Title

Dietary niche partitioning between sympatric brown hares and rabbits

Short title

Dietary niche partitioning of sympatric mammals

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Abstract

Coexistence of ecologically similar species is sustained by niche partitioning, a fundamental element of which is diet. Overlapping of resource requirements between sympatric species can create interspecific competitive or facilitative effects on the foraging behaviour of herbivores. Brown hares and rabbits are similar in size, morphology, feeding type and occupy the same habitats, but direct evidence of competition for resources between them is lacking. Both species are widespread and simultaneously pests and species of conservation concern in different parts of their range. We investigated dietary overlap of brown hares and European rabbits in pastures in relation to pasture management and hare and rabbit abundance. Grasses were the predominant component in both hare and rabbit diets with high overlap of plant species. Both rabbits and hares showed some selectivity for particular plants with evidence of consistent selection for *Phleum spp.* and relative avoidance of *Poa spp*. However, differences in the smaller components of hare and rabbit diet resulted in significant differences in diet overall. There was no evidence that higher relative density of one species led to dietary shifts but pasture management affected the diet of both species. Nutritional composition of diets of both species also differed between cattle and sheep pastures with higher fibre, ash and fat in the former. Our data provide no evidence of competitive exclusion between rabbits and hares on the basis of diet, but suggest that the effects of livestock on their respective diets may influence indirect competition in favour of rabbits over hares.

Key words: brown hares, coexistence, dietary niche, foraging, interspecific competition, rabbits

Introduction

Dietary niche partitioning has been used to explain the coexistence of ecologically similar large mammalian herbivores in both African and Asian herbivore assemblages (Ahrestani, Heitkönig & Prins, 2012; Kartzinel *et al.*, 2015). Diet similarity and overlap between sympatric species could create interspecific competition for resources, particularly if population densities are high and resources are low (Cheng & Ritchie, 2006; Bakker, Olff & Gleichman, 2009). However, dietary niches can be partitioned through differences in body size, morphology and feeding types (e.g. grazer, browser or mixed) (Hofmann & Stewart, 1972; Arsenault & Owen-smith, 2002). Competition between species can also be affected by other species, for example, through facilitation whereby larger herbivores create more favourable habitat for smaller herbivores by maintaining shorter more nutritious forage or reducing vegetation height to allow better access to preferred forage (Stahl *et al.*, 2006; Bakker *et al.*, 2009). Differences in body size have also been related to diet selectivity, with smaller herbivores being more selective than larger species that can ingest higher quantities of lower quality food, as described by the Bell-Jarman principle (Bell, 1971; Jarman, 1974; Gordon & Illius, 1996). Differences in dietary composition are thought to influence the partitioning of resources at the species level but data on individual species' diets are not always available for sympatric species (Kartzinel *et al.*, 2015).

Diet can be affected by a number of factors including resource availability, the quality of forage, home range size, and therefore access to a range of forage and the risk of predation in limiting patch choice (Galende & Raffaele, 2012). Studying diet preferences can help explain habitat use through foraging choice and identify potential competition between herbivores for resources that could impact on the management of a species or their habitat (Galende &

Raffaele, 2012). Intensification of agricultural landscapes has caused changes in resource availability that may have affected the dynamics of competition and coexistence between species within agro-ecosystems, potentially driving declines in some and overabundance of others.

Brown hares (*Lepus europaeus*) and European rabbits (*Oryctolagus cuniculus*) are similar in size, morphology and together occupy a range of agro-ecosystems. Individually they have achieved pest status in parts of their natural and introduced ranges but elsewhere declines have made them species of conservation concern. In the UK hares have declined markedly while rabbit populations have increased and continue to be an important agricultural pest. There is indirect evidence that the two species can exhibit competitive exclusion, however despite a number of studies reviewed by Flux (2008) there has been little evidence of direct competition for resources between the two lagomorphs.

