Sociobiology 63(1): 693-698 (March, 2016) DOI: 10.13102/sociobiology.v63i1.854

Sociobiology
An international journal on social insects

RESEARCH ARTICLE - WASPS

Morphological Differences between Reproductive and Non-reproductive Females in the Social Wasp *Mischocyttarus consimilis* Zikán (Hymenoptera: Vespidae)

TS Montagna[1], WF Antonialli-Junior[1,2]

1 - Universidade Federal da Grande Dourados, Dourados-MS, Brazil
2 - Universidade Estadual de Mato Grosso do Sul, Dourados-MS, Brazil

Article History

Edited by
Kleber Del-Claro, UFU, Brazil
Received 22 June 2015
Initial acceptance 28 January 2016
Final acceptance 16 March 2016
Publication date 29 April 2016

Keywords
Caste determination, Division of labor, Dominance hierarchy, Neotropical wasp, Polistinae, Reproductive status.

Corresponding author
Thiago Santos Montagna
Prog. de Pós-graduação em Entomologia
e Conservação da Biodiversidade
Universidade Federal da Grande Dourados
CEP: 79804-970, Dourados-MS, Brazil
E-Mail: thiagomontag@yahoo.com.br

Abstract

Phenotypic divergence plays an important role in establishment of the reproductive division of labor among castes in eusocial insects; however, little is known about this subject in social wasps. We tested the hypothesis that alpha foundressesin colonial foundations of the independent-founding polistine wasp *Mischocyttarus consimilis* Zikán show greater body size and ovarian development than auxiliary and solitary foundresses. The hypothesis was also tested that females produced in the late post-emergence stage (gynes) are larger than those produced at the beginning (workers) of the colony cycle of this species. Our results showed that the body size of alpha foundresses was significantly greater than that of auxiliary foundresses, but did not differ from that of solitary foundresses. In addition, the alpha had greater ovarian development than the auxiliary and solitary. We also demonstrated that gynes were significantly larger than workers. These results therefore suggest that the phenotype of females emerging in colonies of *M. consimilis* can vary with the progress of the colony cycle, and that body size and ovarian state are closely linked to the function performed by the foundress.

Introduction

Insect societies are characterized by the division of labor between the reproductive and non-reproductive castes, which is essential for the success of their societies (Robinson, 1992). In advanced eusocial species, castes are determined pre-imaginally and there is a clear physical divergence between queen and worker (Bourke, 1999). However, in less-advanced eusocial species, morphological divergences between females are less pronounced, and the factors affecting caste differentiation are not well known (Smith et al., 2011; Murakami et al., 2009; 2013; Jandt et al., 2014; Montagna et al., 2015). Nevertheless, evidence suggests that the morphological attributes, such as body size and ovarian state, can play an important role in establishment of the reproductive division of labor in independent-founding (IF) polistine wasps (Tibbetts & Dale, 2004; Tibbetts, 2006; Cervo et al., 2008).

IF polistine wasps are an important model for study of the division of labor in less-advanced eusocial species. Colonies of IF polistine wasps can be initiated individually (haplometrosis), when a reproductive female unaccompanied by other females starts the colony; or by association (pleometrosis), when two or more reproductive females start the colony (West-Eberhard, 1969; Reeve, 1991). In haplometrosis, the foundress performs all the intra- and extra-nidal tasks until the workers emerge (Jeanne, 1972; Gadagkar, 1991). In pleometrosis, the colony tasks are shared among the foundresses, although the reproductive function is performed by one female, who dominates the others (Röseler, 1991; Keeping, 1992; Prezoto et al., 2004). Hence, females with a greater capacity for dominance are more likely to perform the colony reproductive function (Cervo et al., 2008; Zanette & Field, 2009). Since physical attributes are linked to the capacity for dominance, it has been suggested that body size could influence the

Open access journal: http://periodicos.uefs.br/ojs/index.php/sociobiology
ISSN: 0361-6525

reproductive strategies in pleometrotic foundations (Fukuda et al., 2003; Tannure-Nascimento et al., 2008).

