Daily activity pattern, space use and habitat preferences of the European hare (*Lepus europaeus*)

A Doctoral Thesis presented to the
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(Photo: Stéphanie Schai-Braun)

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Preface

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Introduction and overview

A. Background

Originally the European hare (*Lepus europaeus*) comes from the savannas of Eurasia. From there, the species has spread out over the agriculture areas of Europe (Averianov, 2003). Long-since the European hare belongs to the appearance of our cultural landscape. A range of mentions in poetries, ballads and proverbs give evidence of its importance in our culture. Hunters appreciate the animal as a considerable game species. Due to its high reproduction rate, the European hare withstood for a long time the changes in its habitat. However, it seems as if the species has been brought on the edge of its adaptation capacity. Over recent decades a general decline in hare densities – indicated on the basis of hunting bag statistics – all over Europe has been recorded, also in Switzerland and Austria (Fig. 1). Hence, the European hare is classified as threatened (CH) and near threatened (A) on the Red List (Duelli, 1994; Spitzenberger *et al.*, 2005).

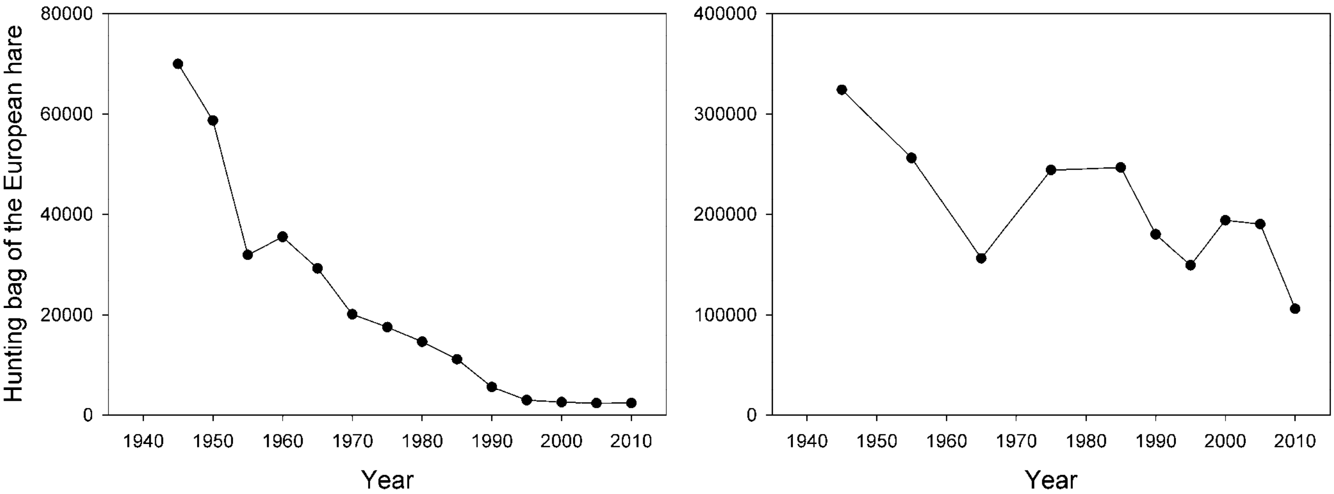

Figure 1: Hunting bags of the European hare have been decreasing both in Switzerland (left) and Austria (right). (Sources: Bundesamt für Umwelt BAFU & Statistik Austria)

B. Cause(s) for the decline of European hares

The decreasing hare density has been investigated by numerous scientists in Europe. In the process, many conclusive theories about the reasons for the population decline have been formulated and measures have been deduced to increase hare abundances (cf Tapper & Barnes, 1986; Pépin, 1989; Slamečka *et al.*, 1997;

Vaughan *et al.*, 2003; Rühe & Hohmann, 2004; Schmidt *et al.*, 2004; Smith *et al.*, 2004; Smith *et al.*, 2005b; Panek *et al.*, 2006; Báldi & Faragó, 2007; Karmiris & Nastis, 2007). Overall, there is a large degree of agreement that the living conditions for European hares have worsened in modern cultivated agriculture areas. Finally, a meta-analysis of the European hare literature revealed as main cause for the population decline habitat changes caused by agricultural intensification (Smith *et al.,* 2005a). It seems as if climate changes and alterations in the number of predators are reinforced in their impact by the loss of cover and food due to agricultural intensification (Smith *et al.,* 2005a).

C. How does the agricultural intensification affect the European hares?

The agricultural intensification changed both the agrarian landscape and its processing in Europe. As an example, the number of agricultural labourers in Austria decreased by a third from 21.0 to 6.4 persons per 100 ha during the 20th century, whereas the number of machinery increased more than a tenfold from 0.4 to 4.4 tractors per 100 ha (Österreichisches Statistisches Zentralamt, 1954; Dötzl, 2006; Dötzl, 2008). This agricultural mechanisation led to the still ongoing tendency of larger field sizes and faster processing. Firstly, there seems to be a positive relationship between European hares' home-range size and field size (Tapper, 1986). Secondly, a fast processing changes the wildlife's habitat dramatically within short time. Both aggravate the accessibility of resources, and a possible consequence for the European hare might be an increase in energy expenditure. Apart from that, the agricultural intensification reduced landscape diversity due to the loss of unfarmed habitat types such as hedges, field margins and fallow land. This is crucial as it has been widely shown that European hares prefer especially unfarmed habitat types (Tapper & Barnes, 1986; Smith *et al.,* 2004; Pépin & Angibault, 2007; Vidus-Rosin *et al.,* 2011; Cardarelli *et al.,* 2011). Unfarmed habitat types are, on the one hand, rich in structure and provide shelter for resting hares (Tapper & Barnes, 1986). On the other hand, they offer high plant diversity including weeds and are therefore attractive for active European hares as foraging areas (Reichlin *et al.*, 2006).

D. Actual state of the European hare research

European hares' locomotor behaviour has been investigated widely by radio-telemetry and visual observation (cf Pielowski, 1972; Broekhuizen & Maaskamp, 1982; Parkes, 1984; Tapper & Barnes, 1986; Kovács & és Búza, 1988; Reitz & Léonard, 1994; Pépin & Cargnelutti, 1994; Marboutin & Aebischer, 1996; Kunst *et al.,* 2001; Stott, 2003; Rühe & Hohmann, 2004; Smith, 2004). Because these two methods are likely to disturb the animals, data in most studies on European hares' space use were collected with large intervals and hence the results focused on large time periods. Accordingly, effects of short-time incidents such as cereal harvest on this species are poorly documented. Only one study investigated the effect of harvest on the European hares' space use and recorded no negative impact (Marboutin & Aebischer, 1996). Since the above mentioned two methods are also impaired by high vegetation, the species' locomotor activity pattern is only recorded for the plants' dormant season. During this time, the nocturnal animals' start and cessation of activity matches the light-dark-cycle created by the sun (Homolka, 1986; Pépin & Cargnelutti, 1994; Holley, 2001). GPS-tracking, which is now available for mammals of smaller sizes, provides the opportunity to investigate an animal's space use at fine temporal scales. This allows, firstly, a more dynamic view of the home-range concept (Kie *et al.*, 2010) along with the possibility to concentrate on short-time events and, secondly, predications about the European hares' locomotor activity pattern during summer.

Several European hare studies have investigated habitat selection. However, all studies on habitat selection have been conducted in areas where European hare densities are between medium and high as densities range between 15 to 74 animals per 100 ha (Pielowski, 1966; Jezierski, 1968; Pépin, 1986; Tapper & Barnes, 1986; Marboutin & Aebischer, 1996; Smith *et al.*, 2004; Smith *et al.*, 2005b; Pépin & Angibault, 2007; Vidus-Rosin *et al.*, 2009; Ferretti *et al.*, 2010; Cardarelli *et al.*, 2011; Bertolino *et al.*, 2011; Vidus-Rosin *et al.*, 2011). The possibility to find habitat preferences is limited at high densities as all available habitats are occupied (Frylestam, 1979) due to intraspecific competition for resources and the use of unpreferred habitats by subordinate individuals. Therefore, European hares' habitat preference or avoidance in areas with high densities may differ from those in areas with low densities. A study in a landscape with low European hare density offers the chance to scrutinise the species' true habitat selection.

E. Contents of the doctoral thesis

To increase the European hares' living conditions, fundamental aspects of this species' ecology have to be known. Within this doctoral thesis, four different topics of European hare ecology were studied which are presented in the following four chapters. All four chapters are linked by their methodology to draw conclusions about the European hares' ecology by analysing the animals' whereabouts within the habitat.

Chapter 1: The influence of daylight regime on diurnal locomotor activity patterns of the European hare (Lepus europaeus) during summer

During summer, agricultural landscapes are rapidly changing because of the growing crops and ongoing agricultural activities. Investigating the European hares' locomotion behaviour during the vegetation season may provide indications how agricultural intensification influences the European hare population decline. The horal GPS-locations of the nine European hares gave valuable insights into the hares' locomotion behaviour (Fig. 2).

Figure 2: One of the nine European hares equipped with a GPS-collar. (Photos: Stéphanie Schai-Braun)

Not only did the hares show a time of reduced activity during their nocturnal activity, but also was the start and cessation of activity influenced by sunrise and sunset in a seasonally varying manner. When the number of daily night hours was small, the hares showed activity peaks in full daylight, whereas when the number of daily night hours was large the hares had their time of maximal activity during the dark phase. Both results imply that the hares' activity pattern is much more complex than results of previous studies have indicated.

Chapter 2: The influence of cereal harvest on the home-range use of the European hare (Lepus europaeus)

A consequence of the agricultural intensification is a reduction in arable crop diversity resulting in agricultural landscapes where one field crop is predominantly cultivated. We studied the European hares' space use in an area consisting of more than 50% cereals (Fig. 3).

Figure 3: The Austrian study area consists predominantly of cereal fields (left) and is located in Lower Austria (right). (Photo and figure: Stéphanie Schai-Braun)

After harvesting, home-range size of active animals increased significantly. The effect was best observable on a small time scale, i.e. over a period of 24 hours. Although harvesting is an incident which changes the animals' habitat in a sudden and holistic way, it seems nevertheless to have only an influence on certain closely circumscribed behaviour patterns and on a small time scale. This makes the effect difficult to detect, but does not preclude that it might be crucial for the species' well-being in a negative way.

Chapter 3: Spring and autumn habitat preferences of active European hares (Lepus europaeus) in an agricultural area with low hare density

Considering the European Union's agricultural policy (European Commission, 2010), the ongoing agricultural intensification in Europe will continue in the next decades. Habitat preferences reveal which habitat types have a special value for the species and might therefore be decisive to enhance the quality of an agricultural landscape. We studied European hares' habitat selection in an agricultural area with low hare density, high landscape diversity and small field sizes (Fig. 4). This ensured that the study animals had a free choice, i.e. true selection was possible. The analysis revealed that it was most important to differentiate the habitat types according to their vegetation structure. By pooling habitat types into larger groups, the validity of the preference index diminished severely. Furthermore, our results showed that most habitat types were preferred or avoided corresponding to the availability of food or visibility which are highly important to European hares during activity.

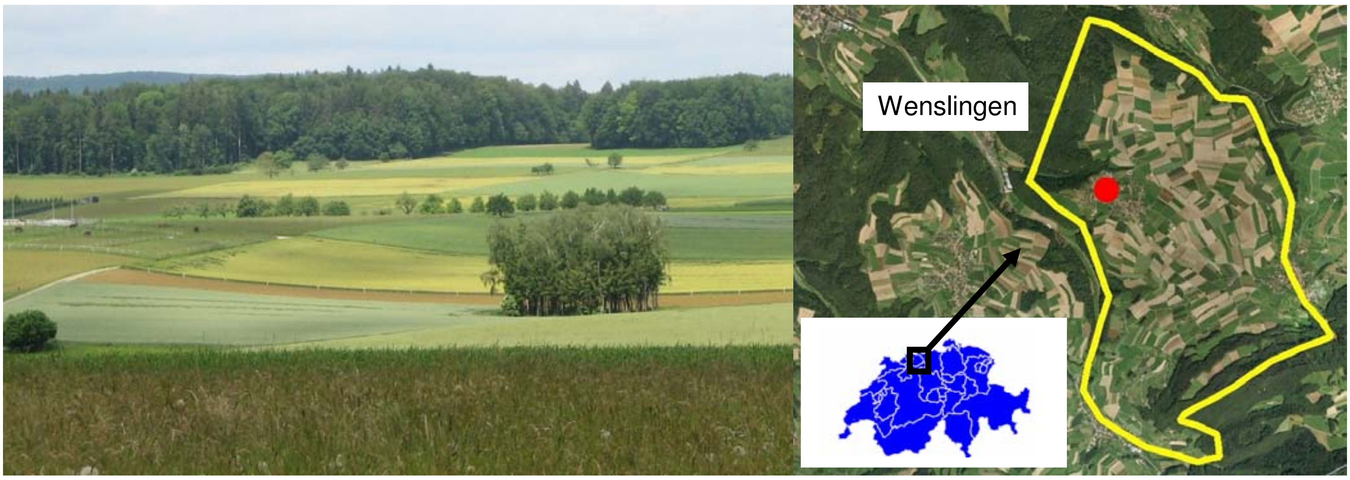

Figure 4: The Swiss study area is an agricultural area with low hare density, high landscape diversity and small field sizes (left) located in Northern Switzerland (right). (Photo and figure: Stéphanie Schai-Braun)

Chapter 4: European hares select resting places for providing cover

During the day, European hares' primary resting time, the animals are known to use structured habitat providing cover (Tapper & Barnes, 1986). A consequence of the agricultural intensification is a reduction of agricultural unexploited habitat types such as hedges, edges or fallow land which offer a rich variety of structure. This loss might result in a shortage of required habitat types for the hares' resting period and be a reason of the European hares' impaired living conditions. Our intention was to clarify the importance of vegetation characteristics for the resting hares. We could show that the vegetation at European hares' resting places offered shelter to the animals. In addition, hares resting in sparse vegetation fled further away than animals lying in dense vegetation when disturbed. The results indicate that not only structured habitat types but also small patches of vegetation structure are important for European hares for offering cover during the day.

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First Chapter

The influence of daylight regime on diurnal locomotor activity patterns of the European hare (*Lepus europaeus*) during summer

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Photo: Stéphanie Schai-Braun

Abstract

Knowledge on diurnal locomotor activity pattern in wild nocturnal medium-sized mammals, such as the European hare (*Lepus europaeus*) is scarce. In this study, we tracked nine European hares during the vegetation period using GPS-transmitters. In particular, we focused on the question how the timing of sunset and sunrise influences the activity peaks in this species. The horal distances between two consecutive hare positions were used as a measure of locomotor activity. European hares showed two distinct peaks in their daily activity. If sunset or sunrise were earlier, the maximum activity peaks of individual European hares occurred after sunset or sunrise, whereas activity peaks were shifted before sunset or sunrise when sunset or sunrise were later. During summer, when the nights are probably too short to allow the hares to cover their energetic requirements, the study animals regularly showed activity peaks in full daylight. In conclusion, our results imply that, although daylight regime normally regulates the diurnal locomotor activity pattern in mammals, other additional factors may play a role in modifying this regulation in European hares during summer.

Key Words: *Lepus europaeus*, GPS, activity pattern, locomotion

Introduction

In mammals, circadian rhythms are predominantly regulated by light (Goldman, 1999; Cermakian & Sassone-Corsi, 2002; van der Merwe *et al.*, 2011). Numerous studies have shown that the impact of light as zeitgeber might be affected by various other intrinsic and extrinsic factors, such as food availability, weather, temperature, sex, season, reproductive status, and age (Getz, 1961; Garshelis & Pelton, 1980; Zielinski *et al.*, 1983; Ferguson *et al.*, 1988; Larivière *et al.*, 1994; Kolbe & Squires, 2007; Wronski *et al.*, 2006; Rödel *et al.*, 2012). However, sunrise and sunset have been suggested to trigger the onset and cessation of activity in a wide range of species (Daan & Aschoff, 1975; Benstaali *et al.*, 2001).

Hares (genus *Lepus*) have been described as mostly nocturnal mammals (Chapman & Flux, 2008), although this seems to be true only during winter (Homolka, 1986; Pépin & Cargnelutti, 1994; Holley, 2001). In summer, activity of hares appears to be less consistent and partly diurnal (Mech *et al.*, 1966; Cederlund & Lemnell, 1980; Figala *et al.*, 1984). Irrespective of this, also in hares sunset and sunrise appear to play a major role concerning the onset and cessation of activity, respectively (Mech *et al.*, 1966; Figala *et al.*, 1984; Pépin & Cargnelutti, 1994; Holley, 2001).

In winter, hares start their daily activity shortly after sunset and end it shortly before sunrise (Cederlund & Lemnell, 1980; Pépin & Cargenelutti, 1994). However, studies on different hare species report contradictory results regarding the influence of sunrise and sunset as zeitgebers during late spring or summer. Snowshoe hare's (*Lepus americanus*) cessation of activity has been reported to be on average one hour before sunrise (Mech *et al.*, 1966; Figala *et al.*, 1984), however, with notable variation. For some individuals the onset of activity was one hour after sunset (Mech *et al.*, 1966), whereas another one was observed to start its activity more than two hours before sunset (Figala *et al.*, 1984). European hares began to leave their forms before sunset and to enter them after sunrise as the nights shortened in the early part of the year (Holley, 2001). That means, in all studies during late spring or summer sunrise and sunset somehow trigger onset and cessation of hares' activity, but the impact of these zeitgebers is various.

It has been argued that the impact of sunrise and sunset in summer was altered by the number of daily night hours (Holley, 2001). In this European hare study the duration of the activity period did not remain constant but decreased from 15 hours in January to 12 hours at the end of March, mirroring the number of daily night hours. At this point, the activity period was not further contracted but the hares suddenly started to increase their activity period by including daylight activity. This sudden transition from a totally nocturnal to a partially diurnal regime was explained by an aversion to daylight activity. Consequently, we suppose that the number of daily night hours alter the impact of the predominant zeitgebers sunrise and sunset. Hence, the hares' activity pattern should display a sudden start of daylight activity at the beginning and an abrupt withdrawal from daylight activity at the end of summer.

