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The consequences of predator control for brown hares (*Lepus europaeus*) on UK farmland

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Abstract The brown hare *Lepus europaeus* is a valued game species but also a species of conservation concern owing to its severe decline in abundance on farmland throughout Europe during the twentieth century. Changes in the farmland habitat and predation have both been cited as causative factors. Their relative roles have been unclear, but most conservation action has focused on improving habitat. We analyse data from a sequence of three unique studies (one experiment and two demonstrations) covering the period 1985–2006 in which control of several common predator species was undertaken to increase densities of wild game on farmland in England. Across the three studies, regression modelling of the proportional change in hare numbers between successive years showed that—after site, year differences and harvesting were accounted for—predator control was a significant determinant of hare population change. Where habitat improvement also took place, hares reached autumn densities that were exceptional for the UK and which could sustain substantial harvests. When predation control was stopped, hare densities fell, even where habitat improvements remained in place. This analysis demonstrates that even where farmland habitat is greatly improved, uncontrolled predation prevents hares making full use of its

carrying capacity. This helps explain the mixed—and at best modest—success of agri-environment schemes in the UK and elsewhere in Europe to increase hare densities. Game-shooting estates, on which effective predator control takes place, probably have a special significance within the landscape as source areas for brown hares.

Keywords Brown hare · *Lepus europaeus* · Predator control · Population dynamics · Farmland

Introduction

The brown hare *Lepus europaeus* Pallas, 1778 has declined in abundance in Britain since the 1960s (Tapper and Parsons 1984), and similar trends have been reported from other parts of Northern Europe (Sweden—Lindström et al. 1994; Jansson and Pehrson 2007; Switzerland—Haerer et al. 2001; Poland—Goszczyński and Wasilewski 1992; Denmark—Strandgaard and Asferg 1980; Schmidt et al. 2004). Because the brown hare is valued as a quarry species, as well as being an iconic species of open farmland, efforts have been made in several European countries to understand these population declines. Much interest has also been focused on how realistic management options might help to improve the status of brown hares.

Decline in crop diversity (Tapper and Barnes 1986) and increased predation (Tapper and Hobson 2002) have been suggested as drivers for population decline. Several strands of evidence (reviewed by Reynolds and Tapper 1996) also suggest a powerful influence of predators, especially foxes *Vulpes vulpes* L., in hare population dynamics (e.g., Reynolds and Tapper 1995). More recent work in Denmark suggested that crop diversity can influence hare density, but that the decline in hare numbers from 1955 to 2000 was

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driven mainly by predation by foxes (Schmidt et al. 2004). Vaughan et al. (2003) distinguished between ultimate and proximate causes of decline, implying that predation (for instance) could be the process through which habitat deterioration has its effect. Nevertheless, Panek et al. (2006) showed that experimental removal of foxes from a 32-km² area in western Poland resulted in an immediate increase in hare density relative to a nearby comparison area, which reversed when fox control ceased.

Owing to its decline in Europe, the brown hare is protected under Appendix III of the Convention on the Conservation of European Wildlife and Natural Habitats. In the UK, the brown hare is designated a ‘priority species of conservation concern’ and has a corresponding Species Action Plan, with a target of doubling the UK population by 2010 (Anon 1995). At the same time, the brown hare is regionally common and locally abundant, particularly in the arable farming regions on the east side of Britain (e.g., average 30 hares km⁻² in a 2,322-km² region of west Norfolk; Heydon et al. 2000). Management of wild game species, which includes control of some of their predators, is also more common in these eastern regions. Probably as a result (Heydon and Reynolds 2000), the density of foxes is notably low (0.58 foxes km⁻²) in the west Norfolk region mentioned (see Fig. 1).

