

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

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Abstract

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

Objectives: We show how landscape composition and configuration and 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 differing in landscape composition and configuration (simple vs. complex) 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 then tested whether the amount of behaviours per category changed with landscape composition and configuration, season and sex.

Results: During peak breeding, hares in areas of high habitat diversity rested more, moved less and spent less time searching for resources. In winter, however, hares moved more and rested less in areas of high habitat diversity.

Conclusions: High habitat diversity 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 cover their requirements. Hence, high habitat diversity guarantees species persistence in human-altered agricultural areas throughout the year.

Introduction

As human population growth drives increasing food demand, 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 class 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; Reidsma et al. 2006). 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, changing their behaviour and adjusting their movements are some of the few options available to animals to survive.

Animal movement is a key life-history trait underlying individuals' survival and fitness, and is influenced by landscape composition and configuration (e.g. Turner et al. 2001; Bennett et al. 2006). For example, it was found that increasing habitat fragmentation and decreasing habitat diversity in agricultural landscapes results in a smaller proportion of dispersing animals (Bonte et al. 2006), changes in habitat choice (Smith et al. 2004; Dolný et al. 2014), and increases home ranges and daily travel distances (Diffendorfer et al. 1995; Schai-Braun and Hackländer 2014; Ullmann et al. 2018). Additionally, these animal movement measures, also depend on seasonal changes in the available vegetation structure (Mayer et al. 2019). However, the behavioural mechanisms underlying the changes in movement patterns, i.e. whether travel distances or utilization ranges increase because of increased fleeing or foraging, remain largely unexplored. One promising avenue to investigating the underlying processes is through the animals' daily behaviours. Although daily behaviours of free-ranging animals have recently become a matter of interest (Wilson et al. 2006; Grünwälder et al. 2012, Lush et al. 2016), the influence of landscape composition and configuration as well as the corresponding seasonal dynamics on the actual animals' behavioural modes has rarely been studied.

A landscapes' composition and configuration can be studied on different scales, e.g. at the habitat scale when looking at an animal's utilization range and discerning the habitat diversity within that utilization range, and at the landscape scale when looking at the overall landscape complexity in which the animal lives (i.e. simple versus complex agricultural landscapes). 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, for e.g. 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 potentially forces animals to stay in a patch when encountering barriers, or to travel long distances between habitat patches to meet 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 overcome or moved around 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, which would then result in higher energy expenditure (Mace and Harvey 1983) and ultimately to a decline in body conditions and individual fitness (Daan et al. 1996).

A typical open-habitat species occurring in agricultural landscapes is the European brown hare (*Lepus europaeus*, hereafter hare). 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 smaller 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 composition and configuration is resource availability (e.g. food and shelter), which additionally changes throughout the season and influences hares' spatial movement behaviour (Mayer et al. 2019). Hares forage on cultivated crops, but a high-quality diet also heavily depends on non-cultivated herbs (Reichlin et al. 2006). This need might be exacerbated in the breeding time of

female hares, when a high energy demand to milk the offspring coincides with the need of finding good hiding places to deter predators (Hackländer et al. 2002a; Valencak et al. 2009; Mayer et al. 2019).

Here, we investigate whether changes in animals' behavioural modes are caused by changes in landscape complexity and habitat diversity. We used GPS telemetry with internal tri-axial accelerometers to distinguish between the following behavioural modes of European brown hares: 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 analysed 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. From the landscape scale we "zoomed in" to the habitat scale and used each hare's monthly utilization range to calculate the underlying habitat diversity, in each of the two differently structured landscapes. We related study area (i.e. landscape complexity) and habitat diversity to the hares' behavioural modes and investigate 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:

1. 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, as they must spend more time searching for resources (especially high-quality food items) and travel longer distances.
2. The effect described in hypothesis 1 scales up to the landscape structure. Hares in simple agricultural landscapes with large fields, spend more time moving than hares in complex agricultural areas with small fields, as resources are more spread out, due to the large field sizes.
3. The behavioural modes of males and females will change seasonally following important life-history events like reproduction, resulting in increased moving behaviour during mating and more extended resting periods in the non-reproductive period.

Methods

Study area

The study was carried out in two structurally contrasting agricultural landscapes in Germany (Fig. 1). 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). 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). 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 2018. 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. For each patch in the category "arable land," we also recorded the monthly tillage state and/or crop type for both study areas during the entire study period.

