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COLONY CONDITION AND BIONOMIC ALTERATIONS IN **GEOTRIGONA INUSITATA** (APIDAE, MELIPONINAE)

CONDIÇÃO DA COLÔNIA E ALTERAÇÕES BIONÔMICAS EM **GEOTRIGONA INUSITATA** (APIDAE, MELIPONINAE)

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Several papers (ref. in SAKAGAMI, 1982; ZUCCHI, in press) disclosed highly complex behaviorial pattern underlying the cell provisioning and oviposition process (POP) of the stingless bees. The POP is composed by a chain of strongly interrelated events where cell construction, provisioning, oviposition and operculation constitute the main parts. The cell provisioning behavior which constitutes the main focus of this paper, although keeping the massal condition of the solitary bees is a complex trait performed by several bees which serially deposit drops of food inside the brood cell.

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Normally the terms, weak, medium and strong are tentatively employed to characterize colony stronghold but one must be confident on their arbitrareness since the evaluation of colony condition is generally difficult and sometimes meaningless. To it contributes, for instance, the basic character of the division of labor (polyethism) and its intrinsic dependence on a flexible age related task allocation which, on its turn, is strongly tied to colonial needs as evidenced long ago by NOLAN (1924) and ROSCH (1930) and repeatedly confirmed by several other specialists. The problems is very complex (see NOWOGRODZKI, 1984, for details) since the ergonomic efficiency of the colony can be reached through several and probably interconnected pathways and most details are still lacking. So, the mere numerical evaluation of population size as a tool to characterize colony stronghold is biased by the necessity of precisely identifying the several age cohorts (task classes or temporal castes in the sense of OSTER & WILSON, 1978; SEELEY, 1982) and mainly by the actual impossibility to ascertain the biological meaning of the obtained values on account of its inherent and wide flexibility to face colonial needs. The same difficulties arise even after other indexes (**e.g.**, brood size, amount of food supplies, etc. SIMÕES, 1974; SIMÕES & BEGO, 1979) are employed although a linear relationship was found between the number of workers present in the colony of **Melipona compressipes** and the number of cells that contained eggs (PAGE & KERR, 1990). Comparable results appeared also in **Melipona rufiventris** (CAMILLO-ATIQUE, 1974) between the number of adult workers and pupal cells.

Among the eusocial bees, the Meliponinae constitute the most adequate tool for studies on socio-dynamics. As mentioned long ago (BASSINDALE, 1955), they present a peculiar age-linked pigmentation which facilitates polyethism studies (SAKAGAMI, 1982; SAKAGAMI et. al., 1983; SALMAH, INOUE & SAKAGAMI, 1984; TERADA, GARÓFALO & SAKAGAMI,

1975) but comprehensive analyses are still lacking and many aspects remain obscure in spite of the renewed interested on such matters (NOWOGRODZKI, 1984).

In the course of a long term project aiming the study of the "brood cell provisioning and oviposition process (POP)" of the stingless bees it was gradually evidenced that some features of normal colonies can vary in relation to population size and other characteristics (CAMILO-ATIQUE, 1974, 1977). Among other causes accounted for trait alterations the orphanage, queen supersedure and swarming processes play surely very important roles (BASSINDALE, 1955; SAKAGAMI, 1982; SAKAGAMI, BEIG & AKAHIRA, 1964; TERADA, 1972, 1974; SILVA, 1972; SILVA, ZUCCHI & KERR, 1972; IMPERATRIZ-FONSECA & OLIVEIRA, 1976; SIMÕES & BEGO, 1979). However, the latter factors, constitute natural events generally integrated in the colony cycles and promote short-lived alterations which are more evidenced specially on socio-regulation grounds (SAKAGAMI & ZUCCHI, 1974).

The events to be explored here are basically connected to the population size fluctuation of normal (queen-headed and ergonomic efficient) colonies and on the alterations carried out mainly on POP characteristics.

