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1 **BUTTERFLY COLONISATION OF A NEW CHALKLAND ROAD CUTTING**

2 **Mike HETHERINGTON^{1*}, Phil STERLING², Emma COULTHARD¹**

3 1 – Manchester Metropolitan University, Department of Natural Sciences, John Dalton Building, Chester Street
4 Manchester M1 5GD, United Kingdom.

5 2 – Butterfly Conservation, Manor Yard, East Lulworth, Wareham, BH20 5QP, United Kingdom.

6 * corresponding author

7 **Abstract**

- 8 1. The design of new roads has the potential to provide new habitats and increase biodiversity
9 value. The cutting and verges of the Weymouth Relief Road, Dorset, completed in 2011,
10 replicate low-fertility chalk grassland in an area previously occupied by arable farmland and
11 improved grassland.
- 12 2. We examine the results of post-construction butterfly surveys carried out in 2012-2020 to test
13 whether butterfly abundance, species richness and species diversity increased in the post-
14 construction period. Analysis is also undertaken of the factors affecting the colonisation of the
15 verges by butterfly populations.
- 16 3. Butterfly abundance increased in the post-construction period when assessed by two
17 methods: mean counts per survey visit and maximum counts. Species richness also
18 increased, but no significant trends were observed with respect to species diversity. The 30
19 butterfly species recorded on the verges represent 51% of Britain's resident or regularly
20 occurring migrant species and include habitat-restricted chalkland species.
- 21 4. The most significant factor affecting speed of colonisation of the cutting and verges was an
22 index of local presence, defined as the number of 1 km squares where 2 or more individuals
23 of a species had been recorded prior to road construction in a 10 km square centred on the
24 site. The separation distance between the site and the nearest butterfly population did not
25 significantly affect the speed of colonisation.
- 26 5. Our results validate the low fertility approach to road verge establishment and management.
27 The experience of the Weymouth Relief Road is influencing future road verge construction
28 and management in the UK.

29

30 **Key words**

31 Biodiversity, colonisation, dispersal, butterfly populations, road verges, habitat creation.

32 **Introduction**

33 Urbanisation and infrastructure construction are among the main drivers for habitat loss and
34 biodiversity decline across the globe (Venter et al., 2016). Declines are identified in indicators for
35 many taxa, including negative trends in population change, extinction rates, and the extent and
36 condition of habitats (Butchart et al., 2010). Even highly conservative extinction rates for vertebrate
37 groups have been shown to exceed estimated 'background' extinction rates (Ceballos et al., 2015).
38 More recently, the focus has expanded to consider declines in less well-studied taxa, including
39 insects. Insects perform essential functions within ecosystems, such as pollination services and the
40 provision of food for other animal groups (Schowalter et al., 2018). Studies suggesting a global
41 'insect apocalypse' have been questioned (Montgomery et al. 2020; Didham et al., 2020), with the
42 evidence now pointing towards more complex and heterogenous patterns in insect population trends
43 (Wagner et al, 2021b). Nevertheless, there are clear examples of significant insect declines in
44 Northern Hemisphere regions where human impacts, such as increasing urbanisation, are particularly
45 severe (Fox et al., 2015; Wagner et al, 2021a; Warren et al., 2021; Fox et al. 2021).

46 The construction of new roads is considered to have detrimental biodiversity effects as a result of the
47 disturbance or complete removal of existing ecosystems, habitat fragmentation, pollution and collision
48 mortality (Forman and Alexander, 1998; Skórka et al., 2013). However, the value of road verges as a
49 potential biodiversity resource is becoming increasingly recognized (Gardiner et al., 2018). It has
50 been estimated that there are over 504,000 km of rural road verges in the United Kingdom (Bromley
51 et al., 2019), representing a substantial potential habitat resource, particularly in areas of intensive
52 agriculture containing few opportunities for biodiversity enhancement.

53 The ecological value of road verges has been assessed in the context of wider studies of habitat
54 creation and restoration. Initially focused largely on plant communities and individual plant species
55 (for example Verhagen et al, 2001), these have broadened out to consider animal colonisation of
56 newly created and restored landscapes (for example: Ries et al, 2001; Saarinen et al., 2005; Valtonen
57 et al., 2006). Such studies have informed the debate about the relative importance of limiting factors,
58 notably habitat quality and population isolation, that affect the persistence of animal populations in

59 fragmented landscapes (WallisDeVries and Ens, 2008; Viljur and Teder, 2018). This persistence
60 derives from a balance between the local extinction of individual populations and the colonisation of
61 previously-vacant habitat patches (Thomas et al., 2001).

62 Butterflies are an appropriate study taxon for the evaluation of a grassland habitat creation project.
63 They occupy several ecological niches, exhibit a range of life history strategies and rely upon a variety
64 of larval food resources (Asher et al., 2001). Studies have shown that road verges have the potential
65 to support abundant and diverse butterfly communities, including habitat-sensitive species (Ries et al.,
66 2001; Wynhoff et al., 2011). UK butterflies can be split into habitat specialists and wider countryside
67 species (Dapporto and Dennis, 2013; Warren, 2021). Most UK butterfly species are conspicuous and
68 easy to identify and record. The UK Butterfly Monitoring Scheme (UKBMS) is a well-established and
69 validated methodology for long-term monitoring programmes (Pollard and Yates, 1993; Van Swaay et
70 al., 2008; UKBMS, 2019). Relevant to the present study, butterfly recording is well-established in the
71 county of Dorset, with a succession of 1 km grid square county atlases having been produced since
72 1970 (Thomas and Webb, 1984; Thomas et al., 1998; Butterfly Conservation Dorset Branch, 2020).

