



# Seasonal effects of habitat structure and weather on the habitat selection and home range size of a mammal in agricultural landscapes

Martin Mayer · Wiebke Ullmann · Rebecca Heinrich · Christina Fischer · Niels Blaum · Peter Sunde

Received: 29 March 2019 / Accepted: 1 August 2019 / Published online: 8 August 2019  
© Springer Nature B.V. 2019

## Abstract

**Context** Human land use intensified over the last century and simultaneously, extreme weather events have become more frequent. However, little is known about the interplay between habitat structure, direct short-term weather effects and indirect seasonal effects on animal space use and behavior.

**Objectives** We used the European hare (*Lepus europaeus*) as model to investigate how habitat structure and weather conditions affect habitat

selection and home range size, predictors for habitat quality and energetic requirements.

**Methods** Using > 100,000 GPS positions of 60 hares in three areas in Denmark and Germany, we analyzed habitat selection and home range size in response to seasonally changing habitat structure, measured as vegetation height and agricultural field size, and weather. We compared daily and monthly home ranges to disentangle between direct short-term weather effects and indirect seasonal effects of climate.

**Results** Habitat selection and home range size varied seasonally as a response to changing habitat structure, potentially affecting the availability of food and shelter. Overall, habitat structure and seasonality were more important in explaining hare habitat selection and home range size compared to direct weather conditions. Nevertheless, hares adjusted habitat selection and daily home range size in response to temperature, wind speed and humidity, possibly in response to thermal constraints and predation risk.

**Conclusions** For effective conservation, habitat heterogeneity should be increased, e.g. by reducing agricultural field sizes and the implementation of set-asides that provide both forage and shelter, especially during the colder months of the year.

---

**Electronic supplementary material** The online version of this article (<https://doi.org/10.1007/s10980-019-00878-9>) contains supplementary material, which is available to authorized users.

---

M. Mayer (✉) · P. Sunde  
Department of Bioscience, Aarhus University, Grenåvej  
14, 8410 Rønde, Denmark  
e-mail: martin.mayer@bios.au.dk

W. Ullmann · R. Heinrich · N. Blaum  
Plant Ecology and Conservation Biology, University of  
Potsdam, Maulbeerallee 2, 14469 Potsdam, Germany

W. Ullmann  
Institute for Landscape Biogeochemistry, Leibniz-Centre  
for Agricultural Landscape Research (ZALF),  
Eberswalderstr. 84, 15374 Müncheberg, Germany

C. Fischer  
Restoration Ecology, Department of Ecology and  
Ecosystem Management, Technische Universität  
München, Emil-Ramann-Str. 6, 85354 Freising, Germany

**Keywords** European hare · GPS · Habitat selection · Home range · *Lepus europaeus* · Weather

## Introduction

Over the last centuries, human activity has massively altered the land cover of the earth (Goudie 2018). More than a third of our earth's land surface is covered by agricultural land (Ramankutty et al. 2018), at the expense of natural habitat types, such as forests, grasslands and swamps, impairing key ecosystem functions by reducing biomass and changing nutrient cycles (Haddad et al. 2015). Intensification of agriculture is a major driver of biodiversity loss due to the use of agro-chemicals and reduced landscape heterogeneity (Tschamtko et al. 2005; Sánchez-Bayo and Wyckhuys 2019). Simplified landscapes generally provide less food resources, shelter and migration opportunities for animals, e.g. threatening the persistence of various farmland birds in Europe (Donald et al. 2001; Heldbjerg et al. 2017).

In addition to intensified land use, extreme weather events are predicted to globally increase in frequency due to human-caused climate change (Coumou and Rahmstorf 2012; Cai et al. 2014). Animals can respond to a certain degree to changing climatic conditions, e.g. via shifting distribution, altered habitat use and reproductive season, phenotypic plasticity or evolutionary adaptation (Walther et al. 2002; Bradshaw and Holzapfel 2006). For example, tropical reptiles are capable of rapid shifts in climate-relevant traits, allowing them to react to changing climatic conditions (Llewelyn et al. 2018), whereas other species apparently cannot, e.g. tropical arthropods that have declined up to 60-fold over the past 30 years likely as a result of climate change (Lister and Garcia 2018). Thus, animals living in human-altered landscapes might face additional challenges via changing weather conditions (Travis 2003). However, little is known about the interplay between habitat structure and weather conditions in terms of its effect on animal space use and behavior.

Animals generally have smaller home ranges in heterogeneous landscapes due increased resource availability (Smith et al. 2004; Anderson et al. 2005; Ullmann et al. 2018). Further, home ranges can change seasonally in response to resource availability and the reproductive period (Li et al. 2000; Börger et al. 2006; Braham et al. 2015). Additionally, weather conditions can affect animal activity and space use. For example, with increasing temperature red deer (*Cervus elaphus*) increased their home range size during winter and

decreased home range size during summer (Rivrud et al. 2010), probably as response to thermal stress (Lenis Sanin et al. 2016). Rodents adjusted their activity to temperature and precipitation, probably as response to predation risk (Vickery and Bider 1981). In line with this, predators were shown to be better at detecting prey with increasing humidity and at lower temperatures, due to an increased olfactory capability (Ruzicka and Conover 2012). Moreover, a study in redshanks (*Tringa totanus*) showed that weather determined habitat selection via its direct effects on starvation and predation risk (Yasué et al. 2003). Additionally, variation in weather conditions can affect foraging opportunities and consequently habitat selection, as shown in little owls (*Athene noctua*) (Sunde et al. 2014). Finally, precipitation and colder temperatures were shown to increase heat loss (Selmann et al. 2009), which might force individuals to select for shelter and reduce activity. However, there is little information about how animals adjust their spatial movement patterns in differently structured habitats toward short-term changes in weather (van Beest et al. 2012), and at different temporal scales (Rivrud et al. 2010).

Here, we used the European hare (*Lepus europaeus*, hereafter hare) as a model species that lives in human-modified landscapes, with its principal habitat being agricultural land (Vaughan et al. 2003). Hare populations have decreased throughout Europe since the 1960s, with the decline mostly attributed to agricultural intensification (Smith et al. 2005; Pavliska et al. 2018). Agricultural field size, variation in resource availability and vegetation height are important predictors for hare habitat use and home range size (Tapper and Barnes 1986; Rühle and Hohmann 2004; Mayer et al. 2018; Ullmann et al. 2018), but the role of weather conditions on habitat selection and home range size is less clear. Hares might be especially sensitive to changing weather conditions, because they do not use any burrows or dens (Macdonald and Barrett 1993; Schai-Braun et al. 2015). For example, it was shown that hare abundance increased with temperature, whereas increased precipitation led to a decrease in hare numbers (Smith et al. 2005; Rödel and Dekker 2012). Further, weather conditions might also affect predation risk of hares, as predators are more likely to detect prey at lower temperatures and higher relative humidity (Ruzicka and Conover 2012).

We GPS-collared hares in areas with different habitat structure (large vs. small agricultural fields) to investigate how weather conditions affect habitat selection and home range size at different temporal scales, comparing daily and monthly home ranges to disentangle between direct short-term weather effects (e.g. rainfall events) and indirect seasonal effects of climate (Rivrud et al. 2010). We were particularly interested in testing if the negative effects of simple landscapes (larger fields, less variation in vegetation height) on habitat selection and home range size (Pavliska et al. 2018; Ullmann et al. 2018) were amplified by weather conditions at different temporal scales (hours to days versus weeks to months) and depending on the time of the year. We predicted (1) that hares select for higher vegetation (shelter) and decrease their home range size when temperatures were at their respective extremes, i.e., high temperatures in summer and low temperatures in winter, and with increasing precipitation to avoid thermal stress, and more so in simple landscapes. Further, we predicted (2) that hares select for shorter vegetation and reduce activity (leading to smaller daily home ranges) with increasing wind speed and humidity to increase the probability escape via early detection of predators. Finally, we predicted (3) that hare' home range sizes change in the course of the year due to seasonal patterns, such as resource availability and the breeding season, and that home ranges of males are larger compared to females due to sex-specific behaviors (e.g. mate searching in males and offspring care in females).

