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Source: Wildlife Biology, 2(2) : 83-91

Published By: Nordic Board for Wildlife Research

URL: https://doi.org/10.2981/wlb.1996.036

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Does harvesting arable crops influence the behaviour of the European hare *Lepus europaeus*?

Eric Marboutin & Nicholas J. Aebischer

Marboutin, E. & Aebischer, N.J. 1996: Does harvesting arable crops influence the behaviour of the European hare *Lepus europaeus*? - Wildl. Biol. 2: 83-91.

Behavioural changes of 20 radio-tagged European hares *Lepus europaeus* were analysed in relation to the harvesting of summer crops under intensive large-scale farming in northeastern France. Focal sampling was also performed to estimate activity budgets and to analyse vigilance sequences according to group size and pre/post-harvest factors. Night-time ranges were 40% larger than day-time ranges; the total home range size was 190 ± 53 ha. Both night-time and day-time range sizes were independent of the pre/post harvest factor, although pre-harvest range centres shifted after harvest and the overlap areas were avoided. Habitat use within ranges was independent of the day/night and pre/post harvest factors, and hares made a larger use of cultivated areas than expected by chance ($P < 0.01$). Landscape diversity in the home range of hares was lower after harvest than before, but the animals did not maximise their access to crop diversity. Time spent scanning was negatively correlated with group size ($r = -0.32$, $P < 0.005$) and vigilance levels averaged lower after than before harvest ($P < 0.05$). Inter-scan intervals (ISIs) were non-randomly distributed and periodicity in the scanning behaviour was identified using spectral analysis. Hares foraging alone displayed a stronger cyclic pattern in vigilance sequences (i) than hares foraging communally ($P = 0.043$), and (ii) after than before harvest ($P = 0.047$). These results were analysed in connection with increased predation risks and shifts in resource distribution.

Key words: Lepus europaeus, France, habitat use, activity budget, scanning behaviour, telemetry

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Received 29 March 1996, accepted 8 August 1996

Associate Editor: Henrik Andrén

Bag records have indicated a general decline of European hare *Lepus europaeus* populations in western Europe from the 1960s onwards (for a review, see Tapper 1992). The first step in identifying factors responsible for such changes is to look for geographical overlaps between a given external driving force and consistent population trends. A common denominator in all countries involved could be intensive farming practices and related changes in the landscape structure, as suggested by Tapper & Barnes (1986) and Slamecka (1991). The demographic mechanisms are still not clearly demonstrated (Pépin 1989, Hansen 1992, Reitz & Léonard 1993), but small changes in the survival or breeding parameters can produce consistent changes in the growth rate of a hare population (Marboutin & Péroux 1995). Therefore, cumulative effects of non-lethal factors should not be disregarded.

There is some evidence that population size and stability are linked to habitat characteristics (Pielowski & Raczynski 1976). In areas entirely given over to monocultures, large blocks of cereals are all harvested simultaneously. Such changes in landscape structure may disturb hares and result in a lack of suitable habitat (Frylestam 1992). A behavioural response to heavy agricultural pressure has sometimes been mooted (Barnes et al. 1982, Reitz & Léonard 1994), but never explicitly assessed. The

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present work examines whether hares change their behaviour and habitat use in relation to the cereal harvest. Based on radio-tagged animals, the following characteristics of the day-time/night-time home ranges were compared before and after harvest: size, overlap and shift, crop use and landscape diversity use. Harvest-induced changes in landscape structure could also result in lowered foraging efficiency and increased predation risk as suggested by theoretical work (Bernstein et al. 1988). Consequently, the activity budgets of unmarked hares were assessed before and after harvest and mean proportions of time allocated to basic activities were compared. Particular attention was paid to the vigilance*group size interaction, as vertebrates foraging in groups often display decreasing levels of individual anti-predator vigilance with increasing group size (Elgar 1989, Lima 1995). The structure of the scanning behaviour was further analysed, the functional significance of sequential non-randomness in scan distribution often being related to antipredatory benefits (Roberts 1994).

