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1 **Running head:** Common Buzzard responses to prey on a grouse moor

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4 **Numerical and functional responses of Common Buzzards *Buteo buteo* on a Scottish grouse**  
5 **moor**

6  
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21 Predators will often respond to reductions in preferred prey by switching to alternative prey resources.  
22 However, this may not apply to all alternative prey groups in patchy landscapes. We investigated the  
23 demographic and aggregative numerical and functional responses of Common Buzzards *Buteo buteo*,  
24 in relation to variations in prey abundance, on a moor managed for Red Grouse *Lagopus lagopus*  
25 *scotica* in south-west Scotland over three consecutive breeding and non-breeding seasons. We  
26 hypothesised that predation of Red Grouse by Buzzards would increase when abundance of their  
27 preferred Field Vole *Microtus agrestis* prey declined. As vole abundance fluctuated, Buzzards  
28 responded functionally by eating voles in relation to their abundance, but did not respond  
29 demographically in terms of either breeding success or density. During a vole crash year, Buzzards  
30 selected a wider range of prey typical of enclosed farmland habitats found on the moorland edge, but  
31 fewer grouse from the heather moorland. During a vole peak year, prey remains suggested a linear  
32 relationship between grouse density and the number of grouse eaten (type 1 functional response),  
33 which was not evident in either intermediate or vole crash years. Buzzard foraging intensity varied  
34 between years as vole abundance fluctuated, and foraging intensity declined with increasing heather  
35 cover. Our findings did not support the hypothesis that predation of Red Grouse would increase when  
36 vole abundance was low. Instead, they suggest that Buzzards predated grouse incidentally while  
37 hunting for voles, which may increase when vole abundances are high through promoting foraging in  
38 heather moorland habitats where grouse are more numerous. Our results suggest that declines in main  
39 prey may not result in increased predation of all alternative prey groups when predators inhabit patchy  
40 landscapes. We suggest that when investigating predator diet and impacts on prey, knowledge of all  
41 resources and habitats that are available to predators is important.  
42  
43

44 **Keywords:** Aggregative response, game management, incidental predation, raptors.

45 Predators may respond either numerically or functionally to fluctuations in prey abundance and  
46 availability (Solomon 1949, Holling 1959a, b, 1965). Numerical responses can be further divided into  
47 demographic and aggregative responses. Demographic numerical responses occur through changes in  
48 breeding density, breeding success or survival (Andersson & Erlinge 1977, Reif *et al.* 2004), although  
49 they may be influenced by predator mobility, reproductive potential and generation time (Korpimäki  
50 & Norrdahl 1991, Redpath & Thirgood 1999). Aggregative numerical responses occur when  
51 individuals aggregate to forage in areas of greater net energy gains (Baker & Brooks 1981, Stephens  
52 & Krebs 1986), and are influenced by the territoriality and mobility of predators as well as the  
53 depletion rates of prey (Thirgood *et al.* 2003, Mckinnon *et al.* 2013). Functional responses involve a  
54 change in predator diet towards the most abundant or rewarding prey type. As the profitability of a  
55 preferred prey type declines, a predator may increasingly select an alternative prey (alternative prey  
56 hypothesis; Angelstam *et al.* 1984, Reif *et al.* 2001), or widen its diet by taking a larger range of  
57 alternative prey as a greater range of alternative prey are selected (Pyke *et al.* 1977, Salamolard *et al.*  
58 2000). However, even in relatively simple ecosystems, the availability of two or more alternative prey  
59 can lead to complex interactions between predators and prey (Newton 1998, Zárýbnická *et al.* 2015).  
60 For instance, predator responses can also affect predation rates on incidental prey, which are not the  
61 primary focus of a predator (incidental prey hypothesis; Cornell 1976, Vickery *et al.* 1992). If  
62 incidental and preferred prey have similar habitat requirements, predation may increase on incidental  
63 prey groups when the density of preferred prey is high (Selås 2001, Valkama *et al.* 2005). Conversely,  
64 if incidental prey coexist in space with important alternative prey groups, but both are spatially  
65 separated from preferred prey, incidental predation may be higher when main prey density is low  
66 (Mckinnon *et al.* 2013). The nature of these responses will depend on the range and juxtaposition of  
67 habitats and prey available to predators, as well as their relative profitability (Smout *et al.* 2010).  
68 Numerical and functional responses of predators can influence predation rates on prey (Redpath &  
69 Thirgood 1999, Tornberg *et al.* 2012, Mckinnon *et al.* 2013), and as such, understanding their nature  
70 is essential for effective management of both predators and prey (Morrison *et al.* 2012).

71 The Common Buzzard *Buteo buteo* (hereafter 'Buzzard') is a generalist raptor whose  
72 preferred prey comprises small mammals, especially voles *Microtus* spp., and European Rabbits  
73 *Oryctolagus cuniculus* (Graham *et al.* 1995, Reif *et al.* 2001). When available, Buzzards may also  
74 select Red Grouse *Lagopus lagopus scotica* as alternative prey (Graham *et al.* 1995), which are an  
75 economically important gamebird in parts of upland Britain (Sotherton *et al.* 2009). Buzzards were  
76 restricted to western areas of Britain during much of the 20<sup>th</sup> century due to persecution throughout  
77 the 18<sup>th</sup>, 19<sup>th</sup> and early 20<sup>th</sup> centuries, and their subsequent recovery was hampered by the effects of  
78 organochlorine pesticides and the collapse of rabbit populations from myxomatosis during the 1950s  
79 and 1960s (Moore 1957, Parkin & Knox 2010, Balmer *et al.* 2014). Since the 1970s, population  
80 recovery and range expansion in Britain (Musgrove *et al.* 2013, Balmer *et al.* 2014) has created

81 concern amongst some game managers about the impact of Buzzard predation on gamebirds (Lees *et*  
82 *al.* 2013, Parrott 2015).

83 Studies in Fennoscandia on the functional responses of generalist predators, including  
84 Buzzards, have shown that predation of grouse *Tetraonidae spp.* increased when vole abundance was  
85 low (Reif *et al.* 2001, Tornberg *et al.* 2012, 2016). Therefore, we hypothesised that Buzzard predation  
86 of Red Grouse would increase when vole abundance was low. We investigated the demographic and  
87 aggregative numerical and functional responses of Buzzards in an area of heather moorland managed  
88 for Red Grouse, and in the neighbouring farmland and forest peripheries. In particular, we were  
89 interested in determining how any response of Buzzards could influence predation of Red Grouse.

90

## 91 **METHODS**

92

### 93 **Study area**

94 The study was conducted at Langholm Moor in south-west Scotland (55°10'N, 02°55'E) between  
95 2011 and 2014. The study area consisted of *c.* 220 km<sup>2</sup> of a mosaic of semi-natural, unenclosed  
96 acidic-grassland and heather *Calluna vulgaris* moorland, which has been fragmented by livestock  
97 grazing (Thirgood *et al.* 2003), surrounded by enclosed fields of improved grassland, coniferous  
98 forest and mixed deciduous woodland (Redpath & Thirgood 1997, Francksen *et al.* 2016). The study  
99 area was chosen to include 114 km<sup>2</sup> managed under the Langholm Moor Demonstration Project  
100 (LMDP; Langholm Moor Demonstration Project 2014) plus a 2 km buffer zone, the latter chosen to  
101 include Buzzards which may hunt within the LMDP area based on previous estimates of home range  
102 size at Langholm (Graham *et al.* 1995). Management to benefit Red Grouse for potential shooting,  
103 including rotational heather burning and legal control of corvids, foxes and mustelids, was undertaken  
104 by a team of five gamekeepers within the area designated under the LMDP. Between 2009 and 2011,  
105 prior to the start of data collection for the current study, sheep density on the study area was reduced  
106 by 21% from 0.75 sheep per hectare to 0.59 sheep per hectare to promote heather recovery.  
107 Furthermore, 37% of the remaining sheep flock was grazed away from the study area between  
108 October and March each year (Langholm Moor Demonstration Project 2014). All raptors were strictly  
109 protected from interference.

