

1 TITLE: Hoverflies are imperfect mimics of wasp colouration
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18 ABSTRACT

19

20 Many Batesian mimics are considered to be inaccurate copies of their models, including a
21 number of hoverfly species which appear to be poor mimics of bees and wasps. This
22 inaccuracy is surprising since more similar mimics are expected to deceive predators more
23 frequently and therefore have greater survival. One suggested explanation is that mimics
24 which appear inaccurate to human eyes may be perceived differently by birds, the probable
25 agents of selection. For example, if patterns contain an ultra-violet (UV) component, this
26 would be visible to birds but overlooked by humans. So far, indirect comparisons have been
27 made using human and bird responses to mimetic stimuli, but direct colour measurements of
28 mimetic hoverflies are lacking. We took spectral readings from a wide range of hoverfly and
29 wasp patterns. They show very low reflectance in the UV range, and do not display any
30 human-invisible colour boundaries. We modelled how the recorded spectra would be
31 perceived by both birds and humans. While colour differences between wasps and hoverflies
32 are slightly more distinct according to human visual abilities, bird vision is capable of
33 discriminating the two taxa in almost all cases. We discuss a number of factors that might
34 make the discrimination task more challenging for a predator in the field, which could
35 explain the apparent lack of selection for accurate colour mimicry.

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37

38 INTRODUCTION

39

40 Colour is widely used by animals as a signal, for example to attract mates (Andersson 1994)
41 or as an anti-predator warning display (Ruxton et al 2004). However, colour is an experience
42 as much as a physical property, and therefore the perceived signal depends on the visual and
43 cognitive abilities of the observer (Endler 1990). For example, male blue tits (*Cyanistes*
44 *caeruleus*) use an ultra-violet (UV) signal to attract a mate, which is striking to female
45 conspecifics but invisible to humans (Andersson et al 1998). The butterfly *Heliconius numata*
46 displays a colourful wing pattern that conveys different signals to other butterflies and to
47 potential predators (Llaurens et al 2014). Cases like these demonstrate the importance of
48 considering the signal receiver when assessing the colour component of any biological signal,
49 and show that doing so can shed new light on well-studied systems.

50

51 Some harmless organisms attempt to deceive predators by mimicking the display of a more
52 dangerous “model”, in a process known as Batesian mimicry (Bates 1862). Mimetic displays
53 can incorporate a range of different cues, including shape (Jones et al 2013), pattern (Bain et
54 al 2007) and movement (Golding et al 2005), but among these, colour is thought to be
55 particularly salient to predators (Marples et al 1994, Aronsson and Gamberale-Stille 2012,
56 Kazemi et al 2014). Most experimental evidence suggests that Batesian mimics should gain
57 the greatest protection by resembling their models as accurately as possible (Dittrich et al
58 1993, Lindström et al 1997). However, to human eyes there is great variation in the degree of
59 resemblance between mimics and models in nature, which raises the question of why the less
60 accurate mimics persist in the face of predicted selection towards perfect resemblance
61 (Edmunds 2000, Kikuchi and Pfennig 2013).

62

63 One proposed solution to the problem is that a perceived lack of mimetic accuracy as
64 observed by humans might be specific to our particular visual abilities (Cuthill and Bennett
65 1993). If mimicry is in the “eye of the beholder”, those mimics that we (as humans) consider
66 to be inaccurate might be highly accurate when viewed by an observer with different sensory
67 and cognitive capabilities. A key part of Cuthill and Bennett’s (1993) argument was that in
68 systems with avian predators, the birds’ ability to detect UV light (Chen and Goldsmith
69 1986) might lead them to interpret patterns very differently to humans.

70

71 In their “eye of the beholder” hypothesis, Cuthill and Bennett (1993) make particular
72 reference to hoverflies (Diptera: Syrphidae), which, together with their models, are a key
73 study system for understanding the evolution of imperfect mimicry (see e.g. Dittrich et al
74 1993, Azmeh et al 1998, Holloway et al 2002, Penney et al 2012). The family comprises a
75 large number of species, many of which are abundant and widespread, ranging from non-
76 mimetic to highly accurate mimics of various hymenopteran models (bees and wasps; Apidae
77 and Vespidae), with a wide range of accuracy in between (Gilbert 2005, Rotheray and Gilbert
78 2011).

