Evolution of social behaviour in the primitively eusocial wasp *Ropalidia marginata*: do we need to look beyond kin selection?

Raghavendra Gadagkar

Centre for Ecological Sciences, Indian Institute of Science, Bangalore 560012, India

*Ropalidia marginata* is a primitively eusocial wasp widely distributed in peninsular India. Although solitary females found a small proportion of nests, the vast majority of new nests are founded by small groups of females. In such multiple foundress nests, a single dominant female functions as the queen and lays eggs, while the rest function as sterile workers and care for the queen’s brood. Previous attempts to understand the evolution of social behaviour and altruism in this species have employed inclusive fitness theory (kin selection) as a guiding framework. Although inclusive fitness theory is quite successful in explaining the high propensity of the wasps to found nests in groups, several features of their social organization suggest that forces other than kin selection may also have played a significant role in the evolution of this species. These features include lowering of genetic relatedness owing to polyandry and serial polygyny, nest foundation by unrelated individuals, acceptance of young non-nest-mates, a combination of well-developed nest-mate recognition and lack of intra-colony kin recognition, a combination of meek and docile queens and a decentralized self-organized work force, long reproductive queues with cryptic heir designates and conflict-free queen succession, all resulting in extreme intra-colony cooperation and inter-colony conflict.

1. *Ropalidia marginata*

Social insects are classified as primitively or highly eusocial based primarily on whether or not there is morphological differentiation between queens and workers. The absence or the presence of such morphological caste differentiation is correlated with a suite of contrasting traits. In primitively eusocial species, caste determination is largely post-imaginal, adults have flexible roles and can switch from worker to queen roles, colony sizes are usually small, and physical aggression—especially by the queen—is important for the maintenance of social organization. In highly eusocial species, on the other hand, caste determination is pre-imaginal, adults often have fixed roles making it impossible for adult workers to become queens, colonies are usually very large, and chemical regulation by pheromones has largely replaced physical aggression as a key mechanism for the regulation of social organization [1]. Because workers can potentially switch to queen roles, implying that workers are behaving altruistically even though they are potentially capable of behaving selfishly, primitively eusocial species offer attractive model systems for testing theories of social evolution. In addition to all the features of primitively eusocial species mentioned above, *Ropalidia marginata* has the additional advantage of being in the tropics, making it possible for the species to have a nesting cycle that is largely aseasonal, perennial and indeterminate—new nests can be founded at all times and do not have a fixed lifespan. This additional feature makes it possible for female wasps to have several different options available to them—(1) founding new solitary nests, (2) founding new multi-female nests, (3) staying back and working at their natal nests for all of their lives, and (4) staying back to work for some time and eventually take over the role of queen in their natal nests (figure 1). Male wasps
leave their natal nest about a week after eclosion to lead a nomadic life and will therefore be ignored in the rest of this discussion. We have contrasted the two options for female wasps, of leaving to found solitary nest (option 1 = selfish, single foundress strategy) on the one hand and staying back to work for their entire lives (option 3 = altruistic worker strategy) on the other, to ask why some wasps pursue the altruistic strategy while others do not. In doing so we have often neglected the fourth option of working first and then taking over as queens (mixed altruistic and selfish strategy). This neglect, necessitated by technical difficulties, is at least partly responsible for the open question in the title—do we need to look beyond kin selection? [2].

2. Hamilton’s rule

When workers spend their whole lives caring for the queen’s brood and do not reproduce themselves, they are said to behave altruistically. Such altruism is paradoxical from the point of view of natural selection because an allele that causes a worker to selfishly reproduce rather than altruistically refrain from reproduction should spread in the population. This paradox was recognized by Darwin and has occupied centre-stage in evolutionary biology ever since. The most prominent and successful solution to this paradox is the theory of kin selection, often referred to as inclusive fitness theory or Hamilton’s rule (I will henceforth use these three terms interchangeably). According to this theory, an altruistic allele can be favoured by natural selection when the condition \(b \cdot r > c\) (Hamilton’s rule) is satisfied, where \(b\) is the benefit to the altruist, \(r\) is the coefficient of genetic relatedness between the altruist and the recipient of the altruism and \(c\) is the cost incurred by the altruist. In proposing this theory, Hamilton expanded the concept of Darwinian fitness to include fitness gained by helping genetic relatives and hence he termed it inclusive fitness [3]. This theory makes explicit that altruistic alleles can be favoured when the altruism is directed towards kin, and hence the name kin selection. Inclusive fitness theory has inspired a large body of theoretical and empirical research, not only in ants, bees and wasps but also in all living organisms including microbes, plants and humans. Nevertheless, there is now a rather bitter controversy about the mathematical generality and validity of inclusive fitness theory [4–6].