Before going further it should be stressed that such approach bears a prime difficulty. It concerns to the limitations posed by the actual impossibility of adequately assigning colony condition to a given population density rank or even to other colonial characteristics. But in spite of the above mentioned difficulties interesting results appeared in CAMILLO-ATIQUE (1974). By experimentally changing the colony conditions of **Melipona rufiventris** it produced weak, medium and strong colonies and evidenced two sets of behavioral traits: qualitative or species-specific (independent on colony conditions); quatitative (dependent on colony conditions). Besides, persistent behavioral and morphological alterations were detected and these could be assigned to at least two different patterns of colony conditions, namely weak and strong.

MATERIAL

Mainly at the generic level the taxonomy of stingless bees is a matter of controversy among the several specialists. Based on MOURE (1971) and also on our serial ethological studies (ZUCCHI in press; LACERDA, 1986, for details) the generic position of **Geotrigona** is here adopted. **Geotrigona inusitata** Moure was recently recognized as a distinct species and the taxon is being described (MOURE, 1991). As in other species of the genus the bees occupy large underground cavities, probably the deserted parts of the nests of leafcutter ants. The three used colonies (one weak, two strong) were collected at the University Campus in Ribeirão Preto, São Paulo State, southeasthern Brazil.

During the observation period the colonies were transfered to observations hives (SAKAGAMI, 1966) and kept at about 28º C.

METHODS

The statistical analyses followed Mann-Whitney U Test and Mediane Test (SIEGEL, 1956).

a. Characterization of the colonial condition -- in the lack of more efficient mean of characterization an arbitrary but comparatively estabelished method was employed (CAMILLO-ATIQUE, 1974, 1977). Since such a method relies on the development of gradative familiarity to the material, colony characterization is obviously time consuming. After sometime the main characteristics of the colonies can be comparatively recognized (higher or low nest population, amount of stored food, number of combs, brood area, flight activity and pattern, waste removal, size of the advancing front, interval between sequencial POP; number of oviposited cells per POP, etc.) and efficiently assigned to strong or weak colonial condition (LACERDA, 1986).

b. Volume of food deposited into the brood cells -- A portion of comb containing freshly oviposited cells was taken from each colony (weak and strong) and fixed with melted paraffin to a Petri dish. After eliminating the egg, a sample of 48 cells (24 of each colony condition) had their food volumes measured using a micro-pipet under a binocular microscope.

c. Food density -- Comb pieces and samples were prepared as above. A micro pipet (20 microliters) was weighed before and after food collection at each cell. The obtained values (weight and volume) were employed to calculate the density of the brood food.

d. Brood cell volume -- The samples of fresh combs were prepared as afore mentioned. The cell caps were carefully removed until its limit to the comb surface and the empty cells were washed and dried out at room temperature. A previously water filled and weighed micro pipet (50 microliters) was used to fill the cells with distilled water. After it the pipet with the remaining water inside was weighed again enhancing the calculation of the volume and weight of water deposited at every cell.

e. Size of worker bees -- Following MEDLER (1962) the size of workers was evaluated by measuring the maximum length of the right wing submarginal cell.

f. Ontogenetic development -- Freshly oviposited cells were mapped. As soon as the first workers appeared the comb was tranfered to an incubator at 28º C facilitating the connection between the emerged bee, cell number and developmental period from egg to emergence.

Table I summarizes the obtained results. Some years ago (KERR, STORT & MONTENEGRO, 1966) under a comprehensive attempt aiming the identification of the factors probably accounted for caste determination in **Melipona** first arrived to the unexpeted conclusion that the higher the number of bees feeding a brood cell the least the volume of food deposited there. Later on (CAMILLO-ATIQUE, 1977; FERREIRA, ALBUQUERQUE & HADJ-IDRIS, 1989) arrived to similar conclusions in **Melipona rufiventris, Friesella schrottkyi** and **Melipona scutellaris,** respectively. In addition, it was demonstrated that higher feeding numbers and larger periods necessary for cell feeding were characteristics of weak colonies since the strong ones evidenced just the opposite trends. After similar results appeared also in **Geotrigona inusitata** (LACERDA, 1986; itens 4 and 5, table 1) it was decided to learn more on the biological meaning of the event and several other aspects were measure (volume and density of the food deposited into the cell, volume of the cell, size of the worker bees, duration of the immature stages (LACERDA, 1986). The results are in table 1 (items 1,2,3,6 and 7).

