

Agri-environmental measures and the breeding ecology of a declining farmland bird

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1 **Agri-environmental measures and the breeding ecology of a declining**
2 **farmland bird**

3

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16

17 **Abstract**

18 Agricultural intensification is a key cause of the population declines shown by many
19 farmland bird species across Europe. Changes in land management through agri-environment
20 schemes (AES) are frequently cited as the best tool to reverse these trends, to date however
21 they have received mixed support. This study tested whether AES options in England that
22 provide winter seed food or insect-rich foraging during the breeding season, were associated
23 with improved breeding performance in tree sparrow, *Passer montanus*, and/or the formation
24 of larger breeding colonies. Breeding attempts (n=428) representing 210 pairs of tree sparrow
25 comprising 22 colonies were compared in Wiltshire, England in 2013 and 2014. The area of

26 margin AES, an insect-rich habitat, was positively correlated with fledgling success per
27 breeding attempt and per breeding pair. Colony size increased with increasing wild bird seed
28 mix AES area, a winter seed food resource, but this option negatively affected hatching
29 success and the number of fledglings produced per breeding attempt. The observed
30 association between colony size and this habitat was expected given that wild bird seed
31 mixtures provide important seed food resources for granivorous birds during winter. The
32 negative correlation with fledgling success, on the other hand, requires further investigation
33 to determine whether this relationship relates to a lack of invertebrate and seed food during
34 the breeding period. These results highlight the importance of providing a suite of AES
35 habitats that are appropriately located to deliver both overwintering and breeding
36 requirements of target, declining farmland birds.

37

38 **Keywords**

39 Farmland birds; Common Agricultural Policy; Insect; Conservation; Agro-ecology

40 **1. Introduction**

41 Changes in agricultural practices across Europe and North America, have, over the last four
42 decades resulted in habitat destruction, fragmentation, and degradation which have been
43 linked to farmland bird declines across these regions (Askins, 1999; Donald et al., 2006;
44 Murphy, 2003). These changes included field enlargement through hedgerow removal
45 reducing the availability of suitable nesting and foraging habitats for many species, the use of
46 more efficient farm machinery (leading to less spilled grain) and reduced areas of uncropped
47 land (important as a foraging, roosting and nesting habitat; Sotherton and Self, 2000;
48 Marshall and Moonen 2002; Newton 2004; Tscharntke et al, 2005). In addition, changes in
49 crop management have reduced bird food supplies, for example, the more extensive use of
50 inorganic herbicides and pesticides has removed weeds and their associated invertebrates and
51 a switch to autumn sown crops means over-winter stubbles have become less common
52 (Newton, 2004; Tscharntke et al, 2005). These changes, have in turn allowed changes in
53 extent and diversity of crops (e.g. loss of oats and growth in oilseed rape), and to regional
54 specialisation in agriculture (leading to a loss of traditional, rotational mixed farming in many
55 areas). Consequently, birds associated with agricultural landscapes have fewer places to nest,
56 raise fewer offspring and have poorer overwinter survival (Newton, 2004). These aspects of
57 agricultural intensification occurred concurrently, making it hard to isolate their individual
58 impacts (Newton, 2004), but collectively they have contributed to the simplification of
59 farmland ecosystems (Matson et al. 1997; Tscharntke et al. 2005).

60

61 The reduced availability of key resources has been linked to severe farmland bird population
62 declines and on average the abundance of common farmland birds has halved since 1980
63 (Voříšek et al., 2005). Across Europe farmland bird declines are considered a high

64 conservation priority and Agri-Environment Schemes (AES) have been the main policy
65 mechanism adopted for addressing these concerns (Donald et al., 2006). In England AES
66 have attempted to help improve habitat heterogeneity by creating or restoring habitats
67 focused on providing food to aid over-winter survival and also to help ensure both chick food
68 and nesting habitat are plentiful over the breeding season (Natural England, 2013a, 2013b).

69

70 Associations between farmland birds and AES habitats have been used by a wide number of
71 studies across Europe in an attempt to evaluate their success (e.g. Burgess et al., 2014; Bright
72 et al., 2015; Davey et al., 2010a,b; Douglas et al., 2009; Gilroy et al., 2009; Kleijn et al.,
73 2001; Princé et al., 2012; Wilson, 2001). Studies have defined AES success in terms of their
74 impact on bird density and use of AES habitats while foraging. Current studies however, lack
75 information on potential mechanisms for such relationships i.e. habitat accessibility and/or
76 improved invertebrate chick-food supplies (but see McHugh et al. 2016a). Insufficient chick
77 food is known to reduce breeding success of grey partridge *Perdix perdix*, Eurasian skylark
78 *Alauda arvensis*, corn bunting *Emberiza calandra* and yellowhammer *Emberiza citrinella*
79 (Brickle et al., 2000; Boatman et al., 2004; Potts, 2012) and, may also impact other farmland
80 birds whose chicks are provisioned largely with invertebrates when in the nest (Newton,
81 2004). The abundance of invertebrates has also been impacted by modern agricultural
82 practices; for example, the abundance of grey partridge chick-food taxa on the Sussex
83 Downs, where annual monitoring has taken place since 1969, show an overall downward
84 trend in abundance and are thought to be representative of the situation on a national scale
85 (Potts, 2012). Indeed, the grey partridge chick food index, the only measure available that
86 relates chick-food abundance to chick-survival, was below the level necessary to sustain a
87 population of grey partridge in all arable crops in the study area (Potts, 2012).