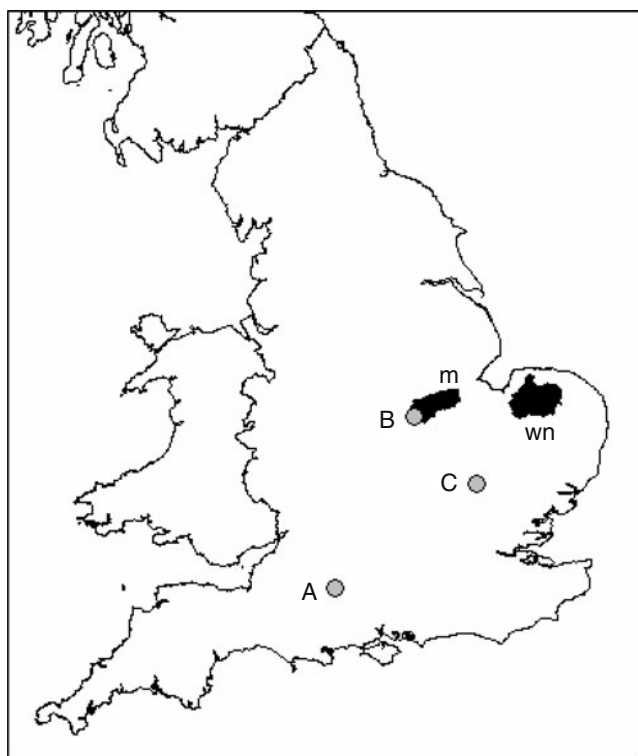


Fig. 1 Location of the three study sites (circles): **a** Salisbury Plain, Wiltshire, **b** Loddington and Horninghold, Leicestershire, **c** Royston, Hertfordshire. The filled patches indicate two study areas of Heydon et al. (2000), cited in the text: *m* Midlands and *wn* West Norfolk

Where it is abundant, the brown hare is regarded by many farmers as a pest of arable crops (Vaughan et al. 2003) and hare shoots may be organised with the aim of reducing numbers considerably (Stoate and Tapper 1993). The shooting of hares may also be allowed on game bird shooting days, dependent on the policy of individual shoots. Hares are held in high culinary regard as game meat. This, and their consequent commercial value, may be an additional or sole motivation for shooting. An estimated 200,000 to 300,000 hares are shot annually in the UK (Macdonald et al. 2000). Hunting of hares using dogs has been outlawed in the UK since the Hunting Act of 2004.

Manipulations of habitat and predator density in which hare numbers are monitored are expensive and therefore unusual. In this paper, we make use of three consecutive studies, during which, the abundance of several common predator species was controlled by a gamekeeper. The three studies are a mixture of formal designed experiment and demonstration projects, but form a chronological sequence in which the same professional gamekeeper (M. H. Brockless) was employed to carry out the predator control. The (positive) consequences of this management for bird species have been discussed for each study elsewhere (Tapper et al. 1996; Stoate 2007; Aebischer et al. 2007). In this paper, we explore the relationship between hare density and predation control across the three studies.

Methods

Study areas

The three studies took place at (1) Salisbury Plain, Wiltshire (51°14'57N –2°2'50W); (2) Loddington, Leicestershire (52°36'53N 0°50'31W); and (3) near Royston, Hertfordshire (52°3'19N 0°1'31W; Fig. 1). In each study, hares were surveyed simultaneously, both on predator control areas and on comparison areas nearby.

Salisbury Plain study (1983–1990)

This was a formal field experiment (Tapper et al. 1996) designed to establish the consequences of predator control for wild grey partridges (*Perdix perdix* L.). Two similar study areas measuring 5.64 km² (Collingbourne) and 4.96 km² (Milston) were selected within the Ministry of Defence training area on the basis that they had similar densities of grey partridge. The two areas were separated by 6 km of intervening grassland. Each area included both unenclosed ground in regular use for army exercises and enclosed farmland rented to tenant farmers and subject to only occasional military use. Unenclosed ground consisted mainly of unimproved chalk grassland which was either left

rough, grazed in sections by sheep and cattle, or cut for hay. Each area contained some small woods as well as areas of scrub. The enclosed farmland was principally used for arable crops (wheat, barley, oilseed rape, and turnips).