110

### 111 **Prey abundance**

112 To interpret any numerical (demographic and aggregative) and functional responses observed in  
113 Buzzards, we assessed the abundances of Field Voles *Microtus agrestis* and lagomorphs, which are  
114 key prey for Buzzards in Britain, and Red Grouse, which are alternative Buzzard prey (Graham *et al.*  
115 1995) of interest to our study. On sites in Britain such as ours, Red Grouse are principally associated  
116 with areas of heather-dominated moorland, where the heather provides food and nesting cover

117 (Jenkins *et al.* 1963). Field Voles are most numerous in the grass-dominated areas of moorland  
118 vegetation (Redpath & Thirgood 1997, Wheeler 2008). On our study site, sightings of lagomorphs,  
119 either rabbit or Brown Hare *Lepus europaeus*, during other prey surveys indicated their abundance  
120 within the heather-dominated moorland and acidic grassland habitats was low (< 0.1 individuals/km)  
121 in all years. Instead, lagomorphs were largely confined to the enclosed fields on the moorland  
122 periphery, where other alternative prey of Buzzards are also likely to be most abundant (Tubbs 1974,  
123 Redpath & Thirgood 1997, Thirgood *et al.* 2003).

124 Field Vole abundance was assessed annually in March/April from 50 unbaited snap traps set  
125 over two nights at 10 locations across the study area, i.e. 1000 trap nights per annum (Redpath *et al.*  
126 1995) between 2011 and 2014 inclusive. All trapping locations were on the heather-moorland and  
127 unenclosed acidic-grassland areas within the LMDP area. The number of voles caught per 100 trap  
128 nights was used as an annual abundance index. Field Voles comprised 83% of all small mammals  
129 trapped over all trap lines. Annual variation in vole abundance between 2011 and 2013 was assessed  
130 by comparing the annual mean number of voles trapped per 100 trap nights at the ten trapping  
131 locations with a two-way ANOVA, specifying year and individual trapping location as factors. For  
132 this analysis, we were not interested in any effect of trapping location, but we included it in the model  
133 as part of the data structure. The purpose was to relate any variation in vole abundance to any  
134 evidence of Buzzard responses during the same period.

135 Red Grouse were counted twice each year: in March or early-April to assess pre-breeding  
136 density and in July to assess post-breeding density. Counts were conducted in ten 0.5 km<sup>2</sup> moorland  
137 blocks using a pointing dog (Jenkins *et al.* 1963). Within each block, transects spaced 150 m apart  
138 were walked with the dog quartering either side of the transect. Additionally, grouse were also  
139 counted on 18 transects across the moorland part of the study area (mean transect length = 1.95 km,  
140 range = 0.96 – 3.46; see Redpath & Thirgood 1997 and Langholm Moor Demonstration Project 2014  
141 for more details of survey methods). Distance sampling corrections were applied to grouse data to  
142 correct for detectability differences between individual dogs and observers. The perpendicular  
143 distance from the transect line to the point at which each single grouse or group of grouse were  
144 flushed was recorded, and subsequently an effective strip width using a detectability curve was  
145 calculated using the program DISTANCE (Thomas & Buckland 2010). Mean densities (grouse/km<sup>2</sup>)  
146 were then calculated for each block or transect using:

$$147$$
$$148 \text{ Grouse density} = \frac{\text{Total grouse counted}}{\text{Total transect length} \times (\text{effective strip width} \times 2)}$$
$$149$$

150 Annual variation in pre- and post-breeding grouse densities were assessed by comparing the annual  
151 mean densities from the ten blocks and 18 transects ( $n = 28$ ), again with a two-way ANOVA with  
152 year and transect as factors.

153 Lagomorphs were counted on twelve 1-km transects in the enclosed fields on the moorland  
154 periphery, which were walked between 05:00 and 09:00 in June 2012 and June 2013. Rabbits  
155 comprised 94% of all lagomorphs seen, and so the number of rabbits seen per km of transect was used  
156 as the annual index. Between-year variation in rabbit abundance was tested with a paired t-test.

157

## 158 **Buzzard responses**

### 159 *Demographic numerical response*

160 To assess the demographic numerical response, Buzzard nests were located within the study area both  
161 on and off the moor between 2011 – 2013 inclusive. Searches were conducted in suitable nesting  
162 sites, especially where displaying Buzzards were seen from vantage points in early spring (Hardey *et*  
163 *al.* 2013). Nests were considered active if they were freshly lined, had fresh prey remains and/or  
164 pellets nearby, or if territorial adults were heard calling (Tubbs 1974, Hardey *et al.* 2013). Between  
165 2011 and 2013, 58 active Buzzard nests were found in 29 territories. The same territory was assumed  
166 if nests were found within the same 1 km<sup>2</sup> in each year, according to approximate territory sizes at  
167 Langholm (Graham *et al.* 1995). The nearest-neighbour distance (NND) was calculated for all nests in  
168 each year, excluding nests where we felt the nearest neighbour may have been missed (2011: 15 nests  
169 used, 1 excluded; 2012: 12 used, 4 excluded; 2013: 21 used, 5 excluded).

170 Breeding success was expressed as the number of chicks fledged, first from all successful  
171 nests (where at least one chick fledged), and then from all breeding attempts (including failed nests  
172 and territories where pairs failed to lay eggs). The latter was the same as chicks per pair because no  
173 pairs were observed to lay repeat clutches if their first attempt failed. Chicks were considered to have  
174 fledged if seen at the nest site at  $\geq 4$  weeks old (Hardey *et al.* 2013). The mean annual breeding  
175 density was compared between years with ANOVA. Breeding success data could not be normalised  
176 and so non-parametric Kruskal-Wallis tests were used to analyse between-year differences.

177

### 178 *Aggregative numerical response*

179 To assess the aggregative numerical response, we explored Buzzard foraging patterns during three  
180 breeding seasons (2012 – 2014) and three non-breeding seasons (winters 2011/12 – 2013/14).  
181 Observations of Buzzards were conducted from fixed vantage points over moorland blocks of  
182 approximately 1 km<sup>2</sup>. Summer observations were conducted twice per month in May, June and July  
183 for three hours on each occasion over 10 blocks in 2012 and 12 in 2013 and 2014, giving a total of  
184 552 hours. Observations were conducted once per month in winter (October – March) over nine of the  
185 blocks in 2011/12 and over 12 in 2012/13 and 2013/14, totalling 661 hours. Observations were made  
186 only under appropriate weather conditions, when blocks were scanned for hunting Buzzards  
187 (quartering, soaring, hovering and scanning while perched) every two minutes.

188 Habitat composition within the 12 observation blocks was estimated from the Land Cover  
189 Map 2007 dataset (Morton *et al.* 2011), whereby each 25 × 25-m grid cell was categorized by its  
190 dominant habitat class. The habitat composition of each block was calculated within ArcGIS. Heather  
191 moorland (dwarf shrub heathland and ericaceous bog) and grassland (rough, neutral and acidic  
192 grassland) together averaged 96% of habitat within the blocks (range: 90 – 100%), therefore one  
193 habitat composition index was derived by log-transforming the ratio of heather moorland to grassland.  
194 Vole abundance data were available for all observed blocks within the period that foraging patterns  
195 were assessed, whilst grouse were counted on ten observation blocks only because the remaining two  
196 blocks contained little or no heather. For the purposes of analyses, we assumed that grouse were  
197 absent from these two blocks, which was supported by no grouse being observed during general  
198 breeding bird surveys. There were no differences in results from models that either included or  
199 excluded these two blocks, so here we include them.

200 We explored Buzzard foraging patterns using GLMMs with Poisson errors and log-link  
201 functions. The number of sightings of Buzzards hunting summed across visits within each season for  
202 each block was used as the response variable, with total scans per season and block fitted as an offset  
203 and block as a random factor. We were not interested in the effect of ‘block’ in itself, but included this  
204 as random factor as an important part of the model structure. We summed data across visits within  
205 each season. We related Buzzard foraging intensity to spatial variation in the heather-grass ratio and  
206 the spatial and temporal variation in grouse and vole indices (covariates), but not lagomorphs, which  
207 were uniformly low in abundance (<0.1 individuals / km) on all blocks, and year (factor), with first-  
208 order interactions between year and the covariates to explore differing relationships between years.  
209 Separate models were constructed to explore relationships during summer and winter. For all models,  
210 we calculated Wald statistics using the Anova function of the car package in R version 3.2.2 (Fox &  
211 Weisberg 2011, R Core Team 2013). Significant interactions with year were explored using separate  
212 GLMs for each year, which included habitat and prey index covariates. Overdispersion of models was  
213 tested using the gof function of the aods3 package in R (Lesnoff & Lancelot 2014), and where  
214 necessary accounted for by including an observation-level random effect (OLRE; Bates *et al.* 2012).  
215 In all models, no two variables were found to be strongly correlated ( $r < |0.45|$ ; Dormann *et al.* 2013),  
216 so all were retained.

