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Research

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

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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, Chalcidoids, 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

Insects show an exceptional variety of colors with complex and diverse patterns. Coloration can be produced by diverse forms of surface and epidermal structures (structural colors) or by pigments in the outer body layers that selectively absorb, reflect, or scatter specific wavelengths of light. Pigments are responsible for most of the orange, red, yellow, and brown-black colors observed in insects while most blue or green colors result from nanostructural features that reflect these colors (Schroeder et al. 2018). Both the colors themselves and the way they are arranged into patterns often vary among individuals of a species.

Insect colors can have important biological functions such as thermoregulation (Stuart-Fox et al. 2017), secondary sexual characters (Jorge García et al. 2016), and predator avoidance via camouflage (crypsis and masquerade) (Skelhorn and Rowe 2016), warning (aposematic) coloration (Stevens and Ruxton 2012), or mimicry (Mallet and Joron 1999). Conspicuous coloration is often, but not always, indicative of aposematism, whereby predators learn to associate a particular color pattern with noxious chemical defenses, although this learning process is more complex than simply developing an aversion to certain types of prey (Skelhorn et al. 2016). Moreover, the visual and cognitive capacities of predators vary; for example, orange shield-back stinkbugs (Hemiptera: Scutelleridae) on a green background are probably conspicuous to birds but much less so to mantids (Fabricant and Herberstein 2015).

Compared with Lepidoptera and Coleoptera there are relatively few studies of conspicuous (potentially aposematic) color patterns in Hymenoptera, and what studies exist are mostly restricted to the yellow and black pattern in Vespidae (Vidal-Cordero et al. 2012, Marchini et al. 2016). However, it has long been recognized that many smaller hymenopterans, especially scelionids, show a recurring color pattern of black head, orange mesosoma, and black metasoma (BOB). (While we recognize that scelionids are currently placed in Platygastridae (Murphy et al. 2007, Sharkey 2007), we shall use the informal term 'scelionid' in the traditional sense.) Lubomir Masner (1988) was probably the first to emphasize the widespread occurrence of this color pattern in Hymenoptera (referring to it as a black, red, black). This BOB pattern appears to occur in 90% of the currently known species of *Chromoteleia*, 70% of *Acanthoscelio* and *Triteleia*, 50% of *Baryconus*, 40% of *Pseudoheptascelio*, 30% of *Opisthacantha*, *Scelio*, and *Sceliomorpha*, and 15% of *Macroteleia* (Valerio et al. 2013). It has also been documented in some species of *Lapitha*, *Leptoteleia*, *Oethecoctonus*, and *Probaryconus* (Masner and Hanson 2006). While the BOB color pattern is best known in scelionids, it also occurs in many other hymenopteran families, and even in species of other orders (we have observed it, for example, in some paederine staphylinids, and a few bibionid and stratiomyiid flies).

To the best of our knowledge, the taxonomic distribution of this color pattern in Hymenoptera has never been tabulated, except at the generic level in scelionids as noted above and in some mutillids (Wilson et al. 2015). Thus, the primary objective of the present investigation was to provide a compilation of hymenopteran taxa showing a black-orange-black color pattern in order to draw attention to this widespread phenomenon and to provide an initial framework for future studies.

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 of 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 10× to 30×. 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 Neartic 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 BOB 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 (Platygastroidea), 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 Platygastriodea), BOB 2 (Evanioidea and Aculeata), and BOB 5 (Braconidae, Platygastriodea, 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 *Trogaspidia* (Mutillidae). In the Australasian realm, some *Orgilus* and *Syngaster* (Braconidae) had a black or orange mesosoma, and a combination of orange and black on the metasoma.