Predator control (see [Loddington study \(1992–2006\)](#) section) was implemented on Collingbourne in 1985 and continued for a 3-year period, Milston acting as an unmanaged comparison. Treatments were then switched for the next 3 years, with predator control implemented at Milston; and Collingbourne left unmanaged. No habitat management or modification of the farming system was implemented.

The dynamics of hares were reported previously by Tapper et al. (1996), who calculated an annual statistic of hare abundance by averaging population estimates for each winter. Road traffic killed a significant number of hares. These were recorded only during years of predator control (when the gamekeeper was present to record them), but illustrate a likely difference between the sites. On Collingbourne, which was bisected by a busy road, during predator control (1985–1987), 82 hares were killed by road traffic. During predator control on Milston (1988–1991), only two hares were killed by road traffic.

Shooting by syndicates took place on both sites and was outside our control. Partridges were the chief quarry and were either shot by walking guns or occasionally (when numbers were high) driven towards standing guns. In years when partridge numbers were low, shooters had more opportunity on shoot days to shoot hares.

Loddington study (1992–2006)

Based at Loddington Farm, this study was a demonstration of how modern farming coupled with game management could generate biodiversity (Stoate and Leake 2002). Loddington Farm consisted of 2.97 km² of arable fields and grassland enclosed by hedges and numerous small woods. Soils were mainly heavy clay. A 3.12-km² farm to the southeast at Horninghold, similar in character to Loddington Farm in the first study year and separated from the latter by 2 km of intervening farmland, was selected to act as a comparison site.

Game management at Loddington commenced in 1993, following a year of baseline monitoring. The management package (Boatman and Brockless 1998) included thinning and planting of woods and active management of hedges in order to increase the area of shrubby vegetation. Game crops (Stoate et al. 2004) were established on 20 m wide mid-field and field edge strips in order to provide invertebrate-rich foraging areas for pheasant broods in summer, and cover and seed food in winter. Pesticide use in cereal crops was restricted, especially on crop headlands (Sotherton 1991), in order to increase arable invertebrate abundance. Beetle banks

(Thomas et al. 1991) were created in one-third of the fields, and herbaceous strips in all field boundaries to provide nesting cover for game birds and suitable summer and winter habitat for beneficial invertebrates. Throughout the winter, grain was provided by hand and from hoppers widely distributed across the farmland and woodland habitats. The game management package was not applied to the surrounding area although there was low level management associated with the releasing of reared pheasants *Phasianus colchicus* L. on a neighbouring farm.

Predator numbers were controlled from 1993 to 2001 as on Salisbury Plain. In order to dissociate the effects of predator control and habitat management, predator control was halted at Loddington Farm in the winter of 2001 and 2002 but all other components of the game management system were maintained. Little or no game management took place at Horninghold throughout the entire 1992–2006 study period.

Royston study (2002–2006)

This was another demonstration study targeted at showing how to restore wild grey partridge numbers in a modern farmed environment (Aebischer and Ewald 2004). It took place on 20 km² of chalk farmland near Royston, most of which was arable. Predator control and habitat management were implemented in 2002 on the central 10 km² covering six farms and continued through to 2006. A further 10 km² in six farms forming two blocks immediately to the west and east of the managed area were adopted as comparison sites.

On the demonstration and comparison areas, game birds and hares were counted annually. Of the six farms on the comparison area, two had a full-time gamekeeper and a third had a part-time gamekeeper; nevertheless, because these keepers were heavily involved with the husbandry of released game, the management for wild game was regarded as less intensive than on the central area.

Predator control

Predator control was carried out by the same gamekeeper through all three separate studies. The aim was to suppress numerically common predator species known to be predators of small game birds and mammals: fox *Vulpes vulpes*, stoat *Mustela erminea* L., weasel *Mustela nivalis* L., brown rat *Rattus norvegicus* Berkenhout, 1769, carrion crow *Corvus corone* L., magpie *Pica pica* L., rook *Corvus frugilegus* L., and jackdaw *Corvus monedula* L. UK legislation allows a range of shooting and trapping methods throughout the year (The Game Conservancy 1994). Control effort was concentrated in the period February–July to protect game species during the breeding season.