A mere glance at the table shows that cell volume (item 3), food volume (item 1), food density (item 2) and duration of the immature stages (item 6) increase from weak to strong colony conditions. Especially the trends observed under itens 1 and 2 are quite unexpected since in the weak colony condition not only the individual acts of cell feeding were more numerous (item 4) but also occupied a large time-span (item 5). Obvious conclusion is that under weak colony condition more bees deposited ther minor and more diluted amounts of food. These tendencies are apparently confirmed at item 7 since the size of the produced imago is smaller under weak than under strong colony condition. Not less interesting are the results concerning item 3; since cell volume is smaller under weak colony condition, which confirm the trend observed in relation to item 7, including its connection to itens 1 and 2. In the honeybee BUCHNER (1953) evidenced that smaller worker bees originate from smaller cells whose volumes were diminished on account of the accumulation of cocoons remains from previous pupal occupants.

Table 1. Some characteristics related to strong and weak colonies of ***Geotrigona inusitata.***

	weak colony	*sample size*	*strong colony*	*sample size*	*statistical analysis*
1. food volume(ul)(*)	*19.03±2.25*	*42*	*22.72±1.60*	*42*	*20 = 6.62* $p < 0.001$
2. food density (mg/ml)(*)	*1.143±0.045*	*24*	*1.171±0.024*	*24*	*20 = 2.12* $p < 0.002$
3. cell volume(ul)(*)	*40.88±2.06*	*24*	*41.24±14.37*	*24*	*20 = 3.75* $p < 0.001$
4. nr. of food depositions per cell (*)	*4.47±0.94*	*49*	*3.77±0.58*	*51*	$X^2 = 15.96$ $p < 0.001$
5. time of cell provisioning (sec)(*)	*7.93±1.17*	*46*	*6.70±1.11*	*46*	*20 = 2.96* $p < 0.002$
6. duration of immature stages(days)	*51.72±1.47*	*39*	*52.86±1.58*	*21*	$x^2 = 0.47$ $p > 0.05$
7. wing length (mm)(*)	*3.54±0.10*	*23*	*3.65±0.05*	*23*	*20 = 2.09* $p < 0.002$

* *Significant results. The* X^2 *was used for items 4 and 6 while the remaining data was compared by Man-Whitney U test. Explanation in the text.*

Presently we are not in a position to explain the origin and basis of the obtained results. Otherwise, it seems clear that the smaller amount of food deposited per bee into the cell cannot be explained only by the lesser amounts of food supplies present in the weak colony. Indeed, even if under food shortage such colonies never reached starvation and colony life proceeded quite normally except for the observed slow rate of development and activity (LACERDA, 1986). Conversely and although being slightly smaller (see Table 1, item 7) the bees in the weak colony are not believed to bear significantly smaller crops mainly on account of the extensible disposition of such organ and the detected diluted condition of the food deposited into the brood cells. In the lack of better explanation we can suggest that under weak colony condition an adjustive social regulation arises enhancing an adaptative kind of strategy to face the unusual situation. If so, the importance of such mechanism is the obvious and to reinforce it there is evidence that a given colony kept its weak condition for more than 2 years (LACERDA, 1986).

