

1 **Both habitat change and local lek structure influence patterns of**  
2 **spatial loss and recovery in a black grouse population**

3

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6 **Abstract**

8 Land use change is a major driver of declines in wildlife populations. Where human economic or  
9 recreational interests and wildlife share landscapes this problem is exacerbated. Changes in UK  
10 black grouse *Tetrao tetrix* populations are thought to have been strongly influenced by upland land  
11 use change. In a long-studied population within Perthshire, lek persistence is positively correlated  
12 with lek size, and remaining leks clustered most strongly within the landscape when the population  
13 is lowest, suggesting that there may be a demographic and/or spatial context to the reaction of the  
14 population to habitat changes. Hierarchical cluster analysis of lek locations revealed that patterns of  
15 lek occupancy when the population was declining were different to those during the later recovery  
16 period. Response curves from lek-habitat models developed using MaxEnt for periods with a  
17 declining population, low population, and recovering population were consistent across years for  
18 most habitat measures. We found evidence linking lek persistence with habitat quality changes and  
19 more leks which appeared between 1994 and 2008 were in improving habitat than those which  
20 disappeared during the same period. Generalised additive models (GAMs) identified changes in  
21 woodland and starting lek size as being important indicators of lek survival between declining and  
22 low/recovery periods. There may also have been a role for local densities in explaining recovery  
23 since the population low point. Persistence of black grouse leks was influenced by habitat, but  
24 changes in this alone did not fully account for black grouse declines. Even when surrounded by  
25 good quality habitat, leks can be susceptible to extirpation due to isolation.

27 **Key words:** Conservation • Dispersal • Distribution • Landscape-scale • Land use • Scotland.

29

**30 Introduction**

31

32 Many species occupy human-dominated landscapes (Tharme et al. 2001) but this makes them  
33 potentially vulnerable to changes in land use (e.g., Virani et al. 2011). Identifying species-habitat  
34 associations is an important step towards understanding the species' reaction to land use changes  
35 (Thuiller et al. 2008; Elith and Leathwick 2009). Species-habitat associations can be complex,  
36 particularly for taxa which inhabit mosaic habitats (e.g., Wolff et al. 2002). In these cases, it is not  
37 only the presence of habitat types but also their accessibility and spatial structure which should be  
38 taken into consideration (Law and Dickman 1998). Relationships may differ depending on the  
39 resolution being considered, and so a multi-scale approach can be key to understanding how species  
40 may respond to changes at small scales as well as across the wider landscape (e.g., Geary et al.  
41 2013). During periods of population change, it may also be important to consider connectivity  
42 within the population, as isolation can result in population decline or hinder recolonisation (Hanski  
43 2005).

44

45 In common with many other working landscapes worldwide, the UK uplands have experienced  
46 considerable land use changes in recent times (Warren 2002). The resultant landscape is, for the  
47 most part, far from 'natural' and is maintained by anthropogenic processes (Watson and Moss  
48 2008). Several bird species are known to have declined recently in the UK uplands, with particular  
49 concern over waders (Douglas et al. 2014), and the black grouse, a species which has suffered  
50 severe declines over many parts of Western Europe (Sim et al. 2008; Watson and Moss 2008). It is  
51 known that agricultural and forestry management practices have contributed to some black grouse  
52 declines (Ludwig et al. 2009, Ludwig et al. 2010; Signorell et al. 2010). Grazing pressure, although  
53 lower than its historic maximum, is high in upland areas and has considerable ecological impact

54 (Fuller and Gough 1999). Large, intensive forestry plantations, established during the last century,  
55 initially had some positive impact on black grouse, but the canopy closure which followed produced  
56 a less valuable ecological resource (Fielding and Haworth 1999). As these plantations are now  
57 harvested, the uplands are experiencing further changes some of which may be more sympathetic to  
58 their ecological impact (Warren 2002). Along with these industries, renewable energy schemes  
59 (Drewitt and Langston 2006) and sporting interests (Whitfield et al. 2003) have also made their  
60 mark on the landscape, and have had a considerable impact on a range of species including breeding  
61 waders (Tharme et al. 2001), mammals (Fuller and Gill 2001), invertebrates (Fuller and Gough  
62 1999) and, particularly, birds-of-prey (e.g., Whitfield et al. 2003). As land use and management  
63 changes continue to occur, it is vital that we assess their impacts on species of conservation concern  
64 so that we can mitigate the effect of future changes (Thuiller et al. 2008). In this way, working  
65 landscapes can be beneficial for wildlife as well as the economy (Polasky et al. 2008).

