

# Spatiotemporal variability in resources affects herbivore home range formation in structurally contrasting and unpredictable agricultural landscapes

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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 as a proxy.

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**Results** Hares in simple landscapes showed increasing home range sizes with increasing resource

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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.

**Keywords** Resource variability · Resource availability · Home range size · European brown hare · GPS tracking · Telemetry · *Lepus europaeus*

## 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. Relyea et al. 2000; Johnson et al. 2002; 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 Bunnell 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 (McCloughlin 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 (McCloughlin 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 high 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 in 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.

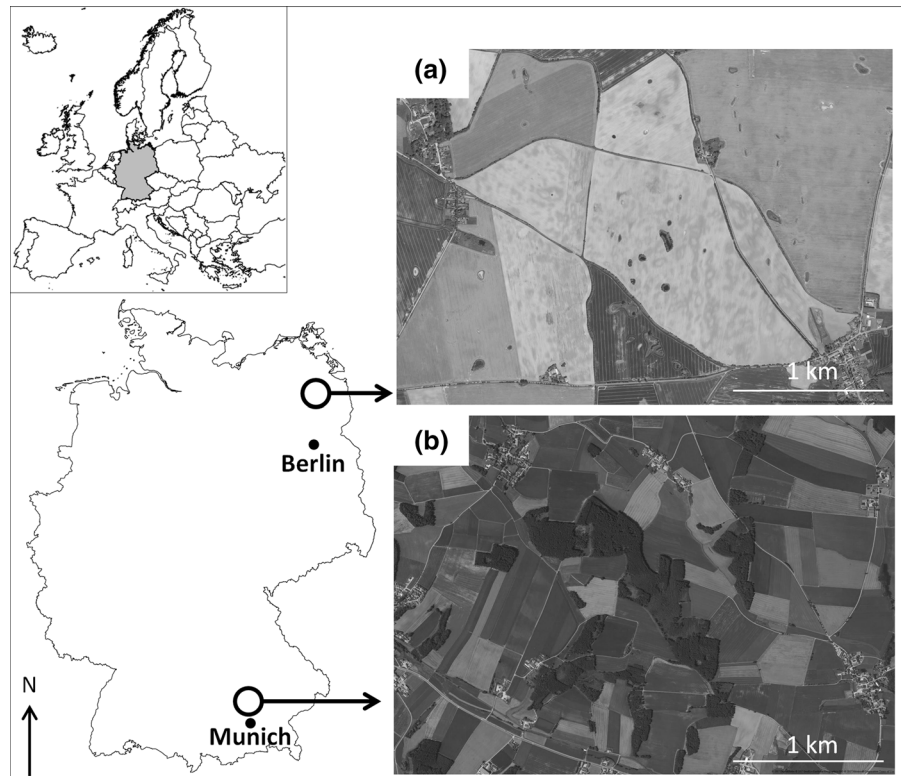
## Materials and methods

### Study area

We selected two study areas which strongly differed in landscape structure (Fig. 1). 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 km<sup>2</sup> study area is characterized by small-scale agriculture with an average field size of  $2.9 \pm 0.04$  ha (mean  $\pm$  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/](http://www.biomove.org/about-biomove/study_area/)). The 213 km<sup>2</sup> area is characterized by large-scale agriculture with an average field size  $27.5 \pm 1.1$  ha (mean  $\pm$  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).

**Fig. 1** Location of Germany in Europe (upper left panel) and the two study areas in North-east 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 (1:12,000)



## Model organism and GPS tracking

European brown hares (*Lepus europaeus* L.) 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 Online Appendix A1).

Hares were driven into woollen nets, then weighed, sexed and collared according to R uhe and Hohmann (2004). The 69 g collars (Model A1, e-obs GmbH, Munich, Germany, [www.e-obs.de](http://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 4 h. 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](http://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 were 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, NDVI 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  $30 \times 30$  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).

The NDVI raster file time series was used to extract and calculate the mean (hereafter NDVI<sub>mn</sub>) as proxy for potential resource availability and the standard deviation of the NDVI (hereafter NDVI<sub>sd</sub>) as proxy for resource variability in time within each 10-day home range (Fig. 2c, 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 NDVI<sub>mn</sub> and NDVI<sub>sd</sub> (see Online Appendix 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 Online 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 NDVI<sub>mn</sub> and NDVI<sub>sd</sub> for each hares' home range on that image and also calculated each home range size.

