On reconfirming the evidence for pre-imaginal caste bias in a primitively eusocial wasp

RAGHAVENDRA GADAGKAR, SEETHA BHAGAVAN, RASHMI MALPE and C VINUTHA

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012, India

Abstract. Caste is usually thought to be determined entirely in the adult stage in most primitively eusocial wasps and bees. A pre-imaginal caste bias has however been recently discovered in the primitively eusocial wasp *Ropalidia marginata*. This study also suggested that reigning queens and possibly other adults may influence the production of new queens and implied at least partial support to the parental manipulation or sub-fertility hypothesis for the evolution of insect sociality. The interest of these results prompted an attempt at their reconfirmation. Complete reconfirmation has now been obtained using data from an independent experiment and two additional methods of data analysis. We therefore conclude that caste is at least partly determined prior to eclosion in the primitively eusocial wasp *Ropalidia marginata* which lacks morphological differentiation between egg-layers and non-egg-layers.

Keywords. *Ropalidia marginata*; social wasps; caste determination; evolution of sociality.

1. Introduction

Evolution of altruistic behaviour is one of the prime concerns of sociobiology. Eusocial insects such as ants, bees and wasps, which are characterized by overlap of generations, co-operative brood care and reproductive caste differentiation, show the most extreme forms of altruism and hence are often favoured as model systems in sociobiology. Of these, primitively eusocial insects such as many species of bees and wasps lack morphological differences between reproductive and non-reproductive castes and thus show considerable flexibility in the social roles that individuals may adopt. For this reason, such species are particularly suited for asking questions concerning the forces that mould the evolution of worker behaviour.

Most studies on these species however have assumed that caste is entirely determined in the adult stage. To verify this assumption, an experiment was set up to test the null hypothesis that 'all eclosing females in the primitively eusocial wasp, *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae) are potentially capable of laying eggs'. Of the 197 freshly eclosed females tested in this experiment, only about 50% built nests and laid eggs, although all animals were isolated from conspecifics and were provided with *ad libitum* food since eclosion. This result therefore permitted rejection of the null hypothesis and suggested that caste is at least partly determined prior to eclosion. In addition, the number of empty cells on the nest from which an animal ecloses and its own rate of feeding during adult life were found to be good predictors of the probability that it would become an egg-layer. The presence of empty cells may be considered an indication of the queen's declining condition. These findings were therefore interpreted to mean that

potential workers are produced when the queen of a colony is young and healthy or has a high influence on her colony for other reasons. Conversely, potential egg-layers were thought to be produced when the queen is old and unhealthy or her influence is otherwise low (Gadagkar *et al* 1988).

Because of the interest of these results and certain features of our methodology, we have considered it worthwhile to repeat the experiment. Here a complete reconfirmation of all our previous results using data from a new experiment and employing two additional methods of data analysis is reported.

2. Materials and methods

2.1 *Experimental procedures*

All experiments were performed using the primitively eusocial wasp *R. marginata* whose biology and social organisation have been described in some detail (Gadagkar 1980, 1985, 1990; Gadagkar *et al* 1982; Gadagkar and Joshi 1983). Naturally occurring nests were collected from around Bangalore (13°00' N and 77°32' E), cleared of adults and maintained in the laboratory. Females eclosing from these nests were isolated into individual $22 \times 11 \times 11$ cm ventilated plastic jars. The animals so isolated were provided with a piece of soft wood as a source of building material and were provided an *ad libitum* diet of final instar *Corcyra cephalonica* larvae, honey and tap water from the same source. Records were maintained of the number of *C. cephalonica* larvae consumed by each animal throughout the experiment. The animals were observed for signs of nest-building and egg laying every day. Our experimental procedures are described elsewhere in more detail (Gadagkar *et al* 1988).