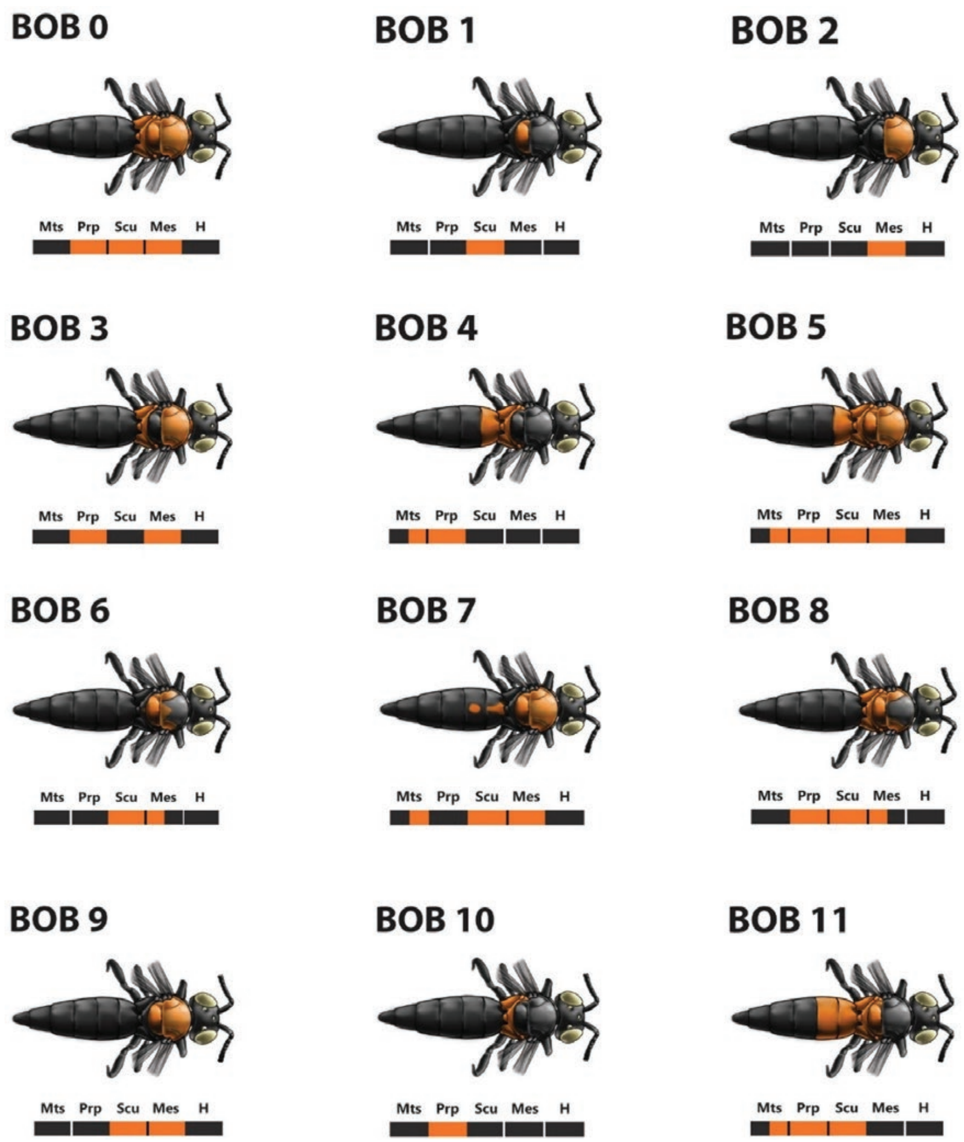

Fig. 1. Eleven variations of the black head, orange mesosoma, black metasoma (BOB pattern) in Hymenoptera. Mts = metasoma, Prp = propodeum, Scu = scutellum, Mes = mesoscutum, H = head. This simplified color code does not include the pronotum and metanotum.