Methods

Study area and data collection

The study took place in northeastern France in 1991-93, on a 6.5-km^2 area of large-scale cereal farming bordered by busy main roads (natural barriers to hare movement in this study). Mean field size was 20 ha and the density of hedgerows and dirt tracks was only 50 m/ha. Wheat was grown on 50% of the land, sugar beet on 30%, peas on 9%, the remainder being grass and woodland. The number of hares in the study area was 175 (SE = 27) in December 1991 and only 130 (SE = 23) in December 1992, using Bailey's modification of the Peterson-Lincoln index and correcting for annual survival rate (Begon 1979). Both hunting bags and abundance indices decreased from year to year.

Biotrack radio-transmitters were fitted to 35 hares, caught in December 1992 as part of a study of population dynamics (Marboutin & Péroux 1995). Tracking was deliberately more intensive at night than by day to obtain a reliable estimate of habitat use (Beyer & Haufler 1994). The hares were located three times per week during the day, and nine times per week at night, from May to September. Day-time locations were recorded during 12.00-15.00, and night-time locations during 19.00-22.00, 00.00-03.00 and 05.00-08.00. Locations were determined by taking three synchronous bearings from fixed radio-tracking towers 9 m high, using null-peak switch boxes and 10-element Yagi aerials. A 95% confidence ellipse around the estimated location point was calculated using the LOCATE II software (Pacer 1990), and the point was discarded if the area of the ellipse exceeded 0.5 ha. Such a threshold for data inclusion was much smaller than the minimum patch size, so that habitat use could be determined correctly (Saltz 1994). Locations obtained at dawn and dusk were pooled with night locations to estimate the activity ranges, as hares were equally active during these periods (Pépin & Cargnelutti 1994).

During the period of the tracking study, groups of 1-7 hares were also observed at dawn and dusk, using a 20-60x telescope from a hide, and behavioural data were recorded on audiotapes for later transcription. Activity budgets were estimated by continuous focal sampling (Altmann 1974), with special reference to the group size factor, i.e. the so-called 'many-eyes' effect (Lima 1995). Focal sampling was carried out for at least 5 minutes, and the following types of behaviour were recorded: feeding, scanning and grooming (comfort activity); resting, running and encountering were pooled together, as they occurred rarely. During pilot trials, some hares were found to spend all time during sampling performing only one or two activities. Thus, some longer focal samples lasting 10 minutes or more were taken too, to increase the likelihood of recording each activity. Recording was aborted if group size changed during the observation period. Because animals were unmarked, no more than two samples were taken per group per session, with at least a 10-minute lag between samples, to limit autocorrelation in the data. Hares were sampled only when in habitats with vegetation less than 30 cm high, in various crops adjacent to wheat fields, and in stubble fields after harvest.

Data analysis

Radio-tracking data

Home-range size and shifts of range centres were computed using Ranges IV (Kenward 1990) and the minimum convex polygon estimator (MCP, with 95% of fixes; White & Garrot 1990). Distribution-free statistics were used where the distribution of variables was non-normal. Comparisons were made in relation to the day/night, pre/post harvest factors. For each hare, overlaps of the 4 MCPs corresponding to all combinations of day/night and pre/post harvest were analysed in pairs following Doncaster (1990). For each pair, the utilisation pattern within an MCP was obtained from the sum of fixes in each cell of a grid superimposed on both ranges. Cells were ranked separately for each MCP, and a Spearman's correlation coefficient (r_s) was calculated from the pairs of fix scores obtained from all the grid-cells present in one or both ranges. Values of r_s ranged from +1.0 (perfectly matched utilisation distributions) to -1.0 (cells heavily used in one home range are avoided in another). Compositional analysis was used to compare habitat compositions of MCPs during day/night and pre/post harvest (Ae-

