Widespread Occurrence of Black-Orange-Black Color Pattern in Hymenoptera

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Subject Editor: Phyllis Weintraub

Received 19 October 2018; Editorial decision 3 February 2019

Abstract

Certain color patterns in insects show convergent evolution reflecting potentially important biological functions, for example, aposematism and mimicry. This phenomenon has been most frequently documented in Lepidoptera and Coleoptera, but has been less well investigated in Hymenoptera. It has long been recognized that many hymenopterans, especially scelionids (Platygastridae), show a recurring pattern of black head, orange/red mesosoma, and black metasoma (BOB coloration). However, the taxonomic distribution of this striking color pattern has never been documented across the entire order. The main objective of our research was to provide a preliminary tabulation of this color pattern in Hymenoptera, through examination of museum specimens and relevant literature. We included 11 variations of the typical BOB color pattern but did not include all possible variations. These color patterns were found in species belonging to 23 families of Hymenoptera, and was most frequently observed in scelionids, evaniids, and mutillids, but was relatively infrequent in Cynipoids, Diaprioids, Chalcidoïds, and Apoids. The widespread occurrence of this color pattern in Hymenoptera strongly suggests convergent evolution and a potentially important function. The BOB color pattern was found in species from all biogeographic regions and within a species it was usually present in both sexes (with a few notable exceptions). In better studied tropical regions, such as Costa Rica, this color pattern was more common in species occurring at lower elevations (below 2,000 m). The biology of the tabulated taxa encompasses both ecto- and endoparasitoids, idiobionts and koinobionts, from a diversity of hosts, as well as phytophagous sawflies.

Key words: aposematism, Braconidae, Evaniidae, Ichneumonidae, Platygastridae, Scelioninae
Materials and Methods

This investigation was primarily restricted to hymenopteran specimens within the general size range of scelionids showing BOB coloration, approximately 3–20 mm in body length. Thus, some groups (e.g., Ceraphronoidea, Aphelinidae, Encyrtidae, Mymaridae) were excluded as being too small while others (many aculeates) were excluded as being too large. However, within the focal size range, all hymenopteran specimens were examined, independently of whether the taxa were previously known to include species with BOB colorations. R.M. examined ca. 418,000 hymenopteran specimens in the collections of the Museo Nacional de Costa Rica (MNCR, formerly the Instituto Nacional de Biodiversidad) from August to December 2015, and ca. 783,000 specimens in the Canadian National Collection of Insects, Arachnids and Nematodes (CNC) in Ottawa from August to December 2016. P.E.H. examined ca. 81,000 hymenopteran specimens in the Museo de Zoología at the Universidad de Costa Rica (MZUCR) from 2016 to 2017, and reviewed the relevant taxonomic literature to supplement museum records since the majority of microhymenopteran specimens in museums are not identified to species level.

Observations were made with various stereomicroscopes using magnifications ranging from 10x to 30x. Color patterns were recorded in dorsal view since the pattern often differed in lateral view. Even when restricting the observations to dorsal view, there was considerable variation. Eleven of the observed variations of the BOB pattern were used for coding the included species (Fig. 1). We did not include tricolored patterns that deviated from head black, mesosoma at least partially orange, and metasoma mostly black. Bicolored patterns were also excluded, for example, orange head and mesosoma, with black metasoma, or black head and mesosoma with orange metasoma. However, the diversity of black-orange patterns of all the observed specimens was documented.

For each species showing BOB coloration we recorded the exact morphological location of the black and orange colors (as coded in Fig. 1), the geographic distribution of the species and the source of these data (acronyms for museums mentioned above and literature references). Unidentified species were only included for genera where there were no identified species showing BOB coloration. For higher level classification of Hymenoptera, we follow Branstetter et al. (2017) and Peters et al. (2017).

A chi-square test was used to evaluate the distribution of color (orange and black, vs all black) with respect to altitude (greater than 2,000 m and less than 2,000 m). Using a contingency table, the number of insects found within each combination was counted. Then a comparison of the expected value of each combination with the observed value was divided by the expected value. The probability value was obtained with the sum of these values and a chi-square distribution with 1 df.

Three limitations in our approach should be mentioned. First, determining what constitutes orange versus, for example, reddish brown, was sometimes difficult. We attempted to include only the orange or reddish orange color as exemplified by numerous scelionids, but other, similar colors are mentioned in the text for some taxa. Second, due to the breadth of this study, it was not possible to exhaustively record all intraspecific color variation, but some examples of such variation are noted. Third, this compilation is geographically biased toward the Neotropical and Nearctic regions, and is certainly incomplete even for these regions.

Results

In total, 66 orange and black color patterns were observed in Hymenoptera (Figs. 2 and 3), and of these 66 patterns, four patterns in braconids, one in chrysidids, and five in mutillids also showed whitish markings, mainly on the metasoma. The results for species showing one or more of the patterns illustrated in Fig. 1 are presented in Tables 1–7. The BO 0 and BOB 9 patterns were found in all taxa (though sawflies lack a propodeum so what appears as BOB 0 is actually BOB 9). Other BOB variations were found in only one taxon, for example, such BOB 3 and BOB 4 (Platygastridae), BOB 8 (Proctotrupomorpha), BOB 10 (Braconidae), and BOB 7 and BOB 11 (Ichneumonidae). Other patterns were found in two or more groups: BOB 1 (Braconidae and Platygastridae), BOB 2 (Evanioidea and Aculeata), and BOB 5 (Braconidae, Platygastridae, and Ichneumonidae).

