

Centre for Ecological Sciences, Indian Institute of Science, Bangalore

Behavioural Castes, Dominance and Division of Labour in a Primitively Eusocial Wasp

K. CHANDRASHEKARA & RAGHAVENDRA GADAGKAR

CHANDRASHEKARA, K. & GADAGKAR, R. 1991: Behavioural castes, dominance and division of labour in a primitively eusocial wasp. *Ethology* 87, 269—283.

Abstract

Female wasps of the primitively eusocial species *Ropalidia marginata* may be classified, by a statistical analysis of their time-activity budgets, into three behavioural castes namely Sitters, Fighters and Foragers. We show that Foragers are primarily responsible for the risky task of foraging for food and have very poorly developed ovaries. Sitters and Fighters forage rarely if at all but share the bulk of the intra-nidal tasks such as feeding larvae and building the nest. Both Sitters and Fighters have better developed ovaries than Foragers. Queens of most colonies belong to the Sitter caste. There are no obvious morphological differences between queens and workers or between the behavioural castes. Queens are not necessarily the most dominant individuals in their colonies. Instead, most dominance behaviour is performed by a group of workers (the Fighters). Division of labour and social organization are achieved through behavioural caste differentiation and not, as in many other species studied, through a dominance hierarchy led by a despotic queen suppressing all her nestmates into worker roles. This suggests that behaviour patterns in such primitively eusocial insects are likely to be moulded by a complex interaction between selection at the individual and colony levels.

Corresponding author: Dr. Raghavendra GADAGKAR, Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India.

Introduction

Eusocial insects, namely those that live in colonies comprising individuals of more than one generation, cooperate in brood care and relegate reproduction to one or a small number of their colony members (MICHENER 1969; WILSON 1971), may be classified into two broad groups. Highly eusocial insects such as all termites, most ants and some bees and wasps are characterized by a morphological distinction between reproductive and worker castes and often between different subcastes among the workers as well. This leaves little or no reproductive opportunity for workers who are destined to remain sterile but leads to

efficient division of labour and a near harmonious social organization (WILSON 1971; SPRADBERY 1973; MICHENER 1974; HÖLLDOBLER & WILSON 1990). Primitively eusocial insects such as many species of bees and wasps on the other hand lack morphological caste differentiation. This provides considerable flexibility in the social roles that the adult insects may adopt but raises questions such as: why do some individuals accept sterile worker roles and how division of labour and social organization are achieved?

These questions have motivated many investigations of primitively eusocial polistine wasps (e.g. WEST-EBERHARD 1969; JEANNE 1972; LITTE 1977, 1979, 1981; STRASSMANN 1981 a, b; for reviews and additional references see ROSS & MATTHEWS 1991). Most of these studies have used one of the two large polistine genera, *Polistes* and *Mischocyttarus*. *Ropalidia* is a polistine genus that is often thought to be crucial for an understanding of social organization and evolution of social life in wasps (e.g. WILSON 1971; JEANNE 1980). Although several studies on *Ropalidia* have been published in recent years (e.g. GADGIL & MAHABAL 1974; DARCHEN 1976; SUZUKI & MURAI 1980; GADAGKAR 1980; GADAGKAR et al. 1982; GADAGKAR & JOSHI 1983, 1984; KOJIMA 1984, 1989; ITÔ 1985, 1986; YAMANE 1986; for a review and additional references see GADAGKAR 1991), our understanding of the biology and social organization of *Ropalidia* lags considerably behind that of other polistine genera. Many investigators have therefore called for more intensive studies of this genus (e.g. KOJIMA 1984; ITÔ 1985).

Here we describe a study of post-emergence colonies of *Ropalidia marginata* (Lep.), a primitively eusocial wasp lacking morphological castes, which attempts to understand the roles of behavioural dominance and behavioural caste differentiation in division of labour and social organization.

Materials and Methods

Study Sites

The study was conducted between Jan. 1986 and May 1987 on 12 naturally occurring post-emergence colonies of *R. marginata*. 7 of the 12 colonies studied were located in Bangalore (13° 00' N and 77° 32' E) and 5 were in Mysore (12° 25' N and 76° 50' E), India. All colonies were built on eaves of buildings or other man-made structures.

Data Collection

Behavioural data presented in this paper are based on 230 h of observation of 12 natural colonies by methods described earlier (GADAGKAR & JOSHI 1983, 1984). In all colonies only one individual was ever seen laying eggs. This individual was designated the queen. At the end of the observations, nests were collected along with all the adults present on them. All female wasps present on a nest (nest 10 was an exception) at the time of collection were examined under a binocular dissection microscope to measure their body size, dissected to assess their ovarian condition and dried at 80 °C to record their dry weight. The non-structural fat content of each wasp was estimated following the method of FOLCH et al. (1957).

Variables Used in the Study

In all, 20 variables were used in this study. They are the proportions of time spent in five common behaviours, (1) Sit and Groom, (2) Raise Antennae, (3) Walk, (4) In cells, (5) Absent from nest, and the frequencies per h of 11 rare behaviours, (6) Dominance behaviour, (7) Subordinate

behaviour, (8) Bring food, (9) Snatch food, (10) Lose food, (11) Feed larva, (12) Bring building material, (13) Snatch building material, (14) Lose building material, (15) Extend walls of cells, (16) Build new cells; (17) an Index of ovarian condition (computed as the amplitude along the first principal component of six input measures of ovarian condition namely, length of the largest oocyte, width of the largest oocyte, mean length of the proximal oocytes, mean width of the proximal oocytes, number of mature eggs (proximal oocytes that, on microscopical examination, appeared to have a fully formed chorion which gave them a characteristic pearly white appearance) and the total number of oocytes), (18) an Index of body size (computed as the amplitude along the first principal component of seven input measures of body size namely, inter-ocellar distance, right ocello-ocular distance, head width, head length, mesoscutum width, mesoscutum length and right wing length), (19) Dry weight (mg) and (20) Non-structural fat content (mg).

