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Colony founding in the primitively eusocial wasp, *Ropalidia marginata* (Hymenoptera: Vespidae)

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Abstract. 1. In a 16-month study in Bangalore, India, about 35% of the newly founded colonies of *Ropalidia marginata* were single foundress colonies and the remainder were multiple foundress colonies with two to twenty-two individuals.

2. Larger colonies did not have a significantly higher per capita productivity, did not produce significantly heavier progeny and did not produce them significantly faster than smaller colonies did.

3. Predation by the hornet *Vespa tropica* appeared to be independent of group size.

4. Single foundress colonies failed more often but not often enough to make them have a lower average per capita productivity, compared to multiple foundress colonies.

5. Some of the advantages of multiple foundress associations came from the greater predictability of their attaining the mean per capita productivity, the relatively lower rates of usurpation experienced by them compared to single foundress colonies, and the opportunities provided by queen turnovers for workers to become replacement queens and gain direct individual fitness.

Key words. Social wasp, *Ropalidia marginata*, multiple foundress associations, colony founding, eusociality.

Introduction

Primitively eusocial polistine wasps show considerable plasticity in their social behaviour. Different individuals in the same population often pursue different social strategies, such as remaining as workers on their natal nests, working on their natal nests for some time and then taking over as the next queen, joining another nest as a subordinate, joining another nest and usurping it, adopting an orphaned nest, and nesting alone (Gadagkar, 1991a; Reeve, 1991; Itô, 1993; Nonacs & Reeve, 1993). Such social plasticity makes them excellent model systems for investigations into the evolution of social behaviour.

As in many independent colony founding polistines, new colonies of *Ropalidia marginata* (Lep.) (Hymenoptera: Vespidae) may be founded either by a single female or by a group of females. A solitary foundress builds a nest, lays eggs, forages to feed her growing larvae, guards them from predators and parasites, and brings them to adulthood all by herself, until her daughters eclose and begin to stay back and assist her in rearing subsequent batches of brood. In multiple foundress colonies, only one individual becomes the egg layer or queen, while the rest act as subordinate workers and perform the tasks of nest building, nest maintenance and brood care (Gadagkar, 1991a). An obvious question, and one that has received considerable theoretical (West-Eberhard, 1969; Queller & Strassmann, 1988; Queller, 1989; Gadagkar, 1990a, 1991b; Reeve & Nonacs, 1992; Keller & Reeve, 1994) and empirical (Metcalf & Whitt, 1977; Gamboa, 1978; Gibo, 1978; Noonan, 1981; Klahn, 1988) attention in studies of polistine wasps, is why do the subordinate workers not become solitary foundresses and rear their own offspring instead of working to rear the brood of another individual? Nevertheless, comparative data on the relative success and productivity of single and multiple foundress nests are meagre. We therefore report here the results of a 16-month study of spontaneous colony founding in a field site and a site protected from the predator, *Vespa tropica*, and attempt to examine the adaptive significance of multiple foundress associations.

Materials and Methods

Data collection. A total of 145 naturally-initiated pre-emergence nests of *Ropalidia marginata* were monitored from June 1991 to September 1992, both in the field (sixty-five nests) and

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in the vespiary (eighty nests). Our field sites included selected buildings at the Indian Institute of Science campus, University of Agricultural Sciences, G.K.V.K. campus, and New Public Office, all in Bangalore (13°00'N and 77°32'E). The vespiary is a room measuring 9.3 × 6 × 4.8 m, with wire mesh of 0.75 × 0.75 cm dimension, located in the Indian Institute of Science. The mesh, by virtue of its size, prevents the hornet, *Vespa tropica*, the major predator on the brood of *R.marginata*, from entering, but permits *R.marginata* to fly in and out freely. When a nest was found, it was given a unique nest code and all the animals on the nest were individually marked using quick-drying paints. Thereafter, records were maintained on the number of wasps attending the nest (census) and the brood composition (nest-map) at intervals of 1–2 days, at least till the first adult eclosed. The census was conducted either before sunrise or at night when most wasps were present on the nest. Each nest was also subjected to several hours of behavioural observations, to determine the egg layer. Each colony is known to have only one egg layer at any given time (Gadagkar *et al.*, 1993). Upon loss of the original egg layer, the new egg layer was similarly identified and a queen turnover was said to have occurred.

Since *R.marginata* follows a perennial, indeterminate nesting cycle (Gadagkar, 1991a), it is virtually impossible to continue monitoring the nests till the end of the colony cycle, to measure productivity. Besides, there is no strict demarcation between workers and potential reproductives. Females eclosing at any time in the colony cycle can become reproductives if an opportunity presents itself. Since the number of individuals in the nest changes after the first eclosion, this time point was chosen as most convenient to terminate monitoring of nests and compare the productivities of colonies with different numbers of foundresses. The total and per capita productivities were estimated from the nest-map and census records.

To examine possible seasonality of nest initiation, an intensive search was carried out once a week, for a period of a year, both in the field sites and in the vespiary, to record all newly initiated nests. This gave an estimate of the number of nests initiated each month. Only nests discovered in the egg stage were used for this analysis.