In addition, a high ambient temperature might influence the activity pattern of mammals. For example, in black bears (*Ursus americanus*) it was shown that temperatures above 25°C substantially reduced the level of activity (Garshelis & Pelton, 1980). Furthermore, the meadow vole (*Microtus pennsylvanicus*) was found to abandon diurnal activity in favour of nocturnal and/or crepuscular activity when the temperature rose above 20°C (Getz, 1961). We hence assumed that the impact of the zeitgebers sunrise and sunset might be altered by a high ambient temperature in which case the hares' activity would be restricted to the dark period.

However, detailed quantitative and individual-based data on daily activity pattern in this genus are still scarce. In this study we investigated the European hare's (*Lepus europaeus*) diurnal locomotor activity patterns during summer. In particular, we did not only focus on the timing of onset and cessation of activity but also studied subtle changes of activity during 24 hours. Our hypothesis was that sunrise and sunset, the predominant zeitgebers for the European hare's diurnal locomotor activity pattern, are slightly altered in their impact by the number of daily night hours (season) and the temperature. We tested this hypothesis by equipping nine individuals with GPS collars, allowing us to assess their diurnal locomotor activity patterns.

Material and Methods

1. Study area

The study was conducted in Lower Austria near Zwerndorf (48°20'N, 16°50'E) and the study area consisted of 270 ha arable land with cereals as the main crop and an average field size of 3.1 (± 0.3 SE) ha. Hare density in the study site was estimated in autumn 2009 by spotlight counts (Langbein *et al.*, 1999) and accounted 35 European hares per 100 ha (SSB & KH, unpubl.).

2. Data collection

Nine adult European hares (4 males, 5 females) were caught in un-baited box traps from May until September 2009. All animals were sexed according to secondary sexual characteristics and equipped with a 70 g GPS collar (Telemetry Solutions, Quantum 4000 Enhanced). The collars were programmed to start working right after the animal's release and take 1 fix per hour. For additional information on the individual hares' GPS-data see the supplementary material. The accuracy of the GPS collars was tested beforehand (see Harris *et al.*, 1990) and yielded a mean precision of 3.5 m (± 1.0 SE). Weather data and the time of sunrise and sunset were provided by the Austrian Central Institute for Meteorology and Geodynamics. Temperatures were recorded daily at 7 am and 7 pm CET.

3. Calculation of positional data

The positional data were digitised using the software ArcGIS 9.2 (ESRI). We only included locations with a solution in three-dimensional mode (based on ≥ 4 satellites) (Frair *et al.*, 2010). The distances (in metres) between two consecutive hare positions (horal distance) were calculated. Although the horal distance does not reveal the effective distance the hare covered between these two fixes, it exposes a minimal distance the hare must have moved during this hour. In the following, the "horal distance" is used as a measure of hares' activity, and the term "activity" is always used in the sense of the hares' locomotor activity.

4. Statistical data analysis

We analysed the data using multivariate (generalized) linear mixed-effects models, allowing for the use of repeated measurements. Statistical analyses were done with the software R 2.12.0 (R Development Core Team, 2011). Generalized linear mixed-effects models were fitted using the package lme4 (Bates, 2005). P-values were extracted by likelihood ratio tests (Faraway, 2006). When using linear models, we visually checked normality of the model residuals by normal probability plots. For all models, the homogeneity of variances and goodness of fit were examined by plotting residuals versus fitted values (Faraway, 2006).

We initially included sex in all models tested. However, since there were never any significant effects of sex in our multivariate analyses ($p > 0.10$), this factor was omitted from the models before re-calculation.

4.1. Diurnal activity pattern

We tested the effect of time of the day (covariate, in hours) on the response variable horal distance by a linear mixed-effects model. In addition, we tested similar models only including data subsets: one subset included all positional data with a shorter time interval to sunset than to sunrise, and the other one comprised the remainder. For all models, the response variable (horal distance) was log-transformed in order to obtain a normal distribution of the model residuals.

Since we expected a non-linear time course with at least one maximum peak, we used polynomials to model the data. For this, we gradually increased the complexity of the polynomials until the 9th order. All of these models were tested for significance, and, in addition, we directly compared the support of these models by using AICc (Burnham & Anderson, 1998). The model with the lowest AICc score can be considered as the best approximating model of the model set. Note that different models can be considered to find equally good support by the data when the ΔAICc is smaller than 2.

All (mixed-effects) models included hare identity as a random factor in order to allow for the repeated measurements collected from the different hares, and also an individual-specific code for the day (“date”) as a second random factor in order to account for the time series measured for each of the study animals during the different days of the study. As is could be expected, there was significant individual variation among the hares’ locomotor activity (significant random factor "individual hare": χ^2 = 199.44, $p < 0.001$) with a variance of 0.21 m/h (± 0.55 SD).

4.2. Influence of different parameters on the activity peaks

A peak can be described mathematically by a parabola, i.e. by a 2nd-order polynomial. The first derivative is used to find the vertex of a parabola as the first derivative equals zero at the vertex. At the maximum point of the parabola the hare's activity is highest. Therefore, if the horal distance is a function of the time interval to and since sunrise or sunset, the independent variable of this function indicates the time interval of maximum locomotor activity.

Firstly, the time interval with the highest activity was determined. As the time of sunset and sunrise changes at about one minute per day in summer, and as each of the nine hares provided a different number of horal distances, several maximum points for each animal were calculated. The horal distances of one day did not yield enough data to calculate a morning and an evening maximum point. For this reason, we pooled the horal distances of five days for every hare to calculate one evening and one morning maximum point. If the first derivative at zero described a minimum point or an impossible maximum point, the point was excluded from further analysis. Out of 171 individual hare days (comprising 3506 hare locations) 36 extrema were calculated for the morning as well as for the evening. 47% of the morning extrema and 75% of the evening extrema were sensible maximum points.

Secondly, the mean time of sunset and sunrise was calculated for every five day interval. Each evening maximum point was paired with its corresponding time of sunset and each morning maximum point with its corresponding time of sunrise. Subsequently, the correlations were tested by two linear mixed-effects models with hare identity as random factor (see Fig. 3a, b). The same models were used to test for correlations between activity peaks and the number of daily night hours (see Fig. 3c, d) and the temperature, respectively.

4.3 Light conditions and the occurrence of a morning activity peak

Here, we analysed two subsets of the data. One subset included all fixes taken when the evening activity peak was during the dark phase, the other one comprised the remainder (see Fig. 4a). To test the effect of the light conditions on the occurrence of a morning activity peak, we used a generalized linear mixed-effects model for binomial data with a logit-link function ("logistic regression"). Also here, hare identity was included as a random factor (see Fig. 4b).

Results

The mean number of satellites used for the location of the fixes was 7 (± 0.03 SE). The overlapping individual study periods were on average 11 days (± 9.2 SE) long with a minimum of 2 and a maximum of 91 days. That is, the number of GPS-fixes taken per animal ranged from 25 to 2127 with an average of 230 (± 219.4 SE). This resulted in a total of 3528 fixes and thus a total of 3519 horal distances available for analysis (709 for males, 2810 for females). For additional information on the individual hares' GPS-data see the supplementary material.

1. Diurnal activity pattern

The daily time course of the hares' activity, measured as the horal distance covered between two fixes, was significantly explained by a 6th order polynomial (χ^2_6 = 1078.6, $p < 0.001$). This model predicted for the European hares' diurnal locomotor activity two distinct activity peaks during night time (see model graph in Fig. 1). We also verified that the 6th order polynomial was the best approximating model describing this relationship by a comparison with higher and lower parameterised models using AICc values. This model selection procedure revealed that this model had the lowest AICc score, with ΔAICc > 87 in comparison to all lower parameterised models, and ΔAICc > 1 in comparison to higher parameterised models.

In relation to sunset and sunrise, the model including a 4th order polynomial predicted that the hares' activities were highest one hour after sunset and again 5 hours later (χ^2_4 = 489.75, $p < 0.001$; Fig. 2a). Furthermore, a model including a 3rd order polynomial predicted that hares were most active 5 to 3 hours before sunrise (χ^2_3 = 445.18, $p < 0.001$; Fig. 2b). The animals did not show any notable activities 5 to 8 hours before sunset and 1 hour before sunrise until 8 hours after sunrise, when the average distance moved by the hares was less than 10 metres within one hour. Also here, we verified by model selection with AICc, that the chosen polynomials were the best approximating models compared to models including lower-order (ΔAICc > 76 and ΔAICc > 70, respectively) or higher-order polynomials (ΔAICc > 2 and ΔAICc > 2, respectively).

2. Influence of different parameters on the activity peaks

2.1. Daylight regime

There were significant and negative correlations between both sunset and the timing of the evening activity peak and between sunrise and the timing of the morning activity peak (Tab. 1). If sunset or sunrise were earlier, the maximum activity peaks of individual hares occurred later, whereas activity peaks were shifted before sunset or sunrise when sunset or sunrise were later (Fig. 3a, b). Note that the regression slope of the correlation between sunrise and the timing of the morning activity peak was steeper than between sunset and the timing of the evening activity peak.

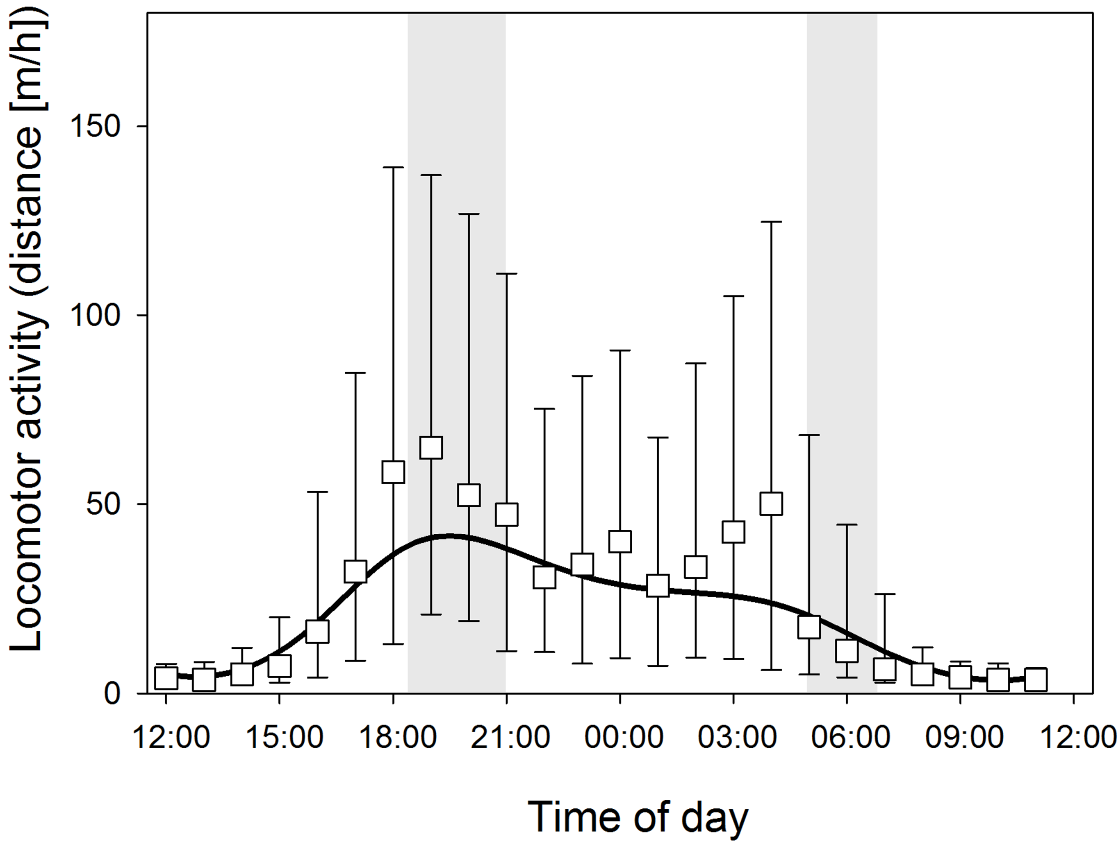

Figure 1: Locomotor activity (measured as the horal distances moved by the hares) described by a 6th-order polynomial regression model. Data (squares) are shown as medians with 25th/75th percentiles. Time of sunrise/sunset during the study period is indicated by grey shading. See text for details on statistics.

2.2. Number of daily night hours

As expected, we found similar effects when testing the variable number of daily night hours on hare activity peaks (Fig. 3c, d, Tab. 1), simply because the number of daily night hours was highly collinear with sunrise and sunset (correlation of sunrise vs. number of daily night hours: $R^2 = 0.99$, $F_{1,100} = 1.5\times10^{31}$, $p < 0.001$, sunset vs. number of daily night hours: $R^2 = 0.97$, $F_{1,100} = 3628$, $p < 0.001$).

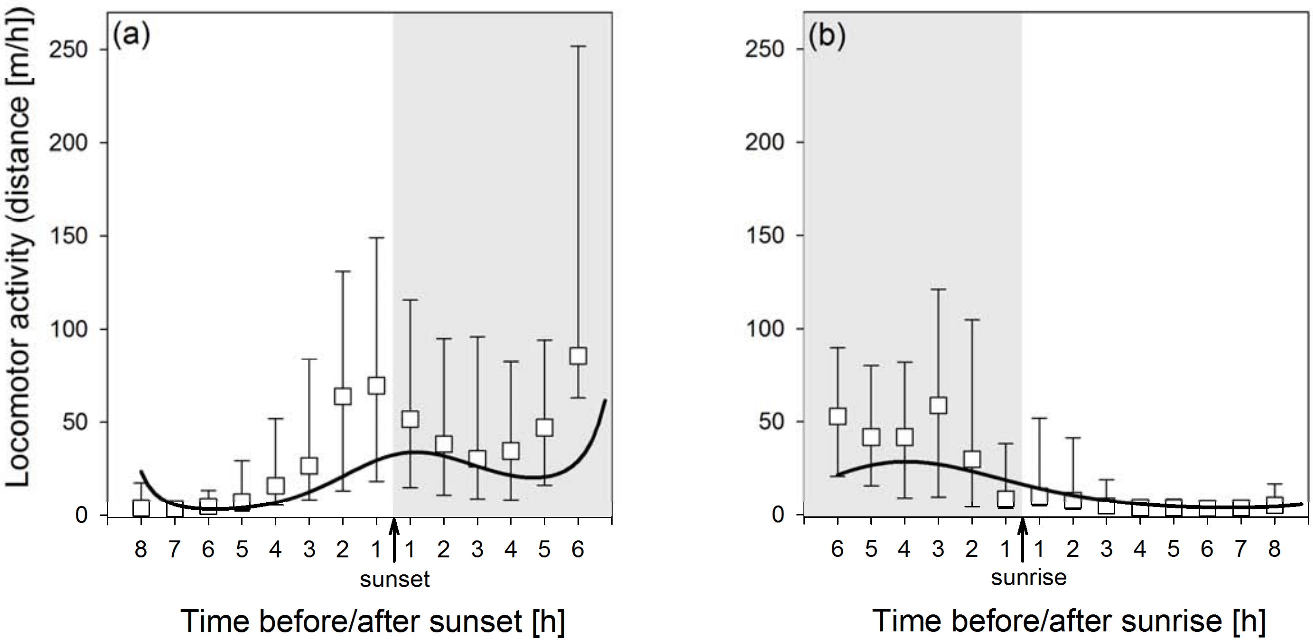

Figure 2: Locomotor activity (measured as the horal distances moved by the hares) in relation to the time of (a) sunset described by a 4th-order polynomial regression model and (b) sunrise described by a 3th-order polynomial regression model. Data (squares) are shown as medians with 25th/75th percentiles. Dark phase is indicated by grey shading.

Table 1: Results of linear mixed-effects models for the effects of different predictor variables on the timing of locomotor activity peaks, including hare identity as a random factor. Analyses are based on $n_{evening}$ = 27 and $n_{morning}$ = 17 five-day activity intervals of repeated measurements of nine hares.

Response variables	Predictor variables	Slope	χ^2_1	*p*
Morning activity peak	Sunrise	–5.16	25.06	<0.001
	Number of daily night hours	–2.31	22.88	<0.001
	Morning temperature	0.39	1.57	0.21
Evening activity peak	Sunset	–1.82	10.68	<0.001
	Number of daily night hours	1.02	11.06	<0.001
	Evening temperature	–0.18	1.09	0.30

2.3. Temperature

There were no statistically significant correlations between the morning temperature and the timing of the morning activity peaks and between evening temperature and the timing of the activity peaks in the evening (Tab. 1).