89 The central aim of this paper is to document whether the productivity of a hole-nesting
90 granivorous farmland bird, the tree sparrow *Passer montanus*, whose chicks are dependent on
91 invertebrate food resources, is limited by the availability of invertebrate-rich foraging habitat.
92 In the United Kingdom over a 31 year period tree sparrows have suffered a decline of over
93 97% (BTO, 2015). When breeding, tree sparrows can adapt their foraging radius to prey
94 densities and conspecifics, but have been found to forage within an average distance of 200 m
95 from their nests (Deckert, 1962; Summer-Smith, 1995). Here, we tested whether colony size,
96 total productivity and per-attempt productivity in tree sparrows was linked to the area of
97 different agricultural habitats, including those provided by AES, within 200 m of their nest
98 boxes. We predicted that higher fledgling success may be more frequently associated with
99 habitats that are rich in chick food invertebrates such as margin AES (Vickery et al., 2002)
100 due to the dependence of chicks on invertebrate food resources. We expected that fledgling
101 success would be negatively affected by the habitat wild bird seed mixture (WBSM) as this
102 habitat is aimed at winter seed food provision, and annual mixes are thought to be a poor
103 source of chick-food resources (McHugh et al., 2016b). Additionally, we examine probable
104 causes for these relationships by comparing tree sparrow chick food abundance in the
105 available agricultural habitat types. Finally, breeding success-habitat area relationships may
106 relate to density dependence mechanisms (Pärn et al., 2011; Ringsby et al., 2002; Svensson et
107 al., 2006), influencing competition for available chick-food resources, therefore we
108 investigated the relationship between tree sparrow colony size and breeding success.

109

110 **2. Methods**

111 **2.1 Study area**

112 Data collection took place in the south of England, in the mixed farming landscape of the
113 Marlborough and Pewsley Downs, within the North Wessex Downs Area of Outstanding
114 Natural Beauty (AONB). The study is centred around 51.42, -1.84 WGS84. 84% of this land
115 is used for agricultural production and the principal land use (over 60%) is arable farming
116 (AONB, 2014). The study sites under investigation were conventionally farmed and form part
117 of a long-term tree sparrow monitoring project run by the Wiltshire Ornithology Society
118 (WOS). It is important to note that the number of nest boxes was uneven across sites. As
119 colony size increases, more nest boxes are provided by WOS and none of the sites had
120 reached capacity. This ensures that nest box availability is not a factor limiting colony size.

121

122 Within and between each of the 11 farm sites, groups of nest boxes that were separated by
123 more than 400m were defined as separate sampling units, resulting in 22 discrete tree sparrow
124 colonies (Figure 1). The maximum distance between neighbouring nest boxes was 253 m
125 (49.46 ± 10.54 m) and minimum distance was 0.49 m (3.50 ± 0.76 m). All habitat types
126 found within 200m of colonies were mapped using farm maps received from farmers and
127 through on-site verification. Individual nest box data was later extracted and analysed. 200m
128 was chosen as the area adult tree sparrows were most likely to forage within when collecting
129 insects to feed chicks. Habitat data was digitised using ArcMap GIS v. 10.2. 200m was
130 chosen as the area adult tree sparrows were most likely to forage within when collecting
131 insects to feed chicks (Deckert, 1962; Summers-Smith, 1995; McHugh et al., 2016b; Zhang
132 and Zheng, 2010). Nest boxes with overlapping 200m buffers were classified as members of
133 the same tree sparrow colony. Individual nest box data was later extracted and analysed.

134

135 The habitat types present on these farms included permanent and temporary grassland; arable
136 crops (cereals: barley, *Hordeum*, and wheat, *Triticum*; broadleaf crops: oilseed rape, *Brassica*
137 *napus spp.*). AES margin (an aggregate group of structurally similar grassy semi-natural
138 habitats, and includes grass buffers, uncropped field corners, floristically enhanced margins,
139 and pollen and nectar mix. Note: non-AES grass habitats, such as grazed grassland, were
140 excluded from this category); wild bird seed mixture (plots sown with seed rich plants to
141 provide seed to granivorous farmland birds over winter; WBSM) and woodland habitats. To
142 increase statistical power for analysis, these habitats were classified into 11 groups according
143 to structural and functional similarities (Table A1).

144

145 **2.2 Productivity Data**

146 This study was conducted over two consecutive years, 2013 and 2014, during the tree
147 sparrow breeding season (April to August). Nest boxes were checked every 2-3 days to
148 obtain the following basic reproductive parameters; clutch size, total eggs (per pair), hatching
149 success (proportion of hatched eggs), number of fledglings, fledging success (proportion of
150 hatchlings that resulted in fledglings) and the number of breeding attempts. This resulted in
151 two productivity datasets 1) total productivity data where breeding measurements were
152 pooled for pairs of birds across the breeding season and 2) per-attempt productivity data,
153 where individual breeding attempts were investigated.

154

155 Tree sparrows have multiple clutches per pair per year; the assignment of chicks to a brood
156 category (1st, 2nd or 3rd) is based on three assumptions: 1. Consecutive clutches laid in the
157 same nest box belong to the same pair, 2. Pairs do not change nests for successive broods and
158 3. Clutches laid in new boxes after the end of May were assumed to be second broods (n=13)

159 and after mid-July were assumed to be third broods (n=3). Deckert (1962) and Summer-
160 Smith (1995) suggest that these assumptions are largely valid, although during their
161 behavioural studies, colour ringed birds were occasionally found to use more than one nest
162 site.

163

164 **2.3 Invertebrate Monitoring in Agricultural Habitats**

165 Between the 9th and 24th July 2013, two sweep net samples were taken from permanent and
166 temporary grassland, grass buffer strips, floristically enhanced margins, pollen and nectar
167 margins, uncropped field corners, oilseed rape, spring wheat, spring barley, wild bird seed
168 mixture (WBSM), winter wheat and winter barley (n=178). For the purpose of analysis these
169 habitats were grouped into six broader categories representing structurally or functionally
170 similar habitat types (Table A.1). Where more than one replicate of a component habitat was
171 available to a colony the replicate to be sampled was randomly chosen using R. Random
172 points within these habitats were chosen as sampling locations using ArcGIS v10.3. Samples
173 comprised ten 180 degree sweeps, covering a distance of approximately 10m. There are
174 however, some limitations relating to this method including the variance in sampling
175 efficiency relating to habitat type sampled and variation in the species recorded depending on
176 their vertical distribution (Southwood, 1987).

177

178 **2.4 Data Analysis**

179 Data exploration and statistical analysis was conducted in Rv3.03 (R Core Development
180 Team, 2014). The data were explored using the procedure outlined by Zuur et al. (2010).
181 Dotplots together with histograms were used to determine whether transformations of

182 covariates were necessary. This led to the use of the ArcSine square-root transformation on
183 habitat area variables.