A number of studies have looked at hare diet (Homolka, 1982; Reichlin, Klansek & Hackländer, 2006; Puig *et al.*, 2007; Katona *et al.*, 2010), or rabbit diet (Bhadresa, 1987; Martin, Marrero & Nogales, 2003) across Europe, but comparisons of brown hare and European rabbit diets within the same pastures have been extremely scarce (Homolka, 1987). Understanding the dietary species composition of these medium-sized mammalian herbivores and whether there is evidence of diet selectivity could help identify indirect competition or niche partitioning of resources that allows them to co-exist. This could have implications for management of both species and help in the conservation of hares and control of rabbit numbers through manipulation of the availability of preferred forage within their ranges.

We sought to elucidate the mechanisms governing coexistence between two similar sympatric herbivores. We aimed to assess whether dietary niche partitioning or competition explained the ability of rabbits and hares to exist in sympatry by comparing their diets within the same pastures. Furthermore, we investigated the effects of livestock grazing on lagomorph diets to understand whether this may have influenced dietary competition between the species.

The study aimed to assess the following hypotheses:

1. Hares and rabbits show dietary selectivity for plant species in their diet. We posit that similar plant selectivity reveals forage competition and differences reveal possible niche partitioning.
2. Rabbits maintain a consistent proportion of preferred forage in their diets across a range of densities, whereas that of hares declines, revealing interspecific competition.
3. Diets of hares and rabbits are related to the nutritional composition of plant species.
4. Livestock grazing affects the nutritional composition of forage, which influences hare and rabbit diet.

Materials and methods

The study site was in Wykeham, North Yorkshire, UK, (54°12’59.21” N, -0°30’54.05” E) a landscape of lowland mixed arable and pastural farmland. Eighteen fields with an average field size of 6.4 ha (SD = 4.63 ha) were intensively studied. Fields were either continuously or rotationally grazed by 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). To measure hare and rabbit density at least one visit per week of all study fields was made 1 h after sunset during data collection. Each field was scanned using a 1 mega candlepower spotlight (Clubman CB2, Cluson Engineering Ltd, Hampshire, UK) and 8 × 42 binoculars, and the number of hares and rabbits was counted. Observations were recorded of 358 hares and 733 rabbits over 13 repeat surveys of all study fields in 2011 and 1332 hares and 2258 rabbits across 21 repeat 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 (Lush et al. 2014).

Faecal analysis

Hare and rabbit droppings were collected over two years from all study fields by walking at a slow pace and searching along three transects in each field. Droppings were collected twice per year between March and June during the grazing season. They were identified using a number of characteristics; hare droppings were larger in size, lighter in colour, consisting of larger fragments, although sometimes they did appear darker. Rabbit droppings were smaller in size, circular and darker in colour and were often found in latrines or by burrow entrances. The number of droppings collected varied between species and surveys (Table 1)

Microhistological techniques were used to prepare the slides following the methods of Katona and Altbäcker (2002). Droppings were dried at room temperature and stored before analysis. For each sample ten droppings (per transect per field) were mixed with water and sieved through 1.0 mm and 500 μm sieves. Fragments from the 500 μm sieve were used for analysis. Three subsamples from the composite sample (Fitzgerald & Waddington, 1979) were stained using Toluidine blue solution and mounted onto slides using glycerol.

Plant composition and nutritional analysis

Plant composition and grass height was recorded within each of the study fields during June 2011 and 2012. The percentage cover of all grasses and herbs was recorded in 1 m^2 quadrats with at least 10 quadrats per transect and 10 grass height measurements per quadrat using the direct method (Stewart, Bourn & Thomas, 2001). This was carried out along three transects per field; one along the edge, one in the middle and an intermediate transect (20–30 m from the field boundary). Plant samples were taken to analyse the nutritional composition of forage by cutting all above ground green plant material from three 1 × 0.1 m plots per transect (Bakker *et al.*, 2005). Plant cuttings were oven dried at 100°C for 36 h, finely ground and mixed using a Retsch rotor mill. Standard methods were used to determine nutritional content, as described fully in Lush *et al.*, (2014).

