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Farming for pests? Local and landscape-scale effects of grassland management on rabbit densities

**Silviu O. Petrovan · Isabel C. Barrio ·
Alastair I. Ward · Philip M. Wheeler**

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Abstract In recent decades in the UK, there has been an increasing trend in numbers of the European wild rabbit, a significant agricultural pest typically associated with grassland habitats. However, the relationship between rabbit abundance and grassland management, in particular grazing, has not been sufficiently explained. We studied rabbit densities in seven pasture-dominated sites in north-east England between autumn and spring in two consecutive years, and used generalised linear mixed models and generalised additive models to explore relationships between habitat and management variables and rabbit abundance at local (field) and landscape scales. At the local scale high rabbit densities were significantly associated with small fields and the very short, homogeneous swards created by intensive sheep grazing during autumn and winter. At the landscape scale, high rabbit numbers were associated with sites with most field margins and a predator removal policy. Our results indicate that landscape management may play a central role in explaining rabbit abundance and distribution in grasslands. We suggest that current pasture management may create favourable conditions for high rabbit densities, and consequently boost numbers of this significant pest species.

Keywords Rabbit · *Oryctolagus cuniculus* · Grassland management · Pasture · Sheep · Pest

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S. O. Petrovan (✉) · P. M. Wheeler
Centre for Environmental and Marine Sciences,
University of Hull, Scarborough Campus,
Filey Road YO11 3AZ, UK
e-mail: s.petrovan@hull.ac.uk

I. C. Barrio
Departamento de Zoología, Universidad de Córdoba,
Campus de Rabanales 14071,
Córdoba, Spain

S. O. Petrovan · A. I. Ward
The Food and Environment Research Agency,
Sand Hutton, York YO41 1LZ, UK

Introduction

In Great Britain, populations of the European wild rabbit (*Oryctolagus cuniculus*) have recovered from the myxomatosis epidemic of the 1950s, which eliminated over 99% of the population (Lloyd 1970) and there has been a subsequent increase in rabbit numbers (Lees and Bell 2008; Trout et al. 1986). Contrary to the situation within the rabbit's native distribution range in the Iberian Peninsula, in which the slow recovery of rabbit populations has only recently led to emerging pest situations (Barrio et al. 2010) and despite recent reports of declines following the spread of rabbit haemorrhagic disease in both England and Scotland (Battersby 2005), in many areas in the UK rabbits have reached pest status causing approximately £115 million of damage to the British agricultural industry (Smith et al. 2007). The impact of rabbits is especially significant in grass-dominated areas, which are the typical habitat for the species (Hulbert et al. 1996; Iason et al. 2002) and which dominate much of the British agricultural landscape, covering around 68% of the total agricultural area (approximately 12.7 million ha; Anonymous 2009). Damage and crop losses associated with rabbits may be more easily overlooked by farmers in pastures and silage grass areas than in other types of crops and can result in little or no control even when rabbit numbers are high (Dendy et al. 2003). For these reasons, understanding the factors that shape rabbit distribution and densities in grassland could allow more effective targeting of resources for rabbit management.

Previous studies in the United Kingdom investigating the factors associated with rabbit abundance at a national scale have identified several variables which positively influenced rabbit densities such as aspects of woodland, soil wetness, predator removal policy and inclusion in agri-environment schemes (Reid et al. 2007; Trout et al. 2000). Pest species, such as the European rabbit, are capable of utilising much of the landscape in which they live (Hamilton et al. 2006) and this is particularly the case in a highly anthropogenic and productive landscape, such as UK farmland, where rabbits can be found in almost every type of habitat (Trout et al. 2000). In such heterogeneous landscapes, resources are spread relatively continuously across a wide area but with variation in resource quality (Hamilton et al. 2006). In grassland habitats, grazing is a primary determinant of sward structure and composition since grazing livestock create a short, dense canopy of highly nutritious plant material and there is some evidence that this can affect rabbit distribution. Bakker et al. (2004, 2009) demonstrate that rabbit grazing is facilitated by the presence of cattle grazing in a productive agroecosystem. Experimental evidence suggests that at the local scale, rabbits select for foraging areas with short sward irrespective of low crop biomass (Iason et al. 2002). Preference for shorter swards by rabbits is attributed to anti-predator strategies, as the perceived predation risk may be lowest in short vegetation (Bakker et al. 2009; Iason et al. 2002).