184

185 Pearson correlation coefficients (<-0.5 and >0.5) and Variance Inflation Factors (VIFs; >3)
186 were used to remove correlated variables (Ieno and Zurr, 2015). Pearson's correlation was
187 highest between winter cereal and oilseed rape (-0.56 for all datasets) resulting in VIFs >10
188 for grassland (in per-attempt productivity data), spring cereal (in all datasets), winter cereal
189 (in all datasets), and oilseed rape (in all datasets). By excluding winter cereal from datasets,
190 VIFs for all variables were reduced to an acceptable level, below 3 (Ieno and Zurr, 2015).

191 The spread of the data was investigated using Cleveland dotplots and led to the exclusion of
192 spring cereal, water and other arable from analysis as these habitats were present on land
193 surrounding $<5\%$ of occupied nest boxes.

194

195 For our colony size-habitat area model, colony size was modelled against the average area of
196 each habitat within 200 m of tree sparrow nestboxes in each colony and year, in a
197 quasipoisson distributed generalised linear model (GLM; Table 1). Only permanent habitat
198 variables (boundary, farmyard buildings, grassland, margin AES, woodland and WBSM)
199 were included in our full model as they are present before tree sparrows establish their
200 breeding territories. The model was simplified via backward stepwise selection (Crawley,
201 2012). Model assumptions were tested using diagnostic plots from the package lme4.

202

203 Backward stepwise selection of explanatory variables from Generalised Linear Mixed Effects
204 Models (GLMMs) was conducted to model total productivity per pair, per-attempt
205 productivity and tree sparrow chick food invertebrate abundance (Table 1). Tree sparrow

206 chick food abundance was calculated, using our sweep net data, as the sum of food items
207 representing >5% of chick diet and was composed of Araneae, Coleoptera, coleopteran
208 larvae, Diptera, Lepidoptera larvae and Tipulidae (McHugh et al., 2016b). For the chick food
209 abundance model, a full model was fitted to model invertebrate abundance and habitat types.
210 Sampled habitats were grouped into six broad categories representing structurally or
211 functionally similar habitat types; grassland, margin AES, oilseed rape, spring cereal, WBSM
212 and winter cereal (Table A.1). Wald Z-tests were used to measure the influence of
213 independent variables that were included in models as fixed effects (Aebischer et al., 2014).
214 The most complicated models that could be fitted to the data contained eight additive fixed
215 effects, the inclusion of additional terms led to model overparameterization and non-
216 convergence.

217

218 GLMM model overdispersion was investigated by calculating the sum of squared Pearson's
219 residuals, divided by the number of observations, minus the number of parameters. A
220 dispersion statistic greater than 1 indicates model overdispersion, our GLMM models were
221 not found to be overdispersed. Model assumptions were tested through diagnostic plots
222 produced with the package ggplot2 (Wickham, 2009) and model prediction plots were
223 produced using the effects package (Fox, 2003).

224

225 Density dependence was examined by modelling mean clutch size, hatching success, number
226 of fledglings and fledgling success per colony against colony size, whilst accounting for
227 seasonality by including year and brood as fixed effects in GLMs (Table 1). Where
228 appropriate quasibinomial and quasipoisson distributions were used to account for model
229 overdispersion, model assumptions were checked using the plot function in the lme4 package.

230

231 **3. Results**

232 **3.1. Colony size**

233 22 colonies were monitored in total (19 were active in 2013 and 18 in 2014), consequently
234 productivity data for 7 colonies were only collected in one of the two years. Colonies ranged
235 in size from 1 to 24 pairs in both years (mean 5.47 ± 1.26 in 2013 and 6 ± 1.41 in 2014), with
236 a total of 104 actively breeding pairs in 2013 and 106 in 2014, and 428 breeding attempts
237 over the two-year period.

238

239 Colony size increased significantly with the area of WBSM present and decreased in relation
240 to increasing grassland area (Table 2; Figure 2).

241

242 **3.2. Total productivity per pair**

243 Between 1 and 3 breeding attempts per pair were made per year (April to August). We found
244 no effect of habitat area variables on the number of broods produced per pair.

245

246 The mean total number of eggs produced by a breeding pair was 10.31 ± 1.02 in 2013 and
247 12.25 ± 1.19 in 2014. According to our Minimum Adequate Model (MAM; Table 2), the
248 predicted total number of eggs produced by a pair over the breeding season decreased with
249 the area of woodland.

250

251 In 2013 7.91 ± 0.77 chicks hatched compared with 9.92 ± 0.96 in 2014. Hatching success
252 decreased relative to the areas of margin AES, WBSM, grassland and woodland available and
253 increased relative to the area farmyard building area coverage (Table 2).

254

255 An average of 5.96 ± 0.59 chicks successfully fledged in 2013 compared to 9.1 ± 0.88 in
256 2014. The MAM for fledgling success per pair showed that over the breeding season the
257 fledgling success increased relative to margin AES, oilseed rape, boundary and farmyard
258 buildings area coverage (Table 2; Figure 3).

259

260 **3.3. Per-attempt productivity**

261 The mean clutch size was 5.44 ± 0.38 in 2013 and 5.60 ± 0.29 in 2014. There was no
262 evidence of a relationship between clutch size per-breeding attempt and habitat variables as
263 our MAM was the null model.

264

265 Tree sparrows hatched an average of 4.15 ± 0.29 and 4.53 ± 0.29 chicks per breeding attempt
266 in 2013 and 2014, respectively. Estimates from our model of tree sparrow hatching success
267 per-attempt suggest that success significantly decreased with the area of margin AES,
268 WBSM, grassland and woodland, and increased with the area of farmyard buildings (Table
269 2).

270

271 The number of fledglings per-attempt in 2013 was 3.13 ± 0.22 and 4.15 ± 0.11 in 2014. The
272 MAM showed that fledging success increased as the areas of boundary, margin AES, oilseed
273 rape, habitat and farmyard buildings increased but was reduced with increased woodland

274 coverage (Table 2). Fledgling success was higher in second and third broods when compared
275 to first broods. The number of fledglings per-attempt, however, was negatively correlated
276 with the area of WBSM and woodland surrounding nest boxes and positively correlated with
277 the area of oilseed rape. The number of fledglings was higher in second broods when
278 compared to first broods.