In tropical regions, colonies of IF polistine wasps are started at any time of the year, so different colonial stages can occur in the same population in the same period. This nesting cycle pattern is termed asynchronous (Poltronieri & Rodrigues, 1976; O'Donnell & Joyce, 2001; Giannotti, 1998; Torres et al., 2011). The workers are produced at the beginning of the post-emergence stage, and they are mainly dedicated to defending the colony and foraging for food and nest material (Jeanne, 1972; Torres et al., 2011). In contrast, gynes are produced in the late post-emergence stage and generally invest in their own reproduction, contributing little to the maternal colony (Jeanne, 1972; Torres et al., 2011). It is therefore possible that the conditions for the development of immature vary with the progress of the colony cycle, due to fluctuations in the work force, which may be reflected in differences in the body size of emerging females (O'Donnell, 1998; Schmidt et al., 2012).

Mischocyttarus consimilis Zikán is an IF polistine wasp belonging to the subgenus *Phi*, one of the largest groups in the tribe Mischocyttarini, with the most extensive geographic distribution. In *M. consimilis*, the caste system is based on the division of tasks between the reproductive and non-reproductive females, in which the behaviors of oviposition, physical dominance, and nest presence characterize the reproductive caste, while behaviors such as alarm and resource foraging characterize the non-reproductive caste (Torres et al., 2012). In order to investigate morphological differences among castes in *M. consimilis*, we measured the body size and ovarian development of foundresses from haplometrosis and pleometrosis foundations, as well as the body size of females emerging in different phases of the colony cycle.

Materials and Methods

Field procedures and data collection

Colonies of *M. consimilis* were collected from the eaves of vacant houses situated in rural areas in the municipality of Dourados (22º13' S, 54º48' W) in Mato Grosso do Sul, from March 2011 through February 2012. To prevent the loss of individuals, colonies were collected in the early evening when foraging activity had ceased. All the individuals collected were killed by freezing (-20°C), prior to any manipulation procedure.

A total of 59 foundresses from 29 foundations were evaluated for body size and ovarian development. The foundresses were classified as: alpha (female performing the reproductive function in a pleometrotic foundation); auxiliary (each female subordinate to the alpha); and solitary (female of a haplometrotic foundation). Alpha foundresses were identified by direct observation of the oviposition behavior. We encouraged oviposition by the alpha by removing a larva with the aid of tweezers, leaving an empty cell in the comb. Our study did not require an ethics statement; however, we endeavored to minimize the stress caused by manipulation.

Additionally, we evaluated the body sizes of a total of 90 newly-emerged females (<24 h old), from 47 colonies. The newly-emerged females were classified as: worker (female created only by the foundresses); intermediate (female created by foundresses and workers); and gyne (female emerging in the colony reproductive phase). The reproductive phase in colonies of *M. consimilis* occurs in the final post-emergence, when males appear among the offspring (Torres et al., 2011).

Measurements of body size and ovarian development

The measurements of body size, obtained according to Gunnels (2007), were: head height; maximum distance between the inner margins of the eyes; minimum distance between the inner margins of the eyes; mesonotum length; mesonotum width; thorax length; mesopleura height; tibia length; and forewing length. For analysis of ovarian development, the gasters were fixed by immersion in Dietrich's solution, stored in 70% ethanol, and dissected in a petri dish containing physiological saline solution. The ovarian development index was obtained for each female, based on the mean length of the six largest oocytes (Sledge et al., 2004). All measurements of body size and ovarian development were obtained with the aid of a Stemi 2000C stereomicroscope (Carl Zeiss Microscopy, Oberkochen, Germany) fitted with a micrometer eyepiece.

Statistical analyses

All statistical analyses were carried out using R Statistical Environment software (R Development Core Team, 2013), with significance level of 0.05. Morphometric data were subjected to principal component analysis (PCA), and the first PCA component was used as the body size index (Gunnels, 2007). In all cases, the data for body size were normally distributed (Shapiro-Wilk test, $P>0.05$) and showed homogeneity of variance (Bartlett's test, $P>0.05$), so the differences among the categories of females were evaluated by parametric tests, including analysis of variance (one-way ANOVA) and Tukey's test (HSD) for multiple comparisons. The ovarian development data were not normally distributed (Shapiro-Wilk test, $P<0.05$), so differences among groups were assessed by nonparametric tests, including the Kruskal-Wallis and Steel-Dwass test for multiple comparisons.

