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Title

Opposing effects of agricultural intensification on two ecologically similar species

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Abstract

Brown hares and rabbits are widely distributed in agricultural landscapes across the UK, occupy similar habitats and have considerable dietary overlap. However, as agriculture in the UK has intensified, hares have declined and become a species of conservation concern while rabbits have become an increasing pest. An intensive study of hares, rabbits and the dynamics of pastures over two grazing seasons was undertaken, in order to understand the environmental factors associated with hare and rabbit abundance at field level. Linear mixed models were utilised to assess the environmental variables, in terms of the structure, nutritional components and effects of livestock grazing that are associated with the abundance of the two species. The models revealed that hares were negatively associated with grazing intensity and plant diversity, whereas rabbits showed the strongest associations with nutritional content of pastures, in particular fat, nitrogen and fibre content in forage, as well as a positive association with short grass swards. The data suggest that, at the field-scale, intensification of pasture use may have contributed to declines in hares and increases in rabbits.

Keywords

Agricultural intensification; biodiversity; brown hare; livestock grazing; pasture; rabbit

1. Introduction

Agricultural land accounts for 70% of the UK land area with 46% consisting of permanent grassland, some of which is grazed by approximately 9.9 million cattle *(Bos Taurus*, Linnaeus, 1758) and 32 million sheep *(Ovis aries*, Linnaeus, 1758) (DEFRA, 2012). Sheep grazing has increased from around 19.7 million sheep in the 1950s (Fuller and Gough, 1999), whilst cattle grazing has experienced a decline from 10.6 million (Hood, 1982). The increase in sheep grazing and reduction in cattle grazing has resulted in shorter more uniform sward structures across the landscape, as sheep are able to graze to 3 cm, whereas cattle graze to around 5 cm and create patchy tussocks around dung, which increases habitat heterogeneity (Vickery et al., 2001).

Brown hares (*Lepus europapaeus* Pallas, 1778) suffered a dramatic population decline in the UK, with numbers falling from an estimated 4 million in 1880 to just over 800 000 in 1993 (Hutchings and Harris, 1996). In contrast the population of the European rabbit (*Oryctolagus cuniculus*, Linnaeus, 1758) in the UK has increased significantly in recent decades and was estimated to be growing at around 2 % each year (Trout, 2003), despite the spread of myxomatosis (Lees and Bell, 2008). Damage to UK crops caused by rabbits has been valued at £115 million each year (Smith et al. 2007).

Livestock grazing and pasture management affect the nutritional quality of forage and intensification of grazing has been shown to increase levels of protein, nitrogen and reduce fibre (Bakker et al., 1983; Pavlů et al., 2006). The amount of fat content in forage has been shown to affect the condition of hares (Hackländer et al., 2002), although Smith et al. (2005a) found no link between broad habitat selection and forage quality, in terms of protein, fat or energy content for hares. Both fibre and higher amounts of nitrogen have been linked to rabbits foraging patch selection (Bakker et al., 2005; Iason et al., 2002), whereas Hewson (1977) found hares were negatively associated with nitrogen content in forage.

At landscape scale hares have been found to be negatively associated with low habitat diversity, hedgerow removal and loss of unfarmed habitat (Tapper & Barnes 1986; Vaughan et al. 2003; Smith et al. 2004, 2005b; Pépin and Angibault 2007). Conversely, rabbits have demonstrated mixed responses to landscape-scale intensification and shown positive associations with aspects of less intensively managed landscapes, such as the presence of woodland and field boundaries, as well as with more intensive practices such as predator control and high levels of sheep grazing (Petrovan et al., 2011; Trout et al., 2000). However, since agricultural landscapes are typically managed at the field-scale, an understanding of how intensification of farming practices is associated with the two species' distribution at this scale could help in the development of practical solutions to hare conservation and rabbit control.

The study aimed to assess the effects of intensification of livestock grazing on field-scale habitat associations of brown hares and rabbits in pastures. The effects of livestock grazing type on pasture forage diversity, height and nutritional composition were examined and related to hare and rabbit distribution.