## Methods

### Study area

Our study areas were located in (1) Syddjurs community, Midtjylland region, Denmark (hereafter Denmark), (2) Uckermark, Brandenburg, Germany (hereafter northern Germany), and (3) the rural district of Freising, Bavaria, Germany (hereafter southern Germany; Fig. 1). All three areas mostly consisted of arable fields (Denmark: 94%, northern Germany: 90%, southern Germany: 83%), tilled with cereals, maize (German areas only), rapeseed, charlock mustard, and to a lesser degree other crops like sugar beet, beans, peas, and clover (Mayer et al. 2018). The rest of

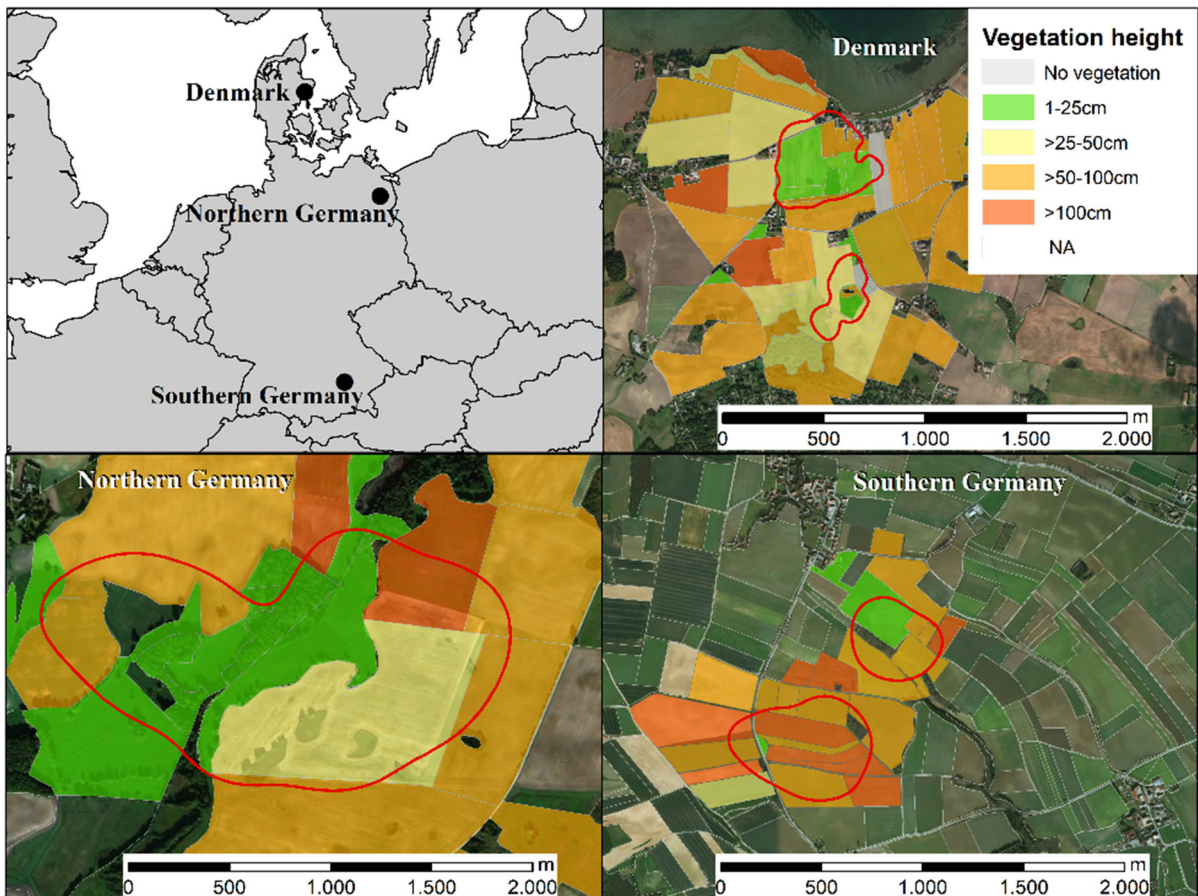
the areas consisted of pastures, game fields, fallow, forest, and built-up areas. Average field sizes varied considerably among the study areas (Fig. 1). Agricultural fields were smallest in southern Germany (mean  $\pm$  SD:  $2.84 \pm 3.13$  ha, median: 1.86 ha), intermediate in Denmark (mean  $\pm$  SD:  $6.25 \pm 7.76$  ha, median: 4.63 ha), and largest in the northern Germany (mean  $\pm$  SD:  $14.86 \pm 22.01$  ha, median: 6.00 ha, ANOVA:  $F_{2, 1772} = 92.3$ ,  $p < 0.001$ ). Average vegetation height varied seasonally, and was highest during June and July (Fig. S1). For a detailed description of the study areas see Mayer et al. (2018) and Ullmann et al. (2018).

### Weather data

We obtained hourly weather data [temperature ( $^{\circ}$ C), precipitation (mm), wind speed (m/s), and relative humidity (%)]. We obtained data from Aarhus airport weather station (<http://www.dmi.dk/>), located 15 km from the center of the study area, for the Danish landscape; from Dedelow weather station (<http://www.zalf.de/en/Pages/ZALF.aspx>), 12 km from the study center, for northern Germany; and from Munich airport (<ftp://ftp-cdc.dwd.de/pub/CDC/>), 9 km from the study center, for southern Germany. For the daily and monthly home range analysis, we calculated the average temperature, wind speed and humidity, and the cumulative precipitation.

### Hare captures and GPS data

In Denmark, we captured 15 hares in 2014 and 2018 ( $n = 7$  males and 8 females) using box traps that were set up in pairs along the edges of agricultural fields. In Germany, we captured 45 hares in 2014 and 2015 (northern Germany:  $n = 17$  males and 10 females; southern Germany:  $n = 10$  males and 8 females) by driving them into nets (Rühe and Hohmann 2004). We transferred captured hares into a canvas cone (Denmark) or a wooden box (Germany), where they were sexed and fitted with a GPS collar (e-obs A1, e-obs GmbH, Gruenwald, Germany) without anesthesia. GPSs recorded one-hourly GPS positions in Denmark. In the two German areas, GPSs recorded one-hourly positions while hares were active, defined by an acceleration threshold (Ullmann et al. 2018), and four-hourly positions when hares were inactive. GPS units recorded data for 7 to 217 days (mean  $\pm$  SD:



**Fig. 1** Map showing the location of the three study areas (black dots, top left), and exemplary maps showing the field size and vegetation height for June from Denmark (top right), northern Germany (bottom left), and southern Germany (bottom right).

Red lines indicate 95% Kernel Density Estimations of hares (2 individuals in Denmark and Southern Germany, and one individual in Northern Germany). (Color figure online)

123 ± 69 days), and between 110 and 4348 individual GPS positions (1789 ± 1215 positions) that we assigned to habitat parameters. We obtained GPS data from April until December, and removed the first day of individual GPS data from the analysis to avoid possible effects of capture and handling. We defined hares as being ‘active’ or ‘inactive’ based on the average distance moved between consecutive GPS positions, because hares have different habitat requirements when active (foraging) and inactive (shelter) (Schai-Braun et al. 2012; Mayer et al. 2018). Overall, 107,348 GPS positions (74,057 active and 33,291 inactive positions) of 60 individuals were obtained that we could assign to habitat and weather variables.

### Home range calculation

To get a measure of daily area use and activity, we calculated the daily home range size based on 95% minimum convex polygons (MCP) using the R package ‘adehabitatHR’ (Calenge 2006) in R 3.2.5 (R Core Team 2013). We used MCPs, because they are more robust for small sample sizes (12–24 GPS positions) compared to kernel density estimates (KDE) (Boyle et al. 2009). We set a threshold of ≥ 12 GPS positions to calculate daily home ranges, because a low number of GPS fixes can affect the size of the daily home range (Boyle et al. 2009), and thus could only calculate home ranges for 55 individuals. Further, we calculated biweekly to monthly home ranges (hereafter ‘monthly home ranges’) based on

95% KDEs (data available for 55 individuals). Monthly home ranges had to contain GPS positions of  $\geq 14$  days in a given month to be included in the analysis.

