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The distribution of bumblebee colour patterns worldwide: possible significance for thermoregulation, crypsis, and warning mimicry

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Bumblebee colour patterns can be highly variable within species, but are often closely similar among species. The present study takes a quantitative approach to survey bumblebee colour patterns in order to address some of the most basic questions concerning resemblances: (1) do colour-pattern groups exist; (2) are species within colour-pattern groups geographically clumped; and (3) are some colour-pattern groups associated with particular kinds of habitat? The results using data for 632 worker patterns from all of the world's bumblebee species show that: (1) there are many repeating colour patterns, forming relatively few groups of species with similar patterns; (2) colour-pattern groups can be recognized using simple rules; and (3) species within the 24 largest colour-pattern groups are significantly aggregated in particular areas of the world. Three principal divisions of colour-pattern groups are associated with three likely functions: (1) the darkest bumblebees are associated primarily with the tropics, where a thermoregulatory function is suggested; (2) the palest bumblebees are associated with intermediate northern latitudes, where a cryptic function in drying grasslands is suggested; and (3) the intermediate, strongly banded bumblebees are widespread, although these patterns predominate where banding may have advantages as collective warning signals to predators (Müllerian mimicry). Further studies are needed to test these explanations. © The Natural History Museum, London. Journal compilation © 2007 The Linnean Society of London, *Biological Journal of the Linnean Society*, 2007, **92**, 97–118.

ADDITIONAL KEYWORDS: *Bombus* – biogeography – camouflage – convergence – temperature regulation – warning coloration.

INTRODUCTION

The most obvious feature of bumblebees (genus *Bombus*) is that they are covered in long and often brightly coloured hairs that form distinctive colour patterns. About a century ago, it was realized that not only can bumblebee colour patterns be closely similar among species (Dalla Torre, 1880), but also that they can be highly variable within species, so that within some species, different individuals may resemble a series of other species (Radoszkowski, 1884; Vogt, 1909). Unsurprisingly, bumblebees have therefore long been used as models for discussing character variation, the nature of species, and regional colour-pattern resemblance among species (Vogt, 1909, 1911; Reinig, 1935, 1939, 1970; Pekkarinen, 1979; Owen & Plowright, 1980; Thorp, Horning & Dunning, 1983; Williams, 1991; Estoup *et al*., 1996; Terzo *et al*., 2005). However, there has been little quantitative exploration of colour-pattern variation to test some of the central ideas. In particular, before attempting to study explanations of colour-pattern resemblance in terms of development and possible evolutionary processes, it is important to know: (1) whether there is evidence for the existence of groups of species with similar colour patterns, in the sense that certain colour patterns recur among different species more often than would be expected by chance, and (2) whether species within these colour-pattern groups are associated with the same places or habitats, so that they tend to occur together in the same parts of the world more often than would be expected by chance.

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Some striking examples of colour-pattern resemblance among bumblebee species have been documented. For example, four species (*Bombus trifasciatus* Smith, *Bombus haemorrhoidalis* Smith, *Bombus breviceps* Smith, and *Bombus rotundiceps* Friese) show a series of colour patterns across southern Asia that are rare among bumblebees. Nonetheless, the similar patterns are shared in any one place by all four, and differ and covary together across the different parts of the range (Richards, 1929; Tkalců, 1968, 1989; Williams, 1991). The four species are only distantly related, belonging to four different subgenera, so their colour patterns appear to be convergent. An early study by Richards (1929) considered that this form of close colour-pattern convergence within a region, combined with parallel covariation among regions, might be the result of Müllerian mimicry for warning signals (Müller, 1879). This case appears to parallel the remarkable geographical covariation seen in the well-known aposematic butterflies *Heliconius melpomene* (Linnaeus) and *Heliconius erato* (Linnaeus) (Turner, 1981).

To date, few studies have assessed quantitatively the factors affecting colour patterns among assemblages of bumblebee species. Stiles (1979) questioned the relative roles of warning mimicry and of thermally based convergence in affecting the degree of sexual colour dimorphism in New World bumblebees. He classified colour patterns into just two groups and compared their relative frequencies by latitude, although the generality of his conclusions for all bumblebees was challenged by Sakagami & Ito (1981). At about the same time, Plowright & Owen (1980) classified colour-pattern groups for North American and British bumblebees and then used a contingency-table analysis to test whether their colour-pattern groups were associated with predefined geographical regions. They found evidence for a strong association, which they interpreted as likely to be the result of Müllerian mimicry for warning signals. However, both studies used only a relatively small proportion of bumblebee species (34% and 20%, respectively, of the world fauna of social species), which, in the latter study, were also deliberately selected as a subset from the regional faunas to exclude particular colour patterns. Therefore, studies with broader coverage of all bumblebees are needed.

The present study takes a quantitative approach to address some of the most basic questions, using data for workers of all of the world's known social bumblebee species: (1) do colour-pattern groups exist to the extent that some bumblebee colour patterns recur more often among species than expected by chance; (2) do species within colour-pattern groups tend to occur together, at least at a coarse scale; and (3) are some colour-pattern groups associated with particular kinds of habitat? These questions are necessary first steps before we can study the evolutionary processes affecting colour patterns among bumblebees.

MATERIAL AND METHODS

When coding colour patterns for analysis, the challenge is to identify an appropriate resolution or scale of variation for scoring. This should depend on the processes being studied and the assumptions should be explicit. For example, to study the genetic control of colour patterns (Owen & Plowright, 1980), even small details of the pattern may be genetically controlled (not considered here). By contrast, to study the gross resemblance effects that might result from selection for thermoregulation, crypsis, and warning coloration, then pattern analysis at a coarser resolution may be more appropriate. To study mimetic selection of warning patterns as imposed by a selective agent such as a predator (Vane-Wright, 1976), the resolution ideally should depend on the predator's visual acuity and pattern-recognition ability. This might operate, for example, at the level of pale band or tail colour (see Discussion). Thermoregulatory and cryptic functions of colour patterns might operate at an even coarser resolution, such as whether the bumblebees are predominantly dark or predominantly pale.

SCORING INDIVIDUALS

Most bumblebees encountered in the field are workers (small females that usually do not lay eggs but care for the queen's offspring). Scoring workers therefore deals with the bumblebees that have perhaps the greatest exposure to selective processes (including physiological stress). For the great majority of species, workers and queens have nearly identical colour patterns. For the minority of remaining species, scoring workers alone avoids (for an initial analysis) problems of strong caste-dependent dimorphism (Ito, Matsumura & Sakagami, 1984; Williams, 1991; Sianturi *et al*., 1995; Hofstede, Det & Asperen de Boer, 2001).

Scoring workers also excludes the workerless cuckoo bumblebees (subgenus *Psithyrus*), which again simplifies the problem for an initial analysis because their different behaviour as parasites in the nests of other social bumblebees might change which selective processes act upon them. For example, Sladen (1912) and Plowright & Owen (1980) suggested that *Psithyrus* may have been selected to mimic the colour patterns of their particular host species. However, colour-pattern mimicry of hosts by parasites to aid their entry into (dark) host nests was rejected by Vogt (1909: 56) and the generality of colour-pattern resemblance between particular parasite–host species pairs was rejected by Richards (1927). This would still admit Müllerian mimicry as a possibility among broader groups of parasite and host species (Alford, 1975; Prŷs-Jones & Corbet, 1987; Mallet, 1999; Goulson, 2003). The scored patterns include those of small females of *Bombus inexspectatus* Tkalců, although this species is probably an obligate ‘workerless’ social parasite in colonies of *Bombus ruderarius* (Müller) and the rare small females are unlikely to be true workers (Yarrow, 1970; Müller, 2006). Scoring only workers excludes phases in colony development (e.g. when queens are founding colonies alone) that might conceivably have an important effect on reproductive success (Pekkarinen, 1979) and hence on selection for colour patterns. Undoubtedly, queens, males, and *Psithyrus* all deserve future investigation.

SCORING BODY REGIONS

Whether bumblebees are visiting flowers or flying slowly between them, it is the dorsum of the body that is usually exposed to the greatest radiation load from the sun, or to perception by predators, often vertebrates, approaching from above (there is no evidence that predators approaching from other directions, often invertebrates, show any discrimination based on colour pattern e.g. crab spiders which attack from the side; Dukas & Morse, 2003). Therefore, it is the dorsum of the body that is considered here for coding into colour-pattern elements.

The body was coded by dividing it into 24 elements (Fig. 1): one representing the lower sides of the thorax, five representing the thoracic dorsum, and 18 representing the gaster (or metasoma) posterior to the narrow waist. Although the first true abdominal segment is fused with the thorax (i.e. gastral tergum 1 is actually abdominal tergum 2), this first abdominal segment contributes no hair to the dorsal colour pattern. The colour of the lower sides of the thorax (element 2) is usually the same as that of the underside of the thorax and gaster. It is excluded from this analysis of the dorsal colour pattern. The thorax is otherwise divided into anterior, medial, and posterior regions. The medial and posterior regions are divided into central and paired (identical) elements on each side (e.g. to allow distinguishing a black band from a black central spot). Gastral terga 2–5 are divided into two central and two paired (identical) lateral elements to account for the complexity of their patterns. These elements may be small for tergum 5, but this system does allow for the coding of posterior pale fringes on each of terga 2–5. Gastral tergum 6 is excluded because it is rarely clearly visible from the dorsal aspect and usually has only sparse shorter hair.

SCORING COLOURS

A colour-pattern element is usually coded as being of the colour of the pubescence (‘hair’) that occupies more than 50% of the area of the element. A minority colour may be coded if the majority colour is identical to the neighbouring element and if the minority colour occupies more than 5% of the element. This allows for narrow but strongly contrasting and obvious fringes or spots to be recorded.