In terms of geographical distribution, the most widespread patterns worldwide were BOB 0 and 9. Among scelionids BOB 0 was very well represented in the Neotropics but was also found in the other biogeographical regions (Table 1). The same was generally true for Braconidae and Ichneumonidae (Tables 3 and 4). BOB 2, BOB 5, and BOB 9 were found in three to five geographical regions, and the remaining patterns in just one region. The vast majority of specimens showing a black-orange-black pattern were collected below 2,000 m. In a statistical analysis ($n = 100$), altitude was categorized in two groups, greater than 2,000 m and less than 2,000 m, and an association was found ($P < 0.0001$) between all black coloration and an altitude greater than 2,000 m.

As in the BOB patterns, several other black-orange dorsal patterns were found in all or most biogeographical regions. Some examples include the following. 1) Black head and mesosoma, with orange metasoma, was observed in all regions except the Indo-Malayan realm. 2) Black head and mesosoma, with metasoma orange anteriorly (the first tergites) and black posteriorly (the remaining tergites), was observed in all regions except the Afrotropical and Australasian realms. 3) Black head, with mesosoma and metasoma orange except last tergite(s) black, was observed in all regions.

On the other hand, the majority of unique patterns (found only in a specific region and within a particular taxon) were found predominantly in three realms: Afrotropical, Indo-Malayan, and Australasian. These unique patterns were characterized in the Indo-Malayan and Afrotropical realms by black or whitish markings on the mesosoma or metasoma, embedded in an orange background, as in some Macroteleia (Scelioninae), Therophilus (Braconidae), and Trogaspida (Mutillidae). In the Australasian realm, some Orgilus and Synagaster (Braconidae) had a black or orange mesosoma, and a combination of orange and black on the metasoma.
Fig. 1. Eleven variations of the black head, orange mesosoma, black metasoma (BOB pattern) in Hymenoptera. Mts = metasoma, Prp = propodeum, Scu = scutellum, Mes = mesoscutum, H = head. This simplified color code does not include the pronotum and metanotum.

Fig. 2. Total number of observed black-orange patterns in some genera of Platygastridae, including those illustrated in Fig. 1 plus additional patterns not illustrated (for example, bicolored patterns and tricolored patterns that did not follow the sequence of head black, mesosoma at least partially orange, metasoma mostly black).
Table 1. Species of Platygastridae (Platygastridae) with BOB color patterns

| Species | Color | Distribution | Reference |
|---------|-------|--------------|-----------|
| Acanthoscelio acutus | BOB 0, 2 | Neotropical | CNC |
| A. radiatus | BOB 2, 4 | Neotropical | CNC |
| Baryconus sp. | BOB 0, 2, 5, 9 | Neotropical | CNC |
| Chromoteleia: 22/27 spp. | BOB 0 | Neotropical | MZUCR |
| Lapitha sp. | BOB 0 | Neotropical | CNC |
| Leptoteleia majkae Masner | BOB 0 | Neotropical | CNC |
| Macroteleia eximia Muesebeck | BOB 0 | Neotropical | CNC |
| M. insignis Muesebeck | BOB 0 | Neotropical | CNC |
| M. simulans Muesebeck | BOB 0 | Neotropical | CNC |
| Oethecoctonus sp. | BOB 0 | Neotropical | MZUCR |
| Parascelio sp. | BOB 0 | Neotropical | CNC |
| Probaryconus sp. | BOB 0, 9 | Neotropical | CNC |
| Pseudobeptascelio rex Johnson & Musetti | BOB 0 | Neotropical | CNC |
| P. tico Johnson & Musetti | BOB 0 | Neotropical | CNC |
| Scelio fulvithorax Dodd | BOB 0 | Australasian | CNC |
| S. schmelio Dangereur & Austin | BOB 1 | Australasian | CNC |
| S. semisanguineus Girault | BOB 3 | Palearctic | CNC |
| S. variegatus Kozlov & Kononova | BOB 5 | Neotropical | CNC |
| Scelionomphra rufithorax Kieffer | BOB 0 | Neotropical | MZUCR |
| Trimorus sp. | BOB 0 | Neotropical | CNC |
| Tyannoscelio genieri Masner & Johnson | BOB 0 | Neotropical | MZUCR |

Platygastridea
Most ‘platygastrids’ (in the traditional sense) and Telenominae are below the size range included in our survey, but BOB coloration was not encountered in either of these groups. In contrast, this color pattern was found in 14 genera of Sclioninae and one Teleasinae (Trimorus) (Table 1). In Chromoteleia, a neotropical genus except for one African species, 13 show the BOB 0 pattern, four the BOB 9 pattern, three the BOB 2 pattern, one the BOB 5 pattern, and one has just the pronotum orange (based on images in Chen et al. 2018). Intraspecific variation in color appears to be quite common in Sclioninae, including variation between individuals of the same sex. For example, in several species of Acanthoscelio (Dotseth and Johnson 2001) and in Pseudobeptascelio rex (Johnson and Musetti 2011) the mesosoma varies from orange to entirely black. In addition to the typical BOB 0 pattern and the 11 variations illustrated in Fig. 1, numerous other black-orange combinations are present, including a total of at least 19 combinations in species of Scelio (Fig. 2).