Here, we investigate the role of habitat and management variables at two spatial scales in explaining rabbit densities in several large grassland-dominated sites in north-east England. At a wide, multi-farm scale, variables reflecting land use, patchiness of the landscape and management practices, i.e. culling of predators or rabbit populations, were considered. At a local scale, additional variables describing habitat features, field management and survey season were also included. We aimed to identify which habitat, pest/predator and grazing management factors most parsimoniously explained variation in rabbit densities both at local and landscape scales.

Methods

Study site

Rabbit distribution and densities were recorded in seven study sites located in a lowland/marginal upland pastural landscape in North Yorkshire, England at altitudes between 30 and 250 m. Sites were selected by investigating remotely sensed images using Google Earth (http://earth.google.com) and searching for large areas dominated by pastures, subsequently verified in the field. Sites were spaced between 3.5 and 14 km apart (mean 10.4 km).

Mean annual temperature and mean annual precipitation for the past 30–40 years were 8°C (SD=0.5) and 704 mm (SD=63) for three of the study sites, situated closer to the coast and 7°C (SD=0.5) and 924 mm (SD=85) for the other four sites (Environment Agency 2009; MetOffice 2007).

Sites were dominated by improved and semi-improved grassland (<50% *Juncus* spp. dominated and no artificial fertilisers) but also included a few arable fields, patches of woodland and rural development. In most areas, the landscape was undulating, with gentle sloping hills and wide, flat valleys. Grass fields were used in a rotational system and were extensively grazed by sheep *Ovis aries* and cattle *Bos taurus* at variable stocking densities. A small percentage of fields were used for silage production with two to three cuts per year and sheep grazing during autumn and winter. Fields were bounded by dry stone walls, hedgerows and barbed wire fences and size varied considerably (mean=2.98 ha, SD=2.91, range=0.33–22.72 ha). Shooting for game birds took place at most sites but only four sites included a permanent gamekeeper whose role included predator and pest control.

Sampling design

In each of the seven selected sites we established a series of two to six transects, each approximately 2–3 km in length (Table 1), by identifying farmers who would give permission to survey their land at night while aiming to cover as much of the area as possible throughout the site. Only three of more than 60 farms identified did not grant access for surveys. To minimise the possibility of double counting of animals in each site transects were spaced at a minimum of 300–400 m distance or separated by natural or artificial barriers such as streams, large blocks of woodland or robust fences. Transects did not follow any landscape or manmade features, such as streams, valleys, roads or foot paths and each transect encompassed between six and 22 fields (mean=9; SD=2.3).

Data collection

Rabbit surveys

Rabbit density surveys were carried out between October 2007 and March 2009. Sampling effort was concentrated during autumn–winter (October to December) and early spring (January to March), when vegetation was generally short and when rabbit population surveys are most effective (Poole et al. 2003). However, due to the poor weather conditions in spring 2008, with high rainfall and frequent fog, surveys were extended until early May for a small number of transects. During the first survey periods, i.e., autumn 2007 and spring

Table 1 Sampling design

Site	Season surveyed	Fields (number)	Transect (number)	Effort (km)
A	Autumn 07	39	5	9.4
	Spring 08	38	5	9.2
B	Autumn 07	58	5	11.8
	Spring 08	53	5	10.5
C	Autumn 07	78	6	13.9
	Spring 08	75	6	13.2
	Winter 08-09	119	12	23.3
D	Autumn 07	23	3	8.4
	Spring 08	21	3	8.2
E	Autumn 07	17	2	6.5
	Spring 08	17	2	6.5
F	Autumn 07	38	4	9.3
	Spring 08	34	4	8.3
G	Autumn 07	24	3	8.0
	Spring 08	22	3	7.8
	Winter 08-09	47	6	15.3
Total per season	Autumn 07	277	29	67.3
	Spring 08	260	29	63.4
	Winter 08-09	166	18	38.6
Total				169.6

Autumn 07 Oct–Dec, *Spring 08* Feb–May, *Winter 08–09* Oct–Mar.