Animal tracking

In 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 seconds, resulting in 110 data points per burst per axis. Within 3.27 seconds, hares can easily conduct more than one or two different behaviours, hence we cut each burst into 1-second intervals and classified the behaviour of each of these 1-second acceleration bursts.

From the 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. We used the area of each hares' monthly utilization range to calculate monthly habitat diversity. Furthermore, we used the value of each hourly step length to calculate a median step length for each month. We did this to consider that 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 chose step length as confounding variable instead of utilization range size, because utilization range size and monthly median step length were highly correlated (Pearson's $r = 0.72$, t -value = 12.65, $df = 147$) and step length resulted in higher R^2 values in our models than using utilization range size. We received data from collared hares from April to January for both study years (2014 and 2015). All tracking and acceleration data were stored at www.movebank.org (Wikelski and Kays 2015).

Determination of habitat diversity

We used the Simpson diversity index to emphasize evenness due to the agricultural setting of the landscape in which areas are often dominated by large 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 each landscape element "arable land", we added the information on the field's current 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

For the behaviour classification we first directly observed four different hares to match the performed behaviour with the corresponding accelerometer output and to train a random forest model (Fig. 2). 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 S3, Table S3.1). 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 *randomforest* 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. 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 S3.

We classified the behaviour of hares into five main behavioural modes: resting, foraging, moving, grooming and vigilance behaviour. 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 S3). Thus, for further statistical analyses we only used resting, moving, and foraging behaviours, but did not consider grooming and vigilance.

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 count of monthly behavioural modes (resting, moving, and foraging): study area (i.e. landscape complexity), habitat diversity (Simpson diversity index), animal sex (male or female), seasonality (month) and median monthly step length. We ran the analyses for each behavioural mode separately to assure normally distributed residuals. This resulted into three linear mixed models (one for resting, moving and foraging respectively). Animal ID was used as random intercept. We included two-way interactions between study area and habitat diversity, study area and animal sex, habitat diversity and month, habitat diversity and animal sex, animal sex and month. The fixed factors were tested for collinearity according to Zuur et al. 2009 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 polynomial term to shape the curve of the variable and selected the model with the lowest AIC value. The model with the third polynomial for month showed the lowest AIC value, hence we included the third polynomial of month into all models. 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 build into the R package *MUMIn* (Barton 2013). We averaged all models with delta AIC values below 7 (Burnham and Anderson 2003). 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 and display the corresponding numbers in our output table (Table 1). However, that unit is rather unintuitive, therefore, we transformed the number of behaviours per month to hours per day (within the respective month) and provide this measure in the text and graphs.

Results

When month and sex were not considered, hares in the simple landscape showed a stable duration of resting per day (17.9 ± 0.2 h) throughout the year, regardless of the underlying habitat diversity (Fig. 3, Table 1). Hares in the complex landscape on the other hand increased the time they rested per day with increasing habitat diversity, from 16.6 ± 0.2 h in low diverse areas (Simpson diversity index = 0.5) to 18.2 ± 0.2 h per day in habitats with high diversity (Simpson diversity index = 0.9).

Table 1

Here we show the output of the three averaged models analysing the number of monthly counts of resting, moving and foraging behaviour depending on study area (SA), 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 SA(s) for the study area with a simple landscape structure and Sex(m) stands for males. We show informative fixed effects in bold and italic. Marginal and conditional R² are shown for each of the three global models in the last row.

