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Proportions of aposematic colouration in bees and wasps (Hymenoptera, Aculeata) and their main mimics – hoverflies, clearwing moths and longhorn beetles

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Abstract

Although bees and wasps are well known as aposematically coloured insects, the role of their aposematic patterns has not been studied to the same extent as other animal and insect groups, i.e., butterflies or beetles. We focused on the fauna of Central Europe, a region with a high diversity of bees and wasps, with more than 1200 species recorded. For each species, we recorded whether aposematic colouration was present as well as which of the main four colouration combinations was present, for both males and females. The same was studied for the three main groups of mimics: clearwing moths, hoverflies, and longhorn beetles. We found that more than 73% of bees and wasps were aposematically coloured, with the black-yellow combination being the most common, recorded in more than half of all aposematically coloured species. The proportions of the main colour combinations varied among the studied groups of bees and wasps. All Chrysididae were metallic. Pompilidae were dominantly black-red, while most Mutillidae exhibited a black-red-white colouration. Parasitic species were more often aposematic (more than 95%) than nesting predators and nesting herbivores were. Regarding the mimics, clearwing moths were nearly all aposematic, and they used Batesian mimicry as their main defence against predators. In contrast, only approximately half of the longhorn beetles were aposematic, whereas the rest of the species used crypsis. All groups of mimics were most commonly coloured black-yellow, but several species in all three groups also possessed the other three colour combinations. Aposematic coloration, along with both Batesian and Müllerian mimicry, functions as a warning signal to vertebrate predators but can also deter insect predators and parasites. However, these interactions remain understudied and deserve further investigation.

Keywords
Anthophila, Apoid wasps, Chrysididae, Cerambycidae, Batesian mimicry, Müllerian mimicry, predators, parasites, Syrphidae, Sesiidae

Introduction

Animal colouration is an important means of communication (Clusella-Trullas and Nielsen 2020; Badejo et al. 2020). Colouration allows animals to transmit signals to each other or adapt to their environment. These animals can use colouration to camouflage themselves in their environment, or to mimic other animals (Caro and Ruxton 2019). There are several types of colouration based on their purpose, including aposematism, mimicry and crypsis. Crypsis, or cryptic colouration, allows a species to blend in with the environment in which it exists. The opposite of cryptic colouration is semantic colouration, which is usually conspicuous and involves contrast of colours (Komárek 2016; Ruxton et al. 2018). Aposematism is probably the most widespread form of semantic colouration. This type of colouration, also referred to as warning colouration, was first defined by Poulton in 1890. Aposematic colouration is associated with species that are unpalatable, toxic, or otherwise dangerous. Most of these species have very distinctive colourations, most often contrasting colours such as black with yellow or red, metallic, or others (Waldbauer 1988; Flegr 2018). Species exhibiting distinctive aposematic characteristics may not be cautious and, as a result, may occupy a new niche that would be disadvantageous for cryptic species (Sherratt 2002). However, these warning signals are not limited to just the visual aspect. There is much evidence for nonvisual aposematic signals as well, which include odour and sound cues (Willadsen 2022).

The term mimicry refers to one animal imitating another animal or the imitation of plants, which is not caused by relatedness but as a convergent adaptation driven by predation pressures (Kirby and Spence 1817; Komárek 2016; Ruxton et al. 2019). Mimics are species that resemble other species, often better-protected ones, and they typically gain advantages from this similarity. Similarity may guarantee protection from predators or reinforce a signal that helps predators learn to avoid such prey. The two most common types of mimicry are Müllerian mimesis and Batesian mimesis. However, the process involves entire mimetic rings that include not only animals that mimic each other and are completely edible but also some that are inedible (Winhard 1996; Chatelain et al. 2023).

Among bees and wasps (Infraorder Aculeata), we often encounter aposematic species due to their weapon – the sting. This group comprises over 70,000 described species, divided into approximately 40 families (Michener 2007; Broad and van Noort 2024). Their colouration is carried by adults of Aculeata but also by some nonstinging groups, such as sawflies, where some larvae also have this conspicuous colouration (Willadsen 2022). The most common aposematic colour combinations include red, orange, or yellow (rarely white) with black. Occasionally, dark brown or blue may substitute for black. These colours can then be combined in various ways. Furthermore, metallic shiny colouring is also considered aposematic (Komárek, 2016; Ruxton et al. 2018). Thus, the main colour types include black-yellow, black-red, black-red-yellow, and metallic colourations. While the first types of colouration are produced by pigments, metallic colouration arises from physical effects within the insect cuticle (Krizek 2011; Ruxton et al. 2018).

