Landscape configuration is a major determinant of home range size variation

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

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INTRODUCTION

With increasing human wildlife conflicts it is necessary to understand and predict the changes of wildlife behavior in general and specifically changes in animal movement patterns (Wilcove and Wikelski 2008). Such conflicts can be due to growing human populations, changing landscapes as a consequence of anthropogenic land use like agriculture or to natural changes like fires and bark beetle outbreaks. A correct interpretation of the causes of animal movement and dispersal is pivotal for understanding habitat selection and more generally the diversity and distribution of species (e.g., Chave et al. 2002).

Most animals do not move randomly through a landscape (Nathan et al. 2008, Gautestad and Mysterud 2010, Fronhofer et al. 2013) and restrain their movement activities to familiar areas. While central place foragers, such as bees or ants, return to their nest after a foraging bout (Wakefield et al. 2014) and territorial animals,

such as some felids, defend well defined landscape stretches (Valeix et al. 2012), a large majority of animals use familiar areas without defending them (Burt 1943). The latter behavior leads to the establishment of home ranges, which are generally defined as the spatial expression of all behaviors an animal performs in order to survive and reproduce (Burt 1943). As home ranges link individual movement to dispersal and (meta-)population dynamics (Hanski and Gilpin 1998, Fronhofer et al. 2012) understanding why and how home range sizes vary between and among species is a fundamental issue in ecology.

While theory still struggles to explain the emergence of home ranges (Börger et al. 2008) the availability of large movement data sets allows us to formulate some testable hypotheses. Progress in GPS-sensor technology and satellite techniques makes it possible to track animals over long time spans with high temporal and spatial resolution and to analyze their habitat requirements and movement paths (Tomkiewicz et al. 2010, Thiebault and Tremblay 2013). Early analyses have shown that home range size depends on a number of variables. Generally, home range size was shown to decrease with decreasing body size (Swihart et al. 1988) and good forage availability (Tufto et al. 1996). Increasing intraspecific competition leads to smaller home range sizes (Riley and Dood 1984) while interspecific competition leads to increasing home range sizes (Loft et al. 1993; see van Beest et al. 2011 for a more complete list). Besides these factors it is well known that the spatial arrangement of different habitat types can influence the distribution of large mammals (Clutton-Brock and Harvey 1978) as this will influence movement trajectories.

A large number of studies have shown that the landscape is an essential determinant of home range size and dynamics in ungulates. Yet, these studies typically only took the dominant habitat type within a home range into account. For example, the landscape composition was included only as the fraction of meadow or forest within the home range (Frair et al. 2005, Börger et al. 2006a, Rivrud et al. 2010). However, natural landscapes are heterogeneous in the spatial arrangement of resources, as these are often autocorrelated and form resource clusters or patches of varying size and density (see Fig. 1). In Fig. 1 we illustrate the extent to which the appearance of a landscape may differ depending on the arrangement of habitats by two artificial landscapes, derived from our true natural landscape. In both cases the fraction of land cover types is kept constant but arranged randomly in space (Fig. 1B) or ordered (Fig. 1C). These different landscape configurations will likely affect home range size. Specifically, home ranges in a randomized landscape may be expected to become much smaller, as a large number of different land cover types satisfying a diversity of needs can be found on a much smaller spatial scale. On the other hand, an artificially ordered landscape could lead to longer movement paths: when an animal needs to reach the land cover type "meadow" after having been in "deciduous forest," for example, and therefore needs to cross a block of "mixed forest."

It is only recently that the explicit spatial configuration of habitat types, the arrangement of all land cover types within the home range, and the size of these patches is being taken into account in the study of home range sizes (e.g., Moorcroft et al. 2006, Moorcroft 2012).

Finally, previous studies have mostly focused only on large spatio-temporal scales like the landscape scale as spatial scale and seasonal scale as temporal scale (Kie et al. 2002, Saïd and Servanty 2005, Walter et al. 2009, Quinn et al. 2013). Yet, smaller scales might also be relevant, depending on the degree and scale of landscape heterogeneity. In addition, mechanisms that affect variation in home range size may differ depending on the temporal and spatial scale under investigation (van Beest et al. 2011).

