Morphological, colour and behavioural mimicry of cuckoo bees by the hoverfly *Eumerus tricolor* (Fabricius) (Diptera: Syrphidae)

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The hoverfly *Eumerus tricolor* is morphologically very similar to the females of cuckoo bees of the genus *Sphecodes* Latreille. This hoverfly was observed in two localities in central (Čertoryje NNR, Czech Republic) and southern (Kladhas, Greece) Europe together with females of these cuckoo bees at nest sites of the bee hosts (*Lasioglossum* Curtis) of the cuckoo bees. Females of *E. tricolor* were sitting on the ground, slowly flying low over the ground and walking on the nesting site. This can be interpreted as Batesian mimicry of *Sphecodes*. This Eumerus species is the only European hoverfly of this genus with a very similar colour pattern to *Sphecodes*, and it also prefers the warm and sunny slopes and/or rocky steppes where *Sphecodes* are abundant. Within red-and-black hoverflies, *E. tricolor* is the only species showing this behaviour. It thus uses not only morphological but also behavioural mimicry.

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1. Introduction

Similarity in morphology and colouration between two unrelated insects represents a very common natural phenomenon, usually being explained as some form of mimicry. Although mimicry was first described in butterflies (Kirby & Spence 1817), which have been intensively studied, more recent work shows that it is more common in dipterans and hymenopterans (Maier 1978, Howarth *et al.* 2000, 2004, Easley & Hassall 2014), and especially in the hoverflies (Syrphidae), a well-known group of Diptera resembling many species of bees, wasps and related aculeate Hymenoptera (Howarth *et al.* 2000, 2004, Rashed & Sherratt 2007, Easley & Hassall 2014). Within this family there are well-known mimics of bumblebees (*Volucella bombylans* (Linnaeus), see Rupp 1989, Edmunds & Reader 2014), social wasps and hornets (*V. inanis* (Linnaeus), *V. zonaria* (Poda), species of *Eupeodes* Osten Sacken, *Helophilus* Meigen and other genera: see Howarth *et al.* 2000) and bees (especially members of the genus *Eristalis* Latreille: see Golding & Edmunds 2000, Golding *et al.* 2001), as well as other species with poorly studied mimicry (Howarth *et al.* 2000). In their resemblance to stinging Hymenoptera, hoverflies are usually thought of as Batesian mimics, palatable species without any protection. Their mimicry is very of-

Fig. 1. Female of the mimetic species, *Eumerus tricolor*. Photo by Cor Zonneveld.

ten not only in general appearance (colouration and morphology) but also in behaviour (e.g. flying style), and in some cases chemical mimicry has also been proven (Rupp 1989). Rashed *et al.* (2009) studied the sound produced by syrphid mimics and its similarity to that of the hymenopteran models, but sound mimicry was not proven.

Red and black colouration is very rare in hoverflies, when compared to wasp-like black-yellowish bands and bee-like brownish colouration. Within 59 species of Syrphidae marked as mimics of aculeate Hymenoptera (Howarth *et al.* 2000), only two were described as possible mimics of cuckoo bees of the genus *Sphecodes* Latreille: *Platycheirus granditarsus* (Forster) of *S. spinulosus* Hagens (together with other reddish-coloured bees *Nomada fabriciana* (Kirby), *Andrena labiata* (Fabricius) and *A. marginata* (Fabricius)), and *Rhingia campestris* Meigen of *S. gibbus* (Linnaeus) (and *Andrena marginata*). Another species with red markings, *Brachypalpoides lentus* (Meigen), was linked with the red-and-black digger wasp *Astata boops* (Schrank). It is interesting that some other species of hoverflies also possess red-and-black colouration, but no mimetic associations have been suggested, e.g. the aphidophagous *Paragus bicolor* (Fabricius) (Stubbs & Falk 2002).

Similar colouration is very common among aculeate Hymenoptera and also other groups of this order. Bogusch (2006) recorded that 62% of European cuckoo bees have red colour on their body, with red being the dominant colour in 24%. In some families a red-and-black pattern dominates, e.g. in spider wasps (Pompilidae), where nearly all species of the most numerous genera (*Arachnospila* Kincaid, *Priocnemis* Schiödte and *Evagetes* Lepeletier) are black with a reddish base to the abdomen. In addition, many digger wasps (Crabronidae, e.g. *Tachysphex* Kohl, *Miscophus* Jurine, *Mimesa* Shuckard, *Didineis* Wesmael and many others, and Sphecidae, e.g. *Ammophila* Kirby, *Sphex* Linnaeus) are red and black (Macek *et al.* 2010). An explanation of this colour pattern has not been suggested, but in many groups it is probably an aposematic signal for predators (Bogusch 2006), as in red-and-black bugs (Heteroptera: *Pyrrhocoris apterus* (Linnaeus), *Spilostethus saxatilis* (Scopoli), *Graphosoma lineatum* (Linnaeus) and many other species) and some groups of beetles (Coleoptera: Pyrochroidae, Lycidae). Male Hymenoptera do not have a sting, and so they cannot be evaluated as aposematic, but in some cases the male pattern slightly or strongly differs from that of females (O'Neill 2001, Michener 2007, Macek *et al.* 2010). It is also interesting that among bees

Fig. 2. Female of the model, a *Sphecodes* species. Photo by Cor Zonneveld.

