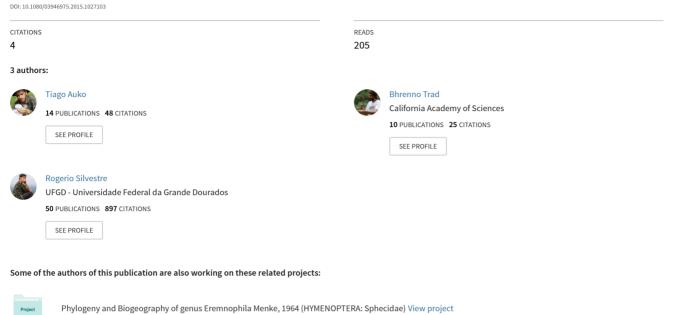
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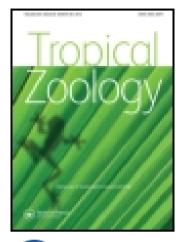
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Bird dropping masquerading of the nest by the potter wasp *Minixi* suffusum (Fox, 1899) (Hymenoptera: Vespidae: Eumeninae)

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The nest of *Minixi suffusum* offers a rare form of mimicry: bird dropping masquerading of the nest by the potter wasp was recorded in mid-western Brazil, in the municipality of Dourados MS. Nesting biology of *M. suffusum* and the material involved in the action of the camouflage were observed. Eleven nests were sampled, with a total of 38 cells. Use of uric acid for staining the cell was evident in all nests. The way that the wasp stains the cells was observed. Substrate nest site, seasonality, larvae biology, sex ratio, prey and parasitoids of *M. suffusum* were reported. Nest camouflage may be related to defense against natural enemies.

Keywords: Ceyxia ventrispinosa; nesting biology; nest camouflage; microlepidoptera; uric acid

Introduction

Some plants and animals are able to mimic inanimate objects such as rocks, twigs, leaves and bird droppings; this adaptation has recently been termed masquerade (Skelhorn, Rowland, Ruxton, et al. 2010; Skelhorn, Rowland, Speed, et al. 2010). Masquerading, crypsis and Batesian mimicry are examples of colourful body signals that may be expressed under high predation risk. Masquerading is an anti-predator adaptation that occurs when an animal's body color and shape mimic an inanimate object (Ruxton et al. 2004; Buresch et al. 2011). Behavior involving bird dropping masquerading by a larval Lepidoptera was recorded by Minno and Emmel (1992), and the effect of bird dropping masquerading by a spider to avoid predators has already been tested (Liu et al. 2014); however, the behavior of masquerading the nest had not been recorded for potter wasps.

Eumeninae has more 3579 species recognized worldwide (Pickett and Carpenter 2010); adults are nectivorous while the larvae are feeding with Lepidoptera (Budriené 2003; Hunt et al. 2003; Budrys and Budriené 2012; Vargas et al. 2014). These wasps have a wide diversity of nesting behavior, ranging from digging nests in the soil, occupying preexisting cavities or building mud nests (West-Eberhard et al. 1995; Sarmiento and Carpenter 2006). Some species possess greater behavior plasticity and construct more than one form of nests (Cooper 1979; Willink and Roig-Alsina 1998; Hermes et al. 2013). More complex nesting biology with the use of vegetable matter for structuring the cell (Bohart and Stange 1965) or nest camouflage (Hermes et al. 2013) has been observed.

Minixi Soika, 1978 is a genus restricted to the Neotropics, with four species known (Giordani Soika 1978; Carpenter and Garcete-Barrett 2002). Analysis of the phylogenetic relationships among species of *Minixi* suggests that the genus is not monophyletic, and

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Minixi suffusum (Fox, 1899) is sister of *Minixi mexicanum* (de Saussure, 1857). *Minixi suffusum* occurs in Bolivia, Paraguay, Argentina and Brazil and all that is known of its nesting biology was the description of one cell of *M. suffusum* collected in Brazil (Corumbá – MS) by Giordani Soika (1978). This cell measured $10 \text{ mm} \times 7 \text{ mm} \times 7 \text{ mm}$ and small stones were added to the mud.