Fixed Effect	Resting				Moving				Foraging			
	β	SE	LCI	UCI	β	SE	LCI	UCI	β	SE	LCI	UCI
Intercept	22503	2158	18255	26751	449	478	-497	1395	6680	3261	275	13086
SA	2562	2388	-2138	7261	102	378	-646	849	-834	2709	-6156	4489
SD	3169	2561	-1871	8210	-123	571	-1252	1006	-4252	4209	-12523	4020
Sex	85	1372	-2620	2789	178	354	-522	879	-1891	2980	-7748	3965
MM	2614	1000	637	4591	-351	383	-1110	407	-369	1059	-2451	1712
MM ²	421	578	-723	1565	275	234	-188	738	357	390	-411	1125
MM ³	98	358	-610	807	-394	146	-683	-105	13	215	-412	439
Med.SL	-10	3	-16	-5	11	1	9	13	3	3	-3	8
SA(s):SD	-4660	2341	-9289	-30	274	916	-1538	2086	5112	2854	-518	10742
SA(s):Sex(m)	99	818	-1517	1716	64	237	-406	534	-995	923	-2818	829
SD:MM	-4058	1274	-6575	-1541	264	487	-700	1228	2647	1351	-22	5316
SD:MM ²	-908	733	-2357	541	-301	297	-890	287	-685	732	-2133	762
SD:MM ³	-42	460	-952	867	523	188	152	893	-67	468	-993	859
SD:Sex(m)	-2075	2516	-7046	2896	-42	893	-1809	1724	5752	2820	185	11318
Sex(m):MM	999	228	548	1450	-532	91	-712	-352	-596	255	-1099	-92
Sex(m):MM ²	-160	111	-380	59	153	45	63	242	158	115	-69	385
Sex(m):MM ³	-274	79	-431	-116	106	32	43	170	202	86	33	371
	mR ² = 0.38 and cR ² = 0.87				mR ² = 0.82 and cR ² = 0.93				mR ² = 0.26 and cR ² = 0.86			

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 from 15.7 ± 0.7 h to 18.0 ± 0.3 h per day (from low to high Simpson diversity index values). The relationship becomes less important over the summer and then starts to decrease in winter. In December, for example, hares rested for 18.4 ± 0.4 h in areas with low habitat diversity and 15.8 ± 0.3 h in areas with high habitat diversity.

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 3.2 ± 0.6 h per day) in areas of low habitat diversity compared to areas of high habitat diversity (0.8 ± 0.3 h per day). This relationship as well becomes less expressed during summer. In winter, hares moved about 40 min less (in December: 0.4 ± 0.2 h per day), probably hiding instead of moving, in areas of low diversity than hares in areas of high diversity (1.1 ± 0.1 h per day). For the behavioural mode “foraging” and the interaction between habitat diversity and month, the lower confidence interval slightly overlapped zero, but as the mean and the upper confidence interval are rather distant from zero we deduced that the interaction is informative (Table 1, see Foraging and the fixed effect SD:MM). The relationship between the time spent foraging and habitat diversity is eminent mainly during peak breeding. Hares use up more of their time to search for resources in areas of low diversity (e.g. 5.8 ± 0.7 h per day in May) than in areas of high diversity (3.3 ± 0.4 h per day in May).

Female and male hares show strong seasonal differences in their behaviours (all three behavioural modes). The resting activity for female hares peaked in summer (e.g. July: 18.2 ± 0.2 h per day) and was lowest in winter (e.g. January: 16.7 ± 0.6 h per day, Fig. 5, Table 1). Male hares rested most in late summer (e.g. September: 17.6 ± 0.2 h per day) and, like females, least in winter (e.g. January: 15.1 ± 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 almost an hour more than females (female: 1.0 ± 0.1 h, male: 1.8 ± 0.1 h per day, Fig. 5). Males and females moved least in early autumn (females: 0.7 ± 0.1 h, males: 0.6 ± 0.1 h per day). Daily foraging activity was highest during winter for both sexes, and while the foraging peaked for males in January (5.1 ± 0.3 h) it was highest for females in November (4.2 ± 0.3 h, Fig. 5).

The interaction between animal sex and habitat diversity, on a yearly average, was informative only in the model for the behavioural mode “foraging”. Female hares searched less for resources the higher the habitat diversity within their utilization range (Fig. 6, Table 1), while male hares foraged for the same amount of time each day (3.9 ± 0.2 h per day), regardless of habitat diversity. Female hares searched for resources up to 4.9 ± 0.6 h per day in areas of low habitat diversity, but only for 3.3 ± 0.3 h in areas with high habitat diversity.

