

Do the parasitic *Psithyrus* resemble their host bumblebees in colour pattern?*

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Abstract – It has been claimed for the parasitic *Psithyrus* bumblebees that each parasite species resembles closely its particular narrow range of bumblebee host species in colour pattern. The generality of colour-pattern resemblance is assessed by applying quantitative tests at three levels of resolution in the detail of the colour patterns. The results show that at all three levels the parasites and hosts are significantly more likely to share similar colour patterns than would be expected by chance in Europe, but not in North America. Parasites do not appear to be significantly more specialised in host choice in Europe than in North America, although there is more evidence of parasite-host co-speciation in Europe than in North America. Parasite-host resemblance appears most likely to be explained by Müllerian mimicry. For the host-specific *Psithyrus*, the host species might serve as the most influential model because necessarily the host species must co-occur with the parasite and must be common.

bumblebee / *Bombus* / cuckoo bee / colour pattern / mimicry

1. INTRODUCTION

The subgenus *Psithyrus* includes approximately 30 species of bumblebees that are all obligate social parasites (inquiline or ‘cuckoo’ bumblebees) in colonies of the social bumblebees, which constitute almost all of the rest of the genus *Bombus* (another 220 species: Williams, 1998). Obligate parasitism is evident for *Psithyrus* because females of all of the species lack a worker caste and lack the structures on the hind legs that are necessary to enable foragers to collect pollen, so that *Psithyrus* are completely dependent on diverting their hosts’ resources for the nutrition of their larvae and hence for their reproduction (for descriptions of *Psithyrus* behaviour see e.g. Hoffer, 1889; Sladen, 1912; Plath, 1934; Alford, 1975; Fisher, 1987). Those *Psithyrus*

species for which hosts are reliably recorded (Tab. I: 16/30 world species) often parasitize just one host species (for 8/16 studied species), or at most, relatively few (2–5) host species. The central issue for this paper is that Reing (1935) concluded that each parasitic *Psithyrus* species shows a ‘similar’ or ‘very marked’ resemblance in colour pattern to its particular host species within each geographical region. And yet so far, the generality of parasite-host colour-pattern resemblance has not been demonstrated quantitatively. A re-assessment is necessary because, despite his broad review, much of Reing’s work on parasite-host colour patterns (Reing, 1930, 1935) focussed primarily on one species, *B. (Ps.) rupestris* (Fabricius), which varies strongly in colour pattern across Europe and Asia, showing especially close resemblance in geographical variation to its principal hosts, *B. lapidarius* (Linnaeus) and *B. sichelii* Radoszkowski. Consequently, it is possible that the close parasite-host resemblance in this particular case is atypical and has biased people’s perceptions of the other species. Taking the opposing view,

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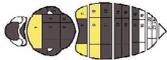
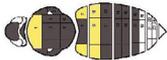
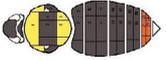
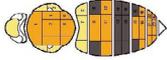
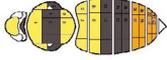
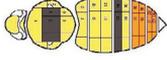
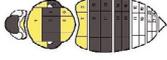
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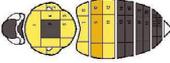
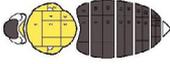
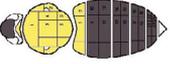
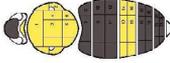
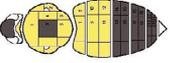
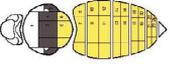
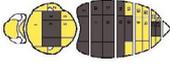
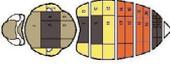
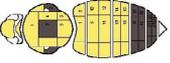
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Table I. Records of parasitic species of the subgenus *Psithyrus* (left column) breeding in colonies of host (other *Bombus*) species (right column) with colour patterns coded as described in Table II.

<i>Psithyrus</i> species + colour group*		Host species + colour group*		Location	Source
EUROPE					
<i>barbutellus</i> 333D		<i>hortorum</i> 333D		Europe	Løken 1984
<i>barbutellus</i> 333D		<i>hypnorum</i> 324D		Europe	Løken 1984
<i>bohemicus</i> 332		<i>lucorum</i> 333D		Europe	Løken 1984
<i>campestris</i> 333D		<i>humilis</i> 324P		Europe	Løken 1984
<i>campestris</i> 333D		<i>pascuorum</i> 124D		Europe	Løken 1984
<i>campestris</i> 333D		<i>pomorum</i> 100		Europe	Løken 1984
<i>campestris</i> 333D		<i>pratorem</i> 132		Europe	Løken 1984
<i>flavidus</i> 333D		<i>jonellus</i> 333D		Europe	Løken 1984
<i>maxillosus</i> 332		<i>argillaceus</i> 333D		S Europe	Popov 1931
<i>maxillosus</i> 300		<i>ruderatus</i> (<i>corsicola</i>) 300		Corsica	Rasmont & Adamski 1996
<i>norvegicus</i> 332		<i>hypnorum</i> 324D		Europe	Løken 1984

<i>perezi</i> 100		<i>terrestris (xanthopus)</i> 100		Corsica	Friese 1923
<i>quadricolor</i> 332		<i>soroensis</i> 333D		Europe	Løken 1984
<i>quadricolor (globosus)</i> 132		<i>soroensis</i> 333D		Europe	Løken 1984
<i>quadricolor (meridionalis)</i> 100		<i>soroensis (proteus)</i> 100		Europe	Løken 1984
<i>rupestris</i> 100		<i>lapidarius</i> 100		Europe	Løken 1984
<i>rupestris</i> 132		<i>lapidarius</i> 100		Europe	Løken 1984
<i>rupestris</i> 133		<i>lapidarius (decipiens)</i> 133		Europe	Løken 1984
<i>rupestris</i> 100		<i>pascuorum</i> 124D		Europe	Løken 1984
<i>rupestris</i> 133		<i>sichelii</i> 133		Europe	Løken 1984
<i>rupestris</i> 100		<i>sylvarum</i> 133		Europe	Løken 1984
<i>sylvestris</i> 332		<i>jonellus</i> 333D		Europe	Løken 1984
<i>sylvestris</i> 332		<i>pratorum</i> 132		Europe	Løken 1984
<i>vestalis</i> 332		<i>terrestris</i> 333D		Europe	Løken 1984

NORTH AMERICA

<i>ashtoni</i> 332		<i>affinis</i> 033		Boston	Plath 1934
<i>ashtoni</i> 332		<i>terricola</i> 033		Boston	Plath 1934
<i>citrinus</i> (<i>laboriosus</i>) 034		<i>impatiens</i> 034		Boston	Plath 1934
<i>citrinus</i> 334D		<i>vagans</i> 033		Boston	Plath 1934
<i>insularis</i> 333D		<i>appositus</i> 343P		Alberta	Hobbs 1966
<i>insularis</i> 333D		<i>fervidus</i> (<i>californicus</i>) 332		Alberta	Hobbs 1966
<i>insularis</i> 333D		<i>flavifrons</i> 113		British Columbia	Sladen 1915
<i>insularis</i> 333D		<i>nevadensis</i> 033		Alberta	Hobbs 1965
<i>insularis</i> 333D		<i>ternarius</i> 233		Saskatchewan	Craig 1953
<i>suckleyi</i> 333D		<i>terricola</i> (<i>occidentalis</i>) 332		Alberta	Hobbs 1968
<i>variabilis</i> 033		<i>pensylvanicus</i> 033		Illinois	Frison 1916

* Colour-pattern groups as defined by Williams (2007).