Field identity, transect position and survey effort were the same in all repeat surveys of individual sites with minor exceptions caused by fields changing management (i.e. grassland in autumn but sown in spring). In sites C and G during winter 2008–2009 transects were surveyed twice

2008, all transects at all seven sites were surveyed twice, once in autumn and once in spring. These surveys were used in landscape-scale analyses. In addition, two of the seven sites (C and G) were surveyed again twice in autumn 2008 and spring 2009 using the same transects. Local scale analyses used these data from sites C and G in conjunction with data from all sites (A–G) collected in spring 2008 when detailed measures at the field level were taken.

Rabbit densities were assessed by spotlight counts which have been shown to produce accurate and consistent estimations of rabbit densities in a comparative study (Poole et al. 2003). Rabbit numbers were recorded as an exact number or as an estimate in intervals of five or ten when densities were very high. All night-time surveys were started at least 1 h after sunset and finished before 23:30. In accordance with previous rabbit studies, surveys were not performed on days where visibility was poor due to fog or heavy rain; similarly particularly cold, windy or bright nights were also avoided due to their negative impact on rabbit activity (Reid et al. 2007). Surveys were carried out by two people, with the same observer, collecting all data in order to avoid between-observer differences in detecting animals while the second person recorded the data. Transects were paced slowly and silently on a straight line through the middle of the field while continuously scanning the area in front in a semicircle with 8×42 binoculars and a 1 million candlepower spotlight (Clubman CB2, Cluson Engineering Ltd, Hampshire, UK). For all transects that were surveyed more than once in the same season, there was an interval of at least a week between visits to minimise any effect of animal disturbance due to spotlighting. To ensure that no animals were counted twice while moving through successive fields, all rabbits which were displaced by the surveyors were followed with the lamp as they moved away to establish with precision the direction of movement and were consequently discounted if they relocated to other fields that were on the transect. The distance walked was recorded at all times as tracks with a GPS (Garmin GPSMAP76C, Garmin International Inc., Kansas, USA) and later superimposed on 1:10,000 scale Ordnance Survey digital map data tiles of the area provided by the Digimap service (http://edina.ac.uk/digimap). Tracks were manipulated in ArcGIS 9.1 (ESRI, CA, USA) to remove sections where rabbits were not surveyed (e.g. distance walked to and from the access point in the field, avoidance of farm buildings or woodland). The remaining sections were used to calculate transect length to the nearest metre in each field. Rabbit densities were computed as the total number of rabbits detected in each field divided by field size.

Habitat variables

We considered several variables reflecting field management and surrounding habitat structure both at a local and a landscape scale.

At the local scale, fields were classified into two types according to their grazing management, specifically if they were grazed by sheep or not. Sward height data were collected concurrently with spotlight counts by the direct measurement method which has been shown to be the only method capable of producing accurate measurements in short swards (Stewart et al. 2001). Measurements to the nearest 1 mm, were collected in each field along the transect, from the moment of the entrance into the field until the exit, every 50 paces in large fields and every 25 paces in smaller fields, with a minimum of six measurements per field. The minimum number of sward height measurements needed to give a stable mean for sheep grazed fields was verified at an early stage of the project. Additional measurements were taken in fields where sward height was very heterogeneous to account for the greater variability.

Field margins can provide diversity and additional habitat for a range of animal species (Marshall and Moonen 2002), and they form an important part of Agri-Environment Schemes which can have a positive effect on rabbits, but also on fox abundance (Reid et al. 2007). For each field, we quantified the extent of field margins inside the field by giving them a class between I and IV; I corresponding to field margins between 0 and 10 cm wide (in which the vegetation was taller or more diverse than the rest of the field), II for 10–20 cm, III for 20–30 cm and IV for 30 cm and above.

In each field, we recorded the presence of livestock, either as a direct count or as an estimate for large groups of sheep or cattle. Field size and proximity to woodland or bracken patches, representing shelter for rabbits or harbourage for their warrens, were also measured. The proximity to these refuges was taken as a four-level categorical variable, separating those fields adjacent to woodland or bracken, those up to 100 m away, those lying between 100 and 200 m away, and those further away.