73 Investigation of local butterfly movement patterns has identified the role of habitat differences in
74 restricting dispersal; for example, open-habitat species are known to avoid crossing boundaries
75 between their habitat and a dense treeline (Cant et al., 2005). Nevertheless, dispersal over
76 apparently inhospitable habitats, and the resulting colonisation of isolated patches, has been shown
77 to take place (Viljur and Teder, 2018). It has been suggested that this occurs mostly through special
78 movements that are designed for net displacement and settlement away from the point of origin rather
79 than routine movements associated with, for example, foraging or other resource exploitation (Van
80 Dyck and Baguette, 2005). Dispersal therefore may be a less important limitation on the colonisation
81 of new habitat patches than the quality of the new habitat itself (WallisDeVries and Ens, 2008; Viljur
82 and Teder, 2018). However, given that the potential for an individual species to move through a
83 landscape is varied, it is also necessary to consider both the capacity of a species to undergo such
84 movements and the nature of the environment through which the movements are taking place, for
85 example in respect of consumables (such as food plants) and utilities (such as sites to pupate) – the
86 resource-based habitat concept (Dennis, 2010; Dennis et al, 2013).

87 Construction of the Weymouth Relief Road (WRR) in Dorset, southern England, provides an
88 opportunity to examine colonisation by butterflies of a new habitat designed to replicate low-fertility
89 chalk downland, located within a landscape of arable farmland and improved grassland. This study
90 explores how the new cutting and verges have been colonised by butterfly species in the nine years
91 following road construction, reviewing changes in butterfly abundance, species richness and species
92 diversity and relating these data to previous surveys in the locality. The specific hypotheses tested
93 were, first, that butterfly abundance, species richness and species diversity would all exhibit a linear
94 increase in the years following road construction and, second, that the speed of colonisation for
95 individual species would have a significantly positive relationship with the proximity of the nearest
96 previously-established population, the degree of presence of that species in the wider locality, the
97 mobility of the species concerned and/or its ecological traits (voltinism and whether it is a generalist or
98 habitat specialist).

99 **Methods**

100 *Study Site*

101 The Weymouth Relief Road (WRR) is an approximate 5 km section of the A354 road linking
102 Dorchester and Weymouth in Dorset, southern England. Constructed between 2009 and 2011 to
103 bypass a residential area experiencing traffic congestion, the road cuts through Ridgeway Hill, an
104 Upper Chalk escarpment at a height of approximately 140 metres above sea level (ASL). Prior to
105 road construction, the land was in use as arable farmland with some improved grassland (Dorset
106 County Council, 2005). Creation of a species-rich chalk grassland was an explicit aim of the design
107 and construction of the Ridgeway Hill cutting and verges (Sterling, 2019). Ridgeway Hill was not
108 subject to detailed pre-construction butterfly surveys. The present study site, which comprises the flat
109 verge on the eastern side of the road and the steep sparsely vegetated slopes above (which have
110 been fenced), totals some 3.6 ha in area, and is between 26 and 80 metres wide.

111

112

113 Contrary to usual practice, which is to apply 150mm of topsoil to areas destined for grassland, the
114 eastern cutting was not treated with topsoil, save for a scattering of 15mm in some places. In

115 2010/2011 the site was hand-sown with a mix of characteristic calcareous grassland plants recorded
116 from the area, with further sowing in 2012/13 (Edwards, 2013). Sowing took place at a rate of 2g per
117 square metre. A resurvey in 2019 showed that all of the sown species remained, with *Hippocrepis*
118 *comosa* L., *Anthyllis vulneraria* L. and *Leucanthemum vulgare* being the most common, and that
119 additional species had become established, notably chalkland indicators such as *Thymus drucei*
120 Ronninger, *Blackstonia perfoliata* Huds., *Cirsium acaule* Scop. and *Pilosella officinarum* F.W. Schulz
121 & Sch. Bip (Edwards, 2019). The cutting is fenced and subject to occasional grazing. However, a
122 formal management regime is yet to be finalised (A. King, pers. comm.).

123

124 *Field Surveys*

125 In 2018 a UKBMS site containing nine transect sections was established at Ridgeway Hill. However,
126 butterfly counts broadly consistent with UKBMS protocols had commenced on the eastern cutting and
127 verges (Ridgeway Hill East) in 2012. These counts followed the route that now comprises UKBMS
128 transect sections 1 and 2 – a combined transect length of some 625 metres. Public access to the
129 cutting is limited, and the transect sections follow footpaths from a high point of 140 metres ASL to
130 finish at a point where the road emerges from the cutting onto an embankment to the south of
131 Ridgeway Hill (90 metres ASL).

132 For the purposes of comparison, the present study combines 2012-2017 survey data from Ridgeway
133 Hill East with 2018-2020 data from sections 1 and 2 of the UKBMS transect. As noted above, the
134 earlier data are from the same route as the later transects. Local survey personnel, all of whom were
135 experienced in operating UKBMS procedures, overlapped the two periods. Between 10 and 20
136 transects were walked each year during the combined survey period. Butterflies were identified to
137 species level. Butterfly nomenclature and species order in this paper follows Agassiz et al. (2013).
138 Plant nomenclature and authority abbreviations follow Stace (2019). Survey data are summarised in
139 table S1 (supporting information).

140 Surveys were undertaken where possible on suitable days every week from April to September,
141 although surveys in the initial year (2012) only took place between late May and mid-August, resulting
142 in a reduced number of visits. While a number of early-flying species such as *Pyrgus malvae* L.,
143 *Erynnis tages* L. and *Anthocharis cardamines* L. may have been under-counted in that year, the

144 survey periods included a substantial part (>50%) of the local flight periods of the species concerned
145 (Thomas et al., 1998). It is therefore likely that these species would have been recorded if present.
146 In a number of cases where the transects were walked more than once during a single survey week,
147 the data have been averaged for that week and the number of visits adjusted accordingly.

148 *Colonisation Study*

149 The number of years taken for a species to colonise the site was calculated for all species, with the
150 exception of three species – *Colias croceus* (Geoffroy, 1785), *Vanessa atalanta* (Linnaeus, 1758) and
151 *Vanessa cardui* (Linnaeus, 1758) – where populations are largely, or entirely, maintained by
152 continental migration (Dapporto and Dennis, 2013). In order to exclude single vagrant butterflies,
153 colonisation was taken to have occurred when 2 or more individuals of a species were recorded at the
154 site in the same year (maximum count data). This is a somewhat more robust criterion than the initial
155 record of a species applied by Woodcock et al. (2012). A total of 20 species were therefore
156 considered in the colonisation study (table S2 – supporting information).