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

All three analysed behavioural modes (resting, moving, and foraging) proved to be sensitive to habitat diversity, animal sex and seasonality. 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 environmental changes for example 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; Lovari et al. 2013; Morellet et al. 2013; Bevanda et al. 2014). This is in line with our results showing that, from April to June, hares in diverse habitats are resting more and spend less time moving and searching for resources. April to June corresponds to the time of peak breeding in hares (Frylestam 1980). Breeding and caring for young is a strenuous time that is characterized by an increased need for certain nutrients (Hackländer et al. 2002a, b; Wanless et al. 2005; Schai-Braun et al. 2015), which is also shown by the fact that the body condition of female hares is a strong predictor for 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. The female hares in those areas find all their daily requirements met easily and do not need to spend much time in search for resources, instead they can rest for up to an hour more per day and save energy. Such high importance of habitat quality during the breeding season was also found in other species, such as roe deer (*Capreolus capreolus*), song sparrow (*Melospiza melodia*), and the little owl (*Athene noctua*) (McLoughlin et al. 2007; Germain et al. 2015; Gruebler et al. 2018).

In winter, however, the relationship between the behavioural modes and habitat diversity shifts. During the cold and wet season hares move more and rest 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 low diversity areas may not have the luxury to move as much as they might need to, as limiting activity is a key to reducing the risk of predation (Ellsworth et al. 2016), and a lack of high vegetation signifies difficulties to find 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 recent study by Mayer et al. (2019) 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 and that hares move less during full moon, probably due to increased predation risk. Subsequently, choosing a home range within high quality habitat 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, involving edge structures (e.g. hedges, field edges and field paths) between different landscape elements are also directly beneficial for the survival of the young (Voigt and Siebert 2019; Karp and Gehr 2020; Schai-Braun et al. 2020). Moreover, animals in high quality habitats are able to allocate more energy into reproduction as other requirements (e.g. food and shelter) are easily available, this is especially true during the breeding season (Trivers 1972; Tieleman et al. 2008).

In particular, the behaviours of male hares were impacted by the annual reproductive cycle. They moved most during May, peak reproduction, and least during October, the end of the reproductive phase (Flux 1965; Frylestam 1980; Hansen 1992). The social behaviour during the breeding season is characterized by males competing for oestrous females, mainly by boxing or chasing competitors away from the female (Holley 1986, Alves et al. 2008). These behaviours relate to an increased amount of moving during the breeding season, as demonstrated in our study. We furthermore showed, that increased movement is causally related to hares exhibiting longer step length and thereby larger utilization ranges. These adjustments in step length (and with it in utilization range size) are most likely caused by changes in the proportion of behavioural modes, and might (besides others) be driven by changes in habitat quality and diversity. These changes, for example, may affect hare movement behaviour seasonally. 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). This allows them to keep their step length short and their utilization range small, as they move only short distances between e.g. field edges and foraging grounds, and therefore move less in general. 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 habitat diversity 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). Eventually, low habitat diversity forces animals to move more and search longer for food, allocating less energy into reproduction, which can result in a decline in fitness and, over the long term, may lead to the local extinctions frequently observed in intensified agricultural landscapes (Benton et al. 2003; Tschamtkke et al. 2005).

Through our research, we have shown that habitat diversity changes the animals' behaviour, especially during the breeding season but as well in the cold and wet season. Habitat diversity has to be increased to assure the future survival of wildlife in agricultural areas. This aim may be reached by planting wild flower strips (Meichtry-Stier et al. 2014; Sliwinski et al. 2019; Weber et al. 2019), increasing the proportion of organic farming (Winqvist et al. 2011; Fischer et al. 2017), decreasing field size (Tapper and Barnes 1986; Schai-Braun and Hackländer 2014; Fahrig et al. 2015; Batáry et al. 2017) and implementing agri-environmental schemes (Fischer et al. 2011).

Declarations

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Competing interests

The authors declare that they have no conflicting or competing interests.

Authors' contributions

WU, CF, SKS, KPW, JAE and NB developed the concept of the work. WU and CF collected the data. PW, AH, KS collected, prepared and analysed the data that was used to train the random forest. WU and MSC prepared the data for the analyses. WU performed the statistical analyses and wrote the manuscript. CF, SKS, KPW, JAE, PW, AH, KS, MSC, MG and NB commented and improved the manuscript. All authors read and approved the final manuscript.

Data availability

The GPS and accelerometer data are deposited in Movebank (study name: “AgroScapeLabs”). Access to the data will be granted by the corresponding author on reasonable request.

Ethics approval

All procedures involving animals for the research were obtained in accordance with the Federal Nature Conservation Act (§ 45 Abs. 7 Nr. 3) and approved by the local nature conservation and animal protection authority (reference number LUGV V3-2347-22-2013 for hares in northeast Germany and 55.2-1-54-2532-229-13 for hares in southern Germany).

