



Vegetation structure influences foraging decisions in a declining grassland bird: the importance of fine scale habitat and grazing regime

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1 **Vegetation structure influences foraging decisions in a declining grassland bird: the**
2 **importance of fine scale habitat and grazing regime**

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34 **SUMMARY**

35
36 **Capsule** Whinchat *Saxicola rubetra* foraging behaviour was significantly influenced by differences in

37 habitat structure and grazing.

38

39 **Aims** To assess how habitats selected by breeding Whinchats for foraging differed from wider territory
40 attributes in multiple marginal upland areas in Scotland under contrasting grazing management:
41 grazed principally by domestic sheep, Red Deer *Cervus elaphus* or ungrazed. Additionally, to identify
42 any limitations in suitable foraging areas imposed by differences in land-use.

43

44 **Methods** We compared fine-scale vegetation structure in patches chosen for foraging by Whinchats in
45 contrasting grazing management regimes.

46

47 **Results** Whinchats were less likely to forage in patches with a greater cover of bracken and tall non-
48 bracken vegetation, regardless of grazing regime. Grass cover influenced foraging behaviour,
49 however, only in ungrazed habitats. Here, Whinchats were less likely to forage in areas with high grass
50 cover.

51

52 **Conclusion** Whinchats appear to require a mosaic or range of sward structures within a breeding
53 territory, which highlights the importance of exploring the influence of vegetation structure on breeding
54 birds at different spatial scales. Our results suggest that suitable foraging patches were plentiful within
55 grazed habitats but potentially limited in ungrazed habitats. Further work is needed to identify
56 management regimes and interventions to maintain conditions suitable for breeding Whinchats that
57 are compatible with other land use and conservation objectives.

58 **INTRODUCTION**

59

60 Farmland birds in Europe have undergone large population declines and range contractions over the
61 past several decades (Pain & Pienkowski 1997, Donald *et al.* 2001). This has been attributed primarily
62 to the intensification of agriculture leading to widespread reductions in habitat quality and food
63 availability (Fuller *et al.* 1995, Siriwardena *et al.* 1998, Chamberlain *et al.* 2000, Donald *et al.* 2001).
64 The majority of agricultural land in Britain is grassland (McGilloway 2005). Changes in management -
65 notably increased fertilizer loads and, where applicable, changes in cutting regimes such as more
66 frequent and earlier mowing and increased silage production - have altered the habitat by reducing
67 vegetation complexity and heterogeneity (Vickery *et al.* 2001). This has rendered these habitats less
68 suitable for breeding birds (Donald *et al.* 2001, Vickery *et al.* 2001). Certain species have retreated to
69 upland and marginal upland areas where agricultural intensification has tended to be less severe and
70 suitable conditions likely remain (Archaux 2007, Calladine & Bray 2012). These marginal uplands
71 areas describe the indistinct and often variable boundary between the 'true' uplands, an area of
72 relatively high altitude and exposure where agriculture is restricted to low intensity grazing, and lower
73 or less exposed land where more intensive agricultural practices have proven to be economically
74 viable.

75

76 One such grassland species which was formerly widespread across lowland Europe but has recently
77 declined is the Whinchat *Saxicola rubetra* (Bastian *et al.* 1997, Broyer 2009, Harris *et al.* 2014).
78 Changes in meadow management practices, in particular earlier mowing dates and reductions in
79 vegetation complexity and habitat heterogeneity leading to reduced availability of arthropod prey, have
80 been suggested as likely drivers in mainland Europe (Müller *et al.* 2005, Britschgi *et al.* 2006, Fischer
81 *et al.* 2013). As an Afro-Palearctic migrant, the Whinchat also faces pressures both during migration
82 and on their wintering grounds, which could be contributing to their declines. However, studies report
83 evidence of favourable conditions from a wintering location in Nigeria, possibly shifting the focus of
84 declines away from these areas (Hulme & Cresswell 2012, Blackburn & Cresswell 2015). In Britain,
85 severe, accelerating, long-term declines have become widespread, and now affect historic stronghold
86 areas for the species (Henderson *et al.* 2014). Overall, breeding populations have declined in
87 abundance by 55% since 1995 (Harris *et al.* 2014). Following a 40% range contraction since 1970 in
88 Britain (Balmer *et al.* 2013), the species is now largely associated with less intensively managed
89 pasture (including moorland) in the uplands and marginal uplands (Henderson *et al.* 2004, Fuller *et al.*
90 2006, Calladine & Bray 2012, Balmer *et al.* 2013). This provides an interesting example of a species
91 impacted by 'altitudinal squeezing' where the population is apparently limited at lower altitudes by
92 intensive agricultural management and at higher altitudes by environmental constraints upon its
93 breeding biology (Calladine & Bray 2012). Consequently, land management decisions within this

94 'narrow belt', where suitable conditions remain, will be of critical importance for the remaining
95 populations of Whinchats as even within this remaining stronghold, declines have become widespread
96 (Henderson *et al.* 2014).

