

# COMMON KNOWLEDGE:

## THE CHALLENGE OF TRANSDISCIPLINARITY

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## 2.1 War and Peace: Conflict and Cooperation in a Tropical Insect Society

by Raghavendra Gadagkar<sup>1</sup>

*It is lamentable, that to be a good patriot one must become the enemy of the rest of mankind.*

Voltaire (1694-1778), Philosophical Dictionary

### The Insect Societies

Most insect species appear to complete their life cycles without the need for any significant interaction with other members of their species except during the act of mating. Other species however, practice group life with varying degrees of dependence on interaction with conspecifics<sup>2</sup>. The most extreme of such dependence is seen in the so called eusocial species that spend all or most of their lives in colonies. These include some bees and wasps and all ants and termites. We often refer to these social insect species as insect societies. Indeed, as we will see below, the insect societies rival if not surpass human societies in the complexity of their social organization and integration, division of labor, communication and even their caste systems. A matter of great interest, but probably of little relevance to our present discussion is that (with the exception of the termites) the insect societies are “feminine monarchies”. I borrow the phrase first used by the cleric Charles Butler in 1634 to describe the honeybee society; their colonies consist of queens and female workers while the males play no domestic role – they merely mate and die. The most striking feature of insect societies is reproductive division of labor – only one or a small

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<sup>2</sup> Other members of their own species.

number of individuals reproduce (the queens) while the rest remain sterile (the workers) and perform all the tasks associated with nest building and maintenance, foraging and brood care. In addition to reproductive division of labor between the queens and the workers, there is often further division of non-reproductive labor among the workers. It is this division of labor, first between the queen caste and worker caste and then between the different worker sub-castes that appear to be the secret of the unparalleled ecological success and dominance of social insects as compared to non-social species, insect or otherwise (Wilson, 1971; Wilson, 1990; Hölldobler and Wilson, 2009).

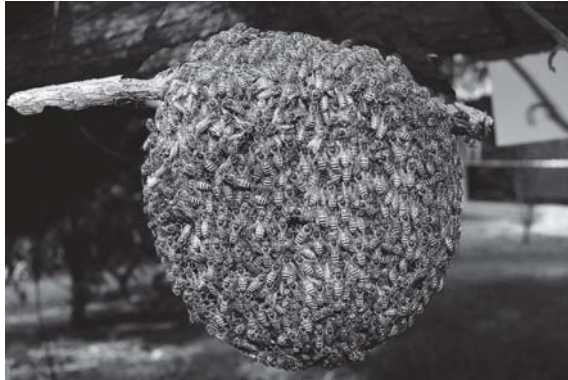
Although all dichotomies will eventually break down under careful scrutiny, it is useful to recognize two sub-divisions among the eusocial species, the primitively eusocial and the advanced eusocial. The following is a brief and somewhat oversimplified description of our current understanding of the contrast between primitively and highly eusocial species. The primitively eusocial species live in relatively small colonies (<100 adults) with limited division of labor so that neither queens and workers nor the sub-castes among workers are morphologically differentiated. Relative to the highly eusocial species, these colonies are organized through top-down control by a physically aggressive queen. In contrast, the highly eusocial species live in large colonies (sometimes up to a million adults) and are largely self-organized through bottom-up regulation in a decentralized manner through worker-worker interactions. In primitively eusocial species the physically stronger queen suppresses worker reproduction and also drives the workers to labor for the colony through physical aggression and harassment of the workers. In highly social species queens produce and release chemicals (pheromones) that are a reliable signal of their superior fertility. The workers are selected to “obey” and suppress their own reproduction as it is in their best fitness interests to do so. It is also in their own best interests to efficiently organize their labor in the colony since their fitness now derives from efficient reproduction of their mother queen rather than from their own reproduction (Wilson, 1971; Hölldobler and Wilson, 2009; Keller and Nonacs, 1993), (Figures 1-3).

## A Tropical Primitively Eusocial Wasp Society

There occurs quite commonly in urban areas of southern India, a remarkable primitively eusocial wasp. Known scientifically as *Ropalidia marginata* (Figure 4), we refer to this commonly as the Indian paper wasp. The name paper wasp comes from the fact that these (and nearly all social wasps) construct their nests, not from wax as bees do, nor from leaves as many ants do or from soil as termites do, but from paper – paper which they manufacture by scraping cellulose fibers from plants, adding their own secretions and chewing it into a fine pulp. Apart from being quite common, there are many features of this wasp that make it an excellent model system for our research. Unlike many other social wasps, they build small open nests so that all adults and brood, and more importantly, all social interactions, are easily visible to the human observer. The number of adult wasps in a nest is often in the 20's and 30's and almost never exceeds a 100. The small number of wasps and their easy visibility make it possible to individually mark<sup>3</sup> all the wasps in a colony and