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Figures

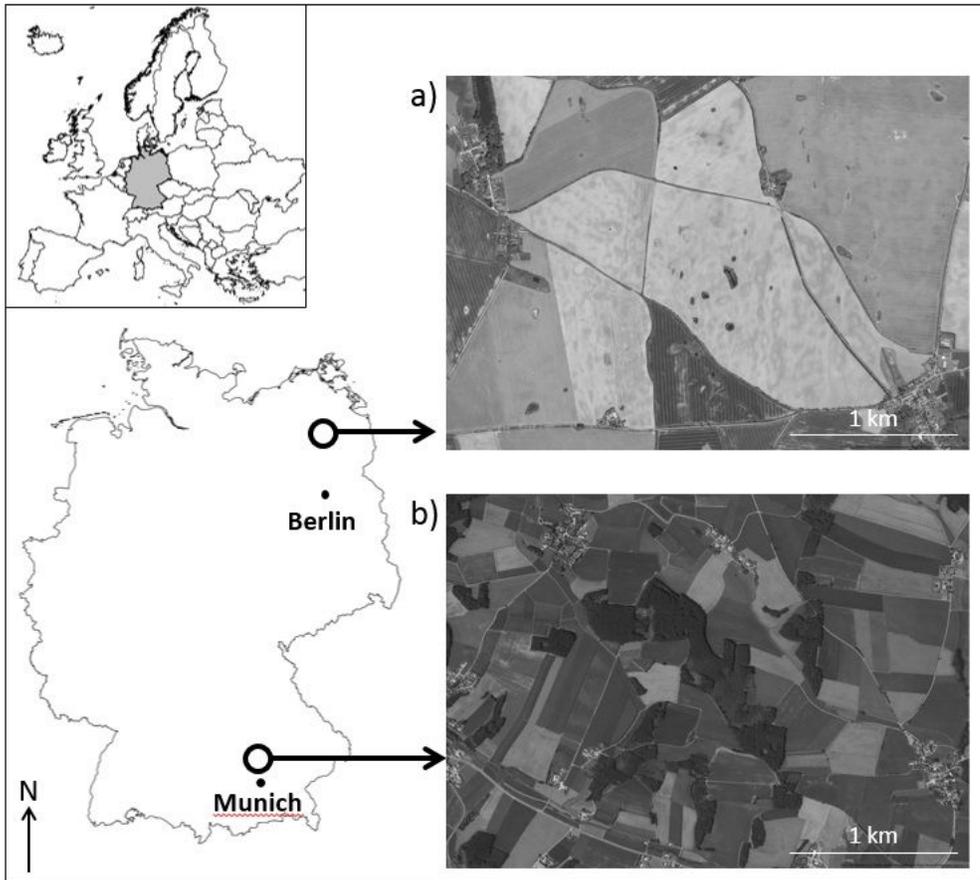


Figure 1

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

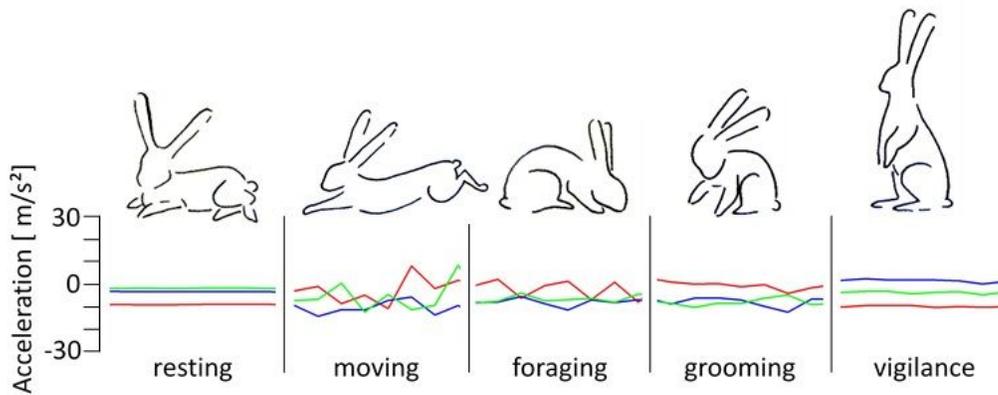


Figure 2

The accelerometer output of the five different behavioural modes. The x-axis is shown in red, the y-axis in blue and the z-axis in green. Resting shows the normal position of the three 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 (as opposed to resting).