Results

The PCA with the morphometric data for the foundresses recovered most of the variation among the groups, with the first principal component explaining 82.9% of the total variation and being positively associated with all the measured variables. The second principal component explained an additional 6.7% of the variation. Considering the first principal component as the explanatory variable in the analysis of variance, it was demonstrated that the foundresses differed in body size (one-way ANOVA, $F_{2,56}=9.26$, $P<0.001$, Fig 1).

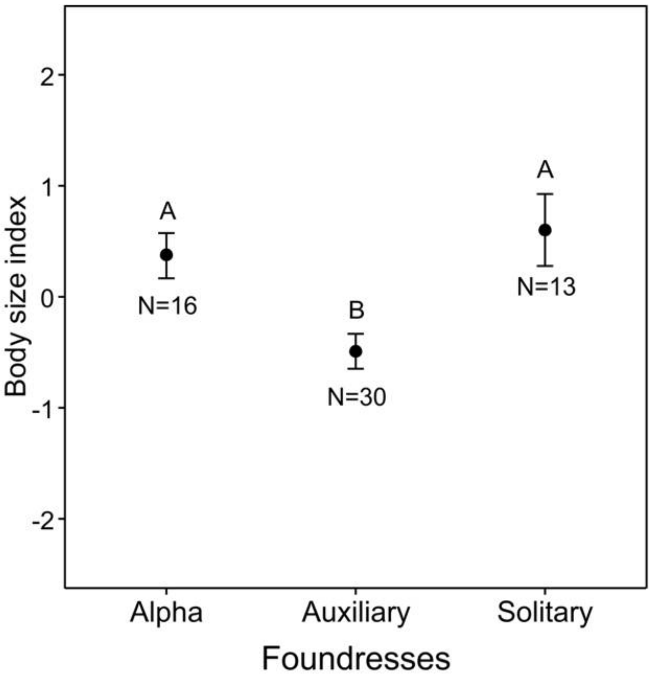

Fig 1. Variation in body size index (mean ± SD) for foundresses of *Mischocyttarus consimilis*. Different letters indicate statistical significance ($P<0.05$).

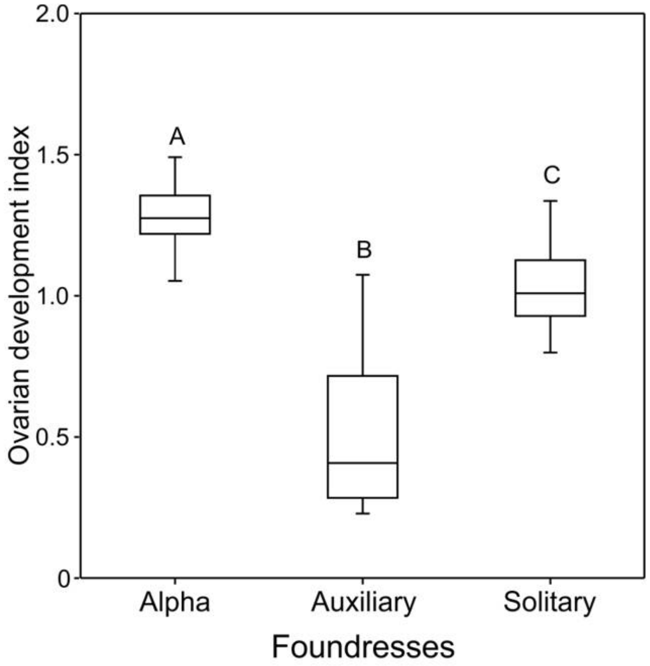

Fig 2. Variation in ovarian development index for foundresses of *Mischocyttarus consimilis*. Box-plot represents the median, 25% - 75% percentiles and minimum/maximum range. Different letters indicate statistical significance ($P<0.05$).

