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1 **Title**

2 Dietary niche partitioning between sympatric brown hares and rabbits

3

4 **Short title**

5 Dietary niche partitioning of sympatric mammals

6

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23 **Abstract**

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

42

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

45 **Introduction**

46

47 Dietary niche partitioning has been used to explain the coexistence of ecologically similar large
48 mammalian herbivores in both African and Asian herbivore assemblages (Ahrestani, Heitkönig
49 & Prins, 2012; Kartzinel *et al.*, 2015). Diet similarity and overlap between sympatric species
50 could create interspecific competition for resources, particularly if population densities are high
51 and resources are low (Cheng & Ritchie, 2006; Bakker, Olf & Gleichman, 2009). However,
52 dietary niches can be partitioned through differences in body size, morphology and feeding
53 types (e.g. grazer, browser or mixed) (Hofmann & Stewart, 1972; Arsenault & Owen-smith,
54 2002). Competition between species can also be affected by other species, for example, through
55 facilitation whereby larger herbivores create more favourable habitat for smaller herbivores by
56 maintaining shorter more nutritious forage or reducing vegetation height to allow better access
57 to preferred forage (Stahl *et al.*, 2006; Bakker *et al.*, 2009). Differences in body size have also
58 been related to diet selectivity, with smaller herbivores being more selective than larger species
59 that can ingest higher quantities of lower quality food, as described by the Bell-Jarman
60 principle (Bell, 1971; Jarman, 1974; Gordon & Illius, 1996). Differences in dietary
61 composition are thought to influence the partitioning of resources at the species level but data
62 on individual species' diets are not always available for sympatric species (Kartzinel *et al.*,
63 2015).

64

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

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

74

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

83

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

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

98 The study aimed to assess the following hypotheses:

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

107

108

109 **Materials and methods**

110 The study site was in Wykeham, North Yorkshire, UK, (54°12'59.21" N, -0°30'54.05" E) a
111 landscape of lowland mixed arable and pastoral farmland. Eighteen fields with an average
112 field size of 6.4 ha (SD = 4.63 ha) were intensively studied. Fields were either continuously
113 or rotationally grazed by cattle (n = 11; mean field size = 8.66 ha, SD = 5.07 ha) or sheep (n
114 = 7; mean field size = 3.41 ha, SD = 1.66 ha). To measure hare and rabbit density at least one
115 visit per week of all study fields was made 1 h after sunset during data collection. Each field
116 was scanned using a 1 mega candlepower spotlight (Clubman CB2, Cluson Engineering Ltd,
117 Hampshire, UK) and 8 × 42 binoculars, and the number of hares and rabbits was counted.
118 Observations were recorded of 358 hares and 733 rabbits over 13 repeat surveys of all study
119 fields in 2011 and 1332 hares and 2258 rabbits across 21 repeat surveys of all study fields in
120 2012. Hares were recorded in all study fields (mean = 3.57, SD = 3.34) and rabbits were
121 present in all but three of the fields (mean = 6.76, SD = 7.74) although abundance varied
122 between fields and surveys (Lush et al. 2014).

123

124 **Faecal analysis**

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

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

138

139 **Plant composition and nutritional analysis**

140 Plant composition and grass height was recorded within each of the study fields during June
141 2011 and 2012. The percentage cover of all grasses and herbs was recorded in 1 m² quadrats
142 with at least 10 quadrats per transect and 10 grass height measurements per quadrat using the
143 direct method (Stewart, Bourn & Thomas, 2001). This was carried out along three transects per
144 field; one along the edge, one in the middle and an intermediate transect (20–30 m from the
145 field boundary). Plant samples were taken to analyse the nutritional composition of forage by
146 cutting all above ground green plant material from three 1 × 0.1 m plots per transect (Bakker
147 *et al.*, 2005). Plant cuttings were oven dried at 100°C for 36 h, finely ground and mixed using
148 a Retsch rotor mill. Standard methods were used to determine nutritional content, as described
149 fully in Lush *et al.*, (2014).

150

151 **Plant cell identification**

152 Reference slides were prepared of the different plant species to aid identification. A single layer
153 of leaf and stem epidermis cells was scraped from each plant and mounted onto slides using
154 glycerol (Wolfe, Whelan & Hayden, 1996). Key identifying features of the cells (shape and
155 size of cells, presence and shape of silica bodies, presence and shape of hair structures and

156 stoma, as well as the shape of the cell wall, if it was sinuous or straight) (Bhadresa, 1987;
157 Matrai & Katona, 2004), were noted. Plant stems were very similar between species so these
158 remained unidentified.

159

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

164

165 **Data analysis**

166 Differences in diets between cattle-grazed and sheep-grazed fields were analysed separately
167 for rabbits and hares using MANOVA. Only the main eight plant species that were found
168 with prevalence above 5% in both hare and rabbit diets were included (Katona *et al.*, 2004).

