0014-4754/93/080714-04$1.50 + 0.20

Queen success is correlated with worker-brood genetic relatedness in a primitively eusocial wasp (*Ropalidia marginata*)

R. Gadagkar, K. Chandrashekara, S. Chandran and S. Bhagavan*

*Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560 012 (India) and *Department of Entomology, Ohio State University, Columbus, Ohio 43210 (USA)*
Received 1 February 1992; accepted 20 April 1993

Abstract. Ropalidia marginata is a primitively eusocial polistine wasp in which, although there is only one queen at any given time, frequent queen replacements lead to a system of serial polygyny. One of the most striking features of this system is the enormous variation in the success of different queens. Measuring queen success as queen tenure, total number of offspring produced, number of offspring produced per day of tenure, and proportion of eggs laid that develop into adults, we show here that each measure of queen success is correlated with worker-brood genetic relatedness and not correlated with worker:brood ratio or the age of the queen at takeover. We interpret these results as meaning that queens are better able to obtain the cooperation of workers when worker-brood genetic relatedness is high.
Key words. Ropalidia marginata; primitively eusocial wasp; queen success; worker-brood genetic relatedness; inclusive fitness theory; Hymenoptera.

The most ecologically and socially diverse group of social wasps belongs to the subfamily polistinae. Members of this family can be subdivided into two functional groups: the swarm-founding species which are relatively more socially advanced and found new nests by swarms of individuals, consisting of queen(s) as well as workers, and the independent-founding species, which are relatively socially primitive and in which nests are founded by one or a group of queen(s) or potential queens, without the aid of workers. This implies that in the independent-founding species, neither behavioural specialisation nor caste differentiation is complete or irreversible. *Polistes*, *Mischocyttarus*, *Parapolybia* and some sub-genera of *Ropalidia* are the prime representatives of the independent-founding polistines, and together occupy tropical and temperate regions of both the Old and the New World[1-3].

Ropalidia marginata (Lep.) (Hymenoptera: Vespidae) is a tropical independent-founding polistine wasp abundantly distributed in Southern India. New colonies may be founded by one or a group of females. Even in the latter case, only one female assumes the role of queen, and the others become workers. Eclosing daughters may either leave to found new single- or multiple-foundress nests, stay in the colony and become workers, or stay and work for a while and then replace their mothers, assuming the role of queens in their natal nests. Colonies are initiated at all times of the year and may continue to exist for indefinite periods of time[1,4]. This gives opportunities for queen replacements, resulting in a succession of queens referred to as serial polygyny[5,6]. Here we show that, in accordance with the prediction of inclusive fitness theory[7,8], queens of this primitively eusocial wasp are more successful when worker-brood genetic relatedness is high.

Methods

Four colonies of *Ropalidia marginata* were established by transplanting post-emergence nests into cages located at the Centre for Ecological Sciences, Indian Institute of Science, Bangalore. These cages were made of wire mesh, of a size which allowed workers to forage outside freely but prevented the hornet *Vespa tropica* from entering and preying on the brood. A nest-map, indicating the contents of each cell, was prepared and brought up to date every other day. All adults were marked, immediately upon eclosion, with a unique spot of coloured paint for individual recognition. The cell from which they eclosed was also noted. A census of all individuals present on the nest was taken every other night after 20.00 hrs. These colonies were under behavioural observation of varying intensity for other experiments. Consequently, the identity of the queen laying each egg was known for all nests at all times. A change of the queen of any nest became known within a day or two of the event.

The four colonies were studied for 606, 472, 335 and 261 days; during these periods they had from 7-148 adult females and 41–535 items of brood (eggs + larvae + pupae), 5–27 adult females and 29–186 items of brood, 4–30 adult females and 42–136 items of brood, and 2–19 adult females and 29–261 items of brood respectively. Although there was only one queen per colony at any given time, the four colonies had a total of 4, 5, 10 and 2 queens respectively during the period of study[5,6].

Results

The most striking feature of this study is the enormous variation from queen to queen in what might be called their success. We have computed four possible indicators of the success of queens (cf. tables): queen tenure, total number of offspring produced, number of offspring produced per day of tenure and proportion of eggs laid that developed into adults. The first three are obvious indictors of queen success, but the fourth may need some justification. A substantial fraction of eggs laid by the queens failed to reach adulthood, mostly because of cannibalism by workers. The proportion of eggs laid that successfully develop into adults is therefore not only an important indicator of queen success, but is perhaps a more direct measure of the extent of cooperation that the queen is able to obtain from the workers. In addition, we have computed three other variables which may be thought of as possible determinants of queen success. These are: age in days at the time of take over, mean worker: brood ratio during the tenure and mean worker-brood genetic relatedness during the tenure. We consider age at takeover as a possible determinant of queen success because young queens may have the advantage of a long tenure ahead of them. High worker:brood ratio is of obvious advantage in increasing the efficiency of brood rearing. High worker-brood genetic relatedness may ensure better cooperation in brood-rearing on the part of the workers, as they would obtain higher inclusive fitness compared to the situation with low worker-brood genetic relatedness.