79

80 Predation from birds is thought to provide the main selective pressure on hoverfly colour
81 patterns (Waldbauer 1988, Gilbert 2005, Bain et al 2007). Bees and wasps are unpalatable to
82 most birds due to their sting and tough cuticle (Mostler 1935), although a few specialists do
83 prey on them despite these defences, usually by removing the sting prior to consumption
84 (Birkhead 1974). Hoverflies do not appear to have any chemical or physical defence, being
85 readily accepted and consumed by birds that have not previously encountered a model
86 (Mostler 1935). Models such as *Apis mellifera* and *Vespula vulgaris* are widespread in the
87 Palearctic and overlap extensively with the ranges of many hoverfly species, while other

88 potential models (e.g. *Mellinus arvensis*) are more restricted geographically and may be
89 present in only part of the range of a given mimic (Richards REF). Most hoverflies, bees and
90 wasps are also likely to overlap at smaller spatial scales, with many being frequent flower
91 visitors. In the UK, most species of hoverfly first emerge between March and May and
92 remain active until at least September (Stubbs and Falk 2002), with workers of social
93 Hymenoptera generally reaching peak abundance in July/August (Richards 1980).

94

95 Given the discrepancy between bird and human visual abilities, it is vital to consider avian
96 perception of the mimetic signals (Cuthill and Bennett 1993). Suitable methods are well-
97 developed for both collection of spectral data and its subsequent interpretation through the
98 eyes of a particular observer (Endler 1990, Vorobyev and Osorio 1998, Endler and Mielke
99 2005). These methods have been used to investigate mimetic accuracy in animals such as fish
100 (Cheney and Marshall 2009), butterflies (Llaurens et al 2014) and salamanders (Kraemer and
101 Adams 2014), but to our knowledge, detailed colour analysis is lacking for hoverflies and
102 their hymenopteran models.

103

104 Most animals, including birds, are thought to perceive the chromatic (hue and saturation) and
105 achromatic (brightness) components of colour separately, and the information in these
106 different channels may be used in different contexts by the signal receiver (Giurfa et al 1997,
107 Osorio et al 1999). Chromatic stimuli are useful for comparison among disparate objects, as
108 the chromatic properties do not change much under different illumination conditions.

109 Achromatic signals are strongly affected by illumination, but are useful for detecting local
110 changes in spectral properties, such as at the border between two colour patches (Osorio et al
111 1999). From this, we predict two possible ways in which spectral properties could be used by
112 an observer to discriminate between models and mimics. The absolute values of chromatic

113 stimuli could be important, as birds have been shown to learn and recognise particular colour
114 combinations in potential prey (Svádová et al 2009, Aronsson and Gamberale-Stille 2012,
115 Kazemi et al 2014). For achromatic stimuli, the absolute values are less likely to be relevant,
116 since they are difficult to compare for samples that are separated in space and time (Osorio et
117 al 1999). However, the achromatic contrast between colour patches within a single pattern
118 will be easier to detect, and could form an important signal (Aronsson and Gamberale-Stille
119 2013).

120

121 In this study, we present data on both chromatic and achromatic components of the colours of
122 wasp-mimicking hoverflies and their potential models, confirming that there is no “hidden”
123 signal in the patterns of either taxon. Then, we interpret the colours through the eyes of avian
124 predators and estimate the level of mimetic accuracy that is achieved. In doing so, we show
125 that mimicry of wasp colours by hoverflies is, to varying degrees, imperfect.

126

127 MATERIALS AND METHODS

128

129 **Specimens**

130

131 Insects were collected using a hand net from wild communities in Nottinghamshire, UK and
132 surrounding areas, during July to September 2014. Target insects were any hoverflies or
133 stinging Hymenoptera bearing a two-colour (typically yellow and black) pattern (Fig. 1), but
134 excluding bumblebees and their putative mimics because they are very likely part of a
135 different mimicry ring (Gilbert 2005), and their hairiness makes taking reliable colour
136 measurements difficult. A total of 247 individuals were identified to species level and sexed
137 using relevant keys (Richards 1980, Stubbs and Falk 2002).