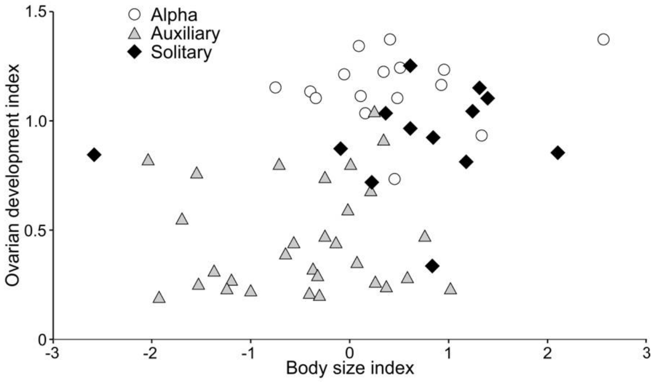

Fig 3. Correlation analyses between the body size index and ovarian development index for foundresses of *Mischocyttarus consimilis* (r=0.41; $P<0.01$).

The analysis comparing the groups demonstrated that alpha foundresses were significantly larger than auxiliary (Tukey's HSD, $P<0.01$, Fig 1), but did not differ from solitary (P=0.78, Fig 1). In addition, solitary foundresses were significantly larger than auxiliary ($P<0.01$, Fig 1).

The three categories of foundresses also differed significantly in the degree of ovarian development (Kruskal-Wallis, H=38.20, df=2, $P<0.001$, Fig 2). Comparison of the groups showed that alpha foundresses had greater ovarian development than auxiliary (Stell-Dwass, $P<0.001$, Fig 2) and solitary (P=0.01, Fig 2), while solitary foundresses had greater ovarian development than auxiliary ($P<0.001$, Fig 2). There was a significant positive correlation between body size and ovarian development when the foundresses were evaluated together (Pearson correlation coefficient; r=0.41, $P<0.01$, n=59, Fig 3).

The PCA performed with the morphometric data for the newly-emerged females recovered most of the variation among the groups. The first principal component was positively associated with all the variables and explained 75.8% of the total data variation. The second principal component explained an additional 5.6% of the variation. Considering the first principal component as the explanatory variable in the analysis of variance, significant differences in body size were found among the categories of newly-emerged females (one-way

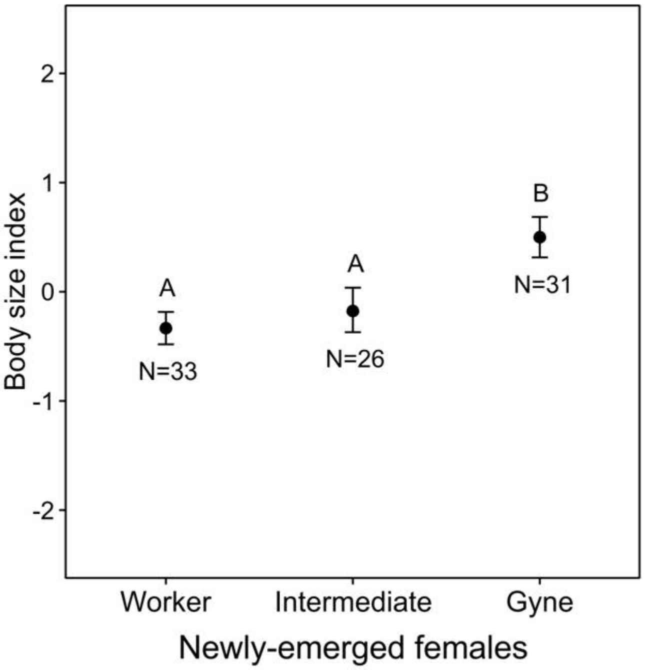

Fig 4. Variation in body size index (mean ± SD) for newly-emerged females in colonies of *Mischocyttarus consimilis*. Different letters indicate statistical significance ($P<0.05$).

ANOVA, $F_{2,87}$=6.86, *P*<0.01, Fig 4). Comparison of the groups showed that the gynes were significantly larger than the workers (Tukey's HSD, *P*<0.01, Fig 4) and the intermediates (*P*=0.02, Fig 4). However, the body size of the workers did not differ significantly from that of the intermediates (*P*=0.79, Fig 4).

