06.2014	85	1533
3397	North Germany	f	4.45	02.06.2014	05.12.2014	186	3080
3398	North Germany	m	3.95	27.07.2014	08.02.2015	196	3426
3400	North Germany	f	4.2	22.05.2015	27.07.2015	66	1156
3401	North Germany	m	4.2	01.06.2014	07.12.2014	189	2888
3406	North Germany	f	4.9	23.06.2014	21.09.2014	90	1500
3407	North Germany	m	3.75	16.06.2014	17.01.2015	215	3805
3408	North Germany	f	3.95	09.03.2014	10.08.2014	154	2529
3409	North Germany	f	5.1	22.06.2014	19.11.2014	150	2813
3411	North Germany	m	3.9	22.05.2015	21.11.2015	183	3319
3413	North Germany	m	3.75	04.05.2014	27.10.2014	176	3355
3415	North Germany	m	3.75	17.05.2014	16.07.2014	60	1180
3419	North Germany	f	5.1	28.05.2015	31.08.2015	95	1757
3420	North Germany	f	4.05	05.05.2014	01.11.2014	180	3124
3426	North Germany	m	3.7	08.06.2014	12.09.2014	96	1651
3427	North Germany	m	4	31.03.2014	22.10.2014	205	4013
3429	North Germany	m	4.35	25.03.2014	11.10.2014	200	3556
3432	North Germany	m	3.95	29.05.2015	28.09.2015	122	2282
4067	North Germany	m	4.35	19.06.2015	24.12.2015	188	3246
4461	North Germany	f	5	06.06.2015	13.01.2016	221	3778
3399	South Germany	f	4.6	14.05.2014	30.11.2014	200	3479
3402	South Germany	m	3.85	13.05.2014	28.11.2014	199	3738
3403	South Germany	f	4.4	15.05.2014	11.11.2014	180	3274
3404	South Germany	f	3.35	15.05.2014	10.12.2014	209	3757
3412	South Germany	m	4	14.05.2015	31.07.2015	78	1449
3421	South Germany	m	4.1	11.07.2014	31.01.2015	204	3724
3422	South Germany	f	3.6	13.07.2014	12.01.2015	183	3288
3423	South Germany	m	3.25	13.07.2014	02.02.2015	214	3007
3424	South Germany	m	3.95	05.06.2014	25.12.2014	203	3628
3425	South Germany	m	3.6	03.05.2015	06.11.2015	187	3533
3428	South Germany	m	4	15.05.2015	28.10.2015	166	3122
3430	South Germany	m	3.5	01.05.2015	22.10.2015	174	3210
3435	South Germany	m	3.5	08.05.2015	18.11.2015	194	3762
3436	South Germany	f	3.4	05.05.2015	19.09.2015	137	2378
3437	South Germany	f	4.55	15.07.2014	22.12.2014	160	4772

Supplementary material ST1 – Reduced model summary tables

ST1.1 – Number of GPS fixes: Results of the reduced models after model selection of negative binomial model, according to Burnham and Anderson (2003) using the lowest AICc score to select the reduced model. Shown are the effects of event state (before and after agricultural management events), management type (baseline, with and without the change of resources), study year (2014 and 2015), Julian date (as quadratic term) and landscape structure (simple and complex) on the number of GPS fixes on the focal field. Parameter estimates with standard error (Std. Error) and z-values are provided. “*” indicates two-way interaction. The reference levels are: “before” for event state, “baseline” for management type, “complex” for landscape structure and “2014” for study year. Abbreviations: Management type = Manag.type, Landscape structure = LS.

All Crops

```
Explanatories                             Estimate  Std. Error   z value
(Intercept)                                  1.757       0.205     8.584
Event.status(after)                          0.841       0.220     3.821
Manag.type(without)                          0.823       0.199     4.137
Landscape structure(simple)                  0.514       0.185     2.775
Event.status(after):Manag.type(without)     -1.055       0.260    -4.062
```

Wheat

```
Explanatories                             Estimate  Std. Error   z value
(Intercept)                                  2.291       0.263     8.716
Event.status(after)                         -0.477       0.214    -2.227
Manag.type(with)                            -0.156       0.358    -0.435
JulianDate^1                                 0.005       0.208     0.023
JulianDate^2                                 0.308       0.158     1.951
Event.status(after):Manag.type(with)         1.065       0.434     2.455
```

Meadow

```
Explanatories                             Estimate  Std. Error   z value
(Intercept)                                  2.328       0.282     8.257
```

Maize

```
Explanatories                             Estimate  Std. Error   z value
(Intercept)                                  1.979       0.285     6.940
Event.status(after)                          0.477       0.303     1.572
Landscape structure(simple)                  0.880       0.304     2.891
```

Rape Seed

```
Explanatories                             Estimate  Std. Error   z value
(Intercept)                                  2.413       0.272     8.864
Event.status(after)                         -0.237       0.298    -0.793
Manag.type(with)                            -2.091       0.476    -4.395
Landscape structure(simple)                  0.656       0.285     2.302
Event.status(after):Manag.type(with)         1.812       0.630     2.876
```

ST1.2 – Home range shift: Results of the reduced models after model selection linear mixed effects model according to Burnham and Anderson (2003) using the lowest AICc score to select the reduced model. Shown are the effects of management type (baseline, with and without the change of resources), study year (2014 and 2015), Julian date (as quadratic term) and landscape structure (simple and complex) on home range shift. The response variable (home range shift) was log-transformed to assure normality. Parameter estimates with standard error (Std. Error), degrees of freedom (DF) and t-values are provided. “*” indicates two-way interaction. The reference levels are: “baseline” for management type, “complex” for landscape structure and “2014” for study year.

All Crops

```
Explanatories       Value   Std.Error  DF  t-value
(Intercept)           4.070     0.118 635  34.461
Manag.type(with)      0.489     0.097 635   5.013
Manag.type(without)   0.361     0.083 635   4.323
LS(simple)            0.390     0.145  33   2.697
JulianDate^1         -2.611     1.028 635  -2.541
JulianDate^2          0.967     0.894 635   1.082
```

Wheat

```
Explanatories       Value   Std.Error  DF  t-value
(Intercept)           4.136     0.149 238  27.752
Manag.type(with)      0.336     0.178 238   1.888
Manag.type(without)   0.370     0.133 238   2.772
LS(simple)            0.342     0.179  33   1.912
```

Meadow

```
Explanatories       Value   Std.Error  DF  t-value
(Intercept)           3.939     0.172 150  22.851
Manag.type(with)      0.663     0.233 150   2.841
Manag.type(without)   0.195     0.348 150   0.561
LS(simple)            0.606     0.222  27   2.735
```