3. Do wasps obey Hamilton’s rule?

My research group has been concerned with the question of whether animals obey Hamilton’s rule by behaving altruistically when the rule is satisfied and selfishly when it is not. In an attempt to answer this question we have, as stated above, considered two of the four options available to newly eclosed female wasps of R. marginata—the selfish single foundress strategy and the altruistic worker strategy. Because the altruistic worker strategy is the paradoxical one, we ask why it is ever adopted. Inclusive fitness theory predicts that it should be advantageous to adopt the altruistic worker strategy if the inclusive fitness gained by a worker is greater than the inclusive fitness gained by a selfish single foundress. It has been our aim to explicitly consider all the three parameters in Hamilton’s rule namely, \(b\), \(r\) and \(c\). However, inclusive fitness is not so easy to measure [2,7]. To make Hamilton’s rule empirically tractable, we have partitioned inclusive fitness into three multiplicative factors, following [8]. These are an intrinsic productivity factor (\(b\) for single foundresses and \(B\) for workers), a relatedness factor (\(r\) for single foundresses and \(\rho\) for workers) and a demographic correction factor (\(s\) for single foundresses and \(\sigma\) for workers). Thus, the altruistic worker strategy should be favoured over the selfish single foundress strategy when \(\beta \cdot \rho \cdot s > b \cdot r \cdot s\) [9]. This formulation is helpful for empirical investigation although \(\beta\), \(\rho\), \(\sigma\), \(b\), \(r\) and \(s\) also cannot be measured directly in the field. Hence we have considered the three extremes of this inequality namely, \(\beta > b\), \(\rho > r\) and \(\sigma > s\). \(\beta > b\) implies that the intrinsic productivity of a worker is greater than that of a single foundress. This may occur because of physiological reasons; wasps that choose to be workers and those that choose to initiate single foundress nests may be physiologically different from each other. It could also be owing to ecological reasons; the environment may make it harder for single foundresses to raise brood all by themselves, as compared to workers who have the protection and cooperation of their colony. Hence I term the condition \(\beta > b\) as an ecological/physiological predisposition to the evolution of eusociality. \(\rho > r\) implies that workers have access to brood more closely related to themselves as compared to the relatedness of single foundresses to their brood. Hence I term the condition \(\rho > r\) as a genetic relatedness predisposition to the evolution of eusociality. This can happen automatically owing to haplodiploidy. Such automatic predisposition to eusociality because of the condition \(\rho > r\) has been termed the haplodiploidy hypothesis. Finally, \(\sigma > s\) implies that demographic correction factors are different for workers and single foundresses; the cost of dying early may be smaller for workers when compared with single foundresses (see below). Thus, I term the condition \(\sigma > s\) as a demographic predisposition to the evolution of eusociality. In summary, we ask if R. marginata is predisposed to the evolution of eusociality for any of the above three reasons.

4. Genetic relatedness predisposition (\(\rho > r\))

Is R. marginata predisposed to the evolution of eusociality owing to relatedness asymmetries? In other words, do workers...
Figure 2. A pedigree of queens in a colony of the social wasp *Ropalidia marginata*. The figure shows that Q2, Q3 and Q4 were daughters of Q1, and Q5, Q6 and Q7 were daughters of Q3, and so on. The question mark indicates that the relationship of Q2 alone to Q1 was somewhat doubtful. Of the two numbers in parentheses, the first one indicates the tenure in days of each queen and the second one indicates the number of offspring she produced during her tenure. (Reproduced with permission from [11].)

