

Comparative productivity of *Mischocyttarus cerberus styx* (Richards, 1940) and *Mischocyttarus cassununga* Saussure (von Ihering, 1903) in an anthropic environment as evaluation for differences in ecological strategies

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Abstract. The biology and productivity of *Mischocyttarus cerberus* and *Mischocyttarus cassununga* were studied in semi urban conditions at Rio Claro, SP - Brazil. The species presented asynchronous foundation and abandoning of nests throughout the year. As expected, the number of colony foundations differed significantly between the two species and also the success of adult production, but are not different in relation to the causes of colony mortality. The proportion of successful colonies were significantly higher in *M. cerberus*. Colony size, number of cells, number of adults produced and colony life-span did not present differences between species. Covariance analysis just confirmed that the number of adults produced, the number of cells and the colony life-span are all significantly correlated, however, there were no differences between species regarding any response variable. The data suggests that *M. cassununga* and *M. cerberus* despite their similarities should be probably adopting different ecological strategies.

Key words: *Mischocyttarus*, asynchronous foundation, cell reutilization, colony size.

Resumo: Produtividade comparativa de *Mischocyttarus cerberus styx* (Richards, 1940) and *Mischocyttarus cassununga* Saussure (von Ihering, 1903) em ambiente antrópico para avaliação de diferenças nas estratégias ecológicas. A biologia e produtividade de *Mischocyttarus cerberus* e *Mischocyttarus cassununga* foram estudadas em condições semi-urbanas em Rio Claro, SP - Brasil. As espécies apresentaram fundação assíncronica e abandono de ninhos ao longo do ano. Como esperado, o número de fundações diferiu significativamente entre as espécies assim como o sucesso na produção de adultos, mas não foram diferentes em relação as causas da mortalidade. A proporção de sucesso das colônias foi significativamente maior em *M. cerberus*. Tamanho da colônia, número de células, número de adultos produzidos e ciclo de vida da colônia não apresentaram diferenças entre as espécies. A análise de covariância apenas confirmou que o número de adultos produzidos, número de células e ciclo de vida da colônia são todos significativamente correlacionados, entretanto, não foram verificadas diferenças entre as espécies com relação a qualquer variável. Os dados sugerem que *M. cassununga* e *M. cerberus* a despeito de suas similaridades devem provavelmente adotar diferentes estratégias ecológicas.

Palavras-chave: *Mischocyttarus*, fundação assíncronica, reutilização de células, tamanho da colônia.

INTRODUCTION

The tribe Mischocitarini comprehends one of the largest and most important groups of social wasps, formed by a single genus, *Mischocyttarus*, which distribution is restricted to the Neotropical region, differing from the cosmopolitan *Polistes* in terms of biological complexity and number of species. About 206 species are known, of which 116 occur in Brazil (CARPENTER & MARQUES 2001).

In the nests of *Mischocyttarus* species, the combs are uncovered and always suspended from one or more narrow petioles (*stelocytтарous gymnodomous*), and their colonies present initially independent foundation, without the presence of workers, by a female or several fecundated females (JEANNE 1972, 1975). In these colonies the relationships of dominance hierarchy are established through agonistic interactions among the females (ITÔ 1984; NODA *et al.* 2001; PREZOTO *et al.* 2004). Besides agonistic relationships among competing queens are rare, this type of interaction is common in primitively eusocial wasps (PARDI 1946; JEANNE 1972; ROSS & MATTHEWS, 1991).

Although there are records of *Mischocyttarus* species in subtropical climates that present colonies with a seasonal cycle (LITTE 1979; HERMANN & CHAO 1984), in typically tropical regions, *Mischocyttarus* colonies do not present seasonal synchronism (JEANNE 1972; GOBBI & SIMÕES 1988).