217

### 218 *Functional response*

219 Diet data were obtained from three sources in three breeding seasons (2011-13): motion-triggered nest  
220 cameras, collection of prey remains and collection of regurgitated pellets from the vicinity of nests.  
221 Camera image data were collected from each of 32 nests for at least three days during each of three  
222 post-hatching periods: < one week, one to four weeks and > four weeks within a mean nestling period  
223 of 50 days ( $\pm 0.74$  se). Overall, 2,320 hours of footage were collected (mean hours per nest  $80 \pm 15$ ),  
224 yielding 1,005 prey deliveries (mean per nest  $31 \pm 3$ ). Of these, prey in 136 deliveries (14%) were

225 obscured and could not be identified, and were excluded. Prey remains and regurgitated pellets were  
226 collected from inside, and within a 50-m radius of, 46 of the 58 nests. The remaining 12 nests either  
227 failed to hatch chicks or were discovered too late in the nestling period to yield samples. Searches  
228 were conducted at the end of each camera recording period when batteries and memory cards were  
229 replaced, and again during the first week post-fledging, yielding 664 prey remains ( $14 \pm 1$  per nest)  
230 and 295 pellets ( $6 \pm 1$  per nest). Analysis of pellets yielded 655 prey items. Prey were identified to the  
231 lowest possible taxonomic level, and were assumed to represent one individual, unless it was obvious  
232 that more than one was present (Redpath *et al.* 2001). Equipment and detailed methods for collection  
233 of prey composition data are described in Francksen *et al.* (2016). All diet data were expressed as the  
234 proportion of prey items in each prey group.

235 Annual diet breadth (range of prey selected by Buzzards) was calculated for each diet  
236 assessment method and nest following Levins (1968), whereby:

$$237 \quad \text{Diet breadth} = \frac{1}{\sum p_j^2}$$

238 where  $p_j$  is the proportion of total frequency of prey group  $j$ . Annual variation in diet breadth was  
239 explored using a two-way ANOVA with year and territory specified as factors, the latter to recognise  
240 that some nests within the same territories were sampled in multiple years.

241 To estimate the local grouse density around each Buzzard nest for comparisons with diet, we  
242 used post-breeding grouse counts (July) as they coincided more closely with when Buzzards  
243 provisioned chicks (early-May to late-July) than did spring counts (March/early-April). Grouse  
244 densities from the ten blocks and 18 transects were plotted onto a map of the study area. The 18  
245 transects were divided into 34 sections of approximately 1 km length. Grouse density at the centre  
246 point of each transect section was used in kriging analysis in ArcMap (version 10.3) to estimate Red  
247 Grouse density contours across the study area in each year. The LMDP area is surrounded by mature  
248 commercial conifer forest and improved farmland, which are unsuitable for Red Grouse, hence  
249 interpolation of grouse density was limited to this area containing suitable grouse habitat, producing a  
250 raster map with a 500-m cell size of grouse density, onto which Buzzard nest locations were then  
251 plotted. A circle of 1-km radius around each nest represented an approximate average summer  
252 territory size (Graham *et al.* 1995), within which grouse density was estimated using the mean of the  
253 estimated cell values from the underlying grouse density layer, weighted by the area of each cell  
254 within the circle.

255 To determine whether the proportion of grouse in Buzzard diet varied between years (2011-  
256 2013) and in relation to grouse density, we constructed GLMMs with binomial distributions and logit-  
257 link functions. The response variable was grouse as a proportion of total identified prey at each  
258 Buzzard nest, or the proportion of pellets containing grouse in the case of pellet data. ‘Year’ was  
259 included as a factor, ‘local grouse density’ as a covariate, and ‘territory’ as a random effect to account  
260 for nests that were sampled within the same territory in successive years. An interaction term between



261 year and local grouse density was included to explore whether the consumption rate of grouse varied  
262 between years. Separate models were constructed for each of the three diet assessment methods and  
263 significance determined with Wald statistics. Again, we checked for overdispersion and adjusted  
264 using an OLRE when necessary (Bates *et al.* 2012).

265

## 266 **RESULTS**

267

### 268 **Demographic numerical response of Buzzards**

269 Within the three breeding seasons when demographic Buzzard data were collected, vole indices at the  
270 ten trapping locations varied almost 12-fold between years, from 0.6 in 2013 to 7.0 / 100 trap nights in  
271 2011 ( $F_{2,18} = 8.09$ ,  $p = 0.003$ ; Table 1). No variation in pre-breeding grouse density was detected ( $F_{2,54}$   
272  $= 0.38$ ,  $P = 0.686$ ), but post-breeding density varied from 78 grouse/km<sup>2</sup> in 2011, to 138 in 2013 ( $F_{2,54}$   
273  $= 6.23$ ,  $P = 0.004$ ). Lagomorph density did not vary significantly between 2012 and 2013 (paired  $t_{11} =$   
274  $-0.29$ ,  $P = 0.779$ ).

275 We found no demographic numerical response by Buzzards to fluctuations in prey abundance  
276 (Table 2). We detected no annual variations in either nearest neighbour distance (NND;  $F_{2,45} = 1.53$ ,  $P$   
277  $= 0.227$ ), or breeding success (Kruskal-Wallis rank-sum tests: all breeding attempts:  $H = 1.12$ ,  $df = 2$ ,  
278  $P = 0.57$ ; successful nests only:  $H = 0.16$ ,  $df = 2$ ,  $P = 0.92$ ).

### 279 **Aggregative numerical response by Buzzards**

280 Following the crash in vole abundance in 2013, vole abundance rapidly increased to a peak in 2014 of  
281 5.5 ( $\pm 0.8$ ) voles per 100 trap nights. During the three summers between 2012 and 2014, Buzzard  
282 foraging intensity within the observation blocks (sightings of Buzzards hunting per 100 scans) was  
283 three-times higher in 2014 when voles peaked compared to 2013 when voles crashed. Furthermore,  
284 Buzzard foraging intensity during the three winters between 2011/12 and 2013/14 was nine-times  
285 higher in 2013/14 when voles peaked compared to 2012/13 when voles crashed (Table 3). The  
286 number of sightings of Buzzards hunting during observations varied significantly between summers  
287 ( $\chi^2_2 = 12.73$ ,  $P = 0.002$ ) and winters ( $\chi^2_2 = 21.83$ ,  $P < 0.001$ ). In both summer and winter, Buzzard  
288 foraging intensity declined with increasing heather cover (Tables 4a & b). During winter, Buzzards  
289 foraged more in areas with greater pre-breeding grouse densities ( $\chi^2_1 = 6.72$ ,  $P = 0.01$ ; Fig. 1), and the  
290 relationship was best explained as a type 1 (linear) response ( $R^2 = 0.18$ ), compared to either a type 2  
291 ( $R^2 = 0.06$ ) or type 3 ( $R^2 = 0.12$ ) response. Spatial variation in vole abundance had no effect on winter  
292 Buzzard foraging, and spatial variation in the densities of grouse and voles was not related to summer  
293 Buzzard foraging patterns.

294

### 295 **Functional response of Buzzards**

296 As vole indices declined from 2011 to 2013, the proportion of voles provisioned to Buzzard chicks  
297 also declined (52 – 20% in cameras; 16 – 1% in remains; 51 – 31% in pellets; Table 5). Instead,  
298 Buzzards provisioned more ‘other small mammals’ (moles, shrews and mice), ‘other large birds’  
299 (corvids, waders and pigeons) and lagomorphs. Diet breadth differed between years for camera  
300 images ( $F_{2,9} = 5.75, P = 0.025$ ) and pellets ( $F_{2,15} = 6.58, P = 0.009$ ), being greatest in 2013 when voles  
301 crashed, and although not significant, followed the same pattern when considering prey remains ( $F_{2, 15}$   
302  $= 0.82, P = 0.460$ ; Table 6).