Maize

```
Explanatories       Value   Std.Error  DF  t-value
(Intercept)           3.768     0.190 134  19.794
Manag.type(with)      0.673     0.197 134   3.416
Manag.type(without)   0.727     0.181 134   4.006
LS(simple)            0.680     0.236  27   2.876
```

Rape Seed

```
Explanatories       Value   Std.Error  DF  t-value
(Intercept)           3.988     0.164 166  24.310
Manag.type(with)      0.911     0.260 166   3.509
Manag.type(without)   0.368     0.176 166   2.092
LS(simple)            0.557     0.204  29   2.727
```

ST1.3 – Delta home range size: Results of the reduced models after model selection linear mixed effects model according to Burnham and Anderson (2003) using the lowest AICc score to select the reduced model. Shown are the effects of management type (baseline, with and without the change of resources), study year (2014 and 2015), Julian date (as quadratic term) and landscape structure (simple and complex) on delta home range size. Parameter estimates with standard error (Std. Error), degrees of freedom (DF) and t-values are provided. "*" indicates two-way interaction. The reference levels are: "baseline" for management type, "complex" for landscape structure and "2014" for study year.

All Crops

Explanatories	Estimate	Std.Error	DF	t-value
(Intercept)	0.092	0.736	301	0.126

Wheat

Explanatories	Estimate	Std.Error	DF	t-value
(Intercept)	0.358	2.303	98	0.156
Manag.type(with)	-3.187	4.501	98	-0.708
Manag.type(without)	2.195	3.736	98	0.588
LS(simple)	0.764	3.052	33	0.250
Manag.type(with):LS(simple)	19.050	7.560	98	2.520
Manag.type(without):LS(simple)	-8.342	4.843	98	-1.722

Meadow

Explanatories	Estimate	Std.Error	DF	t-value
(Intercept)	0.577	1.189	61	0.485

Maize

Explanatories	Estimate	Std.Error	DF	t-value
(Intercept)	-1.441	1.477	53	-0.976

Rape Seed

Explanatories	Estimate	Std.Error	DF	t-value
(Intercept)	0.724	1.335	68	0.542

ST1.4 – Delta energy expenditure (ODBA): Results of the reduced models after model selection linear mixed effects model according to Burnham and Anderson (2003) using the lowest AICc score to select the reduced model. Shown are the effects of management type (baseline, with and without the change of resources), study year (2014 and 2015), Julian date (as quadratic term) and landscape structure (simple and complex) on delta ODBA. Parameter estimates with standard error (Std. Error), degrees of freedom (DF) and t-values are provided. "*" indicates two-way interaction. The reference levels are: "baseline" for management type, "complex" for landscape structure and "2014" for study year.

All Crops

```
Explanatories Value   Std.Error DF  t-value
(Intercept)     0.247     0.439 289   0.561
```

Wheat

```
Explanatories Value   Std.Error DF  t-value
(Intercept)    -0.051     0.548 164  -0.092
```

Meadow

```
Explanatories Value   Std.Error DF  t-value
(Intercept)    -0.087     0.467 124  -0.187
```

Maize

```
Explanatories Value   Std.Error DF  t-value
(Intercept)     0.116     0.479 137   0.242
```

Rape Seed

```
Explanatories Value   Std.Error DF  t-value
(Intercept)     0.086     0.457 130   0.189
```

Supplementary Material ST2 – Competing models summary tables

ST2.1a – Number of GPS fixes: The reduced model (delta = 0) and the competing models for the negative binomial model with the number of GPS fixes as response variable. Displayed are the models for all crops (crop type is disregarded), wheat, grasslands, maize and rape seed.

Crop type	(Intercept)	Event.status	JulianDate^2	Mag.type	LS	Study.year	Event.status: Mag.type	df	logLik	AICc	delta	weight
All crops					NO competing models.							
Wheat					NO competing models.							
Grassland0	2.32							3	-123.50	253.76	0	0.40
Grassland1	1.94					+		4	-122.55	254.40	0.64	0.29
Grassland2	2.10	+						4	-123.15	255.60	1.84	0.16
Grassland3	1.97				+	+		5	-121.84	255.67	1.91	0.15
Maize0	1.98	+			+			5	-250.96	512.89	0	0.43
Maize1	2.29				+			4	-252.26	513.16	0.27	0.38
Maize2	2.17	+		+	+		+	7	-249.29	514.46	1.56	0.20
Rape seed					NO competing models.							

ST2.1b – Number of GPS fixes: Results of the competing models within deltaAICc < 2 of the negative binomial model, according to Burnham and Anderson (2003). Shown are the effects of event state (before and after agricultural management events), management type (baseline, with and without the change of resources), study year (2014 and 2015), Julian date (as quadratic term) and landscape structure (simple and complex) on the number of GPS fixes on the focal field. Parameter estimates with standard error (Std. Error) and z-values are provided. "*" indicates two-way interaction. The reference levels are: "before" for event state, "baseline" for management type, "complex" for landscape structure and "2014" for study year. Abbreviations: Management type = Manag.type, Landscape structure = LS.

Grassland competing model 1

Explanatories	Estimate	Std. Error	z value
(Intercept)	1.941	0.361	5.374
Study.year(2015)	0.749	0.499	1.501

Grassland competing model 2

Explanatories	Estimate	Std. Error	z value
(Intercept)	2.101	0.389	5.402
Event.status(after)	0.371	0.441	0.842

Grassland competing model 3

Explanatories	Estimate	Std. Error	z value

```
(Intercept)                                1.969        0.296    6.652
LS(simple)                                -0.806        0.584   -1.382
Study.year(2015)                           1.140        0.486    2.346
```

Maize - Competing model 1

```
Explanatories                          Estimate  Std. Error   z value
(Intercept)                                2.287        0.224   10.231
LS(simple)                                 0.800        0.305    2.627
```

Maize - Competing model 2

```
Explanatories                          Estimate  Std. Error   z value
(Intercept)                                2.171        0.314    6.915
Event.status(after)                        0.141        0.365    0.387
Manag.typewith                            -0.742        0.438   -1.691
LS(simple)                                 0.901        0.298    3.021
Event.status(after):Manag.type(with)       1.084        0.614    1.765
```

ST2.2a – Home range shift: The reduced model (delta = 0) and the competing models for the linear mixed effects model with the home range shift as response variable (log-transformed). Displayed are the models for all crops (crop type is disregarded), wheat, grasslands, maize and rape seed.