We here analyze the relationship between the spatially explicit landscape configuration and home range size for two sympatric ungulates, red and roe deer at multiple spatio-temporal scales. Since the explicit spatial configuration of land cover types will affect the movement path of an animal searching for food or shelter (Fig. 1) we hypothesized that the spatial configuration is a central determinant of home range size. More specifically we expected larger home ranges in aggregated landscapes, because larger distances have to be covered regularly in order to utilize resources (food, shelter, etc.) that can be found in different land cover types (Fig. 1).
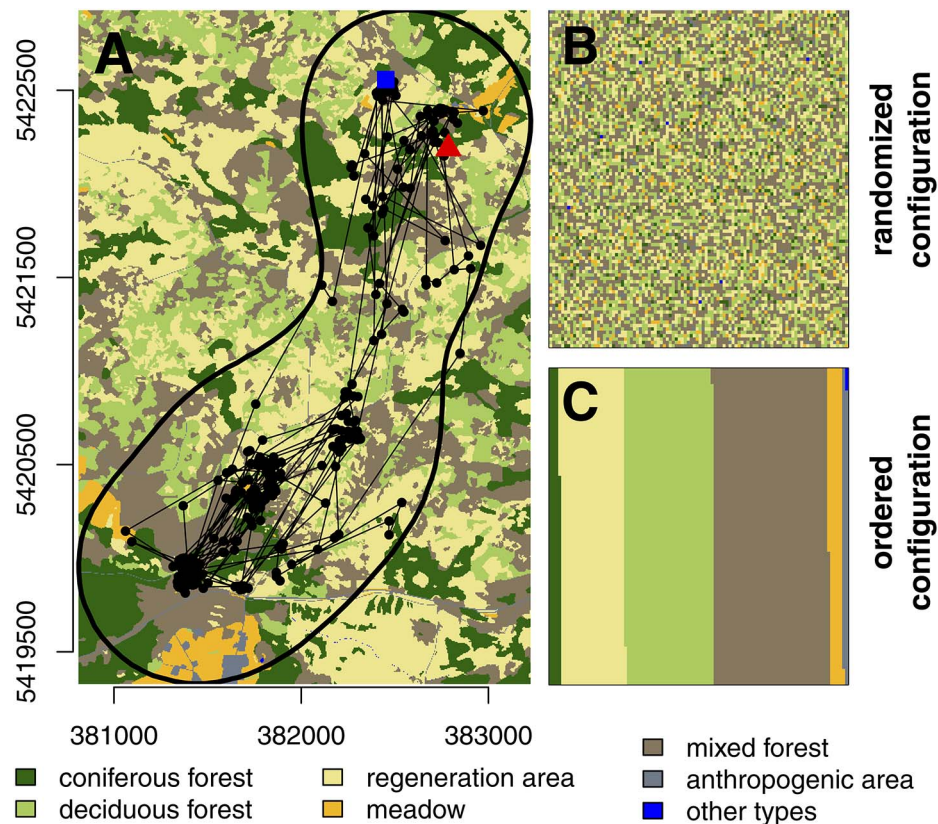
Fig. 1. (A) Example of a home range shown with the trajectory (connected points, red triangle refers to the start of the trajectory and the blue square to the end) of a red deer (individual 668_668_07, female, calculated with the fixed kernel method (90% isopleth) on 286 location points in the month September, projection: WGS84 UTM Zone 33N) in the Bavarian Forest National Park. A land cover map with seven categories is shown in the background. "Regeneration areas" are land stretches that have suffered from massive bark beetle outbreaks during the 90s, "anthropogenic areas" comprise cities, roads, railways and "other types" refers to water and peat bogs. (B) The same landscape with a randomized spatial configuration but the same fraction of land cover types. (C) The same landscape with a blocked spatial configuration but the same fraction of land cover types. These two artificial landscapes illustrate strongly spatial configuration of a landscape can vary for the same composition.