169 A Pearson correlation was calculated on lagomorph densities and t test to assess differences
170 in grass heights between fields. SPSS Statistics (IBM version 19) was used for statistical
171 analysis.

172

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

176

177 **Diet selectivity**

178 Evidence of diet selectivity in hare and rabbit diet was assessed using a compositional analysis
179 (Aebischer, Robertson and Kenward 1993). Data were analysed using R 3.0.1 software (R
180 Development Core Team, 2013) and the package ‘adehabitatHS’ version 0.3.6 (Calenge,
181 2006). The mean percentage frequency of each plant species identified in hare and rabbit
182 droppings was calculated for all study fields for both years (Wolfe *et al.*, 1996). The mean
183 percentage cover of the corresponding plant species was used to calculate the availability of
184 forage in each study field. The value ‘0.01’ was ascribed to plants with 0% cover in fields so
185 that all plant species identified in diets were used in the analysis (Aebischer *et al.*, 1993).

186

187 **Diet similarity and lagomorph densities**

188 To evaluate whether either hare and rabbit diet varied with density of the other lagomorph, the
189 mean percentage of each plant species found in hare and rabbit diet for both years were split
190 into fields that had a relative lower hare to rabbit mean density ratio (0.4 hares and 2.1 rabbits),
191 higher hare to rabbit mean density ratio (1.1 hares and 0.2 rabbits) and fields where the mean
192 density of hares to rabbits was similar (1.2 hares and 1.6 rabbits) (Fig. 1). A similarity matrix
193 was produced to assess diet similarity between hares and rabbits in fields with different density
194 ratios. Using the similarity matrix a non-metric Multi-Dimensional Scaling (MDS) ordination
195 plot was created. The stress value was checked to assess the fit to the data and values below
196 0.2 were regarded as adequate (Clarke, 1993). ANOSIM was used to assess differences in the
197 percentage of each plant species found in hare and rabbit diets depending on hare and rabbit
198 ratios in different fields.

199

200 **Dietary nutrition of hares and rabbits**

201 Logit transformed mean percentage cover of plant species and mean percentage of nitrogen,
202 fat, fibre, ash and energy content (MJ/KG) for each field were used in a linear regression to
203 estimate an approximate figure of nutritional content for each plant species found in the field.
204 Plant species that had large numbers of zeros were excluded from the analysis. The
205 unstandardised coefficients for each plant species were multiplied by the mean percentage
206 found in hares' and rabbits' diets respectively. These were then summed to obtain an overall
207 value of each nutritional component for hares and rabbits in each field. This was done for both
208 years combined and back-transformed to provide a value for hare and rabbit dietary nutrition
209 within each field. A two-way ANOVA was performed on each dietary nutritional value (Table
210 2).

211 **Results**

212 A total of 20,081 plant fragments were identified, 10,737 for hares and 9,342 for rabbits, over
213 the two years across all study fields. Twenty-two different species of plant were identified
214 within hare and rabbit droppings (Table 3), out of 41 plant species identified within the study
215 fields. The mean density of hares across the study fields was 0.82 hares ha⁻¹ (SD = 0.73 hares
216 ha⁻¹) and of rabbits was 1.40 rabbits ha⁻¹ (SD = 1.97 rabbits ha⁻¹). A negative correlation
217 between hare and rabbit densities in the study fields across both years was not significant ($r =$
218 -0.231 , $N = 32$, $P = 0.255$). Grass height varied significantly between fields ($t = 9.68$, $df = 132$,
219 $P = 0.001$) and between cattle-grazed fields (mean = 10.49cm, SD = 10.18cm) and sheep-grazed
220 fields (mean = 5.64cm, SD = 9.45cm), $t = -2.76$, $df = 123$, $P = 0.007$).

221

222 **Comparison of diet**

223 Eighteen different species of plants were found in both hare and rabbit faeces over the two
224 years. Hare diet species richness per field ranged from 5 - 14 species (mean = 11.17, SD = 3.3),
225 while that of rabbits ranged from 7 - 14 species (11.45, SD = 2.81). Mean Simpson's index for
226 hare diet was 0.793 (SD = 0.062) and for rabbits 0.794 (SD = 0.057). There were no significant
227 differences in diet diversity between the two species or between years or fields (ANOVA, $F =$
228 0.025 , $df = 1$, $P = 0.878$; $F = 0.239$, $df = 1$, $P = 0.634$; $F = 2.475$, $df = 15$, $P = 0.454$ respectively).
229 The only plants found in hare droppings but not in rabbit droppings were *Cynosurus cristatus*
230 and *Cirsium spp.* but fragments of these were present only in small numbers.