Besides, both *Mischocyttarus* species studied here are long known and very common in urban environment (LIMA *et al.* 2000), there are few papers discussing the biology, ecology and behavior of these species, but none concerning a comparative approach about colony productivity (GOBBI & SIMÕES, 1988; GIANOTTI & FIERI, 1991; GIANOTTI & SILVA, 1993; GIANOTTI, 1998, 1999a, 1999b; SILVA & NODA, 2000; NODA *et al.*, 2001; PREZOTO *et al.* 2004; MURAKAMI & SHIMA, 2006; PENNA *et al.* 2007). Since they uses the same substract for nest construction and can build nests very close to each other, this paper aimed to evaluate and compare their productivity through number of cells, cells utilizaton, nest duration and adult production in an anthropic environment.

MATERIAL AND METHODS

The study was conducted at buildings next to the Bioterium of the Biosciences Institute of the Universidade Estadual Paulista (UNESP) in Rio Claro, São Paulo, Brazil (22° 25' S 32" W Gr), from February 1987 to March 1990. During this time, we monitored the development of all the new foundations of *Mischocyttarus cerberus* styx Richards, 1940 and *Mischocyttarus cassununga* von Ihering, 1903. The colonies were characterized according to the following parameters:

1. Duration of the colony in days (from foundation to dispersion/destruction/abandonment)
2. Number of cells and adults produced (by meconium count).

Data analysis

Obtained data was correlated with the monthly average rainfall. In order to evaluate the relations between the number of adults and colony duration/number of cells were developed dispersion graphs. The same procedure was used between the variables: colony duration and number of cells produced.

The existence of correlation between the numbers of foundations/abandonment of nests was tested with climatic factors that occurred before and during the period of observations (GOBBI & SIMÕES 1988). The frequency of successful colony foundations, colony mortality and adult production were compared through a Chi-Square test.

A correlation analysis was made between the number of adults, the duration of the colonies, and the number of existent cells in the nests (GOBBI *et al.* 1993). The productivity of the colonies was determined by counting the meconia layers (GOBBI & ZUCCHI 1985).

For each species separately, were made a series of linear and logistic regressions. The linear regressions were carried out to verify the relation between the number of adults produced and both the colony size (measured by total number of cells) and the colony life-span. We assumed that the variables could have allometric relations, which are

appropriately described by a power function of the form $Y = aX^b$; where "Y" is a given response variable, "X" is the independent variable, "a" and "b" are parameters that determines the curve aspect. Allometric relations are ubiquitous in nature, and can be easily found in morphological characters, size related variables like metabolic and other physiological rates, as well as in life-history attributes (GOULD 1966; WOODWARD *et al.* 2005). The power function is linearized by a double logarithm transformation of original variables, assuming the form $\log(Y) = \log(a) + b[\log(X)]$. The exponent "b" of power function is the slope of the correspondent linear form, and can be estimated by a simple linear regression. Its magnitude gives the strength of nonlinearity in the relation between the original variables. When "b" is equal to 1, the relation is *isometric* or simply linear. For values of "b" larger than 1, the response variable increases at increasing rates for larger values of the independent variable (a "positive" *allometric* relation), the contrary occurring for values of "b" lower than 1 (which entails a "negative" *allometric* relation).

Other important variables — the number of adults produced on the second cell layer and on the third cell layer by means of cell reutilizations — could not be used for linear regressions, as the proportion of zeros was quite large. We then categorized the colonies according to the occurrence of double cells (those with two layers) or triple cells. By this way, we could use logistic regressions to verify if either the colony size or colony life-span have any influence over the chance of cell reutilizations to suplementar adult production.

To verify if there are differences between species with respect to the number of adults produced and the colony size, we used t-tests. As it is probable that the number of adults be dependent on both the colony size and life-span, and that these last two variables be also dependent on each other, we used them as covariates in separate analysis of covariance. These analysis could show us if there is species differences based on the adult productivity by colony size or colony life-span, and on the cell productivity by colony life-span.

To test for differences in cell reutilization

frequencies, we employed a general linear model with logit link function and binomial distribution for each of the categorical response variables: the occurrence of double cells and the occurrence of triple cells. The analysis are the same as the previous logistic regressions, having the colony size or colony life-span as covariates, but with the explicit inclusion of the categorical variable "species" as a factor to test for.