279

280 **3.4. Chick food abundance in agricultural habitats**

281 Tree sparrow chick food abundance was significantly higher in margin AES when compared
282 with spring cereal ($z = -3.85$, $p < 0.001$), winter cereal ($z = -6.60$, $p < 0.001$) and WBSM ($z = -$
283 2.25 , $p < 0.05$), but no significant difference between margin AES and oilseed rape ($z = -1.05$,
284 $p = 0.29$) or grassland ($z = -1.03$, $p = 0.31$; Figure 4).

285

286 **3.5. Density Dependence**

287 The average clutch size, hatching success, number of fledglings and fledgling success per
288 breeding attempt showed no significant relationship with colony size (Table B1).

289

290 **Discussion**

291 This study explored tree sparrow habitat associations and productivity over the nesting period
292 in relation to the provision of key resources by AES options. For passerines, previous studies
293 have shown that poorer breeding success was found where invertebrate abundance had been
294 reduced through agricultural intensification (Bradbury and Stoate, 2000; Brickle et al., 2000;
295 Hart et al., 2006). For that reason, our finding that fledging success (in total productivity and
296 per-attempt models) increased with the area of AES margin, confirmed that these AES

297 habitats benefitted tree sparrows. In addition, we demonstrated that the abundance of foliar
298 tree sparrow chick food was significantly higher in this habitat, highlighting the potential role
299 AES margins can play in chick food provisioning. The value of AES margins to farmland
300 biodiversity has been widely studied (Vickery et al, 2009) with studies from the United
301 Kingdom demonstrating that grass margins are heavily exploited by a variety of species
302 including yellowhammer, corn bunting and skylark while provisioning nestlings (Brickle and
303 Harper, 2000; Morris et al., 2001; Douglas et al., 2009). These habitats however, do not
304 always contain appropriate chick food levels for other farmland birds. Holland et al., (2014)
305 found that flower-rich AES habitats contain high levels of grey partridge chick food, but
306 levels of general chick food were no higher than in other commonly found AES habitats.
307 Consequently, given the variation in chick food requirements and foraging strategies
308 (Holland et al., 2006), a range of habitats offering different invertebrate resources and of
309 varying vegetation structure is likely to be needed to adequately provide for a suite of
310 farmland birds. The finding that margin AES habitats had a negative influence on hatching
311 success, is however more difficult to explain. It may be that as this habitat is a poor source of
312 seed resources for granivorous adults it therefore does not help adults reach breeding
313 condition.

314

315 We identified a positive relationship between fledging success (in total productivity and per-
316 attempt models) and farmyard buildings, in addition to the number of fledglings per-attempt
317 and farmyard buildings. These relationships may reflect the role of farmyards in providing
318 spilt grain or livestock feed which might influence the distribution or density of pairs
319 (Gillings et al., 2005; Lack, 1995). Alternatively, untidy yards and buildings with areas of
320 grass, common nettles *Urtica dioica* or European elder *Sambucus nigra* may increase chick
321 food resources. Interestingly Gillings et al., (2005) found that a range of other granivorous

322 species including house sparrow *Passer domesticus*, common chaffinch *Fringilla coelebs* and
323 greenfinch *Carduelis chloris*, are positively associated with farmyard availability. It is
324 important to note that sites were excluded from the study where nest boxes were located on
325 houses or where housing and gardens fell within the absolute foraging range of a colony. This
326 was done to remove the influence of garden feeders on analysis and ensure the results
327 reflected a truly farmland environment.

328

329 Field and Anderson (2004) suggested that tree sparrow colonies utilise winter seed food
330 resources, a finding that is confirmed by this study as colony size was shown to increase with
331 the area of WBSM. Provision of seed food over winter has also resulted in higher breeding
332 densities of other granivorous species (Hole et al., 2002; Robinson et al., 2002; Siriwardena
333 et al., 2007). However, despite the importance of WBSM over winter, our results point to a
334 negative relationship between two measures of breeding success: hatching success per-
335 attempt and the number of fledglings produced per breeding attempt. Contrary to Holland et
336 al., (2014) where suction sampling was used, in this study WBSM were not found to contain
337 high densities of chick food insects (although a different sampling method was used that also
338 collected invertebrates from the ground), therefore, this relationship may reflect the low
339 abundance of chick food resources within one of their preferred habitats. McHugh et al.,
340 (2016b) showed that tree sparrow chick diet was affected by the coverage of WBSM present,
341 with chicks found to consume more seed with increasing WBSM area. This increase in seed
342 consumption may impact the total number of chicks surviving to the fledgling stage as plant
343 foods are a poor source of protein compared to invertebrates (Potts, 2012). Other studies
344 showed that consuming less invertebrates led to reduced growth rates and depressed body
345 conditions in yellowhammer chicks (Douglas et al. 2012), slower growth rates and
346 consequently fledgling weights in great *Parus major* and blue tits *Cyanistes caeruleus* (Naef-

347 Daenzer and Keller, 1999), and delayed fledging in house martins *Delichon urbicum*
348 (Johnston, 1993).

349

350 WBSM was also found to have no significant influence on the other measures of productivity
351 under investigation. Seasonality may be key to the non-significant impact of this habitat.

352 WBSM is primarily a winter habitat and for the majority of the tree sparrow breeding season
353 the mixes sown that year were comprised of bare earth or short vegetation ($0.35\text{m} \pm 0.22\text{m}$)
354 that would support few invertebrates. Invertebrate abundance increases with vegetation
355 height and structural diversity of a habitat (Eyre and Leifert, 2011; Morris and Lakhani,
356 1979), therefore WBSM may only provide invertebrates in high abundance when they have
357 had some time to develop.

358

359 Despite the high abundance of tree sparrow chick food items in grassland, our measures of
360 fledging success showed no relationship with the area of this habitat. Grassland area,
361 however, displayed a significant negative relationship with colony size and hatching success
362 per-attempt and likewise Field and Anderson (2004) found grassland was avoided as a
363 foraging habitat. Tree sparrow may avoid grassland as the vegetation structure of many
364 intensively-managed swards (eg vegetation height, density and lack of heterogeneity) renders
365 it unsuitable as a foraging habitat by inhibiting access to the food resources present or by not
366 allowing birds to conduct their vigilance behaviour to avoid predation (Butler et al., 2005;
367 Shaub et al., 2010; Whittingham and Markland, 2002).