Specifically the study assessed the following hypotheses:

1. Sheep and cattle grazing have different effects on forage diversity, height and nutritional composition.
2. Hare and rabbit distribution is associated with pasture management (livestock type and intensity of use), forage height and nutritional composition.

2. Material and methods

The study was carried out in a lowland, mixed arable and pasture landscape in North Yorkshire, UK, with average field sizes of 6.4 ha (SD = 4.63 ha). Eighteen fields were intensively studied that were grazed by either; dairy/beef cattle (n = 11; mean field size =8.66 ha, SD = 5.07 ha) or sheep (n = 7; mean field size = 3.41 ha, SD = 1.66 ha), and were either continuously or rotationally grazed. The pasture management during the study was similar between fields with cattle grazed fields subject to an annual application of manure and cutting for either silage in cattle fields, or hay in sheep fields when left ungrazed for long periods. Although all fields were subject to grazing during the study, fields were described as 'grazed' if, at the time of survey they had livestock actively grazing them. A field surveyed either before grazing had commenced or after livestock had been removed was classified as 'ungrazed'. Data were collected between March 2011 and July 2011 from the start of the grazing season when the cattle were let out into the fields following winter housing and repeated again from February 2012 until July 2012.

2.1 Survey methods

Data were collected on plant diversity, forage nutrition and grass heights before and after grazing in order to assess the effects of grazing on these variables and relate them to lagomorph distribution. During 2011 habitat surveys were carried out before and after grazing of cattle and sheep. In 2012 data were collected twice before the grazing season started and five times during the grazing season (every two weeks). ArcGIS 9.2 (ESRI, USA) was used to calculate the area of each field from Ordnance Survey maps acquired through the Edina Digimap service (http://edina.ac.uk/digimap) and the percentage amount of different habitat types surrounding the study fields, including arable, semi-improved, improved, unimproved grasslands and woodland. The presence and number of cattle and sheep and the number of days the field was grazed for were also recorded to measure livestock density and grazing intensity. Livestock were counted exactly unless large numbers were present, in which case they were estimated to the nearest 10 animals. Livestock units (LU) were used to calculate the livestock density, using the ratio 1 cow = 0.11 sheep (DEFRA, 2010).

To account for within-field variation, three transects were walked per field, one along the edge, one in the middle and an intermediate transect between the edge and middle of the field, 20-30 metres from the field boundary. Plant samples were taken to analyse the nutritional composition of forage within fields, and between grazed and ungrazed pastures, by cutting all above ground green plant material from three 1 x 0.1 m plots per transect (Bakker et al., 2005).

Vegetation was surveyed in 1 m^2 quadrats along the transects. Quadrats were placed at intervals of 30 or 50 m depending on the size of the field, with a minimum of 6 quadrats per transect. The mean number of quadrats surveyed over the two years was 222.41 per field (SD = 15.44). Ten grass height measurements were taken per quadrat using the direct method, which is suitable for use in measuring grass of varying heights, in particular short swards (Stewart et al. 2001). Percentage cover of all grass and herb species within each quadrat was recorded to the nearest 1 % to assess plant species diversity and richness. Inverse Simpson’s diversity index was chosen as it accounts for evenness, is less affected by sample size and is easier to interpret than other diversity indexes (Magurran, 2004).

One visit per week to all the fields was made at least one hour after sunset during 2011. This was increased to three visits per week of all study fields during 2012. Each field was scanned using a 1 mega candlepower spotlight (Clubman CB2, Cluson Engineering Ltd, Hampshire, UK) and 8 x 42 binoculars, and the number of hares and rabbits was counted.

2.2 Forage analysis

Plant cuttings collected from each field were oven dried at 100 ^{o}C for 36 h, finely ground and mixed using a Retsch rotor mill. The Kjeldahl method was used to determine the amount of protein and nitrogen (AOAC 2006a; method 990.03) and the Soxtherm method to determine crude fat levels within the grass (AOAC 2006b; method 2003.05). Energy content was calculated using a bomb calorimeter and ash was obtained by placing samples in the furnace for 4 h at 400 ^{o}C (AOAC 2005; method 942.05). Crude fibre was ascertained through a process of boiling fat-free samples, using the filter bag method, in sulphuric acid solution for 30 mins followed by boiling in a solution of sodium hydroxide for a further 30 mins. The remaining residue was oven dried at 100 ^{o}C for 4 h, then placed in a furnace at 600 ^{o}C and ashed for a further 4 h (AOAC 2006a).