At the landscape scale, the area occupied by sheep pastures was assessed. The patchiness of the landscape was indirectly measured through ‘edge density’, which was computed in ArcGIS for each site as the length of field borders per unit area (in m ha^{-1}). For analysis purposes, site area was calculated as the sum of field areas that were surveyed in each season (mean=94.51 ha; range 18.59–143.00 ha; SD=41.92). Management practices such as the presence of rabbit or fox *Vulpes vulpes* control were determined by detailed interviews with farmers, gamekeepers, and landowners and were included as a binary (presence–absence) variable. The season in which all field surveys for each site were conducted (i.e. autumn or spring) were also considered. Additionally, the number of foxes encountered in each site during the surveys was taken as a surrogate of predation pressure. Fox records were expressed as foxes seen per kilometre walked. In the case of the field-scale analyses, we took into account the date of field sampling by pooling survey journeys into bimonthly periods.

Data analysis

To investigate the factors that explain variation in rabbit densities at both the field and landscape levels we used linear mixed models (Zuur et al. 2009). Site and field identity nested within site were included as random factors in both analyses. In both cases, the response variable was rabbit density, which was log-transformed to achieve normality. Sward height and heterogeneity, field size and type, proximity of the field to woodland or bracken patches, the presence of field margins and domestic stock, and bimonthly sampling period were included as fixed components in the local scale approach. Edge density, sampling season, predator and rabbit control and percentage of land used by sheep were included as the fixed component in the landscape model. To avoid collinearity problems, highly correlated explanatory variables ($r>0.6$) were excluded from the model (i.e. foxes seen per km and sward height heterogeneity); remaining variables had variance inflation factors <2 (Graham 2003). Model selection was based on Akaike's Information Criterion (AIC) and likelihood ratio tests. In the local scale model, we added a variance structure to the model to account for the heterogeneity in residual spread across sampling months (Pinheiro and Bates 2000). The following models were fitted for the local and landscape scales respectively, as the starting points for the model selection:

Local scale

$$\begin{aligned}\mathrm{Log}(\text{rabbit density}+1)_{ij} = \alpha &+ \beta_1(\text{grass height})_{ij}\\ &+ \beta_2(\text{field size})_{ij}\\ &+ \beta_3(\text{bimonth})_{ij}\\ &+ \beta_4(\text{field type})_{ij}\\ &+ \beta_5(\text{field margins})_{ij}\\ &+ \beta_6(\text{proximity to woodlands})_{ij}\\ &+ \beta_7(\text{livestock})_{ij} + \mathrm{a}_i + \varepsilon_{ij}\end{aligned}$$

$$\varepsilon_{ij} \sim N\left(0, {\sigma_j}^2\right); a_i \sim N\left(0, d^2\right)$$

Landscape scale

$$
\begin{aligned}
\text{Log}(\text{rabbit density}+1)_i = \alpha &+ \beta_1(\%\ \text{sheep})_i \\
&+ \beta_2(\text{edge density})_i \\
&+ \beta_3(\text{season})_i \\
&+ \beta_4(\text{rabbit control})_i \\
&+ \beta_5(\text{predator control})_i + \mathrm{a}_i \\
&+ \varepsilon_i
\end{aligned}
$$

$$\varepsilon_i \sim N\left(0,\sigma^2\right); a_i \sim N\left(0,d^2\right)$$

Where the subscripts i and j refer to each field and sampling month respectively. a_i is the random intercept that differs for each field i, and is assumed to be normally distributed with mean 0 and variance d^2. The residual terms ε_i and ε_{ij} are also assumed to be normally distributed with mean 0 and for ε_{ij} variances are allowed to differ by sampling month j.

Additionally, to investigate the shape of the relationship between sward height and rabbit occurrence in fields we used univariate binomial Generalised Additive Models (GAM) with a logit link (Hastie and Tibshirani 1990). Visual inspection of GAM plots can be used as an exploratory tool to infer the relationship, linear or otherwise, between variables (Pueyo and Alados 2007). The response variable was the presence or absence of rabbits in each field, and the predictor variable, i.e. grass height, was modelled using cubic regression splines, and the optimal amount of smoothing was estimated via cross-validation (Zuur et al. 2009). To improve the fit of the model, grass heights were log-transformed.