138

139 Specimens were euthanised by freezing for 10 to 20 minutes on the day of capture and then
140 pinned. Colour measurements (see below) were taken within one hour of death to minimise
141 any colour changes that might occur (colours of some species fade during the days following
142 death: C Taylor, pers. obs.).

143

144 Eight different model species were sampled, but only four were found more than twice: *Apis*
145 *mellifera* (N = 14), *Vespula vulgaris* (N = 10), *V. germanica* (N = 3) and *Vespa crabro* (N =
146 5). We know from both theory (Getty 1985) and experiments (Lindström et al 1997) that a
147 model's importance in shaping predator behaviour increases with its abundance, and
148 therefore we have excluded rare models (N < 3) from the bulk of the analysis. However, for
149 comparison, we also conducted a repeat analysis using all eight model species.

150

151 **Spectrophotometry**

152

153 Reflectance measurements were taken using a 100 µm bifurcating optic fibre probe (Ocean
154 Optics, Dunedin, FL, USA, custom spec) with one fibre connected to a pulsed xenon light
155 source (Ocean Optics PX-2) and the other to a spectrophotometer (Ocean Optics USB 2000+
156 UV-VIS-ES). The probe was held steady and targeted using a micro-manipulator (Prior,
157 Cambridge, UK). The probe was fixed at an angle of 45° to horizontal, and the patch under
158 measurement was placed as close to horizontal as possible. A custom-made aluminium probe
159 cover cut off at an angle of 45° aided with this alignment, and also helped to maintain a
160 constant distance (approximately 2 mm) between the specimen and the probe (Endler 1990).
161 The light source pulsed at a frequency of 50 Hz and spectral readings were integrated over 10
162 pulses, or 200 ms. Measurements were recorded for wavelengths over the range 300 to 700

163 nm at intervals of 0.4 nm. Measurements were taken in relation to a white standard (Ocean
164 Optics WS-1 Diffuse Reflectance Standard) and recalibrated to the standard after
165 approximately every four specimens in order to account for lamp drift. All measurements
166 were taken in a dark room with the xenon lamp being the only source of light.

167

168 Pilot testing revealed that readings taken from within 0.2 mm of a colour border were
169 inaccurate (see Appendix) and we therefore targeted the centres of insect colour patches that
170 were at least 0.5 mm in width. In order to check that, in doing so, we did not overlook any
171 colour boundaries invisible to humans, we moved the probe across adjacent areas and
172 monitored any changes to the spectral read-out in real time. We recorded an example of such
173 a process in the form of a transect along the abdomen of an individual of *Helophilus*
174 *hybridus*, with intervals of 0.2 mm.

175

176 For each hoverfly or wasp specimen, we took spectral readings from both ‘black’ (low
177 reflectance, black or dark red/brown to human eyes) and ‘coloured’ (higher reflectance,
178 usually yellow or orange to human eyes) patches of the abdomen where possible. In a few
179 cases, patches of one type were too small to take accurate readings and therefore we only
180 recorded spectra of the predominant patch type in those cases. At least three readings were
181 taken for both of the patch types (where present), ideally taken from different patches on
182 different abdominal tergites, again limited in cases where patches were small or absent on
183 some tergites.

184

185 **Spectral analysis**

186

187 Analysis was carried out in R version 3.1.2 (R Core Team 2014) making use of the package
188 ‘pavo’ for spectral processing and visual models (Maia et al 2013). Noise was removed from
189 the spectra using loess smoothing over a span of 0.4. Any smoothed spectra showing negative
190 reflectance values, which can occasionally result from noise or a drift in calibration, were
191 adjusted by adding a constant to the spectrum such that the minimum reflectance value was
192 zero. “Brightness” was calculated as the mean reflectance value across the whole spectrum
193 (300 to 700 nm).