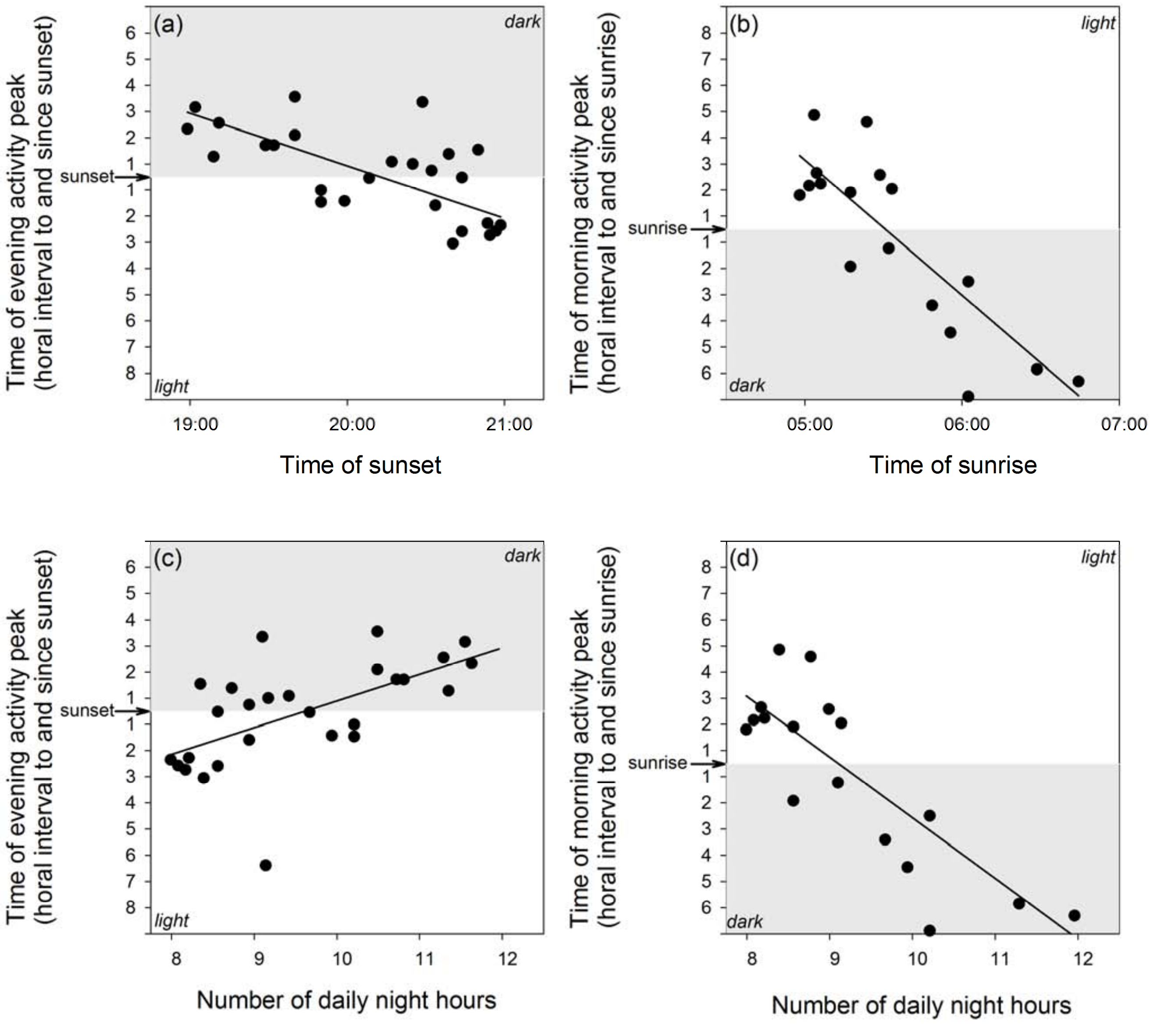

Figure 3: Correlations between (a) evening activity peaks and sunset, (b) morning activity peaks and sunrise, (c) evening activity peaks and the number of daily night hours and (d) morning activity peaks and the number of daily night hours with the regression lines (statistically significant). Dark phase is indicated by grey shading. See text for details on statistics.

3. Light conditions and the occurrence of a morning activity peak

There was a significant effect of light conditions at the time of the evening activity peak on the number of observed activity peaks. The significant models predicted two distinct maxima when the evening activity peak was during daylight (χ^2_6 = 230.09, p < 0.001, Fig. 4a; dashed line), whereas there was only one activity maximum when the evening activity peak was during the dark phase (χ^2_6 = 731.61, p < 0.001, Fig. 4a; solid line). In other words, there was a higher probability of occurrence of a second activity peak (in 79% of cases) when the evening activity peaks of individual hares were in full daylight (χ^2_1 = 15.50, p < 0.001; Fig. 4b).

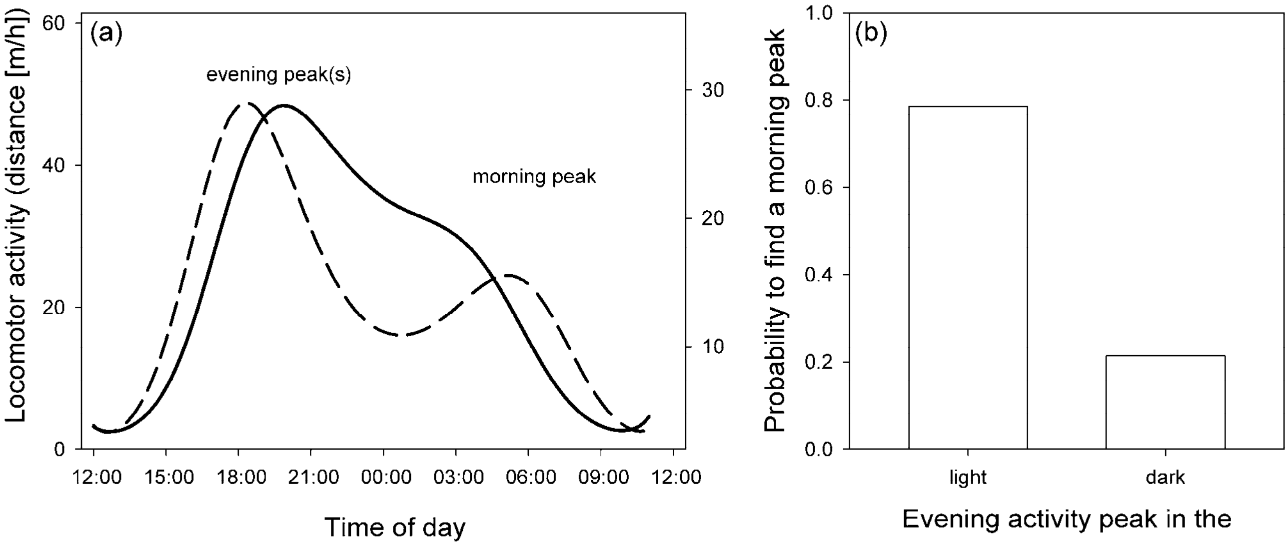

Figure 4: (a) Polynomial regression models describing locomotor activity (measured as the horal distances moved by the hares) with the evening activity peak being in the light (dashed line) or dark phase (solid line). (b) Probability of the existence of a morning activity peak when the preceding evening activity peak was during the dark or light phase. See text for details on statistics.

Discussion

1. Locomotor activity pattern in the course of the day

The hares of our study showed two peaks in their daily activity, having a distinct one in the evening and another less pronounced one in the morning. Thus, it can be concluded that European hares have a time of reduced activity in-between an enhanced activity at the beginning and end of the night. When looking at the activity of the European hare in relation to sunset, the data indicated an activity peak around sunset followed by a decrease and a second increase in activity during the dark phase. During the hour of highest activity, hares moved on average 70 m. As the average field size in the study area was 3.1 ha, we suggest that hares used only a few different field types per night while being active. Furthermore, the model predicted a peak before sunrise followed by a long period of almost no activity. That is, the predicted periods of inactivity did not last for the whole light phase. As a consequence, there was notable locomotor activity well before sunset and after sunrise.

2. Factors influencing the diurnal locomotor activity rhythm

2.1. Influence of sunrise and sunset on the diurnal locomotor activity rhythm

There was a significant negative correlation between both the timing of the morning activity peak and sunrise as well as between the timing of the evening activity peak and sunset. As we assumed that the activity peaks are collinear with onset and cessation of activity, our results imply that the activity and inactivity of European hares in summer are closely tied to sunset and sunrise. This is in accordance with other hare studies describing the major role of sunrise and sunset concerning the onset and cessation of activity (Mech *et al.*, 1966; Figala *et al.*, 1984; Pépin & Cargnelutti, 1994; Holley, 2001). Nevertheless, the negative correlations in summer imply that the impact of sunrise and sunset differ from winter. While in winter European hares consistently started their daily activity shortly after sunset and ended it shortly before sunrise (Pépin & Cargnelutti, 1994; Holley, 2001), in summer the hare's activity peaks occurred after sunset or sunrise when sunset or sunrise were earlier, whereas activity peaks shifted before sunset or sunrise when sunset or sunrise were later. Our results during summer confirm the ones of Holley (2001) who observed European hares' starting to leave their forms before sunset and enter them after sunrise in the early part of the year. Thus, we conclude that the power of the zeitgebers sunrise and sunset is altered in summer by a seasonal factor.

The steep regression slope between sunrise and the timing of the morning activity peak resulted in an 8 to 11 hours shift in the timing of the morning activity peak. In comparison, the shift of the timing of the evening activity peak was much lower i.e. 5 to 6 hours. This result, indicating that sunset might be a stronger zeitgeber for the European hare's diurnal locomotor activity pattern than sunrise, is in line with another European hare study conducted in winter (Holley, 2001). The latter study reported a stronger tie between onset of activity and sunset than between cessation of activity and sunrise.

2.2. Influence of season on the diurnal locomotor activity rhythm

The negative correlation between the timing of the activity peaks and sunrise or sunset might be explained by the European hare's need to fulfil its daily energetic demands, because the length of the dark phase might limit the hare's feeding time. Hackländer *et al.* (2002) showed that European hares fed with a diet comparable to the composition of stomach contents in free-ranging hares had a higher food intake yet assimilated less energy than hares fed with a high fat diet. This might be due to a trade-off between the energy benefit of increasing food-intake and the additional weight load in a flight animal (Hackländer *et al.*, 2002). Such a trade-off might also account for the small resting periods dispersed during activity (Averianov, 2003) which may be used by the European hares to digest before new food intake can take place. The results of another study indicated that the duration of European hares' activity period cannot be contracted further a certain point (Holley, 2001). A possible explanation may be the hare's need to fulfil its daily energetic demands in combination with required digestive breaks. Sunset was late and sunrise early until middle of July and the hare's evening and morning activity peaks proceeded in full daylight. During this time the dark phase seems not to be long enough for the European hare to accomplish its energetic requirements. The number of daily night hours was longer in August and September, and hare's evening and morning activity peaks took place during the dark phase. We propose that during the vegetation period the usual trigger of activity and inactivity, namely sunrise and sunset, is slightly altered in its impact by the hares' instinct to accomplish their daily energetic requirements. Hence, the season in the form of the number of daily night hours had an influence on the activity pattern of the European hare and altered the impact of the usual zeitgebers sunrise and sunset. There was no difference noticeable in the influence of sunrise and sunset and the numbers of daily night hours as these parameters were collinear.

Moreover, the season seems to have an impact on the hare's inactivity period during daytime. Our results are in line with previously reported activity data in European hares (Homolka, 1986; Holley, 2001) showing that activity during the day is displayed predominantly in summer. Outside the summer period, on the contrary, European hare studies reported almost no activity during daytime (Homolka, 1986; Pépin & Cargnelutti, 1994; Holley, 2001). However, our study animal's period of inactivity exceeded the previously reported length of inactivity in European hares during summer. Homolka (1986) showed that in Moravia (Czech Republic) during a one all-day visual observation in July 30 to 50% of the hares were active with foraging throughout the day except for about 4 hours in the middle of the day. The hares' distinct length of inactivity during the day might be explained by the different climate in Southern Moravia and the eastern part of Lower Austria. The Pannonian climate is responsible for hot and dry summers in our study area, whereas the continental climate of Southern Moravia is more moderate. Our study animals may react to the Pannonian climate in summer with an extended period of inactivity during the day. We therefore conclude that the length of inactivity during daytime depends both on season and climatic conditions.

2.3. Influence of temperature on the diurnal locomotor activity rhythm

The ambient temperature has been proposed to influence the activity pattern of some mammal species (Getz, 1961; Garshelis & Pelton, 1980). However, this does not seem to be the case for the European hare, at least not during the vegetation period, as we could not find significant correlations between the activity peaks and the temperature. An explanation might be that the European hare, originally coming from the savannas of Eurasia (Averianov, 2003), is adapted to high ambient temperatures, and, as a result, the impact of the zeitgebers sunrise and sunset is not altered by the daily ambient temperature.

3. Light conditions and the number of activity peaks

Our results revealed a significant influence of light conditions at the time of the evening activity peak on the number of activity peaks. If the evening activity peaks of individual hares were in full daylight, there was a higher probability of occurrence of a second activity peak. It seems as if some unknown factor provokes an increased activity by antedating the evening activity peak into full daylight and hereinafter by evoking a second activity peak in the early morning hours. No such findings were ever reported in the literature regarding hare’s activity patterns. We suggest that future studies on hares’ activity patterns during the vegetation period might carefully examine the number of activity peaks during the night and decipher the factor(s) provoking an increased activity.

Conclusion

In conclusion, our study clearly shows that also in summer, sunrise and sunset were the zeitgebers for the European hare’s diurnal locomotor activity pattern. However, the results indicate that this relationship was altered by the number of daily night hours (season). We speculate that the hares’ feeding activity during the short summer nights is not sufficient to cover their daily energetic requirements during the vegetation period. The temperature, however, had no influence on the locomotor activity pattern of the European hare.

Acknowledgements

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Supplementary material

Hare	Sex	Number Of GPS Positions	Period Of Data Collection	Comments
#1	m	230	23 May - 2 June 2009	Death by predation
#2	f	2127	29 June - 27 September 2009	
#3	m	28	9 July - 10 July 2009	
#4	f	305	20 July - 5 August 2009	Death by predation
#5	m	103	20 July - 24 July 2009	
#6	f	141	29 July - 4 August 2009	
#7	f	25	31 July - 3 August 2009	
#8	f	297	23 August - 8 September 2009	Death by predation
#9	m	385	1 September - 19 September 2009	

Second Chapter

The influence of cereal harvest on the home-range use of the European hare (*Lepus europaeus*)

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Wildlife Biology, submitted

Photo: Stéphanie Schai-Braun

Abstract

In farming areas predominated by one field crop, harvest changes food and cover availability for European hares (*Lepus europaeus*) within a short time frame. In this study, we tracked European hares by GPS (n=9) and VHF (n=19) in an agricultural area with 54% of cereal cropping before, during and after harvest. In particular, we focused on the question whether and how harvest affects European hares' space use. We found that, during activity, hares' 24 hour home-ranges were significantly larger after harvest than before, whereas on weekly home-range size, harvest had only a significant effect when calculated by the MCP method. We suggest that the effect of harvest on the species' home-range size is time scale dependent. Changes in home-range use were mainly due to hares using less cereal fields after harvest. Furthermore, during activity, hares stayed further away from field edges, whereas resting animals were closer to field edges after harvest. In conclusion, our results show that cereal harvest influenced European hares' space use, but this influence might only be discernible on the small time scale.

Key Words: Brown hare, GPS, space use, time scale

Introduction

Since the 1960's the number of European hares (*Lepus europaeus*) has been declining throughout Europe, mainly due to habitat changes caused by agricultural intensification (Smith *et al.,* 2005). The agricultural mechanisation led to the still ongoing tendency of larger field sizes and faster processing. Another consequence of the agricultural intensification was a reduction in landscape diversity due to the loss of non-farmed habitat types. It has been widely shown that European hares especially prefer non-farmed features in agricultural landscapes, such as hedges (Tapper & Barnes, 1986; Pépin & Angibault, 2007; Vidus-Rosin *et al.,* 2011; Cardarelli *et al.,* 2011) and fallow land (Smith *et al.,* 2004; Vidus-Rosin *et al.,* 2011; Cardarelli *et al.,* 2011; Schai-Braun *et al.*, 2013). Modern arable landscapes change dramatically during cereal harvest, as food and shelter will disappear within days or even hours. After body mass is taken into account, residual variation in home-range size and space use patterns in leporids can be explained by a species' ecology and surrounding environment such as the productivity of the habitat (Swihart, 1986). Under these circumstances, one might expect that the harvesting of arable crops in late summer will reduce habitat quality (e.g. food, shelter) for European hares. This may cause behavioural responses such as a home-range shift or a change in home-range size.

One study, which has investigated the effects of harvest on the European hare in cereal dominated agricultural landscapes, supports this hypothesis. Onderscheka & Gattinger (1976) showed that during and after harvest, the animals used effectively only 10 to 15% of the total agricultural area. In contrast, another study presented almost no effect of harvest on the European hare. Marboutin & Aebischer (1996) recorded no difference in home-range sizes before and after cereal harvest. However, European hares' range centres shifted and less overlap was recorded after harvest.

The only European hare study investigating the influence of cereal harvest on the hares' home-range use, compared space use before and after harvest (Marboutin & Aebischer, 1996). Home-ranges of European hares include resting areas and feeding areas, which are often spatially separated due to different habitat requirements (Tapper & Barnes, 1986). Harvest may therefore have a different impact on the European hare depending on its activity state. In addition, this implies that the time scale in general might be decisive to disclose possible modifications of the European hares' space use. Consequently, the effects of harvest on the European hares' space utilisation may be less visible over long than short time scales.

Another study investigating the effect of stand structures on this species' distribution revealed that harvest changed European hares' habitat use by increasing the hares' availability of open space (Rühe, 1999). Lewandowski & Nowakowski (1993) showed that in autumn and winter, hares in areas of monoculture had a preference for resting places close to the field edge where vegetation diversity is generally higher. As cereal harvest alters the availability of cover for the European hare, it may also alter the hares' use of cereal fields and field edges in its home-range.

The aim of this study was to investigate the influence of cereal harvest on the space utilisation of the European hare in an agricultural landscape with small average field size. In particular, we focused on harvest-related changes of 24 hour and weekly home-range use, but also during the hares' active and resting period. Our hypotheses were that (1) harvest influences the European hares' home-range use on the small time scale and, (2) since harvest alters the vegetation density of a landscape, harvest-induced changes in home-range use are due to modifications in the hares' use of cereal fields and field edges. We tested these hypotheses by equipping European hares in the field with GPS and VHF collars, allowing us to assess the animals' space use before, during and after cereal harvest on a fine spatio-temporal scale.

Material and Methods

1. Study area

The study was conducted in Lower Austria near Zwerndorf (48°20'N, 16°50'E) and the study area consisted of 270 ha arable land. 54% of the study site was cereals with winter wheat (*Triticum aestivum*) as the primary crop. In the study years 2006 and 2009, cereal harvest took place during the two last weeks of July (2006: 14-31 July; 2009: 13-24 July). The 'before harvest' period was defined as the time between 23 May 2009 and the start of harvest, whereas 'after harvest' includes the time from the end of harvest until 27 September 2009. Average field size was 3.1 (± 0.3 SE) ha. The field edge index (Pegel, 1986) was 17.79 km per 100 ha and was approximately the same before, during and after harvesting (Tab. 1). The vegetation density for all habitat types was mapped weekly. Vertical vegetation density was estimated by placing a board (43 cm x 33 cm), representing the size of a hare, into the vegetation. The distance between board and observer was measured when only half of the surface was visible to the observer. The vertical density was classified as: nudum/open (>75 cm), sparse (50-75 cm), medium (25-49 cm) and dense (<25 cm). We measured the horizontal vegetation density by assessing the surface covered by vegetation within a frame (25 cm x 25 cm) using the categories: nudum/open (<25%), sparse (25-49%), medium (50-75%) and dense (>75%). Hare density at the study site was estimated in autumn by spotlight counts (Langbein *et al.,* 1999) and differed between years (2006: 90 individuals per 100 ha, 2009: 35 individuals per 100 ha).