97

98 In agricultural areas, grassland vegetation structure can influence bird ecology in many ways (Benton
99 *et al.* 2003). A reduction in vegetation complexity and heterogeneity can reduce arthropod richness
100 and abundance (Dennis *et al.* 1998, Dennis *et al.* 2005, Morris 2000), which in turn can influence
101 breeding productivity and survival through foraging and chick provisioning (Andersson 1981, Verboven
102 & Visser 1998). Adults provisioning young typically need resource rich foraging patches (Morris *et al.*
103 2002, Benton *et al.* 2003). Such patches may be less abundant in lower quality habitats, which may
104 act to increase provisioning distances or reduce provisioning rates, leading to unsustainable energy
105 budgets, poorer body condition of chicks and adults, and ultimately, lower reproductive success
106 (Andersson 1981, Martin 1987, Hinam & Clair 2008). Additionally, vegetation structure can alter
107 predation risk and nesting site availability (Lima & Dill 1990, Benton *et al.* 2003). For example,
108 vegetation can obscure predators and prey from each other, provide cover and assist in camouflaging
109 nesting sites (Whittingham & Evans 2004), all of which can influence reproductive success. The extent
110 to which agriculture impacts habitat and vegetation structure, and therefore its influence on breeding
111 birds, varies according to land use practices (Vickery *et al.* 2001). Within managed pasture, lower
112 intensity land-use practices, which minimize disturbance to vegetation structure, may assist in the
113 preservation of key habitat features required by breeding birds, such as low to moderate grazing,
114 which aids the formation of complex vegetation mosaics and restricts succession (Vickery *et al.* 2001,
115 Evans *et al.* 2006, Dennis *et al.* 2008). Such practices are common in marginal upland areas, since
116 these areas tend to include some of the most extensive 'low-intensity' agriculture largely due to
117 combinations of relative remoteness, inaccessibility for large mechanized equipment and the relatively
118 small (compared to more productive lowlands) returns for agricultural intensification. As such, marginal
119 upland areas can retain suitable conditions for a suite of breeding birds as 'high nature value'
120 farmland, which may serve as potential refuges for declining species such as Whinchats (Archaux
121 2007, Calladine & Bray 2012). Conservation practices would benefit from a better understanding of the
122 role agriculture plays in maintaining high nature value farmland (Fuller & Gough 1999, Evans *et al.*
123 2006).

124

125 Changes in Whinchat breeding abundance within marginal upland areas appear to be spatially non-
126 random, suggesting a general redistribution towards more favoured habitats, however, the overall
127 trend has been for a continued decline (Henderson *et al.* 2014). Furthermore, recent habitat
128 assessments of breeding territories within a favourable marginal upland area have failed to identify
129 predictors of occupancy at the territory level other than altitude and aspect, both measures of

130 environmental exposure (e.g. Calladine & Bray 2012). This suggests that limitations could operate at a
131 finer scale. In this study we therefore assessed within-territory selection of foraging patches by
132 Whinchats breeding within contrasting marginal upland habitats in Scotland. These included areas
133 predominantly grazed by sheep, Red Deer *Cervus elaphus* and areas where grazing had been
134 excluded. Specifically, we asked: 1) For Whinchats breeding in marginal upland areas, does fine-scale
135 vegetation structure (type, height and cover) affect forage patch selection and, if so, which features
136 are important? 2) Are these features the same in areas with contrasting grazing regimes?
137 By comparing what features, if any, are important for foraging by breeding Whinchats and their
138 availability within territories in areas of contrasting land use, we expect to find common attributes that
139 are used within different areas and therefore identify important features for foraging Whinchats.
140 Identification of how any suitable foraging areas might be limited by differences in land use could
141 inform conservation management to improve the status of Whinchats in upland pastoral environments.