Statistical analysis. For analysis of productivity as a function of group size, the mean number of female wasps seen on all days was taken as the number of foundresses. However, in the context of joining, usurpation and predation, the actual number of female wasps present on the day of the event was taken as the number of foundresses. If a nest produced at least one adult, it was considered successful. Total brood (eggs + larvae + pupae) present in the nest on the day of eclosion of the first adult offspring was used as a measure of productivity. Per capita productivity was estimated by dividing the total brood by the number of foundresses, estimated as described above. Freshly eclosed individuals were weighed using an electronic balance accurate to 10 μg.

The null hypothesis that queen turnover are equally likely to occur in nests with two foundresses and in nests with more than two foundresses was tested as follows. The census records correspond to 434 two-foundress nest days and 932 greater than two-foundress nest days. If the queen turnover was equally likely to occur in either category of nests, the ratio of two foundress nests and greater than two foundress nests experiencing queen turnover is expected to be 434:932. The observed ratio of 9:7 was compared with the expected ratio by a G-test.

Computer simulations. To determine whether single or multiple foundress nests were chosen by conspecific joiners, usurpers and the predator *V.tropica* based on their relative abundance or whether there was any specific preference for single or multiple foundress nests, a computer simulation was performed as follows. Taking the case of joining as an example, each of the 217 joining events observed were categorized as joining of a single foundress or a multiple foundress nest, based on the number of foundresses present on the joined nest on the day of the event. Thus the empirical overall observed proportion (out of 217) of joiners preferring single foundress nests was computed. Each event of joining was simulated by drawing a random number uniformly distributed between 0 and 1 and assigning it to the single foundress or multiple foundress category based on the proportion of single and multiple foundress nests available for each joiner at that site on that day. From this, the overall expected proportion of joiners choosing single foundress nests in the simulation was computed. The simulation was repeated 10,000 times to yield as many expected proportions of joiners preferring single foundress nests. The observed proportion of joiners preferring single foundress nests was compared with the distribution of expected proportions. The null hypothesis that the observed proportion preferring single foundress nests was simply based on availability of single foundress nests, was rejected if the observed proportion did not lie in the inner 95% of the distribution of expected (simulated) values. A similar analysis was carried out to test whether preferences of usurpers and the predator for single and multiple foundress nests were significantly different from the proportions of nests available in the two categories.

Results

Seasonality of nest-initiation

Nests were initiated more or less throughout the year, although relatively larger numbers were initiated during May to July and relatively fewer between December and February (Fig. 1). The distributions of nest initiations over different months of the year were not significantly different between the vespiary and the field sites (Kolmogorov-Smirnov two-sample test, $D = 0.194$; $P > 0.35$, data not shown).

Diverse fates of nests

Nests exhibited complex and diverse fates. Some began as single foundress nests whereas others began as multiple foundress nests. There were transitions from the single foundress state to the multiple foundress state and vice versa. Some nests were usurped whereas others were not. Some were successful at producing adult offspring whereas others lost all the foundresses before doing so. Such orphaned nests were sometimes adopted. Some multiple foundress nests experienced queen turnover whereas others did not. The number of nests experiencing each of these diverse fates is shown in Fig. 2.

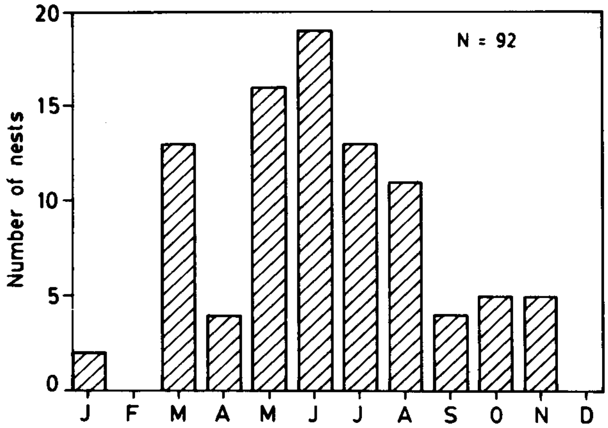

Fig. 1. Numbers of nests initiated during different months of the year (only nests discovered in the egg stage have been included in this analysis).

Group size

The total number of individuals attending any nest ranged from one to thirty-one and the maximum number seen on any given day ranged from 1 to 25. The number of foundresses obtained by averaging over all days of observation ranged from 0.38 to 21.54, and has been rounded off to the nearest integer for clarity of presentation (Fig. 3). Foundress numbers were not significantly different between the vespiary and the field sites (Kolmogorov-Smirnov two-sample test, $D = 0.046$, $P > 0.90$). Twenty-three nests were attended by only a single marked individual throughout the study period. For an additional eight nests a single wasp adopted each of them after the original foundress had disappeared. These thirty-one nests were classified as single foundress nests and account for 21.4% of all nests studied. For yet another additional twenty nests the number of foundresses (averaged over all days of observation), when rounded off to the nearest integer, was one, due to loss of cofoundresses. If all the fifty-one nests are treated as single foundress nests, as it might be appropriate