rear brood more closely related to them than do single foundresses? This can happen owing to haplodiploidy, but the genetic asymmetries created by haplodiploidy can be broken down if queens mate with two or more males and produce different patrilines of daughters. To examine this possibility, we genotyped mothers and daughters from four nests using polymorphic allozyme (esterase) markers. *Ropalidia marginata* queens mate with one to three males and sufficiently mix up sperms from different males to produce daughters who are related to each other by an average value of 0.53. In other words, the genetic asymmetry potentially created by haplodiploidy is broken down owing to multiple mating [10]. We soon discovered that genetic relatedness is further significantly lowered because of multiple matrilines among the workers of a colony (in addition to multiple patrilines). Multiple matrilines arise because one of the options available to the wasps is to work for some time before taking over their colony as new queens. To study this phenomenon, which we term serial polygyny, we conducted a long-term pedigree analysis. Pedigrees of queens in *R. marginata* can be quite complex (figure 2).

New queens may be the daughters, sisters, nieces or cousins of their immediate predecessor queens. Remarkably, workers who are daughters of the previous queen continue to work uninterrupted when a new queen takes over. Therefore, the relatedness between workers and the brood they care for can also be very low. We have shown that the brood cared for may be brothers and sisters, nieces and nephews, cousins, cousins’ offspring, mother’s cousins, mother’s cousins’ offspring and even mother’s cousins’ grand offspring. Our observational techniques permitted us to compute the relative frequencies of each of these worker–brood relationships throughout the observation period. We combined these relative frequencies with the estimate of relatedness between sisters of 0.53 taken from the allozyme analysis and computed a grand mean (average over periods ranging from six to 15 months for four different colonies). The combined effects of polyandry and serial polygyny resulted in worker–brood relatedness values ranging from 0.22 to 0.46, not only below the theoretically expected value of 0.75 (owing to haplodiploidy) but also below 0.5, the expected relatedness between a single foundress and her offspring. Not only is the haplodiploidy hypothesis unsupported but indeed ρ is less than r. In other words, *R. marginata* is not predisposed to the evolution of eusociality on account of genetic relatedness asymmetries. If anything, it is predisposed to the evolution of the selfish single foundress strategy [12].

5. Ecological/physiological predisposition (β > b)

Is *R. marginata* ecologically/physiologically predisposed to the evolution of eusociality, i.e. is β > b? This is possible if the productivity of single foundresses is much less than that of workers. However, it would not be appropriate to compare the productivity of single foundresses with that of workers because such comparison would assume that workers would have the same productivity as single foundresses if they themselves became single foundresses. This may not be true because wasps that become single foundresses may be physiologically different from those who become workers. To test this possibility, we conducted the following experiment. We identified a large number of newly founded nests. Among these, single foundress nests were left undisturbed and labelled as ‘voluntary single foundresses’. Of the remaining, 50% were randomly assigned to the category ‘forced single foundresses’. Here we removed the queen as well as all but one worker. One randomly chosen worker was left on the nest and was thus forced to be a single foundress even though she had herself chosen to be a worker. The remaining 50% were assigned to the category ‘forced solitary queens’. Here we removed all the workers and forced the queen to be alone. We followed these nests until the eclosion of at least one adult offspring and then compared the productivities of the three categories of females. Productivity was measured as the total brood
present on the nest at the time of eclosion of the first adult offspring. We found that the productivities of the voluntary single foundresses and forced solitary queens were not significantly different from each other. However, the productivity of forced single foundresses was significantly lower than the other two categories. A significant conclusion from this experiment is that wasps choose their nesting strategies based on their abilities. Wasps who choose to be workers fare very poorly when forced to become single foundresses compared to those who voluntarily become single foundresses. This is what makes $\beta > b$, because those who choose to be workers give up only a small productivity that they may have gained as single foundresses; those that have a higher intrinsic productivity do not seem to accept worker roles and instead found their own nests [13]. It is not entirely clear why the productivity of forced single foundresses is less than voluntary single foundresses. We suspect that it is a combination of physiological and ecological factors. We have evidence that female wasps in R. marginata have extremely variable reproductive potential [14] and at least half of them fail to build nests and lay eggs in spite of having all the resources to do so [15]. However, we do not fully understand the mechanism by which such variation in reproductive potential is produced. Among the ideas proposed, parental manipulation is a likely candidate [15–18]. We have evidence that the significantly lower productivity of forced single foundresses may also arise owing to their inability to forage and feed a large quantity of brood and yet survive as well as voluntary single foundresses. All this suggests an ecological explanation for $\beta > b$. In summary, we have evidence that R. marginata is predisposed to the evolution of eusociality owing to physiological and ecological reasons.