2.3 Data analysis

To assess the distribution of sheep and cattle fields within the landscape the percentage of arable, semi-improved, improved, unimproved grassland and woodland within a 1 km radius from the centre of each field was calculated. A multivariate ANOVA was used to test if there was a difference between the amount of different types of habitat surrounding sheep and cattle fields on logit transformed percentages (Warton and Hui, 2011). Moran's *I* was calculated using the *ape* package in R 3.0.1 (R Development Core Team, 2013) to test for spatial autocorrelation in the numbers of hares and rabbits across the landscape.

Differences in plant diversity, forage nutrition and grass heights between livestock types and before and after grazing were assessed using two-way analyses of variance. Pearson correlations were used to assess relationships between grazing intensity (stocking density*days grazed) and nutritional composition between fields. Normality and homogeneity were tested to ensure assumptions were met.

Linear mixed models were used to assess the environmental variables that were associated with hare and rabbit abundance. Data were checked for outliers in each variable and collinearity between the explanatory variables was tested. Those where $r > 0.7$ were either removed or combined (Dormann et al., 2012). This process resulted in variables for livestock density and number of days grazed being combined to create a 'grazing intensity' variable by multiplying the two variables together and log transformed to remove significant outliers. Protein values for forage were also removed as these values are derived from the measured nitrogen value with which they are highly correlated ($r = 1.000$, $P = 0.001$). Variance inflation factor values of the new variables were checked and all were below 10, as suggested by Field (2000) to indicate no collinearity issues.

Hare and rabbit abundances were calculated from the mean number counted during the repeated night surveys for each field. Abundances were log transformed to meet normality assumptions and used as the dependent variable for each respective model.

Field area, grazing intensity, grazing type (sheep grazed, sheep ungrazed, cattle grazed or cattle ungrazed), mean grass height, plant diversity and nutritional components of the grass (energy content, percentage of nitrogen, crude fibre, crude fat and ash) were the fixed explanatory variables. The mean value of each explanatory variable was calculated for each field to account for differences in survey effort between years.

An interaction term between grass height and grazing type was also included to account for short grass heights not due to grazing. As data were collected a number of times from each field during the study, a repeated measures term nested within field was included in the model. Year was also included as a random factor to account for possible interannual variation.

An information theoretic approach was used where all permutations of variables were modelled and ranked using the AIC value. The variables were standardised so that each variable had a mean of 0 and standard deviation of 1 (McAlpine et al. 2006; Reid, et al. 2007) to allow comparisons of the parameter estimates between the models. The Akaike weight was calculated to identify which were the best models given the data (Burnham and Anderson, 2002). The models with a delta AIC value less than 10, were used to calculate the relative importance of each predictor variable, as Burnham and Anderson (2002) suggest that models with a delta AIC value above 10 should be ignored. The relative importance was calculated by summing Akaike weights over all the candidate models where the variable was present, the variables were then ranked in order of importance (Burnham and Anderson, 2002). Model validation on the best models was carried out to test for violations to homogeneity, normality and lack of independence. The model residuals were visually inspected on a scatterplot against the fitted values to assess violations of homogeneity, and were plotted against the explanatory variables to check for independence. There were no strong patterns, which indicated assumptions had not been violated. A histogram confirmed that the residuals were normally distributed (Zuur et al., 2009). SPSS Statistics (IBM version 19) was used for all statistical analysis.