142

143 MATERIALS & METHODS

144

145 Study area

146 This study was conducted in 2014 from May to July. Five sites were selected in contrasting marginal
147 upland areas under different grazing managements in central and northern Scotland (Fig. 1). Menstrie
148 Glen (56° 09' N, 3° 51' W; 150 – 300 m above sea level) and Glen Quey (56° 13' N, 3° 39' W; 225 –
149 600 m above sea level) represent areas of current and former upland hill pasture respectively, which
150 consist of grasses with distinct areas of Common Bracken *Pteridium aquilinum*, Rush *Juncus* spp.,
151 herbaceous plants such as Common Nettle *Urtica dioica*, Foxglove *Digitalis purpurea* and Thistle
152 *Asteraceae* spp. and limited ericaceous cover, primarily Heather *Calluna vulgaris* and Bilberry
153 *Vaccinium myrtillus*. Domestic grazing animals have been excluded from Glen Quey since 11 to 12
154 years prior this study. The area was planted with a mix of native broad-leaf tree species that have now
155 grown to a height of approximately 5-10m. Menstrie Glen was extensively grazed by domestic sheep
156 at the time of this study. Other relevant browsing animals include Roe Deer *Capreolus capreolus*
157 which occur in both areas at low densities. In addition to these central sites, three discrete areas in
158 northern Scotland were chosen (Strath Oykel 57° 53' N 4° 35' W; Strath Brora 58° 04' N 4° 02' W;
159 Strath Naver 58° 21' N 4° 15' W, all 30 – 120 m above sea level), all of which are linear valley bottoms
160 no wider than approximately 500 m in most places. These valley bottoms are comprised of either
161 enclosed, agriculturally improved pasture or extensive semi-natural rough grassland with isolated
162 fragments of semi-natural woodland and scrub. The surrounding habitats consist of extensive
163 moorland (rough grasses and ericaceous vegetation), plantations of predominantly coniferous trees
164 (some of which had been clear-felled) with some smaller areas of broad-leaf tree planting. The
165 enclosed pastures are grazed mostly by domestic sheep and moorland areas more extensively by

166 both domestic sheep and relatively high densities of wild Red and Roe Deer. Plantations and other
167 wooded patches are specifically fenced to exclude large herbivores.

168

169 **Location and description of forage patches**

170 A total of 59 territories where Whinchat young were being provisioned were located including: 20
171 territories at Menstrie Glen, 18 at Glen Quey, 11 at Strath Brora, nine at Strath Naver and one at Strath
172 Oykell. Territories were identified by clustered locations of birds through the season and by
173 simultaneous observations of different birds (Bibby *et al.* 2000). Our aim was to assess any
174 differences in vegetation composition and structure between areas where Whinchats successfully
175 foraged and the wider habitat within, or very close to, the breeding territory. Feeding Whinchats were
176 watched to identify areas used for foraging in order to take measurements to describe the vegetation
177 of those patches. For the purposes of this study, we defined a forage patch as the exact area (or very
178 close to it) where a bird was seen to collect food that was then swallowed or carried to a nest or to
179 recently fledged young (which tended to stay within the breeding territories). Locating patches was
180 accomplished by observing foraging birds with binoculars and/or a field telescope and by paying close
181 attention to conspicuous features in the landscape and, when necessary, making sketches to facilitate
182 locating the forage patch upon approach. At the location of each foraging patch, attributes of
183 vegetation structure were sampled by placing 1 m² quadrats and estimating the percent cover in each
184 of three height categories (0-20 cm, 20-50 cm, and 50-100 cm) of: (1) bracken and other ferns, (2)
185 grasses and sedges (graminoids), (3) rushes, (4) non-grassy herbaceous vegetation (forbs) and, (5)
186 ericaceous vegetation (such as Heather and Bilberry). Ground cover of: (1) mosses and lichens and,
187 (2) bare ground was also estimated. In patches where the adult bird was seen to forage in an area
188 large enough for more than one quadrat sample to be taken, up to four quadrats were randomly
189 placed within an area of homogenous vegetation by moving the grid 1 m in a random compass
190 direction (achieved by spinning the compass wheel without looking). For each quadrat within each
191 sampled patch, two reference patches located 10 m to the north and 10 m to the south, were sampled
192 using an identical approach and number of quadrats. This 2:1 ratio in reference to forage quadrats
193 was consistent across management regimes.

194

195 **Statistical Analyses**

196 All analyses were carried out in R version 3.0.2 (R Development Core Team 2013, Crawley 2012). We
197 conducted principle component analyses (PCA) of the measures of habitat structure within the forage
198 and reference patches to reduce the dimensionality of our data to a smaller number of linear
199 combinations. This allowed us to avoid (1) multicollinearity in subsequent models as well as (2)
200 inferred and arbitrary decisions about which habitat measures to include (Peres-Neto *et al.* 2005). For
201 our PCA we included the nine variables that were represented in at least 10% of the surveyed

202 quadrats from the original forage and reference patch habitat datasets (Table 1). These were chosen
203 because the remaining 10 measured habitat features were deemed too scarce to be effectively
204 analysed and were likely not representative of the overall habitat. Factor loadings greater than 0.3
205 were considered to load significantly onto the component (after e.g. Minderman *et al.* 2009). Principle
206 components were retained for further analysis where axes eigenvalues were greater than 1.0 (the
207 Kaiser criteria; Yeomans & Golder 1982).

