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## Comparative Study of the Development of Mischocyttarus cassununga Von Ihering and Mischocyttarus cerberus styx Richards Colonies (Hymenoptera, Vespidae, Mischocyttarini)

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**Abstract**. *Mischocyttarus* is a genus of eusocial wasps belonging to the Polistinae subfamily. They build nests without envelopes, making it easier to take notes and follow the growth of the nest, allowing the observation of oviposition, development of the eggs, larvae and pupae, as well as the addition of new cells to the nest and hierarchical conflicts among adults. *Mischocyttarus cerberus styx* Richards and *Mischocyttarus cassununga* Von Ihering are representatives of a genus and tribe that occur only in the Americas and these species happen to occur in the municipality of Rio Claro (SP). The present work aimed to follow the development of colonies in order to develop a comparative approach of factors that interact with the colony cycle, to verify if the species show similar or diverse profiles from each other. Four locations were chosen to represent the sampling at the Universidade Estadual Paulista campus of Rio Claro, SP. Data collection ranged from April 2014 to April 2015. *M. cerberus styx* showed a more irregular profile of productivity along the four seasons, presenting in general the greatest values on summer and the lowest values on winter. *M. cassununga*, on the other hand, seemed to have a more stable rhythm of productivity, with less discrepancy between seasons, demonstrating a better performance concerning cold seasons, with the greatest productivity values on spring and the lowest values on fall. Both species showed a similar pattern of immature development with the shortest period corresponding to summer and the longest period corresponding to winter.

Keywords: Entomology; Immature Forms; Polistinae; Productivity; Wasp.

# Estudo comparativo do desenvolvimento colonial de *Mischocyttarus cassununga* Von Ihering e *Mischocyttarus cerberus styx* Richards (Hymenoptera, Vespidae, Mischocyttarini)

**Resumo**. *Mischocyttarus* é um gênero de vespas eussociais pertencentes à subfamília Polistinae. Elas constroem ninhos sem envelopes, tornandoos mais facilmente observáveis e favorecendo o acompanhamento do crescimento do ninho, permitindo a observação de oviposição, desenvolvimento dos ovos, larvas e pupas, assim como a adição de novas células ao ninho e interações entre adultos. *Mischocyttarus cerberus styx* Richards (Hymenoptera, Vespidae, Mischocyttarini) e *Mischocyttarus cassununga* Von Ihering (Hymenoptera, Vespidae, Mischocyttarini) são representantes do gênero e tribo que ocorrem apenas nas américas, ocorrendo concomitantemente no município de Rio Claro (SP). O presente trabalho objetivou o acompanhamento do desenvolvimento colonial para elaborar uma abordagem comparativa de fatores que interagem com o ciclo colonial, a fim de verificar se as espécies apresentam perfil similar ou diverso entre si. Quatro locais foram escolhidos para representar a amostragem no campus da Universidade Estadual Paulista de Rio Claro, SP. O período de coleta de dados abrangeu abril de 2014 até abril de 2015, com os mapeamentos das colônias selecionadas na frequência de três vezes por semana, através do auxílio de escadas de diferentes alturas. *M. cerberus* apresentou um perfil mais irregular de produtividade conforme as estações, apresentando geralmente valores maiores no verão e os menores no inverno. *M. cassununga* por outro lado, apresentou um ritmo de produtividade mais estável, com menor discrepância entre as estações e melhor desempenho em períodos frios. Ambas as espécies demonstraram padrão similar no desenvolvimento de imaturos, sendo mais rápido no verão e mais longo no inverno.

Palavras-chave: Entomologia; Formas imaturas; Polistinae; Produtividade; Vespa.

he species represented by the Polistinae subfamily are of great interest in the investigation of the origin and evolution of social behavior, since they are primitively eusocial, being a proper model for the exploration of theories on this matter (HAMILTON 1964a, 1964b; WEST-EBERHARD 1969, 1975; TRIVERS 1971; WILSON 1975). Among its representatives, there's the genus *Mischocyttarus*, the only one of the Mischocyttarini

tribe (CARPENTER 1993), being the largest group with 245 known species divided among 9 subgenders (SILVEIRA 2008), of which mostly are found throughout South America (RICHARDS 1978).