	Crop type	(Intercept)	JulianDate^2	Mag.type	LS	Study.year	Mag.type:LS	df	logLik	AICc	delta	weight
All crops0		4.025		+	+			6	-423.439	859.132	0	0.497
All crops1		4.059	+	+	+			8	-421.849	860.136	1.004	0.301
All crops2		3.989		+	+	+		7	-423.298	860.937	1.805	0.202
Wheat0		4.079		+	+			6	-185.176	382.992	0	0.610
Wheat1		4.243		+				5	-186.717	383.889	0.896	0.390
Grassland0		3.931		+	+			6	-129.786	272.572	0	0.309
Grassland1		4.118			+			4	-132.125	272.716	0.144	0.287
Grassland2		4.317						3	-133.839	273.955	1.383	0.155
Grassland3		4.031			+	+		5	-131.807	274.320	1.747	0.129
Grassland4		3.859		+	+	+		7	-129.547	274.443	1.871	0.121
Maize0	No competing models.											
Rape seed0		3.874		+	+			6	-135.412	283.727	0	0.607
Rape seed1		3.730		+	+	+		7	-134.688	284.594	0.867	0.393

ST2.2b – Home range shift: Results of the competing models within deltaAICc < 2 of the linear mixed model, according to Burnham and Anderson (2003). Shown are the effects of management type (baseline, with and without the change of resources), study year (2014 and 2015), Julian date (as quadratic term) and landscape structure (simple and complex) on the log-transformed home range shift. Parameter estimates with standard error (Std. Error), degrees of freedom and t-values are provided. "*" indicates two-way interaction. The reference levels are: "baseline" for management type, "complex" for landscape structure and "2014" for study year. Abbreviations: Management type = Manag.type, Landscape structure = LS.

All Crops - Competing model 1

```
Explanatories           Value    Std.Error DF  t-value
(Intercept)                4.060     0.125 298     32.599
Manag.type(with)           0.501     0.138 298      3.627
Manag.type(without)        0.379     0.115 298      3.300
Study.area(simple)         0.389     0.144  33      2.705
JulianDate^1              -1.619     0.984 298     -1.645
JulianDate^2               0.694     0.896 298      0.775
```

All crops - competing model 2

```
Explanatories           Value    Std.Error DF  t-value
(Intercept)                3.992     0.141 300     28.231
Manag.type(with)           0.511     0.137 300      3.728
Manag.type(without)        0.435     0.113 300      3.862
Study.area(simple)         0.426     0.145  32      2.943
Study.year(2015)           0.075     0.154  32      0.486
```

Wheat - Competing model 1

```
Explanatories           Value    Std.Error DF  t-value
(Intercept)                4.242     0.112 102     37.884
Manag.type(with)           0.355     0.261 102      1.358
Manag.type(without)        0.460     0.176 102      2.613
```

Grassland - Competing model 1

```
Explanatories           Value    Std.Error DF  t-value
(Intercept)                4.107     0.163  62     25.254
Study.area(simple)         0.413     0.228  27      1.815
```

Grassland - Competing model 2

```
Explanatories           Value    Std.Error DF  t-value
(Intercept)                4.312     0.120  62     35.783
```

Grassland - Competing model 3

```
Explanatories           Value    Std.Error DF  t-value
(Intercept)                3.998     0.210  62     19.004
Study.area(simple)         0.450     0.245  26      1.838
Study.year(2015)           0.198     0.249  26      0.795
```

Grassland - Competing model 4

Explanatories	Value	Std.Error	DF	t-value
(Intercept)	3.816	0.227	60	16.774
Manag.type(with)	0.653	0.332	60	1.969
Manag.type(without)	0.530	0.501	60	1.058
Study.area(simple)	0.596	0.252	26	2.359
Study.year(2015)	0.161	0.251	26	0.644

Rape Seed - Competing model 1

Explanatories	Value	Std.Error	DF	t-value
(Intercept)	3.679	0.258	68	14.243
Manag.type(with)	1.064	0.375	68	2.837
Manag.type(without)	0.557	0.258	68	2.162
Study.area(simple)	0.671	0.277	27	2.422
Study.year(2015)	0.340	0.293	27	1.161

ST2.3a – Delta home range size: The reduced model (delta = 0) and the competing models for the linear mixed effects model with delta home range size as response variable (delta, because it is a subtraction of the "after" home range size from the "before" home range size – after and before each management event). Displayed are the models for all crops (crop type is disregarded), wheat, grasslands, maize and rape seed.

Crop type	(Intercept)	JulianDate^2	Manag.type	Study.area	Study.year	Manag.type:Study.area	df	logLik	AICc	delta	weight
All crops0	0.092						3	-1350.405	2706.882	0	0.730
All crops1	0.205				+		4	-1350.377	2708.875	1.994	0.270
Wheat0	0.358		+	+		+	8	-540.860	1098.845	0	0.554
Wheat1	-1.530		+	+	+	+	9	-539.930	1099.277	0.431	0.446
Grassland0	0.577						3	-345.286	696.852	0	0.559
Grassland1	-0.102			+			4	-345.121	698.713	1.861	0.221
Grassland2	0.015				+		4	-345.124	698.719	1.867	0.220
Maize0	-1.441						3	-328.485	663.278	0	0.464
Maize1	0.064				+		4	-327.655	663.830	0.552	0.352
Maize2	2.179			+	+		5	-327.167	665.124	1.846	0.184
Rape seed0	0.724						3	-396.019	798.290	0	0.689
Rape seed1	0.024				+		4	-395.727	799.879	1.589	0.311

ST2.3b – Delta home range size: Results of the competing models within deltaAICc < 2 of the linear mixed model, according to Burnham and Anderson (2003). Shown are the effects of management type (baseline, with and without the change of resources), study year (2014 and 2015), Julian date (as quadratic term) and landscape structure (simple and complex) on delta home range size. Parameter estimates with standard error (Std. Error), degrees of freedom and t-values are provided. “*” indicates two-way interaction. The reference levels are: “baseline” for management type, “complex” for landscape structure and “2014” for study year. Abbreviations: Management type = Manag.type, Landscape structure = LS.

