RESEARCH ARTICLE

The secret life of wild animals revealed by accelerometer data: how landscape diversity and seasonality influence the behavioural types of European hares

Wiebke Ullmann · **Christina Fischer** · **Stephanie Kramer-Schadt** · **Karin Pirhofer Walzl** ·
Jana A. Eccard · **Jan Philipp Wevers** · **Angelique Hardert** · **Katharina Sliwinski** · **Michael S. Crawford** ·
Michael Glemnitz · **Niels Blaum**

Abstract

Context Landscape composition and configuration, as well as seasonal landscape dynamics shape the behaviour, movement and energy expenditure of animals, i.e. foraging, hiding or fleeing, and ultimately survival. Especially in highly modified agricultural systems, it is crucial to understand how animal behaviour is influenced by landscape context to develop sustainable land management concepts.

Objectives We show how landscape composition and configuration, together with seasonal dynamics affect animal behavioural types, accounting for the different life-history events in both sexes.

Methods We investigated 34 European hares in two contrasting agricultural landscapes (a simple and a complex landscape) by using tri-axial accelerometer data to classify the animals' behaviour into five categories: resting, foraging, moving, grooming and standing upright (i.e. vigilance behaviour). We tested whether the amount of behaviours per category changed with landscape composition and configuration, season and sex.

W. Ullmann (✉) · J. P. Wevers · A. Hardert ·
K. Sliwinski · N. Blaum
Department of Plant Ecology and Nature Conservation,
University of Potsdam, Neues Palais 10, 14469 Potsdam,
Germany
e-mail: wiebke.ullmann@uni-potsdam.de

W. Ullmann · K. Pirhofer Walzl · M. Glemnitz
Leibniz-Centre for Agricultural Landscape Research
(ZALF), Eberswalderstr. 84, 15374 Müncheberg, Germany

C. Fischer
Faunistics and Wildlife Conservation, Department
of Agriculture, Ecotrophology, and Landscape
Development, Anhalt University of Applied Sciences,
Strenzfelder Allee 28, 06406 Bernburg, Germany

S. Kramer-Schadt
Department of Ecological Dynamics, Leibniz Institute
for Zoo and Wildlife Research (IZW), Alfred-Kowalke-Str.
17, 10315 Berlin, Germany

S. Kramer-Schadt
Institute of Ecology, Technische Universität Berlin,
Rothenburgstrasse 12, 12165 Berlin, Germany

K. Pirhofer Walzl
Institute of Biology, Freie Universität Berlin,
Altensteinstraße 6, 14195 Berlin, Germany

J. A. Eccard
Department of Animal Ecology, University of Potsdam,
Potsdam, Germany

M. S. Crawford
Transformation Pathways, Potsdam Institute for Climate
Impact Research, Telegrafenberg, Potsdam, Germany

Results During peak breeding, hares in areas of high habitat diversity rested more, moved less and spent less time searching for resources. During winter, hares moved more and rested less. Females rested less and foraged more in areas with large agricultural fields.

Conclusions A complex landscape is particularly important during the breeding season, allowing animals to allocate enough energy into reproduction. In winter, hares in areas of low habitat diversity may not find enough thermal and anti-predator shelter to move as much as they would need to meet their requirements. Hence, high habitat diversity and small field sizes guarantee species persistence in human-altered agricultural areas throughout the year.

Introduction

As human population growth drives increasing demand for food, land-use expansion and intensification degrade landscape diversity and imperil species' survival (Firbank et al. 2008; Rockström et al. 2009). In particular, agricultural landscapes—the largest land-use category in Europe (Ramankutty et al. 2008)—have been subject to significant anthropogenic stress over the past decades, characterized by habitat fragmentation, land consolidation, increased field sizes, and declines in crop diversity. This has led to a reduction in species abundance and richness (Pimm and Raven 2000; Benton et al. 2003). Animals living in these intensively-managed agricultural landscapes must not only contend with landscape degradation per se, but also with seasonally changing human-caused disturbances, e.g. the application of fertilizers and pesticides, and the sudden removal of large parts of the biomass during harvest in autumn (Ullmann et al. 2020). To adjust to the consequences of agricultural practices, animals change their behaviour and adjust their movements to survive.

Animal movement is a key life-history trait, which underlies individuals' survival and fitness, and is influenced by landscape composition and configuration (e.g. Bennett et al. 2006; Jeltsch et al. 2013). For example, habitat fragmentation and reduced habitat diversity in agricultural landscapes lead to a reduced proportion of dispersing animals (Bonte et al. 2006), changes in habitat selection (Smith et al. 2004), and expanding home ranges and daily travel distances (Schai-Braun and Hackländer 2014; Ullmann et al. 2018). Additionally, these animal movement measures depend on seasonal changes in the available vegetation structure (Mayer et al. 2019). However, the behavioural mechanisms underlying changes in movement patterns, i.e. whether travel distances or utilization ranges become larger because the animals flee or forage more, remain largely unexplored. One promising avenue to investigate these underlying processes is through the animals' daily behaviours. Although daily behaviours of free-ranging animals are increasingly examined (Wilson et al. 2006; Grünewälder et al. 2012; Shamoun-Baranes et al. 2012; Lush et al. 2016; Weterings et al. 2018; Tatler et al. 2021), the influence of landscape composition and configuration, as well as the corresponding seasonal dynamics on the actual animals' behavioural modes, has rarely been studied.

The composition of a landscape (the variety of land-use types) and its configuration (the spatial arrangement of these land-use patches, as described by Fahrig et al. 2011) can be examined at different scales. For example, at the habitat scale, one can investigate an animal's utilization range and assess the habitat diversity within that range, while at the landscape scale, the overall landscape complexity (i.e., simple versus complex agricultural landscapes) in which the animal resides can be evaluated. Areas of high habitat diversity provide all the resources necessary to satisfy the animals' needs for food and cover within a small spatial scale (Anderson et al. 2005; Saïd and Servanty 2005), thus shortening the time animals need for travelling between patches and increasing the amount of time available to them, e.g. for resting or social behaviour (Li and Rogers 2004). In contrast, areas of low habitat diversity consist mainly of agricultural crop fields and few other landscape elements, of which only certain patches may provide food, while other, distant ones provide shelter. Areas of low and high habitat diversity might be found in simple and complex landscapes simultaneously, as even simple landscapes still show small areas of high habitat diversity. In general, however, regions with a simple landscape structure consist of large agricultural

crop fields that often cover vast areas, sparsely interspersed with small (semi-)natural patches. This may force animals to stay in a patch when encountering barriers, or to travel long distances between habitat patches in meeting their daily requirements (Ullmann et al. 2018). Regions with a complex landscape structure, on the other hand, generally show smaller agricultural fields and a higher crop diversity, where inhospitable areas are easier to circumvent than in simple landscapes, resulting in less travel time for animals. Hence, the decline in landscape complexity and habitat diversity seemingly leads to an increase in movement and corresponding decrease in resting, subsequently leading to higher energy expenditure (Mace and Harvey 1983) and ultimately declining physical condition and individual fitness (Daan et al. 1996).