*Mischocyttarus* species found their nests independently (by haplometrosis or pleometrosis), and not by swarms (RICHARDS 1971, 1978; JEANNE 1972). Wasps with such habits are

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characterized by their lack of etary polietism (Jeanne 1991), by absence of external morphological differences between castes and the consequent flexibility of the adult hierarchical roles (GADAGKAR 1991). Since they build combs without the cover of envelopes, they represent an excellent model for the verification of how the environmental factors can influence the dynamics of populational growth, allowing eye contact.

Without the protective envelope, unlike most of the Epiponini wasps, which presents fully covered combs, both immatures and the characteristic low adult numbers (GIANNOTTI 1999a) are exposed to the direct and constant action of the weather (JEANNE 1972; SILVA & NODA 2000; NODA *et al.* 2001).

For *Mischocyttarus cerberus styx* Richards, phenological studies conducted by SIMÕES *et al.* (1985) and GIANNOTTI (1998) showed that the colony development becomes remarkably slow during the cold and dry period. On the other hand, *Mischocyttarus cassununga* Von Ihering showed greater activity and production during the same period (SIMÕES *et al.* 1985), being the most abundant species of the genus in the study area and probably the best adapted for the cold period (MURAKAMI *et al.* 2009, 2013).

In this sense, this study's objective consisted in an analysis of aspects of the colonial development of *M. cerberus styx* and *M. cassununga*, taking into consideration seasonal data of colonial productivity and immature development time for a better understanding of the patters shown by both species.

#### MATERIAL AND METHODS

**Study area.** The study was conducted under field conditions in Rio Claro municipality, at the university campus Universidade Estadual Paulista – UNESP (22°24'36"S; 47°33'36"W), in the State of São Paulo, Brazil.

**Data collection.** All samples were taken for a thirteen month period, ranging from April 2014 to April 2015. Data was collected by the aid of ladders of many sizes, in order to reach colonies from different heights. Colonies preferentially selected were those positioned in a way so that eye contact was possible and easier.

The colonies mapping happened three times a week. We tried to maintain a constant number of at least five to seven colonies of each species being monitored, since eventually there were oscillations on the number of nests due to abandonment, falls, end of the colony cicle, etc. Sampling took place in different hours of the day, ranging from 8:00h to 18:00h, according to availability and weather conditions.

The values of colonial productivity were determined by the number of immatures (eggs, larvae and pupae), adults and constructed cells per colony and were analyzed according to the seasons. Each egg, larvae and pupae that completed its developmental stage had its duration registered in days for each stage of development. Colonies sampled were chosen independently of their development stage, adapted from JEANNE (1972).

**Statistical analysis.** Data was analyzed by the software SigmaPlot Version 12.5. Results were analyzed and compared through the parametric test One Way ANOVA. In case of significant difference between groups, the *post hoc* test Student-Newman-Keuls Method was used. All the data that didn't fill the requisits for normality were analyzed by the non-parametric test Kruskal-Wallis. In the case of significant difference between groups, the *post hoc* test Dunn's Method indicated which groups showed the aforementioned difference.

#### RESULTS

Seasonal colonial productivity. Twenty four *M. cerberus styx* colonies and seventeen *M. cassununga* colonies were sampled in different developmental stages. Data's compiled in the table bellow (Table 1).

Considering *M. cassununga*, the greatest values for all categories were obtained on the spring, except by the main number of constructed cells. *M. cassununga* values were frequently greater, mostly on spring. However, we highlight summer regarding the greatest values for *M. cerberus styx*.

The values of egg, pupae and adult productivity for *M. cerberus styx* showed significant difference between the groups: summer and winter (*post hoc* test Dunn's Method: P = 0.02, P = 0.029, P = 0.009, respectively) shown on Figure 1. Groups of larvae productivity and constructed cells didn't show significant difference between groups (P = 0.182, P = 0.110, respectively).

It was verified for *M. cerberus styx*, as indicated on Table 1, a divergence of the productivity values on summer and winter. The same tendency can be seen on Figure 1, along the seasons of the year: colonial productivity reaches its lowest values on winter, ascending on spring and reaching its maximum on summer, then starts to decline on autumn.

