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7 **Evidence for Batesian mimicry in a polymorphic hoverfly**

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Abstract

Palatable Batesian mimics are avoided by predators because they resemble noxious or defended species. The striking resemblance of many hoverflies to noxious Hymenoptera is a "textbook" example of Batesian mimicry, but evidence that selection by predators has shaped the evolution of hoverfly patterns is weak. We looked for geographical and temporal trends in frequencies of morphs of the polymorphic hoverfly *Volucella bombylans* which would support the hypothesis that these morphs are Batesian mimics of different bumblebee species. The frequency of the black and yellow hoverfly morph was significantly positively related to the frequency of black and yellow bumblebees across 52 sites. Similarly, the frequency of the red-tailed hoverfly morph was positively related to the frequency of red-tailed bumblebees. However, the frequencies of hoverfly morphs were positively spatially autocorrelated, and after controlling for this, only one of the two common hoverfly morphs showed a significant positive relationship with its putative model. We conclude that the distribution of *V. bombylans* morphs probably reflects geographical variation in selection by predators resulting from differences in the frequencies of noxious bumblebee species.

Introduction

Hoverflies (Diptera, Syrphidae) are abundant insects in temperate regions and many of them bear a close resemblance to social hymenopterans. The hypothesis that hoverflies derive protection from this resemblance through Batesian mimicry is paradigmatic in evolutionary biology (Gilbert, 2005; Rotheray and Gilbert, 2011). Nevertheless, despite considerable research effort over the past 150 years (Edmunds, 2008), definitive evidence that natural selection by predators has led to the evolution of Batesian mimicry in hoverflies remains elusive.

41 Batesian mimicry is where a palatable animal (the mimic) gains protection from predators
42 because they mistake it for a noxious or unpalatable animal (the model). It was first described
43 by (and is now named after) Henry Bates (1862) based on his studies of South American
44 butterflies, and there have been numerous reviews of the topic since then (e.g. Cott, 1940;
45 Edmunds, 1974; Ruxton, Sherratt & Speed, 2004). While some hoverflies bear a very close
46 resemblance to their hymenopteran models ('good' mimics) others have a much less precise
47 similarity ('poor' or 'imperfect mimics') so that it has been questioned whether they really do
48 gain protection from this resemblance (Edmunds, 2000). While the existence of imperfect
49 mimics may point to other explanations for hoverfly patterns that do not involve predators
50 generalising avoidance behaviours learned after attacking noxious models, several plausible
51 hypotheses are consistent with the idea that even taxa which do not closely resemble their
52 putative models are Batesian mimics (Gilbert, 2005; Penney *et al.* 2012).

53 Empirical evidence supporting the idea that hoverflies are Batesian mimics comes mostly
54 from studies of predator behaviour under controlled conditions. Mostler (1935) showed that
55 different species of hoverflies resembling honeybees (*Apis mellifera*), wasps (principally in
56 the family Vespidae) or bumblebees (*Bombus* spp.) are palatable to insectivorous birds, and
57 that prior experience of the noxious model caused the birds to reject at least some of the
58 mimics (data summarised by Gilbert, 2005). These experiments were in captivity, but
59 Dlusskii (1984) worked in the field, exposing pairs of tethered insects to local birds. He
60 showed that many birds could distinguish the models from the mimics, avoiding the former
61 and eating the latter, but that some birds were deceived by the mimicry and avoided at least
62 some of the mimics.

63 Obtaining evidence for the effectiveness of mimicry in natural populations is much more
64 difficult. Possible support for hoverflies as Batesian mimics comes from Howarth, Edmunds
65 & Gilbert (2004), who found a positive relationship between hoverfly abundance and the

66 abundance of their putative hymenopteran models for ten out of 18 species studied. However,
67 the association between population sizes of mimics and their models offers only very indirect
68 evidence of selection by predators for mimicry. We might reason that where noxious models
69 are abundant, predators quickly learn to avoid them and other similar-looking taxa, leading to
70 a reduced predation rate on mimics, but the study of population dynamics tells us that
71 reduced predation does not necessarily lead to increased population size. Even in prey
72 populations tightly regulated by density-dependent predation (which may or may not be the
73 case in mimetic taxa), population size can fluctuate dramatically and counter-intuitively for
74 both deterministic and stochastic reasons (e.g. Abrams, 2009); it is therefore inherently risky
75 to infer cause and effect from the study of population sizes alone.

76 More direct evidence for Batesian mimicry in natural populations could come from the study
77 of polymorphic species, where the effectiveness of mimicry in individual morphs might vary
78 depending on the environment. If mimicry really is protective, we would expect selection to
79 favour morphs in environments in which their mimicry is most effective, and hence predation
80 is least common. Under such circumstances, selection might exclude all but the most
81 effective morph in a given population, but gene flow among populations experiencing
82 different selection, or negatively frequency-dependent selection by predators, could easily
83 allow less effective morphs to persist at lower frequencies (Bond, 2007). Thus, we would
84 predict a positive relationship across sites between the frequency of a morph and the
85 effectiveness of its mimicry. Here, we examine this prediction in populations of the
86 polymorphic hoverfly *Volucella bombylans* (L. 1758) across the U.K.

87 The morphs of *V. bombylans* are strikingly different, with each resembling one or more
88 species of bumblebee (Stubbs & Falk, 1983; Howarth, Clee & Edmunds, 1999). The
89 commonest morph in the U.K., *V. bombylans plumata*, resembles black and yellow
90 bumblebees (*Bombus lucorum*, *B. terrestris* and *B. hortorum*). The other morph that is

widespread in the U.K. is *V. bombylans bombylans*, which is black with a red tail and closely resembles *Bombus lapidarius*. A scarce third morph, *V. bombylans haemorrhoidalis*, has both red and yellow bands, and resembles *Bombus pratorum*. The identity and frequency of the species which make up the bumblebee community varies considerably across the sites at which *V. bombylans* is found. If the appearance of *V. bombylans* is the result of selection for mimicry of bumblebees, and if selection is still occurring, we hypothesised that the effectiveness of a morph's mimicry, and hence its relative frequency in the population, will be positively related to the frequency or abundance of the bumblebee taxa that it most closely resembles. We tested this hypothesis using data describing the frequencies of *V. bombylans* morphs and their putative bumblebee models at a large number of sites in the U.K. We also looked for a positive association between model and mimic frequencies across years at a single site where *V. bombylans* was particularly abundant.

Method

Fifty-two sites in Britain where *Volucella bombylans* has been recorded were visited by ME during the flight season (normally June-July) between 2000 and 2011.Twenty nine sites were visited in only one year, 13 were visited in 2 – 6 years, and 10 were visited in more than six years (full details of sites are given in Table S1). All morphs of *V. bombylans* seen resting on flowers or on nearby vegetation were counted, as were all bumblebees visiting the same species of flower. Most bumblebees were identified to species and allocated to one of four common groups according to their appearance (see Table 1).

Of the three principal morphs of *Volucella bombylans* in Britain *V. bombylans plumata* is the commonest: it is typically black with a U-shaped fringe of yellow hairs on the thorax, yellowish hairs at the front of the abdomen, and white hairs at the tip. The amount of yellow on the thorax varies partly because yellow hairs fade and are shed in older, worn insects, but

also because of variation in how much of the thorax is covered with yellow hairs. In a small number of insects the central black area is minute or absent, while the hue varies from dull yellow to yellowish brown or occasionally reddish brown so that a few insects resemble *Bombus pascuorum* rather than *Bombus terrestris* (Fig. 1 A – C). However none of the insects we recorded had the brownish abdomen of the brown morph illustrated in Stubbs & Falk (1983). *V. bombylans bombylans* is black with a red tip to the abdomen, but in older worn insects the red fades to dull yellow (Fig. 1 E, F). Very occasionally (just one insect in the present study) individuals are found with white hairs at the tip of the abdomen (Fig. 1 G). It is possible that this represents a distinct rare morph rather than an extreme fading of the red, but this insect was included in *V. bombylans bombylans* in the present study. The third morph, *V. bombylans haemorrhoidalis*, is exactly like var. *plumata* but with a red tail, and in this form too the yellow hairs on the thorax become sparse in worn insects while the red tail fades to yellowish (Fig. 1 I – L). *V. bombylans plumata* resembles the *Bombus terrestris* group of bumblebees, *V. bombylans bombylans* resembles the *Bombus lapidarius* group of bumblebees, and *V. bombylans haemorrhoidalis* resembles the *Bombus pratorum* group of bumblebees.