66  
67 We aim to identify the relative importance of habitat and spatial demographic parameters as drivers  
68 of population change for a black grouse population in Scotland that decreased between 1990 and  
69 2000, but then which recovered between 2002 and 2008. Habitat data from 1994, 2000 and 2008 are  
70 used to compare habitat suitability at lek sites from MaxEnt modelling, the expectation being that  
71 leks are more likely to be found in areas where habitat has improved. Changed proportions of  
72 individual habitat types within a black grouse territory may provide further information about lek  
73 losses or gains over time. Black grouse exhibit female biased dispersal and leks are maintained by  
74 female immigration (Lebigre et al. 2010). Although not found to be a significant predictor of  
75 decline by Pearce-Higgins et al. (2007), loss of connectivity between leks could be an additional  
76 factor contributing to lek loss in the region. The number of displaying males at lek sites around each  
77 lek will give information on how well connected leks are to the rest of the population. We use  
78 binomial generalised additive models (GAMs) to model changes in lek occupancy across years

79 (1994–2000, 2000–2008, and 1994–2008) in respect to both habitat differences and demographic  
80 measures.

81

**82 Methods**

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84

## 85 Study Area

86

87 The study area (800 km<sup>2</sup>) surrounds Loch Tummel, Perthshire in Scotland, and is dominated by  
88 managed moorland and forestry. It has been included in two national black grouse surveys  
89 (Hancock et al. 1999; Sim et al. 2008), and has been the focus of previous studies on black grouse  
90 (Pearce-Higgins et al. 2007; Geary et al. 2012 and 2013).

91

92

## 93 Species data

94

95 The locations and numbers of displaying males on leks visited between April and May in each year  
96 1990–2008 were provided by the Perthshire Black Grouse Study Group. The survey method was  
97 very similar to methods used in the national black grouse surveys of Hancock et al. (1999) and Sim  
98 et al. (2008). Surveyors travelled to within 500 m of all suitable habitat, listening for male calls.  
99 Once located, dawn counts were performed on two separate occasions for each lek during the  
100 lekking period and their locations recorded as GPS points (for further details see Hancock et al.  
101 1999; Sim et al. 2008; Geary et al. 2012). Leks which were recorded within 300 m of lek sites in the  
102 previous year were considered to be the same lek. Patterns of black grouse population change in this  
103 area are discussed in Geary et al. (2012).

104

105

## 106 Habitat data

107

108 High quality, satellite images were available for three years during the study period. The three  
109 available years were able to represent decline (1994), the lowest population size (2000), and  
110 recovery (2009) for this population. Landsat images from 1994 (NASA Landsat Program 1994),  
111 2000 (NASA Landsat Program 2000) and 2009 (representing habitat in 2008; NASA Landsat  
112 Program 2009) were used to classify habitat types in the study area. Each image was classified into  
113 six broad habitat types using an unsupervised classification in Multispec (Biehl and Landgrebe  
114 2002). As the satellite images are historical, contemporaneous land cover information was  
115 unavailable, so an unsupervised classification was preferred (Gowda 1984). Habitat categories,  
116 identified using Ordnance Survey maps, aerial photographs and personal knowledge of the study  
117 area were: reduced vegetation cover ('mountainous habitat and urban areas'); agricultural habitat;  
118 moorland; open canopy and mixed woodland; closed canopy woodland; and open water. The  
119 proportions of each habitat type were calculated at a 'lek scale' (0.5 km radius from the lek centre),  
120 and at a 'territory scale' (2.0 km radius from the lek centre), the area likely to be used by black  
121 grouse throughout the year (for feeding and brood rearing; Watson and Moss 2008). These two  
122 scales were chosen after scrutiny of black grouse literature (Watson and Moss 2008; Geary et al.  
123 2013). Altitudinal data were obtained from the Ordnance Survey (OS Landform PROFILE).