In all the groups sampled, we found colonies that didn't present addition of new cells, visible on Figure 1-E. The construction of cells, in average  $\pm$  SD, was: 1.9  $\pm$  3.68 cell/colony (n = 13 on fall; 3.3  $\pm$  5.54 cell/colony (n = 13) on winter; 4.7  $\pm$  5.39 cell/colony (n = 8) on spring; 5.6  $\pm$  5.27 cell/colony (n = 6) on summer.

*M. cassununga*, on the other hand, didn't show any significant difference in the statistical analysis. No groups showed significant difference among them: eggs (P = 0.193), larvae (P = 0.110), pupae (P = 0.135), adults (P = 0.095) and construction of cells (P = 0.110), Figure 2.

Figure 2 show us that the lowest values of the colonial productivity of eggs, larvae, pupae and adults for *M. cassununga* are found on autumn and the highest values are found on summer. However, the absence of significant difference amongst the groups reveals that there's no definite pattern.

Seasonal duration of immature development stages. The results can be seen on Table 2 bellow.

Table 1. Compilation of the data on the colonial productivity of *Mischocyttarus cerberus styx* (Mcs) and *Michocyttarus cassunnga* (Ca) according to the seasons. Eggs, larvae and pupae values are in absolute numbers. Adults and constructed cells are in main value  $\pm$  SD per colony.

Seasons	Colonies (n)		Eggs		Larvae		Pupae		Adults		Constructed Cells		
	Mcs	Ca	Mcs	Ca	Mcs	Ca	Mcs	Ca	Mcs	Ca	Mcs	Са	
Aut	umn	13	13	352	276	162	143	54	42	$2.4 \pm 2.25$	$1.8 \pm 2.51$	$1.92 \pm 3.6$	$1.5 \pm 2.25$
Win	nter	13	9	188	346	100	183	36	56	$1.7\pm3.05$	$4.2 \pm 5.56$	$3.3 \pm 5.54$	$12.6 \pm 20.71$
Spri	ing	8	7	259	580	163	299	86	94	8.1 ± 11.8	9.7 ± 11.98	$4.7 \pm 5.39$	11.4 ± 12.29
Sun	nmer	6	7	351	374	196	200	121	87	13.6 ± 13.93	$7.2 \pm 5.02$	$5.6 \pm 5.27$	6.8 ± 9.09

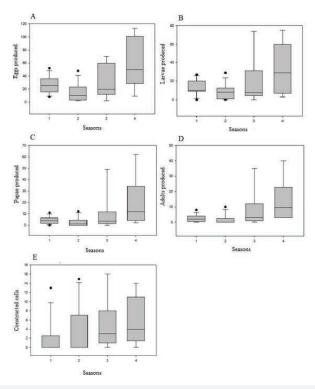


Figure 1. Boxplot representations of *Mischocyttarus cerberus styx* productivity. A: seasonal egg productivity; B: seasonal larvae productivity; C: seasonal pupae productivity; D: seasonal adult productivity; E: constructed cells. 1: autumn; 2: winter; 3: spring; 4: summer.

According to the table, the greatest number of observations (n) belong to the egg category in all the seasons of the year. The larvae category, on its turn, presents the greatest values for the interval of duration (in days) in all the seasons, comparing to the other immatures categories. It's noteworthy that the longest developmental time for all immature forms are seem on winter, whereas the shortest period of development is seen on summer.

Considering *M. cerberus styx*, the values regarding the egg category showed significant difference between groups (P = < 0.001): summer and autumn; summer and winter; summer and spring (Figure 3-A). The larvae category also showed significant difference (P = < 0.001): summer and winter; summer and spring (Figure 3-B).

The values referent to pupae development also showed significant statistical difference between groups (P = < 0.001): winter and summer; winter and autumn; winter and spring; spring and summer. Therefore, we highlight the distinct values obtained on winter.

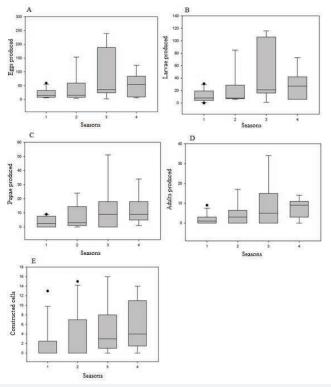


Figure 2. Boxplot representations of *Mischocyttarus cassununga* productivity. A: seasonal egg productivity; B: seasonal larvae productivity; C: seasonal pupae productivity; D: seasonal adult productivity; E: constructed cells. 1: autumn; 2: winter; 3: spring; 4: summer.