Red and roe deer differ in their habitat requirements and behavior. Red deer are widely roaming animals with a broad spectrum of possible food sources (Gebert and Verheyden-Tixier 2001). They rely on open habitats for food supply as well as on covered areas for refuge (Hebblewhite et al. 2008). As the habitat demands a variety of different resource patches and furthermore red deer easily moves across wide areas we expect a high impact of the landscape configuration.

Roe deer on the other hand are smaller, with typically smaller home ranges (Radeloff et al. 1999) and with very selective foraging preferenc-es. As they rely more on highly digestible food items, such as fruits, seeds or sprouting shoots (Demment and Van Soest 1985), the effect of the land cover types should be more pronounced than for red deer. Nevertheless the spatial configuration should play an important role, as it determines the spatial arrangement of the patches.

MATERIAL AND METHODS

Study area

The study was conducted in the Bavarian Forest National Park which is situated in south-

eastern Germany along the border to the Czech Republic (49°3′19″ N, 13°12′9″ E). The National Park covers an area of 240 km². Adjacent to the park, on the Czech side of the border, lies the Šumava National Park with an area of 640 km². These protected areas are embedded within the Bavarian Forest Nature Park (3070 km²) and the Šumava Landscape Protection Area (1000 km²). In its entirety, the area is known as the Bohemian Forest Ecosystem. The area is mountainous, with a variation in elevation between 600 and 1450 m a.s.l. The mean annual temperature varies between 3°C and 6.5°C along higher elevation and ridges.

The mean annual precipitation is between 830 and 2230 mm. Within the park, three major forest types exists: above 1100 m are sub-alpine spruce forests with Norway spruce (*Picea abies* L.) and some mountain ash (*Sorbus aucuparia* L.), on the slopes, between 600 and 1100 m altitude, are mixed montane forests with Norway spruce, white fir (*Abies alba* MILL.), European beech (*Fagus sylvatica* L.), and sycamore maple (*Acer pseudoplatanus* L.). In the valley bottoms, spruce forests with Norway spruce, mountain ash, and birches (*Betula pendula* ROTH. and *Betula pubescens* EHRH.; Fischer et al. 2013).

Since the mid-1990s, the forests of the national park have been affected by massive proliferation of the spruce bark beetle (*Ips typographus*). By 2007, this had resulted in the death of mature spruce stands over an area amounting to 5,600 ha (Lausch et al. 2013), leading to areas which regenerate naturally and go through different successional phases. Today these areas are characterized by shrubby vegetation of spruce and mountain ash.

Deer data

Red deer were caught during winter in the years 2002–2009. Animals were attracted to a corral by food (grass silage, hay, apple, pomace, sugar beets). Within the corral, the deer are guided to a capture facility, were the GPS collars (Vectronic Aerospace, Berlin, Germany) can be attached through hatches in the wall. A second approach was to tranquillize deer by dart gun on sites where they were attracted by food. We collared 14 male and 18 female red deer individuals. Four individuals were collard two or more times over the duration of the study.

Roe deer were captured during the winter months (October–March) in the years 2005–2010 using wooden box traps. A total of 40 roe deer (24 male, 16 female) were collared, with five animals collared two or more times over the years of the study. The most common sampling design was to mark roe and red deer in late winter and retrieve the collars after a year by collar drop-off or recapturing, allowing the collars to be used on new individuals. Animal handling was performed in compliance with German laws and regulations. We restrict our analysis for both species to summer home ranges only.