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bischer et al. 1993). This technique recognises the linear dependence between the proportions that describe habitat composition (they sum to one), and renders them independent by log-ratio transformation. It tests for overall departure from the null hypothesis, e.g. random habitat use, using likelihood ratios (quoted as the equivalent F-statistics in the text), then identifies where differences lie by ranking habitats in order of relative use. Finally, crop diversity within MCPs was compared using two indices: Shannon's $H' = -\Sigma p_k \log_2 p_k$, and the equitability index, $E = H'/\log n = H'/H'_{MAX}$, where p_k is the proportion of habitat k within the MCP, n is the number of habitats, and H'_{MAX} is the largest value of H' obtainable for n different habitats (Scherrer 1984). Because E is independent of n, it allows a comparison of index values based on different numbers of categories; it also represents the percentage of maximum diversity achieved by an individual hare, given the number n of different crops in its home range. In all cases, means are expressed ±1 standard deviation. Statistics were computed using SYSTAT 5.0 (Wilkinson 1990) and NPSTAT 2.6 (Ratsira 1994).

Focal sampling data

The mean proportion of time that individual hares devoted to each type of behaviour was compared in relation to pre/post harvest and group size factors using compositional analysis (see above). Non-random patterns in scanning behaviour were identified by analysing the sequential distribution of inter-scan intervals (ISI). Regularity in ISI sequences was examined using the One-sample runs test (Siegel & Castellan 1988), which compares the number of runs of increasing and decreasing ISI values with that produced by a random model. If H_0 (sequential randomness) was rejected, spectral analysis was conducted using a Qbasic application to identify periodicities of possible cycles (Desportes et al. 1989). For a series of N elements, spectral analysis estimates the proportion g_j of the total variance explained by each periodic component, i.e. the harmonics j = 1,2,...,N/2, in which j measures the number of times a cycle was repeated in the series. Significant gj values were identified using $G_c = -2\log_e[1-(1-\alpha)^{1/q}]/N$ as the minimum critical value, where q = N/2 and α is the type I error rate (Anderson 1971).

Results

Out of the 35 hares tagged, eight died before wheat harvest, four left the study area, and three were lost. For the remaining 20 hares, 2,317 locations were obtained of which 1,308 were night locations (N = 10 hares) and 1,009 were day locations (N = 20 hares). The imbalance between numbers of animals sampled at night and by day occurred because 10 hares could be located only irregularly (probably because they nibbled the whip antennae of the collars and foraged at night in areas of poor signal transmission). The pre-harvest period was 1 May - 14 July (52% of fixes), the post-harvest period was 15 July - 15 September (48% of fixes). Four MCPs were estimated per animal, corresponding to the combinations day/night × pre/post harvest. No tagged hare died as a result of cereal harvesting, and all estimated home ranges were situated entirely within the study area.

Factors affecting home range size

Mean size of the four MCPs differed greatly (Table 1), but so did numbers of radio-locations per MCP. For individual hares, the size of MCPs was not independent of the number of locations ($r = 0.41$, d.f. = 29, $P < 0.05$, using analysis of covariance and a factor identifying individuals). As a result, two-stage sampling was used to obtain a 1:1 ratio in locations registered during the day and at night: for each of the three night periods, only the first location was sampled. Following this, mean size of MCPs was compared using hares as 'blocks' in an analysis of variance. The size of MCPs differed significantly from one hare to the other ($F_{9,27} = 2.42$, $P = 0.04$), and day-time MCPs were, on average, smaller than night-time MCPs ($F_{1,27} = 4.08$, $P = 0.05$). On the other hand, no significant influence of harvest could be demonstrated on the size of MCPs ($F_{1,27} = 1.68$, $P = 0.20$). Before harvest, the size of an individual's day-time MCP was positively correlated with the size of its night-time MCP ($r = 0.85$, d.f. = 8, $P < 0.005$). Comparing the sizes of an individual's night-time MCP pre/post harvest gave a similar result ($r = 0.60$, d.f. = 8, $P < 0.05$). Using all locations registered over the whole period, night-time MCPs were 50% larger, on average, than day-time MCPs ($P = 0.042$, N = 10, Permutation test for paired replicates).

Table 1. Mean home range sizes (in ha ± SD) as calculated by use of the minimum convex polygon method (MCP) for the periods before and after harvest, the whole period, and in total for day-time and night-time observations, respectively. The figures in brackets give mean number of locations.

