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Behaviour of the Indian social wasp *Ropalidia cyathiformis* on a nest of separate combs (Hymenoptera: Vespidae)

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(With 5 figures in the text)

Observations were made on a nest of *Ropalidia cyathiformis* consisting of three combs. The number of eggs, larvae, pupae and adults were monitored at about 3-day intervals for a 2-month period. The behaviour of the adults was observed with special reference to the proportion of time spent on each of the three combs, the proportion of time spent away from the nest site and the frequencies of dominance interactions and egg laying. The adults moved freely between the three combs suggesting that all of them and all the three combs belonged to one nest. However, most of the adults preferred combs 2 and 3 over comb 1. Of the 10 animals chosen for a detailed analysis of behaviour, seven spent varying periods of time away from the nest site and often brought back food or building material. Five of the 10 animals laid at least one egg each but two adults monopolized most of the egg-laying. The animals showed a variety of dominance interactions on the basis of which they have been arranged in a dominance hierarchy. The dominant individuals laid most of the eggs and spent little or no time foraging, while the subordinate individuals spent more time foraging and laid few eggs or none. It is argued that *R. cyathiformis* is different from *R. marginata*, the only other Indian social wasp whose behaviour has been studied, in being at a more primitive stage of social organization.

Contents

Introduction

Social insects with their permanently sterile worker castes and many instances of altruistic behaviour have long been a source of fascination and intrigue for naturalists. Even Darwin

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recognized that the presence of sterile castes is difficult to explain on the basis of natural selection (Darwin, 1859). In recent years Hamilton (1964*a*, *b*) has argued that, although a sterile individual does not raise any of its own offspring, it can indirectly increase its genetic fitness by contributing to the survival of other individuals that share its genes. This has come to be known as the theory of *kin selection* (see West-Eberhard, 1975). Worker castes in Hymenoptera often help to raise their own sisters; and the peculiar mode of sex determination in Hymenoptera namely, *haplodiploidy*, makes her sisters in fact more closely related to a worker than her own potential offspring (see Wilson, 1971; Hamilton, 1972; Michener, 1974). Lin & Michener (1972) have proposed an alternative theory for the evolution of social behaviour in insects; they emphasize that, at least where complete sterility is not present, mutual advantage especially against predation may be an important factor favouring sociality. Alexander (1974), on the other hand, has argued that natural selection operates on the parents to produce a certain fraction of sterile offspring that would help the remaining fraction of fertile offspring to survive and reproduce better. Thus the emergence of a considerable body of theoretical ideas on the origin and evolution of sociality has intensified interest in the study of social insects (West-Eberhard, 1975; Wilson, 1975; Starr, 1979).

The social wasps belong to the family Vespidae which has about 40 genera (Richards, 1962, 1971, 1978; Jeanne, 1980). Of these, *Belonogaster, Parapolybia, Mischocyttarus*, *Polistes* and *Ropalidia* are of particular interest. They form a separate behavioural category characterized by simple, open nests that can be easily studied, and a rather primitive level of sociality because one or a small group of queens (inseminated females) found new colonies and rear the first brood without the aid of a swarm of workers. *Ropalidia* is considered a genus of special interest in this group (Jeanne, 1980). But, while *Belonogaster*, *Mischocyttarus* and *Polistes* have received considerable attention (West-Eberhard, 1969; Pardi & Piccioli, 1970; Piccioli & Pardi, 1970, 1978; Pickering, 1980; Jeanne, 1972; Litte, 1977, 1979; Strassmann, 1979), there is very little information on *Ropalidia* (Roubaud, 1916; Gadgil & Mahabal, 1974; Darchen, 1976; Gadagkar, 1980). This paper is the first report of observations on *Ropalidia cyathiformis* (Fab.).

Materials and methods

The animal

Ropalidia cyathiformis is a common paper wasp measuring about 8 mm from the tip of the head to the end of the abdomen. It builds small open nests of carton suspended by one or more pedicels on the walls of buildings or on the leaves of small plants such as croton. A nest is founded by one or a few females and large nests may contain 30 or more adults. The time taken for an egg to develop into an adult is about 9 weeks and the mean time of residence of adults on a nest is about 4 weeks.