One nest of *M. suffusum* was observed in April 2012 in Dourados municipality MS, Brazil with a whitish substance attached to the mud, characterizing the bird dropping masquerading. Nesting biology of *M. suffusum* with details of larval biology, prey choice and seasonal activity is presented here.

Material and methods

Sampling was carried out in the municipality of Dourados, in the transition area between the Savanna and Atlantic Forest in the mid-western region of Brazil (22°13′S; 54°50′W), from March 2012 to August 2014. Nests were photographed, measured, and removed from the substrate to examine their content and kept at approximately 26°C in the Laboratório de Ecologia de Hymenoptera, Universidade Federal da Grande Dourados (UFGD).

The construction of four cells from two different nests was observed in August 2014. Two of these cells were opened in the laboratory so that we could perform the identification and quantification of prey, and to observe the larval morphology of *M. suffusum* and their parasitoids. Nesting biology of *M. suffusum*, including the behavior of masquerading, was described and filmed based on these four cells. For the videos editing, the software Freemake Video Converter[®] was used.

The sex ratio of *M. suffusum* was analyzed in all cells, which can be determined due to the difference in diameter of the opening occasioned at the time of emergence: the female diameter head is greater (3.9 mm) than the male (3.4 mm) (see Starr 2012). Voucher specimens were deposited in the Museu da Biodiversidade at the UFGD.

Results and discussion

Substrate

Minixi suffusum nests were found on five different substrates (horizontally and vertically), some natural such as branches and vines, while other substrates were derived from humanbuilt structures such as glass, wood and iron (Figure 1). Thus, we conclude that areas with human construction serve as sites with high potential for hosting patches of nests of *M. suffusum*, as well as other species of potter wasps (Camillo 1999; Matthews and González 2004; Matthews and Matthews 2009; Méndez-Abarca et al. 2012). Nests were

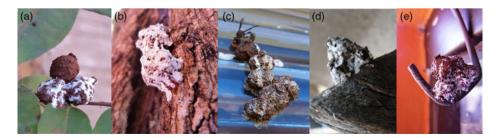


Figure 1. Different types of substrate used by *Minixi suffusum* (Fox, 1899) for fixing the nests. (a) Twigs, (b) liana, (c) glass, (d) wood and (e) iron.

found at different heights ranging from 0.5 to 3.0 m above ground, as noted by Collins and Jennings (1987) for other species of Eumeninae.

Nests

A total of 11 nests of *M. suffusum* were found, totaling 38 cells; the nests varied between two and seven cells. All nests presented a whitish substance, which our observations of *M. suffusum* masquerading the nest showed that it is uric acid obtained in fresh bird droppings, which is inserted into the mud after the construction of the cell. Evidence of the use of uric acid was obtained with stereomicroscope, where we observed arthropod fragments outside the cell (Figure 2), resulting from the feeding of birds.

Seasonality

One nest was found in April 2012, three nests were collected in winter 2013 and seven in winter 2014. They were built in the months of May, June, July and August, during the dry season, contrasting with the nesting activity of other Eumeninae observed in Brazil (Camillo 1999; Buschini and Buss 2010). The period of *M. suffusum* activity was recorded between 9 am and 5 pm, which is common for most Hymenoptera (Hanson and Gauld 1995). The seasonality of wasps probably may be related with the prey activity.

Cell construction

A solitary female can take about 1 h for the construction of a cell. It was observed that the wasp takes about 2-5 min to return to the nest with mud, and the time it takes to transfer all of her mud from mandible to the nest, with the help of the front legs, ranges from 60 to 180 s. The entrance is located by the cell's center, slightly displaced toward the upper part, with an average diameter of 2 mm. A funnel-shaped structure is built by the female around the entrance orifice.

Oviposition

After the end of the construction of the cell, the wasp patrols around the nest possibly checking for the presence of ants. Then, the wasp carries out oviposition, which can take some 85 s. The egg is laid in an empty cell before prey are introduced of the, as is general in Eumeninae (Hanson and Gauld 1995).