Table 1: Field edge index for the study area before, during and after harvest in the year 2009.

	Field edge index [km/100 ha]
Before harvest	17.56
During harvest	18.26
After harvest	17.81

2. Data collection

Nineteen adult European hares (8 males, 11 females) were caught in box traps from March 2006 until September 2009. All animals were sexed according to secondary sexual characteristics. Ten hares received a VHF collar (Biotrack, TW-3 medium), nine hares a GPS collar (Telemetry Solutions, Quantum 4000 Enhanced). The GPS collars were programmed to take hourly fixes. The accuracy of the fixes was tested beforehand (see Harris *et al.,* 1990) and yielded a mean precision of 3.5 m (± 1.0

SE). The data of the GPS collars was analysed regarding the influence of harvest (Tab. 2). Some animals could not be included in all analyses as the data quantity did not meet the requirements (see Data analysis, supplementary material). Thus, we use variable sample sizes in the text and figure legends. VHF positions of nineteen European hares were obtained on foot by triangulation using a Yagi antenna and a Regal 2000 receiver (Titley Electronics, Australia). Each hare was located three to seven times per fortnight between 7 am and 3 pm. VHF- and GPS-tracking data were not combined but analysed separately (see data analysis below).

Table 2: The duration of GPS tracking for the nine study animals in relation to cereal harvest.

Hare	Before harvest	During harvest	After harvest
#1	x		
#2	x	x	x
#3	x		
#4		x	x
#5		x	
#6			x
#7			x
#8			x
#9			x

3. Data analysis

The positional data were mapped in ArcGIS 9.2 (ESRI). We included only GPS-locations with a solution in three-dimensional mode (Frair *et al.,* 2010). The GPS-data were differentiated into an active (4:00 pm - 6:59 am) and resting (7:00 am - 3:59 pm) period. The resting period included all hours with an horal distance's median of less than 10 m (see Schai-Braun *et al.,* 2012). Only GPS-data sets consisting of 24 fixes in sequence were used for the analyses of 24 hour intervals. Normal distribution of all variables was assessed by QQ-plots and histograms. We chose the transformation based on the data's distribution. Weekly home-range centre shift and MCP home-range were transformed by natural logarithm, whereas 24 hour home-range centre shift, kernel home-range, distance to the nearest field edge and distance to home-range centre by square root transformation.

We analysed all data using multivariate (generalized) linear mixed-effects models. Statistical analyses were done with R 2.12.2 (R Development Core Team, 2011). Models were fitted using the package lme4 (Bates, 2005). P-values and parameter estimates were extracted by Markov chain Monte Carlo sampling based on 10000 simulation runs (Baayen *et al.,* 2008) using restricted maximum likelihoods. We visually checked normality of the model residuals by normal probability plots. The homogeneity of variances and goodness of fit were examined by plotting residuals versus fitted values (Faraway, 2006).

All models included hare identity as random factor in order to allow for the repeated measurements collected from the different hares, and a specific code for the day or week as second random factor in order to account for the time series measured for each of the animals during the different days or weeks. When analysing the distance to the field edge, a specific code for each field was included as third random factor in order to account for 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_{MCMC} > 0.10), sex was omitted from the models before re-calculation. To exclude an interaction between season and harvest, we tested the effect of month. Apart from the MCP24hr, we found no significant interaction effects of month (p_{MCMC} < 0.05) and harvest (p_{MCMC} < 0.05). Accordingly, month was omitted from the models before re-calculating significant harvest effects but for the MCP24hr.

3.1. Harvest's influence on the European hares' space use on different spatio-temporal scales

3.1.1. Influence of harvest on hares' home-range size

The home-ranges were calculated by the Minimum Convex Polygon (MCP) and the fixed kernel estimator. Most European hare studies use these two methods (e.g. Broekhuizen & Maaskamp, 1982; Kovács & és Búza, 1988; Reitz & Léonard, 1994; Marboutin & Aebischer, 1996; Kunst *et al.,* 2001; Stott, 2003; Smith *et al.,* 2004; Rühe & Hohmann, 2004) which allows comparisons. Because for each hare and day only 9 resting and 15 active locations were available, we calculated the 100% MCP (Harris *et al.,* 1990). Kernel home-ranges were calculated with the 95% probability level (Worton, 1989; Worton, 1995). An *ad hoc* smoothing parameter ($h_{ad\ hoc}$) 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. $h_{ad\ hoc}$ = a * h_{ref}) is chosen (Berger & Gese, 2007; Kie *et al.,* 2010). As fixes were taken in hourly intervals, duplicate X, Y coordinates occurred which poses 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 each once showed a sally outside of the normally used area. Since occasional sallies should not be considered as a part 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 hour home-ranges (MCP24hr, kernel24hr) for each active, resting and total period were computed (n = 9).

The same method was used to calculate weekly home-ranges. They were 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, resting and total period were calculated (n = 7).

The effect of harvest was tested either on the response variable MCP24hr, kernel24hr, MCP1wk or kernel1wk for the active, resting and total periods. As the effect of harvest was significant, we explored the differences in MCP24hr, kernel24hr, MCP1wk and kernel1wk between before, during and after harvest by post-hoc tests (see Fig. 1, 2).

3.1.2. Influence of harvest on the hares' resting position within the home-range

For every VHF-tracked hare the home-range centre for each fortnight was determined by calculating the median of the locations' coordinates. Subsequently, the distance between the hares' home-range centre and locations was measured (n = 19). The effect of time of the year (covariate, in fortnights) was tested on the response variable distance to home-range centre by polynomials (see Fig. 3). We gradually increased the complexity up to the 6^{th} order and tested each model for significance.

3.1.3. Influence of harvest on the shift of home-range centres

For every hare and day the shift of home-range centre was calculated. We distinguished between centre shifts of two successive active-active (24hrAAS), resting-resting (24hrRRS), active-resting (24hrARS) and of two consecutive 24 hour periods (24hrS). 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 centre one and two was then measured. In total, 129 24hrAAS, 90 24hrRRS, 107 24hrARS and 75 24hrS were computed (n = 7).

The same method was used to calculate the shift of weekly home-range centre. Again, only weeks with a minimum of 101 fixes were used for analyses. Shifts of weekly home-range centres were calculated for two successive active-active (1wkAAS), resting-resting (1wkRRS), active-resting (1wkARS) and two consecutive 7*24 hour (1wkS) periods. In total, 15 1wkAAS, 1wkRRS, 1wkS (n = 4) and 22 1wkARS (n = 7) were calculated.

The effect of harvest was tested on the shift of the response variable 24hrAAS, 24hrRRS, 24hrARS, 24hrS, 1wkAAS, 1wkRRS, 1wkARS or 1wkS.

3.2. Alteration of the vegetation density and European hares' use of cereal fields and field edges due to harvest

For the periods before, during and after harvest the relative frequency of vegetation density was calculated (see Tab. 3).

We analysed the modification in the hares' use of cereal fields by dividing the data into two subsets. One subset included all fixes taken when the hares (n=9) were located on a cereal field (classified during the last week before harvest), the other one comprised the remainder. The effect of harvest on the hares' use of cereal fields was tested by a linear mixed-effects model for binomial data with a logit-link function including hare location on cereal field/not cereal field as response variable and harvest as covariate. Furthermore, we analysed the data for active and resting periods separately (Fig. 4). We investigated the hares' use of cereal fields during harvest more thoroughly by dividing all positional data located on cereal fields during harvest into cut and uncut cereal fields and calculating the relative frequencies.

The distance to the nearest field edge for every hare position (n = 9) was calculated by the dist2Line function using the R package geosphere. The effects of activity and harvest and their interaction were tested on the response variable distance to the field edge. As the interaction term was significant, the data was divided into two subsets. One subset included all distances to the field edge during activity, the other one during resting. Accordingly, harvest was analysed by post-hoc tests for the two subsets (see Fig. 5).

Results

The mean number of satellites used for the location of the fixes was 7 (± 0.03 SE). The overlapping individual study periods for the GPS-collared hares were on average 11 days (± 9.2 SE) long, with a minimum of 2 and a maximum of 91 days. That is, the number of GPS-fixes taken per animal ranged from 25 to 2127 with an average of 230 (± 219.4 SE). This resulted in a total of 3641 GPS-fixes available for analysis (746 for males, 2895 for females). The individual study periods for the VHF-collared hares were on average 75 days (± 10.4 SE) long with a minimum of 6 and a maximum of 160 days. The number of VHF-fixes taken per animal ranged from 4 to 63 with an average of 27 (± 4.4 SE). This resulted in a total of 538 VHF-fixes available for analysis (231 for males, 307 for females).

1. Harvest's influence on the European hares' space use on different spatio-temporal scales

1.1. Influence of harvest on hares' home-range size

Cereal harvest had a significant effect on hares' MCP24hr and kernel24hr. Post-hoc tests revealed that MCP24hr and kernel24hr during activity and total MCP24hr and kernel24hr were significantly larger after cereal harvest than before (Fig. 1a, c), whereas MCP24hr and kernel24hr during resting either were not affected by cereal harvest (Fig. 1b) or were significantly smaller after than before cereal harvest, depending on the calculation method. Note that the hares' MCP24hr during resting was, in addition to harvest, significantly influenced by the month in which the observation was made ($p_{MCMC} < 0.01$).

Cereal harvest had a significant effect on hares' MCP1wk. Post-hoc tests revealed that MCP1wk during activity and total MCP1wk were significantly larger after than before and during cereal harvest, whereas during resting hares' MCP1wk was not affected by cereal harvest (Fig. 2). Kernel1wk was never significantly influenced by harvest (Fig. 2).

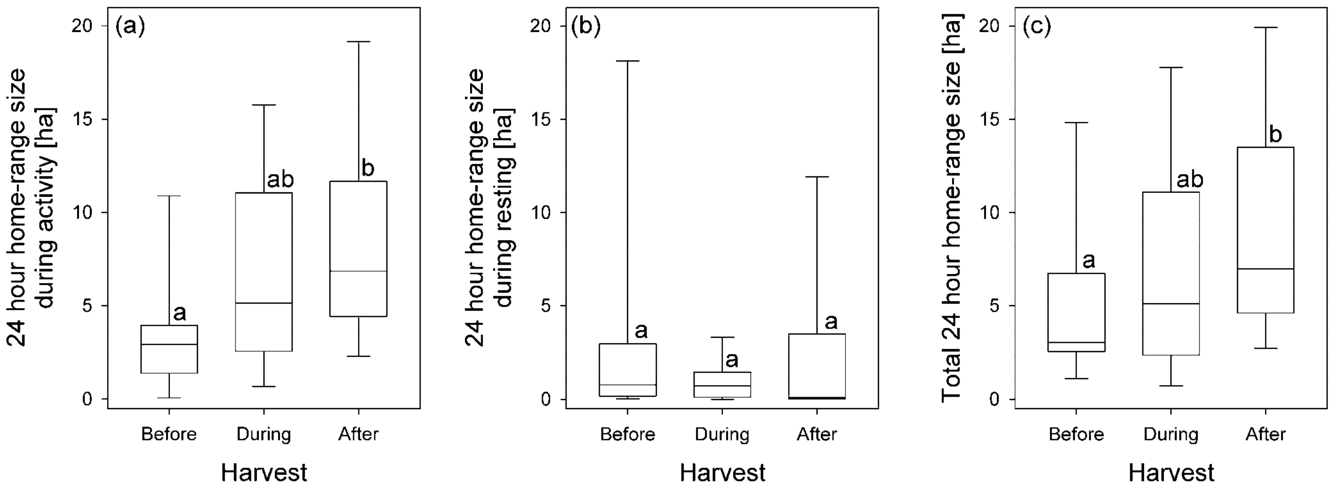

Figure 1: The influence of cereal harvest on hares' 24 hour home-range size (n = 9) during (a) active, (b) resting and (c) total periods calculated by using the fixed kernel estimator (medians with $25^{th}/75^{th}$ and $10^{th}/90^{th}$ percentiles). Different letters indicate significant differences among groups (post hoc: $p_{MCMC} < 0.01$). See text for details on statistics.

1.2. Influence of harvest on the hares' resting position within the home-range

Only the 1^{st}-order polynomial was significant. This model predicted a decrease of the distance between hares' resting position and hares' home-range centre in the course of the year (χ_1^2 = 7.999, p_{MCMC} < 0.01; Fig. 3). That means, the model indicated no apparent influence of cereal harvest on the hares' resting position within home-range use.

1.3. Influence of harvest on the shift of home-range centres

24hrS averaged 69.28 m (± 9.15 SE) and 1wkS was on average 65.12 m (± 14.81 SE). We did not find any significant effect of cereal harvest on the shift of 24 hour and weekly home-range centres during periods of different hare activity (p_{MCMC} > 0.05).

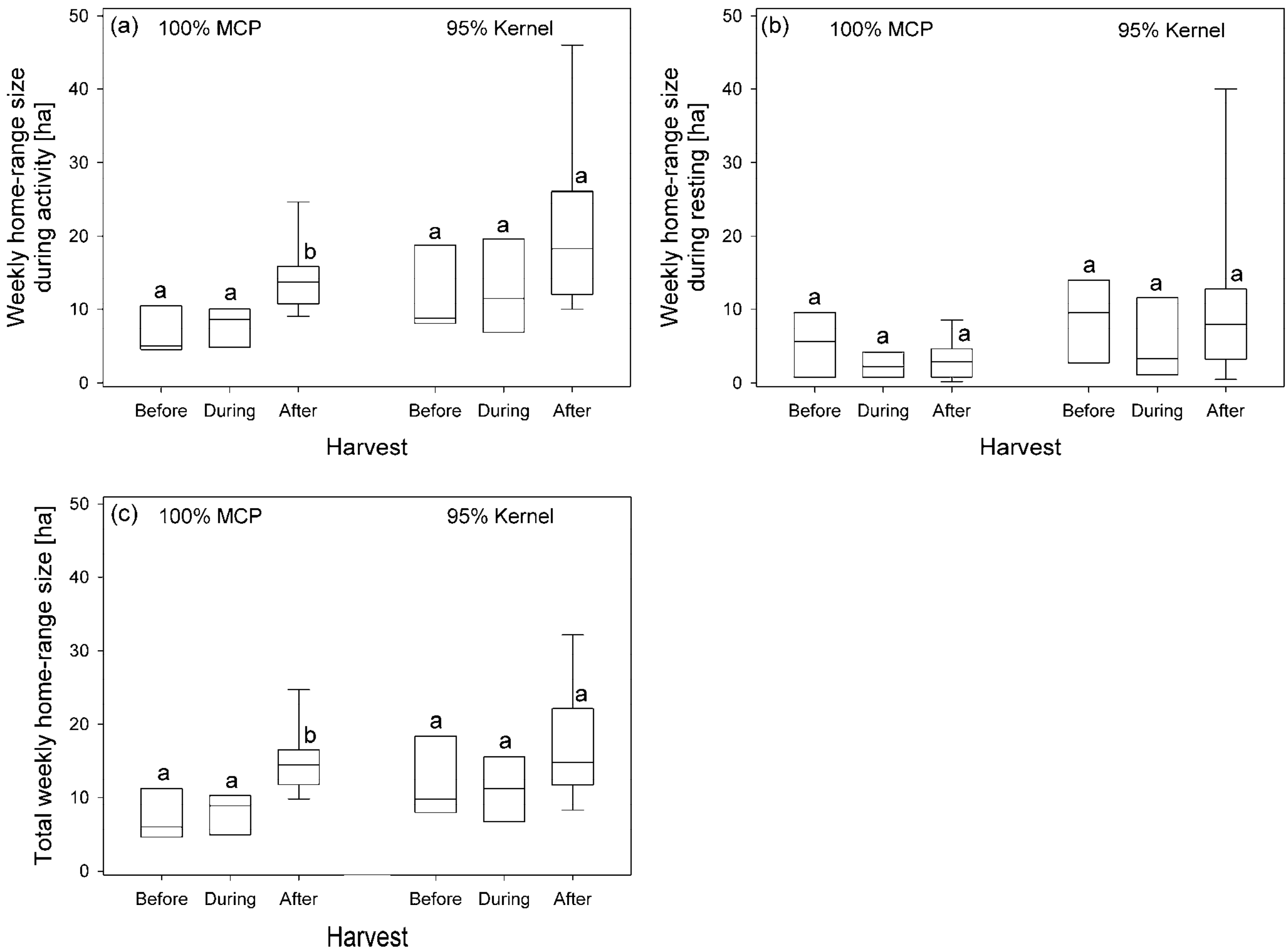

Figure 2: The influence of cereal harvest on hares' weekly home-range size (n = 7) during (a) active, (b) resting and (c) total periods calculated by using the Minimum Convex Polygon and the fixed kernel estimator (medians with 25th/75th and 10th/90th percentiles). Different letters indicate significant differences among groups (post hoc: p_{MCMC} < 0.01).

2. Alteration of the vegetation density and European hares' use of cereal fields and field edges due to harvest

The composition of the vegetation density in the study area changed considerably during cereal harvest. Medium and dense vegetation dominated the landscape before harvest, whereas during and after harvest open vegetation and bare acres prevailed (Tab. 3).

There was a significant effect of harvest on the hares' use of cereal fields (χ^2_2 = 152.59, p < 0.001). When analysing the use of cereal fields for hares during activity, the use before, during and after harvest differed significantly from each other (χ^2_2 = 83.93, p < 0.001; Fig. 4a). For resting hares, the use before and during harvest differed significantly from after harvest (χ^2_2 = 76.10, p < 0.001; Fig. 4b). During the harvest period, 55% of the hares during activity using cereal fields were located on cut cereal fields consisting of either stubble fields or chisel-ploughed acres.