The present study was carried out on a group of three small combs built on a metallic pole at the Indian Institute of Science, Bangalore (13°00'N and 77°32'E). The three combs, each with about 15–30 cells were within 2–3 cm of each other. As shown later, these combs formed a single nest and the adults moved freely between them.

Sampling methods

Three kinds of sampling methods were used in this study (Altmann, 1974).

***Ad libitum** sampling*

Initial *ad libitum* observations revealed that the adults not only moved between the combs but also

spent a considerable portion of time away from the nest site, at the end of which they often returned with food or building material. There were also many agonistic interactions on the basis of which the dominant and the subordinate individual could be recognized. It was therefore decided to employ unbiased sampling methods to quantify the extent to which each animal performed each of these activities. All the adults were individually identified by marking with one or more spots of quick drying paint without removing them from the nest. A census of all the wasps present was made on alternate days before 0530 hrs since none of the wasps ever left the colony before this time. During the census the comb on which each wasp was present was also recorded, and this information is used to calculate the proportion of time spent by the wasps on each of the combs at night; the wasps did not appear to move between the combs at night time.

Instantaneous scans

At randomly chosen times all the animals were instantaneously scanned to determine whether they were present on comb 1, 2, 3 or were temporarily away from the nest site.

All occurrences of some behaviour

Ad libitum observations showed that the wasps engaged in a number of kinds of dominance interactions (see results for description of the behaviour). To determine the frequency with which each animal dominated or was dominated by any other animal, every occurrence of a dominance interaction in randomly chosen 5-min intervals was recorded.

Since egg-laying was considered one of the most crucial activities in the present study, every instance of egg-laying seen during the entire period of observation was noted.

In all, 135 h of observations were spread evenly between 0630 and 1830 hrs during the 2-month period between 19 February and 19 April, 1980.

Results

The combs and their contents

The numbers of cells, eggs, larvae and pupae in each of the three combs are shown in Fig. 1. The total number of cells did not increase significantly on any of the combs during the period of study. On comb 1, the number of eggs varied around a mean of 3·4, the larvae around a mean of 6·3 and pupae between 0 and 1. In terms of the number of cells, comb 3 was bigger than comb 2 which in turn was bigger than comb 1. On both combs 2 and 3, the number of eggs varied around a mean of about 10, the larvae around a mean of about 12 and the pupae around a mean of about 3.

The adults

The number of adults present on these combs during the period of study (Panel (a) of Fig. 1) varied between 15 and 21. Ten of the longest lived animals, on which a considerable amount of information therefore exists, were selected for analysis of their behaviour. These animals are numbered from 1 to 10 and the time during which they were present is shown in Fig. 2.

Movement between combs

The adults moved freely between the combs. It was therefore of interest to determine whether different animals had special preferences for any of the combs. In other words did

