Cerumen collection accompanied by thieving and attacking in a stingless bee, Nannotrigona (Scaptorigona) postica (Latreille), with a consideration on territoriality in social insects*

by

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The observations given in the present paper are a byproduct of the comprehensive treatise on ethology and sociology of Nannotrigona (Scaptotrigona) postica Latreille, (Trigona (Scaptotrigona) postica Latreille in the system by Schwarz), developed by one of us (S.F.S.) during his stay in Rio Claro, in collaboration with Mr. Ronaldo Zucchi. In addition, a brief consideration is given to the territoriality of social insects, though this does not relate directly to the facts observed.

At the end of March, 1963, we received an enormous nest of *Trigona* (*Tetragona*) clavipes (Fabricius) from Dr. Paulo Nogueira-Neto; it had been found within a hollow tree-trunk about 46 cm in diameter. On April 9, the colony was transferred to an artificial hive and the old nest was left exposed at a corner of the apiary of the Departamento de Biologia Geral, Faculdade de Filosofia, Ciencias e Letras de Rio Claro. After that time, many social bees visited

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the trunk for nearly two months to collect cerumen, from which the honey and pollen pots, pillars and involucrum of the clavipes nest were made. It was interesting that only two species, the introduced African honeybee, Apis mellifera adansoni Latreille and a stingless bee, N. postica, visited the trunk, although the apiary possessed nearly thirty colonies belonging to more than fifteen species of stingless bees, including very active colonies of certain species such as Trigona (Tetragonisca) jaty Smith and Melipona quadrifasciata anthidioides Lepeletier. We attempted to force T. jaty to collect the cerumen from the trunk without results. Between honeybees and N. postica, there was a difference in diurnal activities, the honeybees being more abundant and active in the forenoon and N. postica in the afternoon. It is plausible that differential thermal sensitivity caused such segregation, because the tendency became, though not quantitatively measured, clearer in late April to May, with the seasonal decrease of air tempera-tures. The foragers of N. postica came at least from two different colonies. In these colonies we noticed a remarkable extension of entrance tubes, 3-4 cm more than the inicial lengths. The newly extended parts were easily recognized by the distinctly paler coloration. It must also be noted that the foragers took from the pollen pots only cerumen, leaving the pollen itself intact. In the summer of 1962, one of us (S.F.S.) observed an opposite case; N. postica worked at an abandoned nest of T. jaty. In this case the foragers collected only pollen, leaving the cerumen walls of the pots intact. Of course the pollen stored by different stingless bee species may act differently as releasing stimuli. Yet it is probable that here we have another example of the behavioral adjustment depending on the requirement of the colony.

The cerumen collecting behavior is as follows: On arrival at the trunk, the forager first searches for a suitable place for a variable time. After such exploration, she settles on a definite spot. The body is supported by out-stretched middle and hind legs, and the metasoma slightly bent downward. In this posture, accompanied by continuous touchings of the cerumen by the antennae, the mandibles successively take off tiny particles of cerumen, which are joined together and constantly manipulated by mandibles. Often the fore legs participate in such manipulation, more frequently as the lump to be carried grows (Fig. 1, A). The bee often stops to add new particles, raises the fore body, and manipulates the lump with the mandibles and fore legs. When the lump attains an appropriate size, one of the middle legs reaches forward (Fig. 1, B), and using bristles on its underside, the bee transfers the lump very rapidly to the corbicular surface of the hind leg of the same side, which is synchronously moved a little forward (Fig. 1, C). By repetitions of this elementary behavior pattern, the cerumen lump on the corbicula grows little by little. Often the middle leg is extended afterward against the corbicula and presses the growing lump gently. With the gradual growth of lumps in both corbiculae, a peculiar raising of the hind legs appears. The legs are frequently raised upward during a pause, either on one side alone (Fig. 2) or often on both sides simultaneously. In the latter case, body totters momentarily because of the loss of balance. The behavior pattern resembles that of some phytophagous scarabeid beetles resting on leaves when stimulated gently. This behavior might involve the estimation of the loads by the bee, their absolute weight as well as the balance between the sides. But no honeybee working at the same place showed such an act. Except for the lack of this raising of the hind legs, the cerumen collection of the honeybees is essentially identical to that in *N. postica*. Only differences are that the metasoma is more raised and the middle legs are moved farther forward than in *N. postica*.

Besides the normal cerumen collection activities as mentioned above, thieving of ready made lumps from the corbiculæ of other bees was frequently observed. This activity can be segragated into primary and secondary thievings, but the behavior pattern is the same in both cases. Primary thieving is further divided into two: Some bees are restless after arriving at the trunk, seeking out other bees which have lumps on their corbiculæ, and stealing those lumps. Other bees only steal on occasional close contact with the corbiculæ. But this correspondence is not strict, often the newly arrived thieved by the occasional contact and *vice versa*.