231

232 The main components of both hare and rabbit diet were grasses (Hares 2011 = 93.37%, 2012
233 = 98.21% and rabbits 2011 = 88.02%, 2012 = 90.85%). *Triticum aestivum* (wheat) made up
234 22.62% (2011) and 11.46% (2012) of hares diets and 8.33% (2011) and 0.74% (2012) of rabbits

235 diets. *Poa spp.* and *Lolium perenne* were the main non-crop grasses found in the diet of both
236 lagomorphs (Table 3); together with *Holcus lanatus* (which did not form a substantial
237 component), these grasses made up over 85% of plant percentage cover in the study fields
238 (Table 4).

239

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

246

247 **Diet selectivity**

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

251

252 **Diet similarity and lagomorph density**

253 Although the plants most frequently eaten by both lagomorphs were the same (*Lolium perenne*
254 and *Poa spp.*), their diets overall were significantly different (ANOSIM, Global $R = 0.179$, P
255 $= 0.013$). They were also significantly different between sheep and cattle fields (ANOSIM,
256 Global $R = 0.143$, $P = 0.005$). However, there was no significant difference in their diet

257 between fields with different density ratios of hares to rabbits (ANOSIM, Global R = 0.006, P
258 = 0.497) (Fig. 1).

259

260 **Nutrition in diet**

261 The only nutritional difference between hare and rabbit diet was the amount of fibre (Table 2).
262 Hares had slightly more fibre in their diet (mean = 64.3%, SD = 6.2%), particularly in cattle
263 fields (mean = 59.9%, SD = 2.9%; sheep fields: mean = 65.3%, SD = 5.0%) than rabbits (mean
264 = 60.6%, SD = 2.7%). The percentage of ash in both species' diets was higher in cattle fields
265 (mean = 34.8%, SD = 3.6%) than sheep fields (mean = 27.4%, SD = 6.8%) but there was no
266 difference between hares and rabbits dietary intake of ash. The mean fat content of diets in
267 sheep fields (15.2%, SD = 5.3%) was slightly lower than that of cattle fields (20.3%, SD =
268 6.8%) but this difference was not significant.

269

270

271 **Discussion**

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

281

282 **Dietary differences and selectivity**

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

293

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

307

308 **Nutritional intake**

309 Nutritional availability between fields (Lush *et al.*, 2014) and the estimated nutritional intake
310 of hares and rabbits were similar, except that hares had higher estimated amounts of fibre in
311 their diets. This could be due to their selection for fields with taller grasses (Karmiris & Nastis,
312 2007; Lush *et al.*, 2014) whereas rabbits prefer shorter, less fibrous grass and selected for higher
313 quality forage rather than higher quantities, which would enable optimal intake rates to be
314 achieved (Bakker *et al.*, 2005). Whilst there was no strong association between the lagomorphs'
315 distribution and cattle or sheep grazed fields (Lush *et al.*, 2014) their diet varied between fields
316 grazed by different livestock. This is most likely due to the fewer plant species found in cattle

317 fields compared to sheep fields and therefore a difference in availability, which was reflected
318 in the diet.

319 **Effect of pasture management**

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

327

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

340

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

353

354 **Conclusion**

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

360 Dietary species composition was important and highlighted the significance of plant diversity
361 in creating suitable habitat to manage a species. Agro-ecosystems with intensively managed
362 pastures, such as silage fields, could provide less suitable habitat for both lagomorphs in terms
363 of forage quality, as greater variability of plant species in pastures were shown to benefit both

364 hares and rabbits. Therefore, pasture management to help conserve hare populations might
365 inadvertently also promote rabbit numbers.

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

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375

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- 479
- 480

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

483

	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)

484

485

486 **Table 2:** Results from 2-way ANOVA on dietary nutrition of hares and rabbits in sheep and
 487 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		

488

489

490

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

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

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

Plant species	Mean % cover	SD	497
<i>Agrostis capillaris</i>	7.49	9.05	
<i>Conopodium majus</i>	5.73	6.90	
<i>Cynosurus cristatus</i>	9.15	9.18	
<i>Holcus lanatus</i>	22.01	18.96	
<i>Lolium perenne</i>	48.84	27.44	
<i>Phleum pratense</i>	6.88	7.28	
<i>Poa annua</i>	5.15	5.10	
<i>Poa trivalis</i>	10.65	10.16	
<i>Trifolium repens</i>	7.19	9.93	

498

499

500 **Table 5:** Ranking matrix of hare diet (rows) against plant availability (columns) across all
 501 study fields. 1 = most selected for, 9 = least selected. + = plant eaten more than plant species
 502 in columns, - = less eaten, --- = significantly less eaten and +++ = significantly eaten more at
 503 $P < 0.05$.

