

1 **Testing bespoke management of foraging habitat for European Turtle Doves**

2 *Streptopelia turtur*

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14 Abbreviations: AES Agri-Environment Scheme

15 ES Environmental Stewardship

16 HLS Higher Level Stewardship

17 ELS Entry Level Stewardship

18 GLMM Generalized Linear Mixed-effects Model

19 Running head: Testing vegetation structure and seed provision

20 **Abstract**

21 Agri-environment schemes (AES) are increasingly being employed to mitigate against
22 biodiversity loss in agricultural environments. The European Turtle Dove *Streptopelia*
23 *turtur* is an obligate granivorous bird in rapid decline within both the UK (-96% since
24 1970) and across continental Europe (-77% since 1980), despite widespread uptake of
25 AES. Here, we assess the efficacy of a potentially new, sown agri-environment option
26 designed to provide abundant, accessible seed for *S. turtur* during the breeding
27 season. During summer 2011 we compared vegetation structure and seed provision on
28 trial plots to control habitat types (existing agri-environment options thought to
29 potentially provide *S. turtur* foraging habitat) to assess whether trial plots performed
30 better for foraging *S. turtur* than control habitats. In September 2011 all trial plots
31 were topped (cut) and half of a subset of trial plots were then scarified (60% of soil
32 surface disturbed). Vegetation structure on topped, and topped and scarified trial
33 plots was measured during summer 2012 to determine which management regime was
34 most effective in maintaining suitable sward structure and seed provision into the
35 second year. No control habitat type produced as much seed important in *S. turtur* diet
36 as trial plots at any point during year one. Trial plots provided accessible vegetation
37 structure early in the season with no difference in vegetation metrics between trial
38 plots and previously published data on *S. turtur* foraging locations. However, to allow
39 later access, management is required during mid-June to open up the sward through
40 localized topping or scarification. Vegetation structure during year two was generally
41 too dense to attract foraging *S. turtur*. However, scarifying trial plots during the
42 September following sowing encouraged self-seeding of *Fumaria officinalis* (a plant
43 species historically forming a significant proportion of *S. turtur* diet during the
44 breeding season) into the second year, with this species present in 16% of scarified

45 trial plots compared to only 4% of topped trial plots during year two. Thus, autumn
46 scarification, possibly followed by topping or scarification of part of the trial plots in
47 June, is necessary for trial plots to provide more seed and access for *S. turtur* than
48 existing agri-environment options during year two. We recommend modifications to
49 our original seed mix in order to reduce vegetation density and improve vegetation
50 structure. The study provides an example of the need to strike the right balance
51 between food abundance and accessibility, through vegetation structure, when
52 designing agri-environment scheme management options that provide food for birds.

53

54 **Keywords:** agri-environment; arable plant; *Fumaria officinalis*; seed plot; farmland
55 management; food abundance; food accessibility; vegetation management

56 **Introduction**

57 Agricultural intensification over recent decades has been linked to declines in
58 farmland wildlife, as agricultural efficiency and productivity have increased to feed a
59 growing human population (Donald et al. 2001, Robinson and Sutherland 2002,
60 Reidsma et al. 2006). In recent decades, agri-environment schemes (AES) have been
61 increasingly utilised to mitigate farmland biodiversity declines across Europe and
62 North America. However, the impacts of most of these schemes on widespread
63 species have been modest or mixed (Kleijn et al. 2006, Birrer et al. 2007). Some of
64 the strongest evidence of AES reversing declines involve range-restricted bird
65 species, e.g. *Emberiza cirrus* (Peach et al. 2001) and *Tetrax tetrax* (Bretagnolle et al.
66 2011), when subject to much higher levels of targeting and advisory support than that
67 available under standard AES (Perkins et al. 2011), but population-level benefits are
68 not apparent for most widespread bird species (e.g. Davey et al., 2010).

69 As of February 2014, 57 % of English farmland was managed under Entry
70 Level Stewardship Agreements, with a further 14 % managed under Higher Level
71 Stewardship Agreements (Natural England 2014); despite this, the UK population of
72 *S. turtur* has declined by 95 % since 1970 (Eaton et al., 2013). This is paralleled by a
73 75 % decline across Europe since 1980 (PECBMS 2012). As the species is a long-
74 distance migrant, it is possible that carry-over effects from wintering grounds or
75 migration may have contributed towards the decline (e.g. Norris & Marra, 2007;
76 Eraud et al., 2009). However, factors operating on the breeding grounds are thought,
77 at least in part, to be driving the UK population trend: evidenced by the fact that the
78 number of breeding attempts per pair has halved since the onset of the decline
79 (Browne and Aebischer 2004). Nesting habitat is thought unlikely to be limiting, as
80 nesting areas previously utilized by *S. turtur*, in which habitat has not altered, are no

81 longer used due to a reduced density of breeding birds (Dunn & Morris, 2012). Over
82 the same time-scale as the population decline, *S. turtur* has shown a dietary switch
83 from the seeds of wild plants typical of arable fields to anthropogenic sources of
84 cereal grain and oilseed rape (e.g. following harvest operations or as spills in
85 farmyards), reflected in the diet of both adults and nestlings (Browne & Aebischer,
86 2003a), while territories have been lost from areas with less bare ground and fallow
87 (Dunn and Morris 2012); traditionally, habitats rich in arable plants. This suggests
88 that a reduced availability of arable plant seeds has led to an increased reliance on
89 anthropogenic food resources, especially early on in the breeding season (Browne and
90 Aebischer 2003a).

91 *S. turtur* is ecologically unique in Europe, being the only Afro-Palaearctic
92 migrant that is an obligate granivore, and in the UK, with the exception of *Carduelis*
93 *cannabina*, the only species reliant upon seed food throughout the annual cycle
94 (Wilson et al., 1996). Other dove and pigeon species have more generalist diets,
95 taking invertebrates and green plant matter when seed availability is low (Murton et
96 al., 1964). The reduction in the availability of seeds from arable plants has been
97 largely driven by the susceptibility to herbicides (Marshall et al., 2001; Moorcroft et
98 al., 2006) and the switch to autumn sown crops, which has reduced the amount of
99 overwinter fallow for arable plants to mature and, in the case of *Fumaria officinalis*,
100 a plant historically important in *S. turtur* diet (Murton et al. 1964), has also reduced
101 tillage during the peak germination period in the spring. The switch in *S. turtur* diet
102 may have additional implications: wheat is generally considered a low-quality diet for
103 columbiformes (e.g. Costantini, 2010) and this switch may have contributed to the
104 truncation of the breeding season (Browne and Aebischer 2003b). Diet quality can
105 have knock-on effects on a range of ecological traits (e.g. sexually selected traits

106 (Meadows et al., 2012), clutch size (Vergauwen et al., 2012), and survival (Browne et
107 al., 2006)), and the nutritional implications for *S. turtur* of this dietary change are
108 unknown. A more direct result of the change in *S. turtur* feeding ecology might be an
109 increased risk of transmission of disease: *Trichomonas gallinae*, a protozoan parasite
110 directly transmitted at food and water sources, has been found at very high prevalence
111 in *S. turtur* and in grain piles and water on UK breeding grounds (Lennon et al.,
112 2013), and confirmed as likely cause of death in both adult and nestling birds
113 (Stockdale et al., in press). Thus, without stringent hygiene precautions, the option of
114 supplementary feeding by providing seed in piles or via hoppers has the potential to
115 increase parasite transmission and, alone, is unlikely to provide a satisfactory solution
116 for this species. The provision of sown or naturally regenerating semi-natural foraging
117 habitat in close proximity to nest sites (crucial to minimize energetic costs to breeding
118 adults) is therefore likely to be key conservation measure for the species on its UK
119 breeding grounds.

120 Current English agri-environment options deliver nesting habitat for *S. turtur*
121 through management of hedgerows, scrub and orchard under Environmental
122 Stewardship (ES) management, but options providing semi-natural seed food
123 resources are limited. Baker et al. (2012) found a positive localized population
124 response to arable margins (an amalgam of several different option types), but many
125 of these margin management options often result in a relatively tall, dense sward that
126 is unlikely to be used by foraging *S. turtur*, which prefer relatively open foraging sites
127 with sparse vegetation cover (Murton et al., 1964; Browne & Aebischer, 2003a). In
128 the ES AES in England, uncropped, cultivated margins (primarily designed to benefit
129 arable plants) and the addition of wildflowers to field corners and buffer strips may be
130 better suited to the requirements of foraging *S. turtur*, but they have low uptake, e.g.

131 due to perceived or actual problems with pernicious weeds on some soil types, or high
132 costs of establishment and management to maintain the correct sward structure.
133 Although many European AES contain rotational fallow options, the withdrawal of
134 the set-aside scheme funded under Pillar One of the Common Agricultural Policy and
135 other economic drivers, has led to a Europe-wide reduction in the amount of fallow
136 available (Morris et al., 2011), further reducing the area of potentially suitable
137 foraging habitat for *S. turtur*.

138 Here, we describe a two-year trial of a sown seed mix designed to provide an
139 accessible source of seed for *S. turtur* throughout the breeding season. We used 29
140 trial plots across six farms to address the following questions:

- 141 1. How do the *S. turtur* trial plots compare to existing AES options in providing
142 a source of accessible seed food during the first year after sowing?
- 143 2. Which management (scarification or topping in the autumn of the first year) is
144 more successful at continuing the provision of accessible seed into the second
145 year, and how does this compare to existing AES options that may provide
146 food for *S. turtur*?
- 147 3. How do trial plots compare to previously published data documenting
148 vegetation structure of foraging locations used by *S. turtur*?

149

150 **Methods**

151 **Site selection**

152 Six trial plot farms were selected during summer 2010, according to the
153 presence of at least two pairs of territorial *S. turtur* within a 1 km² consisting mostly
154 of ‘typical’ arable land, with no more than 5 % land currently under seed-rich non-
155 cropped management such as wild bird seed mix or fallow. Between two and seven
156 (mean \pm 1 SE: 5.67 \pm 0.4) trial plots covering two ha in total were sown on each farm
157 (except one farm where trial plots only covered 1 ha), giving a total of 29 trial plots;
158 trial plots ranged in size from 0.063 to 1.178 ha (mean \pm 1 SE: 0.301 \pm 0.046 ha). Six
159 control farms were within 26 km (mean \pm 1 SE: 11.84 \pm 3.15 km) of their
160 corresponding trial plot farm and selected on the same basis, but with no trial
161 intervention: ideally control farms would have been within 10 km of their respective
162 trial farm, but we were restricted by low *S. turtur* numbers.