In both cases, the thief stands on middle and hind legs, raises the fore body and, after rapid antennal touchings to the lump (Fig. 2), takes off the latter with mandibles. The attitudes of individuals being robbed are: 1) Complete indifference, 2) Mild resistance by raising the hind leg concerned in a manner similar to that described above (Fig. 2), 3) Escape from the thief, usually continuing work at a slightly distant place. 4) Mild counterattack with mandibles. The most frequent cases are 1) and 2). Very rarely a rather severe combat develops from 4), but usually does not continue long. In any case, the stolen lump is transferred to one of the corbiculæ as in normal collection.

Secondary thieving is seen in the individuals, which performed or suffered from primary thieving, and appears quite frequently. Such individuals become, less persistent in their work, probably due to the imbalance in the load, *i. e.*, a large lump on only one side, often wandering to and fro and thieving in the manner already described. The stolen lump is, in most cases, transferred to the corbicula which does not have the large load. Occasionally two robberies, A from B and B from C were seen synchronously. Through the frequent occurrence of such thieving, either primary or secondary, the cerumen collection is seemingly governed by a curious efficiency. Apparently the thieving may increase the efficiency of particular individuals at the sacrifice of that of others. And the total efficiency of the collecting party may decrease. Thieving was seen, though much more rarely, among honeybees, and occasionally *N. postica* robbed honeybee but never the reverse.

As mentioned above, mild counter-attcks by robbed individuals occasionally developed into rather severe combats, "facing each other, gripping tightly with interlocked mandibles or tumbling over each other like two wrestlers, head to head, and body to body" (SCHWARZ, 13). But such combats were relatively rare, and did not continue long when they did occur¹. On the other hand, much

¹As mentioned previously, at least two colonies of *N. postica* were working at the place. It is probable but uncertain that such severe combats took place between the individuals of different colonies.

more severe and lasting attacks were made by *N. postica* on the honeybees. In this case, the attack began occasionally from the attempt to thieve by *N. postica* and the resulting resistance by the honeybee. But in most cases, the attacks were initiated by *N. postica* and further intensified when the honeybee responded by the defensive attitude, stretching the antennae and producing high-pitched buzzing. The attack was usually unilateral. *N. postica* usually clung with her jaws to one of the wing bases or occasionally to one leg of the honeybee (Fig. 3). When biting, the *postica* became very persistent; probably aimless movements of the honeybee to liberate herself may give further stimulus to continue to cling. In one instance, the clinging lasted one hour after one of us (S.F.S.) brought such pair to the laboratory. The costal vein of the fore wing of the honeybee is often cut through or nearly so, and the honeybees, incapable of flight, walk around aimlessly on the ground and ultimately become the victim of ants.

With respect to the cerumen collection without thieving, the behavior sequence of both N. postica and honeybees coincides with that of propolis collecting described by MEYER (10), including the transferal to the corbicula in the sitting position, instead of in flight as for pollen packing. The only difference is the occurrence of characteristic raising of the hind legs in N. postica. On the other hand, the same author (9) asserted that the honeybee, at least in northern Germany, forages for wax from outside of the hive only when forced experimentally, but not spontaneously. Apparently this does not fit the present case. The stingless bee cerumen is different from bees' wax, but this may be of minor importance. In this instance, the honeybee workers participated in the work without any previous training, and, though we have no quantitative measure, the total amount of cerumen brought back to the Apis hives wa apparently considerable.

The thieving of ready-made cerumen lumps is nothing other than a manifestation of the widespread tendency for economy of labor among insects which perform some "works". Usually any such construction is made by a sequence of sub-processes, the order of which is often stereotypically determined. But the stereotypy varies from case to case, and, in some instances the presence of more or less worked-over material elicits its acceptance, with the resulting omission of some usually intervening sub-processes. Many classical examples of such are seen in the thieving of ready-made dung balls in scarabeid beetles and of prey captured by the other individuals in hunting wasps, notably among pompilid wasps. The fact that many social insects can be reared in artificial nests essentially depends on this ability to economize labor by accepting readymade material. Such tendencies are occasionally fixed genetically, resulting in the cleptobiotic mode of life.

As to the attacks of *N. postica* on honeybee workers, it must be remarked that the attacks did not possess the role of territorial defense. The place was open to both species, and the individual combats did not develop to the monopoly of the place by any species, nor, apparently, by any colonies. This situation leads us to the following brief commentary on territoriality in social insects.