Except for survival analysis, all quantitative variables used for interspecific comparisons were transformed to $\ln(\text{variable}+1)$. The log-transformation normalized the data and avoided problems with asymetry in original distributions. Also, we used a Wilcoxon

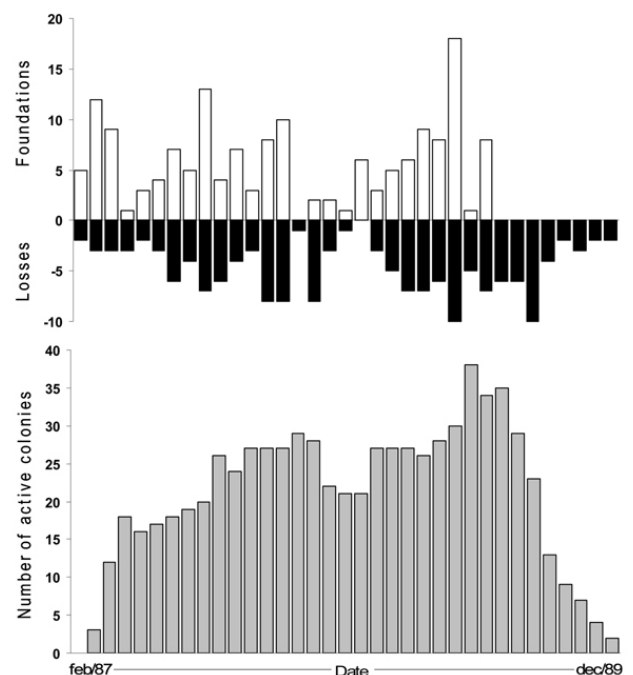


Figure 1. Month pattern of nest foundation, losses (mortality by abandonment, destruction or predation) and number of active colonies of *Mischoctytarus cassununga* from February 1987 to December 1989.

Gehan's test for differences between two samples.

RESULTS AND DISCUSSION

M. cassununga

For *M. cassununga*, we observed 160 nest

foundations, of which 26 (16,3%) were destroyed, 16 (10%) predated, 65 (40,6%) abandoned and 53 (33,1 %) completed the cycle.

The life-span of colonies ranged from 56-714 days with mean $274,26 \pm 165,33$ days, producing 7-234 cells with mean $59,15 \pm 54,84$ cells and 1-609 adults with mean $44,3 \pm 90,56$ adults. There was observed a maximum of three utilizations/cell. Colony foundations and abandonments were observed all around the years, suggesting that the species present an asynchrony nesting behavior (Fig.1) as observed for other *Mischocyttarus* species (JEANNE 1972; POLTRONIERI & RODRIGUES 1976; RAPOSO FILHO 1981; GOBBI & SIMÕES 1988).

Table 1 presents the results from linear regressions for the variables transformed to logarithms. All regressions were highly significant. If we assume that the original variables can be described appropriately by power-functions, then some interesting results arise from the confidence limits for the slopes of regressions. First, the slope of regression for the log-transformed number of adults produced (response variable) with both the number of cells and the colony life-span (independent variables) was significantly higher than 1. This means that the exponents of the correspondent power-functions were higher than 1 (a positive allometric relation), which by their way imply that the number of adults produced increases more than proportionally with the number of cells or the colony life-span. As expected, the data shows clearly that larger/older colonies tends to produce proportionally more adults by colony size/age than