(Apiformes), red and black colouration is quite rare, present mostly in some groups of cuckoo bees (*Ammobates* Latreille, *Sphecodes*). The most likely explanation is that cuckoo bees do not nest and hence spend much more time exposed in their habitat, so aposematism is more important for them than for their nesting hosts (Bogusch 2006).

Cuckoo bees represent about 25% of all European bees (Bogusch 2003), and about 15% of all bees worldwide (Batra 1984, Michener 2007). Females lay their eggs into the nests of other bees, usually putting the egg directly into the brood cell, where their larvae feed on the pollen, nectar or oil resources collected for the brood of the host bee. The genus *Sphecodes* has about 30 species in central Europe, and more than 40 species in Europe as a whole; their colour pattern is uniformly red and black (Bogusch & Straka 2012). They are usually nest cleptoparasites of the bee genera *Halictus* Latreille and *Lasioglossum* Curtis, but some species have switched to other genera such as *Andrena* Fabricius and *Colletes* Latreille (Habermannová *et al.* 2013). Within *Sphecodes* there are specialists with only one known host, as well as generalists with more than ten known hosts (Bogusch *et al.* 2006, Bogusch & Straka 2012, Astafurova & Proshchalykin 2014). Some species are common and obvious components of their ecosystems, usually using their searching flight (slow and low over the ground) to find nest sites, or walking on the ground and entering the nests of their hosts.

This article describes the hoverfly *Eumerus tricolor*, its coloration (which is very similar to that of *Sphecodes* cuckoo bees, Figs. 1 and 2), and its co-occurrence with and similar behaviour to ovipositing female of *Sphecodes*. Discussion of Batesian mimicry of *Eumerus tricolor* is included.

2. Materials and methods

The results of this study were obtained during studies on the cuckoo bees at *Lasioglossum* nests. The author observed ovipositing female *Sphecodes* invading host nests, but also female hoverflies at the nest site. The same behaviour of *Eumerus tricolor* was observed independently twice in relation to different *Sphecodes* species at the nest sites of different *Lasioglossum* hosts; the behaviour is not exceptional, but the normal behaviour of *Eumerus tricolor*. Female hoverflies

were observed together with female *Sphecodes* between 10 a.m. to 3 p.m. The weather was sunny at both localities, around 28 °C, with mild wind.

Localities and material of *Eumerus tricolor* collected:

1) Greece, Peloponnese Peninsula, Kladhas env. (4 km NE of Sparti), 37.121611° N, 22.447404° E, 160–245 m a. s. l., 8.–10.IV. 2005, 1 ♂, 4 ♀♀, P. Bogusch & J. Skuhrovec leg., R. Rozkošný det., coll. P. Bogusch;
2) the Czech Republic, Moravia, Bílé Karpaty Protected Landscape Area, Radějov env., Čertoryje National Nature Reserve, 48.856952° N, 17.407278° E, around 370 m a. s. l., 12.VI.2015, 2 ♀♀, P. Bogusch leg., det. et coll.

The author determined the bees and *Eumerus tricolor* from the Czech Republic and the nomenclature follows Macek *et al.* (2010) and Bogusch and Straka (2012). Rudolf Rozkošný (Brno, the Czech Republic) determined the material of *E. tricolor* from Greece and provided information about its biology. All the material is in the collection of the author (P. Bogusch, Hradec Králové). The photos were taken during the fieldwork of the author.

3. Results

During the field studies on cuckoo bees in Greece, I observed female *Sphecodes gibbus* and *S. monilicornis* (Kirby) entering nests of two host species, *Lasioglossum malachurum* (Kirby) and *L. marginatum* (Brulle). The nests of both eusocial host bees were on a sandy path reaching from the road connecting the villages of Kladhas and Voutiani in the southern part of the Peloponessos Peninsula, Greece to the river Eurotas at the bottom of the valley. The path leads from the hill to the valley, and is surrounded by Mediterranean steppe habitat, with various plants in flower and many insects, especially gold beetles (Cetoninae), butterflies, bumblebees (*Bombus* Latreille) and carpenter bees (*Xylocopa* Latreille). The nests of the host bees were usually aggregated at some parts of the path, with greatest numbers when the path was wide. I counted 1–18 nests per m^2, meaning that the populations can be evaluated to be dense. There were also nests of smaller bees (small *Lasioglossum*) and digger wasps in large numbers, but neither the *Sphecodes* females nor the females of *E. tricolor* showed any interest in them.

