

Home range use by the European hare (*Lepus europaeus*) in a structurally diverse agricultural landscape analysed at a fine temporal scale

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Abstract An animal's home range use is influenced by the landscape type. European hare (*Lepus europaeus*) home ranging behaviour has been studied only in agricultural areas with medium to large fields. In agricultural areas with small fields, European hares' locomotor behaviour is expected to be more localised. We tracked nine European hares by means of global positioning system (GPS) and very high-frequency (VHF) collars during summer in an agricultural area with small fields in Lower Austria. In particular, we analysed the hares' space use at a fine temporal scale, such as when they were active and resting within single 24-h periods. Furthermore, we compared data (day–day distances and day–night distances travelled) calculated from GPS and VHF telemetry. Home ranges were smaller, and the distances between areas used for activity and inactivity were shorter, in this agricultural area with small fields than has ever been measured in other agricultural areas with larger fields. Both active and inactive European hares expressed a preference for areas near field edges. Our findings suggest that with GPS, it is possible to distinguish between the movement path and the relative location of distinctly used areas within an animal's home range, whereas with VHF these two parameters may be difficult to separate. In conclusion, our results show that in areas where resources are easily accessible, such as in agricultural areas with small fields, the European hare is able to reduce its home range size to almost half of the minimum size that has been recorded so far in other habitats. As small home ranges involve less energy expenditure for movement, our results suggest that animals living in agro-ecosystems may benefit from small fields.

Keywords Brown hare · GPS · VHF · Field edge · Activity · Field size

Introduction

The European hare (*Lepus europaeus*), which originates from the grasslands of the Middle East, has spread out over the agricultural areas of Europe (Averianov et al. 2003). Today, the species inhabits a wide array of different habitats, from intensive arable land to extensively managed agricultural areas, which differ greatly in crop types, field size, landscape diversity and proportion of non-farmed habitat types (e.g. Frylestam 1979; Meriggi and Alieri 1989; Lewandowski and Nowakowski 1993; Marboutin and Aebischer 1996; Langbein et al. 1999). Nevertheless, the European hare has been in decline throughout Europe since the 1960s (e.g. Broekhuizen 1982; Pielowski 1990; Tapper 1992; Mitchell-Jones et al. 1999; Jenny and Zellweger-Fischer 2011). Use of space by European hares has been investigated through radio-telemetry (very high frequency, VHF) (cf. Broekhuizen and Maaskamp 1982; Tapper and Barnes 1986; Kovács and Búza 1988; Reitz and Léonard 1994; Pépin and Cargnelutti 1994; Marboutin and Aebischer 1996; Kunst et al. 2001; Stott 2003; Rühle and Hohmann 2004; Smith et al. 2004). VHS telemetry is time-consuming and the observer may influence the radio-collared animal, so researchers take fixes irregularly and with long intervals. Global positioning system (GPS) tracking, which allows to collect a large amount of data within a short time period, provides the opportunity to investigate an animal's home range use at fine temporal scales (Reid and Harrison 2010; Schai-Braun et al., submitted), and thus, the traditional home range can be examined dynamically (Cagnacci et al. 2010; Kie et al. 2010). To be able to compare information on European hares' home range use derived from GPS data with information from studies based on VHF data, it is therefore

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important to determine the differences between GPS-based and VHF-based calculations.

The home range size of the European hare has been measured in several countries and has been found to range between 21 and 330 ha depending on the landscape type (Pielowski 1972; Broekhuizen and Maaskamp 1982; Tapper and Barnes 1986; Kovács and Búza 1988; Reitz and Léonard 1994; Marboutin and Aebischer 1996; Kunst et al. 2001; Stott 2003; Rühle and Hohmann 2004; Smith et al. 2004). It has been suggested that there may be a positive relationship between home range size and field size in arable land, due to variation in the accessibility of resources, i.e. forage during active periods and shelter during resting periods (Tapper and Barnes 1986). Whether food and/or cover are limiting resources for European hares may vary between landscape types and seasons (Smith et al. 2004). The distances between daytime locations on two successive days (day–day distance, DDD) and between one daytime location and a location the night after (day–night distance, DND) are used to quantify hares' locomotor behaviour (Reitz and Léonard 1994; Rühle and Hohmann 2004). Areas used by European hares during periods of activity are generally in open landscapes with short vegetation (Tapper and Barnes 1986), whereas areas used during inactivity are in structured landscapes (Tapper and Barnes 1986; Neumann et al. 2011). Therefore, European hares' active and inactive locations are often not only temporally but also physically separated (Tapper and Barnes 1986), which makes DNDs especially informative. The distance between nocturnal and diurnal locations of European hares is 300 to 400 m during the hunting season (Reitz and Léonard 1994).

Up to now, differentiation between active and inactive periods from telemetry data has been difficult due to methodological limitations. Therefore, the times of sunrise and sunset are generally used to separate these two periods for the European hare (Marboutin and Aebischer 1996; Rühle and Hohmann 2004; Smith et al. 2004). But especially during summer, this species regularly has activity peaks in full daylight (Schai-Braun et al. 2012). For the analysis of the European hares' distinct home range use during activity and inactivity, it is therefore crucial to assess the animal's activity state at the time of location determination.

One study showed that in autumn and winter, in areas of monoculture, European hares prefer areas close to the field edge where vegetation diversity is generally higher. In contrast, they showed no significant preference for field edges in a farming area with small fields (Lewandowski and Nowakowski 1993). The importance of field edges for the European hare during summer is not known. As their habitat requirements during activity and inactivity differ, their use of field edges is expected to differ depending on their activity state.

For many years, calls for the management of arable land to support European hares and other species dwelling there have continued unabated (Vickery et al. 2002; Moreira et al. 2005;

Zellweger-Fischer et al. 2011). So far, all studies on European hares' home range size have been conducted in agricultural areas where mean field sizes range from 6 to 50 ha (Reitz and Léonard 1994; Marboutin and Aebischer 1996; Stott 2003; Rühle and Hohmann 2004; Smith et al. 2004). Landscape diversity is higher in agricultural areas with small fields than in those with medium to large fields, mainly because there are more non-farmed habitat types such as hedges, field edges and fallow land in areas with small fields (Benton et al. 2003). It has been shown that European hares prefer non-farmed features in agricultural areas (Tapper and Barnes 1986; Smith et al. 2004; Pépin and Angibault 2007; Vidus-Rosin et al. 2011; Cardarelli et al. 2011; Schai-Braun et al. 2013). Resource availability is therefore believed to be higher in agricultural areas with small fields, as hares can access a variety of crops and fields over a small area (Tapper and Barnes 1986). We predict that in this habitat, European hares may be able to reduce their movements, by having smaller home ranges and shorter distances between areas used for activity and inactivity. Testing this prediction might lead to suggestions regarding the conservation and management of the European hare and other species living in agroecosystems.

