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DOMINANCE HIERARCHY AND DIVISION OF LABOUR IN THE SOCIAL WASP, *ROPALIDIA MARGINATA* (LEP.) (HYMENOPTERA : VESPIDAE)

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ABSTRACT

The presence of a dominance hierarchy among the workers of a *Ropalidia marginata* colony can be recognized on the basis of pair-wise interactions. This hierarchy influences the division of labour on the colony in a manner such that the subordinate individuals spend more time making trips to places away from the nest to bring back food, building material, water etc. while the dominant ones like the queen, sit around and at best give alarm reactions. This is consistent with the result that it is the heavier individuals that develop their ovaries and are capable of becoming egg layers.

INTRODUCTION

It is a well established fact that dominance hierarchies are an important component of social life in animals (Schein[7], Kramer *et al.*[2]). However, there have been relatively few studies of dominance hierarchies in the social insects. The few reports that do exist are primarily concerned with dominance among foundresses on pre-emergence colonies or dominance of workers over subordinate foundresses (Pardi[6]; West-Eberhard[10]; Hermann and Dirks[5]; Spradbery[8]; West[9]; Wilson[11]). In this paper I report the presence of a dominance hierarchy among the workers of a *Ropalidia marginata* colony and examine its consequences for division of labour.

Ropalidia marginata is a very common wasp in India that builds small, open nests either on the eaves of undisturbed buildings or on the twigs of cypress bushes. The nests may grow as large as 500 cells with as many as 100 adults and 200 immature stages although small nests are more common. The nests are perennial and often have multiple queens (Gadgil and Mahabal[4]; Gadagkar *et al.*[3]). This study was carried out on a small nest that had been built on a cypress bush in Cubbon Park in the city of Bangalore (13°00′ N and 77°32′ E).

Methods

As a part of an ongoing long term study of the behaviour and social organization of *Ropalidia marginata*, I have recorded the proportion of time spent in different behaviours by different individually marked adults.

Three kinds of sampling methods were used (Altmann[1]). *Ad libitum* sampling was used for the initial qualitative cataloguing of different behavioural patterns and for some preliminary data on the basis of which other sampling methods were chosen. Focal animal sampling was carried out on randomly chosen animals for five minutes at a time. Instantaneous scanning of the behaviour of all animals was carried out at random intervals of time. All sampling sessions were begun and terminated by time-contingent rules. In all 10 hours have been spent in focal animal sampling and instantaneous scanning and 45 hours on *ad libitum* sampling.

RESULTS AND DISCUSSION

In this paper, I present data on the following four behavioural categories :

1. *Sitting :* By sitting is meant simply sitting quiety without doing anything in particular and without being alert to any external disturbance. This is the primary behaviour at night but it is also indulged in during daylight hours. The wasps sit with their body held compactly in one plane with legs and wings drawn very close and the antennae lowered.

2. *Sitting alert :* This involves sitting with wings drawn close to the body but the antennae are raised. When disturbed, the first reaction is to raise the antennae, *i.e.*, a transition from sitting to sitting alert.

3. *Alarm reaction :* Sitting alert is followed by an alarm reaction if the disturbance continues. This involves sitting with both antennae and wings raised. The legs may still be folded or may be stretched so as to raise the body above the substratum.

4. *Temporary absence from the nest :* A wasp temporarily absent from the nest may return with food, building material, water or nothing. However, temporary absence from the nest is considered here as one category. This seems justified because even if a wasp does not bring back anything, it might have attempted to collect food or building material and in any case the very act of making trips to places away from the nest predisposes a wasp to a certain amount of risk and consumes a certain amount of energy.

The wasps fight amongst themselves and this is the basis for ranking them in a dominance hierarchy. In an aggressive interaction, one individual is very subdued and keeps its body as stiff and compact as possible. This is the subordinate individual. The dominant individual climbs over the dorsal part of its opponent and bends itself so as to bite its mouth parts. All individuals do not fight as often or with every body else. However, when they do fight, it is easy to see which one is dominant.

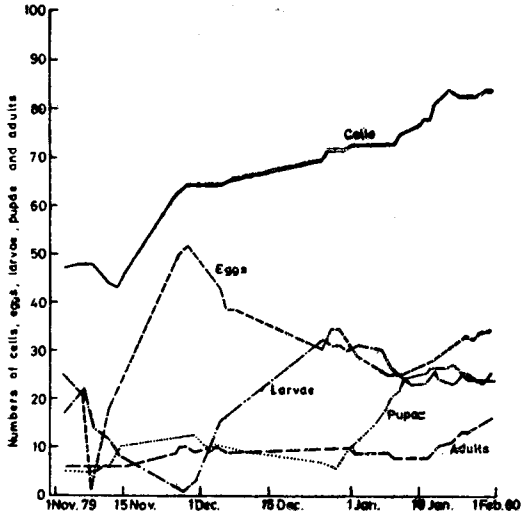

FIG. 1. Growth of the *Ropalidia marginata* nest during the period of study.