MCP	Before harvest	After harvest	Whole period	Total home range
Day-time	72 ± 37 ha (30)	53 ± 33 ha (33)	92 ± 38 ha (63)	190 ±53 ha (195) (min: 80 ha; max: 315 ha)
Night-time	92 ± 43 ha (55)	89 ± 38 ha (77)	138 ± 52 ha (132)	

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Overlap and shifts of home ranges

Distances between the centres of MCP ranges before and after harvest averaged larger for night-time ranges than for day-time ranges (530 ± 282 m vs. 322 ± 148 m, $P < 0.05$, Permutation test for paired replicates). For comparison, the mean distance between two consecutive night locations was 320 ± 79 m. On the other hand, distances between simultaneous day and night range centres were independent of the harvest period (before harvest: 328 ± 210 m; after harvest: 285 ± 145 m; N.S.). Animals varied greatly both (i) in shifts of MCP night ranges (min: 170 m, max: 1,080 m) and (ii) in distances between simultaneous day and night ranges (min: 30 m, max: 915 m). Overlap of day-time/night-time ranges was on average 70%, but asymetry was observed as a direct consequence of difference in their sizes. Use of home range overlaps depended on day-time/night-time and pre/post harvest factors when estimated from the distribution of r_s values (Fig. 1). Overlap of simultaneous day-time/night-time MCPs were heavily used ($r_s > 0$) in 8 out of 10 cases after cereal harvesting ($P = 0.04$, binomial distribution). Overlaps of consecutive pre/post harvest MCPs were poorly used during day-time ($r_s < 0$ in 9 out of 10 cases, $P = 0.01$); a similar, but non-significant tendency was observed for night-time ranges ($r_s < 0$ in 7 out of 10 cases, $P = 0.12$).

Habitat utilisation

Four habitat types were considered: 1) wheat, 2) sugar beet, 3) peas, and 4) pasture + set-aside + woodland. Utilised and available habitat were compared at two levels: home range composition vs. total study area, and proportional habitat use based on radio locations vs. home range composition (Table 2). Habitat utilisation based on the distribution of radio locations differed from one hare to the other ($F_{27,76} = 3.52$, $P < 0.001$), so a factor identifying the individual animals was included in the analysis. The pattern of habitat use within MCPs did not significantly change according to either the day/night ($F_{3,26} = 0.87$, $P = 0.47$) or pre/post harvest factor ($F_{3,26} = 0.98$, $P = 0.42$). Similar results were obtained when comparing use of harvested (1+3) with non harvested (2+4) habitat ($F_{1,28} = 0.10$, $P = 0.76$, $F_{1,28} = 0.71$, $P = 0.41$, for each factor respectively). After pooling the data over these two factors, habitat utilisation was random with respect to the habitat composition of the MCPs ($F_{3,17} = 0.59$, $P = 0.63$). When comparing home range composition [harvested (1+3), non-harvested (2+4)] with total study area, neither the day/night nor the pre/post harvest factor gave significant values ($F_{1,28} = 0.001$, $P = 0.99$, $F_{1,28} = 1.48$, $P = 0.23$, respectively). On the other hand, the overall comparison of habitat composition within MCP ranges with habitat availability in the study area demonstrated non-random establishment of home range ($F_{3,17} = 5.68$, $P < 0.01$). A ranking based on mean log-ratio differences ordered habitat types in the sequence 1>2>3>>4, where >> indicates that habitat 4 was ranked significantly lower ($P < 0.05$) than all other habitat types.

Table 2. Habitat availability (in %) of the total study area, compared with the average percentage of habitat use by radio-tracked hares calculated from the habitat composition of their minimum convex polygon (MCP) home ranges and from the distribution of radio locations.

