Reprinted from:

The Biology of Social Insects

Proceedings of the Ninth Congress of the
International Union for the Study of
Social Insects, Boulder, Colorado, August 1982

**edited by Michael D. Breed,
Charles D. Michener,
and Howard E. Evans**

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Westview Press / Boulder, Colorado

A Comparative Study of Social Structure in Colonies of *Ropalidia*

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Ropalidia is a large old world genus in the family Vespidae whose systematics has been studied by van der Vecht (1962) and Richards (1978). There is very little information on the biology of *Ropalidia* (summarised by Richards, 1978) and even less regarding social organization (summarised below). However, the genus *Ropalidia* is considered to be of special interest primarily because of its diversity in social organization and nest architecture. The genus contains both independent- and swarm-founding species with both open as well as enveloped nests (Jeanne, 1980; van der Vecht, 1962).

Some information on social organization is available for 2 African and 2 Indian species. In Africa, Roubaud (1916) reported that *R. guttatipennis* colonies consist of a mixture of morphologically indistinguishable females, some with functional ovaries and some without. The colonies of *R. cincta* studied by Darchen (1976) were monogynous and there was a dominance hierarchy with the queen at the top of the hierarchy and the males at the bottom.

In India, *R. marginata* has colonies which may be either monogynous or polygynous with the adults all morphologically identical. New colonies are founded by one or a group of females (Gadagkar et al. 1978). Gadgil and Mahabal (1974) showed that females with well developed ovaries tend to be among the heaviest individuals in a colony and hypothesized that workers spend more energy in food gathering but receive a disproportionately smaller share of the food and thus suffer from 'nutritional castration'. Gadagkar (1980) demonstrated that there is a dominance hierarchy in the colonies which influences division of labour in such a fashion that the dominant individuals including the queens spend most of their time sitting on the nest and at best show alarm reactions while the subordinate individuals spend a great deal of time making trips to places away from the nest to bring back food, building material, water etc. *R. cyathiformis* appears to be similar except that it is conjectured to be at a more primitive level of social organization because several individuals lay eggs as well as forage and therefore combine the roles of queen and worker (Gadagkar and Joshi, submitted).

Here we analyse time-activity budgets of individually identified wasps of *R. marginata* and *R. cyathiformis* by multivariate

statistical techniques such as principal components analysis and hierarchical cluster analysis and show that wasps of both species fall into three distinct clusters or behavioural castes which we call sitters, fighters and foragers.

MATERIALS AND METHODS

Observations were made on two colonies of R.marginata for 165 hours and six colonies of R.cyathiformis for 170 hours in Bangalore (13°00'N and 77°32'E). Individual wasps were identified by marking with a spot of paint.

Ad libitum sampling was used to describe the behavioural repertoire, instantaneous scanning to estimate the proportion of time spent in different behaviours and all occurrences of rare behaviours were recorded in separate sessions to calculate the frequencies with which these were performed (Altmann, 1974).

Time-activity budgets for 20 animals of R.marginata and 32 animals of R.cyathiformis were used in principal components analysis (Anderberg, 1973; Frey and Pimental, 1978) and hierarchical cluster analysis (using the single linkage algorithm, and Pearson product moment correlation as an index of similarity between animals, De Gheet, 1978).

RESULTS

The time-activity budgets (data not shown) reveal that every animal spends most of its time (85-100%) in the six activities, sitting plus grooming, sitting alert (antennae raised), mild alarm reaction (antennae and wings raised), walking, inspection of cells and temporary absence from nest. However, the manner in which an animal allocates its time between these activities is highly variable. For example, the time spent by an animal in sitting varied between 7-56% in R.marginata and between 0-67% in R.cyathiformis; the time spent in temporary absence from the nest varied between 0-69% in R.marginata and between 0-88% in R.cyathiformis. This suggests that most individuals are capable of, and do perform most activities and, the differences between individuals are likely to be quantitative rather than qualitative. For this reason we have subjected the time-activity budgets to multivariate analysis. The results of principal components analysis show that temporary absence from the nest and sitting have the highest weightage in the first two principal components respectively in R.marginata and temporary absence from the nest and sitting alert have the highest weightages in the first two principal components in R.cyathiformis respectively. 92.5% and 98.1% of the total variance are accounted for by the first two principal components in R.marginata and R.cyathiformis respectively. Wasps of both species fall into three distinct clusters when each animal is represented as a point in the coordinate space of the first two principal components (Figs.1 and 2). The distinctness of the three clusters was confirmed by the method of nearest centroid. The method of hierarchical cluster analysis gives identical clusters for both species (not shown). In both the species members of one cluster rank highest in sitting (see Figs.3 and 4)

Figure 1. Behavioural castes in *R. marginata* obtained by principal component analysis. Each point represents an animal. $\odot$ = centroid of the cluster

Figure 2. Behavioural castes in *R. cyathiformis* obtained by principal components analysis. Each point represents an animal. $\odot$ = centroid of the cluster.

Figure 3. Mean behavioural profiles for the three clusters obtained in Fig. 1 for *R. marginata*. A, percentage time spent in the six activities used in the analysis: 1, sitting plus grooming; 2, sitting alert; 3, mild alarm reaction; 4, walking; 5, inspection of cells; 6, temporary absence from nest. B, mean frequency per hour of 5 other activities not used in the analysis: 1, bringing food loads; 2, attacking; 3, being attacked; 4, snatching food; 5, losing food.

Figure 4. Mean behavioural profiles for the three clusters obtained in Fig. 2 for *R. cyathiformis*. A, percentage time spent in the six activities used in the analysis. Numbering as in Fig. 3. B, mean frequency per hour of 4 other activities not used in the analysis.

and we call these 'sitters'. Members of a second cluster rank highest in temporary absence from the nest. Wasps temporarily absent from the nest often returned with food, building material or water and hence we call these 'foragers'. The third cluster has the highest rank for sitting alert, an activity that is positively correlated with fighting (labelled as attacking in R.marginata and dominance behaviour in R.cyathiformis) and we have therefore labelled this cluster as 'fighters'.

DISCUSSION

Multivariate analysis of time-activity budgets reveals the presence of three clusters or behavioural castes namely sitters, fighters and foragers in R.marginata as well as R.cyathiformis. It is interesting to note that although data on egg-laying were not used in the analysis, both the queens of R.marginata (individuals 1 and 13) fall into the same cluster, 'sitters'. Thus R.marginata queens seem to do little other than egg-laying and spend most of their time sitting - perhaps the best strategy to develop their ovaries and maximise their egg-laying capacity. The rest of the sitters in R.marginata could either be hopeful queens or naive workers yet to be recruited into the worker force. This is being investigated by queen removal experiments. The situation in R.cyathiformis is somewhat different. One of the colonies was polygynous and some animals did both egg laying and foraging. However, individual 2 was the most dominant one which did most of the egg laying. Individual 17 was the next most dominant individual on the same colony which may be called a 'potential queen' because it later left this colony and went on to found a new colony in which she was the queen. The data on this animal after she became the queen on the new colony are treated separately in form of 17* in Fig.2. Note that individuals 2, 17 and 17* fall into the same cluster but, in this species they are the fighters. Although probably too early to generalise, it is very suggestive that in R.marginata, where the colonies studied were monogynous and the roles of queen and worker rather distinct, the queens are 'sitters'. In R.cyathiformis on the other hand, where one of the colonies was polygynous and the distinction between queen and worker was not always present, the 'queens' are 'fighters'. Reproductive competition must obviously be more intense in R.cyathiformis than in R.marginata. Details are being published elsewhere.

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