Figure 1 shows the numbers of cells, eggs, larvae, pupae and adults that were present in the nest during the three months of this study. This is a relatively small nest which has just reached the size of 80 cells. Previous work has shown that it is only when nests grow beyond this size that multiple queens begin to appear (Gadagkar *et al.*[3]). This nest, as expected has only one egg layer (queen). Figure 2 shows the periods for which each of the adults was present on the nest. The life span of an adult on the nest varied from 2 days to 9 weeks and only the queen has been there for the entire three month period. She is the only one left of the 6 foundresses and thus we have on this nest a situation of daughters helping mothers to raise more offspring. Figure 3 shows the dominance relationships between individuals where, A → B means that A is dominant over B. The reason why all individuals cannot be arranged in one linear dominance hierarchy is that all individuals do not fight with all others. However, it has always been observed that if A is dominant over B and B over C then A is dominant over C. Although the queen does not fight with the workers and therefore cannot strictly be ranked with the workers, she appears to be at the top of the hierarchy because even the very dominant workerseither make very inhibited approaches with the queen or often avoid her.

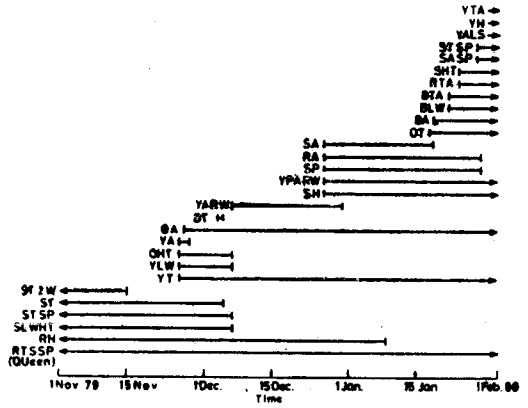

FIG. 2. Life span of adults on the *Ropalidia marginata* nest during the period of study. Arrow head indicates that the fate of the animal beyond the time indicated is not known.

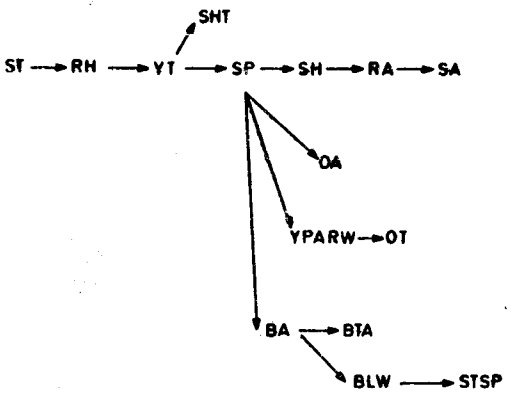

FIG. 3. Dominance hierarchy on a *Ropalidia marginata* nest. ST → RH means that ST is dominant over RH.

Figure 4 shows the percentage of time spent in different activities by four representative individuals. The queen spends most of her time sitting (62%). SP, a very dominant individual spends 30% of its time sitting, SH, an intermediate individual 11% while OA a very subordinate individual only 4%. On the other hand, the time spent away from the nest decreases as one goes up the dominance hierarchy. OA, the subordinate individual spends 58% of its time, the intermediate individual 28%, the dominant individual 8% and the queen 0% of her time away from the nest. It is possible that sitting alert and alarm reaction are functions important for the well being of the

nest. These functions are performed to a greater extent by the dominant and intermediate individuals than by the queen or the subordinate individual. The four activities together constitute 79–94% of the total time of the four individuals being considered.

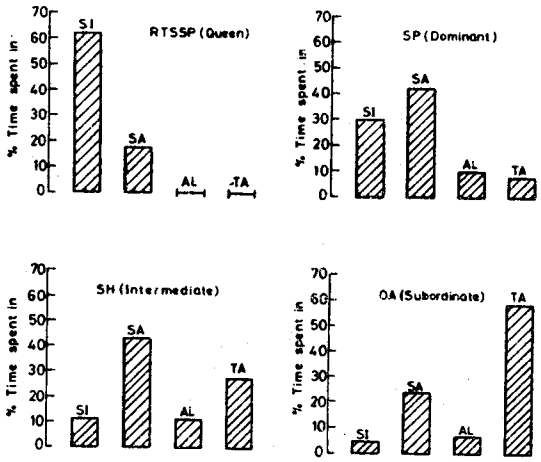

FIG. 4. Percentage of time spent in different activities by four representative adults on a *Ropalidia marginata* nest. Data was pooled from focal animal sampling and instantaneous scanning.

(SI, sitting; SA, sitting alert; AL, alarm reactions; TA, temporary absence from nest).

Thus we see that dominance hierarchies play a significant role in the division of labour among workers on the colony. The manner in which this hierarchy influences the division of labour is consistent with earlier findings. Gadgil and Mahabal[4] showed that females with well developed, functional ovaries were always amongst the heavier individuals on *R. marginata* colonies. The dominant individuals spend more time performing such functions (sitting alert and alarm reaction) that require expenditure of relatively little energy while the subordinate ones spend more time performing high-risk and more energy consuming functions. Given that there is extensive food sharing among the adults (Gadagkar, unpublished observations) dominant individuals are the ones that are likely to become heavier and are in a better position to develop their ovaries and become egg-layers. It must be noted that dominance status is not correlated with age of the animal. For example, OA, the subordinate individual is older than SP and SH. Thus a dominant individual can conserve its energy from a very early age before its ovaries become irreversibly atrophied.

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