



# Homogeneous habitat can meet the discrete and varied resource requirements of hares but may set an ecological trap

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## ABSTRACT

In common with other farmland species, hares (*Lepus* spp.) are in widespread decline in agricultural landscapes due to agricultural intensification and habitat loss. We examined the importance of habitat heterogeneity to the Irish hare (*Lepus timidus hibernicus*) in a pastoral landscape. We used radio-tracking during nocturnal active and diurnal inactive periods throughout one year. In autumn, winter and spring, hares occupied a heterogeneous combination of improved grassland, providing food, and *Juncus*-dominated rough pasture, providing refuge. In summer, hares significantly increased their use of improved grassland. This homogeneous habitat can fulfil the discrete and varied resource requirements of hares for feeding and shelter at certain times of year. However, improved grassland may be a risky habitat for hares as silage harvesting occurs during their peak birthing period of late spring and early summer. We therefore posit the existence of a putative ecological trap inherent to a homogeneous habitat of perceived high value that satisfies the hares' habitat requirements but which presents risks at a critical time of year. To test this hypothesis in relation to hare populations, work is required to provide data on differential leveret mortality between habitat types.

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## 1. Introduction

Homogenisation of landscapes due to agricultural intensification is widely recognised as the principal cause of declining farmland wildlife populations (Siriwardena et al., 1998; Krebs et al., 1999; Aebischer et al., 2000; Robinson and Sutherland, 2002; Wretenberg et al., 2007), including hares (Tapper and Barnes, 1986; Slamačka, 1991; Smith et al., 2004, 2005). Habitat heterogeneity is generally associated with high biodiversity at the landscape scale (Benton et al., 2003). On farmland, the loss of hedgerows, amalgamation of fields and temporal and spatial synchronicity of farm management processes are major contributing factors to biodiversity loss (Benton et al., 2003).

While maintaining and enhancing habitat heterogeneity is widely acknowledged to be of benefit to biodiversity conservation (Benton et al., 2003; Smith et al., 2004; Reid et al., 2007), it is not the loss of heterogeneity *per se* that results in the loss of biodiversity. Rather it is the associated reduction in the availability of various resources and niches that diverse habitats provide. The life-history traits of many species necessitate the use of different resources at different times and in an anthropogenic landscape these various needs are most frequently addressed by different habitat

types. However, in some cases, homogeneous habitats may address some, many or all of the discrete and varied resource requirements of a species at different points in its life cycle. The requirement of hares for food and refuge from predators has been demonstrated previously, and diversity in habitat and landscape structure has been concluded to be particularly important to hares (Frylestam, 1980; Tapper and Barnes, 1986; Lewandowski and Nowakowski, 1993; Vaughan et al., 2003; Smith et al., 2004, 2005).

In Great Britain, as elsewhere in Europe, European hares *Lepus europaeus* Pallas are in general decline (Pielowski and Pucek, 1976; Tapper, 1992; Mitchell-Jones et al., 1999; Smith et al., 2005). Recent work on habitat selection by hares in pastoral landscapes (Smith et al., 2004) supports earlier work in arable areas (Tapper and Barnes, 1986) highlighting the importance of habitat heterogeneity. After an extensive review of 77 papers from 12 European countries, Smith et al. (2005) concluded that agricultural intensification was the ultimate cause of hare population declines with spatio-temporal variation in climate and predator numbers magnifying the impact of the loss of high-quality year-round forage. Smith et al. (2004) advocated the enhancement of within-habitat and within-field structural diversity as a means of realising conservation targets for hares in pastoral landscapes.

The Irish hare (*Lepus timidus hibernicus* Bell) is the only lagomorph native to Ireland (Fairley, 2001) and is an endemic sub-species (Hamill, 2001) of the mountain hare (*L. timidus* L.). It differs

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markedly from mountain hares elsewhere by mainly inhabiting lowland areas (Wolfe and Hayden, 1996; Wolfe et al., 1996) and in common with other *Lepus* spp. it relies almost entirely on grasses in its diet (Walker and Fairley, 1968; Tangney et al., 1995; Jeffery, 1996; Dingerkus and Montgomery, 2001; Strevens and Rochford, 2004). Declines in the Irish hare population prompted conservation concern for the species during the late 20th century (Dingerkus and Montgomery, 2002). The Irish hare is now one of the highest priority species for conservation action in Ireland (Anon, 2005).