163 The trial plot seed mix (detailed in Table 1) consisted of plants known to be
164 important in *S. turtur* diet (Wilson et al., 1996; Browne & Aebischer, 2003a), to
165 provide seed throughout the *S. turtur* breeding season (May – September), and to be
166 largely non-pernicious to cropping and thus acceptable to farmers. The mix was
167 designed to last for at least two years, in order to encourage farmer uptake. Trial plots
168 were sown at the rate recommended by the seed supplier (Kings of Holbeach) at 20
169 kg.ha⁻¹, intended to form a fairly sparse ground cover and ensure seed accessibility.
170 The recommended sowing date for the mix was early – mid September; however, due
171 to late seed delivery and subsequent wet weather the trial plots were sown between
172 late September and mid November (five farms) and during March 2011 on the final
173 farm due to wet ground conditions.

174

175 **Trial Plot Management**

176 During September 2011, following the first *S. turtur* breeding season, trial
177 plots were assessed for structure and invasion by agriculturally pernicious weeds.
178 Trial plots with low weed burdens that were unlikely to be exacerbated by the creation
179 of sparsely vegetated swards (n=19 plots across five farms) were selected for further
180 management trials. Farmers were requested to mow each selected plot, and then
181 scarify half using a power harrow set to scarify 60 % of the plot to a depth of 2.5 cm
182 during September 2011. However, two farmers (nine plots) misinterpreted these
183 instructions and mowed the entirety of half the total number of plots (n=4), scarifying
184 the entirety of the other half of the plots (n=5).

185

186 **Control plot selection and plot measurements**

187 During year one (2011), between two and six (mean \pm 1 SE: 5.5 ± 0.34)
188 control plots were selected on each trial and control farm, giving 66 control plots in
189 total. Control plots were areas considered to form potential alternative *S. turtur*
190 foraging habitats currently available on farms; either options in AES, or other
191 naturally occurring areas or management practices outwith AES. They fell into the
192 following categories (sample size in parentheses): meadow, defined as low-input
193 grassland not cut for silage (seven), floristically enhanced margins (seven), grass
194 margins including paths (17), nectar flower margins (five), wild bird seed mix (17),
195 fallow including areas of failed or sparse crop, areas subsequently planted with
196 vegetable crops, and nesting habitat for *Vanellus vanellus* (13). During year two

197 (2012), between two and four (mean \pm 1 SE: 3.0 ± 0.4) control plots were selected on
198 trial plot farms only. These consisted either of fallow controls (defined as an area
199 where the ground had been disturbed during the previous autumn, and not since been
200 cultivated; n=9) for scarified trial plot sections or second year or older nectar flower
201 controls for mown trial plot sections (n=9), providing a total of 18 control plots in
202 year two.

203 During 2011, measurements were taken from four points within each trial and
204 control plot on three occasions (rounds) throughout the *S. turtur* breeding season,
205 during mid-May, late June- early July, and late July-early August. During 2012,
206 measurements were taken as for 2011, but on only two rounds during May and late
207 June. Two points were 2 m from opposing edges of each plot; two were central at
208 evenly spaced intervals. Points were selected semi-randomly on each occasion by
209 throwing a 0.5 m square quadrat. The % bare ground (to the nearest %) within each
210 quadrat was recorded by eye, along with maximum vegetation height at each point
211 (the highest piece of vegetation touching a disc of 60 mm diameter placed at the
212 central point of the quadrat; \pm 1 cm): measurement of these two variables allowed a
213 direct comparison with previous data from turtle dove foraging locations (Browne and
214 Aebischer 2003a). Vegetation density was assessed at the central point of the quadrat
215 to assess the likelihood of a foraging turtle dove accessing any seed present, using a
216 drop-disc sward stick (disc diameter: 200 mm; disc weight 83 g) lowered gently on to
217 the vegetation; the point at which the disc stopped was considered the density of the
218 vegetation (\pm 1 cm). Vegetation cover was assessed to determine the visibility of
219 potential predators by a foraging turtle dove using a Sigma fish-eye 180° lens attached
220 to a Nikon D50 camera placed at the central point of the quadrat facing upwards.
221 Images were analyzed subsequently to establish % vegetation cover using Gap Light

222 Analyzer (Frazer et al., 1999) version 2.0, with a blue color plane, and with the
223 threshold manually adjusted to control for differing background light intensities.

224 To establish seed density, a standing seed sample was taken from a 20 x 20 cm
225 square adjacent to each quadrat; standing vegetation rooted within the square was
226 collected and frozen for subsequent analysis. The soil within the square was also
227 collected to a depth of 0.5 cm and frozen for subsequent analysis of any fallen seed
228 accessible to *S. turtur*. Subsequently, seed was extracted from standing seed and soil
229 samples, separated according to species, identified to family level (or species level
230 where possible) and dried in a 50 °C oven for at least 48 hours, allowing the
231 calculation of dry seed weight of each species within each plot.

232 Seed weight constituted the dry weight of seeds known to be found in *S. turtur*
233 diet as determined through previous dietary studies (Murton et al., 1964; Browne &
234 Aebischer, 2003a; detailed in Appendix A), with the exception of grass. Whilst some
235 grass species are eaten by *S. turtur* (Murton et al., 1964; Browne & Aebischer,
236 2003a), we did not identify grass seeds to species, although the majority of the
237 vegetative grass seeds found within our trial plots were *Alopecurus myosuroides*. As
238 *A. myosuroides* is not considered to be important in *S. turtur* diet (Appendix A), grass
239 species were excluded from analysis.

240 At each trial plot point, the presence or absence of each sown species was
241 recorded, along with vegetation cover of each on a three point categorical scale (1:
242 <10 %; 2: 10-50 %; 3: >50 %). Any other species with greater than 5 % cover was
243 also recorded for each quadrat to examine invasion by unsown plants.

244

245 **Statistical analyses**

246 *Establishment*

247 To determine whether sown species differed in establishment success between
248 trial plots, species was included as a fixed effect in a generalized linear mixed-effects
249 model (GLMM) with binomial error structures, with presence or absence from each
250 point for each species during year one as the response variable. The analysis was
251 carried out at the plot scale; thus Plot ID within Farm were included as nested random
252 effects to control for pseudo-replication of multiple measures within plots and non-
253 independence of plots on the same farms; Round was included as a fixed factor.

254 As sowing rate differed between species, establishment was also expected to
255 differ, so the establishment of each species between plots was considered separately
256 in subsequent analyses to determine whether establishment differed between rounds
257 (time of year sampled), and between sowing periods, for both years one and two
258 separately. For each species, a binomial GLMM was constructed with presence or
259 absence at each point as the response variable. The minimal model contained just the
260 nested random terms of Plot ID within Farm. Round (May, early July and
261 July/August) and sowing date (Sep 2010, Oct 2010, Nov 2010 and Mar 2011) were
262 tested separately against the minimum model and included when $p < 0.1$. An
263 interaction between round and sowing date was also considered.

264

265 *Vegetation Structure and Seed availability*

266 To determine how vegetation structure differed between trial and control plot
267 habitats in year one, GLMMs were constructed with each of vegetation height,

268 density, cover and % bare ground as the response variables, transformed where
269 necessary to fit assumptions of either Poisson (vegetation height and density) or
270 binomial (vegetation cover and % bare ground) error structure. As vegetation
271 changed throughout the season, a separate model was run for each of the three survey
272 rounds. Each model consisted of plot habitat, and nested random effects of Plot ID
273 within farm to control for localized geographic and management effects. To
274 determine whether trial plots produced more seed than control habitats, three Poisson
275 GLMMs (one for each round) were constructed as described above with total seed
276 weight (both fallen and standing) as the response variable. Post hoc contrasts
277 (Crawley, 2007) were used to identify where any differences lay.

278 For year two data, three separate analyses were run, to determine a) whether
279 vegetation structure and seed availability of mown and scarified trial plot sections
280 differed, b) whether vegetation structure and seed availability of mown halves of trial
281 plots differed from nectar flower controls, and c) whether vegetation structure and
282 seed availability of scarified trial plots differed from fallow controls.

283

284 *Comparison of trial plots during years one and two*

285 To examine differences between trial plot structure and seed provision during
286 years one and two, GLMMs were constructed as previously described. Each model
287 consisted of year as a fixed factor, with nested random effects of trial plot ID within
288 farm to control for localized geographic and management effects.

289

290 *Comparison of trial plot vegetation structure to S. turtur foraging sites*

291 To determine whether the vegetation structure within trial plots was
292 significantly different from *S. turtur* foraging sites located during a previous intensive
293 study (Browne & Aebischer, 2003a), we used the published mean, SE and sample size
294 of both vegetation height (0.13 ± 0.01 ; n=114) and % bare ground (59.09 ± 4.41 ,
295 n=114) of locations at which *S. turtur* individuals were observed feeding during 1998
296 – 2000. We compared Browne & Aebischer's (2003a) data from foraging locations to
297 the vegetation height and % bare ground within our trial plots separately, during
298 rounds 1, 2 and 3 of Year 1, and during rounds 1 and 2 of Year 2 in topped and
299 scarified trial plot sections separately using t-tests. Our analysis assumed that feeding
300 habitat preferences of this species have not changed during the previous 15 years.

301 **Results**

302 *Trial plot establishment*

303 During year one, establishment rates differed significantly between sown
304 species at the plot scale ($\chi^2_5=795.61$; $p<0.001$; Figure 2) with establishment in order
305 of highest to lowest rate: *Trifolium pratense* > *T. repens* > *Vicia sativa* > *Medicago*
306 *lupulina* > *Fumaria officinalis* > *Cerastium fontanum*. All species were influenced by
307 the sampling round, with increased establishment as the season progressed for *T.*
308 *repens*, *V. sativa*, *M. lupulina* and *T. pratense*, and decreased establishment for *F.*
309 *officinalis* and *C. fontanum* (Figure 2; Full model results in Appendix B). Sowing
310 date did not directly influence the establishment of any species but an interaction
311 between round and sowing date influenced the establishment of *M. lupulina*, *F.*
312 *officinalis*, *T. pratense* and *T. repens* (Figure 2). *M. lupulina* showed nil
313 establishment early and late in the season in spring-sown trial plots and there was later
314 establishment of *F. officinalis*, *T. repens* and *T. pratense* in spring-sown trial plots
315 (very low establishment during May in spring-sown trial plots; Figure 2).