The European brown hare (*Lepus europaeus*, hereafter referred to as hare) is a common open-habitat species found in agricultural landscapes throughout most of Europe and parts of Asia, as well as in introduced populations in regions such as Great Britain, South America, and Australia. The breeding season of hares lasts from January to September during which does produce on average three litters (Frylestam 1980). A reproductive pause occurs from October to December in which male hares produce less testosterone and their tests retract into their body (Simeunovič et al. 2000). Since the 1960s, hare populations have declined strongly throughout Europe, primarily due to agricultural intensification and an associated decline in landscape diversity (Smith et al. 2005). Hares in less diverse landscapes are less abundant, have lower survival rates, are lighter, and have smaller litters (Frylestam 1980; Tapper and Barnes 1986). One of the main aspects that might change with declining landscape diversity is resource availability (e.g. food and shelter), which additionally changes throughout the season and influences the hares' spatial movement behaviour (Mayer et al. 2019). Hares forage on cultivated crops, but a high-quality diet heavily depends on non-cultivated herbs (Reichlin et al. 2006). This requirement may be greater during the breeding time of female hares, when a high energy demand to produce milk competes with the need to find safe hiding places to avoid predators (Valencak et al. 2009; Mayer et al. 2019).

Hares and specifically their daily behavioural modes have been studied with the use of acceleration sensors in the past. For example, Lush et al. (2016) found that hares spend about 25% of their time feeding when they are active. Studd et al. (2019) found that snowshoe hares spend about 50% of their time foraging, but less so during the full moon, when they move more. In a study by Majchrzak et al. (2022), accelerometers revealed that snowshoe hares reduced their foraging time in winter when they were food supplemented. Furthermore, Weterings et al. (2018) showed that forage quality and quantity have a stronger effect on foraging behaviour than predation and competition. However, none of these studies researched the link between the hares' behavioural modes and the underlying landscape.

Here, we investigate whether changes in hares' behavioural modes are caused by changes in habitat diversity (i.e. landscape composition) and the size of agricultural crop fields (i.e. landscape configuration). We used GPS telemetry with internal tri-axial accelerometers and subsequent classification based on random forest models (Tatler et al. 2018) to distinguish between the following behavioural modes: resting, moving, foraging, grooming and standing upright on the hind legs (i.e. vigilance behaviour). We defined foraging behaviour as the search for resources and not necessarily the process of feeding. We studied landscape complexity by choosing a structurally simple landscape with large fields in northeast Germany and a structurally complex landscape with small fields in southern Germany. We first calculated the habitat diversity within each hare's monthly utilization range in both the structurally simple and complex landscapes. We then related study area (i.e. the average field size within the monthly utilization range) and habitat diversity to the hares' behavioural modes and investigated the relevance of seasonal changes in habitat diversity for sex-specific behavioural responses within certain life-history stages (e.g. mating during spring and summer, versus reproductive pause in late autumn and beginning winter).

Specifically, we hypothesize that:

- Hares in diverse habitats move less and have more time to rest, as most of their resources are found within a small spatial scale. Hares in habitats of low diversity rest less and move more frequently, travelling longer distances, as they must
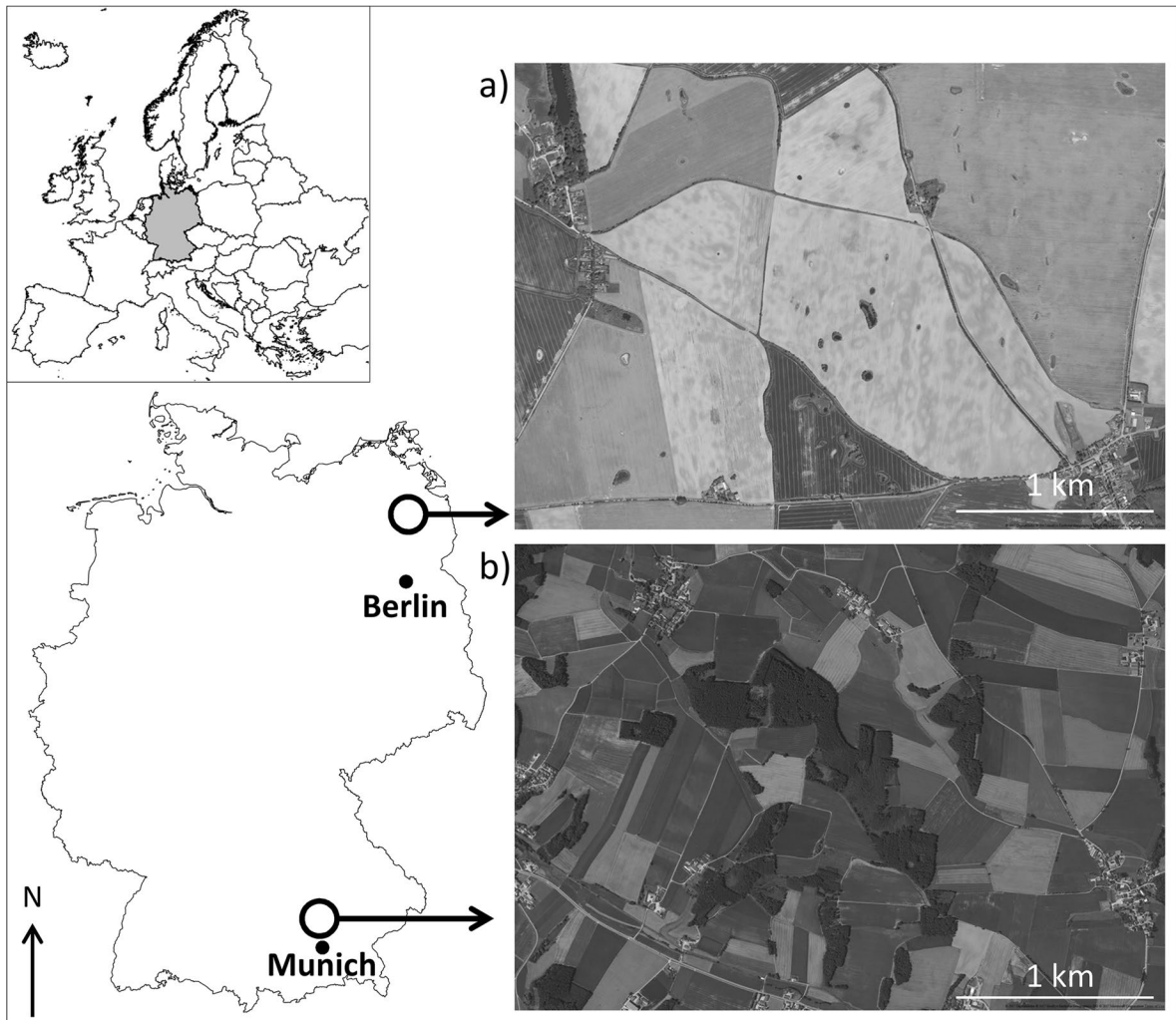
Fig. 1 The location of Germany in Europe (upper left panel) and the study areas in northeast Germany and southern Germany (GADM http://gadm.org/). Satellite images (Google maps 2017) show representative extracts of **a** the simple land-scape in northeast Germany and **b** the complex landscape in southern Germany. Both landscape representations have the same scale (1:12,000)

spend more time searching for resources (especially high-quality food items).

- Hares inhabiting areas with large fields move more than those in areas with small fields, because resources are more dispersed.
- The behavioural modes of males and females will change throughout the season, with important life-history events like reproduction, and result in increased moving behaviour during mating and more extended resting periods in the non-reproductive period.

Methods

Study area

The study area in southern Germany, representative of a complex agricultural landscape, was characterized by intensive but small-scale agriculture with an average field size of 2.9 ± 0.04 ha (mean $\pm$ SE, Fig. 1). The area was covered to 62% by arable land, with the main production cover types: wheat, maize, and grassland (Bayerisches Landesamt für Statistik und Datenverarbeitung 2016). The study area in

northeast Germany, representative of a simple agricultural landscape, was characterized by large-scale farming with an average field size of 27.5 ± 1.1 ha (mean $\pm$ SE, Fig. 1). The simple landscape consists to 73% of arable land with the following main crop types: wheat, maize, and oilseed rape. Landscape metric calculations were based on shapefile information from Landesvermessung und Geobasisinformation Brandenburg (InVeKoS 2014), Bayerische Vermessungsverwaltung (2014) and Corine Land Cover (European Environment Agency 2018a, b). More details about the two study areas (e.g. differences in temperature and precipitation) can be found in the Supplementary Material S1 and in Ullmann et al. (2018, 2020). Both study areas were classified into 11 different landscape elements: arable land, forest, grassland, loose woody vegetation, parks, quarries, streets, urban areas, water, field paths, and wetlands.