Richards (1927, p. 262) challenged the generality of bumblebee parasite-host resemblance in colour pattern: 'The resemblance between *Psithyrus* species and their hosts is scarcely greater than might be expected on the laws of chance in such polymorphic genera'. Despite this, the assertion of close parasite-host colour-pattern resemblance, whatever the cause, has often been repeated in subsequent texts on bumblebees (e.g. Plath, 1934; Free and Butler, 1959; Alford, 1975; Plowright and Owen, 1980; Prys-Jones and Corbet, 1987; Goulson, 2003; Benton, 2006) and deserves a quantitative assessment.

Three possible causes of any resemblance between *Psithyrus* and their hosts have been considered. First, some authors (Vogt, 1909; Plowright and Owen, 1980) have suggested that *Psithyrus* species could have been selected to converge upon the colour patterns of their particular host species to facilitate parasitism, as a form of aggressive mimicry, implicitly to deceive the host. However, the idea that colour-pattern mimicry of hosts by parasites might aid parasite entry into host nests was rejected by Vogt parasites: Command not found.

(1909, p. 56), Plowright and Owen (1980), and by recent reviews (Free and Butler, 1959; Alford, 1975; Goulson, 2003; Benton, 2006). Accounts of *Psithyrus* entering nests write of aggressive interactions with host queens or workers inside the nest, where it is usually dark, rather than in the light at the nest entrance (Sladen, 1912; Plath, 1934; Fisher, 1987). Furthermore, even conspecific intruders (with identical colour patterns) from other colonies are usually attacked (Fisher, 1987). No more recent evidence or argument in favour of this deceit idea for colour pattern resemblance has been presented. It is currently believed that pheromones play the central role in how *Psithyrus* females gain entry into host colonies (e.g. Dronnet et al., 2005).

Second, some authors (Richards, 1927; Reinig, 1935) have concluded that *Psithyrus* species are likely to have evolved independently of one another (convergently) and from each of their respective host species or species-groups. In this case, colour-pattern resemblance between parasite and host species might be expected by default through evolutionary conservatism within each monophyletic host-parasite lineage (Plath, 1922).

However, *Psithyrus* in its entirety has come to be accepted as a monophyletic group (e.g. Pérez, 1884; Gaschott, 1922; Popov, 1931; Plowright and Stephen, 1973; Obrecht and Scholl, 1981; Ito, 1985; Williams, 1985; Pamilo et al., 1987; Williams, 1991, 1995; Kawakita et al., 2004; Cameron et al., 2007; Michener, 2007). Consequently, evolutionary conservatism within monophyletic lineages containing both hosts and parasites cannot explain the colour-pattern resemblance. Nonetheless, there is likely to be some phylogenetic component to colour-pattern resemblances among the different parasite species, resulting from some degree of evolutionary conservatism within co-speciating lineages of hosts and parasites. For example, red tails (*rupestrus*-group) or black tails (*citrimus*-group) are characteristic of different species groups within the subgenus *Psithyrus*, and these might specialize on different species groups of hosts.

Third, a more general explanation for resemblance among *Psithyrus* and their hosts is Müllerian mimicry (Müller, 1879), in which species share a warning colour pattern to advertise the painful sting to common predators (e.g. Sladen, 1912; Free and Butler, 1959; Plowright and Owen, 1980; Prys-Jones and Corbet, 1987; Goulson, 2003; Benton, 2006). A particular parasite would not necessarily have to resemble its own host, but instead might only resemble other abundant (stinging) bumblebees that frequently co-occur.

The first step for this paper is to establish whether or not there is resemblance in colour pattern between each *Psithyrus* species and its particular host species, irrespective of the causes (including shared ancestry within groups of co-speciating hosts and parasites). Quantitative tests are applied at three levels of resolution in the detail of the colour patterns. First, at a coarse resolution, is there a match between parasite and host in the colour of the most prominent component, the 'tail' of the abdomen? Second, at an intermediate resolution, is there a match in the colour-pattern group to which parasite and host are assigned? Third, at a finer resolution, is there a match

Table II. Criteria for classifying colour-pattern groups from Williams (2007).

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 abdomen 2 one pale band only, on part of thorax 3 at least two separated pale bands, on thorax or thorax and abdomen 4 all pale, at least on thorax

The colour of the ‘tail’ usually refers to the colour of the palest hair covering all or parts of the posterior metasomal terga 3–5 (see text); ‘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. Colour-pattern groups can be specified by their values for the three criteria (ABC) from this table, e.g. ‘133’ specifies the most frequent pattern among all female bumblebees (criterion A scores 1 for tail red; criterion B scores 3 for pale bands yellow; criterion C scores 3 for pale bands two). Where groups were further subdivided (see Williams, 2007, for details), these are described as ‘D’ for dark subgroups (with extensive black on the abdomen) and ‘P’ for pale subgroups (with extensive yellow on the abdomen).

in the details of the colour pattern? In seeking to understand the causes of any resemblance, I also test the hypothesis of co-speciation between *Psithyrus* and their hosts.

2. METHODS

2.1. Data for parasite-host associations

The only parasitic bumblebees considered here are species in the subgenus *Psithyrus* (for others see Alford, 1975). *Psithyrus* females have been found in the nests of many more of the social species than they have been confirmed to breed within (Sladen, 1912; Plath, 1934; Reinig, 1935; Løken, 1984). Furthermore, some putative ‘hosts’ have been suggested merely on the basis of supposed colour similarity (e.g. Bequaert and Plath, 1925; Frison, 1934;

Reinig, 1935), making these records especially unsuitable for use as data in this analysis. Therefore the fundamental form of datum required is a record of a particular parasite species breeding successfully within a colony of a particular host species.

Parasite-host records have been reviewed critically for northern Europe by Løken (1984). Her Table II is accepted as the best available authoritative summary. For southern Europe, records for *B. (Ps.) maxillosus* Klug are given by Popov (1931) and by Rasmont and Adamski (1996). For the endemic Corsican *B. (Ps.) perezi* (Schulthess-Rechburg), Ferton (1901, cited in Rasmont and Adamski, 1996) argues that at the time that females are searching for host nests in autumn, only *B. terrestris* (Linnaeus) are founding nests (this species is also given as the host by Friese, 1923, but without detailed evidence). For eastern North America, records from Plath (1934) are accepted as an authoritative summary.

For western North America, records from Hobbs (1965, 1966a, b, 1968) are accepted as authoritative together with some additional records from Sladen (1915), Frison (1916), and Craig (1953). This leaves one North American species without suitable records, despite being widespread: *B. (Ps.) fernaldae* (Franklin). The only inferences of likely hosts are either arguments based on colour-pattern similarity (Bequaert and Plath, 1925), or comments that *B. (Ps.) fernaldae* was recorded from nests of unnamed species of the subgenus *Pyrobombus* (Hobbs, 1967). Other more recent reviews mentioning host associations for *B. (Ps.) fernaldae* (Thorp et al., 1983; Laverty and Harder, 1988) are based on literature records, not on direct observations of breeding (R. Thorp, in litt., and L. Harder, in litt.). For Asia and for Central America there are no published records that come from direct observations of parasite reproduction (Maa, 1948, states that in China *B. trifasciatus* Smith is the host for *B. (Ps.) pieli* (Maa), a synonym of *B. (Ps.) bellardii* (Gribodo), but does not present any supporting evidence). Unfortunately there are insufficient data at present to weight different host records by their relative frequencies.

Records of parasites on hosts rarely specify the colour patterns involved, so these generally had to be inferred from locality data and material in the Natural History Museum (London) collection (e.g. for *B. (Ps.) rupestris*, *B. (Ps.) insularis* (Smith), and their hosts). Records of the North American *B. rufocinctus* Cresson as a host are excluded because of the uncertainty concerning which of the many colour forms were involved in each case.