Plant cell identification

Reference slides were prepared of the different plant species to aid identification. A single layer of leaf and stem epidermis cells was scraped from each plant and mounted onto slides using glycerol (Wolfe, Whelan & Hayden, 1996). Key identifying features of the cells (shape and size of cells, presence and shape of silica bodies, presence and shape of hair structures and stoma, as well as the shape of the cell wall, if it was sinuous or straight) (Bhadresa, 1987; Matrai & Katona, 2004), were noted. Plant stems were very similar between species so these remained unidentified.

Each slide was viewed using a Nikon Eclipse E400 compound microscope and systematically scanned using 10 x magnification, magnifying to 40 x to identify each fragment of plant. Where congeneric species were very similar in their epidermal structure, the fragments were identified to genus level only.

Data analysis

Differences in diets between cattle-grazed and sheep-grazed fields were analysed separately for rabbits and hares using MANOVA. Only the main eight plant species that were found with prevalence above 5% in both hare and rabbit diets were included (Katona *et al.*, 2004). A Pearson correlation was calculated on lagomorph densities and t test to assess differences in grass heights between fields. SPSS Statistics (IBM version 19) was used for statistical analysis.

Simpson's Index of Diversity was calculated using the mean percentage of plant species in their respective diets for both years to examine plant diversity in hare and rabbit diets across all study fields. A two-way ANOVA was used to assess differences in diet diversity.

Diet selectivity

Evidence of diet selectivity in hare and rabbit diet was assessed using a compositional analysis (Aebischer, Robertson and Kenward 1993). Data were analysed using R 3.0.1 software (R Development Core Team, 2013) and the package ‘adehabitatHS’ version 0.3.6 (Calenge, 2006). The mean percentage frequency of each plant species identified in hare and rabbit droppings was calculated for all study fields for both years (Wolfe *et al.*, 1996). The mean percentage cover of the corresponding plant species was used to calculate the availability of forage in each study field. The value ‘0.01’ was ascribed to plants with 0% cover in fields so that all plant species identified in diets were used in the analysis (Aebischer *et al.*, 1993).

Diet similarity and lagomorph densities

To evaluate whether either hare and rabbit diet varied with density of the other lagomorph, the mean percentage of each plant species found in hare and rabbit diet for both years were split into fields that had a relative lower hare to rabbit mean density ratio (0.4 hares and 2.1 rabbits), higher hare to rabbit mean density ratio (1.1 hares and 0.2 rabbits) and fields where the mean density of hares to rabbits was similar (1.2 hares and 1.6 rabbits) (Fig. 1). A similarity matrix was produced to assess diet similarity between hares and rabbits in fields with different density ratios. Using the similarity matrix a non-metric Multi-Dimensional Scaling (MDS) ordination plot was created. The stress value was checked to assess the fit to the data and values below 0.2 were regarded as adequate (Clarke, 1993). ANOSIM was used to assess differences in the percentage of each plant species found in hare and rabbit diets depending on hare and rabbit ratios in different fields.

Dietary nutrition of hares and rabbits

Logit transformed mean percentage cover of plant species and mean percentage of nitrogen, fat, fibre, ash and energy content (MJ/KG) for each field were used in a linear regression to estimate an approximate figure of nutritional content for each plant species found in the field. Plant species that had large numbers of zeros were excluded from the analysis. The unstandardised coefficients for each plant species were multiplied by the mean percentage found in hares' and rabbits' diets respectively. These were then summed to obtain an overall value of each nutritional component for hares and rabbits in each field. This was done for both years combined and back-transformed to provide a value for hare and rabbit dietary nutrition within each field. A two-way ANOVA was performed on each dietary nutritional value (Table 2).