	Wheat	Sugar beet	Peas	Pasture, set-aside & woodland
Habitat availability	49.2	24.6	8.8	17.4
Habitat use (% MCP home range)	53.2	28.2	8.7	9.9
Habitat use (% radio locations)	50.1	29.4	10.3	10.2

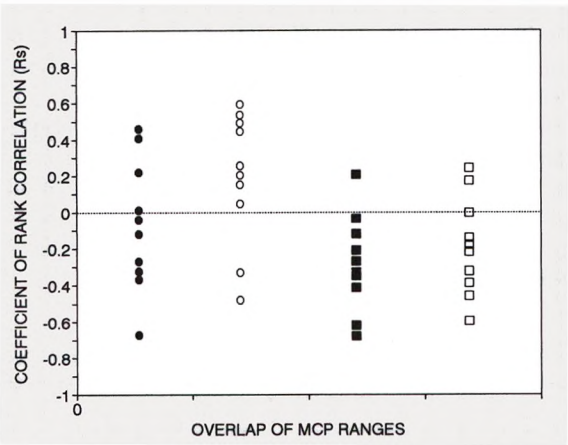


Figure 1. Index of concordance (Spearman' coefficient of rank correlation, r_s) in the utilisation of simultaneous day-time/night-time ranges (●: before harvest;○: after harvest), and consecutive pre/post harvest ranges (■: by day;□: at night). Overlaps of consecutive ranges are avoided both by day and at night; the overlaps of simultaneous ranges are selected only after harvest.

Use of crop diversity

Changes in the Shannon index (H') and the equitability index (E) were analysed using two-way factorial ANOVA with randomised blocks for individual hares. H' did not differ, on average, between night MCPs and day MCPs (1.39 ± 0.33 and 1.32 ± 0.27, $F_{1,27} = 0.45$, N.S.). Crop diversity in MCP ranges was higher before than after harvest (1.60 ± 0.29 and 1.10 ± 0.31, $F_{1,27} = 19.50$, $P < 0.001$). The decrease in H' after harvest was not, however, balanced by an increase in E: equitability was even lower after than before harvest (0.66 ± 0.09 and 0.74 ± 0.08, $F_{1,27} = 7.00$, $P = 0.01$).

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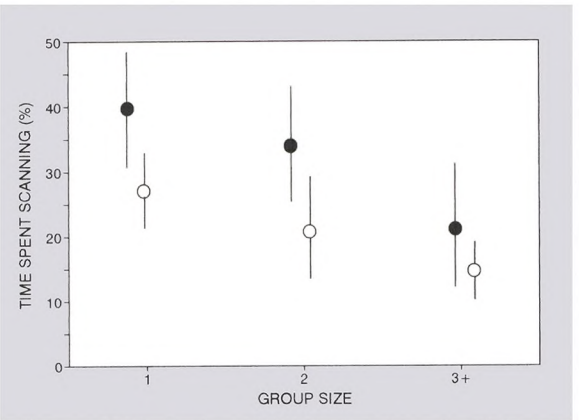


Figure 2. Mean proportion of the time (±SD) individual hares spent scanning, according to group size and observation period. Hares spent significantly less time scanning after harvest (empty symbols) than before (full symbol), whatever the group size.

Activity budget, group size and harvest factor

By focal sampling, 164 hares were observed; 67 (40%) were observed before harvest. Total observation time amounted to approx. 25 hours. Hares were observed alone (on 59 occasions), or in group sizes of 2 (on 66 occasions), 3 (on 33 occasions) or more (6.2 on average, on 6 occasions). The mean proportion of time devoted by the individual hare to each activity (scanning, feeding, grooming, other) was independent of group size ($F_{3,159} = 2.06$, $P = 0.11$) and harvest ($F_{3,159} = 0.49$, $P = 0.69$) factors. The corporate vigilance of groups was estimated from $V_C = 1-(1-V_I)^N$, where V_I = proportion of time individuals are vigilant and N = group size (from Monaghan & Metcalfe 1985). V_C increased significantly with group size ($r = 0.57$, d.f. = 162, $P < 0.001$) though the time cost of vigilance to an individual hare was stable. When using only the long focal samples (≥10 min.), group size and time spent scanning were negatively correlated ($r = -0.32$, d.f. = 78, $P < 0.005$). Time spent scanning was also less after than before harvesting ($F_{1,74} = 4.26$, $P < 0.05$, Fig. 2), and interaction with the group-size factor was non-significant ($F_{2,74} = 1.39$, N.S.).