All eggs laid during the tenure of a queen were assumed to be her offspring, because of strict monogyny at any given time. All eggs were followed through their development into adults so that the numbers of the brood and workers belonging to each matriline at any given time could be computed. No information could be obtained about relative investment between male and female brood. Assuming single mating by queens, and outbreeding, mean coefficients of genetic relatedness between workers and brood were computed, assuming that all brood were female[5,6]. We believe that this is reasonable because worker-female brood genetic relatedness values vary far more than worker-male brood relatedness values[5,6] and because sex ratios are so highly biased in favour of females that only small numbers of males are occasionally produced[6].

There is considerable variation from queen to queen in both the indicators and in the possible determinants of queen success (table 1). With every indicator of queen success, there is a statistically significant dependence on worker-brood genetic relatedness but no dependence on age at takeover or on worker:brood ratio. These results are evident both from a correlation analysis and from a linear regression analysis (table 2, fig.).

Discussion

Taken together, the results suggest that queens of *Ropalidia marginata* are more successful when the worker-brood genetic relatedness during their tenure is high. Long queen tenures may, of course, give rise to high worker-brood genetic relatedness (because of the absence of multiple matrilines) and might independently lead to a higher total number of offspring (simply because of the long tenure). However, even other measures of queen success such as the number of offspring produced per day of tenure and the proportion of eggs that become adults, yield the same results. There is unlikely to be a trivial link between queen tenure and the latter two measures of queen success, which are independent of worker-brood genetic relatedness, as is the total number of offspring produced. A reasonable

Table 1. Variability of indicators and possible determinants of queen success in *R. marginata*

Variables	Minimum	Maximum	Mean	Standard	Median deviation
Indicators of queen success					
Queen tenure (days)	7	219	74.8	71.8	53
No. of offspring produced	0*	394	72.3	123.6	20
No. of offspring produced/day	0*	2.3	0.66	0.63	0.46
Proportion of eggs that develop into adults	0*	0.37	0.19	0.11	0.18
Possible determinants of queen success					
Age at take over (days)	4	78	35.18	19.88	42
Worker:brood ratio	0.04	0.25	0.14	0.06	0.14
Worker-brood genetic relatedness	0.26	0.70	0.43	0.14	0.38

*Note that each queen laid a number of eggs, some of which developed into larvae or pupae. However, in some cases none matured into adult offspring. Hence the zero values.