The general goal of this study was to investigate space use by European hares during summer in an agricultural area with small fields. In particular, we focussed not only on 24-h periods and on individual weeks but also on European hares' movement during active and inactive periods, by examining home ranges and distances between home range centres. Our hypotheses were: (1) European hares' home ranges are smaller, and the distances between areas used for activity and inactivity are shorter, in an agricultural area with small fields (our data) than in agricultural areas with large fields (data from the literature); (2) European hares prefer field edges in summer, and their use of field edges differs between active and inactive periods and (3) results from the analysis of space use differ, depending specifically on whether calculations are based on data derived from VHF or GPS. We tested these hypotheses by equipping European hares with GPS collars containing VHF transmitters and thus revealing their space use at a fine temporal scale.

Material and methods

Study area

The study was conducted in Lower Austria, in the Marchfeld near Zwerndorf (48°20'N, 16°50'E). The study area consisted of 270 ha of arable land, used mainly for growing cereals. The cultivated cereal types were, by area of land used for each, 38 % winter wheat (*Triticum aestivum*), 12 % summer barley (*Hordeum vulgare*), 4 % durum wheat (*Triticum durum*) and 1 % rye (*Secale cereale*). Other field crops were 11 % sugar beet

(*Beta vulgaris*), 5 % poppy (*Papaver somniferum*), 3 % sunflowers (*Helianthus annuus*) and 11 % legumes. Furthermore, the study area included 1 % forest, 1 % hedges/thickets, 4 % unimproved grassland, 1 % ditches, 3 % gravel pits, 1 % bare ground and 4 % rural development. The field size averaged 3.1 (± 0.3 SE) ha. The Pannonian climate is responsible for hot and dry summers in our study area. The accumulated precipitation per year is on average 524.7 l/m², and the daily mean temperature is on average 9.5 °C with a maximum of 37 °C and a minimum of -22.7 °C (Central Institute for Meteorology and Geodynamics, Austria 2013). Hare density in the study site was estimated each year in autumn by means of spotlight counts (Langbein et al. 1999); there were an estimated 35 European hares per 100 ha in 2009 (SSB & KH, unpublished).

Data collection

Nine adult European hares (four males, five females) were caught in unbaited box traps during the study period between May and September 2009. All animals were sexed according to secondary sexual characteristics and equipped with a 70-g GPS collar including a VHF transmitter (Telemetry Solutions, Quantum 4000 Enhanced). The collars were programmed to take one GPS fix per hour. The accuracy of the collars was tested beforehand; mean precision was 3.5 m (± 1.0 SE). Some animals could not be included in all analyses as the data quantity did not meet requirements, so variable sample sizes are indicated in the text and figure legends. To collect VHF data, each European hare was located once daily between sunrise and sunset by triangulation using a three-element Yagi antenna and a Regal 2000 receiver (Titely Electronics, Australia).

Data analysis

The positional data were mapped in ArcGIS 9.2 (ESRI). We included only locations with a solution in three-dimensional mode (Frair et al. 2010). The GPS data were allocated to active (1600–0659 hours) and inactive (0700–1559 hours) periods. We chose these two categories based on an analysis of the same data set to quantify European hares' daily activity patterns (see Schai-Braun et al. 2012). Hence, the inactive period included all hours in which there was a median distance of less than 10 m between subsequent hourly fixes. Only GPS data sets consisting of 24 fixes in sequence were used for the analyses of 24-h periods. Normal distribution of all variables was assessed by QQ-plots and histograms, and data were appropriately transformed based on the distribution of the data. DDDs, DNDs, hourly day–day distances, hourly day–night distances and MCP (minimum convex polygon) home ranges were transformed by natural logarithm, whereas kernel home ranges, differences between GPS and VHF DDDs, distances between two centres and distances to the nearest field edge were square-root transformed.

We analysed all data using multivariate (generalized) linear mixed-effects models, using the software R 2.12.2 (R Development Core Team 2011). Models were fitted using the package lme4 (Bates 2005). The *p* values and parameter estimates were extracted by Markov chain Monte Carlo sampling, based on 10,000 simulation runs (Baayen et al. 2008) using restricted maximum likelihoods. We checked for normality of the model residuals visually by examining normal probability plots and statistically by the Shapiro test. For all models, the homogeneity of variances and goodness of fit were examined by plotting residuals versus fitted values (Faraway 2006).

All models included hare identity as a random factor in order to allow for the repeated measurements collected from the different hares. Some models included paired testing (see Figs. 1 and 5; model description in “Home range size” and “Differences between DDDs and DNDs calculated from VHF and GPS data”). Therefore, these models contained an individual-specific code for the paired variable (“pairing”) as the second random factor. All other models included as the second random factor an individual-specific code for the day (“date”) or week (“week”), in order to account for the time series measured for each of the study animals during the different days and weeks of the study. When analysing the distance to the nearest field edge, an individual-specific code for each field (“field identity”) was included as the third random factor, in order to account for the particular field characteristics.

The effect of sex was tested in all models. Since there were never any significant effects of sex in our multivariate analyses ($p_{\text{MCMC}} > 0.10$), the factor sex was omitted from the models before re-calculation.