2.2 *Data analysis*

2.2a *Logistic regression analysis*: Each animal in our experiment was classified either as an egg-layer or a non-egg-layer. This classification thus yields a binary variable (which shall henceforth be called the dependent variable). We have therefore used the method of logistic regression analysis (Shanubhogue and Gore 1987) rather than simple linear regression analysis to analyse two models. In each model, several variables (which shall be referred to as independent variables) associated with each animal such as the number of eggs, larvae, etc. on its parental nest, its own feeding rate during adult life and indices of its body size were modelled to influence the probability of egg laying by females such that:

$$\ln \left[p/(1\text{-}p) \right] = \beta_{o} + \Sigma \, \beta_i \, X_i.$$

This can be rewritten as

$$p = e^{\beta_o + \Sigma \beta_i X_i} / 1 + e^{\beta_o + \Sigma \beta_i X_i}.$$

Values of β_o and β_i associated with each independent variable were obtained using the maximum likelihood criterion:

$$L = \left(\prod_{i=1}^{m} p_i \right) \left(\prod_{i=m+1}^{n} [1 - p_i] \right),$$

where p is the probability of becoming an egg-layer, $1-p$ the probability of becoming a non-egg-layer, β_0 the intercept, β_i the regression coefficients, X_i the independent variables, L the likelihood, animals 1 to m the egg-layers, and animals $m+1$ to n the non-egg-layers.

2.2b *Comparison of means*: Mean values of independent variables for egg-layers were compared with those for non-egg-layers using a t test. Because some of the independent variables may not be normally distributed, we have also compared means using the non-parametric Mann-Whitney U-test.

2.2c *Correlation analysis*: Although the dependent variable is binary in nature, a corresponding variable which is not binary is the proportion of egg-layers among the animals eclosing from each nest. The association of this variable with those independent variables concerning the nests such as number of eggs, larvae, etc. was investigated by computing Kendall's rank correlation coefficient.

3. Results

3.1 *Need for reconfirmation*

The experiment described in Gadagkar *et al* (1988) showed that about half the animals tested became egg-layers and the other half non-egg-layers. The correlates of becoming an egg-layer or a non-egg-layer were investigated by performing what is sometimes known as a 'fishing expedition'. In other words, we had no specific hypothesis about which variables may be influencing the probability of an animal becoming an egg-layer. All variables for which data were available were tested and 2 out of 15 so tested were found to be significantly correlated with an animal's probability of becoming an egg-layer. Therefore the confidence one may entertain in such a result is perhaps limited. On the other hand, the results obtained by Gadagkar *et al* (1988) were novel and somewhat unexpected. Besides, they led to the discovery of the phenomenon of pre-imaginal caste bias in a primitively eusocial insect which lacks morphological caste differentiation. Although the extent of pre-imaginal caste bias seen cannot by itself account for eusociality in this species, these results imply at least some support for the parental manipulation (Alexander 1974) or sub-fertility (West-Eberhard 1975) hypothesis for the evolution of eusociality. All these factors prompted us to seek a reconfirmation of these results.

3.2 *Two methods of reconfirmation*

We have attempted to reconfirm the results of Gadagkar *et al* (1988) by the combination of two methods. First the experiment was repeated using a new set of animals from a new set of nests. Secondly, the possible involvement of the same variables was studied using two additional statistical techniques, viz. (i) comparison of mean values of independent variables for egg-layers and those for non-egg-layers and (ii) estimating correlation coefficients between the independent variables and the proportion of egg-layers among the animals eclosing from each nest. These two techniques and the original technique of logistic regression analysis have now been

applied to data from each of the two experiments as well as for data pooled from the two experiments.

3.3 *Strategies to deal with results from different statistical tests and different experiments*

One obvious problem that would arise when the same variables are studied by different statistical techniques or by using data from independent experiments is that the results may not be identical. The following strategy was used to deal with such potentially confirming or conflicting results.

When conflicting results were obtained within the same experiment but between different statistical tests, the variables involved were treated with suspicion and only those variables which were shown to be significant by all statistical tests were considered important.

