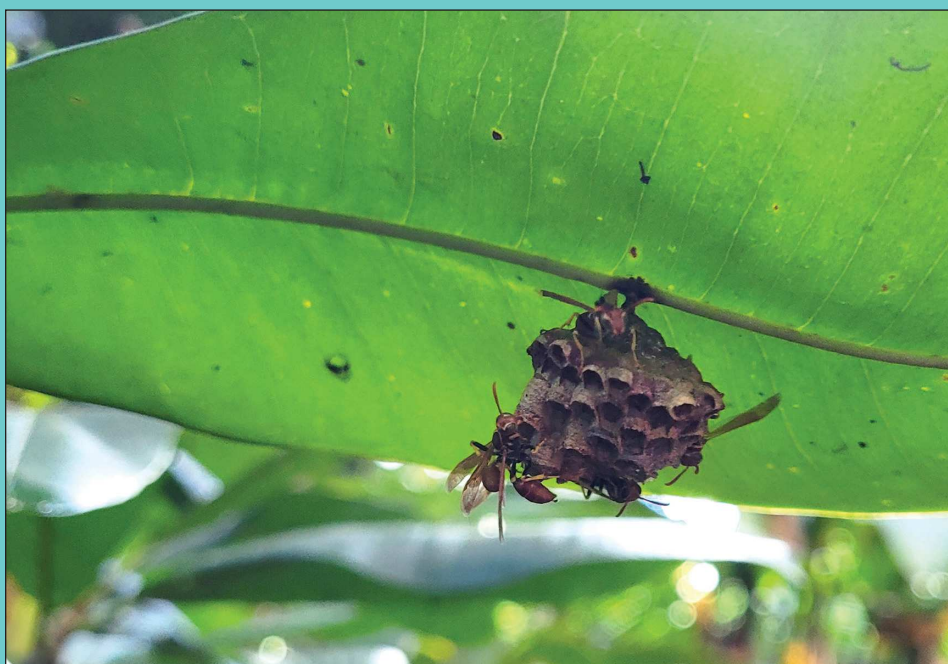


Notes on the Natural History and Climatic Specializations of an Endemic Caribbean Paper Wasp (Hymenoptera: Vespidae: *Mischocyttarus phthisicus*)

Alycia Johnson, Clayton H. Ziemke,
Donald A. Yee, and Kaitlin M. Baudier



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Cover Photograph: A moderately sized centric nest of *Mischocyttarus phthisicus* attached to the species' most typical nesting substrate, the underside mid-rib of a leaf. Photograph © Kaitlin Baudier.

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Notes on the Natural History and Climatic Specializations of an Endemic Caribbean Paper Wasp (Hymenoptera: Vespidae: *Mischocyttarus phthisicus*)

Alycia Johnson¹, Clayton H. Ziemke¹, Donald A. Yee¹, and Kaitlin M. Baudier^{1,*}

Abstract - *Mischocyttarus phthisicus* is a locally abundant social wasp in Puerto Rico with little known of its natural history. Using our own on-site observations and citizen-science reports from iNaturalist, we compiled data on and described this species' occurrence, nesting biology, and colony size. To understand the degree of its climatic specialization, we also compared thermal tolerance across elevations. Nests were most often found on the undersides of broad leaves and were comparable in size to nests of congeners, though likely slightly larger. Heat tolerance, but not cold tolerance, changed with elevation, a result which does not follow Brett's rule.

Introduction

Vespidae is a speciose family that contains nearly all eusocial wasps, including paper wasps in subfamilies Polistinae and Vespinae (Lopez-Osorio et al. 2017). *Mischocyttarus* is the largest genus, with 249 known species distributed primarily in the New World tropics (Carpenter and Genaro 2011, Gadagkar 1991, O'Donnell 2021, Prezoto et al. 2021, Silveira 2008). Like most insects, these are small-bodied ectotherms whose body temperatures are heavily influenced by environmental temperature (Deutsch et al. 2008). Understanding insect thermal biology is important for describing their ranges and dispersal capabilities (Sinclair et al. 2012). Predictions of insect responses to changes in temperature, especially biologically important groups such as pollinators, are necessary going forward into a future of rapid global climate change.