504

Hare diet 2011, Wilks' Lambda = 0.071, P = 0.048										
	<i>Agrostis</i> <i>spp.</i>	<i>Dactylis</i> <i>glomerata</i>	<i>Deschampsia</i> <i>cespitosa</i>	<i>Festuca</i> <i>rubra</i>	<i>Holcus</i> <i>lanatus</i>	<i>Lolium</i> <i>perenne</i>	<i>Phleum</i> <i>spp.</i>	<i>Poa</i> <i>spp.</i>	<i>Trifolium</i> <i>spp.</i>	Rank
<i>Phleum spp.</i>	+++	+	+	+	+++	+++		+++	+++	1
<i>Festuca rubra</i>	+	+	+		+++	+++	-	+++	+	2
<i>Deschampsia cespitosa</i>	+	+		-	+++	+++	-	+++	+++	3
<i>Dactylis glomerata</i>	+		-	-	+++	+++	-	+++	+++	4
<i>Agrostis spp.</i>		-	-	-	+++	+++	---	+	+	5
<i>Trifolium spp.</i>	-	---	---	-	+	+	---	+		6
<i>Poa spp.</i>	-	---	---	---	+	+++	---		-	7
<i>Lolium perenne</i>	---	---	---	---	+		---	---	-	8
<i>Holcus lanatus</i>	---	---	---	---		-	---	-	-	9
Hare diet 2012, Wilks' Lambda = 0.111, P = 0.026										
<i>Phleum spp.</i>	+++	+	+++	+	+++	+++		+++	+++	1
<i>Festuca rubra</i>	+++	+	+++		+++	+++	-	+++	+++	2
<i>Dactylis glomerata</i>	+		+++	-	+++	+++	-	+++	+++	3
<i>Agrostis spp.</i>		-	+++	---	+	+++	---	+	+++	4
<i>Poa spp.</i>	-	---	+	---	+	+++	---		+++	5
<i>Holcus lanatus</i>	-	---	+	---		+	---	-	+++	6
<i>Deschampsia cespitosa</i>	---	---		---	-	+	---	-	+++	7
<i>Lolium perenne</i>	---	---	-	---	-		---	---	+++	8
<i>Trifolium spp.</i>	---	---	---	---	---	---	---	---		9

505

506 **Table 6:** Ranking matrix of rabbit diet (rows) against plant availability (columns) across all
 507 study fields. 1 = most selected for, 9 = least selected. + = plant eaten more than plant species
 508 in columns, - = less eaten, --- = significantly less eaten and +++ = significantly eaten more at
 509 $P < 0.05$.

510

Rabbit diet 2011, Wilks' Lambda = 0.016, P = 0.024										
	<i>Agrostis</i> <i>spp.</i>	<i>Dactylis</i> <i>glomerata</i>	<i>Deschampsia</i> <i>cespitosa</i>	<i>Festuca</i> <i>rubra</i>	<i>Holcus</i> <i>lanatus</i>	<i>Lolium</i> <i>perenne</i>	<i>Phleum</i> <i>spp.</i>	<i>Poa</i> <i>spp.</i>	<i>Trifolium</i> <i>spp.</i>	Rank
<i>Phleum spp.</i>	+++	+++	+++	+++	+++	+++		+++	+++	1
<i>Dactylis glomerata</i>	+++		+	+	+++	+++	---	+++	+++	2
<i>Deschampsia cespitosa</i>	+	-		+	+++	+++	---	+++	-	3
<i>Festuca rubra</i>	+	-	-		+++	+++	---	+	+	4
<i>Trifolium spp.</i>	+	---	-	-	+	+++	---	+		5
<i>Agrostis spp.</i>		---	-	-	+	+	---	+	-	6
<i>Poa spp.</i>	-	---	---	-	+	+++	---		-	7
<i>Lolium perenne</i>	-	---	---	---	+		---	---	---	8
<i>Holcus lanatus</i>	-	---	---	---		-	---	-	-	9
Rabbit diet 2012, Wilks' Lambda = 0.059, P = 0.02										
<i>Dactylis glomerata</i>	+++		+++	+++	+++	+++	+	+++	+++	1
<i>Phleum spp.</i>	+	-	+++	+	+	+++		+	+	2
<i>Festuca rubra</i>	+	---	+++		+	+++	-	+	+	3
<i>Holcus lanatus</i>	+	---	+	-		+++	-	+	+	4
<i>Agrostis spp.</i>		---	+	-	-	+++	-	+	+	5
<i>Poa spp.</i>	-	---	+++	-	-	+++	-		+	6
<i>Trifolium spp.</i>	-	---	+	-	-	+++	-	-		7
<i>Deschampsia cespitosa</i>	-	---		---	-	+++	---	---	-	8
<i>Lolium perenne</i>	---	---	---	---	---		---	---	---	9

511

512

513 **Figure Legends**

514

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

519

520

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