The aposematic combinations of bees and wasps are mimicked by other insect species. Some belong to the order Lepidoptera – clearwing moths (Sesiidae), others to Diptera – hoverflies (Syrphidae), or to Coleoptera – longhorn beetles (Cerambycidae). We can also find bee and wasp mimics within these three orders and in other insect or invertebrate groups – Hemiptera, Cicadomorpha and many others (Malcolm 1990; Chatelain et al. 2023).

The black-yellow wasp-like colouring is the most widespread colour and is best known in Hymenoptera. However, there have been no more detailed studies on the distribution of aposematic types in bees and wasps in Europe. The aim of this study was to evaluate the representation of aposematism and individual types of aposematic colouration in bees and wasps, to focus on individual groups according to taxonomy and ecology, and to compare them with the representation of individual types of aposematic colouration in the best-known bee and wasp mimetics – clearwing moths, hoverflies and longhorn beetles. Moreover, we focused on whether there are differences in colouration between males and females in some of the studied species and whether males are as aposematic as expected.

Materials and methods

We studied the colouration patterns in the four main groups. The first was Hymenoptera: Aculeata (bees and wasps), excluding the four families that have different life strategies – Bethylidae, Dryinidae, Embolemidae and Formicidae. We then focused on three main groups of mimics of bees and wasps – Sesiidae (Lepidoptera), Syrphidae (Diptera) and Cerambycidae (Coleoptera). This study focused on the fauna of the Czech Republic, which is rich in these species and a good representative of the European fauna of the studied groups. The lists of species were adopted from Bogusch et al. (2007) and Hejda et al. (2017) for bees and wasps, Macek et al. (2012) for Sesiidae, Reverté et al. (2024) for Syrphidae, and Hrbek (2014) for Cerambycidae. For better understanding, taxonomic names in English are used further in the text – clearwing moths for Sesiidae, hoverflies for Syrphidae and longhorn beetles for Cerambycidae.

We observed the colour of each species via the private collection of the first author, the National Museum in Prague (NMPC), and the main internet photographic resources (iNaturalist, Flickr, Biolib). For each species, we recorded whether they possessed aposematic colouration for males and females separately. The aposematic colouration was divided into four types: 1) black-yellow, including white or creamy white; 2) black-red; 3) black-yellow-red; and 4) metallic colourations. For all colouration types, we recorded both the colouration of the cuticle and hairs (bands of yellow or white hairs on the body were also recorded as aposematic patterns, as was the combination of black and red body colour with white hairy spots or bands). Fig. 1 shows the typical repre-