368

369 Our results showed a positive relationship between oilseed rape and fledgling success in total
370 productivity per pair and per-attempts models and with the per-attempt number of fledglings.

371 Winter wheat and oilseed rape are linked through common rotational practices and the high
372 multi-collinearity of these two variables led to the exclusion of winter wheat from our models.
373 The positive effect of oilseed rape on fledgling success implies that crop type could be a
374 central driver of foraging habitat selection, and its relationship with winter wheat suggests
375 that habitat use may be dependent on the landscape context of farms as has been shown in
376 other taxa (e.g. Winqvist et al., 2011). Oilseed rape was also found to contain one of the
377 highest levels of chick-food. This has also been reported in Western Poland, where the mean
378 biomass of insects populating oilseed rape was higher than either spring or winter cereals
379 (Karg and Ryszkowski, 1996). Additionally, Perkins et al., (2007) showed in a seed food
380 preference experiment that oily seeds such as brassicas are exploited by tree sparrow and it is
381 possible that oilseed rape seeds may play an important role in the diet of older chicks because
382 they are small and therefore easy for chicks to handle, in addition to being high in energy
383 (Jones and Earle, 1966; Duke, 1983; Diaz, 1990). Ripening oilseed rape seeds are also know
384 to be important in diet of other granivorous birds i.e. linnet, reed bunting and turtle dove
385 (Gruar et al, 2006).

386

387 Fledgling success was also positively related to the proportion of boundary habitat present,
388 tree sparrows have previously been recorded collecting Lepidoptera larva and aphids by
389 searching shrub leaves (Summer-Smith, 1995). A negative relationship was recorded between
390 woodland area and: 1. total eggs in our total productivity model, 2. Per-attempt hatching
391 success, 3. The number of fledglings per-attempt and 4. per-attempt fledging success. This
392 may due to the association of tree sparrows with open habitats such as farmland (Field and
393 Anderson, 2004; Field et al., 2008).

394

395 Contrary to Svensson (2006) we found no significant relationship between population density
396 and breeding success. We expect that population density is more likely to limit tree sparrow
397 productivity where competition for nest boxes is high, as found by Svensson (2006). In his
398 study, 67% of boxes were occupied compared to our 39.54% and 41.06% occupancy rates in
399 2013 and 2014 respectively. WBSM was negatively related to several measures of breeding
400 success and the lack of a population density impact on our results implies that WBSM is
401 influencing settlement patterns, attracting birds in winter which then stay in these areas to
402 breed if boxes are nearby. Provisions of over-winter food may, therefore, have removed one
403 limiting factor for this species (overwinter survival), only for it to be replaced by another, this
404 is perhaps evidenced by the fact that the colonies were still growing. Future schemes must
405 ensure that a package of measures are provided (i.e. winter seed food and invertebrate-rich
406 habitat) around nest boxes if colonies are to prosper.

407

408 **6. Conclusions**

409 The results of this study suggest that placing AES habitats which provide an abundance of
410 chick-food invertebrates within the summer foraging range of occupied nest boxes benefits
411 the breeding performance of tree sparrows. The association of large tree sparrow colonies
412 with WBSM was not surprising as this habitat is designed to provide seed for granivorous
413 species during the winter (Hancock and Wilson, 2003) and tree sparrows are relatively
414 sedentary. The implications of reduced fledging success in relation to WBSM is an important
415 aspect of tree sparrow conservation that needs to be addressed and highlights the importance
416 of providing a package of AES measures that deliver the year-round requirements of target,
417 declining bird species on farms. More specifically, we have demonstrated the need to provide

418 suitable invertebrate-rich AES options close to (and certainly within the foraging range of)
419 suitable nesting habitats for birds that provision their nestlings primarily on invertebrates.

420

421 **7. Acknowledgements**

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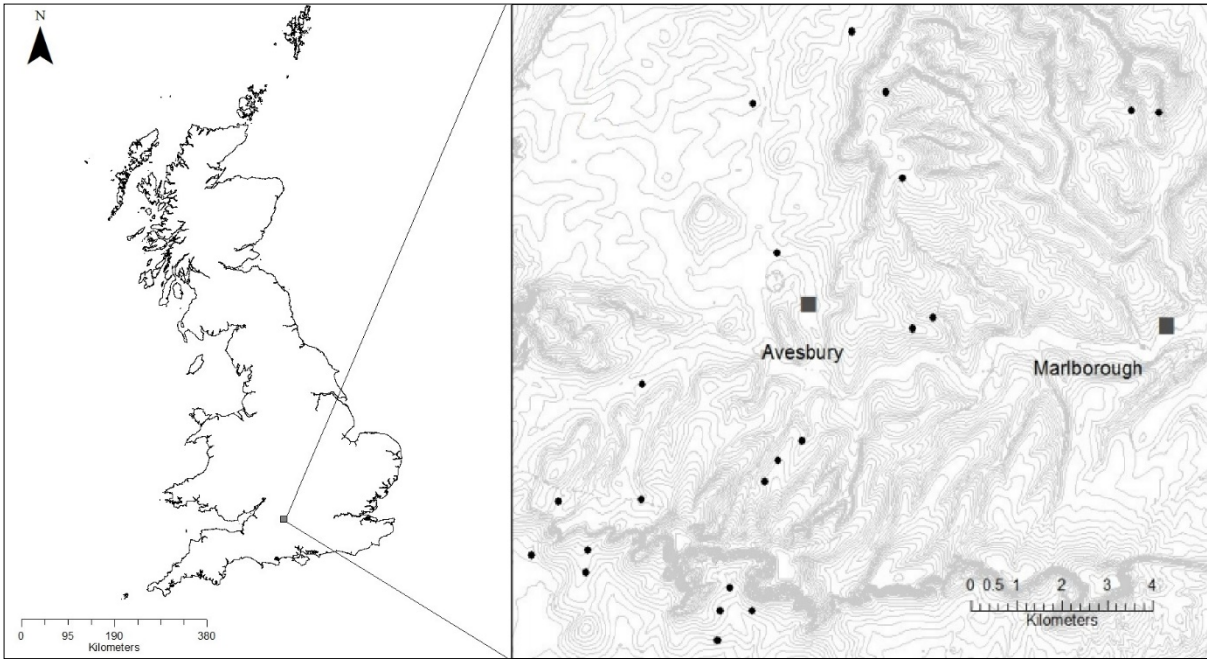


Figure 1. Map showing (a) the location of the sampling region in Southern England and (b) the tree sparrow colony locations within this region relative to two settlements.