6. Demographic predisposition ($\sigma > s$)

Is R. marginata demographically predisposed to the evolution of eusociality? To examine this possibility, I have constructed a hierarchy of inclusive fitness models that explore different demographic reasons why a worker may have higher inclusive fitness than a single foundress [19]. For lack of space, I will illustrate below only one of these models, the assured fitness returns model [9]. A single foundress must survive until her brood becomes independent of her. Since eggs, larvae and pupae are dependent on care and protection from the adult wasps, they only become independent after eclosion. If a single foundress dies before her brood eclose she will certainly lose everything to predation, especially by ants. Thus, a single foundress does not have assured fitness returns for her daily investment of work for her brood. She gets her returns once and for all after her offspring eclose. The probability that she survives until her offspring eclose is therefore her demographic correction factor—a factor by which her intrinsic productivity should be devalued because of expected mortality. Ropalidia marginata brood take an average of 62 days to complete development from egg to adulthood. Based on survival of marked individuals in many colonies, we estimated that the probability of a wasp surviving up to 62 days is 0.12. Thus, $s = 0.12$. The situation is quite different for a worker. If a worker dies before she brings her brood to adulthood, the brood will not necessarily die, other workers will care for them. Thus, even workers with short lifespans can possibly divide labour and cooperatively rear brood with long developmental times, sharing fitness returns along the way, in proportion to the duration of their work. In other words, workers have relatively more assured fitness returns for their daily investment, at least in small colonies [20]. I have captured this feature of their fitness by the expression

$$\sigma = \sum_{i=1}^{n-1} p_i (i/n) + \sum_{i=n}^{\infty} p_i,$$

where $p_i$ is the proportion of wasps surviving up to age $i$, and $n$ is the maximum age of the wasp. With the same data on the survivorship of wasps from many colonies, which yielded $s = 0.12$, the above expression yields a value of 0.43 [9]. In other words, the intrinsic productivity of a worker should only be devaluated by 0.43 while that of a single foundress should be devaluated by 0.12. In other words, $\sigma > s$ and R. marginata is indeed demographically predisposed to the evolution of eusociality [9].

7. A unified theory

The analysis described above showed that although R. marginata is not predisposed to the evolution of eusociality on account of genetic relatedness asymmetries, it is predisposed on account of ecological/physiological and demographic asymmetries between single foundresses and workers. With the hope of integrating these three predispositions—one against and two for the evolution of eusociality—and having estimates of the quantitative extents of these predispositions (based on the ratios of $\beta/b$, $\rho/r$ and $\sigma/s$), I have built a unified model. First we must ask what we want from a unified model. Ideally, I would have liked to make a prediction for each wasp about whether each should become a single foundress or a worker. However, I do not yet see a way of making such a prediction. A more modest expectation from a unified model would be to predict the proportion of the population of wasps that should opt for the single foundress strategy and the proportion that should opt for a worker strategy. With some more simplifying assumptions, it turns out that this can be achieved. Using the condition that worker behaviour will be favoured when $\sigma/s$ should be greater than $rb/\rho\beta$, I calculated graphically that single nesting behaviour is favoured only in 5.1% of the parameter space when worker–brood relatedness is at its highest, the ratio of demographic correction factors for worker/single foundress is at its lowest and the productivity of a solitary foundress is at its highest (figure 3).
A long-term field study of 145 pre-emergence nests shows that 4.6–7.5% of the wasps nested solitarily and 92.5–95.4% of the wasps nested in groups [13]. There is thus a remarkable similarity between the predictions of the unified model and the empirical data. Even if one does not take the quantitative fit between model and data very seriously (and one should not), the fact that both the model and the data show that an overwhelming proportion of wasps should and do opt for the worker strategy and that only a small proportion of wasps should and do nest solitarily is very satisfying [2]. Clearly, Hamilton’s rule provides a powerful framework for understanding the evolution of social and altruistic behaviour in R. marginata. Even though I have often complained that most investigators focus excessively or exclusively on r and neglect the b and c terms in Hamilton’s rule, the power of the theory is evident when all three factors are considered, as I have attempted to do for R. marginata.