316 During year two, sampling round influenced the establishment of *T. pratense*
317 only (full model results in Appendix C), with establishment lower during the second
318 round than the first (Figure 3). Management marginally influenced the establishment
319 of both *V. sativa* and *F. officinalis*, with marginally significant trends towards higher
320 establishment of *V. sativa* in mown trial plot sections and higher establishment of *F.*
321 *officinalis* in scarified trial plot sections (Figure 3).

322

323 *Seed availability and vegetation structure*

324 Direction and significance of differences in vegetation structure and seed
325 availability between trial and control plots during year 1 are summarized in Table 3,
326 with full model results and estimates given in Appendix D. No control habitat
327 produced as much seed of plants known to be important in *S. turtur* diet than autumn-
328 sown trial plots during any sampling period (Table 2). During May, vegetation
329 structure was consistently favourable when compared to nectar flower margins, grass
330 margins and meadow but unfavourable when compared to spring-sown trial plots and
331 seedbeds for new wild bird seed mixes (Table 2). Mid- and late-season, vegetation
332 structure was no better in autumn sown trial plots than any control habitat (Table 2).

333 In year two, Habitat only influenced a difference in seed availability in an
334 interaction with round between scarified trial and fallow control plots (full model
335 results in Appendix E), with seed availability on scarified trial plots increasing more
336 than on fallow control plots between rounds (Figure 4a). Bare ground differed
337 between all three habitat comparisons, although the apparent biological difference in
338 round 1 was statistically only marginal between mown and scarified trial plots. Less
339 bare ground was present on both trial managements than their respective controls, and
340 there was marginally more bare ground on scarified trial plots than on mown trial
341 plots (Figure 4b). Vegetation cover differed between both trial habitats and their
342 respective control types, but an apparent biological trend between mown and scarified
343 trial plots during round 1 was not statistically significant. Vegetation cover was
344 higher on both trial habitats than on their respective controls (Figure 4c). Vegetation
345 height and density differed only between scarified trial plots and fallow controls, with
346 both measures higher on scarified trials than on fallow controls (Figures 4d & 4e).

347

348 *Comparison between trial plots during years one and two*

349 Vegetation height, density and cover were all higher during year two than year
350 one (Height: $z_1=2.64$, $p=0.008$; Density: $z_1=3.24$, $p=0.001$; Cover: $z_1=2.80$, $p=0.005$;
351 Figure 5). Bare ground was much reduced, but seed weight was greater during year 2
352 than year 1 (Bare ground: $z_1=-4.45$, $p<0.001$; Seed weight: $z_1=2.01$, $p=0.045$; Figure
353 5).

354

355 *Comparison of trial plot vegetation structure to S. turtur foraging sites*

356 Trial plot vegetation structure, in terms of vegetation height and % bare
357 ground, was similar to previously assessed *S. turtur* foraging locations (Browne &
358 Aebischer, 2003a) only early during Year 1 (round 1; Tables 3a & b). Scarified trial
359 plots early in Year 2 had similar vegetation height (round 1; Table 3a) but
360 significantly lower % bare ground (Table 3b). Trial plot structure at all other times
361 was significantly different from foraging locations (Tables 3a & 3b).

362

363 **Discussion**

364 The rapid decline of the *S. turtur* in the UK and across Europe means that
365 practical conservation action to attempt to reverse the population decline is urgently
366 needed. Previous studies have identified reduced reproductive success (Browne and
367 Aebischer 2004), probably linked to food limitation (Browne and Aebischer 2003a),
368 as the most likely driver of the decline, but existing measures designed to provide
369 seed food may not be appropriate or sufficiently widely adopted to benefit *S. turtur*.
370 Here, we describe a new seed mix tailored to provide *S. turtur* with the seed and
371 vegetation structure needed throughout its breeding season, with an emphasis on seed
372 provision early in the breeding season when food resources are thought to be limiting
373 (Browne and Aebischer 2003a). The trial plots provided plentiful and accessible seed
374 early in the first breeding season. However, refinements in the seed mix and
375 management are required to provide better foraging conditions subsequently.

376 During year one, no control habitat type performed consistently better in terms
377 of seed provision and vegetation structure than autumn-sown trial plots. Habitats that
378 had a more open vegetation structure favoured by *S. turtur* (such as fallow and wild
379 bird cover during late June) produced less seed: indeed, no habitat produced as much
380 seed than autumn-sown trial plots at any point during the season. However, the
381 vegetation in autumn-sown trial plots did grow rapidly and, in many cases, was too
382 dense to allow access by foraging *S. turtur* by late June. Indeed, mean vegetation
383 structure was similar to known *S. turtur* foraging locations (Browne & Aebischer,
384 2003a) only early in Year 1. *S. turtur* were observed using some autumn-sown trial
385 plots during our study: the foraging areas used tended to be those containing areas of
386 bare ground and good establishment of *F. officinalis* (J. C. Dunn, unpubl. data). This
387 is likely to be due to both seed accessibility and availability, and *S. turtur* are known

388 to prefer relatively open areas for foraging (Browne & Aebischer, 2003a), possibly to
389 reduce perceived predation risk (e.g. Whittingham et al., 2006). This suggests
390 management intervention, similar to that carried out for other current AES options, on
391 part of the trial plots would be required during June in order to alter vegetation
392 structure to make them more attractive to foraging *S. turtur* without reducing seed
393 availability within the trial plots. This could be done by mowing strips through each
394 trial plot in order to allow foraging birds access to seeds, or by scarification of strips
395 through each trial plot to create a heterogeneous mosaic. Douglas et al. (2009) suggest
396 similar measures for improving accessibility for birds foraging for invertebrates in AE
397 habitats during the summer months. Whilst we did not assess invertebrate abundance
398 overall within our plots, we demonstrate elsewhere that our plots perform well in
399 terms of attracting foraging pollinators (Dunn et al., 2013) and are thus likely to
400 provide additional benefits for other invertebrate, and consequently avian, taxa (e.g.
401 Moorcroft et al., 2002; Douglas et al., 2009; Dunn et al., 2010a).

402 Differences in establishment between sown species during year one largely
403 correlated with differential sowing rates during the first sampling round, with the less
404 competitive species (*F. officinalis* and *C. fontanum*) decreasing in abundance during
405 the second and third sampling rounds, and the more competitive species (*Trifolium*
406 *spp.*, *V. sativa* and *M. lupulina*) increasing. The lower establishment rates, especially
407 of *F. officinalis*, in spring-sown trial plots, suggests that spring-sowing is unlikely to
408 be viable for the provision of seed early in the *S. turtur* breeding season when birds
409 return from wintering grounds and food availability is thought especially limiting
410 (Browne & Aebischer, 2003a).

411 During year two, management marginally influenced the establishment of both
412 *V. sativa* and *F. officinalis*, with more *V. sativa* in mown trial plots and more *F.*

413 *officinalis* in scarified trial plots. However, establishment of *F. officinalis* was very
414 low overall and was, in fact, four times higher in scarified trial plots, being present at
415 16 % of points in scarified trial plots compared to 4 % of points in mown trial plots.
416 Seed availability increased more between rounds, and was consistently higher on
417 scarified trial plots than on the fallow controls; however, vegetation structure was
418 poorer on scarified trial plots than their controls, especially during the second
419 sampling round. This again suggests that management interventions will be required
420 within the breeding season in order to increase the accessibility of the seed resource to
421 foraging *S. turtur*. Scarification of part of the trial plots during March could also
422 improve establishment during the subsequent breeding season of *F. officinalis*, which
423 is primarily a spring germinating species benefiting from spring cultivation. No
424 beneficial differences in terms of seed provision or vegetation structure were present
425 between mown trial plots and their nectar flower controls. This suggests that mown
426 trial plots performed similarly to second year nectar flower mixes, with no discernible
427 additional benefits for *S. turtur* and indicates that autumn mowing is unlikely to be a
428 viable management strategy for *S. turtur* trial plots, also suggesting that the benefits
429 of mowing in terms of trial plot structure are relatively short-lived. Importantly, seed
430 provision on all trial plots increased between years one and two, suggesting that
431 management which promotes suitable vegetation structure for foraging will also
432 maintain seed supply into the second year and, possibly, beyond.

433 During the 1960s, when the UK *S. turtur* population was increasing, the
434 distribution of *S. turtur* was noted to be very similar to that of *F. officinalis*,
435 suggesting a tight link between the two species (Murton et al. 1964). In the 1960s, *F.*
436 *officinalis* seeds formed 35 – 60 % of *S. turtur* diet. More recently, when wheat and
437 oil seed rape seeds were found to dominate *S. turtur* diet, *F. officinalis* remained in

438 12.8 % and 12.7 % of adult and nestling diets, respectively (Browne & Aebischer,
439 2003a), and foraging sites containing *F. officinalis* were strongly selected in
440 proportion to their availability (Browne & Aebischer, 2003a). This leads to the
441 question of whether *S. turtur* have a specific nutritional requirement fulfilled by *F.*
442 *officinalis*, or whether this species happens to occur more frequently (alone or as part
443 of a wider community of arable plants) in habitat structures selected by foraging *S.*
444 *turtur*. *F. officinalis* has a semi-prostrate structure, with seeds being easily accessible
445 to ground-foraging birds. It is also a poor competitor although it can become a weed
446 in certain crop types, and tends to occur amongst relatively sparse vegetation (more
447 often on light soils), so it may well be that the foraging habitats of *S. turtur* happen to
448 coincide with *F. officinalis* distribution. The potential implications of nutritional
449 differences between past and present *S. turtur* diet warrant further investigation;
450 however, until more is known it might be prudent to assume that *F. officinalis* should
451 remain an important component of the *S. turtur* trial plot seed mix, despite its
452 comparative expense when compared to other components of both our trial plot mix,
453 and of standard nectar flower mixes (current payments under HLS per hectare of
454 nectar flower mix are £450, and is set to rise to £511 per hectare under the new
455 Countryside Stewardship (see
456 [https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/389521](https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/389521/Countryside_Stewardship_Rates.pdf)
457 [/Countryside Stewardship Rates.pdf](https://www.gov.uk/government/uploads/system/uploads/attachment_data/file/389521/Countryside_Stewardship_Rates.pdf)) with standard nectar flower seed costing £145 -
458 £197.50 per ha. The *S. turtur* trial plot mix costs £337.50 per ha when sown at 15kg /
459 ha, due mostly to the high cost of *F. officinalis* seed). Additional management costs,
460 estimated by one farmer on our trial plot sites to be £175 per year for topping and
461 scarification (unpubl. data), mean that payments under the current schemes for nectar

462 flower mixes are unlikely to cover the seed and management costs of the *S. turtur* trial
463 plot mix.