Animal tracking

In spring and summer of 2014 and 2015, hares were caught by driving them into woollen nets (Rühe and Hohmann 2004). During the capture, we weighed the hares, determined their sex, and collared them. We equipped 34 adult hares (simple landscape: 12 males and 5 females, complex landscape: 9 males and 6 females) with GPS collars in both study areas simultaneously (for detailed information and deployment times see Supplementary File S2). Each collar had a weight of 69 g (Model A1, e-obs GmbH, Munich—Germany, www.e-obs.de) and included a tri-axial acceleration sensor (ACC sensor). Acceleration samples were taken every 4 min. Each accelerometer was calibrated before deployment, according to the orders proposed by the manufacturer. This ensured the comparability between the single devices. The ACC sensor was set to sample at 33 Hz, each sampling burst lasted for 3.27 s, resulting in 110 data points per burst per axis. Within 3.27 s, hares can easily conduct more than one or two different behaviours, hence we cut each burst into 1-s intervals and classified the behaviour of each of these 1-s acceleration bursts. However, as the behaviours for each 1-s interval within one burst (3.27 s) are correlated, we only used the first 1-s interval for the analyses to avoid dependency issues in the data set.

From the hourly GPS points, we calculated monthly 99% Kernel utilization distributions with the smoothing parameter h_{ref} from the *adehabitatHR* package (Calenge 2006). We used 99%, instead of the usual 95% Kernel distribution because we also wanted to include habitat that the hare used rarely yet might be important for its behaviour and ecology. Furthermore, we used the value of each hourly step length to calculate a median step length for each month. The step length is the distance (in meters) between two consecutive GPS locations. We included step length as a confounding variable to account for (un)explained variance in the model, as the amount of resting or moving a hare conducts might depend on a temporally increased/decreased utilization range or on larger/shorter step length. We selected step length as a confounding variable instead of utilization range size because the two were highly correlated (Pearson's $r = 0.72$, t-value $= 12.65$, df $= 147$), and incorporating step length into our models resulted in higher R^2 values compared to using utilization range size. However, we also ran the models with utilization range size to check for significant differences in comparison to step length. Both models showed very similar outcomes (see Supplementary Material S3). We received data from collared hares from April to January for both study years (2014 and 2015). One hare (ID: 3408) was removed from the data set as an outlier as the hare mainly lived in a forest. All tracking and acceleration data were stored at http://www.movebank.org/ (Wikelski and Kays 2015).

Determination of habitat diversity

To determine habitat diversity, we used the Simpson diversity index–emphasizing evenness–as the agricultural landscapes under study are frequently characterized by the dominance of extensive crop fields. To calculate the Simpson diversity index, we used each hares' monthly utilization ranges and the underlying habitat information on crop fields and landscape element properties (Finder et al. 1999; Su et al. 2014) extracted with the R package *vegan* (Oksanen et al. 2013). For 'arable land', we added the information on the field's current (monthly mapping) crop type or tillage state, which was included in the monthly Simpson diversity index calculation. Further, we counted the corresponding number of

each behavioural mode per month and hare. We used monthly counts to account for shifts in hare behaviour and space use over the course of the year.

Behaviour classification

To classify behaviors, we directly observed four hares and correlated their exhibited behaviors with the corresponding accelerometer output. We then trained a random forest model (Fig. 2) using these observations. We observed two hares in an enclosure and two free-ranging hares, collecting 4351 acceleration bursts. All four hares exhibited all behavioural modes except for vigilance behaviour, which was not sampled for one of the free-ranging hares (Supplementary Material S4, Table S4.1). Each acceleration sample (i.e. each axis within one burst) was used to calculate the following predictors in order to be used in the random forest algorithm (R package *random-forest* by Liaw and Wiener 2002) for the prediction of all unobserved behaviours: standard deviation, mean, range (maximum value minus minimum value) and the mean of the burst before the current burst (more predictors were tested but the once chosen where the most parsimonious, please see Supplementary S4). We also conducted a cross validation study to test the potential of the random forest algorithm for the classification accuracy, for the results please see Supplementary Material S4.

We classified the behaviour of hares into five main behavioural modes: resting, foraging, moving, grooming and vigilance behaviour (Fig. 2). We defined resting behaviour as lying down and all kinds of sitting positions that did not include any further movements of the limbs. Foraging behaviour was defined as slowly moving forward and swaying with the head from side to side or up and down. The actual feeding behaviour, however, is part of the behavioural mode 'resting', as feeding itself (i.e. sitting still and chewing) is a very subtle behaviour, even below the threshold of 'fine-scale behaviours' (Chakravarty et al. 2020) and therefore could not directly be extracted from the accelerometer attached to the animals' neck. Hence, in our study we use the behavioural mode 'foraging' in the sense of searching for resources. We defined the behavioural mode 'moving' as all kinds of displacement, like running or hopping from one location to another. Grooming was classified when the animals were licking, scratching, shaking or stretching themselves. Vigilance behaviour in our study was defined as standing up on the hind legs (while the front paws do not touch the ground). However, we disregarded behavioural modes for the analysis when the behaviours were often misclassified. This was the case for grooming and vigilance behaviour (Supplementary Material S4). Thus, for further statistical analyses we only used resting, moving, and foraging behaviours, but did not consider grooming and vigilance.
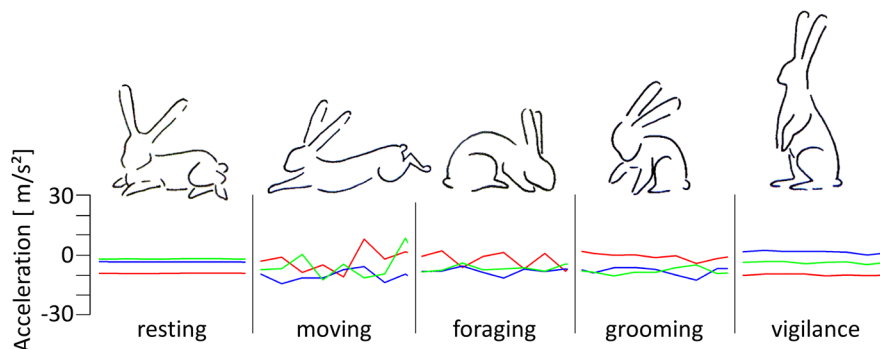
Fig. 2 The accelerometer output of the five different behavioural modes. The x-axis is shown in red, the y-axis in blue and the z-axis in green. Resting shows the normal position of the three axes. During a bout of moving (e.g. running) the hare executes strong movements and shows a wide variation of acceleration. When the hare forages, the head is turned to the ground, therefore the x-axis is located above the other two axes. Grooming shows a similar pattern but usually with less peaks. During vigilance behaviour the hare stands upright on its hindlegs, therefore the y-axis is located above the z-axis