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## 126 Patterns of lek occupancy

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128 Patterns of lek presence/absence across years (1990–2008) were investigated using Ward's  
129 hierarchical cluster analysis (Ward 1963) to group years according to how similar their lek  
130 occupancy patterns were. Years which were temporally close were expected to be more similar and

131 this was investigated by plotting the Euclidean distance between similarity of occupancy patterns  
132 against temporal distance between years.

133

134

135 Habitat suitability and changes in lek occupancy and size

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137 For each of 1994, 2000 and 2008, habitat suitability was assessed using the machine learning,

138 presence-only method MaxEnt (Phillips et al. 2006). MaxEnt is suitable in this case because

139 confirmed absence data were unavailable. The method has been shown to be effective in

140 characterising habitat suitability in a number of conservation situations and can outperform both

141 presence/absence and other presence-only methods of habitat suitability modelling (e.g., Elith and

142 Graham 2009).

143

144 MaxEnt models were constructed at two spatial resolutions, representing the lek (0.5 km) and

145 territory (2.0 km) habitat (Watson and Moss 2008; Geary et al. 2013) around leks for each of the

146 three years, using the default values (convergence threshold =  $10^{-5}$ ; maximum iterations = 500;

147 background points = 10,000) and 'auto features' selected allowing the fitted functions to take any of

148 the available forms. Models were run with ten cross-validated replicates. Cross-validation was

149 preferred to other replication methods, due to the relatively small size of the presence dataset ( $n =$

150 71 in 1994 and 2008;  $n = 56$  in 2000), so that each presence record could be used for both training

151 and testing of the models (Elith et al. 2011). Differences between MaxEnt models across years were

152 assessed visually by comparing partial response curves, which avoid any problems of

153 multicollinearity by showing the relationship between relative suitability and a single variable while

154 controlling for the effects of the others (Zuur et al. 2007).

155

156 We built a contingency table of potential changes in habitat suitability across years (suitable area  
157 remains suitable, unsuitable area remains unsuitable, suitable area becomes unsuitable, unsuitable  
158 area becomes suitable) versus change in lek presence (lek disappeared, lek established) and tested  
159 observed against expected with chi-square tests. Categories for each lek were calculated by  
160 reclassifying output maps from the 1994 MaxEnt model projected onto habitat in 1994, 2000 and  
161 2008. Rather than a binary threshold we used a range of values which we considered to be  
162 ‘marginal habitat’. This was decided to be a range  $\pm 0.1$  around the value which maximises the sum  
163 of sensitivity and specificity (0.5 km = 0.3, 2.0 km = 0.2). This was done because there is no single  
164 value which determines the boundary between ‘suitable’ and ‘unsuitable’ habitat but rather we tried  
165 to capture the direction of change into a ‘zone’ where small habitat quality differences may reflect  
166 well the probability of habitat actually holding a lek. Leks which were unsuitable in the first of the  
167 two years which were then found within this range in later years were considered to have become  
168 suitable, and leks which were considered suitable in the first of the two years which were found  
169 within this range in later years were considered to have become unsuitable.

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171

172 Modelling lek occupancy based on habitat and demographic changes

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174 Models were designed to distinguish between leks which were present in both of a pair of years:  
175 1994 and 2000 (period of population decline); 1994 and 2008 (entire study period), and; 2000 and  
176 2008 (population recovery) from those present in the first of the two years, but which subsequently  
177 disappeared. Predictor variables were the change in the proportions of three habitats known to be  
178 most important to black grouse: moorland, open canopy/mixed woodland and closed canopy  
179 woodland (Geary et al. 2013), plus two demographic variables. These were lek size in the first of  
180 the two years, and, to represent connectivity between leks, the density of black grouse males within

181 a 15.0 km radius of each lek scaled for population size (i.e., density of nearby males divided by total  
182 population size in that year). A 15.0 km radius was chosen as it is larger than the mean natal  
183 dispersal distance reported by Caizergues and Ellison (2002), although smaller than the maximum  
184 dispersal distance.