464

465 *Conclusions and management recommendations*

466 The development of an extensive, seed-provisioning option for *S. turtur* is
467 considered vital for the conservation of this species, where a switch in diet has
468 occurred (Browne and Aebischer 2003a) concurrently with a reduction in breeding
469 output sufficient to explain the population decline (Browne and Aebischer 2004).
470 Most existing AES options are suboptimal in providing accessible food for *S. turtur*
471 and, alone, short-term provision of seed through supplementary feeding risks the
472 spread of parasite infection and disease (Stockdale et al., in press, Lennon et al., 2013)
473 and they do not provide a sustainable solution for *S. turtur*.

474 Seed provision within our mix was greater than any control habitat types
475 during year 1, and early in the season trial plot vegetation structure was no different
476 from previously published data documenting the vegetation structure of *S. turtur*
477 foraging locations. However, management intervention is required in order to
478 maintain a favourable sward that will remain attractive to foraging *S. turtur*. The
479 ground disturbance provided by scarification is likely to be the best way to encourage
480 the germination of *F. officinalis* that seeds in early summer, whilst suppressing the
481 dense growth of *Trifolium spp.* and *V. sativa* encouraged by topping, and seems the
482 best recommendation for management of *S. turtur* trial plots into the second year.
483 Scarification of whole (autumn) or part of the trial plots (spring / summer) may be
484 required at multiple and various times of the year, depending on local conditions.

485 We recommend alterations to the seed mix composition, reducing the rates of
486 *V. sativa* and *T. pratense* to decrease the overall vegetation height, removing *C.*
487 *fontanum* from the mix entirely and reducing the sowing rate of the modified mix (10
488 – 15 kg/ha depending on soil type) in order to encourage a longer-lasting, open sward,
489 although mid-season management is still likely to be necessary to keep the sward
490 open. The addition of *Lotus corniculatus* to the mix, which has a relatively prostrate
491 structure, may help to keep the overall vegetation structure low. The efficacy of the
492 new mix will be trialed on six sites during 2012-14; however, this new mix was made
493 available to selected new and existing HLS agreement holders in key hotspots for *S.*
494 *turtur* in East Anglia, UK, during 2012 and 2013, as a modified nectar flower mixture
495 (HLS option HF4), as part of *Operation Turtle Dove*. Elsewhere, we show that the *S.*
496 *turtur* trial plots perform just as well, if not better, than nectar flower plots in terms of
497 attracting foraging pollinators (Dunn et al., 2013), so the inclusion of the *S. turtur* mix
498 as a modified nectar flower option provides only additional benefits above and
499 beyond that provided by a standard nectar flower mix. However, further testing of
500 this new mix is needed, along with monitoring of *S. turtur* utilizing the trial plots in
501 order to determine whether the provision of semi-natural food resources impacts
502 positively on *S. turtur* abundance and reproductive success. More generally, AES
503 options should seek to address the trade-off between food abundance and accessibility
504 through management of vegetation structure (Douglas et al., 2009; Dunn et al.,
505 2010b).

506

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514 RSPB and Natural England through the *Action for Birds in England* partnership.

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627

628

629 Table 1. Trial plot seed mix

630

Species	% weight
Common Fumitory <i>Fumaria officinalis</i>	2.88
Corvus Red Clover <i>Trifolium pratense</i>	14.3
Avoca White Clover <i>Trifolium repens</i>	14.3
Virgo Black Medick <i>Medicago lupulina</i>	14.3
Early English Common Vetch <i>Vicia sativa</i>	54.1
Common Mouse-Ear <i>Cerastium fontanum</i>	0.12

631

632

633 Table 2. Summary of significance levels and direction of effects (Dir), mean \pm 1 SE from the raw data for habitat comparisons during year 1 in
634 a) May, b) late June and c) late July/August, compared to autumn sown trial plots. Full model details and effect sizes can be found in Appendix
635 B. The desired direction of effect in comparison to autumn-sown trial plots is given in brackets after each vegetation variable, and significance
636 levels along with actual direction of effect are denoted as: (+) or (-) $p < 0.1$, + or - $p < 0.05$, ++ or -- $p < 0.01$. Abbreviations are NF: nectar flower
637 plots; SS trial: spring sown trial plots; WBC: wild bird cover; and FEM: floristically enhanced margins; all apart from Autumn trial and SS trial
638 are control habitats.

639

640 2a)

Habitat	Seed availability x 100 (more)			% bare ground (more)			% vegetation cover (less)			Vegetation height (less)			Vegetation density (less)		
	Direction	Mean	SE	Direction	Mean	SE	Direction	Mean	SE	Direction	Mean	SE	Direction	Mean	SE
Autumn trial		3.62	1.04	N/A	42.28	4.02		9.67	1.94		16.68	2.37		7.63	1.42
Fallow		0.95	0.33		44.69	6.67		7.07	2.02	+	11.14	2.08	+	4.34	1.01
Grass	(+)	0.71	0.46	++	4.90	1.18	-	25.73	3.39		19.04	2.47		9.54	1.64

Meadow	0.55	0.40	+	23.04	7.60		16.29	4.13		19.71	3.64		10.00	2.30
NF	1.12	0.89	+	49.44	18.69		6.22	3.92	-	9.75	3.84	--	5.69	2.19
SS trial	0.10	0.06	-	95.48	1.46		0.56	0.37	++	0.25	0.15	++	0.29	0.29
WBC	2.24	0.86	--	83.74	4.49		4.61	1.40	++	3.16	1.09	++	1.20	0.75
FEM	2.25	2.18		40.50	5.64		9.29	2.33		12.69	2.86		5.06	1.50

641

642 2b)

Habitat	Seed availability x 100 (more)			% bare ground (more)			% vegetation cover (less)			Vegetation height (less)			Vegetation density (less)		
	Direction	Mean	SE	Direction	Mean	SE	Direction	Mean	SE	Direction	Mean	SE	Direction	Mean	SE
Autumn		43.34	11.41		9.53	1.69		39.70	3.15		29.21	2.62		18.28	2.02
trial															
Fallow	(+)	0.74	0.26	--	39.08	5.69	+	18.01	3.18	++	16.81	2.77	++	8.85	1.63
Grass	+	2.14	0.87		8.28	2.96	+	20.44	2.76	++	14.91	2.18	++	5.80	0.98
Meadow		0.78	0.38		17.52	6.63		23.59	4.75		25.44	4.74		11.11	2.45

NF		116.07	31.22		20.17	9.11		49.21	7.00		26.33	4.54		8.75	1.79
SS trial		0.00	0.00	--	81.89	3.95		0.80	0.51	++	1.20	0.51	++	0.27	0.18
WBC	+	20.25	8.61	--	58.76	4.21	++	10.40	2.06	++	4.29	0.82	++	1.68	0.36
FEM		12.85	10.05	-	22.71	5.31	+	13.32	3.56	++	13.59	2.29	++	7.77	1.51

643

644 2c)

Habitat	Direction	Seed availability x 100 (more)		% bare ground (more)		% vegetation cover (less)			Vegetation height (less)			Vegetation density (less)			
		Mean	SE	Direction	Mean	SE	Direction	Mean	SE	Direction	Mean	SE	Direction	Mean	SE
Autumn		145.82	30.62		6.33	1.64		45.07	2.98		29.48	2.47		18.57	1.92
trial															
Fallow	+	14.02	5.92	--	42.00	6.01	+	13.79	2.80	++	14.33	2.34	++	5.14	1.09
Grass	++	7.17	4.08		7.07	2.42	+	21.58	3.23	++	14.82	1.97	++	5.58	1.23
Meadow		3.14	1.37		19.83	7.49		28.89	4.97		23.70	5.18		15.33	3.89
NF		16.93	7.89		11.50	4.41		43.82	6.99		19.60	3.19		5.55	1.38

SS trial	24.55	10.11		29.11	6.07		16.88	4.65	(+)	10.79	3.78	++	6.21	2.67
WBC	29.11	14.29	--	32.40	4.30		35.68	4.33		20.69	2.87	++	4.66	1.00
FEM	5.18	3.54		15.98	3.66	+	17.84	4.44		18.21	3.64	++	7.25	1.31

645

646 **Table 3.** Results of t-tests comparing a) vegetation height and b) % bare ground on trial plots during 5 surveys with that of known *S. turtur*
 647 foraging locations (from Browne & Aebischer, 2003a). Trial plot structure not differing significantly from foraging site structure is highlighted
 648 in bold.