The latitude and longitude of each site was recorded to allow consideration of spatial (geographical) autocorrelation among the frequencies of the *Volucella bombylans* morphs.

Statistical analysis

Geographic and temporal patterns in the frequencies of *Bombus* spp. and *V. bombylans* morphs were analysed using general linear models (GLMs) in R Version 2.14.0 (R Development Core Team, 2011). Binomial response variables were constructed describing

141 the proportion of all *V. bombylans* individuals which belonged to each morph, and the
142 proportion of all bumblebees which belonged to each taxon. To test our main hypothesis that
143 the frequency of mimic morphs is determined by the frequency or abundance of appropriate
144 model taxa, the relative frequencies and abundances of putative model *Bombus* taxa were
145 fitted as independent variables. Relative frequency was calculated as the proportion of all
146 bumblebees recorded at a site that were of the relevant taxon. Because sampling effort varied
147 among sites, an unbiased measure of absolute abundance was not available; instead,
148 bumblebee abundance was calculated as the number of bees of the relevant taxon observed
149 per individual *V. bombylans* observed.
150
151 In preliminary descriptive analysis of bumblebee and *V. bombylans* morph distributions, we
152 used GLMs to test for simple linear effects of latitude and longitude on the probability of
153 occurrence. Exploratory analysis suggested that more complex polynomial effects of latitude
154 or longitude were not present. The significance of terms was tested by deletion from a
155 saturated model (including the interaction between latitude and longitude), with terms which
156 appeared to have the least explanatory power deleted first. Non-random sampling in space
157 meant that there was partial collinearity between latitude and longitude; the results should be
158 interpreted with care in this context.
159
160 We tested our main hypothesis in a spatial context by looking at the relationship between
161 model *Bombus* taxa and their putative mimic *V. bombylans* morphs across sites. This analysis
162 was complicated by the possibility that morph frequencies in neighbouring sites were
163 autocorrelated. Such spatial autocorrelation might result, for example, from gene flow among
164 populations, and would mean that sites are not statistically independent, thus increasing the
165 chances of making a type-1 error when testing our hypothesis. To deal with this problem, we

166 examined both the "raw" relationships between the frequencies of the model and mimic taxa,
167 and the relationships which remained once the effects of spatial autocorrelation had been
168 removed. This was achieved by employing spatial eigenvector mapping, following Dormann
169 *et al*. (2007); see also Bivand *et al*. (2013) and Griffith & Peres-Neto (2006). First, we fitted a
170 GLM for each *V. bombylans* morph, with the frequency or abundance of the putative model
171 species as a predictor. Eigenvectors representing the spatial patterns of our sampling sites
172 were then generated using the spdep package in R (Bivand, 2011). Those eigenvector(s)
173 which substantially reduced spatial autocorrelation in the residuals of the fitted GLMs were
174 selected and added as predictors to the model. We used all the eigenvectors required to leave
175 no significant autocorrelation in the model residuals (Moran's I: $\alpha = 0.05$; usually only one
176 eigenvector was needed); in cases where there was no strong autocorrelation initially, we
177 adopted a conservative approach by increasing α to a level at which at least one eigenvector
178 was required, except in one case where there was no detectable autocorrelation even at $\alpha =$
179 0.5.
180
181 Both before and after adding the eigenvetors as predictors, the effect of the frequency or
182 abundance of the putative model species on the frequency of the relevant hoverfly morph was
183 tested by deletion of the relevant term from the model. F-tests or Chi-squared tests, and
184 binomial or quasi-binomial error-structures, were used depending on whether there was
185 evidence of strong over-dispersion (see Crawley, 2007). One-tailed p-values were used to test
186 the relationships between the frequencies of model *Bombus* taxa and their putatively mimetic
187 *V. bombylans* morphs because the prediction *a priori* was that these relationships would be
188 positive. It is important to note that the data describing the frequencies of the different
189 *Bombus* taxa, and of the different *V. bombylans* morphs, are not independent, because an
190 individual which belongs to one taxon cannot by definition belong to the other taxa. Thus, the

191 p-values presented for the different taxa are not statistically independent, and they should be
192 interpreted with caution in this context. A conservative approach to the interpretation of the
193 results would be to consider only the statistics presented for the most common *Bombus* taxon
194 (*B. terrestris* group) and the commonest *V. bombylans* morph (*V. bombylans plumata*). In
195 both the temporal and geographic analyses, we focussed on the putative model *Bombus*
196 groups as predictors of each *V. bombylans* morph frequency, lumping other bumblebees
197 together as non-models in each case. For comparison, however, we also ran analyses where
198 the frequencies of common *Bombus* groups which were *not* the putative models for each *V.*
199 *bombylans* morph were fitted as independent variables. The results of these analyses are
200 presented in the supplementary information.
201
202 Because most sites were only surveyed in a subset of the 12 years for which the study ran, a
203 complete simultaneous analysis of geographic and temporal patterns in the frequencies of the
204 taxa of interest was not possible. We therefore pooled data across years for an analysis which
205 considered geographic variation across all sites, before examining temporal patterns at the
206 three most comprehensively sampled sites (clustered near Bispham, Lancashire) in detail.
207 The Bispham sites were visited three times each year for 11 years, with at least 12 days
208 between visits. Using this method, the chances of recording the same insect on successive
209 visits were minimised: the occasional rarer morph, var. *haemorrhoidalis*, was never found at
210 the same site on consecutive visits, while a mark-release-recapture study of a population of *V.*
211 *bombylans* in Northamptonshire found that no insects were recaptured after more than 7 days,
212 and there was a daily survival rate of 0.71 (Ball & Morris, 2004).
213
214 For the analysis of temporal patterns, GLMs were first fitted with year as a covariate,
215 sampling date (early, mid-season or late) as a fixed factor, and the interaction between year

and date. Early samples were taken between 4th and 22nd of June; mid-season samples were taken between 23rd June and 6th July, and late samples were taken between 7th July and 8th August. Exploratory analysis suggested that, while some linear trends were evident over the years, there was not a strong case for the inclusion of polynomial temporal effects in the models. Terms were deleted from the saturated model until no non-significant terms remained, and we then tested the significance of adding the frequency or abundance of the putative model species as a predictor. For comparison, we also tested the frequency or abundance of the putative model in the absence of temporal effects. We checked for remaining temporal structure in the data by testing whether model residuals for samples which were close together in time were either more or less alike than would be expected at random using Mantel tests.

Results

Flowers used for nectar

Table S1 shows the flowers on which *V. bombylans* was found at all of the sites. At almost all sites the flies were on or resting close to just one species of flower, so the bumblebees recorded were also on the same species of flower. Most of the *V. bombylans* were on bramble (*Rubus fruticosus* agg.), marsh thistle (*Cirsium palustre*) or occasionally ragged robin (*Lychnis flos-cuculi*), more rarely on other nearby flowers. Almost all insects were on red, purple or white flowers and only one insect was seen briefly on a yellow flower (*Ranunculus repens*) before flying to its usual flower.

Geographical patterns across sites

239 Before examining the geographical distribution of the different morphs of *V. bombylans* at
240 sites across the U.K., we looked for patterns in the distribution of the different bumblebee
241 groups. Overall, the *B. terrestris* group was the most frequently encountered (57.0 % of
242 18,117 bees), followed by *B. pratorum* (17.4 %), *B. pascuorum* (12.3 %) and *B. lapidarius*
243 (9.0 %). *B. monticola* (a montane red-tailed bumblebee very similar to *B. lapidarius*) and
244 unidentified all-black *Bombus* spp. were scarce (4.3 % combined), and were not considered
245 further in the analysis. There were significant latitudinal and/or longitudinal gradients in the
246 frequencies of *B. terrestris*, *B. pratorum* and *B. lapidarius* (see Table 2; Figures 2a, 2b and
247 3). *B. terrestris* was relatively more common in the north, while the reverse was true for *B.*
248 *pratorum*. *B. lapidarius* was generally more common in the west, with the opposite being true
249 for *B. pratorum*. The frequency of *B. pascuorum* did not vary significantly with either
250 latitude or longitude.