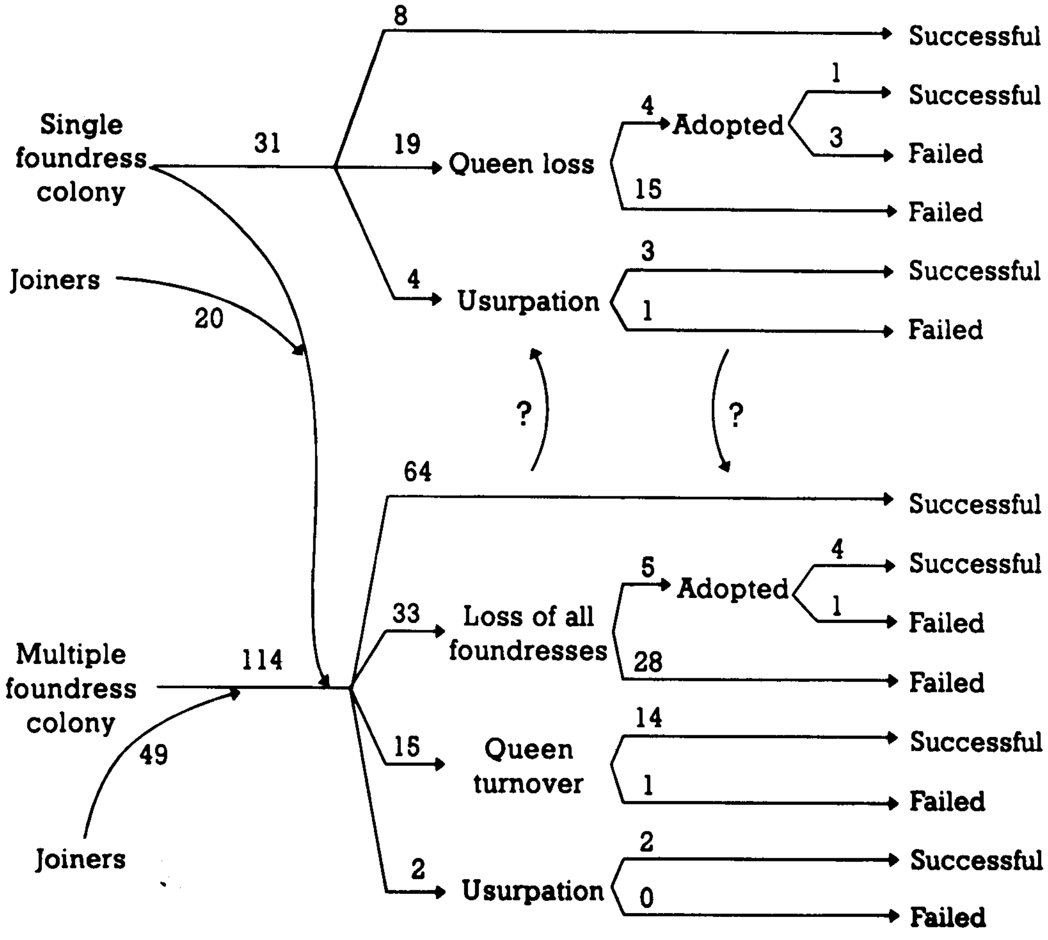

Fig. 2. Diverse fates of pre-emergence nests. See text for definitions of terms used. All numbers refer to nests and not to wasps. Many multiple foundress nests lost all but one foundress and became single foundress nests and some of these later received joiners to revert back to the multiple foundress state. The number of nests undergoing such transitions are not shown.

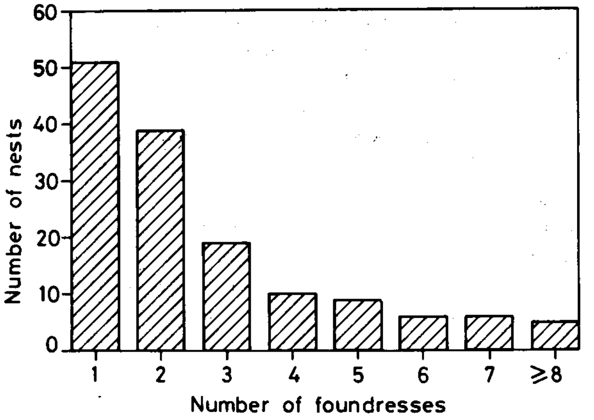

Fig. 3. Numbers of nests with different numbers of foundresses. Data from the field and vespiary sites are pooled as the foundress number distributions are not significantly different between the two sites (Kolmogorov-Smirnov two-sample test, $D = 0.046$, $P > 0.9$).

to do in studies of productivity, then the percentage of single foundress nests in the study population amounts to 35.2%. The remaining ninety-four nests had a mean number of foundresses ranging from 1.5 to 21.5. Since a total of 676 individuals as recorded and marked in the study, 4.6–7.5% (depending on whether thirty-one or fifty-one is taken for the number of single foundress nests) of the founding population can be said to have nested solitarily whereas 92.5–95.4% of the individuals nested in groups.

Colony success

The overall success rate was significantly higher in the vespiary (59/80; 73.8%) than in the field (37/65; 56.9%) ($G = 4.48$, $P < 0.05$). Multiple foundress colonies survived better than single foundress colonies, both in the field (survival of multiple foundress = 28/41; 68.3%, survival of single foundress = 9/24; 37.5%; $G = 5.73$, $P < 0.05$) and in the vespiary (survival of multiple foundress = 44/53; 83.0%, survival of single foundress = 15/27; 55.6%; $G = 6.52$, $P < 0.05$).