208

209 To assess the associations between habitat metrics (the PCA scores) and the probability of a patch
210 being used for foraging by Whinchats, we fitted a generalized linear mixed-effects model (GLMM)
211 specifying a binomial error distribution and logit link function (logistic regression) with the 'glmer'
212 function in the R package lme4 (v. 1.0-6; Bates *et al.* 2014). In 18 quadrats (4 patches; the single
213 territory from the Strath Oykell study site) the management regime was undetermined and so these
214 data were only included in the PCA and excluded from the main analysis. Random terms were
215 included in our model to account for the variation inherent across different study sites and amongst
216 individual foraging patches where repeated measures occurred (Bolker *et al.* 2009). For our maximal
217 model, the dependent variable was 'patch type' (binary; 1 for a patch used by a foraging bird and 0 for
218 a reference patch). Possible predictor variables were the PCA-derived habitat metrics (PC scores;
219 Table 2) with eigenvalues >1. Additionally, in order to ask whether the effect of vegetation structure on
220 the probability of a patch being foraged or not is dependent upon the management regime we included
221 the interaction between each derived habitat metric and the three-level categorical 'management
222 regime' variable (sheep-grazed, deer grazed or ungrazed). The number of days elapsed since the
223 beginning of the study was also included as an additional fixed covariate. Random variables included
224 in the model were 'patch identity' (each with a minimum separation distance of 5m) nested within
225 'study site'. Prediction plots were created by plotting the raw data with lines fitted from the regression
226 predictions of the final model. Confidence limits were obtained via simulation (n = 1000 simulations) at
227 estimated parameter values using the 'sim' function in the R package arm (v. 1.7-07, Gelman *et al.*
228 2014). The full model was simplified to a minimum adequate model using Likelihood Ratio Tests
229 (Sokal & Rohlf 1995), with the exception of 'Julian day' which was left in the model as a control
230 variable to account for the expected change in habitat variables over time (seasonal growth of
231 vegetation). Likelihood ratio tests represent a robust method for model simplification and are generally
232 appropriate for inference on random factors (Bolker *et al.* 2009). We confirmed that all candidate final
233 models adequately met model assumptions, and were not excessively over or under dispersed
234 (Crawley 2012).

235

236 RESULTS

237

238 **Vegetation metrics**

239 In total we sampled 1532 quadrats from 307 distinct foraging patches from our five study sites (Table
240 1). Within these territories, 1049 quadrats (from 170 patches) were sampled in areas where the
241 dominant management regime was grazing by sheep, 127 quadrats (from 36 patches) in habitats
242 where wild deer grazing represented the dominant management, 338 quadrats (from 97 patches) in
243 habitats where domestic and wild grazing were largely excluded by fencing supplemented by active
244 monitoring and removal of incidental grazing intruders.

245 A PCA of habitat measures yielded 3 axes with eigenvalues > 1.0 (Table 2): *First axis* (PC1,
246 accounting for 30.1% of the total variation) – Represents an index of bracken cover at all three height
247 levels. A high PC1 score indicates greater cover with bracken; *Second axis* (PC2, accounting for
248 21.2% of the total variation) – Represents an index of grass cover at all three height levels. A high PC2
249 score indicates greater cover by grasses and lower cover by herbaceous plants and mosses; *Third*
250 *axis* (PC3, accounting for 14.2% of the variation) – Represents an index of vegetation height that is
251 not bracken. A high PC3 score represents greater cover by taller herbaceous vegetation and tall
252 grasses with lower ground cover by mosses. In our study sites this likely represents tall rank grasses,
253 Nettle, Foxglove, Thistle or Rosebay Willowherb (Fireweed) *Chamerion angustifolium*.

254

255 **Forage patch selection**

256 The probability of a patch being used for foraging was significantly affected by differences in habitat
257 structure and grazing regime (Table 3). Areas with a greater cover of bracken (PC1) were used less
258 frequently for foraging, as shown by the negative association between the probability of a patch being
259 used for foraging and PC1 (Fig. 2). Additionally, patches containing a greater cover of tall vegetation
260 (combined with a lower cover of mosses and lichens; PC3) were used less frequently for foraging,
261 evident from the negative relationship between probability of a patch being used for foraging and PC3
262 (Fig. 3). These negative trends were similar across all three management regimes for both PC1 and
263 PC3, as shown by the lack of a significant interaction of management regime with PC1 or PC3 in our
264 model (Table 3). Fine-scale habitat structure also influenced foraging in patches containing a greater
265 cover of grass and a lower cover of herbaceous plants and mosses (PC2), however, this varied
266 depending upon the grazing regime (Fig. 4). In ungrazed habitats, the probability of a patch being
267 used for foraging was lower for patches with higher PC2 scores (more grass, and less herbaceous
268 plant cover, which was indicative of taller swards). By contrast, in grazed habitats this pattern was
269 reversed; patches with more grass and less herbaceous plant cover (higher PC2 scores) were more
270 likely to be selected. This can be seen from both the significant interaction of management regime and
271 the negative association between probability of a patch being used for foraging and PC2 in ungrazed
272 habitats compared to the non-significant relationship in both deer and sheep-grazed habitats.