As indicated for the egg stage, the only group that distinguishes most is summer, with the shortest periods of development, being the overall average  $16.5 \pm 4.85$  days (n = 169 eggs). The season with the longest period of development is winter, along with the lowest number of observations:  $21.6 \pm 6.42$  days (n = 47 eggs).

*M. cassununga*, on its turn, showed significant difference between the following groups of egg development categories: winter and summer; winter and spring; autumn and summer; spring and summer (Figure 4-A).

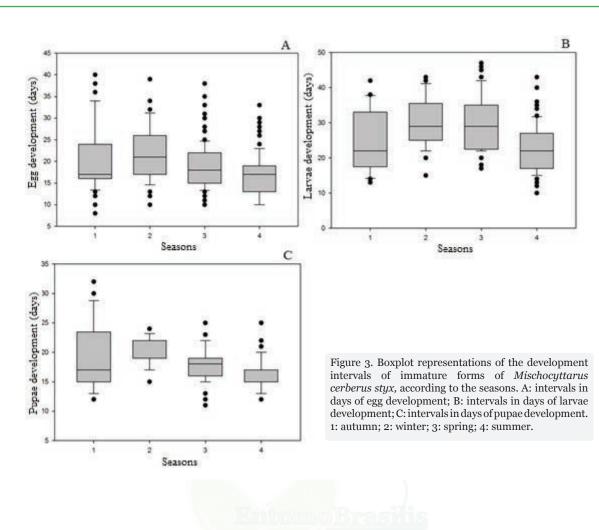
The values for the larval stage were the only data that presented normal distribution, therefore analyzed by the parametric test One Way ANOVA and the *post hoc* Student-Newman-Keuls Method, indicating significant difference between the groups (P = < 0.001): winter and summer; winter and spring; winter and autumn (Figure 4-B).

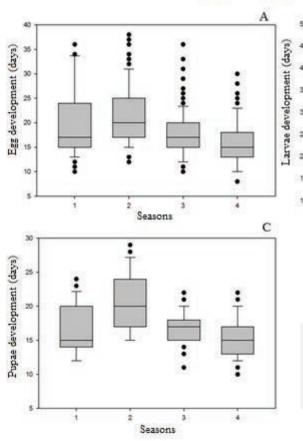
As well as the other immature categories, pupae also showed significant difference between the groups (P = < 0.001): winter

Table 2. Main values ± SD for the intervals of development (in days) for each immature stage sampled, according to the seasons.

Seasons	Colonie	Colonies (n)		gs	Lar	vae	Pupae		
	Mcs	Ca	Mcs	Ca	Mcs	Ca	Mcs	Ca	
Autumn	12	9	$20.3\pm7.42$	$20.2\pm6.89$	$25 \pm 9.03$	$26.9 \pm 4.33$	$19.2 \pm 5.94$	$16.6 \pm 3.53$	
Autumn			n = 93	n = 80	n = 21	n = 26	n = 25	n = 23	
Winter	_	8	$21.6\pm6.42$	$21.9\pm5.93$	$29.8\pm6.88$	$31.7\pm6.55$	$20.5\pm2.52$	$20.4\pm4.02$	
	5		n = 47	n = 178	n = 33	n = 57	n = 23	n = 47	
Spring	7	7	$18.8\pm4.85$	$17.6\pm4.32$	$29.6 \pm 7.58$	$28.2\pm5.89$	$17.8 \pm 2.52$	$16.9 \pm 2.21$	
Spring			n = 122	n = 277	n = 76	n = 97	n = 77	n = 84	
Summer	7	-	$16.5 \pm 4.85$	$16.1 \pm 4.43$	$22.6\pm6.78$	$26.9\pm6.88$	16 ± 2,65	$15.4 \pm 2.75$	
Summer		7	n = 169	n = 157	n = 82	n = 58	n = 102	n = 67	

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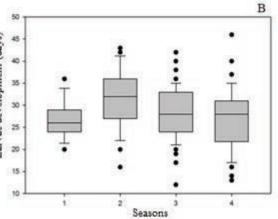


Figure 4. Boxplot representations of the development intervals of immature forms of *Mischocyttarus cassununga*, according to the seasons. A: intervals in days of egg development; B: intervals in days of larvae development; C: intervals in days of pupae development. 1: autumn; 2: winter; 3: spring; 4: summer.