Total and per capita productivity

The mean per capita productivity (compared by t-test) as well as the slope of productivity as a function of the foundress group size (compared as described in Sokal & Rohlf, 1981, p. 499) were not significantly different between the two study sites ($P > 0.05$; data not shown). Hence, data from both these sources were pooled and analysed. Linear regression analysis indicated that total productivity increased significantly with increasing foundress group size (Fig. 4A). However, the slope of the per capita productivity as a function of foundress group size was not significantly different from zero (Fig. 4B). Indeed, the slope was significantly less than zero when failed nests were excluded from the data set (data not shown). These results were independent of whether or not the foundress numbers were rounded off to the nearest integer and whether or not nests with large number of foundresses (more than thirteen), which may possibly be outliers, were excluded from the data set. Regression of per capita productivity on foundress number suggests that, on average, each individual, whether in a solitary foundress nest or in a multiple foundress nest, accounts for about seven cells, three eggs, two larvae and one pupa at the time of eclosion of the first adult offspring.

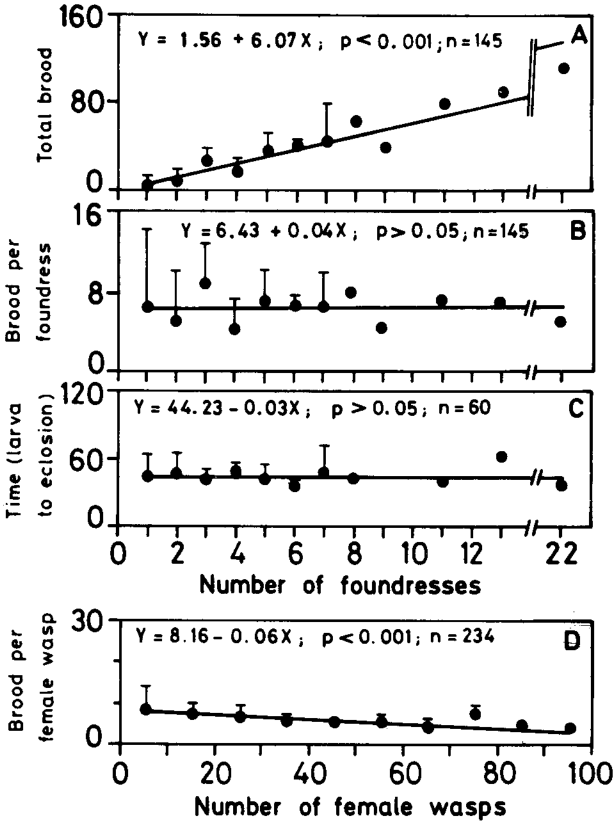

Fig. 4. Total productivity (A) and per capita productivity (B) at the time of the eclosion of the first adult, time elapsed from the hatching of the first egg to the eclosion of the first adult (C), all as a function of the number of foundresses on pre-emergence nests and per capita productivity as a function of the number of adults present on 234 nests at the time of their collection. Mean, one standard deviation, linear regression equations, sample size and P values relating to testing deviation of the slopes from zero, are shown.

It is possible that although the per capita productivity does not increase with group size in the pre-emergence period, it may increase in the post-emergence period of the colony cycle. In other words, post-emergence nests may be qualitatively different from pre-emergence nests with better cooperation or more efficient division of labour. To test this possibility, the total brood per female was plotted against the total number of females present on 234 nests collected for various experiments in our laboratory during the last 12 years (Fig. 4D). The nests used here are a haphazard sample representing the range of natural colony sizes in different stages of development. Here, a significant negative relationship between the number of females present and brood per female could be established. All females present on post-emergence nests may not of course necessarily contribute to labour in their colonies. Nevertheless, it can at least be stated that no increase in per capita productivity as a function of group size has been discovered so far.

The mean fresh weight of the newly eclosing individuals was also not significantly different between those that eclosed on single foundress nests (40.66 ± 8.61 mg, $n = 27$) and those that eclosed on multiple foundress nests (42.10 ± 6.80 mg, $n = 86$) ($t = 0.198$, $P > 0.90$) (data not shown). Duration of the nesting period from the time of hatching of the first egg (which, unlike that of the laying of the first egg, was precisely known for many nests) to the eclosion of the first adult was also not significantly related to foundress group size (Fig. 4C).

Movement of wasps between nests

When an unmarked individual or a marked individual known to belong to a different nest was seen on any nest during the census, that nest was said to have received a joiner. Of the 676 wasps recorded during the study, 217 (32.1%) were seen to join previously-established nests. Of the 145 nests recorded during the study, 69 (47.6%) received at least one joiner each. Nests received joiners in their egg stage and larval stage as well as pupal stage (Table 1). The porportions of nests that were joined were not significantly different between the vespiary and the field sites ($G = 0.097$, $P > 0.50$). The source of 191 of the 217 joiners remains unknown. They could have come from the same natal nest from which the first set of animals came or may have come from different nests. However, twenty-six of the joiners were marked individuals from the founding population and they thus clearly represent movement of foundresses from one pre-emergence nest to another. Therefore our records shown that at least sixteen nests consisted of individuals from two or more source nests, at least three nests consisted of individuals from three or more source nests, and at least one nest consisted of individuals from four or more source nests.Computer simulations indicate that joiners appear to choose multiple foundress nests significantly more often than was expected from their availability (Figs 5A and 5B).