Other Proctotrupomorpha (Cynipoids, Proctotrupoidea, Diaprioids, Chalcidoidea)
Given the prevalence of BOB coloration in Platygastridae it is curious how infrequent this pattern is in the other Proctotrupomorpha (Table 2). Several species of Cynipoids have a black head and mesosoma with an orange metasoma, but BOB colorations seems to be very rare and when present (a couple of Callaspida species) individuals often vary in color. In Proctotrupoidea, some Proctotrupidae and Roproniidae have an orangish metasoma but no examples of BOB coloration were found. In Diaprioids a few Trichopria approach a BOB coloration and among larger-sized Chalcidoidea (>3 mm) the color pattern occurs primarily in a few species of Chalcididae and Eurytomidae. Bephrata and Isosomodes show considerable variation in color between species, and species with BOB coloration often have light colored markings on the sides of the metasoma; a few species show extreme variations of BOB not included in our color codes (Fig. 1). Some pteromalids (e.g., Epistenia and Neocatolaccus) superficially fit the BOB 9 pattern, but the mesosoma is metallic bronze instead of orange. Eulophidae is probably the most speciose chalcidoid family, yet the BOB pattern appears to be virtually absent, at least in the specimens we examined. A few Tetrastichinae and Eulophinae approach the BOB pattern, although they are more yellowish, as opposed to orange.

Ichneumonidae
The BOB color pattern was found in species belonging to six subfamilies of Ichneumonidae (Table 3). Some of these species show intraspecific variation, for example, in females of Glypta...
Species Color Distribution Reference

| Species                  | Color | Distribution | Reference          |
|--------------------------|-------|--------------|--------------------|
| Callaspidea notata       | BOB 8 | Palearctic   | Ros-Farré and Pujade-Villar (2009) |
| Helorina                 | BOB 0 | Neotropical  | CNC, MZUCR         |
| Helorus brethesi Ogloblin| BOB 0 | Neotropical  | MZUCR              |
| Chalcididae              |       |              |                    |
| Brauchymeria sp.         |       |              |                    |
| Stypnia dentipes         | BOB 0 | Neotropical  | MZUCR              |
| Eupelmidae               |       |              |                    |
| Brasema sp.              | BOB 0 | Neotropical  | MZUCR              |
| Eurypomidae              |       |              |                    |
| Aximopsis masneri Gates  | BOB 9 | Neotropical  | MZUCR              |
| Bebratia flava Gates & Hanson | BOB 0 | Neotropical  | MZUCR              |
| B. ticos Gates & Hanson  | BOB 2 | Neotropical  | MZUCR              |
| Isosomodes aozifai Gates & Hanson | BOB 0 | Neotropical  | CNC, MZUCR         |
| L. colombia Gates & Hanson| BOB 9 | Neotropical  | Gates and Hanson (2009) |
| Rileya tricolor Gates    | BOB 9 | Neotropical  | MZUCR              |
| Pteromalidae             |       |              |                    |
| Lelps sp.                | BOB 0 | Neotropical  | MZUCR              |

Table 2. Species of Proctotrupomorpha (excluding Platygastroidea) with BOB color patterns

metadecoris and Zaglyptomorpha cornuta where the mesoscutum varies from entirely orange to almost entirely black (Godoy and Gauld 2002). Many Banchinae, Pimplinae, and Tryphoninae show a BOB-like pattern but the mesosoma is reddish brown instead of orange and these are not included in the table. Ten Neotropical species of Stethantyx (Tersilochinae) (Khaliain and Broad 2013) were also excluded for this reason. Some ichneumonids (e.g., several Xiphosomella, Cremastinae) have a BOB pattern in lateral view but not in dorsal view. Also excluded are numerous species having a black-orange-black sequence but where only the anterior part of the metasoma is orange. Just a few of the many examples of this color pattern include some species in the following subfamilies and genera: Banchinae (Cryptopimpla, Glypta), Campopleginae (Casinaaria), Cryptinae (Agrothereutes, Artrisan, Atractodes, Ceratophygaeneum, Gambrus, Idiolispa, Mastrus, Mesoleptus, Phygaedon, Rhombobius, Sphecophaga, Therscapus, Thyrisus), and Tersilochinae (Barycenis).

Braconidae

The BOB color pattern was found in species belonging to 13 subfamilies of Braconidae (Table 4). Some species of Agathidinae (Alabagrus, Bassus, Pharta), Meteorinae, and Rodaginae have a black-orange-black sequence, but the orange is restricted to the anterior segments of the metasoma and often the propodeum as well. Most species of Alabagrus have bright color patterns (Leathers and Sharkey 2003), but the majority do not fit the BOB pattern. Intraspecific color variation is present in several braconids. For example, most Alabagrus ixtilion Sharkey from Mexico are all black but a few (8%) have an orange mesoscutum (BOB 2 pattern). Odontobracon jansenii females vary in coloration, with the mesoscutum usually orange but occasionally partially to entirely black (Marsh 2002).

Evanioidea

Within the superfamily Evanioidea, Aulacidae and Gasteruptiidae were not extensively examined since most are larger than our focal size range. A cursory examination of these two families revealed no BOB coloration as defined here, although some have the base of the metasoma orange with the rest of the body dark colored. On the other hand, BOB coloration was common in Evanidae, being present in nearly half of the extant genera (Table 5). All genera with species showing this coloration also have entirely dark-colored species, and often species with some other type of black-orange combination.

Aculeata

The BOB color pattern was found in species belonging to 10 families of aculeates (Table 6). Many aculeates are larger than the size range included in this study. Nonetheless, BOB coloration appears to be scarce in groups such as Scoliidae and Vespidae. Although many Pompilidae are also larger than our focal size range, it is notable that when orange coloration is present it is often just on the anterior part of the metasoma, which results in a black-orange-black sequence but with the metasoma mostly to entirely black. A similar pattern can be seen in a few other groups: some Ammophila and Podalonia (Sphecidae); a few Crabronidae, such as some Mimesa (Pemphredoninae), Miscophus, Tachysphex (Larrinae), Didines and Harpactus (Nyssoninae); a few Andrena (Andrenidae); and most Speecodes (Halictidae) (BWARS 2016).