194

195 Given that the main selective pressure on hoverfly mimicry is considered to come from
196 passerine birds (Dlusski 1984, Gilbert 2005) but that no single species stands out as an
197 obvious candidate, we modelled the colour perception on a generalised ‘UV-type’ retina, with
198 four cone types (U, S, M and L) with peak sensitivity at 372, 456, 544 and 609 nm
199 respectively (Ödeen and Håstad 2003, Maia et al 2013). Achromatic stimulation was based
200 on a blue tit double cone with peak sensitivity of 566 nm. We used models of photon catch to
201 calculate cone stimulation values for each spectrum (Vorobyev and Osorio 1998, Maia et al
202 2013). Given the wide range of species included in this study, it is not possible to record
203 precise illumination conditions that will be valid for all sampled individuals; however all
204 were collected from locations with low canopy cover, and therefore we modelled illumination
205 as ‘D65’, which is representative of daylight in open areas (Endler 1993). We then used
206 receptor noise models to calculate the chromatic (ΔS) or achromatic (ΔL) contrast between a
207 given pair of spectra, with units of ‘Just Noticeable Differences’ or JNDs (Vorobyev and
208 Osorio 1998, Maia et al 2013), and based on a Weber fraction (a measure of signal to noise
209 ratio) of 0.06 (Olsson et al 2015).

210

211 In accordance with the way in which birds are thought to perceive spectral information
212 (Osorio et al 1999), we analysed chromatic and achromatic components of the signals
213 separately. To compare the chromatic properties of patterns from a pair of species, we treated
214 black and coloured patch types separately, and calculated ΔS for each. We then made the
215 assumption that, in attempting to discriminate two patterns, a predator will attend to the patch
216 type within the patterns that shows the larger difference. Thus the chromatic distance within a
217 given model-mimic pairing was taken as the larger of the ΔS values for black and coloured
218 patches.

219

220 As achromatic signals are typically used to detect within-pattern variation (Osorio et al 1999),
221 we calculated the within-pattern achromatic contrast (ΔL) between the black and coloured
222 patches for each individual insect. We then calculated the absolute difference between model
223 and mimic in values of within-pattern contrast as a measure of achromatic distance.

224

225 We repeated the model-mimic comparisons using a different visual model based on human
226 vision, in order to examine any differences from bird perception. Human cone sensitivity data
227 was taken from Stockman and Sharpe (2000) and we assumed a Weber fraction of 0.018
228 (Wyszecki and Stiles 2000). Achromatic stimulation was calculated as the sum of M and L
229 cones (Wyszecki and Stiles 2000). To compare achromatic perception between the two
230 systems, we regressed human against avian estimates of within-pattern contrast across the
231 insect species sampled, with the intercept fixed at zero. The slope value gives an estimate for
232 the ratio in achromatic sensitivity between birds and human. We carried out similar
233 regressions on chromatic contrast data, with separate regressions for the four different model
234 species and for the two patch types (these eight sets of data could not be pooled as they are
235 not independent of each other).

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RESULTS

We examined spectra from 209 individual hoverflies of 33 species, and 38 individual Hymenoptera of eight species, sampling both “black” (very low reflectance) and “coloured” (higher reflectance; usually yellow or orange) patch types within the pattern. At no point did we detect a marked change in spectral properties of any individual that did not correspond to a human-visible boundary (see example with *Helophilus pendulus*, Fig. 2). None of the patterns sampled has a strong UV component in either the coloured or black patches (Fig. 3).

Human “Just Noticeable Difference” (JND) estimates for within-pattern achromatic contrast (ΔL) are related to but considerably higher than the avian equivalents (slope = 4.4, $r^2 = 0.996$, $p < 0.001$). Human and avian JND estimates for chromatic similarity (ΔS) are closer to each other, but human values are usually higher. Slopes for black patches range from 0.88 to 1.41, and for coloured patches from 1.19 to 1.94 (all $r^2 > 0.75$, $p < 0.001$; Fig. 4). Hence, the colour differences that we perceive among model and mimic species are generally rather larger than those evident to avian predators.