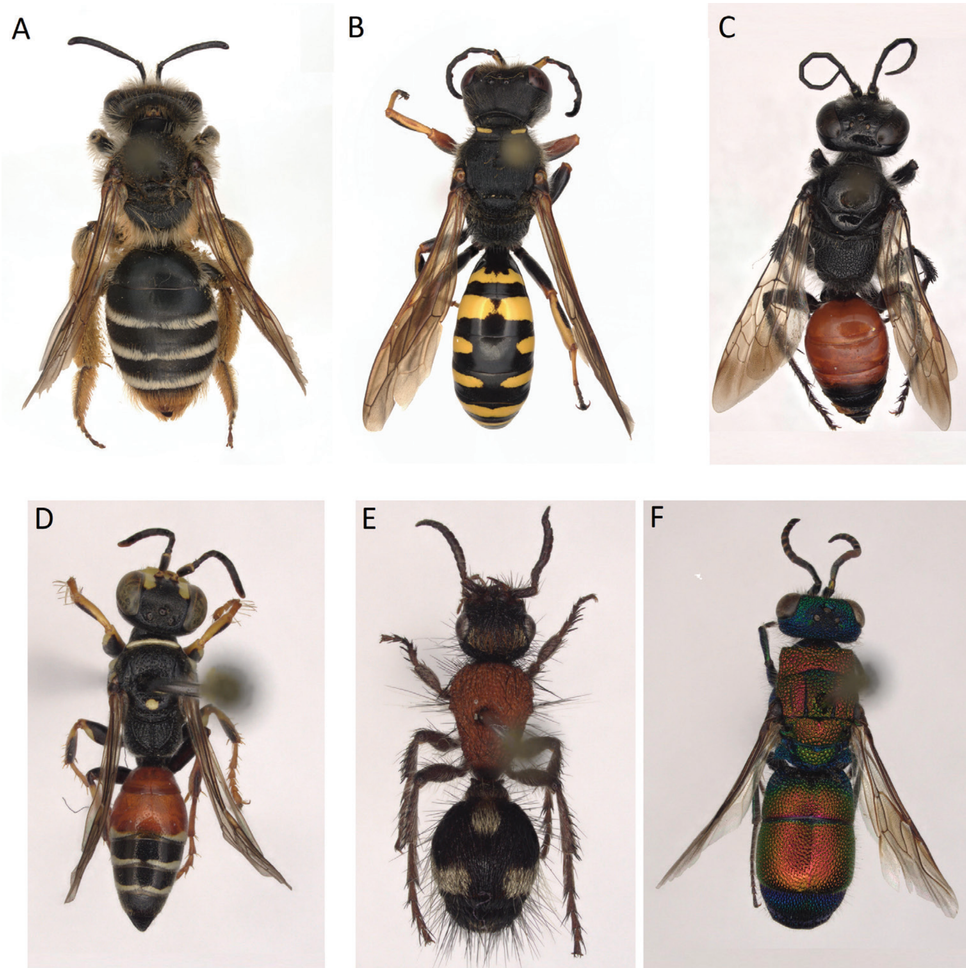

Figure 1. Typical representatives of the main aposematic patterns of bees and wasps. **A** Black-white coloured female of *Andrena chrysopyga* (Apiformes: Andrenidae) with dark brown body and conspicuous whitish bands **B** black-yellow pigment colouration of male of *Ectemnius fossorius* (Apoid wasps: Crabronidae) **C** black-red pigment colouration of female of *Astata boops* (Apoid wasps: Crabronidae) **D** black-yellow-red pigment colouration of male of *Harpactus elegans* (Apoid wasps: Crabronidae) **E** black-red pigment colouration with whitish hairy spots of female of *Dasylabris maura* (Vespoidea: Mutillidae) **F** metallic colouration of male of *Chrysis viridula* (Chrysidoidea: Chrysididae). Photos by Petr Bogusch.

sentatives of each colour pattern. For all groups, we evaluated the proportion of species with aposematic colouration (in %) and the proportions of the four studied types of aposematic colouration (in %). Furthermore, we did the same for bees and wasps, which were divided according to their phylogeny with the excetion for bees which was evaluated independently (Chrysidoidea, Vespoidea, Apoid wasps and Anthophila) and then according to their foraging strategies (nesting predators, nesting herbivores and parasitic species). We adopted information on the taxonomy and foraging strategies from Macek et al. (2017); Bogusch and Horák (2018) and Bogusch et al. (2020). If the males and females were coloured differently, we recorded ½ of each colouration in the dataset.

For the presentation of the results, we used column graphs prepared in SigmaPlot 11.0. Differences in colouration between males and females in some of the species studied are discussed only in a specific part of the Results section. Photographs of representative specimens were done using the photographing microscope Keyence VHX-100.

Results

A total of 1,221 species of bees and wasps were included in the analyses. Among these species, 900 had aposematic colouration, which corresponds to 73.83%. All 424 species of hoverflies found in the Czech Republic were studied, and 322 species presented aposematic colouration. Among the 205 species of longhorn beetles found in the Czech Republic, 104 had aposematic colouration, and of the 43 species of clearwing moths, 36 had aposematic colouration (Fig. 2a).