## Habitat data

### *Habitat selection*

For the analyses of habitat selection, we described the variation in the habitat structure using agricultural field size and vegetation height. We obtained vector data of agricultural fields for northern Germany (InVeKoS 2014), southern Germany (Vermessungsverwaltung 2014) and Denmark ([https://kortdata.fvm.dk/download/Index?page=Markblokke\\_Marker](https://kortdata.fvm.dk/download/Index?page=Markblokke_Marker)), and calculated the size of agricultural fields in ArcMap 10.4.1 (Esri, Redlands, CA, USA). Further, we measured vegetation height in every field bi-weekly to monthly (depending on the study area and year), and grouped vegetation height into four categories due to variation in vegetation height within fields: no vegetation (ploughed, raked and freshly sown fields), 1–25 cm, > 25–50 cm, > 50–100 cm, and > 100 cm. We did not include the vegetation type in our analysis, because it was previously shown that vegetation height is a better predictor for habitat selection by active hares (Mayer et al. 2018). To get a measure of habitat availability for the habitat selection analysis, we created five times the number of random GPS positions than we had obtained for each individual (e.g., if we recorded 2400 individual GPS positions, we created  $5 \times 2400 = 12,000$  random positions for this individual). The random positions were located within an individuals' home range, defined as the 95% KDE of all individual hare GPS positions. We then paired the date and time from hare GPS positions with the random positions, in order to assign weather data (temperature, precipitation, wind and humidity) to the random positions.

### *Home range size*

To get a measure for the available habitat structure within the hares' monthly home ranges, we intersected monthly home ranges with the agricultural fields, and calculated the average field size and the standard deviation (SD) of the field sizes (hereafter 'field size variation') within each home range. To get a measure

for average vegetation height and the SD of the vegetation height (hereafter 'vegetation height variation') we created 100 random positions within each individuals' monthly home ranges and assigned each position to the respective vegetation height category using the join tool in ArcMap. From this, we calculated the average vegetation height and vegetation height variation, using a height index: No vegetation = 0, 1–25 cm = 1, > 25–50 cm = 2, > 50–100 cm = 3, > 100 cm = 4. We also assigned the monthly average and SD field size and vegetation height, respectively, to the daily home range as a measure of available habitat for the hares. This was not done on a daily basis, because vegetation height was measured too infrequently, and because we used the habitat structure as a measure of availability (and we assumed that the entire monthly home range area was available to hares every day).

## Statistical analysis

### *Habitat selection*

We used resource selection functions (RSF) to investigate the effect of weather conditions on habitat selection by active and inactive hares. To test if habitat selection shifts seasonally, we further separated the analysis into pre-harvest (April–July), post-harvest (August–October), and winter (November–December) period. We built generalized linear mixed-effects models, using the R package 'lme4' (Bates et al. 2015), with a logit link and hare occurrence as a binomially distributed dependent variable (1 = used position versus 0 = random position). Temperature and humidity were included as residuals obtained from a quadratic regression against Julian day to remove the seasonal trend in these weather parameters within a year. The wind and precipitation data were included as original data since no clear seasonal trend was noticeable. We included vegetation height, field size (log-transformed), precipitation, wind speed, and the residuals of temperature and humidity as fixed effects, and the hare ID nested within the study area as random intercept. We included the two-way interactions of the weather variables with field size and vegetation height, respectively, to investigate if weather conditions affect habitat selection (Table 1). We used the vegetation height category '1–25 cm' as reference, because this was the most common height category, and pooled the

**Table 1** Informative estimates of the fixed effects for the analyses of European hare (*Lepus europaeus*) habitat selection, separately for active and inactive hares and for the pre-harvest (April–July), post-harvest (August–September) and winter (November–December) period

Variable	Active hares			Inactive hares		
	Pre-harvest	Post-harvest	Winter	Pre-harvest	Post-harvest	Winter
Veg. height no veg.			– 0.41	– 0.66		0.79
Veg. height > 25–50 cm	– 0.23					0.44
Veg. height > 50 cm	– 0.44	– 0.36	– 1.06	– 0.38	0.21	1.09
log (field size)	– 0.12					
Veg. height no veg. × temperature			0.26			0.30
Veg. height > 25–50 cm × temperature			0.25			
Veg. height > 50 cm × temperature	0.07	0.18			0.10	
Veg. height no veg. × precipitation	0.05					
Veg. height > 25–50 cm × precipitation	0.05					
Veg. height > 50 cm × precipitation	0.04	– 0.06				
Veg. height no veg. × humidity						
Veg. height > 25–50 cm × humidity	– 0.09	– 0.18				0.40
Veg. height > 50 cm × humidity			– 0.66			
Veg. height no veg. × wind speed		0.09	– 0.19			
Veg. height > 25–50 cm × wind speed			– 0.20			
Veg. height > 50 cm × wind speed			– 0.73	– 0.08	– 0.16	– 0.45
log (field size) × temperature	0.03			0.05		– 0.14
log (field size) × humidity				0.04		
log (field size) × wind speed				0.04		

Uninformative estimates are not shown

categories > 50–100 cm and > 100 cm as ‘>50 cm’, because selection did not differ between the two categories (Mayer et al. 2018). To calculate robust standard errors (SE), accounting for autocorrelation of the hare locations, we fitted generalized estimating equations (GEE) for the most parsimonious model with an independent correlation structure, using the R package ‘geepack’ (Halekoh et al. 2006). To evaluate the robustness of the top-ranking models (Table S1), we used 10-fold cross validation (Boyce et al. 2002). We first estimated RSFs based on 90% of the data, withholding 10% for evaluation. We extracted the model coefficients of the fixed effects for each training set and used them to predict the RSF values of the corresponding validation set (withheld data). The validation set was then split into 10 equal-sized bins. For each bin, we calculated the relative frequency of used positions. The degree of correlation (Spearman rank correlation  $r_s$ ) between the rank of the bin and the relative frequency of used positions was used as an indicator of model fit.

### Home range size

We used linear mixed-effects models with an identity link to investigate which factors affected the daily and monthly home range size (dependent variable), which was log-transformed to meet the assumption of residual normality. Average field size and field size variation were highly and positively correlated (Spearman rank correlation  $r = 0.89$ ,  $p < 0.001$ , Fig. S1), i.e. areas with on average larger fields also experienced larger field size variation. After creating single-effects models, we included field size variation in the analysis, because it fitted better than average field size ( $\Delta AIC = 22.56$ ). Moreover, we initially created single-effects models including average vegetation height and vegetation height variation, and found that average vegetation height fitted better ( $\Delta AIC = 29.43$ ). We included the number of GPS positions (to correct for potential biases in home range estimation), the interaction of sex and month (to control for sex-dependent seasonal differences), average

vegetation height, field size variation, precipitation, wind speed, the residuals of temperature and humidity, and the two-way interactions of the weather variables with the field size variation and average vegetation height as fixed effects (Table 2). Individual ID nested within the study area was included as a random intercept effect. For the monthly analysis, we included average monthly temperature and humidity, because using the residuals did not remove the seasonal trend in this case. We evaluated model fit by calculating the marginal  $R^2$ , i.e., the variation explained by the fixed effects, and the conditional  $R^2$ , i.e., the variation explained by fixed and random effects (Nakagawa and Schielzeth 2013). We did this separately for the best model and the best model excluding the weather variables and their interactions to get a measure of the variance explained by the weather variables alone.

### Model selection

We scaled and centered all numeric fixed effects to avoid convergence issues and to be able to compare the relative effect sizes. Model selection for all analyses was based on a stepwise variable selection using AIC, selecting the model with the lowest AIC (Murtaugh 2009), using the R package ‘MuMIn’ (Barton 2016). 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

### Habitat selection

Generally, the models were robust to cross-validation regardless of the period ( $r_s$  for the most parsimonious models:  $> 0.9$ , Table S1). Vegetation height was the most important variable explaining habitat selection, and the effects of the weather variables were overall small (and often uninformative), but were more pronounced during the winter period (Table 1).

### Active hares

Active hares avoided  $> 50$  cm high vegetation independent of the season, and selected for 1–25 cm high vegetation during pre-harvest and winter (Fig. 2, Table 1; for details see Table S1 and S2). The selection for a specific vegetation height was less pronounced post-harvest compared to the other periods (Fig. 2). During pre- and post-harvest, hares increasingly used  $> 50$  cm high vegetation with increasing temperature and avoided  $> 25$ –50 cm high vegetation with increasing humidity (Fig. S2). The interaction of vegetation height with precipitation and wind speed was partly informative, but effect sizes were small (Table 1). During winter, hares strongly avoided  $> 50$  cm high vegetation with increasing wind speed and humidity and selected for areas without vegetation and  $> 25$ –50 cm high vegetation with increasing temperature (Fig. 2). Regarding agricultural field size, hares avoided larger fields during the pre-harvest period and more so during colder temperatures (Table S2). This effect was absent during the post-harvest and winter period (Table S2).