Figure 2. Fragments of arthropods typical of bird droppings found in the whitish substance that are used by *Minixi suffusum* (Fox, 1899) for nest masquerading.

Provisioning of prey

With the end of oviposition, the wasp leaves the nest and returns in a few minutes, and begins inserting microlepidoptera into the cell. Once the unidentified moth larva is captured by the female, it manipulates the caterpillar with the mandibles and prothoracic legs (Video 1). The average time she returned to the nest with prey in the mandibles was every eight minutes, a procedure which continued for 12 h. It took about two seconds for transfer of prey inside the cell. In two open cells, one day after the imprisonment of prey, 42 and 58 larvae were recorded (Figure 3(a)).

Prey choice

Only one species of Lepidoptera was recorded, measuring approximately 4 mm in medium length (Figure 3(b),(c)). This is the first prey record for the genus *Minixi*. The prey of potter wasp is little known for Neotropical species; elsewhere, four species of Eumeninae have been recorded as preferring a single family of Lepidoptera (Collins and Jennings 1987; Sears et al. 2001; Vargas et al. 2014). The specificity of the prey is correlated with the solitary habit in Vespidae, as the social species (e.g., Polistinae) have a greater variety in their choice of prey (Silva and Jaff 2002).

Larval biology

Five specimens of *M. suffusum* were observed from oviposition to emergence in the laboratory: the time taken for development of female larvae was 27-34 days, while that of the male was 27 days. Removal of the nest possibly hindered the development of some immatures (Figure 4). In some species of eumenine, it has been observed that the male emerges first and awaits the emergence of the female to copulate (Cowan 1986).

Sex ratio

The sex ratio of *M. suffusum* was 2:2 female/male (Table 1), and the difference for other species of Eumeninae was observed in Brazil, where males were more abundant (Budriené and Budrys 2007; Silva 2008). Some sampled nests had already seen emergence but could be included due to the hole diameter of the emerging adult, as the size difference between the sexes' heads is evident (Figure 5). Cells of both sexes have relatively similar sizes, which is unusual if compared to other species of potter wasps (Fateryga 2013).



Figure 3. Microlepidoptera found in cells of *Minixi suffusum* (Fox, 1899). (a) Contents of one cell opened in the laboratory; (b) dorsal view and (c) ventral view.

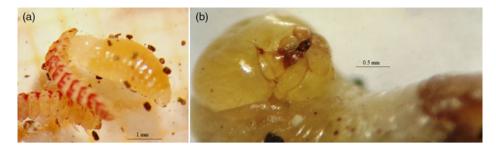


Figure 4. *Minixi suffusum* (Fox, 1899) larvae. (a) Feeding of caterpillar five days after oviposition and (b) 11 days after oviposition the mandible presented signs of sclerotization.

Parasitoids

Ceyxia ventrispinosa Girault, 1911 (Hymenoptera, Chalcididae, Brachymeriini) (Figure 6) was found parasitizing *M. suffusum*. Emergence of the parasitoid occurred 35 days after cell building. This is the first record for a host of *C. ventrispinosa* (Andrade and Tavares 2009).

Uric acid staining

After closing the opening of a cell, the wasp starts to stain the cell and then retouch the entire nest with uric acid obtained from fresh bird droppings approximately two hours old. This group of cells (which together create a nest) is covered by an extra layer of uric acid to provide mechanical strength to the nest covers. The same behavior is recorded to another eumenine species, but only employing mud (Camillo 1999; Matthews and Matthews 2009; Méndez-Abarca et al. 2012). It could be suggested that the extra layer is just to enhance the masquerade. For painting the cells, the wasp collects uric acid with its mandibles, stains the cell, incorporating the uric acid into the mud and allowing a more robust framework for the nest, a greater attachment to the substrate, and strengthens the bond between cells (Video 2).

During the capture of uric acid, we observed that the wasp could take between two and five minutes to return to the nest with the substance. Giordani Soika (1978) did not observe the addition of uric acid by *M. suffusum* described here, when he described a cell from another location of Mato Grosso do Sul, Brazil, where the clay had a grayish color, different from the dark red clay color found in the municipality of Dourados – MS.