All crops - Competing model 1

```
Explanatories                     Value   Std.Error  DF  t-value
(Intercept)                        0.205      0.881 301    0.233
Study.year(2015)                  -0.375      1.607  33   -0.234
```

Wheat - Competing model 1

```
Explanatories                     Value   Std.Error  DF  t-value
(Intercept)                       -1.530      2.698  98   -0.567
Manag.type(with)                  -1.612      4.640  98   -0.347
Manag.type(without)                3.540      3.859  98    0.917
LS(simple)                         1.728      3.128  32    0.552
Study.year(2015)                   3.442      2.582  32    1.333
Manag.type(with):LS(simple)       18.399      7.554  98    2.436
Manag.type(without):LS(simple)    -9.566      4.915  98   -1.946
```

Grassland - Competing model 1

```
Explanatories                     Value   Std.Error  DF  t-value
(Intercept)                       -0.102      1.688  61   -0.061
LS(simple)                         1.359      2.387  27    0.569
```

Grassland - Competing model 2

```
Explanatories                     Value   Std.Error  DF  t-value
(Intercept)                        0.015      1.556  61    0.010
Study.year(2015)                   1.367      2.426  27    0.564
```

Maize - Competing model 1

```
Explanatories                     Value   Std.Error  DF  t-value
(Intercept)                        0.064      1.884  53    0.034
Study.year(2015)                  -3.856      3.015  27   -1.279
```

Maize - Competing model 2

```
Explanatories                     Value   Std.Error  DF  t-value
(Intercept)                        2.179      2.878  53    0.757
LS(simple)                        -3.111      3.199  26   -0.973
Study.year(2015)                  -5.097      3.275  26   -1.556
```

Rape Seed - Competing model 1

Explanatories	Value	Std.Error	DF	t-value
(Intercept)	0.024	1.626	68	0.015
Study.year(2015)	2.166	2.860	29	0.757

ST2.4a – Delta ODBA: The reduced model (delta = 0) and the competing models for the linear mixed effects model with delta ODBA (energy expenditure) as response variable (delta, because it is a subtraction of the “after” ODBA values from the “before” ODBA values – after and before each management event). Displayed are the models for all crops (crop type is disregarded), wheat, grasslands, maize and rape seed.

Crop type	(Intercept)	JulianDate^2	Mag.type	Study.area	Study.year	Mag.type:study.area	df	logLik	AICc	delta	weight
All crops0	-0.293						3	-1277.646	2561.368	0	0.405
All crops1	0.152				+		4	-1277.111	2562.348	0.980	0.248
All crops2	-1.604		+				5	-1276.318	2562.825	1.457	0.195
All crops3	-0.040			+			4	-1277.600	2563.325	1.957	0.152
Wheat0	-0.927						3	-814.837	1635.797	0	0.457
Wheat1	-0.071				+		4	-814.003	1636.211	0.414	0.372
Wheat2	-0.488			+			4	-814.776	1637.758	1.961	0.171
Grassland0	-1.227						3	-633.145	1272.450	0	0.388
Grassland1	-0.233				+		4	-632.590	1273.450	0.999	0.236
Grassland2	0.184			+			4	-632.654	1273.579	1.128	0.221
Grassland3	1.544			+	+		5	-631.937	1274.282	1.831	0.155
Maize0	-0.929						3	-686.964	1380.076	0	0.526
Maize1	-0.257				+		4	-686.656	1381.559	1.483	0.251
Maize2	-0.056			+			4	-686.774	1381.795	1.720	0.223
Rape seed0	-0.998						3	-663.019	1332.192	0	0.483
Rape seed1	-0.072				+		4	-662.343	1332.942	0.751	0.332
Rape seed2	-0.317			+			4	-662.922	1334.100	1.908	0.186

ST2.4b – Delta ODBA: Results of the competing models within deltaAICc < 2 of the linear mixed model, according to Burnham and Anderson (2003). Shown are the effects of management type (baseline, with and without the change of resources), study year (2014 and 2015), Julian date (as quadratic term) and landscape structure (simple and complex) on delta ODBA. Parameter estimates with standard error (Std. Error), degrees of freedom and t-values are provided. "*" indicates two-way interaction. The reference levels are: "baseline" for management type, "complex" for landscape structure and "2014" for study year. Abbreviations: Management type = Manag.type, Landscape structure = LS.

All Crops - Competing model 1

```
Explanatories           Value   Std.Error DF  t-value
(Intercept)              0.111      0.947 290    0.118
Study.year(2015)        -1.881      1.766  32   -1.065
```

All Crops - Competing model 2

```
Explanatories           Value   Std.Error DF  t-value
(Intercept)             -1.604      1.075 288   -1.492
Manag.type(with)         2.674      1.985 288    1.347
Manag.type(without)      2.068      1.526 288    1.355
```

All Crops - Competing model 3

```
Explanatories           Value   Std.Error DF  t-value
(Intercept)              0.026      1.269 290    0.021
LS(simple)              -0.817      1.662  32   -0.491
```

Wheat - Competing model 1

```
Explanatories           Value   Std.Error DF  t-value
(Intercept)             -0.031      1.431 165   -0.021
Study.year(2015)        -3.408      2.624  32   -1.299
```

Wheat - Competing model 2

```
Explanatories           Value   Std.Error DF  t-value
(Intercept)             -0.538      1.932 165   -0.279
LS(simple)              -0.854      2.490  32   -0.343
```

Grassland - Competing model 1

```
Explanatories           Value   Std.Error DF  t-value
(Intercept)             -0.199      1.864 125   -0.107
Study.year(2015)        -3.431      3.073  26   -1.116
```

Grassland - Competing model 2

```
Explanatories           Value   Std.Error DF  t-value
(Intercept)              0.205      2.214 125    0.092
LS(simple)              -2.872      2.931  26   -0.980
```

Grassland - Competing model 3

```
Explanatories           Value   Std.Error  DF  t-value
(Intercept)              1.900      2.723 125    0.698
LS(simple)              -3.432      3.133  25   -1.095
Study.year(2015)        -3.953      3.218  25   -1.228
```

Maize - Competing model 1

```
Explanatories           Value   Std.Error  DF  t-value
(Intercept)             -0.109      1.919 138   -0.057
Study.year(2015)        -3.049      3.195  27   -0.954
```

Maize - Competing model 2

```
Explanatories           Value   Std.Error  DF  t-value
(Intercept)              0.003      2.402 138    0.001
LS(simple)              -1.990      3.096  27   -0.643
```

Rape Seed - Competing model 1

```
Explanatories           Value   Std.Error  DF  t-value
(Intercept)             -0.001      1.744 131   -0.001
Study.year(2015)        -3.909      3.087  28   -1.267
```

Rape Seed - Competing model 2

```
Explanatories           Value   Std.Error  DF  t-value
(Intercept)             -0.249      2.376 131   -0.105
LS(simple)              -1.574      2.987  28   -0.527
```

Appendix – Chapter 3

Supplement SA1 – Summary tables

SA1 – Final models: Results of the model selection process showing seasonal, sex and landscape structure effects on the number of behavioural modes conducted per month. Parameter estimates with standard error (Std.Error) and degrees of freedom (DF) are given. The variable names are: the animals' sex (Sex, male and female), Landscape structure (LS, simple and complex), month, ":" indicates interactions. The reference levels are: "complex" for landscape structure and "female" for the animals' sex.