303 The proportion of grouse in Buzzard diet declined across years when considering prey  
304 remains ( $\chi^2_2 = 20.07, P < 0.001$ ) and pellets ( $\chi^2_2 = 10.36, P = 0.006$ ), but not for camera images ( $\chi^2_2 =$   
305  $3.50, P = 0.17$ ). The spatial relationship between grouse density and grouse in Buzzard diet differed  
306 between years when considering prey remains data ( $\chi^2_2 = 7.01, P = 0.03$ ), with more grouse consumed  
307 at Buzzard nests located in areas with higher grouse densities during the peak vole year of 2011 than  
308 in ones with lower grouse densities ( $\chi^2_1 = 15.39, P < 0.001$ ; parameter estimate =  $0.06 \pm 0.01$ ), but not  
309 in either of the other years, 2012 and 2013 ( $\chi^2_1 \leq 2.23, P \geq 0.13$ ; Fig. 2). The relationship in 2011 most  
310 closely fitted a type 1 (linear) response ( $R^2 = 0.33$ ) compared to either a type 2 ( $R^2 = 0.30$ ) or type 3  
311 ( $R^2 = 0.09$ ) response, There was no relationship between grouse density and grouse in Buzzard diet  
312 using pellets ( $\chi^2_1 = 1.53, P = 0.22$ ) or camera data ( $\chi^2_1 = 2.23, P = 0.13$ ).

## 313 DISCUSSION

314  
315 The impact of predation on prey populations largely depends on the numerical and functional  
316 responses of predators (Solomon 1949, Holling 1959a, b, 1965). In this study, we documented the  
317 demographic and aggregative numerical and functional responses of Common Buzzards, the most  
318 numerous avian predator on our study area. Our results showed that when vole abundance was  
319 reduced, Buzzard hunting intensity declined across our study area, and breeding Buzzards selected  
320 more prey typical of the enclosed farmland habitats on the moorland periphery, which appeared to  
321 result in a reduction in incidental predation on Red Grouse.

322 Predation rates on incidental prey largely depend on the spatial distribution of prey. For  
323 example, Selås (2001) found that incidental predation of Adders *Vipera berus* by Buzzards increased  
324 during peak vole years, because Adders (also vole predators) were attracted to vole rich habitats in  
325 these years. Similarly, Kenward (1999) found that predation rates on released pheasants by Goshawks  
326 *Accipiter gentilis* were greater when rabbit abundance was higher. On the other hand, Mckinnon *et al.*  
327 (2013) found that incidental predation of shore-bird nests by Arctic Foxes *Vulpes lagopus* increased  
328 during years of low abundance of their preferred Lemming *Lemmus trimucronatus* prey, because  
329 foxes were then attracted to goose nests which were in close proximity to shore-bird nests. Studies  
330 showing that generalist predators increase their predation of grouse species when vole abundances are  
331 low (Reif *et al.* 2001, Tornberg *et al.* 2012, 2016) have often been conducted in comparatively  
332 homogenous landscapes (Zárybnická *et al.* 2015). Our study involved a heterogeneous landscape of

333 heather and grass mosaics managed for grouse, surrounded by woodland and enclosed fields of  
334 improved grassland (Redpath & Thirgood 1997, Francksen *et al.* 2016). In this varied landscape,  
335 different prey groups are likely to be more patchily distributed. Furthermore, historical overgrazing by  
336 sheep has resulted in a heather-grass mosaic on our study area (Thirgood *et al.* 2003), which is likely  
337 to promote the spatial proximity or even coexistence of voles and grouse (Redpath & Thirgood 1997,  
338 Wheeler 2008). On the other hand, the enclosed fields on the moorland periphery, which are generally  
339 separated from the heather-moor by 1-2km on our study area, support higher abundances of  
340 alternative prey such as rabbits, moles, earthworms, corvids and pigeons (Glue 1967, Swann &  
341 Etheridge 1995, Redpath & Thirgood 1997). Here, Buzzards showed both an aggregate numerical and  
342 functional response to fewer voles by hunting away from the moor and, in doing so, by widening their  
343 diet breadth and selecting a greater range of alternative prey more typical of farmland habitats,  
344 thereby reducing their incidental predation on grouse. This was in direct contrast to our hypothesis  
345 that predation on grouse would decline when vole abundance was high, and contrasts with the  
346 findings of a number of studies conducted in Fennoscandia (Reif *et al.* 2001, Tornberg *et al.* 2012,  
347 2016).

348         It is important to note that whilst all methods of diet assessment showed that Buzzards  
349 increased their selection of prey associated with farmland and moorland fringe habitats as vole  
350 abundance declined, a corresponding decrease in predation on Red Grouse was apparent only from  
351 prey remains and pellet data, and not from camera image data. All methods of diet assessment carry  
352 sources of inherent bias (Redpath *et al.* 2001, Francksen *et al.* 2016). For example, prey remains and  
353 pellets may overestimate larger and more conspicuous prey, while direct observations, such as with  
354 cameras, may miss prey that are relatively rarely selected or delivered to nests by raptors (Simmons *et*  
355 *al.* 1991, Sonerud 1992, Lewis *et al.* 2004). Indeed, in this study we found Red Grouse remains at  
356 Buzzard nests at which camera data recorded no grouse delivered. Therefore, whilst we cannot be  
357 certain that our findings have not been affected by some of these inherent biases, a change in Buzzard  
358 diet was apparent across all methods whereby a greater proportion of total diet consisted of prey  
359 associated with farmland habitats found on the moorland fringe.

360         On our study area, Hen Harriers *Circus cyanaeus* have shown a demographic numerical  
361 response of elevated breeding density in response to small mammal and passerine abundances, and  
362 were predicted to have more impact on grouse when these main prey abundances were high (Redpath  
363 & Thirgood 1999). However, we found no evidence of a demographic numerical response by  
364 Buzzards to vole abundance, symptomatic of the generalist nature of Buzzards that are able to switch  
365 to alternative prey to offset reductions in preferred prey, so that breeding performance is not affected  
366 (Reif *et al.* 2004). However, Buzzard foraging patterns indicated an aggregative numerical response  
367 (Baker & Brooks 1981, Smout *et al.* 2010, Mckinnon *et al.* 2013), whereby more were seen foraging  
368 on moorland observation blocks during a peak vole year, and that there was a general tendency for  
369 more Buzzard sightings where there was less heather cover. The absence of any relationship between

370 spatial variations in vole abundance and Buzzard foraging patterns seemingly contradicts previous  
371 studies of *Buteo* species (Baker & Brooks 1981, Preston 1990). However, as Thirgood *et al.* (2003)  
372 concluded, the spatial scale at which we assessed raptor foraging may have been too coarse to detect  
373 spatial responses of Buzzards to variation in voles, which may occur at scales of 1-ha or less.

374 The shape of the functional response curve is critical for assessment of predation impacts on  
375 prey (Korpimäki & Norrdahl 1991, Redpath & Thirgood 1999, Salamolard *et al.* 2000). Here, we  
376 found evidence from prey remains that Buzzards responded to grouse density in a linear fashion (i.e. a  
377 type 1 response), but only during a peak vole year. Seemingly, this was because Buzzards focused on  
378 important alternative prey groups occurring outside grouse habitats when vole abundance was low.  
379 Whilst prey remains can overestimate the occurrence of large birds in raptor diet (Redpath *et al.*  
380 2001a, Lewis *et al.* 2004), this bias is likely to be relatively constant between years (Francksen *et al.*  
381 2016). Our analyses of the functional curve shape were also unavoidably linked to the spread of  
382 grouse densities available to us on our study area. Indeed, a type 2 response was a worse fit for our  
383 data than a type 1 response, but only marginally so. This may indicate that Buzzard predation rates on  
384 Red Grouse would plateau at higher grouse densities. However, without measuring predation rates  
385 over the range of densities that grouse may reach on other moors, density-dependent processes may  
386 not have been fully explored in this study (Redpath & Thirgood 1999). This remains an important area  
387 of future research.