Statistics

We used linear mixed-effects models (R package *lme4*; Bates et al. 2014) to test for the influence of the following fixed factors on the three main behavioural modes (resting, moving, and foraging): average field size (i.e. study area, numeric), habitat diversity (Simpson diversity index, numeric), animal sex (male or female, categorical), seasonality (month, numeric) and median monthly step length (numeric). We ran the analyses for each behavioural mode separately to assure normally distributed residuals. Animal ID was used as random intercept in each model. We included two-way interactions between average field size and habitat diversity, average field size and animal sex, habitat diversity and month, habitat diversity and animal sex, animal sex and month. The variable 'average field size' was log transformed due to very different field sizes in the two study regions and because the values were right skewed for the locality representing the complex landscape structure. The fixed factors were standardized using the *scale* function in R. Then they were tested for multi-collinearity according to Zuur et al. (2009) (GVIF was lower than three in all cases, hence we dismissed multi-collinearity) and for non-linear relationships by using generalized additive models [GAMs—package *mgcv* (Wood 2001)]. The variable 'month' was determined to be non-linear. We tested a quadratic, the third and the fourth order polynomial term to shape the curve of the variable and selected the model with the lowest AIC value. For resting and moving behaviour we used the third order polynomial for month, while the model for foraging had the lowest AIC value when month was included as a quadratic term. Scaled residuals were used [R package *DHARMa* (Hartig 2017)] to test for linearity and temporal autocorrelation. Each global model as well as its corresponding nested submodels were used for model selection (Dochtermann and Jenkins 2011) with an information theoretic approach built into the R package *MUMIn* (Barton 2013). We averaged all models with delta-AIC values below 7 (Anderson 2008; Bolker et al. 2009). Fixed effects were considered informative when the estimates' 95% confidence interval excluded zero (Arnold 2010). We also show pseudo R^2-values for the global model, represented by marginal (m) and conditional (c) R^2- values using *MuMIn*. Throughout the text, we show estimates and

their respective standard errors, while the graphs show estimates and 95% confidence intervals.

We used the monthly counts of each behavioural mode as dependent variable (Table 1) and transformed them to hours per day (within the respective month). Therefore, we multiplied the number of bursts associated with that behaviour by 24 h, and then divided the result by the total number of monthly bursts. As the acceleration data was sampled every 4 min–resulting in 360 bursts per day–over a 30-day period we collected 10,800 bursts per individual hare.

Results

The overall model accuracy for the random forest was 80%. The precision (true positives/(true positives + false positives) for resting was 0.94, for moving 0.48 and for foraging 0.67 (for further information please see Supplementary S4). The average size of agricultural fields within the hares' monthly utilization ranges ranged from 1.7 to 64.3 ha and was significantly smaller in the complex landscape (3.3 ± 1.1 ha) than in the simple landscape (23.8 ± 1.2 ha, $F_{1,31} = 124$, $p < 0.001$). Average field size was contained in all three averaged models, with an informative main term for foraging (Table 1). Females rested less and foraged more when the average field sizes were large. When the field sizes were very small (e.g. 1.7 ha) females rested 18.8 ± 0.4 h per day, but when the field sizes were very large (e.g. 64.3 ha) they rested 1.5 h less per day (17.3 ± 0.5 h, Fig. 3). On the other hand, females foraged only 2.7 ± 0.4 h when fields were small and 5.0 ± 0.5 h when the fields were large, i.e. they foraged 46% more in simple landscapes.

The relationship between habitat diversity and the time hares spent for each of the three behaviours per day changed seasonally (Fig. 4, Table 1). Across both study areas, hares rested more with increasing habitat diversity during the peak breeding-season. In May, for example, resting increased by 15.5% per day from 15.3 ± 0.8 to 18.1 ± 0.4 h per day (from low to high Simpson diversity index values—please note that these values are based on the fitted model, i.e. the actual data for a certain month does not necessarily cover the entire range of the x-axis in Fig. 4). The relationship became less important over the summer and then started to decrease in winter. In December,

Table 1 Three averaged models analysing the number of monthly counts of resting, moving and foraging behaviour depending on average field size (FS), habitat diversity (SD for Simpson diversity), animal sex (Sex), the third polynomial of month (MM), median step length per month (Med.SL), and their respective interactions, where sex (m) stands for males

Fixed effect	Resting					Moving					Foraging				
	Est.	SE	LCI	UCI	Im.	Est.	SE	LCI	UCI	Im.	Est.	SE	LCI	UCI	Im.
Intercept	*8197*	*111*	*7977*	*8417*	*NA*	*356*	*35*	*287*	*424*	*NA*	*1676*	*118*	*1443*	*1908*	*NA*
FS	−185	108	−398	28	0.8	37	28	−18	91	0.6	*297*	*121*	*59*	*535*	*1*
SD	31	47	−62	124	1	−3	16	−35	29	1	−27	71	−166	113	0.7
Sex (m)	−115	137	−386	156	1	43	43	−42	128	1	154	149	−140	448	0.9
MM	*−222*	*70*	*−361*	*−84*	*1*	−31	28	−87	25	1	*100*	*35*	*31*	*169*	*1*
MM²	*−111*	*47*	*−203*	*−18*	*1*	29	19	−8	67	1	*68*	*31*	*7*	*128*	*1*
MM³	31	43	−55	116	1	−10	17	−44	25	1					
Med.SL	*−133*	*38*	*−207*	*−58*	*1*	*146*	*15*	*116*	*175*	*1*	26	38	−50	101	0.3
FS:SD	−29	36	−100	42	0.2	10	14	−18	38	0.2	5	38	−70	79	0.2
FS:Sex (m)	*283*	*118*	*50*	*517*	*0.6*	−48	37	−122	26	0.2	*−286*	*133*	*−549*	*−23*	*0.6*
SD:MM	*−100*	*37*	*−173*	*−28*	*1*	8	15	−21	37	1	*55*	*26*	*3*	*107*	*0.5*
SD:MM²	−3	22	−45	40	1	−10	9	−27	8	1	*−37*	*17*	*−71*	*−3*	*0.5*
SD:MM³	−14	13	−40	13	1	*15*	*5*	*4*	*26*	*1*					
SD:Sex (m)	−48	75	−195	99	0.3	6	27	−48	59	0.2	121	78	−33	276	0.3
Sex (m):MM	*345*	*86*	*175*	*516*	*1*	*−182*	*35*	*−251*	*−113*	*1*	−64	56	−174	45	0.2
Sex (m):MM²	−54	50	−153	44	1	35	20	−5	75	1	59	47	−34	151	0.2
Sex(m):MM³	*−97*	*45*	*−187*	*−7*	*1*	*47*	*18*	*10*	*83*	*1*					
	mR²=0.48 and cR²=0.88					mR²=0.83 and cR²=0.93					mR²=0.36 and cR²=0.86				

We show informative fixed effects in bold and italic. Estimates are in the column 'Est.', and the variable importance, based on the averaged models, is listed under 'Im.' (importance). Note that the model for foraging only had a quadratic term for month, therefore some rows are missing. Marginal and conditional R² are shown for each of the three global models in the last row
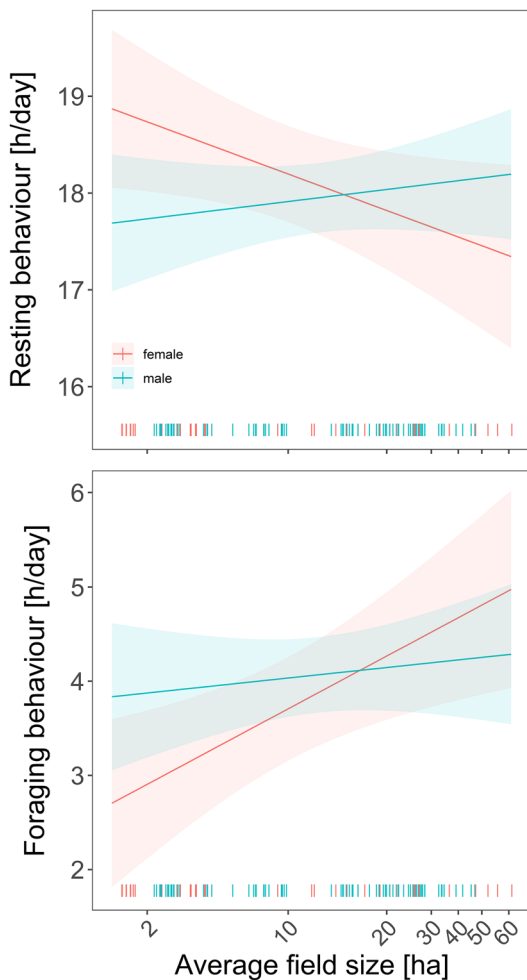
Fig. 3 The number of hours per day female and male hares spent foraging and resting in relationship to the average agricultural field size in the hares' monthly utilization range. The slope for male hares is shown in blue and for female hares in red. Please note the logarithmic scale on the x-axis