Our strategy to deal with results from replicate experiments has been somewhat different. First, a new experiment was performed under conditions identical to those in the first experiment. Secondly, data pooled from both experiments were reanalysed. This gave us 3 sets of results namely those from experiment 1, from experiment 2 and from data pooled from experiments 1 and 2. Only those variables which were significant in the pooled data as well as in at least one of the individual experiments were accepted as being important in influencing the outcome of the experiment.

3.4 *Logistic regression analysis*

Results of both models using logistic regression are in table 1 and those pertaining to experiment 1 are from Gadagkar *et al* (1988). In experiment 1, three variables, viz. number of empty cells on parental nest, an animal's feeding rate during its adult life and its ocello-ocular distance (an index of body size) had coefficients which were significantly different from zero ($P < 0.05$). In the second experiment, only feeding rate has a regression coefficient which is significantly different from zero ($P < 0.05$). When data pooled from the two experiments are analysed, 3 variables, viz. number of pupae, number of empty cells and feeding rate are found to have coefficients significantly different from zero ($P < 0.05$). Using the strategy outlined in the previous section, we consider the roles of number of empty cells and feeding rate as having been reconfirmed. This strategy requires that the two other variables, viz. ocello-ocular distance and number of pupae not be considered important at this stage. It might be mentioned here that similar results are obtained if the proportion of empty cells is considered instead of the absolute number of empty cells.

3.5 *Comparison of means*

The mean values of each variable for egg-layers were compared with those for non-egg-layers as another method of detecting the correlates of egg laying. Our conclusions arising from such comparisons using a parametric *t*-test (shown in table 2) are similar to those from logistic regression analysis. Once again, the roles

Table 1. Results of logistic regression analysis.

Variables	Data from experiment 1			Data from experiment 2			Data pooled from experiments 1 and 2			Remarks[†]
	Estimated coefficient (β)	Standard error	Z	Estimated coefficient (β)	Standard error	Z	Estimated coefficient (β)	Standard error	Z	
Model 1: Nest properties as determinants of the probability of egg laying by eclosing females										
No. of eggs	−0·0071	0·0154	−0·4597	0·1610	1·0874	0·1480	−0·0031	0·0087	0·3550	
No. of larvae	0·0043	0·0149	0·2869	0·1486	0·9882	0·1504	−0·0111	0·0101	−1·0976	
No. of pupae	0·0155	0·0226	0·6841	1·0208	1·3245	0·7707	0·0305	0·0148	2·0518*	
No. of parasitized cells	−0·1347	0·1442	−0·9340	10·9547	10·4664	1·0466	0·0368	0·0639	0·5762	
No. of empty cells	0·0525	0·0217	2·4169*	0·3039	3·0698	0·0990	0·0401	0·0126	3·1943*	Accept
No. of males	0·1532	0·1736	0·8827	2·2228	56·1278	0·0396	0·0483	0·0813	0·5943	
No. of females	−0·0158	0·0195	−0·8131	−1·6864	1·7881	−0·9431	−0·0268	0·0137	−1·9588*	
Model 2: Feeding rate and body size as determinants of the probability of egg laying										
Feeding rate	5·9180	1·4919	3·9666**	9·3788	3·7503	2·5008*	6·0943	1·3484	4·5197**	Accept
Inter-ocular distance	−1·8912	7·2793	−0·2598	−1·8777	10·7721	−0·1743	−4·4015	5·5478	−0·7934	
Ocello-ocular distance	−12·7920	6·0868	−2·1016*	2·8892	7·5265	0·3839	−8·4351	4·5252	−1·8640	
Head width	1·3801	1·4764	0·9348	−1·5973	2·8099	−0·5685	0·4546	1·1975	0·3796	
Head length	1·4794	1·4561	1·0160	−1·9246	2·0181	−0·9537	0·3137	1·0554	0·2972	
Mesoscutum width[††]	−1·2484	1·5386	−0·8114	1·1383	1·8972	0·6000	−0·2781	1·1218	−0·2479	
Mesoscutum length[††]	1·3517	1·3390	1·0095	0·7408	2·1653	0·3421	−0·8050	1·0595	0·7598	
Wing length	−0·2133	0·3223	−0·6618	0·5895	0·3727	1·5817	0·0482	0·2200	0·2189	

[†]Based on the strategies described in section 3·3.