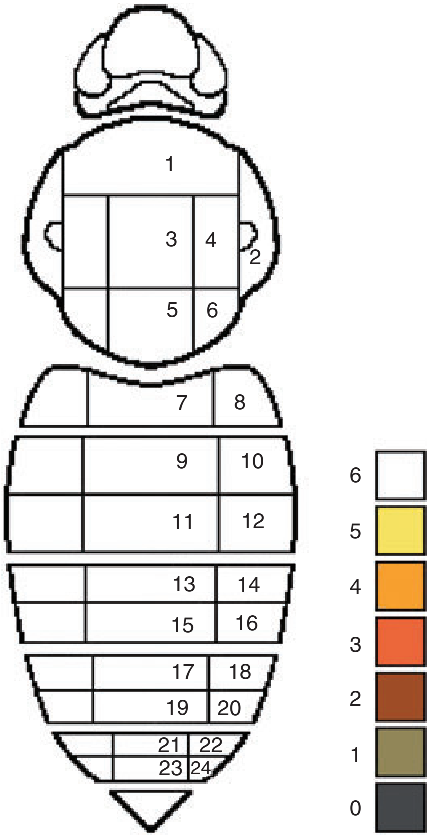


Figure 1. Division of the worker dorsum into 23 colour-pattern elements for scoring colour patterns (plus element 2 on the lower sides of the thorax, which is excluded from the analyses). The seven colour classes (Table 1) are shown to the right.

Spectral analysis of colours would be possible, but is unnecessarily complex for a preliminary analysis. Ultraviolet (UV) reflectance patterns, which are known for some butterflies (Beccaloni, 1997), are not considered here because photographs of a few common British and North American bumblebees taken in UV light with UV-sensitive emulsions have so far shown no apparent patterns (D. Goulson, pers. comm.; L. Day, pers. comm.). This needs further study. Care has been taken to avoid including specimens faded by prolonged exposure to the sun. These older foragers can usually be recognized by their more severe wing wear. Museum specimens exposed to light for too long usually lack any brightly coloured or intensely black hairs.

In the present study, an intermediate resolution of classes of colours, with simplifying rules, is used. By classifying bumblebee colours into a few of the large colour classes used traditionally in bumblebee descriptions, much subtle variation is lost, but large groups of similar species may then be more easily detected in a simple analysis (see Discussion). Interpretation of colours could suffer from context-dependent bias in the coding. For example, for bumblebees of the subgenus *Thoracobombus*, very similar colours may have been interpreted as brown on the thorax and as red on the 'tail' (see below) because these are the traditional colour descriptions of these body regions in this group (Sladen, 1912; Alford, 1975). By reducing the number of colour classes used, some of these similarities may be recognized.

Some bumblebee colour patterns have been suggested (Richards, 1929; Plowright & Owen, 1980) to have a warning function to predators. Traditionally, this has been associated with alternating bands of strongly contrasting colours, as in the familiar black and yellow 'bee pattern'. Therefore, to represent this contrast quantitatively, the colours were scored in an approximate rank order by their brightness or luminosity, from black (0) to white (6) (Fig. 1, Table 1).

DATA SOURCES

Colour patterns were scored from worker bumblebees in the collections of the Natural History Museum (NHM), London, and of the Oxford University Museum, and from material collected in China (on loan from the Institute of Zoology, Beijing). A total of 632 patterns were scored, representing all 219 social species currently recognized (Williams, 1998, updated online). Each scored pattern represents a particular individual worker bumblebee, without weighting for relative abundance. No doubt, other patterns exist. Workers of several species were unavailable, but were scored either from published descriptions of workers (e.g. *Bombus haueri* Handlirsch and *Bombus tucumanus* Vachal; Milliron, 1973), or from specimens of queens (*Bombus amurensis* Radoszkowski, *Bombus melanopoda* (Cockerell), *Bombus rubriventris* Lepeletier), on the assumption that their unknown workers are likely to be similar in colour pattern. These patterns inferred from queens represent only 1% of the species, which is unlikely to affect the results. Distribution data were extracted from the NHM collection and from Williams (1991) and Williams (1998). The area extent of vegetation cover for assessing habitat associations is taken from Global Land Cover Facility (GLCF) classification data (http://glcf.umiacs.umd.edu/data/landcover/) and area extent at elevations from GLCF shuttle radar data (http://glcf.umiacs.umd.edu/data/srtm/).

CLASSIFYING COLOUR-PATTERN GROUPS

Classifying colour-pattern groups among bumblebees is not straightforward. Unsurprisingly, the groups obtained depend on the criteria used. A priori, a reasonable technique was expected to be to use the combination of: (1) raw colour-pattern element data; (2) Manhattan distances among patterns; and (3) an undirected hierarchical divisive classification (S-Plus; http://www.insightful.com/products/splus/default.asp). However, this proved to be very sensitive to variation in the extent of black on the body, and particularly to the most variable parts of the body, and therefore divides apparent colour-pattern groups in a counter-intuitive way (classification available online at: http://www.nhm.ac.uk/research-curation/projects/bombus/downloads/bumblebeedivclass.pdf). For example, workers of *Bombus marussinus* Skorikov, with a simple yellow–black–red pattern (from anterior to posterior), are placed on both sides of the first division of the classification, depending on whether or not the yellow extends from gastral tergum 1 to the anterior part of tergum 2. This is despite the fact that the workers share similar patterns that can require close examination to distinguish. Therefore the most variable colour-pattern elements (Fig. 2B), which are emphasized by this technique, appear not to be the

Table 1. Colour classes used for scoring colour patterns

Colour class	Colour description	*Bombus* species exemplifying each colour to illustrate the scope of the colour classes
0	Black	*morio*, *waltoni*
1	Black with grey/yellow intermixed ('olive')	*funerarius*, *grahami*, *infrequens*, *melanopygus*, *mixtus*
2	Dark brown	*simillimus*, *tunicatus*, *friseanus*, *mlokosievitzii*
3	Orange–red	*lapidarius*, *lapponicus*, *atripes*, *morawitzi*, *rubicundus*
4	Orange–brown	*pratorum*, *pascuorum*, *hypnorum*, *breviceps*, *dahlbomii*
5	Yellow	*lucorum*, *terrestris*, *sylvarum*
6	Grey–white	*lucorum*, *incertus*, *convexus*

most critical for membership of intuitive colour-pattern groups. Consequently, this technique appears to emphasize what may be functionally irrelevant details at the edges of the principal colour bands.

Instead, an explicitly directed classification was chosen in the present study. Even though their visual systems may be very different (Endler & Mielke, 2005), it remains possible that people collecting bumblebees recognize bumblebee colour-pattern groups using pattern criteria that are broadly similar to those used by other vertebrate predators. For example, people and pigeons rank similarity in colour pattern among aposematic wasps and hoverflies in a similar order (Dittrich *et al.*, 1993). The classification in Table 2 uses simple criteria to describe three components of the colour pattern. It is based on experience of watching bumblebees foraging, as well as experience of the difficulties in identifying species that arise from colour-pattern similarities. For example, somewhat ironically, photographs in the study of mimicry by Brower & Brower (1962), ostensibly using *Bombus americanorum* Fabricius [a synonym of *Bombus pensylvanicus* (DeGeer)], actually show several different species of bumblebees.

Another problem for the first, more conventional, method above is that a mimic might have patches of colour on slightly different body segments or elements than a model, and yet still be an effective mimic [e.g. *Bombus vandykei* (Frison) and *Bombus vosnesenskii* Radoszkowski share similar isolated yellow bands on

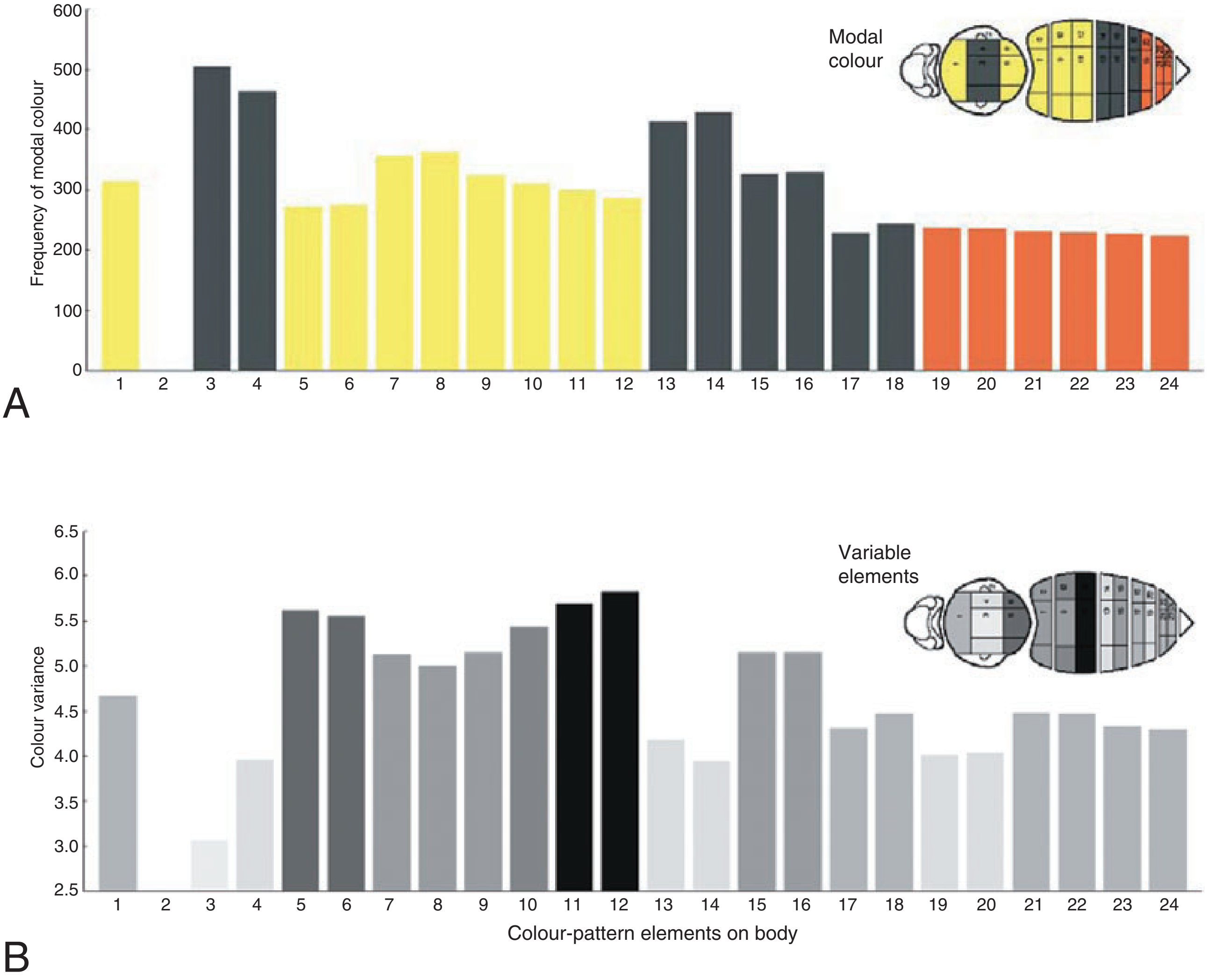


Figure 2. Variation in colour-pattern elements (excluding element 2, the sides of the thorax). A, colour bars show the most frequent colour for each colour-pattern element (by position on the *x*-axis; its position on the bumblebee is shown in the diagram to the right) and histogram bars show the frequency of this colour (*y*-axis score). B, grey histogram bars show the variance (*y*-axis score and bar grey intensity) in the colour score for each element (by position on the *x*-axis; its position on the bumblebee is shown in the diagram to the right).