Parasite-host records satisfying all of the criteria above are available for only 24 unique species colour-pattern pairs in Europe and 11 species colour-pattern pairs in North America (Tab. I).

2.2. Data for colour patterns

Colour patterns refer here to the variable colours of the pubescence (hair) on the dorsum of the body, which are the most obvious exposed parts when bumblebees are flying or walking. Colour-pattern resemblance is analysed between *Psithyrus* females and the workers or queens of the social *Bombus*. In the relatively few cases in which workers and queens differ in colour pattern, e.g. *B. argillaceus* (Scopoli) in Europe and *B. affinis* Cresson in North America, worker patterns are used. This is because if Müllerian mimicry were important, at the time

of year when *Psithyrus* females are most frequently seen, it is the workers of the social species that are most frequently seen.

Colour patterns can be quantified by breaking them down into body regions and colour classes using the methods described previously (Williams, 2007). This system of data coding uses 23 pattern elements (body regions) and 7 colour classes (see the example diagrams in Tab. I). In addition, groups of similar colour patterns are recognised using the classification criteria described in Table II. The resulting colour-pattern groups are listed for each of the species of parasites and hosts in Table I.

2.3. Analyses

2.3.1. Low resolution: tail colour

One of the most conspicuous components of bumblebee colour patterns is the 'tail' at the posterior tip of the abdomen, which often presents a bright and strongly contrasting colour. The colour of the 'tail' is usually considered to be the colour class of the palest colour of the long hair of terga 3–5 (Tab. II). This colour is most often yellow and/or white (Tab. I), or sometimes orange or red. More rarely there may be both yellow and red (or orange) hair, or occasionally at least terga 4–5 may be completely black (contrasting with pale terga 2–3).

I use the familiar randomization-test approach (Manly, 1991) in all of the tests here, but adapted to each case. For tail colour, the test assessed whether there are significantly more matches in tail colour between parasites and hosts than would be expected by chance. Different randomly selected 'host' colour-patterns were drawn with equal probability (with replacement, because there are fewer unique hosts than there are parasite records) 9999 times from the species pool of potential hosts and compared with the parasite colour patterns for tail-colour matches. The resulting frequency distribution of expected numbers of tail matches is used to estimate the probability of getting by chance at least as many as the observed number of tail matches.

The composition of the appropriate pool of potential 'host' species for random draws needs careful consideration. At its simplest, this pool might be thought to include the entire European and North American faunas of social (non-*Psithyrus*) bumblebee species (excluding the faunas of Turkey and Mexico, because there are no specific records of

host colonies rearing *Psithyrus* from there). However, treating these entire faunas as the 'host' pools to be sampled could be misleading, particularly if the subsets of species that are actually observed to be hosts in Table I are those species among the regional faunas that are substantially more likely to be suitable for supporting parasite populations. For example, this might be because the observed host species are more widespread and abundant and so better able to support sustainable reproduction by the parasite populations. Constraining the species pools for the random draws in this way will make for a more conservative test (confirmed in trials for both regions, unpublished), because the options for drawing additional random 'hosts' are more rapidly constrained with each draw made. Therefore these analyses use only the subset of observed hosts as the populations from which to make the random draws.

Treating the faunas of Europe and North America together as a single uniform host-species pool to be sampled (in effect by the parasites) could also be misleading. This is because the two different regional faunas are dominated by species that belong to two very different sets of colour-pattern groups (Williams, 2007). Therefore, in these analyses, the two regional species pools are sampled separately. In contrast, many of the parasite species, host species, and colour-pattern groups are widespread within either one of the two regions. For example, in North America although host colour patterns differ between eastern and western areas, parasites and their colour patterns tend to be widespread (e.g. *B. (Ps.) insularis*, although less true for *B. (Ps.) citrinus* (Smith) and *B. (Ps.) variabilis* (Cresson)) and therefore are exposed to most of the range of potential host patterns. In Europe, a few parasites are much more geographically restricted (e.g. *B. (Ps.) perezii* in Corsica), but where they occur they are still exposed to the range of potential host patterns. At present it is considered premature to constrain the simulation further within each of the two continental regions, although this might be desirable when a greater and more representative regional spread of parasite-host association records becomes available from North America.

2.3.2. Intermediate resolution: colour group

To test whether there are significantly more matches in colour-pattern group than would be expected by chance, 'host' colour groups were drawn

at random from the observed host pools for Europe and for North America to estimate the probability of getting at least as many as the observed number of group matches.

2.3.3. Fine resolution: colour element

The 7 colour classes (Tab. II) are ranked in order of increasing brightness or luminance, giving scores from 0 to 6 from black to white. It is then possible to compare crudely any two bumblebee colour patterns by summing the colour-score differences between pairs of colour-pattern elements across the 23 pattern elements of the body. To test whether there are significantly more colour-pattern-element colour-score differences than would be expected by chance, 'host' colour patterns were drawn at random from the observed host pools for Europe and for North America to estimate the probability of getting at least as many as the observed mean sum of colour-pattern-element colour-score differences.

Computational software for the randomization tests was written in C (see online appendices).

2.3.4. Co-speciation of parasites and hosts

Well supported *Psithyrus* and host phylogenetic trees are available from Cameron et al. (2007). Co-speciation was tested by counting the numbers of differences in resolved triplets (groups of three species with a resolved relationship of the form (a+b)+c within each tree) between the parasite and host trees when compared to randomly generated trees, using the COMPONENT software (Page, 1993).

3. RESULTS

Because results were found to differ between Europe and North America, those results are presented separately rather than combined.

3.1. Do parasites and hosts have similarly coloured tails?

Among all of the parasite-host records in Table I, there are 24/35 (68%) tail-colour matches. For Europe with 19/24 (79%)

matches the estimated probability that such a high observed number of matches could be due to chance is $P = 0.004$, and for North America with 5/11 (45%) matches it is $P = 0.26$. Therefore, while there is a statistically significant association (threshold $P < 0.05$) between parasite and host tail colour in these data for Europe, there is no significant association in these data for North America.

3.2. Do parasites and hosts belong to the same colour-pattern groups?

Among all of the parasite-host records in Table I, there are 10/35 (28%) colour-pattern-group matches. For Europe with 8/24 (33%) matches the estimated probability that such a high observed number of matches could be due to chance is $P = 0.024$, and for North America with 2/11 (18%) matches it is $P = 0.21$. Therefore, while there is a statistically significant association (threshold $P < 0.05$) between parasite and host colour-pattern group in these data for Europe, there is no significant association in these data for North America.

3.3. Do parasites and hosts share similarly coloured body-pattern elements?

For Europe, the observed mean number of colour-pattern-element differences is 38.58 per species pair, whereas for North America the mean number of differences is 52.36 (out of a possible range of values between 0–161 in each case). For Europe the estimated probability that such a low observed number of differences could be due to chance is $P = 0.037$, and for North America it is $P = 0.18$. Therefore, while there is a statistically significant association (threshold $P < 0.05$) between parasite and host colour-pattern elements in these data for Europe, there is no significant association in these data for North America.

3.4. Is there evidence for co-speciation of parasites and hosts?

Tests of the numbers of differences in resolved triplets of species between the parasite

and host trees compared to randomly generated trees show significant similarity between parasite and host trees for Europe ($P = 0.016$), but not for North America ($P = 0.227$).

4. DISCUSSION

4.1. Interpretation of the results and caveats

The results show that the parasites and hosts are significantly more likely to share similar colour patterns than would be expected by chance in Europe, but not in North America. This result is consistent across three levels of resolution in colour-pattern similarity.