In the superfamily Chrysidioidea the greatest number of species showing BOB coloration was found in chrysidids belonging to the subfamilies Cleptinae and Amiseginae (Table 6), although the black coloration in these species often includes some metallic reflections. It appears that a majority of Cleptidea species have some form of BOB coloration (Kimsey 1986; only a few examples are included in Table 6) and their color pattern is often complemented by banded wings. We observed several dryinids with orange coloration, but relatively few conformed to the BOB pattern. Orange coloration appears to be extremely scarce in Bethylidae although some apterous females of Sclerodermus domestius approach the BOB pattern.

Orange to red coloration is very common in female Mutillidae although there are a diversity of patterns and their size ranges from 2 to 25 mm. BOB coloration is found in several species of Timulla, as well as some Ephuta, Darditilla, Dasymutilla, Hoplocrates, Horcomutilla, Lynchiatilla, Pertyella, Pseudomethoca, Pitolomutilla, and Xystromutilla. Species in these genera showing a BOB pattern usually have pubescent or tegumentary markings (white, yellow, orange-red) on the metasoma, especially the second tergite. BOB coloration appears to be less common in male Mutillidae although it is found, for example, in both sexes of the Palearctic Mutilla europaea and Smicronyrmus rufipes (BWARS 2016).
| Species | Color | Distribution | Reference |
|---------|-------|--------------|-----------|
| Banchinae | | | |
| Apophua schoutedeni (Benoit) | BOB 0 | Afrotopical | Van Noort (2017) |
| Cryptopimpla bantani* | BOB 0 | Afrotopical | Reynolds Berry and van Noort (2016) |
| C. rubritoraxa* | BOB 0 | Afrotopical | Reynolds Berry and van Noort (2016) |
| C. swartii* | BOB 0 | Afrotopical | Reynolds Berry and van Noort (2016) |
| Glypta cuerciensis* | BOB 0 | Afrotopical | Reynolds Berry and van Noort (2016) |
| G. geognensis* | BOB 0 | Afrotopical | Reynolds Berry and van Noort (2016) |
| G. metaedecoris* | BOB 0 | Afrotopical | Reynolds Berry and van Noort (2016) |
| G. punctata* | BOB 9 | Afrotopical | Reynolds Berry and van Noort (2016) |
| G. tumifrons* | BOB 9 | Afrotopical | Reynolds Berry and van Noort (2016) |
| Zaglyptomorpha bella* | BOB 9 | Afrotopical | Reynolds Berry and van Noort (2016) |
| Cremastinae | | | |
| Pristomerus mexicanus Cresson | BOB 0 | Neotropical | Gauld (2000) |
| Traithala flaca* | BOB 0 | Neotropical | CNC, Gauld (2000) |
| T. gifa* | BOB 0 | Neotropical | Gauld (2000) |
| T. henryia* | BOB 9 | Neotropical | Gauld (2000) |
| T. horaa* | BOB 9 | Neotropical | Gauld (2000) |
| T. paulaa* | BOB 9 | Neotropical | Gauld (2000) |
| Crytinae | | | |
| Apotemnus truncatus Cushman | BOB 9 | Neotropical | CNC |
| Artrani sp. | BOB 0 | Neotropical | CNC |
| Astomaspis violaceipennis (Cameron) | BOB 9 | Neotropical | Van Noort (2017) |
| Bathybrix sp. | BOB 2 | Nearctic | CNC |
| Diapetimorpha sp. | BOB 11 | Neotropical | CNC |
| Dracaela latifasciata (Cameron) | BOB 0 | Neotropical | Van Noort (2017) |
| Gelis apterus (Ponstoppidan) female | BOB 0 | Neotropical | Korenko et al. (2014) |
| Madastenus mgnrutos Seyrig | BOB 0 | Neotropical | CNC |
| Polycyrus condylolbus* | BOB 5 | Neotropical | Zúñiga Ramírez (2004) |
| P. duplarisa* | BOB 5 | Neotropical | Zúñiga Ramírez (2004) |
| P. latigulus* | BOB 5 | Neotropical | Zúñiga Ramírez (2004) |
| P. luist* | BOB 5 | Neotropical | Zúñiga Ramírez (2004) |
| P. naia* | BOB 5 | Neotropical | Zúñiga Ramírez (2004) |
| Ichneumoninae | | | |
| Jacotitypus sp. | BOB 0 | Neotropical | CNC |
| Jotpha sp. | BOB 0, 7 | Neotropical | CNC |
| Pimplinae | | | |
| Acrotaphus chedelae Gauld | BOB 5 | Neotropical | MNCX |
| A. fasciatus (Brullé) | BOB 5 | Neotropical | Gauld (1991) |
| A. franklini Gauld | BOB 11 | Neotropical | MNCX |
| A. latifasciatus (Cameron) | BOB 5 | Neotropical | MNCX |
| A. timialis (Cameron) | BOB 5 | Neotropical | MNCX |
| Callisteptiales grapholithae (Cresson) | BOB 9 | Nearctic | MNCX |
| C. guesvarae* | BOB 11 | Neotropical | MNCX |
| C. leodezmae* | BOB 0 | Neotropical | MNCX |
| Clydonium moragaia* | BOB 9 | Neotropical | MNCX |
| Polysphincta janzeni* | BOB 9 | Neotropical | MNCX |
| Tryphoninae | | | |
| Boethus taeniatus Townes & Gupta | BOB 0 | Neotropical | Gauld (1997) |
| Oedemopis cyranoa* | BOB 9 | Neotropical | Gauld (1997) |
| O. dentipara* | BOB 9 | Neotropical | Gauld (1997) |
| O. noyesi* | BOB 9 | Neotropical | Gauld (1997) |
| O. ojasa* | BOB 0 | Neotropical | Gauld (1997) |
| O. quemadoi* | BOB 9 | Neotropical | Gauld (1997) |
| O. ryato* | BOB 0, 9 | Neotropical | Gauld (1997) |