Nest	Cells	Ŷ	0 [*]
1	7	2	
2	3	2	1
3	2	2	_
4	5	3^{a}	2
5	2	2^{a}	_
6	2	_	2^{a}
7	2	_	1
8	3	2	1
9	4	3 ^a	1 ^a
10	3	1	_
11	5	3	1

Table 1. Number of cells per nest of Minixi suffusum (Fox, 1899) and its sex ratio.

^aCells of *Minixi sufussum* with signals of emergence.

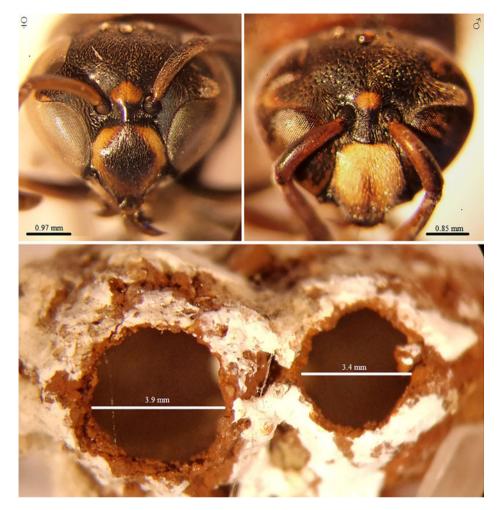


Figure 5. Heads of Minixi suffum (Fox, 1899) and entrances to the cells.



Figure 6. Ceyxia ventrispinosa Girault, 1911, found parasitizing Minixi suffusum (Fox, 1899).

Adaptations in the mandible may be the key to understand this behavior of M. *suffusum*, as has been observed in the mandible adaptations that occur in other eumenines using vegetable raw materials to add to the mud (Cooper 2012).

Bird dropping masquerading

Uric acid added after the construction of cells by *M. suffusum* is probably a defense against natural enemies, causing the nests to resemble a bird dropping (Figure 1). This defensive strategy is assuming to avoid predation by be misidentified as an inedible object by their predators (Skelhorn, Rowland, Speed, et al. 2010). This behavior may be related to defense mainly against parasitoids, ants, bats and birds (Krombein 1979; West-Eberhard et al. 1995; Liu et al. 2014). Nest masquerading can hinder the action of parasitoids that use the mandible and the ovipositor to puncture the cell wall of mud, but not for parasitoids that act during the nesting (Berland and Bernard 1938; Gauld and Hanson 1995). Auko et al. (2014) recorded *M. suffusum* being parasitized by *Chrysis* sp. (gr. *intricans*) that possibly occurred during cell construction, as recorded for other *Chrysis* species (Kimsey and Bohart 1990). This possibly happened with *C. ventrispinosa* recorded here. Chapman (1969) noted that the parasitoids of wasps that nest in mud prefer unprotected cells. We realize that when the nest is fixed to dark substrates, the wasp inserts a smaller amount of uric acid, leaving the nest as clearly white.

Use of arthropod fragments for nest camouflage (Auko et al. 2013) or protection (Staab et al. 2014) has been observed in other species of solitary wasps. Nest camouflage in potter wasps involving other materials in addition to mud has already been recorded, such as lichens (Bertoni 1918), lumps of mud (Jayakar and Spurway 1965) and vegetable matter (Hermes et al. 2013). This is the first time that this particular masquerading behavior has been reported in eumenines. Species using the masquerading strategy in the form of a bird dropping in with intent of avoiding parasitic wasps is already known for other invertebrates (Minno and Emmel 1992; Liu et al. 2014). Although this is the first use of this strategy for masquerading of the nest, the knowledge of nesting biology of eumenines is restricted to a few species in the Neotropical region (Bertoni 1929; Camillo 1999, 2001; Méndez-Abarca et al. 2012).

Perhaps, in addition to masquerading, the chemical composition of uric acid can serve as a repellent to their natural enemies, with chemical requirements, e.g. ants, or even influence the climatic conditions of the nest, since these nests are found at sites exposed to sunlight and thus uric acid may function as a reflector of light. Future research may reveal whether there is more than one function involved in this behavior of staining the nest.