Table 2. Criteria for classifying colour-pattern groups

Criterion	Values
A Tail colour	0 Black 1 Brown/red/orange 2 Brown/red/orange followed by yellow/white 3 Yellow/white
B Pale band colour	0 Pale bands absent (black) 1 Olive 2 Brown/red/orange 3 Yellow 4 White
C Pale band position	0 Pale bands absent 1 One pale band only, on gaster 2 One pale band only, on part of thorax 3 At least two separated pale bands, on thorax or thorax and gaster 4 All pale, at least on thorax

For definitions of 'tail' and 'pale band', see text. Colour-pattern groups can be specified by their values for the three criteria (ABC) e.g. '133' specifies the modal pattern shown in Fig. 2A: criterion A scores 1 for tail red; criterion B scores 3 for pale bands yellow; criterion C scores 3 for pale bands two.

the gaster, but these are on different terga; Thorp *et al*., 1983]. The criteria in Table 2 can accommodate this by moving away from comparing rigidly between anatomically fixed colour-pattern elements towards comparing the more flexibly defined 'tail' and 'pale band' components of the pattern on the body. The 'tail' refers to the palest hair covering all or parts of the posterior gastral terga 3–5. 'Pale bands' refer to transverse bands of any colour, surrounded by black, where the band is of a colour other than black (most often the colour is yellow or white), and where the band must cover parts of the body other than the 'tail' or head. Differences in colours other than black between adjacent colour-pattern elements are not counted as defining separate pale bands. Several other qualifications need to be recognized. First, a black bumblebee with terga 2–5 red is counted as being unbanded black with a red tail (group 100). Second, bumblebees with a yellow band on tergum 3 or 4 (with no red on terga 3–5) and with black immediately anteriorly are counted as yellow tailed (e.g. group 332). However, if bumblebees have pale terga 2–3 with black terga 4–5, then they are counted as black tailed (e.g. group 033). Consequently, the rule-based system adopted in Table 2 is intermediate between the spatially rigid approach of the Manhattan distances above and the location-free method of Endler & Mielke (2005).

TESTING GEOGRAPHICAL ASSOCIATION WITHIN COLOUR-PATTERN GROUPS

This test is designed to assess whether species within a colour-pattern group are associated in space more often than would be expected by chance. There is no reference to a priori biogeographical regions. The distribution of each colour form (defined from the colour-pattern groups above) of each species (i.e. not the entire species) is scored as presence data on a coarse-scale equal-area grid (area of each cell approximately 611 000 km^2; Williams, 1998). When species richness is plotted for a colour-pattern group, geographical association among the group members can be measured using the mean richness among the cells occupied by the group (completely unassociated species would show a mean richness of 1; more highly associated species would show higher mean richness, up to N for N species if they were to co-occupy all cells).

The observed mean richness for a group can be compared with the distribution of expected mean richnesses from 100 000 simulated group distributions. The simulation places distributions at random using a set of four rules. First, the simulated species' colour forms have the same set of range sizes as the real species' colour forms. Second, simulated range 'centres' are allowed to be allocated only within the 248 grid cells that are actually occupied by any social bumblebees worldwide. Third, within this region, the placement of each range 'centre' is random, but its probability of placement is made to depend upon the relative species richness of each cell for all social (non-*Psithyrus*) bumblebees worldwide. This tends to concentrate species in certain regions to mirror real bumblebee distributions, which will increase range clumping and make the test more conservative. Fourth, simulated ranges are 'grown' outwards from these randomly allocated centres in a spiral of cells, but are still confined to the 248 cells actually occupied by any social bumblebees worldwide. The null hypothesis that the observed geographical association within a colour-pattern group is no greater than random will be rejected if the observed mean richness falls beyond a threshold in the upper tail of the distribution of mean richness scores expected based on the random simulation. Computational software for the simulation was written in C.

RESULTS

Variability in colour-pattern elements

The modal colour scores of each colour-pattern element and their frequencies are shown in Figure 2A. The modal colour pattern presents strongly contrasting black and yellow bands in combination with a red tail. Figure 2B shows the variance of the colour scores for the colour-pattern elements. The most frequent and least variable element of the colour pattern is a black spot on the thoracic dorsum between the wings (element 3), which is often expanded into a black band between the wing bases (sometimes known as the 'interalar' band). The black areas on the thorax and gaster are more consistent than the yellow because the yellow bands may be replaced by other pale colours more often than the black is replaced by a pale colour. Particularly variable colour-pattern elements are element 2 (the sides of the thorax and underside, not used below), elements 11–12 (reflecting variation in the extent of the pale anterior gastral band), elements 5–6 (the presence or absence of a pale posterior thoracic band), and elements 15–16 (the extent of the black mid gastral band).

Do colour-pattern groups exist?

Among the 632 worker colour patterns that were coded, 427 different colour patterns are discerned at the level of resolution of 23 colour-pattern elements and seven colour classes. Therefore, 204 patterns (one third) are exact duplicates among species. In the unlikely event that colours were truly randomly distributed among these patterns (being independent among body elements and species and without developmental, phylogenetic, or selective constraints), there would be 7^{23} possible different patterns ($> 10^{19}$), so repeats should be almost unknown among 632 patterns. This is easily confirmed, because no repeat patterns are found among 10 000 draws of sets of 632 randomly chosen patterns ($P < 0.001$). Therefore, a subset of the possible colour patterns are recurring exactly among bumblebee species much more often than would be expected by chance. These precisely recurring patterns form the most narrowly defined colour-pattern groups.

Which are the principal colour-pattern groups?

The three criteria and 14 values for discriminating colour-pattern classes in Table 2 would permit 68 possible classes to be distinguished. Of these, 44 classes are actually observed among the 632 colour patterns coded (Fig. 3). Consequently, 24 possible classes in this colour-pattern 'space' have not been observed and are 'missing'. Another 12 of the 44 classes cannot be considered to be groups of similar or convergent colour patterns because each class includes just one species.

The success of the criteria from Table 2 in distinguishing intuitively sensible colour-pattern classes appears to be variable. Some of the classes in Figure 3, including some of the largest (e.g. class 133, corresponding to Fig. 2A), are reasonably homogeneous in pattern. However, other classes in Figure 3 (particularly 124, 143, 324, 333, 334, 343) appear to be a mixture of at least two distinctive subclasses. Classes 143 and 324 can both be split between bumblebees with and without yellow on the gaster [e.g. *Bombus lepidus* Skorikov/*Bombus incertus* Morawitz; *Bombus muscorum* (Linnaeus)/*Bombus hypnorum* (Linnaeus)]. Classes 124, 333, 334 and 343 can be split between extensively pale bumblebees (e.g. *Bombus distinguendus* Morawitz) and those with a broad black band covering all of either gastral tergum 2 or 3, or of adjacent parts of tergum 2 and 3 [e.g. typical *Bombus hortorum* (Linnaeus)]. The classes with a single species (a tiny minority among all worker patterns) can then either be reunited with closely similar classes: 041 with 141, 200 with 100, 213 with 113, 313 with 013, 322 with 323, 321 with 331, 341 with 331; or deleted if they have only one or two dissimilar species: 042, 043, 224, 342, 344. This brings the total number of colour-pattern classes that have more than one co-occurring species distinguished in this scheme to 38 (Table 3). Many more subtle subclasses could be discerned within these if required, but these 38, which will be referred to below as colour-pattern 'groups', provide a starting point for testing geographical associations of similar colour patterns among species (all of these modifications to the classes are made without reference to distribution patterns). Figure 4 shows that there is substantial variation in the size of the 38 colour-pattern groups in Table 3, with 32 small groups of 2–15 species and six larger groups of 21–54 species (033, 100, 133, 143 white, 333 dark, 333 pale).

Are colour-pattern groups geographically clumped?