Home range size

The home range sizes were calculated by using the MCP and the fixed kernel estimators. The hourly fixes taken by the GPS collars provided 24 locations per hare per day. Therefore, only nine inactive and 15 active locations for each hare and day were available, so we chose to calculate the 100 % MCP (Harris et al. 1990). Kernel home ranges were calculated with the 95 % probability level (Worton 1989, 1995). An ad hoc smoothing parameter ($h_{\text{ad hoc}}$) prevented over- or under-smoothing. Thereby, the smallest increment of the reference bandwidth (h_{ref}) that results in one contiguous polygon without lacuna (i.e. $h_{\text{ad hoc}} = a \times h_{\text{ref}}$) is chosen (Berger and Gese 2007; Kie et al. 2010). As fixes were taken in hourly intervals, duplicate *X*, *Y*-coordinates occurred which pose computational problems in kernel analyses (Amstrup et al. 2004; Hemson et al. 2005). We jittered all duplicate locations by adding random noise (median = 1.02 m, SE = ± 0.03 m). Two animals were each recorded once outside the area they normally used. Since occasional outliers should not be considered to be part

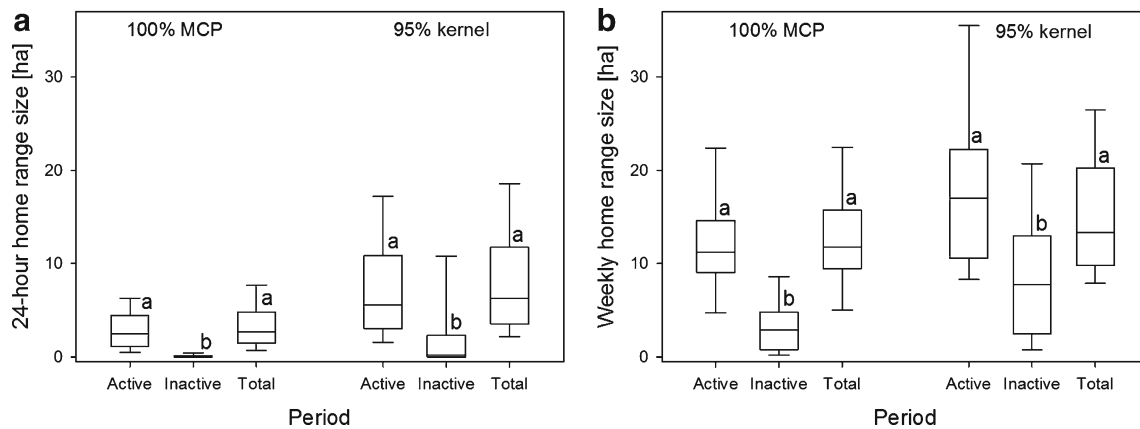


Fig. 1 European hares' **a** 24-h (nine collared hares) and **b** weekly (seven collared hares) home range sizes during active, inactive and total periods, calculated by using the minimum convex polygon and the fixed kernel

estimator (medians with 25th/75th and 10th/90th percentiles). *Different letters indicate significant differences between groups (post hoc: $p_{MCMC} < 0.01$).* See text for details of statistics

of the home range (Burt 1943), these two points were discarded. All home range analyses were performed using the R package *adehabitat* (Calenge 2006). In total, 103 24-h home ranges (MCP24hr, kernel24hr) for each active, inactive and total period were obtained using fixes from the nine collared individuals.

A similar method was used to calculate weekly home ranges, each based on a minimum of 101 fixes, i.e. 60 % of a complete week. In total, 22 weekly home ranges (MCP1wk, kernel1wk) for each active, inactive and total period were obtained using fixes from seven collared individuals.

We tested the effect of the period (covariate) on the response variable MCP24hr, kernel24hr, MCP1wk or kernel1wk. As the effect of the period was significant, we explored the differences in MCP24hr, kernel24hr, MCP1wk and kernel1wk between the active, inactive and total periods by means of post hoc tests (see Fig. 1). Additionally, we tested the effect of the time scale (covariate) on the response variable home range size (100 % MCP and 95 % kernel) for the active, inactive and total periods.

Distance between areas used during activity and inactivity

For every hare and day, the distances between the centres of pairs of successive active–active periods (AAD), inactive–inactive periods (IID) and active–inactive periods (AID) were calculated. The centres were determined by taking the median of all fixes of the first period as centre one and the median of all fixes of the second period as centre two. The distance between centres one and two was then measured. In total, 129 AAD, 90 IID and 107 AID were computed ($n=7$).

The effect of the period was tested on the response variable AAD, IID and AID. As the effect of the period was significant, we investigated the differences between AAD, IID and AID by means of post hoc tests (see Fig. 2).

Use of field edges

The distance to the nearest field edge was calculated for every position obtained from the nine collared hares. In each field which was used by hares, the same number of random points was created as there were hare positions. Subsequently, the distances between the random points and the nearest field edge were quantified.

The effect of the type of point (covariate, random point vs. hare position) was tested on the response variable distance to the nearest field edge (see Fig. 3a). As the effect of the type of point was significant, we explored the distances between hare positions and nearest field edges further. Therefore, the effect of activity (covariate, two levels) was tested on the hares' distances to the nearest field edge (see Fig. 3b).

Differences between VHF and GPS

How many fixes are needed before the distance a hare is estimated to move during 24 h reaches an asymptote? We conducted simulations to find out how many fixes are needed to estimate a hare's movement path within a consecutive day and night. DDDs (71, from six hares) were quantified from VHF data according to Reitz and Léonard (1994). For every VHF DDD, we also had a complete hourly GPS data set. The VHF DDD start and end points were used to calculate the GPS DDD. Between one and 34 additional fixes between the start and end points were randomly selected from the GPS data set. The intervals between the start and end points ranged between 11 and 35 h, so the number of DDDs available for analyses decreased after the number of additional fixes exceeded 10 (see the figures on the upper whiskers in Fig. 4). The random selection of additional points was repeated 100 times for every GPS DDD and for every number of additional fixes (1–34). The distances between the fixes were added up for every GPS