### Statistical analysis

We first tested whether home range size, NDVI<sub>mn</sub> and NDVI<sub>sd</sub> 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  $\sim$  landscape structure,
- (2) NDVI<sub>mn</sub>  $\sim$  landscape structure and
- (3) NDVI<sub>sd</sub>  $\sim$  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

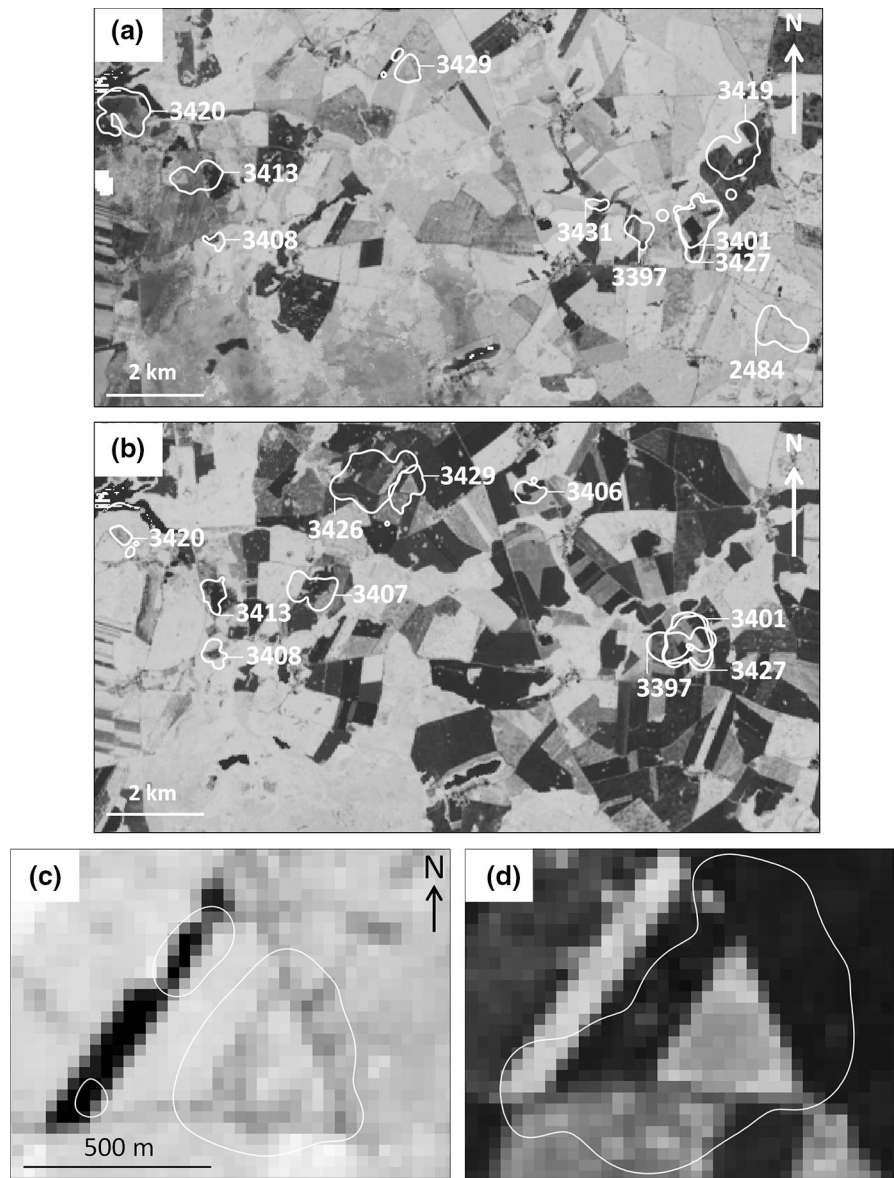
*nlme* (Pinheiro et al. 2014)) to test whether home range size is affected by NDVI<sub>sd</sub>, NDVI<sub>mn</sub>, landscape structure (simple vs. complex) and season (Julian day):

$$\begin{aligned} 10\text{-day home range size} &\sim \text{NDVI}_{sd} \\ &\times \text{landscape structure} + \text{NDVI}_{mn} + \text{day} + \text{day}^2 \end{aligned}$$