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Disclosure statement

No potential conflict of interest was reported by the authors.

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Supplementary material

Supplementary data for this article can be accessed at doi: 10.1080/03946975.2015.1027103.

References

- Andrade TV, Tavares MT. 2009. Revisão de Ceyxia Girault, stat. Rev. (Hymenoptera, Chalcididae, Brachymeriini). Revista Brasileira de Entomologia. 53(4):511–548. doi: 10.1590/S0085-56262009000400004
- Auko TH, Silvestre R, Pitts JP. 2013. Nest camouflage in the spider wasp *Priochilus captivum* (Fabricius, 1804) (Hymenoptera: Pompilidae), with notes on the biology. *Tropical Zoology*. 26(3):140–144. doi: 10.1080/03946975.2013.835636
- Auko TH, Trad BM, Silvestre R. 2014. Five new associations of parasitoids in potter wasps (Vespidae, Eumeninae). *Revista Brasileira de Entomologia*. 58(4):376–378. doi: 10.1590/ S0085-56262014005000004
- Berland L, Bernard F. 1938. Faune de France. In: Hymenoptères vespiformes III. Paris: Fédération Française des Sociétés de Sciences Naturelles; 146 p.
- Bertoni AW. 1918. Contribución al conocimiento de los himenópteros diplópteros americanos (especies y nidos nuevos o pocos conocidos). Anales Científicos Paraguayos. 2:184–202.
- Bertoni AW. 1929. Nidificación en colonias de abejas antofóridas sus huéspedes y parasitos. *Revista de la Sociedad Científica del Paraguay*. II(5):223–224.
- Bohart RM, Stange LA. 1965. A revision of the genus Zethus Fabricius in the western hemisphere (Hymenoptera: Eumenidae). Vol. 40. Los Angeles (CA): University of California Press: Publications in Entomology; 208 p.
- Budriené A. 2003. Prey of Symmorphus wasps (Hymenoptera: Eumeninae) in Lithuania. Acta Zoologica Lituanica. 13(3):306–310.
- Budriené A, Budrys E. 2007. Comparison of mating of ten Eumeninae wasp species with a brief review of sexual selection theories: a framework for future research. Acta Zoologica Lituanica. 17(2):87–104.
- Budrys E, Budriené A. 2012. Adaptability of prey handling effort in relation to prey size in predatory wasps (Hymenoptera: Eumeninae). *Annales Zoologici Fennici*. 49(1–2):58–68. doi: 10.5735/ 086.049.0106
- Buresch KC, M\u00e4thger LM, Allen JJ, Bennice C, Smith N, Schram J, Chiao C-C, Chubb C, Hanlon RT. 2011. The use of background matching vs. masquerade for camouflage in cuttlefish Sepia officinalis. Vision Research. 51(23–24):2362–2368. doi: 10.1016/j.visres.2011.09.009
- Buschini MLT, Buss CE. 2010. Biologic aspects of different species of *Pachodynerus* (Hymenoptera; Vespidae; Eumeninae). *Brazilian Journal of Biology*. 70(3):623–629. doi: 10. 1590/S1519-69842010000300020
- Camillo E. 1999. A solitary mud-daubing wasp *Brachymenes dyscherus* (Hymenoptera: Vespidae) from Brazil with evidence of a life-cycle polyphenism. *Revista de Biologia Tropical*. 47:949–958.
- Camillo E. 2001. Inquilines of *Brachymenes dyscherus* nests with special reference to *Monobia* schrottkyi (Hymenoptera, Vespidae, Sphecidae). Revista de Biologia Tropical. 49(3-4): 1005–1012.
- Carpenter JM, Garcete-Barrett BR. 2002. A key to the Neotropical genera of Eumeninae (Hymenoptera: Vespidae). *Boletín del Museo Nacional de Historia Natural del Paraguay*. 14(1-2):52–73.
- Chapman RF. 1969. The insects, structure and function. London: English Universities Press; 819 p.
- Collins JA, Jennings DT. 1987. Nesting height preferences of eumenid wasps (Hymenoptera: Eumenidae) that prey on Spruce Budworm (Lepidoptera: Tortricidae). *Annals of the Entomological Society of America*. 80(3):435–438. doi: 10.1093/aesa/80.3.435
- Cooper KW. 1979. Plasticity in nesting behavior of a renting wasp, and its evolutionary implications. Studies on eumenine wasps VIII (Hymenoptera, Aculeata). *Journal of the Washington Academy* of Sciences. 69:151–158.
- Cooper M. 2012. New species of *Pararhaphidoglossa* von Schulthess (Hymenoptera: Vespidae, Eumeninae): I, the Mestiza and Cressoniana groups. *Entomologist's Monthly Magazine*. 148:163–171.
- Cowan DP. 1986. Sexual behavior of eumenid wasps (Hymenoptera: Eumenidae). Proceedings of the Entomological Society of Washington. 88(3):531–541.