### Inactive hares

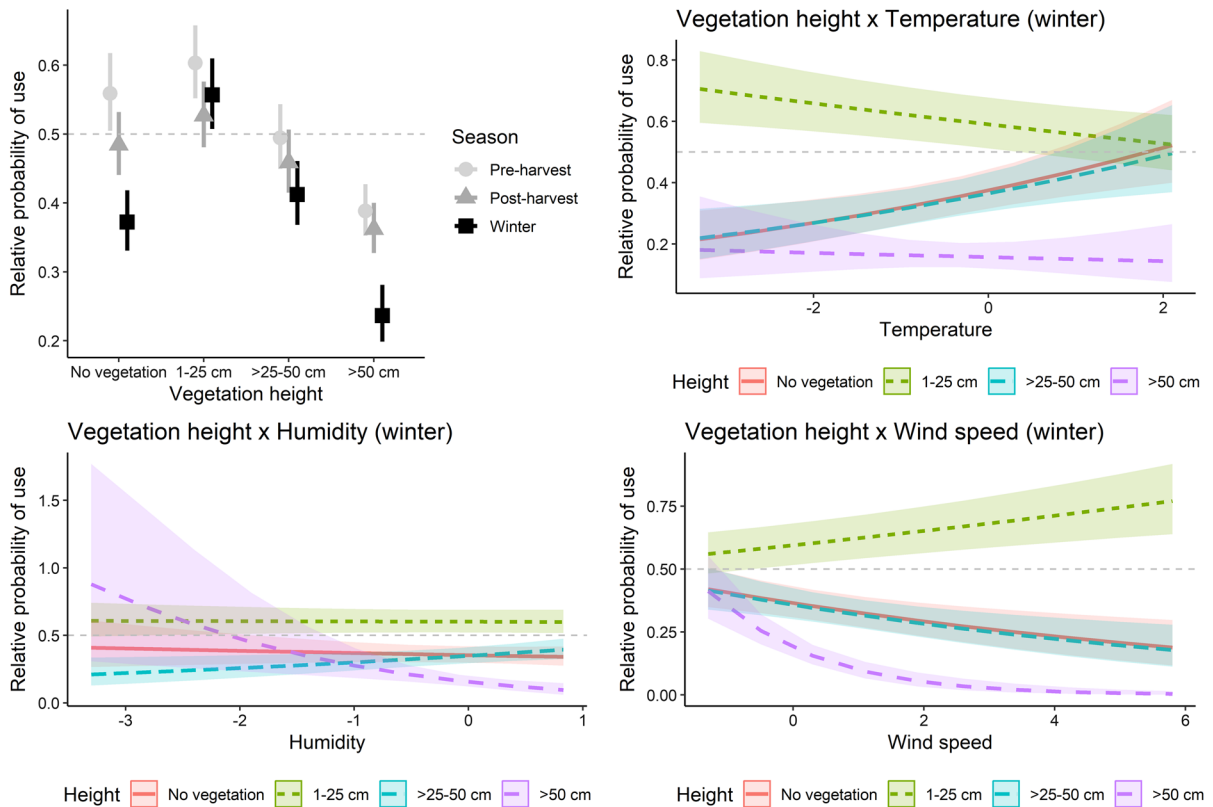
The selection for a specific vegetation height by inactive hares varied seasonally (Table 1; for details see Tables S1 and S3). During the pre-harvest period, hares selected for 1–50 cm high vegetation, and avoided higher vegetation and areas without vegetation (Fig. 3). Post-harvest, selection for a specific vegetation height was less pronounced, with hares selecting for  $> 25$  cm high vegetation (Fig. 3). In winter, hares strongly selected for  $> 50$  cm high vegetation and to a lesser degree  $> 25$ –50 cm high vegetation and areas without vegetation, and avoided 1–25 cm high vegetation (Fig. 3). Independent of the season, hares increasingly avoided  $> 50$  cm high vegetation with increasing wind speed (Table 1). Further, during winter hares increasingly used areas without vegetation with increasing temperature and  $> 25$ –50 cm high vegetation with increasing humidity. The other weather-vegetation height interactions were uninformative or weak, especially during pre- and post-harvest (Table 1, S3). The interactions of the weather variables and field size were informative, but small during the pre-harvest season (Fig. S3), and an effect of field size was absent during post-harvest

**Table 2** The model selection results for the analysis of the (1) daily and (2) monthly home range size of European hares (*Lepus europaeus*) showing the best, full, and intercept only model

Model	df	LogLik	AIC <sub>c</sub>	Delta AIC <sub>c</sub>	AIC <sub>c</sub> weight	R <sup>2</sup> m	R <sup>2</sup> c
<b>(1) Daily home range size</b>							
Number of GPS positions + month + precipitation + wind + temperature + humidity + sex + average vegetation height + log (field size variation) + log (field size variation) × (precipitation + wind + temperature + humidity) + average vegetation height × (precipitation + wind + temperature + humidity) + month × sex	30	- 5963	11,987	0	0.94	0.266	0.489
Number of GPS positions + month + precipitation + wind + temperature + humidity + sex + average vegetation height + log (field size variation) + log (field size variation) × (precipitation + wind + temperature + humidity) + average vegetation height × (precipitation + wind + temperature + humidity) + month × sex	34	- 5962	11,993	6	0.06	0.267	0.489
Number of GPS positions + month + sex + average vegetation height + log (field size variation) + month × sex	22	- 5994	12,032	45	0.00	0.254	0.481
Intercept only	4	- 6319	12,646	659	0.00	0.000	0.424
<b>(2) Monthly home range size</b>							
Month + sex + log (field size variation)	13	- 185	397	0	1.00	0.352	0.686
Number of GPS positions + month + precipitation + wind + temperature + humidity + sex + average vegetation height + log (field size variation) + log (field size variation) × (precipitation + wind + temperature + humidity) + average vegetation height × (precipitation + wind + temperature + humidity) + month × sex	34	- 173	426	29	0.00	0.425	0.713
Intercept only	4	- 215	438	41	0.00	0.000	0.661

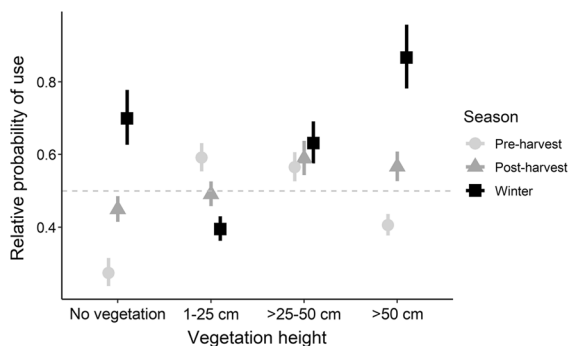
For the daily home range analysis, we also show the best model without weather variables. Hare ID nested within area was included as random effect. R<sup>2</sup>m = marginal R<sup>2</sup>, R<sup>2</sup>c = conditional R<sup>2</sup>





**Fig. 2** The effect of vegetation height on habitat selection by 60 GPS-collared active European hares (*Lepus europaeus*) shown for the pre-harvest (April–July; light grey circles), post-harvest (August–October; dark grey triangles) and winter (November–December; black squares) period (top left). The 95% confidence intervals are given as bars. Further, the effect of

the interactions between vegetation height × temperature (top right), vegetation height × humidity (bottom left), and vegetation height × wind speed (bottom right) on habitat selection by active hares during winter. The 95% confidence intervals are given as shading



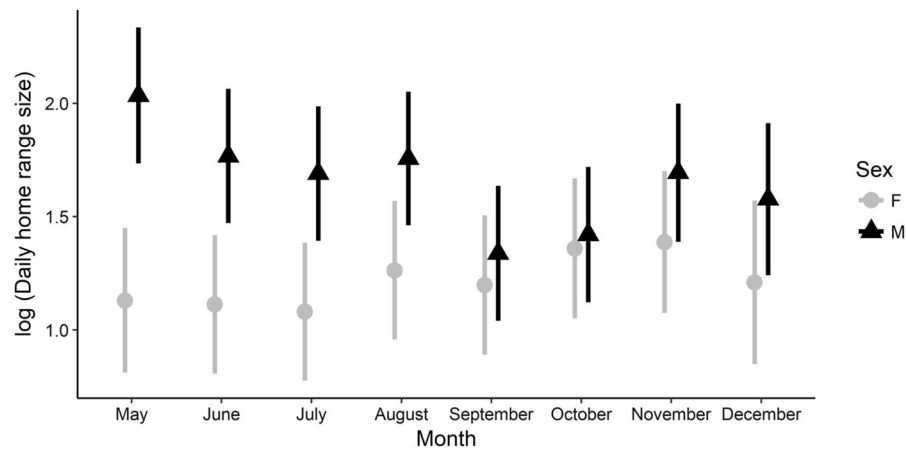
**Fig. 3** The effect of vegetation height on habitat selection by 60 GPS-collared inactive European hares (*Lepus europaeus*) shown for the pre-harvest (April–July; light grey circles), post-harvest (August–October; dark grey triangles) and winter (November–December; black squares) period. The 95% confidence intervals are given as bars

(Table 1, S3). During winter, inactive hares increasingly used smaller fields, an effect that was weaker during warm temperatures (Table S3).

