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CAMOUFLAGED NESTS OF *Mischocyttarus mirificus* (Zikán, 1935) (HYMENOPTERA, VESPIDAE)

Juiz de Fora

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Dissertação apresentada ao Instituto de Ciências Biológicas, Programa de Pós-Graduação em Comportamento e Biologia Animal da Universidade Federal de Juiz de Fora, como requisito para obtenção do título de Mestre

Orientador: Prof. Dr. Fábio Prezoto

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A todos aqueles que sabem a resposta para

a Vida, Universo e tudo mais.

“Aprecie o mundo natural,

porque você é parte dele

e depende dele”

Sir *David Attenborough*

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Resumo para divulgação científica

As vespas sociais são insetos conhecidos popularmente no Brasil por Marimbondos ou Cábas. Os ninhos destes insetos, estruturas utilizadas para abrigar os indivíduos jovens das espécies, também são amplamente conhecidos pela população, sendo chamadas de “caixas-de-marimbondo”, e que algumas pessoas até associam a boa sorte em tê-las fixadas em seus telhados. Os ninhos dos marimbondos podem variar de formato, cor e tamanho. Com relação ao formato podem ser redondos, ovais, discoides e até mesmo longos em formato de fio. Os ninhos em fio são especialmente difíceis de serem avistados. Acredita-se que isso se deva a dois motivos principais: (1) são construídos por espécies que não suportam a presença humana, sendo sensíveis a devastação do meio ambiente, e (2) devido ao aspecto de fio, geralmente são confundidos com galhos secos e cipós. Esta confusão pode ser “intencional” por parte das vespas, pois sabe-se que não é coincidência que seus ninhos se aparentem com objetos inanimados, sendo esta uma estratégia de camuflagem da espécie. A camuflagem é comportamento defensivo na qual um animal se assemelha em cor e formato a um objeto inanimado (“sem vida”), como uma folha, pedra ou galho. Algumas análises foram realizadas com fotografias dos ninhos de *Mischocyttarus mirificus*, uma vespa que constrói ninho de fio, e pode se atestar que esta estratégia está presente nos ninhos da espécie. Esta camuflagem dos ninhos, é uma maneira de oculta-lo de seus preadores, evitando assim um gasto de energia das vespas na defesa de sua prole.

Ninhos Camuflados de *Mischocyttarus mirificus* (Zikán, 1935) (Hymenoptera, Vespidae)

Resumo

As vespas sociais apresentam variados padrões arquitetônicos para seus ninhos, que podem diferir em formato, tamanho, cor e material utilizado na construção. *Mischocyttarus mirificus* possui um padrão de distribuição das células do favo, em que estas se mantém na vertical com uma única célula de espessura, apresentando um formato filiforme que camufla-se em meio ao substrato, sendo então o objetivo deste estudo detalhar os hábitos de nidificação da espécie, produtividade e quantificar o grau de camuflagem dos ninhos. Ao todo foram analisadas 40 colônias em seu hábitat natural e seis dissecadas em laboratório para coletas de dados sobre os hábitos de nidificação da espécie e produtividade, além de um teste realizado com fotografias dos ninhos, para quantificar a porcentagem de camuflagem destes quando inseridos no substrato de nidificação. As colônias foram encontradas principalmente em florestas ripárias quando haviam elementos na paisagem que permitissem sua camuflagem. De acordo com as análises das fotografias das colônias, estas apresentam níveis de camuflagem que pode variar de acordo com a posição em que a fotografia é registrada. A produtividade das colônias de *M. mirificus* foi semelhante quando comparada a outras espécies do grupo. É evidente que as fundadoras de *M. mirificus* selecionam locais em que possam camuflar suas colônias, e isso lhes confere vantagens em explorar um novo ambiente.

Palavras-Chave: Hábitos de Nidificação, Vespa social, Produtividade, Mischocyttarini, Polistinae.

Camouflaged Nests of *Mischocyttarus mirificus* (Zikán, 1935) (Hymenoptera, Vespidae)

Abstract

The social wasps present varied architectural patterns for their nests, which may differ in shape, size, color and material used on its construction. In *Mischocyttarus mirificus* nests, comb pattern consists in vertical, single-cell wide combs in a filiform shape, which allows for camouflaging nests amidst their substrate. The objective of this study was to investigate the species' nesting habits and colony productivity, and to quantify its ability to camouflage. A total of 40 colonies were analyzed in their natural habitat, and six of which were dissected in the laboratory to verify nesting habits and productivity. Images taken from the nests *in natura* were used to quantify their camouflage potential in contrast to the nesting substrate. Colonies were found mainly in riparian forests with availability of landscape elements that facilitated their camouflage. According to the image analysis, the camouflage level can vary according to the position from which the images are captured. The productivity of *M. mirificu*s also varied in some aspects when compared with other species of the group. Is evident that the founders of *M. mirificus* select sites where they can camouflage their colonies, and this gives them advantages in exploring novel environments. Although row colonies are an energetically costly architectural alternative, *M. mirificus* presents productivity similar to that of other species of the genus.

Keywords: Nesting habits, Social wasp, Productivity, Mischocyttarini, Polistinae.

Introdução Geral

As vespas sociais são conhecidas popularmente no Brasil por Marimbondos ou Cabas, e fazem parte de histórias e conhecimentos populares por todo o planeta. Entretanto, muito da importância destes insetos é desconhecido do público geral, que erroneamente associam-nas a perigo por considerarem apenas as ferroadas provocadas por estes insetos, que são apenas um método utilizado para defesa individual ou da colônia. As relações ecológicas estabelecidas pelas vespas sociais nos ecossistemas são bastante variadas, atuando como agentes polinizadoras e visitantes florais de diversas espécies de angiosperma, são também bioindicadoras de qualidade de ambiente, pois muitas espécies são sensíveis a alterações no hábitat e também desempenham importante função no controle biológico de diversos artrópodes, tanto em ambientes naturais quanto agrícolas (Souza & Zanuncio, 2012). Todavia, outro ponto característico destes insetos, são suas colônias que parecem feitas de papelão, fazendo com que sejam chamadas de Vespas-do-papel em alguns países.