Modelling assumptions of normality, homogeneity and independence were checked (Zuur et al. 2009). All statistical analyses were performed using R 2.8.1 (R Development Core Team 2008) and particularly the packages *nlme* (Pinheiro and Bates 2000) and *mcgv* (Wood 2006).

Results

During the 2 years of this study we surveyed 260 individual fields on 170 km of transects by spotlighting, collected over 2,700 grass height measurements and recorded a total of 4,543 rabbit observations. We surveyed 94 fields in two sites four times while all the rest were surveyed twice. Rabbits were present in 63% of all surveyed fields but densities varied widely, with only a small proportion of fields (16%) exhibiting very high rabbit abundances. Overall, we saw an average rabbit density of 4.7 rabbits ha^{-1} (SD=8.77; range=0.00–69.68). Rabbit densities varied between study sites (Fig. 1; ANOVA, F=43.275, p< 0.001). We recorded a total of 33 foxes (mean=0.25 foxes km^{-1}; SD=0.24; range=0.00–0.67), and fox sightings were significantly lower in sites where predator control was carried out (t test; t=4.130, n=7, p=0.035; Fig. 1). At the landscape scale log-transformed rabbit densities across sites were significantly associated with the field boundary length per unit area ('edge density') and the presence of predator control policy at a site (Table 2). At the local scale, rabbit densities were correlated with grass height, field size and field type (Table 3). Grass height ranged from 0.5 to 17.9 cm (mean=3.7, SD=2.7), and was negatively correlated with rabbit densities; it was also significantly different between field types (ANOVA, F=75.768, p=0.0001; Fig. 2). Field size was negatively related to rabbit densities, with smaller fields having higher rabbit densities. Field type, specifically those fields devoted to sheep grazing, was positively associated with rabbit densities. However, neither the proximity to woodlands or bracken patches, field margins, nor the presence of livestock in the fields during the survey, were significantly associated with rabbit densities, and were therefore excluded from the final model.

Grass height showed a non-linear relationship with rabbit presence (Fig. 3). After cross-validation, the effective degrees of freedom were set to 5.51. Effective degrees of freedom reflect the ruggedness of the smoothing parameter: values close to 1 represent straight lines, higher values indicate non-

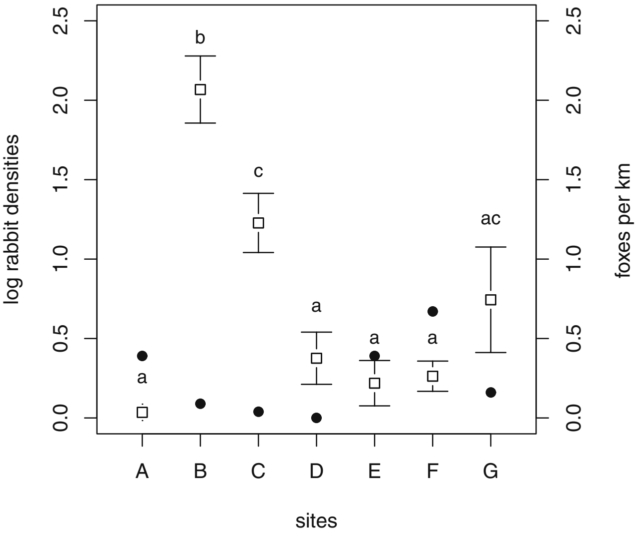

Fig. 1 Rabbit densities and foxes per km, i.e. numbers of foxes seen per kilometre walked at seven sites in NE England. *Open squares* are log mean rabbit densities and corresponding 95% confidence intervals; *letters* indicate significant differences between groups (p< 0.01). *Filled dots* indicate foxes seen per kilometre values in each site. Predator control was carried out at sites *B*, *C*, *D* and *G*

Table 2 Linear mixed models results for rabbit densities at the landscape scale

Linear mixed model for rabbit densities—landscape scale

	Estimate (±SE)	*df*	*t* value	Sig.
Intercept	−1.640 (±0.718)	7	−2.284	0.056
Edge density	0.009 (±0.003)	4	2.808	0.048
Predator control	1.036(±0.357)	4	2.898	0.044

Response variable: rabbit densities log-transformed. Random factor: sampling site. Log Likelihood: −11.11

linearities (Zuur et al. 2009). The smoothing term was highly significant (χ^2=22.93, p=0.001). The density of rabbits was greatest at grass heights of 1.12 cm, and again but to a lower extent at 4.31 cm and declined at higher grass heights.