We examined diel and seasonal variation in home ranging behaviour and habitat use of adult Irish hares living in a low-intensity, lowland pastoral landscape. We hypothesised that hares required habitat heterogeneity to address their dual needs for food and shelter. We, therefore, investigated the separate roles that homogenous and heterogeneous habitat types play in fulfilling the discrete resource requirements of hares at different times of year through the provision of either short uniform vegetation or tall uneven vegetation. We go on to posit the existence of a putative ecological trap inherent to a homogeneous habitat of perceived high value that satisfies the hares' discrete and varied habitat requirements but presents risks at a critical time of year.

## 2. Materials and methods

### 2.1. Study site

The study site (197 ha) was located in a lowland pastoral landscape in south Armagh, Northern Ireland, UK (54°15'46"N, 06°48'04"W). Habitats were mapped and digitised at a scale of 1:10,000 using a modified Phase 1 habitat survey technique (Parkins, 1990) and GIS Arcview 3.3 software (ESRI, California, USA). Field areas were small (mean = 0.9 ha, s.d. = 0.5 ha,  $n = 195$ ). Three habitats dominated the site covering 95% of the study area (Table 1); improved grassland consisting entirely of perennial ryegrass (*Lolium perenne*) monocultures harvested for silage production twice to three times from May to September, semi-improved grassland containing a mix of native and agricultural grasses with <50% *Juncus* cover harvested for silage production once to twice from May to September and *Juncus*-dominated rough pasture consisting of native grasses with >50% *Juncus* cover used for extensive grazing only and often left fallow. Less common habitat types, including marsh, scrub, amenity grass, neutral grassland, arable and woodland accounted for 5% of the study site (Table 1).

Common soft-rush (*Juncus effusus*) can grow up to 1.5 m tall (Phillips, 1980) and forms dense tufts and clumps that amalgamate to create expansive stands. Tall uneven vegetation provides hares with cover and camouflage from predators and shelter from wind and rain and thus makes ideal diurnal lie-up sites. Improved grasslands provide high quality forage but their vegetation structure is

generally short (<20 cm) and uniform for most the year except immediately prior to silage harvest when grass may reach up to 1 m.

### 2.2. Capture and tagging

Hares were captured from December 2003 to August 2004 using 6z gauge static nylon long nets 1.5 m tall and of varying length (5–30 m each; total length = 120 m, Euroguns, Yorkshire, UK). Hares were flushed from their diurnal lie-up sites by a line of beaters and driven into nets placed across openings in hedgerows and habitual hare runs. Captured animals were placed in a cloth bag to minimise handling stress, sexed and tagged using cable-tie TW-3 (173 MHz band) medium (39 × 20 × 20 mm) small-mammal radio collars with a lifespan of 1.5 years (1/2AA battery, Biotrack Ltd., Dorset, UK). Collars weighed 25 g and were <1% of the animal's body weight. To minimise stress, hares were processed and released *in situ* within 15 min of capture.

### 2.3. Radio-tracking

Hares were tracked over one calendar year between December 2003 and December 2004. To avoid autocorrelation of locational radio fixes (Harris et al., 1990), each animal was discontinuously tracked with 2–4 fixes collected each week during both their inactive and active periods until either the animal died or the end of the study was reached. The active period was defined as the crepuscular and nocturnal period from one hour prior to sunset until one hour after sunrise. The inactive period was the diurnal period from one hour past sunrise until one hour prior to sunset. The seasons were defined as spring (March–May), summer (June–August), autumn (September–November) and winter (December–February). Animals were located by triangulation using a Mariner 57 radio receiver with a flexible 3-element Yagi antenna (Biotrack Ltd., Dorset, UK). Triangulation generally included 5–10 bearings taken throughout the study site on foot. Accuracy was not formally tested but animals were occasionally located by tracking the radio-signal to source with an estimated triangulation error <50 m.

### 2.4. Statistical analyses

Range size was determined using a robust fixed kernel method (Worton, 1987) using individual smoothing parameters determined by least squares cross-validation (Silverman, 1986) during seasonal active and inactive data subsets. The number of fixes within these periods varied between animals. Consequently, the number of fixes used in range calculation was accounted for in subsequent analyses. Hereafter, 95% kernel ranges (95% of radio fixes) will be referred to as 'ranges'. All radiotelemetric analyses were conducted using the Animal Movement extension (Hooge and Eichenlaub, 2000) for Arcview GIS 3.3 software.