The representation of the different types of aposematic colouration varies across the different groups (Fig. 2b). In all four groups studied, black-yellow colouration was strongly predominant, being most common in hoverflies (271 species; 84%) and least common in longhorn beetles (185 species; 51%). The representations of the other colouration types were less prominent, between 5% and 20%. Black-red colouration was the most common in longhorn beetles (24 species; 23%) and least common in hoverflies (26 species; 8%). Metallic colouration was also most common in longhorn beetles (23 species; 22%).

However, the representation of the different types of aposematic colouration varies considerably across the different groups of bees and wasps, e.g., in the family Pompilidae, black-red colouration was strongly represented, whereas in the family Chrysididae, 100% of the species were metallic. On the other hand, black-yellow colouration was significantly more prevalent in the family Vespidae, whereas black-yellow-red colouration was more prevalent in the family Mutillidae. Within each group, the representation of aposematics also varies. While the family Chrysididae includes only aposematic representatives with metallic colouration, the representation of aposematic species was only slightly above half that of Apoid wasps (Apoidea without bees) (165 out of 281 species, i.e., 58%). In bees (Anthophila), the representation of aposematically coloured species was greater (433 species; 71%), but in nonparasitic bee species, black-yellow colouration was strongly predominant, with yellow, or mostly white, colour most often produced by hair bands or spots on the body (Fig. 2c).

The different types of aposematic colouration were represented differently in the main groups. While all cuckoo wasps (Chrysididae) are metallic, there was no other type of colouration. This type of colouration was absent in the superfamily Vespoidea and in Apoid wasps but was least common in bees. In all three groups, black-yellow colouration was the most common colouration, accounting for 69% (92 species) of the bees, whereas black-red colouration was also frequent in the superfamily Vespoidea (78 species; 40%). The proportions of each type of aposematic colouration in each taxonomic group are shown in Fig. 2d.