Among the 38 colour-pattern groups tested, 24 groups show a mean species richness for those parts of the species showing each colour pattern that is significantly higher than expected from the random model

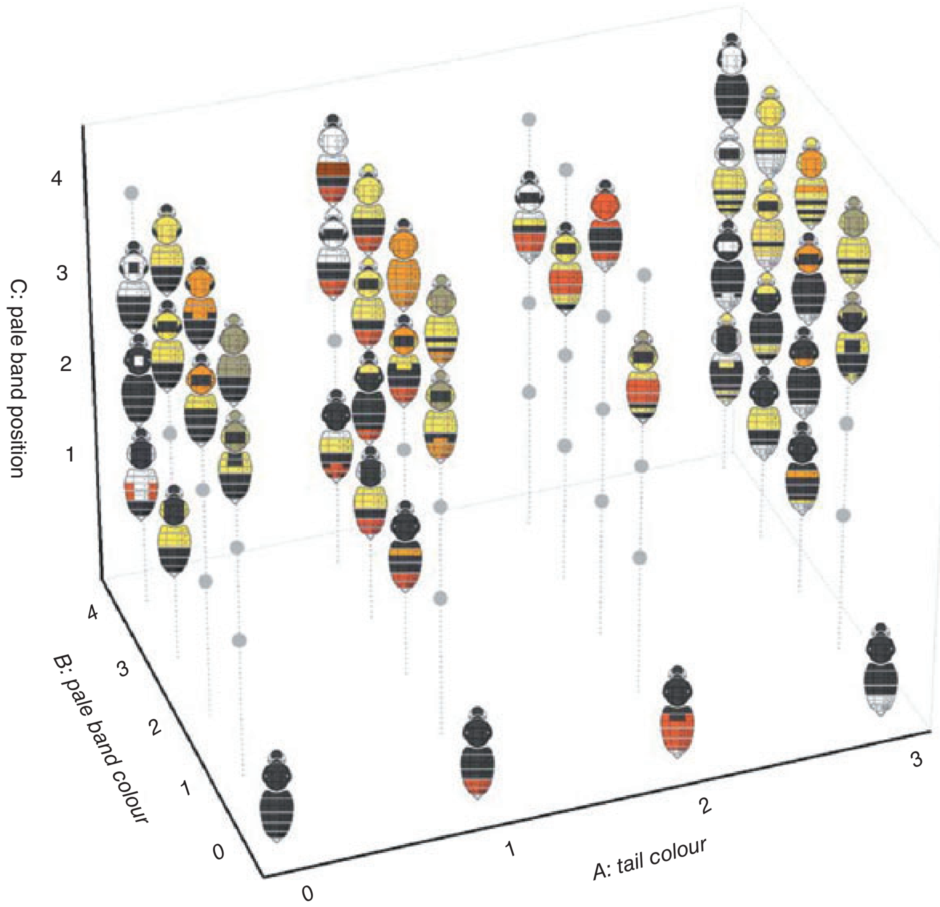


Figure 3. Plot of the three-dimensional 'colour-pattern space' defined for bumblebees in Table 2. The *x*-axis shows the four classes for criterion A (tail colour); the *y*-axis shows the classes of criterion B (pale band colour); and the *z*-axis shows the classes of criterion C (pale band position). Each colour-pattern group is represented by an example of a closest-to-modal colour pattern (closest-to-modal colour patterns are identified as the closest realized match, from the lowest number of cumulative colour-score differences summed across all colour-pattern elements, to the modal colours found within the group for the colour-pattern elements, Fig. 1). Grey spots represent the 24 'missing' colour-pattern groups (out of 68 possible groups) that are not observed.

(Table 3). Consequently, parts of species (subsets of individuals) with these colour patterns are significantly associated with one another among grid cells (at least at this coarse spatial scale). The locations of these geographical associations are mapped in Figure 5. Figure 4 shows that the groups that do not show significant geographical association are all among the smallest colour-pattern groups. In some cases, these smaller groups may represent transitional (and possibly genetically recombinant) forms between other groups.

ARE DIFFERENT COLOUR-PATTERNS ASSOCIATED WITH PARTICULAR KINDS OF HABITAT?

The colour patterns that are likely to have the most divergent thermoregulatory functions are expected to be the most extreme dark and pale patterns because of the greater differences in reflectance and absorption of these colours (Fig. 5A, W). Figure 6 shows how the mean brightness or luminosity of all colour patterns in Table 3 varies with latitude. The brightness of the colour patterns is scored by summing the colour-class values (Table 1; $0 \leq c_i \leq 6$) for all 23 dorsal body elements and expressing it as a proportion of the possible range of values from all black to all white $[(\Sigma_{i:1-23}c_i)/(23 \times 6)]$. Unavoidably, there are few species or occupied grid cells in the far south. The mean brightness among all of the colour patterns scored is 0.46. All-black (brightness 0.0) and predominantly black bumblebees are most frequent near the equator. The species with the palest patterns (the maximum observed brightness is 0.83) are most consistently frequent at mid latitudes (there are a few pale species at

Table 3. Tests of geographical coincidence within colour-pattern groups against 100 000 random simulations

Colour-pattern group code	Number of species	Number of coded patterns	Number of occupied equal-area grid cells	Maximum richness per grid cell	Mean richness per occupied grid cell	Estimated probability of such a high mean richness	Significance (threshold $P = 0.0013$)
000	15	15	60	4	1.90	< 0.0001	*
013	2	4	12	2	1.33	< 0.0071	NS
014	2	2	8	2	1.12	< 0.0072	NS
023	3	5	4	3	1.50	< 0.0206	NS
024	6	9	23	2	1.39	< 0.0035	NS
031	8	9	10	3	1.80	< 0.0001	*
033	28	36	161	9	2.31	< 0.0001	*
034	10	12	57	4	2.01	< 0.0001	*
100	30	35	88	10	2.69	< 0.0001	*
113	4	11	27	3	2.29	< 0.0001	*
114	8	12	12	6	2.83	< 0.0001	*
121	4	6	23	1	1.00	1.0000	NS
123	5	8	13	4	1.92	< 0.0001	*
124 dark	3	9	50	2	1.02	< 0.0209	NS
124 pale	8	9	30	2	1.20	< 0.0127	NS
131	9	23	27	5	1.70	< 0.0001	*
132	5	5	36	4	1.55	< 0.0014	NS
133	54	96	167	12	2.89	< 0.0001	*
134	12	18	28	6	1.46	< 0.0005	*
141	4	4	6	2	1.16	< 0.0411	NS
143 white	21	36	54	12	2.14	< 0.0001	*
143 yellow	13	24	30	6	1.90	< 0.0001	*
144	6	6	2	4	3.00	< 0.0001	*
233	8	11	96	5	1.55	< 0.0005	*
243	6	14	14	5	2.21	< 0.0001	*
300	14	18	44	5	1.45	< 0.0002	*
314	2	2	7	2	1.14	< 0.0069	NS
323	3	3	10	1	1.00	1.0000	NS
324 dark	5	10	66	3	1.96	< 0.0001	*
324 pale	10	16	74	7	2.62	< 0.0001	*
331	6	6	19	2	1.05	< 0.1007	NS
332	9	11	41	6	1.43	< 0.0010	*
333 dark	40	65	173	15	3.86	< 0.0001	*
333 pale	27	46	119	8	2.63	< 0.0001	*
334 dark	4	4	12	1	1.00	1.0000	NS
334 pale	9	9	36	4	1.47	< 0.0009	*
343 dark	4	4	32	2	1.21	< 0.0416	NS
343 pale	9	11	48	5	2.18	< 0.0001	*

A Bonferroni correction for a conservative probability threshold among 38 single tailed tests of 0.05/38 = 0.0013 is used to decide significance (*).

low latitudes, all of which occur at high altitudes in the Neotropical mountains). But at the highest (northern) latitudes, brightness again declines.

Table 4 shows a preliminary assessment of the positive associations at the coarse scale of the equal-area grid from Figure 5 between each of the three principal divisions of colour-pattern groups and each of five of the principal kinds of habitats in turn. The habitat data represent the area extent (coverage) within each equal-area grid cell of four biomes or vegetation classes and of land above 1500 m. At this coarse scale, the results cannot be definitive but may still be indicative, and do at least provide a summary of patterns with global coverage. The black bumblebees appear to be most strongly associated with broadleaf evergreen forest but are not associated with mountains, a com-

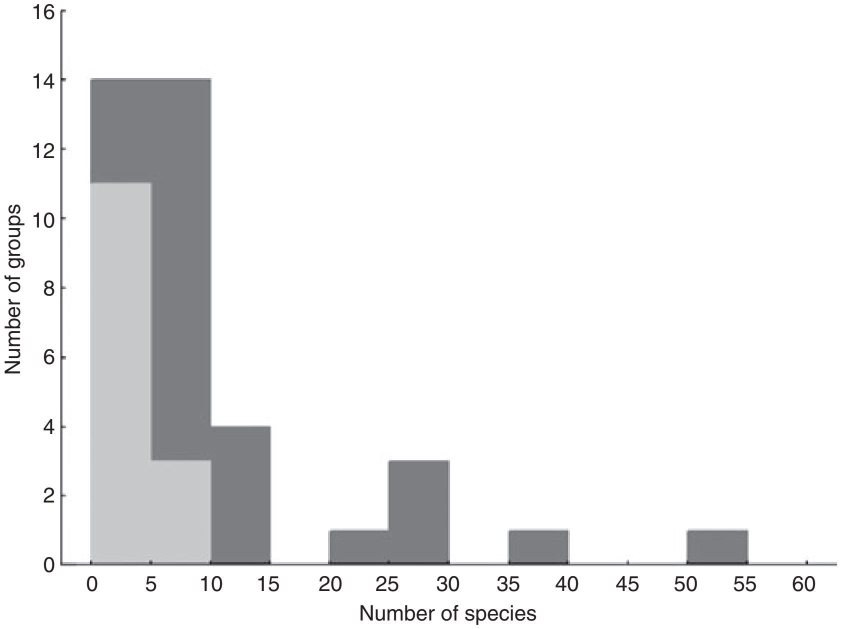


Figure 4. Histogram of the frequency of the 38 multispecies colour-pattern groups from Table 3 by the number of species that they contain. Light grey bars show the 14 groups without significant geographical associations among species and dark grey bars show the 24 groups with significant associations.