Radiotelemetry studies examining habitat use have the difficulty that animals may not use different habitats within their home range equally (White and Garrott, 1990). This is particularly problematic when using the 100% minimum convex polygon method of range analysis as it is strongly influenced by peripheral fixes often including large areas which are never visited (Harris et al., 1990). However, the probabilistic kernel method of range estimation used here accounts not only for the location of radio fixes but also their density. This equates to the time spent by the animal in any given area or the probability of its occurrence known as 'utilization distribution' (Worton, 1989). Moreover, restricting analysis to 95% of radio fixes excludes outlying points reducing the likelihood of including areas used infrequently. Indeed, previous studies have shown that kernel range estimators are good proxies of habitat use (Kernohan et al., 1998).

**Table 1**

Habitat availability to Irish hares defined as the area and percentage composition of the study site. Habitats are rank in order of prevalence.

Habitat	Area (ha)	% of study site
Improved grassland	108.02	54.76
Semi-improved grassland	52.45	26.59
<i>Juncus</i> -dominated grassland	26.38	13.37
Marsh	3.37	1.71
Scrub	3.22	1.63
Amenity grass	1.68	0.85
Neutral grassland	0.96	0.49
Arable	0.60	0.31
Woodland	0.59	0.30
<b>Total</b>	<b>197.27</b>	<b>100.00</b>

General linear mixed models assuming a normal distribution and using an identity link function were employed to examine the dependent variables of (a) range size and habitat use, defined as the percentage of the range that was (b) improved grassland, (c) semi-natural grassland and (d) *Juncus*-dominated pasture. Exploratory analysis of six less common habitat types found no significant relationships. Moreover, each remaining habitat accounted for between 0.3% and 1.7% of the study area (Table 1) and were considered too scarce for inclusion in formal analyses. Seasonal ranging data were unbalanced with some individuals tracked across multiple seasons while others only in one, thus the number of radio fixes from which ranges were calculated was treated as a covariate. For range size, activity, season and sex were treated as independent fixed factors and hare ID was fitted as a random factor. For simplicity, models of habitat use excluded sex as it was shown to have no significant effect on range size. Moreover, initial exploratory analyses demonstrated that it had no significant on habitat use. Activity\*Season was the only interaction term included to determine the extent to which ranges and habitat use varied between day and night throughout the year. To conform to the assumptions of the test, including homogeneity of variances, range size was normalised using a logarithmic transformation ( $\log_{10} + 1$ ). All statistics were performed using GenStat® (v6).

### 3. Results

Seventeen hares were tracked; 16 remained near to the point of capture. One young male dispersed approximately 2 km over a period of several months and was excluded from all analyses. Sampling effort, defined as the number of fixes, did not significantly affect calculated range size nor did ranging behaviour differ between the sexes (Table 2). Range size was affected significantly by hare activity, season and their interaction (Table 2). Hares were non-territorial and individual ranges overlapped one another, often to a great extent. Active nocturnal ranges were significantly larger than inactive diurnal ranges in all seasons except during summer (Fig. 1a). In general, ranges were significantly larger in winter and spring than in summer and autumn.

Habitat use, described as range habitat composition, varied significantly with hare activity and season for improved grassland and *Juncus*-dominated pasture but not semi-improved grassland

(Table 2). There was no significant interaction between Activity\*Season suggesting that patterns of habitat use were consistent between day and night across seasons.

Improved grassland was used more frequently during active periods when it was typically used at a frequency greater than its availability and used least during inactive periods when it was typically used at a frequency less than its availability; except during summer (Fig. 1b). In summer, hares used significantly more improved grassland during inactive periods than during any other season. Semi-improved grasslands were consistently used at a frequency less than their availability throughout the year (Fig. 1c). *Juncus*-dominated pasture was used most frequently during inactive than active periods and generally always used at a frequency greater than its availability; except during active periods in summer when it was used at a frequency less than its availability (Fig. 1d).