388 Responses of generalist predators and any effects these have on predation rates of prey will  
389 depend on a number of factors, including the range and juxtaposition of habitats and prey, and the  
390 relative profitability of prey resources (Redpath & Thirgood 1999, Smout *et al.* 2010, Mckinnon *et al.*  
391 2013). As such, predator responses may vary between locations with varying physical and biological  
392 conditions (Salamolard *et al.* 2000). Our study was conducted on an area of heather-moorland  
393 managed for potential Red Grouse shooting, which included control of generalist predators (i.e. foxes,  
394 mustelids and carrion crows; Ludwig *et al.* in press). Generalist predators can limit populations of  
395 both small mammals (Andersson & Erlinge 1977, Erlinge *et al.* 1983) and Red Grouse (Fletcher *et al.*  
396 2010, Ludwig *et al.* in press). Consequently, the reduced abundance of legally controllable generalist  
397 predators during this study (Ludwig *et al.* in press) may have influenced the nature of the responses of  
398 Buzzards that we documented here. Equally, our results may have also been influenced by habitat  
399 management measures aiming to increase heather cover (Ludwig *et al.* in press). Heather-dominated  
400 habitats provide inherently poorer conditions for voles compared to grass dominated habitats  
401 (Wheeler 2008), and whilst reducing sheep grazing can lead to increases in heather cover and a  
402 resulting decline in vole abundance on upland areas (Evans *et al.* 2006, Wheeler 2008) this may only  
403 be seen over a period of more than 10 years (see Smith *et al.* 2001 and references therein). On our  
404 study area, sheep numbers were reduced prior to the start of this study with the aim of stimulating  
405 heather recovery (Ludwig *et al.* in press). Other studies have found that, in the years immediately  
406 following reductions in grazing, vegetation height and vole abundances increase, before heather cover

407 increases and vole abundance declines once more (Hill *et al.* 1992, Hope *et al.* 1996, Smith *et al.*  
408 2001). Therefore, it remains uncertain whether the responses of Buzzards we documented here would  
409 occur following any long-term recovery of heather. Clearly, there is a need for further study, over a  
410 greater time period than that studied here, to fully explore these predator-prey-habitat relationships.

411 Our results may have implications for management efforts aimed at mitigating grouse losses  
412 to raptors. High mortality rates of Red Grouse chicks and breeding adults, predominately attributed to  
413 raptor predation, have been identified as an important factor in determining overall breeding success  
414 of grouse at Langholm since 2008 (Ludwig *et al.* in press). Although grouse formed a minor part of  
415 Buzzard diet, the response of Buzzards to fluctuating vole abundance may be indicative of the  
416 responses of other generalist predators (controlled or not). By maintaining habitats rich in preferred  
417 prey on the moorland periphery, or alternatively by making heather-moorland habitats less attractive  
418 by increasing heather cover, it may be possible to exploit the natural flexibility in the foraging  
419 behaviour of Buzzards and encourage them to forage away from Red Grouse habitats (Löhmus 2003).  
420 Whilst reductions in sheep grazing may promote vole abundance in the short-term (Smith *et al.* 2001),  
421 over a longer time-period grazing reductions can promote heather recovery with the dual benefit to  
422 grouse managers of providing more habitat for grouse (Jenkins *et al.* 1963) and reducing vole  
423 abundance (Wheeler 2008), with an associated reduction in incidental predation from generalist  
424 predators.

425 Here, we have provided some evidence that increased vole abundance may increase generalist  
426 predation on Red Grouse. However, it is important to note the short period of study, in which results  
427 from just one year can have a sizeable effect on conclusions. The true nature of the interactions  
428 between habitat, predators, and prey is likely to be more complex than those documented here.  
429 Improving our understanding of these responses will rely on further study over a greater time period,  
430 and at other sites with different habitat compositions and prey resources. The effect of predator  
431 responses and apparent competition between prey should be further investigated to explore how  
432 bottom-up and top-down processes may act together or in opposition (Smout *et al.* 2010). Our results  
433 suggest that, in an ideal world with unlimited funding, studies investigating predator-prey dynamics  
434 and their management should consider all resources and habitats available to predators.

435  
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440 **REFERENECS**

441

442 **Andersson, M. & Erlinge, S.** 1977. Influence of predation on rodent populations. *Oikos* **29**: 591–  
443 597.

444 **Angelstam, P., Lindström, E. & Widén, P.** 1984. Role of predation in short-term population  
445 fluctuations of some birds and mammals in Fennoscandia. *Oecologia* **62**: 199–208.

446 **Baker, J.A. & Brooks, R.J.** 1981. Distribution patterns of raptors in relation to density of meadow  
447 voles. *Condor* **83**: 42–47.

448 **Balmer, D., Gillings, S., Caffrey, B. & Swann, B.** 2014. *Bird Atlas 2007-11: The Breeding and*  
449 *Wintering Birds of Britain and Ireland*. British Trust for Ornithology, Thetford.

450 **Bates, D., Maechler, M. & Bolker, B.** 2012. lme4: Linear mixed- effects models using S4 classes.  
451 Available from <http://lme4.r-forge.r-project.org/>.

452 **Cornell, H.** 1976. Search strategies and the adaptive significance of switching in some general  
453 predators. *Am. Nat.* **110**: 317–320.

454 **Dormann, C.F., Elith, J., Bacher, S., Buchmann, C., Carl, G., Carré, G., Marquéz, J.R.G.,**  
455 **Gruber, B., Lafourcade, B., Leitão, P.J., Münkemüller, T., McClean, C., Osborne, P.E.,**  
456 **Reineking, B., Schröder, B., Skidmore, A.K., Zurell, D. & Lautenbach, S.** 2013.  
457 Collinearity: a review of methods to deal with it and a simulation study evaluating their  
458 performance. *Ecography* **36**: 27–46.

459 **Erlinge, S., Göransson, G., Hansson, L., Högstedt, G., Liberg, O., Nilsson, I.N., Nilsson, T., von**  
460 **Schantz, T., Sylvén, M., Goransson, G., Hogstedt, G., von Schantz, T. & Sylven, M.** 1983.  
461 Predation as a Regulating Factor on Small Rodent Populations in Southern Sweden. *Oikos* **40**:  
462 36–52.

463 **Evans, D.M., Redpath, S.M., Elston, D.A., Evans, S.A., Mitchell, R.J. & Dennis, P.** 2006. To  
464 graze or not to graze? Sheep, voles, forestry and nature conservation in the British uplands. *J.*  
465 *Appl. Ecol.* **43**: 499–505.

466 **Fletcher, K., Aebischer, N.J., Baines, D., Foster, R. & Hoodless, A.N.** 2010. Changes in breeding  
467 success and abundance of ground-nesting moorland birds in relation to the experimental  
468 deployment of legal predator control. *J. Appl. Ecol.* **47**: 263–272.

469 **Fox, J. & Weisberg, S.** 2011. *An {R} Companion to Applied Regression*. 2nd Edition. Sage,  
470 Thousand Oaks CA, USA.

471 **Francksen, R.M., Whittingham, M.J. & Baines, D.** 2016. Assessing prey provisioned to Common  
472 Buzzard *Buteo buteo* chicks: a comparison of methods. *Bird Study* **63**: 303–310.

473 **Glue, D.E.** 1967. Prey taken by the Barn Owl in England and Wales. *Bird Study* **14**: 169–183.

474 **Graham, I.M., Redpath, S.M. & Thirgood, S.J.** 1995. The diet and breeding density of Common  
475 Buzzards *Buteo buteo* in relation to indices of prey abundance. *Bird Study* **42**: 165–173.

476 **Hardey, J., Crick, H., Wernham, C., Riley, H., Etheridge, B. & Thompson, D.B.A.** 2013.  
477 *Raptors: A Field Guide for Surveys and Monitoring.*, 3rd ed. The Stationery Office, London.

478 **Hill, M.O., Evans, D.F. & Bell, S.A.** 1992. Long-Term Effects of Excluding Sheep from Hill  
479 Pastures in North Wales. *J. Ecol.* **80**: 1–13.