*$0·05 \geqslant P > 0·001$; **$P < 0·001$.

[††]This was erroneously labelled as mesoscutellum in Gadagkar et al (1988).

Table 2. Results of parametric comparison of means.

Variables	Data from experiment 1			Data from experiment 2			Data pooled from experiments 1 and 2			Remarks[†]
	Mean ± SE (egg-layers)	Mean ± SE (non-egg-layers)	Z	Mean ± SE (egg-layers)	Mean ± SE (non-egg-layers)	Z	Mean ± SE (egg-layers)	Mean ± SE (non-egg-layers)	Z	
No. of eggs	85·6970 ± 5·5302	85·2755 ± 5·9025	0·0521	93·1522 ± 9·7799	118·2105 ± 10·9205	−1·7093	88·0621 ± 4·8761	94·4779 ± 5·3655	−0·8849	
No. of larvae	68·9798 ± 5·2515	74·0204 ± 5·6169	−0·6555	71·7174 ± 8·4424	104·8158 ± 10·5772	−2·4457*	69·8483 ± 4·4600	82·6250 ± 5·1300	−1·8796	
No. of pupae	41·4747 ± 3·7161	43·8673 ± 4·0792	−0·4336	59·0870 ± 5·4363	72·7632 ± 7·3868	−1·4911	47·0621 ± 3·1326	51·9412 ± 3·7469	−0·9990	
No. of parasitized cells	1·3434 ± 0·2922	1·5306 ± 0·3311	−0·4238	2·3843 ± 0·5577	0·6579 ± 0·2566	2·6822**	1·6483 ± 0·2681	1·2868 ± 0·2509	0·9845	
No. of empty cells	10·2929 ± 1·3680	6·2959 ± 0·8551	2·4776*	23·9783 ± 4·1328	8·4737 ± 2·5568	3·1904***	14·6345 ± 1·6866	6·9044 ± 0·9414	4·0021***	Accept
No. of males	1·0808 ± 0·2650	0·9082 ± 0·2271	0·4947	2·6522 ± 0·4798	0·2632 ± 0·1494	4·7546***	1·5793 ± 0·2432	0·7279 ± 0·1704	2·8669***	
No. of females	41·8384 ± 3·3054	43·6531 ± 3·5963	−0·3715	54·6522 ± 4·3480	69·6316 ± 5·8058	−2·0651*	45·9035 ± 2·6829	50·9118 ± 3·2069	−1·1978	
Feeding rate	0·2240 ± 0·0132	0·1485 ± 0·0107	4·4522***	0·1606 ± 0·0089	0·1259 ± 0·0088	2·7685**	0·2019 ± 0·0094	0·1410 ± 0·0077	4·9948***	Accept
Inter-ocular distance	0·3134 ± 0·0024	0·3183 ± 0·0023	−1·4433	0·3187 ± 0·0043	0·3190 ± 0·0037	−0·0529	0·3153 ± 0·0022	0·3185 ± 0·0020	−1·1037	
Ocello-ocular distance	0·5164 ± 0·0025	0·5240 ± 0·0032	−1·8485	0·5125 ± 0·0049	0·5118 ± 0·0030	0·1071	0·5150 ± 0·0024	0·5199 ± 0·0024	−1·1535	
Head width	3·1981 ± 0·0121	3·1923 ± 0·0159	0·2867	3·1896 ± 0·0208	3·2000 ± 0·0187	−0·3708	3·1951 ± 0·0107	3·1949 ± 0·0123	0·0144	
Head length	2·8237 ± 0·0135	2·8188 ± 0·0151	0·2453	2·8349 ± 0·0227	2·8510 ± 0·0243	−0·4849	2·8276 ± 0·0118	2·8295 ± 0·0129	−0·1082	
Mesoscutum width	2·2478 ± 0·0146	2·2620 ± 0·0164	−0·6498	2·2255 ± 0·0217	2·2088 ± 0·0237	0·5203	2·2400 ± 0·0121	2·2443 ± 0·0136	−0·2352	
Mesoscutum length	2·3422 ± 0·0175	2·3424 ± 0·0188	−0·0088	2·3049 ± 0·0250	2·2861 ± 0·0255	0·5257	2·3292 ± 0·0144	2·3237 ± 0·0153	0·264!	
Wing length	9·9697 ± 0·0667	10·0867 ± 0·0742	−1·1730	9·8792 ± 0·0900	9·6592 ± 0·1227	1·4460	9·9382 ± 0·0536	9·9442 ± 0·0661	−0·0713	