To summarise: hare home ranging behaviour and habitat use in summer was markedly different from the rest of the year. Home ranges were at their smallest with little difference between nocturnal active and diurnal inactive ranges suggesting that hares were relatively sedentary. Hare habitat use during the summer inactive period was more similar to habitat use during the active rather than inactive periods of any other season whilst habitat use during the summer active period demonstrated greatest use of improved grassland and least use of *Juncus*-dominated pasture (Fig. 2).

### 4. Discussion

This study supports indirectly the view that hares have discrete and varied resource requirements for food, in terms of high quality grazing, and shelter, in terms of tall uneven vegetation that provides cover from predators. As the characteristics of each habitat change over the year, an individual's requirements may be satisfied not only by heterogeneous habitats but also differential use of homogeneous habitat at different times.

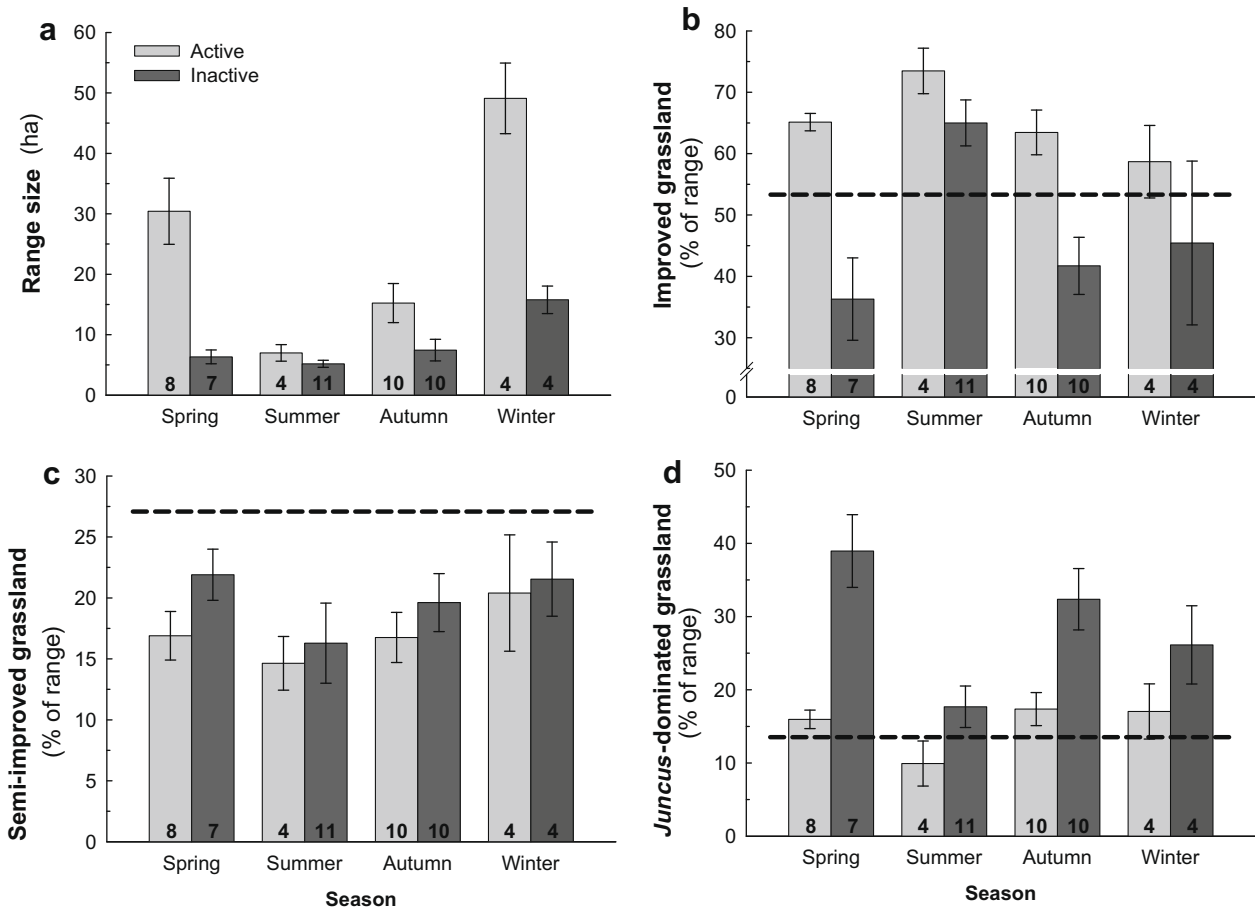
It is generally accepted that hares are predominantly active with greater ranges at night and inactive with smaller ranges during the day (Holley and Greenwood, 1984; Homolka, 1987; Pépin and Cargnelutti, 1994; Holley, 2001; Smith et al., 2004). During active periods, Irish hares tended to inhabit both improved grassland and *Juncus*-dominated pasture at frequencies greater than their respective availabilities. During darkness, hares spend most of their time feeding (Homolka, 1986). It seems likely that both improved grassland and *Juncus*-dominated pasture provided good grazing and were chosen as nocturnal foraging areas. In general during inactive periods, Irish hares used *Juncus*-dominated pasture at a frequency greater than its availability whilst generally utilising improved grasslands at a frequency less than its availability suggesting that cover and shelter are much more important during daylight periods.