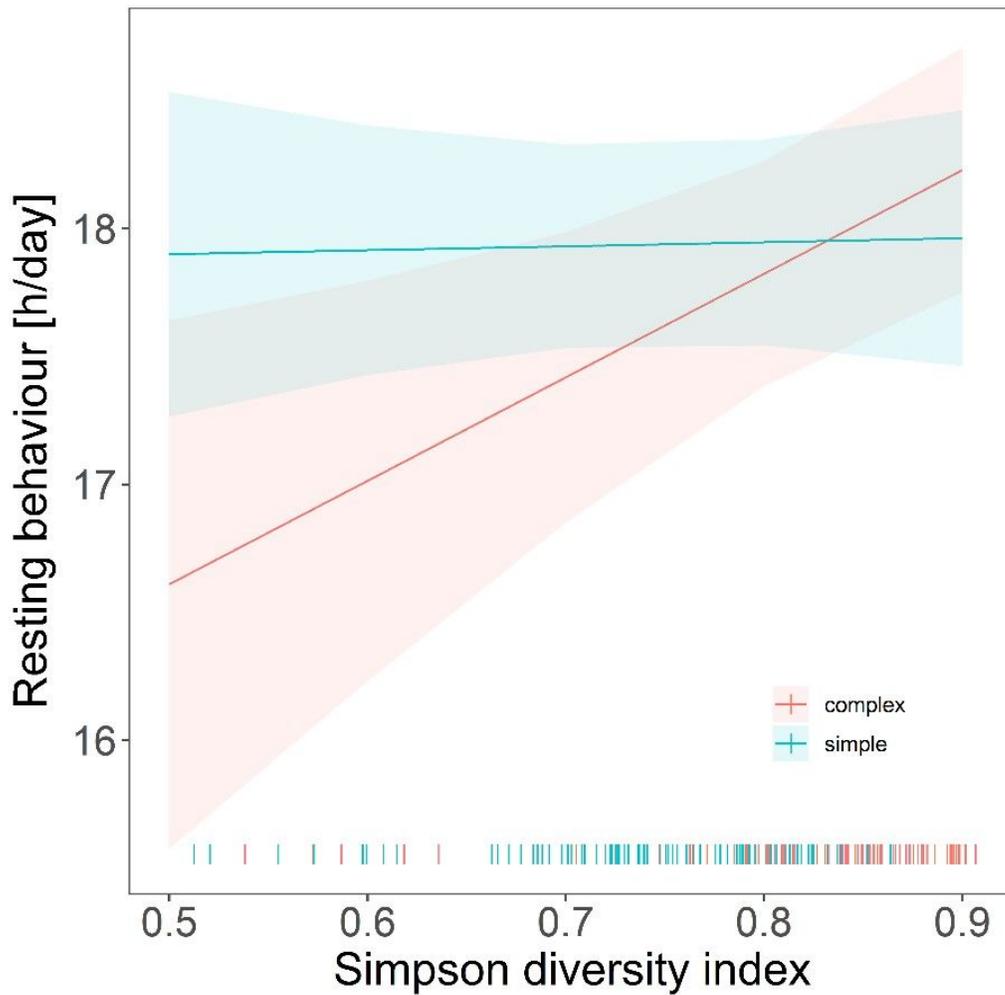


Figure 3

The amount of time hares rested in relation to the underlying habitat diversity in the two differently structured agricultural landscapes, seen as an average over the entire year. The complex study area, southern Germany, is depicted in red and the simple landscape, northeast Germany, is depicted in blue.