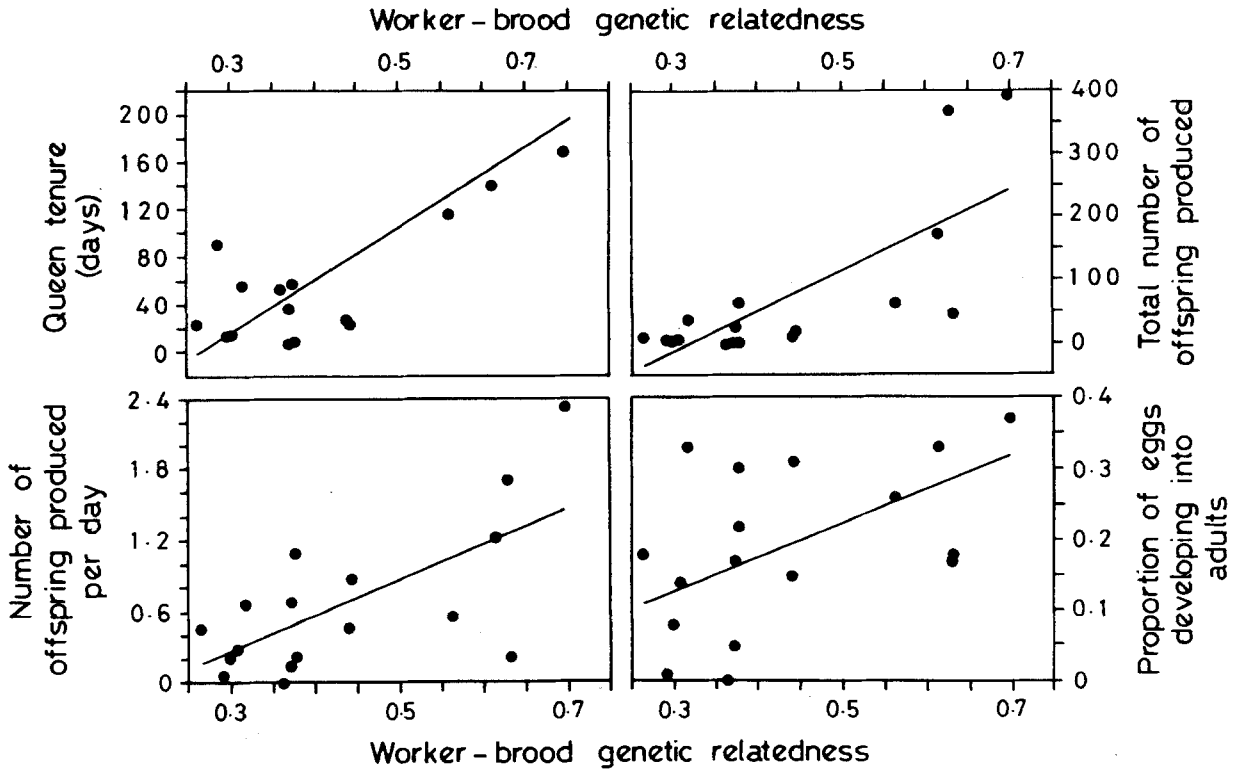

Figure. Relationship between each of the four measures of queen success and worker-brood genetic relatedness. For queen tenure, $Y = -117 + 442\,X$; for total number of offspring produced, $Y = -206 + 641\,X$; for number of offspring produced per day, $Y = -0.641 + 2.99\,X$; for proportion of eggs laid that develop into adults, $Y = -0.017 + 0.48\,X$. All slopes are significantly greater than zero (see table 1). A non-linear relationship may provide a better fit for some of these variables, but the purpose here is not to describe the functional relationships between the variables, nor is it to predict the exact value of queen success for different values of worker-brood genetic relatedness; it is merely to show the dependence of queen success on worker-brood genetic relatedness.

Table 2. Relationships between indicators and possible determinants of queen success

Indicators of queen success \ Possible determinants of queen success	Age at take over		Mean worker:brood ratio		Mean worker-brood genetic relatedness	
	r or tau	b	r or tau	b	r or tau	b
Queen tenure (days)	−0.15	−0.76	0.32	336	0.84[c]	442[c]
Total number of offspring produced	0.06	1.41	0.21	403	0.52[c]	641[d]
Number of offspring produced per day of tenure	0.16	0.01	0.13	0.42	0.48[c]	2.99[e]
Proportion of eggs laid that develop into adults	0.44	0.002	0.11	−0.39	0.49[a]	0.48[a]

The body of the table gives the values of the Pearson product moment correlation (r) or Kendal's rank correlation coefficient (tau) between the variable in the row heading and that in the column heading, and Model II regression coefficients (b)[10] computed using Bartlett's three-group method with the variable in the row heading as the dependent variable and that in the column heading as the independent variable. Correlation and regression coefficients significantly different from zero are marked and the p values indicated in footnotes. All variables except total number of offspring produced and number of offspring produced per day are normally distributed. For these two variables, correlation was measured by the non-parametric Kendall's rank correlation tau and the significance of the regression coefficient tested by a randomization test[10]. [a]$p < 0.05$; [c]$p < 0.02$; [c]$p < 0.01$; [d]$p < 0.002$.

interpretation of these results is therefore that when worker-brood genetic relatedness is high, queens receive better cooperation from workers in brood-rearing. Higher levels of cooperation by workers in brood-rearing when worker-brood genetic relatedness is high is a general prediction of inclusive fitness theory, and has also been found in honey bees[9].

Acknowledgments. We thank M. Gadgil, V. Nanjundiah and J. T. Bonner for comments and discussions. This work was sup-

ported in part by a grant from the Department of Science and Technology, Government of India.

1 Gadagkar, R., in: The Social Biology of Wasps, p. 149. Eds K. G. Ross and R. W. Matthews. Cornell University Press, Ithaca, New York 1991.
2 Reeve, H. K., in: The Social Biology of Wasps, p. 99. Eds K. G. Ross and R. W. Matthews. Cornell University Press, Ithaca, New york 1991.
3 Jeanne, R. L., in: The Social Biology of Wasps, p. 191. Eds K. G. Ross and R. W. Matthews. Cornell University Press, Ithaca, New York 1991.
4 Gadagkar, R., Gadgil, M., Joshi, N. V., and Mahabal, A. S., Proc. Indian Acad. Sci. (Anim. Sci.) *91*, (1982) 539.
5 Gadagkar, R., Chandrashekara, K., Chandran, S., and Bhagavan, S., Naturwissenschaften *78*, (1991) 523.
6 Gadagkar, R., Chandrashekara, K., Chandran, S., and Bhagavan, S., in: Queen number and Sociality in Insects, p. 187. Ed. L. Keller. Oxford University Press, Oxford 1993.
7 Hamilton, W. D., J. theor. Biol. *7* (1964) 1.
8 Hamilton, W. D., A. Rev. ecol. Syst. *3* (1972) 193.
9 Ratnieks, F. L. W., and Visscher, P. K., Nature *342*, (1989) 796.
10 Sokal, R. R., and Rohlf, F. J., Biometry. W. H. Freeman and Co., San Fransisco 1981.