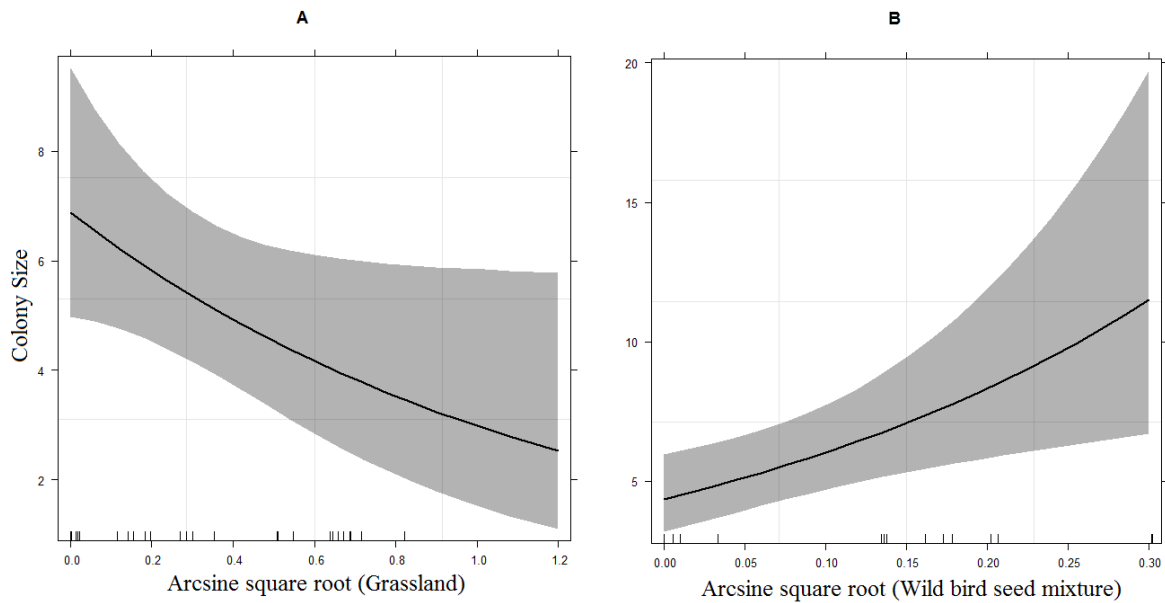


Figure 2. Predicted values for colony size relative to two significant variables (Table 2) chosen by backward stepwise deletion from the full GLM: a) grassland and b) wild bird seed mixture. For each covariate displayed probabilities are adjusted relative to the effects of the other variables modelled. A 95% confidence interval is drawn around the estimated effect.

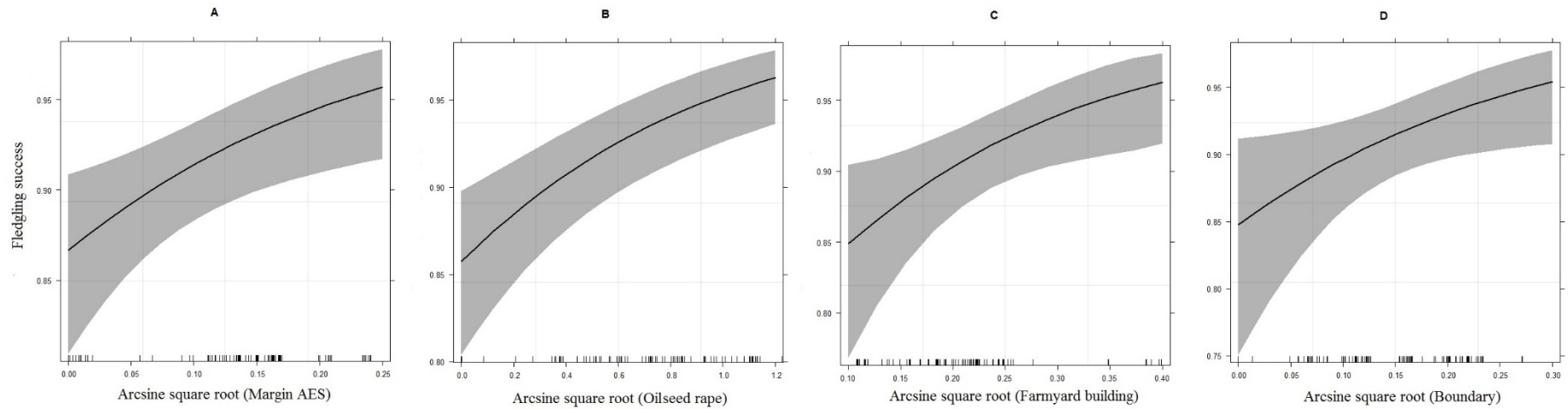


Figure 3. Predicted values for fledging success per pair relative to four significant variables (Table 2) chosen by backward stepwise deletion from the full GLMM: a) margin AES, b) oilseed rape, c) farmyard building and d) boundary. For each covariate displayed probabilities are adjusted relative to the effects of the other variables modelled. A 95% confidence interval is drawn around the estimated effect.