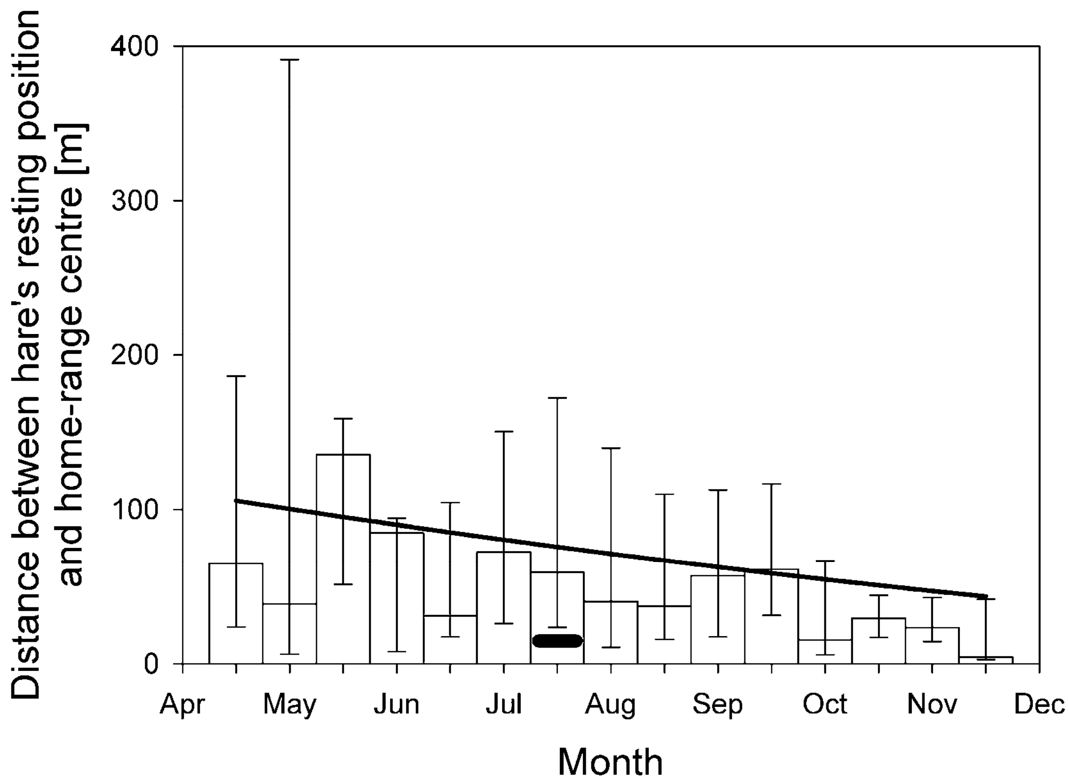

Figure 3: Distance between hares' resting position (n = 19) and home-range centre described by a polynomial regression model. Data (columns) are shown as medians with 25th/75th percentiles (error bars). Black bar indicates time of harvest for the years 2006 and 2009.

Table 3: Relative frequency of (a) horizontal and (b) vertical vegetation density in the study area before, during and after harvest.

a)	Nudum/open	Sparse	Medium	Dense
Before harvest	0.12	0.11	0.41	0.37
During harvest	0.59	0.05	0.11	0.25
After harvest	0.63	0.02	0.14	0.21

b)	Nudum/open	Sparse	Medium	Dense
Before harvest	0.10	0.23	0.33	0.33
During harvest	0.63	0.04	0.13	0.20
After harvest	0.66	0.02	0.06	0.26

Hares during active periods were significantly further away from field edges after cereal harvest (Fig 5a), whereas resting animals stayed significantly closer to field edges after harvest (Fig 5b).

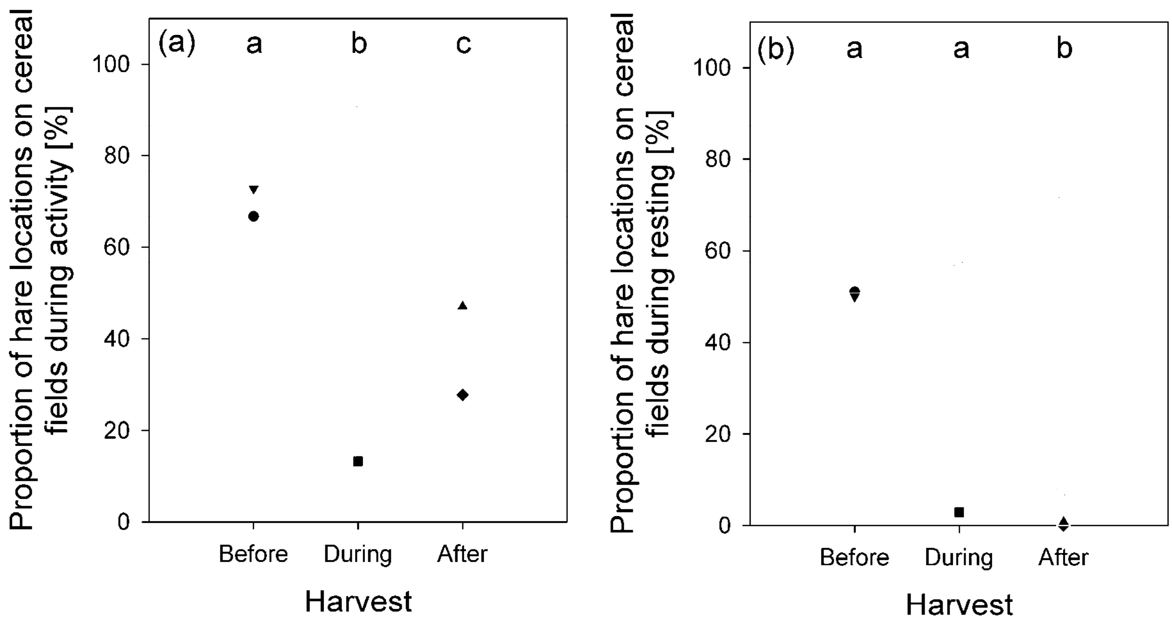

Figure 4: The proportion of hare locations on cereal fields (n = 9) during (a) activity and (b) resting in relation to cereal harvest (in percent). Different symbols indicate different study animals, whereas different letters indicate significant differences among groups (post hoc: $p_{MCMC} < 0.01$).

Discussion

Harvest influences the European hares' home-range use on a small time scale

Harvest influenced the European hares' movement behaviour on the small time scale i.e. over a period of 24 hours, irrespective of the calculation method. On weekly home-range size, the influence of harvest depended on the calculation method used. Therefore, we suggest that the influence of harvest on the hares' space use is not conspicuous on the large time scale i.e. one week. This assumption might also explain why Marboutin & Aebischer (1996) found no influence of harvest on the European hares' home-range size. The home-range sizes of the French study were calculated for a 2 and 2.5 month interval, i.e. before and after harvest. Hence, we assume that the effect of harvest on the European hares' home-range size is time scale dependent. That means, cereal harvest might influence the European hares' space use only at the small time scale. The increasing size of home-ranges during activity and total home-ranges in the course of harvest implies an enhanced energy expenditure (Swihart, 1986). Future studies have to show, whether harvest may negatively affect the European hares' daily energy balances.

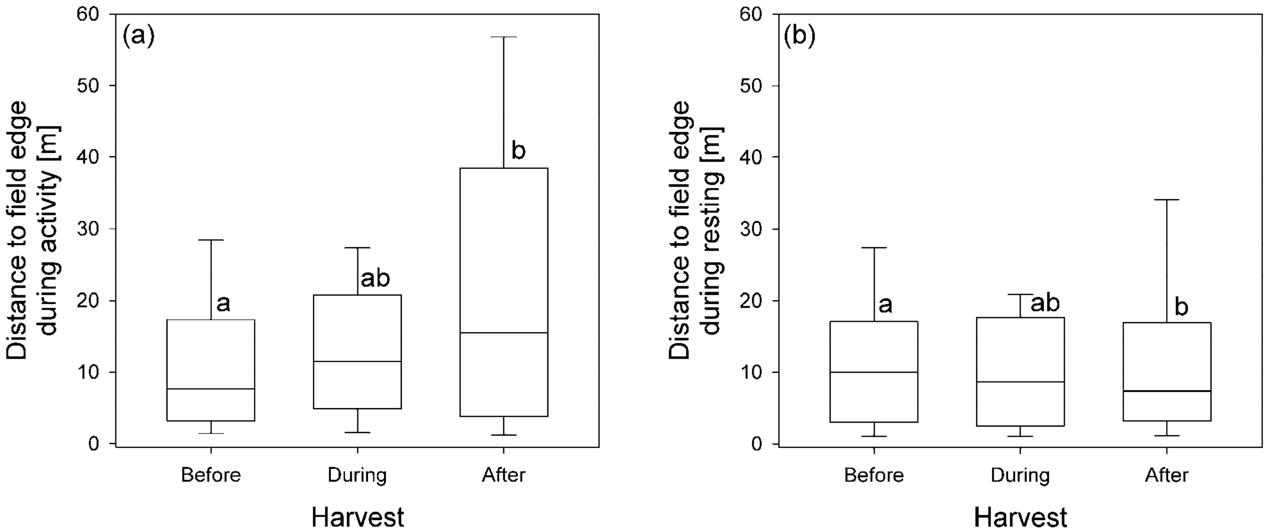

Figure 5: The influence of cereal harvest on the hares' distance to the field edge (n = 9) during (a) activity and (b) resting (medians with $25^{th}/75^{th}$ and $10^{th}/90^{th}$ percentiles). Different letters indicate significant differences among groups (post hoc: $p_{MCMC} < 0.05$).

No influence of harvest on the hares' home-range size during resting

During resting, harvest had no effect on European hares' home-range size except in the case of MCP24hr when home-range size decreased after harvest. Additionally, harvest did not have an apparent influence on the hares' resting position within home-range use. The results of a study done by Pépin & Angibault (2007) suggested that hares benefit from non-farmed features only if the area contains more than 10% of such habitats. In our study site, areas not under crops comprised 12% of the land use. As home-range sizes during the resting period were extremely small, we assume that in an agricultural area with small average field size and enough non-farmed features, European hares are able to find small habitat patches suitable for resting, irrespective of changes in agricultural land use.

No influence of harvest on the shift of home-range centres

In our study, hares shifted their home-range centre on a 24 hour and weekly basis irrespective of cereal harvest. The 24 hour and weekly home-range centre shifts of our study animals did not differ greatly and were smaller than the approximately 200 m monthly shifts in intensive arable land with an average field size of 10 ha (Reitz & Léonard, 1994) and the 131 m two-month shifts in arable land with an average field size of 6.5 ha (Rühe & Hohmann, 2004).

Modifications in the European hares' use of cereal fields and field edges because of harvest

Although European hares during activity prefer open landscapes with short vegetation (Tapper & Barnes, 1986), the overall dominance of medium and dense vegetation before harvest did probably effectuate the study animals' high proportional use of cereal fields. 55% of the cereal fields frequented during harvest were already cut. This might be explained by Späth (1989) who reported hares feeding on fallen grains in freshly cut stubble fields. During activity, our study animals visited significantly more alternative habitats after harvest. One of the main occupations during activity is foraging (Averianov *et al.,* 2003). We propose that the change to use different, less well known fields for foraging increased the European hares' movement behaviour i.e. home-range size. As resting European hares prefer landscapes providing shelter (Tapper & Barnes, 1986; Neumann *et al.,* 2011), we assume that harvested cereal fields were less attractive for hares. Although after harvest the resting hares' use of cereal fields changed significantly, no significant modification in hares' home-range size was recorded. We suggest that the agricultural area characterised by small average field sizes provided enough equivalent habitats in non cereal fields suitable for resting.

The landscape after harvest was easier to view for the hares than before and during harvesting. During activity, when hares are occupied with different activities (Averianov *et al.,* 2003), it might be safer to stay further away from field edges where there is a better overview and predators easier detectable, whereas during resting field edges might be favourable because they provide some enhanced vegetation diversity. In contrast to Lewandowski & Nowakowski (1993), our results imply that field edges are of great importance to resting hares, also in farming areas with small average field size.

Conclusion

In summary, we found that the influence of cereal harvest on the European hares' space use was evident on the small time scale (24 hour), but not conspicuously on the larger scale (one week). Consequently, the impact of harvest might be noticeable only on small time scales and become undetectable on larger scales. Changes in home-range use were due to hares using less cereal fields after harvest. Furthermore, hares during activity stayed further away from whereas resting animals were closer to field edges after harvest. In agricultural areas with large field sizes, resting hares might be faced with difficulties in using their preferred habitats near field edges. Whether such difficulties might impact the hare management, further research has to show.

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Supplementary material

			Number Of 24 Hour Home-Ranges			Number Of Weekly Home-Ranges		
Hare	Number Of GPS Positions	Period Of Data Collection	Before Harvest	During Harvest	After Harvest	Before Harvest	During Harvest	After Harvest
#1	230	23 May - 2 June 2009	8			1		
#2	2127	29 June - 27 September 2009	10	7	54	2	2	9
#3	28	9 July - 10 July 2009	1					
#4	305	20 July - 5 August 2009		2	1		1	1
#5	103	20 July - 24 July 2009		3			1	
#6	141	29 July - 4 August 2009			5			1
#7	25	31 July - 3 August 2009			1			
#8	297	23 August - 8 September 2009			6			2
#9	385	1 September - 19 September 2009			5			2

Third Chapter

Spring and autumn habitat preferences of active European hares (*Lepus europaeus*) in an agricultural area with low hare density

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Abstract

The number of European brown hares (*Lepus europaeus*) has been declining throughout much of Europe since the 1960's. Consequently, many studies have focused on analysing habitat selection of European hares in order to improve the suitability of the habitat for this species. Habitat preferences of European hares are known to be affected by hare density, but most studies have been conducted in agricultural areas where hare densities were medium to high. Finding habitat preferences at high densities is difficult as most available habitats are occupied. In addition, in agricultural areas field size might influence the hares' habitat selection because it affects the distribution and availability of certain habitat types. However, most studies relate to areas with large field sizes. In this study, we analysed the habitat preferences of European hares in spring and autumn during the activity period, in the early hours of the night, in an agricultural area with low hare density and small average field size using Chesson's electivity index. Moreover, we focused on the question whether two different habitat classifications varying in their specificity might cause contradictory results regarding European hares' habitat preferences. Our results show that in this agricultural area with low hare density, European hares avoided several habitat types which were preferred in other study areas with higher hare densities. Therefore, we assume that hare density has an influence on the species' habitat selection. In contrast, the small average field size of our study area seemed not to have an effect on hare habitat preference. Furthermore, by pooling habitat types into broader groups substantial information was lost in some categories. Hence, for some categories, e.g. grassland or agricultural crop land, more detail might be needed than for others, such as urban areas, when analysing hares' habitat selection. In conclusion, our results imply that studies on habitat preferences have to be conducted in areas with low hare density to be able to gain knowledge on the species' habitat requirement and hereinafter improve the suitability of the habitat for this species.

Key Words: Brown hare, habitat selection, habitat avoidance, field size, Chesson's electivity index

Introduction

The European hare (*Lepus europaeus*) is an important game species in Europe. Since the 1960's, the number of European hares throughout Europe has been declining, also in Switzerland. The European hare is classified as threatened on the Swiss Red List (Duelli, 1994). For that reason, the hare abundances in 56 study sites have been determined annually in the Swiss Hare Monitoring since the year 1991 (Jenny &

Zellweger-Fischer, 2011). During the Europe-wide decline phase, many studies have been conducted to analyse habitat selection of European hares to be able to improve the suitability of the habitat for this species (see supplementary material for an overview). Some habitat types are consistently reported in the literature to be avoided by the European hare, e.g. residential areas (Roedenbeck & Voser, 2008; Vidus-Rosin *et al.*, 2009), or preferred by it, e.g. fallow land (Smith *et al.*, 2004; Bertolino *et al.*, 2011a; Bertolino *et al.*, 2011b). However, evidence of use of most other habitat types from different studies is contradictory in part. As an example, woodland and hedges are reported to be avoided in some studies (Tapper & Barnes, 1986; Roedenbeck & Voser, 2008; Ferrettti *et al.*, 2010; Cardarelli *et al.*, 2011; Bertolino *et al.*, 2011b) and preferred in others (Tapper & Barnes, 1986; Homolka *et al.*, 1988; Bertolino *et al.*, 2011a).

One reason why some habitat types are contentiously discussed in the literature might be that there are differences in habitat classification in the various studies. Detailed habitat type mapping is costly and the additional effort has to be compensated by producing valuable information. It is open to question how detailed a habitat classification has to be in order to represent European hares' habitat preferences satisfactorily. Moreover, some habitat categories may be more prone to change their importance for European hares than others if they are pooled into broader categories. It is therefore important to know which habitat categories have to be mapped in more detail than others to record European hares' habitat preferences.

Habitat selection in this lagomorph species is known to be affected by hare density (Jezierski, 1973; Pépin, 1986). However, all studies on habitat selection have been conducted in areas where European hare densities are between medium and high as densities range between 15 to 74 animals per 100 ha (Pielowski, 1966; Jezierski, 1968; Pépin, 1986; Tapper & Barnes, 1986; Marboutin & Aebischer, 1996; Smith *et al.*, 2004; Smith *et al.*, 2005; Pépin & Angibault, 2007; Vidus-Rosin *et al.*, 2009; Ferretti *et al.*, 2010; Cardarelli *et al.*, 2011; Bertolino *et al.*, 2011b; Vidus-Rosin *et al.*, 2011). Finding habitat preferences at high densities is difficult as most available habitats are occupied (Frylestam, 1979) due to intraspecific competition for resources and the use of unpreferred habitats by subordinate individuals. Therefore, European hares' habitat preference or avoidance in areas with high densities may differ from those in areas with low densities.

In addition, all detailed studies on habitat preferences were conducted in agricultural areas where mean field sizes range from 7 to 20 ha (Pépin, 1986; Marboutin & Aebischer, 1996; Smith *et al.*, 2004; Smith *et al.*, 2005; Pépin & Angibault, 2007). Thus, certain habitat types such as fallow land or hedges, which are often reported to be preferred by hares, might be either clumped or rare. This may influence European hares' habitat selection and effectuate different results for habitat preferences of hares living in agricultural areas with small field sizes compared to those with medium to large field sizes.