Resting behaviour

```
Explanatory Variables                  Estimate     Std.Error   DF
(Intercept)                            37025.00     22312.52    81
Sex(male)                               3261.99      7390.88    29
Diversity                              -5809.33     12171.69    81
LS(simple)                              2296.96      1164.57    29
month^1                                -7445.70      8086.48    81
```

```
month^2                                      1013.55      943.86    81
month^3                                       -40.80       35.78    81
Sex(male):month^1                           -3342.54     2833.44    81
Sex(male):month^2                             550.25      354.64    81
Sex(male):month^3                             -25.01       14.46    81
Diversity:month^1                            3622.64     4384.22    81
Diversity:month^2                            -480.41      506.31    81
Diversity:month^3                              18.12       18.90    81
Diversity:LS(simple)                        -1462.73      628.12    81
```

Running behaviour

```
Explanatory Variables                    Estimate     Std.Error   DF
(Intercept)                                 23186.01    12511.36    82
Sex(male)                                   -2774.04     4138.18    29
LS(simple)                                    632.78      211.71    29
Diversity                                  -13697.16     6835.25    82
month^1                                     -6611.32     4519.86    82
month^2                                       645.38      527.68    82
month^3                                       -20.98       20.03    82
Sex(male):month^1                            2398.54     1592.04    82
Sex(male):month^2                            -380.84      199.61    82
Sex(male):month^3                              16.99        8.15    82
Diversity:month^1                            4348.43     2454.35    82
Diversity:month^2                            -456.95      283.31    82
Diversity:month^3                              16.01       10.58    82
```

Foraging behaviour

```
Explanatory Variables                    Estimate     Std.Error   DF
(Intercept)                                -18095.94    16902.22    85
Sex(male)                                     733.55      434.45    30
Diversity                                   12349.33     9816.05    85
month^1                                     10482.27     6079.31    85
month^2                                     -1333.14      703.32    85
month^3                                        53.13       26.31    85
Diversity:month^1                           -5218.97     3525.76    85
Diversity:month^2                             639.75      406.98    85
Diversity:month^3                             -24.06       15.19    85
```

SA2 – Competing models: Models with deltaAIC scores < 2 showing seasonal, sex and landscape structure effects on the number of behavioural modes conducted per month. Parameter estimates with standard error (Std.Error) and degrees of freedom (DF) are given. The variable names are: the animals' sex (Sex, male and female), Landscape structure (LS, simple and complex), month, ":" indicates interactions. The reference levels are: "complex" for landscape structure and "female" for the animals' sex.

Resting behaviour - Competing model

Explanatory Variables	Estimate	Std.Error	DF
(Intercept)	32951.72	22843.10	82
Sex(male)	3463.34	7583.53	30
Diversity	-4388.60	12458.64	82
month^1	-5327.32	8242.94	82
month^2	754.97	961.56	82
month^3	-31.20	36.48	82
Sex(male):month^1	-3301.33	2908.07	82
Sex(male):month^2	531.20	363.89	82
Sex(male):month^3	-23.97	14.83	82
Diversity:month^1	2731.94	4469.05	82
Diversity:month^2	-366.59	515.41	82
Diversity:month^3	13.77	19.23	82

Moving behaviour - Competing model 1

Explanatory Variables	Estimate	Std.Error	DF
(Intercept)	21892.88	13139.74	84
Sex(male)	868.55	253.73	29
LS(simple)	739.85	697.09	29
Diversity	-13906.38	7645.69	84
month^1	-5350.00	4755.65	84
month^2	413.75	551.76	84
month^3	-9.69	20.67	84
LS(simple):Diversity	-77.30	381.19	84
Diversity:month^1	4389.54	2757.10	84
Diversity:month^2	-454.18	318.93	84
Diversity:month^3	15.60	11.92	84

Moving behaviour - Competing model 2

Explanatory Variables	Estimate	Std.Error	DF
(Intercept)	-1965.89	3678.71	86
Sex(male)	-257.62	4181.22	29
LS(simple)	689.11	202.99	29
month^1	1486.22	1415.42	86
month^2	-218.75	178.25	86
month^3	9.77	7.32	86
Sex(male):month^1	1457.90	1604.92	86

```
Sex(male):month^2                                   -266.70       200.58    86
Sex(male):month^3                                     12.47         8.15    86
```

Foraging behaviour - Competing model

```
Explanatory Variables                           Estimate     Std.Error   DF
(Intercept)                                     -1965.89       3678.71    86
Sex(male)                                        -257.62       4181.22    29
LS(simple)                                        689.11        202.99    29
month^1                                          1486.22       1415.42    86
month^2                                          -218.75        178.25    86
month^3                                             9.77          7.32    86
Sex(male):month^1                                1457.90       1604.92    86
Sex(male):month^2                                -266.70        200.58    86
Sex(male):month^3                                  12.47          8.15    86
```

Supplement SD1 – Hare Data Information

SD1: Information on individual hares including their tag number, the study area in which they were caught, sex, weight in kg (on the day of collar deployment), deployment date, date of last movement, the amount of days the collar recorded GPS fixes and the total number of valid GPS fixes.

Tag ID	Study area	Sex	Weight [kg]	Deployment Date	Date of last Movement	Deployment Days	Valid GPS fixes
1647	North Germany	m	4.3	02.07.2015	28.12.2015	179	2123
2484	North Germany	m	4	24.03.2014	17.06.2014	85	1533
3397	North Germany	f	4.45	02.06.2014	05.12.2014	186	3080
3398	North Germany	m	3.95	27.07.2014	08.02.2015	196	3426
3401	North Germany	m	4.2	01.06.2014	07.12.2014	189	2888
3406	North Germany	f	4.9	23.06.2014	21.09.2014	90	1500
3407	North Germany	m	3.75	16.06.2014	17.01.2015	215	3805
3408	North Germany	f	3.95	09.03.2014	10.08.2014	154	2529
3409	North Germany	f	5.1	22.06.2014	19.11.2014	150	2813
3411	North Germany	m	3.9	22.05.2015	21.11.2015	183	3319
3413	North Germany	m	3.75	04.05.2014	27.10.2014	176	3355
3420	North Germany	f	4.05	05.05.2014	01.11.2014	180	3124
3426	North Germany	m	3.7	08.06.2014	12.09.2014	96	1651
3427	North Germany	m	4	31.03.2014	22.10.2014	205	4013
3429	North Germany	m	4.35	25.03.2014	11.10.2014	200	3556
3432	North Germany	m	3.95	29.05.2015	28.09.2015	122	2282
4067	North Germany	m	4.35	19.06.2015	24.12.2015	188	3246
3399	South Germany	f	4.6	14.05.2014	30.11.2014	200	3479
3402	South Germany	m	3.85	13.05.2014	28.11.2014	199	3738
3403	South Germany	f	4.4	15.05.2014	11.11.2014	180	3274
3404	South Germany	f	3.35	15.05.2014	10.12.2014	209	3757