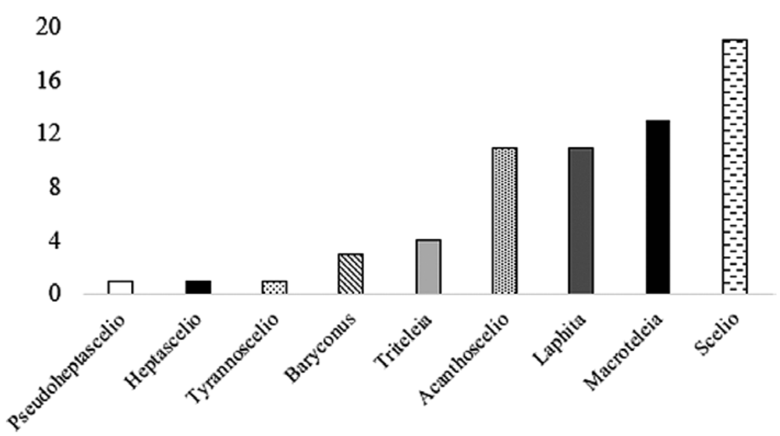

Fig. 2. Total number of observed black-orange patterns in some genera of Platygastridae, including those illustrated in Fig. 1 plus additional patterns not illustrated (for example, bicolored patterns and tricolored patterns that did not follow the sequence of head black, mesosoma at least partially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

Platygastroidea

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 Scelioninae and one Teleasinae (*Trimorus*) (Table 1). In *Chromoteleia*, a neotropical genus except for one African species, 13 species 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 Scelioninae, including variation between individuals of the same sex. For example, in several species of *Acanthoscelio* (Dotseth and Johnson 2001) and in *Pseudoheptascelio 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).

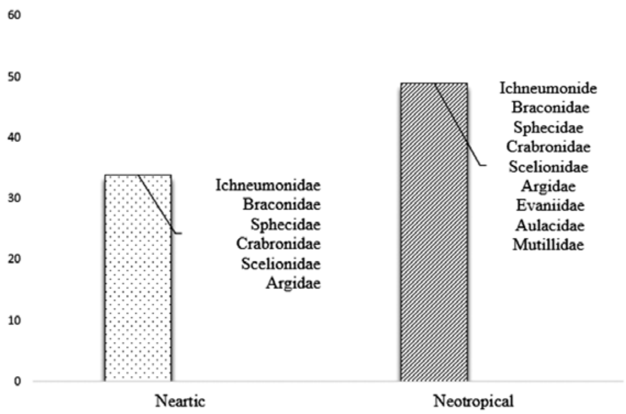

Fig. 3. Total number of observed black-orange patterns in all Neotropical and Neartic specimens examined, which are the geographical areas best represented in our survey. These include the patterns illustrated in Fig. 1 as well as others not illustrated (for example, bicolored patterns and tricolored patterns that did not follow the sequence of head black, mesosoma at least partially orange, metasoma mostly black).

Other Proctotrupomorpha (Cynipoids, Proctotrupoidea, Diaprioids, Chalcidoids)

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 *Callaspidia* 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 Chalcidoids (>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*

Table 1. Species of Platygastroidea (Platygastridae) with BOB color patterns

Species	Color	Distribución	Reference
Acanthoscelio acutus Dotseth & Johnson	BOB 0, 2	Neotropical	CNC
A. radiatus Dotseth & Johnson	BOB 2, 4	Neotropical	CNC
Baryconus sp.	BOB 0	Neotropical	MZUCR
Chromoteleia: 22/27 spp.	BOB 0, 2, 5, 9	Neotropical	Chen et al. (2018)
Lapitha sp.	BOB 0	Neotropical	MZUCR
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
Pseudoheptascelio rex Johnson & Musetti	BOB 0	Neotropical	CNC
P. tico Johnson & Musetti	BOB 0	Neotropical	CNC
Scelio fulvithorax Dodd	BOB 0	Australasian	CNC
S. schmelio Dangerfield & Austin	BOB 1	Australasian	CNC
S. semisanguineus Girault	BOB 3	Australasian	CNC
S. variegatus Kozlov & Kononova	BOB 5	Palearctic	CNC
Sceliomorpha rufithorax Kieffer	BOB 0	Neotropical	CNC
Triteleia sp.	BOB 0	Neotropical	MZUCR
Tyrannoscelio genieri Masner & Johnson	BOB 0	Neotropical	CNC
Trimorus sp.	BOB 0	Neotropical	MZUCR

Valerio et al. (2013) also mention *Opisthacantha*.