The tests at the three levels of pattern resolution are not independent of one another as all three are based on some of the same colour-pattern elements. The results are subject to the effects of errors or biases arising particularly from: (1) errors in ascertaining whether parasites reproduced in a nest; (2) misidentifications of parasite and host species; (3) parasite-host associations are not weighted by their relative frequencies where different hosts are involved; (4) problems with coding colour patterns and assigning colour-pattern groups (Williams, 2007); (5) host records are available from only 16 out of 30 *Psithyrus* species world-wide and include none from the fauna of Asia or Central America, and more records are also needed from across the entire ranges of all of the *Psithyrus* species in Table I, especially in North America. The approach taken to selecting the data admitted for this analysis should have minimised errors from the first two sources. Source (3) is unlikely to obscure the true general pattern because the data from experienced review sources do not appear to be dominated by many atypical rare records. Source (4) appears not to be a problem because the results here are robust with respect to how colour pattern resemblance is measured. Even though the colour coding used here obscures some subtle additional resemblances noted by Richards (1927) among common British parasite-host pairs (part-orange tails for some *B. (Ps.) sylvestris* (Lepeletier) and *B. pratorum* (Linnaeus); yellow rather than white tails for

B. (Ps.) campestris (Panzer) and *B. pascuorum* (Scopoli)), the results still support a general resemblance. Source (5) cannot be assessed at present and more data are needed.

4.2. Interpretations of parasite-host colour-pattern resemblance

The difference between Europe and North America in whether there is an association between parasite and host colour patterns does not seem to be explained by any difference in the degree of host specificity between the two continents. Different *Psithyrus* species do vary in host specificity (Fisher, 1987) and it might have been expected that parasites that are less host-specific might also have shown weaker associations with particular hosts in their colour patterns (Plowright and Owen, 1980). However, from the data on host specificity of parasites in Table I, the North American parasites (with weaker association in colour pattern with host species) do not have significantly more recorded hosts per parasite than the European parasites (assessed using 9999 simulated random draws of 5 from among 16 parasite species and comparing the observed mean within North America of 2.2 hosts per parasite with the expected distribution: estimated probability of finding such a high value by chance $P = 0.34$). These data appear to contradict the difference in host specificity between continents suggested (without supporting data) by Plowright and Owen (1980). However, the data could be biased because they do not represent similar sample sizes for all *Psithyrus* species, so standardised data are still needed to confirm the result.

Although the association of colour-pattern groups between parasites and hosts is statistically significant in Europe, nonetheless with only 8 colour-pattern-group matches among the 24 records, parasite-host resemblance is hardly a universal pattern even there. The 8 precise European matches occur within 4 different colour-pattern groups. Where these colour-pattern-group matches do occur, many involve particularly the black red-tailed bees (group 100: 3/8 cases). This includes the ex-

ample (*B. (Ps.) rupestris* parasitizing primarily *B. lapidarius* in Europe) that originally attracted the attention of Reinig for his influential review (Reinig, 1935). Although there are also many red-tailed social bumblebees in North America, there are no red-tailed parasites there.

According to the well-supported trees in Cameron et al. (2007), the overall phylogenetic tree for *Psithyrus* species does not appear to map especially closely onto that of their host species as listed in Table I. For example, Figure 1 shows that several individual *Psithyrus* species attack species in both of the two largest clades of hosts. Nonetheless, the greater support for co-speciation between parasites and hosts in Europe may be because there is a greater diversity of *Psithyrus* in the Old World (Williams, 1998) and because only a few of all *Psithyrus* clades have spread later to the New World (Cameron et al., 2007), where in some cases they may have ‘colonised’ new host clades. However, the test used here is weakened by the many shared hosts and parasites. These trees are now being used to study the evolution of colour characters more directly. It will be interesting to incorporate information from more of the very variable parasite species in China, Europe, and North America when more host-parasite records become available.

Intriguingly, the result that parasites are significantly more similar to each of their observed hosts than to hosts of other species is inconsistent with the driving process being diffuse Müllerian mimicry with any co-occurring abundant social species. Nonetheless, the resemblance between parasite and host may still be driven by Müllerian mimicry. This could be explained if the particular host species were the most influential model because, of necessity, it must always co-occur with the parasite and must also be sufficiently common for the parasite to encounter sufficiently frequently to maintain its population.

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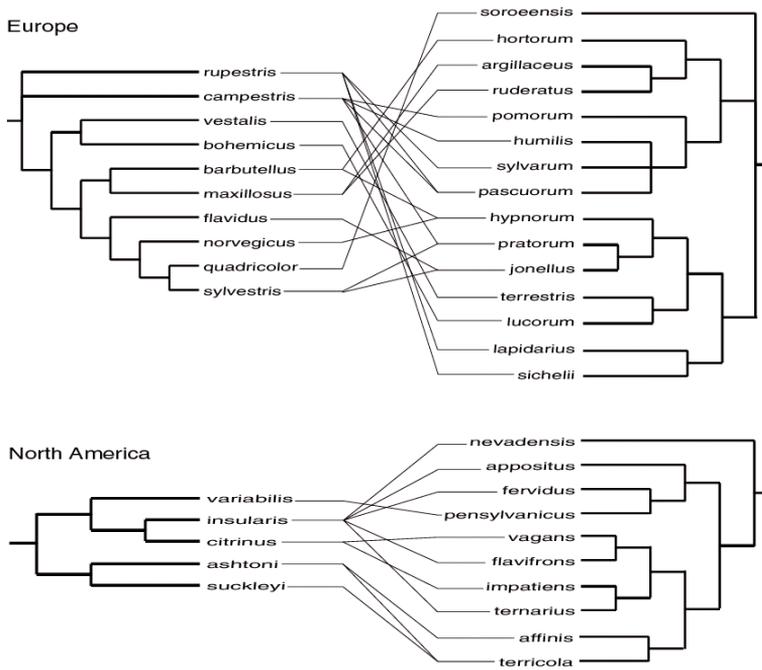


Figure 1. Parasite-host associations mapped against phylogenetic trees. Records of parasitic species of the subgenus *Psithyrus* (left column) breeding in colonies of host (other *Bombus*) species (right column) from Table I are represented by lines linking the species in the centre. Estimates of phylogeny are subtrees for the included species alone, taken from Figure 2 in Cameron et al. (2007), but resolving only those clades with strong support (Bayesian posterior probability ≥ 0.95).

Les *Psithyrus* parasites et leurs bourdons hôtes ont-ils un patron de couleurs semblable ?

***Bombus* / *Psithyrus* / mimétisme / coloration / relation hôte-parasite**

Zusammenfassung – Ähneln die parasitischen *Psithyrus*-Hummelarten ihren Wirten im Farbmuster? Die Untergattung *Psithyrus* schließt ca. 30 Hummelarten ein, von denen alle obligate Parasiten bei sozialen Hummeln sind. Dabei werden fast alle Vertreter der Gattung *Bombus* mit etwa 220 Arten parasitiert. Einige Autoren behaupten, dass parasitische Arten, die auf nur wenige Wirtsarten spezialisiert sind, ein ähnliches Farbmuster wie ihre Wirte aufweisen. In dieser Arbeit wird untersucht, ob es eine allgemein gültige Übereinstimmung im Farbmuster zwischen Parasiten und Wirten gibt (Tab. I). Hierfür werden quantitative Tests mit drei unterschiedlichen Auflösungen zur Erfassung der Färbung des Endstücks des Abdomens, (2) Vergleich von „Farbmuster-Gruppen“ bei Parasiten und Wirtsarten sowie (3) auf der Basis von 7

Farbklassen für jede von insgesamt 23 definierten Körperregionen auf dem Rücken des Hummelkörpers. Die Ergebnisse zeigen, dass bei allen drei Versuchsansätzen die Parasiten und ihre Wirte in Europa eine signifikant höhere Wahrscheinlichkeit für ein ähnliches Farbmuster aufweisen. Dies gilt aber nicht für Nordamerika, so dass sich die Farbmuster-Ähnlichkeit in beiden Kontinenten unterschiedlich darstellt. Auch gibt es in Europa mehr Anhaltspunkte für eine gemeinsame Artbildung von Parasiten und Wirten als in Nordamerika (Abb. 1), wo einige Wirtsarten möglicherweise erst vor kurzem von Parasiten besiedelt worden sind. Ich schließe daraus, dass die Parasit-Wirt-Ähnlichkeit am ehesten durch Müllersche Mimikry erklärt werden kann, wenn für die wirtsspezifischen *Psithyrus* in erster Linie die jeweilige Wirtsart den größten Einfluss darauf hat. Dies macht Sinn, weil die Wirte zwangsläufig immer mit den Parasiten gemeinsam auftreten und außerdem so häufig vorkommen müssen, dass ausreichende Begegnungen mit den Parasiten stattfinden.