251 The most common *V. bombylans* morph seen was *V. bombylans plumata* (83.1 % of 2,098
252 insects), followed by *V. bombylans bombylans* (15.1 %). The third morph, *V. bombylans*
253 *haemorrhoidalis*, was very rare (1.8 %). The two common morphs showed reciprocal
254 geographic patterns: *V. bombylans plumata* was relatively more common in eastern and
255 northern sites, while the reverse was true for *V. bombylans bombylans* (see Table 3; Figures
256 4a, 4b and 5). Before and after accounting statistically for spatial autocorrelation, there was a
257 significant positive relationship between the frequency of *V. bombylans plumata* and both the
258 frequency and the abundance of its putative model, the *B. terrestris* group (see Figure 6a and
259 Table 4). A similar pattern was seen for *V. bombylans bombylans*, the frequency (but not
260 abundance) of which was positively related to the frequency of its model *B. lapidarius* (see
261 Figure 6b), but this relationship was not significant after accounting for spatial
262 autocorrelation and was further weakened (slightly) if data for the rare red-tailed *B. monticola*
263 were combined with those for *B. lapidarius* (results not shown). The distribution of *V.*

bombylans haemorrhoidalis did not show any clear geographic pattern, or any relationship with the frequency or abundance of its putative model, *B. pratorum*, although both were generally less common later in the season.

When analyses were run with non-model *Bombus* groups as predictors, significant negative relationships with the frequency of *V. bombylans plumata* were revealed, both before and after (with one exception) accounting for spatial autocorrelation (see Tables S2 and S3); these negative relationships can be interpreted simply as the reciprocals of the observed *positive* relationships involving the putative model *B. terrestris*. The expected negative relationships between the frequency of the *B. terrestris* group and the frequencies of *V. bombylans bombylans* and *V. bombylans haemorrhoidalis* were also significant, although the latter was not significant after controlling for autocorrelation. Surprisingly, there were also *positive* relationships between the rarer two morphs and the other non-model taxa, some of which remained even after controlling for spatial autocorrelation.

Temporal patterns at Bispham over eleven years

There were no overall differences in *V. bombylans* morph frequencies among the three Bispham sites (Chi-squared = 2.085, p = 0.353, n = 1993), and more detailed preliminary investigations showed no evidence of an effect of site as a factor, so we pooled the data from the three sites for the main analysis.

Before looking for temporal patterns in the frequency of *V. bombylans* morphs at Bispham, we examined patterns in bumblebee frequencies (see Table 5). Overall, the frequencies of the different *Bombus* groups encountered mirrored those seen at all sites combined (see above); about half (51.8 % of 5,156 individuals) were from the *B. terrestris* group, while *B. pratorum* (16.4 %), *B. lapidarius* (18.1 %) and *B. pascuorum* (13.8 %) groups were roughly equal in abundance. There were no long-term trends in the frequencies of *B. terrestris* and *B.*

pratorum groups across the 11 years of sampling, but there were reciprocal significant seasonal differences in the frequencies of these two groups (see Figures 7a and 7b). *B. terrestris* was more abundant relative to the other groups later in the season, while the opposite was true for *B. pratorum*. *B. lapidarius* was significantly less abundant early in the season than later, and was slightly more common in recent years. Finally, there was a small but significant interaction between the effects of year and season on the frequency with which *B. pascuorum* was encountered: it was seen less frequently late in the season in recent years.

Of the three *V. bombylans* morphs, *plumata* was the most frequently seen at Bispham (77.1 % of 1,016 individuals), followed by *bombylans* (20.3 %) and the much rarer *haemorrhoidalis* (2.7 %). Before accounting for seasonal and yearly differences, there were no obvious relationships between the frequencies of any of the morphs and the frequencies or abundances of the appropriate model bumblebee species (fourth and sixth lines of Table 6). However, the frequencies of the two common *V. bombylans* morphs at Bispham varied significantly with season and across years (see Figures 8a and 8b). *V. bombylans plumata* was seen more frequently earlier in the season, and in recent years, while the opposite was true for *V. bombylans bombylans*. For both common morphs, samples in which frequencies were higher than expected given the effects of year and season tended to be those in which higher frequencies of the appropriate model bumblebee species were observed, but these effects were not significant (fifth and seventh lines of Table 6). Frequencies of *V. bombylans haemorrhoidalis* showed no significant patterns either seasonally or across years. The frequencies of the three *V. bombylans* morphs showed no significant associations with non-model bee taxa at Bispham (see Tables S4 and S5).

Once the effects of year and season were accounted for statistically, there was no evidence of additional temporal autocorrelation, which might be expected if negative frequency

312 dependence was influencing changes in morph frequency over time (Mantel tests of the
313 residuals from the minimum adequate generalised linear models: $p > 0.1$ for all morphs).

314 ## Discussion

315 ### Batesian mimicry

316 Our results show that the frequencies of *V. bombylans plumata* at sites from south Wales to
317 northern England and southern Scotland are positively related to the frequencies and
318 abundances of the *B. terrestris* group of bumblebees whilst being, if anything, negatively
319 related to the frequencies of other bumblebee groups. This finding supports the hypothesis
320 that the commonest *V. bombylans* morph gains protection through Batesian mimicry of black
321 and yellow bumblebees. Our results also show that frequencies of the less common morph, *V.*
322 *bombylans bombylans*, are positively related to the frequencies of its putative model, *B.*
323 *lapidarius*, but negatively related to the frequencies of the *B. terrestris* group. This again is
324 exactly what we predicted we would find if *V. bombylans* gains protection through Batesian
325 mimicry of bumblebees. However, our findings were not entirely clear-cut. After controlling
326 for spatial autocorrelation, the relationship between *V. bombylans bombylans* and its putative
327 model was no longer statistically significant, and the frequencies of this morph also showed
328 unexpected positive relationships with the frequencies of some non-model taxa. Although the
329 results are not unequivocal, to our knowledge our study is the first to have identified a
330 positive association between model and mimic frequencies at a large geographical scale. Our
331 findings thus provide some support for the long-held but seldom tested hypothesis that
332 hoverflies are Batesian mimics of the aversive Hymenoptera that they resemble.

333 Because this is an observational study, there are of course other possible explanations for the
334 relationships we have observed. Model and mimic frequencies may correlate because they are
335 both influenced by factors other than predation which vary geographically. For example,

bumblebee and hoverfly colouration may influence thermoregulation (e.g. Holloway, 1993) or crypsis (although this seems unlikely given their conspicuous yellow, red and black colouration), which in turn may influence fitness, and ultimately relative abundance, in different ways in different locations. Given the intricate and subtle ways in which *V. bombylans* morphs and other syrphids resemble their supposed models, however, such hypotheses seem to us much less plausible than the idea that mimicry explains hoverfly morphology.

It is possible that mimicry in *V. bombylans* is not Batesian. The larvae live in bumblebee nests, feeding on its contents, sometimes including host larvae, although probably only when they are undefended and not of use to the colony (Rupp, 1989; F. S. Gilbert, unpublished). While it is not clear whether this behaviour reduces host fitness, and there is no evidence that *V. bombylans* morphs specialise in inhabiting the colonies of matching host species, it is possible that the resemblance of the adult hoverfly to the host helps *V. bombylans* evade detection and attack by the host colony when laying eggs. Further experiments are required to investigate this hypothesis of "aggressive" mimicry, but at present it seems less plausible than the idea that *V. bombylans* is a Batesian mimic (F. S. Gilbert, unpublished).

Residuals from preliminary GLMs of *V. bombylans* morph frequencies were spatially autocorrelated, and controlling for this autocorrelation weakened the statistical support for some of the predicted relationships (most notable the positive relationship between *V. bombylans bombylans* and *B. lapidarius*). There are many possible sources of spatial structure in the residuals, but an obvious explanation is that neighbouring hoverfly populations are not independent because they are connected by dispersal. The persistence of the predicted positive association between *V. bombylans plumata* and *B. terrestris* when autocorrelation was removed suggests, however, that this association is not a statistical artefact. Nevertheless, while much work has been done recently to devise methods to account

361 for the effects of spatial autocorrelation on type-1 error rates in observational studies of
362 spatial patterns in biology (Dormann *et al.*, 2007), the causal relationships underpinning
363 observed correlations in space will remain unconfirmed unless their study is augmented by
364 appropriate manipulative experiments.