- Fateryga AV. 2013. The nest structure in four wasp species of the genus *Euodynerus* Dalla Torre (Hymenoptera, Vespidae: Eumeninae). *Entomological Review*. 93(4):412–421. doi: 10.1134/ S0013873813030027
- Gauld ID, Hanson PE. 1995. The chrysidoid families. Hanson, P.E. & Gauld, I.D. (Orgs.) In: Hymenoptera of Costa Rica. London: Oxford Science Publications, The Natural History Museum; p. 464–503.
- Giordani Soika A. 1978. Revisione degli Eumenidi Neotropicali appartenenti ai generi Eumenes Latr., Omicron (Sauss.), Pararhaphidoglossa Schulth. ed affini. Bollettino del Museo Civico di Storia Naturale di Venezia. 29:1–420.
- Hanson PE, Gauld ID. 1995. Hymenoptera of Costa Rica. London: Oxford Science Publications, the Natural History Museum; p. 893.
- Hermes MG, Melo GAR, Carpenter JM. 2014. The higher-level phylogenetic relationships of the Eumeninae (Insecta, Hymenoptera, Vespidae), with emphasis on *Eumenes sensu lato*. *Cladistics*. 30(5):453–484. doi: 10.1111/cla.12059
- Hermes MG, Somavilla A, Garcete-Barrett BR. 2013. On the nesting biology of *Pirhosigma* Giordani Soika (Hymenoptera, Vespidae, Eumeninae), with special reference to the use of vegetable matter. *Revista Brasileira de Entomologia*. 57(4):433–436. doi: 10.1590/S0085-56262013005000044
- Hunt JH, Buck NA, Wheeler DA. 2003. Storage proteins in vespid wasps: characterization, developmental pattern, and occurrence in adults. *Journal of Insect Physiology*. 49(8):785–794. doi: 10.1016/S0022-1910(03)00115-X
- Jayakar SD, Spurway H. 1965. Normal and abnormal nests of *Eumenes emarginatus conoideus* (Gmelin) including notes on *crèpissage* in this and other members of the genus (Vespoidea, Hymenoptera). *Journal of the Bombay Natural History Society*. 62:193–200.
- Kimsey LS, Bohart RM. 1990. The chrysidid wasps of the world. New York (NY): Oxford University Press; 652 p.
- Krombein KV. 1979. Vespoidea. In: Krombein KV, Hurd Jr, PD, Smith DR, Burks BD, editors. Catalogue of hymenoptera in America North of Mexico. 2th ed. Washington (DC): Smithsonian Institution Press; p. 1469–1522.
- Liu M-H, Blamires SJ, Liao C-P, Tso I-M. 2014. Evidence of bird dropping masquerading by a spider to avoid predators. *Scientific Reports*. 4:1–5.