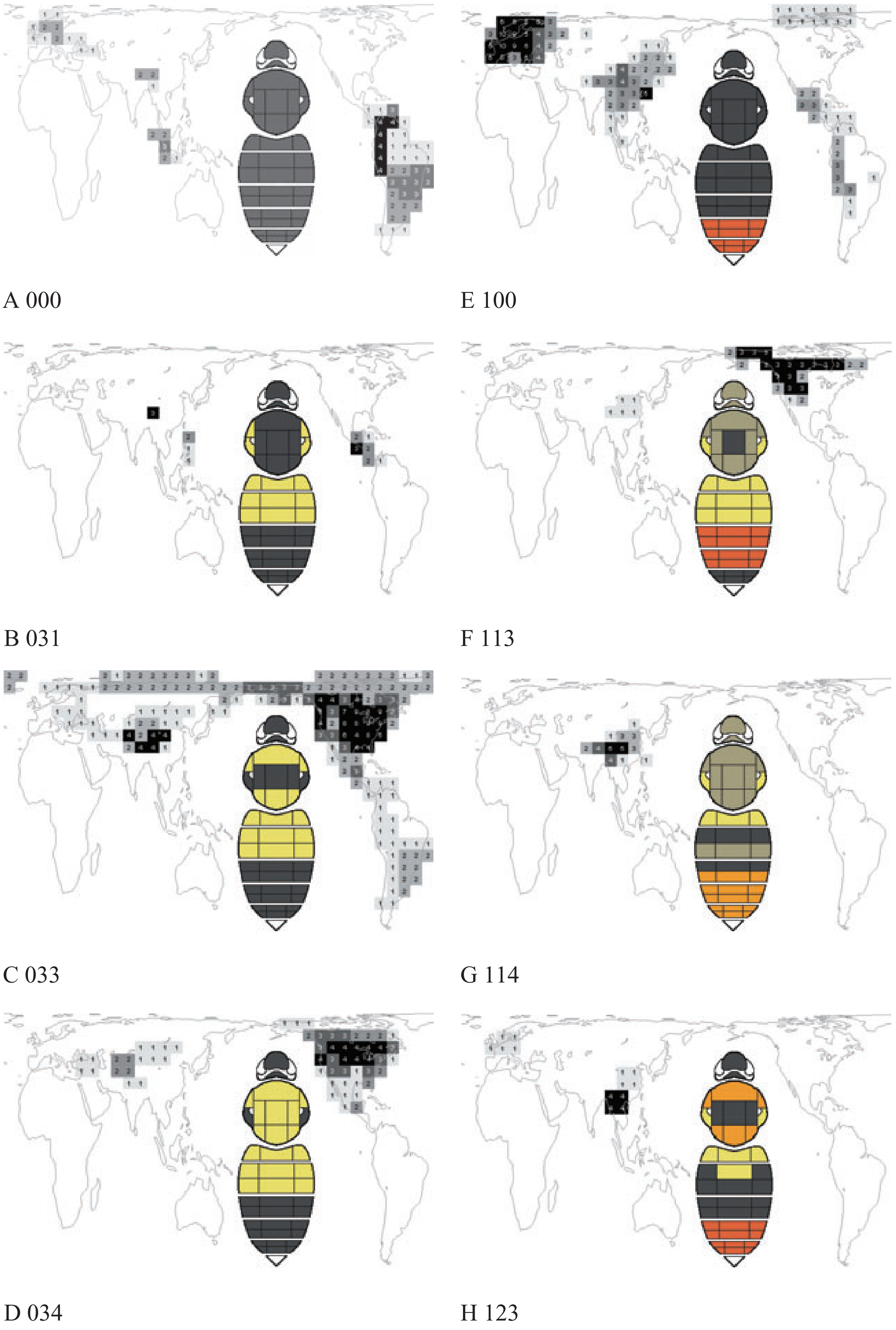
Table 4. Spearman rank correlation coefficients for the positive associations between the worldwide species richness per grid cell of each of the three principal divisions of bumblebee colour-pattern groups from Fig. 8 and the area extent per grid cell of the highlands and of each of four Global Land Cover Facility vegetation classes

	Black bumblebees	Pale bumblebees	Banded bumblebees
Land above 1500 m	0.012 NS	0.174 NS	0.374*
Grassland	–0.035 NS	0.347*	0.407*
Broadleaf evergreen	0.528*	–0.330 NS	–0.445 NS
Broadleaf deciduous	0.125 NS	0.221*	0.219*
Tundra	–0.285 NS	–0.113 NS	0.106 NS

Broadleaf evergreen forest is primarily tropical and broadleaf deciduous is primarily temperate. Three principal divisions of bumblebee colour-pattern groups from Fig. 8: black bumblebees (000); predominantly pale bumblebees (324 pale, 333 pale, 334 pale, 343 pale); and bumblebees with multiple strongly contrasting bands (033, 034, 133, 134, 143 white and yellow, 144, 233, 333 dark, 243). Associations are assessed at the coarse scale of the equal-area grid from Fig. 5 and within the 248 grid cells covering the total global range of social bumblebees. A Bonferroni correction for a conservative probability threshold among 15 single tailed tests of 0.05/15 = 0.0033 is used to decide significance (*).

bination that defines much of tropical lowland forest. The predominantly pale bumblebees are most strongly associated with grassland and not with mountains. The banded bumblebees are also associated with grasslands but are associated more strongly than the other groups with mountains, which is consistent with grasslands at high altitudes being more important for this banded group. Further studies at a finer resolution are needed to confirm these results.

Looking in more detail, the colour-pattern groups in Figure 5 show broadly six forms of distribution patterns: (1) the largest consists of red-tailed groups (113, 114, 123, 131, 133, 134, 143 yellow and white, 144, 233, 243) and is primarily mid-latitude montane; (2) the large white-tailed groups with extensive black on the abdomen (324 dark, 333 dark) are primarily northern boreal but extend southwards more weakly into the mountains and lowlands; (3) the palest groups (324 pale, 333 pale, 334 pale, 343 pale) are primarily of the Old World lowland grassland and semidesert zone; (4) two black-tailed groups (033, 034) are richest in the lowlands and hills of central



A 000

E 100

B 031

F 113

C 033

G 114

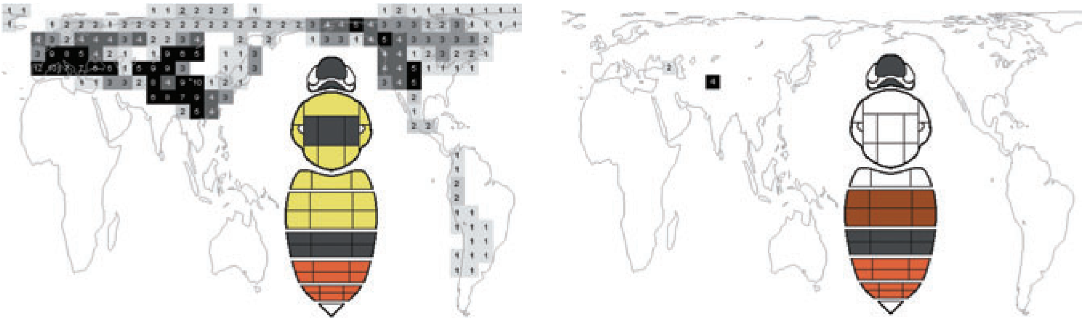
D 034

H 123

Figure 5. Mapping geographical coincidence among species for the 24 multispecies colour-pattern groups from Table 3 that show significant geographical association. Numbers on the maps (and the equal-frequency grey scale) show counts of those parts of species with the particular group colour pattern within equal-area (611 000 km^2) grid cells. Details of the grid, map projection, and species data are given in Williams (1998). Examples of closest-to-modal colour patterns are shown (identified as described in the legend to Fig. 3).