*Author names same as reference.
Table 4. Species of Braconidae with BOB color patterns

| Subfamily, species | Color | Distribution | Reference |
|--------------------|-------|--------------|-----------|
| **Agathidinae**     |       |              |           |
| Aerophilus vaughntani (Sharkey) | BOB 2 | Neotropical | Sharkey et al. (2011) |
| Agathacrista depressifera (van Achterberg & Long) | BOB 2 | Indo-Malayan | Sharkey and Stoelb (2013) |
| Bassus calculator (Fabricius) | BOB 9 | Paleartic | CNC |
| B. ebulus (Nixon) | BOB 9 | Indo-Malayan | CNC |
| Brainsia fumipennis (Cameron) | BOB 9 | Indo-Malayan | Sharkey and Cluts (2011) |
| Cremnops violaceipennis (Cameron) | BOB 10 | Neotropical | Tucker et al. (2015) |
| Eusathidinae sphenippum (Cameron) | BOB 0 | Indo-Malayan | van Achterberg and Long (2010) |
| Zeolida angustosa | BOB 9 | Indo-Malayan | van Achterberg and Long (2010) |
| Zelomorpha similis (Szépligeti) | BOB 5 | Neotropical | Sarmiento-Monroy (2006) |
| **Alysiinae**       |       |              |           |
| Gnathopleura sp. | BOB 5 | Neotropical | MNCR |
| Phaenocarpa sp. | BOB 0 | Neotropical | CNC |
| **Brachistinae**    |       |              |           |
| Eubazus sp. | BOB 0 | Nearctic | CNC |
| Eubazus sp. | BOB 9 | Neotropical | MNCR |
| Nealiolus sp. | BOB 0 | Neotropical | CNC |
| **Braconinae**      |       |              |           |
| Aphrastobracon biroi (Szépligeti) | BOB 9 | Neotropical | MNCR |
| Bracon campyloneurus Szépligeti | BOB 0 | Nearctic | CNC |
| Cadabracon sp. | BOB 0 | Neotropical | MZUCR |
| Campodobracon sp. | BOB 9 | Neotropical | MZUCR |
| Cyanopterus sp. | BOB 0 | Neotropical | CNC |
| Digonogaster sp. | BOB 0 | Neotropical | CNC |
| Gracibracon sp. | BOB 0, 1 | Neotropical | MZUCR |
| Megasbracon sp. | BOB 5 | Neotropical | MNCR |
| Pycnoitraconoides mutator (Fabricius) | BOB 0 | Australasian | CNC |
| **Cardiochilinae**  |       |              |           |
| Cardiochiles fallax Kokujev | BOB 9 | Nearctic | MZUCR |
| Cardiochiles sp. | BOB 2 | Neotropical | CNC |
| Toxoneuron leve (Mao) | BOB 9 | Nearctic | CNC |
| **Cenocoelinae**    |       |              |           |
| Capitonius pulcher (Cameron) | BOB 5 | Neotropical | CNC, MNCR |
| C. tricolorvalvus Ent | BOB 0 | Neotropical | MNCR, MZUCR |
| Cenoelus sp. | BOB 0 | Neotropical | CNC |
| **Charmontinae**    |       |              |           |
| Charmon cruentatus Haliday | BOB 0 | Holarctic | CNC |
| C. extensor (Linneaus) | BOB 0 | Holarctic | CNC |
| **Cheloninae**      |       |              |           |
| Leptodrepana atalanta Dadelahi & Shaw | BOB 0 | Neotropical | Dadelahi et al. (2018) |
| L. cynthia Dadelahi & Shaw | BOB 9 | Neotropical | Dadelahi et al. (2018) |
| L. conleye Dadelahi & Shaw | BOB 0 | Neotropical | Dadelahi et al. (2018) |
| L. dementer Dadelahi & Shaw | BOB 0 | Neotropical | Dadelahi et al. (2018) |
| L. ioreae Dadelahi & Shaw | BOB 9 | Neotropical | Dadelahi et al. (2018) |
| L. munjanae Dadelahi & Shaw | BOB 9 | Neotropical | Dadelahi et al. (2018) |
| L. ninae Dadelahi & Shaw | BOB 9 | Neotropical | Dadelahi et al. (2018) |
| L. schuttei Dadelahi & Shaw | BOB 0 | Neotropical | Dadelahi et al. (2018) |
| L. stasia Dadelahi & Shaw | BOB 0 | Neotropical | Dadelahi et al. (2018) |
| Macrochelonus rubescens | BOB 0 | Neotropical | Papp (2010) |
| M. ruficollis Vierreck | BOB 9 | Neotropical | Papp (2010) |
| **Doryctinae**      |       |              |           |
| Gymnoitracon megistus Marsh | BOB 0 | Neotropical | CNC, MNCR |
| Megaloprocus strongylaster (Cameron) | BOB 3 | Neotropical | MNCR |
| Odontobracon batesi Roman | BOB 0 | Neotropical | CNC |
| O. jancezi Marsh | BOB 5 | Neotropical | MNCR |
| Pedinotus columbianus Enderlein | BOB 0 | Neotropical | CNC |
| **Macrocentrinae**  |       |              |           |
| Macrocentrus bicolor Curtis | BOB 0 | Neotropical | van Achterberg (1993) |
| **Meteorinae**      |       |              |           |
| Meteorus sp. | BOB 0 | Nearctic | CNC |
| **Orgilinae**       |       |              |           |
| Orgilus sp. | BOB 9 | Neotropical | MZUCR |
| **Rogadininae**     |       |              |           |
| Aleoidea lucidus (Szépligeti) | BOB 0 | Neotropical | Shimbori and Penteado-Dias (2011) |
| A. melanopterus (Erichson) | BOB 0 | Neotropical | CNC |
| A. shaworuma | BOB 10 | Neotropical | Shimbori and Penteado-Dias (2011) |