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

Species	Color	Distribution	Reference
Figitidae			
Callaspidia notata (Fonscolombe)	BOB 8	Palearctic	Ros-Farré and Pujade-Villar (2009)
Heloridae			
Helorus brethesi Ogloblin	BOB 0	Neotropical	CNC, MZUCR
Chalcididae			
Brachymeria sp.		Neotropical	MZUCR
Stypiura dentipes (Fabricius)	BOB 0	Neotropical	MZUCR
Eupelmidae			
Brasema sp.	BOB 0	Neotropical	MZUCR
Eurytomidae			
Aximopsis masneri Gates	BOB 9	Neotropical	MZUCR
Bephrata flava Gates & Hanson	BOB 0	Neotropical	MZUCR
B. ticos Gates & Hanson	BOB 2	Neotropical	MZUCR
Isosomodes azofiefai Gates & Hanson	BOB 0	Neotropical	CNC, MZUCR
I. colombia Gates & Hanson	BOB 9	Neotropical	Gates and Hanson (2009)
Rileya tricolor Gates	BOB 9	Neotropical	MZUCR
Pteromalidae			
Lelaps sp.	BOB 0	Neotropical	MZUCR

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) (Khalaim 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 (*Casinaria*), Cryptinae (*Agrothereutes*, *Aritranis*, *Atractodes*, *Ceratophygadeuon*, *Gambrus*, *Idiolispa*, *Mastrus*, *Mesoleptus*, *Phygadeuon*, *Rhembobius*, *Sphecophaga*, *Theroscopus*, *Thrybius*), and Tersilochinae (*Barycnemis*).

Braconidae

The BOB color pattern was found in species belonging to 13 subfamilies of Braconidae (Table 4). Some species of Agathidinae (*Alabagrus*, *Bassus*, *Pharpa*), Meteorinae, and Rogadinae 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 ixtilton* Sharkey from Mexico are all black but a few (8%) have an orange mesoscutum (BOB 2 pattern). *Odontobracon janzeni* 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 Evaniidae, 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 mesosoma 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), *Didineis* and *Harpactus* (Nyssoninae); a few *Andrena* (Andrenidae); and most *Sphecodes* (Halictidae) (BWARS 2016).

In the superfamily Chrysidoidea 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 domesticus* 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*, *Ptilomutilla*, 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 *Smicromyrme rufipes* (BWARS 2016).