All remaining values in the results section are calculated with respect to avian vision. The four main model species (those with $N \geq 3$) are distinguishable from each other in terms of their spectra (Fig. 3). For coloured patches, chromatic contrast ranges from 2 to 12 JNDs (Table S1). Differences among black patches are smaller, ranging from 0.6 to 4.7, with the largest differences being between *Vespa crabro* and the other three models. The three vespid species (*Vespa crabro*, *Vespula vulgaris* and *V. germanica*) have similar levels of within-

260 pattern achromatic contrast ($\Delta L = 40\text{-}45$ JNDs), whereas contrast for *Apis mellifera* is much
261 lower ($\Delta L = 22$; Table 1).

262

263 All of the mimic species sampled are theoretically distinguishable from each of the four main
264 model species in chromatic terms, although some have ΔS values only just larger than one
265 (e.g. *Episyrphus balteatus* differs from *A. mellifera* by $\Delta S = 1.3$; Table 1, Figs. S2 and S3).

266 The species sampled are split roughly half and half between being most similar to *A.*
267 *mellifera* (15) and *Vespula vulgaris* (14), with two being closest to *Vespa crabro* and two to
268 *Vespula germanica*.

269

270 Achromatic differences span a wider range of values than chromatic differences, and are
271 usually larger than the latter (Fig. 5). The hoverflies generally show lower within-pattern
272 contrast than the Hymenoptera (Fig. S4), but some model-mimic pairings were highly similar
273 in achromatic terms, with five mimics differing from their closest model by $\Delta L < 1$ (Table 1).
274 When mimics are allocated to models according to the lowest achromatic difference, we find
275 twelve mimics of *Vespula vulgaris*, ten mimics of *A. mellifera*, ten of *Vespa crabro* and one
276 of *Vespula germanica*. Agreement between the chromatic and achromatic measures is poor –
277 the closest model in chromatic terms matches the achromatic for only 14 of the 33 mimics
278 (Table 1).

279

280 We repeated the above analysis taking into account all eight sampled species of
281 Hymenoptera, including those with very low abundance. Results in this re-analysis were very
282 similar, with only nine of 33 hoverfly species having one of these rare species as their closest
283 model (Table S2).

284

285 DISCUSSION

286

287 This study represents the first attempt to characterise, in detail, the colours of hoverflies and
288 their hymenopteran models. From our measurements of insect specimens, we find no
289 evidence that there are pattern elements or colour boundaries in either hoverflies or their
290 models that are invisible to the human eye, a fact which until now has only been indirectly
291 inferred (Green et al 1999, Penney et al 2012). Our estimates of colour similarity according to
292 the sensory abilities of humans and birds correlated closely with one another.

293

294 Model and mimic colours were usually less distinct (smaller JND values) when calculated
295 using the avian as opposed to the human visual model. This tallies well with recent
296 behavioural data, which have shown that humans are at least as good at discriminating
297 colours as chickens are, thanks to lower levels of receptor noise (Olsson et al 2015).
298 Nonetheless, none of the mimics differs from its nearest model by less than one avian JND,
299 which implies that, in the eyes of birds, any given mimic-model pair should in theory be
300 distinguishable in terms of colour (Vorobyev and Osorio 1998).

301

302 A number of researchers have speculated that a threshold of one JND may not be realistic in a
303 natural context, instead adopting higher threshold values in the range two to four (Siddiqi et
304 al 2004, Feeney et al 2014, Limeri and Morehouse 2014). There is no behavioural evidence to
305 support the choice of a particular threshold other than one (Olsson et al 2015) but there are a
306 number of factors which might make the discrimination task more difficult for a predator in
307 the wild than in the controlled laboratory settings on which JND values are based. Firstly,
308 predators will rarely have the opportunity to compare two prey items side by side. Temporal

309 separation of the stimuli, as experienced by a predator learning to discriminate between
310 models and mimics, will increase the difficulty of the task (Dyer and Neumeyer 2005).