During much of the year, habitat heterogeneity was clearly important to hares as they often moved between patches of improved grassland and *Juncus*-dominated pasture between day and night. Similar behaviour has been described before (Tapper and Barnes, 1986; Hiltunen et al., 2004; Smith et al., 2004) and our results corroborate those of Dingerkus and Montgomery (2002) who suggest that Irish hares select *Juncus*-dominated grasslands as diurnal lie-up sites, whilst the importance of *Lolium perenne* in their diet (Stevens and Rochford, 2004) suggests improved grasslands are used for grazing at night. However, when a habitat becomes suitable for both feeding and resting, hares need not move between habitats (Reitz and Léonard, 1994; Marboutin and Aebischer, 1996; Smith et al., 2004). During summer, Irish hares used improved grassland during both active and inactive periods. The height of grass during summer approaches that of rushes and is more uniformly dense providing not just high quality grazing but

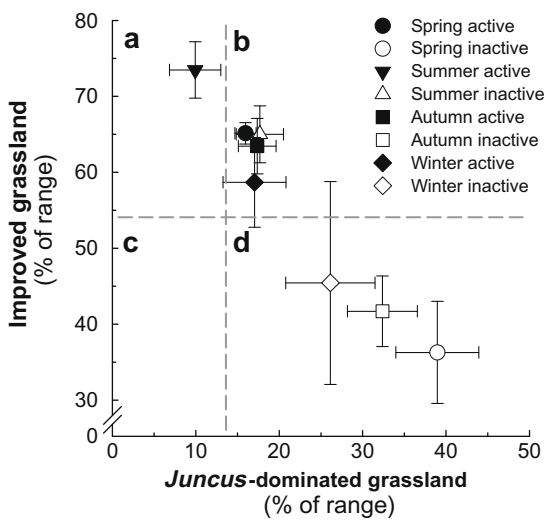
**Table 2**

Variation in the (a) 95% kernel ranges of hares and the percentage composition of ranges that were (b) improved grassland, (c) semi-improved grassland and (d) *Juncus*-dominated grassland determined by GLMM.

Explanatory variable	F	d.f.	p
<i>(a) Range size (log<sub>10</sub> transformed)</i>			
Activity	87.07	1	<0.001
Season	9.20	3	<0.001
Activity * Season	3.88	3	0.009
Sex	0.08	1	0.780
Number of radio fixes	0.02	1	0.894
<i>(b) % Improved grassland within range</i>			
Activity	26.66	1	<0.001
Season	9.80	3	<0.001
Activity * Season	1.69	3	0.167
<i>(c) % Semi-improved grassland within range</i>			
Activity	1.70	1	0.192
Season	2.41	3	0.065
Activity * Season	0.24	3	0.871
<i>(d) % Juncus-dominated grassland within range</i>			
Activity	35.38	1	<0.001
Season	9.85	3	<0.001
Activity * Season	2.25	3	0.080



**Fig. 1.** Variation in (a) Irish hare range size and the percentage composition of ranges that were (b) improved grassland, (c) semi-improved grassland and (d) *Juncus*-dominated pasture ± standard errors. Sample sizes are given in bold text within the bars. Dashed lines represent habitat availability within the study site (see Table 1).