Table 3. Species of Ichneumonidae with BOB color patterns

Species	Color	Distribution	Reference
Banchinae			
Apophua schoutedeni (Benoit)	BOB 0	Afrotropical	Van Noort (2017)
Cryptopimpla hantami[a]	BOB 0	Afrotropical	Reynolds Berry and van Noort (2016)
C. rubrithorax[a]	BOB 0	Afrotropical	Reynolds Berry and van Noort (2016)
C. zwarti[a]	BOB 0	Afrotropical	Reynolds Berry and van Noort (2016)
Glypta cuericiensis[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
G. geoginensis[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
G. metadecoris[a]	BOB 0	Neotropical	Godoy and Gauld (2002)
G. punctata[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
G. tumifrons[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
Zaglyptomorpha bella[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
Z. cornuta[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
Z. gabrieli[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
Z. hebeae[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
Z. pediflava[a]	BOB 9	Neotropical	Godoy and Gauld (2002)
Cremastinae			
Pristomerus mexicanus Cresson	BOB 0	Neotropical	Gauld (2000)
Trathala flaca[a]	BOB 0	Neotropical	CNC, Gauld (2000)
T. gifa[a]	BOB 0	Neotropical	Gauld (2000)
T. henryi[a]	BOB 9	Neotropical	Gauld (2000)
T. hora[a]	BOB 9	Neotropical	Gauld (2000)
T. paula[a]	BOB 9	Neotropical	Gauld (2000)
Cryptinae			
Apotemnus truncatus Cushman	BOB 9	Neotropical	CNC
Aritranis sp.	BOB 0	Palearctic	CNC
Astomaspis violaceipennis (Cameron)	BOB 9	Afrotropical	Van Noort (2017)
Bathythrix sp.	BOB 2	Nearctic	CNC
Diapetimorpha sp.	BOB 11	Neotropical	CNC
Diracela latifasciata (Cameron)	BOB 0	Afrotropical	Van Noort (2017)
Gelis apterus (Pontoppidan) female	BOB 0	Palearctic	Korenko et al. (2013)
Madastenus nigrinotus Seyrig	BOB 0	Afrotropical	CNC
Polycyrtus condylobus[a]	BOB 5	Neotropical	Zúñiga Ramírez (2004)
P. duplaris[a]	BOB 5	Neotropical	Zúñiga Ramírez 2004
P. latigulus[a]	BOB 5	Neotropical	Zúñiga Ramírez (2004)
P. luisi[a]	BOB 5	Neotropical	Zúñiga Ramírez (2004)
P. nanii[a]	BOB 5	Neotropical	Zúñiga Ramírez (2004)
Ichneumoninae			
Jacotitypus sp.	BOB 0	Afrotropical	CNC
Joppa sp.	BOB 0, 7	Neotropical	CNC
Pimplinae			
Acrotaphus chedelae Gauld	BOB 5	Neotropical	MNCR
A. fasciatus (Brullé)	BOB 5	Neotropical	Gauld (1991)
A. franklini Gauld	BOB 11	Neotropical	MNCR
A. latifasciatus (Cameron)	BOB 5	Neotropical	MNCR
A. tibialis (Cameron)	BOB 5	Neotropical	CNC, MNCR
Calliephialtes grapholithae (Cresson)	BOB 9	Nearctic	CNC
C. guevarae[a]	BOB 11	Neotropical	Gauld (1991)
C. ledezmae[a]	BOB 0	Neotropical	Gauld et al. (1998)
Clydonium moragai[a]	BOB 9	Neotropical	Gauld et al. (1998)
Polysphincta janzeni[a]	BOB 9	Neotropical	Gauld (1991)
Tryphoninae			
Boethus taeniatus Townes & Gupta	BOB 0	Neotropical	Gauld (1997)
Oedemopsis cyranoi[a]	BOB 9	Neotropical	Gauld (1997)
O. dentipara[a]	BOB 9	Neotropical	Gauld (1997)
O. noyesi[a]	BOB 9	Neotropical	Gauld (1997)
O. ojoa[a]	BOB 0	Neotropical	Gauld (1997)
O. quemadoi[a]	BOB 9	Neotropical	CNC, Gauld (1997)
O. riyitoi[a]	BOB 0, 9	Neotropical	Gauld (1997)