157 Butterfly presence prior to WRR construction was calculated from 2005-2009 butterfly survey data
158 supplied on 1 km grid maps prepared by Dorset Environmental Records Centre using DMAP for
159 Windows. A variety of sources contributed to these data, notably surveys organized by Butterfly
160 Conservation Dorset Branch. Separation distances to the nearest established population were
161 calculated between the centroid of the 1km square containing the WRR survey transects (SY6785)
162 and the centroid of the nearest 1 km square containing 2 or more individuals of the relevant species.
163 Squares containing a record of a single butterfly were discounted in order to exclude vagrant records.

164 An index of local presence was calculated by counting the number of 1 km squares where two or
165 more individuals of a species had been recorded in a 10 km square centred on the survey 1 km
166 square during the 2005-2009 period. These range from 0 squares (*Thymelicus lineola*
167 (Ochsenheimer, 1808) and *Cupido minimus* (Fuessly, 1775)) to a maximum of 26 squares (*Maniola*
168 *jurtina* (Linnaeus, 1758)). Given that 69 squares within the 10 km square contain at least one record
169 in the data set, this represents a well-recorded locality, with records from 71% of terrestrial 1 km
170 squares (three squares are exclusively maritime). The potential effect of species' mobility was
171 investigated using a mobility score derived by Dennis (2010) (quoted in Warren, 2021). Species'

172 habitat preferences (either habitat specialists or wider countryside generalists) were taken from
173 Warren (2021), while data on voltinism uses Dorset flight periods (Thomas et al., 1998).

174 *Statistical Analysis*

175 All statistical analyses were carried out in R 3.6.1 (R Core Team, 2020). Significance for tests was
176 adopted as $P=0.05$.

177 Given the variation in sampling effort over the survey period, abundance data are presented as mean
178 butterfly numbers per survey visit. However, in order to check the validity of the use of mean butterfly
179 numbers per survey visit, abundance was also calculated using maximum count data.

180 Shannon-Weiner and Simpson's diversity indices were calculated from the mean butterfly numbers
181 per survey visit. Along with mean abundance per visit and species richness, these variables were
182 found to be normally distributed through the survey period. Trends in these data over the study
183 period were therefore investigated by linear regression, with the exception of six species where
184 numbers were too low for meaningful analysis. The linear models were verified to test for normal
185 distribution of residuals. The trend in the cumulative number of species recorded on the WRR was
186 investigated by a polynomial regression, which was found to explain more variation than a logarithmic
187 relationship.

188 For analysis of the colonisation data with arrival year as the response variable, generalized linear
189 models with Poisson errors and a log link function were used. We tested whether the speed of
190 colonisation was affected by the proximity of existing populations and the index of local presence
191 using a Poisson GLM with arrival year as the response variable and separation distance, index of
192 local presence and mobility score as three explanatory variables. The numeric explanatory variables
193 had a weak collinearity (all pairwise correlations ≤ 0.57), so none were initially excluded from analysis.
194 However, the proximity of existing populations, the species' mobility scores and their ecological traits
195 (degree of habitat specialisation and voltinism) were found to have no significant effect on the year of
196 arrival, so were removed from the Poisson GLM. The effect of the ecological traits on arrival year
197 were separately explored using Wilcoxon *U*-tests.

198 **Results**

199 *Survey Effort*

200 Two butterfly transects along the eastern cutting of the Weymouth Relief Road (WRR) were surveyed
201 over nine years following the road's construction in 2010/11. The transects were walked during a total
202 of 173 weeks between April and September of each year, with 5845 butterflies of 30 species being
203 recorded in total. The number of butterfly species present in any one survey year ranged from 13
204 species in 2012 (the first survey year) to a peak of 27 species in 2017.

205 *Abundance*

206 There was a significant increase in total butterfly abundance per survey visit during the period
207 (F=81.54, DF = 1, 7; R-squared = 0.92; P<0.001) (figure 1). A similar trend was found with the
208 maximum count for all species combined (the sum of each species' maximum counts for the year
209 concerned), which was found to significantly increase over the study period (F=7.56, DF = 1, 7; R-
210 squared = 0.52; P=0.029).

211 Changes in the abundance of individual species were analysed using both mean butterfly abundance
212 and maximum count data. Only three species showed significant increases in both analyses:
213 *Melanargia galathea* (Linnaeus, 1758) (P<0.001 and P<0.01 respectively), *Aphantopus hyperantus*
214 (Linnaeus, 1758) (P=0.024 and P=0.030) and *C. minimus* (P=0.047 and P=0.049). Significant
215 increases in mean butterfly abundance alone were found for *M. jurtina* (P=0.034) and *Pyronia tithonus*
216 (Linnaeus, 1771) (P=0.049), while maximum counts increased significantly for *T. lineola* (P=0.031)
217 and *Polyommatus bellargus* (Rottemburg, 1775) (P=0.023). Maximum counts of *Lasiommata megera*
218 (Linnaeus, 1767) showed a significant decline (P<0.001), while no significant declines were found in
219 mean abundance of any species. The differences in the findings between the two analyses, the
220 relatively small numbers of some of the species sampled and, in some cases, the marginal degree of
221 statistical significance, suggest that species-level findings should be viewed with caution.
222 Nevertheless, it is clear that at least one grassland species (*M. galathea*) has benefitted significantly
223 from the creation of this habitat.

224

225 *Species richness*

226 Initial colonisation of the site by butterfly species was rapid, with the rate of new additions decreasing
227 markedly during the study period. This pattern was best explained by a polynomial regression
228 ($F=56.9$; $DF = 2, 6$; $R\text{-squared}=0.95$; $p<0.001$) (figure 2). Several species ceased to be recorded
229 during the study period, suggesting either a dynamic pattern of arrivals and local extinctions, or, in the
230 case of species with very small counts such as *Gonepteryx rhamni*, (Linnaeus, 1758), vagrancy.
231 Annual species richness showed a significant increase during the study period ($F=6.55$, $DF = 1, 7$; $R\text{-}$
232 $squared = 0.48$; $p=0.038$) (figure 1).