**Fig. 2.** Relative use of improved grassland and *Juncus*-dominated pasture by Irish hares during active and inactive periods throughout the year. Symbols represent mean values and whiskers are standard errors. In quadrant (a) hares used improved grassland more than its availability but *Juncus*-dominated pasture less than its availability, (b) hares used both improved grassland and *Juncus*-dominated pasture more than their respective availabilities, (c) no animals used both improved grassland and *Juncus*-dominated pasture less than their respective availabilities and (d) hares used improved grassland less than its availability and *Juncus*-dominated pasture more than its availability.

also suitable cover. This may also contribute to ranges being smallest during summer, with little difference in the sizes of active and inactive ranges. Indeed, summer range size in the current study was one of the smallest recorded for any *Lepus* spp. suggesting that movement activity was minimal and animals were largely sedentary at this time of year.

This study provides evidence that whilst Irish hares still used *Juncus*-dominated pasture during summer their use of improved grasslands significantly increased. Variability in habitat use can have serious conservation implications for population growth in some species (Schlaepfer et al., 2002; Battin, 2004; Bro et al., 2004). Peak parturition of *L. timidus* in Scotland is between May and July (Flux, 1970) whilst that of *L. europaeus* in England and mainland Europe is between April and June (Lincoln, 1974; Hewson and Taylor, 1975; Broekhuizen and Maaskamp, 1981). Comparable data do not exist for the Irish hare but it is likely that a peak birthing coincides with silage harvesting during late spring and early summer. For the first few weeks of life leverets remain motionless close to the natal area (Broekhuizen and Maaskamp, 1982), which is generally in open habitats, such as the middle of fields. Mechanised harvesting may endanger young hares and has been shown to be a significant cause of mortality in agricultural areas (Kaluziński and Pielowski, 1976; Milanova and Dimov, 1990; Milanov, 1996; Marboutin and Hansen, 1998). This study did not extend to the selection of natal areas by female Irish hares. However, it is not unreasonable to propose that if hares restrict their activity and increase their use of improved grasslands during

summer due to their perceived high value for food and shelter that leverets may well be placed in the same habitat. If this is the case, the sudden destruction of this habitat during silage harvesting may reduce leveret survival, recruitment and erode population densities. Therefore, we believe that it is desirable to test the hypothesis that selection of homogeneous improved grasslands during summer may constitute an ecological trap at a critical time of year. This would require work to provide data on natal area selection criteria and differential leveret mortality between habitat types.

Management of pastoral land for maximum grass harvest results in structural uniformity (Frame et al., 1995). Smith et al. (2004) suggested that the maintenance and promotion of within-field, within-farm and landscape structural heterogeneity may be important to hares whilst habitat heterogeneity benefits farmland biodiversity as a whole (Vickery et al., 1999; Robinson and Sutherland, 2002; Benton et al., 2003). Habitat 'patchiness' may encourage a uniform coverage of hare populations but may not be sufficient to arrest population declines if individuals favour patches that compromise their fitness. Conservation strategies that increase habitat heterogeneity through the provision of permanent cover have been shown to increase hare numbers (Slamačka, 1991). Moreover, Smith et al. (2004) claimed that a reduction in silage production, through reduced livestock density, would decrease leveret mortality attributable to mechanised harvest. Despite conservation measures being part of existing agri-environment schemes these have been shown not to work for hares (Reid et al., 2007). However, a hare specific option for 'delayed cutting and grazing of grassland' was implemented during 2008 in the Northern Ireland Countryside Management Scheme (Anon, 2008). This demonstrates that species-specific conservation is possible by modification of the existing agri-environment scheme network.

In addition to the intuitively appealing promotion of a habitat 'patchwork', further research into the effect of crop management on hare survival is required urgently to assess the impact of changes to harvesting regimes on hare population growth. This applies not only to the harvesting of silage but ongoing trends towards growing cereal crops, such as winter wheat and barley, which are harvested earlier in the year. The adoption of 'hare-friendly' mowing regimes, similar to those adopted for restoration of corncrake *Crex crex* L. populations (Tyler et al., 1998; Schaffer and Weisser, 1996) would be the corollary of evidence from such studies of leveret survival. Enhancing habitat heterogeneity, with respect to type and structure, coupled with sensitive harvesting techniques within current agri-environment scheme measures may be one way of reversing the decline of many farmland species, including hares.

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