Tag ID	Study area	Sex	Weight [kg]	Deployment Date	Date of last Movement	Deployment Days	Valid GPS fixes
3412	South Germany	m	4	14.05.2015	31.07.2015	78	1449
3421	South Germany	m	4.1	11.07.2014	31.01.2015	204	3724
3422	South Germany	f	3.6	13.07.2014	12.01.2015	183	3288
3423	South Germany	m	3.25	13.07.2014	02.02.2015	214	3007
3424	South Germany	m	3.95	05.06.2014	25.12.2014	203	3628
3425	South Germany	m	3.6	03.05.2015	06.11.2015	187	3533
3428	South Germany	m	4	15.05.2015	28.10.2015	166	3122
3430	South Germany	m	3.5	01.05.2015	22.10.2015	174	3210
3435	South Germany	m	3.5	08.05.2015	18.11.2015	194	3762
3436	South Germany	f	3.4	05.05.2015	19.09.2015	137	2378
3437	South Germany	f	4.55	15.07.2014	22.12.2014	160	4772

Supplement SG1 – Grooming and Vigilance

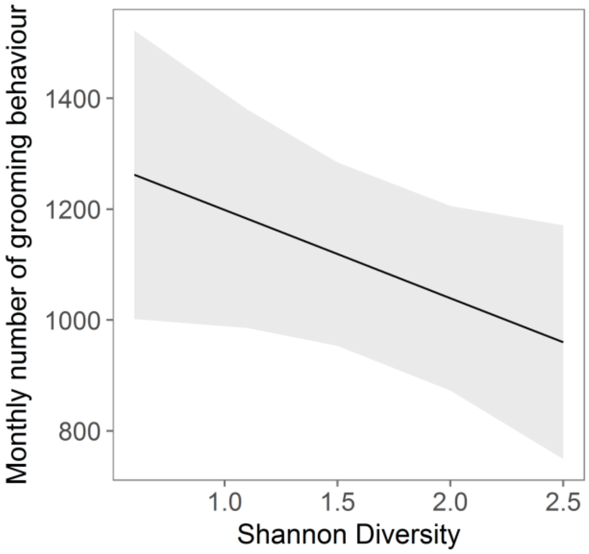
SG1 – Final models: Results of the model selection process showing seasonal, sex and landscape structure effects on the number of behavioural modes conducted per month. Parameter estimates with standard error (Std.Error) and degrees of freedom (DF) are given. The variable names are: the animals' sex (Sex, male and female), Landscape structure (LS, simple and complex), month, ":" indicates interactions. The reference levels are: "complex" for landscape structure and "female" for the animals' sex.

Grooming behaviour

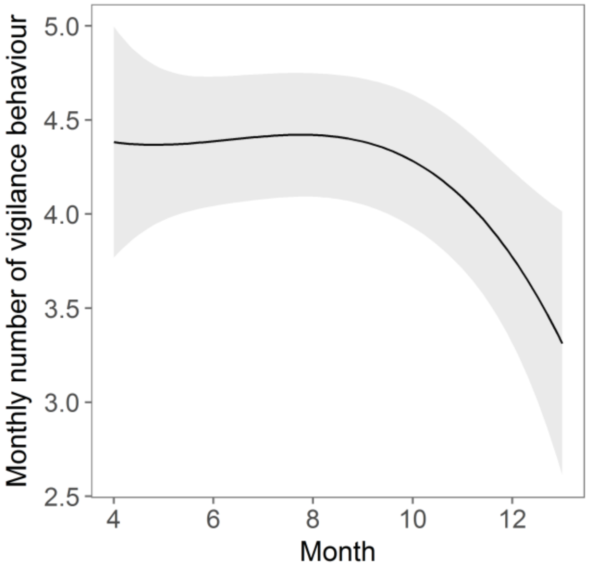
```
Explanatory Variables    Estimate     Std.Error   DF
(Intercept)                   9472.60     2086.94    85
Diversity                     -159.16       91.11    85
LS(simple)                   -6415.15     2364.14    30
month^1                      -2946.82      753.25    85
month^2                        349.09       87.85    85
month^3                        -13.08        3.32    85
LS(simple):month^1            2090.97      866.19    85
LS(simple):month^2            -233.09      102.83    85
LS(simple):month^3               8.24        3.95    85
```

Vigilance behaviour (log)

```
Explanatory Variables    Estimate     Std.Error   DF
(Intercept)                     5.269       2.087    89
month^1                        -0.471       0.781    89
month^2                         0.079       0.095    89
month^3                        -0.004       0.004    89
```



SG2 – Effects plot for grooming: The amount of grooming behaviour declines with increasing landscape diversity. Landscape diversity was measured as Shannon Diversity index over the number of landscape elements and different crop types within each hares' home range.



SG3 – Effects plot for vigilance behaviour: The amount of vigilance behaviour plotted against the month of the year.

SG4 – Competing models: Models with deltaAIC scores < 2 showing seasonal, sex and landscape structure effects on the number of behavioural modes conducted per month. Parameter estimates with standard error (Std.Error) and degrees of freedom (DF) are given. The variable names are: the animals' sex (Sex, male and female), Landscape structure (LS, simple and complex), month, ":" indicates interactions. The reference levels are: "complex" for landscape structure and "female" for the animals' sex.

Grooming behaviour - Competing model 1

Explanatory Variables	Estimate	Std.Error	DF
(Intercept)	9473.40	2132.48	86
LS(simple)	-6845.83	2399.17	30
month^1	-3074.02	765.43	86
month^2	364.74	89.21	86
month^3	-13.65	3.37	86
LS(simple):month^1	2298.87	875.61	86
LS(simple):month^2	-259.13	103.84	86
LS(simple):month^3	9.21	3.99	86

Grooming behaviour - Competing model 2

Explanatory Variables	Estimate	Std.Error	DF
(Intercept)	4779.32	987.49	88
LS(simple)	-501.71	161.27	30
Diversity	-206.46	87.61	88
month^1	-1267.16	360.04	88
month^2	161.23	43.67	88
month^3	-6.38	1.72	88

Grooming behaviour - Competing model 3

Explanatory Variables	Estimate	Std.Error	DF
(Intercept)	9883.76	2061.52	84
Sex(male)	-595.62	376.80	29
LS(simple)	-6292.52	2326.53	29
Diversity	-430.83	171.67	84
month^1	-2937.43	740.34	84
month^2	349.55	86.34	84
month^3	-13.15	3.26	84
Sex(male):Diversity	357.28	196.29	84
LS(simple):month^1	2051.46	851.78	84
LS(simple):month^2	-230.37	101.08	84
LS(simple):month^3	8.19	3.88	84