649 a)

Vegetation height	Year 1			Year 2 topped		Year 2 scarified	
	Round 1	Round 2	Round 3	Round 1	Round 2	Round 1	Round 2
t	1.102	5.027	4.635	3.620	7.558	1.888	9.292
df	134	134	130	124	123	126	126
p	0.274	<0.001	<0.001	<0.001	<0.001	0.061	<0.001

650

651 b)

% bare ground	Year 1			Year 2 topped		Year 2 scarified	
	Round 1	Round 2	Round 3	Round 1	Round 2	Round 1	Round 2
t	1.450	4.871	4.752	4.224	4.143	4.097	4.672
df	134	134	130	124	123	126	126
p	0.149	<0.001	<0.001	<0.001	<0.001	<0.001	<0.001

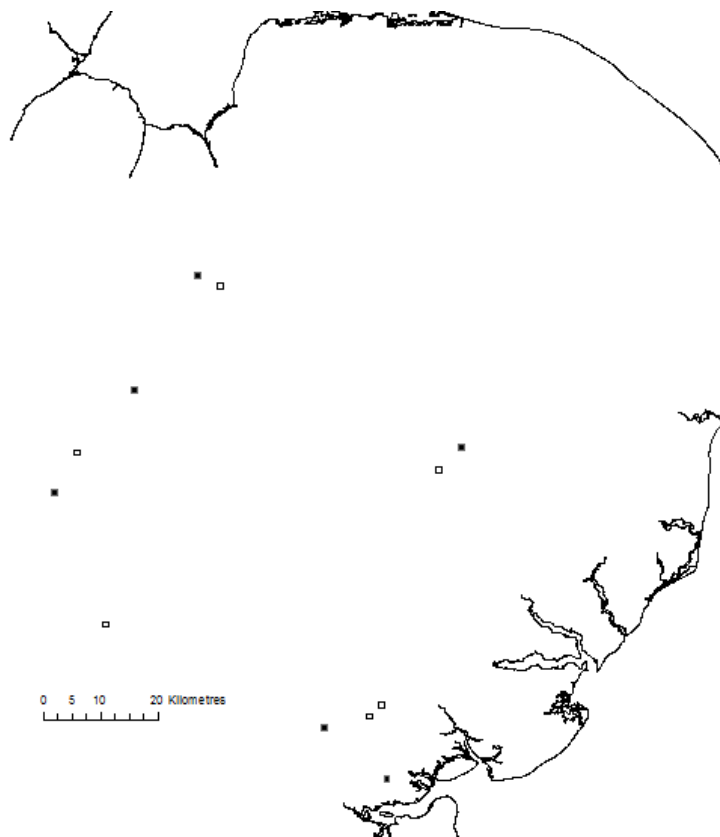
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655 Figure 1. a) A map showing locations of trial and control farms within the UK, with
656 trial plot farms shown as black boxes and control farms as white boxes (© Crown
657 Copyright. All rights reserved. RSPB licence 100021787) and b) a schematic diagram
658 showing our sampling design within plots. Numbers of trial and control plots varied
659 between farms (mean \pm 1 SE plots: trial: 5.67 ± 0.4 ; control year 1: 5.5 ± 0.34 ; control
660 year 2: 3.0 ± 0.4)

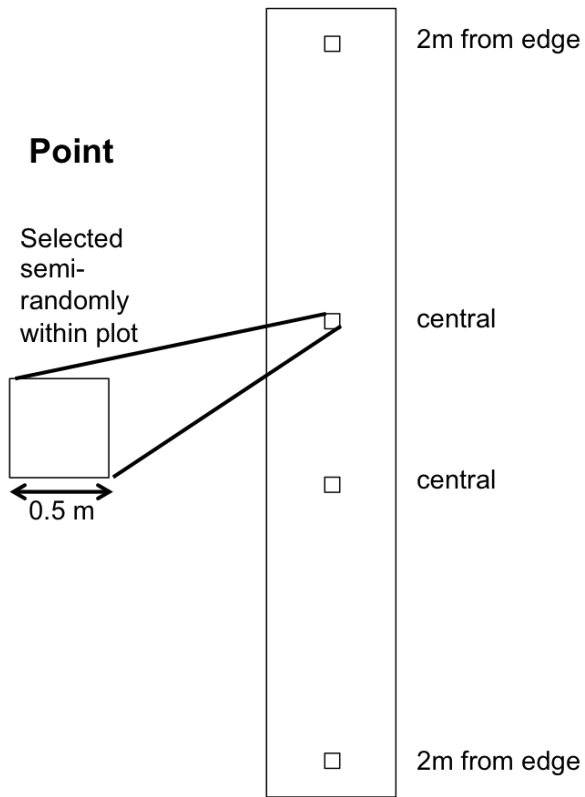
661 a)



662

663 b)

Trial or control plot



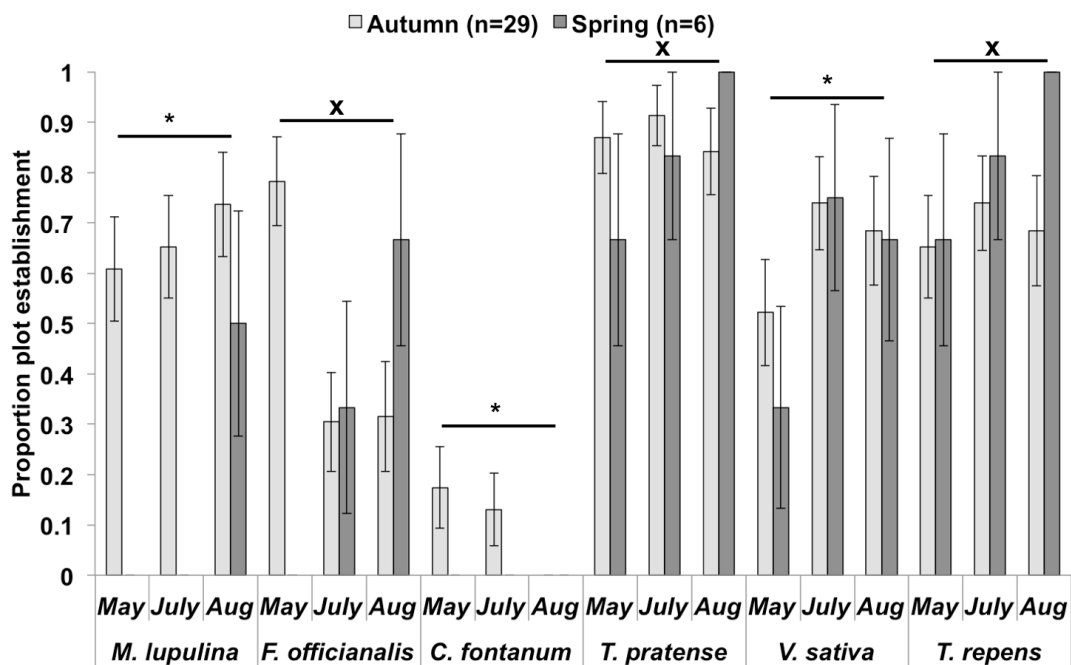
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666

667 Figure 2. Establishment of trial plot species (proportion of plots within which each
 668 species was detected) according to sowing date (autumn or spring) during May, early
 669 July and late July/August of year one. Bars depict mean \pm 1 SE from the raw data. *
 670 above a line indicates a significant effect of round only at $p < 0.05$; x above a line
 671 indicates a significant effects of an interaction between round and sowing date at
 672 $p < 0.05$. Sowing date alone did not significantly affect the establishment of any trial
 673 plot species; full model results and estimates are available in Appendix 2.

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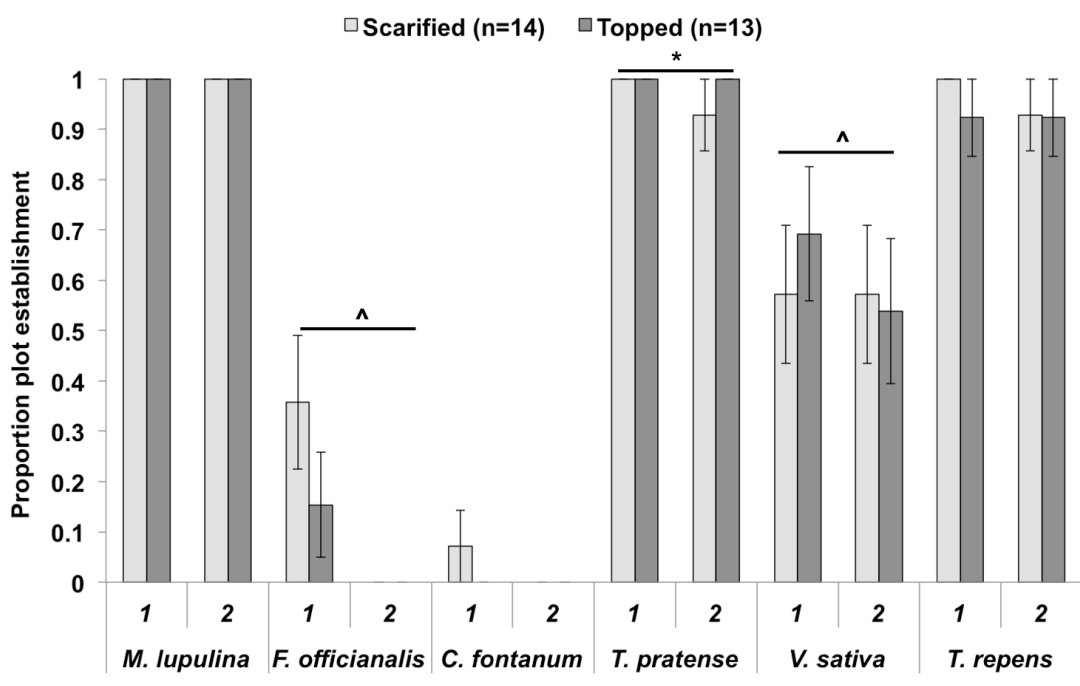
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680

681 Figure 3. Establishment of each species (proportion of plots within which each
 682 species was detected) in Rounds 1 or 2 in mown or scarified trial plots during Year
 683 two. Bars depict mean \pm 1 SE from the raw data. * above a line indicates a
 684 significant effect of round only at $p < 0.05$; ^ above a line indicates a near significant
 685 effect of management at $p < 0.1$. Interactions between round and management did not
 686 significantly affect the establishment of any trial plot species; full model results and
 687 estimates are available in Appendix 3.