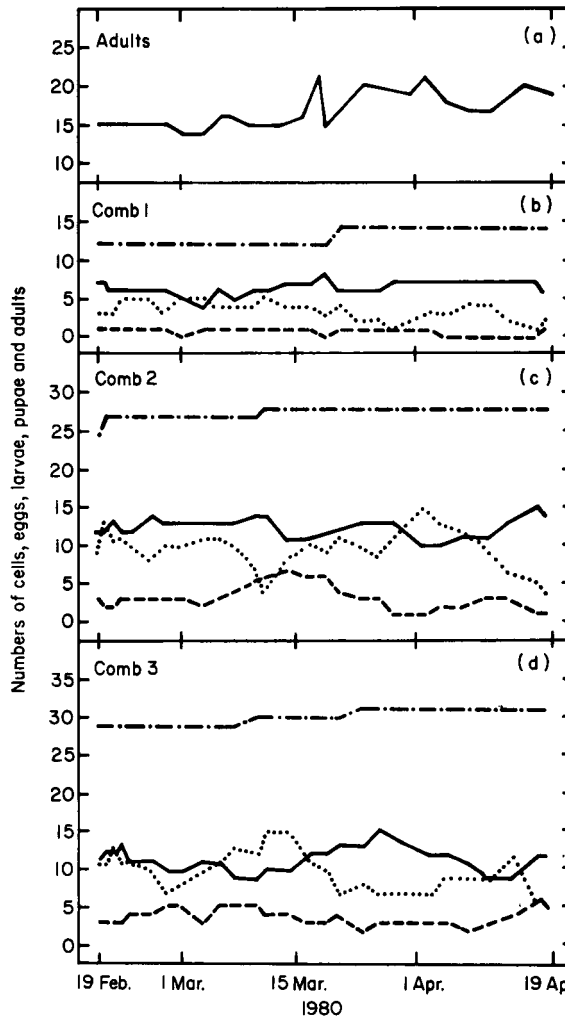

FIG. 1. (a) Numbers of adults (———); (b)–(d) cells (–·–·–), eggs (· · · ·), larvae (———) and pupae (– – – –) at different times on the nest and its constituent combs.

all the animals and all the combs belong to one nest? Figure 3 reveals that although the proportion of time spent on each of the combs varied between the animals, and between day and night, no animal or group of animals appeared to possess any of the combs at the exclusion of the others. Hence all the combs and all the animals may be said to belong to a single nest. Most of the animals however preferred combs 2 and 3 which were bigger and had a larger fraction of the brood than comb 1.

Time spent away from the nest site

The proportion of time spent away from the nest site by each of the ten animals (Fig. 4) was between 0 and 73%. Except animals 3 and 7, all spent at least some portion of their

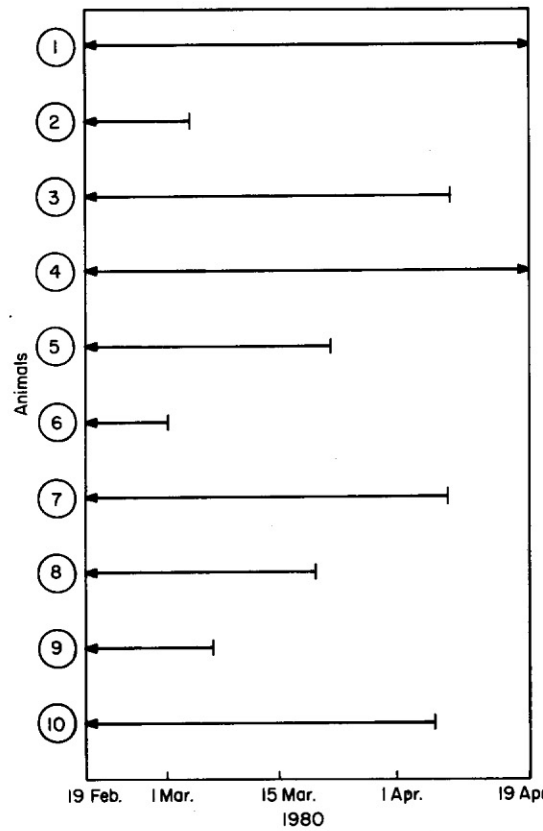

FIG. 2. The period of residence of adults on the nest. Arrowhead indicates that the fate of the animal beyond the time indicated is not known.

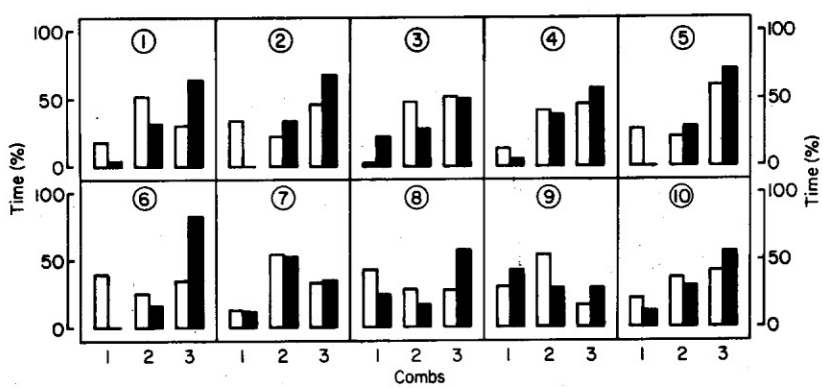

FIG. 3. The proportion of time spent by the ten animals both during day time (unshaded bars) and night time (shaded bars) on the three combs.