273

274 **DISCUSSION**

275

276 **Forage patch attributes**

277 This study provides clear evidence that fine-scale vegetation structure within territories influences the
278 foraging behaviour of Whinchats breeding in marginal upland areas. Furthermore, the influence of
279 some habitat characteristics differed according to management regime, suggesting that prescribed
280 land management practices can influence Whinchat ecology by affecting the availability of some of the
281 fine-scale habitats that they use for foraging.

282

283 In all management regimes, Whinchats typically foraged in patches with lower bracken cover
284 compared to reference patches. Likely, this is because bracken cover influences food availability for
285 species foraging in open areas. Dense bracken represents a homogeneous habitat that is associated
286 with lower arthropod richness and abundance (Dennis *et al.* 1998, 2005), and greater cover probably
287 obscures prey on the ground. Foraging opportunities are therefore expected to be lower in such
288 habitats for species that require open areas to forage and those that typically seek out resource rich
289 patches, of which Whinchats are a typical example (Morris *et al.* 2002, Benton *et al.* 2003, Richter &
290 Düttmann 2004). Similarly, in all management regimes, Whinchats foraged in patches where the sward
291 height was relatively short, and avoided tall herbaceous vegetation (mainly thistle, foxglove, nettle,
292 and willowherb), grasses and bracken; features that may limit foraging opportunities for the same
293 reasons as above. At lower cover, these features likely increase the vertical and horizontal structural
294 complexity of forage patches and provide the high vegetation diversity that has been shown to be
295 beneficial for grassland birds (Schaub *et al.* 2010), the perching structures important for effective
296 foraging (Oppenman 1990, Bastian & Bastian 1997, Fischer *et al.* 2013) and probably support higher
297 arthropod diversity and abundance (Dennis *et al.* 1998). Accordingly, the vast majority of sampled
298 forage patches had at least some herbaceous vegetation and only rarely consisted of purely open
299 grassy areas, and we often observed Whinchats perching on individual herbaceous plants and
300 bracken stalks when foraging.

301

302 Our results suggest that suitable foraging patches are plentiful within grazed habitats but potentially
303 limited in ungrazed habitats. In these ungrazed habitats, the index describing the gradient of
304 herbaceous plants to grass cover (PC2) had a strong negative effect on foraging patch selection, so
305 that areas composed predominantly of grasses were less likely to be used for foraging compared to
306 those composed of short herbs (typically *Gallium saxatile* and *Potentilla erecta*) and mosses. By
307 contrast, in grazed habitats this pattern was either absent (in sheep grazed areas) or reversed (in deer
308 grazed areas and in both cases non-significant (possibly an artefact of relatively small sample size for
309 deer grazed areas). The fact that Whinchats specifically sought out preferred areas for foraging whilst

310 avoiding the habitat at the wider territory scale suggests that such favourable areas may be limited,
311 especially when compared to grazed areas. In these areas, suitable foraging patches appear to be
312 more widely available since birds did not seek them out, but rather foraged freely throughout the
313 territory. Most likely, the exclusion of grazing animals allows taller swards to develop more extensively
314 resulting in reduced food availability and rendering them less suitable for foraging for the same
315 reasons that dense bracken and herbaceous vegetation are also unsuitable for foraging (see above).
316 In contrast, low-level grazing both creates and maintains complex vegetation mosaics and restricts the
317 succession of less favourable vegetation (Vickery *et al.* 2001). For example, lowered sward height due
318 to grazing has been shown to increase prey availability and influence the foraging behaviour of many
319 grassland birds (Milsom *et al.* 1998, Evans *et al.* 2006). In our study, foraging patches in ungrazed
320 habitats contained on average more short herbaceous vegetation and mosses (as opposed to areas of
321 tall grasses), further supporting a preference for areas with higher vegetation diversity.

322

323 **Conservation implications**

324 Our study highlights the importance of exploring the influence of vegetation structure on breeding birds
325 at different spatial scales (e.g. Johnson 1980). Landscape-scale studies link Whinchats to open, non-
326 forested areas (Suter 1988), and territory-scale studies show associations with relatively tall
327 vegetation, which in pastoral areas particularly includes bracken (Stillman & Brown 1994, Britschgi *et al.*
328 2006, Pearce-Higgins & Grant 2006). To satisfy all requirements for breeding Whinchats, there is a
329 need for taller swards (for song posts, nest cover and predator avoidance; Greig-Smith 1982, Fischer
330 *et al.* 2013) as well as short swards for efficient foraging (this study). These vegetation mosaics need
331 to be present within an area of a Whinchat's breeding territory, which is typically less than 1 ha
332 (Calladine & Bray 2012). Within our study areas, taller swards mostly consisted of bracken as well as
333 some tall grass and herbaceous species, which created stands that approached or were greater than
334 100 cm throughout the breeding season. Shorter swards, which were favoured by Whinchats for
335 foraging typically included grasses, herbs and mosses in areas generally less than 20 cm in height.