Hummeln / *Bombus* / Kuckucksbienen / Farbmuster / Mimikry

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Online Material

APPENDIX

Paul Williams

Programs written for Dev-C++ version 4.9.9.2

from Bloodshed Software <http://www.bloodshed.net>

```

//=====
//(1) COLTAIL4.c
//by Paul Williams, the Natural History Museum, London
//version 15.xi.2007
//for Dev-C++ 4.9.9.2
//
//Randomization test for Psithyrus and host data:
//At a coarse scale, is there an association between parasites and hosts
//in their tail colour in the sample of records?

#include <stdio.h>
#include <stdlib.h>
#include <string.h>
#include <math.h>
#include <time.h>

#define RECORDSEU 24 // number of European parasitism records
#define HOSTSEU 18 // number of unique European hosts
#define RECORDSNA 11 // number of N American parasitism records
#define HOSTSNA 11 // number of unique N American hosts
#define SIMULATIONS 9999

int main(int argc, char *argv[])
{
int i, j, k,
choiceEU[RECORDSEU], choiceNA[RECORDSNA], result[SIMULATIONS+1],
orderEU[RECORDSEU], orderNA[RECORDSNA],
randn, randmax,
mark, gap, tempv, step;
FILE *fp_out;

//data
char parasite_groups_EU[RECORDSEU][5]= {
"333D",
"333D",
"332x",
"333D",
"333D",
"333D",
"333D",
"333D",
"333D",
"332x",
"300x",
"332x",
"100x",
"332x",
"132x",
"100x",
"100x",
"132x",
"133x",
"100x",
"133x",
"100x",
"332x",
"332x",
"332x"},
parasite_groups_NA[RECORDSNA][5]= {
"332x",
"332x",
"034x",

```

```

"334D",
"333D",
"333D",
"333D",
"333D",
"333D",
"333D",
"333D",
"033x"},
host_groups_EU[HOSTSEU][5]= { //excluding non-unique hosts as comments
"333D",
"324B",
"333D",
"324Y",
"124D",
"100x",
"132x",
"333D",
"333D",
"300x",
//  "324B",
"100x",
"333D",
//  "333D",
"100x",
"100x",
//  "100x",
"133x",
//  "124D",
"133x",
"133x",
//  "333D",
//  "132x",
"333D"},
host_groups_NA[HOSTSNA][5]= {
"033x",
"033x",
"034x",
"033x",
"343L",
"332x",
"113x",
"033x",
"233x",
"332x",
"033x"};

//open files
if ((fp_out=fopen("simresults.txt","w+")) == NULL)//clear contents of file
{
printf("file opening error\n");
return EXIT_FAILURE;
}

//simulation
srand((unsigned)time(NULL)); // seed start of number table
randn= (int)(RAND_MAX/HOSTSEU);
randmax= HOSTSEU*randn; // max acceptable score
for (i=1; i<=SIMULATIONS; i++) // sim 1->9999
{
result[i]= 0;

//Europe
//choose offsets into HOSTS codes
for (j=0; j<RECORDSEU; j++)// for each sim choice with replacement
{
do {
randn= rand();
} while (randn>randmax);
}
}

```

```

        choiceEU[j]= (randn%HOSTSEU);      // offsets 0 -> N-1
    }

    for (j=0; j<RECORDSEU; j++)
    {
        if (strncmp(parasite_groups_EU[j],host_groups_EU[choiceEU[j]],1)==0)
            ++result[i];
    }
}

//extract results
gap= SIMULATIONS/2;                                //Shell binary sort
while (gap > 0)
{
    for (i=1; i<=SIMULATIONS-gap; i++)
    {
        for (j=i; j>=1; j--)
        {
            mark= j+gap;
            if (result[j] > result[mark])    //sort to increasing values
            {
                tempv= result[j];
                result[j]= result[mark];
                result[mark]= tempv;
            }
            else
                j= 0;
        }
    }
    gap /= 2;
}

//write results
fprintf(fp_out,"\n\n Results Europe ###\n\n");
step= SIMULATIONS/1000;
fprintf(fp_out," percentage points:\n");
for (i=1; i<=SIMULATIONS; i++)                // sim 1->100...
{
    if ((i%(100))==0)
    {
        if (i==500)
        {
            j= 1;
            fprintf(fp_out,"%5d (%6.2f):    %4d\n",
                i, ((double)i/SIMULATIONS), result[i]);
            fprintf(fp_out,".....\n");
        }
        else if (i==9500)
        {
            fprintf(fp_out,".....\n");
            fprintf(fp_out,"%5d (%6.2f):    %4d\n",
                i, ((double)i/SIMULATIONS), result[i]);
        }
        else
            fprintf(fp_out,"%5d (%6.2f):    %4d\n",
                i, ((double)i/SIMULATIONS), result[i]);
    }
}
fprintf(fp_out,"\n upper tail threshold:\n");
for (i=1; i<=SIMULATIONS; i++)                // sim 1->100...
{
    if (i>9400 && i<=9999)
    {
        fprintf(fp_out,"%5d (%6.4f):    %4d\n",i,1-((double)i/SIMULATIONS), result[i]);
    }
}

randn= (int) (RAND_MAX/HOSTSNA);

```

```

randmax= HOSTSNA*randn; // max acceptable score
for (i=1; i<=SIMULATIONS; i++) // sim 1->9999
{
  result[i]= 0;

  //N America
  for (j=0; j<RECORDSNA; j++)// for each sim cell
  {
    do {
      randn= rand();
    } while (randn>randmax);
    choiceNA[j]= (randn%HOSTSNA); // offsets 0 -> N-1
  }

  for (j=0; j<RECORDSNA; j++)
  {
    if (strcmp(parasite_groups_NA[j],host_groups_NA[choiceNA[j]],1)==0)
      ++result[i];
  }
}

//extract results
gap= SIMULATIONS/2; //Shell binary sort
while (gap > 0)
{
  for (i=1; i<=SIMULATIONS-gap; i++)
  {
    for (j=i; j>=1; j--)
    {
      mark= j+gap;
      if (result[j] > result[mark]) //sort to increasing values
      {
        tempv= result[j];
        result[j]= result[mark];
        result[mark]= tempv;
      }
      else
        j= 0;
    }
  }
  gap /= 2;
}

//write results
fprintf(fp_out, "\n\n Results N America ####\n\n");
step= SIMULATIONS/1000;
fprintf(fp_out, " percentage points:\n");
for (i=1; i<=SIMULATIONS; i++) // sim 1->100...
{
  if ((i%(100))==0)
  {
    if (i==500)
    {
      j= 1;
      fprintf(fp_out, "%5d (%6.2f): %4d\n",
        i, ((double)i/SIMULATIONS), result[i]);
      fprintf(fp_out, ".....\n");
    }
    else if (i==9500)
    {
      fprintf(fp_out, ".....\n");
      fprintf(fp_out, "%5d (%6.2f): %4d\n",
        i, ((double)i/SIMULATIONS), result[i]);
    }
    else
      fprintf(fp_out, "%5d (%6.2f): %4d\n",
        i, ((double)i/SIMULATIONS), result[i]);
  }
}

