

1 **Breeding ground correlates of the distribution and decline of the Common Cuckoo**  
2 ***Cuculus canorus* at two spatial scales**

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20 **Running head:** Breeding ground correlates of Cuckoo declines

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22 **Keywords:** distribution shift, Dunnock, Meadow Pipit, moth caterpillars.

23

24 Many migratory bird species are undergoing population declines as a result of potentially multiple,  
25 interacting mechanisms. Understanding the environmental associations of spatial variation in  
26 population change can help tease out the likely mechanisms involved. Common Cuckoo *Cuculus*  
27 *canorus* populations have declined by 75% in England, but increased by 29% in Scotland. The  
28 declines have mainly occurred in lowland agricultural landscapes, but their mechanisms are  
29 unknown. At both the local scale within the county of Devon (SE England) and at the national (UK)  
30 scale, we analysed the breeding season distribution of Cuckoos in relation to habitat variation, the  
31 abundance of host species and the abundance of moth species whose caterpillars are a key food of  
32 adult Cuckoos. At the local scale, we found that Cuckoos were more likely to be detected in areas  
33 with more semi-natural habitat, more Meadow Pipit *Anthus pratensis* (but fewer Dunnock *Prunella*  
34 *modularis*) and where, later in the summer, higher numbers of moths were captured whose larvae  
35 are Cuckoo prey. Nationally, Cuckoos have become more associated with upland heath characterised  
36 by the presence of Meadow Pipit hosts, and with wetland habitats occupied by Eurasian Reed  
37 Warbler *Acrocephalus scirpaceus* hosts. The core distribution of Cuckoos has shifted from south to  
38 north within the UK. By the end of 2009, the abundance of macro-moth species identified as prey  
39 has also declined four times faster than that of species not known to be taken by Cuckoos. The  
40 abundance of these moths has shown the sharpest declines in grassland, arable and woodland  
41 habitats and has increased in semi-natural habitats (heaths and rough grassland). Our correlative  
42 data suggest that Cuckoos are likely to remain a very scarce bird in lowland agricultural landscapes  
43 without large scale changes in agricultural practices.

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47 Many long-distance, migratory birds are in long-term decline (Robbins *et al.* 1989, Sanderson *et al.*  
48 2006, Vickery *et al.* 2014, Bairlein 2016). Reversing such population declines is a major nature  
49 conservation challenge and involves identifying and addressing the underlying causes (Caughley  
50 1994). This is often not straightforward, as there may be multiple interacting mechanisms operating  
51 on breeding or wintering grounds or on migration routes (Vickery *et al.* 2014). These include the  
52 effects of climate change, which are manifested through the impact of changing temperature on  
53 physiology (Şekercioğlu *et al.* 2012), on laying dates in breeding grounds (Ockendon *et al.* 2013), on  
54 the mismatch between timing of food requirements and food availability (Both *et al.* 2010), and  
55 through the effects of rainfall on seasonal resources in wintering grounds (Ockendon *et al.* 2014).  
56 Other mechanisms affecting migratory birds include habitat loss and fragmentation in breeding and  
57 non-breeding areas (Vickery *et al.* 2014), reduced food abundance in breeding areas (Townsend *et*  
58 *al.* 2016, Bairlein 2016), hunting and predation during migration (Lehikoinen *et al.* 2011) and  
59 possible increases in deleterious effects of competitors, parasites and pathogens (Fuller *et al.* 2012),  
60 Wittmer *et al.* 2015).

61 Obligate brood parasite such as the Common Cuckoo *Cuculus canorus* (henceforth, 'Cuckoo')  
62 face an additional challenge, as the impacts of environmental change on both the brood parasite  
63 and its host must be considered. The Cuckoo has declined by 27% across Europe over the period  
64 1980-2015 (www.ebcc.info), but in the UK, the overall decline is more severe, with a 43% decline  
65 between 1994 and 2014 (Harris *et al.* 2016). However, there is spatial variation in these trends.  
66 Harris *et al.* (2016) found that population declines were most severe and long-term in England (75%  
67 between 1967 and 2014, and 68% between 1995 and 2014), whereas, by contrast, there has been a  
68 recent increase in Scotland (29% between 1995 and 2014). This pattern has also been found in a  
69 range of other migratory bird species (Ockendon *et al.* 2012, Morrison *et al.* 2013, Morrison *et al.*  
70 2016). Recent trends are also habitat-specific. In lowland farmland habitats, where the Dunnock  
71 *Prunella modularis* is the main host species, rates of decline have exceeded the overall mean, whilst  
72 there has been little change since the 1990s in wetland and semi-natural grassland and heathland  
73 habitats where Eurasian Reed Warbler *Acrocephalus scirpaceus* and Meadow Pipit *Anthus pratensis*,  
74 respectively, are the main host species (Brooke & Davies 1987, Newson *et al.* 2009, Robinson *et al.*  
75 2015).

76 The causes of Cuckoo population declines remains unknown (Thorogood & Davies 2013).  
77 Changing conditions on the equatorial African wintering rounds and increasing phenological  
78 mismatch with the timing of breeding of host species have been suggested, but there is no strong  
79 empirical evidence that either of these mechanisms is playing a significant role (Saino *et al.* 2009,  
80 Douglas *et al.* 2010, Ockendon *et al.* 2012). Evidence of a possible driver of decline outside the

81 breeding grounds derives from recent satellite tagging of 42 adult male Cuckoos breeding in the UK  
82 over a four year period, which has revealed two distinct autumn migratory routes to a common  
83 equatorial wintering area (Hewson *et al.* 2016). Birds following a more westerly route (via the  
84 Iberian peninsula, and the western side of the Sahara) had a significantly higher mortality probability  
85 than birds following a more easterly route (via Corsica, Italy or Greece, and the central Sahara), but  
86 only during the phase of migration between leaving the UK and crossing the Sahara, with excess  
87 mortality tending to occur in Spain. Notably, birds following this apparently riskier migration route  
88 are more likely to have bred in lowland, southern and eastern areas of the UK where long-term  
89 population declines have been greatest (Hewson *et al.* 2016).

90 In this paper, we compliment these previous studies by analysing correlates of spatial  
91 patterns of change in Cuckoo populations on the UK breeding grounds. Cuckoos have declined  
92 particularly in the UK's lowland agricultural landscapes where the impacts of agricultural  
93 intensification have caused serious population declines of a wide range of breeding birds (Donald *et al.*  
94 *al.* 2001, Newton 2004, Wilson *et al.* 2009). Moreover, adult Cuckoos prey upon large invertebrates  
95 that are known to be highly sensitive to agricultural intensification (Wilson *et al.* 1999). These  
96 include lepidopteran larvae, notably of large, aposematic, hairy species avoided by other birds, or  
97 smaller species which can be found aggregated in high numbers (e.g. some Geometridae and  
98 Pieridae), as well as some adult beetles (e.g. Scarabeidae and Chrysomelidae), grasshoppers and  
99 odonates (Wyllie 1981, Cramp 1985). This relative dependence on large-bodied invertebrates and,  
100 especially, large caterpillars highlights the importance of gaining a greater understanding of the  
101 extent to which Cuckoo declines may be associated with changes in the abundance of their prey.