Discussion

The results showed that foundresses of *M. consimilis* performing the reproductive function in pleometrotic foundations were significantly larger than their auxiliary. Several studies have shown that in pleometrotic foundations of IF polistine wasps, the colony reproductive function is aggressively disputed among potential females, and larger females have increased chances of subduing smaller competitors (Cant & Field, 2001; Tannure-Nascimento et al., 2008). Under these conditions, the reproductive organization is highly dependent on a dominance hierarchy, with larger females occupying higher positions in this hierarchy (Turillazzi & Pardi, 1977; Cervo et al., 2008). Larger females are therefore more likely to assume colony reproductive functions, suggesting that attributes established during immature development are relevant for the adult behavioral phenotype (Zanette & Field, 2009). Recent studies have shown that pre-imaginal caste determination can occur in IF polistine wasps, and that subtle morphological differences can be decisive in establishing the reproductive division of labor among foundresses (Fukuda et al., 2003; Judd et al., 2015; Montagna et al., 2015). These results provide evidence that body size affects the reproductive organization in pleometrotic foundations of *M. consimilis*.

It was also shown that the solitary foundresses were similar in size to the alpha. In a study with *M. consimilis*, Torres et al. (2011) demonstrated that haplometrotic foundation is the most common strategy adopted by the foundress. Our results suggest that large females with high reproductive potential invest in direct reproduction using the strategies of either fighting for the alpha position in pleometrotic foundations, or founding colonies individually. In addition, individual foundation could be an alternative strategy for large females who refrainfrom disputing the reproductive function in pleometrotic foundations. Nevertheless, these hypotheses need to be evaluated, considering the origins of the females that found colonies alone.

Alpha foundresses had a significantly greater degree of ovarian development, compared to the auxiliary. Furthermore, a significant positive correlation was found between body size and ovarian development, when the foundresses were evaluated together. These data suggest that the degree of ovarian development is closely relatedto both body size and the function performed by the foundress. Other studies have shown that foundresses performing reproductive functions (i.e., alpha and solitary), must invest more in ovarian development (Turillazzi & Pardi, 1977; Dropkin & Gamboa, 1981; Fukuda et al., 2003; Tannure-Nascimento et al., 2008). Moreover, auxiliary foundresses performing activities with high energy costs, such as foraging for resources, are likely to undergo ovarian regression (Keeping, 2000; Cervo et al., 2008).

It was also found that gynes were significantly larger than workers and intermediates, in agreement with other studies that evaluated differences in the body size of offspring females in IF polistine wasps (West-Eberhard, 1969; Haggard & Gamboa, 1980; Miyano, 1983). For example, females of *Polistes fuscatus* (Fabricius) produced in the late post-emergence stage, which were possibly gynes, were larger than workers produced at the beginning of this stage (West-Eberhard, 1969). Since the adult body size in holometabolous insects is fixed before emergence, it is possible that in IF polistine wasps it could be influenced by pre-imaginal trophic factors (Miyano, 1998; Karsai & Hunt, 2002). Differential feeding is known to be the main factors influencing caste determination in the honey bee, *Apis mellifera*, where larvae fed a highly nutritious diet (based on royal jelly) develop into queens (Winston, 1987). The effect of differential feeding in caste determination has also been demonstrated in the bumblebee, *Bombus terrestris*, where larvae that have access to greater amounts of food emerge as queens (Cnaani et al., 2002). In the case of IF polistine wasps, Judd et al. (2010) showed that the development of larvae of *Polistes metricus* into either workers or gynes was significantly influenced by the levels of nutrients in the hemolymph, including lipids, carbohydrates, and proteins, and that the differences were associated with possible variations in nutritional quality. In studies of the same species, Judd et al. (2015) showed that an increase in the quality of larval nutrition led to the development of larger females. In *M. consimilis,* workers and gynes emerge in different phases of the colony cycle, so the conditions for development of the immature are different (Torres et al., 2011). These findings suggest a link between body size and colonial stage, which needs to be further investigated.