```

```

    }
    fprintf(fp_out, "\n upper tail threshold:\n");
    for (i=1; i<=SIMULATIONS; i++) // sim 1->100...
    {
        if (i>9400 && i<=9999)
        {
            fprintf(fp_out, "%5d (%6.4f): %4d\n", i, 1-((double)i/SIMULATIONS), result[i]);
        }
    }

fclose(fp_out);
return EXIT_SUCCESS;
}

//=====
// (2) COLGROUPS4.c
// by Paul Williams, the Natural History Museum, London
// version 15.xi.2007
// for Dev-C++ 4.9.9.2
//
// Randomization test for Psithyrus and host data:
// At an intermediate scale, is there an association between parasites and hosts
// in their colour-pattern groups (from Williams, 2007) in the sample of records?

#include <stdio.h>
#include <stdlib.h>
#include <string.h>
#include <math.h>
#include <time.h>

#define RECORDSEU 24 // number of European parasitism records
#define HOSTSEU 18 // number of unique European hosts
#define RECORDSNA 11 // number of N American parasitism records
#define HOSTSNA 11 // number of unique N American hosts
#define SIMULATIONS 9999

int main(int argc, char *argv[])
{
    int i, j, k,
        choiceEU[RECORDSEU], choiceNA[RECORDSNA], result[SIMULATIONS+1],
        orderEU[RECORDSEU], orderNA[RECORDSNA],
        randn, randmax,
        mark, gap, tempv, step;
    FILE *fp_out;

    //data
    char parasite_groups_EU[RECORDSEU][5]= {
        "333D",
        "333D",
        "332x",
        "333D",
        "333D",
        "333D",
        "333D",
        "333D",
        "333D",
        "332x",
        "300x",
        "332x",
        "100x",
        "332x",
        "132x",
        "100x",
        "100x",
        "100x",
        "132x",
        "133x",
        "100x",
        "133x",
    }

```

```

"100x",
"332x",
"332x",
"332x"},
parasite_groups_NA[RECORDSNA][5]= {
"332x",
"332x",
"034x",
"334D",
"333D",
"333D",
"333D",
"333D",
"333D",
"333D",
"033x"},
host_groups_EU[HOSTSEU][5]= { //excluding non-unique hosts as comments
"333D",
"324B",
"333D",
"324Y",
"124D",
"100x",
"132x",
"333D",
"333D",
"300x",
// "324B",
"100x",
"333D",
// "333D",
"100x",
"100x",
// "100x",
"133x",
// "124D",
"133x",
"133x",
// "333D",
// "132x",
"333D"},
host_groups_NA[HOSTSNA][5]= {
"033x",
"033x",
"034x",
"033x",
"343L",
"332x",
"113x",
"033x",
"233x",
"332x",
"033x"};

//open files
if ((fp_out=fopen("simresults.txt","w+")) == NULL)//clear contents of file
{
printf("file opening error\n");
return EXIT_FAILURE;
}

//simulation
srand((unsigned)time(NULL)); // seed start of number table
randn= (int)(RAND_MAX/HOSTSEU); // max acceptable score
randmax= HOSTSEU*randn; // sim 1->9999
for (i=1; i<=SIMULATIONS; i++)
{
result[i]= 0;
}

```

```

//Europe
//choose offsets into HOSTS codes
for (j=0; j<RECORDSEU; j++)// for each sim choice with replacement
{
    do {
        randn= rand();
        } while (randn>randmax);
    choiceEU[j]= (randn%HOSTSEU);    // offsets 0 -> N-1
}

for (j=0; j<RECORDSEU; j++)
{
    if (strncmp(parasite_groups_EU[j],host_groups_EU[choiceEU[j]],4)==0)
        ++result[i];
}

}

//extract results
gap= SIMULATIONS/2;                                //Shell binary sort
while (gap > 0)
{
    for (i=1; i<=SIMULATIONS-gap; i++)
    {
        for (j=i; j>=1; j--)
        {
            mark= j+gap;
            if (result[j] > result[mark])    //sort to increasing values
            {
                tempv= result[j];
                result[j]= result[mark];
                result[mark]= tempv;
            }
            else
                j= 0;
        }
    }
    gap /= 2;
}

//write results
fprintf(fp_out, "\n\n Results Europe ###\n\n");
step= SIMULATIONS/1000;
fprintf(fp_out, " percentage points:\n");
for (i=1; i<=SIMULATIONS; i++)                // sim 1->100...
{
    if ((i%(100))==0)
    {
        if (i==500)
        {
            j= 1;
            fprintf(fp_out, "%5d (%6.2f):    %4d\n",
                i, ((double)i/SIMULATIONS), result[i]);
            fprintf(fp_out, ".....\n");
        }
        else if (i==9500)
        {
            fprintf(fp_out, ".....\n");
            fprintf(fp_out, "%5d (%6.2f):    %4d\n",
                i, ((double)i/SIMULATIONS), result[i]);
        }
        else
            fprintf(fp_out, "%5d (%6.2f):    %4d\n",
                i, ((double)i/SIMULATIONS), result[i]);
    }
}
fprintf(fp_out, "\n upper tail threshold:\n");
for (i=1; i<=SIMULATIONS; i++)                // sim 1->100...

```

```

{
if (i>9400 && i<=9999)
{
fprintf(fp_out, "%5d (%6.4f): %4d\n", i, 1-((double)i/SIMULATIONS), result[i]);
}
}

//simulation
randn= (int) (RAND_MAX/HOSTSNA);
randmax= HOSTSNA*randn; // max acceptable score
for (i=1; i<=SIMULATIONS; i++) // sim 1->9999
{
result[i]= 0;

//N America
for (j=0; j<RECORDSNA; j++)// for each sim cell
{
do {
randn= rand();
} while (randn>randmax);
choiceNA[j]= (randn%HOSTSNA); // offsets 0 -> N-1
}

for (j=0; j<RECORDSNA; j++)
{
if (strcmp(parasite_groups_NA[j], host_groups_NA[choiceNA[j]], 4)==0)
++result[i];
}
}

//extract results
gap= SIMULATIONS/2; //Shell binary sort
while (gap > 0)
{
for (i=1; i<=SIMULATIONS-gap; i++)
{
for (j=i; j>=1; j--)
{
mark= j+gap;
if (result[j] > result[mark]) //sort to increasing values
{
tempv= result[j];
result[j]= result[mark];
result[mark]= tempv;
}
else
j= 0;
}
}
gap /= 2;
}

//write results
fprintf(fp_out, "\n\n Results N America ###\n\n");
step= SIMULATIONS/1000;
fprintf(fp_out, " percentage points:\n");
for (i=1; i<=SIMULATIONS; i++) // sim 1->100...
{
if ((i%100)==0)
{
if (i==500)
{
j= 1;
fprintf(fp_out, "%5d (%6.2F): %4d\n",
i, ((double)i/SIMULATIONS), result[i]);
fprintf(fp_out, ".....\n");
}
else if (i==9500)