688



689

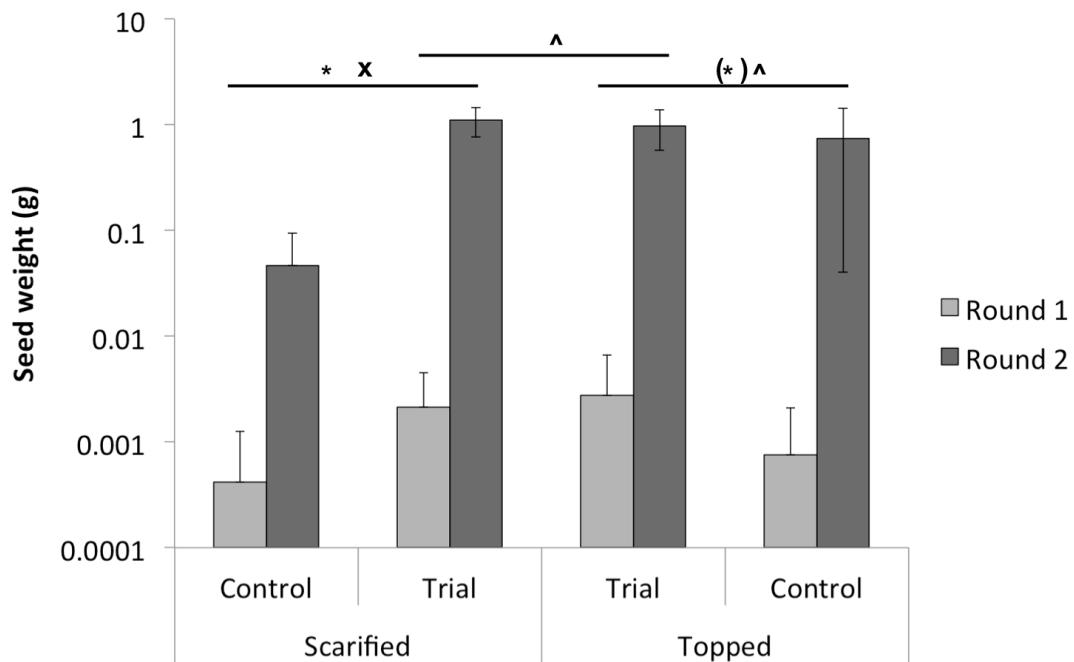
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693 Figure 4. Mean \pm 1 SE (A) Seed weight, (B) Bare ground, (C) Vegetation cover, (D)
 694 Vegetation height and (E) Vegetation density in different trial and control plots during
 695 year 2 from the raw data. Note log y-axis for 4(A). Significant differences at $p < 0.05$
 696 are demonstrated by symbols above lines: * denotes an effect of habitat; ^ denotes an
 697 effect of round and x denotes a significant Habitat x Round interaction. Near
 698 significant differences (< 0.1) are denoted by the same symbols in parentheses. Full
 699 model results and estimates are given in Appendix E.

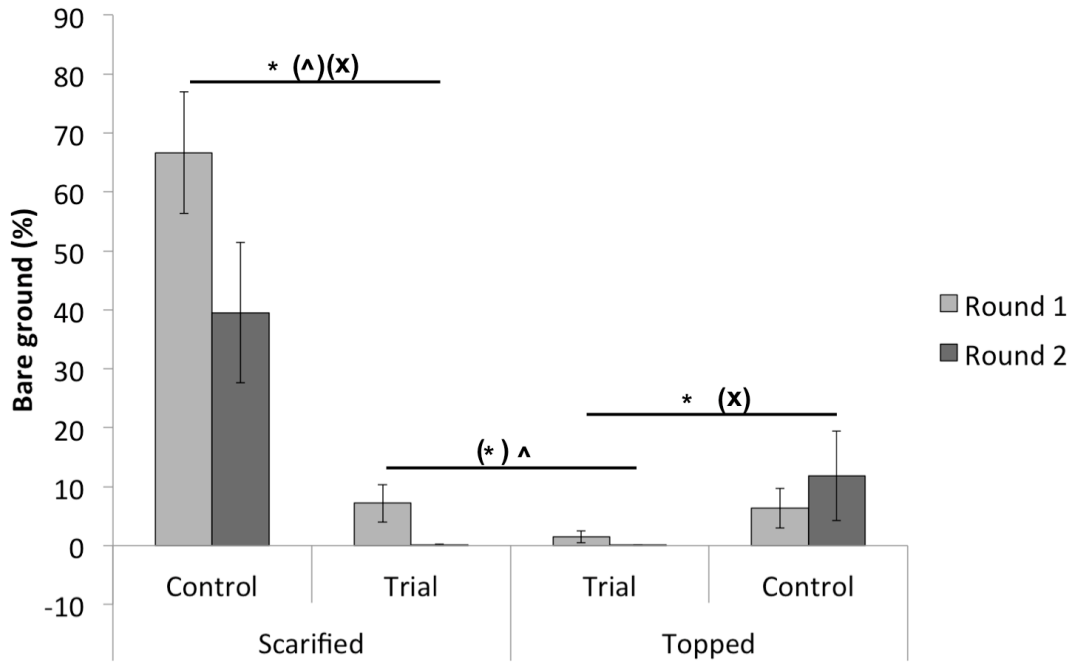
700 4(A) Seed weight



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702

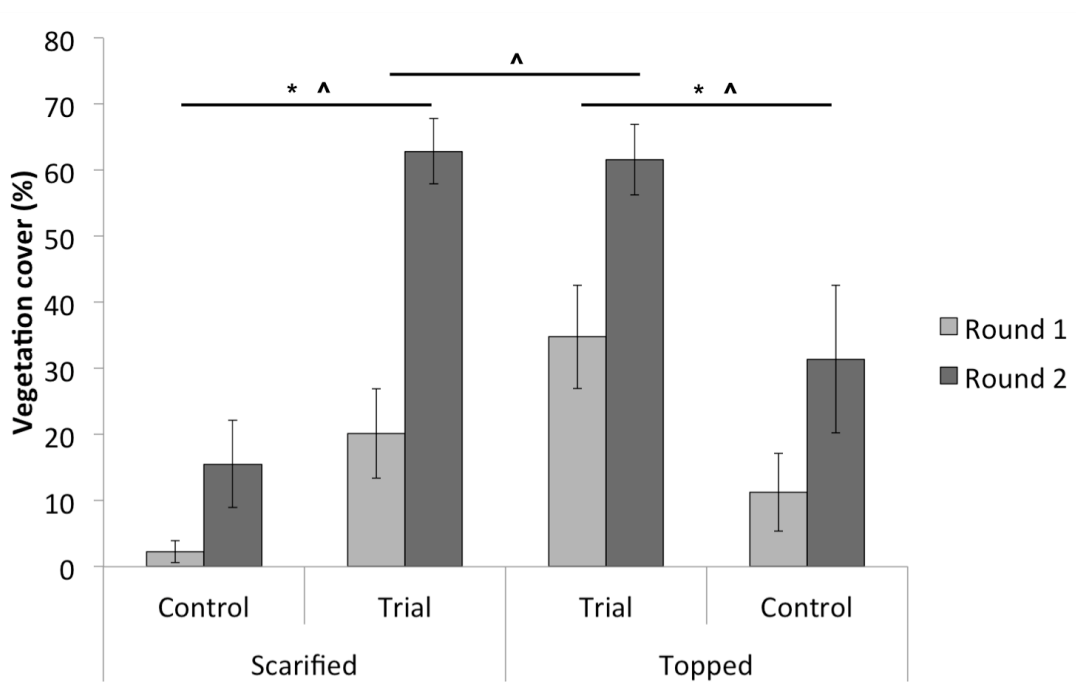
703 4(B) Bare ground



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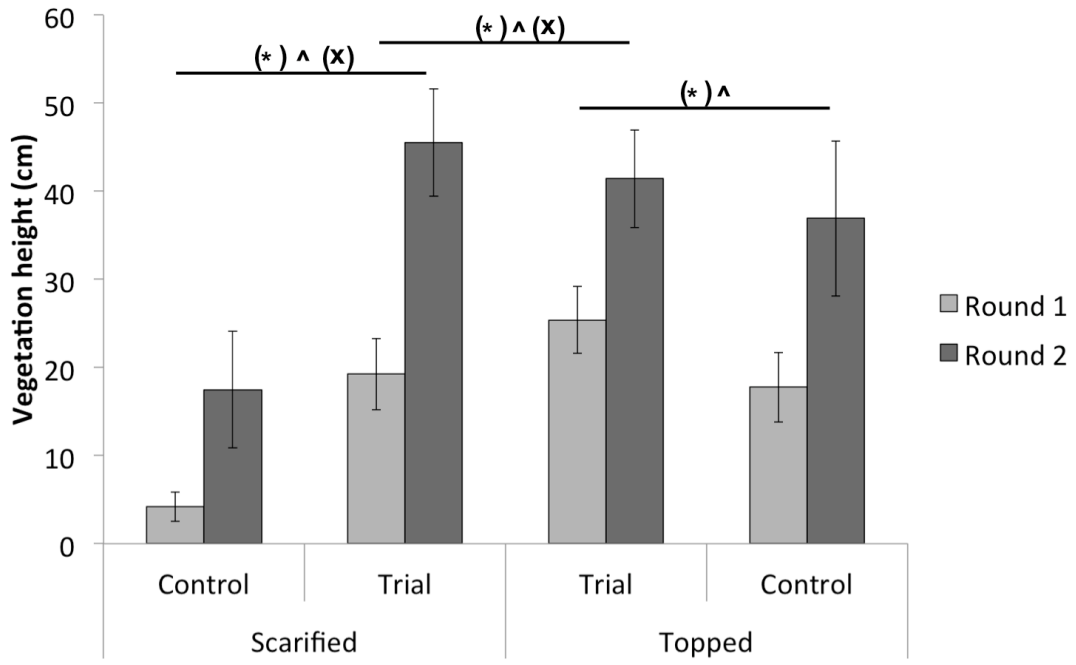
706 4(C) Vegetation cover