O aspecto de papel apresentado pelos ninhos das vespas é devido a utilizarem materiais vegetais, como raspas de celulose, que são maceradas e misturadas a secreções salivares e utilizadas tanto na construção quanto na manutenção das colônias, a qual apresentam diversos padrões arquitetônicos. O padrão utilizado por cada espécie está intimamente relacionado com a evolução e seleção das mesmas para explorarem diferentes hábitats. Diversas espécies constroem seus ninhos com um invólucro protetor (proteção contra predadores, mudanças climáticas e intempéries) que circunda os favos onde ficam abrigadas os ovos, pupas e larvas, como acontece nos gêneros *Polybia, Brachygastra, Protonectarina, Synoeca,* entre outros. Certas espécies como *Agelaia pallipes e Agelaia multipicta* procuram por ocos de árvores ou cupinzeiros abandonados, que fazem as vezes de um invólucro, e onde constroem os favos. E temos também as espécies que fixam suas colônias por um pedicelo ao substrato e não apresentam invólucro protetor como *Apoica, Polistes e Mischocyttarus* (RICHARDS, 1978)*.*

Mischocyttarus é o gênero com maior número de espécies de vespas sociais e apresenta vasta gama de padrões arquitetônicos para seus ninhos, sendo alguns com menos de 10 células, até aqueles que apresentam mais de 100 (CARPENTER & Marques, 2001). Além da quantidade de células, outro fator que varia bastante nas espécies do gênero são as disposições, formatos e cores destas células que formam os favos, e que juntamente com o hábitat escolhido, são vitais no sucesso de nidificação. As espécies do gênero podem ser facilmente encontradas nidificando em ambientes antrópicos, todavia, quando em seu hábitat natural as colônias podem ser bastante crípticas e camufladas, como ocorre com *Mischocyttarus mirificus* (Zikán, 1935) onde elas são confundidas com lianas, galhos e raízes de epífitas. Passando desapercebidas aos olhos pouco treinados.

Sabe-se que as fundadoras de *M. mirificus* procuram por substratos de nidificação que facilitem a camuflagem visual por parte das colônias. Entretanto, muitos ainda são os questionamentos por parte desta arquitetura diferenciada da espécie, e de seus hábitos de nidificação. Sendo assim, entender mais sobre os hábitos ímpares de nidificação de *M. mirificus*, assim como a produtividade da espécie, ajudará a compreender seu comportamento de nidificação e fornecer informações para as demais espécies deste grupo. Portanto objetivou-se caracterizar a produtividade da espécie, além de seus hábitos de nidificação. E propor uma nova técnica para quantificação de camuflagem presente nas colônias das espécies de vespas sociais, utilizando como base os ninhos de *M. mirificus.*

Revisão da literatura

A Ordem Hymenoptera (Abelhas, Formigas e Vespas) é tradicionalmente dividida em duas subordens, Symphyta e Apocrita, sendo nesta segunda onde se encontra a superfamília Vespoidea e a família Vespidae (RAFAEL *et al.,* 2012). Vespidae abrange mais de 5.000 espécies distribuídas em seis subfamílias ativas, sendo elas: Euparagiinae, Masarinae, Eumeninae, Stenogastrinae, Vespinae e Polistinae (PICKETT & CARPENTER, 2010). As três primeiras são de vespídeos com hábitos solitários e as últimas de vespas com diferentes graus de socialidade (CARPENTER & MARQUES, 2001).

Polistinae possui ampla distribuição, entretanto a maior diversidade é encontrada nas regiões tropicais. Ao todo a fauna mundial é constituída de 26 gêneros e mais de 900 espécies. O Brasil apresenta a maior diversidade de Polistinae do mundo, onde são registradas cerca de 350 espécies, tendo 104 destas como endêmicas do país (CARPENTER & ANDENA, 2013). Esta subfamília apresenta quatro tribos, Mischocyttarini, Polistini e Epiponini que podem ser encontradas no Brasil e Ropalidini que possui representantes na Austrália, Índia, sudeste da Ásia, África e Madagascar (CARPENTER & MARQUES, 2001).

Mischocyttarini é representada por um único gênero (*Mischocyttarus*), entretanto é a mais diversificada das tribos, com nove subgêneros e aproximadamente 245 espécies descritas (SILVEIRA, 2008). As espécies de *Mischoccyttarus* fundam seus ninhos de forma independente, podendo ser por uma única fêmea (Haplometrose) ou em associação com outras fêmeas (Pleometrose) (WENZEL, 1998).Na haplometrose todas as tarefas são realizadas pela fundadora até que novas fêmeas emerjam para auxiliá-la, já na pleometrose os trabalhos são divididos entre as fêmeas fundadoras, podendo desta forma aumentar o sucesso na nidificação e manutenção da colônia nos primeiros momentos (CASTRO *et al.,*2014, MONTAGNA & ANTONIALLI-JUNIOR, 2016).

As colônias do gênero *Mischocyttarus* consistem em um único favo, sem um invólucro protetor e fixado ao substrato por um pedicelo (WENZEL, 1998; SOMAVILLA *et al.,* 2012). Devido à suscetibilidade de algumas espécies deste gênero a predadores por fatores como ferrões atrofiados, colônias com poucos indivíduos e desprovidas de invólucro protetor (JEANNE, 1975; RAPOSO-FILHO &

RODRIGUES, 1984), algumas estratégias de defesas diretas e indiretas podem ser observadas, como mimetizar espécies agressivas de Epiponini, principalmente as do gênero *Agelaia* e *Polybia* (RICHARDS, 1978, WENEL, 1998) ou o ocultamento das colônias, os auxiliando na defesa contra inimigos naturais. Ocultar a colônia é uma estratégia presente em muitas espécies de *Mischocyttarus* (SILVEIRA, 2008).