102 We worked at two scales, local and national, to analyse the distribution of Cuckoos in  
103 relation to habitat variation, the abundance of host species and the abundance of moth  
104 (Lepidoptera) species, whose caterpillars are a key food of adult Cuckoos (Wyllie 1981, Cramp 1985).  
105 Specifically, we address the following hypotheses and predictions:

106

107 H1. At a national scale, Cuckoos' habitat associations have changed over the period of  
108 population decline (1995-2010), with the probability of detecting Cuckoos becoming more  
109 positively associated with suitable semi-natural habitats and the hosts which characterise  
110 those habitats (Reed Warbler and Meadow Pipit), and less positively (or negatively)  
111 associated with intensively managed agricultural habitats and the hosts which most  
112 characterise these habitats (Dunnock).

113 H2. At a local scale, cuckoos are more likely to be associated with semi-natural habitats and  
114 the abundance of Meadow Pipits.

115 H3. Moth species whose caterpillars are known to be preyed upon by Cuckoos have declined  
116 nationally over the long-term at a greater rate than those not known to be Cuckoo prey and  
117 abundance trends of moth species preyed on by Cuckoos differs between habitat types.  
118 H4. The presence of territorial Cuckoos locally is associated with higher abundance of moth  
119 species whose larvae are exploited as prey by adult Cuckoos.

120

## 121 **METHODS**

122

### 123 **Local Scale**

#### 124 *Field data collection*

125 We chose the county of Devon as our study area as Cuckoos were recorded in 81% of 2 km tetrads ( $n$   
126 = 1,858) in 1977-1985 (Sitters 1988), but this occupancy had declined to 18% by 2007-2013, with  
127 distribution increasingly limited to the semi-natural heathland habitats of the Dartmoor and Exmoor  
128 National Parks (Fig. 1; Beavan & Lock 2016). We used the Centre for Ecology and Hydrology's Land  
129 Cover Map 2000 (LCM2000) data (Fuller *et al.* 2002) to select all 1 km squares which had no more  
130 than 10% cover of unsuitable habitat (water, bare rock and sediment, saltmarsh, and built habitats)  
131 and contained 10-30% woodland cover, recognising that Cuckoos require trees and other vantage  
132 points to parasitize hosts (Øien *et al.* 1996, Roskaft *et al.* 2002, Fuller *et al.* 2007). 1x1 km squares  
133 were selected to account for the more fragmented nature of habitats in the area. Using these  
134 criteria, 223 potential 1 km squares were identified across Devon. These were then ranked by semi-  
135 natural habitat cover (Table S1) and divided into five evenly sized groups. Nine sites were then  
136 randomly selected from each group to give a total sample of 45 squares. Each site was surveyed to  
137 estimate Cuckoo presence and measure host abundance.

138 Cuckoo surveys took place during daylight hours by one observer (CD) at the centre of each  
139 1x1 km square in May and June 2012. Adult male Cuckoos respond well to playback recordings  
140 (Wyllie 1981), so we played an amplified recording of a male Cuckoo song for one minute towards  
141 each of the four cardinal points. The recording was audible to an observer over 200 m. After playing  
142 the song, the observer waited for 15 minutes for a response. One survey was conducted per square  
143 and surveys were not conducted in high winds (Beaufort scale 5 or above) or heavy rain. The main  
144 potential Cuckoo hosts in this area, Meadow Pipits and Dunnocks, were also counted once in each  
145 square along two parallel 1 km transects, 500m apart, in late April or early May, using standard  
146 Breeding Bird Survey (BBS) techniques (Harris *et al.* 2016).

147 Moths were sampled once between late June and the end of July, using Ranger traps fitted  
148 with 40W actinic bulbs, run from a 12V battery. This timing was designed to coincide with the flight

149 period of those moths whose larvae are preyed upon by adult Cuckoos on return to the breeding  
150 grounds. Four moth traps were placed, one in each of four main available habitat types (semi-  
151 natural grassland, heath, improved grassland and arable) in each square where all these habitats  
152 were present. Where only three habitats were present, then a second trap was placed in the  
153 dominant habitat by area, where two habitats were present then two traps were placed in each, and  
154 in one square where only one habitat was present, all four traps were placed in that habitat. Traps  
155 were always placed >50m away from the nearest habitat edge and 100m from the nearest other  
156 trap (Dodd *et al.* 2008) to reduce the risk that one trap influenced the catch rate of another. Exactly  
157 as for bird surveys, no trapping took place in heavy rain or strong wind. The total count of all macro-  
158 moths caught and, secondly, the total count of all those species whose caterpillars have been  
159 identified as Cuckoo prey (Table 1) were used as response variables in subsequent analyses. A  
160 temperature logger was attached to each trap to record minimum air temperature (°C) on the  
161 trapping night, and wind speed was recorded (Beaufort scale) when the trap was set at dusk. In  
162 total, moths were trapped in 21 of the 45 squares where it was possible to locate traps according to  
163 the criteria described above and where overnight trapping was secure and permitted by the  
164 landowner.

165

#### 166 *Data analysis*

167 First, we modelled the probability of Cuckoo detection (1) or non-detection (0) in the 45 study  
168 squares as a function of their habitat composition and host abundances using a Generalized Linear  
169 Model (GLM), and specifying a binomial error distribution. To do this, we added 0.01 to all mean  
170 counts of Dunnocks and Meadow Pipits (to allow zero counts to be transformed) and  $\log_e$ -  
171 transformed these counts (lnD and lnMP) as the two measures of host abundance. The proportion  
172 of the square covered by each of semi-natural grassland (SNG), heathland (HEATH), arable farmland  
173 (ARABLE), and agriculturally improved, sown grasslands (GRASS), as derived from LCM 2000 data  
174 (Table S1) were the four measures of habitat composition. However, all six variables showed  
175 moderate or high collinearity (Pearson's  $r$  for pairwise correlation coefficient > 0.5 for at least one  
176 pairwise correlation for every variable) so we carried out a Principal Components Analysis. The first  
177 two principal components had Eigenvalues >1 (PC1 - Eigenvalue = 3.40, proportion of variance  
178 explained = 0.567; PC2 – Eigenvalue = 1.11, proportion of variance explained = 0.185), so these two  
179 components were taken forward as explanatory variables in a final model in which both were fitted.  
180 The partial correlation coefficients (Table 2) show that PC1 describes a gradient from squares rich in  
181 semi-natural habitats and with higher densities of Meadow Pipits and lower densities of Dunnocks  
182 (high values) to squares rich in agriculturally improved grasslands with lower densities of Meadow

183 Pipits and higher densities of Dunnocks (low values). PC2 describes a gradient between squares  
184 where the agriculturally improved component is dominated by grassland to those where it is  
185 dominated by arable crops.