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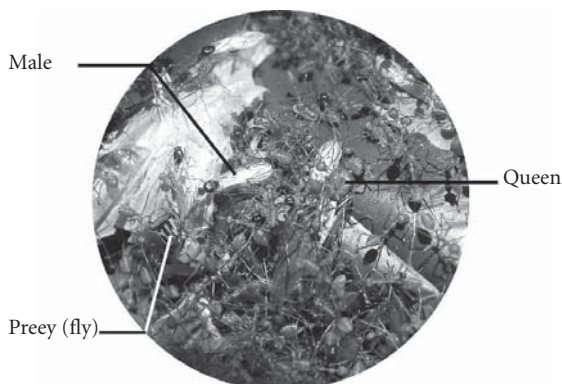
<sup>3</sup> With small spots of quick drying, non-toxic, coloured paint of different colours, on different parts of their body.



**Figure 1** The honeybee is the most widely known example of a highly eusocial insect society. Shown here is the nest of perhaps the least advanced of the honeybees, the Asian dwarf honeybee, *Apis florea*. (Photograph: Dr. Thresiamma Varghese). The underlying wax comb, brood and food stores are all covered by the large numbers of bees on the nest surface.

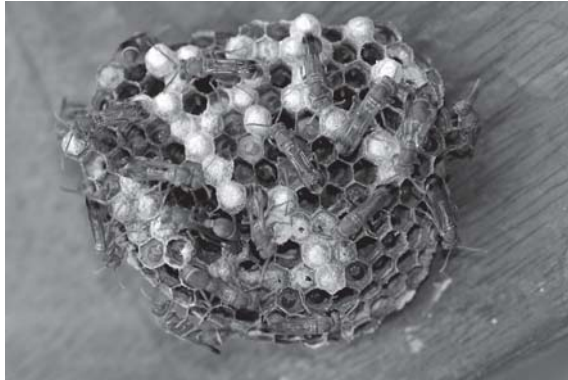


**Figure 2** A close up of a portion of the honeybee nest on figure 1, showing the morphologically differentiated queen surrounded by a group of workers. (Photograph: Dr. Thresiamma Varghese).



**Figure 3** Another example of a highly eusocial insect, the Asian weaver ant, *Oecophylla smaragdina*, showing the large queen, some males and an item of prey (a fly) brought into the nest as food. (Photograph: Dr. Thresiamma Varghese).

observe them throughout their lives. The nest is a small honeycomb like structure with typical hexagonal cells that are used by the wasps to rear their brood.



**Figure 4** A typical nest of the primitively eusocial wasp, *Ropalidia marginata*, showing the paper comb with hexagonal cells, many adult wasps and some capped brood (pupae). (Photograph: Dr. Thresiamma Varghese).

New nests may be founded either by a single female wasp or by small groups of them. In the single-foundress nests the lone female naturally does everything by herself – she builds the nest, lays eggs, forages for food and feeds her larvae when they hatch, guards them when they pupate and rears them to adulthood unaided, thus combining the duties of queen and worker. In multiple-foundress nests there is a clear division of labor. One individual lays eggs while the others work toward nest building, foraging and brood care. We designate the egg-layer as the queen and the remaining wasps as workers, even though (to us) they appear morphologically indistinguishable from each other. The first adult wasps to eclose<sup>4</sup>, both in single as well as in multiple-foundress nests are usually female wasps and normally stay back in their nest of birth and function as workers. Males are produced later and they stay on in their nest of birth only for about a week. The week-old males depart to lead a nomadic life, attempting to mate with female wasps from various other nests that may be out in search of food or cellulose fibers for building their nests. Thus our systematic observations are generally concerned only with female wasps on the nest.

Female wasps have at least four different life-style options available to them. They may leave their nest of birth and start single-foundress nests of their own, they may leave and join other multiple foundress nests, they may stay back in the nest of their birth and spend their entire lives functioning as sterile workers and finally, they sometimes work for a while and then, at an opportune moment, replace the original queen as the new queen of the colony. Workers appear to mate opportunistically during their foraging flights so that some but not all workers in a colony are mated. Mated females store sperm received from one or more males, in their spermatheca<sup>5</sup> and can use them when required. Female

<sup>4</sup> Emerge as adults from the pupa, after metamorphosis.