Nest usurpation

When a joiner replaced the resident queen within a day or two of her joining, the nest was said to have been usurped. The replaced queen always disappeared, but only after the coming of the usurper. The proportion of nests that were usurped in the vespiary (5/80) was not significantly different from the corresponding proportion in the field site (8/65) ($G = 1.606$, $P > 0.10$). Eleven single foundress nests were usurped, whereas only two nests with two foundresses were usurped. There were no instances of usurpation of nests with three or more foundresses. Computer simulations indicate that usurpers preferred to usurp single foundress nests more often than was expected from the availability of single foundress nests (Figs 5A and 5B).

Queen turnovers

When a resident worker (not a joiner, who had come in the preceding 1 or 2 days) replaced the existing queen, the nest was said to have experienced a queen turnover. As in the case of usurpation, the original queen always disappeared. The proportion of nests experiencing queen turnovers in the vespiary (9/80) was not significantly different from the corresponding proportion in the field site (5/65) ($G = 0.529$, $P > 0.25$). Nests with two foundresses (9/434) experienced queen turnovers significantly more often compared to nests with more than two foundresses (7/932) ($G = 3.96$, $P < 0.05$).

Adoption

When a wasp not belonging to a nest was seen on that nest after all the resident wasps had disappeared, that nest was said to have been adopted. Among the nests that lost all foundresses, the proportion that were adopted were significantly higher in the vespiary (9/26) than in the field (0/28) ($G = 10.78$, $P < 0.001$). We failed to detect any influence of the amount of brood present

Table 1. Movement of foundresses between nests.

	Total no. of joiners[*]				No. of nests receiving at least one joiner[†]			
	Egg stage	Larval stage	Pupal stage	Total	Egg stage	Larval stage	Pupal stage	Total
Marked joiner[‡]	7	10	9	26	5	9	4	16
Unmarked joiner[§]	83	76	32	191	26	34	18	53
Total	90	86	41	217	31	43	22	69[¶]

[*] The total number of wasps recorded in the study, including joiners and non-joiners was 676.

[†] Total number of nests was 145.

[‡] These individuals were known to be on other nests under observation.

[§] The sources of these individuals were not known.

[¶] Note that this is not equal to the sum of the three numbers to the left of it, because some nests received joiners during all the three stages of colony growth.

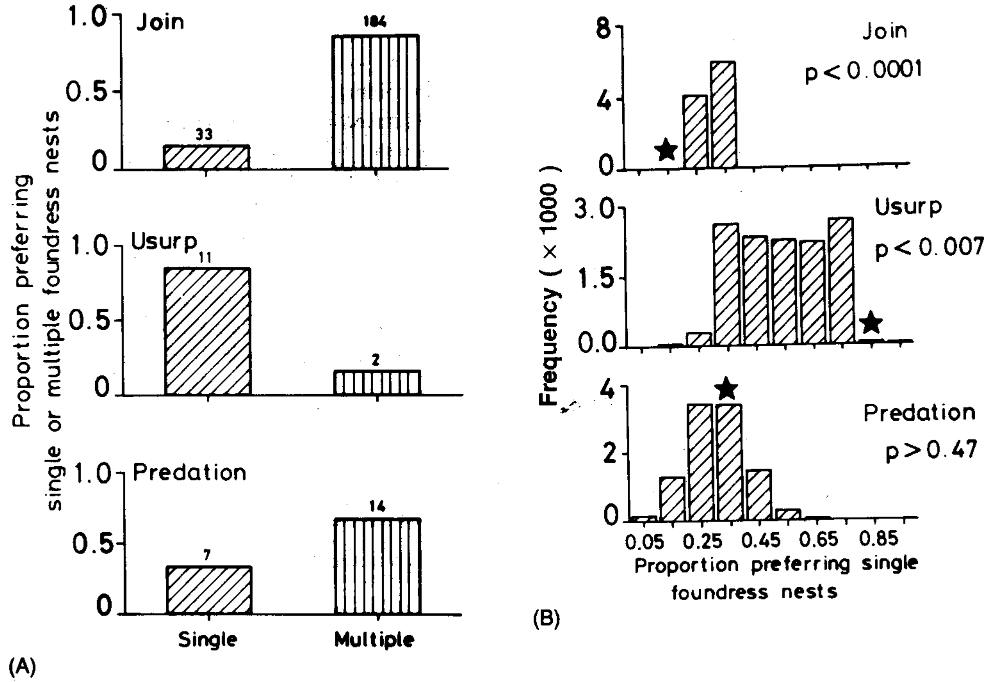

Fig. 5. (A) Proportions of animals prefering single and multiple foundress nests for joining, usurpation and proportions of single and multiple foundress being attacked by *V.tropica*. The actual numbers leading to these proportions are indicated above the bars. (B) Results of simulations (see Materials and Methods for details). Frequency distribution of expected proportion of conspecifics choosing single foundress nests for joining (upper panel). The observed proportion was significantly different from the expected proportions ($P < 0.0001$, the observed proportion of animals preferring to join single foundress nests fell completely outside the distribution of expected values, * indicates the location of the empirically observed value from Fig. 5A). Frequency distribution of expected proportion of conspecifics choosing to usurp single foundress nests (middle panel). Single foundress nests were usurped significantly more often than expected from the availability of single foundress nests ($P < 0.007$, only sixty-eight of the 10,000 expected values were more extreme than the observed proportion, * indicates the location of the empirically observed value from Fig. 5A). Frequency distribution of expected proportions of single foundress nests attacked by predator *V.tropica* (lower panel). Single and multiple foundress nests were attacked at relative rates expected from their availability ($P > 0.47$, 4774/10,00 expected values were more extreme than observed value, * indicates the location of the empirically observed value from Fig. 5A).

on the nest at the time of loss of all foundresses on the probability of its being adopted ($P > 0.05$, logistic regression analysis).