480 **Holling, C.S.** 1959a. The Components of Predation as Revealed by a Study of Small-Mammal  
481 Predation of the European Pine Sawfly. *Can. Entomol.* **91**: 293–320.

482 **Holling, C.S.** 1959b. Some Characteristics of Simple Types of Predation and Parasitism. *Can.*  
483 *Entomol.* **91**: 385–398.

484 **Holling, C.S.** 1965. The Functional Response of Predators to Prey Density and its Role in Mimicry  
485 and Population Regulation. *Mem. Entomol. Soc. Can.* **97**: 5–60.

486 **Hope, D., Picozzi, N., Catt, D.C. & Moss, R.** 1996. Effects of Reducing Sheep Grazing in the  
487 Scottish Highlands. *J. Range Manage.* **49**: 301–310.

488 **Jenkins, D., Watson, A. & Miller, G.** 1963. Population studies on red grouse, *Lagopus lagopus*  
489 *scoticus* (Lath.) in north-east Scotland. *J. Anim. Ecol.* **32**: 317–376.

490 **Kenward, R.E.** 1999. Raptor predation problems and solutions. *J. Raptor Res.* **33**: 73–75.

491 **Korpimäki, E. & Norrdahl, K.** 1991. Numerical and functional responses of kestrels, short-eared  
492 owls, and long-eared owls to vole densities. *Ecology* **72**: 814–826.

493 **Langholm Moor Demonstration Project.** 2014. *The Langholm Moor Demonstration Project: Seven*  
494 *Year Review*. The Langholm Moor Demonstration Project Ltd., Langholm.

- 495 **Lees, A.C., Newton, I. & Balmford, A.** 2013. Pheasants, Buzzards, and trophic cascades. *Conserv.*  
496 *Lett.* **6**: 141–144.
- 497 **Levins, R.** 1968. *Evolution in Changing Environments; Some Theoretical Explorations*. Princeton  
498 University Press, Princeton, N.J.
- 499 **Lewis, S.B., Fuller, M.R. & Titus, K.** 2004. A comparison of three methods for assessing raptor diet  
500 during the breeding season. *Wildl. Soc. Bull.* **32**: 373–385.
- 501 **Löhmus, A.** 2003. Are certain habitats better every year? A review and a case study on birds of prey.  
502 *Ecography* **26**: 545–552.
- 503 **Ludwig, S.C., Roos, S., Bubb, D. & Baines, D.** In press. Long-term trends in abundance and  
504 breeding success of red grouse and hen harriers in relation to changing management of a  
505 Scottish grouse moor. *Wildl. Biol.* doi:10.2981/wlb.00246.
- 506 **Mckinnon, L., Berteaux, D., Gauthier, G. & Bêty, J.** 2013. Predator-mediated interactions between  
507 preferred, alternative and incidental prey in the arctic tundra. *Oikos* **122**: 1042–1048.
- 508 **Moore, M.W.** 1957. The past and present status of the Buzzard in the British Isles. *Br. Birds* **50**: 173–  
509 197.
- 510 **Morrison, M.L., Marcot, B. & Mannan, W.** 2012. *Wildlife-Habitat Relationships: Concepts and*  
511 *Applications*. Island Press, Washington D.C.
- 512 **Morton, D., Rowland, C.S., Wood, C.M., Meek, L., Marston, C., Smith, G., Wadsworth, R.A. &**  
513 **Simpson, I.C.** 2011. *Final Report for LCM2007 - the New UK Land Cover Map. Countryside*  
514 *Survey Technical Report No 11/07*. NERC/Centre for Ecology & Hydrology.
- 515 **Musgrove, A., Aebischer, N.J., Eaton, M., Hearn, R., Newson, S.E., Noble, D.G., Parsons, M.,**  
516 **Risely, K. & Stroud, D.** 2013. Population estimates of birds in Great Britain and the United  
517 Kingdom. *Br. Birds* **106**: 64–100.
- 518 **Newton, I.** 1998. *Population Limitation in Birds*. Academic Press, London.
- 519 **Parkin, D.T. & Knox, A.G.** 2010. *The Status of Birds in Britain and Ireland*. Christopher Helm,  
520 London.
- 521 **Parrott, D.** 2015. Impacts and management of common Buzzards *Buteo buteo* at pheasant *Phasianus*  
522 *colchicus* release pens in the UK: a review. *Eur. J. Wildl. Res.* **61**: 181–197.
- 523 **Preston, C.** 1990. Distribution of raptor foraging in relation to prey biomass and habitat structure.  
524 *Condor* **92**: 107–112.
- 525 **Pyke, G.H., Pulliam, H.R. & Charnov, E.L.** 1977. Optimal foraging: a selective review of theory  
526 and tests. *Q. Rev. Biol.* **52**: 137–154.
- 527 **R Core Team.** 2013. *R (Version 3.2.2): A Language and Environment for Statistical Computing,*  
528 *Vienna, Austria.* <http://www.r-project.org/>.
- 529 **Redpath, C.J., Thirgood, S.J. & Redpath, S.M.** 1995. Evaluation of methods to estimate field vole  
530 *Microtus agrestis* abundance in upland habitats. *J. Zool.* **237**: 49–55.
- 531 **Redpath, S.M., Clarke, R., Madders, M. & Thirgood, S.J.** 2001. Assessing Raptor Diet:  
532 Comparing Pellets, Prey Remains, and Observational Data at Hen Harrier Nests. *Condor* **103**:  
533 184–188.
- 534 **Redpath, S.M. & Thirgood, S.J.** 1997. *Birds of Prey and Red Grouse*. The Stationery Office,  
535 London.
- 536 **Redpath, S.M. & Thirgood, S.J.** 1999. Numerical and functional responses in generalist predators:  
537 hen harriers and peregrines on Scottish grouse moors. *J. Anim. Ecol.* **68**: 879–892.
- 538 **Reif, V., Tornberg, R., Jungell, S. & Korpimäki, E.** 2001. Diet variation of common Buzzards in  
539 Finland supports the alternative prey hypothesis. *Ecography* **24**: 267–274.
- 540 **Reif, V., Jungell, S., Korpimäki, E., Tornberg, R. & Mykrä, S.** 2004. Numerical response of  
541 common Buzzards and predation rate of main and alternative prey under fluctuating food  
542 conditions. *Ann. Zool. Fennici.* **41**: 599–607.
- 543 **Salamolard, M., Butet, A., Leroux, A. & Bretagnolle, V.** 2000. Responses of an Avian Predator to  
544 Variations in Prey Density at a Temperate Latitude. *Ecology* **81**: 2428–2441.
- 545 **Selås, V.** 2001. Predation on reptiles and birds by the common Buzzard, *Buteo buteo*, in relation to  
546 changes in its main prey, voles. *Can. J. Zool.* **79**: 2086–2093.
- 547 **Simmons, R.E., Avery, D.M. & Avery, G.** 1991. Biases in diets determined from pellets and  
548 remains: correction factors for a mammal and bird-eating raptor. *J. Rap. Res.* **25**: 63–67.
- 549 **Smith, A.A., Redpath, S.M., Campbell, S.T. & Thirgood, S.J.** 2001. Meadow pipits, red grouse

550 and the habitat characteristics of managed grouse moors. *J. Appl. Ecol.* **38**: 390–400.

551 **Smout, S., Asseburg, C., Matthiopoulos, J., Fernández, C., Redpath, S.M., Thirgood, S.J. &**  
552 **Harwood, J.** 2010. The functional response of a generalist predator. *PloS one*, **5(5):e1076**, DOI:  
553 10.1371/journal.pone.0010761.

554 **Solomon, M.** 1949. The natural control of animal populations. *J. Anim. Ecol.* **18**: 1–35.

555 **Sonerud, G.A.** 1992. Functional responses of birds of prey: biases due to the load-size effect in  
556 central place foragers. *Oikos* **63**: 223–232.

557 **Sotherton, N., Tapper, S. & Smith, A.** 2009. Hen harriers and red grouse: economic aspects of red  
558 grouse shooting and the implications for moorland conservation. *J. Appl. Ecol.* **46**: 955–960.