336

337 Low-intensity and uneven grazing is likely to create and maintain the vegetation mosaics and perching
338 structures (Crofts & Jefferson 1999, Evans *et al.* 2006) that are required within Whinchat breeding
339 territories. The modification of grazing regimes can sometimes successfully achieve conservation aims
340 (Ward *et al.* 1995, Evans *et al.* 2006, Calladine *et al.* 2002). Further work is needed to identify the
341 management regimes and interventions that are required to maintain a mosaic of sward structures that
342 is suitable for breeding Whinchats and that is compatible with other land uses and conservation
343 objectives. Our study suggests that both sheep and deer grazed regimes can provide such conditions
344 but the roles of spatial, seasonal and long term variations and changes in grazing intensities deserves
345 further attention.

For Peer Review

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348

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For Peer Review

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566 TABLES

567

568 **Table 1** Summary statistics of the raw habitat variables and the first three extracted PC axes displayed as
 569 means (± 1 se). For the raw habitat variables, the proportion of total quadrants in which they occurred per
 570 management regime is also provided. Variables shown in bold (those which occurred in at least 10% of
 571 the sample quadrants) were selected for analysis and included in the PCA

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Habitat Variables	Sheep Grazed (n = 1049 quadrats)		Deer Grazed (n = 127 quadrats)		Ungrazed (n = 338 quadrats)	
	Mean (% ± 1 se)	Proportion	Mean (% ± 1 se)	Proportion	Mean (% ± 1 se)	Proportion
Herb. Veg. (0-20 cm)	9.4 \pm 0.5	0.42	20.4 \pm 1.7	0.82	19.7 \pm 1.2	0.69
Herb. Veg. (20-50 cm)	4.2 \pm 0.4	0.21	1.6 \pm 0.6	0.12	3.9 \pm 0.8	0.15
Herb. Veg. (50-100 cm)	1.7 \pm 0.3	0.08	0.3 \pm 0.3	0.01	2.4 \pm 0.7	0.06
Grasses (0-20 cm)	59.0 \pm 1.2	0.83	24.3 \pm 2.1	0.77	61.2 \pm 1.6	0.97
Grasses (20-50 cm)	26.6 \pm 1.0	0.58	21.1 \pm 2.1	0.76	35.7 \pm 1.8	0.88
Grasses (50-100 cm)	4.0 \pm 0.4	0.19	1.2 \pm 0.6	0.05	5.7 \pm 1.0	0.17
Rushes (0-20 cm)	4.1 \pm 0.4	0.11	0.1 \pm 0.1	0.01	1.8 \pm 0.5	0.07
Rushes (20-50 cm)	3.8 \pm 0.4	0.11	0.8 \pm 0.2	0.09	1.7 \pm 0.5	0.06
Rushes (50-100 cm)	2.3 \pm 0.3	0.07	0.7 \pm 0.3	0.06	1.4 \pm 0.5	0.04
<i>Ericaceous</i> veg. (0-20 cm)	1.6 \pm 0.3	0.05	3.7 \pm 1.1	0.23	1.7 \pm 0.6	0.04
<i>Ericaceous</i> veg. (20-50 cm)	1.3 \pm 0.3	0.03	1.1 \pm 0.4	0.06	1.1 \pm 0.5	0.01
<i>Ericaceous</i> veg. (50-100 cm)	0.3 \pm 0.1	0.01	0.0 \pm 0.0	0.00	0.0 \pm 0.0	0.00
Bracken (0-20 cm)	9.1 \pm 0.7	0.26	0.1 \pm 0.1	0.02	4.3 \pm 1.0	0.06
Bracken (20-50 cm)	26.7 \pm 1.1	0.56	3.0 \pm 0.8	0.20	5.2 \pm 1.0	0.10
Bracken (50-100 cm)	26.2 \pm 1.2	0.46	9.1 \pm 2.1	0.22	7.2 \pm 1.2	0.12
Mosses	5.0 \pm 0.4	0.23	19.9 \pm 1.9	0.79	12.3 \pm 0.9	0.61
Bare ground	3.0 \pm 0.4	0.10	14.2 \pm 2.0	0.62	2.2 \pm 0.6	0.07
Extracted PC axes	Mean (± 1 se)		Mean (± 1 se)		Mean (± 1 se)	
PC1	-0.30 \pm 0.05		-0.51 \pm 0.05		-0.74 \pm 0.07	
PC2	0.19 \pm 0.04		-1.08 \pm 0.08		-0.14 \pm 0.08	
PC3	0.08 \pm 0.03		-0.59 \pm 0.08		0.01 \pm 0.07	