8. Why then look beyond?

There are three different reasons why I think it is worth trying to look beyond kin selection. The first is the publication of Nowak et al. [4] (see also [5,6]). Personally, I have no basis to rule out the possibility that they may be right in their claim that the mathematics of inclusive fitness may be wrong or may have limited applicability [22] and there is no resolution in sight [21,23,24]. I am therefore more interested in their claim that old-fashioned, standard population genetic modelling can serve equally well (never mind whether better) in understanding the evolution of social behaviour. My second reason is that there were a number of simplified assumptions that went into our analysis of Hamilton’s rule described above. Perhaps the most important one, as already mentioned at the beginning, is the complete neglect of the fourth option that the wasps have: namely to combine selfish and altruistic strategies by working first and taking over as queens later in their lives. It seems reasonable to argue that individual selection for maximizing direct reproduction would have a role in selecting for such behaviour. My third reason and the only one I will discuss below is that during the course of nearly four decades of studying these wasps, we have uncovered many phenomena that do not immediately appear to be the result of kin selection. Indeed, some of them appear to be contrary to the predictions of kin selection. Hamilton’s rule may be satisfied in spite of these counterintuitive phenomena, but why should these phenomena have evolved in the first place? I will briefly describe below eight such phenomena.

9. Lowering and apparent irrelevance of genetic relatedness

As already described above, polyandry and serial polygyny significantly reduce intra-colony genetic relatedness, not only below the expected value of 0.75 for a haplodiploid species but indeed below 0.5, the value expected for a selfish single foundress. It is true that Hamilton’s rule appears to be satisfied in spite of such low relatedness but the question is why have polyandry and serial polygyny evolved? Surely they must have evolved owing to other constraints for the evolutionary competitiveness of R. marginata and its relatives, in spite of working against kin selection. The very least we must admit is that forces other than kin selection must have been important in moulding the overall social organization of R. marginata.

10. Nest foundation by unrelated individuals

As mentioned above, we conducted a long-term field study of pre-emergence nests in which all adult wasps on all nests were uniquely marked. When an unmarked individual or a wasp marked on another nest was seen on any nest, such a wasp was termed a ‘joiner’ and the nest on which it was seen was said to have received a joiner. Of the 676 wasps recorded in this study, 217 (32.1%) were joiners and of the 145 nests studied, 69 (47.6%) received at least one joiner. Of the 217 joiners, 191 were unmarked individuals so that we are not sure where they came from. Some of them could be unrelated to the individuals in the nest that they joined. However, we had previously marked 26 of the joiners on another nest and they thus represent unambiguous evidence of movement of foundresses from one nest to the other [25]. If kin selection is the sole arbitrator of social evolution, why should nests accept such joiners and why should joiners move from nest to nest?

11. Strong nest-mate discrimination and lack of intra-colony kin recognition

To understand whether the break down (by polyandry and serial polygyny) of the genetic asymmetries created by haplodiploidy can be overcome behaviourally, we investigated the phenomenon of nest-mate and kin discrimination. We found strong evidence for nest-mate discrimination. Further investigation of the possible mechanism of nest-mate discrimination showed that the ability to tell apart nest-mates from non-nest-mates depended on labels on the discriminating wasps and templates in the discriminating wasps. However, both labels and templates were clearly acquired by the wasps from their nests and/or nest-mates, after their eclosion. Wasps denied the opportunity to so acquire either the labels or the templates were unable to make efficient nest-mate discrimination. This suggests that all wasps on a nest will have similar labels and templates and that intra-colony kin discrimination is not possible [26]. In a species where intra-colony relatedness is lowered owing to polyandry and serial polygyny, bringing together wasps of multiple patrilines and matrilines, the ability to discriminate more related kin from less related kin within the colony would be of obvious benefit for the operation of kin selection. And yet, such intra-colony kin discrimination has not evolved. Why? What forces are powerful enough to counteract the demands of kin selection?