Differences in thermal tolerances across a geographic gradient typically follow both Janzen's rule (Janzen 1967) and Brett's rule (Brett 1956). Janzen's rule, also referred to as the Climatic Variability Hypothesis, states that the thermal tolerance range of an organism broadens with increased environmental temperature variation, such as along a latitudinal or elevational gradient (Janzen 1967). Brett's rule states that the lower thermal limit of an organism is more likely to vary with climatic gradients than the upper limit (Brett 1956). There is a large change in precipitation along the elevational gradient of Puerto Rico, which creates different climatic areas even across relatively small changes in elevation (Beusekom et al. 2015). The degree to which this variation selects for different climatic specializations across life zones is underexplored. Wasps in the genera *Polistes* and *Mischocyttarus* typically build exposed, single-combed nests (Prezoto et al. 2021), making ambient climate

¹University of Southern Mississippi, School of Biological, Environmental, and Earth Sciences, Hattiesburg, MS 39406, USA. *Corresponding author - kaitlin.baudier@usm.edu.

a potentially important selective pressure on their biology. Four such species can be found in Puerto Rico: *Mischocyttarus phthisicus* (Fabricius), *Polistes crinitus* (Felton), *Polistes major* Palisot de Beauvois, and *Polistes minor* Palisot de Beauvois (Carpenter and Genaro 2011). Here, we explore the biology of and potential changes in thermal tolerances across geographic gradients in *M. phthisicus*.

Mischocyttarus phthisicus is native to the Greater Antilles and belongs to the same subgenus (*Phi*) along with 5 other species distributed throughout the Caribbean, Central America, and North America: *Mischocyttarus alfkeni* (Ducke), *Mischocyttarus cassununga* (von Ihering), *Mischocyttarus mexicanus* (de Saussure), *Mischocyttarus baconi* Starr, and *Mischocyttarus flavitarsus* (de Saussure) (Clouse 2001; Gunnels et al. 2008; Litte 1979; Richards 1978; Scobie and Starr 2012, 2016). Despite local abundance of *M. phthisicus* in Puerto Rico, there is little to no published information on its natural history (Arévalo et al. 2004, Starr 2014). Here we provide the first accounts of the nesting biology of *M. phthisicus* while also expanding our understanding of the occurrence of the species across elevations and islands in the Caribbean.

Measuring the thermal limits of an animals' physiological function can be useful for exploring evolutionary processes that have given rise to extant variation in phenotypes, but these metrics can also be used to estimate relative risk of extirpation due to anthropogenic warming (Deutsch et al. 2008, Sinclair et al. 2012). We tested hypotheses related to how climatically specialized *M. phthisicus* is across elevations in Puerto Rico. Under the Climatic Variability Hypothesis, we predicted that *M. phthisicus* would show a widening thermal tolerance range as elevation increased. In line with Brett's Rule, we predicted that most of this change would be driven by changes in cold tolerance and not heat tolerance. However, Puerto Rico exhibits only a moderate elevational range of 1339 m, which according to first principles is expected to generate less than 2 °C difference in average air temperature between high-elevation and low-elevation sites (Lazaridis 2010, MacAurthur 1972). For this reason, we expected that differences in thermal tolerance across elevations, if present, would be small.

Methods

Estimating range, colony size, and nesting locations using citizen-science data

We downloaded 70 "research-grade" observations of *M. phthisicus* from iNaturalist that had been recorded between 2003 and 2022 and used these data to describe geographic occurrence, nesting substrate, and nest cell number (iNaturalist 2023). To be accepted as research-grade, the entry must include a location and a picture, and the identification must be widely agreed upon in the iNaturalist community. We then confirmed correct species identification in each photo using a dichotomous key (Silveira 2008). We compiled location data into a map using QGIS version 3.26.3 (<https://www.qgis.org>). Based on user-submitted photos from each observation, we categorized nest substrate (the surface to which the nest pedicel attached) as: leaf, vine, manmade, or grass. We excluded 6 observations with unclear nest habitats and 5 observations in which no nest was pictured. We then categorized observations as

low elevation (below 490 m) or high elevation (above 490 m). In each observation photo, we counted the number of nest cells.

