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EUROPEAN HARES SELECT RESTING PLACES FOR PROVIDING COVER

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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, vegetation cover, resting place, Switzerland

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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 and 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 and 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, while those habitats providing both food and resting places seem to be used both at night and during the day (Tapper and 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 and 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 and Barnes 1986; Pépin 1987; Rühe and Hohmann 2004; Pépin and 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.

MATERIALS AND METHODS

Field work took place from January 2008 to October 2009 in two agricultural landscapes in the Canton of Baselland, northwestern 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 field 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 ± SE, 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 ($\chi^2_4 = 10.62$, $p = 0.031$). When grouping all open habitats into a single category called “field”, resting places were mainly found in fields from April to August, and in forest from September to March ($\chi^2_1 = 4.53$, $p = 0.033$).

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

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.

Habitat/Month	Resting places		Control points	
	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

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 ($\chi^2_1 = 0.78$, $p = 0.38$). In contrast, from September to March, the distribution of resting places was significantly different from the distribution of control points ($\chi^2_1 = 7.16$, $p = 0.007$), suggesting that in autumn and winter, hares preferred to rest in forests rather than in fields.

2. Characterization of forms

Forms of hares were mainly found at places that offered cover: the mean (± SE) 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, $t_{41} = -0.35$, $p = 0.73$).

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.

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, SE = 0.049, t = -2.30, p = 0.028, r^2 = 0.14).

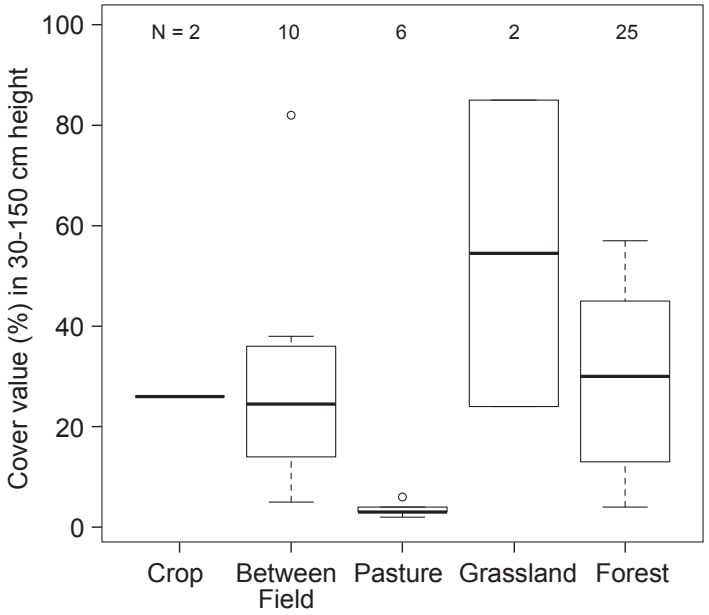

Figure 1 - Percent cover values at hare forms for five main habitats; boxes are median and 25th and 75th percentiles, whiskers are non-outlier ranges, dots are outliers.

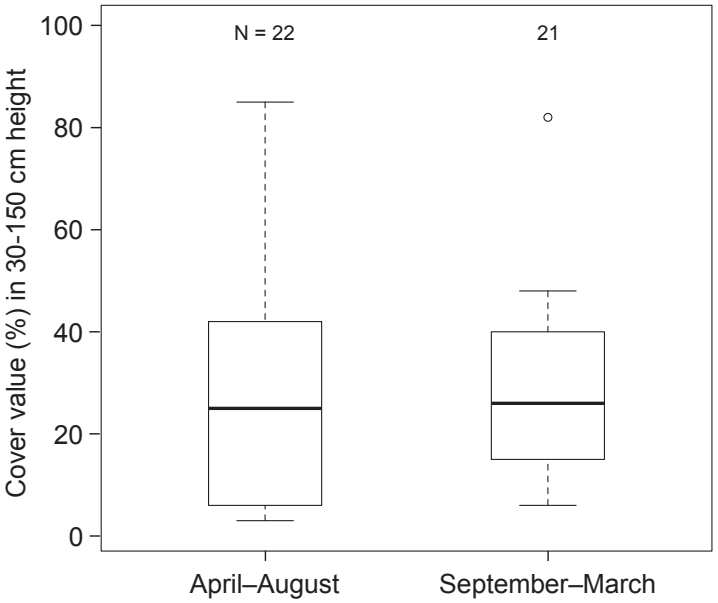

Figure 2 - Percent cover values at hare forms in the two study periods.