311

312 Secondly, predators may not have the opportunity to view their prey from close range before
313 deciding whether to attack, reducing the visual information available. It is not clear at what
314 typical distance a bird might make its decision. Dlusski (1984) showed that hoverflies would
315 not give flight until a mock predator approached to within 30 cm or less, suggesting that
316 relatively close inspection might be possible on occasion, but he also observed that
317 insectivorous birds could find prey from a distance of 10 m or more. The spatial resolution of
318 the perceived pattern will decline with distance. Passerines can discriminate objects separated
319 by a visual angle of about 1-3 arc minutes (0.017 to 0.05 °; Donner 1951). This would give a
320 spatial resolution of about 0.2 mm at a distance of 30 cm, which would be enough to perceive
321 the pattern of most hoverflies, but even at a distance of a few metres, very little detail would
322 be visible (2 mm resolution at a distance of 3 m). At that range, rather than perceiving
323 separate patches of colour, the bird would perceive a spectrum that is an average of the two
324 spectra (weighted by area), but it might still be able to learn differences among species based
325 on this colour information.

326

327 Thirdly, if the prey is moving, this may make the discrimination more difficult. Notably,
328 motion creates blur which will make borders within the colour pattern less distinct, although
329 (at least in humans) cognitive processing can remove much of the blur (Burr 1980). Hoverflies
330 are fast fliers and highly active, but one might expect birds to target them when they are at
331 rest on flowers or vegetation rather than in flight (Dlusski 1984), which would minimise the
332 impact of blur. Motion blur would have a similar effect to the low resolutions described
333 above, in that above a certain level, the pattern would not be visible, and colours of different

334 patches would become merged together. However, a strong colour difference would certainly
335 still be visible under those circumstances.
336 Importantly, there is considerable variation among species in the levels of mimetic accuracy,
337 with several showing chromatic contrast of less than three JNDs with their nearest model, and
338 others with values of 10 or more. In their natural context, it is likely that the most accurate
339 hoverflies are more or less “perfect” colour mimics. However, contrary to the “eye of the
340 beholder” hypothesis (Cuthill and Bennett 1993), those mimics at the lower end of the
341 accuracy scale should be clearly distinguishable from their models, even if we allow for the
342 difficulties described above. If birds do indeed provide the main selective pressure on
343 hoverfly colours, the observed variation in mimetic accuracy cannot be explained solely by
344 the eye of the beholder hypothesis.

345

346 Our data do hint at an alternative explanation for at least some instances of mimetic
347 inaccuracy. The model species that we sampled were all distinguishable in terms of their
348 colours; even *Vespula vulgaris* and *V. germanica*, two very closely related wasps, differ by
349 five JNDs. Models and mimics do not segregate neatly according to their colour (Figures S2
350 and S3). In contrast to other characteristics such as antenna length, in which models and
351 mimics are consistently separated (Penney et al 2012), there is no simple rule that could be
352 followed to reliably distinguish hoverflies from wasps on the basis of colour. A predator can
353 therefore adopt one of two strategies: it can learn each species and its colour entirely
354 separately, which would carry a high cognitive burden as well as requiring repeated sampling
355 of potentially dangerous prey (Kikuchi and Sherratt 2015), or it may generalise over a range
356 of colours (Richards-Zawacki et al 2013, Veselý et al 2013). In the latter strategy, a large area
357 of colour space would be protected, including many (though perhaps not all) of the hoverfly

358 colours (Figs. S2 and S3), and this would explain the lack of selection for increased mimetic
359 accuracy in those cases.

360

361 It is interesting to note that, in the majority of cases, achromatic distances between model and
362 mimic are larger than chromatic distances (Fig. 5 and Table 1). This implies that the
363 chromatic properties of the colour pattern may be under stronger selection from predators
364 than the achromatic properties. The same appears to be true of mimetic salamanders
365 (Kraemer and Adams 2014), another system in which birds are thought to provide the main
366 selective pressure on colours. Birds may find it difficult to compare achromatic signals that
367 are separated in time and space given changing light conditions (Osorio et al 1999). In
368 addition, their sensitivity to achromatic contrast declines at small spatial scales ($< 1^\circ$ visual
369 angle; Ghim and Hodos 2006), meaning that they may exert little selection for accurate
370 mimicry of luminance properties.