for example, hares rested for 17.7 ± 0.2 h in areas with low habitat diversity and 16.0 ± 0.3 h in areas with high habitat diversity, which is a relative decrease of 9.6%.

Non-resting implies the patterns for the behavioural modes 'moving' and 'foraging' to show opposing relationships with habitat diversity within their utilization range. Hares moved a lot during spring (e.g. in April 3.5 ± 0.6 h per day) in areas of low habitat diversity compared to areas of high habitat diversity (1.1 ± 0.3 h per day, a relative decrease of 70%). This relationship became less expressed during

summer. In winter, hares moved about 40 min less (in December: 0.4 ± 0.2 h per day) in areas of low diversity than hares in areas of high diversity (1.1 ± 0.1 h per day). The relationship between the time spent foraging and habitat diversity was eminent mainly during peak breeding. Hares used up more of their time to search for resources in areas of low diversity (e.g. 5.9 ± 0.7 h per day in May) than in areas of high diversity (3.1 ± 0.4 h per day in May, a relative decrease of 47.5%).

Female and male hares showed strong seasonal differences in their resting and moving behaviours. The resting activity for female hares peaked in June (18.3 ± 0.3 h per day) and was lowest in January (16.5 ± 0.7 h per day, Fig. 5, Table 1). Male hares rested about 17% more per day in late summer (e.g. September: 18.0 ± 0.2 h per day) than in winter (e.g. January: 14.9 ± 0.3 h per day). Furthermore, males rested about an hour less than females during peak breeding in June. Both sexes moved most during spring, but males moved half an hour more than females (female: 1.2 ± 0.2 h, male: 1.7 ± 0.1 h per day). Males moved only a third of their spring levels in early autumn (0.6 ± 0.1 h per day). Daily foraging activity was highest during winter for both sexes (about 5.0 ± 0.3 h per day). In April females spent 3.1 ± 0.6 h per day foraging while males foraged for 4.7 ± 0.3 h per day, a relative difference of 34%.

The confounding variable step length showed that hares rested more when step length decreased and moved more when step length increased. Although the confounding variable was kept in the model for 'foraging' the lower confidence interval for step length overlapped zero and was therefore determined as uninformative.

Discussion

In spring and early summer, we found that hares in areas of low habitat diversity were resting less, moving more, and spending more time searching for food than animals in diverse habitats. Habitat quality affects movement behaviour in most mobile animals (e.g. Turner et al. 2001; Saïd and Servanty 2005). Hares, as well as other species—such as roe deer (*Capreolus capreolus*), red deer (*Cervus elaphus*), red fox (*Vulpes vulpes*), wild turkey (*Meleagris gallapovo silvestris*), and lynx (*Lynx lynx*)—react to
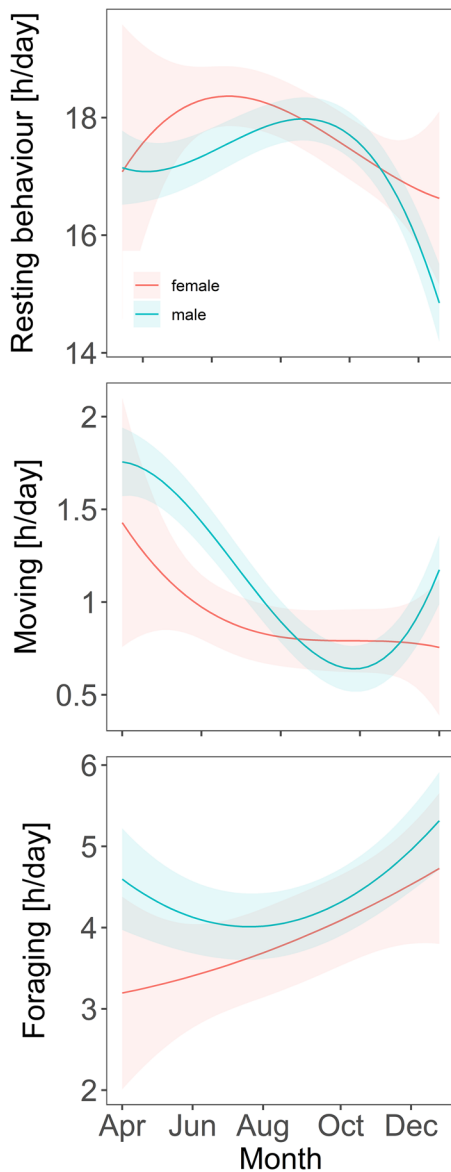
Fig. 4 The average hours hares spent resting, moving and foraging per day and season in relation to habitat diversity (measured as Simpson diversity index of landscape elements within 99% Kernel utilization ranges of each month). Both animal sexes and both study areas are pooled together in this graph. Light coloured bands display 95% confidence intervals. Please be aware of the different scales on the y axis and the data distribution for each month on the x-axis
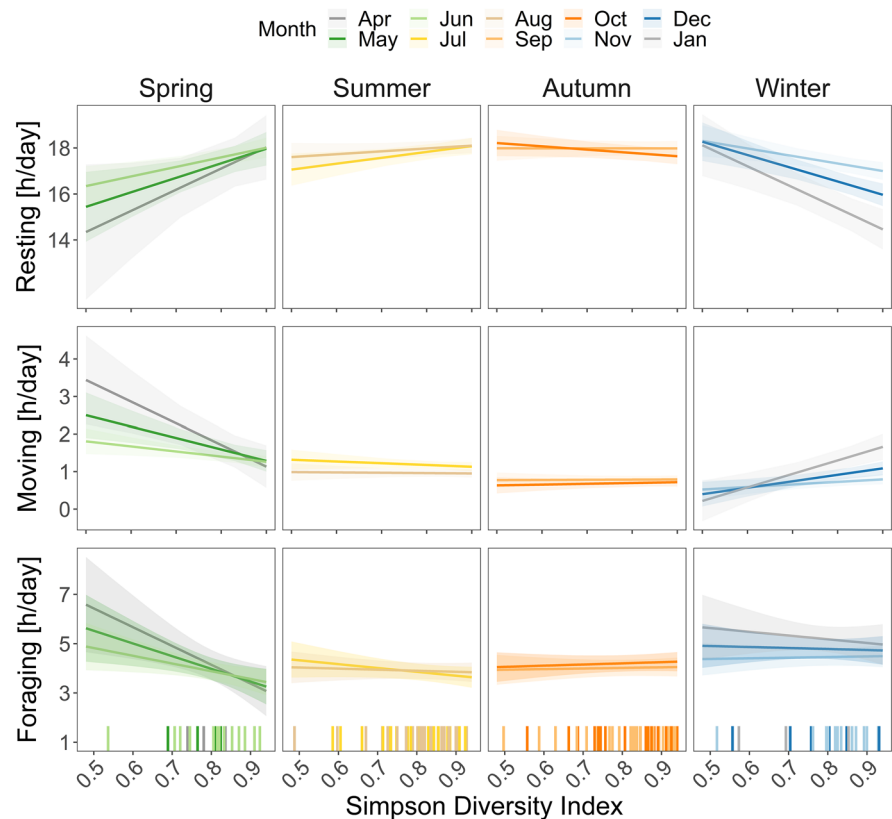
environmental changes by altering their utilization range size (Lucherini and Lovari 1996; Herfindal et al. 2005; Saïd and Servanty 2005; McLoughlin et al. 2007; Marable et al. 2012). This is in line with our results showing that, from April to June (peak breeding Click or tap here to enter text.), hares in diverse habitats rest more and spend less time moving and searching for resources. Breeding and caring for young is strenuous, and drives an increased need for nutrients (Hackländer et al. 2002; Schai-Braun et al. 2015), reflected by female hares' body condition strongly predicting their subsequent reproductive output (Schai-Braun et al. 2021). Hence, well-fed mother hares in areas with high habitat diversity will have more and heavier offspring. We also showed that female hares are particularly sensitive to the landscape context, as they rested more and foraged less when field sizes were smaller. The female hares in those areas find their daily requirements more easily and thus can rest for up to an hour and a half more per day. Such high importance of habitat quality and overall landscape complexity during the breeding