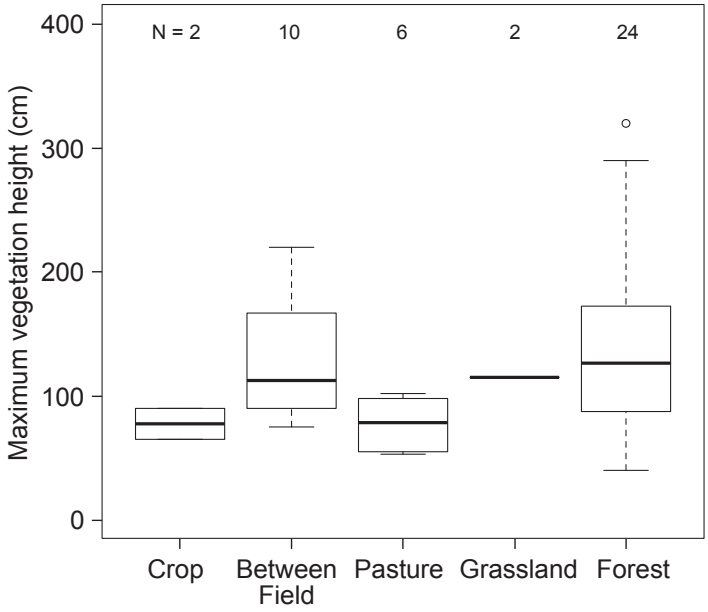

Figure 3 - Maximum vegetation height at hare forms for five main habitats.

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 and 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 and Barnes 1986; Vaughan et al. 2003; Roedenbeck and 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 and 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

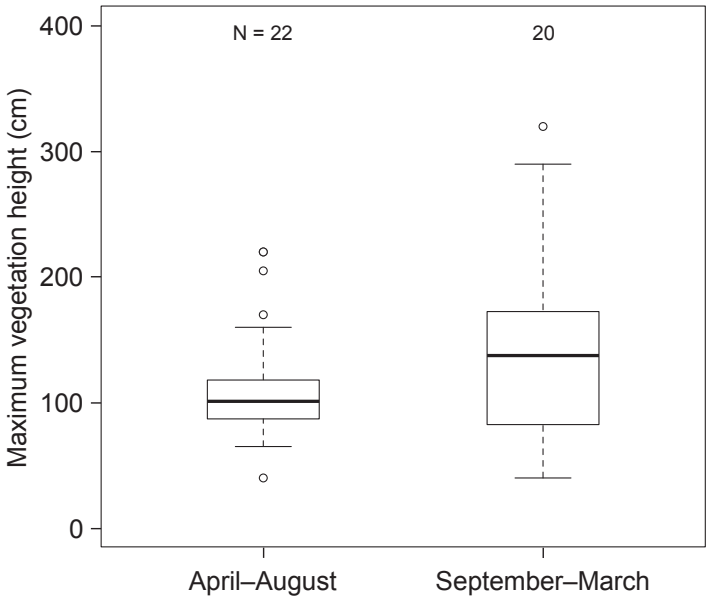

Figure 4 - Maximum vegetation height at hare forms in the two study periods.

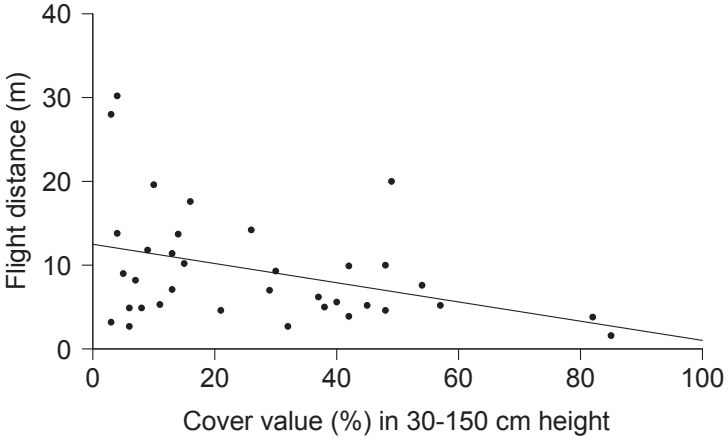

Figure 5 - Regression of flight distance of hares on cover value at hare forms (N=35).

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 enhanc-

ing the availability of cover in agricultural landscapes, both in time and space. Because hares change their resting places frequently (Angelici et al. 1999; Rühe and 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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