365 Experimental manipulation of mimic frequencies and direct measurement of selection
366 coefficients could confirm once and for all that hoverflies are Batesian mimics, but such
367 experiments are extremely difficult to conduct. Close parallels, however, can be found in
368 studies which have sought to demonstrate the adaptive value of cryptic colouration. In several
369 polymorphic cryptic species, it has been shown that on appropriate backgrounds, better
370 camouflaged morphs receive less predation than more conspicuous morphs. Most of these
371 studies involved observations of attacks by captive predators on prey such as praying
372 mantids, grasshoppers, fish, moths and caterpillars placed against appropriate backgrounds
373 (e.g. Edmunds, 1974 for references to earlier experiments; Mariath, 1982; Edmunds &
374 Grayson, 1991). Because they are conducted in artificial conditions, such experiments do not
375 provide direct evidence of selection pressures acting on natural populations. The best known
376 study of selective predation on different morphs in wild populations is that of Sheppard
377 (1951) on the banded snail (*Cepaea nemoralis*). He found that, in April, song thrushes
378 (*Turdus merula*) took many more yellow snails (yellow-green in life) because these were
379 conspicuous on the brown woodland floor, but by late May when the ground was green with
380 low-growing plants they took fewer yellow and more brown snails because by then the
381 browns were more conspicuous than the yellows. So in this instance the direction of selective
382 predation varies seasonally, but over the geographical range of the snail there are many other
383 factors known to be important in determining the fitness of different morphs, including the
384 effect of shell banding, apostatic selection and climate (e.g. Ożgo & Schilthuisen, 2012, who
385 give references to many earlier papers).

386 The only study that we know of involving selective predation of a polymorphic mimetic
387 insect involved the diadem butterfly (*Hypolimnas misippus*) in tropical and southern Africa,
388 the females of which resemble different morphs of the African queen (*Danaus chrysippus*).
389 The African queen is now considered to be a superspecies comprising four semispecies which
390 evolved in different parts of the continent, but which meet and hybridise in east and central
391 Africa (recently reviewed by Gordon, Edmunds, Edgar, Lawrence & Smith, 2010). The
392 diadem has four morphs corresponding to these four semispecies, but, contrary to expectation
393 if they are Batesian mimics, all morphs occur throughout sub-saharan Africa, irrespective of
394 the local model, with the same two morphs predominating in all populations. Initial work on
395 a population in Ghana showed that when the white hind-winged model was common, the
396 diadems with some white on the hind wings were at a relatively high frequency in the
397 population and had a high survival rate, but when the model became scarce the white hind-
398 winged diadems became rarer and had a lower survival rate (Edmunds, 1969). This supports
399 the contention that diadems in Ghana gain protection through Batesian mimicry for part of
400 the year. More extensive studies on populations in Ghana and Tanzania showed that the
401 situation is much more complex: in both populations, occasional changes in morph frequency
402 favouring rarer and mimetic morphs were followed by linkage disequilibrium between
403 forewing and hindwing patterns (Gordon *et al*., 2010). In both populations the evidence was
404 consistent with selective predation of non-mimetic forms and selection for perfection of
405 mimicry of the hindwings in Ghana and of forewings in Tanzania, but such selection only
406 occurred occasionally.

407 Although the frequencies of *V. bombylans* morphs were also positively associated with those
408 of their putative bumblebee models across years at our best sampled site(s), these temporal
409 relationships were not significant. It is possible that this is the result of a similar situation to
410 that seen in the diadem: if differential selective predation on one or other morph only occurs

411 occasionally, a longer time-series of observations or a different approach such as mark-
412 release-recapture studies might be required to detect it.

413 Alternatively, lags in the effect of relative abundance of models on predation rates may make
414 the influence of selection difficult to detect in our time-series. Further analysis showed no
415 evidence of a seasonally- or annually-lagged relationship between model and mimic
416 frequencies (data not shown), but ultimately a longer time-series is needed to investigate fully
417 temporal feedback between model and mimic relative abundances. It may also be the case
418 that the temporal resolution of three sampling periods per year was not appropriate to detect
419 the effects of interest: a study of three sites in northern England with hourly sampling found
420 evidence of associations at a finer temporal scale between the frequencies of mimetic
421 hoverflies, including *V. bombylans*, and their models (Howarth *et al.*, 2004). These
422 associations are suggestive of behavioural mimicry by hoverflies, but are generally consistent
423 with the geographic patterns in *V. bombylans* morph frequencies.

424 **Seasonal and geographical patterns in relative abundance**

425 We found both seasonal and geographical variations in the relative abundances of different
426 species of bumblebee. It is well known that *Bombus pratorum* starts its colonies early in the
427 season and rears males and fertile females in early summer so that the colonies decline in
428 mid- to late summer, well before most other species of bumblebee (Prŷs-Jones & Corbet,
429 1987), and our results confirm this. However, our findings that the *B. terrestris* group is more
430 frequent in the north relative to *B. pratorum* while *B. lapidarius* is more frequent in the west
431 relative to *B. pratorum* do not appear to have been reported before. *V. bombylans* also shows
432 geographical variation, with *V. bombylans plumata* more frequent in the east and north while
433 *V. bombylans bombylans* is more frequent in the south and west. There were insufficient data
434 on the third morph, *V. bombylans haemorrhoidalis*, to draw any conclusions, but we note that

this morph is widespread in France; for example at two sites in Brittany in 2011 it replaced *V. bombylans bombylans* as the second most frequent morph, yet the frequencies of the bumblebee taxa were very similar to those in the U.K. (ME unpublished data).

Most bumblebee species forage from a wide variety of flowers according to availability, with the relative frequencies foraging on a particular flower varying in different species of bumblebee (Benton, 2006). At Bispham and some other sites it was noticeable that *B. lapidarius* and *B. pascuorum* were more commonly seen on low growing Fabaceae (e.g. *Trifolium* and *Lotus* spp.) than were species in the *B. terrestris* group, but we only counted those bees that were seen on the plant used by *V. bombylans* for feeding and resting (*Rubus fruticosus* at Bispham). Thus the relative numbers of the different species of bumblebee at each site may have been different from those recorded here, but we justify this on the grounds that if there is selective predation of *Volucella* morphs then it is likely to be in the vicinity of the plant where it is most commonly found. Whether bumblebee frequency or abundance is a more important determinant of predator behaviour towards putative mimics is unknown; if birds, for example, really do learn to avoid mimetic hoverflies through prior experience with aversive model taxa, both the relative and absolute rates of encounter with models could conceivably influence the effectiveness or speed of learning.

Conclusion

Our results provide indirect evidence that the remarkable resemblance of *V. bombylans* morphs to common bumblebee species provides them with protection from predation, and hence that bumblebee community composition determines equilibrium morph frequencies in any given *V. bombylans* population. This and other recent research underlines the fact that the study of conspicuously polymorphic animals, which has a rich history stretching back over

150 years, continues to contribute to our understanding of the selective forces which have shaped the evolution of phenotypes in natural populations.

Acknowledgements

We wish to thank everyone who has helped with facilitating visits to sites and other advice and encouragement, especially Staff of Natural England and the Field Studies Council (Preston Montford), Stuart Ball, Barry Brigden, Janet Edmunds, Francis Gilbert, Brigitte Howarth and Yvonne Golding. We are also grateful to two anonymous reviewers for comments on an earlier version of the manuscript.

466 Table 1. Bumblebee groups identified in surveys of sites for *V. bombylans* morphs and their putative models. The vast majority of bees recorded
467 were *Bombus* spp., but a few cuckoo bees (*Psithyris* spp.) were encountered. In addition to those species in the four groups listed, *Bombus*
468 *monticola*, a black bumblebee with a large red tail, was seen at low frequencies at upland sites, and a small number of unidentified all-black
469 bumblebees were encountered (possibly *B. ruderatus*, but more likely a black mutant of a common bumblebee); these scarce taxa were excluded
470 from analyses.

Group	Taxa included	Description
Bombus terrestris	*B. terrestris*, *B. lucorum*, *B. hortorum*, *B. soroeensis*, *B. (Psithyris) vestalis*, *B. (P.) barbutellus, B. (P.) bohemicus*	Black and yellow bumblebees
Bombus lapidarius	*B. lapidarius* & *B. (P.) rupestris*	Black bumblebees with red tails
Bombus pratorum	*B. pratorum* & *B. (P.) sylvestris*	Black and yellow bumblebees with rusty red tails
Bombus pascuorum	*B. pascuorum*, *B. hypnorum* & *B. (P.) campestris*	Reddish or yellowish brown bumblebees, though with some black, especially in worn specimens

471

472

Table 2. Results of generalised linear models with quasi-binomial errors testing the effect of latitude and longitude on the proportion of different species of bumblebees seen at sites in the U.K. Statistics are reported for the effect of deleting the term of interest from the model during backwards step-wise model selection. Statistically significant results are in bold.