186 Secondly, we modelled moth abundance as a function of whether or not Cuckoos had been  
187 detected in the square during playback surveys in the subset of 21 squares in which moth trapping  
188 took place. We again used a GLM, and specified a Poisson error distribution whilst correcting  
189 denominator degrees of freedom for overdispersion using DSCALE in SAS9.4 (SAS Institute Inc.  
190 2014). Cuckoo detection, or not, during the prior playback session in the square was recorded as a  
191 binary categorical variable (CKDET). We also included minimum air temperature recorded on the  
192 night of moth trapping (MINAIR) and wind speed (WIND) because we expected that these weather  
193 conditions would be confounding effects on the number of moths caught. The best-approximating  
194 model was identified by fitting all seven possible models and finding the model which minimised  
195 AICc.

196

## 197 **National scale**

### 198 *Data preparation*

199 At a national scale, we used data from the UK Breeding Bird Survey (BBS) and Rothamsted Insect  
200 Survey (RIS) light trap network in conjunction with Land Cover Map (LCM) data. The BBS is based on  
201 a random sample of 1 x 1 km squares across the UK, within which volunteer observers carry out two  
202 breeding season visits (one between early April and mid-May, and one between mid-May and late  
203 June) and record birds along two 1 km transects (Harris *et al.* 2016). Specifically, we extracted BBS  
204 data for Cuckoos and the three main host species for two time periods, 1995-1999 ( $n = 2767$ ) and  
205 2006-2010 ( $n = 4101$ ), to examine correlates of change in Cuckoo presence and abundance over this  
206 15-year period. Separately for each time period, for each square, the detection (1) or non-detection  
207 (0) of at least one adult Cuckoo during the years in which a square was surveyed was used as the  
208 response variable in models. The first (April – May) count of each host species was used as an  
209 explanatory variable to reduce the risk of young birds affecting counts, and the mean count was  
210 calculated, for each time period, over all years in which a square was surveyed. Given that territorial  
211 Cuckoos may range over several kilometres (Wyllie 1981), we then measured the habitat  
212 composition of each BBS square plus its surrounding buffer of eight squares (i.e. a 3 km square in  
213 total) using the LCM 1 km raster data set for both 2000 (target year 1998, Fuller *et al.* 2002) and  
214 2007 (target year 2007, Morton *et al.* 2011). These two data sets were the best available matches in  
215 time to the two BBS periods. The 1 km raster data set provides a measure of the coverage of each 1  
216 km square by each of 26 (LCM2000) or 23 (LCM2007) land cover categories, but we pooled these

217 into seven explanatory variables: woodland (WOOD), semi-natural grassland (SNG), heathland  
218 (HEATH), arable farmland (ARABLE), agriculturally improved, sown grasslands (GRASS), 'fen, marsh  
219 and swamp' (FMS) and 'OTHER' for this study (Table S1), and calculated the proportion of land  
220 covered by each of these land uses for each 3 x 3 km square.

221 The Rothamsted Insect Survey (RIS) light-trap network was established in 1968 and consists  
222 of a national network of approximately 100 volunteer-operated light traps of standard design with a  
223 200W tungsten bulb, each emptied daily. The RIS light-trap network has generated the largest and  
224 longest-running dataset of terrestrial invertebrate population dynamics anywhere in the world, and  
225 has been used to document national-scale changes in abundance and distribution of UK macro-moth  
226 populations (Conrad *et al.* 2004, 2006a; Fox *et al.* 2013).

227 First, we used annual rates of abundance change for 337 macro-moth species published by  
228 Conrad *et al.* (2006a) from the RIS database (1868 – 2002) to test whether these differed between  
229 those species known to be taken by Cuckoos as prey ( $n = 17$ ) and the remainder. We then extracted  
230 the total annual count of each macro-moth species recorded in the Cuckoo diet (Table 1) for every  
231 RIS trap that was operated for more than one year between 1975 and 2009 ( $n = 274$ , Fig. 2a). We  
232 chose 1975 as the start year because annual samples of traps were low before this year, but had  
233 increased to 90 by 1975. We summed this count over all these species for each site. We used the  
234 same approach as for the BBS squares to calculate the habitat composition of each 1 km square  
235 containing a light trap (using LCM2007 data) and, because of the small number of traps in semi-  
236 natural habitats, we pooled the three semi-natural habitat categories of HEATH, SNG and FMS into  
237 one (SN). We then determined which habitat type covered the greatest area in the square and  
238 considered that as the habitat allocated to that trap for further analysis. The final sample sizes were:  
239 SN ( $n = 26$ ), WOOD ( $n = 49$ ), ARABLE ( $n = 93$ ), and GRASS ( $n = 106$ ).

240

#### 241 *Cuckoo detection probability as a function of host abundance and habitat composition*

242 As in the local scale analysis, we used SAS 9.4 (SAS Institute Inc. 2014) , and we first modelled the  
243 probability of Cuckoo detection in BBS squares as a function of their habitat composition and host  
244 abundance using a GLM, and specifying a binomial error distribution. We modelled these  
245 relationships separately for 1995-1999 and 2006-2010.  $\log_e$  of the number of years surveyed  
246 ( $\ln\text{YEARS}$ ) was fitted as a nuisance variable in all models to control for variation in survey effort  
247 between squares. We added 0.01 to all mean counts of Dunnocks and Meadow Pipits and  $\log_e$ -  
248 transformed these counts ( $\ln\text{D}$  and  $\ln\text{MP}$ ). We expressed squares with (1) and without (0) Reed  
249 Warblers as a two-level, categorical effect (RW) given the rarity of BBS squares in which this species  
250 was recorded ( $n = 70$  in 1995-1999 and  $n = 148$  in 2006-2010). Habitat areas (except 'OTHER' to