Results

A total of 20,081 plant fragments were identified, 10,737 for hares and 9,342 for rabbits, over the two years across all study fields. Twenty-two different species of plant were identified within hare and rabbit droppings (Table 3), out of 41 plant species identified within the study fields. The mean density of hares across the study fields was 0.82 hares ha^{-1} (SD = 0.73 hares ha^{-1}) and of rabbits was 1.40 rabbits ha^{-1} (SD = 1.97 rabbits ha^{-1}). A negative correlation between hare and rabbit densities in the study fields across both years was not significant (r = - 0.231, N = 32, P = 0.255). Grass height varied significantly between fields (t = 9.68, df = 132, P = 0.001) and between cattle-grazed fields (mean =10.49cm, SD = 10.18cm) and sheep-grazed fields (mean = 5.64cm, SD = 9.45cm), t = -2.76, df = 123, P = 0.007).

Comparison of diet

Eighteen different species of plants were found in both hare and rabbit faeces over the two years. Hare diet species richness per field ranged from 5 - 14 species (mean = 11.17, SD = 3.3), while that of rabbits ranged from 7 - 14 species (11.45, SD = 2.81). Mean Simpson's index for hare diet was 0.793 (SD = 0.062) and for rabbits 0.794 (SD = 0.057). There were no significant differences in diet diversity between the two species or between years or fields (ANOVA, F = 0.025, df = 1, P = 0.878; F = 0.239, df = 1, P = 0.634; F = 2.475, df = 15, P = 0.454 respectively). The only plants found in hare droppings but not in rabbit droppings were *Cynosurus cristatus* and *Cirsium spp.* but fragments of these were present only in small numbers.

The main components of both hare and rabbit diet were grasses (Hares 2011 = 93.37%, 2012 = 98.21% and rabbits 2011 = 88.02%, 2012 = 90.85%). *Triticum aestivum* (wheat) made up 22.62% (2011) and 11.46% (2012) of hares diets and 8.33% (2011) and 0.74% (2012) of rabbits diets. *Poa spp.* and *Lolium perenne* were the main non-crop grasses found in the diet of both lagomorphs (Table 3); together with *Holcus lanatus* (which did not form a substantial component), these grasses made up over 85% of plant percentage cover in the study fields (Table 4).

Analysis of droppings in both years revealed that the proportions of *Phleum spp.*, *Triticum aestivum*, *Ranunculus spp.* and *Trifolium spp.* were significantly different between hare and rabbit diets (Table 3). Hare droppings contained more *Phleum spp.* and *Triticum aestivum* than rabbits (Fig. 2). Whereas rabbit droppings contained more fragments of *Trifolium spp.* and *Ranunculus spp.* than hares. There was no significant difference in the composition of hare and rabbit diets between sheep or cattle fields for either years (GLM, df = 1, P > 0.05 in all cases).

Diet selectivity

Phleum spp. were selected more than other plant species in hare and rabbit diets for both years (Table 5). *Holcus lanatus* and *Trifolium spp.* were the least selected plants by hares and *Holcus lanatus* by rabbits (Table 6).

Diet similarity and lagomorph density

Although the plants most frequently eaten by both lagomorphs were the same (*Lolium perenne* and *Poa spp.*), their diets overall were significantly different (ANOSIM, Global R = 0.179 , P = 0.013). They were also significantly different between sheep and cattle fields (ANOSIM, Global R = 0.143, P = 0.005). However, there was no significant difference in their diet between fields with different density ratios of hares to rabbits (ANOSIM, Global R = 0.006, P = 0.497) (Fig. 1).

Nutrition in diet

The only nutritional difference between hare and rabbit diet was the amount of fibre (Table 2). Hares had slightly more fibre in their diet (mean = 64.3%, SD = 6.2%), particularly in cattle fields (mean = 59.9%, SD = 2.9%; sheep fields: mean = 65.3%, SD = 5.0%) than rabbits (mean = 60.6%, SD = 2.7%). The percentage of ash in both species' diets was higher in cattle fields (mean = 34.8%, SD = 3.6%) than sheep fields (mean = 27.4%, SD = 6.8%) but there was no difference between hares and rabbits dietary intake of ash. The mean fat content of diets in sheep fields (15.2%, SD = 5.3%) was slightly lower than that of cattle fields (20.3%, SD = 6.8%) but this difference was not significant.