*Author names same as reference.*
Among ants (Formicidae), BOB coloration is relatively uncommon (Table 6), occurring primarily in Myrmecinae (Myrmecia) and Formicinae (a few Camponotus and Formica). Examples of Myrmecia species showing BOB coloration include M. aberrans, M. cephalotes, M. desertorum, M. fuscipes, M. nigriceps, M. nigrocincta, M. nobilis, and M. sueler. In addition to an orange mesosoma, many of these ants often have the petiole and postpetiole orange colored as well, and some (e.g., M. nigrocincta) have black orange colored as well, and some (e.g., M. nigriceps, M. swalei). In addition to an orange middle of the mesosoma, resulting in a BOBOB pattern. In the Neotropical region the most common ant showing BOB coloration is Myrmecia nobilis (Fabricius)

Table 5. Species of Evaniidae with BOB color patterns

| Species                          | Color | Distribution      | Reference                           |
|----------------------------------|-------|-------------------|-------------------------------------|
| Acanthinevania clavaticornis (Kieffer) | BOB 0 | Australasian      | Deans et al. (2017)                  |
| Exania stenochela Kieffer        | BOB 0 | Palearctic        | Deans et al. (2017)                  |
| Exaniella erythropis (Cameron)    | BOB 6 | Neotropical       | Deans et al. (2017)                  |
| E. nana (Schletterer)            | BOB 9 | Neotropical       | Deans et al. (2017)                  |
| E. nobilis (Westwood)            | BOB 0 | Neotropical       | Deans et al. (2017)                  |
| E. ruficornis (Fabricius)        | BOB 0 | Neotropical       | Deans et al. (2017)                  |
| E. rufosparsa (Kieffer)          | BOB 9 | Neotropical       | Deans et al. (2017)                  |
| E. semaeoda (Bradley)            | BOB 9 | Nearctic          | Deans et al. (2017)                  |
| Exsinusius rufithorax Enderlein   | BOB 9 | Neotropical       | Mullins et al. (2012)                |
| Hyptia chalcidipennis (Enderlein) | BOB 0, 9 | Neotropical       | Deans et al. (2017)                  |
| H. persanus (Enderlein)          | BOB 9 | Neotropical       | Deans et al. (2017)                  |
| H. reticulata (Say)              | BOB 0 | Nearctic          | Deans et al. (2017)                  |
| H. rufpectus Dewitz              | BOB 0, 9 | Neotropical       | Deans et al. (2017)                  |
| H. rufipes (Fabricius)           | BOB 9 | Nearctic          | Deans et al. (2017)                  |
| H. stimulata (Schletterer)       | BOB 0 | Neotropical       | Deans et al. (2017)                  |
| Parevania kriegeriana (Enderlein) | BOB 9 | Indo-Malyan       | Deans et al. (2017)                  |
| P. mcholitzi (Enderlein)         | BOB 9 | Indo-Malyan       | Deans et al. (2017)                  |
| Proevania erythrosoma (Schletterer) | BOB 0 | Indo-Malyan       | Ramage and Martiré (2016)            |
| P. lombokensisis (Szépligeti)    | BOB 9 | Afrotropical      | Deans et al. (2017)                  |
| P. rufoniger (Enderlein)         | BOB 0, 9 | Indo-Malyan       | Deans et al. (2017)                  |
| P. satheri (Enderlein)           | BOB 0 | Indo-Malyan       | Deans et al. (2017)                  |
| P. tricolor (Szépligeti)         | BOB 0 | Indo-Malyan       | Deans et al. (2017)                  |
| Semaeomyia magnus (Enderlein)    | BOB 9 | Neotropical       | Deans et al. (2017)                  |
| S. pygmaea (Fabricius)           | BOB 9 | Neotropical       | Deans et al. (2017)                  |
| L. reticolifera (Enderlein)      | BOB 9 | Neotropical       | Deans et al. (2017)                  |
| Szepligetella formosa (Kieffer)  | BOB 0 | Australasian      | Deans et al. (2017)                  |
| Zeuxevania lamellata Benoit       | BOB 9 | Afrotropical      | Deans et al. (2017)                  |

Sawflies
Our examination of sawflies was less thorough than in other groups, and was limited to three families in the New World (Table 7). Intraspecific variation occurs in at least some species, sometimes with males being all black (e.g., Scobina dorsalis), and in some cases females vary in color, as in Scobina lepida (Klug) and S. melanocephala (Lepeletier) (Smith 1992). In Perreya tropica some males have just the mesoscutum orange (especially at higher elevations) while in others the entire thorax and abdomen is orange; females have both the thorax and abdomen orange, but the dark wings cover the abdomen.