251 avoid the unit sum constraint) were converted into proportions. The longitude and latitude (LONG,  
252 LAT - degrees) and elevation (ELEV - metres above sea level) of the square were also calculated. All  
253 twelve of these variables were considered initially as explanatory variables for modelling, but  
254 HEATH, LAT, ELEV, lnD and lnMP showed moderately high collinearity (Pearson's  $r$  for pairwise  
255 correlation coefficient of approximately 0.5 for all pairs in this group), so we subjected this group of  
256 five variables to a Principal Components Analysis. Only the first principal component had an  
257 Eigenvalue >1 (Eigenvalue = 3.00 and 2.89; proportion of variation explained = 0.600 and 0.576 for  
258 1995-1999 and 2006-2010, respectively), and so this component (PC1) was taken forward as a  
259 covariate in further modelling together with other seven explanatory variables. The partial  
260 correlation coefficients of the original variables and PC1 were (LAT 0.424 and 0.395; ELEV 0.431 and  
261 0.444, lnMP 0.463 and 0.464, lnD -0.439 and -0.428, HEATH 0.477 and 0.498 for 1995-1999 and  
262 2006-2010 respectively). So, in both time periods, this indicates a gradient from squares at higher  
263 elevations and latitudes, rich in heath cover and with more Meadow Pipits and fewer Dunnocks, to  
264 lower elevation and latitude squares with less heathland, more Dunnocks and fewer Meadow Pipits.  
265 The best-approximating model was identified by fitting all possible main effects models ( $n = 255$ ) and  
266 identifying the model which minimised AICc. If the variable PC1 was not included in the best-  
267 approximating model, then all possible combinations of the five original variables comprising PC1  
268 were added to the model to test whether any of these further reduced AICc.

269

#### 270 *Comparing population trends of moths that are known to be Cuckoo prey and those not known to be* 271 *Cuckoo prey*

272 To test whether moth species known to be Cuckoo prey show different long-term trends than those  
273 not known to be Cuckoo prey, we modelled the (1968 – 2002) annual population change (taken from  
274 Conrad *et al.* 2006a) in Table 1 as a function of these two categories (Cuckoo prey species = 1; non-  
275 Cuckoo prey species = 0), using a linear, mixed model (PROC GLMM) with normal errors. Moth  
276 family was fitted as a categorical, random effect as a basic correction for phylogenetic non-  
277 independence of trends (Sanderson *et al.* 2016).

278

#### 279 *Modelling habitat-specific trends of moths known to be Cuckoo prey*

280 For the macro-moth species forming part of the diet of Cuckoos (Table 1), we used a GLM to model  
281 moth count in the RIS database as a function of HABITAT (fixed, categorical effect with four levels:  
282 SN, WOOD, ARABLE, GRASS), SITE (fixed, categorical effect with 274 levels) and the YEAR x HABITAT  
283 interaction term in order to generate year and habitat-specific indices of moth abundance,  
284 specifying a Poisson error structure and log link. We corrected for overdispersion using the DSCALE

285 option in SAS 9.4. We then re-fitted the same model, but with YEAR fitted as a covariate in order to  
286 test whether annual rate of moth abundance change differed between the four habitat types.

287

## 288 **RESULTS**

289

### 290 **Local scale**

291 Cuckoos were detected in 14 of 45 (31.1%) sites surveyed across Devon. The probability of Cuckoo  
292 detection increased strongly with values of PC1 (PC1 =  $0.89 \pm 0.25$ , Wald  $\chi^2_1 = 12.55$ ,  $P = 0.0004$ ) but  
293 was unrelated to PC2 (PC2 =  $0.41 \pm 0.47$ , Wald  $\chi^2_1 = 0.77$ ,  $P = 0.38$ ). This indicates that Cuckoos were  
294 more likely to be detected in squares with a high cover of semi-natural habitats, which also tended  
295 to have higher numbers of Meadow Pipits and lower numbers of Dunnocks (Fig. 3). Agricultural land  
296 cover, along the spectrum from grassland to arable crops (PC2), had no influence on the probability  
297 that Cuckoos would be detected.

298 Total catches of macro-moths fell strongly with increasing wind speed (WIND =  $-0.407 \pm$   
299  $0.159$ , Wald  $\chi^2_1 = 6.5$ ,  $P = 0.01$ ), but there was no significant additive effect of either night-time air  
300 temperature or whether the square had previously recorded a territorial Cuckoo. Nonetheless, the  
301 best- approximating model ( $\Delta\text{AICc} = 41.4$ ) contained all three variables. When the data set was  
302 restricted to moth species known to be taken as prey by adult Cuckoos, the wind speed effect was  
303 no longer significant and there was a significant additive tendency for squares which had previously  
304 recorded Cuckoos to have higher catches than squares that did not (mean = 7.1 vs. 3.4 per trap;  
305 Wald  $\chi^2_1 = 5.1$ ,  $P = 0.024$ ). Again, the best-approximating model ( $\Delta\text{AICc} = 8.7$ ) included all three  
306 explanatory variables. There was no collinearity between the two most important explanatory  
307 variables; squares which had recorded Cuckoos did not experience different wind strength on moth  
308 trapping nights than those that had not recorded Cuckoos (two-sample  $t_{16} = 0.86$ ,  $P = 0.4$ ). In  
309 summary, at the local scale in Devon, Cuckoos were more likely to be detected in areas with more  
310 semi-natural habitat, more Meadow Pipits (but fewer Dunnocks) and, later in the summer, higher  
311 numbers of moths whose larvae are known to be preyed upon by adult Cuckoos are captured at sites  
312 at which territorial Cuckoos have previously been recorded.

313

### 314 **National scale**

315 During 1995-1999, Cuckoos were encountered in 59.2% of squares over the five years pooled ( $n =$   
316  $2767$  surveyed square-years), but this had fallen to 39.3% by 2006-2010 ( $n = 4101$  surveyed square-  
317 years). In 1995-1999, the best-approximating model was clear-cut ( $\Delta\text{AICc} = 51$ ). Using this model for  
318 inference, Cuckoos were more likely to be encountered at lower elevation and at more southerly

319 and easterly sites (i.e. the lowland south and east of Britain), and likelihood of detection increased  
320 with the proportion of all habitats other than the rarest (FMS; Table 3). However, there was no  
321 additive effect of the abundance of Dunnocks or Meadow Pipits, and the effect of presence of Reed  
322 Warblers was very weak (Table 3). In 2006-2010, the best-approximating model was moderately  
323 clear ( $\Delta AICc = 5$ ). Using this model for inference, the same habitat associations existed, but the  
324 associations with ARABLE and GRASS habitats had much reduced slopes, and there was now a clear  
325 positive association with sites with Reed Warblers and, as reflected by PC1, with northerly, higher  
326 elevation sites with more heathland and Meadow Pipits and fewer Dunnocks (Table 3). In summary,  
327 over a 10-15 year period, Cuckoos had become detected less often on BBS plots. Moreover, they  
328 had become more associated with upland heath characterised by the presence of Meadow Pipit  
329 hosts, and with wetland habitats occupied by Reed Warbler hosts, and relatively less associated with  
330 lowland sites associated with agricultural land and Dunnocks as the most available host. In addition,  
331 the core distribution of Cuckoos had shifted from south to north within the UK.