[a]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	Palearctic	CNC
B. ebulus (Nixon)	BOB 9	Indo-Malayan	CNC
Braunsia fumipennis (Cameron)	BOB 9	Indo-Malayan	Sharkey and Clutts (2011)
Cremnops violaceipennis (Cameron)	BOB 10	Neotropical	Tucker et al. (2015)
Euagathis ophippium (Cameron)	BOB 0	Indo-Malayan	van Achterberg and Long (2010)
Zelodia anginota[a]	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 0	Australasian	CNC
Bracon campyloneurus Szépligeti	BOB 0	Afrotopical y Australasian	CNC
Calobracon sp.	BOB 0	Nearctic	CNC
Compsobracon sp.	BOB 9	Neotropical	MZUCR
Cyanopterus sp.	BOB 0	Neotropical	CNC
Digonogastra sp.	BOB 0	Neotropical	CNC
Gracilibracon sp.	BOB 0, 1	Neotropical	MZUCR
Megabracon sp.	BOB 5	Neotropical	MNCR
Pycnobraconoides mutator (Fabricius)	BOB 0	Australasian	CNC
Cardiochilinae			
Cardiochiles fallax Kokujev	BOB 9	Palearctic	Farahani et al. (2015)
Cardiochiles sp.	BOB 2	Neotropical	MZUCR
Toxoneuron leve (Mao)	BOB 9	Nearctic	CNC
Cenocoelinae			
Capitonius pulcher (Cameron)	BOB 5	Neotropical	CNC, MNCR
C. tricolorvalvus Ent	BOB 0	Neotropical	MNCR, MZUCR
Cenocoelius sp.	BOB 0	Neotropical	CNC
Charmontinae			
Charmon cruentatus Haliday	BOB 0	Holarctic	CNC
C. extensor (Linnaeus)	BOB 0	Holarctic	CNC
Cheloninae			
Leptodrepana atalanta Dadelahi & Shaw	BOB 0	Neotropical	Dadelahi et al. (2018)
L. conda Dadelahi & Shaw	BOB 9	Neotropical	Dadelahi et al. (2018)
L. conleyae Dadelahi & Shaw	BOB 0	Neotropical	Dadelahi et al. (2018)
L. demeter Dadelahi & Shaw	BOB 0	Neotropical	Dadelahi et al. (2018)
L. lorenae Dadelahi & Shaw	BOB 9	Neotropical	Dadelahi et al. (2018)
L. munjuanae 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 9	Neotropical	Dadelahi et al. (2018)
L. scottshawi Dadelahi	BOB 0	Neotropical	Dadelahi et al. (2018)
L. stasia Dadelahi & Shaw	BOB 0	Neotropical	Dadelahi et al. (2018)
Microchelonus rubescens[a]	BOB 0	Neotropical	Papp (2010)
M. ruficollis Viereck	BOB 9	Neotropical	Papp (2010)
Doryctinae			
Gymnobracon megistus Marsh	BOB 0	Neotropical	CNC, MNCR
Megaloproctus strongylogaster (Cameron)	BOB 5	Neotropical	MNCR
Odontobracon batesi Roman	BOB 0	Neotropical	CNC
O. janzeni Marsh	BOB 5	Neotropical	MNCR
Pedinotus columbianus Enderlein	BOB 0	Neotropical	CNC
Macrocentrinae			
Macrocentrus bicolor Curtis	BOB 0	Palearctic	van Achterberg (1993)
Meteorinae			
Meteorus sp.	BOB 0	Nearctic	CNC
Orgilinae			
Orgilus sp.	BOB 9	Neotropical	MZUCR
Rogadinae			
Aleiodes lucidus (Szépligeti)	BOB 0	Neotropical	Shimbori and Penteado-Dias (2011)
A. melanopterus (Erichson)	BOB 0	Neotropical	CNC
A. shaworum[a]	BOB 10	Neotropical	Shimbori and Penteado-Dias (2011)

[a]Author names same as reference.