Data Analysis

Principal components analysis. Time-activity budgets constructed from data on proportions of time spent in five common behaviours were subjected to principal components analysis (FREY & PIMENTEL 1978). Principal components analysis and identification of the resulting clusters were performed separately for each colony as described by GADAGKAR & JOSHI (1983, 1984). For all subsequent analysis data from all the colonies were combined.

Logistic regression analysis. Each of the 20 variables used in the study was modelled to test its influence on the probability of an animal being a Sitter, a Fighter or a Forager such that,

$$\begin{aligned}\ln(p_1/p_3) &= a_1 + \beta_1 X \\ \ln(p_2/p_3) &= a_2 + \beta_2 X\end{aligned}$$

where p_1 , p_2 and p_3 are the probabilities of being a Sitter, a Fighter or a Forager respectively ($p_1 + p_2 + p_3 = 1$), a_1 and a_2 are intercepts, β_1 and β_2 are regression coefficients and X is the independent variable. The unknown parameters in the above regression equations were estimated by maximizing the likelihood:

$$L = \left(\prod_{i=1}^k p_1\right) \cdot \left(\prod_{i=k+1}^m p_2\right) \cdot \left(\prod_{i=m+1}^n p_3\right)$$

and the estimates were used to calculate p_1 , p_2 , and p_3 . 1 to k are Sitters, $k+1$ to m are Fighters and $m+1$ to n are Foragers (for further details see, SHANUBHOGUE & GORE 1987; GADAGKAR et al. 1988, 1990 b; COX & SNELL 1989).

Correlates of Dominance. Each of the 20 variables used in the study were examined as potential correlates of dominance. Pooling all dominance interactions seen in the 12 colonies, the number of interactions 'h' where the dominant animal had a larger value for a variable and those 's' where the dominant animal had a smaller value for the variable were computed. The departures of these numbers from those predicted on the basis of a null hypothesis postulating no effect of the variable ($h = s$) were tested by a normal approximation of the binomial distribution where the test statistic was computed as

$$z = (h - np) / \sqrt{npq}$$

where n is the total number of interactions, and $p = q = 0.5$ (FELLER 1968). This was repeated for each of the 20 variables.

Results

Identification of Behavioural Castes

Time-activity budgets constructed for individually identified animals from 12 colonies of *R. marginata* revealed that female wasps spend 69%—100% ($\bar{x} \pm SD = 94.61 \pm 5.23$) of their time in the five common behaviours, Sit and Groom, Raise Antennae, Walk, In cells and Absent from nest. The manner in

which each wasp allocated her time between these five behaviours was however highly variable. In an attempt to discern a pattern in the allocation of their time, these time-activity budgets were subjected to principal components analysis. Our results show that the first two principal components together account for 97.9%—99.7% of the variance in the input data. The position of each wasp is therefore plotted as a point in the space of the first two principal components (Fig. 1). This results in a distribution of the points into three distinct clusters. The boundaries of the three clusters were not equally obvious in all 12 colonies but the distinctness of the clusters was always confirmed by the nearest centroid criterion (GADAGKAR & JOSHI 1983). Following GADAGKAR & JOSHI (1983, 1984) the cluster showing the highest mean proportion of time in Sit and Groom was labelled Sitters, the cluster showing the highest mean proportion of time in Raise antennae or the highest frequency of Dominance behaviour was labelled Fighters and that showing the highest mean proportion of time spent in Absent from nest was labelled Foragers. In 11 out of 12 colonies the queen belonged to the Sitter caste while in colony 3 alone the queen was a Fighter.