Sabe-se que as colônias apresentam importante valor taxonômico e sua arquitetura pode contribuir para a classificação dos grupos as quais pertencem (GIANOTTI, 1999; WENZEL 1991, 1998), sendo por vezes, quando descrita uma nova espécie, de costume descrever também a arquitetura de sua colônia, e para colônias do gênero *Mischocyttarus,* algumas obras da literatura são ricas em descrições, como as de (RICHARDS, 1978; Silveira, 2008, 2015).

Principalmente na obra de Richards (1978) onde existe uma vasta gama de descrições de colônias, por vários autores e para diversas espécies do gênero *Mischocyttarus*, em certos casos, nota-se claramente a intenção do descritor em sugerir uma possível camuflagem da colônia em seu meio, baseado em aspectos morfométricos. Parte da descrição da colônia de *Mischocyttarus punctatus* (Ducke) traz o seguinte texto: "O ninho pode ser muito longo e depois se assemelhar a um galho seco ou raiz de uma liana" ou "e as costas das células são cobertas com partículas de musgo de modo a assemelhar-se ao substrato" para a colônia de *Mischocyttarus iheringi* Zikán.

Apesar dos 40 anos da publicação do livro de Richards, pouco ainda se é visto sobre aspectos morfológicos das colônias que retratem possíveis camuflagens. Tendo como um recente trabalho acerca do tema o de Barbosa *et al.,* (2016) com uma espécie do Grupo de *Mischocyttarus iheringi* Zikán 1935, e em uma pequena parte do trabalho de (SILVEIRA, 2015) para espécies do Grupo *Mischocyttarus (Omega) punctatus* (Ducke, 1904). Entretanto muitas ainda são as espécies do gênero que possuem os padrões arquitetônicos de suas colônias diferenciados, mas que ainda são quase ou nada estudados, sendo exemplo disso a espécie *Mischocyttarus mirificus* Zikán, 1935.

Colônias de *M. mirificus* têm sido encontradas em áreas de mata ciliar de dois municípios do sul de Minas Gerais, principalmente quando existem epífitas e lianas na região, que aparentemente reforçam sua camuflagem. Este mesmo aspecto foi citado no trabalho de Silveira *et al* (2015), onde a arquitetura dos ninhos de algumas espécies do gênero, em que o padrão se assemelha com *M. mirificus,* foram descritos, relacionando em um dos casos com o substrato onde eles haviam sido encontrados, sendo sugerida uma possível estratégia de camuflagem por parte da espécie *Mischocyttarus ryani* (Silveira, 2015).

Camouflaged Nests of *Mischocyttarus mirificus* (Zikán, 1935) (Hymenoptera, Vespidae)

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1. Introduction

Mischocyttarus mirificus (Zikán, 1935) has been recorded in Southeastern Brazil in the Parque Nacional do Itatiaia (RJ) and in the Área de Proteção Ambiental (APA) São José (MG) (Barbosa *et al.,* 2016a). *M. mirificus* is part of the *Haplometrobius* subgenus and the *Mischocyttarus artifex* species group. These groups have variable architectural patterns, and some species such as *Mischocyttarus artifex* (Ducke, 1914)*, M. mirificus, Mischocyttarus oecothrix* Richards, 1940 and *Mischocyttarus ypiranguensis* Fonseca, 1926 build string-like combs, with a single cell of width (Richards, 1978).

This filiform architecture pattern presented by *M. mirificus* nests is a subject of curiosity because, when in their natural environment, they are often mistaken for branches, vines and roots of epiphytic plants (Souza et al., 2010a). However, studies that aimed to investigate aspects related to the camouflage behavior of nests in social wasps are scarce (Turillazzi, 2012; Barbosa et al., 2016b), while a few others address them briefly (Richards 1978; Giannotti 1999; Smith 2004; Starr 2014).

In 1978, O. W. Richards described the architectural pattern of colonies of many *Mischocyttarus* species and provided insights into the possible camouflage potential of patterns for many of them. Edilberto Giannotti, in 1999, wrote that colonies of *Mischocyttarus cerberus styx* Richards, 1940 were well camouflaged in their substrate, since their coloration resembled the bark of the trees in which they were found; besides, he described the behavior of adult wasps covering the nest's naturally white pupae cells with plant material so that they do not contrast in relation to the background. Another report pointed out that the nests of *M. collarellus* are extremely cryptic: not only were about the same stained color as the trunk of the tree they were in, but were also similar in shape and size to a hanging tree bark piece (Smith, 2004). It is also suggested that the elongated and filiform shape of the *Mischocyttarus punctatus* (Ducke, 1904) nests (similar to the *M. mirificus* pattern) consists in a defensive camouflage strategy (Starr, 2014).

Animals capable of camouflaging themselves are under strong pressure to minimize their conspicuity to possible predators, and the efficiency of this behavior is related to the mechanisms used by the predator in the search for prey (Pike, 2018). Investigating more thoroughly the aspects involved in the camouflage behavior of the *M. mirificus* nests will assist in the better understanding of its evolutionary and adaptive meaning. And if there is success in the colonies camouflage, this can result in to productivity near or superior of the M. mirificus when compared to the other genus species. Thus, the aim of this study was to measure the productivity of *M. mirificus* colonies, describe their nesting habits and quantify the percentage of camouflage presented in the nest color.

2. Material and Methods

2.1. *Study area*

Were realized monthly field visits from 12:00 a.m. to 5:00 p.m. from March 2017 to February 2018, totaling 15 days of fieldwork and 75 hours of sampling. The study was carried out at riverbank forest fragments in the municipalities of Inconfidentes (22 ° 19 '1 "S, 46 ° 19' 40" W) and Bueno Brandão (22 ° 26 '27 "S, 46 ° 21' 3" W), south of Minas Gerais state, Brazil, being under the influence of the Atlantic montane semi-deciduous forest phytophysiognomy (Machado et al. 2004), and where colonies of the species have typically been found. Both areas present warm climate, with an average of 17.3 and 19.3 degrees Celsius for Bueno Brandão and Inconfidentes respectively according to Koppen and Geiger (Climate-date, 2018).