185

186 We used binomial GAMs (Zuur et al. 2007), which do not assume linear relationships between the  
187 probability of lek persistence and habitat features. To fit these models we used the ‘mgcv’ package  
188 (Woods 2011). Previous research indicates that a range of habitat combinations in different  
189 proportions can be beneficial for black grouse (Pearce-Higgins et al. 2007; Geary et al. 2013). Due  
190 to strong collinearity ( $r_s > 0.5$ ) between change in closed canopy forestry and change in open  
191 canopy forestry in the 1994–2000 data, the former was omitted from the 0.5 km model (Freckleton  
192 2010). Similarly, change in proportion of moorland was omitted from the 1994–2008 model from  
193 both the 0.5 km and 2.0 km models (strong correlation with both forestry measures).

194

195 Spatial autocorrelation of persistence among lek locations was assessed after model fitting using  
196 Moran's I correlograms on model residuals, however, none was detected, so the models did not  
197 require a spatial error term. For each predictor variable in each model, the optimum number of  
198 knots to be used in smoothing was calculated by including that single predictor in a model and  
199 selecting the number of knots with the lowest Akaike's Information Criterion (AIC) value.

200

201 For each period, all combinations of the predictor variables were considered and the best model  
202 combination selected using AIC-based methods (the model with the lowest AIC value or, if  $\Delta\text{AIC} <$   
203 7.0, the highest Akaike weight and comparison of evidence ratios; Burnham and Anderson 2002;  
204 Burnham et al. 2011). To identify variables most likely to be included in best models, relative  
205 Akaike variable weights were calculated (combined Akaike weight of all models including that

206 variable divided by the sum of all Akaike model weights) using model averaging in the ‘MuMIn’  
207 package in R (Grueber et al. 2011; Barton 2013). All analyses were performed in R 3.0.2 (R Core  
208 Team 2013).

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211

212 **Results**

213

214

## 215 Patterns of lek occupancy

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217 Two main clusters of lek occupancy patterns emerged, with annual patterns pre–2003 distinct from  
218 those in later years (Fig. 1). The larger cluster (1990–2003) was further split, with lek patterns in the  
219 period 1997–2002 relatively distinct from those of the earlier years. Years which were temporally  
220 closer to each other were more similar in terms of their occupancy pattern when measured by  
221 Euclidean distance.

222

223

## 224 Habitat suitability and changes in lek occupancy and size

225

226 Habitat suitability models using lek locations and habitat in 1994, 2000 and 2008 (Fig. 2) were all  
227 successful at predicting relative habitat suitability, with  $AUC > 0.8$  for all models (AUC scores  
228 above 0.7 indicate a 'good' model; Fielding and Bell 1997). Altitude was an important predictor in  
229 all three years (mean contribution 48.3 %; SD 14.5%) along with the proportion of grouse moor  
230 (mean contribution 23.7%; SD 6.3%). Open canopy/mixed forestry was more important in the 2008  
231 models (per cent contribution to MaxEnt models at 0.5 and 2.0 km radii was 16% and 11%  
232 respectively). The response curves relating habitat suitability to proportions of individual habitat  
233 types were similar across the three models (Fig. 3). Only plantation forestry showed a markedly  
234 different relationship with suitability in 1994.

235

236 The proportion of leks appearing between 1994 and 2000 that appeared in areas of improving  
237 habitat (those with an increase in MaxEnt suitability score) or good habitat, was no different to the  
238 proportion of leks that disappeared from areas of improving habitat during the same period using a  
239 0.5 km radius ( $\chi^2 = 6.7, n = 70, df = 3, P = 0.08$ ), but significantly more leks appeared in areas of  
240 good or improved habitat at a 2.0 km radius ( $\chi^2 = 9.7, n = 70, df = 3, P = 0.02$ ). A greater proportion  
241 of leks which appeared between 1994 and 2008 were in good or improving areas than the  
242 proportion which disappeared from improving habitat during the same period using a 0.5 km radius  
243 ( $\chi^2 = 15.2, n = 106, df = 3, P = 0.002$ ), but not a 2.0 km radius ( $\chi^2 = 6.6, n = 106, df = 3, P = 0.09$ ).  
244 Significantly more leks appeared in good or improving habitat than disappeared between 2000 and  
245 2008 at the 0.5 km radius ( $\chi^2 = 9.4, n = 84, df = 3, P = 0.02$ ), but there were no significant  
246 associations at the 2.0 km radius ( $\chi^2 = 3.3, n = 84, df = 3, P = 0.35$ ).