Estimating thermal tolerance

In June 2022, we collected 18 female wasps from unique colonies (2 wasps per colony) at high- and low-elevational sites in the Luquillo Mountains of Puerto Rico. The first site was near El Verde Field Station at 350 m. The second site was near the Palo Colorado Recreation Area in El Yunque National Park at 630 m (the highest site where this species was observed in El Yunque).

We transported collected wasps to the lab in 5-dram plastic vials, each containing moistened paper towel to provide water ad libitum. The wasps were then subjected to maximum critical temperature (CT_{max}) or minimum critical temperature (CT_{min}) assays within 4 hours of capture. We used standard dynamic methods to estimate upper and lower critical temperatures (Bishop et al. 2017, Lutterschmidt and Hutchison 1997). We placed subjects into 1.5-mL conical tubes capped with cotton to prevent thermal refuge in the upper portion of the tube. We placed 1 wasp from each colony into a dry heat bath set to 30 °C for CT_{max} . We placed the other collected wasp into a digital chilling dry bath set to 20 °C for CT_{min} . During the assay, temperature increased or decreased (respectively) by 1 °C every 10 mins. After every 10-min interval, we checked all wasps for a movement response to light flicking of the vial (physical stimulus). We deemed any wasp without an observed movement 10 sec following the flick to have exceeded its CT_{max} or CT_{min} , respectively.

Extrapolated climate data

We compared temperature across high and low elevations using extrapolated climate data. We used nest coordinates collected using a phone GPS (iPhone 11; Apple, Cupertino, CA, USA) to extract historic climate data from Worldclim using the ‘raster’ package (Fick and Hijmans 2017, Hijmans 2022). We downloaded Bioclimatic variables Bioclim 5 (hottest temperature in the hottest month) and Bioclim 6 (coldest temperature in the coldest month) at a resolution of 1 km².

Statistical analyses

We compared critical temperature data across elevations using Mann–Whitney U tests because the data were not normally distributed. We used a chi-squared analysis to test whether nesting substrate differed between high and low elevations. We performed all analyses in R version 4.2.1 (R Core Team 2022).

Results

Geographic distribution

Research grade iNaturalist records of *M. phthisicus* were from 4 islands: eastern Hispaniola (Dominican Republic), Puerto Rico, and St. Thomas and St. John of the US Virgin Islands (Fig. 1A). The island with the most observations was Puerto Rico. *Mischocyttarus phthisicus* were reported across elevations varying from sea level to 1025 m.

Preferred nesting substrate

Of the 70 research-grade observations from iNaturalist, there were 22 and 48 observations from high and low elevations, respectively (18 high and 41 low observations of wasps in the same image as their nest; Table 1). Over half of 59 observed nests (~53%) used a leaf or some other wide organic cover at the nest substrate, whereas ~26% of colonies were observed nesting on vines or narrow organic cover (Table 1). Only 2 observations showed a nest on a manmade structure, and 2 observations showed a nest on grass. High- and low-elevation sites did not differ in nesting substrate (chi-squared test: $\chi^2 = 1.36$; $df = 3$; $P = 0.714$).