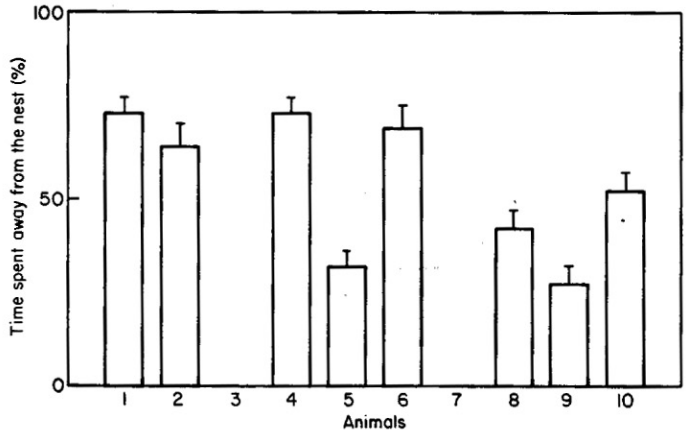

FIG. 4. The proportion of time (mean and standard deviation) spent away from the nest site by the ten animals.

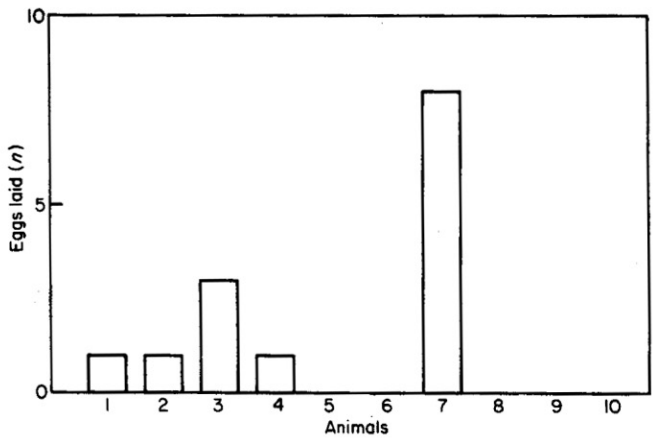

FIG. 5. The number of eggs laid by the ten animals.

time away from the nests. Wasps temporarily absent from the nests often returned with food or building material and even when they did not, they might have spent certain amount of time and energy and incurred certain risks in order to search for food. Moreover, foraging is very difficult to observe, let alone quantify directly. The proportion of time spent in being temporarily absent from the nests is therefore taken as an approximate index of time spent in foraging (see also Gadagkar, 1980).

Egg-laying

Five of the ten animals studied laid at least one egg (Fig. 5) showing that this was a polygnynous nest. Animals 3 and 7, which did most of the egg laying, spent no time at all foraging (Fig. 4).

Dominance behaviour

The wasps engaged in a variety of agonistic interactions. In the most common type of aggressive encounter one individual climbed on top of another and tried to bite its mouth parts. Such an animal is called dominant. The opponent (the subordinate animal) remained very still and kept its body as compact as possible. In a second kind of interaction, one individual (also called dominant) sat on top of another for several minutes. Sometimes one (again called dominant) sat close to another and held one of the latter's legs or antennae in its mouth. In other kinds of interactions one wasp (dominant) chased, nibbled or pecked the other (subordinate). These kinds of interactions were not distinguished in our records: an individual was said to be dominant if it behaved in any of the ways described above.