I 131

M 143 yellow

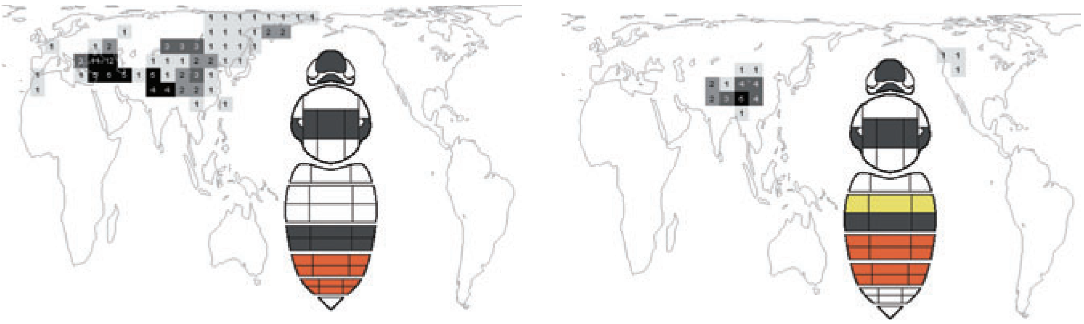


J 133

N 144

K 134

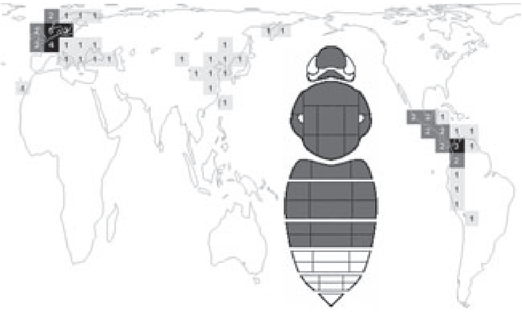
O 233



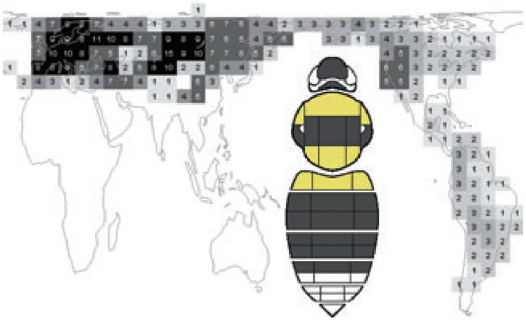
L 143 white

P 243

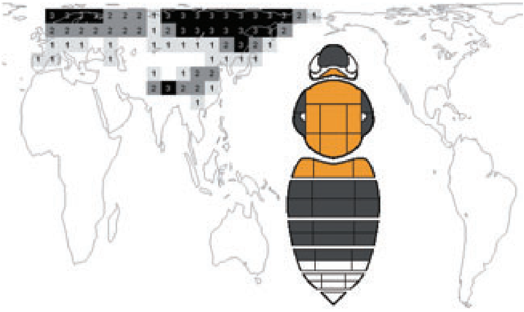
Figure 5. *Continued*



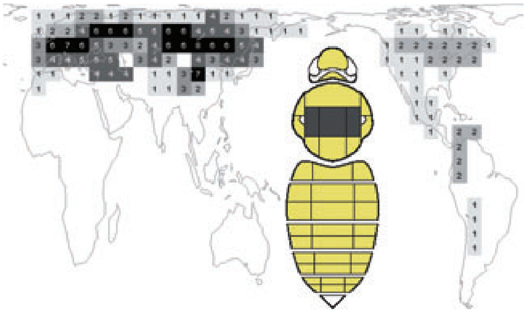
Q 300



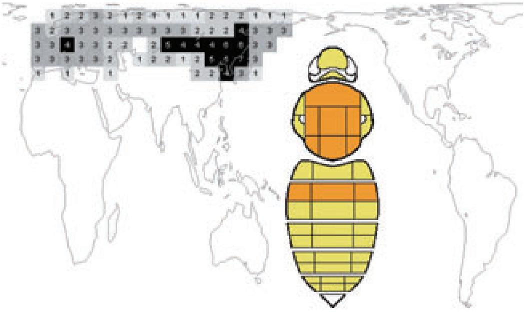
U 333 dark



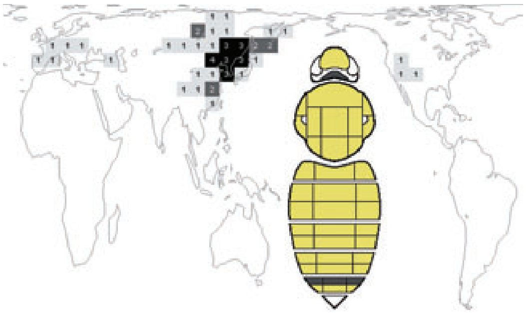
R 324 dark



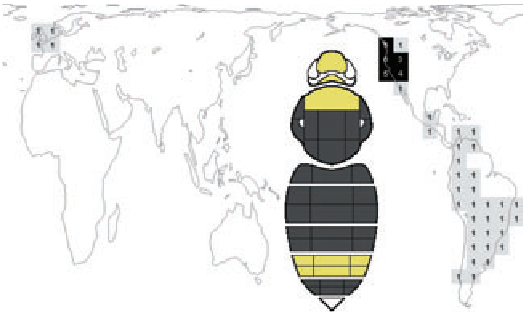
V 333 pale



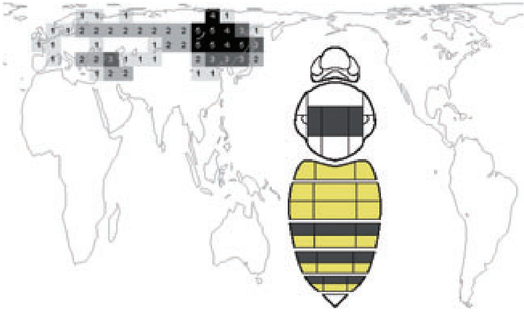
S 324 pale



W 334 pale



T 332



X 343 pale

Figure 5. *Continued*

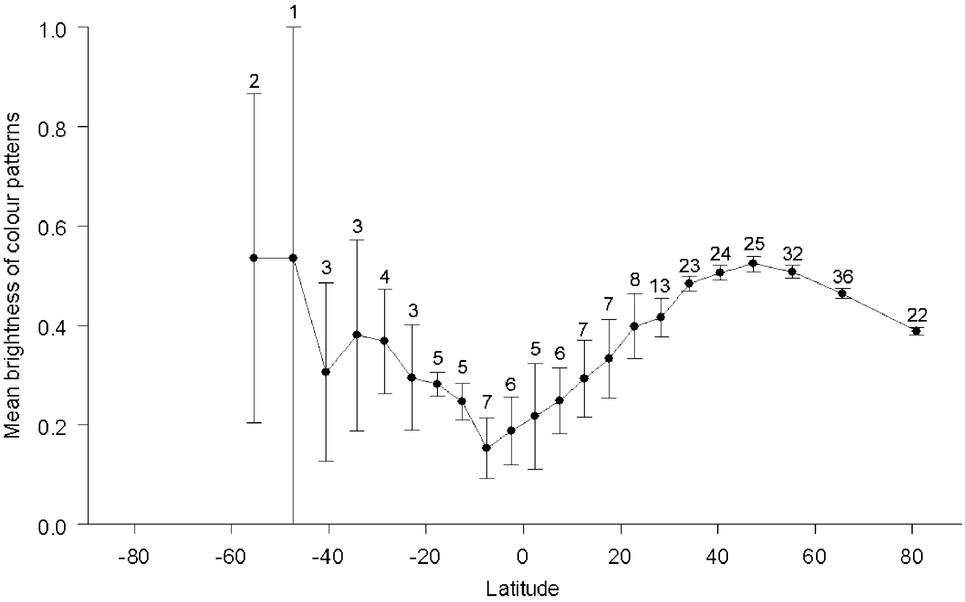


Figure 6. Plot of the mean brightness of colour patterns (from summed colour scores for pattern elements of each pattern, see text) by latitudinal band of the equal-area grid (from Fig. 5). Mean brightness is scored for each equal-area grid cell from Fig. 5, then among the cells within each latitudinal band, the means (as points) and the standard errors of the means (as error bars) are plotted, together with the numbers of occupied equal-area grid cells per latitudinal band (as figures above the bars).

and eastern North America; (5) two dark groups with more restricted yellow bands (031, 332) are richest in Central America and in western North America; and (6) three of the darkest groups without pale bands (000, 100, 300) are richest in Europe and in South America.

DISCUSSION

COLOUR-PATTERN SIMILARITY, GEOGRAPHY, AND CONVERGENCE

The results of this preliminary quantitative analysis of bumblebee colour patterns worldwide are interpreted as showing that: (1) there are many repeating colour patterns, forming relatively few groups of species that share similar colour patterns; (2) colour-pattern groups can be recognized using simple rules; and (3) species within the larger colour-pattern groups are significantly clustered or aggregated within particular regions of the world.

These three results are subject to the effects of errors or biases arising particularly from: (1) the choice of colour classes (Table 1); (2) the choice of body regions to be scored (Fig. 1); (3) the choice of grouping rules (Table 2); (4) the choice of spatial scale for the geographical analysis; and (5) errors in identification of species and in distribution data. Adopting different rules for any of these factors would affect the outcome to some degree. However, the significant associations found for so many of the colour-pattern groups within independent geographical data are taken as evidence that the method has detected groups with some reality, showing that the patterns in the data appear to be robust to the errors and biases.

Although there may be groups of species with colour-pattern resemblance, and these groups may have a recognizable geographical association and identity, the present results are unable to demonstrate whether there is colour-pattern convergence among their constituent species. To discover this requires colour-pattern changes to be mapped onto a reliable estimate of the phylogenetic tree (when available) to explore patterns of colour-pattern inheritance and evolution.

In the interim, there is anecdotal evidence that striking convergence has taken place in at least a few cases. It may be a likely explanation for the case described in the introduction involving the southern Asian *B. trifasciatus* and the three other species (Richards, 1929), which are morphologically disparate and apparently not closely related (Williams, 1995). Even stronger evidence comes from two morphologically disparate and commonly co-occurring species from higher altitudes around the southern and eastern edges of the Tibetan plateau, *Bombus* (*Melanobombus*) *rufofasciatus* Smith and *Bombus* (*Alpigenobombus*) *kashmirensis* Friese. Workers of these species appear to be identical when seen flying together, with a red tail, tipped with white. However, for *B. rufofasciatus*, there are separate bands of red hairs (gastral tergum 4) and white hairs (tergum 5) on the tail. By contrast, for *B. kashmirensis*, both terga have hairs that are red at the base and white at the tips, but which are white for more of their length on tergum 5. These bi-coloured hairs achieve a very similar visual effect to *B. rufofasciatus*, but with a different developmental basis (Williams, 1991).

It is usually assumed that the different colour patterns have advantages of greater fitness under different environmental conditions. Possible factors affecting the evolution of insect colour patterns in general were listed by Stiles (1979) as including their potential functions in thermoregulation, crypsis, and warnings to predators. For bumblebees in particular, previous studies have focused on the roles of colour patterns in communicating warnings, and to some extent in aiding thermoregulation, but have not considered in any detail the possible role of crypsis. Inter-sexual selection is unlikely to be a factor for bumblebees, because Free (1971) found that colour pattern had no effect on acceptance of females by mate-searching males of British *Bombus pratorum* (Linnaeus). Furthermore, there was no evidence of selection as disequilibrium from the inferred gene frequencies among the more visually mate-searching and highly colour-variable *Bombus asiaticus* (Morawitz) in the Himalaya (Williams, 1991). The present study aims only to describe the geographical distribution of different colour patterns and cannot settle the relative roles of the various selective processes, which will require future field and experimental studies.

BUMBLEBEES ‘WITHOUT’ COLOUR PATTERNS?

Many nocturnal Hymenoptera, particularly in the tropics, share a similar, nearly uniformly orange–brown colour of both the pubescence and the underlying sclerites. This may represent a convergent loss of other colour pigments in a situation where these pigments have no advantage or, possibly, it could be a special form of nocturnal crypsis (see below). Examples include many Ophioninae, the pompilid genus *Hemipepsis*, the vespid genera *Provespa* and *Apoica*, and the carpenter bee, *Xylocopa myops* Ritsema (NHM collection). Among bumblebees, a similar orange–brown colour pattern of both hair and sclerites is known from the Oriental tropics (part of group 124), in the Cameron Highlands of Peninsular Malaysia, where it is shared by distantly related species of the *trifasciatus*-group (‘*maxwelli*’ Pendlebury) and of the *flavescens*-group (‘*rufoflavus*’ Pendlebury). However, it remains unknown whether these bumblebees are nocturnal.

THERMOREGULATION

Most early explanations for regional resemblances in colour patterns among bumblebee species looked to ideas of shared ‘environmental’ effects and especially to the effects of climate (Vogt, 1909; Friese & Wagner, 1912; Franklin, 1913; Reinig, 1935; Pittioni, 1943). In a more recent example, Pekkarinen (1979: fig. 23) showed quantitatively that, on a regional scale within Scandinavia, darker colour patterns within *B. hortorum* are associated with longer cool periods in spring. This may help these bumblebees absorb energy from the sun and warm up more quickly in cool conditions (Pereboom & Biesmeijer, 2003). Figure 7 shows evidence supporting a similar trend among all bumblebees towards progressively darker colour patterns when moving from mid to high northern latitudes.