Nest size and morphology

The number of cells per nest varied from 2 to 362 (Fig. 1B), although few exceeded 100 cells. The median number of cells per nest was 32. Nests of *M. phthisicus*

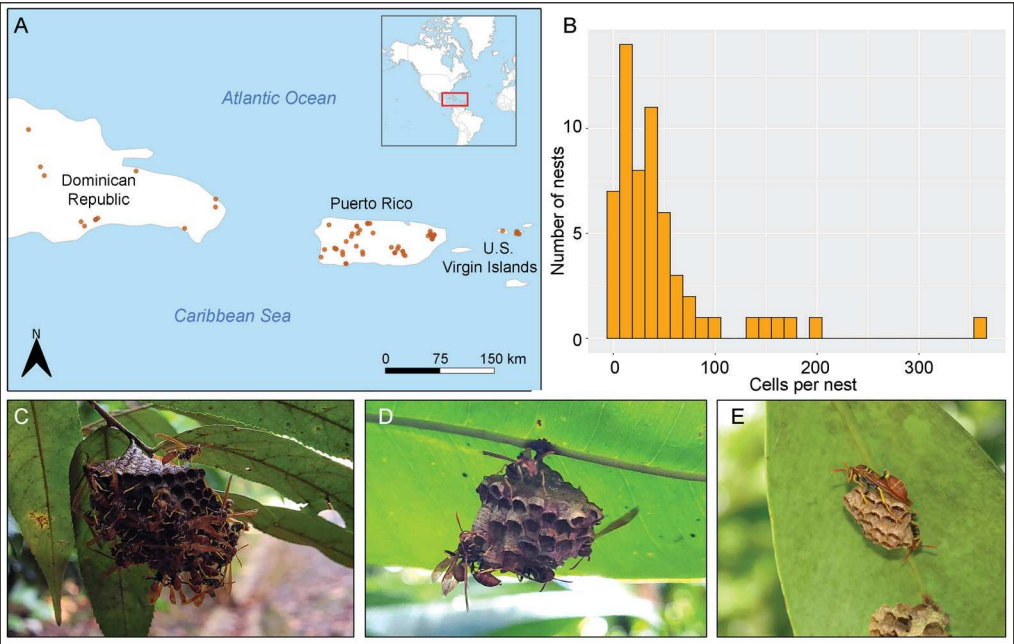


Figure 1. (A) Geographic distribution of 70 research-grade iNaturalist observations of *Mischocyttarus phthisicus* recorded between 2003 and 2022 (orange points). (B) Histogram of nest size frequency among a subset of observations in which a nest was visible in the photo ($n = 59$). (C) A mature eccentric nest with asymmetric distribution of cells around nest pedicel (Photograph © by K.M. Baudier). (D) A mid-size centric nest (Photograph © K.M. Baudier). (E) An early centric nest founded within centimeters of a conspecific, abandoned nest (Photograph © C. Ziemke).

Table 1. Summary of wasp colony nesting site choice across high and low elevations based on iNaturalist observations.

Elevation	Leaf	Vine	Grass	Manmade
High	12	4	1	1
Low	25	14	1	1
Total	37	18	2	2

were open and varied between centric (round, pedicel attached towards the middle of the nest) and eccentric in form (elongate, pedicel attached asymmetrically), with nests more commonly centric when attached to the underside of broad leaves, and more commonly eccentric when attached to stems, vines, or twigs (Fig. 1C–E).

Thermal tolerance across elevations

The low-elevation site (330–350 m) had a maximum temperature of 29 °C and a minimum of 16.4 °C. The high-elevation site (600–630 m) had a maximum temperature of 26 °C and a minimum of 14.1 °C. CT_{max} was significantly lower at the high-elevation site than at the low-elevation site (Mann–Whitney U test: $U = 1$, $P = 0.0304$; Fig. 2A), but there was no change in CT_{min} across the sampled elevations (Mann–Whitney U test: $U = 8$, $P = 0.7037$; Fig. 2B). Thermal tolerance breadth ($CT_{max} - CT_{min}$) did not significantly differ across elevations (Mann–Whitney U test: $U = 6$, $P = 0.3749$; Fig. 2C).