233 *Species Diversity*

234 Changes in species diversity were assessed using the Shannon-Weiner and Simpson's diversity
235 indices (Gardener, 2017). In both cases, an initially high species diversity reduced during the first two
236 years following the road's construction but then returned to its original level towards the end of the
237 study, following a V-shaped pattern (figure 3). No significant linear relationship was observed in
238 respect of species diversity during the overall study period (Shannon-Weiner: $F=1.96$, $DF = 1, 7$;
239 $P=0.204$; Simpson's: $F=0.82$, $DF = 1, 7$; $P=0.396$).

240 *Colonisation*

241 There was a significant negative relationship between the year of butterfly arrival and the local
242 presence of the species, defined as the number of 1 km squares previously occupied by the species
243 in a 10km square centred on the survey site ($Z=2.62$, $DF=19$, $R\text{-squared}=0.42$, $P=0.0089$) (figure 4).
244 Greater local presence was therefore found to increase the speed of butterfly arrival. However, the
245 proximity of existing populations, the species' mobility scores and their ecological traits (degree of
246 habitat specialisation and pattern of voltinism) were found to have no significant effect on the speed of
247 arrival.

248

249 **Discussion**

250 *Overview*

251 This study documents the expansion and development of the butterfly fauna on a roadside cutting and
252 verges designed to replicate low-fertility chalk downland. It demonstrates that suitably designed and
253 seeded verges can create an impressively species-rich butterfly habitat, supporting the view that road
254 verges can support biodiversity conservation (Gardiner et al., 2018; Bromley et al., 2019).

255 Thirty butterfly species were recorded, with a maximum of 27 in any one year (table S1). Butterfly
256 abundance and species richness were found to increase significantly during the nine-year study
257 period, although species diversity measured by two indices did not show significant linear trends.

258 Investigation of butterfly data for the wider locality demonstrated that the speed of colonisation of the
259 road verges by butterfly species was significantly related to the degree of local presence of that
260 species but had no significant relationship to the proximity of the nearest population of that species,
261 its mobility score as defined by Dennis (2010) or other ecological traits.

262 *Creation of a species-rich butterfly habitat*

263 The 30 butterfly species recorded on the WRR verges represent 51% of Britain's resident or regularly
264 occurring migrant species (Asher et al., 2001), and 63% of those occurring regularly in Dorset
265 (Thomas et al., 1998). It is a substantial number by British standards, and approaches that of
266 comparable chalk downland nature reserves. For example, 35 butterfly species have been recorded
267 at the Dorset Wildlife Trust reserve of Fontmell and Melbury Downs, which is designated as a Site of
268 Special Scientific Interest and Special Area of Conservation (Branson, 2015). Five of the species
269 recorded on the WRR verges are identified as priority terrestrial invertebrate species in the UK
270 Biodiversity Action Plan 2007 (JNCC, 2007): *Coenonympha pamphilus* (Linnaeus, 1758), *C. minimus*,
271 *Erynnis tages* (Linnaeus, 1758), *L. megera* and *Pyrgus malvae* (Linnaeus, 1758). In addition, two
272 geographically restricted species – *Polyommatus coridon* (Poda, 1761) and *P. bellargus* – that
273 exclusively use chalk and limestone grassland (Asher et al., 2001) were recorded in the study; these
274 have not previously been recorded within the site's immediate locality (Thomas et al, 1998). This
275 finding amplifies the view, discussed further below, that the restoration success of the cutting and
276 verges was not significantly impeded by dispersal limitation.

277 The increase in butterfly abundance and species richness that followed construction of the road and
278 seeding of the cutting is consistent with a model of populations establishing at the site as the

279 vegetation has increased in maturity and diversity. Although a theoretical limit to abundance may be
280 expected based upon the site's carrying capacity in respect of food resources, notably the availability
281 of food plants and nectar (Curtis et al., 2015), there is no evidence that this has yet been reached on
282 the Weymouth Relief Road cutting. As such, the biodiversity value of the site can be expected to
283 continue to improve for the time being, subject to continued appropriate management.

284 Given the significant increases in abundance and species richness, it might have been expected that
285 species diversity would also have increased during the study period. However, analysis of two
286 diversity indices (Shannon-Weiner and Simpson's) showed no significant linear trend. For both
287 indices, species diversity declined sharply in the first two years before increasing towards the end of
288 the study period, creating a U-shaped pattern. This is explained by the dominance of two species –
289 *Pieris rapae* (Linnaeus, 1758) and *Polyommatus icarus* (Rottemburg, 1775) – which together
290 accounted for 57% of the total mean butterfly abundance in 2014, followed by the sole dominance of
291 *P. icarus* which accounted for 52% of mean butterfly abundance in 2015.

292 Although several roadside butterfly faunas have been previously studied – for example in Iowa, USA
293 (Ries et al., 2001), Finland (Saarinen et al., 2005; Valtonen et al., 2006) and Poland (Skórka et al.,
294 2013) – most are not directly comparable to the WRR site, given the UK's relatively low butterfly
295 species richness. An exception is a study in Dorset and Hampshire, UK, where twelve road verges
296 were examined using similar transect methods to the present study (Munguira and Thomas, 1992).
297 Those authors recorded a total of 27 species across all sites, with the richest site (Bere Regis, Dorset)
298 containing 23 species. The verges sampled in the 1992 study were therefore markedly less species
299 rich than the WRR site. This may be a function of the geological characteristics of the verges
300 surveyed at that time, as well as the shorter survey length (100 metre transects compared with the
301 625 metres surveyed at the WRR) and the larger size of the WRR verges and cutting (for example,
302 the Bere Regis verge totalled 1.4 ha in area, under half the area of the WRR site) (Munguira and
303 Thomas, 1992). Nevertheless, a comparison of the two studies suggests that the adoption of the low
304 fertility approach on the WRR cutting and verges has resulted in the creation of a richer butterfly
305 habitat than other road verges in the county and its neighbour.