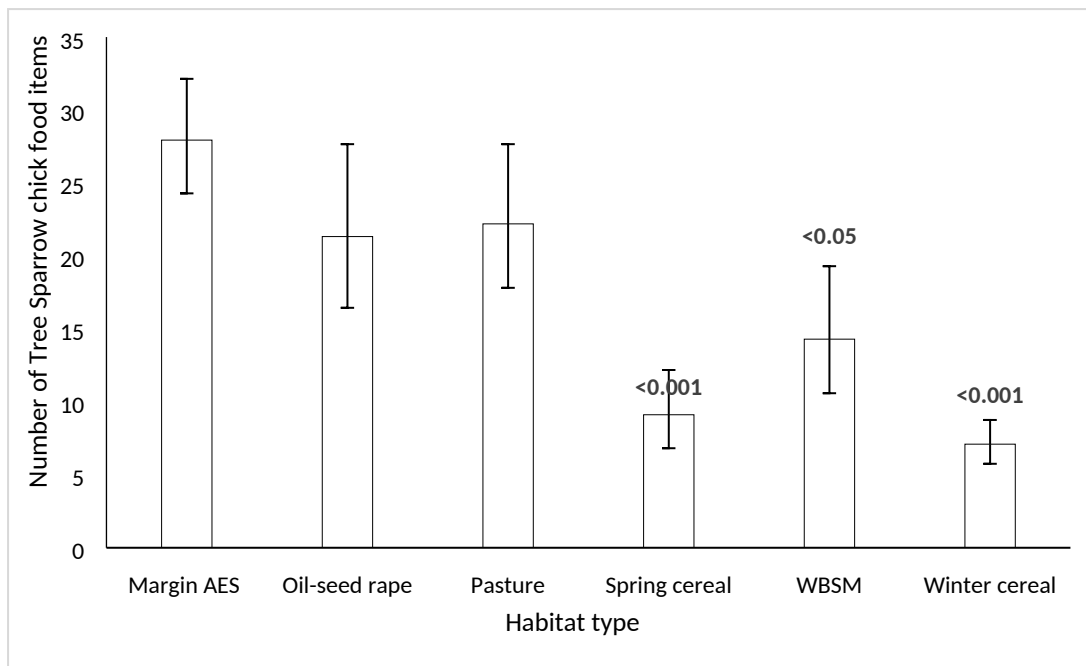


Figure 4. The number of tree sparrow chick food items (mean \pm SE) recorded in pooled habitat types. The mean and standard errors of model estimates were back transformed for graphical representation. P-values refer to significant deviations from the reference variable, margin AES.

Table 1. Structure of GLMs and GLMMs used for analysis, fixed effects were included in models simultaneously. Habitat area measurements refer to Appendix 1 “habitat category” codes and represent habitats present within the 200m adult foraging ranges from nest boxes.

| | Model type | Response | Error structure/ link function | Fixed Effects | Random effects |
|------------------------------------|-------------------|--------------------------------------|---|---|------------------------|
| Colony size | GLM | Colony size | Quasipoisson/log | Mean permanent habitat category area measurements, year | N/A |
| Total productivity per pair | GLMM | Total eggs | Poisson/log | Habitat category area measurements | Colony, Nest box/Year |
| | GLMM | Hatching success | Binomial/logit | Habitat category area measurements | Colony, Nest box/Year |
| | GLMM | Total fledglings | Poisson/log | Habitat category area measurements | Colony, Nest box/Year |
| | GLMM | Fledgling success | Binomial/logit | Habitat category area measurements | Colony, Nest box/Year |
| | GLMM | Number of attempts | Poisson/log | Habitat category area measurements | Colony, Nest box/Year |
| Per-attempt productivity | GLMM | Clutch size | Poisson/log | Habitat category area measurements, brood | Colony, Nest box/ Year |
| | GLMM | Hatching Success | Binomial/logit | Habitat category area measurements, brood | Colony, Nest box/ Year |
| | GLMM | Fledging’s per brood | Poisson/log | Habitat category area measurements, brood | Colony, Nest box/Year |
| | GLMM | Fledging success | Binomial/logit | Habitat category area measurements, brood | Colony, Nest box//Year |
| Chick Food abundance | GLMM | Chick food | Poisson/log | Habitat category | Colony |
| Density dependence | GLM | Mean clutch size per colony | Poisson/log | Colony size, year, brood | N/A |
| | GLM | Mean hatching success per colony | Quasibinomial/logit | Colony size, year, brood | N/A |
| | GLM | Mean number of fledglings per colony | Poisson/log | Colony size, year, brood | N/A |
| | GLM | Mean fledgling success per colony | Quasibinomial/logit | Colony size, year, brood | N/A |

Table 2. Estimated parameter and p values for each fixed effect present in MAMs relating to colony size, total productivity per pair of sparrows and per-attempt productivity. Null models are not presented.

| | Model | Fixed Effects | Estimate ± SE | Z-value | P | |
|------------------------------------|---------------------------------|--------------------------|------------------------|----------------|----------|--------|
| Colony size | Colony size | Intercept | 1.76 ± 0.19 | 6.43 | <0.001 | |
| | | Wild bird seed mixture | 3.22 ± 1.10 | 2.92 | <0.01 | |
| | | Grassland | -0.84 ± 0.41 | -2.02 | <0.05 | |
| Total productivity per pair | Total eggs | Intercept | 2.42 ± 0.04 | 58.24 | <0.001 | |
| | | Woodland | -0.93 ± 0.32 | -2.91 | <0.01 | |
| | Hatching success | Intercept | 1.78 ± 0.42 | 4.22 | <0.001 | |
| | | Margin AES | -3.81 ± 1.69 | -2.26 | <0.05 | |
| | | Wild bird seed mixture | -6.72 ± 1.76 | -3.82 | <0.001 | |
| | | Farmyard building | 6.32 ± 2.14 | 2.95 | <0.01 | |
| | | Grassland | -1.16 ± 0.53 | -2.21 | <0.05 | |
| | | Woodland | -3.63 ± 1.78 | -2.04 | <0.05 | |
| | Fledgling success | Intercept | -0.39 ± 0.56 | -0.71 | 0.47 | |
| | | Margin AES | 4.91 ± 1.79 | 2.74 | <0.01 | |
| | | Oilseed rape | 1.22 ± 0.28 | 4.39 | <0.001 | |
| | | Farmyard building | 5.09 ± 1.97 | 2.59 | <0.01 | |
| | | Boundary | 4.38 ± 2.01 | 2.18 | <0.05 | |
| | Number of Broods | Intercept | 0.69 ± 0.06 | 11.45 | <0.001 | |
| | | Woodland | -0.60 ± 0.49 | -1.24 | 0.216 | |
| | Per-attempt productivity | Hatching success | Intercept | 1.62 ± 0.44 | 3.69 | <0.001 |
| | | | Margin AES | -3.88 ± 1.73 | -2.25 | <0.05 |
| | | | Wild bird seed mixture | -6.75 ± 1.80 | -3.76 | <0.001 |
| Farmyard building | | | 6.55 ± 2.20 | 2.98 | <0.01 | |
| Grassland | | | -1.18 ± 0.56 | -2.11 | <0.05 | |
| Woodland | | | -3.70 ± 1.82 | -2.04 | <0.05 | |
| Brood (2 nd) | | | 0.57 ± 0.15 | 3.86 | <0.001 | |
| Brood (3 rd) | | | -0.12 ± 0.16 | -0.76 | 0.44 | |
| Number of fledglings | | Intercept | 1.08 ± 0.10 | 11.14 | <0.001 | |
| | | Wild bird seed mixture | -1.08 ± 0.34 | -3.22 | <0.001 | |
| | | Oilseed rape | 0.15 ± 0.06 | 2.62 | <0.001 | |
| | | Farmyard buildings | 1.22 ± 0.43 | 2.81 | <0.001 | |
| | | Woodland | -0.85 ± 0.38 | -2.11 | <0.01 | |
| | | Brood (2 nd) | 0.22 ± 0.05 | 3.96 | <0.001 | |
| Fledgling success | | Brood (3 rd) | 0.09 ± 0.07 | 1.31 | <0.01 | |
| | | Intercept | -0.90 ± 0.57 | -1.56 | 0.12 | |
| | | Margin AES | 5.12 ± 1.78 | 2.89 | <0.05 | |
| | | Oilseed rape | 1.09 ± 0.26 | 4.16 | <0.001 | |
| | Farmyard buildings | 7.12 ± 2.17 | 3.29 | <0.05 | | |
| | Boundary | 3.96 ± 1.99 | 1.99 | <0.05 | | |
| | Woodland | -3.28 ± 1.65 | -1.99 | <0.05 | | |
| Brood (2 nd) | 0.94 ± 0.19 | 5.04 | <0.001 | | | |
| Brood (3 rd) | 0.45 ± 0.20 | 2.16 | <0.05 | | | |