However, in IF polistine wasps, other factors are associated with the caste ontogeny, which vary as the colony grows. For example, larvae of *P. fuscatus* developing in the pre-emergence stage are subjected to higher levels of vibration, compared to larvae that develop in the later post-emergence stage (Suryanarayananet al., 2011). The vibration is produced by adults using their antennas to touch the walls of cells occupied by larvae. Adult females subjected to high levels of vibration in the larval stage show a worker-like phenotype, while those subjected to low levels of vibration show a gyne-like phenotype (Suryanarayanan & Jeanne, 2008; Suryanarayanan et al., 2011). This form of manipulation of the caste ontogeny is essential for the success of the colony, because it allows adults to control the caste production throughout the colony cycle.

The results presented in this study suggest that individual attributes such as body size and ovarian development are linked to the function performed by the foundresses in *M. consimilis*. In addition, it is clear that gynes are larger than workers, suggesting that factors associated with the pre-imaginal caste determination vary with the development of the colony. Knowledge of the caste ontogeny in IF polistine wasps sheds light on individual attributes that increase the chances for direct reproduction, in the context of disputes, and also helps to understand the conditions under which the castes are produced in less-advanced eusocial wasps.

Acknowledgements

The authors acknowledge the Coordenação de Aperfeiçoamento de Pessoal de Nível Superior (CAPES) for a scholarship granted to the first author. The Fundação de Apoio ao Desenvolvimento do Ensino, Ciência e Tecnologia do Estado de Mato Grosso do Sul (FUNDECT) provided financial support (Proc. No. 23/200.767/2012). WFAJ thanks the Conselho Nacional de Desenvolvimento Científico e Tecnológico (CNPq) for research productivity scholarship.

References

Bourke, A.F.G. (1999). Colony size, social complexity and reproductive conflict in social insects. Journal of Evolutionary Biology, 12: 245-257. doi:10.1046/j.1420-9101.1999.00028.x

Cant, M.A. & Field, J. (2001). Helping effort and future fitness in cooperative animal societies. Proceedings of the Royal Society of London B, 268: 1959-1964. doi: 10.1098/rspb.2001.1754

Cervo, R., Dapporto, L., Beani, L., Strassmann, J.E. & Turillazzi, S. (2008). On status badges and quality signals in the paper wasp *Polistes dominulus*: body size, facial colour patterns and hierarchical rank. Proceedings of the Royal Society of London B, 275: 1189-1196. doi:10.1098/rspb.2007.1779

Cnaani, J., Schmid-Hempel, R. & Schmidt, J.O. (2002). Colony development, larval development and worker reproduction in *Bombus impatiens* Cresson. Insectes Sociaux, 49: 164-170. doi: 10.1007/s00040-002-8297-8

Dropkin, J.A. & Gamboa, G.J. (1981). Physical comparisons of foundresses of the paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). Canadian Entomologist, 113: 457-461.doi: 10.4039/Ent113457-6

Fukuda, H., Kojima, J., Tsuchida, K. & Saito, F. (2003). Size-dependent reproductive dominance in foundresses of *Ropalidia plebeiana*, an Australian paper wasp forming nest aggregations (Hymenoptera: Vespidae). Entomological Science, 6: 217-222. doi: 10.1046/j.1343-8786.2003.00025.x

Gadagkar, R. (1991). *Belonogaster*, *Mischocyttarus*, *Parapolybia*, and independent founding *Ropalidia*. In K.G. Ross & R.W. Matthews (Eds.), The social biology of wasps (pp. 149-190). Ithaca, NY: Cornell University Press.

Giannotti, E. (1998). The colony cycle of the social wasp, *Mischocyttarus cerberus styx* Richards, 1940 (Hymenoptera, Vespidae). Revista Brasileira de Entomologia, 41: 217-224.

Gunnels, C.W. (2007). Seasonally variable eusocially selected traits in the paper wasp, *Mischocyttarus mexicanus*. Ethology, 113: 648-660. doi: 10.1111/j.1439-0310.2007.01358.x

Haggard, C.M. & Gamboa, G.J. (1980). Seasonal variation in body size and reproductive condition of a paper wasp, *Polistes metricus* (Hymenoptera: Vespidae). Canadian Entomologist, 112: 239-248. doi: 10.4039/Ent112239-3

Jandt, J.M., Tibbetts, E.A. & Toth, A.L. (2014). *Polistes* paper wasps: a model genus for the study of social dominance hierarchies. Insectes Sociaux, 61: 11-27. doi: 10.1007/s00040-013-0328-0

Jeanne, R.L. (1972). Social biology of the neotropical wasp *Mischocyttarus drewseni*. Bulletin of the Museum of Comparative Zoology, 144: 63-150.