306 While systematic surveys of the Lepidoptera of Ridgeway Hill were not undertaken prior to the WRR's
307 construction, historic butterfly survey data for the 1 km square suggests that species richness was

308 markedly lower; for example, during the survey period 1980-1996, only 22 species of butterfly were
309 recorded (Thomas et al., 1998), although the degree of survey activity at that time is unlikely to have
310 been consistent with efforts in the present study. No survey data for this 1 km square is available for
311 the period (2005-2009) immediately prior to WRR construction. Nevertheless, it appears that the road
312 verges' establishment within an area previously occupied by arable farmland and improved grassland
313 has resulted in a material biodiversity gain.

314 *Colonisation*

315 Construction of the Weymouth Relief Road cutting has created habitat of a suitable quality to attract
316 colonisation by both generalist (wider countryside) and habitat specialist butterfly species (Dapporto
317 and Dennis, 2013; Warren, 2021). However, the finding that speed of colonisation is not related to
318 the separation distance between the site and the nearest population of the species concerned is, at
319 first sight, surprising. The relationship between degree of local presence and arrival year suggests
320 that colonisation is not a simple process involving small scale movements from a single population,
321 but is more likely to be the product of more complex movements involving a number of local
322 populations. Such movements may well be amplified by longer range dispersal – the special
323 movements described by Van Dyck and Baguette (2005). In the present study, a number of outlying
324 data points suggest movements of this nature, notably the colonisation by *C. minimus* and *T. lineola*
325 in years 1 and 3 respectively – species that had no 2005-2009 records within the 10km square
326 centred on the study site and nearest populations some 8-10 km distant. This degree of dispersal is
327 unexpected; both species are classed as 'sedentary' by Pollard and Yates (1993), while Dennis
328 (2010) attaches mobility scores of 2 (low) and 4 (medium) respectively to these species. It is however
329 also possible that both species have been previously under-recorded in the site's wider vicinity, a
330 concern that especially applies to *T. lineola* given the potential for confusion with the similar
331 *Thymelicus sylvestris* (Poda, 1761). Nevertheless, the present study is consistent with a resource-
332 based habitat model that shows a wide variability in the dispersal and colonisation activity of UK
333 butterfly species (Dapporto and Dennis, 2013). It also accords with the view of Dennis et al. (2013)
334 that all butterfly species, even the most sedentary, are to some extent capable of crossing apparently
335 'empty' landscape areas.

336 Looking forward, it is noted that two species that have previously been recorded in the survey 1 km
337 square – *Hipparchia semele* (Linnaeus, 1758) and *Thymelicus acteon* (Rottemburg, 1775) – have yet
338 to appear on post-construction transect surveys. *H. semele* is a species generally declining in
339 abundance and distribution in the British Isles (Asher et al., 2001). The nearest record of this species
340 during the 2005-2009 survey period was some 4 km east of the WRR site. This species uses a
341 variety of grasses as larval foodplants, favouring sites with sparse vegetation and bare ground.
342 These factors suggest it as a potential future colonist of the WRR cutting and verges. The distribution
343 of *T. acteon*, which in the British Isles is restricted to south Dorset, is strongly determined by the
344 presence of its larval foodplant *Brachypodium rupestre* Host. Although not part of the original seed
345 mix, and not recorded in 2013, this grass species is now present on both the eastern and western
346 cuttings, suggesting that *T. acteon* could be a potential future colonist.

347 A further species of South Dorset's calcareous grasslands is *Plebejus argus* (Linnaeus, 1758). Its
348 nearest populations to the WRR cutting and verges are on limestone grassland at Portland, some 12
349 km to the south, and on heathland at Tadmoll, some 12 km to the east (Butterfly Conservation Dorset
350 Branch, 2020). This is a somewhat greater degree of separation than the largest distance suggested
351 by the present study (10.2 km for *T. lineola*). Intervening habitats, comprising urban areas and open
352 water to the south of the WRR site and farmland (mainly arable and improved grassland) to the east,
353 appear unfavourable for this species and may indeed form a true barrier to dispersal. Taking these
354 factors together, and bearing in mind its particularly low relative mobility (Cowley et al., 2001), *P.*
355 *argus* would therefore appear to be an unlikely coloniser of the WRR site, despite the presence of
356 suitable larval foodplants such as *H. comosa* and *Lotus corniculatus* L..

357 As already noted, several species that have been observed on the WRR did not appear in sufficient
358 quantities in the present survey to be considered as colonists. One of these (*P. coridon*), first
359 recorded on the transects in 2017, has the potential to become established at the site given the
360 abundance of *H. comosa* in the cutting. Absence of this larval food plant has been suggested as the
361 main factor limiting recolonisation of previously suitable sites by this species (Brereton et al., 2007).
362 Several of the other species (including *Anthocharis cardamines* L., *G. rhamni*, *Polygonia c-album* L.
363 and *Celastrina argiolus* L.) depend upon larval food plants that are either rare or absent on the WRR
364 eastern cutting, which at present lacks substantial hedgerows, areas of shrubs or shading – the last
365 factor being also likely to deter *Parage aegeria* L. *Gonepteryx rhamni* has been recorded breeding in

366 an area of planted scrub on the opposite side of the WRR, to the south of the present survey site.
367 Future woody shrub growth on or adjacent to the eastern cutting, for example through natural
368 succession, could increase the range of butterfly species colonising the study site, although excessive
369 cover could threaten those grassland species that are presently established.

370 *Conclusions*

371 This study provides a validation of the low fertility approach to road verge establishment and
372 management. Road verges represent previously-overlooked resources with the potential to provide
373 good quality habitat in their own right as well acting as corridors or 'stepping stones' that can create
374 linkages in presently fragmented landscapes. Appropriate road verge design and management can
375 therefore form part of a wider strategy aimed at reducing declines in butterfly populations (Warren et
376 al., 2021). Encouragingly, the example of the Weymouth Relief Road cuttings and verges has been
377 cited by Highways England in support its recent Major Project Instruction (MPI) on the adoption of
378 Low Nutrient Grasslands for major schemes on the strategic road network. This MPI is intended to
379 create a step change towards a long-term objective of maximising biodiversity opportunities through
380 the delivery of road improvement projects, through the creation of grassland biodiversity on its soft
381 estate while also reducing maintenance requirements (Highways England, 2020).