Term	*Bombus terrestris*			*Bombus pratorum*			*Bombus lapidarius*			*Bombus pascuorum*		
	F	df	P	F	df	P	F	df	P	F	df	P
Latitude	12.458	1,51	**< 0.001**	11.542	1,51	**0.001**	1.131	1,50	0.293	2.217	1,51	0.143
Longitude	0.111	1,50	0.740	1.9591	1,50	0.168	6.643	1,51	**0.013**	1.106	1,50	0.298
Latitude x longitude	0.176	1,49	0.677	0.177	1,49	0.676	0.069	1,49	0.794	1.726	1,49	0.195

482 Table 3. Results of generalised linear models with quasi-binomial errors testing the effect of latitude, longitude on the proportion of different
483 morphs of *V. bombylans* seen at sites in the U.K. Statistics are reported for the effect of deleting the term of interest from the model during
484 backwards step-wise model selection. Statistically significant results are in bold.

Term	*Volucella bombylans plumata*			*Volucella bombylans bombylans*			*Volucella bombylans haemorrhoidalis*		
	F	df	P	F	df	P	F	df	P
Latitude	3.228	1,50	0.078	4.653	1,50	**0.036**	0.101	1,51	0.752
Longitude	12.053	1,50	**0.001**	12.353	1,50	**< 0.001**	3.676	1,50	0.061
Latitude x longitude	2.339	1,49	0.133	2.815	1,49	0.100	1.192	1,49	0.280

485

Table 4. Results of generalised linear models with quasi-binomial errors testing the effect of the relative frequency and abundance of the appropriate model bumblebee species on the proportion of different morphs of *V. bombylans* seen at sites in the U.K. The effect of the frequency/abundance of the appropriate model species was tested both with and without spatial filters (generated by spatial eigenvector mapping) fitted as covariates to remove spatial autocorrelation. All tests are one-tailed because the null hypothesis for each was directional (relationships were predicted to be positive). Statistically significant results are in bold.

Morph	Bumblebee frequency as predictor						Bumblebee abundance as predictor					
	Without eigenvector maps			With eigenvector maps			Without eigenvector maps			With eigenvector maps		
	F	df	P	F	df	P	F	df	P	F	df	P
Volucella bombylans plumata	27.728	1,51	**< 0.001**	20.655	1,50	**< 0.001**	17.308	1,51	**< 0.001**	No detectable autocorrelation		
Volucella bombylans bombylans	9.070	1,51	**0.001**	0.017	1,50	0.552	0.003	1,51	0.494	0.209	1,50	0.325
Volucella bombylans haemorrhoidalis	0.089	1,51	0.384	0.400	1,50	0.265	8.278	1,51	0.503	8.434	1,50	0.502

494 Table 5. Results of generalised linear models with quasi-binomial errors testing the effect of year and sampling date (early-, mid- and late-
495 season) on the proportion of different groups of bumblebees seen at Bispham. Statistics are reported for the effect of deleting the term of interest
496 from the model during backwards step-wise model selection. Statistically significant results are in bold.

Term	*Bombus terrestris*				*Bombus pratorum*				*Bombus lapidarius*				*Bombus pascuorum*			
	Residual deviance	Change in deviance	df	P	Residual deviance	Change in deviance	df	P	Residual deviance	Change in deviance	df	P	Residual deviance	Change in deviance	df	P
Year	156.73	0.822	1	0.710	399.51	35.643	1	0.134	193.74	43.037	1	**0.015**	78.697	5.209	1	**0.023**
Sampling date	157.55	47.839	2	**0.016**	435.15	400.47	2	**< 0.001**	193.74	178.58	2	**< 0.001**	78.697	4.686	2	0.096
Year x sampling date	151.73	5.002	2	0.670	380.86	18.642	2	0.564	189.92	3.8126	2	0.780	72.126	6.571	2	**0.038**

497

Table 6. Results of generalised linear models with binomial errors testing the effect of year, sampling date (early-, mid- and late-season) and the relative frequency and abundance of the appropriate model bumblebee species on the proportion of different morphs of *V. bombylans* seen at Bispham. Statistics are reported for the effect of deleting the term of interest from the model during backwards step-wise model selection. The effect of the appropriate model species was tested both before and after accounting for variation among years and sample dates (fifth and seventh lines). Statistically significant results are in bold.

Term	*Volucella bombylans plumata*				*Volucella bombylans bombylans*				*Volucella bombylans haemorrhoidalis*			
	Residual deviance	Change in deviance	df	P	Residual deviance	Change in deviance	df	P	Residual deviance	Change in deviance	df	P
Year	39.375	7.363	1	**0.007**	26.190	16.913	1	**< 0.001**	27.663	3.469	1	0.063
Sampling date	39.375	6.833	2	**0.033**	26.190	12.611	2	**0.002**	27.055	0.609	2	0.738
Year x sampling date	37.483	1.893	2	0.388	25.985	0.204	2	0.903	26.246	0.809	2	0.667
Frequency of model species alone	54.552	0.456	1	0.250[a]	56.486	0.009	1	0.538[a]	31.009	0.123	1	0.725
Abundance of model species alone	54.988	0.020	1	0.444[a]	61.222	0.288	1	0.296[a]	31.092	0.040	1	0.421[a]
Frequency of model species with year and sampling date	37.326	2.050	1	0.076[a]	26.163	0.027	1	0.435[a]	NA (year and sampling date not significant)			
Abundance of model species with year and sampling date	38.098	1.277	1	0.129[a]	38.936	0.527	1	0.234[a]	NA (year and sampling date not significant)			

503 [a]one-tailed p-value

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574

575 **Figure Legends**

576 Figure 1. The three morphs of *Volucella bombylans*: A-C *plumata*; E-G *bombylans*; I-K
577 *haemorrhoidalis*, and examples of putative model bumblebee taxa (D, H & L). A, E & I are
578 fresh insects with bright colours, A & I with almost no black in centre of thorax; B is
579 unusually reddish brown; B & J have typical U-shaped yellow mark on thorax; C, F & K are
580 worn insects with faded colours; G is possibly a different morph rather than var. *bombylans*
581 with white tail. D is *B. hortorum*, from the *B. terrestris* group, H is *B. lapidarius* and L is *B.*
582 *pratorum*.

583 Figure 2. Effect of a) latitude and b) longitude on frequencies of different *Bombus* groups
584 (data pooled across sites).

585 Figure 3. Distribution of different *Bombus* groups across sites in the U.K. Sample size is
586 indicated by the size of the pies: small $n < 20$, medium $20 < n < 200$, large $200 < n < 4200$.

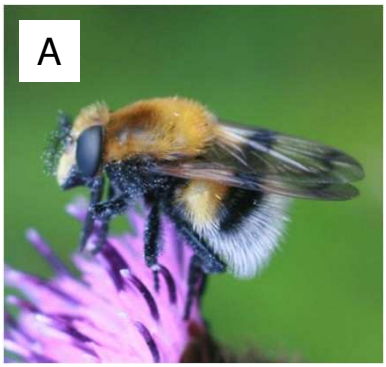
587 Figure 4. Effect of a) latitude and b) longitude on frequencies of different *V. bombylans*
588 morphs (data pooled across sites).

589 Figure 5. Distribution of different *V. bombylans* morphs across sites in the U.K. Sample size
590 is indicated by the size of the pies: small $n < 10$, medium $10 < n < 100$, large $100 < n < 700$.

591 Figure 6. Relationship between the frequency of two mimetic *V. bombylans* morphs and their
592 putative bumblebee models across sites in the U.K: a) *V. bombylans plumata* and its putative
593 model *B. terrestris* and b) *V. bombylans bombylans* and its putative model *B. lapidarius*. The
594 diameter of each data point is proportional to the sample size for *V. bombylans*.