In any social insects, the areas around the nests are defended, though the intensity of such defense varies greatly among species. Outside this area, however, territorial defense within the home range is usually limited. In ants, there are various degrees of such extra-nidal defense, which were reviewed and discussed by BRIAN (2). Except for the arboreal Oecophyla the extra-nidal defense appears usually only at the places which are important to the maintenance of the colony, for instance, on the branches inhabited by aphid colonies, but not throughout the home range. In winged social insects, too, such local defense is seen when there is concentrated and more or less lasting food in limited places, as seen among social wasps at exuding tree sap (SAKAGAMI & FUKUSHIMA, 12; KIKUCHI, 5). In the honeybees, such a situation is experimentally brought about by artificial training to a small but concentrated food source. The defense is more severe between different races (KALMUS, 4) and results in monopoly by one species when different species are involved (SAKAGAMI 11). But under natural conditions, the food sources of bees are usually scattered throughout wide areas, and each source is relatively small and does not last for a long time. It is known that some competitive attitudes exist among flower visitors (Bombus, BRIAN, 1; various insects, KIKUCHI, 6, 7, 8). But in these cases, competition does not go beyond mild aggressive and avoidance responses. "Ownership" stimuli seemingly do not attain the level at which violent defense is elicited. The defense of particular flowers is known in some bees, such as in Osmia (VLEUGEL, 14), Centris² and Bombus (DODSON, 3). But such defense is exhibited by the males, hence, probably relates to mating habits. In our case, the source of cerumen was about 1m², and the concentration of working bees was quite definite and lasting. Yet no territorial defense was aroused. This suggests, together with the other cases cited above, that extranidal territorial defense in social insects appears only under extreme situations, i. e., under the extreme concentration of food or building material in very limited spaces. Such limited territorial defense, or limited spatial projection of ownership, may secondarily be produced among vertebrates, as an adjustment of relations among different families, each occupying its own territory, or may arise as an outcome of economy of labor, in connection to the developed nervous ability, both central and peripheral. On the other hand, it is open to question whether such limited territorial defense in social insects is caused by the same mechanism (the advanced, secondary type), or, conversely, by their limited ability to make a topographical perspective of their own home range, due to the lower associative ability (the primary type). In other words, the limited territorial defense could be an advanced, secondary type in vertebrates, but must be the primary type in social insects.

²Such male territorial defense at the flowers seems to be common, at least in the smaller species of this genus. One of us (S.F.S.) frequently observed such behavior in 1962 at Foz de Iguaçu, Paraná, Brazil, and its counterpart in the Paraguayan frontier, Puerto Presidente Franco.

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SUMMARY

The cerumen collecting behavior of a stingless bee, Nannotrigona (Scaptotrigona) postica Latreille was observed. The behavior pattern seen in this activity resembles that in the propolis collecting of the honeybee, except for the peculiar raising of hind legs. Beside such normal collecting, the thieving of the ready-made cerumen loads from the hind legs of other individuals was frequently seen, which often resulted in secondary thieving by the robbed bees. Furthermore, the attacks of N. postica on honeybees working at the same place was occasionally observed. In connection with the fact that such attacks did not possess the role of territorial defense, a brief commentary is given concerning territorial defense in social insects.

RESUMEN

Se observa el comportamiento al colectar cerumen de la abeja melipónida Nannotrigona (Scaptotrigona) postica. Este comportamiento es muy similar al que se observa en la abeja doméstica cuando colecta propolis, excepto el levantamiente peculiar de las patas traseras. Además de dicha forma normal de colectar cerumen, se pudo observar con frecuencia el robo del material ya puesto en las patas traseras por otros individuos, los cuales alguna vez eran, a su vez, robados por los primeros. Ocasionalmente se observaron ataques de N. postica contra la abeja doméstica que colectaba en el mismo lugar. En vista de que dichos ataques no desempeñan un papel en la defensa territorial, se da un breve comentario sobre ésta en los insectos sociales.

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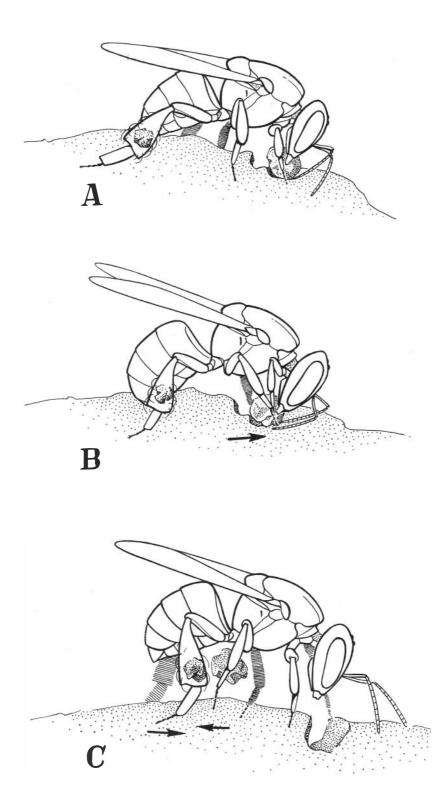
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Fig. 1. Cerumen collection behavior in N. postica.

A. Collection and manipulation of cerumen particles with mandibles and fore legs. B. and C. Successive stages in transferring a cerumen lump to the hind leg corbicula by means of the middle leg. Arrows indicate movements of middle and hind legs.



- Fig. 2. Raising of hind leg by a cerumen collecting worker of N. *postica*. Another worker is attempting to steal the cerumen lump.
- Fig. 3. Clinging of a *N. postica* worker to the wing base of a honeybee.