Judd, T.M., Magnus, R.M. & Fasnacht, M.P. (2010). A nutritional profile of the social wasp *Polistes metricus*: differences in nutrient levels between castes and changes within castes during the annual life cycle. Journal of Insect Physiology, 56: 42-56. doi: 10.1016/j.jinsphys.2009.09.002.

Judd, T.M., Teal, P.E.A., Hernandez, E.J., Choudhury, T. & Hunt, J.H. (2015). Quantitative differences in nourishment affect caste-related physiology and development in the paper wasp *Polistes metricus*. PLoS One, 10: e0116199. doi:10.1371/journal.pone.0116199

Karsai, I. & Hunt, J.H. (2002). Food quantity affects traits of offspring in the paper wasp *Polistes metricus* (Hymenoptera: Vespidae). Environmental Entomology, 31: 99-106.

Keeping, M.G. (1992). Social organization and division of labour in colonies of the polistine wasp, *Belonogaster petiolata*. Behavioral Ecology and Sociobiology, 31: 211-224. Keeping, M.G. (2000). Morpho-physiological variability and differentiation of reproductive roles among foundresses of the primitively eusocial wasp, *Belonogaster petiolata* (Degeer) (Hymenoptera, Vespidae). Insectes Sociaux, 47: 147-154. doi: 10.1007/PL00001693

Miyano, S. (1983). Number of offspring and seasonal changes of their body weight in a paperwasp, *Polistes chinensis antennalis* Pérez (Hymenoptera: Vespidae), with reference to male production by workers. Research on Population Ecology, 25: 198-209. doi: 10.1007/BF02528793

Miyano, S. (1998). Amount of flesh food influences the number, larval duration, and body size of first brood workers, in a Japanese paper wasp, *Polistes chinensis antennalis* (Hymenoptera: Vespidae). Entomological Science, 1: 545-549.

Montagna, T.S., Raizer, J. & Antonialli-Junior, W.F. (2015). Effect of larval topical application of juvenile hormone on caste determination in the independent-founding eusocial wasp *Mischocyttarus consimilis* (Hymenoptera: Vespidae). Open Journal of Animal Science, 5: 174-184. doi: 10.4236/ojas.2015.52020

Murakami, A.S.N., Shima, S.N. & Desuó, I.C. (2009). More than one inseminated female in colonies of the independent-founding wasp *Mischocyttarus cassununga* von Ihering (Hymenoptera, Vespidae). Revista Brasileira de Entomologia, 53: 653-662. doi: 10.1590/S0085-56262009000400017

Murakami, A.S.N., Desuó, I.C. & Shima, S.N. (2013). Division of labor in stable social hierarchy of the independent-founding wasp *Mischocyttarus* (*Monocyttarus*) *cassununga*, Von Ihering (Hymenoptera, Vespidae). Sociobiology, 60: 114-122. doi: 10.13102/sociobiology.v60i1.114-122

O' Donnell, S. (1998). Reproductive caste determination in eusocial wasps (Hymenoptera: Vespidae). Annual Review of Entomology, 43: 323-446. doi: 10.1146/annurev.ento.43.1.323

O' Donnell, S. & Joyce, F.J. (2001). Seasonality and colony composition in a Montane Tropical eusocial wasp. Biotropica, 33: 727-732. doi: 10.1111/j.1744-7429.2001.tb00233.x

Poltronieri, H.S. & Rodrigues, V.M. (1976). Vespídeos sociais: estudos de algumas espécies de *Mischocyttarus* Saussure, 1853 (Hymenoptera.Vespidae. Polistinae). Dusenia, 9: 99-105.

Prezoto, F., Vilela, A.P.P., Lima, M.A.P., D'ávila, S., Sinzato, D.M.S., Andrade, F.R., Santos-Prezoto, H.H. & Giannotti, E. (2004). Dominance hierarchy in different stages of development in colonies of the primitively eusocial wasp *Mischocyttarus cassununga* (Hymenoptera, Vespidae). Sociobiology, 44: 379-390.