<sup>5</sup> A small pouch that is connected to the oviduct and has several accessory glands associated with it so that the sperm are nourished and kept viable for the duration of the life of the individual, which incidentally can be a few decades in some ants.

wasps can lay both unfertilized, haploid<sup>6</sup> eggs as well as fertilized diploid<sup>7</sup> eggs. The unfertilized eggs develop parthenogenetically into adult males while the fertilized eggs develop into adult females. Thus mothers have complete control over the sex of their offspring, producing sons and daughters as required. The first brood in single as well as in multiple-foundress colonies is generally female and the ensuing daughters generally stay back as workers and assist their mother in producing more brood. Workers perform all domestic tasks in an orderly fashion, working intranidally (at home) at brood care, at nest building and maintenance when relatively young and away from home, and at gathering food and cellulose fibers when relatively old. Workers live on an average for about four weeks although their life spans range from a few days to several months. Queen tenures are also highly variable, ranging from just about a week to nearly a year.

I have spent the past 30 years studying these wasps, often in collaboration with a large number of enthusiastic students. My research has been driven entirely by my insatiable curiosity about how these wasps organize their lives, coordinate their activities and manage to function as an orderly and efficient society. In other words, I wish to understand the rules that govern the lives of these wasps and the mechanisms they employ to create, follow and perhaps enforce these rules. As an evolutionary biologist I am simultaneously interested in the evolutionary forces that mould the social and altruistic behavior that these wasps display. This is an especially fascinating conundrum because most of the wasps that impress me with their social accomplishments are sterile and therefore not subject to simple natural selection through “survival of the fittest”. We have made many discoveries and learnt a great many odd and amazing facts about these wasps (Gadagkar, 2001). It is hard to pick a winner but perhaps the most fascinating aspect of the lives of these wasps is the fine balance that they tread between conflict and cooperation, and the manner in which they are able to use a subtle mix of conflict and cooperation to achieve success as a society. This is therefore the aspect that I will focus on for the rest of this chapter. One of our most interesting findings in this context is that these wasps display extreme aggression and intolerance toward conspecifics that do not belong to their colonies. However, the wasps are highly tolerant of each other and display almost no aggression to members of their own colony, even when there is a great potential for conflict. Here I will describe and contrast such “war” with foreigners and “peace” with insiders displayed by the wasps. I will also illustrate our research methodology that permits an understanding of these insect societies and conclude with some remarks about what we might learn from these primitive insect societies.

## Nestmate Discrimination

Seeing the wasps flying in and out of their colonies<sup>8</sup> without any apparent hesitation, even the casual observer will wonder how the wasps know which is their colony and which is not. This ability becomes even more intriguing when we see that two or more colonies are sometimes built very close to each other. Is it indeed that the wasps know exactly which

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<sup>6</sup> Containing only one set of [maternal] chromosomes.

<sup>7</sup> Containing two sets of chromosomes, one maternal and one paternal.

<sup>8</sup> I will use colony and nest somewhat interchangeably.

their nest is and never make mistakes or is that they sometime enter the wrong colony? The casual observer is unlikely to find out. But anyone who observes these wasps longer than the casual observer is likely to be rewarded by occasional breakdown of this apparent orderly behavior. Wasps do occasionally land on alien nests, either because they have made a mistake or because they wish to deliberately sneak into a foreign colony. Whatever be the reason for the unusual action, a drama ensues that would rivet anyone's attention. The intruder is intensely and aggressively repelled by one or more resident wasps from the colony on which she has landed. The intruder quickly beats a retreat and if she fails to do so she may be mauled, stung and even killed. How does this happen? How do the wasps recognize and repel the intruder? In other words, how do the wasps discriminate between their nestmates and non nestmates? We decided to investigate these questions using an experimental approach (Gadagkar, 1985).

In the first set of experiments we put three wasps in a plastic jar and recorded all behavioral interactions shown by each of them toward each of the other two. We called this the triplet assay. The three wasps were so chosen that two were nestmates of each other and one was a non nestmate of the other two. We observed 15 types of interactions among the wasps including antennation, approach, nibble, peck, chase, attack and so on (for a list of the 15 behaviors and their tolerance ranks<sup>9</sup>, see Table 1). Considering how tolerant or intolerant these behaviors seemed to be and how often each type of behavior was shown, we computed a numerical index of tolerance. The tolerance index was computed by multiplying the proportional representation of each individual behavior (such as nibble, peck etc.) multiplied by the tolerance rank of that behavior and then summing over all the behaviors shown. Since each of the three wasps can initiate interactions with each of the other two, we could compute six tolerance indices per experiment (Figure 5) and then compute separate average tolerance indices for all interactions among nestmates and all interactions among non nestmates. Thus we could make a quantitative assessment of whether individual wasps were able to discriminate their nestmates from non nestmates, based on statistical significance of differences in the tolerance indices among nestmates and those among non nestmates.