We checked the data before the statistical analysis and removed spatial and temporal outliers. Temporal outliers were locations that were less than 60 minutes apart and spatial outliers were removed by visual inspection of the data. This leads to a removal of 19% of the raw data for red deer and 16% for roe deer. We used only the summer months (May–September; red deer stay in enclosures during winter time) for the analysis and only if the calculated home ranges had at least 95% overlap with the land cover map. Further, we classified the samples from the multiple collared animals over the single years as independent. As red deer spend the winter in enclosures, we restricted the analysis temporally from May to the end of September. The schedules of the collars are adjusted to take a location every 15 min for one day of the week. We took a random sample of animals with sequences of short time intervals to ensure that all locations have a minimum interval of one hour. The elapsed time between locations for each animal averaged 157.57 min for red deer and 365.77 min for roe deer with an overall position acquisition rate of 72.8% and a median accuracy of 16.5 m (Stache et al. 2012).

Home range estimation

Home ranges were estimated with a commonly used approach, the fixed kernel method (Worton 1989) using the reference method for the smoothing factor h (Kernohan et al. 2001).

Mechanisms that affect variation in home range size may differ depending on the scale under investigation (van Beest 2011). Therefore, we consider multiple spatial and temporal scales in our study which have been used to study

home range variation before (e.g., Rivrud 2010). The spatial resolution was realized by calculating home range isopleths with 50%, 70% and 90%.

In addition, all home ranges were estimated on three temporal scales: weekly, biweekly and monthly. We only estimated home ranges for individuals with at least six relocations for the temporal scale under study (Börger 2006*b*) and restricted our analyses to summer months, as red deer live in enclosures during the winter time. The software R version 3.0.2 using the package "adehabitatHR" was used for the analysis (R Development Core Team 2013, Calenge 2006).

Land cover types and environmental data

To characterize the landscape in our study area we considered five land cover types: "coniferous forest," "deciduous forest," "mixed forest," "meadow" and "regeneration areas," i.e., areas containing mature trees killed by bark beetles and showing now regrowing vegetation, characterized by a shrubby appearance. Anthropogenic areas (e.g., roads) and water bodies were not taken into account as they cover only a negligible area within the study area. The land cover classification was derived through digitalization from aerial images from the year 2008. In order to take into account the rapid forest dynamics due to bark beetle outbreaks, we update the land cover classification for every year of the study (2002–2010).

As a measure of the landscape's spatial configuration we calculated different landscape indices within a given home range (McGarigal et al. 2002). As the calculation of the landscape indices require a raster, we converted the land cover classification into a grid with a resolution of 5 m. We choose as index for landscape configuration the percentage of like adjacencies (PLADJ). This index measures the patchiness of a landscape and we could show that this index is the most scale-independent (see the Appendix for details). Henceforth, we will refer to this index as configuration index. Furthermore, we estimated the mean elevation of the home ranges using ASTER GDEM (resolution: 30 m; http://asterweb.jpl.nasa.gov/gdem.asp).

Statistical methods

To investigate the influence of different land cover types and the landscape configuration on home range sizes, we used linear mixed models (R version 3.0.2, R Development Core Team 2013; package "nlme", Pinheiro et al. 2013) on the log transformed home range areas (km^2) and included spatio-temporal autocorrelation structures following the framework proposed by (Börger et al. 2006*a*).We used the year of measurement nested in individuals (ID) as a random effect, as individuals were sampled repeatedly in subsequent years.

After inspection for colinearity we removed the variables "mixed forest" and "elevation" for the red deer data set as both variables showed a Pearson correlation index > 0.7 with "regeneration area" and "configuration index". Furthermore preprocessing steps revealed a quadratic fit of elevation and configuration index, hence these two variables were fitted with a quadratic term in the model. For the roe deer data we only removed "mixed forest" as it showed a correlation with elevation (Pearson correlation index > 0.7).

Therefore we fitted as fixed effects the variables coniferous, deciduous, meadows, regeneration areas, configuration index, sex and additionally elevation for roe deer.

We first selected the best autocorrelation structure using AIC on the full models and subsequently simplified our models using ANOVA as described in Crawley (2013).