Percentage of egg layers

Since each nest has a single egg layer at any given time, and since 145 nests were recorded during the study period and there were thirteen cases of usurpation, fourteen cases of queen turnover and nine cases of adoption of abandoned nests, a total of 181 out of 676 (26.8%) females were egg layers in the founding population.

Predation

The hornet, *Vespa tropica*, is the major predator on the brood of *R.marginata*. Although predation was prevented in the vespiary, both single and multiple foundress nests in the field sites were attacked at relative rates expected from the availability of single and multiple foundress nests, as seen from the computer simulations (Figs 5A and 5B).

Discussion

Probable proximate causes of the observed patterns

The large number of nests initiated during May to July is perhaps due to warmer and more favourable temperatures and emergence of large numbers of prey items during this period of the year which results in the production of a large number of adults at this time of the year (Chandrashekara, 1991) which leave their natal nests and initiate new nests. Conversely, the observation that very few nests are initiated between December and February is probably attributable to the low temperatures resulting in the production of very few adults at this time of the year (Chandrashekara, 1991) that can leave to found new nests.

Nests failed significantly more often in the field sites than in the vespiary. Can this increased failure rate in the field sites be attributed entirely to the predator pressure which was lacking in the vespiary? 21/80 (26.2%) nests failed in the vespiary, obviously due to causes other than predation by *V.tropica*. In the field sites, 28/65 (43.1%) nests failed. However, only sixteen nests were attacked by the predator. Of the remaining forty-nine nests not attacked, sixteen (32.7%) failed. This rate of failure in the field can be attributed to causes other than predation. The failure rate of 21/80 nests in the vespiary, and 16/49 nests in the field (due to causes other than predation) are not significantly different ($G = 0.59$, $P > 0.05$). We conclude therefore that the higher overall failure rate in the field as compared to the vespiary can be attributed to predation by *V.tropica*.

Why do single foundress colonies have significantly lower success rates than multiple foundress colonies? This cannot be due to predation pressure from *V.tropica* for two reasons. First, single foundress colonies have a significantly lower success rate compared to multiple foundress colonies both in the field and in the vespiary. Second, *V.tropica* does not preferentially attack single foundress nests in the field sites. Nest usurpation also cannot account for the observed pattern. Since we were interested in productivity as a function of group size rather than fitness of individual wasps, usurped nests were not considered as failed nests; only nests that failed to produce any adults were considered failed. Loss of foundresses which is obviously of more serious consequence for single foundress colonies is therefore the most likely cause of the lower success rate of single foundress colonies.

The total colony productivity in *R.marginata* increased with increasing number of foundresses. Such an increase was documented for the social Hymenoptera in general, in a classic paper by Michener (1964). The increase in total productivity as a function of the number of foundresses seen in *R.marginata* is possibly a reflection of the increasing amount of resources, such as building material and food, brought into the nest with increasing group size. However, the per capita productivity did not vary significantly with increasing number of foundresses in one of our data sets and decreased significantly in another data set. Michener (1964) reported a decreasing per capita productivity for social insects in general. Why does the per capita productivity not increase significantly as a function of number of foundresses? Notice that the lack of a significant increase in per capita productivity is not compensated by either significantly faster development or significantly heavier progeny in multiple foundress nests compared to single foundress nests in *R.marginata*. One might have expected that, due to division of labour, there would have been an increase in the efficiency of brood rearing and hence a significant increase in the per capita productivity in large nests. However, there appears to be a decrease in brood-rearing efficiency as the number of foundresses increases; in spite of relatively lower rates of failure, multiple foundress colonies have about the same mean per capita productivity as single foundress nests do. We speculate that the apparent decrease in efficiency with increase in foundress group size has to do with the primitively eusocial status of *R.marginata*. Unlike most highly eusocial species, where workers are expected to rely almost entirely on the indirect component of inclusive fitness, workers in primitively eusocial species such as *R.marginata* are clearly attempting to obtain both individual fitness (by becoming queens in their natal or other nests at some time in the future) and indirect fitness (by caring for the queen's brood). This probably prevents an increase in efficiency due to division of labour in a primitively eusocial species as might occur in a highly eusocial species.