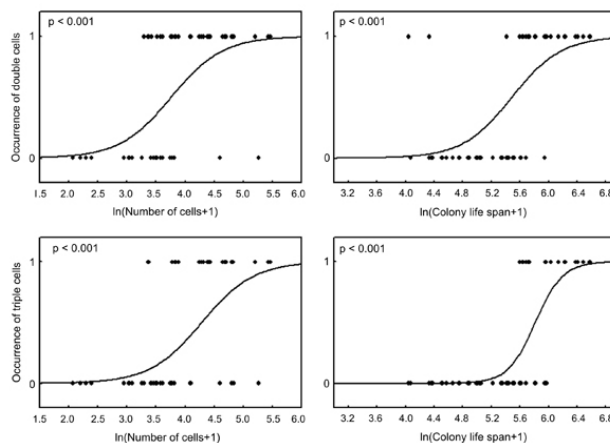


Figure 2. Scatterplots from logistic regressions with their correspondent estimated curves for *Mischocyttarus cassununga*. The occurrence of double (or triple) cells was coded to “0” when none of these cells were observed on a colony and to “1” when at least one of them were observed. Each point consists in a colony data. The hypothesis test results (p values) are shown on the top-left of each graph.

smaller/younger ones. Second, the same conclusion does not apply to the relation between the number of cells and the colony life-span. It must be considered that the first variable increases proportionally with the last, as the slope of regression is not significantly different from 1. So, the improved adult productivity by colony age could not be a simple indirect result from the cell productivity. Third, when we consider only those adults produced from the first cell layer as the response variable, the slope of regression with both the number of cells and the colony life-span turns to be equal to 1. Therefore, the improved adult productivity with colony size/age is certainly caused by cell reutilizations, which is confirmed by the logistic

Table 1. Results from linear regressions for *Mischocyttarus cassununga*. Before analysis, all variables were transformed to $\ln(\text{variable}+1)$. The confidence limits are those for 95% confidence intervals using the t-distribution with 51 degrees of freedom.

Response variable	Independent variable	Intercept	Slope	Confidence limits for slope	R ²	p
Adults produced	Number of cells	-2.4	1.375	1.110 -- 1.640	0.674	<0.001
Adults produced	Colony life-span	-6.076	1.623	1.190 -- 2.056	0.517	<0.001
Adults from the first cell layer	Number of cells	-1.946	1.194	0.984 -- 1.405	0.713	<0.001
Adults from the first cell layer	Colony life-span	-4.757	1.339	0.963 -- 1.715	0.491	<0.001
Number of cells	Colony life-span	-1.038	0.879	0.593 -- 1.164	0.417	<0.001

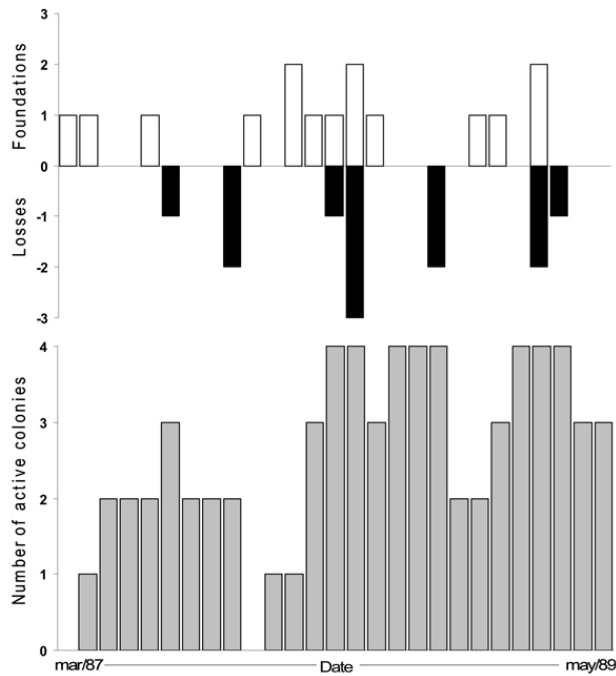


Figure 3. Month pattern of nest foundation, losses (mortality by abandonment, destruction or predation) and number of active colonies of *Mischocyttarus cerberus* from March 1987 to May 1989.

regressions presented in Figure 2.

All logistic regressions were highly significant. Thus, the probability of a colony utilizing two or three times the same cells for adult production is highly dependent on the colony size/age, and the relation between them is positive. In other words, there is a greater chance of cell reutilization in larger/older colonies.