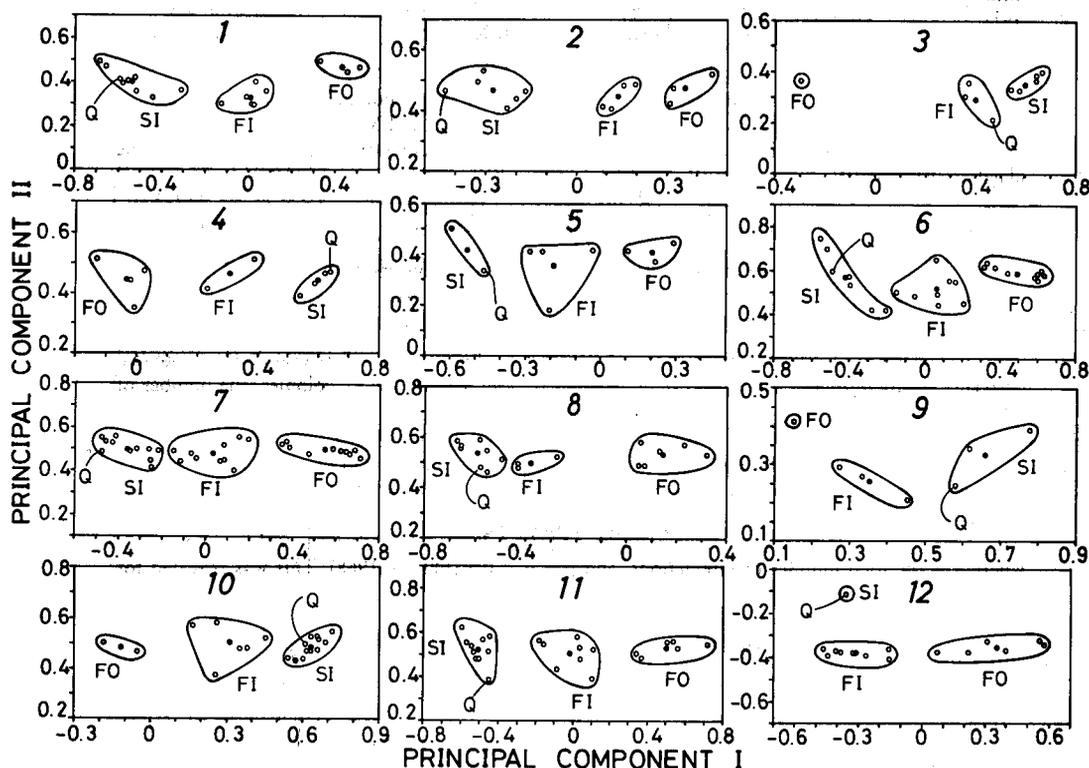


Fig. 1: Behavioural castes in 12 colonies of *Ropalidia marginata* identified by principal components analysis of time-activity budgets. Each point (open circles) plotted in the coordinate space of the first two principal components represents a wasp. Solid circles are the centroids of their respective clusters. SI = Sitters, FI = Fighters, FO = Foragers, Q = queen

Table 1: Correlates of the behavioural castes assessed by logistic regression analysis

	Sitters vs. Fighters			Sitters vs. Foragers			Fighters vs. Foragers		
	estimated coeff.	SE	test statistic Z	estimated coeff.	SE	test statistic Z	estimated coeff.	SE	test statistic Z
Sit and groom	14.7247	2.2954	6.4148***	38.3711	5.4040	7.1004***	23.1266	4.7865	4.8316***
Raise antennae	-20.2737	5.0746	-3.9951***	11.6375	6.3765	1.8251	31.9113	6.6997	4.7631***
Absent from nest	-20.0904	3.3298	-6.0336***	-39.6311	5.3988	-7.3407***	-19.5407	4.2070	-4.6448***
Dominance behaviour	- 1.6502	0.8424	-1.9589*	5.4913	2.0838	2.6353**	7.1415	2.0966	3.4062***
Bring food	- 8.8942	2.9594	-3.0054**	-11.1089	2.9671	-3.7440***	- 2.2147	1.1199	-1.9776*
Snatch food	1.2926	0.7559	1.7099	9.5742	1.8177	5.2673***	8.2816	1.8173	4.5569***
Feed larva	- 0.3546	0.2980	-1.1896	0.9110	0.4446	2.0490*	1.2656	0.4490	2.8187**
Extend walls of cells	- 0.0022	0.4641	-0.0048	1.9292	0.7622	2.5311*	1.9068	0.7790	2.4477*
Index of ovarian condition	0.2195	0.0099	2.1961*	0.8109	0.2319	3.4959***	0.5914	0.2332	2.5362*
Index of ovarian condition#	0.1125	0.1714	0.6565	0.7469	0.2449	3.0498**	0.6344	0.2479	2.5586*
Index of body size	- 0.1295	0.1054	-1.2288	0.0061	0.1187	0.5166	0.1909	0.1248	1.5288
Dry weight (mg)	0.0025	0.0067	-0.3727	0.1707	0.0097	1.7466	0.1955	0.1004	1.9473
Fat (mg)	0.1326	0.2668	0.4968	0.5816	0.3453	1.6814	0.4490	0.3642	1.2330

*: $0.05 > p > 0.01$; **: $0.01 > p > 0.001$; ***: $p < 0.001$.

#: index of ovarian condition was retested after the queens (egg layers) were deleted from the data set.

Correlates of the Behavioural Castes

In what ways are Sitters, Fighters and Foragers different from each other? In other words which, if any, of the 20 variables studied here permit us to distinguish different behavioural castes? We have attempted to answer this question by using the method of logistic regression analysis (Table 1).

The coefficient of regression associated with Sit and Groom is significantly greater than zero ($p < 0.001$) in a comparison of Sitters either with Fighters or Foragers. This is interpreted to mean that Sitters spend significantly more time in Sit and Groom than either Fighters or Foragers. Interpreting other coefficients similarly, we find that Fighters spend significantly more time in Raise antennae than either Sitters or Foragers ($p < 0.001$) and Foragers spend significantly more time in Absent from nest than either Sitters or Fighters ($p < 0.001$). These results were expected on the basis of the mean behavioural profiles of the castes which were used to name the clusters. However, we have included these variables as internal controls to establish the correct interpretation of the results of logistic regression analysis and to justify the use of this method to identify the correlates of the behavioural castes.

By examining other variables which were not used in deriving the clusters, we have attempted to establish the patterns of task allocation between the castes. Foragers brought food significantly more often than either Sitters or Fighters ($p < 0.05$) and Fighters did so significantly more often than Sitters ($p < 0.01$). Fighters showed Dominance behaviour significantly more often than either Sitters or Foragers ($p < 0.05$) and Sitters did so significantly more often than Foragers ($p < 0.01$). Sitters and Fighters showed Snatch food, Feed larva and Extend walls of cells significantly more often than Foragers ($p < 0.05$). However Sitters and Fighters were indistinguishable from each other by any of these three variables.