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and autumn; winter and spring; winter and summer; spring and summer (Figure 4-C).

Through Figure 4-A, referent to the egg period of development, one could notice that the values belonging to summer are made of the shortest intervals. This group, with the lowest main values (16.1  $\pm$  4.43 days, n = 157 eggs), differs significantly from the others. The presence of *outliers* in the graphical representations are related to the different range of intervals (developmental time) of all the observations per season (i.e. eggs: n = 80 on autumn; n = 178 on winter; n = 277 on spring; n = 157 on summer) that distinguishes from the rest of the groups.

Considering larvae category on Figure 4-B, one can see that the longest period of development corresponds to winter, being the main value  $31.7 \pm 6.55$  days (n = 57). The same trend stands for the pupae category, since the longest period of development also occurs on winter (20.4 ± 4.02 days, n = 47).

The main values of the intervals of immature development time are found represented in Figure 5 for *M. cerberus styx* and in Figure 6 for *M. cassununga* for a better visualization of the general pattern shown by both species according to the seasons.

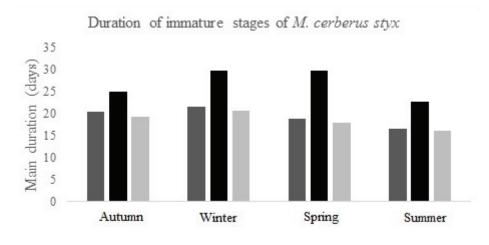
Both figures demonstrate two general patterns, according to the main values of the duration in days, corresponding to the seasons for all immature stages categories. First, it is seen that the winter represents the season with the longest periods of development for both species. Second, both species show the shortest periods of development on summer.

#### DISCUSSION

Considering the general pattern of the duration of the immature stages of *M. cerberus styx* and *M. cassununga* (Figure 5 and Figure 6) and their corresponding main values (Table 2), one can see that the larval stage presents the longest interval of development, for both species, independently of the season. This is due to, besides the fact that the development and metabolism of insects are directly linked to the temperature, the larval stage that is subjected to the workforce of the colony (JEANNE 1972). The duration of immature stages could also vary according to the stage of development of their own colony, as seen to *Protopolybia exigua* Saussure (ROCHA *et al.* 2009).

*M. cerberus styx* showed its greatest main values of immaure development on winter, with a subsequent decrease of the values on spring and another decrease on summer, reaching the point of the shortest period of development. The main values begin to rise afterwards, on autumn (Table 2).

Egg development on summer differed from the other seasons, by its shortest interval (Figure 2-A), with the main value  $16.5 \pm 4.85$  days. Larvae development was also faster on summer, differing



Egg Larvae Pupae

Figure 5. Main duration in days of immature stages of Mischocyttarus cerberus styx, according to the seasons.

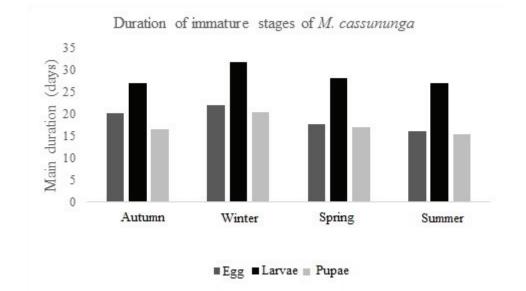


Figure 6. Main duration in days of immature stages of Mischocyttarus cassununga, according to the seasons.

from winter and spring, which showed close main values (Figure 2-B). Winter was an important season, considering pupae development, since it differed from all other seasons by the longest period of development (Figure 2-C).

It is clear that for *M. cerberus styx* the development of immatures is faster on hot seasons like summer and slower on cold seasons like winter, being the other two seasons intermediates on this transition. TORRES *et al.* (2009b) studying *Polistes canadensis* Linnaeus, found significant difference between the period of egg, larvae and pupae development on hot-wet and cold-dry seasons, being the shortest period corresponding to  $12.7 \pm 4.27$  days for egg;  $21.1 \pm 6.24$  days for lavae;  $16.5 \pm 3.07$  for pupae (hot-wet season).