The contrasting effects of different colour patterns on thermoregulation should be associated most clearly with the very lightest and darkest patterns because these colours differ most in reflectivity and absorption. What is most interesting with respect to Figure 6 is that the broader global relationship shown for all bumblebee workers is the opposite to that expected (Pekkarinen, 1979): the darkest patterns occur most frequently in the tropics (e.g. black patterns, Fig. 5A), not in the highest latitude faunas, where the greater absorption of light by black might have been expected to be advantageous for warming in these cool environments (especially in the early morning). The correlation between latitude and temperature may not be precise, especially when taking altitudinal variations into account, but the relationship still holds broadly in that warm habitats occur only at low latitudes. Furthermore, near the equator, the entirely black bees are most frequent at the lowest altitudes occupied by bumblebees (e.g. as reported for Andean bumblebee faunas in Colombia; Lievano Leon, Ospina Torres & Nates Parra, 1991). The physical effects of colour on bumblebee thermoregulation are not yet well understood, particularly when this involves the possibilities of radiation and reflection within the dense coat of long hairs. Any consideration of bumblebee thermoregulation must allow that constraints on their activity are likely to be different in the early morning and in the early afternoon, even in the tropics.

An observation of local foraging activity in the western Himalaya corroborates the broader latitudinal pattern. In Kashmir, *B. haemorrhoidalis* and *B. trifasciatus* have the hair of the thorax entirely black and they too inhabit the lowest (1000 m) and warmest altitudes occupied by bumblebees in the western Oriental region. On warm midsummer days, they forage only in the cooler mornings and evenings, and only in the shade (Williams, 1991). When their food plants (*Impatiens glandulifera* Royle and

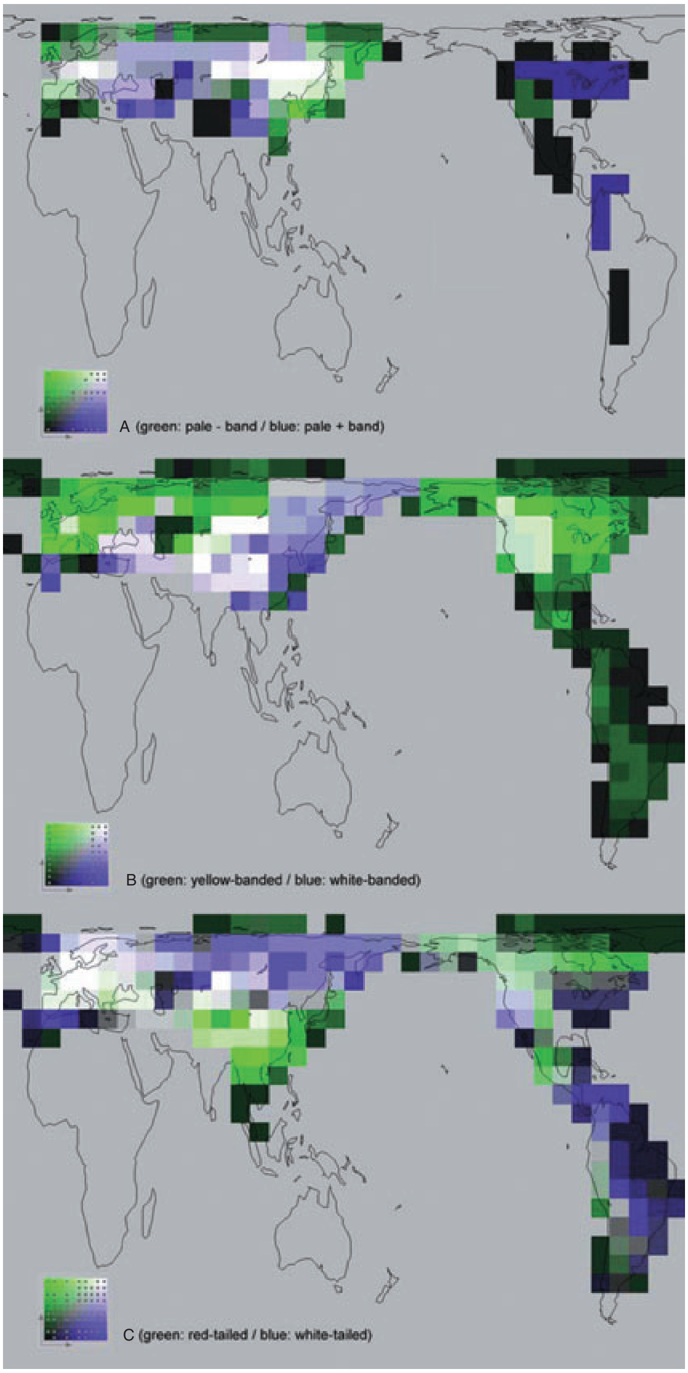


Figure 7. Mapping comparisons of spatial patterns in some colour-pattern features. The maps overlay counts of two sets of colour-pattern groups in green and blue (Williams & Gaston, 1998) within equal-area (611 000 km^2) grid cells (Fig. 5). Both colour axes are transformed to give near-uniform frequency distributions among classes along these axes (see the colour-scale boxes). Areas of high richness on both green and blue axes appear white and areas of low richness on both axes appear black, with areas of intermediate and precisely covarying richness appearing grey. By contrast, deviations from an overall positive relationship appear as increasingly saturated green or blue, showing an 'excess' richness on one axis over the other (colour values plotted on the map are indicated on the scale boxes with grey spots). A, predominantly pale bumblebees with a black band (blue: 333 pale, 343 pale) and without a black band (green: 324 pale, 334 pale) between the wings. b, yellow-banded (green: 033, 034, 133, 134, 233, 333 dark) and white-banded (blue: 143 white and yellow, 144, 243) bumblebees (and with red or white tails). c, red-tailed (green: 100, 113, 114, 123, 131, 133, 134, 143 white and yellow, 144) and white-tailed (blue: 300, 324 dark, 332, 333 dark) bumblebees.

Pteracanthus urticifolius (Kuntze) Bremek.) were no longer in the shadow of the trees, these bumblebees stopped foraging and could be found nowhere else. However, other large bees (e.g. *Amegilla* sp.) continued to forage on the same flowers, so presumably nectar and pollen were still present. More generally among bumblebees, the analysis of colour variation among body elements here (Fig. 2) shows that a black spot or black band above the indirect flight muscles between the wing bases is the most frequent and invariant component of bumblebee colour patterns worldwide (often in combination with unusually short and sparse hair on the mid thoracic dorsum). Perhaps black hair above the main flight muscles may be particularly important for thermoregulation in some situations. Many female bumblebees also have sparse and often black hair on the underside of their abdomens, an area that they have been shown to use to incubate the brood within their nests (Heinrich, 1979).

By contrast, worker bumblebees at mid latitudes tend to show the lightest colour patterns (Fig. 6). This geographical pattern was claimed to be even more pronounced for male bumblebees by Stiles (1979), although for that case it was challenged by Sakagami & Ito (1981) on the grounds that it was confounded by comparing two large groups (subgenera *Fervidobombus* and *Pyrobombus*) that have different latitudinal distributions and also different colour-pattern trends. Sakagami & Ito (1981) reported finding no trends within each group. For the data from workers used here, all species worldwide are included, so the results describe a general pattern among all bumblebees, even if it does have a phylogenetic component that has still to be elucidated. Bumblebees at the highest elevations where they could be recorded in Kashmir (up to 4800 m) tend to have the palest queen and worker colour patterns, whereas Kashmiri males are palest at the upper limit of the closed-canopy forest at around 3000 m (Williams, 1991).

In climates where the advantage of dark colour patterns may be less of a constraint, paler colour patterns might offer other benefits in addition to any thermoregulatory function.

CRYPSIS

The possibility that some colour patterns shared among bumblebee species might help to conceal them from predators has not been considered previously in any detail. Skorikov (1914) appears to have been suggesting the advantage of crypsis when describing the almost uniformly yellow *Bombus anachoreta* (Skorikov) from the Russian–Korean border: 'The colouring of this species is very much in its favour owing to the sandy aspect of the locality [translation]'. Pekkarinen (1979) mentioned camouflage as a possible explanation of 'variegated' bumblebee colour patterns, but gave no examples or discussion of how he saw this working. It is possible that bands of contrasting colours provide camouflage by the disruptive effect (Endler, 1981, 2006) for some bumblebees, by visually breaking up familiar body outlines in a similar way to military camouflage. However, to this observer, bumblebees' banded colour patterns do not appear to provide obvious protective benefits, at least when they are flying or on flowers (although it might work when they are resting on the ground). Banded bumblebees (e.g. British *Bombus terrestris*) are often simultaneously both sufficiently dark and sufficiently light in colour as to be fairly obvious whether flying in light grassland or within dark forest. Experimental work is needed to assess the possible benefits of the disruptive effect for bumblebees.

Effective crypsis (Edmunds, 1974) might depend on habitats that are reliably of a particular colour, to provide a consistent background that prey species might match (Cott, 1940; Endler, 1978; Merilaita & Lind, 2005). One of the most important bumblebee habitats (Williams, 1988, 2005) that is most reliably of one colour is flower-rich tall grassland. As it dries in summer, when worker bumblebees reach their peak abundances, this grassland tends to become predominantly yellow–brown. Some brown butterflies of seasonally dry grassland have been suggested to be cryptic (Brakefield & Larsen, 1984). Similarly, extensively yellow–brown bumblebees seen flying among the drying grass and herb stems are much more difficult to follow for human observers than are the darker and more strongly banded bumblebees (from field observations in Europe, North America, and in the high steppe of the eastern Tibetan plateau). Possibly of even greater importance, many of these bumblebees nest on the surface of the ground in balls of dry grass (e.g. the 'carder bees'; Sladen, 1912), and workers of these bumblebees are well hidden when working on the outside of the nest (Benton, 2006: fig. 43), which also helps to hide the location of the nest. Predation of nests may be a severe problem for bumblebee populations (Alford, 1975; Goulson, 2003). Friese & Wagner (1912) noted that steppe bumblebees are characterized by extensive yellow. Similarly, present data show the most predominantly pale, grey/yellow/brown bumblebees (324 pale, 333 pale, 334 pale, 343) are richest in the temperate grasslands around Mongolia and westwards through the Russian steppes (Figs 5, 7A). By comparison, tropical low-altitude grasslands are not a preferred habitat of bumblebees, probably because they are usually too hot and either often too dry for flowers to produce nectar, or too prone to flooding that drowns nests.