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389 **Conflict of interest**

390 The authors declare that there is no conflict of interest.

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TABLES (SUPPORTING INFORMATION)

	2012		2013		2014		2015		2016		2017		2018		2019		2020	
	Total/visit	Max Count																
<i>Erynnis tages</i>	0.00	0	0.00	0	0.05	2	0.20	2	0.31	2	0.74	7	0.35	6	2.26	18	0.06	1
<i>Pyrgus malvae</i>	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.05	2	0.00	0	0.00	0	0.00	0
<i>Thymelicus lineola</i>	0.00	0	0.00	0	0.00	0	0.13	2	0.00	0	0.32	8	0.00	0	0.26	5	1.76	13
<i>Thymelicus sylvestris</i>	0.00	0	0.00	0	0.37	3	1.00	7	1.08	7	2.63	34	0.90	5	0.26	2	2.18	7
<i>Ochlodes sylvanus</i>	0.00	0	0.05	1	0.11	2	0.27	2	0.23	2	0.21	3	0.80	5	0.26	4	0.12	1
<i>Anthocharis cardamines</i>	0.00	0	0.05	1	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0
<i>Pieris brassicae</i>	1.20	8	0.70	11	0.05	1	0.47	4	0.38	3	0.42	3	0.65	3	0.42	5	1.29	5
<i>Pieris rapae</i>	0.60	2	4.80	33	0.74	5	1.33	9	2.00	8	0.63	3	1.10	3	2.11	16	3.29	9
<i>Pieris napi</i>	0.00	0	0.15	2	0.05	3	0.20	3	0.15	3	0.05	1	0.10	1	0.00	0	0.06	1
<i>Colias croceus</i>	0.00	0	1.70	21	0.47	6	0.07	1	0.08	1	0.26	2	0.30	5	0.68	6	0.18	1
<i>Gonepteryx rhamni</i>	0.00	0	0.10	1	0.05	1	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.06	1
<i>Lasiommata megera</i>	0.30	3	0.25	3	0.26	3	0.13	2	0.23	2	0.21	2	0.10	1	0.05	1	0.29	1
<i>Pararge aegeria</i>	0.00	0	0.00	0	0.00	0	0.07	1	0.15	1	0.05	1	0.00	0	0.00	0	0.00	0
<i>Coenonympha pamphilus</i>	0.00	0	0.00	0	0.00	0	0.27	2	0.31	2	0.05	1	0.20	3	0.05	1	0.06	1
<i>Aphantopus hyperantus</i>	0.10	1	0.00	0	0.05	1	0.00	0	0.00	0	0.21	4	0.35	4	0.16	2	0.35	4
<i>Maniola jurtina</i>	2.30	16	1.75	20	3.58	21	4.87	26	5.62	27	12.37	51	10.05	26	5.58	22	7.94	33
<i>Pyronia tithonus</i>	0.20	2	0.20	3	0.47	5	0.33	2	0.23	2	1.89	17	0.30	3	1.05	7	4.88	33
<i>Melanargia galathea</i>	1.30	9	0.20	2	1.37	16	1.87	19	2.15	19	5.00	46	6.50	45	7.11	104	12.59	57
<i>Vanessa atalanta</i>	0.30	2	0.25	2	0.16	1	0.20	2	0.08	1	0.37	2	0.05	1	0.21	1	0.06	1
<i>Vanessa cardui</i>	0.20	1	0.10	1	0.00	0	0.40	3	0.54	3	0.16	2	0.20	2	1.16	5	0.00	0
<i>Aglais io</i>	0.00	0	0.25	2	0.26	2	0.33	3	0.31	3	0.21	2	0.20	1	0.21	2	0.41	4
<i>Aglais urticae</i>	0.80	4	2.75	18	2.53	19	1.07	7	0.92	3	0.74	4	0.70	5	0.16	1	0.53	3
<i>Polygonia c-album</i>	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.16	1	0.00	0	0.00	0	0.06	1
<i>Lycaena phlaeas</i>	0.00	0	0.05	1	0.05	1	0.07	1	0.00	0	0.05	1	0.00	0	0.16	1	0.06	1
<i>Cupido minimus</i>	1.10	10	0.75	5	0.58	7	2.93	20	2.08	20	2.53	31	4.95	30	16.47	76	5.47	21
<i>Celastrina argiolus</i>	0.00	0	0.00	0	0.00	0	0.00	0	0.00	0	0.05	1	0.00	0	0.00	0	0.00	0
<i>Aricia agestis</i>	0.10	1	0.05	1	0.05	1	0.40	4	0.31	4	0.37	3	0.00	0	0.53	3	0.12	1
<i>Polyommatus icarus</i>	0.7	5	7.55	58	11.95	89	13.87	35	10.77	61	6.05	24	7.35	19	4.47	11	2.06	5
<i>Polyommatus bellargus</i>	0	0	0.00	0	0.16	2	0.00	0	0.00	0	0.53	7	2.65	24	4.84	25	1.00	10
<i>Polyommatus coridon</i>	0	0	0.00	0	0.00	0	0.00	0	0.00	0	0.00	1	0.00	0	0.05	1	0.00	0
All Species	9.20		21.70		23.37		30.47		27.92		36.32		37.80		48.51		44.88	
Number of visits	10		20		19		15		13		19		20		19		17	

Table S1: Weymouth Relief Road eastern cutting – mean annual butterfly numbers per survey visit maximum counts for each species. Mean annual butterfly numbers and visit numbers have been adjusted to correct for several occurrences of multiple visits during a single survey week.