### Home range size

#### Daily home range size

We obtained 6274 daily home ranges of 55 individuals that varied between 0.01 and 67.2 ha (mean ± SD = 6.0 ± 7.6 ha; median = 3.3 ha). The number of GPS positions, the interaction of sex and month, and the interactions of the weather variables with the average vegetation height and field size variation explained 26.6% of the variation in daily home range size, and the random intercept (individual nested within study area) explained another 22.3% (Table 2). Males had



**Fig. 4** The effect of month on daily home range size of 55 GPS-collared European hares (*Lepus europaeus*) separately for females (grey circles) and males (black triangles). The 95% confidence intervals are given as bars

2.1 times larger daily home ranges than females, an effect that was more pronounced during May–July (we did not obtain data from females in April). Female daily home range size was comparatively stable, whereas male home range size decreased from May–September, and then increased again (Fig. 4, Table 3). Generally, daily home range size increased with field size variation and decreased with average vegetation height (Table 3). The effect size of field size variation was 8 to 15 times greater compared to the effect sizes of the weather variables and their interactions, indicating that weather effects were generally small. Daily home range size decreased with precipitation and increased with temperature in areas with large field size variation, but not when field size variation was smaller (Fig. S4). When vegetation was on average high, daily home range size increased with temperature, but not when vegetation was short (Fig. S4). Home ranges decreased with increasing humidity independent of the habitat structure (Table 3).

#### Monthly home range size

We obtained 243 monthly home ranges of 55 individuals that varied between 3.4 and 161.9 ha (mean  $\pm$  SD =  $30.4 \pm 25.7$  ha). Field size variation, month, and sex explained 35.2% of the variation in monthly home range size, and the random intercept explained another 33.4% (Table 2), i.e., there was considerable variation among individuals across study areas. Monthly home range size increased with increasing

field size variation (Fig. 5, Table 3). Males had 1.9 times larger monthly home ranges compared to females, and home ranges for both sexes were smallest in June and July (Fig. 5). No weather variables were retained in the best model.

#### Discussion

We found that habitat structure, i.e. agricultural field size and seasonal changes in vegetation height affected habitat selection and home range size of European hares, whereas direct weather effects had little influence. Nevertheless, hares partly adjusted habitat selection with changing weather conditions, possibly responding to thermal stress (prediction 1) and predation risk (prediction 2). Additionally, daily and monthly home range size changed seasonally and sex-dependent, likely due to the reproductive season and sex-specific behaviors (prediction 3). Our study adds to the limited knowledge on the interactive effects of weather, season and habitat structure on animal habitat selection and activity (Sunde et al. 2014; Amor et al. 2019).

Recording one-hourly GPS positions of hares in three different study areas that varied considerably in their landscape structure enabled us to obtain detailed patterns and to draw general conclusions regarding habitat selection and home range size. The fact that habitat effects (especially agricultural field size in the case of home ranges) were much larger compared to

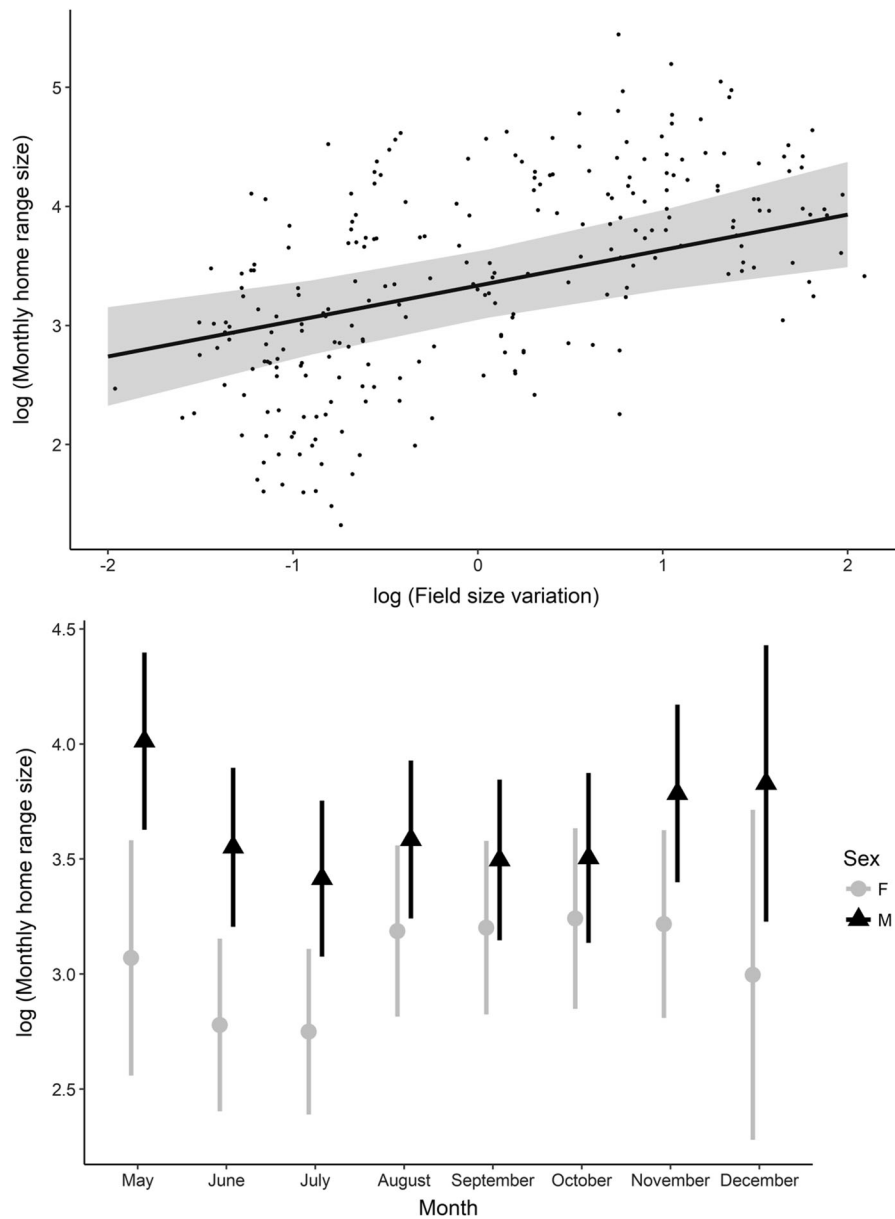
**Table 3** Effect size ( $\beta$ ), standard error (SE), lower 95% confidence interval (LCI) and upper 95% confidence interval (UCI) of explanatory variables for the analyses of the (1) daily and (2) monthly home range size of 55 European hares