Table 5. Species of Evaniidae with BOB color patterns

Species	Color	Distribution	Reference
Acanthinevania clavaticornis (Kieffer)	BOB 0	Australasian	Deans et al. (2017)
Evania stenochela Kieffer	BOB 0	Palearctic	Deans et al. (2017)
Evaniella erythraspis (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	CNC
Evaniscus rufithorax Enderlein	BOB 9	Neotropical	Mullins et al. (2012)
Hyptia chalcidipennis (Enderlein)	BOB 0, 9	Neotropical	Deans et al. (2017)
H. peruanus (Enderlein)	BOB 9	Neotropical	Deans et al. (2017)
H. reticulata (Say)	BOB 0	Nearctic	CNC
H. rufipectus Dewitz	BOB 0, 9	Neotropical	Deans et al. (2017)
H. rufipes (Fabricius)	BOB 9	Neotropical	Deans et al. (2017)
H. stimulata (Schletterer)	BOB 0	Neotropical	Deans et al. (2017)
Parevania kriegeriana (Enderlein)	BOB 0	Indo-Malyan	Deans et al. (2017)
P. micholitzi (Enderlein)	BOB 9	Indo-Malyan	Deans et al. (2017)
Prosevania erythrosoma (Schletterer)	BOB 0	Afrotropical	Ramage and Martiré (2016)
P. lombokiensis (Szépligeti)	BOB 9	Indo-Malyan	Deans et al. (2017)
P. rufoniger (Enderlein)	BOB 0, 9	Indo-Malyan	Deans et al. (2017)
P. sauteri (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)
S. reticulifer (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)

Among ants (Formicidae), BOB coloration is relatively uncommon (Table 6), occurring primarily in Myrmeciinae (*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. swalei*. 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 in the middle of the mesosoma, resulting in a BOBOB pattern. In the Neotropical region the most common ant showing BOB coloration is *Pseudomyrmex gracilis* (Pseudomyrmecinae), although the coloration is highly variable, ranging from all black to predominantly orange.

There are very few examples of BOB coloration in Apoids, a group that includes Heterogynaeidae, Ampulicidae, Sphecidae, Crabronidae, and bees. Moreover, there is often intraspecific variation in those that do have this color pattern (Table 6). Most *Incastigmus* are predominantly black but a few have BOB coloration: some females of *I. hexagonalis*, and females and some males of *I. pyrrhopyris*. Two other species, *I. ignithorax* Finnamore and *I. thoracicus* Finnamore, show similar intraspecific variation but are yellow-orange instead of red-orange (Finnamore 2002). A few bees, for example, *Andrena clarkella* (Kirby) and *A. thoracica* (Fabricius), have reddish hairs on the mesosoma (BWARS 2016), but these were not included.

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 having this coloration in each family is not currently possible. Nonetheless, our preliminary compilation suggests that BOB coloration is very infrequent in certain taxa (e.g., Cynipoids, Diaprioids, Chalcidoids, and Apoids) and quite common in others (Scelioninae, Evaniidae, 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 these 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