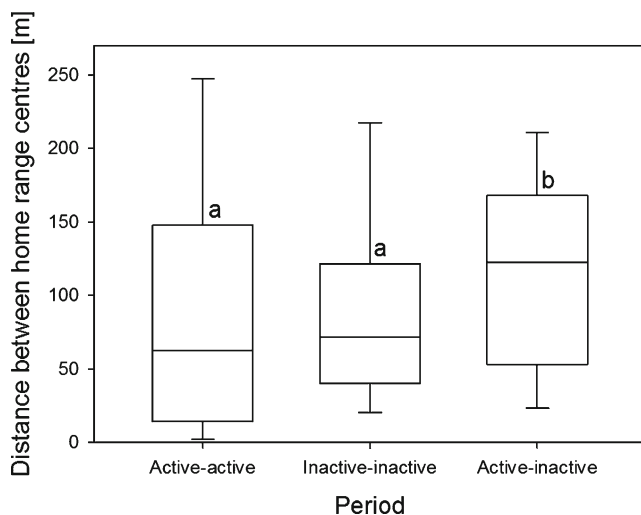
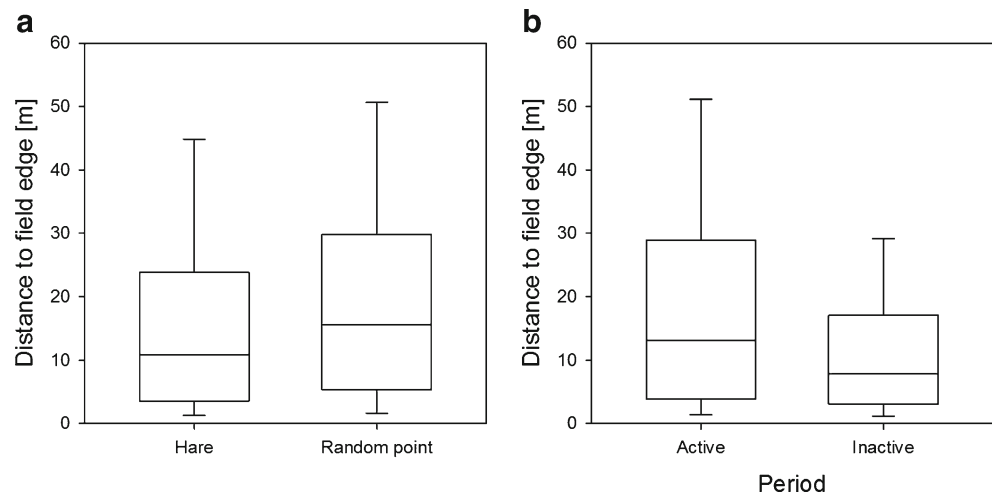


Fig. 2 Distances between the home range centres for two consecutive periods of European hares' activity or inactivity (seven collared hares; medians with 25th/75th and 10th/90th percentiles). Different letters indicate significant differences between groups (post hoc: $p_{\text{MCMC}} < 0.01$). See text for details of statistics

DDD. From the 100 simulations, the median was used to calculate the absolute difference between GPS and VHF DDD (see Fig. 4).

Differences between DDDs and DNDs calculated from VHF and GPS data We aimed to show that with our GPS data, we could simulate calculations from our VHF data. For 55 VHF DDDs calculated from two fixes from consecutive days, we had a complete GPS data set (48 fixes from the same consecutive days; $n=6$). For each of these 55 VHF DDDs, a corresponding GPS DDD was calculated by randomly choosing 100 start points (from the 24 fixes of the first day) and end points (from the 24 fixes of the second day). We then calculated the GPS DDD and selected the median.

Fig. 3 Distances to the field edge of **a** hare positions and random points and **b** hare positions during activity and inactivity (nine collared hares; medians with 25th/75th and 10th/90th percentiles). See text for details of statistics



The effect of the type of data (covariate, VHF vs. GPS) was tested on the response variable DDD. As the effect of the type of data was not significant ($\beta = -0.01$, $p_{\text{MCMC}} = 0.80$), we hereafter simulated VHF DDD and DND with the GPS data.

Hourly day–day distances (hDDD) and hourly day–night distances (hDND) represent the movement path between the start and end points of the DDD or DND connected by hourly GPS fixes. In total, 78 DDD or hDDD and 94 DND or hDND ($n=7$) were calculated. The effect of the calculation method (covariate) was tested on the response variables DDD and hDDD or DND and hDND (see Fig. 5).

Results

The mean number of satellites used for locating GPS fixes was $7 (\pm 0.03 \text{ SE})$. The overlap in individual periods of GPS tracking was on average 11 days ($\pm 9.2 \text{ SE}$; minimum 2, maximum 91 days). The number of GPS fixes taken per animal ranged from 25 to 2,127 with an average of 230 ($\pm 219.4 \text{ SE}$). This resulted in a total of 3,641 GPS fixes for analysis (746 for males, 2,895 for females). The duration of radio tracking for each hare ranged from 7 to 130 days with an average of 67 days ($\pm 13.6 \text{ SE}$). The number of VHF fixes taken per animal ranged from 7 to 134 with an average of 74 ($\pm 14.3 \text{ SE}$). This resulted in a total of 580 VHF fixes for analysis (240 for males, 340 for females).

Home range size

Influence of activity on home range size

The level of activity had an influence on the hares' home range sizes (see Table 1): The MCP24hr, kernel24hr, MCP1wk and kernel1wk for the inactive period differed significantly from those of the active or total period. The average

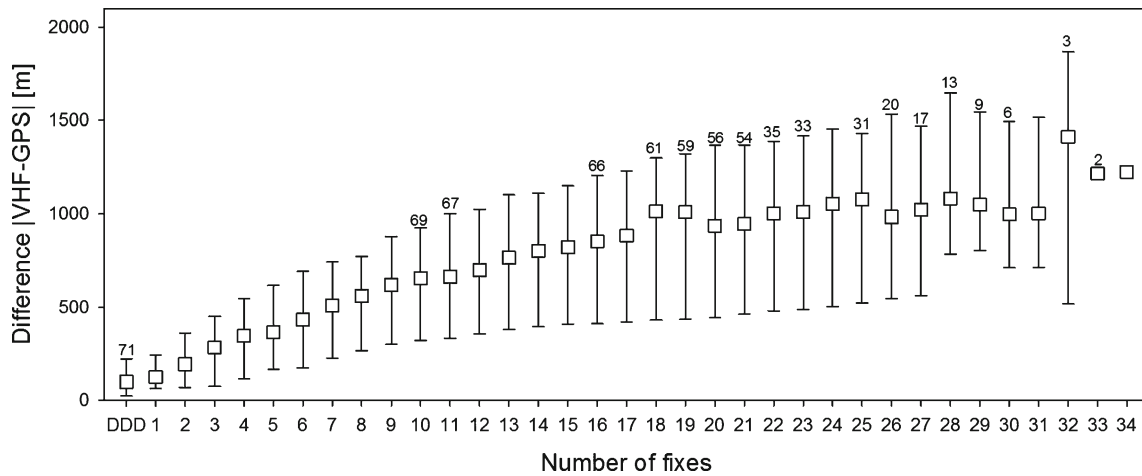


Fig. 4 Difference between DDDs of two VHF fixes and two GPS fixes taken at the same time, but with a different number of additional fixes taken randomly in between (six collared hares). Data (squares) are shown

as medians with 25th/75th percentiles; figures indicate the number of DDDs available for analyses. See text for details of statistics

MCP24hr was 97 times smaller during inactivity (median=0.03 ha, SE=±0.03) than during activity (median=2.48 ha, SE=±0.28; Fig. 1a), whereas the average kernel24hr was 24 times smaller during inactivity (median=0.23 ha, SE=±0.64) than during activity (median=5.55 ha, SE=±0.70).