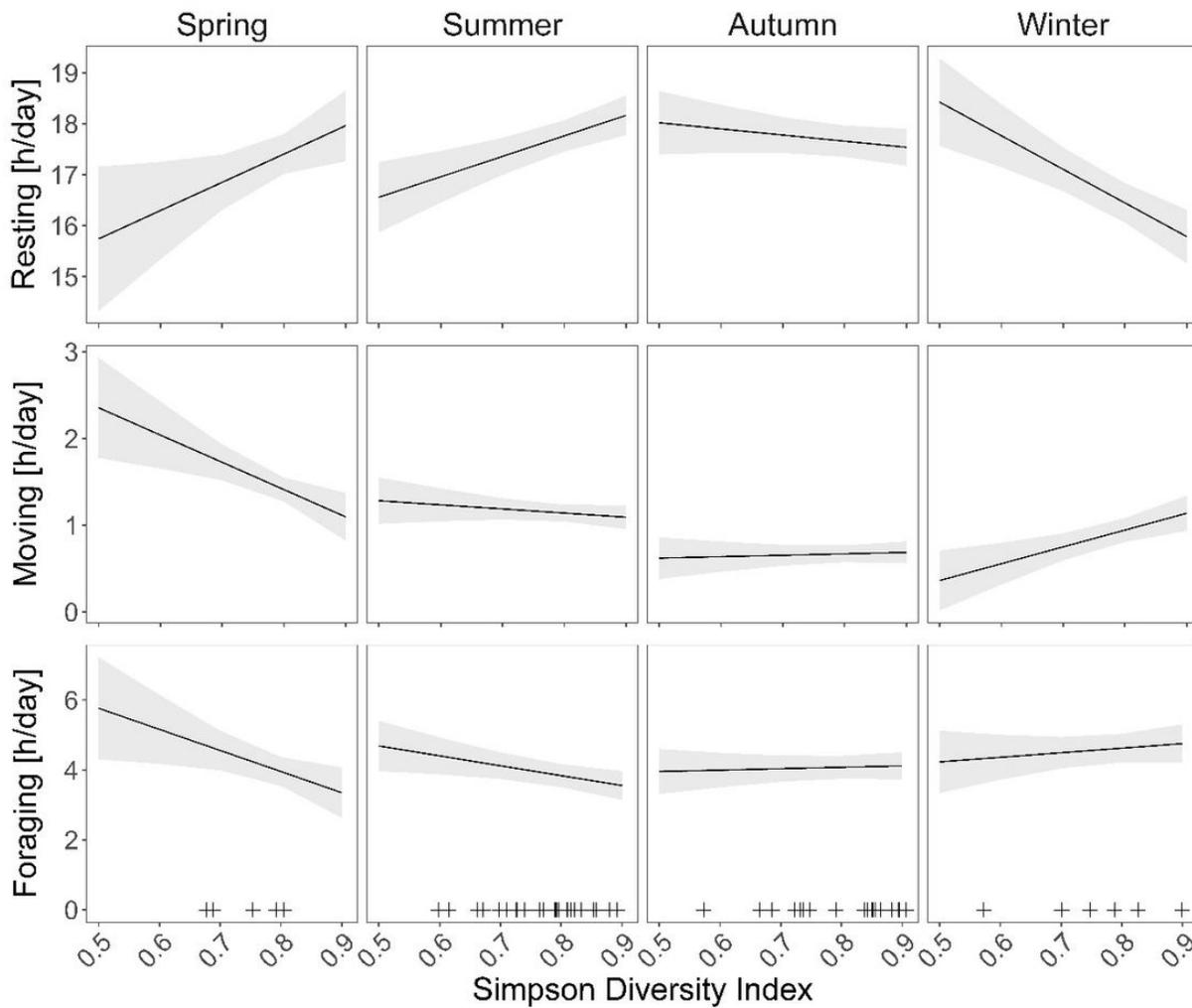


Figure 4

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; data shown with '+'). Represented are the following month: May for spring, July for summer, October for autumn and December for winter. Both animal sexes and both study areas are pooled together in this graph. Light grey bands display 95% confidence intervals. Please be aware of the different scales on the y axis.