Discussion

Both on-site observations and iNaturalist data confirm that *M. phthisicus* is abundant in Puerto Rico. The geographic range of iNaturalist observations was restricted to 4 islands in the Greater Antilles, stretching from Hispaniola in the west to the Virgin Islands in the east. Presence of this species in all these islands has been previously reported (Richards 1978). Whether this represents the full extent of this species' distribution in the Caribbean remains an open question. Citizen-science data can be prone to biases of underreporting in remote areas or those less frequented by tourism (Skvarla and Fisher 2023). As such, additional systematic surveys are needed to establish a more accurate range map for *M. phthisicus*.

Our results provide the first information on the nesting biology of *M. phthisicus*. This species shares many physical and behavioral traits with closely related species, with some key differences in nest size and substrate preference. *Mischocyttarus*

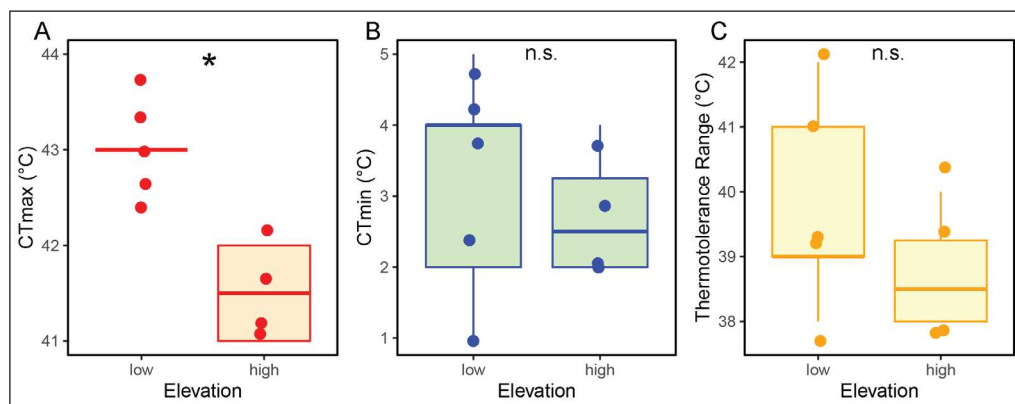


Figure 2. (A) Critical thermal maxima (CT_{max}) across 2 elevations. (B) Critical thermal minima (CT_{min}) across 2 elevations. (C) Thermotolerance range ($CT_{max} - CT_{min}$) across 2 elevations. “*” indicates significant difference ($P < 0.05$) and “n.s.” indicates no significant difference ($P \geq 0.05$). Points are plotted with jitter to improve visibility.

phthisicus seldom nested on manmade structures, preferring to nest on the undersides of plants with broad leaves. This pattern contrasts with several closely related species that readily nest (sometimes preferentially) on manmade structures, including *M. cassununga* (Castro et al. 2014), *M. alfkenii* (O'Connor et al. 2011), and *M. baconi* (Scobie and Starr 2012, 2016). Nesting substrate preferences of *M. phthisicus* appear more like those of *M. mexicanus* (Litte 1977), both commonly nesting on the undersides of broad plant leaves. There were a variety of common substrate plants observed bearing nests of *M. phthisicus* in this study. In Puerto Rico this included species of *Philodendron*, *Dendropanax*, *Epipremnum*, *Anthurium*, *Lagerstroemia*, and *Casearia*. Nests in Puerto Rico also appeared to frequently occur near one another (Fig 1E), often on different leaves of the same plant. This clustering can occur in other polistines when satellite nests are formed (Page et al. 1989). The maximum number of cells observed in our survey exceeded 300, with 10% of nests having more than 100 cells. These results suggest that colonies of *M. phthisicus* vary from comparable in size to slightly larger than those of *M. baconi*, *M. falvitarisus*, and *M. mexicanus* (Litte 1979, Scobie and Starr 2012).