371

372 Numerous experiments have demonstrated that colour is an important stimulus for predators
373 attempting to discriminate among prey items (Morrell and Turner 1970, Svádová et al 2009,
374 Veselý et al 2013, Kazemi et al 2014). However, all of these experiments have used stimuli
375 that are well separated in colour space, corresponding to different named colour categories.
376 More behavioural studies are needed to establish predator responses to colour stimuli that
377 differ by more subtle degrees, and to separate the response to achromatic and chromatic
378 properties of the stimulus. Most importantly, future work on inaccurate mimicry must
379 consider the natural history of the predator-prey interactions in order to take account of
380 highly influential variables such as viewing distance and movement.

381

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517

518 SUPPLEMENTARY MATERIAL

519 Supplementary text: testing spatial resolution.

520 Fig. S1. Testing the accuracy of spectral readings at small spatial resolutions.

521 Fig. S2. Coloured patches of models and mimics plotted in 2D colour space.

522 Fig. S3. Black patches of models and mimics plotted in 2D colour space.

523 Fig. S4. Histograms showing the distribution of values for contrast between black and

524 coloured areas, across all model and mimic species sampled.

525 Table S1. Comparison of spectral properties among the four most abundant model species.

526 Table S2. A comparison of achromatic and chromatic similarity values when rare

527 Hymenoptera are either excluded or included as possible models.

528 FIGURE LEGENDS

529 Fig. 1. Examples of colour and pattern variation in hymenopteran (**a** and **b**) and hoverfly (**c-j**)
530 abdominal patterns. Scale bars each show 1 mm. **a** – *Vesupla vulgaris*. **b** – *Apis mellifera*. **c** –
531 *Eristalis tenax*. **d** – *Eristalis pertinax*. **e** – *Melangyna labiatarum*. **f** – *Sericomyia silentis*. **g** –
532 *Syrphus ribesii*. **h** – *Sphaerophoria scripta*. **i** – *Episyrphus balteatus*. **j** – *Platycheirus*
533 *albimanus*.

534

535 Fig. 2. Colour variation along a transect on an abdomen of *Helophilus hybridus*. **a** – The
536 abdomen, with locations of spectral readings shown in red. **b** – All 22 spectra from the
537 transect. **c** – Variation in spectral brightness along the transect.

538

539 Fig. 3. Reflectance spectra for all sampled species with $N > 3$. Solid and dashed lines show
540 means for black and coloured patches respectively, shaded areas show standard error. For
541 species abbreviations, see Table 1.

542

543 Fig. 4. Comparison of estimates of chromatic contrast as calculated in models based on avian
544 and human vision. Each point represents a single model-mimic pairing. Values are in units of
545 Just Noticeable Difference. The two panels show data on black and coloured patch types
546 separately. For model abbreviations, see Table 1.

547

548 Fig. 5. Comparison of chromatic and achromatic distances between mimic species and each
549 of the four main model species. Each point represents a single model-mimic species pairing.
550 For model abbreviations, see Table 1.

551

552

553 **Table 1. Achromatic and chromatic distances of each hoverfly species to its closest**
 554 **model.** All values are given in units of Just Noticeable Differences.