season was also found in other species, such as roe deer (*C. capreolus*), song sparrow (*Melospiza melodia*), and the little owl (*Athene noctua*) (McLoughlin et al. 2007; Germain et al. 2015; Grüebler et al. 2018).

In winter, however, the relationship between the behavioural modes and habitat diversity shifted. During the cold and wet season hares moved more and rested less in areas of high habitat diversity than in areas of low habitat diversity. Concurrently, during winter, areas of low habitat diversity in agricultural landscapes are characterized by vast open areas with low vegetation cover. Hares in areas with low habitat diversity might be unable to move as much as necessary to meet their daily requirements, since limiting activity is crucial for minimizing predation risk (Ellsworth et al. 2016). Additionally, the absence of tall vegetation may lead to challenges in finding thermal shelter (Laiolo 2005; Meichtry-Stier et al. 2018). Hence, areas of high vegetation are especially important as cover for hares during winter (Tapper and Barnes 1986). A study by Mayer et al. (2019)

Fig. 5 The average time male (blue) and female (red) hares spent resting (upper panel), moving (middle panel) and foraging (lower panel) per day in each month from April to January. Shaded areas correspond to 95% confidence intervals. All month were used in the model, here only every second month is ticked to ease visual representation. Beware of the different scales on the y axes

also showed that weather effects on habitat selection in hares are strongest in winter and that resting hares need high vegetation and edge structures during the cold period of the year. Furthermore, Mori et al. (2020) showed that hares are more active in

winter when they have the opportunity for cover in their home ranges. Subsequently, choosing a utilization range within high quality habitat, especially in landscapes with large agricultural fields, plays an important role for individual fitness, as it subsequently results in favourable proportions of resting vs. moving and foraging behaviour, depending on the specific requirements for each season. Highly diverse habitats are also directly beneficial for the survival of the offspring (Karp and Gehr 2020; Schai-Braun et al. 2020) and adults are able to allocate more energy into reproduction as other requirements (e.g. food and shelter) are easily available (Trivers 1972; Tieleman et al. 2008). As a result, animals in areas with low habitat diversity or extensive agricultural fields must prioritize energy allocation towards self-maintenance before reproduction, leading to decreased overall abundance in such poorly structured landscapes.

Our behavioural classification model's accuracy of 80% is lower than some other ACC analyses within the literature (Nuijten et al. 2020; Yu and Klaassen 2021). After we removed grooming and vigilance behaviour from the final statistical model, the largest source of error stems from foraging, which was confused with resting or moving behaviour. We are confident that this source of error within the model is unlikely to dramatically change the results of our analysis. We would expect that the error occurred over the entire range of the independent variables (i.e. average field size, Simpson diversity index and month), which would result in a slight upwards or downwards shift (depending on the focal behaviour) of the curve, with none or minimal changes to the corresponding slope. Thus, the statistical significance of our results and the biological effect size are practically unaffected (please see also the Supplementary Material S4).

While hare populations are declining across Europe, some areas have experienced more significant decreases than others. These regions likely underwent extensive land-use changes, with Germany's land-use change over the past 75 years potentially being representative of other European areas [e.g. Poland as demonstrated in Gryz and Krauze-Gryz (2022)]. Hare populations in eastern Germany declined more sharply than in western Germany (Strauß et al. 2008; Deutscher Jagdverband 2019), which may be attributable to the large field sizes established during land consolidation in the German Democratic Republic.

These larger fields led to reduced habitat diversity (Batáry et al. 2017), potentially contributing to the decline in hare numbers.

We also demonstrated that increased movement correlates with hares displaying longer step lengths and, consequently, larger utilization ranges. These changes are likely a result of alterations in the proportion of behavioral modes, potentially driven by factors such as habitat quality and landscape configuration, among others. When standing crops are high, hares in areas of small agricultural fields and high habitat quality can cross the field by tunnelling through the dense vegetation (Rühe 1999; Mayer et al. 2018; Ullmann et al. 2018). In contrast, when agricultural fields are large and the standing crops are high, they become impassable barriers to hares (Rühe 1999) and have to be circumvented to get to different foraging grounds, thus increasing the amount hares have to move per unit time.

Conclusion

Our observed changes in the behavioural modes of hares relative to landscape composition and configuration will likely apply to other mobile species. For most animals in agricultural landscapes, land-use intensification decreases habitat quality (Chamberlain et al. 2000; Burel et al. 2004). Ultimately, low habitat diversity compels animals to move more and spend more time foraging, allocating less energy to reproduction. This can lead to decreased fitness and, over time, may contribute to the local extinctions often observed in intensively managed agricultural landscapes (Benton et al. 2003).

Our study demonstrates that habitat diversity influences animal behaviour, particularly during the breeding season as well as in cold and wet seasons. To ensure the long-term survival of wildlife in agricultural areas, it is essential to increase habitat diversity and reduce field sizes. This aim may be reached by e.g. planting wild flower strips (Meichtry-Stier et al. 2014; Sliwinski et al. 2019), increasing the proportion of organic farming (Winqvist et al. 2011; Fischer et al. 2017), splitting fields to make them smaller (Tapper and Barnes 1986; Fahrig et al. 2015; Batáry et al. 2017) and implementing agri-environmental schemes (Fischer et al. 2011).