Variable	Estimate	SE	LCI	UCI
<b>(1) Daily home range size</b>				
Number of GPS positions	<b>0.20</b>	<b>0.02</b>	<b>0.16</b>	<b>0.23</b>
Month June	– 0.02	0.07	– 0.15	0.11
Month July	– 0.05	0.06	– 0.18	0.08
Month August	<b>0.13</b>	<b>0.06</b>	<b>0.01</b>	<b>0.26</b>
Month September	0.07	0.07	– 0.06	0.20
Month October	<b>0.23</b>	<b>0.07</b>	<b>0.10</b>	<b>0.36</b>
Month November	<b>0.26</b>	<b>0.07</b>	<b>0.11</b>	<b>0.40</b>
Month December	0.08	0.12	– 0.15	0.31
Precipitation	– 0.01	0.01	– 0.03	0.00
Wind speed	– <b>0.03</b>	<b>0.01</b>	– <b>0.04</b>	– <b>0.01</b>
Temperature	0.01	0.01	– 0.01	0.03
Humidity	– <b>0.03</b>	<b>0.01</b>	– <b>0.05</b>	– <b>0.01</b>
Sex male	<b>0.90</b>	<b>0.12</b>	<b>0.67</b>	<b>1.13</b>
Average vegetation height	– <b>0.14</b>	<b>0.01</b>	– <b>0.17</b>	– <b>0.12</b>
Log field size variation	<b>0.30</b>	<b>0.03</b>	<b>0.23</b>	<b>0.36</b>
Precipitation $\times$ log field size variation	– <b>0.02</b>	<b>0.01</b>	– <b>0.04</b>	<b>0.00</b>
Temperature $\times$ log field size variation	<b>0.02</b>	<b>0.01</b>	<b>0.00</b>	<b>0.04</b>
Wind speed $\times$ average vegetation height	0.02	0.01	0.00	0.04
Temperature $\times$ average vegetation height	<b>0.04</b>	<b>0.01</b>	<b>0.02</b>	<b>0.05</b>
Month June $\times$ sex male	– <b>0.25</b>	<b>0.08</b>	– <b>0.41</b>	– <b>0.09</b>
Month July $\times$ sex male	– <b>0.30</b>	<b>0.08</b>	– <b>0.45</b>	– <b>0.14</b>
Month August $\times$ sex male	– <b>0.41</b>	<b>0.08</b>	– <b>0.57</b>	– <b>0.26</b>
Month September $\times$ sex male	– <b>0.77</b>	<b>0.08</b>	– <b>0.92</b>	– <b>0.61</b>
Month October $\times$ sex male	– <b>0.84</b>	<b>0.08</b>	– <b>1.01</b>	– <b>0.68</b>
Month November $\times$ sex male	– <b>0.60</b>	<b>0.09</b>	– <b>0.78</b>	– <b>0.42</b>
Month December $\times$ sex male	– <b>0.54</b>	<b>0.15</b>	– <b>0.83</b>	– <b>0.25</b>
<b>(2) Monthly home range size</b>				
Month June	– <b>0.44</b>	<b>0.13</b>	– <b>0.70</b>	– <b>0.18</b>
Month July	– <b>0.54</b>	<b>0.13</b>	– <b>0.79</b>	– <b>0.28</b>
Month August	– 0.25	0.13	– 0.51	0.01
Month September	– <b>0.29</b>	<b>0.14</b>	– <b>0.56</b>	– <b>0.03</b>
Month October	– 0.26	0.14	– 0.55	0.02
Month November	– 0.12	0.15	– 0.41	0.18
Month December	– 0.18	0.24	– 0.66	0.29
Sex male	<b>0.57</b>	<b>0.13</b>	<b>0.32</b>	<b>0.81</b>
Log field size variation	<b>0.27</b>	<b>0.08</b>	<b>0.11</b>	<b>0.43</b>

Informative parameters are given in bold. The month May was used as reference level, and April was removed from the analysis, because we only obtained data from males then

the weather effects implies that heterogeneous habitat, i.e., smaller fields and the availability of both high-quality forage (short vegetation) and shelter (high

vegetation during winter), are highly important for hares (Smith et al. 2004; Pavliska et al. 2018). The spring and summer of 2018 was one of the warmest



**Fig. 5** The effect of (1) field size variation (defined as the standard deviation of the field size; top), and (2) month separated by sex (females in grey circles and males in black

triangles; bottom) on the monthly home range size of 55 GPS-collared European hares (*Lepus europaeus*). The 95% confidence intervals are given as shading (top) or bars (bottom)

and driest on record in Central and Northern Europe (Schiermeier 2018; World Meteorological Organization 2018). During this period, we obtained GPS data from eight GPS-collared hares in Denmark and thus, would have expected to see a clear effect, if extreme weather affects hare habitat selection and home range size. However, we did not observe strong effects of

weather during this period (e.g., daily home range sizes in May–July 2018 did not differ from May–July home range sizes from other years). This suggests that extreme heat and drought have little effect on adult hares, at least at its northern distribution range. Alternatively, the northernmost study area in Denmark might have buffered against potential negative effects

of heat and drought, because it was comparatively heterogeneous. Nevertheless, converse extreme events, i.e. wet and cold winters might very well affect hare populations via altered leveret survival (Schmidt et al. 2004), which was also indicated by the stronger effects of the weather variables on habitat selection during the winter period.

Generally, active hares selected for short vegetation (1–25 cm), and avoided > 50 cm high vegetation, likely because short vegetation provides high-quality forage (Rühe 1999; Murray et al. 2016) and allows an early detection of predators (Prevedello et al. 2011), thereby reducing predation risk as shown in farmland birds (Whittingham and Evans 2004). Further, active hares selected for smaller agricultural fields during the pre-harvest season, when vegetation was high on most fields, and had the smallest monthly home range sizes in June and July, when vegetation was highest. This suggests that increased vegetation height might act as a barrier, excluding hares and other species from larger fields (Kay et al. 2016; Mayer et al. 2018). Additionally, home range size might have been decreased during summer due to an increased resource availability via plant growth (Garner and Allard 1920), which means that energetic requirements were achieved on a smaller area (Schai-Braun and Hackländer 2013).

Inactive hares avoided > 50 cm high vegetation pre-harvest, whereas they strongly selected for > 50 cm high vegetation during the colder months, likely to seek thermal shelter (prediction 1). Importantly, high vegetation during this time of the year predominantly constitutes of fallow and forest patches, whereas most agricultural crops are short. Thus, habitats including fallow areas with high vegetation during winter can be highly important for farmland species by providing thermal shelter (Laiolo 2005; Meichtry-Stier et al. 2018). In line with this, hares increasingly utilized areas without vegetation as temperature increased during winter, potentially because they did not rely on shelter as much when it was warmer. Similarly, armadillos (*Euphractus sexcinctus* and *Tolypeutes matacus*) adjusted habitat selection in response to temperature constrains, using forests as thermal shelter (Attias et al. 2018).

Weather effects might have also affected anti-predator behaviors (prediction 2). Independent of the season, inactive hares avoided high vegetation as wind speed increased. Animals potentially struggle to detect

approaching predators visually and acoustically in high vegetation on windy days (due to the noise created by moving vegetation). Thus, they might select for areas where they have an increased probability of detecting potential predators, such as short vegetation (Prevedello et al. 2011). There are other examples showing that predator–prey interactions are influenced by wind conditions; e.g., ringed seals (*Phoca hispida*) face downwind when resting at their breathing holes, enabling them to detect predators approaching from behind (Kingsley and Stirling 1991), and in fact polar bears (*Ursus maritimus*) orientate responding to wind conditions in search of prey (Togunov et al. 2017). Further, daily home ranges decreased with humidity. Predators have an increased olfactory capacity to detect prey when humidity is higher (Ruzicka and Conover 2012), which might lead hares to decrease activity when humidity was high. Alternatively, the stronger interactive effect of vegetation height with wind and humidity, respectively, during the colder months of the year suggest that a reduced hare activity could be the result of thermal constrains (Lenis Sanin et al. 2016).

Month was included in the most parsimonious model for both the analyses of daily and monthly home size, suggesting that hares adjust home ranges to other effects than changing vegetation height alone. Both daily and monthly home ranges of males were much larger than female home ranges, especially during spring and summer (in the case of daily home ranges). This was probably related to the sex-specific reproductive strategies (prediction 3), with males searching a greater area in order to maximize access to females, as shown in other species (Frafjord 2016; Sprogis et al. 2016), and females being constrained to a smaller area to take care of dependent young (Aronsson et al. 2016). Finally, the random effects, i.e., variation between individuals and the study areas, explained much of the variation in both daily and monthly home range sizes. Thus, our results add to the increasing understanding that individual differences are important when studying animal behavior and ecology (Bowler and Benton 2005; DeAngelis 2018). Moreover, the number of GPS positions was positively related to daily, but not monthly, home range sizes. Thus, the inclusion of the number of GPS positions can be a simple tool to control for varying sampling effort, especially when sample sizes are small (Boyle et al. 2009).