In the first experiment, we collected nests from nature, brought them to the laboratory and transferred the adults already present at the time of collection into individual plastic jars and kept them in isolation for several days (See Figure 6 for an illustration of the plastic jars and wood and wire mesh cages used in these experiments). We collected nests from some 10 km apart from each other so that we had both nestmate wasps and non nestmate wasps for the experiment. We then tested these wasps by putting two nestmates and one non nestmate into a fresh plastic jar, allowed them to interact, constructed tolerance indices and compared the tolerance shown toward nestmates and non nestmates. There was clear evidence of nestmate discrimination, i.e., nestmates were significantly more tolerant of each other than they were of their non nestmates. These wasps were able to successfully recognize their nestmates either because they were genetically related, or because they had shared the same nest environment or simply because they were directly familiar with nestmates they encountered in the experiment.

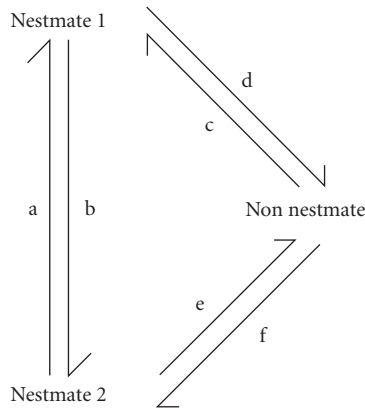
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<sup>9</sup> Our tolerance ranking was based on more than 200 hours of observation of wasps on colonies in nature and in the laboratory.



**Table 1** The 15 behaviors observed in the Triplet assay, ranked by increasing order of tolerance. Reproduced with permission (Venkataraman, *et al.*, 1988).

Tolerance Rank	Behavior
1	Aggressive bite: the most extreme form of aggression seen in this species; sometimes leads to injuries
2	Attack: a ritual act of aggression where the dominant animal climbs onto the subordinate and attempts to bite its mouthparts
3	Peck
4	Chase
5	* <sup>10</sup> Aggressive mutual antennation: a kind of sparring contest
6	Nibble: relatively mild with little chance of injury
7	Crash: the crashing of one wasp into a sitting wasp that results in one or both falling to the ground; very brief and appears much milder than behaviors 1 - 6
8	*Falling fight: two animals grappling with each other and falling to the ground; very brief and appears much milder than behaviors 1 - 6
9	Avoiding
10	Soliciting
11	*Mutual approach with withdrawal
12	Approach I: the other withdraws
13	Approach II: the other does not withdraw
14	Antennation
15	*Mutual antennation



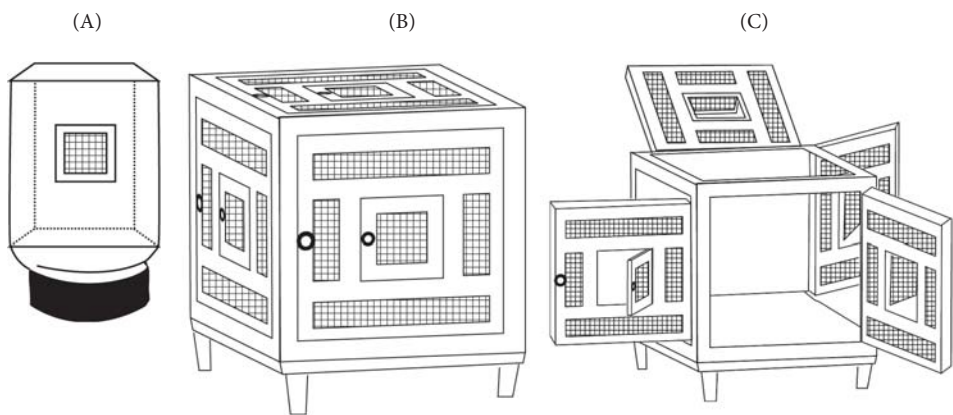
**Figure 5** The triplet assay. The behavioral interactions seen in all experiments are classified into six categories, designated a, b, c, d, e, f, such that all interactions initiated by nestmate 2 towards nestmate 1 are assigned to a, all interactions initiated by nestmate 1 towards nestmate 2 are assigned to b, and so on. Tolerance indices were computed for each category of interaction as described in the text. Reprinted with permission (Venkataraman *et al.*, 1988).

<sup>10</sup> Indicates bidirectional behavior.