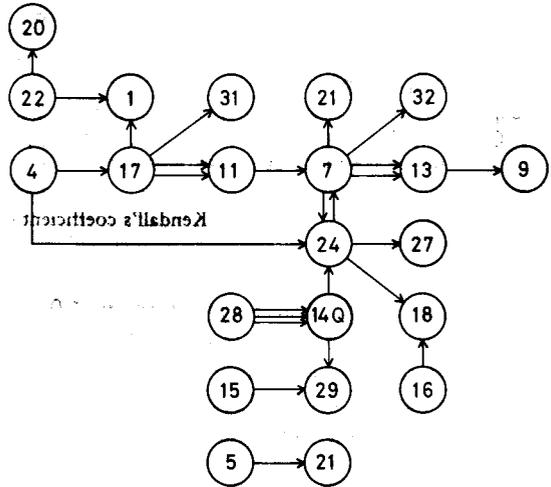
Sitters had significantly better developed ovaries than either Fighters or Foragers ($p < 0.05$) and Fighters had significantly better developed ovaries than Foragers ($p < 0.05$). This result was obviously due to the inclusion of queens among the Sitter caste in 11 out of 12 colonies. When queens of all 12 colonies were excluded from the data set, we found that Sitters and Fighters still had significantly better developed ovaries than Foragers ($p < 0.05$) but Sitters and Fighters were now indistinguishable on the basis of their ovaries. The Index of body size, Dry weight and Fat content however did not differ significantly between castes.

Dominant-Subordinate Relationships

A variety of dominance behaviours were shown towards each other by the wasps in a colony. One animal, dominant by definition, Attacked, Pecked, Chased or Nibbled another, subordinate by definition (see GADAGKAR & JOSHI 1983, 1984 for a description of these behaviours). The frequencies of all these behaviours were pooled to obtain the frequency of Dominance behaviour. One member of a pair of animals was nearly always (in 159 out of 163 pairs of interacting animals observed) dominant over the other in all dominance interac-

tions between them and thus their dominant-subordinate status was unambiguous. We attempted to construct dominance hierarchies for animals in each colony by connecting dominant members of a pair to their subordinate partners by means of arrows. A simple linear dominance hierarchy could not be obtained because all animals did not interact with all the other animals in a colony. Instead a complex network of dominant-subordinate relationships was obtained for most colonies. One such network of intermediate complexity is illustrated in Fig. 2.

Fig. 2: The dominance-subordinate network of colony 7 as an example of intermediate complexity. Arrows connect dominant animals to their subordinate partners. Each arrow represents one instance of Dominance behaviour. Since all animals were observed for the same duration, these numbers are directly comparable. Each circle represents a wasp and the number inside, its code. Of 32 animals, only 22 figure in the dominance-subordinate network shown here; the remaining 10 animals did not show any Dominance or Subordinate behaviour



In 3 out of 12 colonies the queen did not participate in dominance-subordination interactions at all, although several instances of such interactions were recorded among her nestmates. This could not have been merely because our sampling effort may have been insufficient. In one of these 3 colonies, we recorded 75 instances of dominance behaviours and 14 of them by a single animal. Nevertheless, none were shown by the queen. In another 3 of the 12 colonies, the queen participated in dominance-subordination interactions in her colony but was dominated by one or more of her nestmates. Even in the remaining 6 colonies where none dominated the queen and where she participated in dominance-subordination interactions, the queen was never the one to show the highest number of dominance behaviours in her colony. Out of the total number of dominance behaviours shown in a colony, the proportion shown by the queen was indistinguishable from that shown by one or more of her nestmates in 3 of these 6 colonies (test of proportions, $p < 0.05$) and significantly less than that shown by at least one of her nestmates in the remaining three colonies (test of proportions, $p < 0.05$). In no colony and by no criteria can we therefore conclude that the queen is at the top of the behavioural dominance hierarchy of her colony.

We also find that there was a strong and statistically significant positive linear dependence of the frequency per h of Dominance behaviour shown by an animal and the number of animals that it dominates (Fig. 3, $r^2 = 0.75$; $p < 0.01$;

Table 2: Kendall's coefficient of rank correlation between Dominance behaviour and other variables

	tau	SE	z
Subordinate behaviour	0.1874	0.0476	3.9415***
Bring food	0.0041	0.0476	0.0856
Snatch food	0.2186	0.0476	4.5968***
Lose food	-0.0053	0.0476	-0.1123
Feed larva	0.1879	0.0476	3.9520***
Bring building material	0.0741	0.0476	1.5573
Snatch building material	0.1760	0.0476	3.7019***
Lose building material	0.1113	0.0476	2.3403*
Extend walls of cells	0.3560	0.0476	7.4864***
Build new cells	0.1478	0.0476	3.1075**
Index of ovarian condition	0.1856	0.0564	3.2886**
Index of body size	0.2823	0.0564	5.0017***
Dry weight (mg)	0.2326	0.0564	4.1216***
Fat (mg)	0.1972	0.0573	3.4437**

*: $0.05 > p > 0.01$; **: $0.01 > p > 0.001$; ***: $p < 0.001$.