The average MCP1wk was four times smaller during inactivity (median=2.88 ha, SE=±0.64) than during activity (median=11.23 ha, SE=±1.23) or total period (median=11.78 ha, SE=±1.22; Fig. 1b). On average kernel1wk was half the size during inactivity (median=7.79 ha, SE=±2.95) than during activity (median=16.99 ha, SE=±2.56) or total period (median=13.35 ha, SE=±1.66).

Comparison between 24-h and weekly home range size

The time scale (24 h vs. weekly) had an influence on the hares' home range sizes for the active (MCP: $\beta=1.80, p_{MCMC}<0.001$; kernel: $\beta=1.70, p_{MCMC}<0.001$), inactive (MCP: $\beta=4.21,$

$p_{MCMC}<0.001$; kernel: $\beta=1.70, p_{MCMC}<0.001$) and total periods (MCP: $\beta=1.58, p_{MCMC}<0.001$; kernel: $\beta=1.19, p_{MCMC}<0.001$), irrespective of the calculation method. A large difference between 24-h and weekly home range size was observed during the European hares' inactive period. The average MCP1wk was more than 100 times larger than the average MCP24hr. On average, kernel24hr during the inactive period was 34 times smaller than kernel1wk. Differences between 24-h and weekly home range sizes during the active or total time period were small. Weekly home ranges were on average between two and five times larger than 24-h home ranges, depending on the calculation method and period.

Distance between areas used during activity and inactivity

The level of activity had an influence on the distance between two home range centres (AID vs. AAD: $\beta=1.44, p_{MCMC}<0.01$; AAD vs. IID: $\beta=-0.41, p_{MCMC}>0.05$; AID vs. IID: $\beta=1.92,$

Fig. 5 a DDDs and **b** DNDs calculated for fixes taken daily and hourly (seven collared hares; medians with 25th/75th and 10th/90th percentiles). See text for details of statistics

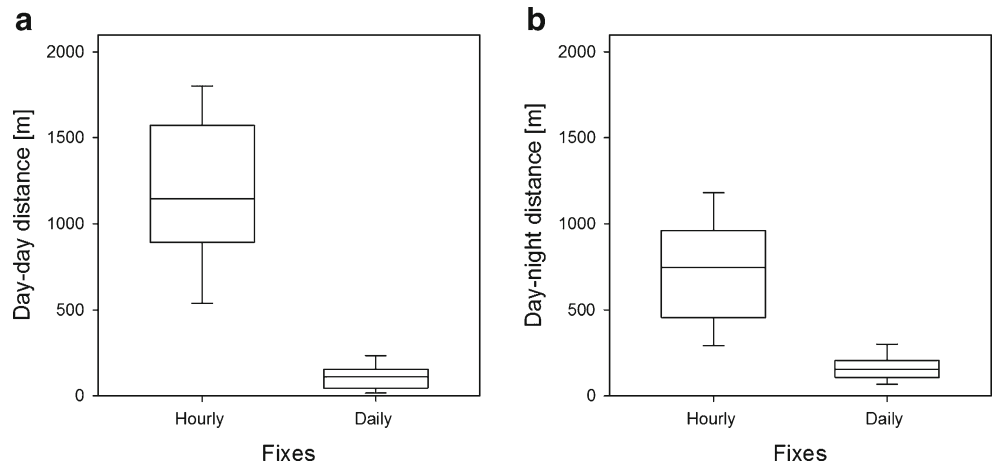


Table 1 Results of the post hoc tests exploring the differences in European hares' MCP24hr, kernel24hr, MCP1wk and kernel1wk home ranges between the active, resting and total periods

Response variables	Covariates	Estimate	<i>p</i>
MCP24hr	Active vs. inactive	-4.25	<0.001
	Active vs. total	0.30	<0.05
	Inactive vs. total	-4.55	<0.001
Kernel24hr	Active vs. inactive	-1.47	<0.001
	Active vs. total	0.16	0.27
	Inactive vs. total	-1.63	<0.001
MCP1wk	Active vs. inactive	-1.70	<0.001
	Active vs. total	0.04	0.69
	Inactive vs. total	-1.75	<0.001
Kernel1wk	Active vs. inactive	-1.38	<0.01
	Active vs. total	-0.30	0.31
	Inactive vs. total	-1.08	<0.01

$p_{\text{MCMC}} < 0.01$). The differences were greater between home ranges in different activity periods (AID: median=122.7 m, SE=±7.4) than between home ranges in the same activity period (AAD: median=62.5 m, SE=±10.7; IID: median=71.8 m, SE=±6.8; Fig. 2).

Use of field edges

Hares exhibited a preference for field edges ($\beta = 0.46$, $p_{\text{MCMC}} < 0.001$; Fig. 3a). The preference was stronger during inactivity than during activity ($\beta = -0.44$, $p_{\text{MCMC}} < 0.001$; Fig. 3b). Inactive hares were on average 7.8 m (SE=±0.5) away from the field edge, whereas during activity the distance between hares and field edges was on average 13.1 m (SE=±0.5).

Differences between VHF and GPS

How many fixes are needed before the distance a hare is estimated to move during 24 h reaches an asymptote?

Approximately 18 additional fixes were needed before the distance a hare had moved within daytime locations of two successive days reached an asymptote (Fig. 4). The hares were estimated to have moved approximately 1,000 m more than the estimation from the DDD based on two fixes.

Differences between DDDs and DNDs calculated from VHF and GPS data

The average times elapsed between DDD locations and DND locations were 23 h 52 min (SE=±3 min 59 s) and 11 h 57 min (SE=±3 min 7 s), respectively. There was a significant difference in DDD and DND in comparison to hDDD and hDND (day–day: $\beta = 2.56$, $p_{\text{MCMC}} < 0.001$; day–night: $\beta = 1.48$,

$p_{\text{MCMC}} < 0.001$). The hDDD (median=1,146.9 m, SE=±53.7) was ten times larger than the DDD (median=112.4, SE=±10.3; Fig. 5a), whereas the hDND (median=748.8 m, SE=±35.6) was five times larger than the DND (median=154.6, SE=±8.6; Fig. 5b).