2.2. *Data collection*

In order to locate colonies, riverbank forest areas of the two municipalities were actively searched. The searches were carried out on pre-existing trails for an unmarked distance with varied proximity to water bodies.

When found, colonies were photographed and measurements were made in their nest length, cell number, number of adults, distance to the nearest water source, distance from the ground, substrate used for nesting and color of the nest peduncle. When nests were found abandoned (absence of adults, eggs, larvae and pupae), they were be collected for laboratory analysis.

Individual wasps were collected and sent to Professor Orlando Tobias da Silveira at the Museu Emílio Goeldi to confirm species identification. The specimens were deposited in the Coleção Biológica de Vespas Sociais of IF Sul de Minas, campus Inconfidentes (00708-2014; 00709-2014; 00710-2014; 03446-2017; 03447-2017; 03448-2017; 03449-2017; 03449-2017).

2.3. *Coloy productivity*

The nests were taken to the Laboratório de Ecologia Comportamental e Bioacustica (LABEC) of the Universidade Federal de Juiz de Fora, where they were dissected to characterize nest architecture and infer productivity rates. Six colonies were dissected, and the following data were recorded from them: cell length, productive cells, number of adult wasps emerged (calculated by counting the meconium layers on cell interiors), number of reused cells and size and width of the nest peduncle (Oliveira, *et al.,* 2010).

Initially, peduncle length and width were measured with calipers. Later, each cell was analyzed individually for length and width. Finally, by dissection under the stereomicroscope, it was possible to assess the amount and width of the meconium layers in each cell.

2.4. *Data analysis*

The Spearman correlation coefficient was used between peduncle width and cell number, the total cells number and the number of adults produced by the colony and the number of meconium layers and the length of the cells. Pearson's correlation was used between colony length and cells number, with a 5% confidence margin. Both analyzes were made in the R Software (R Development Core Team, 2017).

2.5. *Quantification of the camouflage presented by the nest color*

Sixteen colored photos of *M. mirificus* colonies that were taken in the field were used for camouflage quantification. The resolution of the photos is 4608 x 3456, taken with an NIKON® camera (model: COOLPIX P600). The analyzes were carried out by Dr. Rafael Alves Bonfim de Queiroz, from the Departmento de Ciência da Computação of the Universidade Federal de Juiz de Fora.

During the capturing of every photo, we sought an angle that depicted the colony inserted in the landscape, recording surrounding branches, roots and epiphytes. Whenever possible, photographs of different perspectives of the colonies were recorded, front, back, left and right.

In order to process the images, the free open-source program ImageJ (Gonzalez & Woods, 2009) was chosen. The Threshold Color plugin, which is based on a bandpass filter, was used (Schneider et al., 2012). This allows the threshold RGB color images in different color spaces such as the HSB here regarded. The HSB space has three components to define the color of each pixel: saturation (H), brightness (B) and hue (V). The RGB space defines the pixel color through three components: red (R), green (G) and blue (B). Details about color spaces and conversions between them can be seen in (Schneider et al., 2012).

The Threshold Color plugin has as input data the intensity of a pixel or a region of interest (ROI) formed by a set of pixels. This input data is provided to the plugin through ImageJ's graphical interface. As the focus in this study is the wasp nest, each plugin application was provided with a rectangular domain contained within the nest space as the ROI.

Figure 1 illustrates the ROI chosen to be input from the Threshold Color plugin. This region is determined via ImageJ graphical interface using mouse click event by the user. After the user chooses the ROI, the filter determines in the image, regions that have colors close to those contained in the ROI. In column c3 of Figure 4 (later in the text) are shown the colored regions in red that resemble the color pattern of the ROI chosen in the wasp colonies.

Figure 1: The arrow indicates a rectangular ROI (edges in yellow) chosen within the *Mischoyttarus mirificus* colony.

In order to quantify the color area with the application of the Threshold Color plugin, the Color Segmentation plugin (Sage, 2018) was also used, added to ImageJ to determine areas of regions present in an image using a clustering algorithm. This plugin inputs data points in the form of color keys assigned to regions whose area is sought. As an example, column c3 of Figure 4 shows areas recognized by the plugin using the red color.

Below are the metrics proposed for quantifying the results on the plugins mentioned above:

- A1: percentage of colony area in the photo. To do this, a user manually colored the colony area in blue using the Paint program in the Windows operating system. Then the Color Segmentation plugin was used to determine the area of this region in blue. The images used to calculate this metric are present in column c2 of Figure 4.
- A2: percentage of the colored area in red in the photo that resembles the color of the colony. This region colored in red is the result of the

application of the Threshold Color plugin. The images used to calculate this metric are shown in column c3 of Figure 4.

• A3: percentage of the colored area in red resulting from the application of the Threshold Color plugin only to the colony. To obtain this percentage, an algorithm that receives the images considered to calculate A1 and A2 and identifies the region of the colony that has red color was developed. This algorithm has been implemented computationally in the GNU Octave programming environment, which is a free and open source. The images generated to calculate this metric are shown in column c4 of Figure 4.

• M1: ratio between the percentage rates A2 and A1, that is, A2 divided by A1. Through this metric, greater values indicate a more camouflaged wasp colony.

• M2: ratio between the percentage rates A3 and A1, that is, A3 divided by A1. This metric suggests that the closer its value is to 1 (one), the more properly the ROI in the nest for the application of the Threshold Color plugin was chosen.

3. Results

3.1*. Nesting habitats.*

Forty *M. mirificus* colonies were recorded, all fixed on vegetal substrates. This included aerial roots of different epiphytes species, as well as stems or leaves. About 92% of the colonies found were within 15 meters of some body of water, usually in riparian forests (Figure 2).