559 **Stephens, D.W. & Krebs, J.R.** 1986. *Foraging Theory*. Princeton University Press, Princeton, N.J.

560 **Swann, R.L. & Etheridge, B.** 1995. A comparison of breeding success and prey of the Common  
561 Buzzard *Buteo buteo* in two areas of northern Scotland. *Bird Study* **42**: 37–43.

562 **Thirgood, S.J., Redpath, S.M. & Graham, I.M.** 2003. What determines the foraging distribution of  
563 raptors on heather moorland? *Oikos* **1**: 15–24.

564 **Thomas, L. & Buckland, S.** 2010. Distance software: design and analysis of distance sampling  
565 surveys for estimating population size. *J. Appl. Ecol.* **47**: 5–14.

566 **Tornberg, R., Reif, V. & Korpimäki, E.** 2012. What Explains Forest Grouse Mortality: Predation  
567 Impacts of Raptors, Vole Abundance, or Weather Conditions? *Int. J. Ecol.* **2012**: 1–10.

568 **Tornberg, R., Rytkönen, S., Välimäki, P., Valkama, J. & Helle, P.** 2016. Northern Goshawk  
569 (*Accipiter gentilis*) may improve Black Grouse breeding success. *J. Ornithol.* **157**: 363–370.

570 **Tubbs, C.R.** 1974. *The Buzzard*. David & Charles, Newton Abbot, London.

571 **Valkama, J., Korpimäki, E., Arroyo, B.E., Beja, P., Bretagnolle, V., Bro, E., Kenward, R.E.,**  
572 **Mañosa, S., Redpath, S.M., Thirgood, S.J. & Viñuela, J.** 2005. Birds of prey as limiting  
573 factors of gamebird populations in Europe: a review. *Biol. Rev. Camb. Philos. Soc.* **80**: 171–203.

574 **Vickery, P., Hunter, M. & Wells, J.** 1992. Evidence of incidental nest predation and its effects on  
575 nests of threatened grassland birds. *Oikos* **63**: 281–288.

576 **Wheeler, P.** 2008. Effects of sheep grazing on abundance and predators of field vole (*Microtus*  
577 *agrestis*) in upland Britain. *Agric. Ecosyst. Environ.* **123**: 49–55.

578 **Zárybnická, M., Riegert, J. & Kouba, M.** 2015. Indirect food web interactions affect predation of  
579 Tengmalm's Owls *Aegolius funereus* nests by Pine Martens *Martes martes* according to the  
580 alternative prey hypothesis. *Ibis* **157**: 459–467.



581 **Tables and Figures**

582 **Table 1.** Abundances of three Buzzard prey groups at Langholm Moor between 2011 - 2013. Note  
 583 that densities are presented in different units. Red Grouse densities combine data from block counts  
 584 and transects. Significant variations between years ( $P < 0.05$ ) are highlighted in bold. Data are means  
 585  $\pm$  se.

	2011	2012	2013
Voles/100 trap nights ( $n=10$ )	<b>7.0 <math>\pm</math> 1.9</b>	<b>4.0 <math>\pm</math> 1.0</b>	<b>0.6 <math>\pm</math> 0.3</b>
Pre-breeding grouse/km <sup>2</sup> ( $n=28$ )	46.9 $\pm$ 5.4	48.7 $\pm$ 4.9	49.8 $\pm$ 4.3
Post-breeding grouse/km <sup>2</sup> ( $n=28$ )	<b>77.5 <math>\pm</math> 9.7</b>	<b>94.6 <math>\pm</math> 12.0</b>	<b>138.3 <math>\pm</math> 17.5</b>
Rabbits/km ( $n = 12$ )	N/A	8.0 $\pm$ 1.2	8.3 $\pm$ 1.9

586  
 587 **Table 2.** Buzzard breeding density (nearest neighbour distance, NND) and breeding success at  
 588 Langholm Moor between 2011 and 2013. No measures varied significantly between years. Data are  
 589 means  $\pm$  se for breeding density, or means  $\pm$  sd for breeding success.

	2011	2012	2013
Breeding density (NND) (km)	1.61 $\pm$ 0.21 ( $n=15$ )	2.06 $\pm$ 0.23 ( $n=12$ )	1.62 $\pm$ 0.20 ( $n=21$ )
Breeding success (chicks per breeding attempt)	1.56 $\pm$ 0.89 ( $n=16$ )	1.69 $\pm$ 0.79 ( $n=16$ )	1.39 $\pm$ 0.90 ( $n=26$ )
Breeding success (chicks per successful nest)	1.79 $\pm$ 0.70 ( $n=14$ )	1.80 $\pm$ 0.68 ( $n=15$ )	1.71 $\pm$ 0.64 ( $n=21$ )

590  
 591 **Table 3.** Indices of voles, Red Grouse and foraging Buzzards at Langholm Moor in three summers  
 592 (2012 – 2014) and three winters (2011/12 – 2013/14). Values are means  $\pm$  se.  $n$  = number of blocks.  
 593 Vole and grouse densities were calculated from counts on all twelve blocks in each year.

	Summer		
	2012 ( $n=10$ )	2013 ( $n=12$ )	2014 ( $n=12$ )
Voles / 100 trap nights	4.0 $\pm$ 1.0	0.6 $\pm$ 0.3	5.5 $\pm$ 0.8
Post-breeding grouse km <sup>-2</sup>	67.2 $\pm$ 14.2	108.3 $\pm$ 23.0	103.8 $\pm$ 20.3
Buzzards / 100 scans	7.89 $\pm$ 2.02	5.55 $\pm$ 2.00	15.69 $\pm$ 3.86
	Winter		
	2011/12 ( $n=9$ )	2012/13 ( $n=12$ )	2013/14 ( $n=12$ )
Voles / 100 trap nights	4.0 $\pm$ 1.0	0.6 $\pm$ 0.3	5.5 $\pm$ 0.8
Pre-breeding grouse km <sup>-2</sup>	33.8 $\pm$ 8.2	40.5 $\pm$ 7.0	67.8 $\pm$ 12.0
Buzzards / 100 scans	7.18 $\pm$ 2.06	1.01 $\pm$ 0.29	9.29 $\pm$ 1.41

594  
 595

596 **Table 4.** Relationships between the foraging patterns of Buzzards and measures of prey density and  
 597 habitat composition in a) summer and b) winter. Habitat composition refers to the log-transformed  
 598 ratio of heather moorland to grassland. Main effects were tested across the whole study ( $n = 3$  years:  
 599 2012 – 2014) or during each year separately when there was a significant interaction with year. Main  
 600 effects were tested with interaction terms excluded. Parameter estimates were taken from a full model.

601 a) Summer

	<i>Interaction with year</i>			<i>Main effects</i>		
	$X^2_2$	<i>P</i>		Parameter estimate $\pm$ se	$X^2$	<i>df</i>
Year	-	-	-	12.73	2	0.002
Post-breeding grouse	1.53	0.46	0.01 $\pm$ 0.01	1.23	1	0.27
Vole index	1.98	0.37	-0.02 $\pm$ 0.06	0.08	1	0.77
Habitat composition	6.06	0.04	2012 -0.14 $\pm$ 0.06	6.22	1	0.01
			2013 -0.30 $\pm$ 0.08	12.80	1	<0.001
			2014 -0.12 $\pm$ 0.11	1.13	1	0.29

602 b) Winter

	<i>Interaction with year</i>			<i>Main effects</i>		
	$X^2_2$	<i>P</i>		Parameter estimate $\pm$ se	$X^2$	<i>df</i>
Year	-	-	-	21.83	2	<0.001
Pre-breeding grouse	0.96	0.62	0.06 $\pm$ 0.02	6.72	1	0.01
Vole index	2.57	0.28	0.03 $\pm$ 0.07	0.20	1	0.65
Habitat composition	7.31	0.03	2011/12 -0.36 $\pm$ 0.11	11.20	1	<0.001
			2012/13 -0.18 $\pm$ 0.06	6.26	1	0.01
			2013/14 -0.07 $\pm$ 0.08	0.79	1	0.37

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605 **Table 5.** Prey composition (%) delivered to Buzzard nests determined by three different methods.  
 606 Data are pooled across nests within each of three years. Unidentified prey in camera images ( $n = 136$ )  
 607 were removed.