332 At the beginning of the period 1975-2009, moths captured in light traps of those species  
333 whose larvae are known to be prey of adult Cuckoos were many times (up to approximately 15-fold)  
334 more numerous in improved grassland and woodland habitats than in either arable or semi-natural  
335 habitats (Fig. 2b). However, significant and consistent declines in abundance in woodland (4.4% per  
336 annum, Wald  $\chi^2_1 = 402.4$ ,  $P < 0.0001$ ), improved grassland (3.1% per annum, Wald  $\chi^2_1 = 118.1$ ,  $P <$   
337  $0.0001$ ) and arable (3.2% per annum, Wald  $\chi^2_1 = 57.5$ ,  $P < 0.0001$ ) habitats, and a similar magnitude  
338 of annual abundance increase in semi-natural habitats (4.4% per annum, Wald  $\chi^2_1 = 32.8$ ,  $P < 0.0001$ )  
339 mean that moth abundance overall varied only roughly four-fold across these four habitat types by  
340 the end of the time period. By the end of the time period in 2009, numbers in semi-natural habitat  
341 were consistently higher than those in arable habitats, and similar to those in improved grassland  
342 and woodland habitats.

343 The annual population changes of a much larger sample of macro-moths between 1968 and  
344 2002, as published by Conrad *et al.* (2006a) differed significantly ( $P = 0.009$ ) between those species  
345 known to be preyed upon by Cuckoos (mean annual population change =  $-3.2\% \pm 0.9$  se,  $n = 17$ ) and  
346 those not known to be taken as Cuckoo prey ( $-0.7\% \pm 0.4$  se,  $n = 320$ ; Fig. 2c).

347

## 348 **DISCUSSION**

349

350 Our data found support for the hypotheses that Cuckoo habitat associations have changed (H1), with  
351 Cuckoos now more likely to be associated with semi-natural habitats and with the presence of

352 Meadow Pipits (H2). Similarly, the macro-moth prey have declined at a greater rate than other  
353 macro-moth species (H3) and Cuckoo presence is associated with their macro-moth prey (H4).

354 Both at local (Devon) and national (UK) scales, our results show that a declining Cuckoo  
355 population is becoming increasingly associated with upland heath and grassland habitats in which  
356 Meadow Pipit is the predominant host species, and less prevalent in lowland, agricultural habitats in  
357 which Dunnock is the predominant host species. There is also evidence from our national analyses  
358 that remaining lowland populations are now increasingly associated with habitats supporting Reed  
359 Warblers; these are likely to range from extensive freshwater wetland systems, often associated  
360 with nature reserves, to drainage systems in lowland agricultural landscapes where these are  
361 colonised by extensive stands of reed.

362 The changing abundance and distribution of Cuckoos accords broadly with changing  
363 abundance and distribution of macro-moths in the UK (Conrad *et al.* 2004, 2006a, Fox *et al.* 2013),  
364 especially changes in the species with hairy caterpillars which are preyed upon by adult Cuckoos  
365 (Conrad *et al.* 2002, 2003, 2006b). One of these, the Garden Tiger *Arctia caja*, has been studied in  
366 detail and, like the Cuckoo, shows a long-term distributional shift from the south and east towards  
367 the north and west of the UK, which is suggested to reflect the combined influences of climate and  
368 land management change (Conrad *et al.* 2002, 2006b). Specifically, we found that, nationally across  
369 all habitats, the abundance of macro-moth species identified as Cuckoo prey by Wyllie (1981) has  
370 declined over four times faster ( $3.2 \pm 0.9\%$  annual decline) than that of species not known to be  
371 taken by Cuckoos ( $0.7 \pm 0.4\%$  annual decline). Moths preyed upon by Cuckoos have shown steep  
372 declines in lowland landscapes dominated by agriculture and woodland, whilst increasing in semi-  
373 natural habitats, including heathland, semi-natural grasslands and fen, marsh and swamp habitats.  
374 Locally, in Devon, even a modest moth-trapping data set suggested that, after controlling for  
375 weather conditions, sites that had recorded territorial Cuckoos in the preceding breeding season  
376 supported larger, later-summer catches of moth species whose larvae are known to be prey for adult  
377 Cuckoos than sites that did not record Cuckoos.

378 These findings provide strong correlative evidence that Cuckoos are becoming increasingly  
379 confined to areas of semi-natural habitat such as heathlands, moorlands and wetlands, and that  
380 declining populations of key prey species of adult Cuckoos are a strong candidate explanation for  
381 this change. Other factors such as environmental impacts on abundance of hosts (Douglas *et al.*  
382 2010), changing climate or land use on migration routes or in wintering areas (Ockendon *et al.* 2012,  
383 Hewson *et al.* 2016), and mismatches in timing of breeding with some host species (Saino *et al.*  
384 2009, Moller *et al.* 2011, but see Douglas *et al.* 2010), may also contribute. However, our results do  
385 suggest that there are important opportunities to test whether Cuckoo population declines can be

386 reversed through the management of prey and hosts on the breeding grounds. In particular, our  
387 results highlight the need to further test hypotheses related to food resource availability. For a  
388 landscape to support breeding Cuckoos, it must have: i) habitat conditions and prey resources  
389 sufficient to support the host species; ii) habitat conditions necessary to support sufficient  
390 populations of moths (especially in the families Lasiocampidae, Sphingidae, Notodontidae and  
391 Erebididae) whose caterpillars are available when Cuckoos return to the breeding grounds in spring, as  
392 well as other large invertebrates later in the summer; iii) habitat conditions which accommodate the  
393 preferred 'perch-and-scan' behaviour of Cuckoos which is used both to detect prey and host nests;  
394 and, iv) the availability of all the above habitat conditions at an appropriate spatial scale, considering  
395 the Cuckoo home range.