Of course, we are not in a position to inform if such phenomenon is observed under natural condition too. Based, however, in the experience achieved through **G. inusitata, M. rufiventris, F. schrottkyi,** and on the indirect evidence provided by KERR, STORT & MONTENEGRO (1966) and CAMPOS & COSTA (1989) we are inclined to suggest it as a real natural possibility. In addition the adjustive mechanisms allowing weak colony condition persistence would be selectively important to face, at least in part, unusual weather or other environmental restriction. It is frequently suggested that food storage provided several eusocial insects with a relative environmental independence. Such evolutionary acquisition is surely very important but probably developed without restricting other kinds of strategies to face possible unfavorable conditions. The regulatory mechanism suggested above could represent one set of such strategies, that is, restricted ativities, improved cycling pathways and other forms of sparing energy. Of course, presently we can only present and evidence the phenomenon. The final understanding of the problem including several biological implications is surely a fascinating challenge for the future, a position not different from that already held long ago by WILSON (1971: 426).

RESUMO

Estudos visando o conhecimento da dinâmica populacional dos Meliponinae têm se valido de conceitos que pretendem definir as condições das colônias, ou seja, colônias fortes, médias e fracas. Tais conceitos têm, evidentemente, caráter bastante impreciso especialmente se utilizados sem o devido cuidado e sem a necessária familiarização com o material estudado. Se tais providências são tomadas, os conceitos não só são de utilidade, como também, podem ser utilizados para fundamentar dados comparativos. Além disso, o presente trabalho evidencia que o caráter número de abelhas aprovisionando um determinado alvéolo de cria e o tempo dispendido em tal aprovisionamento podem ser empregados como índices auxiliares na determinação de colônias fortes e fracas: maior número de atos de aprovisionamento e maior tempo de aprovisionamento, caracterizam colônias fracas, os valores alternativos, evidenciam colônias fortes. Além disso, nas colônias fracas, o volume de alimento depositado na célula de cria é menor, mais diluido o que ocasiona o surgimento de imagos menores. O volume total da célula também é menor em colônias fracas. A condição de colônia fraca é aqui encarada como uma situação especial de colônia normal que, por apresentar características de prováveis ajustes visando a regulação numa solução temporariamente adversa, propicia a sobrevivência da colônia por largos períodos.

PALAVRAS CHAVE: **Geotriona-inusitata,** bionomia, condições da colônia.

SUMMARY

In the course of several bionomic studies of the Meliponinae, colonies are normally refered as strong, weak or medium sized. Such concepts are difficult to be dealt with precisely unless perfect acquataince to the studied material is reached. Besides, a comparative approach suggests at least two characters as simple and useful tools turning the characterization of weak and strong colonies easier: larger number of bees provisioning a given brood cell in a comparatively larger period -- weak colony; the alternative values evidence strong colonies. In addition, in weak colonies the final volume of food deposited into the cell is smaller, with less density and produces smaller adult bees. The cell total volume is also smaller in weak than in stronger colonies. The weak colony situation is here viewed as a normal colony maintained so through adjustive regulatory mechanisms leading to a diminished but enough to survival condition.

KEY WORDS: **Geotriona-inusitata,** bionomy, colony condition.

RÉSUMÉ

Au cours d'études sur la bionomie des Meliponinae, les colonies sont génerallement considerées fortes, intermediaires et faibles. Cette classification est imprécise et pose des problemes surtout pour personnes pas familiarisées avec les Trigones et Mélipones. Selon nos études dans **Geotrigona inusitata** et apres l'utilization de deux variables, c'est à dire, le numéro d'ouvrieres que nourrissent une certain cellule et la periode de temps necessaire pour remplisser de nourriture la même cellule, une indication tres precise de la situation fonctionelle de la colonie est-il possible. En effect, et concernant les nourrissement des cellules, les colonies fortes sont caracterizées per tres courtes periodes de nourrissement ou s´engagent peu d´abeilles noutrices, la nourriture régurgitée est tres concentrée et en mineur volume. Situations opposées caracterizent les colonies faibles. En effect, les abeilles originées de colonies fortes sont plus grosses quand comparées aux lesquelles provenant de colonies faibles. Il est donc raisonable de conclure que la condition "colonie debile" est caracterizée per des adaptations qui permettent vie normalle quoique réduite ce qui serait important pour affronter un milieu temporairement detrimental.

MOTS CLÉS: **Geotrigona-inusitata,** bionomie, condicion de la colonie.

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