595 Figure 7. Effect of a) year and b) sampling date on frequencies of different *Bombus* groups at
596 Bispham.

597 Figure 8. Effect of a) year and b) sampling date on frequencies of different *V. bombylans*
598 morphs at Bispham.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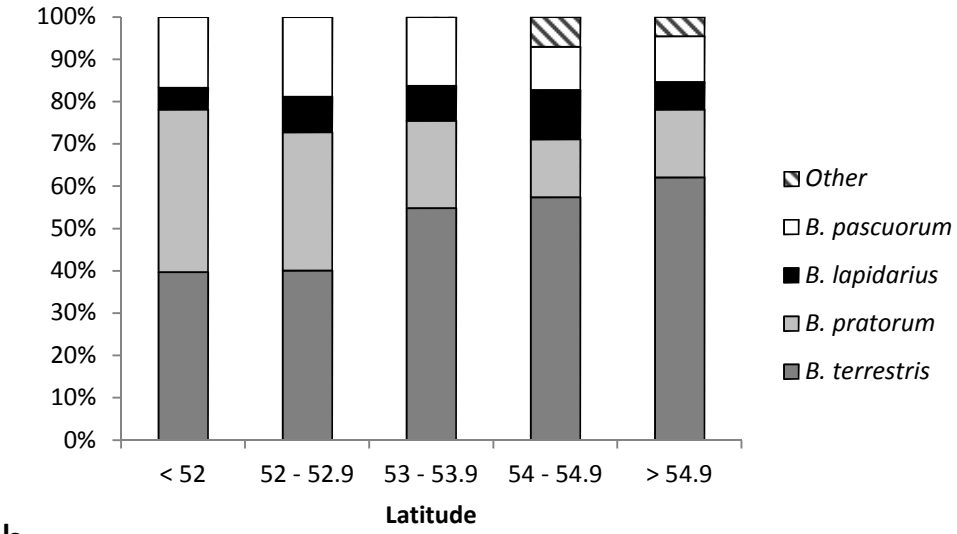
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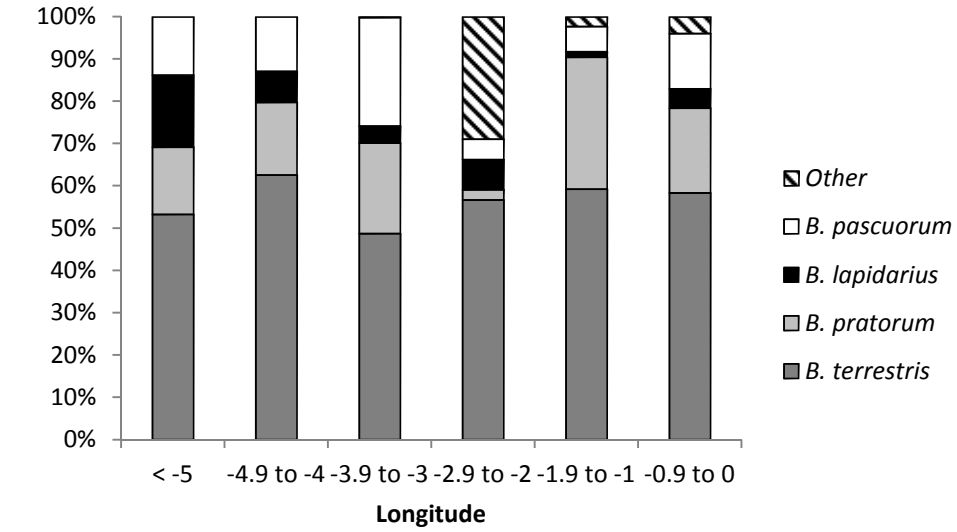
B. lapidarius
B. pratorum
B. terrestris

b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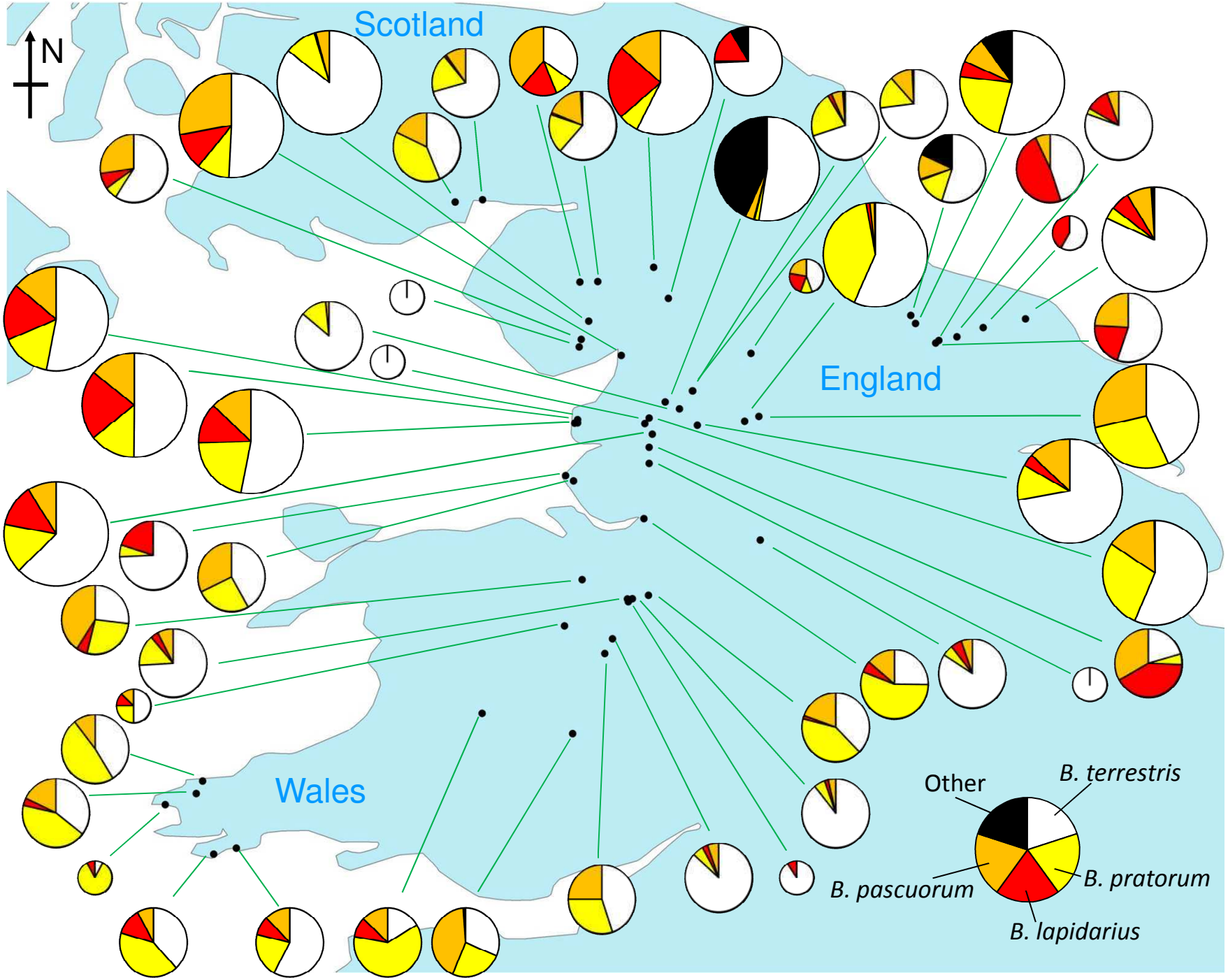
B. terrestris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B. lapidarius