To evaluate the importance of landscape configuration for the model fit, we compared the best models and analogous models without the landscape configuration using an R^2 measure calculated as $1 - \exp(-(2/N \times \delta L))$ with N as the sample size and δL as the difference between the log-likelihood of the model of interest and the log-likelihood of the null model. We repeated the analysis steps for the three definitions of home range size and for the three definitions of temporal scale.

RESULTS

The role of landscape configuration

Home range sizes varied across all spatio-temporal scales, especially for red deer (Table 1; Appendix). The fixed effects of the most parsimonious models explained between 0.19–0.37 R^2 for red deer (Table 1) and 0.12–0.15 R^2 (Table 2)

Table 1. The ΔR^2 values are shown retained from the mixed model with the best correlation structure calculated for all temporal (monthly, biweekly and weekly) and all spatial scales (90%, 70% and 50% isopleths) for red deer with ID and nested year as random structure. The variable configuration was fitted as quadratic term.

Timescale and kernel size	Correlation	Variable	Relationship	t	p	ΔR^2
Monthly						
50	temporal	coniferous	positive	3.47	<0.001	0.05
		deciduous	positive	4.63	<0.001	0.08
		configuration	linear	5.29	<0.001	0.13
		configuration	quadratic	−4.23	<0.001	0.13
70	spatial	coniferous	positive	4.42	<0.001	0.07
		deciduous	positive	5.86	<0.001	0.12
		configuration	linear	6.82	<0.001	0.18
		configuration	quadratic	−5.48	<0.001	0.18
90	none	coniferous	positive	5.71	<0.001	0.10
		deciduous	positive	5.33	<0.001	0.09
		configuration	linear	7.28	<0.001	0.17
		configuration	quadratic	−5.98	<0.001	0.17
Biweekly						
50	temporal	deciduous	positive	1.93	0.05	0.01
		meadows	negative	−2.16	0.03	0.01
		regeneration	negative	−3.93	0.001	0.03
		configuration	linear	7.89	<0.001	0.16
		configuration	quadratic	−6.22	<0.001	0.16
70	temporal	deciduous	positive	4.46	0.05	0.01
		meadows	negative	−2.16	0.003	0.02
		regeneration	negative	−3.93	<0.001	0.04
		configuration	linear	9.55	<0.001	0.19
		configuration	quadratic	−8.38	<0.001	0.19
90	spatial	meadows	negative	−2.16	0.03	0.01
		regeneration	negative	−5.10	<0.001	0.05
		configuration	linear	10.42	<0.001	0.21
		configuration	quadratic	−9.01	<0.001	0.21
Weekly						
50	temporal	deciduous	positive	2.28	0.005	0.01
		meadows	negative	−2.39	0.02	0.01
		regeneration	negative	−5.85	<0.001	0.04
		configuration	linear	8.44	<0.001	0.13
		configuration	quadratic	−6.46	<0.001	0.13
70	temporal	deciduous	positive	3.06	0.002	0.01
		meadows	negative	−3.37	<0.001	0.01
		regeneration	negative	−6.05	<0.001	0.04
		configuration	linear	11.80	<0.001	0.16
		configuration	quadratic	−9.84	<0.001	0.16
90	temporal	meadows	negative	−4.45	<0.001	0.02
		regeneration	negative	−8.66	<0.001	0.07
		configuration	linear	12.05	<0.001	0.15
		configuration	quadratic	−10.32	<0.001	0.15

for roe deer across scales.

Landscape configuration was the key determinant of home range sizes for both species. Especially for red deer the variance explained through the configuration index was high across all scales (0.13–0.21 ΔR^2; Table 1). In the roe deer data set the configuration index played a major role but its impact varied across scales (0.02–0.10 ΔR^2; Table 2) and was highest at the 50% kernel weekly scale. Especially at the monthly scale the configuration index was exceeded by the land cover type "meadow."