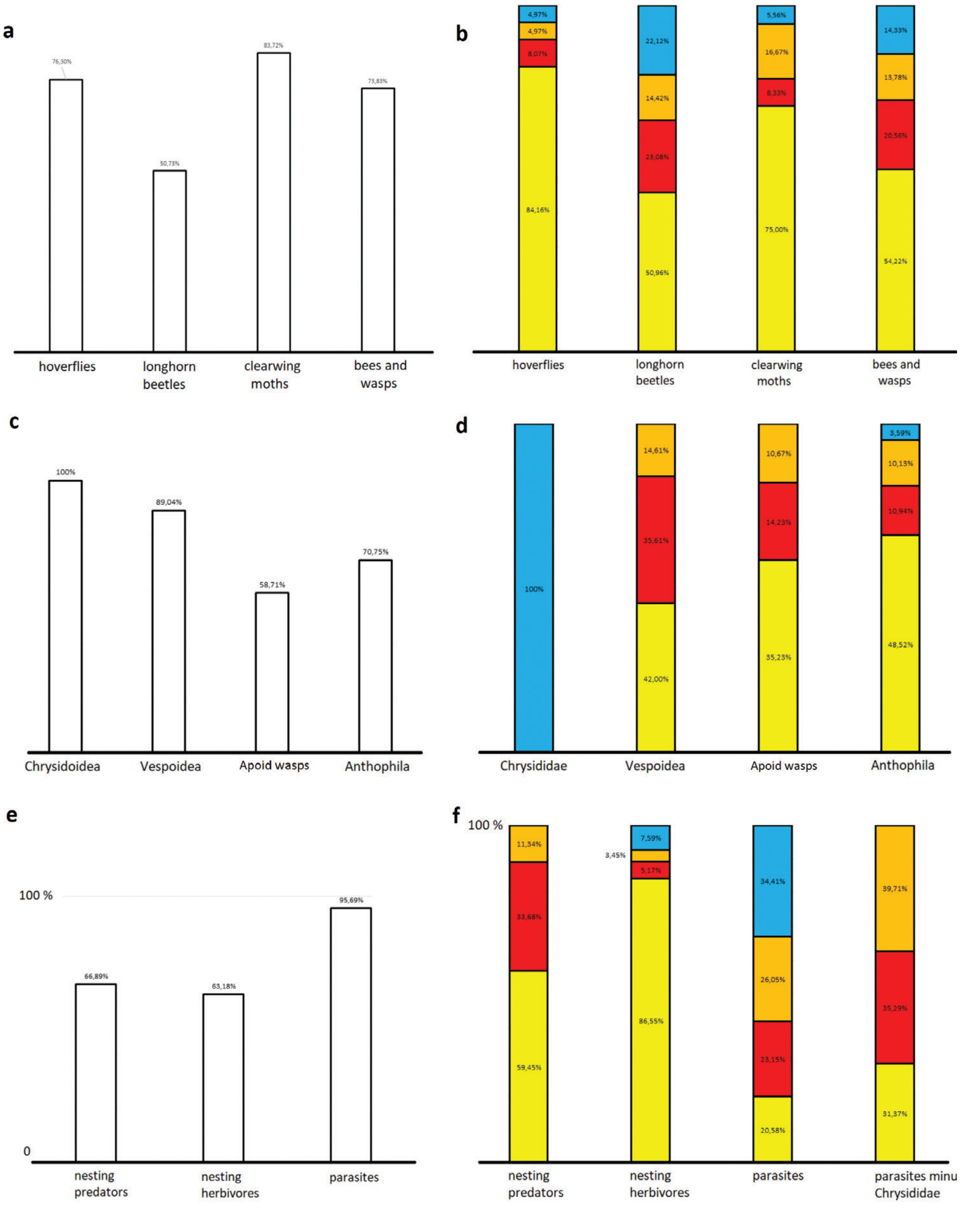

Figure 2. Proportions of **a** aposematically coloured species (in %) among bees and wasps and three main groups of their mimics – clearwing moths, hoverflies and longhorn beetles **b** main four types of aposematic colour combinations (in %) among bees and wasps and three main groups of their mimics – clearwing moths, hoverflies and longhorn beetles **c** aposematically coloured species (in %) in the four main taxonomic groups of bees and wasps **d** main four types of aposematic colour combinations (in %) in the four main taxonomic groups of bees and wasps **e** aposematically coloured species (in %) in the three main foraging groups of bees and wasps **f** main four types of aposematic colour combinations (in %) in the four main foraging groups of bees and wasps. Yellow colour represents black-yellow, red colour black-red, orange colour black-yellow-red and blue colour metallic colouration.

The distribution of aposematic colouration according to feeding strategy was interesting. While nesting predators and herbivores had similar proportions of aposematically coloured representatives, over 60% of parasitic species used aposematic signals frequently, and 96% of these species had aposematically coloured representations (Fig. 2e).

Different types of aposematic colouration were represented differently: while almost 87% of the species in breeding herbivore species were coloured black-yellow, in parasitic representatives, this type of colouration comprised only 21% of all species and was the least frequent colouration type. Among parasites, metallic colouration was the most common (34%), but this was due to cuckoo wasps. If this family was removed from the analysis, metallic colouration was not present in the other parasitic species, and all three other colouration types were roughly equally common (values between 32% and 40%) (Fig. 2f).

Differences in colouration of males and females of the same species

In bees and wasps, males and females were differently coloured in 67 species, or 5.49% of all the species studied. The most frequent situation was when both sexes were black and the female had white hair bands, whereas in the male, they were absent or less pronounced (several species of the genera *Andrena* and *Eucera*). Much more interesting was the difference in the cuckoo bees *Ammobatoides abdominalis* and *Epeoloides coecutiens*, where the male was cryptically coloured, whereas the female was aposematic (in both cases the colouration included black and red with white bands or spots). The same was observed in Mutillidae, e.g., *Dasylabris regalis*, *Myrmosa atra* and *Paramyrmosa brunnipes*, where the females were black and red (with white hairs in the first species), whereas the males were solid black. In this group, the difference in colouration between the sexes was undoubtedly related to their different lifestyles; females were wingless and males had wings. The situation was similar in several Pompilidae, e.g., in the species *Agenioideus cinctellus*, *Myrmecodipogon pannonicus*, *Poecilagenia rubricans* and *Telostegus inermis*, the females were aposematic, whereas the males were black. The same colour was also found in the cuckoo bee *Sphecodes niger*, and many other males of this genus had only a small portion of red colouration, in contrast to the coloured females. In some other species, pigmented black-yellow-red colouration was present in females, but the red colouration was absent in males (*Alysson spinosus*, *Nysson dimidiatus*), as was also the case in *Sapyga quinquepunctata* and *S. similis*. Contrary, in some species, females were less aposematic than the males were usually red-black or rusty brown, e.g., in the smaller species of the genus *Nomada* or in species of the genus *Meria*.