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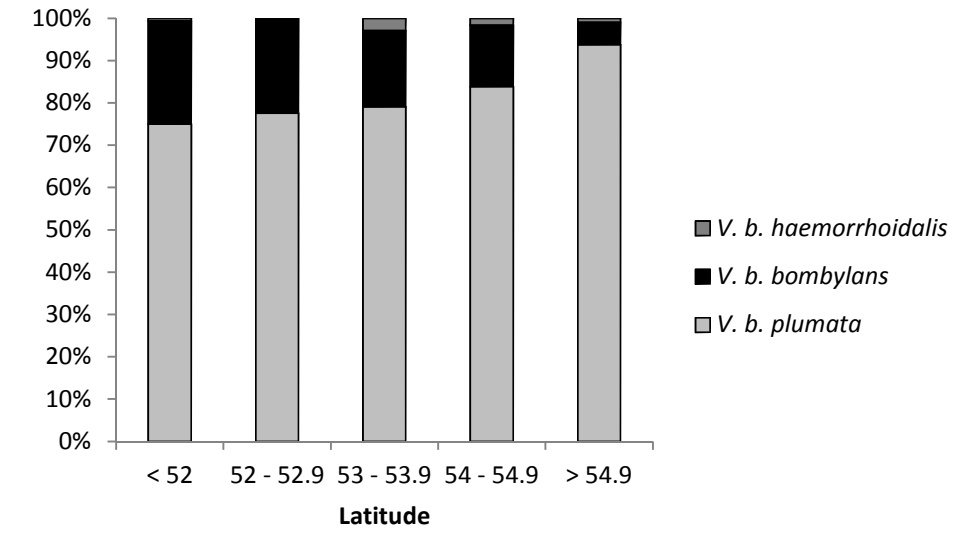
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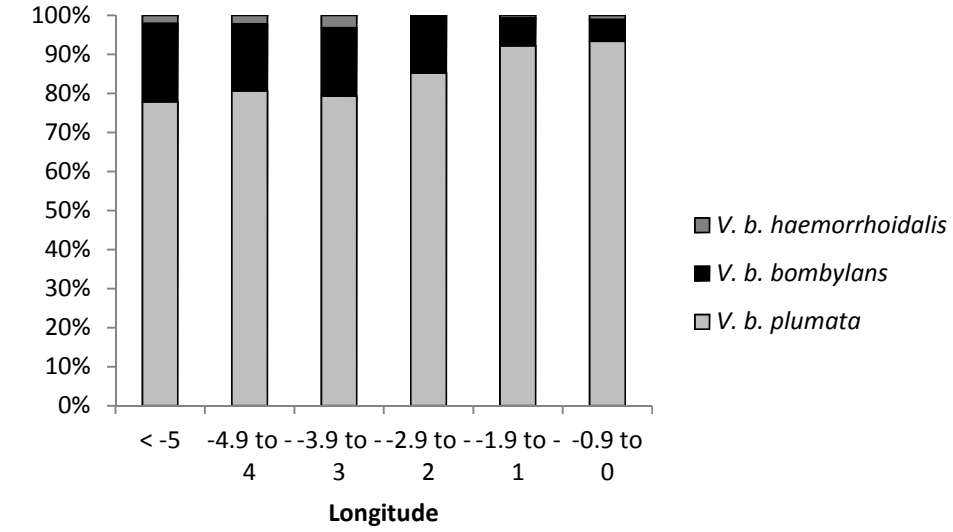
Latitude
V. b. haemorrhoidalis
V. b. bombylans
V. b. plumata

b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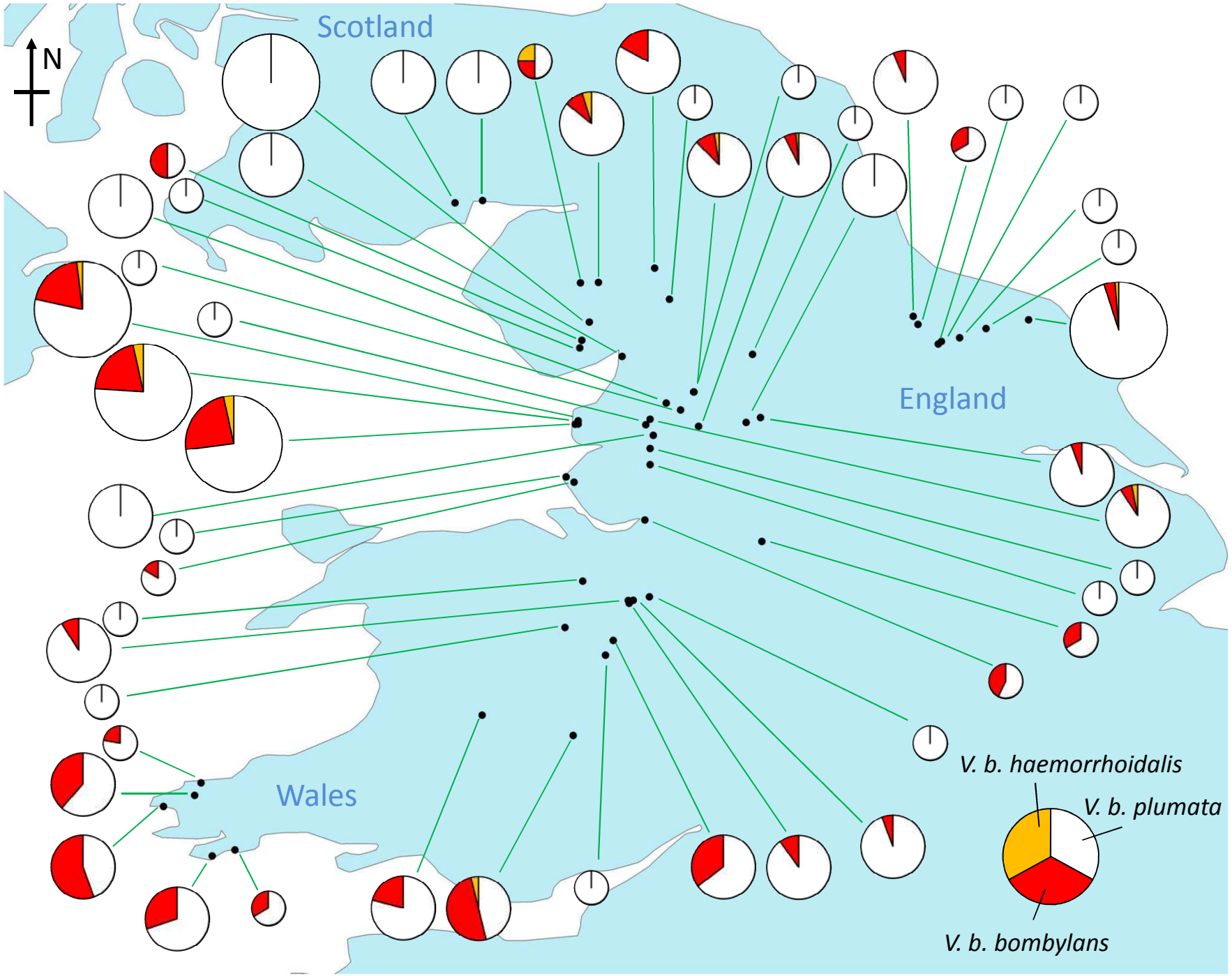
V. b. plumata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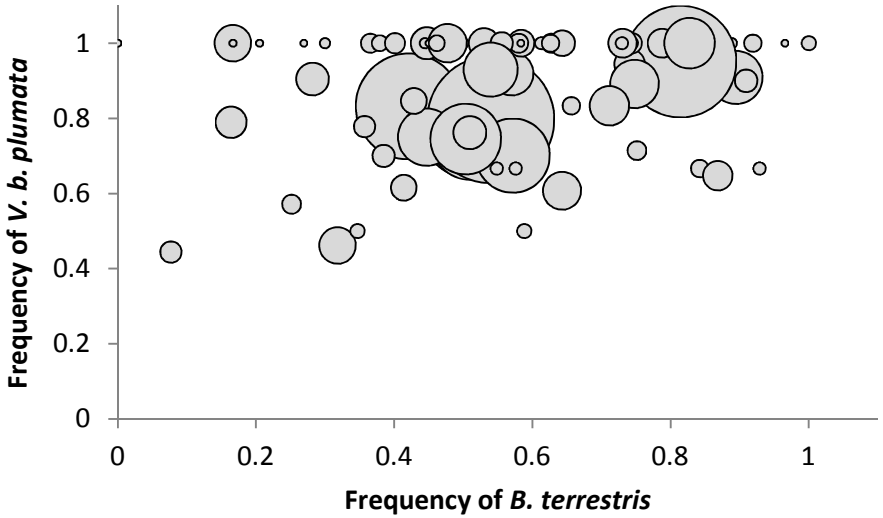
V. b. bombylans