[†]Based on the strategies described in section 3·3.

*0·05 > P > 0·01; **0·01 > P > 0·005; ***P < 0·005

of number of empty cells and feeding rate are reconfirmed. Because some of the variables may not be normally distributed, a non-parametric comparison of means using the Mann-Whitney U-test was also performed. These results (shown in table 3) permitted the same conclusions as the logistic regression analysis and parametric comparison of means. In experiment 2, the mean values of the number of females on the parental nest were significantly different between egg-layers and non-egg-layers but such a result was not obtained either in experiment 1 or in the pooled data. In experiment 2 and in the pooled data, the number of males on the parental nest is significantly different between egg-layers and non-egg-layers but this variable is not considered important because it did not have a coefficient significantly different from zero in the logistic regression analysis.

3.6 Correlation analysis

As far as variables associated with the parental nest (such as number of eggs, larvae, etc.) are concerned, there is yet another way in which the association of such variables with egg laying and non-egg laying by the experimental animals can be investigated. This is to compute the proportion of egg-layers among animals eclosing from each nest and calculate Kendall's rank correlation coefficients between this quantity and each variable. Such an analysis shows that number of empty cells is significantly correlated with the proportion of egg-layers eclosing from each nest (table 4). Three other variables, viz. the number of pupae, number of

Table 3. Results of non-parametric comparison of means.

Variables	Data from experiment 1		Data from experiment 2		Data pooled from experiments 1 and 2		Remarks[†]
	U	Z	U	Z	U	Z	
No. of eggs	4790·50	0·1522	690·50	−1·6998	9387·00	−0·7018	
No. of larvae	4661·50	−0·4767	630·50	−2·2583*	8804·50	−1·5561	
No. of pupae	4850·50	−0·0013	780·50	−0·8662	9756·00	−0·1543	
No. of parasitized cells	4767·00	−0·2599	588·50	2·9719***	9031·50	1·4725	
No. of empty cells	3838·50	2·5527*	521·00	3·3136***	7164·00	4·0115***	Accept
No. of males	4782·50	−0·2276	520·00	3·8954***	8711·50	2·1805*	
No. of females	4833·50	−0·0440	623·50	−2·3224*	9330·00	−0·7865	
Feeding rate	3213·50	4·0970***	898·00	2·6879**	7579·00	4·8130***	Accept
Inter-ocular distance	4283·00	−1·5339	1286·00	0·0882	10344·00	−1·1780	
Ocello-ocular distance	4068·50	−2·0626*	1145·00	1·1267	10345·00	−1·1768	
Head width	4657·50	−0·4876	1241·50	−0·3849	10728·50	−0·5980	
Head length	4652·50	−0·4999	1201·00	−0·6583	10556·50	−0·8289	
Mesoscutum width	4421·50	−1·0807	1295·00	0·0236	10501·50	−0·9023	
Mesoscutum length	4730·50	−0·3023	1277·50	0·1411	11058·50	−0·1523	
Wing length	4280·50	−1·4290	1142·50	1·0485	10749·50	−0·5665	

[†]Based on the strategies described in section 3·3.
*$0·05 > P > 0·01$; **$0·01 > P > 0·005$; ***$P < 0·005$.