Downloaded by [179.145.58.182] at 18:14 28 June 2015

- Matthews RW, González JM. 2004. Nesting biology of Zeta argillaceum (Hymenoptera: Vespidae: Eumeninae) in Southern Florida, U.S. Florida Entomologist. 87(1):37–40. doi: 10.1653/0015-4040(2004)087[0037:NBOZAH]2.0.CO;2
- Matthews RW, Matthews JR. 2009. Nesting behavior of *Abispa ephippium* (Fabricius) (Hymenoptera: Vespidae: Eumeninae): extended parental care in an Australian mason wasp. *Psyche*. 2009:1–15. doi: 10.1155/2009/851694
- Méndez-Abarca F, Mundaca EA, Vargas HA. 2012. First remarks on the nesting biology of *Hypodynerus andeus* (Packard) (Hymenoptera, Vespidae, Eumeninae) in the Azapa valley, northern Chile. *Revista Brasileira de Entomologia*. 56:240–243.
- Minno MC, Emmel TC. 1992. Larval protective coloration in swallowtails from the Florida keys (Lepidoptera: Papilionidae). *Tropical Lepidoptera*. 3(1):47–49.
- Pickett KM, Carpenter JM. 2010. Simultaneous analysis and the origin of eusociality in the Vespidae (Insecta: Hymenoptera). Arthropod Systematics and Phylogeny. 68:3–33.
- Ruxton GD, Sherratt TN, Speed MP. 2004. Avoiding attack, the evolutionary ecology of crypsis, warning signals and mimicry. Oxford: Oxford University Press.
- Sarmiento CE, Carpenter JM. 2006. Familia Vespidae. In: Fernández F, Sharkey MJ, editors. Introducción a los Hymenoptera de la Región Neotropical. Bogotá (DC): Sociedad Colombiana de Entomologia y Universidad Nacional de Colombia; p. 539–555.
- Sears ALW, Smiley JT, Hilker M, Müller F, Rank NE. 2001. Nesting behavior and prey use in two geographically separated populations of the specialist wasp *Symmorphus cristatus* (Vespidae: Eumeninae). *American Midland Naturalist*. 145(2):233–246. doi: 10.1674/0003-0031(2001) 145[0233:NBAPUI]2.0.CO;2
- Silva ER, Jaff K. 2002. Expanded food choice as a possible factor in the evolution of sociality of Vespidae (Hymenoptera). *Sociobiology*. 39(1):1–12.
- Silva JF. 2008. Vespas solitárias (Hymenoptera: Aculeata) nidificando em ninhos-armadilha na Estação Ecológica de Ribeirão Preto, Mata Santa Teresa, Ribeirão Preto, SP [dissertation]. [Faculdade de Filosofia, Ciências e Letras de Ribeirão Preto]: Universidade de São Paulo.

- 10 *T.H. Auko* et al.
- Skelhorn J, Rowland HM, Ruxton GD. 2010a. The evolution and ecology of masquerade. *Biological Journal of the Linnean Society*. 99(1):1–8. doi: 10.1111/j.1095-8312.2009.01347.x
- Skelhorn J, Rowland HM, Speed MP, Ruxton GD. 2010. Masquerade: camouflage without crypsis. Science. 327(5961):51. doi: 10.1126/science.1181931
- Staab M, Ohl M, Zhu C-D, Klein A-M. 2014. A unique nest-protection strategy in a new species of spider wasp. PLoS ONE. 9(7):e101592. doi: 10.1371/journal.pone.0101592
- Starr CK. 2012. Nesting biology and sex ratio in a neotropical spider wasp, *Priochilus captivum* (Hymenoptera: Pompilidae). *Tropical Zoology*. 25(2):62–66. doi: 10.1080/03946975.2012. 682799
- Vargas HA, Vargas-Ortiz M, Huanca-Mamani W, Hausmann A. 2014. Prey identification in nests of the potter wasp *Hypodynerus andeus* (Packard) (Hymenoptera, Vespidae, Eumeninae) using DNA barcodes. *Revista Brasileira de Entomologia*. 58(2):157–160. doi: 10.1590/S0085-56262014000200007
- West-Eberhard MJ, Carpenter JM, Hanson PE. 1995. The vespid wasps (Vespidae). In: Hanson PE, Gauld ID, editors. The hymenoptera of Costa Rica. New York (NY): Oxford Science Publications; p. 561–587.
- Willink A, Roig-Alsina A. 1998. Revision del gênero Pachodynerus Saussure (Hymenoptera: Vespidae, Eumeninae). Contributions of the American Entomological Institute. 30(5):1–117.