The hourly frequencies with which each of the ten animals were dominant or subordinate to any other individual are shown in Fig. 6. There appeared to be four kinds of animals. Animals such as 3 were often dominant and seldom subordinate. Animals such as 8 and 9 were seldom dominant and often subordinate. But animal 5, for example, showed a high frequency of both dominant and subordinate behaviour, while animals 1, 2, 4 and 6 had low frequencies of both.

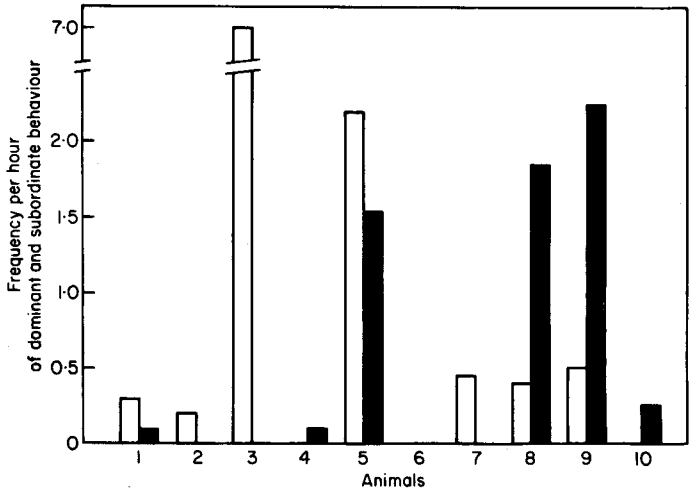

FIG. 6. The frequency per hour of dominance (unshaded bars) and subordinate behaviour (shaded bars) by the ten animals.

A dominance hierarchy for nine of the ten animals is given in Fig. 7. Animal 6, which was never involved in a dominance interaction, could not be represented. No instance of the reversal of a dominant/subordinate relationship was observed. Animals 3 and 7, which had the highest ranks, spent no time at all in foraging, and laid most of the eggs.

Discussion

The three combs of *R. cyathiformis* studied evidently belonged to one nest although most adults spent more time on combs 2 and 3. This species does not, however, always build multiple combs: we have also seen other nests with a single comb (unpublished observations).

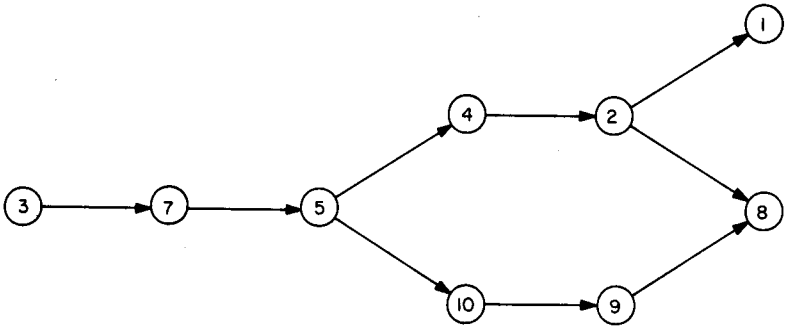

FIG. 7. Dominance hierarchy among the ten animals on the colony: $3 \rightarrow 7$ means that animal 3 is dominant over animal 7. Although the frequency of subordinate behaviour for 7 is shown to be zero in Fig. 6, data from *ad libitum* observations have also been used to construct the dominance hierarchy shown here and therefore 3 is shown to be dominant over 7.

The presence of multiple combs have been reported for other social wasps such as *Polistes canadensis* (Jeanne, 1979), *P. aterrimus* and *P. carnifex* (Rodrigues, 1968), *P. metricus* (Gamboa, 1981), *P. exclamans* (Strassmann, 1981) and *R. marginata* (Gadagkar, unpublished observations), but for none is there quantitative information on differences among adults in their comb preference.