Discussion

Dietary niche partitioning between two medium-sized sympatric mammalian herbivores was observed and could explain their coexistence despite their superficial similarities. Partitioning by body size, morphological differences or feeding types among other assemblages of different sized herbivores, has been used to explain coexistence between ecologically similar herbivores (Kuijper, Beek & Bakker, 2004a; Bakker *et al.*, 2009). However, in this case the body size of hares and rabbits are similar (Cowan & Hartley, 2008; Jennings, 2008), albeit rabbits are slightly smaller. They also share similar morphology and are both mixed feeders, and yet they showed a similar pattern of dietary niche partitioning as larger sympatric mammalian herbivores.

Dietary differences and selectivity

Using species level dietary information, we were able to show that differences in dietary species composition were consistent with partitioning of resources between sympatric medium-sized mammals, which could facilitate coexistence. This has also been observed in larger sympatric mammalian herbivores to mitigate potential interspecific competition (Kartzinel *et al.*, 2015). Whilst grasses formed the predominant component in both hare and rabbit diets with high overlap of plant species between them, there were important differences in their species composition (Wolfe *et al.*, 1996; Katona *et al.*, 2004). *Triticum aestivum* and *Phleum spp.* formed a higher proportion of hares' diets compared to rabbits' (Katona *et al.*, 2004, 2010; Reichlin *et al.*, 2006), with herbs such as *Trifolium spp.* and *Ranunculus spp.* found more in rabbits' diets (albeit at low frequencies), which is consistent with dietary niche partitioning.

Our findings were also consistent with other studies that found hares (Puig *et al.*, 2007; Schai-Braun *et al.*, 2015) and rabbits were selective feeders. This study also showed evidence of consistent selection for *Phleum spp.* and avoidance of *Poa spp.* by both lagomorphs. This supports to some extent the Bell-Jarman principle. However, lagomorphs, as with larger herbivores, are hind gut fermenters and are able to digest higher quantities of lower quality food, enabling them to adapt their diets to the availability of forage rather than select solely for more highly nutritious forage (Sakaguchi, 2003; Kuijper, van Wieren & Bakker, 2004b). This similarity in diet composition and selectivity for particular plant species could suggest high levels of food competition between hares and rabbits. However, other factors such as high forage availability and hares' larger home ranges compared with rabbits, which are more spatially restricted and more selective for nutritious forage than hares (Jennings, 2008; Hulbert *et al.*, 2010; Lush *et al.*, 2014), could help reduce competition for food, thus facilitating coexistence.

Nutritional intake

Nutritional availability between fields (Lush *et al.*, 2014) and the estimated nutritional intake of hares and rabbits were similar, except that hares had higher estimated amounts of fibre in their diets. This could be due to their selection for fields with taller grasses (Karmiris & Nastis, 2007; Lush *et al.*, 2014) whereas rabbits prefer shorter, less fibrous grass and selected for higher quality forage rather than higher quantities, which would enable optimal intake rates to be achieved (Bakker *et al.*, 2005). Whilst there was no strong association between the lagomorphs' distribution and cattle or sheep grazed fields (Lush *et al.*, 2014) their diet varied between fields grazed by different livestock. This is most likely due to the fewer plant species found in cattle fields compared to sheep fields and therefore a difference in availability, which was reflected in the diet.

Effect of pasture management

Intensification of agriculture has caused changes in resource availability and increased productivity within agro-ecosystems providing abundant food resources that could alleviate potential interspecific competition. However, 'improved' pasture fields that are often found in agricultural landscapes consist of a high abundance of *Lolium perenne*, which despite forming a high proportion of hare and rabbits' diets, was the least selected grass when available. This suggests that 'improved' pastures provide lower quality habitat for lagomorphs with respect to forage.