Declarations

References

Anderson D (2008) Model based inference in the life sciences: a primer on evidence. Springer, New York

Anderson DP, Forester JD, Turner MG et al (2005) Factors influencing female home range sizes in elk (*Cervus elaphus*) in North American landscapes. Landsc Ecol 20:257–271

Arnold TW (2010) Uninformative parameters and model selection using Akaike's Information criterion. J Wildl Manage 74:1175–1178

Barton K (2013) MuMIn: multi-model inference. R package version 1.9. 5

Batáry P, Gallé R, Riesch F et al (2017) The former Iron Curtain still drives biodiversity–profit trade-offs in German agriculture. Nat Ecol Evol 1:1279

Bates D, Maechler M, Bolker B, Walker S (2014) lme4: linear mixed-effects models using Eigen and S4. R package version 1:1–23

Bayerisches Landesamt für Statistik und Datenverarbeitung (2016) Erntemengenanteile der Fruchtartgruppen in Bayern 2015 in Prozent [WWW Document]. https://www.statistik.bayern.de/statistik/landwirtschaft/#

Bayerische Vermessungsverwaltung (2014) Geobasisdaten zur tatsächlichen Nutzung. In: http://www.ldbv.bayern.de/produkte/kataster/tat_nutzung.html

Bennett AF, Radford JQ, Haslem A (2006) Properties of land mosaics: implications for nature conservation in agricultural environments. Biol Conserv 133:250–264

Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? Trends Ecol Evol 18:182–188

Bolker BM, Brooks ME, Clark CJ, Geange SW, Poulsen JR, Stevens MHH, White J-S-S (2009) Generalized linear mixed models: a practical guide for ecology and evolution. Trends Ecol Evol 24:127–135

Bonte D, Vanden BJ, Lens L, Maelfait J-P (2006) Geographical variation in wolf spider dispersal behaviour is related to landscape structure. Anim Behav 72:655–662

Burel F, Butet A, Delettre YR, de La Peña NM (2004) Differential response of selected taxa to landscape context and agricultural intensification. Landsc Urban Plan 67:195–204

Calenge C (2006) The package 'adehabitat' for the R software: a tool for the analysis of space and habitat use by animals. Ecol Modell 197:516–519

Chakravarty P, Cozzi G, Dejnabadi H et al (2020) Seek and learn: automated identification of microevents in animal behaviour using envelopes of acceleration data and machine learning. Methods Ecol Evol 11:1639–1651

Chamberlain DE, Fuller JR, Bunce GHR et al (2000) Changes in the abundance of farmland birds in relation to the timing of agricultural intensification in England and Wales. J Appl Ecol 37:771–788

Daan S, Deerenberg C, Dijkstra C (1996) Increased daily work precipitates natural death in the kestrel. J Anim Ecol 65:539–544

Deutscher Jagdverband (2019) Dichte des Feldhasen in den Referensgebieten Deutschlands. Accessed on [22.12.2020]

https://www.jagdverband.de/zahlen-fakten/tiersteckbriefe/feldhase-lepus-europaeus

Dochtermann NA, Jenkins SH (2011) Developing multiple hypotheses in behavioral ecology. Behav Ecol Sociobiol 65:37–45

Ellsworth E, Boudreau MR, Nagy K et al (2016) Differential sex-related winter energetics in free-ranging snowshoe hares (*Lepus americanus*). Can J Zool 94:115–121

European Environment Agency (2018a) Land cover and change 2000–2018 based on corine land cover classes (clc)

European Environment Agency (2018b) Corine land cover (clc) 2018 version 20

Fahrig L, Baudry J, Brotons L, Burel FG, Crist TO, Fuller RJ, Sirami C, Siriwardena GM, Martin JL (2011) Functional landscape heterogeneity and animal biodiversity in agricultural landscapes. Ecol Lett 14(2):101–112

Fahrig L, Girard J, Duro D et al (2015) Farmlands with smaller crop fields have higher within-field biodiversity. Agric Ecosyst Environ 200:219–234

Finder RA, Roseberry JL, Woolf A (1999) Site and landscape conditions at white-tailed deer/vehicle collision locations in Illinois. Landsc Urban Plan 44:77–85

Firbank LG, Petit S, Smart S et al (2008) Assessing the impacts of agricultural intensification on biodiversity: a British perspective. Philos Trans R Soc Lond B: Biol Sci 363:777–787

Fischer C, Thies C, Tscharntke T (2011) Small mammals in agricultural landscapes: opposing responses to farming practices and landscape complexity. Biol Conserv 144:1130–1136

Fischer C, Stadlmann D, Blaum N, Ullmann W (2017) Der Einfluss des ökologischen Landbaus auf das Raumnutzungsverhalten von Feldhasen (Lepus europaeus). In: Wolfrum, S., Heuwinkel, H., Reents, H. J., Wiesinger, K., Hülsbergen, K.-J. (eds) Beiträge zur 14. Wissenschaftstagung Ökologischer Landbau: Ökologischen Landbau weiterdenken - Verantwortung übernehmen - Vertrauen stärken, Verlag Dr. Köster, Berlin, pp 794-796.

Frylestam B (1980) Reproduction in the European hare in southern Sweden. Ecography 3:74–80

Germain RR, Schuster R, Delmore KE, Arcese P (2015) Habitat preference facilitates successful early breeding in an open-cup nesting songbird. Funct Ecol 29:1522–1532

Google maps (2017) Map of Nordwestuckermark and Freising. Google. https://www.google.de/maps/place/Nordwestuckermark/@53.3161736,13.6173236,12z/data=!3m1!4b1!4m5!3m4!1s0x47aa29f485f939db:0x42120465b5e6e40!8m2!3d53.2973849!4d13.7247244. Accessed 30 June 2017

Grüebler MU, Müller M, Michel VT et al (2018) Brood provisioning and reproductive benefits in relation to habitat quality: a food supplementation experiment. Anim Behav 141:45–55

Grünewälder S, Broekhuis F, Macdonald DW et al (2012) Movement activity based classification of animal behaviour with an application to data from cheetah (*Acinonyx jubatus*). PLoS ONE 7:e49120

Gryz J, Krauze-Gryz D (2022) Why did Brown hare (*Lepus europaeus*) disappear from some areas in Central Poland? Diversity 14:465

Hackländer K, Arnold W, Ruf T (2002) Postnatal development and thermoregulation in the precocial European hare (*Lepus europaeus*). J Comp Physiol B 172:183–190

Hartig F (2017) DHARMa: residual diagnostics for hierarchical (multi-level/mixed) regression models. R package version 0.1. 5

Herfindal I, Linnell JDC, Odden J et al (2005) Prey density, environmental productivity and home-range size in the Eurasian lynx (*Lynx lynx*). J Zool 265:63–71

InVeKoS (2014) Integriertes Verwaltungs- und Kontrollsystem—Landesvermessung und Geobasisinformation Brandenburg. In: https://www.geobasis-bb.de/dienstleister/gis_invekos.htm

Jeltsch F et al (2013) Integrating movement ecology with biodiversity research-exploring new avenues to address spatiotemporal biodiversity dynamics. Mov Ecol 1(1):1–13

Karp D, Gehr B (2020) Bad hare day: very low survival rate in brown hare leverets. Wildl Biol 2020(2):1–8

Laiolo P (2005) Spatial and seasonal patterns of bird communities in Italian agroecosystems. Conserv Biol 19:1547–1556

Li Z, Rogers E (2004) Habitat quality and activity budgets of white-headed langurs in Fusui, China. Int J Primatol 25:41–54

Liaw A, Wiener M (2002) Classification and regression by randomForest. R News 2:18–22

Lucherini M, Lovari S (1996) Habitat richness affects home range size in the red fox *Vulpes vulpes*. Behav Proc 36:103–106

Lush L, Ellwood S, Markham A et al (2016) Use of tri-axial accelerometers to assess terrestrial mammal behaviour in the wild. J Zool 298:257–265

Mace GM, Harvey PH (1983) Energetic constraints on home-range size. Am Nat 121:120–132

Majchrzak YN, Peers MJ, Studd EK, Menzies AK, Walker PD, Shiratsuru S, McCaw LK, Boonstra R, Humphries M, Jung TS, Kenney AJ, Krebs CJ, Murray DL, Boutin S (2022) Balancing food acquisition and predation risk drives demographic changes in snowshoe hare population cycles. Ecol Lett 25:981–991

Marable MK, Belant JL, Godwin D, Wang G (2012) Effects of resource dispersion and site familiarity on movements of translocated wild turkeys on fragmented landscapes. Behav Proc 91:119–124