```



```

5, 0,0,0,0,0,0,0,0,0,0,0,0,0,6,0,6,6,6,6,0,0,0,0, //norvegicus
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,4,4,5,5,5,5,6,6, //perezi
5, 0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6,4,4,4,4, //quadricolor
5, 0,0,0,0,0,0,0,0,0,0,4,4,4,5,5,5,4,4,4,4,4, //quadricolor
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,4,4,4,4,4,4, //quadricolor d
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3, //rupestris
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3, //rupestris p
5, 0,0,5,5,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3, //rupestris p
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3, //rupestris
5, 0,0,5,5,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3, //rupestris p
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3, //rupestris
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,0,0,0,0, //sylvestris
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,0,0,0,0, //sylvestris
5, 0,0,0,0,0,0,0,0,0,0,0,5,5,5,6,6,6,6,0,0,0,0, //vestalis

parasitesNA[RECORDSNA][ELEMS]= { //parasite-record colour-pattern elements
//0 X 1 2
//1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,0,6,0,0, //ashtoni
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,0,6,0,0, //ashtoni
5, 5,5,5,5,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0, //citrinus lab
5, 5,5,5,5,0,0,0,0,0,0,5,5,5,5,0,0,0,0,0,0,0,0,0, //citrinus
5, 0,0,5,5,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,0,5,0,5, //insularis
5, 0,0,5,5,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,0,5,0,5, //insularis
5, 0,0,5,5,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,0,5,0,5, //insularis
5, 0,0,5,5,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,0,5,0,5, //insularis
5, 0,0,5,5,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,0,5,0,0, //suckleiy
5, 0,5,5,5,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0, //variabilis

allhostsEU[RECORDSEU][ELEMS]= { //host-record colour-pattern elements
//0 X 1 2
//1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4
5, 0,0,5,5,5,5,5,0,0,0,0,0,0,6,6,6,6,6,6,6,6,6,6,6, //hortorum
4, 4,4,4,4,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6, //hypnorum
5, 0,0,0,0,0,0,0,0,5,5,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6, //lucorum
4, 4,4,4,4,5,5,4,4,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5, //humilis
4, 4,4,4,4,5,5,4,4,0,4,4,0,0,0,4,0,4,4,4,4,4,4,4,4, //pascuorum
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3,3,3, //pomorum
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3, //pratorum
5, 0,0,5,5,5,5,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6,6, //jonellus
5, 0,0,5,5,5,5,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6,6,6, //argillaceus
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,5,5,5,5,5, //ruderatus cors
4, 4,4,4,4,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6, //hypnorum
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,4,4,4,4,4,4,4,4,4, //terrestris xanth
5, 0,0,0,0,0,5,5,5,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6, //soroensis
5, 0,0,0,0,0,5,5,5,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6, //soroensis
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3,3,3, //soroensis prot
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3,3,3, //lapidarius
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3,3,3, //lapidarius
5, 0,0,5,5,5,5,5,5,0,0,0,0,0,0,3,3,3,3,3,3,3,3,3,3, //lapidarius dec
4, 4,4,4,4,5,5,4,4,0,4,4,0,0,0,4,0,4,4,4,4,4,4,4,4, //pascuorum
5, 0,0,5,5,5,5,5,5,0,0,0,0,0,0,4,4,4,4,4,4,4,4,4,4, //sichelii
5, 0,0,5,5,5,5,5,5,5,5,0,0,5,5,4,4,4,4,4,4,4,4,4,4, //sylvarum
5, 0,0,5,5,5,5,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6,6,6, //jonellus
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3, //pratorum
5, 0,0,0,0,0,0,5,5,0,0,0,0,0,0,6,6,6,6,6,6,6,6,6,6, //terrestris

allhostsNA[RECORDSNA][ELEMS]= { //host-record colour-pattern elements
//0 X 1 2
//1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4
5, 0,5,5,5,5,5,4,4,5,5,0,0,0,0,0,0,0,0,0,0,0,0,0, //affinis
5, 0,0,0,0,0,0,5,5,5,5,5,5,5,5,0,0,0,0,0,0,0,0,0, //terricola
5, 5,5,5,5,5,5,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0, //impatiens
0, 5,5,5,5,5,5,5,5,5,5,5,5,0,0,0,0,0,0,0,0,0,0,0, //vagans
6, 0,0,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5, //appositus
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,0,0,0,0, //fervidus cali
1, 0,0,1,1,0,5,0,5,5,5,3,3,3,3,3,3,3,3,3,3,0,0,0,0, //flavifrons

```

```

5, 0,5,5,5,5,5,5,5,5,5,5,5,5,5,5,0,0,0,0,0,0,0, //nevadensis
5, 0,0,5,5,5,5,3,3,3,3,3,3,3,3,3,5,5,5,5,0,0,0, //ternarius
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6, //terricola occ
5, 0,0,0,0,0,0,5,5,5,5,5,5,5,5,5,5,0,0,0,0,0,0, //pennsylvanicus

unighostsEU[HOSTSEU][ELEMS]= { //host-record colour-pattern elements
//excluding non-unique hosts as comments
//0 X          1          2
//1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4
5, 0,0,5,5,5,5,5,5,0,0,0,0,0,6,6,6,6,6,6,6,6,6, //hortorum
4, 4,4,4,4,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6, //hypnorum
5, 0,0,0,0,0,0,5,5,0,0,0,0,0,0,0,0,6,6,6,6,6,6, //lucorum
4, 4,4,4,4,5,5,4,4,5,5,5,5,5,5,5,5,5,5,5,5,5, //humilis
4, 4,4,4,4,5,5,4,0,4,4,0,0,0,0,4,0,4,4,4,4,4,4, //pascuorum
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3, //pomorum
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3, //pratorum
5, 0,0,5,5,5,5,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6, //jonellus
5, 0,0,5,5,5,5,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6, //argillaceus
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,5,5,5,5, //ruderatus cors
// 4, 4,4,4,4,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6, //hypnorum
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,4,4,4,4,4,4,4,4,4, //terrestris xanth
5, 0,0,0,0,0,5,5,5,0,0,0,0,0,0,0,6,6,6,6,6,6,6, //soroensis
// 5, 0,0,0,0,0,5,5,5,0,0,0,0,0,0,0,6,6,6,6,6,6,6, //soroensis
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3,3, //soroensis prot
0, 0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3,3, //lapidarius
// 0, 0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3,3,3,3,3,3, //lapidarius
5, 0,0,5,5,5,5,5,5,0,0,0,0,0,3,3,3,3,3,3,3,3,3, //lapidarius dec
// 4, 4,4,4,4,5,5,4,0,4,4,0,0,0,4,0,4,4,4,4,4,4,4, //pascuorum
5, 0,0,5,5,5,5,5,5,0,0,0,0,0,4,4,4,4,4,4,4,4,4, //sichelii
5, 0,0,5,5,5,5,5,5,5,5,0,0,5,5,4,4,4,4,4,4,4,4, //sylvarum
// 5, 0,0,5,5,5,5,0,0,0,0,0,0,0,6,6,6,6,6,6,6,6, //jonellus
// 5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,3,3,3,3, //pratorum
5, 0,0,0,0,0,5,5,5,5,5,5,5,5,5,5,0,0,0,0,0,0,0, //terrestris

unighostsNA[HOSTSNA][ELEMS]= { //host-record colour-pattern elements
//0 X          1          2
//1 2 3 4 5 6 7 8 9 0 1 2 3 4 5 6 7 8 9 0 1 2 3 4
5, 0,5,5,5,5,5,4,4,5,5,0,0,0,0,0,0,0,0,0,0,0,0, //affinis
5, 0,0,0,0,0,0,5,5,5,5,5,5,5,5,5,5,0,0,0,0,0,0, //terricola
5, 5,5,5,5,5,5,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0, //impatiens
5, 0,5,5,5,5,5,5,5,5,5,5,0,0,0,0,0,0,0,0,0,0,0, //vagans
6, 0,0,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5,5, //appositus
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,5,5,5,5,5,5,0,0,0, //fervidus cali
1, 0,0,1,1,0,5,0,5,5,5,3,3,3,3,3,3,3,3,3,0,0,0,0, //flavifrons
5, 0,5,5,5,5,5,5,5,5,5,5,5,5,5,5,0,0,0,0,0,0,0, //nevadensis
5, 0,0,5,5,5,5,3,3,3,3,3,3,3,3,3,3,5,5,5,5,0,0,0, //ternarius
5, 0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,0,6,6,6,6,6,6,6, //terricola occ
5, 0,0,0,0,0,5,5,5,5,5,5,5,5,5,5,0,0,0,0,0,0,0, //pennsylvanicus