These highly productive agro-ecosystems also supported high densities of rabbits. In fields where the relative rabbit density was higher than hares, the rabbits consumed higher proportions of *Phleum spp.* compared to hares, suggesting that rabbits outcompeted hares for this preferred plant species at high density. The lack of significant correlation between hare and rabbit abundance suggests that any effect of this dietary competition does not translate to a clear effect on field-scale distribution. There was no evidence of competitive exclusion between rabbits and hares on the basis of diet but the effects of livestock and pasture management on diet may influence indirect competition in favour of rabbits over hares. It is perhaps the differences in the ability of hares to consume swards with higher biomass on poorer quality patches when resource competition occurs (Kuijper et al. 2004) that has enabled the coexistence of two herbivore species by providing an adequate nutritional niche (van Langevelde et al. 2008).

Differences in predator avoidance strategies could also influence foraging patch choice and therefore forage availability. Rabbits have been shown to favour predator avoidance (choosing areas of short grass) over intake rate in habitat selection (Iason *et al.*, 2002). No similar evidence exists for brown hares. Our fields had varying grass heights, with a major determinant of grass height being livestock grazing. Since diet composition varied with livestock grazing, it is possible that these differences reflect differing between-fields grass heights and consequently foraging behaviour. In this study hares and rabbits were found foraging in all fields, except for three where rabbits were absent, therefore access to forage species was similar. Differences in spatial foraging within the fields could determine finer scale foraging patch choice that may be limited by predator avoidance strategies and affect forage availability if plant species differed within the field. These finer scale within-field differences need to be examined further.

Conclusion

Patterns of dietary niche partitioning found between medium-sized sympatric mammalian herbivores in this study mirror those found between more distinctly different sized herbivores. However, factors other than body size, morphology and feeding type played important roles in dietary niche partitioning and limitation of food competition between medium-sized sympatric mammalian herbivores in this study.

Dietary species composition was important and highlighted the significance of plant diversity in creating suitable habitat to manage a species. Agro-ecosystems with intensively managed pastures, such as silage fields, could provide less suitable habitat for both lagomorphs in terms of forage quality, as greater variability of plant species in pastures were shown to benefit both hares and rabbits. Therefore, pasture management to help conserve hare populations might inadvertently also promote rabbit numbers.

The differences between hare and rabbit diets indicated sufficient dietary niche partitioning to allow coexistence between ecologically similar species. Other important factors such as high forage availability, differences in home ranges, responses to predators and the ability to digest lower quality food could also help mitigate food competition between these similar sized sympatric mammalian herbivores and need to be investigated further.

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Table 1: Summary of the number of hare and rabbit droppings collected between surveys and year. Standard deviations are in brackets.

	Total number of hare droppings	**Mean number of hare droppings per field**	**Total number of rabbit droppings**	**Mean number of rabbit droppings per field**
2011	320	27 (17)	350	30 (21)
2012	160	11 (4)	180	14 (5)

Table 2: Results from 2-way ANOVA on dietary nutrition of hares and rabbits in sheep and cattle fields (n = 16 fields)

Nitrogen	**df**	**F**	**P**
Lagomorph species	1	1.728	0.202
Livestock species	1	1.264	0.272
Lagomorph*Livestock	1	0.270	0.608
Error	23		
Fibre			
Lagomorph species	1	5.655	**0.026**
Livestock species	1	15.475	**0.001**
Lagomorph*livestock	1	1.442	0.242
Error	23		
Fat			
Lagomorph species	1	0.879	0.358
Livestock species	1	3.868	0.061
Lagomorph*Livestock	1	0.953	0.339
Error	23		
Ash			
Lagomorph species	1	2.381	0.136
Livestock species	1	13.680	**0.001**
Lagomorph*Livestock	1	0.690	0.415
Error	23		
Energy			
Lagomorph species	1	1.123	0.300
Livestock species	1	2.000	0.171
Lagomorph*Livestock	1	0.181	0.674
Error	23		

Table 3: Mean percentage of plant fragments identified in hare and rabbit droppings across all study fields in 2011 and 2012. Main plants eaten, which are classed as ones above 5% in the diet, are shaded (Standard deviations in brackets). * = Significantly different between hare and rabbit diet (MANOVA, df = 1, P > 0.05).