Discussion

Our data support the first part of hypothesis 1: European hares' home ranges are smaller in an agricultural area with small fields (our data) than in agricultural areas with large fields (data from the literature; Table 2). The hares in our study area had extremely small 24-h home ranges during the inactive period. Forms used throughout the day were therefore situated in close proximity to one another. Home ranges during the inactive period were considerably bigger when analysed over a whole week. This suggests that hares changed the locations of the areas they used during inactivity frequently over the course of a week. The weekly active home range was two to four times larger than the inactive home range, suggesting that forms were not spread out over the whole home range. This is in agreement with results from other research on European hares (Marboutin and Aebischer 1996; Ruhe and Hohmann 2004; Smith et al. 2004). However, in our study, the difference between active and resting home range size was larger than in other studies (Table 2). Harris et al. (1990) showed that the calculation method affects home range size, by analysing a European hare's home range with different methods and receiving results between 28 and 153 ha. Although Marboutin and Aebischer (1996), Ruhe and Hohmann (2004) and Smith et al. (2004) used different calculation methods, the trend of increased size difference between active and inactive home ranges in agricultural areas with small fields is discernible. In our results, there was no significant difference between home range size during the active and total periods because the inactive home ranges were very small. Over 24 h, European hares used between 25 and 50 % of their weekly home range, depending on the calculation method. The home ranges of our study animals were distinctly smaller than those recorded in other studies of European hares, independent of the calculation method (Table 2). Our weekly home ranges were calculated over a relatively short time frame. Nevertheless, this does not fully explain the small size of the home ranges recorded in our study area. In another study, observation period and home range size were unrelated, indicating that a large part of the home range was used by the hares within a short time period (Broekhuizen and Maaskamp 1982). The differences between our results and those of other researchers may be related to tracking methods, as VHF telemetry provides less accurate positional data than GPS telemetry (Hebblewhite and Haydon 2010). Nonetheless, inaccuracy does not necessarily result in

Table 2 European hares' home range size in agricultural areas with different average field sizes

Author(s)	Year	Sample size	Mean home range size (ha)	Active/inactive home range size	Average field size (ha)	Hare density (hare/100 ha)	Proportion of non-farmed habitat types	Time period	Method
This study		9	12	2–4	3.1	35	10 %	May–Sep	100 % MCP
Rühe and Hohmann	2004	38	21	1.7	6.5	–	1 %	All year	95 % MCP
Smith et al.	2004	42	29	1.9*	6.6	16	6 %	All year	100 % MCP (*95 % kernel)
Broekhuizen and Maaskamp	1982	13	29	–	–	–	–	All year	100 % MCP
Tapper and Barnes	1986	15	38	–	18	64	6 %	All year	90 % isopleth
Reitz and Léonard	1994	21	113	–	10	15	–	Jul–Dec	100 % MCP
Stott	2003	6	133	–	50	–	13 %	Oct–Apr	100 % MCP
Marboutin and Aebischer	1996	20	138	1.5	20	153	11 %	May–Sep	95 % MCP

enlarged home range size estimations. After body mass is taken into account, residual variation in home range size in leporids can be explained by species' ecology and the surrounding environment (Swihart 1986). The small home ranges found in our study area with small fields are in agreement with the findings of other researchers, who report that in agricultural areas with large fields, European hares mostly enlarge their home ranges in order to include the required habitat types (Marboutin and Aebischer 1996; Reitz and Léonard 1994; Stott 2003; Rühe and Hohmann 2004; Smith et al. 2004; Table 2). The results of Tapper and Barnes (1986) do not support this assumption, but their home ranges were calculated by the isopleths method which provides much smaller (<50 %) home ranges than the MCP method. In contrast, hare density and the proportion of non-farmed habitat types do not seem to affect the home range size (Table 2). We therefore suggest that in agricultural areas with small fields, European hares can reduce their home range size as long as accessibility to resources is high and the animals can fulfil their daily requirements.

The European Union's agricultural policy focusses on a considerable increase in agricultural food production and includes the aim to uphold global contestability (European Commission 2010). This will lead to larger fields in Europe. But authorities should mitigate this by encouraging farmers to increase the proportion of fallow land and/or numbers of strips of unused land within large fields, in order to conserve biodiversity in agricultural landscapes (Berger et al. 2003) and improve the suitability of the habitat for the European hare (Vaughan et al. 2003; Smith et al. 2004). The proportion of land left fallow or unused as linear structures needs to be high enough. Otherwise, a number of species may be concentrated in small isolated areas of non-farmed habitat. In consequence, predators may search these areas systematically, and areas of fallow land may act as ecological pitfalls for prey species such as the European hare (Bro et al. 2004).

The significantly larger distances moved by the hares between home ranges of different activity periods than between home ranges of the same period suggest that, firstly, home ranges used during activity are separate and distinct from those used during inactivity, and secondly, home ranges used during inactivity were located right beside or on the margin of home ranges used during activity. The areas used by hares during the active and inactive periods were on average only 122.7 m apart, which is less than half of the distance measured in intensive arable land with an average field size of 10 ha (DND=306 m; Reitz and Léonard 1994) and around half of the distance measured in arable land with an average field size of 6.5 ha (DND=226 m; Rühe and Hohmann 2004). Hence, our data are in agreement with the second part of hypothesis 1 that the distances between areas used for activity and inactivity by European hares are shorter in an agricultural area with small fields (our data) than in agricultural areas with large fields (data from the literature). When we compared our results from VHF data (DND=154.6 m) with those from other hare studies, we reached the same conclusion. We suggest that in agricultural areas with small fields, the areas used by active and inactive European hares are closer together than in agricultural areas with larger fields, as the habitat offers more opportunities for hares to satisfy their various needs within smaller areas.

Though field size is clearly important, the structure and density of European hare populations can also be affected by factors other than field size, such as habitat composition, landscape structure, types of crops, amount of spontaneous vegetation, open land and forest ratio, weather and climate (Averianov et al. 2003). Therefore, field size can only explain part of the observed behaviour. Another factor is the season. Our study is limited to summer; the behaviour of hares in other seasons may be different (Averianov et al. 2003).