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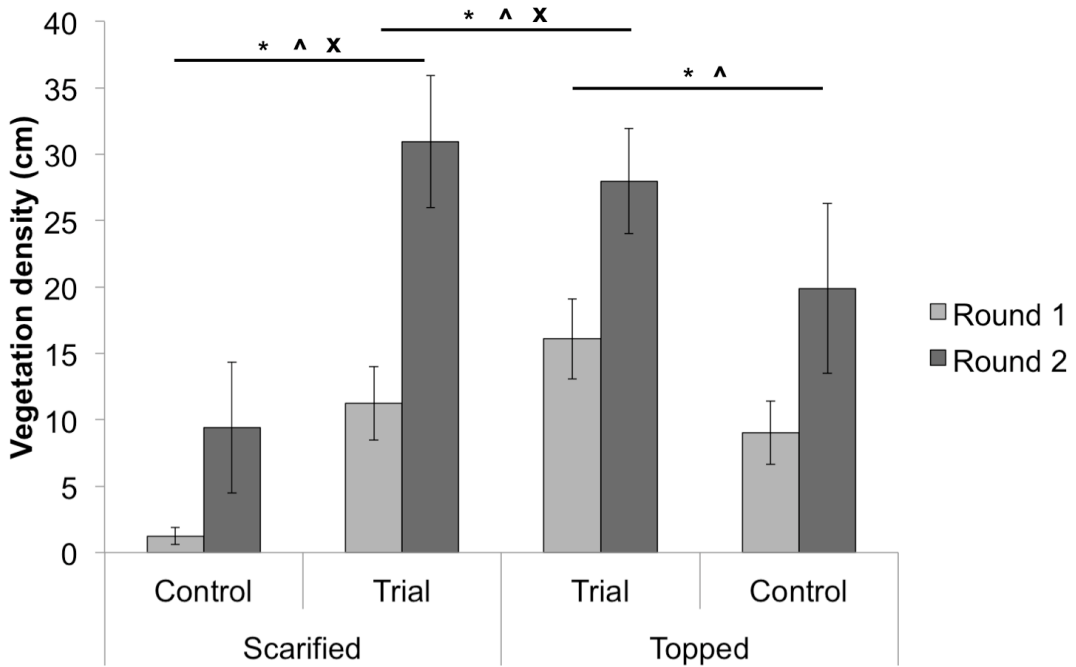
709 4(D) Vegetation height



710

711

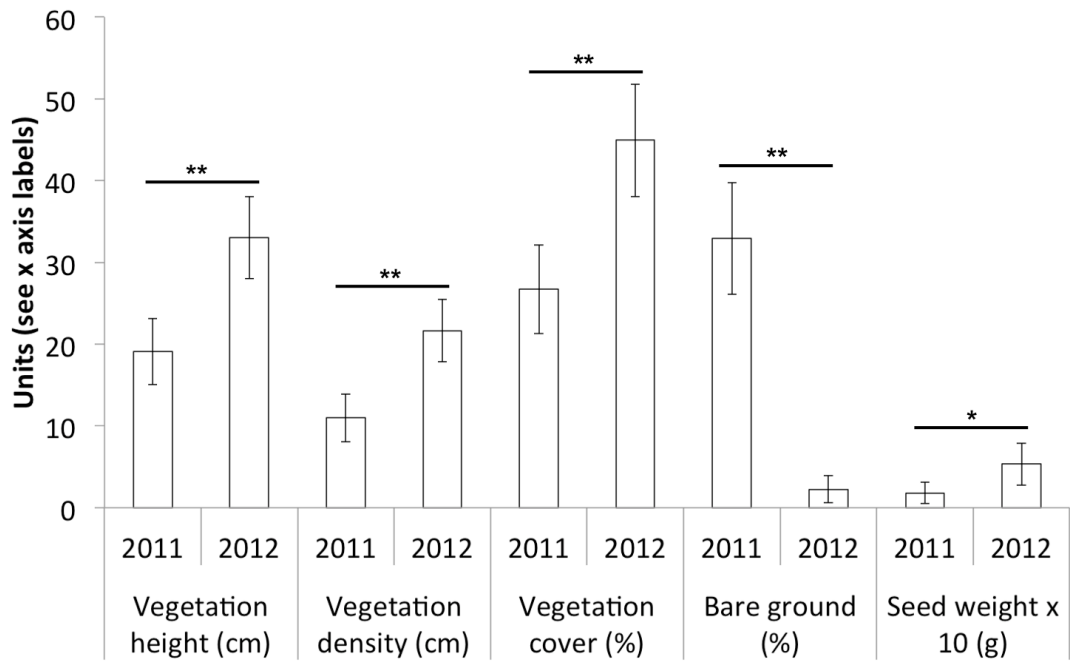
712 4(E) Vegetation density



713

714

715 Figure 5. Mean vegetation and seed parameters on trial plots during Year 1 (2011)
 716 and Year 2 (2012). Between-year significance is denoted by * ($p < 0.05$) and **
 717 ($p < 0.01$).



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722 Appendix A. Seeds considered important in *S. turtur* diet, taken from Murton et al. (1964) and Browne & Aebischer (2003a).

723

Murton et al. (1964)

Browne & Aebischer (2003a)

Brassica *Sinapsis* spp.

Wheat *Triticum aestivum* var

Chickweed *Stellaria media*

Oil seed rape *Brassica napus* var

Knotgrass *Polygonum* sp.

Chickweed *Stellaria media*

Fumitory *Fumaria* spp.

Mignonette *Reseda lutea*

Grass spp. (*Agropyron* spp. and *Festuca* spp.)

Knotgrass *Polygonum aviculare*

Cereals (specifically Wheat and Oil seed rape)

Redshank *Persicaria maculosa*

Creeping buttercup *Ranunculus repens*

Fumitory *Fumaria officinalis*

Wild mignonette *Reseda lutea*

Grass *Graminae* spp.

Heartsease *Viola tricolor*

Field pansy *Viola arvensis*

White campion *Silene alba*

Orache *Atriplex patula*

Bladder campion *Silene vulgaris*

Nettle *Urtica dioica*

Common mouse-ear *Cerastium holosteoides*

Stitchwort spp. *Stellaria spp.*

Corn spurrey *Spergula arvensis*

Fat hen *Chenopodium album*

Orache *Atriplex patula*

Black medick *Medicago spp.*

Clover spp. *Trifolium spp.*

Spurge spp. *Euphorbia spp.*

Dock *Rumex spp.*

Scarlet pimpernel *Anagallis arvensis*

Round-leaf fluellen *Kickxia spuria*

Goosegrass *Galium aparine*

Stinking chamomile *Anthemis cotula*

724

725 Appendix B. a) Results and b) estimates from GLMMs determining the independent and interactive influences of Round (May, early July or
 726 late July/August) and Sowing date (autumn or spring) on the establishment of each trial plot species during Year 1.

727

2a

Trial plot species

Variable	<i>V. sativa</i>			<i>M. lupulina</i>			<i>F. officinalis</i>			<i>C. fontanum</i>			<i>T. pratense</i>			<i>T. repens</i>		
	χ^2	df	p	χ^2	df	p	χ^2	df	P	χ^2	df	p	χ^2	df	p	χ^2	df	p
Round	42.07	2	<0.001	6.75	2	0.034	15.30	2	<0.001	18.68	2	<0.001	6.08	2	0.048	27.14	2	<0.001
Sowing date	0.16	1	0.691	3.00	1	0.083	2.33	1	0.127	2.32	1	0.128	0.10	1	0.755	0.01	1	0.948
Sowing date x Round	4.20	2	0.123	- ^a	- ^a	- ^a	21.84	2	<0.001	- ^a	- ^a	- ^a	19.79	2	<0.001	8.31	2	0.016

728

729 ^a ‘-’ indicates that the model didn’t converge owing to a lack of establishment in spring sown trial plots.

2b

Trial plot species

	<i>V. sativa</i>		<i>M. lupulina</i>		<i>F. officinalis</i>		<i>C. fontanum</i>		<i>T. pratense</i>		<i>T. repens</i>	
Variable	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	-0.41	1.05	-0.41	0.58	-1.99	0.36	-5.82	1.08	0.27	0.55	1.00	0.98
Round (May) ^a	-2.57	0.45	-0.06	0.34	1.47	0.38	1.46	0.73	0.57	0.35	-1.49	0.46
Round (July) ^a	-0.54	0.36	0.77	0.35	-0.55	0.50	* b	* b	0.50	0.37	-0.34	0.51
Sowing date (Spring) -	-	-	-2.57	1.32	-0.69	0.94	-	-	0.21	1.26	-0.49	2.28
Sowing date (Spring) - x Round (May)	-	-	-	-	* b	* b	-	-	-2.59	0.83	-0.66	0.92

Sowing date (Spring) - - - - 1.96 1.05 - - 1.21 0.87 2.15 0.96
x Round (July)

731

732 ^a Estimates for Round are compared to Round 2 (June).

733 ^b “*” indicates a lack of variation in this category, leading to unreliable estimates.

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739 Appendix C. a) Results and b) Estimates from GLMMs determining the independent and interactive influences of Round (May or July) and
 740 Management (mown or scarified) on the establishment of each trial plot species during Year 2.

4a	<i>V. sativa</i>			<i>M. lupulina</i>			<i>F. officinalis</i>			<i>C. fontanum</i>			<i>T. pratense</i>			<i>T. repens</i>		
Variable	χ^2/z	df	p	χ^2/z	df	p	χ^2/z	df	p	χ^2/z	df	p	χ^2/z	df	p	χ^2/z	df	p
Round	1.717	1	0.190	0.729	1	0.393	- ^a	- ^a	- ^a	1.600	1	0.206	23.222	1	<0.001	1.767	1	0.184
Management	3.070	1	0.080	0.099	1	0.753	3.241	1	0.072	0.263	1	0.608	1.487	1	0.223	0.305	1	0.581
Management x Round	0.367	1	0.544	0.810	1	0.368	- ^a	- ^a	- ^a	- ^a	- ^a	- ^a	0.511	1	0.475	0.696	1	0.404

741

742 ^a ‘-’ indicates that the model didn’t converge owing to a lack of establishment in July. b) Estimates for significant terms in a).