However, it should be noted that in the species *Dinetus pictus*, the female was markedly different in colour than the male was, but it included a combination of the same or similar colours.

However, there were also species that showed some colour variation, e.g., in some species of the genus *Andrena* (*A. hattorfiana*, *A. trimmerana*), both females and males may have red terga but they also may not. In some species with black-yellow-red colouration, females were always coloured, but in males, the red colouration was often

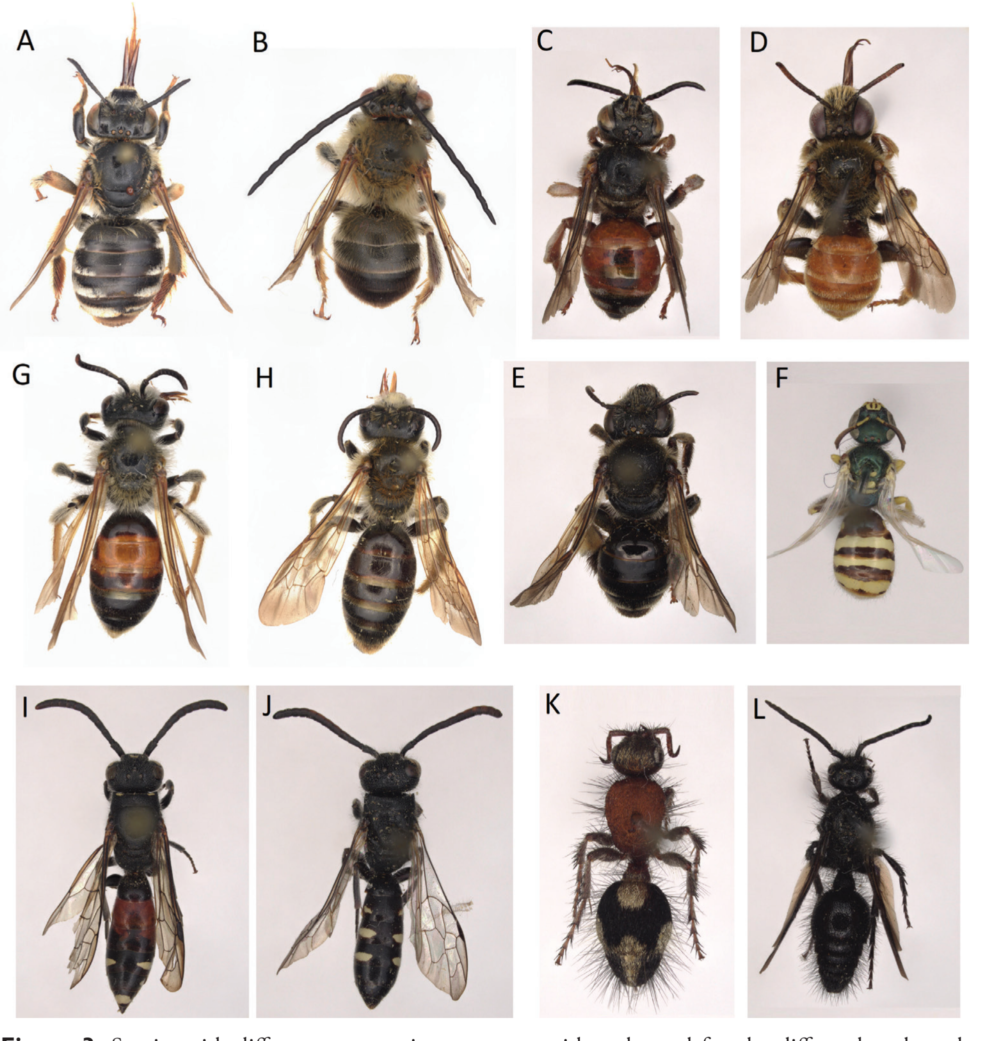

Figure 3. Species with different aposematic patterns or with males and females differently coloured. *Eucera interrupta* **A** female with conspicuous whitish metasomal bands **B** male with these bands missing; *Epeoloides coecutiens* **C** female with aposematic black-white-red colouration **D** non-aposematic male **E** *Macropis europaea* is the host of *E. coecutiens* and the female of the parasite is very similar to the female of the host except the red colouration of the metasoma **F** *Nomioides minutissimus* with combination of black-yellow and metallic colouration; *Andrena hattorfiana* **G** male with reddish colouration on metasoma **H** male without reddish colouration on metasoma; *Sapyga quinquepunctata* **I** female with part of metasoma reddish **J** male with only yellow and black colours; *Dasylabris regalis* **K** female with black-white-red colouration **L** completely black male. Photos by Petr Bogusch.

absent (e.g., in species of *Nysson distinguendus* or *N. maculosus*). A final interesting feature was the combination of several types of aposematic colouration, most often black-yellow or black-red with metallic colouration (e.g., in some cuckoo wasps of the genus *Hedychridium* or in bees of the genera *Nomioides*, *Lasioglossum* and *Seladonia*). Several of above discussed species are on Fig. 3.

For the mimetic groups, males were different in colour than females were among the 41 species. Males were different in colour than females were among the 26 species of hoverflies. However, these differences were minor – mostly the absence of yellow or red markings in males, which develop as small spots or bands in females. In eight species of longhorn beetles, there were differences in colour between females and males. In most of them, males were cryptically coloured, and females were aposematically coloured, e.g., in the species *Anisorus quercus*, *Pachyta almed* or *Stenopterus ater*. In the species *Tetropium castaneum*, the difference between males and females was the opposite. In the *Oxymirus cursor*, the male was black, and the female was metallic in colour. In clearwing moths, there were no differences in the colouration of males and females, but in the two species, there was a combination of two types of aposematic colouration, namely, *Synanthedon culiciformis*, with black-red but also metallic colouration, and *S. cephiformis*, with a combination of black-yellow and metallic colouration.

Discussion