Table 3: Probability of winning or losing in aggressive interactions as a function of behaviour performed, ovarian condition and body size

Variable	No. of cases where dominant and subordinate animals have the same value	No. of cases where animal with higher value of the variable is dominant	No. of cases where animal with lower value of the variable is dominant	Test statistic Z
Raise antennae	30	113	68	3.3448**
Absent from nest	7	71	133	- 4.3409***
Dominance behaviour	11	172	28	10.1823***
Subordinate behaviour	16	38	157	- 8.5218***
Snatch food	37	113	61	3.9421***
Feed larva	31	113	67	3.4286***
Snatch building material	131	55	25	3.3541***
Extend walls of cells	42	114	55	4.5385***
Build new cells	166	33	12	3.1305**
Index of ovarian condition	24	63	45	1.7321
Index of body size	0	84	48	3.1334**
Dry weight (mg)	0	80	52	2.4371*
Fat (mg)	1	73	51	1.9757*

*: $0.05 > p > 0.01$; **: $0.01 > p > 0.001$; ***: $p < 0.001$.

of the Index was dominant and in 45 cases the animal with a lower value of the Index was dominant suggesting no significant influence of Ovarian condition on the outcome of a dominance interaction ($p > 0.05$). (2) Animals with higher values of Index of body size, Dry weight and Fat content were more likely to be dominant rather than subordinate ($p < 0.05$) but, animals that showed higher frequencies of Feed larva, Extend walls of cells and Build new cells were also more likely to be dominant rather than subordinate.

Discussion

Several investigators have found it useful to employ multivariate statistical techniques to discern clusters of functionally similar individuals in social insect colonies that contain morphologically identical or similar individuals. This approach has proved useful in the investigation of inter-individual variability, division of labour and social organization of insect societies (e.g. BROTHERS & MICHENER 1974; PARDI & MARINO PICCIOLI 1981; FRESNEAU et al. 1982; GADAGKAR & JOSHI 1982, 1983, 1984; FRESNEAU & DUPUY 1988; TSUJI 1988; CORBARA et al. 1989; PRATTE 1989). In one such study, GADAGKAR & JOSHI (1983) identified three behavioural castes namely Sitters, Fighters and Foragers in the primitively eusocial wasp *R. marginata*. The queens of both colonies in the study were Sitters. Speculating that some of the remaining Sitters and Fighters were potential queens they argued that Foragers had little or no chance of reproduction. The present study with a larger data base from 12 colonies confirms these basic findings. Three behavioural castes which may be labelled Sitters, Fighters and Foragers, by criteria similar to those used in the previous study, could be identified in each of the 12 colonies. In 11 out of these 12 colonies, the queens were Sitters. The lone exception was colony 3 where the queen was a Fighter. Any speculation to account for this exception would perhaps be premature. It is not clear at this stage whether the behavioural caste of a wasp changes with her age but GADAGKAR & JOSHI (1984) found that in *R. cyathiformis*, most individuals did little work in the first week after eclosion but thereafter followed a relatively constant time-activity budget for the rest of their lives.

Our results suggest that division of labour and social organization are closely linked to behavioural caste differentiation. The extra-nidal task of foraging is performed primarily by the Foragers while the intra-nidal tasks of feeding larvae and nest building are shared between Sitters and Fighters. Because both Sitters and Fighters have better developed ovaries compared to Foragers, but are indistinguishable from each other by their ovaries, potential queens to replace old queens are most likely to be drawn from amongst either Sitters or Fighters. Primitively eusocial species are characterized by the lack of morphological differentiation between queens and workers and the consequent flexibility in the social roles that the adult insects may adopt. The lack of morphological differences between the behavioural castes also adds to this flexibility.

Following the pioneering work of PARDI (1948), dominance hierarchies have been shown to or perceived as having a fundamental role in achieving division of

labour and social organization in many primitively eusocial wasp societies. In most species studied there is usually a despotic queen that is at the top of the dominance hierarchy who actively suppresses aggressive behaviour by nestmates through physical attack. Also, there is a strong correlation between dominance relationships and division of labour such that the most dominant animal monopolizes egg laying while the subordinates are forced to work for the colony both on the nest and outside (PARDI 1948; WEST-EBERHARD 1969, 1986; JEANNE 1972; GADAGKAR 1980; LITTE 1977, 1981; STRASSMANN 1981 a; KOJIMA 1984; ITÔ 1985; RÖSELER 1985; YAMANE 1986; PRATTE 1989). In *Polistes metricus* (DEW 1983) and in *P. fuscatus* (REEVE & GAMBOA 1983, 1987) the queen is the most dominant and active animal in the colony and has been regarded as the central pace-maker and coordinator of colony activity. There are some situations however, where the dominant-subordinate relationships are rather mild or may be nearly absent. But when this happens, the monopoly in egg laying also disappears and several females in a colony are known to have well developed ovaries with mature eggs and/or do actually lay eggs (YAMANE 1973; HOSHIKAWA 1979; KASUYA 1981; ITÔ 1985, 1986; YAMANE 1986).

R. marginata colonies appear to be different in that the queens do not necessarily participate in dominance-subordination interactions and even when they do, the queens are not the most dominant animals in their colonies. And yet during the 230 h of observation reported here as well as during several 100 h of observations of other colonies of *R. marginata* (GADAGKAR 1980; GADAGKAR & JOSHI 1983, unpubl. obs.) we have never observed egg laying by more than one animal in a colony. The queens in *R. marginata* must have some other, more subtle, "non-confrontational" (WEST-EBERHARD 1986), perhaps pheromonal way of suppressing egg laying by their nestmates and thus maintain their unique egg-laying status. Similarly, there must be some other way by which colony activity is stimulated and integrated because the queen does not appear to act as central pace-maker and coordinator of colony activity.

We find a significant correlation between rates of Dominance behaviour and the number of animals dominated. This suggests that Dominance behaviour is not necessarily directed towards one or a small number of animals (perceived as a potential threat), but is distributed over a large number of animals with more or less the same rate of dominance shown towards each opponent. Rates of Dominance behaviour and probabilities of being dominant (rather than subordinate) are correlated with rates of Feeding larva, Extending walls of cells and Building new cells. That dominance behaviour is performed by a group of animals that specialize in several intra-nidal tasks is also consistent with the idea that division of labour and social organization are achieved by behavioural caste differentiation rather than simply by an animal's position in the behavioural dominance hierarchy.