	Arrival Year	Separation Distance (km)	Index of Local Presence	Mobility Score	Habitat Specialisation	Generations
<i>Erynnis tages</i>	3	2.83	4	2	HS	1
<i>Pyrgus malvae</i>	6	7.28	0	2	HS	1
<i>Thymelicus lineola</i>	3	10.2	0	4	WC	1
<i>Thymelicus sylvestris</i>	3	2	5	5	WC	1
<i>Ochlodes sylvanus</i>	3	2	6	5	WC	1
<i>Pieris brassicae</i>	1	1	24	8	WC	2
<i>Pieris rapae</i>	1	1	23	8	WC	2
<i>Pieris napi</i>	2	2	11	7	WC	2
<i>Lasiommata megera</i>	1	1	7	5	WC	2
<i>Coenonympha pamphilus</i>	4	1	7	4	WC	2
<i>Aphantopus hyperantus</i>	6	2	4	3	WC	1
<i>Maniola jurtina</i>	1	1	26	6	WC	1
<i>Pyronia tithonus</i>	1	2	20	4	WC	1
<i>Melanargia galathea</i>	1	2	11	2	WC	1
<i>Aglais io</i>	2	2	13	8	WC	2
<i>Aglais urticae</i>	1	1	9	8	WC	2
<i>Cupido minimus</i>	1	8.06	0	2	HS	1
<i>Aricia agestis</i>	4	2	4	2	WC	2
<i>Polyommatus icarus</i>	1	1	8	6	WC	2
<i>Polyommatus bellargus</i>	3	1.41	7	1	HS	2

Table S2: Colonisation data. Arrival year 1 is 2012. Butterfly survey data for the 2005-2009 period supplied on 1 km grid maps prepared by Dorset Environmental Records Centre using DMAP for Windows. Index of local presence represents the number of 1km squares in which the species was recorded (2005-2009) within a 10km square centred on the Weymouth Relief Road cutting at Ridgeway Hill East. Mobility categories from Dennis (2010) cited in Warren (2021). Habitat specialism - 'Habitat Specialist' (HS) and 'Wider Countryside' (WC) – from Warren (2021). Data on voltinism is from Dorset butterfly records (Thomas et al., 1998).

FIGURES

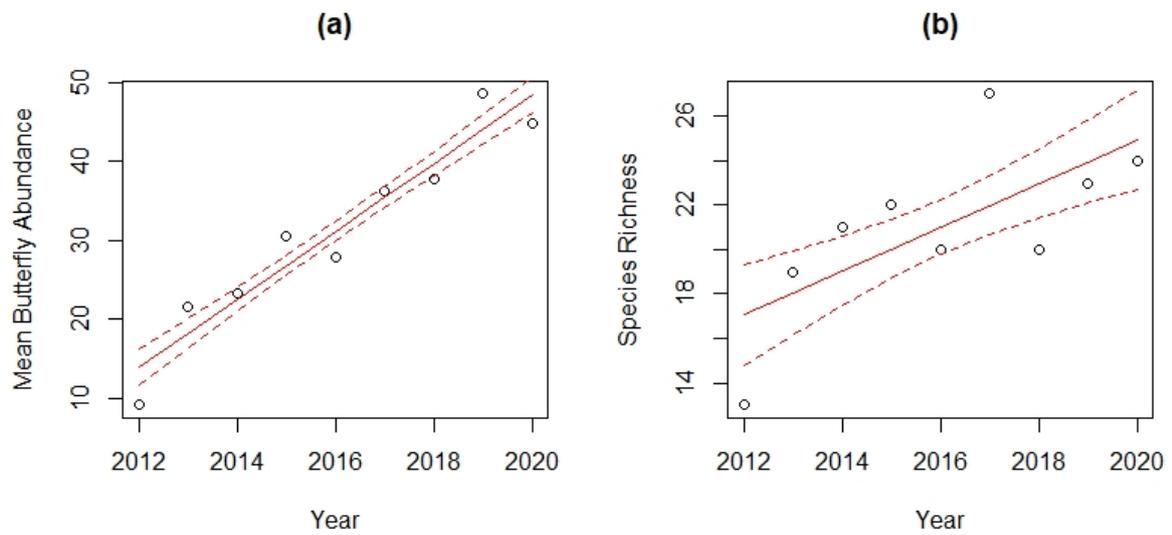


Figure 1: Weymouth Relief Road cutting – (a) mean butterfly numbers per survey visit 2012-2020 (all species). Dotted lines indicate standard errors. ($F=81.54$, $DF = 1, 7$; $R\text{-squared} = 0.92$; $P<0.001$); (b) species richness 2012-2020. Dotted lines indicate standard errors. ($F=6.55$, $DF = 1, 7$; $R\text{-squared} = 0.48$; $p=0.038$).

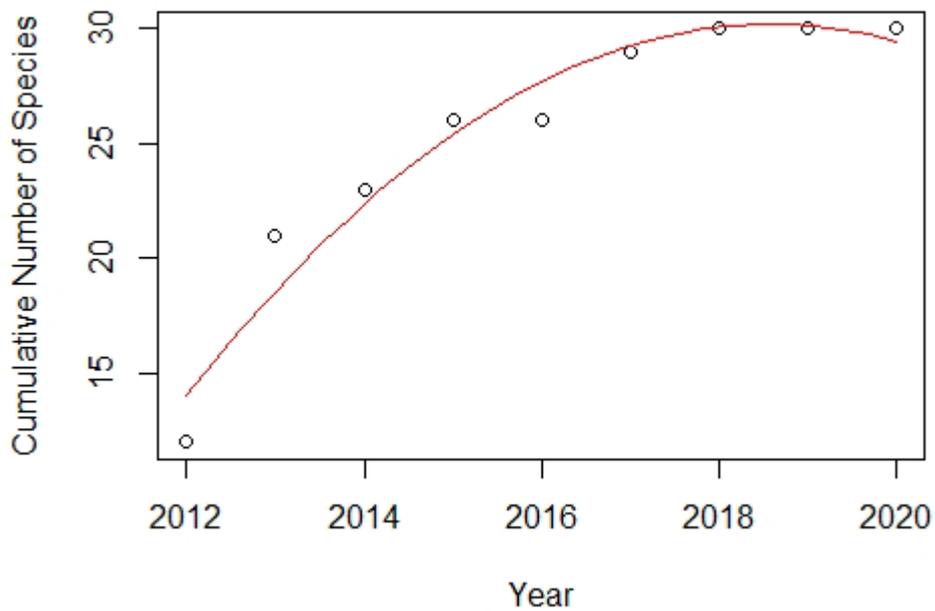


Figure 2: Weymouth Relief Road cutting – cumulative number of species recorded (2012-2020) plotted with a polynomial regression ($F=56.9$; $DF = 2, 6$; $R\text{-squared}=0.95$; $p<0.001$).