The nest studied was polygynous; and five of the ten adults studied in detail each laid at least one egg. Polygyny is known in large nests of social wasps (see, for example, Richards & Richards, 1951). But in such nests there is a clear distinction between egg-layers and workers; other egg-layers in polygynous nests behave like queens in all respects and do no foraging (except when they cease to be queens and become workers; see for example West-Eberhard, 1978). In contrast, several individuals (such as animals 1, 2 and 4) in the nest of *R. cyathiformis* studied here, foraged as well as laid eggs. In addition to the time spent away from the nest (which is taken as an index of foraging), animal 1 for example was observed to bring back food and share it with other adults in the nest both before and after it was observed to lay an egg. It is believed that this is the first documented case of simultaneous egg-laying and foraging by a social wasp when more than one adult is present on a nest.

Although five of the ten animals studied laid eggs and seven of the ten animals foraged, there were considerable differences in the extent to which different animals did so. Animals 3 and 7 spent no time at all foraging and they laid most of the eggs; these animals were also at the top of the dominance hierarchy. Hence the dominant individuals spent the least amount of time foraging and laid most eggs, and the subordinate individuals spent more time foraging and laid few or no eggs. This is consistent with the behaviour of other social wasps such as *Polistes fuscatus* (West-Eberhard, 1969) and *R. marginata* (Gadagkar, 1980) for example.

Another important activity of this species is cannibalism. Several instances of adults eating eggs, larvae and even pupae (after breaking open the cap of the pupal cell) were observed (unpublished observations). It would be of interest to know which of the adults showed this behaviour, but we give no information on this for the following reason. Once one animal

initiates cannibalism by pulling out an egg, a larva or a pupa, several others present on the nest join it and feed on the already killed immature stage. Hence initiation of cannibalism is the significant act; but initiation of cannibalism itself was seldom seen.

Eighty-two species belonging to nine genera of social wasps have been recorded from India (Gupta & Das, 1977). The only other social wasp from India whose behaviour has been studied is, however, *R. marginata* (Gadagkar, 1980; Gadgil & Mahabal, 1974). It would, therefore, be of interest to compare *R. cyathiformis* with *R. marginata.* Small nests of *R. marginata* have a single egg-layer. Large nests have more than one individual with well developed ovaries. However, we have made no careful observations of such large nests. What follows therefore refers only to small monogynous nests in which there is always a clear distinction between egg-layers and workers with no overlap between these roles except when a single foundress is attending a newly founded nest. Furthermore, the egg-layer of a nest of *R. marginata* is dominant over all the other individuals: she does not normally come into contact with her nest mates, and they often withdraw from her presence. No instances of larval or pupal cannibalism have been observed in *R. marginata* except immediately after extensive predation by *Vespa tropica.*

In contrast, the nest of *R. cyathiformis,* which forms the subject of the present paper, had at least five egg-layers and there was no clear distinction between egg-layers and workers. The same individuals have been observed to lay eggs as well as forage within a short period. Moreover, even the most dominant individuals often engaged in actual physical interaction with other adults. The dominance interactions of this species appear to be much more varied than those of *R. marginata.* In addition, several instances of larval and even pupal cannibalism were observed in *R. cyathiformis.* It is therefore suggested that *R. cyathiformis* is at a more primitive stage of social organization than that of *R. marginata.* In fact, *R. cyathiformis* probably represents one of the most primitive levels of eusociality recorded among the Vespidae (except some stenogastrinae). More information on this species should therefore throw some light on the factors responsible for the origin of eusociality in wasps.

Summary

Three combs of the Indian social wasp, *Ropalidia cyathiformis*, built very close to each other were studied. The adults moved freely between the combs and it was concluded that the combs and adults belonged to a single nest. A variety of dominance interactions was observed among the adults on the basis of which they could be arranged in a dominance hierarchy. The most dominant individuals monopolized most of the egg-laying and spent little or no time foraging. The subordinate individuals spent more time foraging but some of them also laid some eggs. This species appears to be unusual among the social wasps studied in that some individuals did both egg-laying and foraging and therefore combined the roles of queen and worker. This is not usually known to occur except when a single foundress is attending a newly founded nest. On the basis of this and other evidence it is argued that *R. cyathiformis* is at a more primitive level of sociality compared to *R. marginata,* another Indian social wasp that has been studied.

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