a


Frequency of V. b. plumata
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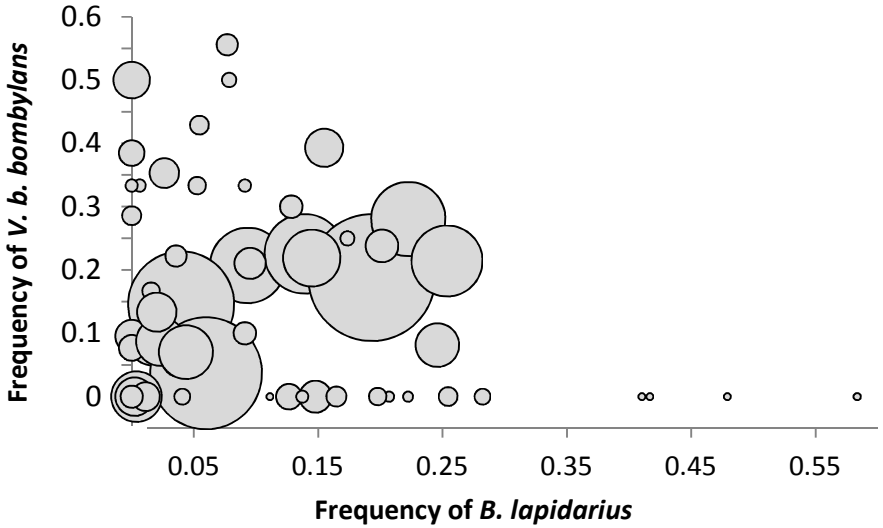
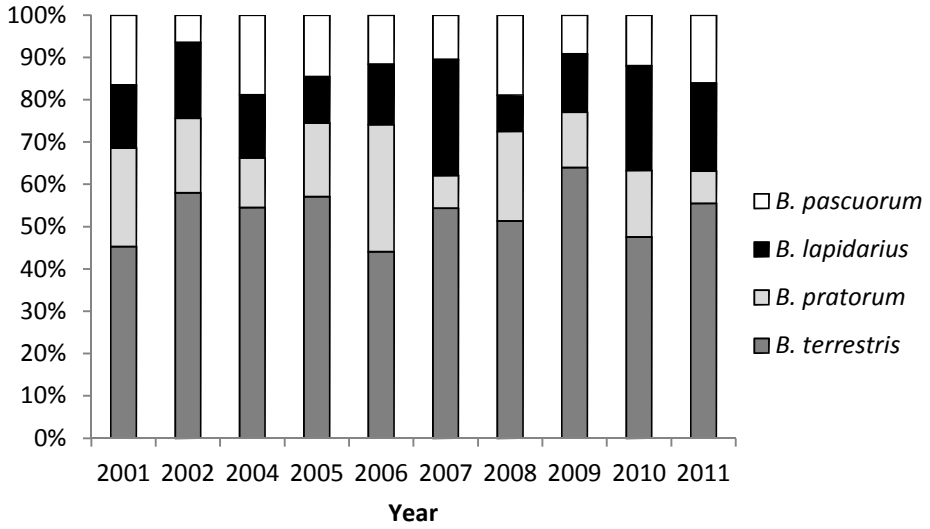
0.2
0.4
0.6
0.8
1
0
0.2
0.4
0.6
0.8
1
Frequency of B. terrestris

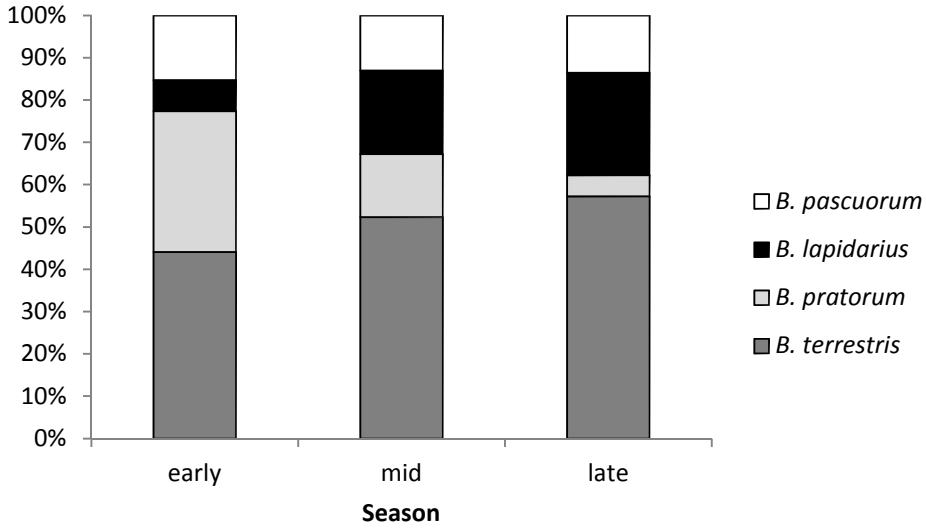
b


Frequency of V. b. bombylans
0
0.1
0.2
0.3
0.4
0.5
0.6
0.05
0.15
0.25
0.35
0.45
0.55
Frequency of B. lapidarius

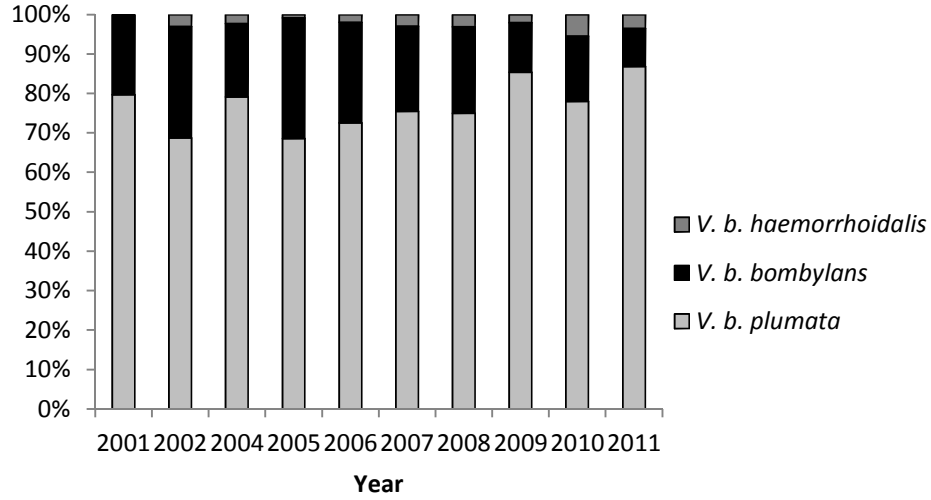
a


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
2001 2002 2004 2005 2006 2007 2008 2009 2010 2011
Year
B. pascuorum
B. lapidarius
B. pratorum
B. terrestris

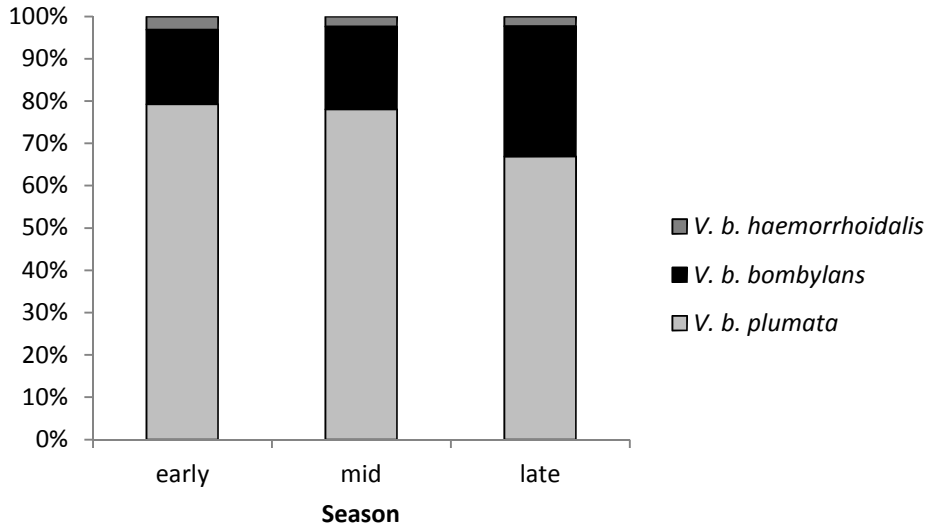
b


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
early
mid
late
Season
B. pascuorum
B. lapidarius
B. pratorum
B. terrestris

a


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
2001 2002 2004 2005 2006 2007 2008 2009 2010 2011
Year
V. b. haemorrhoidalis
V. b. bombylans
V. b. plumata

b


100%
90%
80%
70%
60%
50%
40%
30%
20%
10%
0%
early
mid
late
Season
V. b. haemorrhoidalis
V. b. bombylans
V. b. plumata