M. cerberus

We observed 15 nest foundations, of which one

(6,7%) was destroyed or predated, five (33,3%) were abandoned and nine (60 %) completed the cycle. According to GOBBI et al (1993) we considered as predated the abandoned nests with missing parts and the destroyed ones were separated based on total disappearance of the nest with no apparent cause.

The life-span of colonies ranged from 82-383 days with mean $269,44 \pm 192,89$ days, producing 12-63 cells with mean $34,44 \pm 18,69$ cells, and 1-90 adults with mean $22,89 \pm 29,84$ adults. As was observed for *M. cassununga*, we found a maximum of three reutilizations/cell with asynchronous foundation (Fig.3).

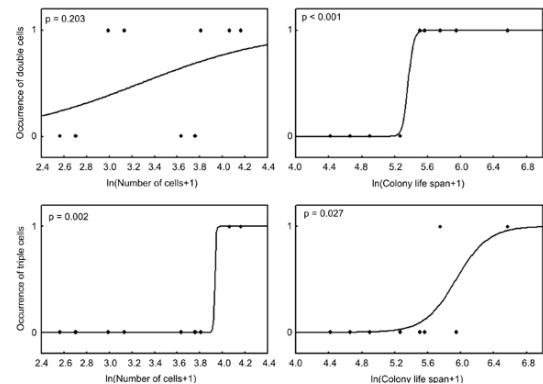


Figure 4. Scatterplots from logistic regressions with their correspondent estimated curves for *Mischocyttarus cerberus*. The occurrence of double (or triple) cells was coded to "0" when none of these cells were observed on a colony and to "1" when at least one of these cells was observed. Each point consists in a colony data. The hypothesis test results (p values) are shown on the top-left of each graph. The regressions in the top-right and in the bottom-left graphs are somewhat problematic, because of the gap on the abscissa dimension between the last "0" occurrence and the first "1" occurrence. Nevertheless, it distrusts only the exact values of parameter estimation for the curves. The significance of the tests is still valid.

Table 2. Results from linear regressions for *Mischocyttarus cerberus*. Before analysis, all variables were transformed to ln(variable+1). The confidence limits are those for 95% confidence intervals using the t-distribution with 7 degrees of freedom.

Response variable	Independent variable	Intercept	Slope	Confidence limits for slope	R2	p
Adults produced	Number of cells	-3.804	1.831	0.742 -- 2.920	0.649	0.005
Adults produced	Colony life-span	-5.373	1.452	0.326 -- 2.579	0.509	0.019
Adults from the first cell layer	Number of cells	-3.188	1.596	0.685 -- 2.508	0.67	0.004
Adults from the first cell layer	Colony life-span	-3.934	1.151	0.087 -- 2.215	0.409	0.038
Number of cells	Colony life-span	1.272	0.399	0.797	0.095	0.217

Considering the number of adults as the response variable, the regressions with both the number of cells and the colony life-span are significant (Tab.2). However, these two last variables are not significantly related. The statistical effect of a lower sample size for *M. cerberus* can be readily perceived at the relatively large confidence intervals for regression slopes. As they encompass the value 1, any nonlinear relation could be inferred.

The logistic regressions show significant results, except that for occurrence of double cells as response variable and the number of cells as the independent variable (Fig.4). Based on the patterns observed for *M. cassununga*, and the other three regressions, we expect that this last relation would

Table 3. Results from the analysis of covariance. The "Effects" are the independent variables, of which "species" is the categorical predictor and the others are continuous covariates. Before analysis, all response variables and covariates were transformed to $\ln(\text{variable}+1)$.

Response variable	Effect	F(1,59)	p
Adults produced	Species	0.3087	0.581
	Number of cells	123.951	<0.001
Adults produced	Species	0.36	0.551
	Colony life-span	66.522	<0.001
	Species	1.391	0.243
Number of cells	Colony life-span	38.944	<0.001

nevertheless become significant if sample size were somewhat larger. Even not considering this, we have already sufficient evidence to conclude that the colony size and/or age affect positively the chance of a colony reutilizing cells for adult production, the same pattern as that found in *M. cassununga*.