Appendix A

Table A1. Pooled and component habitat types present within foraging distance (200m) of tree sparrow nest boxes. The habitat categories are explanatory variables in our colony size, total productivity per-pair and per-attempt models.

| Habitat category | Component | Mean ± SE |
|-------------------------------|---|----------------------------------|
| Boundary | Hedges, tree line, grassy verges, scrub (young plantation or deciduous scrub) | 3120.59 ± 151.91m ² |
| Farmyard building | Roads, tracks, farm buildings | 6642.23 ± 292.68m ² |
| Grassland | Permanent and temporary grassland | 15131.58 ± 1180.56m ² |
| Margin AES | 2m, 4m and 6m grass buffer strips, floristically enhanced margins, pollen and nectar margins, uncropped field corners | 1922.29 ± 99.608m ² |
| Oil-seed rape | Oil-seed rape | 38676.00 ± 2172.01m ² |
| Other arable | Spring beans, maize | 3514.18 ± 595.45m ² |
| Spring cereal | Spring wheat, spring barley | 7441.27 ± 1141.13m ² |
| Water | Lakes, ponds, streams and ditches | 70.61 ± 16.10m ² |
| Wild bird seed mixture | Wild bird seed | 2424.43 ± 148.83m ² |
| Winter cereal | Winter wheat, winter barley | 44946.59 ± 1986.38m ² |
| Woodland | Deciduous and coniferous woodland | 1725.64 ± 162.99m ² |

Appendix B

Table B1. Estimated parameter and p values for each fixed effect present in density dependence models for clutch size, hatching success, number of fledglings and fledgling success.

| Model | Fixed Effects | Estimate ± SE | Z-value | P |
|-----------------------------|--------------------------------------|----------------------|----------------|------------------|
| Clutch size | Intercept | 1.17 ± 0.33 | 3.61 | <0.001 |
| | Colony size | -0.03 ± 0.04 | -0.83 | 0.41 |
| | Brood (2 nd) | 0.47 ± 0.47 | 1.00 | 0.32 |
| | Brood (3 rd) | -0.06 ± 0.48 | -0.13 | 0.90 |
| | Year (2014) | 0.12 ± 0.26 | 0.47 | 0.64 |
| | Colony size:Brood (2 nd) | 0.02 ± 0.06 | 0.37 | 0.71 |
| | Colony size:Brood (3 rd) | 0.04 ± 0.06 | 0.66 | 0.51 |
| Hatching success | Intercept | 1.17 ± 0.33 | 3.61 | <0.001 |
| | Colony size | -0.03 ± 0.04 | 0.81 | 0.41 |
| | Brood (2 nd) | 0.47 ± 0.47 | 1.00 | 0.32 |
| | Brood (3 rd) | -0.06 ± 0.49 | -0.29 | 0.90 |
| | Year (2014) | 0.12 ± 0.26 | 0.47 | 0.61 |
| | Colony size:Brood (2 nd) | 0.02 ± 0.06 | 0.37 | 0.71 |
| | Colony size:Brood (3 rd) | 0.04 ± 0.06 | 0.66 | 0.51 |
| Number of fledglings | Intercept | 1.12 ± 0.15 | 7.72 | <0.001 |
| | Colony size | -0.00 ± 0.02 | -0.24 | 0.80 |
| | Brood (2 nd) | 0.26 ± 0.18 | 1.44 | 0.14 |
| | Brood (3 rd) | 0.12 ± 0.21 | 0.58 | 0.56 |
| | Year (2014) | 0.22 ± 0.10 | 2.07 | 0.56 |
| | Colony size:Brood (2 nd) | 0.00 ± 0.02 | 0.02 | 0.99 |
| | Colony size:Brood (3 rd) | 0.00 ± 0.02 | 0.06 | 0.95 |
| Fledgling success | Intercept | 1.11 ± 0.34 | 3.22 | <0.01 |
| | Colony size | -0.01 ± 0.04 | -0.34 | 0.74 |
| | Brood (2 nd) | 0.69 ± 0.53 | 1.30 | 0.19 |
| | Brood (3 rd) | 0.16 ± 0.53 | 0.29 | 0.77 |
| | Year (2014) | 1.11 ± 0.31 | 3.62 | <0.01 |
| | Colony size:Brood (2 nd) | -0.02 ± 0.06 | -0.27 | 0.79 |
| | Colony size:Brood (3 rd) | -0.01 ± 0.06 | -0.18 | 0.86 |