Discussion

This study aimed to create a better understanding of the mechanisms through which habitat and farming management, in particular grazing, influences rabbit abundance in grasslands at both the field and the landscape scale and as a consequence, to identify ways that management practices could be used to manipulate rabbit densities and the economic impacts associated with their presence in pastures. While we have identified different factors associated with rabbit density at different spatial scales, variables associated with livestock grazing were highly significant at the local scale, implying that grazing management may play a central role in explaining rabbit density in grasslands.

Relationship between habitat management and rabbits at the field scale

At the field level, which represents a spatially and temporally distinct management unit (Atkinson et al. 2005), higher rabbit densities occurred in small fields containing improved sheep pastures. Sheep grazing generates short and homogeneous swards which Iason et al. (2002) demonstrated through manipulative experiments were preferred foraging areas for rabbits but to our knowledge there are no published field-scale evaluations of a link between grazing management and rabbit abundance.

Table 3 Linear mixed models results for rabbit densities at local scale

Linear mixed model for rabbit densities—local scale

	Estimate (±SE)	*df*	*t* value	Sig.
Intercept	0.763 (±0.284)	229	2.690	0.008
Grass height	−0.042 (±0.015)	137	−2.838	0.005
Field size	−0.051 (±0.017)	137	−2.920	0.004
Field type—sheep	0.310 (±0.103)	137	2.994	0.003

Response variable: rabbit densities log-transformed. Random factor: field within sampling site. Variance structure: different standard deviations per sampling period. Log Likelihood: −442.10

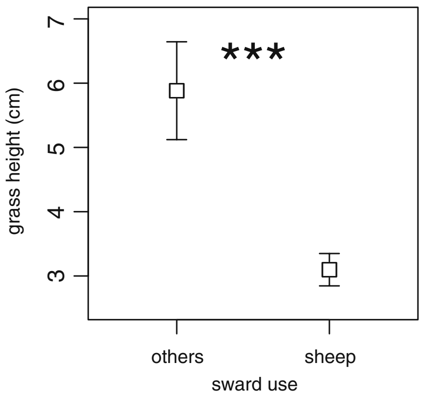

Fig. 2 Mean grass height (cm) ±95% confidence intervals for swards used by sheep and those used for other grazing. A significant difference between means at p=0.001 is indicated by the stars

Sward height selection in herbivores has been attributed to different anti-predator strategies and optimization of food abundance and/or availability (Whittingham and Devereux 2008). In animals relying on visual cues to detect predators, the level of visual obstruction offered by the vegetation within a foraging patch is likely to have a greater influence on their perception of predation risk than the degree of protection it offers (Whittingham and Devereux 2008). In this sense, rabbits' preference for shorter swards in spite of the reduced food resource they represent can be explained

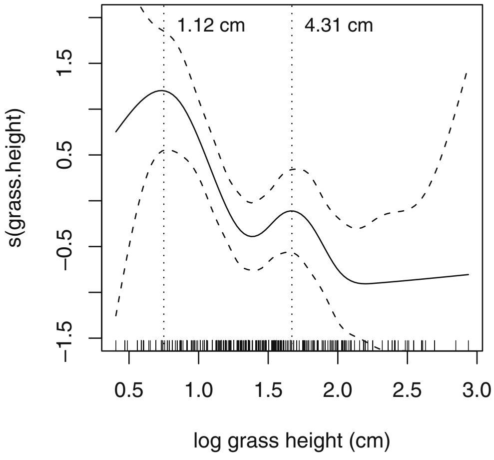

Fig. 3 Estimated smoothing curve (cubic regression splines) and point-wise 95% confidence intervals for the Generalised Additive Models containing log-transformed grass height as predictor variable, and the presence/absence of rabbits in each field as the response variable. The *horizontal axis* shows the observed values of grass height (*short vertical lines*), and the *vertical axis* the contribution of the smoother to the fitted values. Critical values of untransformed grass height are indicated (vertical dashed lines)