Aposematic colouration associated with sting defence is quite abundant in the group of bees and wasps; over 73% of Central European species show conspicuous types of colouration in the main aposematic combinations. Moreover, in the vast majority of species, males are coloured in the same way as females are, although very often, the colouration in males is less conspicuous and contrasting. Thus, it can be concluded that in this group, both the aposematics – the common and conceived species in nature – and their Müllerian mimetics, which are probably the majority of species, as previously reported by Willandsen (2022); Chatelain et al. (2023) and other studies cited in these larger reviews. Aposematic colouration is understood primarily to signal vertebrate predators (Stevens and Ruxton 2012; Summers et al. 2015; Willandsen 2022).

Among the most common mimetics, the representation of aposematic colouration varies. Almost all clearwing moths are aposematic, indicating that this group has relied on Batesian mimicry as their main strategy of defence against predators, which also corresponds with the results of Skowron Volponi et al. (2022). The proportion of mimetics is greater than 70% in hoverflies; however, the remaining species are also mimetics but they mimic nonaposematically coloured species of bees (Leavey et al. 2021). Interestingly, approximately half of the species of longhorn beetles have aposematic colouration, whereas the remaining species are cryptically coloured and rely on a different type of defence against predators (Linsley 1959).

Among all the groups studied, the most common combination was black-yellow; this is mainly related to the fact that the largest proportion of aposematic wasps are black-yellow, and they include those most widespread in the landscape in terms of abundance, such as social wasps (genus *Vespula* and related wasps) (Macek et al. 2010; Boppré et al. 2016). Other colouration types are less abundant, except in certain groups, e.g., many species of cuckoo bees and spider wasps are black-red in colour. Black-red colouration is sporadically represented in all three studied groups of mimetics, and species with this colour combination probably resemble the most widespread black-red bees and wasps in their habitats. In contrast, the cuckoo wasps are all metallic in colour, and few mimetics with metallic body colouration are found among the longhorn beetles, clearwing moths and hoverflies. Interestingly, a number of species or groups present not only morphological or colour mimicry but also behavioural mimicry. The longhorn beetle *Plagionotus arcuatus* has the same colour combination as wasps, which it demonstrably mimics, but the striking similarity is only observed when these beetles move. Similarly, several clearwing moths mimic the flight and buzzing patterns of their models in addition to their colouration. Sometimes, the combination of behavioural and morphological mimicry is of such high quality that the species presents virtually identical to its model when moving in their habitat. The hoverfly *Eumerus tricolor*, which mimics cuckoo bees of the genus *Sphecodes*, is a good example of this (Bogusch 2015).