We hypothesised that European hares in an agricultural area with small fields prefer areas near field edges during summer

and that their use of field edges differs between active and inactive periods (hypothesis 2). Our hares were observed close to field edges, during both inactive and active periods. During summer when vegetation is high and dense, cover for inactive hares seems to be abundant. In pastoral landscapes, heterogeneity at the within-habitat scale was found to be more important to European hares than heterogeneity at the between-habitat scale (Smith et al. 2004). We assume that heterogeneity at the within-habitat scale is also highly important in agricultural areas with small fields, which normally have a high level of habitat diversity. In summer, inactive hares may find more suitable cover near field edges where vegetation diversity is generally higher than away from edges. Since hares prefer to feed on weeds in summer (Reichlin et al. 2006), areas near field edges may provide additional food and may be attractive to active hares. We found that hares' mean distances to field edges during activity and inactivity differed by only 5 m, which is a small distance for this species. Nevertheless, when looking at the distribution of the animals, inactive hares used areas close to field edges more extensively than active hares. Therefore, European hares use the areas close to field edges differently depending on their activity state.

Finally, we focussed on methodological issues in space use analysis, by comparing home range calculations derived from VHF and GPS data (hypothesis 3). In general, less than one fix per hour was enough to estimate a hare's movement path within a consecutive day and night. In another study of European hares with a study area similar to ours, the mean distance travelled over 24 h by the animals was 3,910 m, over three times greater than in our study (Pépin and Cargnelutti 1994). However, the study was conducted during late winter, and hares were located three times per hour during the day and six times per hour during the night. The hares studied in February and March were more active either because reproductive activity was higher than during summer (Raczynski 1964) or because the much higher frequency of taking fixes led to an increased movement path.

Traditional DDDs overestimated the distance between two areas used consecutively for activity by 80 %, and the hares' movement path for this time period was estimated to be around ten times longer (AAD=62.5 m; DDD=112.4 m; hDDD=1,146.9 m). DNDs overestimated the distance between the hares' areas used during activity and inactivity by 26 %, and the hares' movement path for this time period was estimated to be around five times longer (AID=122.7 m; DND=154.6 m; hDND=748.8 m). Thus, traditional DDD and DND overestimated the distance between areas used and underestimated hares' movement paths, within the home range. The over- or underestimation was greater during the hares' active phase. With the large numbers of fixes provided by GPS tracking, it is possible to distinguish between the movement path and the location of distinctly used areas within an animal's home range, whereas with VHF tracking, these two parameters may be difficult to separate. It is

therefore advisable to draw conclusions based on comparisons between VHF and GPS data with caution.

Conclusion

In summary, we found that in our agricultural area with small fields, European hares' home ranges were smaller, and the distances between areas they used for activity and for inactivity were shorter, than ever recorded before in agricultural areas with larger fields. Moreover, European hares expressed a preference for areas near field edges while they were active and inactive during summer. We compared the VHF and GPS methods of telemetry and showed that with GPS data it is possible to distinguish between the movement path and the relative location of distinctly used areas within an animal's home range. Comparisons between results based on VHF data and GPS data should therefore be made with caution. As small home ranges involve less energy expenditure for movement, our results suggest that animals living in agro-ecosystems may benefit from small fields.

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References

- Amstrup SC, McDonald TL, Durner GM (2004) Using satellite radiotelemetry data to delineate and manage wildlife populations. *Wildl Soc Bull* 32:661–679
- Averianov A, Niethammer J, Pegel M (2003) *Lepus europaeus* Pallas, 1778—Feldhase. In: Niethammer J, Krapp F (eds) *Handbuch der Säugetiere Europas, Band 3/II Hasentiere*. AULA, Wiesbaden, pp 35–104
- Baayen RH, Davidson DJ, Bates DM (2008) Mixed-effects modeling with crossed random effects for subjects and items. *J Mem Lang* 59:390–412
- Bates DM (2005) Fitting linear mixed models in R. *R News* 5:27–39
- Benton TG, Vickery JA, Wilson JD (2003) Farmland biodiversity: is habitat heterogeneity the key? *Trends Ecol Evol* 18:182–188
- Berger G, Pfeffer H, Kächele H, Andreas S, Hoffmann J (2003) Nature protection in agricultural landscapes by setting aside unproductive areas and ecotones within arable fields ("Infield Nature Protection Spots"). *J Nat Conserv* 113:221–233
- Berger KM, Gese EM (2007) Does interference competition with wolves limit the distribution and abundance of coyotes? *J Anim Ecol* 76:1075–1085
- Bro E, Mayot P, Corda E, Reitz F (2004) Impact of habitat management on grey partridge populations: assessing wildlife cover using a multisite BACI experiment. *J Appl Ecol* 41:846–857
- Broekhuizen S (1982) Studies on the population ecology of hares in the Netherlands. Annual report 1981 of the Research Institute for Nature Management, Arnhem, Netherlands