The lack of significant change in CT_{min} but significant decrease in CT_{max} as elevation increased was unexpected, given the small change in elevation, but was consistent with a slightly warmer climate at the low-elevation site. Although this is a small study, our observation of more change in heat tolerance than cold tolerance across geographic space opposes the predictions of Brett's rule (Brett 1956, Gaston et al. 2009) and challenges the widely held notion that CT_{max} may be a more phylogenetically constrained functional trait than CT_{min} (Diamond and Chick 2018). We did not observe wider thermal-tolerance breadths at the more variable low-elevation site, but the difference in temperature variation between the 2 sites was $<1^{\circ}C$, which may be insufficient to generate selective pressure on tolerance breadth that is detectable by our methods. The $12^{\circ}C$ difference between the lowest recorded CT_{max} value and the highest temperature during the hottest month in the lowland site suggest this species is not in immediate danger of extirpation due to acute effects of climatic warming. However, there may be sub-lethal challenges associated with deforestation and climatic transformation outside of the scope of this study. Overall, these results prompt a closer look at the climatic specializations and natural history of tropical island ectotherms.

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Literature Cited

Arévalo, E., Y. Zhu, J.M. Carpenter, and J.E. Strassmann. 2004. The phylogeny of the social wasp subfamily Polistinae: Evidence from microsatellite flanking sequences, mitochondrial COI sequence, and morphological characters. *BMC Ecology and Evolution* 4:1–16.

- Beusekom, A.E.V., G. González, and M.M. Rivera. 2015. Short-term precipitation and temperature trends along an elevation gradient in northeastern Puerto Rico. *Earth Interactions* 19:1–33.
- Bishop, T.R., M.P. Robertson, B.J. Van Rensburg, and C.L. Parr. 2017. Coping with the cold: Minimum temperatures and thermal tolerances dominate the ecology of mountain ants. *Ecological Entomology* 42:105–114.
- Brett, J.R. 1956. Some principles in the thermal requirements of fishes. *Quarterly Review of Biology* 31:75–87.
- Carpenter, J.M., and J.A. Genaro. 2011. Vespidae (Insecta: Hymenoptera) of Puerto Rico, West Indies. *Insecta Mundi* 0202:1–35.
- Castro, M.M.D., D.L. Avelar, A.R.D. Souza, and F. Prezoto. 2014. Nesting substrata, colony success, and productivity of the wasp *Mischocyttarus cassununga*. *Revista Brasileira de Entomologia* 58:168–172.
- Clouse, R. 2001. Some effects of group size on the output of beginning nests of *Mischocyttarus mexicanus* (Hymenoptera: Vespidae). *Florida Entomologist* 84:418–425.
- Deutsch, C.A., J.J. Tewksbury, R.B. Huey, K.S. Sheldon, C.K. Ghalambor, D.C. Haak, and P.R. Martin. 2008. Impacts of climate warming on terrestrial ectotherms across latitude. *Proceedings of the National Academy of Sciences* 105:6668–6672.
- Diamond, S.E., and Chick L.D. 2018. The Janus of macrophysiology: Stronger effects of evolutionary history, but weaker effects of climate on upper thermal limits are reversed for lower thermal limits in ants. *Current Zoology* 64:223–230.
- Fick, S.E., and R.J. Hijmans. 2017. WorldClim 2: New 1-km spatial resolution climate surfaces for global land areas. *International Journal of Climatology* 37:4302–4315.
- Gadagkar, R. 1991. *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent-founding *Ropalidia*. Pp. 149–201, *In* K.G. Ross and R.W. Matthews (Eds.). *The Social Biology of Wasps*. Cornell University Press, Ithaca, NY, USA. 696 pp.
- Gaston, K.J., S.L. Chown, P. Calosi, J. Bernardo, D.T. Bilton, A. Clarke, S. Clusella-Trullas, C.K. Ghalambor, et al. 2009. Macrophysiology: A conceptual reunification. *American Naturalist* 174:595–612.
- Gunnels, C.W., A. Dubrovskiy, and A. Avalos. 2008. Social interactions as an ecological constraint in a eusocial insect. *Animal Behaviour* 75:681–691.
- Hijmans, R. 2022. Raster: Geographic data analysis and modeling. R package version 3.6.3. Available online at <https://CRAN.R-project.org/package=raster>.
- iNaturalist. 2023. Observations of *Mischocyttarus phthisicus* from worldwideobserved on/ between March 2003–October 2022. Available online at <https://www.inaturalist.org>. Accessed 21 February 2023.
- Janzen, D.H. 1967. Why mountain passes are higher in the tropics. *American Naturalist* 101:233–249.
- Lazaridis, M. 2010. First principles of meteorology. Pp. 67–118, *In* First Principles of Meteorology and Air Pollution. Springer, New York, NY, USA. 548 pp.
- Litte, M. 1977. Behavioral ecology of the social wasp, *Mischocyttarus mexicanus*. *Behavioral Ecology and Sociobiology* 2:229–246.
- Litte, M. 1979. *Mischocyttarus flavitarsis* in Arizona: Social and nesting biology of a polistine wasp. *Zeitschrift für Tierpsychologie* 50:282–312.
- Lopez-Osorio, F., K.M. Pickett, J.M. Carpenter, B.A. Ballif, and I. Agnarsson. 2017. Phylogenomic analysis of yellowjackets and hornets (Hymenoptera: Vespidae, Vespinae). *Molecular Phylogenetics and Evolution* 107:10–15.
- Lutterschmidt, W.I., and V.H. Hutchison. 1997. The critical thermal maximum: Data to support the onset of spasms as the definitive end point. *Canadian Journal of Zoology* 75:1553–1560.