Female *Sphecodes* were entering host nests while individual *Eumerus tricolor* females were sitting on the path, sometimes slowly flying low above the surface of the ground or walking on the soil near the nest entrances. No contacts among hoverflies, cuckoo and eusocial bees were observed. Although female *Sphecodes* frequently entered host nests, female *E. tricolor* did not enter any nest during the 3-day observation. In all other respects their behaviour and general appearance was nearly the same as in female *Sphecodes*, and were very hard to distinguish, especially when they were flying: they were repeatedly accidentally captured in an entomological net.

The same behaviour of female *Eumerus tricolor* was observed in the Czech Republic in the Bílé Karpaty Protected Landscape Area, Čertoryje National Natural Reserve. Hoverfly females were sitting on the ground near a nest aggregation of *L. malachurum*, where female *S. monilicornis* were entering nests. They were also sometimes flying low over the ground and walking around the nests. No aggression or other kinds of communication between *E. tricolor*, *Sphecodes* and *Lasioglossum* were observed.

4. Discussion and conclusions

Even though many aculeate Hymenoptera are armed with a sting, the number of recorded mimics of most of them is surprisingly low. This is not a result of the real situation in natural biotopes, but more the fact that they have not been studied very much. Accordingly, we know quite a bit about the mimics of hornets, wasps, bumblebees, honeybees and ants, but very little about those of other groups of aculeates (Maier 1978, Howarth *et al.* 2000, Penney *et al.* 2012, 2014, Easley & Hassall 2014). Only one comprehensive study has been done, but this was based only on general appearance (Howarth *et al.* 2000). Some other studies describe relationships within one mimetic

complex (Láska & Bičík 1997). Mimicry is usually multimodal, combining aspects of morphology, colour, behaviour, and in some cases chemistry and sound (Golding & Edmunds 2000). Thus, we can expect that there are plenty of hoverfly species that use mimicry as a protection against various groups of predators. There are also other taxa with general resemblance to bees and wasps, especially particular species of sawflies (Tenthredinidae) and other Symphyta, but not much is known about such mimicry, and most of what is known was published only as short notes within wider taxonomic studies (Haris 2006, Saini & Ahmad 2012).

Thus mimicry of red-and-black aculeate Hymenoptera has not very often been described, compared with that of bumblebees, wasps, honeybees, ants, etc. However, resembling a cuckoo bee is a good strategy because cuckoo-bee females spend most of their life outside because they do not have their own nest, and thus predators meet them more often than nesting species. In addition, they have a powerful sting with strong venom for fighting with the host, which in some species is quite frequent. It is also very interesting that cuckoo bees often have a reddish colouration on their body: in Europe, 62% of cuckoo bee species have a red pattern, while less than 3% of non-parasitic bees have it (Bogusch 2006). Thus, I suggest that the reddish coloration has the same aposematic meaning as in true bugs or some beetles (Pyrochroidae, Lycidae). *Eumerus tricolor* should be classified as a Batesian mimic of an aposematic species, *Sphecodes* females.

Eumerus tricolor is a phytophagous hoverfly, whose larva feeds in stems of *Tragopogon porrifolius* L. (Asteraceae) (Roeder 1990) and probably some other related plants. Adults feed on nectar from various plants, usually of Asteraceae, Apiaceae and Dipsacaceae. There is no specific association of the kind seen in *Volucella* hoverflies whose larvae are parasitoids or commensals in the nests of eusocial bumblebees and wasps (Rupp 1989). *Eumerus tricolor* differs markedly in colouration from other members of this genus, where most species are black or brownish, sometimes with pale leg and/or facial marks (Stubbs & Falk 2002): of all 58 European species, it is the only one with a conspicuous red-and-black color pattern (Lindner 1969, Stubbs & Falk 2002). It has the same colour pattern and size as female *Sphecodes*, being about 7–9 mm long, black with the upper part of the abdomen reddish, the head and mesonotum black, the legs almost black except the knee whitish, and the wings with a slight infuscation similar to *Sphecodes*.

There are other species of hoverflies with similar coloration to *E. tricolor*, but none has been observed in contact with the models at localities or nesting sites of the hosts of the models. Howarth *et al.* (2000) described other mimics of cuckoo bees: *Anasimyia contracta* Claussen and Torp was suggested to resemble *Epeolus* Latreille cuckoo bees, and *A. lineata* (Fabricius) and *Lejops vittata* (Meigen) were said to resemble *Coelioxys* Latreille cuckoo bees. Both genera are very conspicuous cuckoo bees, and *Epeolus* are also aposematic and have a strong sting for fighting with their *Colletes* hosts (Bogusch 2003). However, Howarth *et al.* (2000) do not describe how these mimetic complexes work in general.

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