While the Loddington Farm site was unusually small, the size of the treatment areas in the other two studies were typical of the area that one professional gamekeeper would be employed to manage on a lowland estate.

Hare count methodology

The spotlight count method of Barnes and Tapper (1985) was used in all three studies. The method has been shown to be effective at detecting major population changes over time or large differences in hare density (Langbein et al. 1999), and is appropriate for small areas where the number of observations may be small. Counts were conducted during the winter, once winter crops were established, providing open foraging areas. To detect hares from a raised platform on a vehicle, 300,000–500,000 candle-power lamps and 7×50 or 8×40 binoculars were used. On enclosed ground, there was at least one point per field. The area of ground visible from each count point was plotted on a map in daylight and subsequently measured. Because the visibility of hares is only ever reduced by weather conditions, counts were made only in optimal weather conditions, avoiding nights with sub-zero temperatures, mist, fog, or strong winds. Visibility on each survey night was measured and taken into account by Tapper on Salisbury Plain in calculating the proportion of ground surveyed (21–35%). In the Loddington and Royston studies, 300 m was taken as an empirically determined maximum distance for detection. To calculate the hare population for each site, the observed density was extrapolated to the entire site. This seemed reasonable because habitats likely to hold low hare densities at night (such as woodland) formed a very small percentage of total area. Survey data are presented as densities in Fig. 2, but also modelled as estimated population size in order to take account of the large numbers culled from the high-density populations.

Survey effort, equipment, and personnel were consistent within each of the three studies. On Salisbury Plain, 25 count points were used at Collingbourne and 22 at Milston. These were relatively remote field sites, and local weather conditions were difficult to predict. Hence, one to four (average 2.75) surveys separated by several weeks were made each winter between 1983 and 1990. We considered the possibility of systematic bias introduced by this variable survey effort. Regression of estimated abundance against survey date showed no significant difference in slope between years or treatments, while for data pooled across all winters, the slope did not differ significantly from zero. This justified using annual winter averages, as in Tapper et al. (1996), noting that this under-represented peak abundance detected in individual surveys during periods of predator control.

In the Loddington study, owing to manpower constraints, surveys were made on only a single night in each winter, but

locally-based staff could choose optimal conditions. Thirty-five count points at Loddington and 30 count points at Horninghold covered, respectively, 56% and 60% of the total land area. In the Royston study, hare surveys took place over a number of nights, choosing optimum weather conditions in early winter. The number of count points varied in response to crop patterns and access and was not recorded, but the total area surveyed was recorded and amounted to 25% to 37% of the total land area.

Statistical analyses

All analysis was performed using Genstat release 12.1. Statistical modelling was necessary to dissociate the effects of predator control from those of site, year, and habitat improvement. We used General Linear Modelling with log-transformed change in abundance from one year to the next as the dependent variable. To account for differences among the three studies and between the component study sites, we included two factors as blocking variables: 'site' (a factor with six levels representing the two sites in each of three studies) and 'year nested within study'. This ensured that each study was treated as a separate experimental block. Habitat improvements were essentially permanent relative to the time-scale of each study. At no site were habitat improvements implemented after predator control began. Thus, effects of habitat improvement on hare density are included within the effects of 'site'. Small methodological differences between studies—such as those described for hare counts above—would also be included in the 'site' effects. Similarly differences in geographical area which would influence accessibility to predators would be represented by this term.

Predator control was represented by a factor with two levels indicating whether or not predator control took place at a given site during year t ; because predator control was seasonally focused, this chiefly reflected whether predator control took place during the spring and summer between the two counts. First-order density dependence was examined by including \log_{10} (density in year $(t-1)$) as an explanatory variate. The full model also included an interaction term between predator control and \log_{10} (density in year $(t-1)$). Significance was tested by dropping first the interaction term, then predator control or \log_{10} (density in year $(t-1)$) individually from the full model.