Vigilance behaviour - competing model (log)

Explanatory Variables	Estimate	Std.Error	DF
(Intercept)	5.572	2.096	89
Sex(male)	-0.481	0.330	30
month^1	-0.463	0.781	89
month^2	0.078	0.095	89
month^3	-0.004	0.004	89

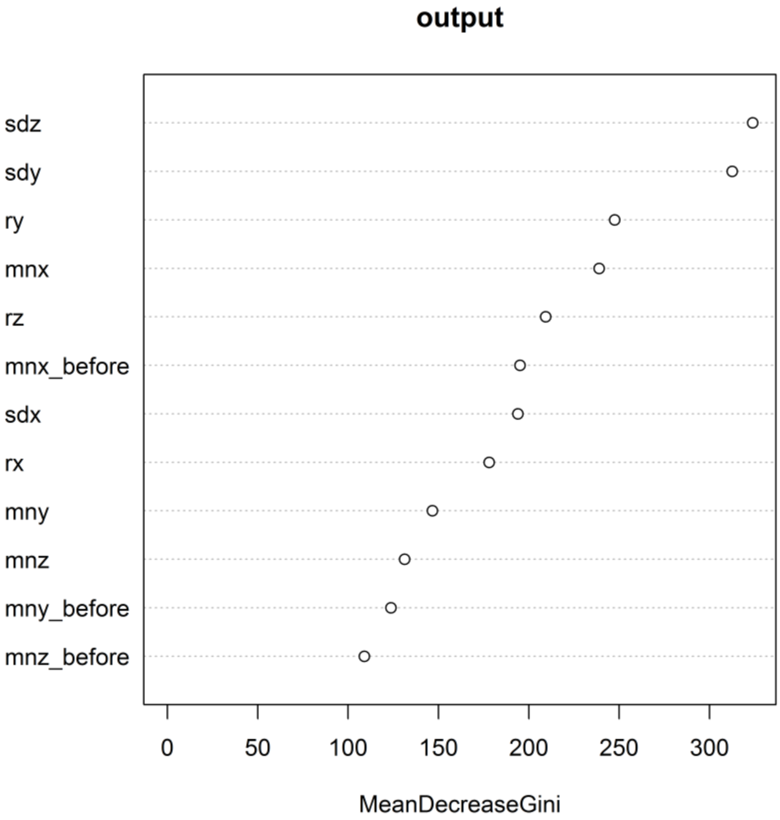
Supplement ST1– Random forest output

ST1: The formula with predictors that was used to train the random forest can be found under "call". The confusion matrix shows how often each behaviour category was classified correctly (within the same behaviour category) or erroneously (within other behaviour categories). The classification error presents the percentage of wrongly classified ACC samples per behaviour category.

```
Call:
 randomForest(formula = behaviour ~ mnx + mny + mnz +
                                    sdx + sdy + sdz +
                                    rx + ry + rz +
                                    mnx_before + mny_before + mnz_before,
                          data = train, na.action = na.omit)

               Type of random forest: classification
                     Number of trees: 500
No. of variables tried at each split: 3

        OOB estimate of  error rate: 10.5%
Confusion matrix:
                 Foraging Grooming Running Resting Vigilance    class.error
Foraging              525       14      39      95         4     0.22451994
Grooming               17      130      16      15         0     0.26966292
Running                25        4     540      13         5     0.08006814
Resting                85       11      32    2510         7     0.05103970
Vigilance               6        1      24      34       104     0.38461538
```



ST2: Variable Importance plot for the random forest depicting the Mean decreased gini index for the predictor variables used to classify the behaviours: foraging, grooming, running, resting, vigilance.