Mayer M, Ullmann W, Sund P et al (2018) Habitat selection by the European hare in arable landscapes: the importance of small-scale habitat structure for conservation. Ecol Evol. https://doi.org/10.1002/ece3.4613

Mayer M, Ullmann W, Heinrich R et al (2019) Seasonal effects of habitat structure and weather on the habitat selection and home range size of a mammal in agricultural landscapes. Landsc Ecol 34:2279–2294

McLoughlin PD, Gaillard J-M, Boyce MS et al (2007) Lifetime reproductive success and composition of the home range in a large herbivore. Ecology 88:3192–3201

Meichtry-Stier KS, Jenny M, Zellweger-Fischer J, Birrer S (2014) Impact of landscape improvement by agri-environment scheme options on densities of characteristic farmland bird species and brown hare (*Lepus europaeus*). Agric Ecosyst Environ 189:101–109

Meichtry-Stier KS, Duplain J, Lanz M et al (2018) The importance of size, location, and vegetation composition of perennial fallows for farmland birds. Ecol Evol 8:9270–9281

Mori E, Lovari S, Cozzi F, Gabbrielli C, Giari C, Torniai L, Romeo G, Ferretti F, Fattorini N (2020) Safety or satiety? Spatiotemporal behaviour of a threatened herbivore. Mamm Biol 100(1):49–61

Nuijten R, Prins EF, Lammers J, Mager C, Nolet BA (2020) Calibrating tri-axial accelerometers for remote behavioural observations in Bewick's swans. J Zoo Aquar Res 8(4):231–238

Oksanen J, Blanchet FG, Kindt R, et al (2013) Package 'vegan.' Community ecology package, version 2:1–295

Pimm SL, Raven P (2000) Biodiversity: extinction by numbers. Nature 403:843

Ramankutty N, Evan AT, Monfreda C, Foley JA (2008) Farming the planet: 1. Geographic distribution of global agricultural lands in the year 2000. Glob Biogeochem Cycles. https://doi.org/10.1029/2007GB002952

Reichlin T, Klansek E, Hackländer K (2006) Diet selection by hares (*Lepus europaeus*) in arable land and its implications for habitat management. Eur J Wildl Res 52:109–118

Rockström J, Steffen W, Noone K et al (2009) Planetary boundaries: exploring the safe operating space for humanity. Ecol Soc. https://doi.org/10.5751/ES-03180-140232

Rühe F (1999) Effect of stand structures in arable crops on brown hare (*Lepus europaeus*) distribution. Gibier Faune Sauvage, Game Wildl Sci 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

Saïd S, Servanty S (2005) The influence of landscape structure on female roe deer home-range size. Landsc Ecol 20:1003–1012

Schai-Braun SC, Hackländer K (2014) 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, Reichlin TS, Ruf T et al (2015) The European hare (*Lepus europaeus*): a picky herbivore searching for plant parts rich in fat. PLoS ONE 10:e0134278

Schai-Braun SC, Ruf T, Klansek E et al (2020) Positive effects of set-asides on European hare (*Lepus europaeus*) populations: leverets benefit from an enhanced survival rate. Biol Conserv 244:108518

Schai-Braun SC, Steiger P, Ruf T et al (2021) Maternal effects on reproduction in the precocial European hare (*Lepus europaeus*). PLoS ONE 16:e0247174

Shamoun-Baranes J, Bom R, van Loon EE et al (2012) From sensor data to animal behaviour: an oystercatcher example. PLoS ONE 7:e37997

Simeunovič B, Štrbenc M, Bavdek SV (2000) Position and histological structure of the testes in the brown hare (*Lepus europaeus*) during seasonal regression and recrudescence. Anat Histol Embryol 29:73–82

Sliwinski K, Ronnenberg K, Jung K et al (2019) Habitat requirements of the European brown hare (*Lepus*

europaeus Pallas 1778) in an intensively used agriculture region (Lower Saxony, Germany). BMC Ecol 19:1–11

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, Vaughan Jennings N, 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

Strauß E, Grauer A, Bartel M, Klein R, Wenzelides L, Greiser G, Muchin A, Nösel H, Winter A (2008) The German wildlife information system: population densities and development of European Hare (*Lepus europaeus* PALLAS) during 2002–2005 in Germany. Eur J Wildl Res 54:142–147

Studd EK, Boudreau MR, Majchrzak YN, Menzies AK, Peers MJ, Seguin JL, Lavergne SG, Boonstra R, Murray DL, Boutin S, Humphries MM (2019) Use of acceleration and acoustics to classify behavior, generate time budgets, and evaluate responses to moonlight in free-ranging snowshoe hares. Front Ecol Evol 7:154

Su S, Xiao R, Li D (2014) Impacts of transportation routes on landscape diversity: a comparison of different route types and their combined effects. Environ Manage 53:636–647

Tatler J, Cassey P, Prowse TA (2018) High accuracy at low frequency: detailed behavioural classification from accelerometer data. J Exp Biol 221(23):jeb184085

Tatler J, Currie SE, Cassey P, Scharf AK, Roshier DA, Prowse TA (2021) Accelerometer informed time-energy budgets reveal the importance of temperature to the activity of a wild, arid zone canid. Mov Ecol 9(1):1–12

Tapper SC, Barnes RFW (1986) Influence of farming practise on the ecology of the brown hare (*Lepus europaeus*). J Appl Ecol 23:39–52

Tieleman BI, Dijkstra TH, Klasing KC et al (2008) Effects of experimentally increased costs of activity during reproduction on parental investment and self-maintenance in tropical house wrens. Behav Ecol 19:949–959

Trivers R (1972) Parental investment and sexual selection. Biological Laboratories, Harvard University, Cambridge

Turner MG, Gardner RH, O'neill RV et al (2001) Landscape ecology in theory and practice. Springer, New York

Ullmann W, Fischer C, Pirhofer-Walzl K et al (2018) Spatiotemporal variability in resources affects herbivore home range formation in structurally contrasting and unpredictable agricultural landscapes. Landsc Ecol. https://doi.org/10.1007/s10980-018-0676-2

Ullmann W, Fischer C, Kramer-Schadt S et al (2020) How do agricultural practices affect the movement behaviour of European brown hares (*Lepus europaeus*)? Agric Ecosyst Environ. https://doi.org/10.1016/j.agee.2020.106819

Valencak TG, Tataruch F, Ruf T (2009) Peak energy turnover in lactating European hares: the role of fat reserves. J Exp Biol 212:231–237

Weterings MJ, Moonen S, Prins HH, van Wieren SE, van Langevelde F (2018) Food quality and quantity are more important in explaining foraging of an intermediate-sized mammalian herbivore than predation risk or competition. Ecol Evol 8(16):8419–8432

Wikelski M, Kays R (2015) Movebank: archive, analysis and sharing of animal movement data. Hosted by the Max Planck Institute of Animal Behavior. http://www.movebank.org/. Accessed 13 April 2020

Wilson RP, White CR, Quintana F et al (2006) Moving towards acceleration for estimates of activity-specific metabolic rate in free-living animals: the case of the cormorant. J Anim Ecol 75:1081–1090

Winqvist C, Bengtsson J, Aavik T et al (2011) Mixed effects of organic farming and landscape complexity on farmland biodiversity and biological control potential across Europe. J Appl Ecol 48:570–579

Wood SN (2001) mgcv: GAMs and generalized ridge regression for R. R nEws 1:20–25

Yu H, Klaassen M (2021) R package for animal behavior classification from accelerometer data—rabc. Ecol Evol 11(18):12364–12377

Zuur AF, Ieno E, Walker N et al (2009) Mixed effects models and extensions in ecology with R. Springer, New York