Shoot data were not available for the comparison site at Horninghold (Leicestershire) or for the adjacent areas at Royston (Herefordshire). At these sites, we assumed the number of hares shot was zero. The effect of errors in this assumption (i.e. if significant numbers of hares were shot on comparison areas) would be to underestimate population growth on these two sites. To a large extent, therefore, such errors would be accommodated by the factor 'site'.

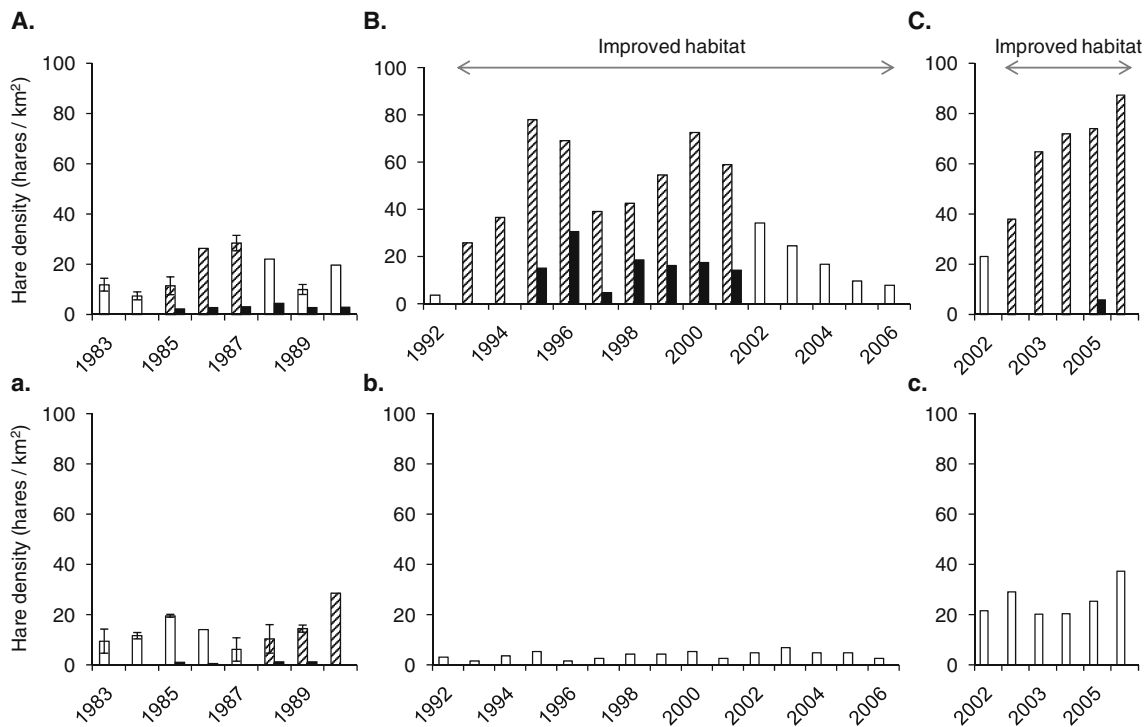


Fig. 2 Density of hares (hares/km²) for the three study sites (Salisbury Plain: A, Collingbourne, **a** Milston. Leicestershire: B-Loddington, **b** Horninghold. Hertfordshire: C—Royston demonstration area, **c** Royston adjacent area). *Hatched bars* winter hare density during

periods of predator control. *Unfilled bars* winter hare density during periods of no predator control. Standard errors are indicated where plotted data are averages of several survey estimates (Salisbury Plain only). *Black bars* hares killed by shooting or accidentally in pest control activity

We used two models with different dependent variables:

- (1) Density model. We calculated the proportional change in hare density between year $t-1$ and year t as $\log_{10}(D_t/D_{t-1})$ where D_t and D_{t-1} are the estimated densities of hares on surveyed areas in successive years. This model assumes that within each study, hare counts were a linear function of hare density, but does not assume identical survey methodology or precision between studies. It does not take into account the often considerable numbers of hares shot during predator control years.
- (2) Population model. To account for known shooting losses, we calculated the proportional change in hare numbers between year $t-1$ and year t as $\log_{10}[(N_t + A_t)/(N_{t-1} - S_{t-1})]$ where N_t and N_{t-1} are the estimated n for each study site in successive years, A_t is the number of hares accidentally killed during pest control operations in summer months, and S_{t-1} is the number of hares shot in the winter months immediately following the count in year $t-1$. (Hares known to have been killed by other causes such as road traffic were not included, because these were recorded only where the keeper was active.) In effect, the dependent variable represented the growth of the un-shot hare population from one annual count to the next. The

(\log_{10}) denominator of this term, lagged by 1 year, was used to test first-order density dependence.