396 Cuckoos are known to fly several kilometres between areas where hosts are nesting to areas  
397 rich in caterpillars, historically in aggregations of many tens of birds (Wyllie 1981, Davis 1996). This  
398 suggests that habitat patches that support high caterpillar concentrations are an important  
399 component of landscapes in which breeding Cuckoos can persist. In this context, the fact that  
400 lepidopteran populations are known to be highly sensitive to the impacts of agricultural  
401 intensification (Wilson *et al.* 1999) suggests that agricultural change over recent decades could have  
402 substantially reduced the ability of the lowland agricultural landscape to support Cuckoos.  
403 Important impacts on Lepidoptera include effects of agrochemical use, hedgerow loss and frequent  
404 mechanical trimming of those that remain, conversion of grassland to arable cultivation,  
405 replacement of semi-natural grassland with sown and heavily grazed or frequently cut ryegrass  
406 *Lolium* swards (Wilson *et al.* 1999, Conrad *et al.* 2006, Woiwod & Gould 2008, Fox 2013) as well as,  
407 potentially, the impact of new generations of pesticides such as neonicotinoids (Pisa *et al.* 2017). In  
408 the summary by Fox *et al.* (2013) of long-term trends (1968 – 2007) of 337 species of the UK's larger  
409 moths, three of the key prey species of Cuckoos had declined by over 90% during this time (Figure-  
410 of-Eight *Diloba caeruleocephala*, -96%; Lackey *Malacosoma neustria*, -93%, Garden Tiger, -92%) but  
411 none were recorded as having increased. Recent evidence of positive responses of moth  
412 abundance and diversity to interventions designed to reverse the impacts of agricultural  
413 intensification, such as organic farming conversion, and agri-environment schemes which provide  
414 sensitively managed hedgerows, hedgerow trees and wide, uncultivated and unsprayed field  
415 margins (e.g. Wickramsinghe *et al.* 2004, Fuentes-Montemayor *et al.* 2011, Merckx & Macdonald  
416 2015), provides further evidence of the causal relationship between agricultural change and moth  
417 populations.

418 Restoring lowland agricultural landscapes capable of supporting breeding Cuckoo  
419 populations and their key prey resources is a major challenge. To test the causality of the

420 relationships found here, and to trial an effective management solution, we suggest that a replicated  
421 landscape-scale intervention be designed. This should focus around the coordinated restoration of  
422 species-rich grasslands, reduced pesticide use on arable land, hedgerows with less-than-annual  
423 trimming and minimal understorey disturbance, and grass field margins not subject to agrochemical  
424 application, ideally located close to a remaining centre of Cuckoo population such as Dartmoor.  
425 Merckx *et al.* (2009) have already tested the effect of landscape-scale targeting of agri-environment  
426 management deigned to benefit macro-moth populations by establishing contiguous blocks of  
427 farmland either subjected to concerted, targeted agri-environment interventions or left as controls.  
428 Using interventions similar to those we list above, that study demonstrated increases of 38% in  
429 species diversity and 60% in abundance of larger moths in the trial landscapes, leading the authors  
430 to suggest that larger moths might be suitable as a bio-indicator of landscape quality. Although such  
431 an intervention may need to be scaled up further in order to also detect any effect on settlement by  
432 territorial Cuckoos, this earlier study shows the potential impact of a landscape-scale trial.  
433 Evaluation of responses in trial and control landscapes should include moth populations, presence  
434 and numbers of territorial Cuckoos, and also the abundance and breeding success of Dunnocks,  
435 given that it is also possible that agricultural intensification has limited the ability of this species to  
436 rear a Cuckoo nestling to fledging. With such a commitment, the restoration of populations of  
437 Cuckoos and the moth species upon which they depend could become emblematic of the  
438 achievement of Lawton *et al.*'s (2010) vision for the restoration of an ecological network across  
439 England. Without such a commitment, the continuing rapid decline of this iconic species suggests  
440 that the Cuckoo, a bird with an exceptionally rich folklore (Cocker & Mabey 2005) may soon  
441 disappear completely from lowland agricultural Britain.

442

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450

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597

598 **Table 1.** Macro-moths recorded in Cuckoo diet by Wyllie (1981) and Cramp (1985).

599

English name	Scientific name	Family
Poplar Hawkmoth <sup>a</sup>	<i>Laothoe populi</i>	Sphingidae
Elephant Hawkmoth <sup>a</sup>	<i>Deilephila elpenor</i>	Sphingidae
Buff-tip	<i>Phalera bucephala</i>	Notodontidae
Antler Moth	<i>Cerapteryx graminis</i>	Noctuidae
Yellow-tail	<i>Euproctis similis</i>	Erebidae
Lackey	<i>Malacosoma neustria</i>	Lasiocampidae
Oak Eggar	<i>Lasiocampa quercus</i>	Lasiocampidae
Drinker	<i>Euthrix potatoria</i>	Lasiocampidae
Lappet	<i>Gastropacha quercifolia</i>	Lasiocampidae
Small Eggar	<i>Eriogaster lanestris</i>	Lasiocampidae
Figure of Eight	<i>Diloba caeruleocephala</i>	Noctuidae
White Ermine <sup>a</sup>	<i>Spilosoma lubricipeda</i>	Erebidae
Buff Ermine <sup>a</sup>	<i>Spilosoma luteum</i>	Erebidae
Garden Tiger	<i>Arctia caja</i>	Erebidae
Cinnabar	<i>Tyria jacobaeae</i>	Erebidae
March Moth	<i>Alsophila aescularia</i>	Geometridae
Winter Moth	<i>Operophtera brumata</i>	Geometridae
Early Thorn	<i>Selenia dentaria</i>	Geometridae
Magpie	<i>Abraxas grossulariata</i>	Geometridae
Mottled Umber	<i>Erannis defoliaria</i>	Geometridae
Dotted Border	<i>Agriopsis marginaria</i>	Geometridae
Six-spot Burnet	<i>Zygaena filipendulae</i>	Zygaenidae

600 <sup>a</sup>Wyllie (1981) identifies hawkmoths and ermines, respectively, as species groups of Cuckoo prey. Poplar and  
601 Elephant Hawkmoths and White and Buff Ermines are identified specifically here as they are the species within  
602 each of these groups with sufficient data for analysis in the RIS database.

603 **Table 2.** Partial Pearson correlation coefficients for Principal Components Analysis of explanatory  
 604 variables in modelling of variation in territorial Cuckoo detection across 45 1 km squares in Devon in  
 605 2012. See text for explanatory variable definitions.

606

<b>Explanatory variable</b>	<b>PC1 (Eigenvalue 3.40; % of variation explained = 56.7)</b>	<b>PC2 (Eigenvalue = 1.11; % of variation explained = 18.5)</b>
HEATH	0.366	-0.285
SNG	0.462	0.104
GRASS	-0.428	0.486
ARABLE	-0.283	-0.776
lnMP	0.492	0.213
lnD	-0.384	0.157

607

608

609

610 **Table 3.** Final GLMs showing relationship between Cuckoo presence on Breeding Bird Survey plots  
 611 and their habitat composition and abundance or presence of host species. Rows in bold refer to  
 612 1995-1999 and rows in italics refer to 2005-2009.