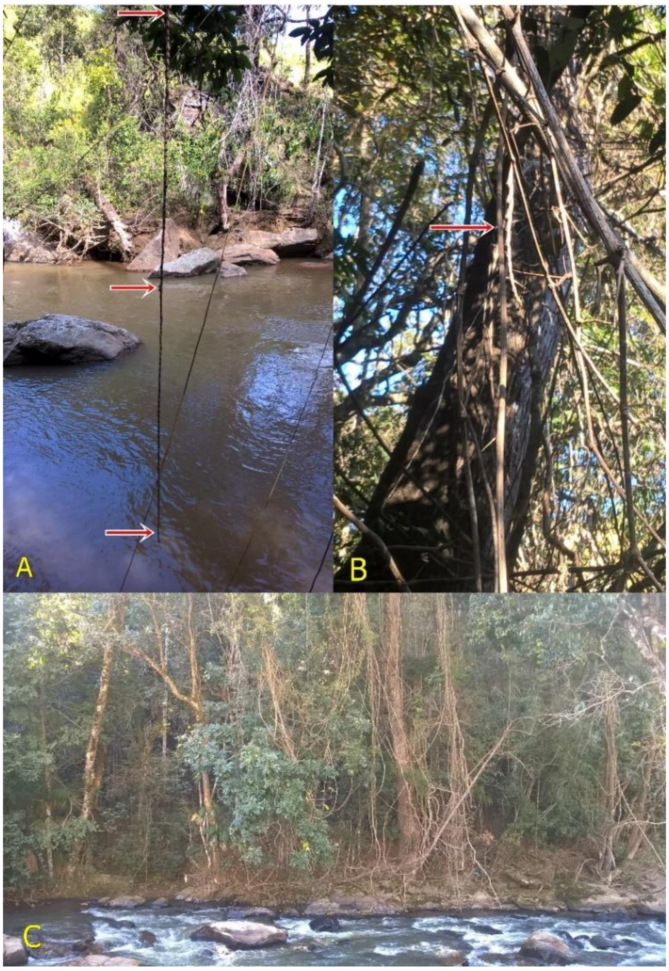

Figure 2: (A): Red arrows highlight the colony of *Mischocyttarus mirificus* amdist the vines. (B): Red arrow highlights the colony of *Mischocyttarus mirificus* among dry branches. (C): Riparian Forest where the colonies of the figures (A) and (B) were found.

The nests presented varying lengths and cells number, however, even though some of them varied considerably in these aspects, the length correlated positively with the cells number ($r = 0.99$ $p = 2.2e^{-16}$).

The smallest colonies recorded in the field had five cells, while the largest of them presented a total of 103 cells. An average of 6.09 ± 5.66 (1 - 24 n = 32) adults per colony were recorded. The mean distance from the nest to the nearest water body was 5.35 m ± 2.77 (1 - 15 n = 38), except for two nests that were approximately 600 m from any bodies of water. Regarding distance from the ground, an average of 3.46 ± 1.81 (0.3 - 8 n = 40) was obtained. However, 95% (n = 38) of the colonies were between the heights of 1.5m and 5m.

3.2. *Nest building*

3.2.1. Peduncle

The substrates used by the wasps for the nest fixation are preferably horizontally inclined. Initially, a resinous peduncle, which is fixed centrally in the first cell, is constructed in a vertical or slightly inclined position. The peduncles maintained a similar width to its initial state, slightly widening as the cell number increased but with no significant correlation ($r = 0.58$ $p = 0.9$). The analyzed nests peduncles showed a mean length of 4.97 ± 2.75 (1.6 - 10 n = 9) mm and a mean width of 1.57 ± 0.71 (1 - 3.1 n = 9) mm. All recorded peduncles were shiny black or bright gray in color.

3.2.2. *Cell construction*

Once the peduncle is completed, the wasps begin the construction of the first cell, which has a conical shape like the rest of the nest. Initially, the cell shows symmetry in the length of its front and dorsal surfaces. As it is being enlarged by workers, the dorsal surface becomes slightly larger than the front one, causing the opening to be inclined. Because of the vertical-filiform disposition of cells on this architectural pattern, it is necessary that the upper cell is at least partially constructed before the lower one can be initiated. The initial cell, which has not yet originated any adult and is considered incomplete, is relatively smaller than a complete cell, which has already originated at least one adult (Figure 3). Cell length correlated positively with the amount of meconium layers found per cell ($r = 0.96$ $p = 0.008$).

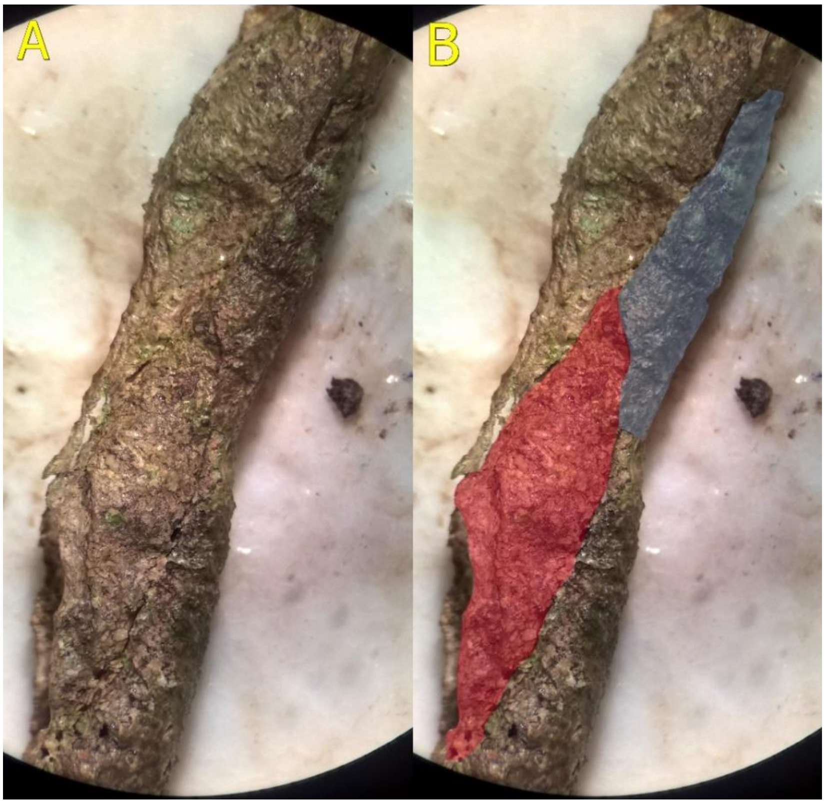

Figure 3: (A) Record of a *Mischocyttarus mirificus* nest part in stereomicroscope (45x). (B) The blue color represents the initial cell initial size while the red color represents the increase in cell size. Both colors together represent the final cell size.