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249 Models of lek occupancy based on habitat and demographic changes

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251 The 'best' models using a 0.5 km radius for 1994–2000 ( $n = 84$ , Dev. Exp = 20.1%), 2000–2008 ( $n$   
252 = 56, Dev. Exp = 48.1%) and 1994–2008 ( $n = 84$ , Dev. Exp = 36.8%), included initial lek size as a  
253 predictor (details of all models and evidence ratios between 'best' models are given in the Electronic  
254 Supplementary Material (ESM)). Deviance explained is the proportion of the null deviance  
255 explained by the model (Woods 2011). Additionally, open canopy forestry was an important  
256 predictor for the 1994–2000 and 1994–2008 models, but was less important for 2000–2008. Initial  
257 lek size had high Akaike variable weights in both the 1994–2000 and 1994–2008 models, as did  
258 change in open canopy forestry and the density of nearby displaying males, with lek persistence  
259 being associated with decreases in open canopy forestry and large lek starting sizes (Fig. 4a & b).  
260 For the 2000–2008 model, lek connectivity had the highest Akaike weight (Table 2), with high

261 connectivity being associated with lek persistence (Fig. 4c). Larger, better-connected leks, and those  
262 areas experiencing both large decreases and small increases in moorland habitat, were those most  
263 likely to remain in 2008.

264

265 At the 2.0 km radius, the best models (see ESM for details) for 1994–2000 ( $n = 84$ , Dev. Exp =  
266 15.4%), 2000–2008 ( $n = 56$ , Dev. Exp = 61.3%) and 1994–2008 ( $n = 84$ , Dev. Exp = 35.8%), also  
267 included initial lek size as a predictor (Fig. 5). Initial lek size had the highest relative importance, as  
268 measured by Akaike weight, from the predictors in the 1994–2000 and 1994–2008 models. In the  
269 1994–2008 model, change in the proportion of close canopy forestry was equally important, with  
270 change in the proportion of open canopy forestry relatively high in importance, too. In the 2000–  
271 and 2008 model, however, the variables with the highest relative importance were density of nearby  
272 displaying males and the change in the proportion of moorland.

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276 **Discussion**

277

278 Although black grouse range in Britain has contracted considerably since the 19th century, our  
279 results indicate the relative stability of habitat requirements in this upland mosaic, over several  
280 decades of population change, and the importance of landscape connectivity to population recovery.  
281 Changes in habitat suitability went some way to explaining differences between lek locations across  
282 time; in the recovery period new leks appeared in areas of improved habitat. However, habitat  
283 suitability alone did not fully explain changes to lek locations and lek growth was not well  
284 explained by changing habitat suitability. Instead, our results highlight the importance of spatial  
285 social factors to black grouse populations and are supported by increased levels of spatial clustering  
286 of lek sites during the recovery period (Geary et al. 2012). The importance of connectivity in  
287 maintaining populations has been shown for a number of taxa (Hanski 2005), with loss of  
288 connectivity being particularly detrimental when habitat is fragmented and population size is low  
289 (Proctor et al. 2005).