Landscape configuration explains home range size

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

Land cover type

In red deer the land cover types "regeneration area" and "meadow" played a secondary role at

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

Timescale and kernel size	Correlation	Variable	Relationship	t	p	ΔR^2
Monthly						
50	temporal	meadows	negative	−3.91	<0.001	0.06
		configuration	positive	3.00	0.004	0.04
		sex	male > female	2.82	0.008	0.03
70	spatial	coniferous	positive	2.55	0.01	0.02
		deciduous	positive	2.62	0.01	0.03
		meadows	negative	−2.96	0.003	0.03
		configuration	positive	2.33	0.02	0.02
		sex	male > female	2.71	0.01	0.02
90	spatial	coniferous	positive	3.36	0.001	0.04
		deciduous	positive	2.01	0.05	0.01
		meadows	negative	−4.05	<0.001	0.05
		sex	male > female	2.39	0.02	0.02
Biweekly						
50	temporal	meadows	negative	−5.93	<0.001	0.05
		regeneration	negative	−2.40	0.02	0.01
		configuration	positive	6.58	<0.001	0.07
		elevation	positive	2.37	0.02	0.01
		sex	male > female	3.18	0.003	0.01
70	spatial	coniferous	positive	2.23	0.02	0.01
		deciduous	positive	2.91	0.004	0.01
		meadows	negative	−3.84	<0.001	0.02
		configuration	positive	6.89	<0.001	0.07
		sex	male > female	2.82	0.007	0.01
90	spatial	deciduous	positive	2.03	0.04	0.01
		meadows	negative	−4.86	<0.001	0.03
		configuration	positive	7.32	<0.001	0.08
		sex	male > female	2.56	0.01	0.01
Weekly						
50	temporal	coniferous	positive	3.72	<0.001	0.01
		deciduous	positive	3.85	<0.001	0.01
		meadows	negative	−5.41	<0.001	0.02
		configuration	positive	11.29	<0.001	0.10
		elevation	positive	3.60	<0.001	0.01
		sex	male > female	2.78	0.009	0.005
70	temporal	coniferous	positive	4.10	<0.001	0.01
		deciduous	positive	4.48	<0.001	0.02
		meadows	negative	−5.85	<0.001	0.03
		configuration	positive	10.46	<0.001	0.08
		elevation	positive	2.95	0.003	0.01
		sex	male > female	2.40	0.02	0.004
90	spatial	coniferous	positive	3.41	<0.001	0.01
		deciduous	positive	3.14	0.002	0.01
		meadows	negative	−8.74	<0.001	0.08
		configuration	positive	2.93	0.003	0.01
		sex	male > female	2.88	0.007	0.01

the biweekly and weekly scale, while "coniferous forest" and "deciduous forest" were more important at the monthly scale. Generally, "regeneration area" and "meadow" led to smaller home ranges, while "coniferous forest" and "deciduous forest" lead to larger home ranges.

In roe deer "meadow" had an impact across scales and lead to smaller home ranges. The land cover types "coniferous forest" and "deciduous forest" showed a positive effect across scales but without clear pattern.