As the nest increases in cell number, the wasps perform small adjustments so that the cell row remains in the same spatial position, thus avoiding nest curvature. Such corrections are made to cells that were initially skewed to either side of its upper neighbor. However, in some nests with a large number of cells, this curvature may still exist, leaving them with a semi-spiral appearance.

3.3. *Colony productivity*

Six nests were dissected and their general data are presented in Tables 1 and 2. The mean number of cells per *M. mirificus* nests was 47.66 ± 14.76 (24-62); the mean percentage of productive cells was 79.3 ± 15.36 (50 - 91.7%) and the mean number of adults produced per colony was 54.16 ± 17.22 (37 - 77). The mean number of individuals produced per cell was 0.93 ± 0.24 (0.7 - 2.25). There was a positive correlation between the total number of cells in the colonies and the number of adults emerged ($r = 0.93$, $p = 0.0005$).

Table 1: Comparative data on the productivity of 6 dissected colonies of *Mischoyttarus mirificus*. CN (Total cell number), NCU (Number of cell uses), % PC (Average percentile rate of productive cells), PA (Produced adults), PA / CN (Produced adults by cell number).

Colonies	**CN**	**NCU**			**% PC**	**PA**	**PA /CN**
		1	**2**	**3**			
L1	35	20	7	--	80	34	0,97
L2	56	34	11	5	89,3	71	1,26
L3	62	43	4	--	77,5	51	0,82
L4	54	16	11	--	50	38	0,7
L5	55	28	11	9	87,3	77	1.4
L6	24	15	6	7	91,7	54	2.25
Average	**47,66**				**79,3**	**54,16**	**0,93**
Standard deviation	**14,76**				**15,36**	**17,22**	**0,24**

Table 2: Height and width (mean, standard deviation and variation) of cells in relation to the meconium layers found deposited at the bottom of each cell of the colonies of *Mischoyttarus mirificus* (n = 230). NML (Number of meconium layers), CN (Total cell number), LL (Layer length in mm), CL (Cell length in mm), CW (Cell width in mm).

NML	CN	LL mm	CL mm	CW mm
1	156	2.03 ± 0.38 (1.04 - 2.51)	15.9 ± 1.6 (9.8 - 20)	2.95 ± 0.14 (2.7 - 3.2)
2	50	1.32 ± 0.33 (0.85 - 1.8)	17.2 ± 1.2 (15.3 - 20)	3.04 ± 0.08 (2.9 - 3.3)
3	24	1.02 ± 0.09 (0.92 - 1.1)	18.0 ± 0.9 (16.1 – 19.9)	3.06 ± 0.06 (2.9 - 3.1)

The most productive *M. mirificus* cells were located near the initial cell, on the oldest region of the comb. The less productive cells, on the other hand, were concentrated from the middle to the end of the nest, the youngest part of the comb.

3.4*. Quantification of the camouflage presented by the nest color*

According to the M1 metric, the nests are satisfactorily camouflaged in their environment, especially those labeled by Dr, El, Ef and Gf. The values stipulated as reference of M1 for the camouflage presented by the nests are: Low 1 to 10, Moderate 11 to 50 and High above 51. The M2 metric confirms that the ROI chosen for the application of the Threshold Color plugin is adequate in the most of cases (Table 3).

Table 3: Quantification of measurements through the processing of *Mischocyttarus mirificus* nests images. Perspective = Nest label + position in which it was recorded by the photograph. Example: (Ab) Back side of nest A.

Nest	Perspective	A1 (%)	A2 (%)	A3 (%)	M1	M2
A	Back (Ab)	0,54	10,71	0,475	19,83	0,88
	Front (Af)	0,7	19,23	0,679	27,47	0,97
B	Front (Bf)	0,62	10,36	0,577	16,71	0,93
	Left (Bl)	1,04	22,29	0,946	21,43	0,91
C	Front (Cf)	0,65	21,4	0,643	32,92	0,99
	Right (Cr)	1,52	20,75	1,201	13,65	0,79
D	Front (Df)	0,28	16,67	0,272	59,54	0,97
	Right (Dr)	0,17	20,68	0,163	121,64	0,96
E	Left (El)	0,15	24,31	0,147	162,07	0,98
	Front (Ef)	0,07	13,22	0,061	188,86	0,87
F	Left (Fl)	1,08	13,42	1,037	12,43	0,96
	Right(Fr)	0,71	37,28	0,703	52,51	0,99
G	Front (Gf)	0,31	28,09	0,254	90,61	0.82
	Left (Gl)	1,19	15,62	1,131	13,13	0,95
H	Front (Hf)	0,67	17,48	0,516	26,09	0,77
	Left (Hl)	0,56	34,76	0,291	62,07	0.52

Figure 4 shows the processed images. In this Figure, column c1 represents the original images, c2 the colonies identified manually in Paint (blue), c3 the images processed by Threshold Color and c4 the nests determined by the algorithm elaborated to determine the metric A3.