Sequential non-randomness of vigilant behaviour

The data set comprised 20 long sequences of inter-scan intervals (ISIs) obtained from hares foraging alone or in groups, before or after harvesting. Out of 20, 17 had a greater number of runs than what would be the mean expectation in a random model. Z-values ranged from 1.92 to 8.83, giving P-levels from 0.06 to <0.001: these ISIs were in a non-random, periodically cycling order. Spectral analysis confirmed these findings: 20% of the variance of a series (N = 20) could be explained on average by significant periodic components (one or two different periods in each case). This pattern was more pronounced in hares foraging alone than in hares foraging communally (30% vs. 8%, P = 0.043, Permutation test). Non-random distribution of ISIs was stronger after than before harvest for hares foraging alone (47% vs. 12%, P = 0.047, Permutation test); no effect of harvest was detected for groups of two or more hares. Series contained either short-term cycles ($T \in [2.1, 8]$) or long-term cycles ($T \in [10.2, 29]$), or both types (Fig. 3).

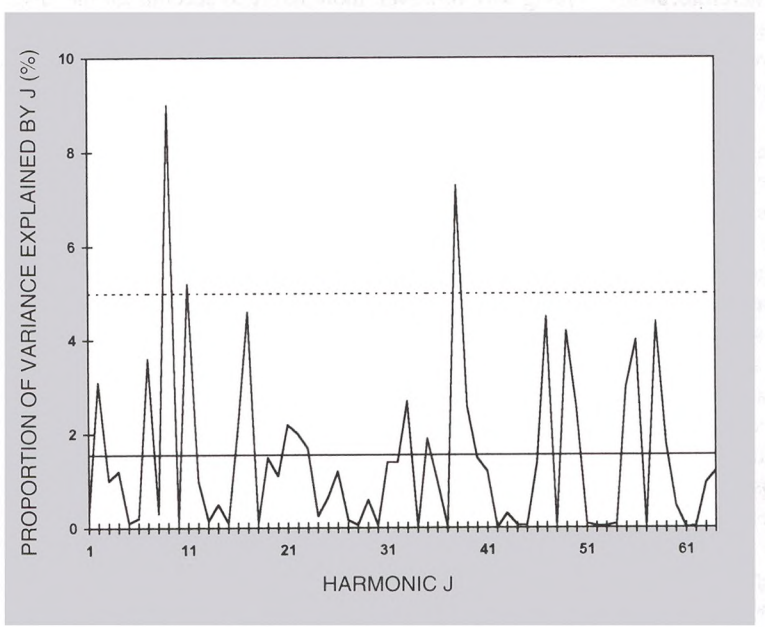


Figure 3. Periodogram of an ISI sequence; the theoretical random periodogram is indicated by the straight line of ordinates 1:(n:2)= 2:n. The dashed line indicates the upper 95% confidence limit.

Discussion

Adult mortality induced by harvesting of summer crops was nil based on survival of tagged animals. Mark-recapture analysis of ear-tagged hares (Marboutin & Péroux 1995) gave an annual adult survival rate of 0.51; usual values ranged from 0.35 to 0.60 (Marboutin & Péroux *op. cit.*). Reitz & Léonard (1993) also estimated high summer survival rates of juvenile and adult hares under similar intensive farming conditions. Harvest-induced changes in the landscape structure

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have, therefore, been further examined here as to their influence on hare behaviour. The results are discussed below in relation to increased predation risk, disturbance of the hares, and shifts in resource distribution and food availability.