- MacArthur, R.H. 1972. Geographical Ecology: Patterns in the Distribution of Species. Princeton University Press, Princeton, NJ, USA. 269 pp.
- O'Connor, T.K., C.K. Starr, and S.A. Cameron. 2011. The Neotropical social wasp *Mischocyttarus 'alfkenii'* Ducke (Hymenoptera: Vespidae) is a pair of ethospecies. Systematic Entomology 36:446–452.
- O'Donnell, S. 2021. *Mischocyttarus*. Pp. 593–598, In C.K. Starr (Ed.). Encyclopedia of Social Insects. Springer, New York, NY, USA. 1075 pp.
- Page, R.E., D.C. Post, and R.A. Metcalf. 1989. Satellite nests, early males, and plasticity of reproductive behavior in a paper wasp. American Naturalist 134:731–748.
- Prezoto, F., F. S. Nascimento, B.C. Barbosa, and A. Somavilla (Eds.). 2021. Neotropical Social Wasps: Basic and Applied Aspects. Springer, New York, NY, USA. 472 pp.
- R Core Team. 2022. R: A language and environment for statistical computing. Version 4.2.1. R Foundation for Statistical Computing, Vienna, Austria.
- Richards, O.W. 1978. The Social Wasps of the Americas Excluding the Vespinae. Pp. 316–317. British Museum (Natural History), London, UK. 580 pp.
- Scobie, A.A., and C.K. Starr. 2012. Nest structure of the Neotropical social wasp *Mischocyttarus baconii* (Hymenoptera: Vespidae). Sociobiology 59:235–239.
- Scobie, A.A., and C.K. Starr. 2016. Notes on colony composition in the social wasp *Mischocyttarus baconii* (Hymenoptera: Vespidae). Living World (Port of Spain) 2016:11–12.
- Silveira, O.T. 2008. Phylogeny of wasps of the genus *Mischocyttarus* de Saussure Silveira (Hymenoptera, Vespidae, Polistinae). Revista Brasileira de Entomologia 52:510–549.
- Sinclair, B.J., C.M. Williams, and J.S. Terblanche. 2012. Variation in thermal performance among insect populations. Physiological and Biochemical Zoology 85:594–606.
- Skvarla, M.J., and R.J. Fisher. 2023. Online community photo-sharing in entomology: A large-scale review with suggestions on best practices. Annals of the Entomological Society of America 116(5):276–304.
- Starr, C.K. 2014. Things we don't know about West Indian social wasps. Living World (Port of Spain) 2014:74–81.