Why is there a behavioural caste differentiation into Sitters, Fighters and Foragers and why do some animals show Dominance behaviour? In primitively eusocial species, many individuals have some chance of direct reproduction in

their lifetime. This should select for behaviours that enhance the possibility of such direct reproduction. Many animals however die without reproducing. This should select for behaviours that enhance the colony's fitness and thereby the indirect component of the individual's inclusive fitness. Thus behaviour patterns in these species should evolve in response to individual as well as colony level selection.

Because Foragers appear to have little or no chance of direct reproduction, we suggest that their behaviour of taking up the risky task of foraging is the direct result of attempts to enhance the colony's fitness and thereby the indirect component of their inclusive fitness. Fighters show high frequencies of Dominance behaviour and we suggest that this serves to enhance both direct as well as indirect component of their inclusive fitness. Exhibiting high frequencies of Dominance behaviour may help individuals to enhance their chances of future reproduction by succeeding old and weak queens. On the other hand Dominance behaviour may also serve to keep the colony members active and working. We have often observed that periods of inactivity on nests are broken by one animal directing dominance behaviour towards one or more of its nestmates (GADAGKAR & CHANDRASHEKARA unpubl. obs., see also GADAGKAR & JOSHI 1983). For this reason and because Fighters perform many intra-nidal tasks, they must also enhance colony fitness. Sitters too appear to enhance colony fitness by performing intra-nidal tasks. But by participating little in foraging and dominance acts and thus avoiding risks and conserving energy, they are probably pursuing an alternate pathway of enhancing their chances of future reproduction. Most individuals therefore work for the colony but without entirely closing their option for direct reproduction and thus seem to attempt to maximize individual fitness without hurting the colony's interests too much. Such a compromise between individual fitness and colony fitness may be essential both due to the uncertainty of direct reproduction and because a female who inherits (as a queen) a large and healthy nest will be able to reproduce more efficiently than one who inherits a small and unhealthy nest.

Fighters are not significantly larger in body size than Sitters or Foragers. But there is a more subtle effect of body size on Dominance behaviour. The frequency of Dominance behaviour per hour is significantly positively correlated with body size (Table 2, $p < 0.05$). However, GADAGKAR et al. (1988, 1990 b) found no effect of body size on the egg laying ability of a large sample of *R. marginata* females under laboratory conditions. In 7 out of 11 colonies in this study (data on body size were not available for colony 10) one or more nestmates were larger than the queen and indeed in one of these colonies the queen was the smallest of all animals in her colony. Larger animals thus may not necessarily have better chances of becoming queens. On the other hand we have argued that dominance behaviour may also increase colony fitness by keeping its members active and working. We speculate therefore that the correlation of body size with frequency of Dominance behaviour is related to its possible colony level function of keeping nestmates active and working — a task perhaps best performed by larger individuals if it is achieved by overt physical aggression rather than by pheromones.

Queens of *R. marginata* are known to mate multiply, use sperm from different males simultaneously and produce mixtures of full and half-sisters (MURALIDHARAN et al. 1986). This, coupled with frequent queen replacements (GADAGKAR et al. 1990 a), should considerably lower worker-brood genetic relatedness. It appears unlikely that full and half-sisters can be discriminated within a colony to restore genetic asymmetries created by haplodiploidy (VENKATARAMAN et al. 1988). Kin-selection facilitated by haplodiploidy (HAMILTON 1964 a, b, 1972) has therefore been considered unlikely to be entirely responsible for maintaining sociality in this species (VENKATARAMAN et al. 1988; GADAGKAR 1991). There is evidence for pre-imaginal caste biasing that programmes some animals to develop into poor eaters and poor egg layers but the extent of this is by itself insufficient to explain the presence of sterile castes in *R. marginata* (GADAGKAR et al. 1988, 1990 b). For these reasons and because of the great deal of behavioural flexibility shown by these wasps GADAGKAR (1991) has argued that opportunities for egg laying in future may be an important factor in maintaining eusociality in such species and indeed that mutualism (LIN & MICHENER 1972) may be the reason why individuals come together and establish groups in the first place. Division of labour and social organization achieved through behavioural caste differentiation, which in turn is moulded through an interaction between individual and colony level selection, rather than by a despotic dominant queen suppressing her nestmates and bullying them into worker roles by constant physical attack, constitutes an appropriate milieu for early social evolution through mutualism.

Acknowledgements

We thank A. SHANUBHOGUE and A. P. GORE for the computer program used to perform logistic regression analysis, Madhav GADGIL, V. NANJUNDIAH, N. V. JOSHI and three anonymous referees for useful comments on a previous version of this paper.

Supported by a grant from the Indian National Science Academy, New Delhi.