Evolutionary advantages of foundress associations

Why do over 90% of the wasps form multiple foundress colonies and why do joiners prefer multiple rather than single foundress colonies, even though it means that only one per group becomes the egg layer? This is even more paradoxical because there is no evidence of any significant increase in per capita productivity as a function of group size. Even if the foundresses were full-sisters of each other, subordinate cofoundresses would be helping to rear their nieces and nephews to whom they are less related than they would be to their offspirng. Therefore a substantial increase in per capita productivity is required to compensate for the lower worker–brood genetic relatedness if workers are to gain sufficient inclusive fitness to make joining a better strategy than being a solitary foundress. Moreover, foundresses are likely to be more distantly related than full-sisters. *R.marginata* exhibits polyandry (Muralidharan *et al.*, 1986; Gadagkar, 1990b) and serial polygyny (Gadagkar *et al.*, 1991a, 1993) resulting in the simultaneous production of several different patrilines and matrilines within a colony. There is no evidence of intra-colony kin recognition (Venkataraman *et al.*, 1988; Gadagkar, 1995). Factors other than genetic relatedness also appear to play a role in the acceptance of joiners (Venkataraman & Gadagkar, 1992). Unrelated wasps may found new nests cooperatively (Venkataraman, 1990). Foundresses often move from one nest to another, perhaps suggesting that they are not sorting strictly along genetic lines. One might expect identification of genetic relatives to be a more definite, one-time process not requiring movement of animals from nest to nest. On the other hand, if the wasps are assessing their potential of becoming future egg layers in the group, then such a process might require continuous monitoring and frequent changes in the nest composition. All these arguments taken together suggest that foundresses probably have rather low genetic relatedness among themselves.

Larger colonies, again as explained earlier, do not appear to produce larger offspring and do not seem to produce them any sooner. However, this does not say anything about the predictability with which the mean per capita productivity is attained by nests with different numbers of foundresses, an important and usually overlooked issue, as pointed out by Wenzel & Pickering (1991). Small groups are expected to be more unpredictable and show larger deviation from the expected mean compared to larger groups (Wenzel & Pickering, 1991). There is indeed a significant reduction in the coefficient of variation of the per capita brood with increase in the number of foundrresses in our data (Fig. 6A), thus confirming Wenzel & Pickering's (1991) claim that reduction in variance constitutes an 'automatic' advantage of group living. There was also a significant decrease in the standard deviation of per capita productivity with increasing number of foundresses, showing that a reduction in variance and not an increase in the mean is responsible for the reduction of the coefficient of variation (data not shown). Besides, we have already seen that the mean per capita productivity does not change significantly with increasing group size. It should be pointed out, however, that the significant decrease in the coefficient of variation in per capita productivity with increasing foundress group

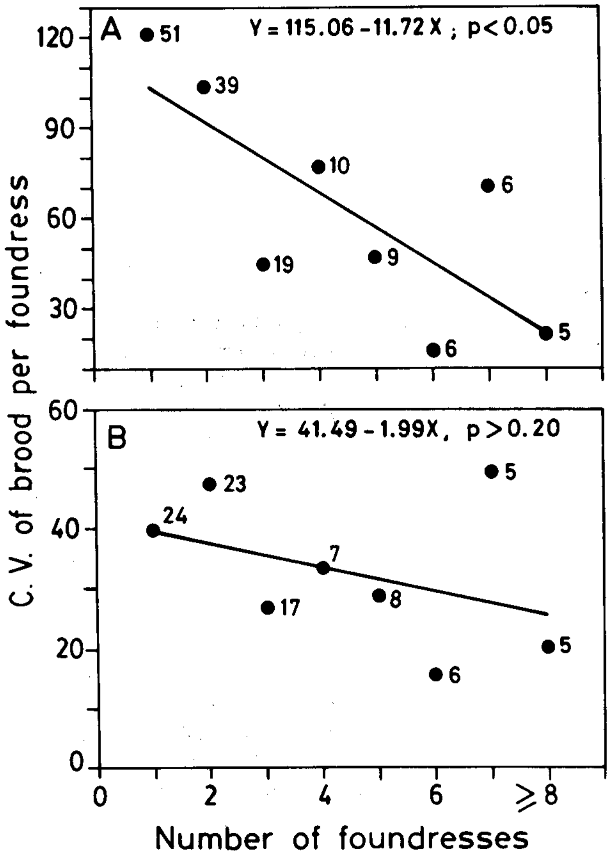

Fig. 6. (A) Coefficient of variation of the per capita brood (eggs + larvae + pupae) as a function of the number of foundresses. The linear regression and the *P* value relating to testing of the deviation of the slope from zero and sample sizes (number of nests) are shown for each point. Note that the coefficient of variation decreases significantly with foundress group size despite the drastic reduction in sample sizes for larger groups. (B) Although the negative trend remains, the slope is no longer significantly less than zero when failed nests are excluded from the data set. Note that failed nests were assigned a value of zero productivity and included in the data set in A.

size in *R.marginata* is due to failure of large numbers of nests in the smaller group sizes to whom we have assigned zero values of per capita productivity. If the data are reanalysed after ignoring the failed nests, the significant decrease in the coefficient of variation disappears, although a decreasing trend remains (Fig. 6B). It might be argued therefore that our data support the 'survivorship insurance' model of Reeve (1991) rather than the central limit theorem (CLT) model of Wenzel & Pickering (1991), because the CLT model attributes the expected lower predictability in smaller groups to statistical fluctuations in food brought to the nest rather than to statistical fluctuations in the probability of foundress survival. However, there is no reason why the low predictability of smaller groups cannot also be attributed to loss of foundresses. In other words, the 'survivorship insurance' model and the CLT model are not really different, at least in the limited context of this study.

Another explanation for multiple foundress associations comes from the observations of nest usurpations. Significantly more single foundress nests were usurped compared to two foundress nests and no nests with three or more foundresses were usurped. Therefore, as in the cases of *Polistes metricus* (Gamboa, 1978) and *Polistes fuscatus* (Klahn, 1988), usurpation pressure from conspecifics appears to provide a selective disadvantage for single foundress nests in particular and small nests in general.