Covariates were tested for collinearity first (Zuur et al. 2009). An interaction term was used for NDVI<sub>sd</sub> and landscape structure to test for different relationships between home range size and resource variability in the two landscape structures. NDVI<sub>mn</sub> 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 (NDVI<sub>mn</sub>: complex landscape =  $0.56 \pm 0.13$ , simple landscape =  $0.59 \pm 0.12$ ,  $F_{1,40} = 0.27$ ,  $P = 0.61$ , Fig. 3a and NDVI<sub>sd</sub>: complex landscape =  $0.17 \pm 0.05$ , simple landscape =  $0.18 \pm 0.05$ ,  $F_{1,40} = 0.29$ ,  $P = 0.59$ , Fig. 3b). However, the mean 10-day home range size in the complex landscape with  $18.5 \pm 13.7$  ha was significantly smaller than those in



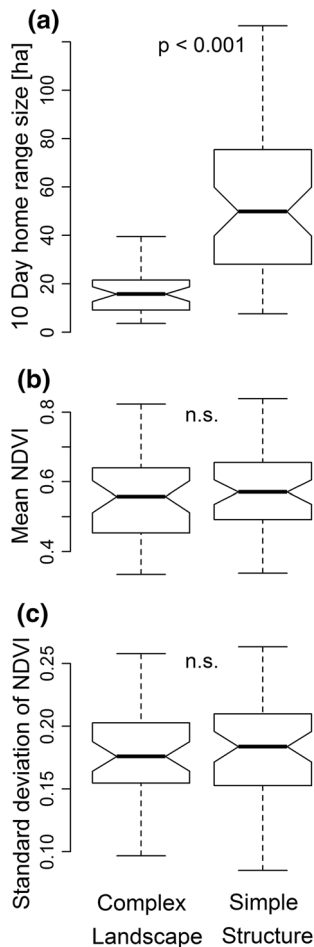
**Fig. 2** NDVI raster image acquired on 10.06.2014 (**a** and **c**) and 13.08.2014 (**b** and **d**) with the corresponding 10-day home ranges. The images show the differences in NDVI within home ranges and between different seasons (June and August 2014). The home ranges are labelled with the hare's 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

to 14.06.2014. The NDVI measures were  $NDVI_{Im} = 0.75$ ,  $NDVI_{sd} = 0.11$ . 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 to 17.08.2014. The NDVI measures were  $NDVI_{Im} = 0.44$ ,  $NDVI_{sd} = 0.17$ . 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  $30 \times 30$  m

simple landscapes with  $55.41 \pm 34.56$  ha ( $F_{1,40} = 38.7$ ,  $P < 0.001$ , Fig. 3c).

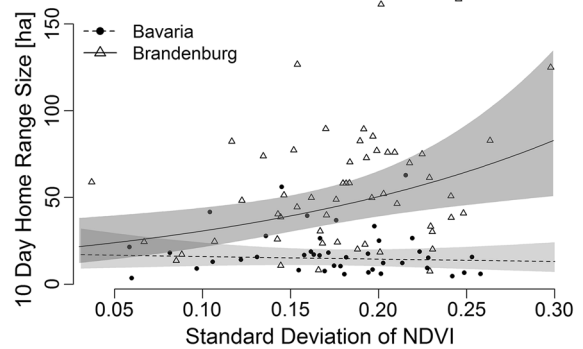
The model selection procedure showed that resource availability ( $NDVI_{mean}$ ) and Julian Day

had no effect on the respective 10-day hare home range sizes in both landscapes. In contrast, increasing spatiotemporal variability of the resources ( $NDVI_{sd}$ ) in the structurally simple landscape led to an increase



**Fig. 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)

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).



**Fig. 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

## 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 (NDVI<sub>mn</sub>) and resource variability (NDVI<sub>sd</sub>) 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



**Table 1** LMM output—degrees of freedom, coefficients, and standard errors (df,  $\beta \pm$  SE) for explanatory variables retained in the most parsimonious model predicting home range sizes of European brown hares. The reference category was the complex landscape

	df	$\beta$	SE
Intercept	54	2.86	0.38
NDVI_sd	54	− 0.97	2.06
Landscape structure (simple landscape)	38	0.06	0.51
NDVI_sd $\times$ 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

landscape (a pattern also found by Tapper and Barnes 1986; Frylestam 1992; Rhe and Hohmann 2004; Smith et al. 2004; Schai-Braun and Hacklnder 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; Tschardt 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<sup>2</sup>) 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 larger 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 size 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 1 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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