Reeve, H.K. (1991). *Polistes*. In K.G. Ross & R.W. Matthews (Eds.), The social biology of wasps (pp. 309-335). Ithaca, NY: Cornell University Press.

Robinson, G.E. (1992). Regulation of division of labor in insect societies. Annual Review of Entomology, 37: 637-665. doi: 10.1146/annurev.en.37.010192.003225

Röseler, P-F. (1991). Reproductive competition during colony establishment. In K.G. Ross & R.W. Matthews (Eds.), The social biology of wasps (pp. 149-190). Ithaca, NY: Cornell University Press.

Schmidt, K.C., Hunt, B.G. & Smith, C.R. (2012). Queen, worker, and male yellowjacket wasps receive different nutrition during development. Insectes Sociaux, 59: 289-295. doi: 10.1007/s00040-012-0220-3

Sledge, M.F., Trinca, I., Massolo, A., Boscaro, F. & Turillazzi, S. (2004). Variation in cuticular hydrocarbon signatures, hormonal correlates and establishment of reproductive dominance in a polistine wasp. Journal of Insect Physiology, 50: 73-83.

Smith, C.R., Suarez, A.V., Tsutsui, N.D., Wittman, S.E., Edmonds, B., Freauff, A. & Tillberg, C.V. (2011). Nutritional asymmetries are related to division of labor in a queenless ant. PLoS One 6: e24011. doi: 10.1371/journal.pone.0024011

Suryanarayanan, S. & Jeanne, R.L. (2008). Antennal drumming, trophallaxis, and colony development in the social wasp *Polistes fuscatus* (Hymenoptera: Vespidae). Ethology, 114: 1201-1209. doi: 10.1111/j.1439-0310.2008.01561.x

Suryanarayanan, S., Hantschel, A.E., Torres, C.G. & Jeanne, R.L. (2011). Changes in the temporal pattern of antennal drumming behavior across the *Polistes fuscatus* colony cycle (Hymenoptera: Vespidae). Insects Sociaux, 58: 97-106. doi: 10.1007/s00040-010-0122-1

Tannure-Nascimento, I.C., Nascimento, F.S. & Zucchi, R. (2008). The look of royalty: visual and odour signals of reproductive status in a paper wasp. Proceedings of the Royal Society of London B, 275: 2555-2561. doi: 10.1098/rspb.2008.0589

Tibbetts, E.A. (2006). Badges of status in worker and gyne *Polistes dominulus* wasps. Annalles Zoologici Fennici, 43: 575-582.

Tibbetts, E.A. & Dale, J. (2004). A socially enforced signal of quality in a paper wasp. Nature, 432: 218-222.doi:10.1038/nature02949

Torres, V.O., Montagna, T.S., Fernandes, W.D. & Antonialli-Junior, W.F. (2011). Colony cycle of the social wasp *Mischocyttarus consimilis* Zikán (Hymenoptera, Vespidae). Revista Brasileira de Entomologia, 55: 247-252. doi: 10.1590/S0085-56262011000200016

Torres, V.O., Montagna, T.S., Raizer, J. & Antonialli-Junior, W.F. (2012). Division of labor in colonies of the eusocial wasp, *Mischocyttarus consimilis*. Journal of Insect Science, 12: 21. doi: 10.1673/031.012.2101

Turillazzi, S. & Pardi, L. (1977). Body size and hierarchy in polygynic nests of *Polistes gallicus* (L.) (Hymenoptera: Vespidae). Monitore Zoologico Italiano, 11: 101-112. doi:10.1080/00269786.1977.10736294

West-Eberhard, M.J. (1969). The social biology of polistine wasps. Michigan, MI: Miscellaneous Publications Museum of Zoology, University of Michigan, nº 140, 101p.

Winston, M.L. (1987). The biology of the honey bee. Cambridge, MA: Harvard University Press, 296p.

Zanette, L. & Field, J. (2009). Cues, concessions, and inheritance: dominance hierarchies in the paper wasp *Polistes dominulus*. Behavioral Ecology, 20: 773-780. doi: 10.1093/beheco/arp060