3 Results

A total number of 358 hares and 733 rabbits were recorded over 13 repeat surveys of all study fields in 2011 and 1332 hares and 2258 rabbits across 21 repeated surveys of all study fields in 2012. Hares were recorded in all study fields (mean = 3.57, SD = 3.34) and rabbits were present in all but three of the fields (mean = 6.76, SD = 7.74) although abundance varied between fields and surveys. Sheep and cattle fields were evenly distributed within the landscape with no difference in the amount of arable (Sheep = 46.82 %, SD = 9.84; Cattle = 51.26 %, SD = 11.13), semi-improved grassland (Sheep = 32.04 %, SD = 8.93; Cattle = 28.69 %, SD = 5.90), improved grassland (Sheep = 10.69 %, SD = 3.77; Cattle = 9.55, SD = 4.92), unimproved grassland (Sheep = 1.24 %, SD = 0.73; Cattle = 0.83 %, SD = 0.42) or woodland (Sheep = 9.21 %, SD = 2.30; Cattle = 9.67 %, SD = 2.49) within a 1km from the centre of each field (ANOVA df = 1, $P > 0.05$ in all cases). The Moran's *I* revealed that there was no significant spatial autocorrelation between hare and rabbit numbers across the landscape (Hares: $I = -0.08$, SD = 0.07, P = 0.81; Rabbits: $I = 0.01$, SD = 0.06, P = 0.21).

3.1 Effects of livestock grazing

Sheep fields were grazed on average for 50 d (SD = 34.52) and cattle fields were grazed for an average of 24.94 d (SD = 28.12). The mean stocking density for sheep was 1.68 LU / ha (SD = 0.88) and the mean cattle stocking density was 9.67 LU / ha (SD = 5.55). The mean grazing intensity (stocking density * days grazed) for sheep was 19.48 (SD = 24.76) and for cattle was 52.68 (SD = 145.19). Sheep grazed fields had significantly shorter grass height (mean = 2.3 cm, SD = 2.2 cm) than cattle grazed (4.9 cm, SD = 4.1 cm), or ungrazed sheep (4.8 cm, SD = 4.4 cm) or ungrazed cattle fields (7.1 cm, SD =

4.7 cm: $F = 11.527$, $df = 3$, $P = 0.001$). There were no significant differences in nutritional composition of fields grazed by either sheep or cattle nor was this affected by removal of grazing (ANOVA $df = 52$, $P > 0.05$ in all cases).

Grazing intensity was also not correlated with the nutritional composition in the fields (Pearson, $n = 53$, $P > 0.05$ in all cases). Sheep fields were found to be more diverse (mean plant diversity = 0.60, SD = 0.09) in terms of plant species than cattle fields (mean plant diversity = 0.42, SD = 0.14; $F = 34.753$, $df = 2$, $P = 0.001$). Species richness was also significantly different ($F = 5.610$, $df = 1$, $P = 0.033$) between sheep (mean = 5.94, SD = 2.12; range = 5 - 8 plant species) and cattle fields (mean = 4.48, SD = 1.71; range = 3 - 7 plant species).

3.2 Hare and rabbit habitat associations

The two best fitting models for hares revealed a negative association with plant diversity and grazing intensity (Table 1). The three best fitting models for rabbits revealed a positive association with crude fat and nitrogen and a negative association with plant diversity and grass height (Table 2). The only variable that appeared in the best models for both hares and rabbits was plant diversity and had the highest importance within both hare and rabbit models (Figure 1). Grazing intensity was also highly important within hare models and crude fat in the rabbit models. Within the candidate models hares were also associated with taller grass swards and rabbits with short grass swards irrespective of livestock type. However, both hares and rabbits were weakly associated with cattle and sheep fields within their respective models.

4 Discussion

The intensification of pasture management had opposing effects on hare and rabbit abundance, with hares being negatively associated with grazing intensity and plant diversity, whereas rabbit abundance was positively associated with nitrogen content in forage, as well as with short grass swards.

This study found no evidence of short term effects of livestock grazing on forage nutrition, indicating that between-field differences in nutrition are likely due to long term management that improved their suitability for rabbits. However, long term intensive grazing has been found to increase the nutritional content of pastures (Pavlů et al. 2006), as well as being influenced through the addition of fertiliser and sowing of specific grass species that affect the nutritional quality of forage (Smith et al., 1997). Often only a few highly nutritious species such as *Lolium spp.* are grown, as they provide a predictable nutrient intake for livestock, thus increasing the nutrient quality of pastures despite decreased plant diversity (Smith et al. 1997; Hopkins and Holz 2006).