Table 2 Eigenvalues, proportion of variation explained and factor loadings of the first 3 axes extracted by PCA of 9 foraging patch structural habitat measurements

	PC1	PC2	PC3
Proportion of variance explained	0.301	0.212	0.142
Eigenvector	2.705	1.905	1.277
% cover herbaceous vegetation at height 0-20 cm	-0.19	-0.48	0.38
% cover herbaceous vegetation at height 20-50 cm	-0.09	-0.30	0.69
% cover grasses at height 0-20 cm	-0.22	0.48	0.02
% cover grasses at height 20-50 cm	-0.25	0.44	0.22
% cover grasses at height 50-100 cm	-0.15	0.34	0.31
% cover bracken at height 0-20 cm	0.45	0.04	0.17
% cover bracken at height 20-50 cm	0.55	0.09	0.11
% cover bracken at height 50-100 cm	0.54	0.05	0.07
% cover mosses at height 0-20 cm	-0.14	-0.36	-0.43

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590 **Table 3** The fixed and random effects exploring the influence of vegetation structure variables and their

591 interaction with land management type on forage patch selection in Whinchats from a minimum adequate
 592 generalized linear mixed effects model (GLMM, binomial errors) of: 'Patch type' ~ PC1 + PC2 *
 593 'management' + PC3 + 'Julian day' + (1 |Study_area/'Patch identity'). The full model was: 'Patch type' ~
 594 PC1 * 'management' + PC2 * 'management' + PC3 * 'management' + 'Julian Day' + (1 |Study_area/'Patch
 595 identity'). The interaction terms with PC1 and PC3 were dropped during the model simplification process
 596 (see 'statistical analyses'). The reference category is ungrazed. N = 307 patches.
 597

<i>Fixed effects</i>	<i>Parameter estimate</i>	<i>se</i>	<i>Z</i>	<i>P</i>
intercept	-1.37	0.29	-4.70	< 0.001
PC1	-0.51	0.056	-9.12	< 0.001
PC2	-0.45	0.087	-5.10	< 0.001
PC3	-0.31	0.058	-5.34	< 0.001
Habitat type (<i>sheep grazed</i>)	0.48	0.26	1.88	0.060
Habitat type (<i>deer grazed</i>)	0.58	0.42	1.38	0.17
Habitat type (<i>sheep grazed</i>) * PC2	0.54	0.10	5.12	< 0.001
Habitat type (<i>deer grazed</i>) * PC2	0.89	0.24	3.68	< 0.001
Julian day	0.005	0.009	0.63	0.53
<i>Random effects</i>	<i>Variance</i>			
Study site	0.030			
Patch identity:Study site	2.34 x 10 ⁻⁹			

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609 **FIGURES**

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611 **Fig. 1** Map of the 5 principal study sites in central and northern Scotland

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613 **Fig. 2** The probability that a sampled patch was used by a foraging bird as a result of the index of bracken
614 cover (PC1; higher scores denote greater bracken cover) in sheep grazed habitats. The raw observed
615 forage (1) or reference (0) values are represented as open circles (jittered for clearer visibility). Solid lines
616 are the predicted relationships, using median observed values for all other parameters, from the model in
617 table 3. The dotted lines represent the 95% quantiles obtained from N = 1000 simulation draws from the
618 estimated parameters. Predicted relationships are significant and statistically similar for deer grazed and
619 ungrazed habitats (not illustrated)

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621 **Fig. 3** The probability that a sampled patch was used by a foraging bird as a result of the index for tall
622 non-bracken vegetation (PC3; higher scores denote a greater cover of taller herbaceous vegetation and
623 tall grasses and lower moss cover) in sheep grazed habitats. Refer to Fig. 2 for explanations of trend lines
624 and symbols. Predicted relationships are significant and statistically similar for deer grazed and ungrazed
625 habitats (not illustrated)

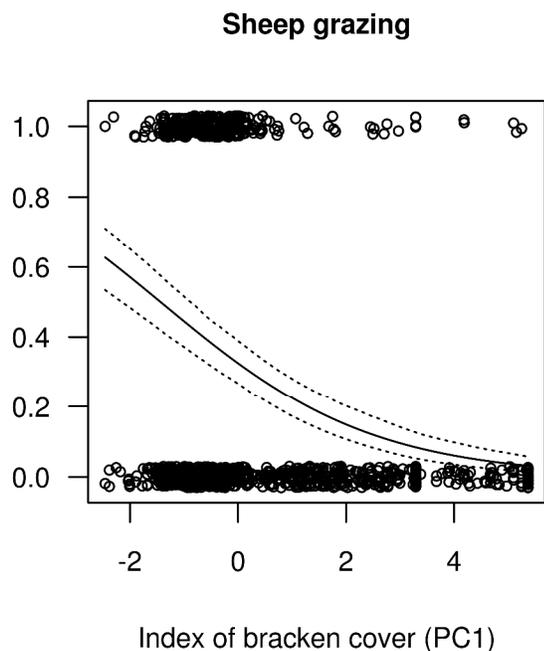
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627 **Fig. 4** The probability that a sampled patch was used by a foraging bird as a result of the index of non-
628 bracken vegetation (PC2; higher scores denote a greater cover of grass at all height levels, lower cover of
629 herbaceous plants at all height levels and a lower ground cover by moss) in sheep grazed, deer grazed
630 and ungrazed habitats. Refer to Fig. 2 for explanations of trend lines and symbols. Note that the
631 relationship in both grazed habitats is non-significant.