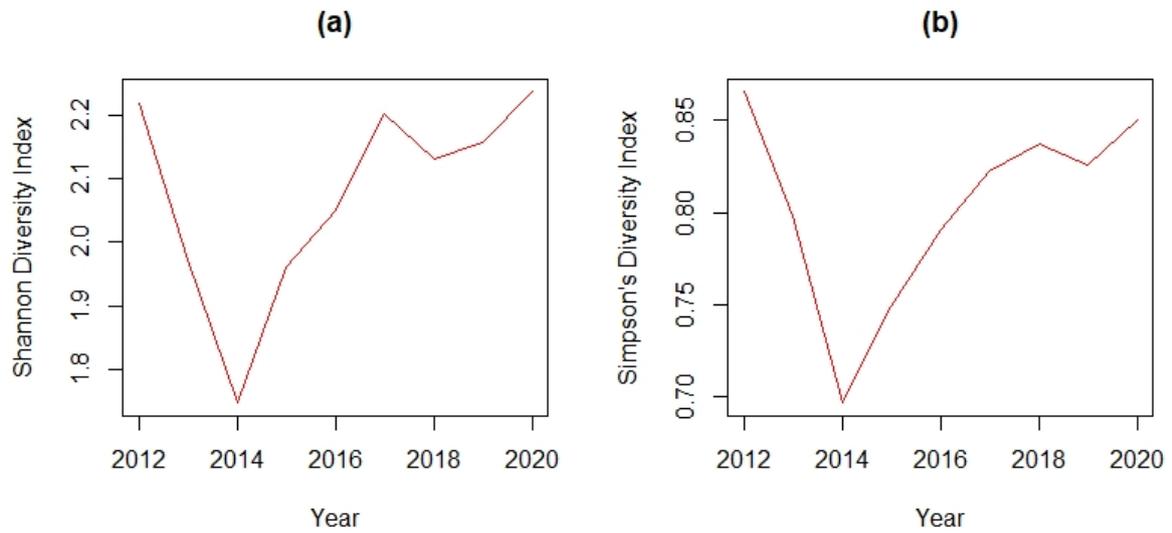


Figure 3: Weymouth Relief Road cutting – changes in (a) Shannon-Weiner Diversity Index and (b) Simpson's Diversity Index during the study period. No significant linear relationships were observed. (Shannon-Weiner: $F=1.96$, $DF = 1, 7$; $P=0.204$; Simpson's: $F=0.82$, $DF = 1, 7$; $P=0.396$)

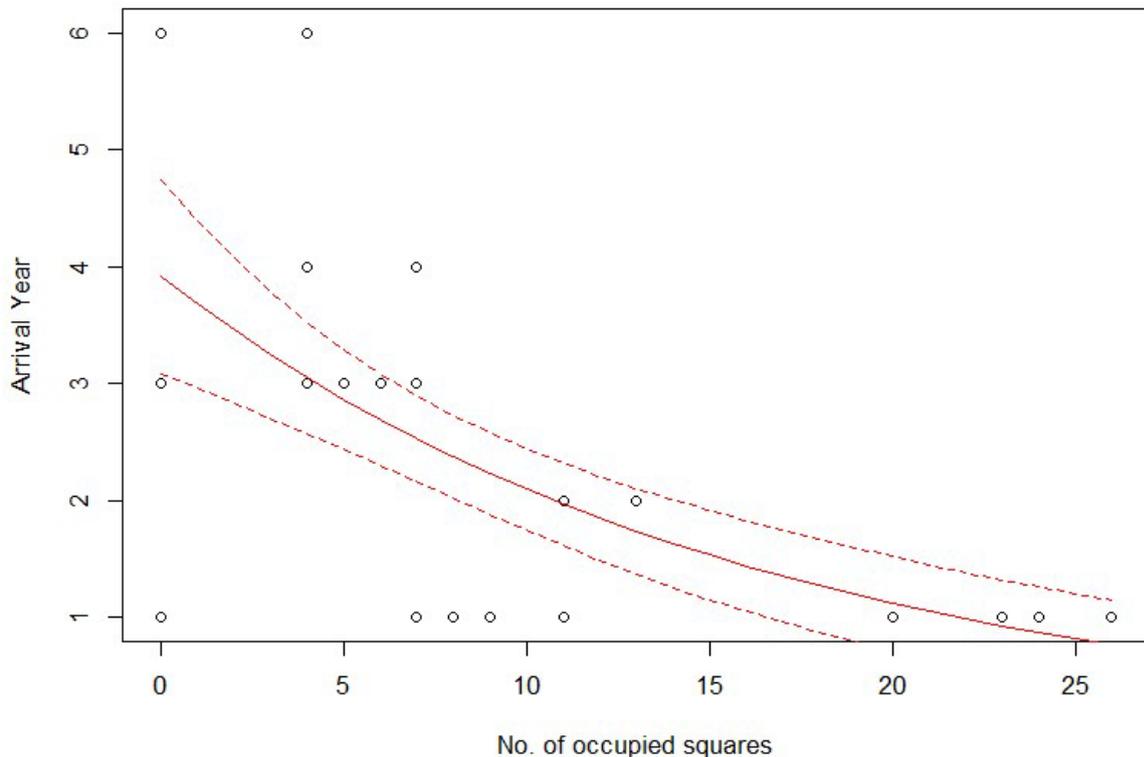


Figure 4: Plot of Poisson GLM showing the relationship (+/- SE) between year of arrival and the degree of local presence of a species (defined as the number of occupied 1 km squares in a 10 km square centred upon the Weymouth Relief Road cutting site) ($Z=2.62$, $DF=19$, $R\text{-squared}=0.42$, $P=0.0089$).