```

```
FILE *fp_out;
```

```

//open file
if ((fp_out= fopen("simresults.txt", "w+")) == NULL) //clear contents of file
{
printf("file opening error\n");
return EXIT_FAILURE;
}

//get test data
observedEU= 0;
observedNA= 0;
for (j=1; j<=RECORDSEU; j++) // for simulated parasite records
{
for (k=1; k<=ELEMS; k++)
{
m= parasitesEU[j-1][k-1]-allhostsEU[j-1][k-1];
if (m>0)
observedEU += m;
}
}

```

```

        else if (m<0)
            observedEU -= m;
    }
}
for (j=1; j<=RECORDSNA; j++) // for simulated parasite records
{
    for (k=1; k<=ELEMS; k++)
    {
        m= parasitesNA[j-1][k-1]-allhostsNA[j-1][k-1];
        if (m>0)
            observedNA += m;
        else if (m<0)
            observedNA -= m;
    }
}
fprintf(fp_out, " Observed mismatch value EU= %6.2f\n Observed mismatch value NA=
%6.2f\n\n",
        ((float)observedEU/(float)RECORDSEU), ((float)observedNA/(float)RECORDSNA));

//simulation
srand((unsigned)time(NULL)); // seed start of number table
randn= (int)(RAND_MAX/HOSTSEU);
randmax= HOSTSEU*randn; // max acceptable score

for (i=1; i<=SIMULATIONS; i++) // sim 1->9999
{
    result[i]= 0;

    //Europe
    //choose offsets into RECORDS codes (from within tdata[RECORDS])
    for (j=0; j<RECORDSEU; j++)// for each sim cell
    {
        do {
            randn= rand();
        } while (randn>randmax);
        choiceEU[j]= (randn%HOSTSEU); // offsets 0 -> N-1
    }
    for (j=0; j<RECORDSEU; j++) // for simulated parasite records
    {
        for (k=1; k<=ELEMS; k++)
        {
            m= parasitesEU[j][k-1]-uniqhostsEU[choiceEU[j]][k-1];
            if (m>0)
                result[i] += m;
            else if (m<0)
                result[i] -= m;
        }
    }
}

//extract results
gap= SIMULATIONS/2; //Shell binary sort
while (gap > 0)
{
    for (i=1; i<=SIMULATIONS-gap; i++)
    {
        for (j=i; j>=1; j--)
        {
            mark= j+gap;
            if (result[j] > result[mark]) //sort to increasing values
            {
                tempv= result[j];
                result[j]= result[mark];
                result[mark]= tempv;
            }
            else
                j= 0;
        }
    }
}

```

```

    }
    gap /= 2;
}

//write results
fprintf(fp_out, "\n\n Simulation results Europe ####\n\n");
step= SIMULATIONS/1000;
fprintf(fp_out, " percentage points:\n");
for (i=1; i<=SIMULATIONS; i++) // sim 1->100...
{
    if ((i%(100))==0)
    {
        if (i==500)
        {
            j= 1;
            fprintf(fp_out, "%5d (%6.2f): %6.2f\n",
                i, ((double)i/SIMULATIONS), (float)result[i]/(float)(RECORDSEU));
            fprintf(fp_out, ".....\n");
        }
        else if (i==9500)
        {
            fprintf(fp_out, ".....\n");
            fprintf(fp_out, "%5d (%6.2f): %6.2f\n",
                i, ((double)i/SIMULATIONS), (float)result[i]/(float)(RECORDSEU));
        }
        else
            fprintf(fp_out, "%5d (%6.2f): %6.2f\n",
                i, ((double)i/SIMULATIONS), (float)result[i]/(float)(RECORDSEU));
    }
}
fprintf(fp_out, "\n lower tail threshold:\n");
for (i=1; i<=SIMULATIONS; i++) // sim 1->100...
{
    if (i>=1 && i<=600)
    {
        fprintf(fp_out, "%5d (%6.4f): %6.2f\n",
            i, ((double)i/SIMULATIONS), (float)result[i]/(float)(RECORDSEU));
    }
}

////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////////
//simulation
randn= (int)(RAND_MAX/HOSTSNA);
randmax= HOSTSNA*randn; // max acceptable score
for (i=1; i<=SIMULATIONS; i++) // sim 1->9999
{
    result[i]= 0;

    //N America
    for (j=0; j<RECORDSNA; j++)// for each sim cell
    {
        do {
            randn= rand();
        } while (randn>randmax);
        choiceNA[j]= (randn%HOSTSNA); // offsets 0 -> N-1
    }
    for (j=0; j<RECORDSNA; j++) // for simulated parasite records
    {
        for (k=1; k<=ELEMS; k++)
        {
            m= parasitesNA[j][k-1]-uniqhostsNA[choiceNA[j]][k-1];
            if (m>0)
                result[i] += m;
            else if (m<0)
                result[i] -= m;
        }
    }
}
}

```

```

//extract results
gap= SIMULATIONS/2;                               //Shell binary sort
while (gap > 0)
{
    for (i=1; i<=SIMULATIONS-gap; i++)
        {
            for (j=i; j>=1; j--)
                {
                    mark= j+gap;
                    if (result[j] > result[mark]) //sort to increasing values
                        {
                            tempv= result[j];
                            result[j]= result[mark];
                            result[mark]= tempv;
                        }
                    else
                        j= 0;
                }
            gap /= 2;
        }

//write results
fprintf(fp_out, "\n\n Simulation results N America ###\n\n");
step= SIMULATIONS/1000;
fprintf(fp_out, " percentage points:\n");
for (i=1; i<=SIMULATIONS; i++)                    // sim 1->100...
{
    if ((i%(100))==0)
        {
            if (i==500)
                {
                    j= 1;
                    fprintf(fp_out, "%5d (%6.2f):    %6.2f\n",
                        i, ((double)i/SIMULATIONS), (float)result[i]/(float)(RECORDSNA));
                    fprintf(fp_out, ".....\n");
                }
            else if (i==9500)
                {
                    fprintf(fp_out, ".....\n");
                    fprintf(fp_out, "%5d (%6.2f):    %6.2f\n",
                        i, ((double)i/SIMULATIONS), (float)result[i]/(float)(RECORDSNA));
                }
            else
                fprintf(fp_out, "%5d (%6.2f):    %6.2f\n",
                    i, ((double)i/SIMULATIONS), (float)result[i]/(float)(RECORDSNA));
        }
}
fprintf(fp_out, "\n lower tail threshold:\n");
for (i=1; i<=SIMULATIONS; i++)                    // sim 1->100...
{
    if (i>=1 && i<=600)
        {
            fprintf(fp_out, "%5d (%6.4f):    %6.2f\n",
                i, ((double)i/SIMULATIONS), (float)result[i]/(float)(RECORDSNA));
        }
}

//close
fclose(fp_out);
return EXIT_SUCCESS;
}

```