Thus, mimetic associations (Joron 2009; Chatelain et al. 2023), consisting of the most abundant aposematics and their Müllerian mimetics, operate in the world of bees and wasps. These associations are supplemented by Batesian mimics clearwing moths, hoverflies and longhorn beetles (Willandsen 2022) and are composed of different species in different habitats and areas (e.g., Hlaváček et al. 2023). Unfortunately, very little is known about the role of chemical signals in bees and wasps. In a number of species or groups, they seem to play a significant role, and it is possible that most mimicry and aposematic colouration are signals to predators and not to the parasites, with which their hosts probably communicate in a chemical way (Willandsen 2022; Chatelain et al. 2023); this is related to the high proportion of aposematically coloured parasitic species. Their colour (often in a black and red combination) is more of a signal to predators than to their hosts, which do not see the red colour (Chittka and Waser 1997). The presence of aposematism in parasitic species may be related to the simple fact that parasites do not hide in nests and are more likely to be present, so aposematic colouration may help them fight against predators. However, sometimes the females of parasitic bees or wasps have been observed to bear a striking resemblance to their host after the red colour is removed (the case of the cuckoo bee *Epeoloides coecutiens* and its hosts of the genus *Macropis*, Bogusch (2006)). Moreover, chemical communication has been demonstrated only in aposematically coloured cuckoo bees of the genus *Nomada*, in which males perfume females with a volatile chemical that is identical to the main communicating substance of their host (Tengö and Bergström 1978). Unfortunately, subsequent studies have not yielded any interesting results, although it is highly likely that similar cases are much more common.

Some authors have suggested that aposematic colouration may not be strictly related to aposematism, but rather it may be a tool for thermoregulation (summarized in detail by, e.g., Chatelain et al. 2023); this may be related to the ability to genetically influence the proportion of light and dark colours, e.g., yellow and black. As a result, the same species in northern Europe has a greater proportion of dark colour, whereas in southern Europe, it has almost 100% light colour (Hines et al. 2017). In other cases, dimorphism is presented, with darker-coloured individuals being more common in colder regions than lighter-coloured individuals (e.g., *Andrena hattorfiana*, *A. trimmerana*, *A. rosae*). In this case, it may be the result of a trade-off, where the species must "decide" whether to choose between defence against predators or a longer activity period that could enhance its overall fitness.

Thus, in Central Europe, almost ¾ of bees and wasps are aposematically coloured. Since most species inhabit similar habitats, breed in the same places, and often share microhabitats, adopting three colour schemes (along with one that combines two of them) can be a very advantageous adaptation for many species. In particular, those species that form weaker populations and are Müllerian mimetics of numerous species, often benefit greatly from this situation (Sherratt 2008; Willandsen 2022). The nature, significance, and efficacy of these signals for vertebrate predators have been studied in considerable detail, although much less frequently than, for example, mimicry and aposematism in diurnal butterflies (Komarek 2009; Willandsen 2022; Chatelain et al. 2023). Experiments with juvenile birds and aposematically coloured insects in particular provide a good indication of the function of this colouration (e.g., Svádová et al. 2009). However, some signals suggest that they may also function between parasitoids, brood kleptoparasites and their hosts (Rupp 1989; Edmunds and Reader 2014), which represents an unexplored research topic for the future.

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Supplementary material 1

List of all species with the description of their colouration

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Data type: xlsx

Explanation note: In column aposematism, Y – yes, N – no; in other columns, the main aposematic patterns are abbreviated: B/Y – black and yellow, B/R – black and red, B/Y/R – black and yellow and red, M – metallic.

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