Both models assume that hare numbers were estimated with comparable accuracy and precision among the three component studies. The log-transformed dependent variable means that the additive effects of explanatory terms in the model represented multiplicative population effects.

Results

In all three studies, comparison areas had initial hare densities very similar to the treatment areas (hares km⁻² for treatment and comparison areas, respectively: Salisbury Plain 15.6, 11.3; Loddington 3.6, 3.2; Royston 23.1, 23.5). In general, hare abundance increased wherever predator control was implemented, while comparison areas often showed no increase or showed a decline (Fig. 2). During predator control years on Salisbury Plain, hare density peaked at 28.5 hares km⁻², compared to average winter hare density prior to predator control between 7.4 and 11.9 hares km⁻². Similarly, at Loddington and Royston, where habitat was also managed for game, hare density reached the highest values under predator control. During the predator control phases at Loddington Farm and the Royston

demonstration area, hare densities were exceptionally high (mean 52.3 hares km⁻², ± S.E. 6.8; mean 67.2, ± S.E. 30.1). After predator control ceased at Loddington Farm, hare density averaged 25.3 hares km⁻² (± S.E. 7.8) over 5 years, even though habitat improvements were still in place. By the most recent count in 2006, hare densities at Loddington Farm had declined to 7.8 hares km⁻².

The two models led to identical conclusions, and the regression coefficient estimates were similar (Table 1). There was no evidence of serial correlation (Breusch-Godfrey test, $\chi^2_1 = 2.31$, n.s.). There was no significant interaction in either model between predator control and hare abundance in the previous year, and this interaction term was dropped from the models. Hare abundance in the year ($t-1$) had a significant negative effect on growth between year ($t-1$) and year t , implying that density-dependent effects were operating. Predator control had a significant positive effect, amounting to an approximate doubling of annual population growth rate and explaining 44% of the variance.

Discussion

Hare density

In this analysis, the interest has been in hare population growth rates rather than density per se. Nevertheless, the actual densities observed are of considerable interest in conservation terms. During the Loddington study reported here, Heydon et al. (2000) estimated hare density by distance sampling in a 1,283 km² region that included Loddington. Loddington Farm lies at the southwestern edge of this region, with the Horninghold site 2 km outside the region. Heydon et al. (2000) estimated mean hare abundance for this region to be 14.5 and 15.9 hares km⁻² between August 1995 and September 1996, respectively (net 95% confidence interval for both estimates=9.6–19.8). Average early winter hare density at Horninghold during 1992–2006 was clearly well below this, and the same would have been true for Loddington Farm prior to predator control in 1992. The estimated density at

Loddington in 2006, 5 years after the cessation of predator control, was very similar to the seven hares km⁻² proposed by Tapper (1999) for sub-optimal land with habitat improvement but without predator control. On the other hand, hare densities at Loddington Farm during the predator control phase were exceptionally high for the region, or indeed for Britain as a whole (Tapper 1999; White et al. 2000). Support for these estimates of very high density is provided by the large bags (up to 30.3 hares shot km⁻² at Loddington) representing up to 40% of estimated density. Despite harvesting, the hare populations at Loddington Farm and Royston maintained average densities during years of predator control that would be regarded as very high anywhere in the UK.