743

4b *V. sativa* *M. lupulina* *F. officinalis* *C. fontanum* *T. pratense* *T. repens*

Variable	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE	Estimate	SE
Intercept	-1.689	0.979	-	-	-2.651	0.511	-	-	5.077	0.931	-	-
Round	-	-	-	-	-	-	-	-	-2.050	0.494	-	-
Management (Mown)	0.713	0.400	-	-	-1.445	0.821	-	-	-	-	-	-
Management x Round	-	-	-	-	-	-	-	-	-	-	-	-

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747 Appendix D. Results of GLMMs comparing a) seed availability, b) % bare ground, c) % vegetation cover, d) vegetation height and e)
 748 vegetation density between trial plots and alternative habitat during each survey in year 1. The first row in the table shows the important of the
 749 habitat term in the GLMM (with χ^2 statistics), the rest of the table shows the significance of post-hoc contrasts comparing each specified habitat
 750 type with autumn sown trial plots (z statistics); habitats significantly different from autumn sown trial plots are denoted in bold. ‘-’ indicates that
 751 the sample size for this term during this time period was too small to give meaningful estimates

752

2a Habitat	May					Late June/early July					Late July/August				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Overall significance	N/A	N/A	9.96	7	0.191	N/A	N/A	26.741	7	<0.001	N/A	N/A	20.189	7	0.005
Fallow	-1.217	0.827	-1.473	7	0.141	-4.038	2.426	-1.664	7	0.096	-1.983	0.837	-2.370	7	0.018
Grass	-1.703	0.936	-1.819	7	0.069	-2.994	1.389	-2.155	7	0.031	-2.673	0.877	-3.048	7	0.002

Meadow	-0.739	0.908	-0.815	7	0.415	-3.989	3.217	-1.240	7	0.215	-3.423	2.088	-1.639	7	0.101
Nectar flower	-1.182	1.947	-0.607	7	0.544	0.498	1.084	0.459	7	0.646	-1.089	1.007	-1.082	7	0.279
Spring sown trial plots	-3.504	2.828	-1.239	7	0.215	-	-	-0.007	7	0.994	-0.544	1.210	-0.450	7	0.653
Wild bird cover	-0.391	0.642	-0.609	7	0.543	-1.371	0.670	-2.047	7	0.041	-0.653	0.623	-1.048	7	0.294
Floristically enhanced margins	-0.928	0.956	-0.971	7	0.332	-1.374	0.953	-1.441	7	0.150	-2.560	1.598	-1.602	7	0.109

753

2b Habitat	May					Late June/early July					Late July/August				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Overall significance	N/A	N/A	93.867	7	<0.001	N/A	N/A	52.264	7	<0.001	N/A	N/A	32.854	7	<0.001

Fallow	0.513	0.445	1.153	7	0.249	1.960	0.540	3.633	7	<0.001	2.412	0.636	3.794	7	<0.001
Grass	-2.120	0.547	-3.876	7	<0.001	-0.145	0.653	-0.222	7	0.824	-0.089	0.770	-0.116	7	0.908
Meadow	-1.305	0.600	-2.177	7	0.029	0.451	0.704	0.641	7	0.522	0.670	0.777	0.863	7	0.388
Nectar flower	-1.665	0.700	-2.379	7	0.017	-0.057	0.838	-0.068	7	0.946	0.250	0.959	0.261	7	0.794
Spring sown trial plots	2.740	1.103	2.485	7	0.013	2.912	0.734	3.966	7	<0.001	0.725	0.804	0.902	7	0.367
Wild bird cover	1.503	0.448	3.357	7	<0.001	1.968	0.489	4.019	7	<0.001	1.739	0.621	2.800	7	0.005
Floristically enhanced margins	0.561	0.568	0.988	7	0.323	1.787	0.756	2.365	7	0.018	1.273	0.849	1.500	7	0.134

754

2c

May

Late June/early July

Late July/August

Habitat	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Overall significance	N/A	N/A	15.33	7	0.032	N/A	N/A	29.991	7	<0.001	N/A	N/A	15.326	7	0.032
Fallow	-0.342	0.733	-0.466	7	0.641	-1.030	0.470	-2.193	7	0.028	-1.282	0.520	-2.467	7	0.014
Grass	1.746	0.540	2.176	7	0.030	-1.053	0.437	-2.412	7	0.016	-1.118	0.439	-2.546	7	0.011
Meadow	0.598	0.705	0.849	7	0.396	-0.733	0.533	-1.375	7	0.169	-0.573	0.553	-1.036	7	0.300
Nectar flower	-0.479	1.528	-0.313	7	0.754	0.376	0.531	0.708	7	0.479	0.001	0.553	0.001	7	0.999
Spring sown trial plots	-2.952	2.780	-1.062	7	0.288	-4.064	2.197	-1.849	7	0.064	-1.210	0.670	-1.805	7	0.071
Wild bird cover	-0.794	0.841	-0.944	7	0.345	-1.648	0.485	-3.398	7	<0.001	-0.191	0.390	-0.490	7	0.624
Floristically enhanced margins	-0.044	0.828	-0.053	7	0.958	-1.625	0.656	-2.479	7	0.013	-1.317	0.612	-2.153	7	0.031

2d Habitat	May					Late June/early July					Late July/August				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Overall significance	N/A	N/A	79.792	7	<0.001	N/A	N/A	83.526	7	<0.001	N/A	N/A	15.794	7	0.027
Fallow	-0.271	0.118	-2.289	7	0.022	-0.410	0.105	-3.816	7	<0.001	-0.302	0.105	-2.868	7	0.004
Grass	0.058	0.101	0.575	7	0.565	-0.434	0.098	-4.412	7	<0.001	-0.264	0.098	-2.678	7	0.007
Meadow	0.107	0.119	0.898	7	0.369	-0.123	0.112	-1.093	7	0.274	-0.090	0.112	-0.801	7	0.423
Nectar flower	0.380	0.127	2.990	7	0.003	0.168	0.123	1.369	7	0.171	0.033	0.130	0.258	7	0.797
Spring sown trial plots	-0.989	0.214	-4.631	7	<0.001	-0.902	0.204	-4.411	7	<0.001	-0.286	0.152	-1.875	7	0.061
Wild bird cover	-0.563	0.117	-4.797	7	<0.001	-0.676	0.108	-6.273	7	<0.001	-0.064	0.088	-0.730	7	0.465

Floristically enhanced margins -0.091 0.137 -0.661 7 0.508 -0.532 0.131 **-4.077** 7 **<0.001** -0.172 0.135 -1.271 7 0.204

756

Habitat	May					Late June/early July					Late July/August				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Overall significance	N/A	N/A	88.374	7	<0.001	N/A	N/A	61.731	7	<0.001	N/A	N/A	45.042	7	<0.001
Fallow	-0.479	0.205	-2.334	7	0.020	-0.570	0.165	-3.465	7	<0.001	-0.881	0.177	-4.984	7	<0.001
Grass	0.080	0.166	0.485	7	0.628	-0.669	0.157	-4.268	7	<0.001	-0.752	0.164	-4.601	7	<0.001
Meadow	0.166	0.189	0.878	7	0.380	-0.189	0.176	-1.069	7	0.285	-0.223	0.173	-1.291	7	0.197
Nectar flower	0.551	0.195	2.823	7	0.005	0.029	0.198	0.147	7	0.883	-0.306	0.231	-1.326	7	0.185

Spring sown trial plots	-2.557	0.721	-3.545	7	<0.001	-1.719	0.583	-2.949	7	0.003	-0.542	0.272	-1.996	7	0.046
Wild bird cover	-1.291	0.249	-5.178	7	<0.001	-1.127	0.195	-5.786	7	<0.001	-0.733	0.160	-4.586	7	<0.001
Floristically enhanced margins	-0.155	0.228	-0.678	7	0.498	-0.533	0.190	-2.797	7	0.005	-0.526	0.214	-2.454	7	0.014

757

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759 Appendix E. Results of GLMMs determining the influence of habitat management and sampling round on a) Seed abundance, b) % bare
 760 ground, c) % vegetation cover, d) vegetation height and e) vegetation density during year 2. Raw data are displayed for significant trends in
 761 Figures 3a, 3b and 3c. Estimates are given for significant terms (shown in bold) considered to influence the response variable. For non-
 762 significant variables, values presented are χ^2 statistics comparing the models with and without the relevant term; for significant variables, z
 763 values are presented.

764 5a) Seed abundance

	Mown trial vs. scarified trial					Mown trial vs. nectar flower					Scarified trial vs. fallow				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Habitat			0.819	1	0.366			1.684	1	0.092			0.069	1	0.793
Round	4.113	0.847	4.855	1	<0.001	4.180	1.190	3.513	1	<0.001	2.337	0.589	3.970	1	<0.001
Habitat x Round			0.001	1	0.992			0.001	1	0.978	4.024	1.053	3.822	1	<0.001

765

766 5b) % Bare ground

	Mown trial vs. scarified trial					Mown trial vs. nectar flower					Scarified trial vs. fallow				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Habitat	-1.255	0.672	-1.868	1	0.062	-1.909	0.718	-2.658	1	0.008	-1.719	0.354	-4.855	1	<0.001
Round	-3.135	1.368	-2.293	1	0.022			0.012	1	0.914			-1.747	1	0.081
Habitat x Round			0.034	1	0.854			3.1	1	0.078			-1.690	1	0.091

767

768 5c) Vegetation cover

	Mown trial vs. scarified trial					Mown trial vs. nectar flower					Scarified trial vs. fallow				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p

Habitat			0.494	1	0.482	0.603	0.221	2.728	1	0.006	1.132	0.283	4.002	1	<0.001
Round	0.695	0.174	3.994	1	<0.001	0.524	0.205	2.553	1	0.011	0.957	0.238	4.018	1	0.001
Habitat x Round			1.340	1	0.247			0.613	1	0.474			0.213	1	0.645

769

770 5d) Vegetation height

	Mown trial vs. scarified trial					Mown trial vs. nectar flower					Scarified trial vs. fallow				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Habitat	0.163	0.092	1.771	1	0.077	0.125	0.073	1.711	1	0.087	1.017	0.181	5.626	1	<0.001
Round	0.480	0.084	5.683	1	<0.001	0.298	0.068	4.397	1	<0.001	0.793	0.168	4.711	1	<0.001
Habitat x Round	-0.207	0.119	-1.739	1	0.082			0.617	1	0.432	-0.313	0.188	-1.664	1	0.096

771

772 5e) Vegetation density

	Mown trial vs. scarified trial					Mown trial vs. nectar flower					Scarified trial vs. fallow				
	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p	Estimate	SE	χ^2/z	df	p
Habitat	0.252	0.106	2.376	1	0.018	0.269	0.085	3.150	1	0.002	1.466	0.232	6.334	1	<0.001
Round	0.596	0.097	6.122	1	<0.001	0.318	0.078	4.102	1	<0.001	1.193	0.233	5.121	1	<0.001
Habitat x Round	-0.287	0.135	-2.123	1	0.034			0.177	1	0.674	-0.598	0.253	-2.367	1	0.018

773

774