4.1 Hare and rabbit habitat associations

In the short-term (within a grazing season), intensive grazing by large numbers of livestock, grazed continuously, resulted in less field use by hares, whilst livestock grazing created short grass swards that contributed to improving the habitat for rabbits.

Rabbits were associated with high nutritional quality pastures and low plant diversity, which is the result of intensively managed pastures, whereas hares had no association with nutrient quality. These field-scale patterns reflect those found at landscape scales for both species, where hares have been shown to select habitat on the basis of structure, rather than nutrition and rabbits were associated with short grass swards (Smith et al. 2005b; Petrovan et al. 2011, 2012). This difference could be due to hares' need for cover from predators and as surface resting sites (Smith et al. 2004), and rabbits' need to escape predation (Iason et al., 2002) and provision of higher quality forage close to burrows (Bakker et al., 2005). Hares have shown selection for cattle fields in other studies (Karmiris and Nastis, 2007; Smith et al., 2004) and avoidance of intensively grazed sheep fields (Petrovan et al. 2012), but this was not strongly evident within these models.

4.2 Impacts of intensification on plant diversity

In this study, cattle grazed fields had lower plant diversity than sheep grazed fields. The negative associations between plant diversity and hares may therefore be an indicator of long-term effects of intensive pasture management in the fields that were studied, where particular plant species have been sown rather than purely due to grazing. However, whilst there was a statistically significant difference in plant diversity between sheep and cattle fields, a comparison of species richness revealed that the difference in actual number of plant species was small.

The data indicate that intensification of pastures has benefited rabbits and been detrimental to hares. Livestock grazing by either sheep or cattle, had short-term impacts on the structure of vegetation, but not significantly on the nutritional content of the forage, although it could have longer term implications for nutritional quality. This affects hare and rabbit abundance in opposite ways and could therefore be used to manage populations more effectively. Reducing grazing intensity and de-intensifying pasture management should simultaneously reduce habitat suitability for a significant agricultural pest whilst benefiting a species of conservation concern. Although, if rabbit numbers are high initial control may be required to reduce the impact of self-facilitation, as rabbits are able to maintain short swards and increase forage nutrients in areas they graze through fertilisation from faeces (Bakker et al., 2005). Future studies should attempt mixed ecological-economic modelling of this system to ascertain the possible gains from de-intensification against loss of productivity and carry out controlled field-scale manipulations of grazing regimes.

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Table 1
Linear mixed models ranked according to AIC and Akaike weight with the environmental variables that are associated with log hare abundance and their corresponding parameter estimates. Those in bold are the best fitting models.

Model	AIC	Delta AIC	Akaike weight	Intercept (SE)	Environmental variables	Estimate (SE)
1	**109.48**	**0**	**0.996**	**0.940 (0.113)**	**Plant diversity**	**−0.784 (0.21)**
					Grazing intensity	**−0.245 (0.39)**
2	**118.63**	**9.15**	**0.004**	**0.550 (0.039)**	**Grazing intensity**	**−0.269 (0.04)**
3	133.878	24.39	0	0.889 (0.136)	Plant diversity	−0.988 (0.25)
4	134.142	32.48	0	0.659 (0.150)	Mean grass height	0.024 (0.008)
					Plant diversity	−0.774 (0.25)
5	141.969	32.49	0	0.223 (0.503)	Mean grass height	0.031 (0.008)
6	148.184	38.40	0	0.662 (0.159)	Plant diversity	−0.722 (0.29)
					Sheep ungrazed × grass height	0.03 (0.01)
					Cattle ungrazed × grass height	0.024 (0.009)
7	153.627	44.15	0	0.889 (0.136)	Cattle ungrazed × grass height	0.03 (0.009)

Table 2
Linear mixed models ranked according to AIC and Akaike weight with the environmental variables that are associated with log rabbit abundance and their corresponding parameter estimates. Those in bold are the best fitting models.