DISCUSSION

The present study highlights the strong effect of a landscape's spatial configuration on individual variation in home range sizes. The influence of landscape configuration was found on different spatio-temporal scales for two sympatric ungulate species, red deer and roe deer. The temporal scales analyzed range from monthly to weekly and the spatial scales from 90% to 50% kernel isopleths.
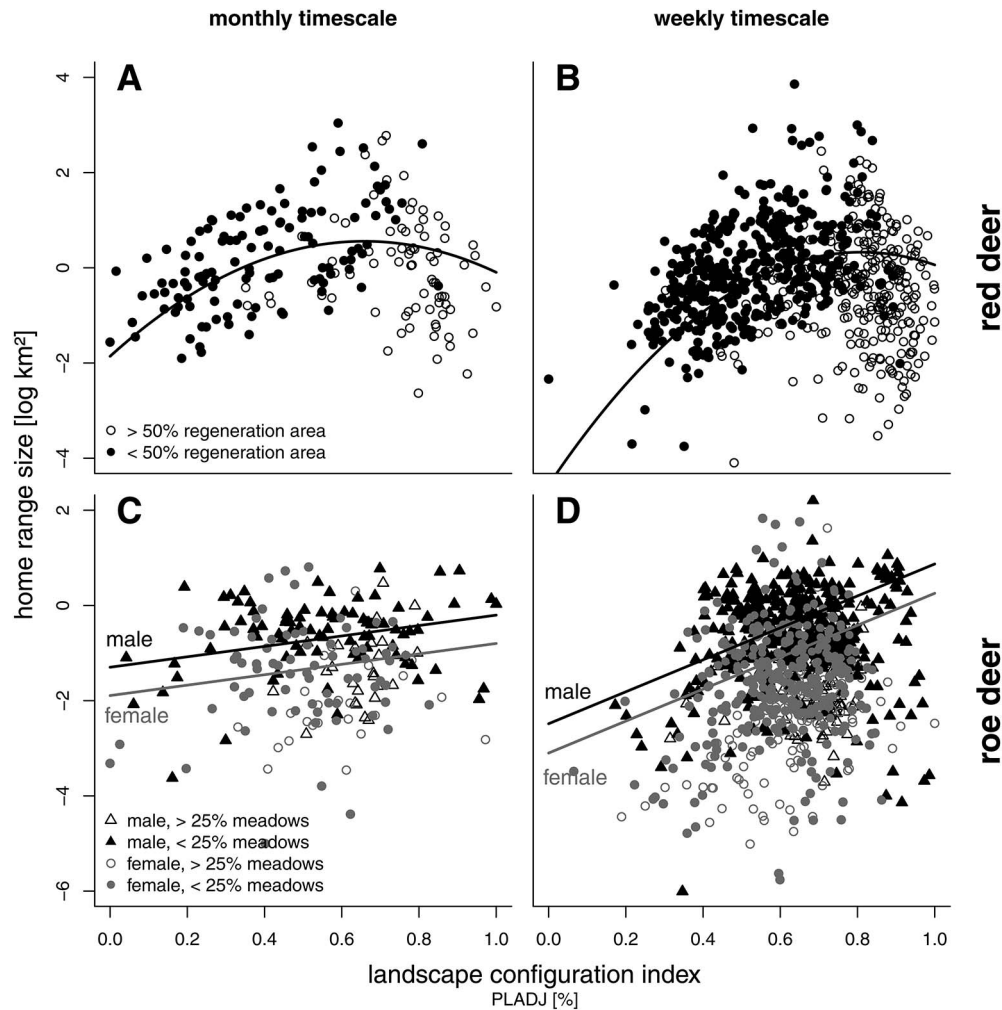
Fig. 2. Home range size (log km²) for red deer (A, B) and roe deer (C, D) as a function of patch aggregation. Home ranges are calculated on 50% monthly scale and 50% weekly scale on each individual home range. The models revealed a different effect of the sexes for roe deer, therefore the male (black, triangle) and female (grey, points) are presented separately. In red deer, filled points show home ranges with less than 50% land cover type "regeneration area" within the home range and unfilled points show home ranges with 50% and more than 50% "regeneration areas" within the home range. In roe deer, filled triangles show male home ranges sizes with less than 25% land cover type "meadow" within the home range and unfilled triangles show home ranges with 25% or more land cover type "meadow" within the home range. The same holds for females, the symbols here are coded as points. Lines show model fit and points true values. Red deer: monthly: $n = 210$, weekly: $n = 753$; male roe deer: monthly: $n = 112$, weekly: $n = 483$; female roe deer: monthly: $n = 99$, weekly: $n = 448$.

Besides quantifying the effect of the landscape configuration we also include further parameters, such as environmental parameters.