The increase in hare density on Salisbury Plain during predator control was relatively modest presumably because predator control was limited to 3 years and because no habitat improvement took place. Hares were shot only as an incidental component of shoot bags, and numbers shot were small. The comparison area at Royston was immediately adjacent to the treatment area and arguably was likely to be influenced by events on the latter. Some predator control also took place on these adjacent farms. Nevertheless, mean hare density on these farms at the latest count (2006; 37.2 hares km⁻²) was only 43% of that on the demonstration area (87.3 hares km⁻²). An unknown number of hares were shot on the comparison area, but it is inconceivable that this was sufficient to explain the differences in growth rate between the demonstration and comparison areas.

Predation as a determinant of hare population density

Under favourable conditions, brown hare populations can have a very high intrinsic population growth rate with up to 13 young produced per surviving adult female per year (Marboutin et al. 2003). Sustained increase in density over the first few years of predator control in each treatment area of the present study shows that we are observing population growth, not merely an increase in winter density. In less favourable circumstances, population growth is believed to be limited by predation, disease, and intra-specific competition,

Table 1 Coefficients for significant explanatory factors from regression models of hare population growth (on a log₁₀ scale)

Parameter	Coefficient	s.e.	t_{21}	P
Model 1				
Dependent variable: log ₁₀ change in estimated hare density between year ($t-1$) and year t				
Predator control	0.2997	0.0826	3.63	0.002
Estimated hare density in year ($t-1$)	-0.617	0.137	-4.51	<.001
Model 2. Dependent variable: log ₁₀ change in estimated hare population size, adjusted for shooting and other losses incurred through pest control, between year ($t-1$) and year t				
Predator control	0.3469	0.0862	4.03	<.001
estimated hare population size in year ($t-1$) after adjusting for shooting losses	-0.546	0.157	-3.48	0.002

all of which are conventionally seen as density-dependent processes and thus regulatory. Our analysis shows that across three studies, control of common predators allowed greater hare population growth from year to year. The extent to which this resulted in a sustained high density of hares clearly depended on habitat, with the greatest improvement shown where habitat management likely to benefit hares was also undertaken.

Any growing population will eventually be constrained by the availability of resources such as food, and there is substantial evidence for density-dependent limitation of productivity in brown hares (Frylestam 1979, 1980). In the analysis reported here, clear evidence was obtained for density-dependent effects. Additionally, shooting probably acted in a crudely density-dependent fashion. Hares were harvested quite heavily at Loddington and Royston when their density exceeded acceptable levels. At Loddington, farm managers were uneasy with densities in excess of about 50 hares km⁻².

Hutchings and Harris (1996) attributed a positive association between gamekeepers and hare density to enhanced habitat management rather than to predator control. Smith et al. (2005) concluded that habitat degradation was the ultimate cause of hare population decline around Europe, with predation acting as a proximate agent. If true, this would imply that in the absence of predators, the decline would still have taken place through other mortality factors; that controlling predator numbers would not in itself restore hare numbers; and conversely, that where favourable habitat characteristics have been restored, predation would not prevent hare population increase. On the contrary, we have shown that predator control is a key component of the game management package that leads to greatly increased hare densities. Specifically, removing predators without habitat improvement led to increased hare densities (Salisbury Plain); a combination of habitat improvement and predator control led to still higher hare densities (Loddington and Royston); and maintaining favourable habitat, while allowing predator levels to increase resulted in a strong decline in hare density (Salisbury Plain and Loddington).

Given that the models explained around 44% of the variance in hare population growth, one might ask what explains the remaining 56%. We would attribute a good deal of the variance to errors in estimating autumn population size—including survey inaccuracies, timing of surveys in relation to hare dispersal, and the inclusion of numbers shot. Density-dependent effects extending over periods longer than 1 year may also play some part. A further likely cause is local and annual variation in predation pressure, which is masked by our representation of ‘predator control’ by a two-level factor. This ignores any variation in effectiveness of that control, and also ignores local and temporal changes in the guild of protected predators that predation control did not

touch, such as raptors (Falconiformes), owls (Strigiformes), and badgers *Meles meles*.