12. Acceptance of young non-nest-mates and cooperation among unrelated individuals

In an experiment designed to study nest-mate discrimination in the context of a nest, we released all members of a nest into the cage of another resident colony with its nest and nest-mates. In this experiment, we found that all (and only) young alien wasps were accepted on to the foreign colony, without aggression. This permitted us to deliberately make genetically mixed colonies by introducing young
non-nest-mate wasps taken from nests more than 10 km away. Studying such genetically mixed colonies, we found no evidence of intra-colony discrimination. Instead we found that the introduced aliens became indistinguishable from the resident wasps and even went on to become future queens, in spite of the presence of resident wasps [27]. Why have these phenomena evolved? They do not appear to be the result of kin selection. What other forces are at play in shaping the complex behaviour of these wasps?

13. Meek docile queens and decentralized work organization

Unlike what is expected of a typically primitively eusocial species, R. marginata queens are remarkably meek and docile individuals, not behaviourally dominant and non-interactive. We now have growing evidence that they nevertheless manage to maintain reproductive monopoly by means of pheromones [28–32]. Also unexpected for a typical primitively eusocial species, queens of R. marginata do not appear to be involved in the regulation of colony labour. Workers appear to self-organize their labour in a decentralized manner in the presence or the absence of the queen [33–35]. For these reasons, we have argued that R. marginata may be intermediate between primitively and highly eusocial species. We really do not understand the forces involved in the evolution of the highly eusocial state, with pheromone-producing, behaviourally docile queens and efficient decentralized self-organization of work. It is not impossible that kin selection has a role in this, although these features appear tantalizing signatures of group- or colony-level selection. I believe that the evolution of the highly eusocial state from a primitively eusocial condition is a whole new field waiting to be investigated. Using comparative genomics and identifying ‘a large number of candidate taxonomically restricted genes that may have played a role in eusocial evolution’, Johnson & Tsutsui [36, p. 1] show one way to do so.

14. Cryptic heir designates and conflict-free queen succession

When an R. marginata queen is lost or experimentally removed, a replacement queen is immediately (within minutes) apparent because one of the workers becomes hyper-aggressive and goes on to become the next queen if the original queen is not returned [37,38]. It is rather remarkable indeed that we are unable to predict the identity of the successor before removing the original queen [39]. It is even more remarkable that the workers themselves appear to know who their next queen is, suggesting the presence of a cryptic heir-designate [40]. We now know whether there is just one heir-designate or a long reproductive queue. It is rather hard to explain why such a pre-designated reproductive queue is implemented without any overt aggression. Upon removal of successive queens or potential queens, one and only one individual becomes hyper-aggressive and takes over the colonies without being challenged by others [41]. What evolutionary forces might lead to such a peacefully organized society? I believe that merely focusing on Hamilton’s rule is unlikely to give us the answer.

15. We need to look beyond kin selection

All the evidence presented above suggests that R. marginata wasps show extraordinary levels of intra-colony cooperation and extreme inter-colony conflict. I suggest that it is this combination of cooperation and conflict that makes social life possible and worthwhile. But how does this contrasting combination of traits evolve? It is very suggestive of group selection indeed. We have also seen apparent signatures of individual selection, described above. And we have already shown the usefulness of kin selection in explaining many features of this species. It seems obvious that a full understanding of the evolution of the entire suite of characters that define the R. marginata society will require consideration of several kinds of evolutionary forces, including individual, kin and group selection. I am open to an even more radical question—Hamilton’s rule may be sufficient to explain the evolution of social behaviour in R. marginata, but is it necessary? Perhaps there are other explanations, equally good or better, who knows? Future work should consider individual selection and group selection in the same detail as has been done with kin selection. Finally, an integrated multi-level selection approach [42] combined with other creative, non-conventional ideas [43–48] may eventually help us achieve a better understanding of the evolutionary logic of the many surprising and remarkable features of R. marginata. I must add that R. marginata is not the only species questioning the importance and exclusivity of kin selection. Recent studies on a number of other species are showing either that inclusive fitness theory is inadequate or when adequate, as in R. marginata, it is not obvious that it is the exclusive explanation. Answers to some of the questions I raise are being found in relation to other species and I plan to test them in the context of R. marginata in the future [49–54].

Ethics. All experiments were done in accordance with the regulations for research involving animal subjects in India.

Competing interests. I declare I have no competing interests.

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