We demonstrate that by including landscape configuration, predictions of home range size can be significantly improved (Tables 1 and 2). This finding can be explained by comparing the artificially ordered landscape in Fig. 1C with the random landscape in Fig. 1B: if we consider an animal located in a patch of "deciduous forest" that aims to reach a "meadow" patch in order to forage, it needs to cross a large block of "mixed forest" to reach its goal. The same animal will reach its goal with a much shorter move-

ment path in a very fine grained landscape (Fig. 1B). Real landscapes contain a mixture of patches differing in size and habitat type and an animal will establish a home range according to its needs in the context of the underlying landscape. Hence the home range will contain patches that provide resources according to the needs of the animal (e.g., food or shelter) as well as patches it needs to traverse when switching between different activity modes. As a consequence, home range size is heavily influenced by the spatial configuration of a landscape.

The differences in habitat preference of our study organisms lead to different relationships for the two species. While roe deer show a positive linear relationship with patch aggregation, this relationship is hump-shaped for red deer.

Red and roe deer differ in their habitat requirements and behavior: red deer are widely roaming animals and intermediate feeders that consume both, high and poor-quality food (Hofmann 1989, Clauss et al. 2009). In our study area very large patches are typically "regeneration areas," i.e., land stretches that have suffered from massive bark beetle outbreaks during the 90s. These outbreaks affected an area of approximately 5,600 ha especially in the subalpine regions, leading to sunny openings (Lausch et al. 2011). After a first succession phase the characteristics of these areas provide exceptionally good habitat for red deer, as these areas show high grass cover. Additionally, with lying dead wood and regrowing vegetation the food supply is diverse and furthermore at the same time these vegetation characteristics provide next to abundant food supply good shelter for the animals. Here both resources occur at small spatial scales. This leads to shorter movement paths and smaller home ranges, an effect that is highly visible in our study and responsible for the hump-shaped relationship depicted in Fig. 2.

Roe deer, on the contrary, show characteristically smaller movement radii, are very selective feeders and only consume highly digestible forage (Barančeková et al. 2009, Mueller et al. 2013). As a consequence the fraction of habitat types containing valuable food resources for roe deer (e.g., "meadow") increases the quality of our model.

As shown in Fig. 2 larger amounts of valuable resources within the landscape ("regeneration areas" for red deer, "meadow" for roe deer) significantly decrease the size of a home range. While for red deer such valuable resources occur especially in large "regeneration areas," which leads to the hump-shaped relationship shown in Fig. 2, meadows can be found all along the patch aggregation axis (open symbols in Fig. 2C and D). Roe deer that have a high amount of "meadow" in their home range typically have smaller home ranges, as open symbols in Fig. 2 occur especially in the lower parts of the graph.

We chose to use the most common estimator for home range size calculation to have a basis for comparison to other studies. While the best home range estimate is under discussion and new methods are continuously proposed (Hemson et al. 2005, Kie et al. 2010, Kranstauber et al. 2012), we expect our results to be robust against the choice of a particular estimator of home range size, since we focused on core areas of home range activity.

Most empirical studies on home range dynamics and size, especially within ungulates, take into account vegetation, i.e., the fraction of land cover types but not the explicit spatial configuration of a landscape (Börger et al. 2006b, Rivrud et al. 2010, van Beest et al. 2011). So far, studies which include landscape heterogeneity have focused exclusively on large scales. For example Kie et al. (2002) analyzed female mule deer in North America at the landscape scale with a multiple regression model, using buffers around home ranges centers and seasonal 95% adaptive kernels on a landscape resolution of 50 × 50 cell grid. At the largest spatial scale the landscape analysis extended the home range size. They found similar results at these scales (larger home ranges in aggregated landscapes) but restricted their analysis to landscape indices only. Similarly Quinn et al. (2013) analyzed home range sizes of white-tailed deer in North America on an annual and seasonal temporal scale using different landscape metrics and linear regressions and found similar results, decreasing home range size with increasing patchiness of the landscape.

Concluding Remarks

Although home ranges have been studied extensively for quite some time, it is only recently

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

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SUPPLEMENTAL MATERIAL

ECOLOGICAL ARCHIVES

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