as an anti-predator strategy (Bakker et al. 2004; Iason et al. 2002). On the other hand, shorter swards are of higher nutritional quality, as forage quality of grasses per unit weight declines with increasing sward height (Riddington et al. 1997). In our study, rabbits were most abundant in sward heights shorter than 1.5 cm; the further, minor apparent selection for sward heights around 4 cm could be explained by a higher availability of swards of that size. Our data suggest that maintaining autumn and winter sward heights above those associated with highest rabbit densities in this study may reduce local abundance of rabbits. This suggestion is supported by small-scale experimental studies: removal of sheep from experimental grazing plots led to abandonment of the area by rabbits (Iason and Hester 1999). However, it is impossible to quantify what proportion of the short sward height in our survey area is due to sheep grazing and what is a consequence of intense rabbit grazing. Rabbits can facilitate habitats for themselves and their conspecifics by creating and maintaining vegetation in a favourable state through repeated grazing (Bakker et al. 2005). It has been shown that grazing by rabbits, particularly at high densities, can represent a significant contribution to overall grass offtake; in the 0.4-ha experimental plots of Iason and Hester (1999) , rabbit offtake was as great as that by sheep. However, rabbits are central-place foragers, foraging closest to their burrows (Bakker et al. 2005); in our study, with mean field sizes of almost 3 ha and grass measurements taken from the middle of fields, i.e. away from most burrows, it is likely that the sward heights we measured were determined for the most part by sheep and not rabbit grazing, although this might not be the case at the very short sward heights of less than 1.5 cm where high rabbit densities might play a significant role in creating and maintaining such short swards.

Woodland was positively and strongly associated with rabbit abundance in a country-wide study (Trout et al. 2000) and surface-living rabbits were found to intensely use the dense cover provided by woodland or scrub rather than burrows during winter (Kolb 1991) but here the proximity to woods or bracken had no significant relationship with rabbit numbers at the field scale. This might be explained by different processes governing distribution at this scale, or the fact that numerous small blocks of woodland were distributed fairly homogenously throughout most of our sites.

Relationship between habitat management and rabbits at the landscape scale

At the wider, landscape-scale edge density and predator control were the most significant factors in determining rabbit densities. Similar results were found by Reid et al. (2007) in Northern Ireland and by Trout et al. (2000) in England and Wales. Both of these previous studies suggest that the presence and density of field boundaries positively influences rabbit abundance.

The presence of a predator control policy explained differences in fox sightings between sites. It has been suggested that predator control might be a consequence of the high numbers of foxes attracted by the abundance of rabbits therefore making it impossible to distinguish between cause and effect (Trout et al. 2000). However, it is likely that in our sites predator control was implemented irrespective of rabbit densities due to the local economic importance of pheasant and grouse shooting for which fox control represents a key management practice even at low predator density (Trout and Tittensor 1989). The fact that lagomorphs, most likely rabbits, represent the most important prey item in fox diets in the UK (Webbon et al. 2006) and the observed impact of fox control on rabbit populations (Banks et al. 1998) supports our finding of higher rabbit densities in areas with fox control, and suggests that this relationship is causal.

Conclusion

Our counts indicate relatively high rabbit densities in several of our sites, but such spotlight counts may represent only ~60% of the total rabbit population using that area and even that percentage can vary widely (Poole et al. 2003). At the local scale, sheep grazing appears to have a substantial influence on rabbit density, in part through its impact on sward height. The results from such a correlatory study as this must not be viewed as confirmation of the relationships reported, which should instead be the basis of further investigation. While there is strong experimental evidence for the local preference of rabbits for foraging in areas with short grass, our results suggest that other relationships, particularity at the landscape scale, should be explored through manipulative studies in the field.

Sheep numbers in Britain more than doubled in the post-war years (Fuller and Gough 1999) and even in upland areas over this long timescale there has been a change from mixed grazing regimes toward those dominated by sheep (Sydes and Miller 1988). If the relationships described here are causative and hold true across the country, recent trends in grazing management in Britain may have had a significant impact on rabbit densities at local and landscape scales by increasing habitat suitability for rabbits in pasture land with the potential for significant concomitant economic losses.

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