In multiple foundress nests only one individual is the egg layer, whereas the others are non-egg laying workers. However, queen turnovers provide opportunities for workers to become queens in their lifetime. Therefore, apart from gaining indirect fitness on account of rearing the queen's brood, workers can also gain direct fitness with some probability, if they take over their colony as replacement queens. A queen on a multiple foundress nest of *R.marginata* produces an average of about seventy-eight offspring, whereas a solitary foundress produces barely one or two (Gadagkar, 1990c). Hence wasps that begin their life as workers with a hope of direct reproduction may sometimes do better than solitary foundresses. This may thus be another factor favouring multiple foundress associations (West-Eberhard, 1978; Gadagkar, 1990c). Although queen turnovers provide a possible explanation for multiple foundresses associations, it is at best a weak explanation. If all foundresses have the same chance of becoming replacement queens, the probability of a given individual becoming the replacement queen is inversely proportional to the number of foundresses on that nest. Therefore even if the probability of a nest experiencing queen turnover is independent of the number of foundresses present on it, joiners are expected to have a higher probability of becoming queens in smaller nests and joiners must therefore prefer them rather than nests with large number of individuals. However, we have shown that nests with two foundresses have a higher probability of experiencing queen turnover compared to nests with three or more foundresses. Multiple foundress nests must therefore be even less preferred by joiners, if joiners are hopeful queens. But our analysis shows that joiners preferred multiple foundress nests over single foundress nests. This appears paradoxical and appear to weaken the hopeful queen hypothesis. However, the observed movement of animals between nests may perhaps be interpreted as an attempt on the part of the foundresses to choose that group to nest with, where they might have a high probability of succeeding as a subsequent queen, on account of their competitive ability relative to the residents of the joined nest.

Using a dynamic optimization model of colony founding in wasps and ants, Nonacs (1989) showed that, for foundresses faced with the dilemma of whether to remain at the present site or leave in the hope of finding a better site, discriminating competitive ability of potential cofoundresses is more valuable than discriminating kinship. Synthesizing the extensive literature on *Polistes* foundress behaviour and using a simple ecological constraints model, Reeve (1991) has shown that when ecological constraints on solitary nest founding are sufficiently weak, only solitary nesting and usurping are favoured. And when ecological constraints on solitary nesting are strong, usurpation and joining are favoured. It is interesting to note that genetic relatedness between cofoundresses drops out of his model completely. In support of this, he finds a negative relationship between mean cofoundress relatedness and percentage of multiple foundress associations in polistine wasps (Reeve, 1991; Ross & Carpenter, 1991). More recently, Hughes *et al.* (1993) have failed to find a positive relationship between genetic relatedness and percentage of foundresses who become subordinate helpers rather than single foundresses or queens of multiple foundress nests in eight species of *Polistes*, and have concluded that 'factors other than relatedness are more important in determining interspecific differences in the incidence of altruism'.

Nest usurpation and queen turnover also cannot provide a complete and satisfactory explanation for multiple foundress associations in *R.marginata*, in the face of low genetic relatedness and the absence of a significant increase in per capita productivity as a function of group size. This is because both nest usurpation and queen turnover are relatively rare phenomena. Only about 9% of the nests in our study were usurped and only about 10% of the nests witnessed queen turnover, and that too only once in the pre-emergence phase. Added to this is the problem that joiners preferred multiple foundress nests even though the probability of queen turnover is higher in nests with two foundresses. Surely these factors must work in conjunction with several others that we have investigated in the past. For instance, individual wasps may be quite different in their egg-laying abilities, and those that have poor egg-laying abilities may choose to become subordinate cofoundresses rather than solitary foundresses.

There is evidence for a larval-nutrition based pre-imaginal caste bias such that better-nourished larvae tend to develop into early egg-layers and poorly-nourished larvae tend to develop into late egg-layers or non-egg-layers under laboratory conditions (Gadagkar *et al.*, 1988, 1990, 1991b). In addition to such differences in fertility, caused by pre-imaginal caste bias, other factors such as delay and variation in the time taken to attain reproductive maturity can also select for worker behaviour as has been shown previously, using inclusive fitness models (Gadagkar, 1991b). Besides, the mere fact that workers work in groups and can serially divide labour whereas solitary foundresses have to necessarily survive for the entire brood developmental period, in order to gain any fitness at all, can make substantial contributions to the inclusive fitness of a worker, relative to that of a solitary nest foundress (Queller, 1989; Gadagkar, 1990a, 1991b). Let us return to the original question of why subordinate workers do not become solitary foundresses and rear their own offspring instead of working to rear the brood of another individual. Taken together with earlier studies referred to above, our results suggest that the apparent increased fitness of the worker strategy over the solitary foundress strategy in the primitively eusocial wasp *R.marginata* does not appear to come from any high degree of worker brood relatedness or from any increased per capita productivity attained by efficient division of labour. It appears to come instead, from (i) the greater predictability of attaining the mean per capita productivity in larger colonies, (ii) lower probabilities of nest usurpation of larger colonies, (iii) opportunities that queen turnovers provide for workers to gain some individual fitness also, (iv) inherent inequalities between individual wasps that make the worker strategy the best of a bad job for some individuals, and (v) the advantage of serial division of labour and the associated relatively higher assured fitness returns for workers as compared to a solitary nest foundress.

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