Some bumblebees of monsoonal Asian mountains show a greenish–grey–yellow pattern, at least for the thorax (Fig. 5G). It is possible that this pattern too is cryptic against the background of their food plants, which tend to remain green throughout more of the summer, rather than turning yellow or brown as in drier habitats. In dense tropical lowland forest, entirely black bumblebees might also be cryptic when flying in deep shade.

If black were important for thermoregulation at lower latitudes and if a black band between the wings were the first component of a black pattern to appear on otherwise pale bumblebees, then this compromise to a cryptic entirely pale pattern would be expected to be more frequent at lower latitudes. For some individual northern species, black-banded individuals may be either more frequent in the south of the species' range (e.g. *Bombus humilis* Illiger), or more frequent in the north of its range (e.g. *Bombus laesus* Morawitz in the broad sense). The general pattern is shown in Figure 7A. This shows that unbanded pale bumblebees (in light green) are more frequent at high latitudes in the northern Old World as well as in northern Iberia and in eastern China and Korea, whereas black-banded pale bumblebees (in light blue) are more frequent at lower latitudes, particularly in the semi-desert areas of the central Old World. Frequencies of both patterns are low (darker colours) in the New World.

WARNING MIMICRY

Warning mimicry (Mallet & Joron, 1999) has become widely accepted as a primary explanation for colour-pattern resemblances among many species of bumblebees only relatively recently (Richards, 1929; Heinrich, 1979; Plowright & Owen, 1980; Thorp *et al.*, 1983; Prŷs-Jones & Corbet, 1987; Goulson, 2003). Contrastingly banded and apparently warning (or 'aposematic') patterns are the most frequent colour patterns among all bumblebees (Fig. 2) and yet the advantage of this warning strategy is apparently not always supreme because seemingly cryptic bumblebee colour patterns are still encountered in some regions (see above). If bumblebee colour patterns were at equilibrium with predator selection (which may be unlikely), this might imply that crypsis could sometimes provide better protection than warnings. There is also the possibility that some bumblebee colour patterns might provide 'dual signals' for both camouflage and warnings, as suggested for some butterflies (Rothschild, 1975; Brown, 1988).

Perhaps where bumblebee habitat is less predictable in its colours (e.g. in less dry subalpine meadows with more diverse and apparent flower colours), bumblebees may be unable to hide from predators by reliably matching the background vegetation in colour. Therefore, another way of avoiding predators would be advantageous. The most common pattern for bumblebees worldwide is the familiar black- and yellow-striped 'bee pattern' of popular literature (e.g. E. H. Shepard in Milne, 1926). These strongly contrasting transverse bands (an 'intrinsic' contrast, within the body, as opposed to extrinsic contrast with the background habitat; Exnerová *et al.*, 2006) are the classic aposematic or warning signal to predators (Poulton, 1890), advertising a distasteful or dangerous sting and thereby providing some demonstrable protection (Brower & Brower, 1962; Evans & Waldbauer, 1982). Such warning patterns could become selected to converge on one pattern within a region because it would be easier for predators to learn just one pattern, which then becomes more effective (Müller, 1879; Beatty, Beirinckx & Sherratt, 2004). Banded warning patterns appear to be more prevalent among bumblebees at mid latitudes, especially in mountainous regions (Fig. 7B: the combined areas of white and light colours on the map show high richness of all banded bumblebees in the region of southern Europe through southern and central Asia, and in the western New World). Not all banded bumblebees are banded with yellow. In some regions, the yellow is largely or completely replaced by grey–white. Figure 7B shows that yellow-banded bumblebees (in green) are relatively more frequent in north-western Europe and in the New World, whereas white-banded bumblebees (in blue) are more frequent in south-eastern Europe and in most of southern and eastern Asia. This parallels variation in the aposematic patterns seen in vespine 'yellowjacket' wasps, which similarly tend to be predominantly white-banded in north-eastern Asia [data from Archer (1989); NHM collection]. However, vespine wasps also tend to be white-banded in the northern Nearctic, where white-banded bumblebees are rare. Experiments show that at least sometimes the particular hue of the pale colour can be important for avoidance of banded patterns by predators (Exnerová *et al.*, 2006) but it is also possible that it is the black component that carries the important warning.

The brightly coloured and contrasting red or white tails of bumblebees (contrasting with bands that are otherwise of different pale colours) are often very obvious. Possibly, they signal the location of the sting, perhaps as a threat, although the advantage of this is unclear. Figure 7C shows that red-tailed bumblebees (in green) are relatively more frequent in mountainous areas, especially from southern Europe eastwards to the Tibetan Plateau and Oriental region, and in the western and northern New World. By contrast, white-tailed bumblebees (in blue) are more frequent in the northern Old World, northern Africa, California and the eastern New World.

DIVERSITY OF COLOUR-PATTERN GROUPS

Figure 5 shows that although different colour-pattern groups are associated with different parts of the world, there is substantial overlap, so that several groups usually co-occupy the same large grid cells. Unsurprisingly, richness in colour-pattern groups and species richness in social bumblebees are highly correlated at the coarse scale of this grid ($\text{rho} = 0.91$, $P < 0.001$). Figure 5 also shows that many colour-pattern groups are associated with the higher mountains of southern Europe, central and southern Asia, and in the west of the New World. One major reason for this is likely to be that habitat diversity is greater among the range of altitudinal zones in high mountain regions, allowing more colour-pattern groups to occur in close proximity while often remaining separated by altitude, as seen within Kashmir (Williams, 1991: fig. 12). Nonetheless, bumblebees rarely show only a single colour-pattern group even at any one local lowland site, a characteristic shared with mimicry systems in Lepidoptera (Papageorgis, 1975; Mallet & Joron, 1999; Mallet, 1999).

In summary, the analysis in the present study identifies three principal groups of colour patterns worldwide, and three likely principal functions are suggested. The relative frequencies are plotted against latitude in Figure 8 for the three groups of: (1) entirely black bumblebees; (2) predominantly pale grey–yellow–brown bumblebees; and (3) bumblebees with multiple strongly contrasting bands. The first two categories include colour patterns at the extremes of dark and pale. The third is a subset of the intermediate banded bumblebees, chosen to exclude some of the darker and paler banded patterns for which a single function may be less clearly predominant (so not all bumblebee colour patterns are represented on this figure). The darkest bumblebees are associated with the tropics, where a thermoregulatory or cryptic function is suggested. The palest bumblebees are associated with intermediate northern latitudes, where a cryptic function in temperate grasslands is suggested. The intermediate, strongly banded bumblebees are widespread but predominate where the other two groups may be at less of an advantage, and where intermediate banded colour patterns might have advantages for both thermoregulation and as warnings to predators.

FURTHER QUESTIONS

The present study describes some of the patterns in the coarse-scale geographical distribution of bumblebee colour patterns but most questions in seeking to explain these patterns remain unanswered. Still

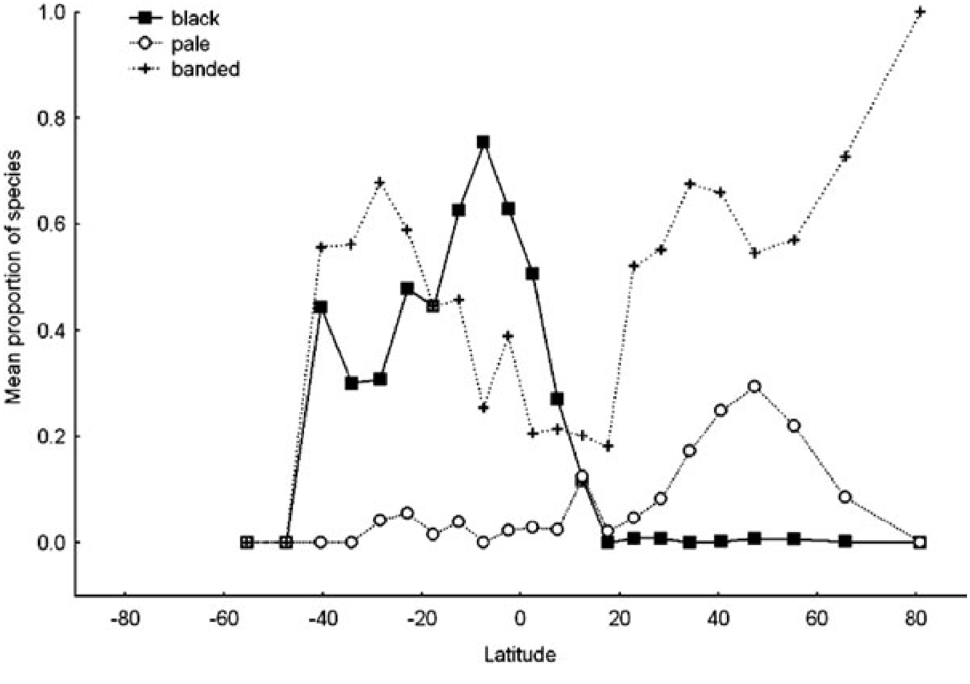


Figure 8. Mean proportions of social bumblebee species (excluding the subgenus *Psithyrus*) within three principal divisions of bumblebee colour-pattern groups plotted for each latitudinal band of the equal-area grid in Fig. 5 (cf. Fig. 6): black bumblebees (000); predominantly pale bumblebees (324 pale, 333 pale, 334 pale, 343 pale); and bumblebees with multiple strongly contrasting bands (033, 034, 133, 134, 143 white and yellow, 144, 233, 333 dark, 243). Mean proportions are used because total numbers of bumblebee species vary strongly with latitude.

required are: (1) phylogenetic studies to determine whether bumblebee species within colour-pattern groups tend to be closely related, or whether these groups are generally the result of evolutionary convergence, as appears to be the case in some examples; (2) empirical studies of heat balance and of cooling rates in relation to colour patterns of foraging bumblebees, both in the laboratrory and in field conditions; (3) field studies of possible predators that might drive bumblebee crypsis, disruptive effects, and warning mimicry; (4) further studies of colour-pattern variation in queen and male bumblebees; and (5) studies of the genetic and developmental control of bumblebee colour patterns.

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