<b>Parameter</b>	<b>Estimate</b>	<b>SE</b>	<b>Wald <math>\chi^2_1</math></b>	<b>Significance</b>
Intercept	<b>-3.448</b>	<b>0.522</b>	<b>43.67</b>	<b>&lt;0.0001</b>
	<i>-3.707</i>	<i>0.325</i>	<i>129.8</i>	<i>&lt;0.0001</i>
lnYEARS	<b>1.172</b>	<b>0.084</b>	<b>194.8</b>	<b>&lt;0.0001</b>
	<i>1.043</i>	<i>0.073</i>	<i>205.3</i>	<i>&lt;0.0001</i>
ARABLE	<b>4.367</b>	<b>0.296</b>	<b>217.2</b>	<b>&lt;0.0001</b>
	<i>1.961</i>	<i>0.194</i>	<i>102.2</i>	<i>&lt;0.0001</i>
WOOD	<b>6.669</b>	<b>0.478</b>	<b>194.6</b>	<b>&lt;0.0001</b>
	<i>5.170</i>	<i>0.331</i>	<i>243.9</i>	<i>&lt;0.0001</i>
SNG	<b>4.932</b>	<b>0.463</b>	<b>113.5</b>	<b>&lt;0.0001</b>
	<i>3.014</i>	<i>0.368</i>	<i>67.0</i>	<i>&lt;0.0001</i>
GRASS	<b>2.916</b>	<b>0.346</b>	<b>71.0</b>	<b>&lt;0.0001</b>
	<i>1.620</i>	<i>0.243</i>	<i>44.6</i>	<i>&lt;0.0001</i>
HEATH	<b>6.076</b>	<b>0.480</b>	<b>160.4</b>	<b>&lt;0.0001</b>
PC1	<i>0.231</i>	<i>0.030</i>	<i>57.9</i>	<i>&lt;0.0001</i>
LONG	<b>0.0021</b>	<b>0.0006</b>	<b>12.4</b>	<b>0.0004</b>
	<i>0.0036</i>	<i>0.0004</i>	<i>76.5</i>	<i>&lt;0.0001</i>
LAT	<b>-0.0027</b>	<b>0.0006</b>	<b>97.6</b>	<b>&lt;0.0001</b>
ELEV	<b>-0.0042</b>	<b>0.0006</b>	<b>50.1</b>	<b>&lt;0.0001</b>
RWP (1)	<b>0.624</b>	<b>0.348</b>	<b>3.2</b>	<b>0.073</b>
	<i>1.521</i>	<i>0.197</i>	<i>59.7</i>	<i>&lt;0.0001</i>

613

614

615 **Figure legends**

616

617 **Figure 1.** Map showing the dramatic change in the distribution of Cuckoos in Devon, south west  
618 England from 1977-1985 to 2007-2014. Dots represent different categories of Cuckoo presence (see  
619 legend). The shaded area to the south represents an area of uplands called Dartmoor and the  
620 shaded area in the north represents Exmoor. Reproduced with permission from Beavan & Lock  
621 (2016), Devon Bird Atlas 2007-2013. © Devon Birds.

622

623 **Figure 2.** Long-term, annual estimates of abundance of moth species known to be key food sources  
624 of adult Cuckoos as recorded by Rothamsted light traps in four broad habitat types in Britain, 1975-  
625 2009 (3a). Precision of individual annual estimates is not shown for clarity, but these data show  
626 significant linear percentage declines in abundance in woodland, improved grassland and arable  
627 habitats, and a significant linear percentage increase in abundance in semi-natural habitats (3b).  
628 Macro-moth species known to be prey for adult Cuckoos ( $n = 17$ ) are declining faster than other  
629 moth species ( $n = 320$ ). Each category is labelled with its maximum annual percentage population  
630 change. Data from Conrad *et al.* (2006a) (3c).

631

632 **Figure 3.** Fitted relationship across 45 1x1 km squares between probability of Cuckoo detection  
633 during a single song playback survey in May/June and Principal Component 1, in which high values  
634 indicate squares with more semi-natural heath and grassland habitat (less agricultural land cover),  
635 more Meadow Pipits and fewer Dunnocks. Filled circles indicate squares in which one or more  
636 Cuckoos were detected in response to playback and open circles indicate squares in which no  
637 Cuckoo was detected.