Discussion
We found BOB coloration in 23 families of Hymenoptera, and in many of the subfamilies of Ichneumonidae and Braconidae. Due to lack of revisionary taxonomic studies, quantification of the proportion of species showing BOB coloration is very infrequent in certain taxa (e.g., Cynipoids, Diaprioids, Chalcidoids, and Apoids) and quite common in others (Scelioninae, Evaninae, and female Mutillidae). As noted in the introduction, the proportion of species showing a BOB pattern, in scelionid genera where this color is present, ranges from about 90% in Chromoteleia to 15% in Macroteleia (Valerio et al. 2013). As more taxonomic revisions become available it will become possible to expand this data; for example, 10 of the 24 Costa Rican species of Leptodrepana (Braconidae) (Dadelahi et al. 2018).

The preliminary nature of our survey as well as the lack of phylogenies for most of the taxa preclude estimating the number of times BOB coloration has evolved. Nonetheless, the widespread occurrence of this color pattern strongly suggests that it has arisen on numerous occasions, which in turn suggests that it has some biological function. It seems unlikely that this color is used in intersexual communication since both sexes usually had the same color, and most of the intraspecific variation we observed included color
variation within the same sex. Among the few cases of intersexual color variation were in groups where females are apterous and males are winged (e.g., Mutillidae and Methocha), and in these cases only females show BOB coloration.

The most likely function of BOB coloration is aposematism (warning coloration) since contrasting orange and black color patterns are known to be aposematic in other insects, for example, ladybird beetles (Coleoptera: Coccinellidae) (María Arenas et al. 2015). It is also possible that at least some of the taxa showing BOB coloration are mimicking ants, for example, P. gracilis. While this species is restricted to the New World, it could be argued that other ants serve as models in other regions (Table 6), for example, Myrmecia spp. in Australia and Formica rufa in the Palearctic region. There are, however, other possible models, namely female Mutillidae (see ‘black-headed Timulla’ mimicry ring in Wilson et al. 2015). Many female mutillids showing the BOB pattern also have lateral white spots on the metasoma, a pattern that also occurs in several other taxa we examined, for example, Bephrata and Issomodes (Eurytomidae), and Cleptidea (Chrysidae); in Leptodrepana (Bracoonidae) there is often a central white spot on the first tergite. If BOB coloration in nonaculeate hymenopterans involves mimicry, it remains to be seen what proportion of these are Batesian mimics (only the model is distasteful) versus Mullerian mimics (both model and mimic are distasteful).

Four factors have been speculated to be correlated with the prevalence of BOB coloration (Masner 1988, Masner and Hanson 2006): insect size, habitat, altitudinal distribution, and geographic distribution. With respect to size, BOB coloration does indeed appear to be especially common in hymenopterans with a body length between 3 and 10 mm, although we included species up to 20 mm in length. Outside the 3–20 mm size range, there were examples of BOB coloration in both smaller specimens (among neotropical scelionids: Table 6.

| Species | Color | Distribution | Reference |
|---------|-------|--------------|-----------|
| Cleptidea balboana Kimsey | BOB 9 | Neotropical | MZUCR |
| C. panamensis Kimsey | BOB 9 | Neotropical | MZUCR |
| Adelpho masneri Kimsey | BOB 0 | Neotropical | CNC |
| Alienicus: both of the two spp. | BOB 0 | Afrotropical | Van Noort (2017) |
| Anadelpho allavarengai | BOB 9 | Neotropical | Kimsey (1987) |
| Atopegae: all six spp. | BOB 9 | Indo-Malayan | Kimsey (2014) |
| Mahinda sulawesiensis | BOB 0 | Indo-Malayan | Kimsey et al. (2016) |

Sclerogibbidiae

Sclerogibba talpiformis Benoit female

Dryinidae

Dryinus collaris (Linnaeus)

Rhopalosomatidae

Olsson myrmoseaforme (Arnold)

Thynnidae

Methocha articulata Lateille female

Pompilidae

Aenennula sp.

Agromyodes rubicundus Evans

Balboana sp.

Dipogon tracundus Townes

Eupomphilus azteca (Cresson)

E. delicatus Turner

Bradyponobaenidae

Gynecastra bimaculata (André) female

Formicidae

Camponotus nigriceps (Smith)

C. vicinus Mayr

Formica rufa Linnaeus

Dolobractyla fousqui Santschi

Myrmecia spp.

Psedomyrmex gracilis (Fabricius)

Tennobzonix isabellae (Wheeler)

Heterogynaidae

Heterogyna saudita Gadallah & Soliman female

Crabronidae

Alysson tricolor Lepeletier & Serville female

Incascognius hexagonalis (Fox) female

I. pyrrhoprus

Stigmus sp.

Trypoxylon sp.

For Mutillidae and Myrmecia (Formicidae) see text.

Author names same as reference.
Table 7. Species of sawflies with BOB color patterns