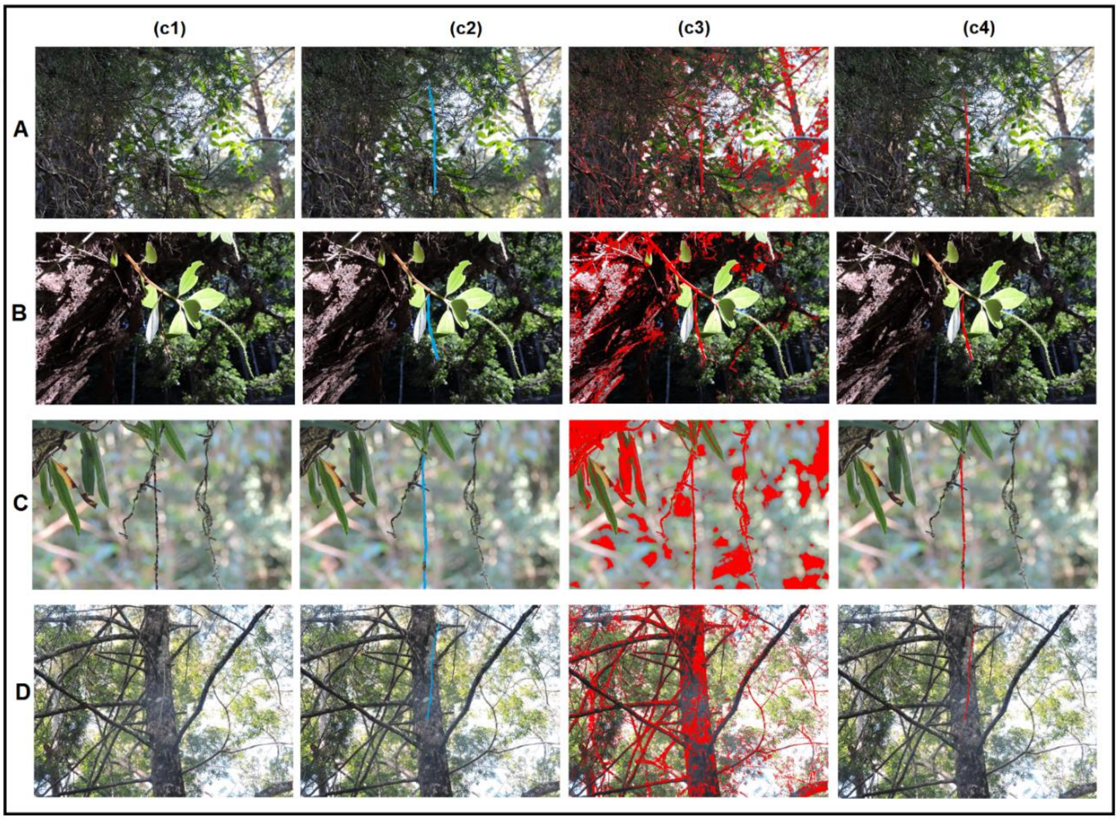

Figure 4: Photographs of *Mischocyttarus mirificus* colonies labeled A, B, C, and D. (c1) in this column are the original photos, (c2) manually the nest was highlighted in blue in the photo (c3) result of the application of the Threshold Color, (c4) identification of only the wasps' nest in the processed images of column c3.

4. Discussion

4.1. *Nesting habitats*

Mischocyttarus mirificus nests were mostly found in riparian forests, where there were elements in the environment that resembled their architecture, such as vines, branches or epiphytic roots, providing support for their camouflage. Riparian forests offer a great complexity in vegetal structures, which can favor social wasps since it provides great variety of physical supports for the colony, increases the amount and heterogeneity in food resources and imposes less micro-climate variability (Lawton, 1983, Souza et al., 2010b). It has also been reported that *Mischocyttarus flavitarsis* (Saussure, 1854) mainly occurs in riparian forests (Little, 1979); in addition to showing habitat complexity, these ecosystems are close to water resources.

Proximity to water also appears to be an important factor in the selection of nesting sites in *M. mirificus.* This factor may have an effect on the passive maintenance of colony temperature, such as shown for *Polistes dominula* (Christ, 1791), where this behavior was emphasized with the choice of nesting sites as a mechanism of thermo regulation (Hocherl *et al.,* 2016). However, some colonies of *M. mirificus* have already been found in other types of vegetation. As an example, in the present study, two nests were recorded in Atlantic montane semi-deciduous forest, being at least 600 meters away from the nearest body of water. In another study, a single colony was recorded in a rocky wall surrounded by hanging roots that helped hide its location (Souza *et al*., 2010a). Both these reports reinforce the theory that what those wasps are attracted to in a potential nesting site are aspects that enable their camouflage.

The nesting substrates used by *M. mirificus* were quite diverse, and there was no obvious preference for a particular plant species. As already reported in another study, social wasps do not seem to be influenced by a particular species of plant, but rather by the complexity generated by to the heterogeneity of the environment (Souza *et al.,* 2014). When nesting, they seem look for certain aspects and factors that can be found in too many substrates.

In a different study, the species *Mischocyttarus collarellus* Richards, 1940 showed a preference for nesting in guava trees (*Psidium* sp.), even with the availability of different potential sites in the area (Smith, 2004). It was also observed that all the substrates used by *M. collerallus* had a common characteristic: the presence of few epiphytes, which corroborates with the hypothesis previously proposed. The author assumes that the epiphytes may be a means for predators to access the colonies (Smith, 2004), which disagrees with the present study, in which *M. mirificus* colonies were generally found amidst those plants.

Mischocyttarus colonies usually do not present large populations, usually less than 30 individuals (Giannotti & Trevisoli, 1993) and the average population found in the present study was quite similar to those described in other studies (Torres *et al*., 2011; Giannotti, 1999). The same was true for the distance of the colony from the ground (Smith, 2004; Guimarães & Prezoto 2007; Castro et al., 2014). As for the number of cells presented by *M. mirificus* nests, and in contrast to what was suggested by Robert L. Jeanne in 1975, half of the colonies found had 24 cells or more, with the largest of the nests reaching 103 cells a colony cycle that extended for more than a year.