- Broekhuizen S, Maaskamp F (1982) Movement, home range and clustering in the European hare (*Lepus europaeus*) in the Netherlands. *Z Säugetierkd* 47:22–32
- Burt WH (1943) Territoriality and home range concepts as applied to mammals. *J Mammal* 24:346–352
- Cagnacci F, Boitani L, Powell RA, Boyce MS (2010) Animal ecology meets GPS-based radiotelemetry: a perfect storm of opportunities and challenges. *Philos Trans R Soc B* 365:2157–2162
- Calenge C (2006) The package adehabitat for the R software: a tool for the analysis of space and habitat use by animals. *Ecol Model* 197:516–519
- Cardarelli E, Meriggi A, Brangi A, Vidus-Rosin A (2011) Effects of arboriculture stands on European hare *Lepus europaeus*. *Acta Theriol* 56:229–238
- Central Institute for Meteorology and Geodynamics, Vienna, Austria (2013) www.zamg.ac.at. Accessed 25 July 2013
- European Commission (2010) Commission communication on the CAP towards 2020. Meeting the food, natural resources and territorial challenges of the future, Brussels, Belgium. <http://ec.europa.eu/agriculture>
- Faraway JJ (2006) Extending the linear model with R. Texts in statistical science. Chapman and Hall/CRC, Boca Raton
- Frair JL, Fieberg J, Hebblewhite M, Cagnacci F, Decesare NJ, Pedrotti L (2010) Resolving issues of imprecise and habitat-biased locations in ecological analyses using GPS telemetry data. *Philos Trans R Soc B* 365:2187–2200
- Frylestam B (1979) Structure, size and dynamics of three European hare populations in Southern Sweden. *Acta Theriol* 24:449–464
- Harris S, Cresswell WJ, Forde PG, Trehwella WJ, Woollard T, Wray S (1990) Home-range analysis using radio-tracking data—a review of problems and techniques particularly as applied to the study of mammals. *Mamm Rev* 20:97–123
- Hebblewhite M, Haydon DT (2010) Distinguishing technology from biology: a critical review of the use of GPS telemetry data in ecology. *Philos Trans R Soc B* 365:2303–2312
- Hemson G, Johnson P, South A, Kenwards R, Ripley R, MacDonald D (2005) Are kernels the mustard? Data from global positioning system (GPS) collars suggest problems for kernel home-range analyses with least-square cross-validation. *J Anim Ecol* 74:455–463
- Jenny M, Zellweger-Fischer J (2011) 20 Jahre Feldhasenmonitoring in der Schweiz.—Wildtiermonitoring I, 18–21
- Kie JG, Matthiopoulos J, Fieberg J, Powell RA, Cagnacci F, Mitchell MS, Gaillard J-M, Moorcroft PR (2010) The home-range concept: are traditional estimators still relevant with modern telemetry technology? *Philos Trans R Soc B* 365:2221–2231
- Kovács G, Búza C (1988) Characteristics of the home range of the brown hare (*Lepus europaeus* PALLAS) in a forested and in a large-scale cultivated agricultural habitat. *Vadbiológia* 2:67–84
- Kunst PJG, van der Wal R, van Wieren S (2001) Home ranges of brown hares in a natural salt marsh: comparisons with agricultural systems. *Acta Theriol* 46:287–294
- Langbein J, Hutchings MR, Harris S, Stoate C, Tapper SC, Wray S (1999) Techniques for assessing the abundance of brown hares *Lepus europaeus*. *Mamm Rev* 29:93–116
- Lewandowski K, Nowakowski JJ (1993) Spatial distribution of brown hare *Lepus europaeus* populations in habitats of various types of agriculture. *Acta Theriol* 38:435–442
- Marboutin E, Aebischer NJ (1996) Does harvesting arable crops influence the behaviour of the European hare *Lepus europaeus*? *Wildl Biol* 2:83–91
- Meriggi A, Alieri R (1989) Factors affecting brown hare density in northern Italy. *Ethol Ecol Evol* 1:255–264
- Mitchell-Jones A, Amori G, Bogdanowicz W, Krystufek B, Reijnders P, Spitzenberger F, Stubbe M, Thissen JBM, Vohralik V, Zima J (1999) The atlas of European mammals. Poyser, London
- Moreira F, Beja P, Morgado R, Reino L, Gordinho L, Delgado A, Borralho R (2005) Effects of field management and landscape context on grassland wintering birds in Southern Portugal. *Agric Ecosyst Environ* 109:1–2:59–74
- Neumann F, Schai-Braun S, Weber D, Amrhein V (2011) European hares select resting places for providing cover. *Hystrix* 22:291–299
- Pépin D, Angibault JM (2007) Selection of resting sites by the European hare as related to habitat characteristics during agricultural changes. *Eur J Wildl Res* 53:183–189
- Pépin D, Cargnelutti B (1994) Individual variations of daily activity patterns in radiotracked European hares during winter. *Acta Theriol* 39:399–409
- Pielowski Z (1972) Home range and degree of residence of the European hare. *Acta Theriol* 17:93–103
- Pielowski Z (1990) Über die Abhängigkeit der Besatzdichte und anderer Populationsparameter des Hasen von der Agrarstruktur und landwirtschaftlichen Aktivitäten. *Beiträge zur Jagd- und Wildforschung* 17:147–156
- R Development Core Team (2011) R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna. www.R-project.org
- Raczynski J (1964) Studies on the European hare. V. Reproduction. *Acta Theriol* 9:305–352
- 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
- Reid N, Harrison A (2010) Post-release GPS tracking of hand-reared Irish hare *Lepus timidus hibernicus* leverets, Slemish, Co. Antrim, Northern Ireland. *Conserv Evid* 7:32–38
- Reitz F, Léonard Y (1994) Characteristics of European hare *Lepus europaeus* use of space in a French agricultural region of intensive farming. *Acta Theriol* 39:143–157
- 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
- Schai-Braun S, Rödel H, Hackländer K (2012) The influence of daylight regime on diurnal locomotor activity patterns of the European hare (*Lepus europaeus*) during summer. *Mamm Biol* 77:434–440
- Schai-Braun S, Weber D, Hackländer K (2013) Spring and autumn habitat preferences of active European hares (*Lepus europaeus*) in an agricultural area with low hare density. *Eur J Wildl Res* 59:387–397
- 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
- Stott P (2003) Use of space by sympatric European hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus*) in Australia. *Mamm Biol* 68:317–327
- Swihart RK (1986) Home range—body mass allometry in rabbits and hares (Leporidae). *Acta Theriol* 31:139–148
- Tapper SC, Barnes RFW (1986) Influence of farming practice on the ecology of the brown hare (*Lepus europaeus*). *J Appl Ecol* 23:39–52
- Tapper SC (1992) Game heritage. An ecological review from shooting and gamekeeping records. Game Conservancy, Hampshire
- Vaughan N, Lucas E-A, Harris S, White PCL (2003) Habitat associations of European hares *Lepus europaeus* in England and Wales: implications for farmland management. *J Appl Ecol* 40:163–175
- Vickery J, Carter N, Fuller R (2002) The potential value of managed cereal field margins as foraging habitats for farmland birds in the UK. *Agric Ecosyst Environ* 89:41–52
- Vidus-Rosin A, Meriggi A, Cardarelli E, Serrano-Perez S, Mariani M-C, Corradelli C, Barba A (2011) Habitat overlap between

- sympatric European hares (*Lepus europaeus*) and eastern cottontails (*Sylvilagus floridanus*) in northern Italy. *Acta Theriol* 56:53–61
- Worton BJ (1989) Kernel methods for estimating the utilization distribution in home-range studies. *Ecology* 70:164–168
- Worton BJ (1995) Using Monte Carlo simulation to evaluate kernel-based home range estimators. *J Wildl Manage* 59:794–800
- Zellweger-Fischer J, Kéry M, Pasinelli G (2011) Population trends of brown hares in Switzerland: the role of land-use and ecological compensation areas. *Biol Conserv* 144:1364–1373