| Species Color Distribution Reference |
|-------------------------------------|
| **Argidae-Arginae**                 |
| Arge pectoralis (Leach) BOB 9 Neartic CNC |
| A. quidia Smith BOB 9 Neartic CNC |
| A. scapularis Klug BOB 9 Neartic CNC |
| Scobina dorsalis (Klug) female BOB 9 Neotropic MZUCR |
| **Argidae-Atomacerinae**            |
| Atomacera decepta Rohwer BOB 9 Neartic CNC |
| A. debilis Say BOB 2 Neartic CNC |
| A. ebena Smith BOB 9 Neotropic MZUCR |
| A. lepidula (Konow) BOB 9 Neotropic MZUCR |
| **Argidae-Erigleninae**             |
| Sericoceros gibbus (Klug) BOB 9 Neotropic MZUCR |
| Argyropilus rubra (Kugel) BOB 9 Neotropic MZUCR |
| **Argidae-Stenipterinae**           |
| Acrophylla pala Smith BOB 9 Neotropic MZUCR |
| **Tenthredinidae-Allantinae**       |
| Decameria similis (Enderlein) BOB 9 Neotropic MZUCR |
| D. variipes Cameron BOB 9 Neotropic MZUCR |
| Perreya tropica (Norton) BOB 9 Neotropic CMC MZUCR |
| **Tenthredinidae-Blennochilinae**   |
| Eriocampa ovata Linnaeus BOB 2 Neartic Smith (1979) |
| Phrontosoma brocca Smith BOB 2 Neartic MZUCR |
| P. nata Smith BOB 9 Neartic MZUCR |
| **Tenthredinidae-Selandrinae**      |
| Waldheimia amazonica (Kirby) BOB 9 Neotropic MZUCR |
| **Tenthredinidae-Selandrinae**      |
| Dolerus rubifolius Ross BOB 9 Neartic MZUCR |

The BOB 0 pattern is not possible in sawflies since they lack a propodeum; what appears as BOB 0 is actually BOB 9.

Laphita, Macroteleia, Tyrannoscelio, Probaryconus) and larger specimens (several Mutillidae and Ichneumonidae), but our impression is that BOB coloration is most prevalent in the size range mentioned above. However, quantitative analyses are required to examine this question in greater detail.

Masner (1988) suggested that BOB coloration is most prevalent among species that inhabit low vegetation, between 1 and 2 m high. Although data on collecting techniques were generally not available and we did not quantify what little was available, there did appear to be more specimens from Malaise traps and screen-sweeping, and fewer from pan traps and other ground-based techniques, but this requires confirmation. The biology of the taxa showing BOB coloration (Tables 1–7) encompasses both ecto- and endoparasitoids, idiobionts and koinobionts, from a diversity of hosts, as well as phytophagous sawflies. It is interesting that egg parasitoids (scelionids, evaniids, amiseine chrysidids) are especially well represented, but more research is needed to determine whether they are in fact proportionately better represented than parasitoids of larval and pupal nests.

With regard to the altitudinal distribution of BOB coloration, the vast majority of specimens showing this color pattern were collected below 2,000 m, as has been previously observed (Masner and Hanson 2006). In a few cases we were able to examine specimens collected at altitudes ranging from sea level to 5,000 m. For example, Triteleia specimens with BOB coloration were common in the lowlands, however, entirely black specimens were found in higher altitudes such as Cotopaxi in Ecuador (5,000 m), Sierra Nevada in Spain (3,200 m), and Chiapas in Mexico (4,000 m). On the other hand, two specimens (less than 3 mm in length) of Probaryconus showing BOB coloration (one with BOB 9) were collected at higher altitudes in Ecuador, one from Napo at 3,000 m and the other from Oyacachi at 3,190 m. In species showing intraspecific color variation there is often a tendency for specimens from higher elevations to be darker. For example, in Costa Rica an unidentified species of Lapitha shows typical BOB coloration in the lowlands, but at higher altitudes (above about 1,300 m) specimens become darker, with a black propodeum (BOB 10) and a darker mesoscutum. Although these altitudinal trends merit further investigation with additional taxa, the scarcity of BOB coloration at higher altitudes appears to be a real pattern, but the reason (e.g., temperature, UV radiation, predators) for this pattern is unknown.

Although it has previously been suggested that BOB coloration occurs mostly in the Neotropics (Masner 1988, Masner and Hanson 2006), our results show that this color pattern is found in all biogeographic regions. Although it is possible that this color pattern is more frequent in the Neotropics, at least among scelionids, our data are insufficient to substantiate this possibility.

While BOB coloration was previously known to occur in Hymenoptera, especially in Scelioninae, our results demonstrate that it is much more widespread than previously realized. Although this color pattern occurs in other insects, we are not aware of any systematic surveys. In addition to extending the survey to other groups of insects, potential research questions for the future include the following. First, the fact that some observers see the mesosoma as orange, while others see it as red, demonstrates the need for spectro-photometric analyses. Moreover, it would be useful to compare scelionids with taxa such as agathidine braconids, where the orange color appears to be slightly different. Second, to the best of our knowledge,
Mutilidae is the only group in which the physical/chemical basis of BOB coloration has been examined, namely orange pheomelanins and black eumelanins (Hines et al. 2017); similar studies are needed in the other groups, especially scelionids. Third, future studies should include other black and orange patterns, for example, where only the base of the metasoma is orange, and bicolored species. In some cases wing coloration contributes to the color pattern; for example, in Cardiochiles nigriceps Vierack (Braconidae) both the mesosoma and metasoma are reddish, but when the black wings cover the metasoma it has a black appearance. Fourth, it would be useful to examine in greater detail species that show intraspecific variation in color. Finally, and perhaps most importantly, in order to address the question of the function of this widespread color pattern, feeding trials with potential predators of species listed in Tables 1–7 are needed to determine whether this color pattern is indeed aposematic. Similarly, the possible presence of repugnatorial glands in species showing BOB coloration needs to be examined, and compared with closely related species that lack this color pattern (for example, completely black species).

Acknowledgments

We would like to give special thanks to Lubomir Masner, for first drawing attention to this color pattern and for his help during R.M.’s visit to the Canadian National Collection, and to Sophie Cardinal for her efforts in arranging this visit. We also thank the staff of the National Museum (INBio) for access to their collections, Roberto Cambra of the University of Panama for providing information on mutilids, J. Albert C. Uy for valuable comments on the manuscript and Jose Vargas Murillo for the support in the design of the illustrations.

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