Literature Cited

- BROTHERS, D. J. & MICHENER, C. D. 1974: Interactions in colonies of primitively social bees. III. Ethometry of division of labour in *LasioGLOSSUM zephyrum* (Hymenoptera: Halictidae). *J. Comp. Physiol.* **90**, 129–168.
- CORBARA, B., LACHAUD, J. P. & FRESNEAU, D. 1989: Individual variability, social structure and division of labour in the ponerine ant *Ectatomma ruidum* Roger (Hymenoptera, Formicidae). *Ethology* **82**, 89–100.
- COX, D. R. & SNELL, E. J. 1989: *The Analysis of Binary Data*. Chapman and Hall, London.
- DARCHEN, R. 1976: *Ropalidia cincta* guêpe sociale de la savane de Lamto (Cote-d'Ivoire) (Hymenoptera, Vespidae). *Ann. Soc. Ent. Fr. (N.S.)* **12**, 579–601.
- DEW, H. E. 1983: Division of labour and queen influence in laboratory colonies of *Polistes metricus* (Hymenoptera; Vespidae). *Z. Tierpsychol.* **61**, 127–140.
- FELLER, W. 1968: *An Introduction to Probability Theory and its Applications*. Vol. I, 3rd ed. John Wiley and Sons, New York.
- FOLCH, J., LEES, M. & SLOANE STANLEY, G. M. 1957: A simple method for the isolation and purification of total lipids from animal tissues. *J. Biol. Chem.* **226**, 497–509.

- FRESNEAU, D. & DUPUY, P. 1988: A study of polyethism in a ponerine ant: *Neoponera apicalis* (Hymenoptera, Formicidae). *Anim. Behav.* **36**, 1389—1399.
- —, GARCIA-PÉREZ, J. & JAISSON, P. 1982: Evolution of polyethism in ants: observational results and theories. In: *Social Insects in the Tropics*. Vol. 1. (JAISSON, P., ed.) Presses de l'Univ. Paris-Nord, pp. 129—155.
- FREY, D. F. & PIMENTEL, R. A. 1978: Principal components analysis and factor analysis. In: *Quantitative Ethology*. (COLGAN, P. W., ed.) John Wiley and Sons, New York, pp. 219—245.
- GADAGKAR, R. 1980: Dominance hierarchy and division of labour in the social wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). *Curr. Sci.* **49**, 772—775.
- — 1985: Evolution of insect sociality — A review of some attempts to test modern theories. *Proc. Indian Acad. Sci. (Anim. Sci.)* **94**, 309—324.
- — 1991: *Belonogaster*, *Mischocyttarus*, *Parapolybia* and independent-founding *Ropalidia*. In: *Social Biology of Wasps*. (ROSS, K. G. & MATTHEWS, R. W., eds.) Cornell Univ. Press, Ithaca, pp. 149—190.
- —, CHANDRASHEKARA, K., CHANDRAN, S. & BHAGAVAN, S. 1990a: Serial Polygyny in *R. marginata*: Implications for the Evolution of Eusociality. XIth Congr. Int. Union Study Soc. Insects, Bangalore, 1990, pp. 227—228.
- —, GADGIL, M., JOSHI, N. V. & MAHABAL, A. S. 1982: Observations on natural history and population ecology of the social wasp *Ropalidia marginata* (Lep.) from Peninsular India (Hymenoptera: Vespidae). *Proc. Indian Acad. Sci. (Anim. Sci.)* **91**, 539—552.
- — & JOSHI, N. V. 1982: A comparative study of social structure in colonies of *Ropalidia*. In: *The Biology of Social Insects*. (BREED, M. D. & MICHENER, C. D., eds.) Proc. IXth Congr. Int. Union Study Soc. Insects, Westview Press, Boulder, pp. 187—191.
- — & — — 1983: Quantitative ethology of social wasps: Time-activity budgets and caste differentiation in *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). *Anim. Behav.* **31**, 26—31.
- — & — — 1984: Social Organisation in the Indian Wasp *Ropalidia cyathiformis* (Fab.) (Hymenoptera: Vespidae). *Z. Tierpsychol.* **64**, 15—32.
- —, BHAGAVAN, S., MALPE, R. & VINUTHA, C. 1990b: On reconfirming the evidence for pre-imaginal caste bias in a primitively eusocial wasp. *Proc. Indian Acad. Sci. (Anim. Sci.)* **99**, 141—150.
- —, VINUTHA, C., SHANUBHOGUE, A. & GORE, A. P. 1988: Pre-imaginal biasing of caste in a primitively eusocial insect. *Proc. R. Soc. Lond. B* **233**, 175—189.
- GADGIL, M. & MAHABAL, A. 1974: Caste differentiation in the paper wasp *Ropalidia marginata* (Lep.). *Curr. Sci.* **43**, 482.
- HAMILTON, W. D. H. 1964a: The genetical evolution of social behaviour I. *J. Theor. Biol.* **7**, 1—16.
- — 1964b: The genetical evolution of social behaviour II. *J. Theor. Biol.* **7**, 17—52.
- — 1972: Altruism and related phenomena, mainly in social insects. *Ann. Rev. Ecol. Syst.* **3**, 192—232.
- HÖLDOBLER, B. & WILSON, E. O. 1990: *The Ants*. Springer-Verlag, Berlin.
- HOSHIKAWA, T. 1979: Observations on the polygynous nests of *Polistes chinensis antennalis* Perez (Hymenoptera, Vespidae) in Japan. *Kontyû* **47**, 239—243.
- ITÔ, Y. 1985: A comparison of frequency of intra-colony aggressive behaviours among five species of polistine wasps (Hymenoptera: Vespidae). *Z. Tierpsychol.* **68**, 152—167.
- — 1986: On the pleometrotic route of social evolution in the Vespidae. *Monitore zool. ital. (N.S.)* **20**, 241—262.
- JEANNE, R. L. 1972: Social biology of the neotropical wasp *Mischocyttarus drewseni*. *Bull. Mus. Comp. Zool. Harvard Univ., Cambridge* **144**, 63—150.
- — 1980: Evolution of social behaviour in the Vespidae. *Ann. Rev. Entomol.* **25**, 371—396.
- KASUYA, E. 1981: Polygyny in the Japanese paper wasp *Polistes jadvigae* Dalla Torre (Hymenoptera, Vespidae). *Kontyû* **49**, 306—313.
- KOJIMA, J. 1984: Division of labor and dominance interaction among co-foundresses on pre-emergence colonies of *Ropalidia fasciata* (Hymenoptera, Vespidae). *Biol. Mag. Okinawa* **22**, 27—35.
- — 1989: Growth and survivorship of pre-emergence colonies of *Ropalidia fasciata* in relation to foundress group size in the subtropics (Hymenoptera: Vespidae). *Insect. Soc.* **36**, 197—218.