Focal sampling of animals foraging at dawn and dusk showed that hares spend more time being vigilant before than after wheat harvest. Moreover, the individual vigilance level was lower when animals foraged in groups, as noted by Monaghan & Metcalfe (1985) during an experiment where food distribution was manipulated. Both results may be related to anti-predator strategies and/or intraspecific competition. Where mammals live in long-term proximity, competition may exist and vigilance may also serve a social function (Roberts 1988). Competition between European hares arises mainly (i) when food is clumped in some high-density food patches (Monaghan & Metcalfe 1985), or (ii) when chasing occurs for access to oestrous does (Holley 1986). In the present study, food distribution was fairly uniform, and social interactions were poorly related to the group-size and pre/post harvest factors. As a result, vigilance patterns probably reflected anti-predator strategy rather than intraspecific competition. First a decrease in habitat obstruction, following the wheat harvest, may improve predator detectability (Elgar 1989): hares would need to devote less time to scanning in order to achieve good vigilance efficiency. Secondly, the basic idea of the group-size effect is the 'many-eyes' hypothesis (Lima 1995). As group size increases in socially foraging animals, there are progressively more eyes scanning the environment for predators. Therefore, an individual forager can devote less time to vigilance with increasing group size, assuming collective detection of predators and individual monitoring of groupmate vigilance.

Spectral analysis of interscan intervals (ISIs) confirmed an underlying structure in vigilance behaviour, especially in hares foraging alone: they were more prone to display periodicity in vigilance than those foraging communally, and this periodicity was stronger after wheat harvest than before. These results were unexpected as the sequential non-randomness of ISIs is usually considered an anti-predator strategy used mainly by animal groups. The predictability of vigilance may promote coordination of scanning, thereby increasing corporate vigilance without increasing the need to monitor the vigilance of others (Desportes et al. 1989, Roberts 1994). Thus, the influence of group size was made up of two components, as both the mean proportion of time spent scanning and the cyclic pattern in ISIs decreased with increasing group size. The interaction between these components was, however, unclear when considering the influence of habitat visibility. Following harvest, the time spent scanning decreased whatever the group size, whereas the cyclic patterns in vigilance increased only for animals foraging alone. Observing such strategies does not necessarily mean that predator-induced selection was strong. Hares usually form a small fraction of predator diet in western Europe (Reynolds & Tapper 1995a), although theoretical work suggests that even a weak predation rate may limit the growth of a hare population (Reynolds & Tapper 1995b). In the present case, five tagged hares were found scavenged - or predated - by red foxes *Vulpes vulpes*, and only two non-breeding foxes foraged in the study area. Fox-induced mortality on adults was probably weak, but its impact on the local hare dynamics was unknown. Indeed, the growth rate of the hare population was very sensitive to light increases in adult mortality (Marboutin & Péroux 1995). Present results suggest that anti-predator behaviour of hares could be based on a range of strategies, as already observed in between-species comparisons (Quenette 1990).

Hares often fed and rested in contiguous fields, without a clear habitat boundary separating night-time and day-time ranges, as in Reitz & Léonard's (1994) study. Although it was estimated from only a five-month period, the average home range size (190 ha) was at least twice as large as most published values (see Reitz & Léonard *op. cit.* for a review). Only Pielowski (1972) gave larger values, but his calculation based on chased animals assumed a circular home range and considered annual ranges. Indeed, the measurement of home range depends on the length of the study and on the estimators used (White & Garrott 1990); the emphasis on night sampling was, however, more likely to account for the large figures estimated herein. Night-time ranges were 50% larger than day-time ranges, as would be expected for a species mainly active at night (Pépin & Cargnelutti 1994). No major change in the size of ranges pre/post harvest was observed. Such a range-size stability could be attributable to constraints on body-size energetics and to patchiness of the habitat: the home range size of leporids scales with body mass allometrically, and is partly determined by perceived habitat productivity (Swihart 1986). Besides the size-stability, the centres of both night-time and day-time ranges shifted after harvesting. The area of overlap of consecutive ranges was poorly used on average, which could be explained by hares (i) using new fields that brought them good resources (forms or food) or (ii) avoiding disturbed areas. Non-harvested habitats could have provided a refuge during harvest, but they were used similarly before and after harvest, as were harvested habitats. So a mixture of both hypotheses is likely to be valid. Habitat use within home ranges was independent of the day/night factor, too. Other studies have suggested a more structured habitat use, although statistics could be partly biased owing (i) to non-independence of habitat proportions (Tapper & Barnes 1986), or (ii) to