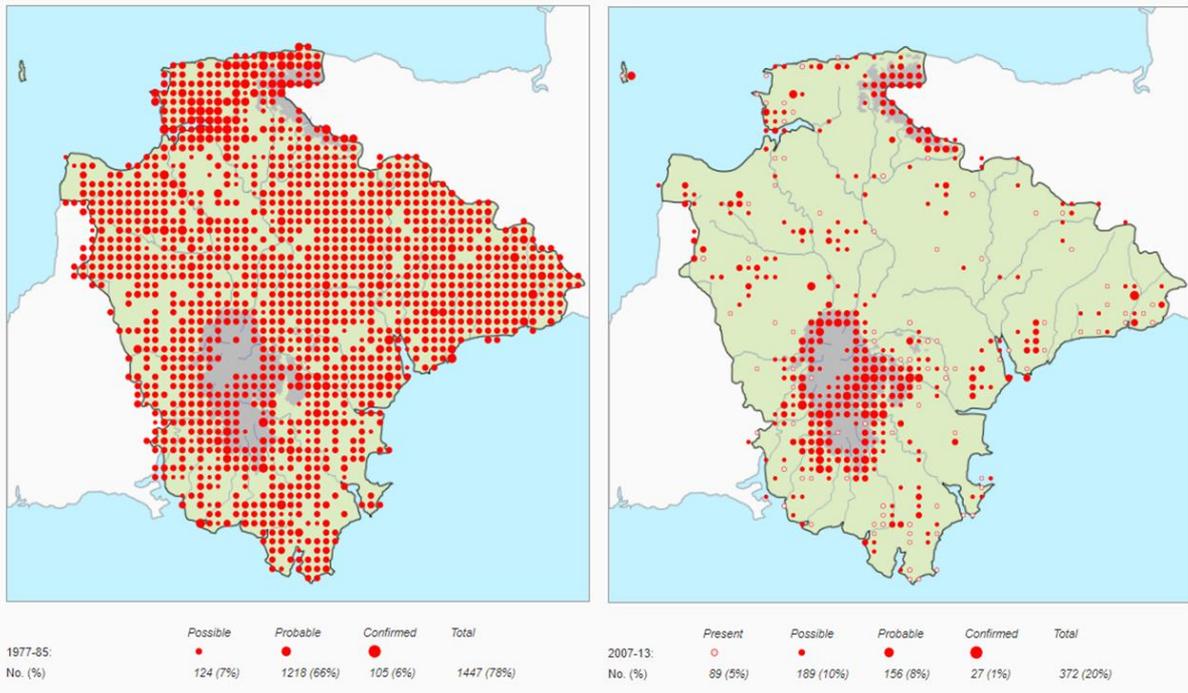
638

639

640 **Figure 1.**

a) 1977-1985

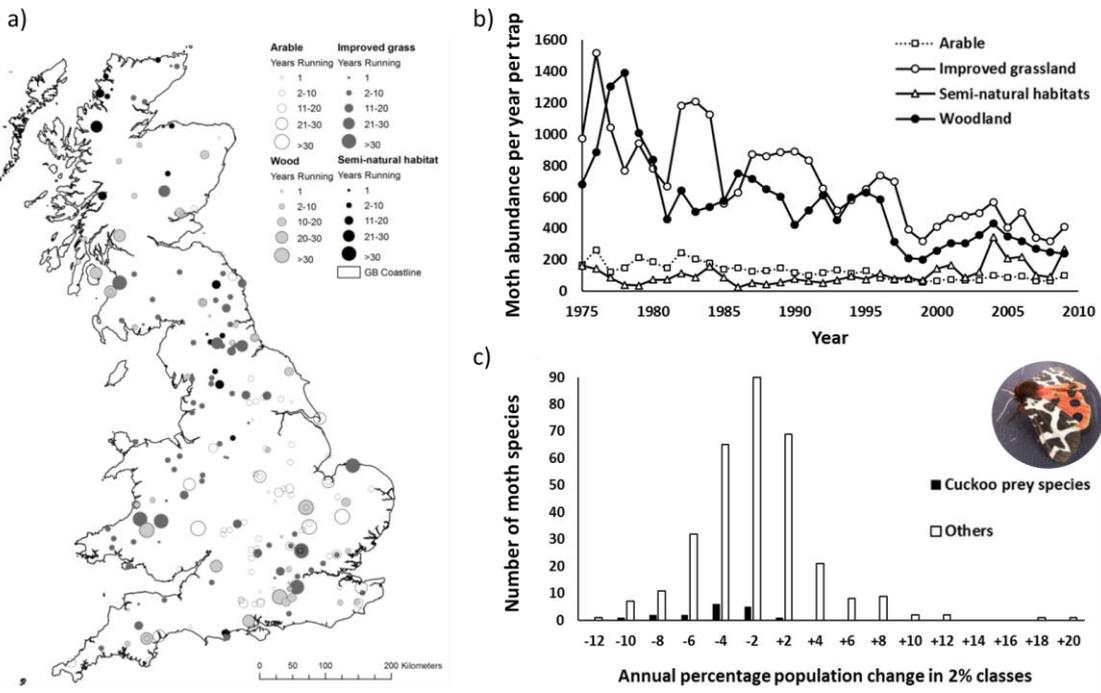
b) 2007-2013



641

642 **Figure 2.**

Figure 2.



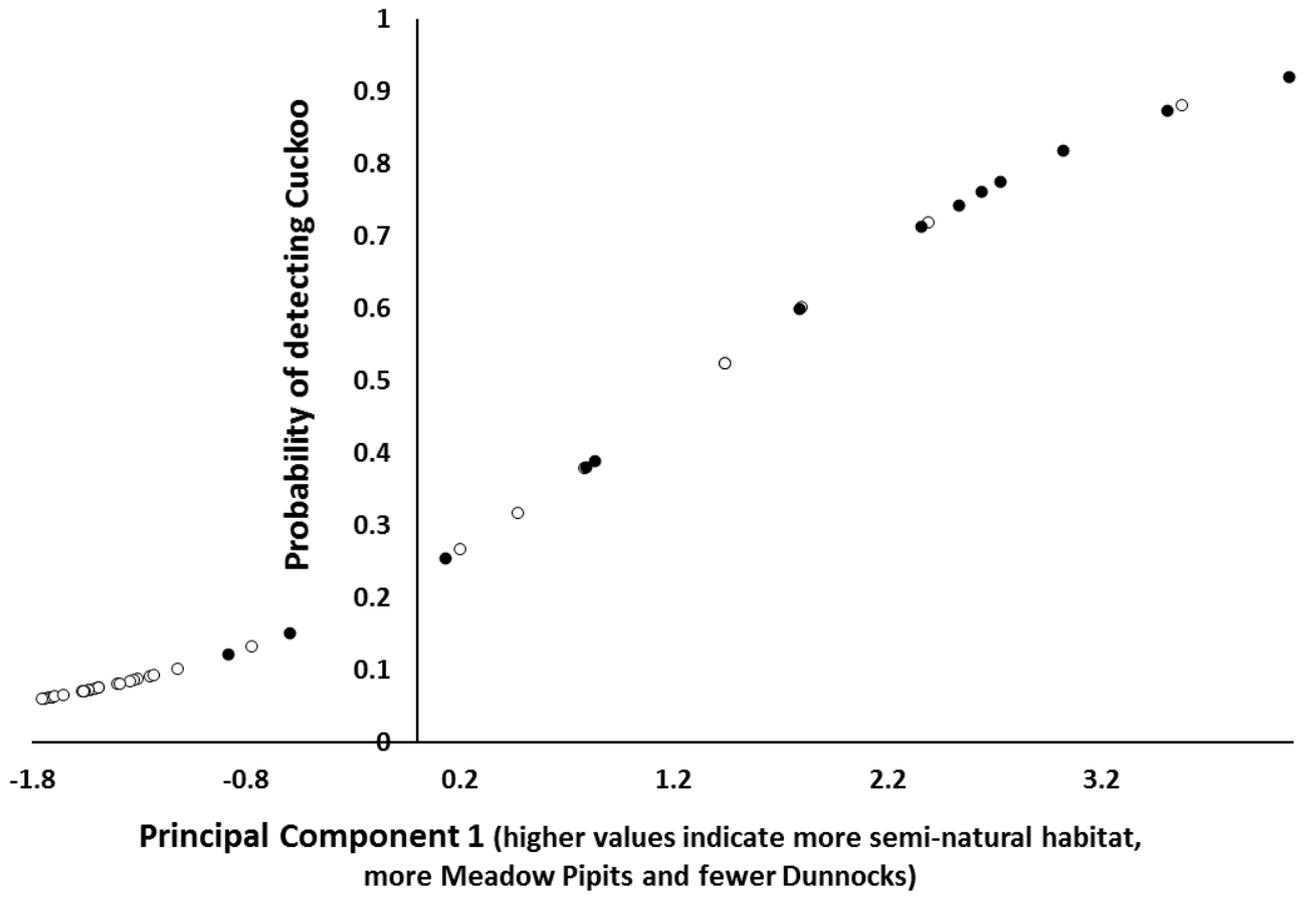
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646

647 **Figure 3.**



648