Table 6. Species of Aculeata (excluding Mutillidae) with BOB color patterns

Species	Color	Distribution	Reference
Chrysididae			
Cleptidea balboana Kimsey	BOB 9	Neotropical	MZUCR
C. janzeni Kimsey	BOB 9	Neotropical	MZUCR
C. panamensis Kimsey	BOB 9	Neotropical	MZUCR
Adelphe masneri Kimsey	BOB 0	Neotropical	CNC
Alieniscus: both of the two spp.	BOB 0	Afrotropical	Van Noort (2017)
Anadelphe alvarengai[a]	BOB 9	Neotropical	Kimsey (1987)
Atoposega: all six spp.	BOB 9	Indo-Malayan	Kimsey (2014)
Mahinda sulawesiensis[a]	BOB 0	Indo-Malayan	Kimsey et al. (2016)
Sclerogibbidae			
Sclerogibba talpiformis Benoit female	BOB 0	Afrotropical	Van Noort (2017)
Dryinidae			
Dryinus collaris (Linnaeus)	BOB 9	Palearctic	BWARS (2016)
Rhopalosomatidae			
Olixon myrmosaeforme (Arnold)	BOB 0	Afrotropical	Van Noort (2017)
Thynnidae			
Methocha articulata Latreille female	BOB 0	Palearctic	Agnoli (2011)
Pompilidae			
Aegeniella sp.	BOB 0	Neotropical	CNC
Agenioideus rubicundus Evans	BOB 0	Nearctic	CNC
Balboana sp.	BOB 0	Neotropical	CNC
Dipogon iracundus Townes	BOB 0	Nearctic	CNC
Epipompilus aztecus (Cresson)	BOB 2	Neotropical	MZUCR
E. delicatus Turner	BOB 0	Neotropical	MZUCR
Bradynobaenidae			
Gynecaptera bimaculata (André) female	BOB 0	Palearctic	Romano (2011)
Formicidae			
Camponotus nigriceps (Smith)	BOB 5	Australasian	AntWeb (2018)
C. vicinus Mayr	BOB 5	Nearctic	AntWeb (2018)
Formica rufa Linnaeus	BOB 5	Palearctic	AntWeb (2018)
Dilobocondyla fouqueti Santschi	BOB 5	Indo-Malayan	AntWeb (2018)
Myrmecia spp.	BOB 5	Australasian	AntWeb (2018)
Psudomyrmex gracilis (Fabricius)	BOB 0	Neotropical	MZUCR
Temnothorax isabellae (Wheeler)	BOB 5	Neotropical	AntWeb (2018)
Heterogynaidae			
Heterogyna saudita Gadallah & Soliman female	BOB 0	Palearctic	Van Noort (2017)
Crabronidae			
Alysson tricolor Lepeletier & Serville female	BOB 0	Palearctic	CNC
Incastigmus hexagonalis (Fox) female	BOB 9	Neotropical	Finnamore (2002)
I. pyrrhopyris[a]	BOB 0	Neotropical	Finnamore (2002)
Stigmus sp.	BOB 9	Neotropical	CNC, MZUCR
Trypoxylon sp.	BOB 9	Neotropical	MZUCR

For Mutillidae and *Myrmecia* (Formicidae) see text.
[a]Author names same as reference.

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, *Mymecia* species 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 *Isosomodes* (Eurytomidae), and *Cleptidea* (Chrysididae); in *Leptodrepana* (Braconidae) 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 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	Neotropical	MZUCR
Argidae-Atomacerinae			
Atomacera decepta Rohwer	BOB 9	Neartic	CNC
A. debilis Say	BOB 2	Neartic	CNC
A. ebena Smith	BOB 9	Neotropical	MZUCR
A. lepidula (Konow)	BOB 9	Neotropical	MZUCR
Argidae-Erigleninae			
Sericoceros gibbus (Klug)	BOB 9	Neotropical	MNCR
Argidae-Sterictiphorinae			
Acrogymnia palama Smith	BOB 9	Neotropical	MZUCR
Durgoa sp.	BOB 9	Neotropical	CNC
Hemidianeura leucopoda Smith	BOB 9	Neotropical	CNC, MZUCR
Neoptilia malvacearum (Cockerell)	BOB 9	Neartic	CNC
N. xicana Smith	BOB 9	Neotropical	CNC
Pergidae-Perreyiinae			
Decameria similis (Enderlein)	BOB 9	Neotropical	MZUCR
D. varipes Cameron	BOB 9	Neotropical	MZUCR
Perreya tropica (Norton)	BOB 9	Neotropical	CNC, MZUCR
Tenthredinidae-Allantinae			
Eriocampa ovata Linnaeus	BOB 2	Nearctic	Smith (1979)
Phrontosoma brocca Smith	BOB 2	Nearctic	CNC
P. usta Smith	BOB 9	Nearctic	CNC
Tenthredinidae-Blennocampinae			
Waldheimia amazonica (Kirby)	BOB 9	Neotropical	MZUCR
Tenthredinidae-Selandrinae			
Dolerus rufilobus Ross	BOB 9	Neartic	CNC

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, amisegine chrysidids) are especially well represented, but more research is needed to determine whether they are in fact proportionately better represented than parasitoids of larvae and pupae.

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 spectrophotometric 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, Mutillidae 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* Viereck (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).

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