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unequal detectability of hares in different habitat types (Frylestam 1992, Prigioni & Pelizza 1992). Habitat selection in this study occurred at a higher level. In their selection of a total home range from within the overall study area, hares made greater use of cultivated areas than should be expected by chance, and less use of non-cultivated areas (i.e. woodland + hedges + grass fields + set-aside fields). On a large scale, similar results were observed in France, where hare densities were higher in highly cultivated than in non-cultivated areas (Fiechter & Benmergui 1986), except when spring cereals were dominant. Habitat diversity of ranges was larger before than after harvest, possibly suggesting a lack of suitable habitats. But hares did not maximise their use of landscape diversity, as deduced from a decrease in the equitability index of ranges before and after harvest. Hansen (in press) also demonstrated that the foraging activity of hares was poorly related to habitat patchiness. However, the food diversity actually available to hares probably exceeded our measure of landscape diversity. Indeed, in a nearby study area, Chapuis (1990) demonstrated that the hares' diet was more varied during summer and autumn, when it included both cultivated and weedy species of plants, than during the rest of the year. Moreover, even hares from high-density populations do not necessarily experience food shortages (Bradshaw in press). Monthly changes in diet may enable a hare to make good use of the trophic potential of its habitat, by adapting its feeding choices to the phenology of crops (Chapuis *op. cit.*). Some spatial correlations between landscape diversity and the autumn mosaic of hare densities have, however, been found in England and Poland (Tapper & Barnes 1986, Lewandowski & Nowakowski, 1993), but not in Italy where diversity was related to the unfavourable presence of maize (Meriggi & Alieri 1989). In France, spatio-temporal changes in numbers of hares are poorly related to changes in landscape diversity (Marboutin & Péroux in press), and in Poland hare densities are independent of the agrarian structure (Bresinski 1976). Until the landscape is oversimplified (e.g. Slamecka 1991), its diversity is, therefore, probably not a critical component of hare behaviour and feeding ecology, at least during summer.

Hares varied in habitat use, range size and movements to such a point that individual animals needed to be regarded as 'blocks' during data analysis. Strong individual variations are usual in this species (Reitz & Léonard 1994), and are sometimes thought to represent adaptive flexibility (Pépin & Cargnelutti 1994). Despite a wide distribution (Chapman & Flux 1990), the European hare occurs mainly in open-field agroecosystems. To a certain extent, these resemble the African savanna where their ancestors evolved (Perez-Suarez et al. 1994): both systems are characterised by low spatial diversity, affected by some unpredictable temporal variability. Individuals might, therefore, be able to respond opportunistically to habitat change by being distributed randomly among habitats (Bryan 1973). The spatial structure of a hare population is, however, time and density-dependent (Jezierski 1972). Social factors, food availability, and human-induced disturbance partly account for this structure (Frylestam 1976, Monaghan & Metcalf 1985, Holley 1986). So colinearity between time-related variables and the behavioural changes observed in this study may be possible. Unpredictable changes in landscape structure are likely to affect animal populations (Wiens 1976), but evolution will have selected adaptive life histories. Owing to a long breeding season, cursorial ability and sociality (Swihart 1984, Cowan & Bell 1986, Krebs 1986), the European hare has probably overcome the environmental changes induced by modern farming in summer, through some slight alterations of its behaviour.

Acknowledgements - the present work has been possible thanks to landowners, farmers and hunters who allowed us to mark the hares. We gratefully acknowledge M. Marchi for setting up and improving the telemetry system, and F. Demoyen, Y. Georgeon, G. Humbert, V. Jacquemin, A. Lequien, C. Marchal, C. Sarignac and S. Undreiner for providing field assistance. F. Reitz, S. Tapper and two anonymous referees made valuable comments on the manuscript. Our work was supported by the Fédération Départementale des Chasseurs de l'Aisne and by grant # 91201 from Secrétariat de la Recherche et du Traitement de l'Information sur l'Environnement.

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