Moreover, European hares' home-ranges include resting areas used during the day and feeding areas frequented at night (Averianov *et al.*, 2003), although during summer the species' active period is not restricted to the dark phase (Holley, 2001; Schai-Braun *et al.*, 2012). Studies analysing day and night habitat preferences separately confirmed that habitat preferences differ widely depending on the European hares' activity state (Tapper & Barnes, 1986; Smith *et al.*, 2004; Cardarelli *et al.*, 2011, Bertolino *et al.*, 2011b). The European hares' feeding areas consist normally of open grounds with short vegetation (Tapper & Barnes, 1986), whereas resting areas are comprised of structured landscapes providing shelter (Tapper & Barnes, 1986; Neumann *et al.*, 2011). One study has shown that European hares selected their habitat with reference to vegetation height, and their preference depended on whether they were foraging or resting, as well as on the time of the year (Smith *et al.*, 2004). It is therefore questionable whether the vegetation height is one factor explaining the European hares' habitat preference.

The objective of this study was to evaluate habitat preferences of European hares in spring and autumn during the activity period, in the early hours of the night, in an agricultural area with low hare density and small field sizes. In particular, we focused on the question whether two different habitat classifications varying in their specificity might cause contradictory results regarding European hares' habitat preferences. Moreover, we hypothesised that the European hares' preference or avoidance for the habitat types in agricultural land during the active period can be explained by vegetation height.

Material and Methods

Study area

The study was conducted in Northern Switzerland in the canton of Basel-Land near Wenslingen (47°26'N, 7°54'E) and consisted of 989 ha of farmland composed of 32% arable crops with cereals as the main crop, 50% grassland, 4% forest, 1% permanent culture, 1% unfarmed area and 11% rural development (including buildings, gardens, etc.). The study area comprised of farmland including small villages surrounded by a forest belt. The forest belt, although not surveyed, was included in the study area in further analyses, since European hares recorded at the forest edge might use the forest as habitat (see data collection below). Field size was typical for Northern Switzerland and averaged 0.66 ha (± 0.01 SE) ranging from small plots with a minimum of 0.003 ha to large fields with a maximum of 12.17 ha. We measured vegetation height on every field in the agricultural land by the drop disc method (Holmes, 1974) to the nearest 5 cm. Excluded were tree-covered habitat types, hedge, thickets and rivulets, as their height could not be quantified accordingly. We measured homogeneous vegetation at a random point of the field, whereas for heterogeneous vegetation, where the vegetation tended to be at two different heights, we recorded the minimum and maximum vegetation heights and afterwards calculated the mean. Plants' dormancy is a period of arrested plant growth which enables for example plants to survive winter in our climate. Plants' dormant season in the study area starts in October and ends at the end of March/early April corresponding with the occurrence of temperatures below zero degrees Centigrade (Federal office of Meteorology and Climatology MeteoSwiss).

Hare density at the study site was estimated each year in autumn and spring by spotlight counts (Langbein *et al.*, 1999) and accounted on average 5.7 European hares per 100 ha (± 0.18 SE) during the study period (Zellweger-Fischer, 2010). Hare numbers remained stable along the three years of the study. As the study site is remotely located, there is little disturbance by leisure activities, such as horse riding, jogging or dog walking, and 47% of the roads surface area is not tarred.

Data collection

From autumn 2007 until spring 2010, European hares were counted twice both in late March/early April and in November. Spotlight counts were done in the agricultural land on roads from a car driving at a speed of 15-20 km per hour. The forest belt and the residential areas were excluded from the spotlight count transect as European hares are reported to use open fields during the activity period (Tapper & Barnes, 1986). Spotlight counts for each hare survey were done on two nights per season along four transects of total 61.48 km length by the local hunters. Thereby, the complete agricultural land of the study area (915 ha) was illuminated during each spotlight count. The position of each European hare was mapped and later digitised with the software ArcGIS 9.1 (ESRI). In the same months of the hare surveys, the landscape composition and agricultural use was recorded and digitised. Thereby, a different map of land use was created for each hare survey by taking a ground-truthed land register map as basis. If the land use of a parcel, the minimum unit mapped, was not consistent, the boundaries within the parcel were determined by using a hand held GPS-device. The land use was mapped as accurately as possible for the season. This resulted in a classification comprising 29 habitat types (Tab. 1, 2).

Table 1: The 29 habitat types used to classify the study site's land use with the vegetation height (cm), a rough classification into five categories and their area covered in percent. A description is only given if necessary.

Landscape Variable	Description	Median (± SE)	Min	Max	N	Classification	Area [%]
Forest	Rich brown-mull beech wood (*Galio odorati-Fagetum pulmonarietosum*)	-	-	-	-	Tree-covered habitat	3.67
Tree nursery		-	-	-	-	Tree-covered habitat	0.17
Dwarf orchard	Intensively managed short-lived, high-density dwarf fruit tree orchards	-	-	-	-	Tree-covered habitat	1.06
Set-aside	Field sown with wildflowers	130 (± 3.2)	5	200	264	Unfarmed areas	1.97
Edge	Strip sown with wildflowers	20 (± 1.7)	20	60	9	Unfarmed areas	0.03
Hedge, thicket	Hedgerows with an herbaceous strip	-	-	-	-	Unfarmed areas	0.98
Rivulet	Rivulets with an herbaceous strip	-	-	-	-	Unfarmed areas	0.11
Fallow land	Uncultivated fields	20 (± 1.4)	15	80	30	Unfarmed areas	0.10
Species-rich pasture	Cattle, sheep or horse pasture not fertilised, species-rich, characteristic plant species are listed in Tab. 2	15 (± 0.5)	10	15	27	Grassland	0.29
Pasture	Cattle, sheep or horse pasture fertilised, plant species listed in Tab. 2 are absent	15 (± 0.2)	0	30	561	Grassland	12.38
Unimproved grassland	Grassland not fertilised, species-rich, characteristic plant species are listed in Tab. 2	15 (± 0.3)	5	30	375	Grassland	4.55
Semi-improved grassland	Grassland lightly fertilised, plant species listed in Tab. 2 are absent	15 (± 0.1)	5	30	1641	Grassland	15.01
Improved grassland	Grassland fertilised, sown with a few grass and/or clover species, ploughed after 1 to 3 years	10 (± 0.1)	5	30	894	Grassland	19.55
Harrowed acre		0 (± 0.0)	0	0	222	Arable crop	1.92
Ploughed acre		0 (± 0.0)	0	0	45	Arable crop	0.52
Grubbed acre		0 (± 0.0)	0	0	6	Arable crop	0.08
Stubble field		15 (± 1.1)	5	30	33	Arable crop	0.41
Germinating seed	Crop plant not yet identifiable	5 (± 0.1)	0	15	213	Arable crop	2.36
Winter grain		10 (± 0.1)	5	19	678	Arable crop	18.37
Winter oilseed rape		25 (± 0.5)	0	35	156	Arable crop	3.93
Grain legumes		5 (± 0.0)	5	5	6	Arable crop	0.34
Vegetables		25 (± 0.0)	25	25	3	Arable crop	0.09
Intertillage	Phacelia, sunflowers, others	40 (± 4.3)	0	150	63	Arable crop	0.59
Track completely vegetated		-	-	-	-	Urban areas	0.34
Gravel walk partially vegetated		-	-	-	-	Urban areas	0.69
Gravel walk unvegetated		-	-	-	-	Urban areas	0.67
Tarred road		-	-	-	-	Urban areas	1.94
Residential area		-	-	-	-	Urban areas	7.39
Gardens, allotments, graveyards		-	-	-	-	Urban areas	0.43

A rough classification containing 5 categories pooled all the 29 study site's habitat types into broader groups. The classifications of the habitat types were the same for each hare survey. Around each point where a European hare was mapped, a circle with the size of 25 ha was drawn. We chose 25 ha circles since small home-range sizes of European hares in agricultural landscapes are recorded to be around 25 ha (see for an overview Smith *et al.*, 2004). We assumed that our study animals had small home-ranges because average field size seems to influence the European hares' home-range size and our study area's average field size was small. Only European hare points whose circle area was located at least 75% within the study area were used for further analyses. Subsequently, the landscape composition within the circle was evaluated assuming that the habitat types within the circle were actually being used by the individual hare. For every 100 ha of the study area eight random points were selected per season and year. Since no data on hare presence were collected in the forest and residential areas, all random points within these two habitat types were discarded to avoid bias. The same procedure as used for the European hare points was applied to the random points. This resulted in a total of 601 random points and 612 European hare positions used for analysis. Note that we performed the same analysis with a larger assumed home-range (50 ha circles), but the results did not differ.

Table 2: Plant species characteristic for the species-rich pasture and unimproved grassland.

Scientific name	
Achillea millefolium	*Gaudinia fragilis*
Achillea roseoalba	*Heracleum sphondylium*
Anthriscus sylvestris	*Knautia arvensis*
Arrhenatherum elatius	*Leucanthemum vulgare*
Avenula pubescens	*Malva moschata*
Campanula patula	*Peucedanum carvifolia*
Carum carvi	*Rhinanthus alectorolophus*
Centaurea jacea	*Silene vulgaris*
Centaurea nigrescens	*Tragopogon orientalis*
Cirsium oleraceum	*Tragopogon pratensis*
Crepis biennis	*Trifolium dubium*
Galium album	*Trisetum flavescens*
Galium mollugo	

In different parts of an area an unequal visibility of hares may be caused by structures e.g. hedges in the landscape (Pegel, 1986; Roedenbeck & Voser, 2008). Such unequal visibility would result in a non-random distribution of the hares missed during the spotlight counts. Nevertheless, we assume this to be negligible in our study since structured habitat types such as set-aside, tree nursery, dwarf orchard, gardens, allotments, graveyards and vegetable fields comprised only 3.7% of the study area's landscape (Tab. 1) and as few as 5.6% of all fields had a hedge.

Data analysis

The European hares' habitat preferences were measured by using Chesson's electivity index ε (Chesson, 1983), an index based on Manly's alpha (Manly *et al.*, 1972) which can be used to analyse habitat preferences (Krebs, 1989), among others. We chose Chesson's electivity index, because it has the advantage that results between cases for which the number of available habitat types vary are comparable. The Chesson's electivity index ranges between -1 and +1, with negative values showing a negative selection, whereas positive values signify a positive selection. If the index value is zero, the habitat type concerned is used in the same proportion as it is available. We calculated on the one hand the Chesson's electivity indices for each of the 29 habitat types and on the other hand for each habitat type of the rough categorisation. The reliability of the electivity indices were tested using the bootstrap method (Dixon, 1993). The original ε_i values (ε_i = Chesson's electivity index for the habitat type i) were resampled 1000 times with replacement and an accelerated bootstrap confidence interval was calculated (Fig. 1). The accelerated bootstrap adjusted the confidence interval for bias and skewness (Efron & Tibshirani, 1993). If the two values of the lower and upper boundary featured the same algebraic sign, the selection for this habitat type was significant. All analyses were done with the software R 2.12.0 (R Development Core Team, 2011).

Results

Rough categorisation of all habitat types

A rough classification of all the study site's habitat types into broader groups showed that both in spring and autumn the European hares avoided urban areas, unfarmed areas and grassland, whereas for agricultural crop land this species displayed no significant preference (Fig. 1). Moreover, the animals preferred tree-covered habitats in spring, while in autumn there was no significant selection for this habitat type recordable. Except for urban areas, the variability in European hare preferences within each of the rough categories was considerable.

The 29 different habitat types

In tree-covered habitats, European hares displayed avoidance of forest and dwarf orchards both in spring and autumn. Compared to this, tree nurseries were not significantly selected. We found that in spring and autumn, hares had a high preference for grubbed acres, but avoided winter oilseed rape and winter grain. The species positively selected germinating seeds and showed no significant selection for the other habitat types within the category agricultural crop land in spring. In contrast, ploughed acre, intertillage, vegetables and stubble fields were preferred and harrowed acre and germinating seed were avoided by the animals in autumn. Note that grain legumes were not available in autumn. In both seasons, our results showed a significant avoidance of all types of grassland except species-rich pasture, which was highly preferred. When looking at the different types of unfarmed areas separately, the European hares expressed in spring and autumn a preference for rivulets and field margins. In contrast, hedges, thickets and set-asides were avoided. Besides, the hares preferred fallow land in spring, but expressed no significant preference for the same habitat type in autumn. European hares avoided residential areas and gardens, allotments and graveyards both in spring and autumn. Furthermore, hares negatively selected all types of roads.

Vegetation height of the habitat types in the agricultural land

The vegetation height of 5226 fields recorded in the agricultural land during the three study years was on average 15 (± 5.9 SE) cm high with a minimum of 0 cm and a maximum of 200 cm. Only in the category unfarmed areas did the measured vegetation heights vary substantially between the different habitat types (Tab. 1).

Discussion

Rough categorisation of all habitat types

The rough categorisation of all habitat types into broader groups revealed a negative selection by the European hares for the unfarmed and urban areas in spring and autumn. That urban areas are avoided by active European hares has been suggested by different studies (Roedenbeck & Voser, 2008; Vidus-Rosin *et al.*, 2009). The avoidance of unfarmed areas is, however, more difficult to interpret. The reason for this might be that different kinds of habitat types with variable vegetation structures were pooled into this one category. European hares showed an electivity index around zero or no selection at all for the other three categories. Our results imply that it is most important to differentiate between the studied habitat types in relation to vegetation height, cover, composition, etc. and to avoid the pooling of habitat types differing in these premises in order to avoid losing information. Hence, for some categories, e.g. grassland or agricultural crop land, where selection varied widely, more detail might be needed as for others, such as urban areas, where all subcategories were systematically avoided. The pooling of habitat types might therefore be responsible for controversially discussed habitat types such as grassland and pastures in the literature about active European hares' habitat preferences (Frylestam, 1980; Barnes *et al.*, 1983; Tapper & Barnes, 1986; Smith *et al.*, 2004; Cardarelli *et al.*, 2011; Bertolino *et al.*, 2011b).

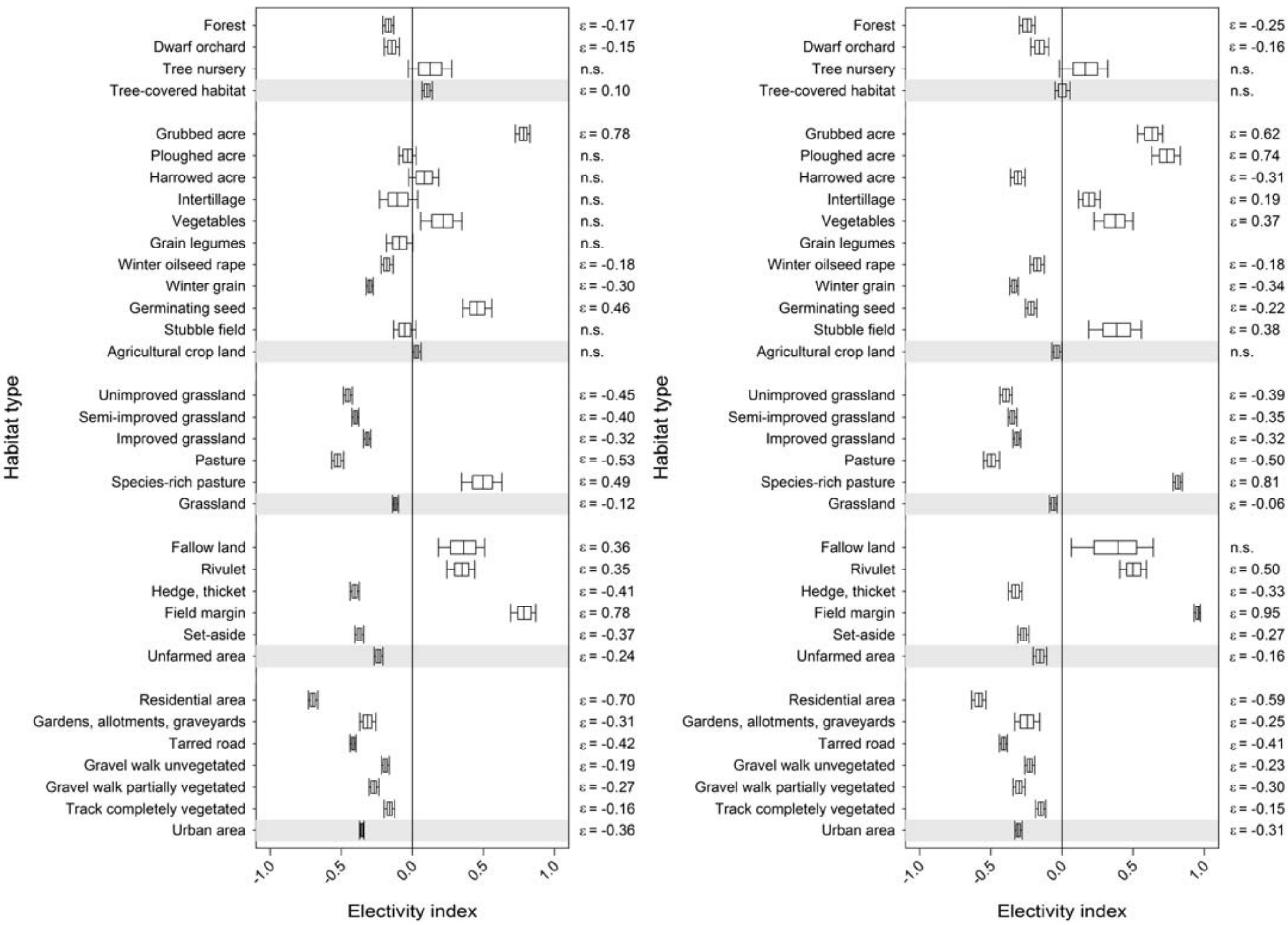

Figure 1: Chesson's electivity indices and their distributions of 1000 bootstrap resamples (medians with 25th/75th and 10th/90th percentiles) for all habitat types based on the analysis of (a) spring and (b) autumn. The habitat types of the rough categorisation are indicated by grey shading. Not significant results are marked with the abbreviation n.s. See text for details on statistics.

The 29 different habitat types

1. Tree-covered habitat types

European hares in spring and autumn negatively selected forests and dwarf orchards, but expressed no significant selection for tree nurseries. All three habitat types are unfavourable for hares during the activity period with respect to the vegetation structure which inhibits an open view. However, hares might use tree nurseries as feeding grounds during the plants' dormant season. In another European hare study, mostly needles of coniferous trees and shoots of trees and shrubs were found in the stomach during winter when availability of herbage is impaired (Homolka, 1982). Dwarf orchards in the study area are protected against large herbivores by wire fences. This might also impede smaller herbivores from using dwarf orchards as feeding grounds because the access to the trees is restricted and, therefore, make this habitat type less accessible for European hares.