Interspecific comparisons

As expected, the number of colony foundations differed significantly between the two species (binomial test, $p < 0.001$). They differed also with respect to the adult production success, but not by the causes of colony mortality. The proportion of

successful colonies were significantly higher in *M. cerberus* (Pearson Chi-square: 4.330, $df = 1$, $p = 0.037$).

The colony size, represented by the total number of cells, the number of adults produced and the colony life-span did not present difference between species (t-test for cells and adults, respectively: $t = 0.996$, $p = 0.323$; $t = 0.499$, $p = 0.619$; Gehan's

Table 4. Results from the general linear models with logit link function and the binomial distribution. The "Effects" are the independent variables; of which "species" is the categorical predictor and the others are continuous covariates. Before analysis, all covariates were transformed to $\ln(\text{variable}+1)$.

Response variable	Effect	Wald chi-square	p
Occurrence of double cells	Species	1.259	0.262
	Number of cells	14.121	<0.001
Occurrence of double cells	Species	0.498	0.48
	Colony life-span	15.433	<0.001
Occurrence of triple cells	Species	0.109	0.741
	Number of cells	14.387	<0.001
Occurrence of triple cells	Species	0.282	0.595
	Colony life-span	12.234	<0.001

Wilcoxon test for colony life-span: test statistic = 0.220, $p = 0.826$) (Tab.3).

As we have already seen for each species separately, covariance analysis just confirmed that the number of adults produced, the number of cells and the colony life-span were all significantly correlated (except for the relation between the last two variables in *M. cerberus*). However, there was no difference between species regarding any response variable, meaning that the proportion of adults produced by number of cells and by days of colony activity and the proportion of cells by days of colony activity should be considered statistically equal for the two species. Unfortunately, as the sample size for *M. cerberus* was inevitably low, it is indeed difficult that any difference be evidenced — unless the pattern be too strong.

The logit analysis also shows no difference regarding species (Tab.4). Nevertheless, the effects of all covariates were highly significant, what is just like the previous results from separate species logistic regressions.

We observed that *M. cassununga* produced a higher number of foundations than *M. cerberus*, suggesting different ecological strategies adopted. Besides both species statistically presented a very similar colony life-span, *M. cerberus* produces a lower number of foundations, which is compensated by a proportionally higher number of colonies with complete life cycle.

GOBBI *et al.* (1993) observed a similar mechanism for *Polistes versicolor* (Olivier, 1791) and *Polistes simillimus* Zikán, 1951 in which *P. simillimus* had more foundations and a less successful colonies than *P. versicolor*. Besides the authors did not identified the reasons, we believe that the assynchronicity is usually connected to bigger colonies where exists an increase in the occurrence of females with developed ovaries, which due to agonistic processes of the dominant against them, are expelled from the colony and this is probably responsible for the increased number of foundations of the species.

The studies of PREZOTO (2001) on *P. simillimus* nest productivity and OLIVEIRA (2005) on *P. versicolor* nest productivity, showed that these species presents very different strategies on nest building behavior. *P. simillimus* presents a tendency in build new cells, showing a low number of cell utilizations. This fact is probably the responsible for the higher number of cells observed in this species. *P. versicolor* shows a tendency for the construction of smaller nests than *P. simillimus*, but with a higher rate of utilization.

According to these considerations plus the lower number of *M. cerberus* colonies founded and the lack of statistical differences between both species regarding the proportion of adults produced by number of cells, by days of colony activity, and the proportion of cells by days of colony activity, we believe that *M. cerberus* is apparently more fitted to the local environmental conditions than *M. cassununga*, showing evidences at least for our data, that in these conditions *M. cerberus* is behaving as a "K" strategist and *M. cassununga* as a "r" strategist.

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