In this sense, a study compiled data from different studies that showed a gradient of immature development intervals for *Mischocyttarus drewseni* Saussure, according to the environment temperature of different locations (GIANNOTTI & TREVISOLI 1993): at Belém (PA) *M. drewseni* showed a duration of 11.1 days for egg stage, 20.2  $\pm$  6.1 days for larvae stage and 14.8  $\pm$  0.8 days for pupae stage. At Rio Claro (SP), *M. drewseni* showed a duration of 15.1  $\pm$  2.9 days for egg stage, 26.5  $\pm$  5.6 days for larvae stage and 18.9  $\pm$  3.1 days for pupae stage. On the other hand, in Curitiba (PR), *M. drewseni* showed a duration of 11.3  $\pm$  1.1 days for egg stage, 34.7  $\pm$  2.6 days for larvae stage and 19.9  $\pm$  2.6 days for pupae stage, resulting on a larger period of overall development.

*M. cassununga*, as well as *M. cerberus styx*, presented the longest period of immature development on winter, and hence, the shortest period on summer. The egg stage, for example, showed significant difference between winter and summer. Winter differed significantly from all other seasons considering larvae and pupae groups, as shown in Figure 3. Therefore, we emphasize the marking difference concerning winter and all other seasons, mainly summer.

*M. cassununga* presented a main value of immature development of 21.9  $\pm$  5.93 days (eggs), 31.7  $\pm$  6.55 days (larvae) and 20.4  $\pm$ 4.02 days (pupae) on winter. On summer, it presented 16.1  $\pm$ 4.43 days (eggs), 26.9  $\pm$  6.88 days (larvae) and 15.4  $\pm$  2.75 days (pupae). On a previous study with the same species, GIANNOTTI & FIERI (1991) found a main value of immature development period of 13.1  $\pm$  2.74 days for eggs, 32.6  $\pm$  7.02 days for larvae and 15.6  $\pm$  4.38 days for pupae. Considering other studies on the genus, *Mischocyttarus labiatus* Fabricius showed a main value of 16.1 days for eggs, 16.1 days for larvae and 16.3 days for pupae (Litte 1981). *Mischocyttarus flavitarsis* Saussure with a main value of 14.1 days for eggs, 23.1 days for larvae and 19.7 days for pupae (LITTE 1979). *Mischocyttarus mexicanus* Saussure with a main value of 13.9 days for eggs, 24.8 days for larvae and 16.3 days for pupae (LITTE 1977).

Some *Polistes* species also had their period of immature development studied in the same area of the present study (Rio Claro, SP, Brazil). Among them, *Polistes simillimus* Zikán, with the main duration value of 10.2 days for eggs, 25.3 days for larvae and 18.7 days for pupae (GIANNOTTI 1994). *Polistes cinerascens* Saussure with the main value of 13 days for eggs, 23.7 days for larvae and the pupal stage lasting 22.2 days (GIANNOTTI 1997). *Polistes subsericeus* Saussure with the main duration period of  $10 \pm 1.4$  days for eggs, 32.7  $\pm 1.5$  days for larvae and  $13 \pm 1$  day for pupae (GIANNOTTI 1995b).

GIANNOTTI & MACHADO (1994) studying *Polistes lanio* Fabricius on Rio Claro (SP), found significant differences among the four seasons. The longest periods of development were those corresponding to winter: 28.2 days for eggs, 46.7 days for larvae and 30.6 days for pupae. On the other hand, the shortest period of development were those corresponding to summer: 16.8 days for eggs, 34.2 days for larvae and 18.6 days for pupae. The observed response of both species studied here is a similar dynamic shown by the immature forms, also verified for other species studied previously, according to the seasons. Both are found within the same context, considering their main values for productivity and immature development.

Data collection about colonial productivity is subjected to the influence of the action of dynamic factors which may, as mentioned by JEANNE (1972), influence data accuracy. Therefore, we emphasize oophagy: an egg could be cannibalized and substituted by another one, exactly in the same position. This new egg could remain undetected by the researcher, causing an error considering egg production.

GADAGKAR *et al.* (1982) also highlighted some other factors that may influence the data collection for colonial productivity and immature development: different placement of the colonies sampled, different stages of development, different nesting substrates and adults present. All those aspects may interfere on the results.