## Conclusions

In contrast to our hypothesis, weather effects did not appear to have a stronger effect on home range size and habitat selection in simpler compared to complex landscapes. Our results show that the selection of a certain vegetation height in agricultural landscapes depends on animal activity, with active individuals generally selecting for shorter vegetation providing high-quality forage (Douglas et al. 2009; Leal et al. 2019) and inactive individuals selecting for higher vegetation providing shelter, especially during the colder parts of the year. Weather had little effect on habitat selection during the warmer months of the year, but affected the selection for vegetation height in the colder months, suggesting thermal constraints. Similarly, home range size was little affected by direct short-term weather conditions, but changed seasonally in response to indirect climatic effects (e.g. a change in vegetation height) and the reproductive season. An increasing frequency of extreme weather events, e.g. greater temperature variation, and droughts (Coumou and Rahmstorf 2012; Cai et al. 2014) might further increase the energetic demands of many species living in human-dominated landscapes. Individuals can respond to a certain degree to changing climatic conditions (Llewelyn et al. 2018). However, it is evident that animal populations cannot cope with the rapid and ongoing human-driven habitat destruction, affecting most of our earth's terrestrial ecosystems (Ceballos et al. 2017; Bar-On et al. 2018). In conclusion, our highest priority should be to conserve remaining habitats to ensure that animal populations persist over time and to buffer against negative effects of climate change. In the case of the hare and other farmland species, the reduction of agricultural field sizes on a landscape scale and farming various crops on a local scale would help to increase habitat heterogeneity and quality. Additionally, habitat heterogeneity can be increased via the establishment of year-round mandatory set-asides consisting of fallow and wildflower areas (Benton et al. 2003; Smith et al. 2004; Petrovan et al. 2013), especially during the colder months of the year, buffering against extreme weather conditions. This could be achieved by increasing the efficiency of Ecological Focus Areas of the European Common Agricultural Policy via a reduction in agrochemical use and prioritizing options that promote biodiversity and provide shelter (e.g.,

fallow land and buffer strips) and excluding ineffective options, such as 'catch crops and green cover' from direct subsidy payments (Pe'Er et al. 2017). More studies investigating fine-scale resource selection are needed to better understand the interactive effects of climate and land use change in different landscapes.

**Acknowledgements** We thank the Leibniz Centre for agricultural landscape research (ZALF), the long-term research platform "AgroScapeLab Quillow" (Leibniz Centre for Agricultural Landscape Research (ZALF) e.V.), the European fund for rural development (EFRE) in the German federal state of Brandenburg and the DFG funded research training group 'BioMove' (RTG 2118-1) for funding the German part of the study. We also thank the Leibniz Institute for Zoo and Wildlife Research Berlin–Niederfinow and Jochen Godt from the University of Kassel for providing the nets to catch hares, all students and hunters that helped with trapping, and the landowners for allowing us to work on their land. Further, we thank Lars Haugaard for hare captures in Denmark, Erik Lykke for allowing us to work on his land, and Sebastian Behnke from the Danish Hunters Association for his help and support. Animal captures were approved by the Federal Nature Conservation Act (§ 45 Abs. 7 Nr. 3) and the local nature conservation authority (reference number LUGV V3-2347-22-2013 and 55.2-1-54-2532-229-13) with economical funding from the Danish Environmental Agency. Finally, we thank two anonymous reviewers for their helpful comments.

## References

- Amor JM, Newman R, Jensen WF, Rundquist BC, Walter WD, Boulanger JR (2019) Seasonal home ranges and habitat selection of three elk (*Cervus elaphus*) herds in North Dakota. *PLoS ONE* 14:e0211650
- Anderson DP, Forester JD, Turner MG, Frair JL, Merrill EH, Fortin D, Mao JS, Boyce MS (2005) Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. *Landscape Ecol* 20:257–271
- Arnold TW (2010) Uninformative parameters and model selection using Akaike's information criterion. *J Wildl Manag* 74:1175–1178
- Aronsson M, Low M, López-Bao JV, Persson J, Odden J, Linnell JD, Andrén H (2016) Intensity of space use reveals conditional sex-specific effects of prey and conspecific density on home range size. *Ecol Evol* 6:2957–2967
- Attias N, Oliveira-Santos LGR, Fagan WF, Mourão G (2018) Effects of air temperature on habitat selection and activity patterns of two tropical imperfect homeotherms. *Anim Behav* 140:129–140
- Bar-On YM, Phillips R, Milo R (2018) The biomass distribution on Earth. *Proc Natl Acad Sci* 115:6506–6511
- Barton K (2016) Package "MuMIn": multi-model inference. R package, Version 1.15.6. Accessed 10 Feb 2018
- Bates D, Maechler M, Bolker B, Walker S (2015) Package 'lme4'. *Convergence* 12

- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol Evol* 18:182–188
- Börger L, Franconi N, Ferretti F, Meschi F, Michele GD, Gantz A, Coulson T (2006) An integrated approach to identify spatiotemporal and individual-level determinants of animal home range size. *Am Nat* 168:471–485
- Bowler DE, Benton TG (2005) Causes and consequences of animal dispersal strategies: relating individual behaviour to spatial dynamics. *Biol Rev* 80:205–225
- Boyce MS, Vernier PR, Nielsen SE, Schmiegelow FK (2002) Evaluating resource selection functions. *Ecol Model* 157:281–300
- Boyle SA, Lourenço WC, Da Silva LR, Smith AT (2009) Home range estimates vary with sample size and methods. *Folia Primatol* 80:33–42
- Bradshaw WE, Holzapfel CM (2006) Evolutionary response to rapid climate change. *Science* 312:1477–1478
- Braham M, Miller T, Duerr AE, Lanzone M, Fesnock, La Pre L, Driscoll D, Katzner T (2015) Home in the heat: dramatic seasonal variation in home range of desert Golden Eagles informs management for renewable energy development. *Biol Conserv* 186:225–232
- Cai W, Borlace S, Lengaigne M, Van Rensch P, Collins M, Vecchi G, Timmermann A, Santoso A, McPhaden MJ, Wu L (2014) Increasing frequency of extreme El Niño events due to greenhouse warming. *Nat Clim Change* 4:111
- Ceballos G, Ehrlich PR, Dirzo R (2017) Biological annihilation via the ongoing sixth mass extinction signaled by vertebrate population losses and declines. *Proc Natl Acad Sci* 114:E6089–E6096
- Coumou D, Rahmstorf S (2012) A decade of weather extremes. *Nat Clim Change* 2:491
- DeAngelis DL (2018) Individual-based models and approaches in ecology: populations, communities and ecosystems. CRC Press, USA
- Donald P, Green R, Heath M (2001) Agricultural intensification and the collapse of Europe's farmland bird populations. *Proc R Soc Lond B* 268:25–29
- Douglas DJ, Vickery JA, Benton TG (2009) Improving the value of field margins as foraging habitat for farmland birds. *J Appl Ecol* 46:353–362
- Fraford K (2016) Influence of reproductive status: home range size in water voles (*Arvicola amphibius*). *PLoS ONE* 11:e0154338
- Garner WW, Allard HA (1920) Effect of the relative length of day and night and other factors of the environment on growth and reproduction in plants. *Mon Weather Rev* 48:415
- Goudie AS (2018) Human impact on the natural environment. Wiley, USA
- Haddad NM, Brudvig LA, Clobert J, Davies KF, Gonzalez A, Holt RD, Lovejoy TE, Sexton JO, Austin MP, Collins CD (2015) Habitat fragmentation and its lasting impact on Earth's ecosystems. *Sci Adv* 1:e1500052
- Halekoh U, Højsgaard S, Yan J (2006) The R package geepack for generalized estimating equations. *J Stat Softw* 15:1–11
- Heldbjerg H, Sunde P, Fox AD (2017) Continuous population declines for specialist farmland birds 1987–2014 in Denmark indicates no halt in biodiversity loss in agricultural habitats. *Bird Conserv Int* 28:1–15
- InVeKoS (2014) Integriertes Verwaltungs- und Kontrollsystem
- Kay GM, Driscoll DA, Lindenmayer DB, Pulsford SA, Mortelliti A (2016) Pasture height and crop direction influence reptile movement in an agricultural matrix. *Agric Ecosyst Environ* 235:164–171
- Kingsley MC, Stirling I (1991) Haul-out behaviour of ringed and bearded seals in relation to defence against surface predators. *Can J Zool* 69:1857–1861
- Laiolo P (2005) Spatial and seasonal patterns of bird communities in Italian agroecosystems. *Conserv Biol* 19:1547–1556
- Leal AI, Acácio M, Meyer CF, Rainho A, Palmeirim JM (2019) Grazing improves habitat suitability for many ground foraging birds in Mediterranean wooded grasslands. *Agric Ecosyst Environ* 270:1–8
- Lenis Sanin Y, Zuluaga Cabrera AM, Tarazona Morales AM (2016) Adaptive responses to thermal stress in mammals. *Rev Med Vet* 31:121–135
- Li B, Chen C, Ji W, Ren B (2000) Seasonal home range changes of the Sichuan snub-nosed monkey (*Rhinopithecus roxellana*) in the Qinling Mountains of China. *Folia Primatol* 71:375–386
- Lister BC, Garcia A (2018) Climate-driven declines in arthropod abundance restructure a rainforest food web. *Proc Natl Acad Sci* 115:E10397–E10406
- Llewelyn J, Macdonald SL, Moritz C, Martins F, Hatcher A, Phillips BL (2018) Adjusting to climate: acclimation, adaptation, and developmental plasticity in physiological traits of a tropical rainforest lizard. *Integr Zool* 13:411–427
- Macdonald DW, Barrett P (1993) Mammals of Britain & Europe. HarperCollins, UK
- Mayer M, Ullmann W, Sunde P, Fischer C, Blaum N (2018) Habitat selection by the European hare in arable landscapes: the importance of small-scale habitat structure for conservation. *Ecol Evol* 8:11619–11633
- Meichtry-Stier KS, Duplain J, Lanz M, Lugin B, Birrer S (2018) The importance of size, location, and vegetation composition of perennial fallows for farmland birds. *Ecol Evol* 8:9270–9281
- Murray C, Minderman J, Allison J, Calladine J (2016) Vegetation structure influences foraging decisions in a declining grassland bird: the importance of fine-scale habitat and grazing regime. *Bird Study* 63:223–232
- Murtaugh PA (2009) Performance of several variable-selection methods applied to real ecological data. *Ecol Lett* 12:1061–1068
- Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R<sup>2</sup> from generalized linear mixed-effects models. *Methods Ecol Evol* 4:133–142
- Pavliska PL, Riegert J, Grill S, Šálek M (2018) The effect of landscape heterogeneity on population density and habitat preferences of the European hare (*Lepus europaeus*) in contrasting farmlands. *Mamm Biol* 88:8–15
- Pe'er G, Zinggrebe Y, Hauck J, Schindler S, Dittrich A, Zingg S, Tschamtker T, Oppermann R, Sutcliffe LM, Sirami C (2017) Adding some green to the greening: improving the EU's ecological focus areas for biodiversity and farmers. *Conserv Lett* 10:517–530
- Petrovan S, Ward A, Wheeler P (2013) Habitat selection guiding agri-environment schemes for a farmland specialist, the brown hare. *Anim Conserv* 16:344–352