Plant species	**Hare**		**Rabbit**	
	2011	**2012**	**2011**	**2012**
Grasses				
Triticum aestivum	22.61 (14.13)*	11.46 (18.65)*	8.33 (11.66)*	0.74 (0.00)*
Lolium perenne	21.67 (14.59)	11.83 (7.71)	30.79 (18.50)	24.32 (7.56)
Phleum spp.	11.73 (8.75)*	9.03 (11.78)*	6.27 (5.45)*	2.53(2.60)*
Poa spp.	11.45 (10.85)	18.30 (12.08)	15.93 (15.50)	27.96 (13.54)
Dactylis glomerata	6.30 (8.90)	5.54 (3.95)	6.92 (7.87)	7.97 (8.22)
Festuca rubra	4.10 (9.61)	10.69 (4.90)	1.64 (1.50)	11.27 (12.30)
Deschampsia cespitosa	3.79 (3.99)	9.46 (1.22)	2.47 (2.44)	0
Holcus lanatus	2.45 (4.40)	4.82 (4.71)	3.07 (3.40)	5.49 (8.34)
Agrostis spp.	1.37 (1.47)	9.16 (9.03)	5.05 (10.60)	2.79 (1.07)
Alopecurus spp.	3.20 (3.66)	2.86 (2.15)	2.54 (2.47)	2.08 (2.64)
Arrhenatherum elatius	3.02 (4.22)	2.57 (2.32)	3.37 (5.53)	3.72 (3.84)
Bromus hordeaceus	1.68 (1.13)	1.77 (1.56)	1.64 (0.89)	1.98 (1.81)
Cynosurus cristatus	0	0.71 (0.31)	0	0
Herbaceous plants				
Trifolium spp.	2.38 (2.89)*	0.80 (0.32)*	3.67 (3.60)*	2.82 (3.71)*
Ranunculus spp.	1.20 (0.96)*	1.00 (0.83)*	2.06 (2.42)*	2.97 (6.40)*
Rumex spp.	0.90 (0.46)		3.78 (8.16)	
Veronica persica	0.72 (0.00)	0	0.82 (0.00)	0.74 (0.00)
Taraxacum officinale	0	0	0.82 (0.00)	0.74 (0.00)
Stellaria media	0	0	0.82 (0.00)	0.74 (0.00)
Cirsium spp.	0.72 (0.00)		0	
Cerastium fontanum	0.72 (0.00)	0	0	1.12 (0.97)

Table 4: Mean percentage of cover of plant species found across all study fields, only those that were above 5% are shown

Plant species	**Mean % cover**	**SD**
Agrostis capillaris	7.49	9.05
Conopodium majus	5.73	6.90
Cynosurus cristatus	9.15	9.18
Holcus lanatus	22.01	18.96
Lolium perenne	48.84	27.44
Phleum pratense	6.88	7.28
Poa annua	5.15	5.10
Poa trivalis	10.65	10.16
Trifolium repens	7.19	9.93

Table 5: Ranking matrix of hare diet (rows) against plant availability (columns) across all study fields. 1 = most selected for, 9 = least selected. + = plant eaten more than plant species in columns, - = less eaten, --- = significantly less eaten and +++ = significantly eaten more at P < 0.05.