Table 4. Kendall's rank correlation coefficients between proportion of egg-layers eclosing from each nest and other variables associated with the nests.

Variables	Data from experiment 1		Data from experiment 2		Data pooled from experiments 1 and 2		Remarks[†]
	τ	Z	τ	Z	τ	Z	
No. of eggs	0·0220	0·1435	0·1633	0·9772	0·1466	1·3139	
No. of larvae	0·0220	0·1435	0·0995	0·5951	0·0963	0·8632	
No. of pupae	0·1733	1·1290	0·3080	1·8425	0·3087	2·7673**	
No. of parasitized cells	−0·0702	−0·4575	0·4739	2·8351***	0·2515	2·2545*	
No. of empty cells	0·2622	1·7081	0·3580	2·1416*	0·3231	2·8966***	Accept
No. of males	−0·1283	−0·8359	0·4561	2·7286**	0·2583	2·3154*	
No. of females	0·1470	0·9575	0·0066	0·0396	0·1784	1·5994	

[†]Based on the strategies described in section 3·3.
*$0·05 > P > 0·01$; **$0·01 \geqslant P > 0·005$; ***$P \leqslant 0·005$.

parasitized cells and number of males are also significantly correlated but by the criteria laid down in section 3·3, we do not accept these variables as being important at this stage.

Figure 1A shows the proportion of egg-layers eclosing from each nest as a function of the number of empty cells in that nest. Although, the number of empty cells is statistically significantly correlated with the proportion of egg-layers (table 4, row 5), there is much scatter in the data, preventing us from discerning any simple relationship between the two variables. A major source of error in this data must arise on account of our attempt to compute proportion of egg-layers for nests from which a very small number of animals were tested (in several cases only one or two animals were tested). For this reason, we have deleted all nests from which 6 or fewer animals were tested. Now our estimates of proportion of egg-layers will have less error and the nature of the relationship between proportion of egg-layers and empty cells should be easier to unravel. Figure 1B shows that animals have a small probability ($\sim 0·28$) of becoming egg-layers even when the number of empty cells is zero and that the probability of becoming an egg-layer rises rapidly to about 0·6 when the number of empty cells is 20 and later rises gradually to about 0·9 when the number of empty cells reaches about 80.

4. Discussion

Gadagkar *et al* (1988) demonstrated a pre-imaginal bias in the caste of female *R. marginata* by showing that only 97 out of 197 females tested under laboratory conditions initiated nests and laid eggs while the remaining died without doing so. The results presented here reconfirm a substantial pre-imaginal caste bias because in a new experiment with 102 animals, only 53 laid eggs and the remaining 49 died without doing so. Gadagkar *et al* (1988) also concluded that the number of empty cells on the parental nest and an animal's feeding rate during its adult life are useful in predicting whether an animal will become an egg-layer or a non-egg-layer. The role of these variables was not postulated beforehand but, as is often inevitable in dealing with complex systems, all available variables were tested and these two were found to be significant.
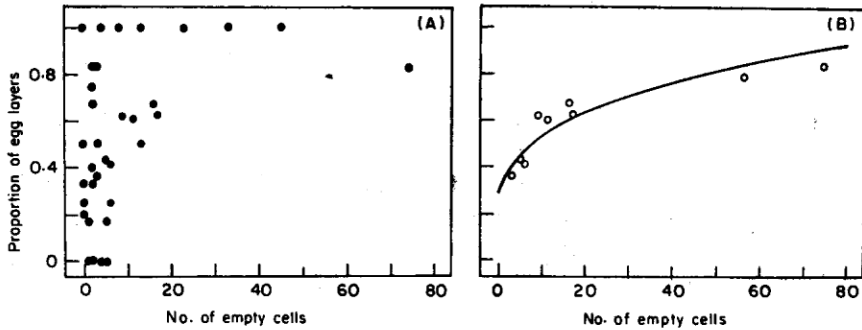
Figure 1. Scatter plot showing the proportion of egg-layers eclosing from each nest versus the number of empty cells on that nest (**A**). The two variables are significantly correlated as seen from Kendall's coefficient of rank correlation ($P < 0.005$; see table 4, row 5). The excessive scatter in the data is on account of our attempt to estimate the proportion of egg-layers for nests from which a very small number of animals were tested. The relationship between proportion of egg-layers and number of empty cells is seen more clearly when nests from which only 6 or fewer animals were tested are deleted (**B**). The solid line is computed using the equation $\ln Y = 0.2710 * \ln(1 + X) - 1.2861$ which was fitted using the method of least square. $r^2 = 0.8501$. The slope 0.2710 has a standard error of 0.0430 and is thus significantly different from zero at $P < 0.0001$.