- Prevedello J, Forero-Medina G, Vieira M (2011) Does land use affect perceptual range? Evidence from two marsupials of the Atlantic Forest. *J Zool* 284:53–59
- R Core Team (2013) R: A language and environment for statistical computing
- Ramankutty N, Mehrahi Z, Waha K, Jarvis L, Kremen C, Herrero M, Rieseberg LH (2018) Trends in global agricultural land use: implications for environmental health and food security. *Ann Rev Plant Biol* 69:789–815
- Rivrud IM, Loe LE, Myrsterud A (2010) How does local weather predict red deer home range size at different temporal scales? *J Anim Ecol* 79:1280–1295
- Rödel HG, Dekker JJ (2012) Influence of weather factors on population dynamics of two lagomorph species based on hunting bag records. *Eur J Wildl Res* 58:923–932
- Rühe F (1999) Effect of stand structures in arable crops on brown hare (*Lepus europaeus*) distribution. *Gibier Faune Sauvage (France)* 16:317–337
- Rühe F, Hohmann U (2004) Seasonal locomotion and home-range characteristics of European hares (*Lepus europaeus*) in an arable region in central Germany. *Eur J Wildl Res* 50:101–111
- Ruzicka RE, Conover MR (2012) Does weather or site characteristics influence the ability of scavengers to locate food? *Ethology* 118:187–196
- Sánchez-Bayo F, Wyckhuys KA (2019) Worldwide decline of the entomofauna: a review of its drivers. *Biol Conserv* 232:8–27
- Schai-Braun SC, Hackländer K (2013) Home range use by the European hare (*Lepus europaeus*) in a structurally diverse agricultural landscape analysed at a fine temporal scale. *Acta Theriol* 59:277–287
- Schai-Braun SC, Rödel HG, Hackländer K (2012) The influence of daylight regime on diurnal locomotor activity patterns of the European hare (*Lepus europaeus*) during summer. *Mamm Biol* 77:434–440
- Schai-Braun SC, Reichlin TS, Ruf T, Klansek E, Tataruch F, Arnold W, Hackländer K (2015) The European hare (*Lepus europaeus*): a picky herbivore searching for plant parts rich in fat. *PLoS ONE* 10:e0134278
- Schiermeier Q (2018) Droughts, heatwaves and floods: how to tell when climate change is to blame. *Nature* 560:20–22
- Schmidt NM, Asferg T, Forchhammer MC (2004) Long-term patterns in European brown hare population dynamics in Denmark: effects of agriculture, predation and climate. *BMC Ecol* 4:15
- Seltmann MW, Ruf T, Rödel HG (2009) Effects of body mass and huddling on resting metabolic rates of post-weaned European rabbits under different simulated weather conditions. *Funct Ecol* 23:1070–1080
- Smith RK, Jennings NV, Robinson A, Harris S (2004) Conservation of European hares *Lepus europaeus* in Britain: is increasing habitat heterogeneity in farmland the answer? *J Appl Ecol* 41:1092–1102
- Smith RK, Jennings NV, Harris S (2005) A quantitative analysis of the abundance and demography of European hares *Lepus europaeus* in relation to habitat type, intensity of agriculture and climate. *Mamm Rev* 35:1–24
- Sprogis KR, Raudino HC, Rankin R, MacLeod CD, Bejder L (2016) Home range size of adult Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in a coastal and estuarine system is habitat and sex-specific. *Mar Mamm Sci* 32:287–308
- Sunde P, Thorup K, Jacobsen LB, Rahbek C (2014) Weather conditions drive dynamic habitat selection in a generalist predator. *PLoS ONE* 9:e88221
- Tapper S, Barnes R (1986) Influence of farming practice on the ecology of the brown hare (*Lepus europaeus*). *J Appl Ecol* 23:39–52
- Togunov RR, Derocher AE, Lunn NJ (2017) Windscapes and olfactory foraging in a large carnivore. *Sci Rep* 7:46332
- Travis J (2003) Climate change and habitat destruction: a deadly anthropogenic cocktail. *Proc R Soc Lond B* 270:467–473
- Tscharntke T, Klein AM, Kruess A, Steffan-Dewenter I, Thies C (2005) Landscape perspectives on agricultural intensification and biodiversity–ecosystem service management. *Ecol Lett* 8:857–874
- Ullmann W, Fischer C, Pirhofer-Walzl K, Kramer-Schadt S, Blaum N (2018) Spatiotemporal variability in resources affects herbivore home range formation in structurally contrasting and unpredictable agricultural landscapes. *Landscape Ecol* 33:1–13
- van Beest FM, Van Moorter B, Milner JM (2012) Temperature-mediated habitat use and selection by a heat-sensitive northern ungulate. *Anim Behav* 84:723–735
- Vaughan N, Lucas EA, Harris S, White PC (2003) Habitat associations of European hares *Lepus europaeus* in England and Wales: implications for farmland management. *J Appl Ecol* 40:163–175
- Vermessungsverwaltung B (2014) Geobasisdaten zur tatsächlichen Nutzung
- Vickery W, Bider J (1981) The influence of weather on rodent activity. *J Mamm* 62:140–145
- Walther G-R, Post E, Convey P, Menzel A, Parmesan C, Beebee TJ, Fromentin J-M, Hoegh-Guldberg O, Bairlein F (2002) Ecological responses to recent climate change. *Nature* 416:389
- Whittingham MJ, Evans KL (2004) The effects of habitat structure on predation risk of birds in agricultural landscapes. *IBIS* 146:210–220
- World Meteorological Organization W (2018) July sees extreme weather with high impacts
- Yasué M, Quinn JL, Cresswell W (2003) Multiple effects of weather on the starvation and predation risk trade-off in choice of feeding location in Redshanks. *Funct Ecol* 17:727–736
- Zuur A, Ieno E, Walker N, Saveliev A, Smith G (2009) In: Gail M, Krickeberg K, Samet JM, Tsiatis A, Wong W (eds) *Mixed effects models and extensions in ecology with R*. Springer Science and Business Media, New York

**Publisher's Note** Springer Nature remains neutral with regard to jurisdictional claims in published maps and institutional affiliations.