The role of habitat

The permutation we have not tried in these studies is to implement habitat improvements without at least initial control of predators. However, this has been implemented elsewhere with modest or equivocal success. Vaughan et al. (2003) found set-aside or fallow to be associated with more frequent sightings of hares on arable farms. The UK’s Arable Stewardship Scheme—which supported a range of wildlife-friendly habitats to partially replace arable crops—had no discernible effect on hare density after 2 years (Tapper and Aebischer 2001). Four years after implementation, it was associated with greater hare density in one region of England (East Anglia), but not in another (the West Midlands); in East Anglia at the start of the scheme, hare densities were one-third higher on Arable Stewardship farms than on comparison farms, but after 4 years, were two-thirds higher (Browne and Aebischer 2003). In the lowlands of Switzerland, similar habitat measures designed specifically to benefit hares had no discernible effect on hare density after 5 years (Pfister et al. 2002). In the present study, hare density at Loddington 14 years after habitat improvement and 5 years after the cessation of predator control was roughly twice that at the outset or on the nearby comparison site, Horninghold, which had neither treatment.

Slamečka (1991) increased habitat diversity in a 15 km² area of the Danube lowlands in Slovakia and showed an 80% increase in hare density (from 38.4 to 66.5 hares km⁻²) with an accompanying threefold increase in the number shot. This study was described by Vaughan et al. (2003) and Smith et al. (2005) as involving ‘no manipulation of fox numbers’, though Slamečka (1991) himself makes no mention of predator control or predator densities. In fact, at the time of Slamečka’s study (1986–1990), foxes were under intense hunting pressure because of the value of their fur (a single fur was then worth roughly 2 weeks’ wages, or 70 l of petrol) and fox density is believed to have been suppressed as a result (Slamečka, personal communication). In a later paper, Slamečka et al. (1997) regard the fox as the key predator of hares, note its recent increase due to oral vaccination against rabies, and conclude that reduction in fox density is ‘highly desirable’ in the management of small game such as hares. Similarly, Panek et al. (2006) argue that the increase of hares in response to experimental removal of foxes supports the hypothesis that an increase in fox numbers is a reason for a decline in hare numbers in Poland since the 1990s, and that fox control is an effective remedial measure.

In the UK Arable Stewardship Scheme, the presence of a gamekeeper did not modify the effect of the habitat changes on hare density in either East Anglia or the West Midlands

(Tapper and Aebischer 2001; Browne and Aebischer 2003), though one should note that presence of a gamekeeper is not synonymous with effective predator control. On the other hand, it may be relevant that fox density in the East Anglia region—as evidenced by shooting bags (Tapper 1992) and direct survey (Heydon et al. 2000)—is low compared with other parts of the UK, probably because of high historical and current intensity of predator control in the region (Heydon and Reynolds 2000).

Game management in the agricultural landscape

Game management is widespread in the UK. Current best estimates (J. Ewald, Game & Wildlife Conservation Trust, personal communication) suggest that gamekeepers are employed on about 21% of the land area of England, 5% of Wales, and 31% of Scotland. In the lowlands, game management is especially associated with arable agriculture and thus with habitats and regions that are relatively favourable for hares (Tapper 1992; Heydon and Reynolds 2000; Heydon et al. 2000). For this reason, the present analysis is helpful in distinguishing the role of predator control within this overall picture.

The game management package in the Loddington and Royston studies is implemented within a commercially-driven agricultural landscape. Relatively unfavourable habitats with predator densities at or above regional averages are replaced with more favourable habitats and lower densities of common predator species. Man becomes the dominant predator of game species, but farming remains economically viable. Considerable use was made of available agri-environment grants to improve the farm landscape for small game species and, wherever possible, farm management options were also chosen to enhance this. Most of these measures have a cost to farming operations in terms of convenience and cost-efficiency (Leake 2007; Stoate and Jarvis 2006).

Effective control of common predators is time-consuming and, therefore, a costly addition to these habitat measures, but for wild game birds, it is a crucial component of the game-management package (Tapper et al. 1996; Boatman and Brockless 1998). This analysis suggests that it is crucial for brown hares as well. The magnitude of population increase observed in these studies suggests that estates with favourable habitat and effective predator control would act as significant source areas to support hare populations in the adjacent countryside.

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