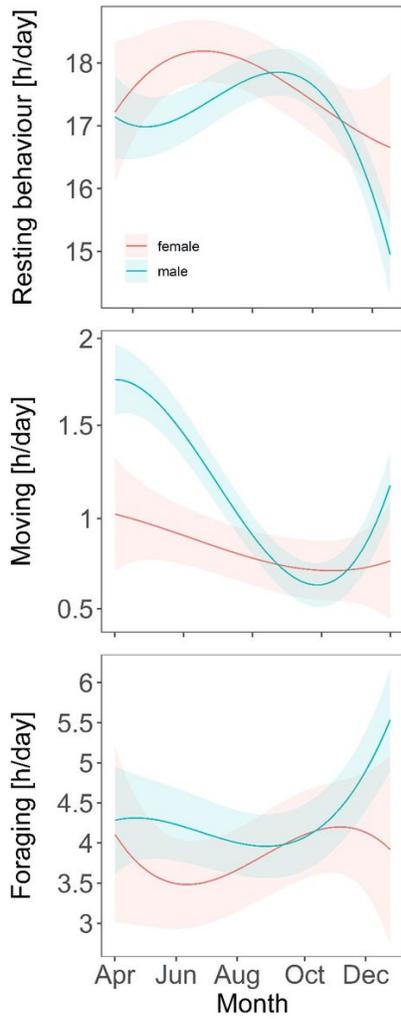


Figure 5

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.

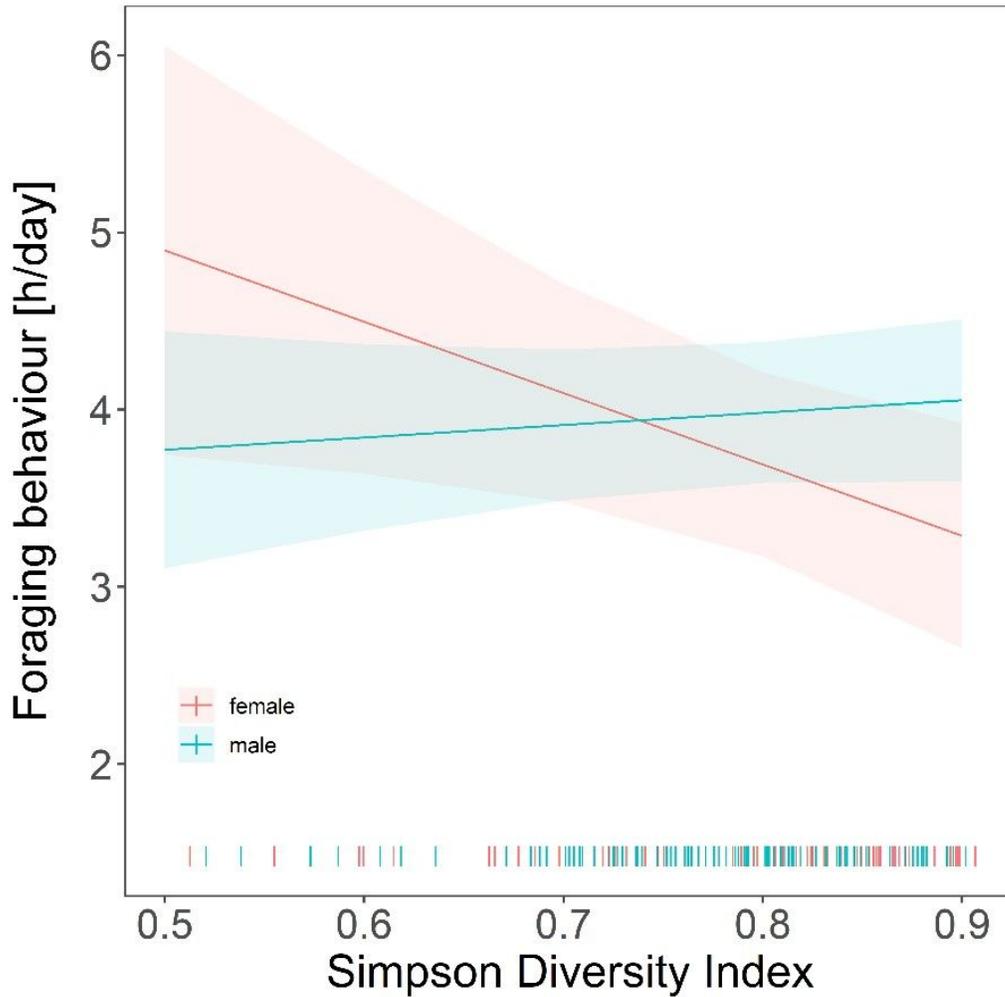


Figure 6
 The number of hours per day female and male hares spent foraging in relationship to habitat diversity displayed by the Simpson diversity index. The slope for male hares is shown in blue and for female hares in red. The respectively coloured shades correspond to 95% confidence intervals

Supplementary Files

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