Model	AIC	Delta AIC	Akaike weight	Intercept (SE)	Variables	Estimate (SE)
1	**51.728**	**0**	**0.62**	**1.038 (0.259)**	**Crude fat**	**0.252 (0.05)**
					Plant diversity	**−1.827 (0.34)**
2	**52.851**	**1.123**	**0.36**	**1.722 (0.338)**	**Nitrogen**	**0.231 (0.062)**
					Crude fat	**0.331 (0.04)**
					Mean grass height	**−0.04 (0.01)**
					Plant diversity	**−1.868 (0.27)**
3	**58.805**	**7.077**	**0.02**	**0.308 (0.436)**	**Crude fat**	**0.297 (0.06)**
					Plant diversity	**−1.607 (0.31)**
					Crude fibre	**−0.04 (0.02)**
					Mean grass height	**−0.043 (0.02)**
4	70.079	18.351	0	−0.089 (0.137)	Crude fat	0.354 (0.06)
5	72.999	21.271	0	−0.128 (0.148)	Field area	0.027 (0.01)
					Crude fat	0.299 (0.06)
6	78.31	26.582	0	0.252 (0.158)	Sheep grazed × grass height	−0.265 (0.06)
					Crude fat	0.271 (0.06)
7	79.863	28.135	0	0.133 (0.150)	Sheep grazed × grass height	−0.176 (0.04)
					Cattle grazed × grass height	−0.103 (0.05)
					Crude fat	0.223 (0.06)
					Field area	0.037 (0.01)
8	86.244	34.516	0	0.938 (0.303)	Nitrogen	0.198 (0.1)
9	88.834	34.516	0	−1.682 (1.124)	Sheep grazed × grass height	−0.265 (0.06)
					Energy content	0.139 (0.06)
10	112.088	60.36	0	1.791 (0.197)	Plant diversity	−2.03 (0.26)
					Mean grass height	−0.037 (0.01)
11	115.134	63.406	0	1.516 (0.156)	Plant diversity	−1.728 (0.256)
12	145.06	93.332	0	0.476 (0.754)	Field area	0.033 (0.01)
13	148.862	97.134	0	0.519 (0.111)	Field area	0.036 (0.01)
					Mean grass height	−0.021 (0.01)
14	163.728	112	0	0.787 (0.104)	Sheep grazed × grass height	−0.111 (0.03)

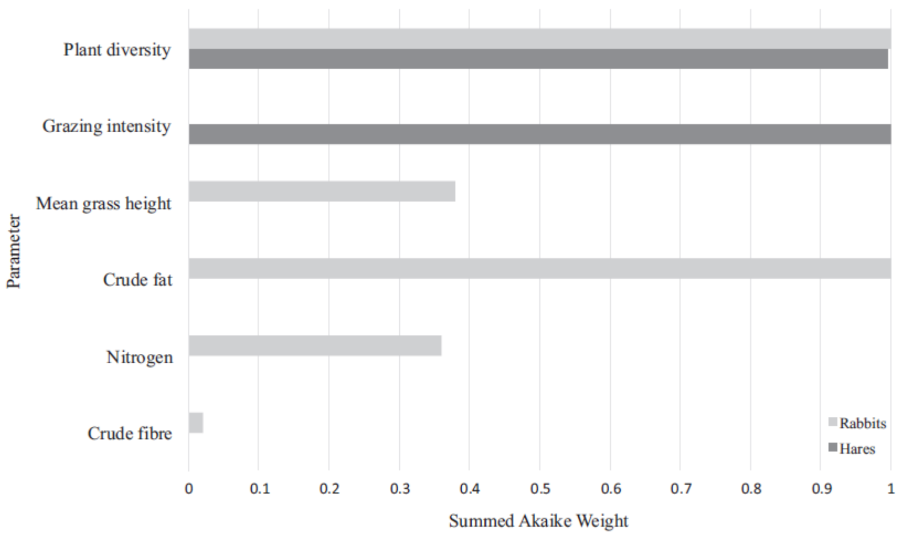

Fig. 1. Relative importance of parameters for the hare and rabbit models based on Akaike weight summed across the best models that contain each parameter.