Hare diet 2011, Wilks' Lambda = 0.071, P = 0.048

	Agrostis spp.	*Dactylis glomerata*	*Deschampsia cespitosa*	*Festuca rubra*	*Holcus lanatus*	*Lolium perenne*	*Phleum spp.*	*Poa spp.*	*Trifolium spp.*	Rank
Phleum spp.	+++	+	+	+	+++	+++		+++	+++	1
Festuca rubra	+	+	+		+++	+++	-	+++	+	2
Deschampsia cespitosa	+	+		-	+++	+++	-	+++	+++	3
Dactylis glomerata	+		-	-	+++	+++	-	+++	+++	4
Agrostis spp.		-	-	-	+++	+++	---	+	+	5
Trifolium spp.	-	---	---	-	+	+	---	+		6
Poa spp.	-	---	---	---	+	+++	---		-	7
Lolium perenne	---	---	---	---	+		---	---	-	8
Holcus lanatus	---	---	---	---		-	---	-	-	9
Hare diet 2012, Wilks' Lambda = 0.111, P = 0.026										
Phleum spp.	+++	+	+++	+	+++	+++		+++	+++	1
Festuca rubra	+++	+	+++		+++	+++	-	+++	+++	2
Dactylis glomerata	+		+++	-	+++	+++	-	+++	+++	3
Agrostis spp.		-	+++	---	+	+++	---	+	+++	4
Poa spp.	-	---	+	---	+	+++	---		+++	5
Holcus lanatus	-	---	+	---		+	---	-	+++	6
Deschampsia cespitosa	---	---		---	-	+	---	-	+++	7
Lolium perenne	---	---	-	---	-		---	---	+++	8
Trifolium spp.	---	---	---	---	---	---	---	---		9

Table 6: Ranking matrix of rabbit diet (rows) against plant availability (columns) across all study fields. 1 = most selected for, 9 = least selected. + = plant eaten more than plant species in columns, - = less eaten, --- = significantly less eaten and +++ = significantly eaten more at P < 0.05.

Rabbit diet 2011, Wilks' Lambda = 0.016, P = 0.024

	Agrostis spp.	*Dactylis glomerata*	*Deschampsia cespitosa*	*Festuca rubra*	*Holcus lanatus*	*Lolium perenne*	*Phleum spp.*	*Poa spp.*	*Trifolium spp.*	Rank
Phleum spp.	+++	+++	+++	+++	+++	+++		+++	+++	1
Dactylis glomerata	+++		+	+	+++	+++	---	+++	+++	2
Deschampsia cespitosa	+	-		+	+++	+++	---	+++	-	3
Festuca rubra	+	-	-		+++	+++	---	+	+	4
Trifolium spp.	+	---	-	-	+	+++	---	+		5
Agrostis spp.		---	-	-	+	+	---	+	-	6
Poa spp.	-	---	---	-	+	+++	---		-	7
Lolium perenne	-	---	---	---	+		---	---	---	8
Holcus lanatus	-	---	---	---		-	---	-	-	9
Rabbit diet 2012, Wilks' Lambda = 0.059, P = 0.02										
Dactylis glomerata	+++		+++	+++	+++	+++	+	+++	+++	1
Phleum spp.	+	-	+++	+	+	+++		+	+	2
Festuca rubra	+	---	+++		+	+++	-	+	+	3
Holcus lanatus	+	---	+	-		+++	-	+	+	4
Agrostis spp.		---	+	-	-	+++	-	+	+	5
Poa spp.	-	---	+++	-	-	+++	-		+	6
Trifolium spp.	-	---	+	-	-	+++	-	-		7
Deschampsia cespitosa	-	---		---	-	+++	---	---	-	8
Lolium perenne	---	---	---	---	---		---	---	---	9

Figure Legends

Fig. 1: Mean percentage of plant species found in hare and rabbit diet for both years split between fields that have relative higher rabbit to hare densities (Fields = 6), fields with higher hare to rabbit densities (Fields = 5) and fields where the ratio of hare to rabbit densities were similar (Fields = 5). Standard deviation is represented by error bars.

Fig. 2: Mean percentage of plant fragments identified in hare and rabbit droppings from samples in 2011 and 2012 that were significantly different between lagomorphs. (Standard deviations represented by error bars)