632 Fig 1.



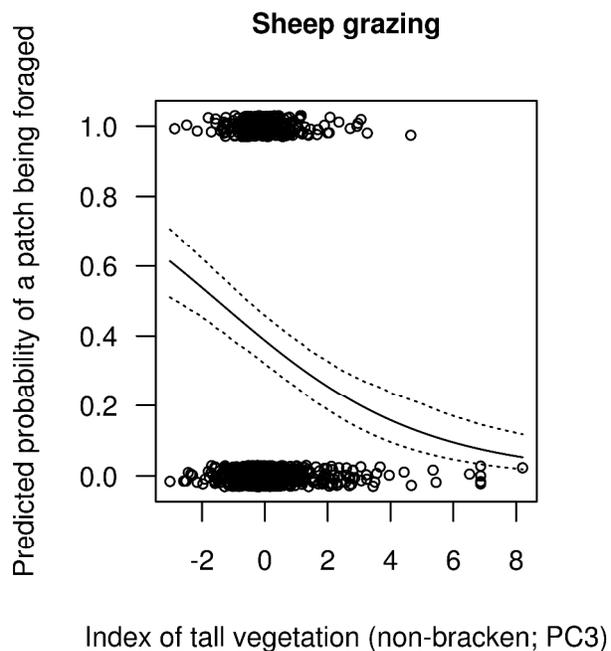
634 Fig. 2



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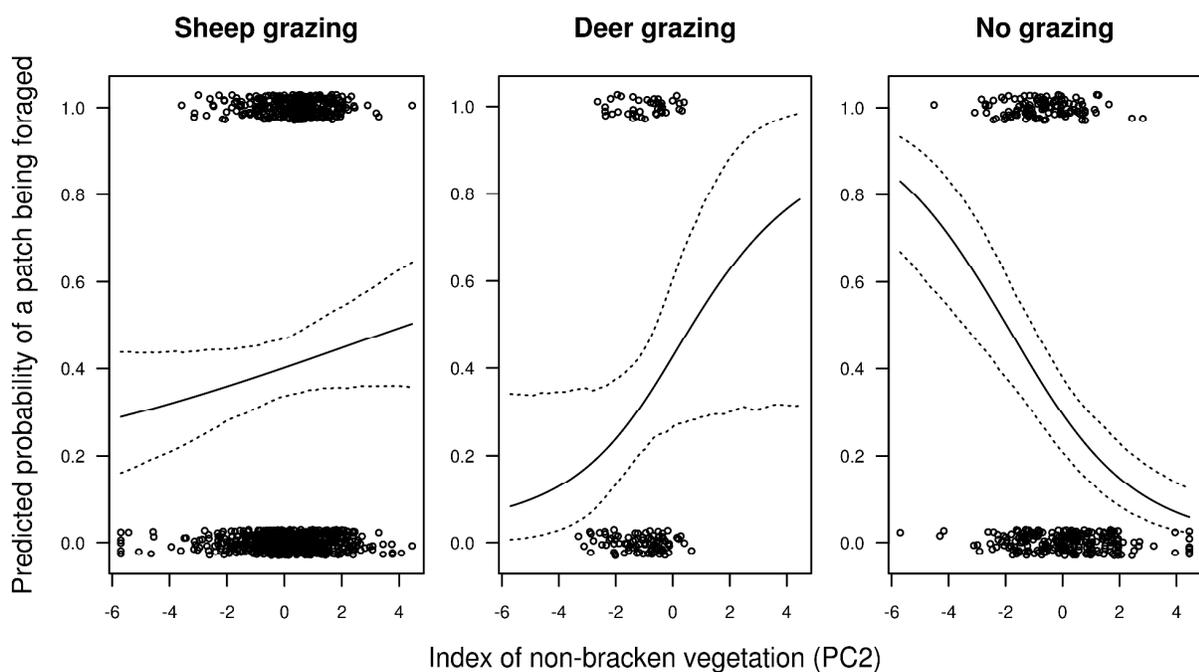
Peer Review

661 Fig. 3



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