2. Agricultural crop land

European hares in spring and autumn expressed a strong preference for grubbed acres. Grubbed acres still offer a fraction of the dug-over field crop or grassland at the field surface which might be used in the plants' dormant season by the European hares as a food source. Winter grain and oilseed rape were negatively selected in spring and autumn by European hares. Freshly grown winter grain is reported to be a widely used food source for European hares (Nesvadbová & Zejda, 1989; Reichlin *et al.*, 2006). Nevertheless, it has been shown that European hares mostly did not positively select winter wheat because its availability was high compared to other food sources (Reichlin *et al.*, 2006). This supports our findings. All other habitat types of the rough category agricultural crop land were selected differently in spring and autumn. In spring, European hares were attracted probably to germinating seeds as a food source. The habitat types which were used by European hares without significant selection in spring might not be attractive as forage because they consist either of bare ground or vegetation from the last year. In contrast, intertillage, vegetables and stubble field might offer forage for the animals in autumn.

3. Grassland

European hares in spring and autumn avoided grassland of any type except species-rich pastures. Jennings *et al.* (2006) argue that European hares from pastural landscapes obtain a good-quality diet, but expend more energy and have a reduced body condition in comparison to those from arable areas. Grassland as a suboptimal habitat for European hares might therefore explain our findings of a general avoidance of this habitat type especially as our study was conducted in the plants' dormant season. Fertilised pastures were avoided most, whereas unfertilised and therefore species-rich pastures were preferred most among the different types of grassland. Because unimproved grassland and species-rich pastures had about the same plant associations, plant diversity alone cannot explain the hares' strong preference for species-rich pastures. Active European hares preferred sheep grazed pastures only during winter (1 February -13 March) but selected cattle pasture throughout the year (Smith *et al.*, 2004). In addition, strong differences between vegetation height of sheep grazed fields and cattle fields during October-March have been recorded (Petrovan *et al.*, 2011). Hence, European hares seem to use pasture differently depending on the season, vegetation height or kind of livestock. In our study, both types of pasture had about the same vegetation height, but we did not distinguish between cattle, horse or sheep pasture. We therefore conclude that the combination of high plant diversity due to omission of fertilisation and the vegetation structure, caused by grazing livestock, created a highly attractive habitat type for European hares during spring and autumn.

4. Unfarmed area

The category unfarmed areas comprised different habitat types. The European hares' selection for the habitat types set-aside, field margin and fallow land was noticeably different. A possible explanation is the different vegetation structure. Since active European hares prefer open grounds with short vegetation for feeding (Tapper & Barnes, 1986), we assume that the open vegetation of field margins and fallow land were preferred, whereas the more structured vegetation of set-asides was avoided. Probably for the same reason, the hedges, thickets with high and dense vegetation were negatively selected by the European hares. The European hares preferred fallow land in spring but showed no significant selection for the same habitat type in autumn. We assume that in autumn the species finds enough alternative habitat types attractive for foraging, whereas in early spring suitable food is less abundant and hence fallow land becomes preferred.

5. Urban areas

Urban areas consisted not only of residential areas but also of gardens, allotments and graveyards. European hares strongly avoided residential areas. Since gardens, allotments and graveyards contain a high variety of different plants, they might be attractive to hares. Despite this fact, European hares in our study negatively selected these habitat types. Possible explanations for this might be that, firstly, the disturbance caused by humans is considerable, and secondly, these areas are mostly surrounded by a wire fence which makes it difficult for animals to enter the property. European hares avoided roads in general. Tarred roads had the lowest preference index, whereas tracks completely vegetated had the highest preference index among the different road types. It has been argued that the vegetation along and on field tracks and unpaved roads contribute to the hares' diet spectrum (Roedenbeck & Voser, 2008). Additionally, the construction level of the road is closely linked with the amount of traffic, i.e. disturbance for the hares (Roedenbeck & Voser, 2008). Both explanations fit our results.

6. Influence of the vegetation height on the European hares' habitat preference

The vegetation height seemed to explain the European hares' habitat avoidance during activity only when the vegetation was substantially high such as in set-asides. For habitat types with a marginally higher vegetation height than average, such as intertillage, vegetables or winter oilseed rape, other criteria for the hares' selection during activity, like suitability for forage, might be more important than the vegetation structure. This supports another European hare study recording some crop types used day and night when fulfilling requirements for feeding and resting (Tapper & Barnes, 1986). Moreover, for European hares not only vegetation height but also cover value are crucial for their habitat selection (Neumann *et al.*, 2011). Vegetation height and cover might vary in the same habitat type especially during the plants' dormant season. A combination of vegetation height and cover value may therefore explain the European hares' habitat preference more accurately during this time of the year.

7. Influence of the hare density on habitat preferences

Some habitat types such as woodland/forest, hedges, cereals and improved grassland were unattractive to the European hares in our study. When comparing our results with other studies on active European hares, it seems that these habitat types changed to being attractive when hare density increased (Tapper & Barnes, 1986; Smith *et al.*, 2004; Vidus-Rosin *et al.*, 2009; Cardarelli *et al.*, 2011; Bertolino *et al.*, 2011b; Tab. 3). A possible explanation might be that at high densities unpreferred habitats become attractive to European hares due to intraspecific competition for resources.

Table 3: Comparison of different studies investigating European hares' habitat preferences during the night classified according to hare density (number of hares per 100 ha). Results for a specific season are indicated by sp (spring), su (summer), au (autumn) and wi (winter).

Autor(s)	Year	Hare density	Urban areas	Hedge, thicket	Rivulet/ shores	Fallow land	Grassland	Pasture	Improved grassland	Agricultural crop land	Stubble field	Germinating/ short crops	Cereals	Ploughed acre	Poplar	Woodland/ Forest
this study		5.7	-	-	+	+ sp, n.s. au	-	-	-	n.s.	n.s. sp, + au	+ sp, - au	-	n.s. sp, + au		-
Bertolino *et al.*	2011b	0-29.9			+	+	+				n.s.			-	-	-
Smith *et al.*	2004	15.9				+ sp, su, au		+	+ wi	- wi						
Cardarelli *et al.*	2011	55	n.s.			n.s.	n.s.				n.s.	n.s.			+	n.s.
Tapper & Barnes	1986	64		+				-					-			+
Vidus-Rosin *et al.*	2009	74.1							+				+	-		

Table 4: Comparison of different studies investigating European hares' habitat preferences classified according to field size. Note that the studies differ in the time of recording (day, night, day & night). Results for a specific season are indicated by sp (spring), su (summer), au (autumn) and wi (winter).

Autor(s)	Year	Mean field size	Fallow land	Pasture	Improved grassland	Agricultural crop land	Cereals	Grain legumes	Harrowed acre	Ploughed acre
this study		0.78 ha	+	-	-	n.s.	-	n.s.	-	+
Smith *et al.*	2005	6.6 ha	n.s.	+ sp, su	+ au		- au			
Smith *et al.*	2004	6.6 ha	+ sp, su, au	+	n.s.	n.s.				
Pépin & Angibault	2007	7 - 12 ha					n.s.		-	+
Pépin	1986	15-20 ha		-			+		-	+
Maroutin & Aebischer	1996	20 ha					+	+		

8. Influence of the mean field size on habitat preferences

Our study animals living in an agricultural landscape with small average field sizes appeared not to select habitat types differently than animals in study areas with larger average field sizes (Tab. 4). This supports the findings of other studies reporting that in agricultural areas with large field sizes European hares mostly enlarge their home-range size in order to include the required habitat types (Reitz & Léonard, 1994; Stott, 2003; Smith *et al.*, 2004). Note that, regarding the influence of mean field size on the habitat preferences, the results of our active study animals were not compared to studies on European hares during activity exclusively, as information on average field size in the literature is mostly missing.

9. Difference between the two seasons spring and autumn

European hares selected more habitat types positively (8 vs. 6) but chose less habitat types without significant selection in autumn than in spring (2 vs. 7). All differences between the two seasons were due to an altered habitat selection in the rough categories agricultural crop land and unfarmed areas. Possibly, these changes in habitat preferences were caused by remaining field crops getting old and new field crops starting to sprout at the end of the plants' dormant season. In contrast, in another study on active European hares changes in preferences of grassland were recorded additionally along the seasons (Smith *et al.*, 2004). Probably this is due to a higher percentage of grassland in Smith's than in our study area (71% vs. 50%)

Conclusion

In summary, we found that substantial information was lost by pooling habitat types into broader groups in some categories. Hence, for some categories more detail might be needed as for others when analysing hares' habitat selection. In this agricultural area with low hare density, European hares avoided several habitat types which were preferred in other study areas with higher hare densities. Therefore, we assume that hare density has an influence on the species' habitat selection. Moreover, the vegetation height seemed to explain the species' habitat selection only when the vegetation was substantially high. In conclusion, our results imply that studies on habitat preferences have to be conducted in areas with low hare density to be able to gain knowledge on the species' habitat requirement and hereinafter improve the suitability of the habitat for this species.

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Supplementary material

Autor(s)	Year	Time	Urban areas	Roads	Field edges	Shrubs	Hedge, thicket	Rivulet/ shores	Fallow land	Grassland	Stock-free pasture	Pasture	Improved grassland	Unimproved grassland	Agricultural crop land	Stubble field
this study		night	-	-			-	+	+	-		-	-	-	n.s.	n.s.
Bertolino *et al.*	2011b	night				-		n.s.	n.s.	+						n.s.
Cardarelli *et al.*	2011	night	n.s.		+				n.s.	n.s.						-
Vidus-Rosin *et al.*	2009	night	-										+			
Roedenbeck & Voser	2008	night	-	-			-							+		
Smith *et al.*	2004	night							+ sp, su, au			+ sp, su, au	+ wi		- wi	
Tapper & Barnes	1986	night					-				n.s.	+				
Barnes *et al.*	1983	night									+	-			-	
Frylestam	1980	night										-	+			-
Bertolino *et al.*	2011a	day				+ sp, su, wi			+	- au, wi						+ au
Bertolino *et al.*	2011b	day				n.s.		+	+	n.s.						n.s.
Cardarelli *et al.*	2011	day	n.s.		+				n.s.	n.s.						-
Ferretti *et al.*	2010	day														
Pépin & Angibault	2007	day														
Smith *et al.*	2004	day							+ sp, su, au			+	n.s.		n.s.	
Homolka *et al.*	1988	day					+									
Pépin	1986	day										-				
Tapper & Barnes	1986	day					+				n.s.	-				
Barnes *et al.*	1983	day									+ au, -wi	- au, + wi			- au, + wi	
Jezierski	1968	day														
Jezierski	1968	day														
Pielowski	1966	day														
Vidus-Rosin *et al.*	2011	day & night	-		n.s.								+ au			
Cardarelli *et al.*	2011	day & night	n.s.		n.s.				n.s.	n.s.						n.s.
Smith *et al.*	2005	day & night							n.s.			+ sp, su	+ au			
Maroutin & Aebischer	1996	day & night														
Tapper & Barnes	1986	day & night					+				+	-				

Autor(s)	Year	Time	Germinating/ short crops	Cereals	Rape	Grain legumes	Root crops	Rice	Harrowed acre	Ploughed acre	Orchard	Vineyards	Poplar	Woodland/ Forest
this study		night	n.s.	-	-	n.s.			-	+				-
Bertolino *et al.*	2011b	night		+				-		-			-	-
Cardarelli *et al.*	2011	night	n.s.							n.s.			n.s.	-
Vidus-Rosin *et al.*	2009	night		+						-		-		
Roedenbeck & Voser	2008	night									+			
Smith *et al.*	2004	night												
Tapper & Barnes	1986	night		n.s.			n.s.							-
Barnes *et al.*	1983	night												
Frylestam	1980	night		+	+		-			-				
Bertolino *et al.*	2011a	day		+ sp, - au			- sp, su			- wi			n.s.	+ au
Bertolino *et al.*	2011b	day		-				-		n.s.			-	-
Cardarelli *et al.*	2011	day	n.s.							-			n.s.	-
Ferretti *et al.*	2010	day									-	-		-
Pépin & Angibault	2007	day		n.s.					-	+				
Smith *et al.*	2004	day												
Homolka *et al.*	1988	day												
Pépin	1986	day		+					-	+				
Tapper & Barnes	1986	day		n.s.			n.s.							+
Barnes *et al.*	1983	day												
Jezierski	1968	day		n.s.						n.s.				
Jezierski	1968	day		-						-				
Pielowski	1966	day		-						- sp, au, + wi				
Vidus-Rosin *et al.*	2011	day & night		n.s.										
Cardarelli *et al.*	2011	day & night	n.s.										+	n.s.
Smith *et al.*	2005	day & night		- au										
Maroutin & Aebischer	1996	day & night		+		+	+							
Tapper & Barnes	1986	day & night		-			+							+

Fourth Chapter

European hares select resting places for providing cover

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Photo: Stéphanie Schai-Braun

Abstract

European hares (*Lepus europaeus*) are thought to select resting places providing cover, to protect themselves against predators and unfavourable weather conditions. We tested this hypothesis by flushing wild hares from their resting places and by assessing the cover at hare forms. The vegetation at resting places was generally found to be higher than 30 cm, *i.e*. higher than the approximate height of a hare. As compared to randomly chosen control points, hares showed a preference for cover at their resting places throughout the year. From April to August, all investigated habitat categories, but most often field habitats were used for resting places, and during this season, vegetation providing cover above 30 cm was found in all habitat categories. From September to March, however, resting places were mostly found in forests or in areas between fields, whereas open fields with little or no vegetation were generally avoided as resting sites. Furthermore, we found that flight distances depended on cover value and were lower in dense vegetation, suggesting that hares valued resting places providing cover as a better protection against predators. We suggest that the loss of cover in agricultural landscapes has reduced the availability of resting places for the European hare and has likely contributed to the population decline in intensely used landscapes.

Key Words: *Lepus europaeus*; Agriculture; Cover value; Form; Resting place

Introduction

In Europe, farmland is the main habitat of the European hare (*Lepus europaeus*). Hares are generally more abundant in arable areas than in pastures, uplands and woodlands (Vaughan *et al*., 2003; but see Karmiris & Nastis, 2007). However, since the second half of the last century, hare populations have declined throughout Europe (Smith *et al*., 2005a). In Switzerland, a nation-wide survey showed that hare populations have continued to decline since 1991 until the end of the century (Fischer, 2009). Nowadays, in Switzerland, mean hare population density is less than 3 hares per km^2 (Zellweger-Fischer, 2010). The main reason for this decline seems to be the intensification of agriculture after World War II, *i.e.* increased mechanization, loss of habitat diversity and increased homogeneity in habitat structure both in time and space (Robinson & Sutherland, 2002; Benton *et al*., 2003; Smith *et al*., 2005a). For hares, heterogeneity within and between habitats seems to be important, heterogeneous habitats allowing a more varied diet and offering cover throughout the year (Smith *et al*., 2004). Open fields or grassland are mostly used when hares are active at night (Tapper & Barnes, 1986), while those habitats providing both food and resting places seem to be used both at night and during the day (Tapper & Barnes, 1986). During the day, hares usually rest on the ground in a depressed area, known as “form”. The cover provided at forms may be essential to protect against predators and unfavourable weather conditions (Tapper & Barnes, 1986; Pépin, 1989; Fernex *et al.*, 2011). In areas with high recreational activity, cover is also likely to be important to protect against man. However, the cover provided by vegetation may change seasonally according to vegetation type. If hares select resting places for cover, also habitat selection should thus vary with the time of the year. Indeed, some studies found seasonal changes in daytime habitat use by European hares (Tapper & Barnes, 1986; Pépin, 1987; Rühe & Hohmann, 2004; Pépin & Angibault, 2007). In intensely used landscapes, habitats offering cover all year round, such as fallow land or forests, are thought to be particularly important (Vaughan *et al.*, 2003; Smith *et al.*, 2004; Holzgang *et al.*, 2005), but little is known about selection for resting places in hares (Angelici *et al.*, 1999).

In this study, we tested the hypothesis that habitats selected by hares for resting places should vary according to seasonal variation in vegetation cover. We predicted that in cultivated fields, resting places should be found more frequently in spring and summer, when crops and grassland are high, than in autumn and winter, when there is little or no cover. We investigated habitat use at daytime resting places by flushing resting hares in north-western Switzerland. We compared the distribution and vegetation structure of resting places between two study periods: from April to August and from September to March. If hares select resting places for providing cover, we predicted that at resting places, there would generally be cover above 30 cm, *i.e.* above the approximate height of a hare. Furthermore, we investigated how flight distance varied with cover values at forms. If dense cover at forms is perceived by hares to enhance their protection from predators, we predicted that flight distance would be lower at forms in denser vegetation.

Material and Methods

Field work took place from January 2008 to October 2009 in two agricultural landscapes in the Canton of Baselland, north-western Switzerland. The first area covered 9.88 km^2 and was located East of Basel, near Wenslingen, on a plateau of the Tabel Jura, at 500-800 m a.s.l. The second area covered 8.42 km^2 and was located about 27 km west of the first area, near Reinach, at 300-450 m a.s.l. In both study sites, hares were counted in spring and autumn from a moving car using spotlights at night (Langbein *et al.*, 1999; Heynen, 2008; Fischer, 2009). Hare population densities varied from about 6 hares per km^2 in the study area at Wenslingen to about 2 hares per

km^2 at Reinach. Wood covered 24.9% of the study area at Wenslingen and 17.8% at Reinach. Vegetation in open fields was dominated by grassland (including pastures; Wenslingen: 58.3%; Reinach: 54.6%), followed by crops (including a small proportion of fallow land; Wenslingen: 39.1%; Reinach: 39.2%) and non-forested natural areas (Wenslingen: 1.3%; Reinach: 2.3%).