- LIN, N. & MICHENER, C. D. 1972: Evolution of sociality in insects. *Q. Rev. Biol.* **47**, 131—159.
- LITTE, M. 1977: Behavioural ecology of the social wasp *Mischocyttarus mexicanus* (Hym., Vespidae). *Behav. Ecol. Sociobiol.* **2**, 229—246.
- — 1979: *Mischocyttarus flavitarsis* in Arizona: social and nesting biology of a polistine wasp. *Z. Tierpsychol.* **50**, 282—312.
- — 1981: Social biology of the polistine wasp, *Mischocyttarus labiatus*: Survival in Colombian Rain forest. *Smithson. Contrib. Zool.* **327**, 1—27.
- MICHENER, C. D. 1969: Comparative social behaviour of bees. *Ann. Rev. Entomol.* **14**, 299—342.
- — 1974: *The Social Behaviour of Bees*. Belknap Press of Harvard Univ. Cambridge.
- MURALIDHARAN, K., SHAILA, M. S. & GADAGKAR, R. 1986: Evidence for multiple mating in the primitively eusocial wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae). *J. Genet.* **65**, 153—158.
- PARDI, L. 1948: Dominance order in *Polistes* wasps. *Physiol. Zool.* **21**, 1—13.
- — & MARINO PICCIOLI, M. T. 1981: Studies on the biology of *Belonogaster* (Hymenoptera, Vespidae). 4. On caste differences in *Belonogaster griseus* (Fab.) and the position of this genus among social wasps. *Monitore zool. ital. (N.S.) Suppl.* **14**, 131—146.
- PRATTE, M. 1989: Foundress associations in the paper wasp *Polistes dominulus* Christ. (Hym., Vesp.). Effect of dominance hierarchy on the division of labour. *Behaviour* **111**, 208—219.
- REEVE, H. K. & GAMBOA, G. J. 1983: Colony activity integration in primitively eusocial wasps: the role of the queen (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behav. Ecol. Sociobiol.* **13**, 63—74.
- — & — — 1987: Queen regulation of worker foraging in paper wasps: A social feedback control system (*Polistes fuscatus*, Hymenoptera: Vespidae). *Behaviour* **102**, 147—167.
- RÖSELER, P. F. 1985: Endocrine basis of dominance and reproduction in polistine paper wasps. In: *Experimental Behavioural Ecology and Sociobiology*. (HÖLLDOBLER, B. & LINDAUER, M., eds.) Gustav Fischer-Verl., Stuttgart, pp. 259—272.
- ROSS, K. G. & MATTHEWS, R. W. 1991: *Social Biology of Wasps*. Cornell Univ. Press, Ithaca, in press.
- SHANUBHOGUE, A. & GORE, A. P. 1987: Using logistic regression in ecology. *Curr. Sci.* **56**, 933—936.
- SPRADBERY, J. P. 1973: *Wasps*. Univ. Washington Press, Seattle.
- STRASSMANN, J. E. 1981 a: Wasp reproduction and kin selection: reproductive competition and dominance hierarchies among *Polistes annularis* foundresses. *Fla. Entomol.* **64**, 74—88.
- — 1981 b: Evolutionary implications of early males and satellite nest production in *Polistes exclamans* colony cycles. *Behav. Ecol. Sociobiol.* **8**, 55—64.
- SUZUKI, H. & MURATI, H. 1980: Ecological studies of *Ropalidia fasciata* in Okinawa island. I. Distribution of single- and multiple-foundress colonies. *Res. Popul. Ecol.* **22**, 184—195.
- TSUJI, K. 1988: Obligate parthenogenesis and reproductive division of labor in the Japanese queenless ant *Pristomyrmex pungens*. *Behav. Ecol. Sociobiol.* **23**, 247—255.
- VENKATARAMAN, A. B., SWARNALATHA, V. B., NAIR, P. & GADAGKAR, R. 1988: The mechanism of nestmate discrimination in the tropical social wasp *Ropalidia marginata* and its implications for the evolution of sociality. *Behav. Ecol. Sociobiol.* **23**, 271—279.
- WEST-EBERHARD, M. J. 1969: The social biology of polistine wasps. *Misc. Publ. Mus. Zool. Univ. Mich.* **140**, 1—101.
- — 1986: Dominance relations in *Polistes canadensis* (L.), A tropical social wasp. *Monitore zool. ital. (N.S.)* **20**, 263—281.
- WILSON, E. O. 1971: *The Insect Societies*. Harvard Univ. Press, Cambridge.
- YAMANE, S. 1973: Discovery of a pleometrotic association in *Polistes chinensis antennalis* Perez (Hymenoptera: Vespidae). *Life Study* **17**, 3—4.
- — 1986: The colony cycle of the Sumatran paper wasp *Ropalidia (Icariola) variegata jacobsoni* (Buysson), with reference to the possible occurrence of serial polygyny (Hymenoptera: Vespidae). *Monitore zool. ital. (N.S.)* **20**, 135—161.

Received: July 18, 1990

Accepted: January 29, 1991 (H.-U. Reyer)