290

291 Our analyses show that this black grouse population had variable occupancy patterns within the  
292 landscape at different times during the study period. Spatial social factors, such as locations and  
293 size of breeding sites, have previously been shown to be important drivers of population changes in  
294 birds (Serrano et al. 2004). Indeed, an attraction towards conspecifics such as at breeding sites is not  
295 always of benefit to the individual (Cardador et al. 2012); large leks in poor quality habitat might  
296 have low reproductive rates (Baines et al. 2007) but still be attractive to natally-dispersing birds,  
297 therefore would effectively function as population sinks (e.g., Lane and Alonso 2001). Dispersal in  
298 black grouse is female-biased and generally occurs during their first year (Watson and Moss 2008).  
299 Caizergues and Ellison (2002) found a mean dispersal distance of 8 km and that dispersal distance

300 can be up to 30 km. Monitoring of radio-tracked females by Warren and Baines (2002) found that  
301 no natively-dispersing birds settled to breed within their 15 km<sup>2</sup> study area, suggesting that the area  
302 required for full connectivity between leks could be large.

303

304 In our study, there was only a slight shift in response to one habitat type over time. Areas with  
305 higher proportions of plantation forestry (a transitional habitat before canopy closure; Fielding and  
306 Haworth 1999) were considered more suitable in 1994 than in later years. In later years, there were  
307 higher proportions of mature conifer stands with full canopy closure in the study area, and these  
308 stands are known to be associated with black grouse population decline (Pearce-Higgins et al.  
309 2007). During recovery, leks were found in areas where the habitat adjacent to potential lek sites  
310 had improved at the 'lek scale' rather than at the territory scale, suggesting that protecting display  
311 sites as well as the habitat mosaic is important for black grouse conservation. Black grouse are  
312 known to have different habitat requirements depending on the scale considered (Geary et al. 2013)  
313 and, indeed, may be affected by different land use drivers at these different scales. Our results also  
314 indicate the importance of the landscape scale, to maintain connectivity within the black grouse  
315 population. This points to the importance of considering species conservation at multiple scales as  
316 has been found in other species, such as the grey long-eared bat (*Plecotus austriacus*; Razgour et al.  
317 2011), and highlights the applications of multi-scale planning in conservation actions (e.g., Cabeza  
318 et al. 2010).

319

320 Habitat management/provision around lek sites will no doubt play a key role in maintaining black  
321 grouse populations in this region (Pearce-Higgins et al. 2007; Geary et al. 2013), but we present  
322 evidence that demographic effects also have an additional role to play in determining relationships  
323 between habitat quality and population size. For species such as black grouse, which have spatially  
324 complex populations, it is vital to consider connectivity between territories when considering

325 conservation actions (Wiegand et al. 2005). Future conservation actions for black grouse  
326 populations in landscapes such as our study area should not only aim to improve habitat quality in  
327 the form of mosaics at a range of spatial scales, but also to maintain or improve the spatial  
328 functionality of the population at a landscape scale.

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330

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332

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454 **Table 1:** Contingency tables for chi-square tests on leks which appeared (gain) and disappeared  
 455 (loss) between each pair of years in habitat which remained unsuitable, was marginal and  
 456 declined in suitability, was marginal and increased in suitability and remained suitable.

457

<b>Radius</b>	<b>Gain/loss</b>	<b>Remained unsuitable</b>	<b>Marginal - decreasing</b>	<b>Marginal - improving</b>	<b>Remained suitable</b>
1994 - 2000					
0.5 km	Gain	2	5	8	6
	Lost	7	14	25	3
2.0 km	Gain	0	4	9	8
	Lost	2	17	26	4
1994 - 2008					
0.5 km	Gain	0	14	20	11
	Lost	15	19	21	6
2.0 km	Gain	1	13	25	6
	Lost	7	24	27	3
2000 - 2008					
0.5 km	Gain	1	13	23	11
	Lost	3	16	16	1
2.0 km	Gain	0	14	26	5
	Lost	1	8	10	1

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461 **Table 2.** Relative Akaike weights (variable Akaike weight divided by sum of all variable Akaike  
 462 weights) for logistic GAMs predicting black grouse presence/absence from habitat (at a radius of  
 463 0.5 km from the lek centre) and demographic changes between 1994–2000, 1994–2008, and 1994–  
 464 2008. The variables are referred to in the table as follows: starting lek size as ‘Size’, change in the  
 465 proportion of open canopy forestry within 0.5 km as 'Open canopy', change in the proportion of  
 466 moorland within 0.5 km as 'Moorland', change in the proportion of closed canopy forestry within  
 467 0.5 km as 'Closed canopy' and the density of lekking males within 15.0 km scaled for population  
 468 size in each year as 'Local density'. A dash indicates that the variable in question was not used in  
 469 model fitting.