Appendix – Chapter 4

Supplement Figures

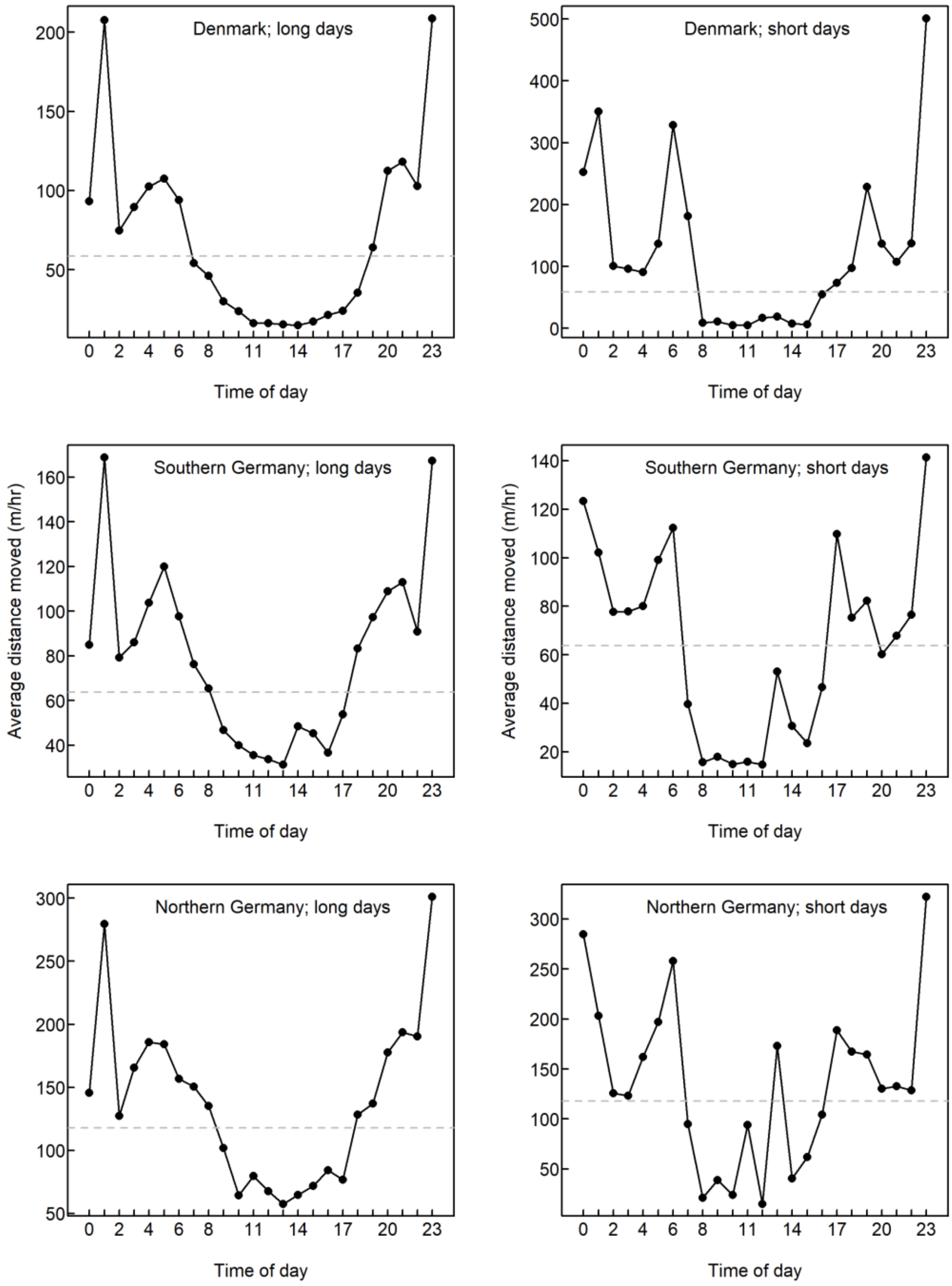


Fig. S1: Plots showing the average distance moved per hour (black dots) as measure of activity separately for long days (>12 hours of daylight; left) and short days (<12 hours of daylight; right) and separately for Denmark (top), Southern Germany (middle) and Northern Germany (bottom). The threshold for activity was set as 75% of the overall average distance moved (grey dashed line), that is, we categorized hares as ‘active’ if hourly distance moved was >75% of the average distance moved, and ‘inactive’ if it was <75% of the average distance moved.

Supplement Tables

Table S1: The 20 candidate models for the analyses of habitat selection by European hares (*Lepus europaeus*) separately for active and inactive GPS positions, ranked by $\text{AIC}_{c.}$ Hare ID, area, and month nested within year were included as random intercept in all models. Hare GPS data were obtained in 2014-2015.

Active GPS positions					
Model	df	logLik	AIC_c	deltaAIC_c	AIC_c weight
Vegetation type + log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2 + Vegetation height x log(Field size) + Vegetation height x log(Edge distance)	27	-81245	162544	0	1
Vegetation type + log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2 + Vegetation height x log(Edge distance)	24	-81356	162760	217	0
Vegetation type + log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2 + Vegetation height x log(Field size)	24	-81361	162769	226	0
Vegetation type + log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2	21	-81566	163174	631	0
Vegetation type + Vegetation height + log(Edge distance) + log(Edge distance)^2	20	-81651	163342	798	0
Vegetation type + log(Field size) + Vegetation height	19	-81670	163378	835	0
Vegetation type + Vegetation height	18	-81812	163660	1116	0
log(Field size) + Vegetation height + Vegetation height x log(Field size)	12	-81881	163787	1243	0
log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2	11	-81931	163884	1341	0
Vegetation height + log(Edge distance) + Vegetation height x log(Edge distance)	12	-81947	163919	1375	0
Vegetation height + log(Edge distance) + log(Edge distance)^2	10	-82026	164072	1528	0

log(Field size) + Vegetation height	9	-82039	164097	1553	0
Vegetation height	8	-82205	164427	1883	0
Vegetation type + log(Field size) + log(Edge distance) + log(Edge distance)^2	18	-82400	164836	2293	0
Vegetation type + log(Edge distance) + log(Edge distance)^2	17	-82466	164967	2423	0
Vegetation type + log(Field size)	16	-82501	165034	2491	0
Vegetation type	15	-82619	165268	2724	0
log(Field size) + log(Edge distance) + log(Edge distance)^2	8	-82976	165968	3424	0
log(Field size)	6	-83096	166205	3661	0
log(Edge distance) + log(Edge distance)^2	7	-83165	166344	3800	0

Inactive GPS positions

Model	df	logLik	AIC$_c$	deltaAIC$_c$	AIC$_c$ weight
Vegetation type + log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2 + Vegetation height x log(Field size) + Vegetation height x log(Edge distance)	27	-28299	56653	0	1
Vegetation type + log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2 + Vegetation height x log(Edge distance)	24	-28318	56683	31	0
Vegetation type + log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2 + Vegetation height x log(Field size)	24	-28359	56766	113	0
Vegetation type + log(Field size) + Vegetation height	19	-28377	56792	139	0
Vegetation type + log(Field size) + Vegetation height + log(Edge distance) + log(Edge	21	-28376	56794	141	0

distance)^2					
Vegetation type + Vegetation height	18	-28382	56800	148	0
Vegetation type + Vegetation height + log(Edge distance) + log(Edge distance)^2	20	-28382	56804	151	0
Vegetation type + log(Field size)	16	-28550	57133	480	0
Vegetation type + log(Field size) + log(Edge distance) + log(Edge distance)^2	18	-28550	57135	482	0
Vegetation type	15	-28554	57139	486	0
Vegetation type + log(Edge distance) + log(Edge distance)^2	17	-28554	57142	490	0
Vegetation height + log(Edge distance) + Vegetation height x log(Edge distance)	12	-28889	57802	1150	0
log(Field size) + Vegetation height + Vegetation height x log(Field size)	12	-28921	57866	1213	0
log(Field size) + Vegetation height	9	-28927	57872	1219	0
log(Field size) + Vegetation height + log(Edge distance) + log(Edge distance)^2	11	-28926	57874	1221	0
Vegetation height	8	-28933	57882	1229	0
Vegetation height + log(Edge distance) + log(Edge distance)^2	10	-28932	57884	1231	0
log(Field size)	6	-29143	58298	1645	0
log(Field size) + log(Edge distance) + log(Edge distance)^2	8	-29142	58300	1647	0
log(Edge distance) + log(Edge distance)^2	7	-29160	58335	1682	0

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In 2015 we moved from the beautiful Maulbeerallee to Golm. “Oh, how miserable!”, but Florian told us that we will be more of a team if we move to Golm. I think he was right.

Although I miss the Maulbeerallee dearly, I had a great time with all the people from our lab and am very grateful to them for all those years that I spend with them. I think there is something to be said for a person who actually *enjoys* going to work. So, a great thanks to all PENCies, for distractive lunch breaks, fast R and GIS support (thanks Robert, Jarro and Mike!), and helpful scientific advice. Thanks to Merlin, Madlen and Uli for sharing my ideas about science and the world :)

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Declaration

Herewith I declare to have prepared this dissertation independently and with the help of my supervisors. I marked all parts, which originate from publications. This thesis has not been submitted to any other university or institution before.

Potsdam, 14. November 2018

Wiebke Ullmann