	Camera images			Prey remains			Pellets		
	2011	2012	2013	2011	2012	2013	2011	2012	2013
<i>n</i> (Identified prey items)	249	266	354	160	169	335	128	141	386
<i>n</i> (nests sampled)	11	10	11	15	13	18	15	13	18
Small mammals									
Field Vole	52.2	40.2	20.1	15.6	5.9	0.9	50.8	38.3	30.6
Mole	9.2	10.5	11.3	1.9	3.0	5.4			
Other small mammals	5.2	9.4	22.3	1.3	3.6	0.9	7.0	12.8	14.5
Large mammals									
Lagomorph spp.	4.8	1.5	8.2	20.6	21.9	28.4	3.1	10.6	17.9
Other large mammals	4.4	4.9	2.0	1.9	0.0	0.6			
Small passerines	10.8	7.5	11.6	15.6	17.8	14.0	6.3	9.2	9.6
Large birds									
Red Grouse	0.0	2.6	0.8	11.9	5.3	2.1	4.7	2.8	2.3
Pheasant	2.0	0.8	0.8	15.0	17.2	17.9	1.6	0.7	2.3
Other large birds	0.0	1.9	5.1	9.4	15.4	21.8	2.3	2.8	3.1
Other prey									
Invertebrates	0.8	0.8	0.3	5.6	1.8	3.6	22.7	22.0	19.2
Amphibians and reptiles	10.4	19.9	17.5	1.3	8.3	4.5	1.6	0.7	0.5

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 609 **Table 6.** Average diet breadth (Levins' Index  $\pm$  se) calculated from prey at Buzzard nests in each of  
 610 three years using three methods of assessment; camera images  $n = 32$  nests; prey remains  $n = 46$ ;  
 611 pellets  $n = 46$ ). Significant variation between years highlighted in bold (see text).

	2011	2012	2013
Camera images	<b>3.24 <math>\pm</math> 0.19</b>	<b>3.64 <math>\pm</math> 0.39</b>	<b>4.72 <math>\pm</math> 0.31</b>
Prey remains	3.65 $\pm$ 0.29	4.27 $\pm$ 0.41	4.39 $\pm$ 0.27
Pellets	<b>3.29 <math>\pm</math> 0.15</b>	<b>3.81 <math>\pm</math> 0.23</b>	<b>4.11 <math>\pm</math> 0.19</b>

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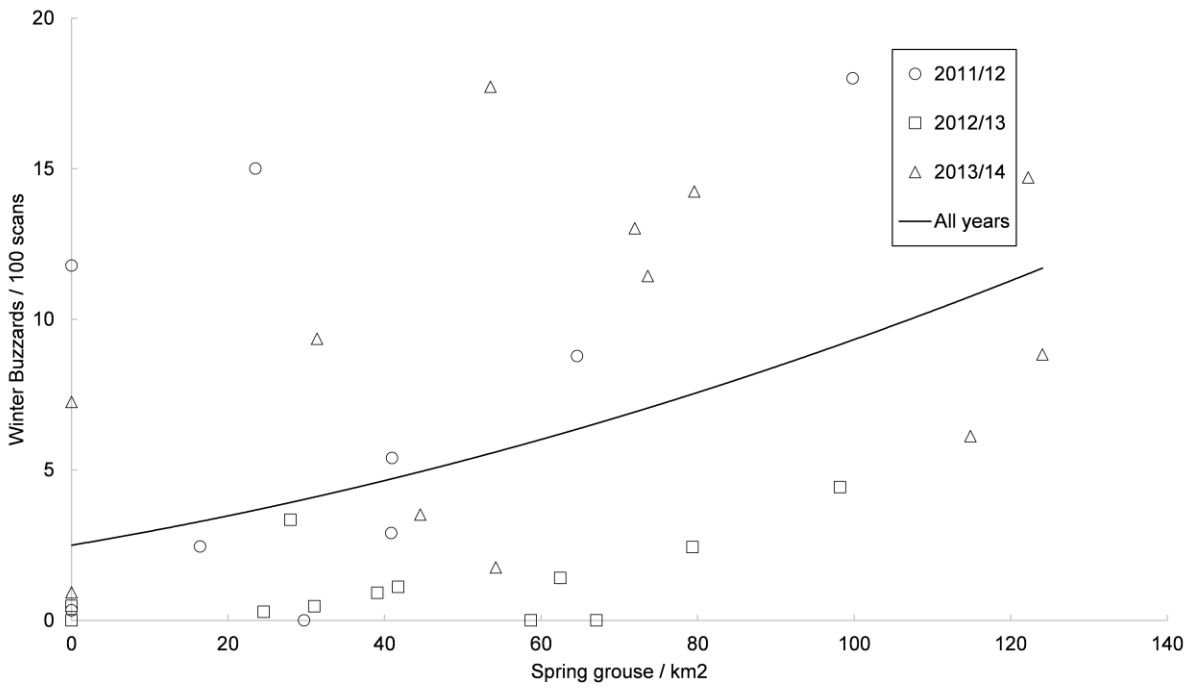


Figure 1. Buzzards foraging in winter in relation to Red Grouse density on 33 observation areas in three years (2011/12: 9, 2012/13: 12, 2013/14: 12). Line represents the relationship across all years (no significant interaction with year).

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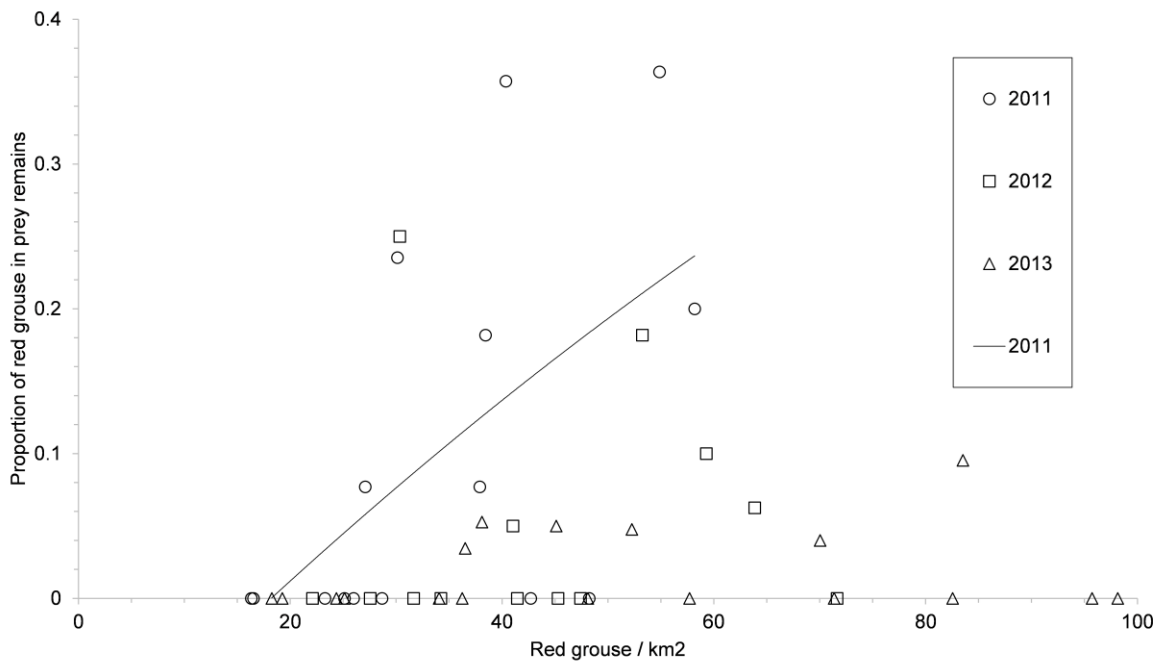


Figure 2. The proportion of Red Grouse in Buzzard diet from prey remains in relation to grouse density within a 1-km radius of each Buzzard nest in three years (2011: nests = 15; 2012: nests = 13; 2013: nests = 18). Line represents a type I functional response in 2011 (peak vole year – circles). There was no significant relationship in 2012 or 2013.

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