Variable	Relative Akaike weight					
	1994–2000		2000–2008		1994–2008	
	<i>0.5 km</i>	<i>2.0 km</i>	<i>0.5 km</i>	<i>2.0 km</i>	<i>0.5 km</i>	<i>2.0 km</i>
Size	0.9	0.9	0.6	0.9	1.0	1.0
Local density	0.5	0.5	1.0	1.0	0.5	0.5
Moorland	0.5	0.4	1.0	1.0	-	-
Open	0.6	0.3	0.4	0.7	1.0	0.7
Closed	-	0.4	0.4	0.7	0.9	1.0

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474 **Figures**

475

476 **Figure 1** Dendrogram showing the results of Ward's method of hierarchical clustering on  
477 presence/absence of birds at lek locations from 1990–2008 in Perthshire Scotland. The y axis  
478 indicates a measure of difference, according to Ward's method, between leks according to the  
479 distance between them on the dendrogram.

480

481 **Figure 2** Lek locations (black filled circles) and habitat types in (a) 1994, (b) 2000, and (c) 2008.

482

483 **Figure 3** Response curves from MaxEnt models predicting black grouse presence from the  
484 proportion of habitat at a radius of 0.5 km and 2.0 km from the lek centre. Percentage contributions  
485 of each variable to Maxent models for 1994, 2000 and 2008 respectively are given in brackets.  
486 Response curves are from models based on a 0.5 km radius from the lek centre for a) grazed land  
487 (0.8, 1.6, 1.6), b) grouse moor (25.3, 23.3, 24.2), c) open canopy forestry (1.9, 3.3, 14.5) and d)  
488 closed canopy forestry (0.2, 0.9, 4.8), and a radius of 2.0 km from the lek centre for e) grazed land  
489 (5.9, 2.9, 6.8), f) grouse moor (11.7, 28.2, 29.2), g) open canopy forestry (6.8, 6.2, 10.8) and h)  
490 closed canopy forestry (5.9, 10, 18.2) around lek sites in 1994 (solid line), 2000 (dashed line) and  
491 2008 (dotted line).

492

493 **Figure 4** Plots of each habitat or demographic variable along with the contribution of the smooth  
494 component to each variable for GAMs (solid line) along with 95% confidence intervals (dashed  
495 line) predicting black grouse presence/absence from habitat (at a radius of 0.5 km) and demographic  
496 changes between 1994–2000 for a) starting lek size in 1994, and b) the proportion of open canopy

497 forestry within 0.5 km, between 2000–2008 for c) starting lek size in 1994, d) the proportion of  
498 moorland within 0.5 km, and e) the density of displaying males within 15.0 km in 1994 and  
499 between 1994–2008 for f) starting lek size in 2000, g) the proportion of open canopy forestry within  
500 0.5 km, and h) the proportion of closed canopy forestry within 0.5 km.

501

502 **Figure 5** Plots of each habitat or demographic variable along with the contribution of the smooth  
503 component to each variable for GAMs (solid line) along with 95% confidence intervals (dashed  
504 line) predicting black grouse presence/absence from habitat (at a radius of 2.0 km) and demographic  
505 changes between 1994–2000 for a) starting lek size in 1994, b) and between 2000 and 2008 for  
506 b) starting lek size in 1994, c) the proportion of open canopy forestry within 2.0 km, d) the  
507 proportion of closed canopy forestry within 2.0 km and e) the proportion of moorland within 2.0 km  
508 and f) the density of displaying males within 15.0 km in 1994 and 1994–2008 for g) starting lek size  
509 in 2000, h) the proportion of open canopy forestry within 2.0 km, i) the proportion of closed canopy  
510 forestry within 0.2 km, and j) the density of displaying males within 15.0 km in 1994 .

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