555

556	Species	Abbrev.	Achromatic			Chromatic			
557			Internal	Closest	Dist ¹	Closest	Dist ²	Patch	Thorax
558			contrast	model		model		colour	width
559	Mimics								
560	<i>Chrysotoxum arcuatum</i>	Car	41.2	Vvu	1.2	Vge	9.3	C	2.6
561	<i>Dasysyrphus albostrigatus</i>	Dal	55.7	Vcr	10.4	Vvu	8.5	C	2.4
562	<i>Dasysyrphus tricinctus</i>	Dtr	49.3	Vcr	4.0	Vvu	11.4	C	2.5
563	<i>Epistrophe grossulariae</i>	Egr	37.5	Vvu	2.5	Ame	3.8	B	3.2
564	<i>Episyrphus balteatus</i>	Eba	25.9	Ame	4.0	Ame	1.3	C	2.2
565	<i>Eristalis arbustorum</i>	Ear	29.6	Ame	7.7	Ame	3.5	B	3.2
566	<i>Eristalis horticola</i>	Eho	35.5	Vvu	4.5	Vvu	2.9	C	3.5
567	<i>Eristalis interruptus</i>	Eip	32.8	Vvu	7.2	Vcr	5.4	C	3.4
568	<i>Eristalis pertinax</i>	Epe	31.3	Vvu	8.7	Ame	1.6	C	3.7
569	<i>Eristalis tenax</i>	Ete	27.4	Ame	5.6	Vcr	3.6	B	4.4
570	<i>Eupeodes latifasciatus</i>	Ela	52.4	Vcr	7.0	Vge	2.6	C	2.0
571	<i>Helophilus hybridus</i>	Hhy	45.9	Vcr	0.6	Vvu	1.9	C	3.8
572	<i>Helophilus pendulus</i>	Hpe	37.9	Vvu	2.1	Vvu	2.2	B	3.0
573	<i>Leucozona glaucia</i>	Lgl	35.4	Vvu	4.6	Ame	16.2	C	2.6
574	<i>Melangyna labiatarum</i>	Mla	53.5	Vcr	8.2	Vvu	10.7	C	1.8
575	<i>Melanostoma scalare</i>	Msc	27.7	Ame	5.8	Ame	2.6	C	1.6
576	<i>Meliscaeva auricollis</i>	Mau	34.6	Vvu	5.4	Vvu	4.4	C	2.0
577	<i>Meliscaeva cinctella</i>	Mci	30.3	Ame	8.4	Ame	3.4	C	1.9
578	<i>Myathropa florea</i>	Mfl	34.1	Vvu	5.9	Vvu	3.9	C	3.8
579	<i>Parhelophilus versicolor</i>	Pve	43.0	Vge	1.0	Vvu	2.7	C	2.9

580	<i>Platycheirus albimanus</i>	Pal	28.7	Ame	6.8	Ame	10.5	C	1.8
581	<i>Platycheirus clypeatus</i>	Pcl	22.9	Ame	1.0	Ame	2.2	B	1.7
582	<i>Platycheirus occultus</i>	Poc	21.5	Ame	0.3	Ame	13.0	C	1.5
583	<i>Sericomyia silentis</i>	Ssi	63.9	Vcr	18.6	Vvu	3.1	B	4.5
584	<i>Sphaerophoria scalare</i>	Ssc	38.5	Vvu	1.5	Vvu	2.7	C	1.6
585	<i>Syrpitta pipiens</i>	Spi	22.3	Ame	0.5	Ame	4.5	C	1.6
586	<i>Syrphus ribesii</i>	Sri	51.1	Vcr	5.8	Vvu	4.9	C	2.8
587	<i>Syrphus torvus</i>	Sto	44.9	Vcr	0.5	Vvu	7.3	C	2.9
588	<i>Syrphus vitripennis</i>	Svi	46.8	Vcr	1.5	Vvu	5.5	C	2.4
589	<i>Volucella inanis</i>	Vin	44.9	Vcr	0.4	Ame	5.7	B	4.8
590	<i>Volucella pellucens</i>	Vpe	32.9	Vvu	7.1	Ame	8.2	C	4.9
591	<i>Volucella zonaria</i>	Vzo	38.6	Vvu	1.4	Ame	3.8	B	6.1
592	<i>Xylota segnis</i>	Xse	15.4	Ame	6.5	Ame	5.7	C	2.6
593	Models								
594	<i>Ancistrocerus trifasciatus</i>	Atr	45.3						2.0
595	<i>Apis mellifera</i>	Ame	21.9						3.6
596	<i>Ectemnius cavifrons</i>	Eca	65.7						2.9
597	<i>Ectemnius continuus</i>	Eco	65.9						2.8
598	<i>Mellinus arvensis</i>	Mar	70.3						2.2
599	<i>Vespa crabro</i>	Vcr	45.3						5.5
600	<i>Vespula germanica</i>	Vge	44.0						3.6
601	<i>Vespula vulgaris</i>	Vvu	40.0						3.1

602 ¹ Achromatic distances are calculated as the absolute difference between values of internal
603 pattern contrast (that is, the achromatic distance between coloured and black patches)
604 between the model and mimic.

605 ² Chromatic distances are the ΔS values between model and mimic for whichever patch type
606 (coloured or black, indicated in the 'patch colour' column) has the larger ΔS .