Resting places were searched for a total of about 11 days each month. Transects were chosen haphazardly, as to cover the following habitat categories at roughly balanced proportions: Crops (cereal, rape), Between Fields (fallow land, hedgerow, field borders), Pasture, Grassland, and Forest. Crops of maize and pea were excluded because they were too dense to observe hares. To find as many hares as possible, transects were walked in loops. In open and low fields, loops were broader (tracks of a transect loop were 20–40 m apart) than in dense and high fields (2–20 m). To avoid field damage in cereal and rape, only machine tracks and fields borders were walked. A total of 48 different resting places were detected by flushing hares and scanning the ground. On 45 occasions, the exact location of the form could be determined from its smell and the presence of hairs. On three additional occasions, the location of the resting place could be determined to an accuracy of about 4 m^2, but the form was not found.

Cover was assessed as the percentage of a 1 m^2 large circle centred on each form (N=45) covered by any sort of material, both natural (mainly herbs and shrubs) and man-made (e.g., fences). We estimated cover value only for structures between 30 cm, which can completely hide a resting hare, and 150 cm. We also measured maximum vegetation height, for which we included structures up to 5 m, but did not include the tree layer. For each resting place (N=48), one control point was randomly selected within a radius of 500 m, and the habitat category around the control point was recorded.

For 35 hares, the flight distance from the observer to the middle of the form at the moment of flushing was measured to the nearest 10 cm.

All statistical analyses were carried out using R 2.9.2 (R Development Core Team, 2009), results are presented as mean ± s.e., and all tests were two-tailed. Chi-square (χ^2) tests were applied to compare the counts of forms in the different habitats between seasons and in relation to control points, while t-tests were used to test for differences in cover values and vegetation height between the two study periods. Linear regression was used to test for the relationship between flight distance and cover value.

Results

1. Daytime habitat use

Resting places (N=48) were found in all five available habitat categories (Tab. 1), but the use of these five habitats differed between the two study periods (χ^2_4 = 10.62, P = 0.031). When grouping all open habitats into a single category called "fields", resting places were mainly found in fields from April to August, and in forest from September to March (χ^2_1 = 4.53, P = 0.033).

In contrast, the distribution of randomly selected control points (N=48) did not significantly differ between the two study periods (χ^2_5 = 1.28, P = 0.94), also when examining the two broader categories fields and forest (χ^2_1 = 0.04, P = 0.85).

When comparing the distribution of resting places in fields and forest from April to August with the distribution of control points for the same study period, we did not find a significant difference (χ^2_1 = 0.78, P = 0.38). In contrast, from September to March, the distribution of resting places was significantly different from the distribution of control points (χ^2_1 = 7.16, P = 0.007), suggesting that in autumn and winter, hares preferred to rest in forests rather than in fields.

Table 1: Numbers of resting places (N=48) of European hares and of randomly selected control points (N=48) per habitat category. See text for details.

	Resting places		Control points	
Habitat/Month	April-August	Sept.-March	April-August	Sept.-March
Crop	2	0	3	4
Between Field	5	5	1	1
Pasture	4	0	5	5
Grassland	3	0	7	4
Road	–	–	2	1
Forest	11	18	7	8
Field	14	5	18	15
Forest	11	18	7	8

2. Characterization of forms

Forms of hares were mainly found at places that offered cover: the mean (± s.e.) cover value in 30–150 cm height was 26 ± 20.6% (Fig. 1). Note that in total, 25 of 45 forms were found in forests. The cover values at forms were similar between the two study periods (Fig. 2; Student's t-test, t_{41} = -0.35, P = 0.73).

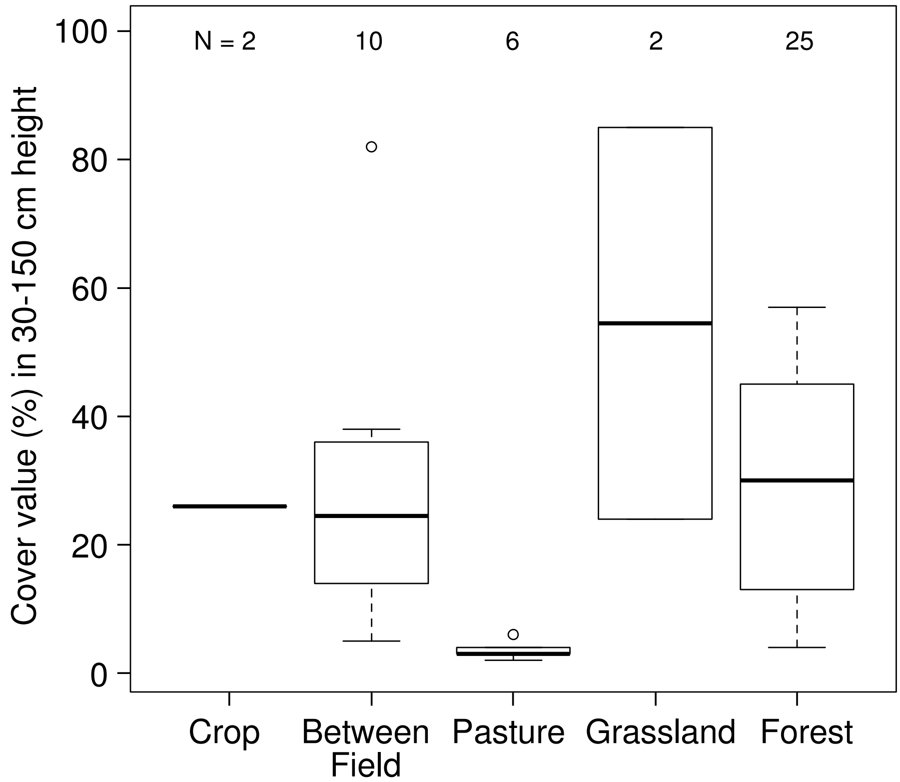

Figure 1: Percent cover values at hare forms for five main habitats; boxes are median and 25th and 75th percentiles, whiskers are non-outlier ranges, dots are outliers.

Mean maximum vegetation height at forms was 125 ± 64.4 cm (Fig. 3), significantly higher than the height of hares (one-sample t-test against an expected value of 30 cm vegetation height: t_{43} = 9.79, P < 0.001), and maximum vegetation height did not significantly vary between the two study periods (Fig. 4; t_{40} = -1.36, P = 0.18).

Between fields, forms were found in high grass, and near or below herbs and bushes. In the forest, forms providing cover were found at the trunks of trees, below bushes, around or below dead wood and broken branches with leaves, and below the European holly (*Ilex aquifolium*). In grassland, forms were often a depressed area surrounded by high grass, while in pastures, forms were next to high herbs or at fences, mostly on less intensely grazed hillsides, and were often deepened into the ground below high herbs. In crops, forms were found only in higher stages, but no resting hare was recorded in the tracks used for agricultural machines.

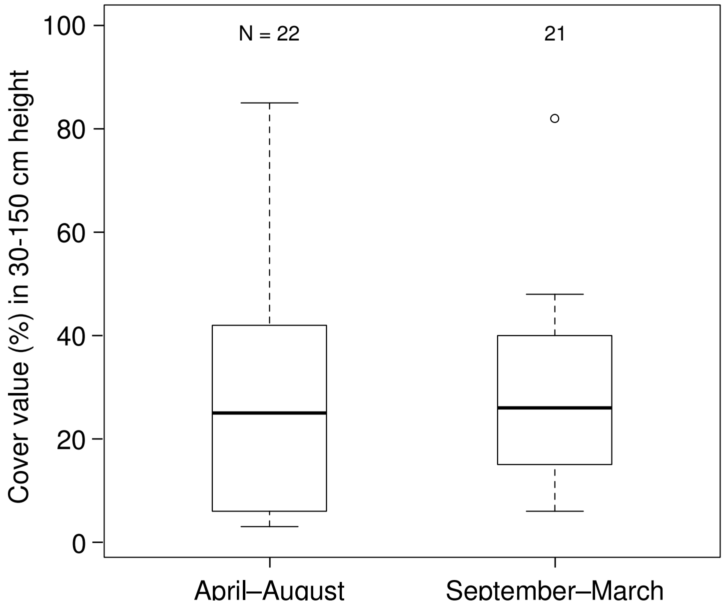

Figure 2: Percent cover values at hare forms in the two study periods.

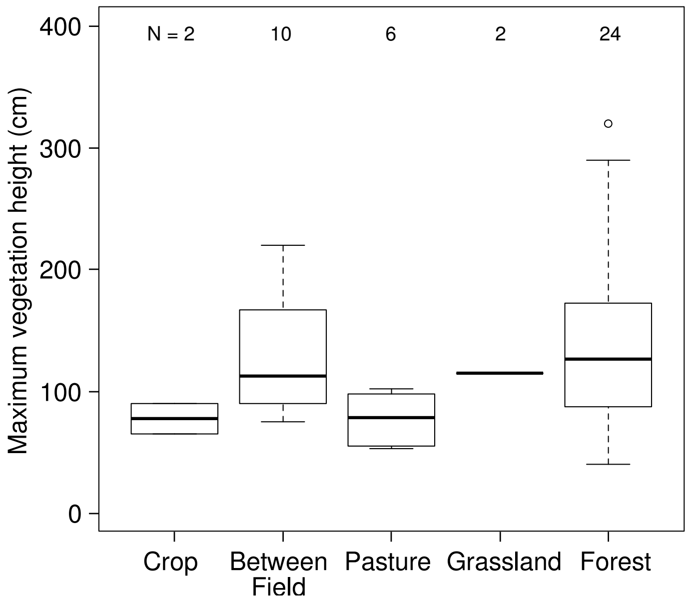

Figure 3: Maximum vegetation height at hare forms for five main habitats.

3. Flight distance

Mean flight distance was 9.4 ± 6.8 m (N=35). Flight distances were shorter at forms offering high cover between 30 and 150 cm height than at scarcely covered places (Fig. 5; regression, slope = -0.11, s.e. = 0.049, t = -2.30, P = 0.028, r^2 = 0.14).

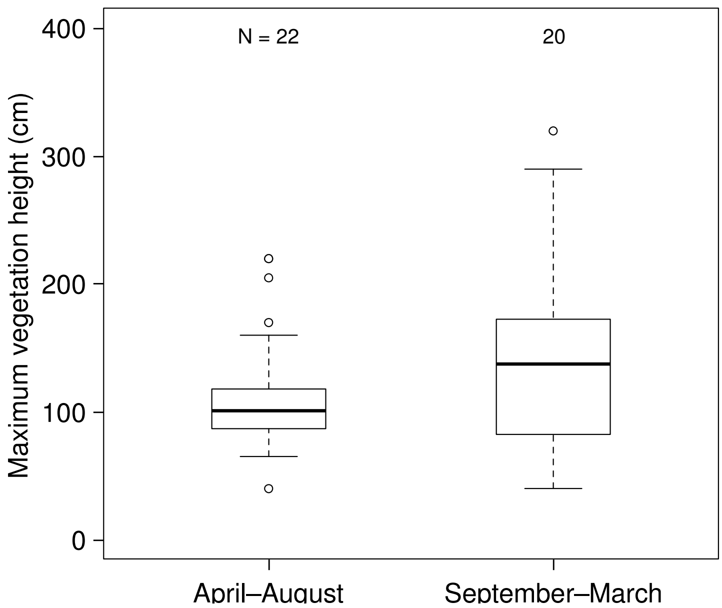

Figure 4: Maximum vegetation height at hare forms in the two study periods.

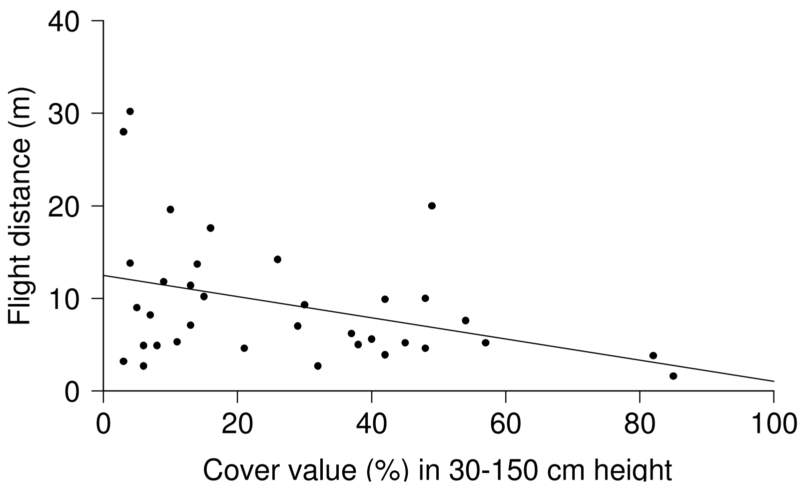

Figure 5: Regression of flight distance of hares on cover value at hare forms (N=35).

Discussion

In our study areas, hares faced with seasonal variation in the cover offered by available habitats apparently responded by changing the location of resting places accordingly. As vegetation at resting places was generally higher than 30 cm, *i.e.* higher than the approximate height of a hare, we conclude that hares selected resting places for providing cover throughout the year. Several studies reported that cover is important for resting hares (Tapper & Barnes, 1986; Pépin, 1987; Smith *et al.*, 2005a, b; Jennings *et al.*, 2006; Macdonald *et al.*, 2007), although this preference for cover had not yet been demonstrated by characterizing form structure. Note that our method for finding resting places was probably biased, because we probably missed more hares in dense and high vegetation than in open fields, but this bias was conservative with regard to the hypothesis that hares select resting places for cover.

In autumn and winter, resting hares showed a preference for forests rather than for fields, and forests are known to offer cover to hares all year-round (Tapper & Barnes, 1986; Vaughan *et al.*, 2003; Roedenbeck & Voser, 2008). In cultivated areas, most field habitats offer little or no cover for about three-quarters of a year, beginning with harvest in late summer. Thus, residual wooded patches in cultivated areas are likely to be fundamental to hares as resting places.

Cover has been suggested to be important as a protection against predators during the day (Tapper & Barnes, 1986; Edwards *et al.*, 2000; Vaughan *et al.*, 2003; Fernex *et al.*, 2011). In our study areas, hares resting in more open places were usually flushed from a greater distance than hares resting in densely covered places, suggesting that hares found denser vegetation safer. Nonetheless, we rarely flushed hares in uniform thick vegetation, except for grassland, suggesting that resting places have also to provide escape routes and to allow oversight of the surrounding area. Hares thus seem to select either patches of denser and higher vegetation in open fields (e.g., in pastures), or more open places in denser vegetation (e.g., in crops).

Based on our results, we recommend supporting hare populations by enhancing the availability of cover in agricultural landscapes, both in time and space. Because hares change their resting places frequently (Angelici *et al.*, 1999; Rühe & Hohmann, 2004), a network of diverse habitat structures providing cover in intensely used agricultural landscapes is probably necessary. Such a network should be connected to residual woodland fragments, as hares often rest in forests after the harvest. Farmers should be encouraged to promote heterogeneous landscapes by increasing diversity both within and between fields.

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Synthesis and preview

Over recent decades a general decline in hare densities all over Europe has been recorded. To increase the European hares living conditions, fundamental aspects of the species' ecology have to be known. In this doctoral thesis, on the one hand, the species' activity pattern and space use and, on the other hand, the European hares' habitat preferences were investigated. Therefore, we equipped nine European hares with GPS-collars programmed to take one fix per hour. We were therefore able to study the influence of daylight regime on the hares' diurnal locomotor activity patterns. As the telemetry was conducted in a cereal dominated agricultural landscape, we moreover investigated the effects of harvest on the hares' space use. Furthermore, the vegetation characteristics at hares' resting places during daytime and hares' habitat selection during activity, i.e. the early night hours, were analysed in an agricultural area with low hare density (6 hares per 100 ha).

Because of their value as a game species and their Europe-wide population decline, the European hare has been studied by numerous scientists from all over Europe. Nevertheless, the results of our studies show that this "well-known" species has still major secrets to reveal.

Photo: Stéphanie Schai-Braun

Our results regarding the European hares' activity patterns indicate that during summer, activity peaks regularly occur in full daylight and within the dark phase there is a time of reduced activity. This species' activity pattern is therefore more sophisticated than suggested by earlier European hare studies. It is hence questionable whether some of our results are only true for summer. Furthermore, other factors than sunrise and sunset seem to have a substantial effect on hares' activity pattern. To reveal the identity of these factors, further studies on the European hares' activity pattern are necessary. GPS-locations of smaller intervals and activity sensors, which are available since recently, will additionally help to identify what kind of locomotion behaviour the animals are expressing characteristically within 24 hours. Physiological experiments might solve questions about the correlation between the hares' activity pattern and its energy budget.

Photo: Stéphanie Schai-Braun

We could show that active European hares increased their home-range size after cereal harvest. Whether the impact of harvesting is negative, future studies have to show. It mostly depends on whether the hares are able to compensate the higher energy expenditure evoked by the larger home-range sizes by beneficial circumstances caused by harvest. For instance, it might be conceivable that along the process of harvesting forage of high nutrition value is becoming available to the European hares. Analyses of stomach contents after the hares have fed may give some indications in this respect. In case the larger home-range size of active hares after harvesting proves to impair their daily energy budget, future studies should focus on the reason why active hares increase their home-range size. This might be done by analysing the hares' habitat use combined with the species' locomotion behaviour. Only by knowing the mechanism of how harvest interferes with the European hares' living conditions, scientifically sound courses of actions can be elaborated to reduce the harvest's negative impact.

Photo: Stéphanie Schai-Braun

The agrarian landscapes in Europe are highly divers. Nevertheless, the European hare populations throughout Europe are declining. Our study about the hares' habitat preferences was conducted in a typical agricultural landscape of Northern Switzerland under the condition to ensure true habitat selection. Yet, our results regarding preferred habitat types will not be applicable everywhere in Europe to improve the European hares' living conditions. As an example, the highly preferred habitat type species-rich pasture is not frequently encountered in intensive arable land. Moreover, our results are based on hare locations sampled in spring and autumn and therefore strictly seasonally to interpret. Prospective studies on European hares' habitat preferences are needed in different kinds of hare habitats and various seasons including the premises that, firstly, they are conducted in areas with low hare densities and, secondly, that habitat types are differentiated with respect to their vegetation structure.

Photo: Stéphanie Schai-Braun

Our results indicated that not only structured habitat types but also small patches of vegetation structure distributed in otherwise uniform habitat types are important for European hares for offering cover during their resting period. It might be interesting to clarify if the provision of small structured vegetation patches in homogenous landscapes improved the European hares' living conditions substantially.