The frequent abandonment and termination of the colonies cycles of *M. cerberus styx* and *M. cassununga*, with the constant replacement of new colonies for sampling along the seasons, was possible due to the asynchrony exhibited by the tropical wasps (West-Eberhard 1969).

As stated before, there was a divergence concerning the main values obtained for the colonial productivity mainly for winter and summer (Table 1). The productivity ascends from winter to spring, subsequently ascending even more from spring to summer, reaching its highest. The overall values for colonial productivity of *M. cerberus styx* on summer are mostly the highest obtained: 351 eggs/colony; 121 pupae/colony and 13.6  $\pm$  13.93 adults/colony, for example. It contrasts to what was found for winter: 188 eggs/colony; 36 pupae/colony and 1.7  $\pm$  3.05 adults/colony.

SIMÕES *et al.* (1985) found the ascension of egg productivity for *M. cerberus styx* on October, reaching its highest on January. In this same study, they found that on early spring (October) the species showed its highest main value of pupae and adults per colony. However, GIANNOTTI (1998) found the highest main values of pupae and adults for the months December, January and February: 5.1; 5.6; 5.9 for pupae and 4.4; 3.5; 3.9 for adults, respectively.

Cell construction is a factor that is related to the colony workforce, as seen for *M. cerberus styx* (GIANNOTTI 1999a), *M. drewseni* (JEANNE 1972), *M. labiatus* (LITTE 1981), *M. mexicanus* (LITTE 1977); but it is also linked to the environmental conditions such as air humidity, temperature and luminosity (SILVA & NODA 2000). It adds to the fact that cell construction didn't show significant differences among the seasons, which is a reminder that those are neotropical wasps, with a constant rhythm of activity throughout the year (RICHARDS 1971, WEST-EBERHARD 1969).

Considering seasonal productivity for *M. cassununga*, it is visible that all the values are mainly higher than those obtained for *M. cerberus styx* (Table 1). This difference is probably related to their own biology and behavior, since *M. cerberus styx* builds nests with a characteristically low number of adults and cells (GIANNOTTI 1998).

It is noteworthy that eventually the environment itself may influence such values, since human activity may lead to a lesser productivity, as seen for *Polistes versicolor* Olivier and for *M. consimilis* (MICHELUTTI *et al.* 2013; TORRES *et al.* 2014).

None of the productivity categories differed significantly among the seasons for *M. cassununga* (Figure 3). The higher values obtained and the absence of significant differences among the seasons may be in indication of some particular biological aspects

of the species, since its hierarchy is stable and there are multiple inseminated females in the nests, being the most abundant species in the study area of the genus *Mischocyttarus* (MURAKAMI *et al.* 2009, 2013). Furthermore, *M. cassununga* is probably better adapted to the environmental conditions of the area, specially cold periods, as suggested by MURAKAMI *et al.* (2009).

SIMÕES *et al.* (1985) studying *M. cassununga* productivity, found the highest absolute values of eggs, larvae, pupae and adults for the months June and July (winter). On this study, done 32 years ago, they showed a good performance of *M. cassunuga* in cold and dry periods. The present study, done in the same area, indicates that *M. cassunuga* has a higher development rhythm considering this period, comparing to *M. cerberus styx*.

Spring could represent, on its turn, a favorable season for colonial productivity, since in this hot and warm season there is a greater amount of available resources for foraging, as seen for *P. versicolor* (ELISEI *et al.* 2010). *P. lanio* showed a higher foraging activity level in the hot and warm period (GIANNOTTI *et al.* 1995a). SILVA & NODA (2000) concluded, equally, that hot and warm seasons are more favorable to foraging and material gathering for *M. cerberus styx*.

Based on the obtained results for both species, we could infer that *M. cerberus styx* presents a more inconstant rhythm of colonial productivity throughout the year, showing its greatest values during the hot and warm period (i.e. summer) and its lowest values during the cold and dry period (i.e. winter). *M. cassununga*, on the other hand, presents a more stable rhythm of colonial productivity, exhibiting less discrepancy between the seasons, reacting better to cold periods.

Both species demonstrates a similar profile concerning the intervals of immature development. They develop faster on spring and summer, whereas they take longer to develop during autumn and winter.

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