Complex systems often cannot be tackled by methods other than such 'fishing expeditions' but it may be argued that one's confidence in the role of any variable detected through such a method is not as high as it would be if its involvement were postulated beforehand on *a priori* grounds (see Martin and Bateson 1986, pp 134–135 for a discussion of this issue). For this reason an attempt was made to reconfirm these results both by performing additional statistical tests as well as by repeating the experiment and performing the original and new statistical tests on data from the new experiment and on data pooled from both experiments. In doing so, we were, as might be expected, confronted with minor discrepancies in the results between experiments and between statistical techniques. Here the rather conservative strategy of accepting only those results which were validated by all statistical techniques in at least one individual experiment and in the pooled data was adopted. Inspite of such reconfirmation, our approach here was to first detect variables that may be important and then construct hypotheses as to their possible mode of involvement in pre-imaginal caste bias. It is for this reason that a conservative strategy which may lead to an error of rejecting an important variable rather than to the converse error of accepting an unimportant variable, was adopted.

Using this strategy, we reconfirm the association of the number of empty cells present on the parental nest and an animal's feeding rate during adult life with its probability of becoming an egg-layer. Such reconfirmation strengthens our model for pre-imaginal caste bias (Gadagkar *et al* 1988) which suggests that a declining influence of the queen leads to the accumulation of empty cells as well as to the production of daughters who are programmed to feed more and become egg-layers while a high influence of the queen leads to fewer or no empty cells and the production of daughters programmed to feed less and become workers. Thus caste is atleast partly determined prior to eclosion even in a primitively eusocial wasp

such as *R. marginata* which lacks morphological differences between egg-layers and non-egg-layers.

References

Alexander R D 1974 The evolution of Social Behaviour; *Annu. Rev. Ecol. Syst.* **5** 325–383

Gadagkar R 1980 Dominance hierarchy and division of labour in the social wasp *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae); *Curr. Sci.* **49** 772–775

Gadagkar R 1985 Evolution of insect sociality—A review of some attempts to test modern theories; *Proc. Indian Acad. Sci. (Anim. Sci.)* **94** 309–324

Gadagkar R 1990 Social biology of *Belonogaster, Mischocyttarus, Parapolybia* and independent-founding *Ropalidia;* in *Social biology of wasps* (eds) K G Ross and R W Matthews (Cornell University Press) (in press)

Gadagkar R, Gadgil M, Joshi N V and Mahabal A S 1982 Observations on the 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

Gadagkar R and Joshi N V 1983 Quantitative ethology of social wasps: time-activity budgets and caste differentiation in *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae); *Anim. Behav.* **31** 26–31

Gadagkar R, Vinutha C, Shanubhogue A and Gore A P 1988 Pre-imaginal biasing of caste in a primitively eusocial insect; *Proc. R. Soc. London* **B233** 175–189

Martin P and Bateson P 1986 *Measuring behaviour* (Cambridge: Cambridge University Press)

Shanubhogue A and Gore A P 1987 Using logistic regression in ecology; *Curr. Sci.* **56** 933–936

West-Eberhard M J 1975 The evolution of social behaviour by kin selection; *Q. Rev. Biol.* **50** 1–33