4.2. *Nest building*

4.2.1. *Peduncle*

The mean length and width of the peduncle was close to that found by some authors for other species of the genus (Giannotti, 1999; Montagna et al., 2010; Scobie & Starr, 2012). In the present study, the peduncle was always central and its increasing width was not significantly correlated with the growing of cell numbers, in opposition to records for other species (Gianotti, 1999; Montagna et al., 2010).

4.2.2. *Cell construction*

Commonly in the colonies of social wasps, the cells are initially rounded, and as neighbor cells are added to they assume their characteristic hexagonal shape. This can be observed in species nests where the cells have hexagonal shapes at the comb's center while the rounded at the comb periphery, especially on the edges (Wenzel, 1998; Oliveira et al., 2010). Notwithstanding, the pattern presented by *M. mirificus* cells always maintain a rounded or oval shape, as they do not share their side walls.

The internal cell space tends to decrease as each new adult emerges. This is due to the fact that the larvae releases excreta before becoming pupae, accumulating in the bottom of the cell in layers known as meconium and leading to necessary maintenance of the structure. Thus, as the pupa develops and grows, adjustments are made in the form of expansion of cell walls to house the pupal cocoon, which increases cell length. This is similar to what was previously recorded for *Polistes lanio lanio* (Fabricius, 1775) (Giannotti, 1992) and *M. cerberus styx* (Giannotti, 1999).

As for cell row architecture, some disadvantages to this pattern are cited in literature. Because this disposition does not allow cells to share their side walls, a greater amount of material and energy is required in the each new cell construction, so one would expect nests with 25 cells or less (Jeanne, 1975). Elongated nests also affect social life, reducing interactions among individuals, and making it harder for the dominant female to maintain a reproductive monopoly (Starr, 1991; 2014).

However, even when considering the aforementioned disadvantages, researchers assume that the filiform nest shape must be related to its camouflage and could be somewhat advantageous (Jeanne 1975; Starr, 1991; 2014). Other possible advantages of filiform nests could be not to be completely knocked over by birds at once, which may happen to more compact nests, and to be less vulnerable to being totally eliminated by parasites migrating from cell to cell (Herre, 1986).

4.3. *Colony productivity*

The mean number of cells produced by *M. mirificus* nests was close to that found in other studies (Giannotti, 1998; Penna *et al* 2007ab; Montagna *et al*., 2010; Castro *et al*., 2014). However, *M. mirificus* had a higher mean number of productive cells than *Mischocyttarus cassununga* (Castro *et al*., 2014) and *Mischocyttarus consimilis* (Montagna *et al*., 2010).

Mischocyttarus mirificus nests seemed to produce fewer cells when compared to other species in the genus. However, the former showed a higher average of adults produced, as well as for the number of adults emerged per cell. The number of uses of each cell was also very close to that recorded by other researchers, and reusing the cells is a way for the social wasps to save on energy and material for the construction of new cells, which can be costly in this architectural pattern. These differences may be related to the intrinsic biological differences between species and/or the environments in which the study was conducted, making comparisons a complicated effort (Castro *et al*., 2014).

Some authors suggest that the most productive cells in colonies of *Mischocyttarus* and *Polistes* are the central ones, since they probably receive greater parental care of the females due to more frequent monitoring (Giannotti & Machado, 1999) and because it is a possible strategy against predation and parasitism (Gobbi *et al*., 1993), besides being the oldest cells of the colony (Castro et al., 2014). The same can occur with *M. mirificus* with the cells closest to the peduncle (upper region), which we found to be the most productive of the colony.

4.4. *Quantification of the camouflage presented by the nest color*

As previously mentioned, the nests of *M. mirificus* resemble the substrate in which they are inserted, requiring careful observation in order to be found. The shape assumed by the vertical and linear cells distribution is easily mistaken by the substrate when observed. However, according to Table 1, nests resemble the substrate not only in shape, but also in coloration.

In Stefano Turillazzi's study in 2012, the author discusses architectural patterns of several species of the subfamily Stenogastrini, many of them resembling the pattern of *M. mirificus.* Several of the colonies brought by the author closely resemble the substrate in which they are inserted in characteristics such as size, shape and color. Still in this study, Turillazzi states that one of the main defenses of the Stenogastrini colonies is camouflage, knowing that Hornet wasps are its main predators and that these use visual cues to find the species' colonies. This suggests that the main selection force, which led *M. mirificus* to present this architectural pattern, may have been a predator that used visual clues to find the colonies.

A very fortuitous event that can further testify to the nest camouflage capability was that during one of the field observations a dragonfly from the Suborder Zygoptera landed in the colony to rest and only took flight when it was attacked by a wasp. Knowing that dragonflies see very well and use mainly the vision to orient themselves (Olberg et al., 2005), the fact that the individual did not perceive the difference of the colony to the branches is worth noting.

As it can be seen in Figure (4), by applying the Threshold Color Plugin, all the substrate in which the nests are inserted is colored red, stating that the coloration presented by them resembles that the substrate. This suggests that the plant material used in the nest construction is taken from the very place where the colonies are found, as observed for *M. cerberus styx* (Giannotti, 1999). Furthermore, from the M1 value variation, some angles in which the colonies are photographed attest more to their camouflage than others due to the incidence of light in the camera lens. The same is possible to occur with possible *M. mirificus* predators guided by visual clues.

5. Conclusion

With the analysis of the nests images, it is possible to affirm that the colors present in the comb corroborate in the degree of visual camouflage of these. The analysis, besides being a pioneer experimental approach with social wasps, proved to be satisfactory for the purpose.

Mischocyttarus mirificus founders look for environments and nesting substrates that provide support for their colony’s camouflage, not having a preference for a particular plant substrate. Although row nests are a energetically costly architectural pattern, *M. mirificus* has a similar productivity to genus species in the genus.

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Author Contributions

L.R.M; F.P and M.M.S, designed, conducted the experiments, analyzed and interpreted the data. In addition to writing the manuscript.

Conflicts of interest

The authors declare no conflict of interest

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