To tease out the effects of these factors on nestmate discrimination, we tested wasps that were genetically related and had the experience of sharing the same nest but were not directly familiar with each other. These wasps also showed clear evidence of nestmate discrimination suggesting that direct familiarity was not necessary for discrimination. Thus to be tolerant to each other it is sufficient for both to have had some experience with their nest of birth, even at different times, without coming in direct contact with each other. But is experience with the same nest necessary for two wasps to recognize each other as nestmates? To test this we used wasps that had been removed from their nests just before they completed their development and had been allowed to complete their development in an incubator. These wasps that did not have the opportunity to smell their nests or nestmates or acquire any information about their nests or nestmates during their adult life, completely failed to discriminate nestmates from non nestmates. We thus showed that familiarity with their nest of birth was both necessary and sufficient for discrimination. We labeled the wasps that had experience with their nests and were capable of discriminating their nestmates from non nestmates as “experienced wasps” and those that did not have such experience necessary for making nestmate discrimination as “naïve wasps”. Thus experienced wasps were able to tell their nestmates apart from their non nestmates even outside the context of their nests and even if they had not encountered their nestmates before. What do experienced wasps possess that naïve wasps do not, which permit nestmate discrimination? We can imagine that effective nestmate discrimination requires that wasps carry some form of label in their bodies (most likely a smell) which indicates which nest they come from and a template in their head indicating what wasps of their nest should smell like. Experienced wasps obviously possess both labels and templates characteristic of their nests while naïve wasps must lack appropriate labels or templates or both. Whether they lack both labels and templates characteristic of their nests or only one of them is unclear from these experiments and somewhat irrelevant at this point in time, although it will become relevant in the next section. These experiments tell us how wasps are able to efficiently repel non nestmate intruders without interfering with the smooth arrival and departure of nestmates. And that is important because on all days with good weather there is a steady traffic of nestmates going in and out of the nest.

On the few occasions that we have been fortunate to see non nestmates land on nests, we have always witnessed efficient repulsion of their attempts to enter a foreign nest and we have never seen a returning nestmate being subjected to anything of the kind of inspection and harassment meted out to non nestmates. Nevertheless we only very rarely witness landing of non nestmates, in nature. We therefore decided to simulate such landings in the laboratory and in somewhat more natural conditions than the previous set of experiments in the plastic jars. We placed two colonies in two large laboratory cages (See Figure 6) and we introduced all the wasps from one of the cages (without their nest or brood) into the cage of the other nest. Now there were several attempts by the introduced wasps to land on the nest in the cage they were introduced into. The response of the resident wasps to the introduced non nestmate wasps was most interesting. The queen among the non nestmate was selectively attacked, dismembered, and killed within a few minutes of her introduction. In contrast the relatively young ones among the introduced non nestmates were not only permitted to land but were actually accepted and allowed to join the non nestmate colony. The rest of the introduced non nestmate wasps that were

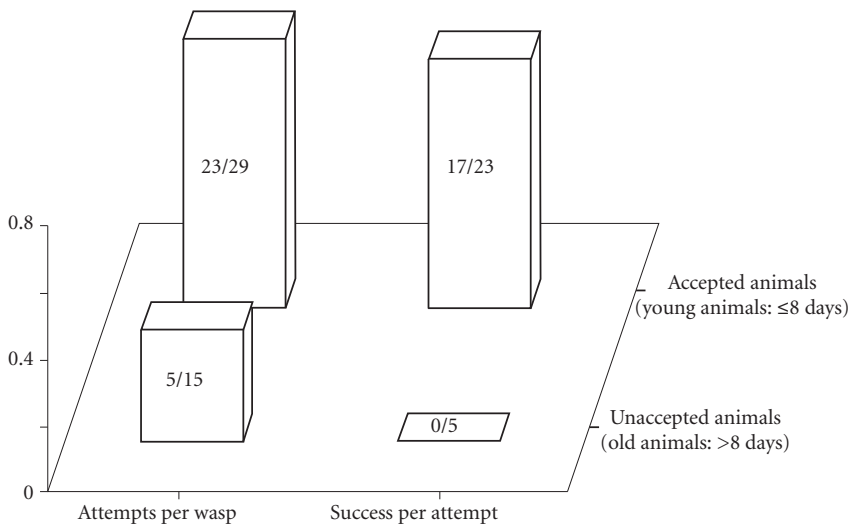
neither the queen nor were very young, were allowed to live in the periphery of the cage without being killed and also without being accepted onto the nest (Venkataraman and Gadagkar, 1993). The treatment meted out to the non nestmate queen was spectacular but not really surprising. A non nestmate queen would be dangerous indeed and it would not be worth taking chances with her; she might enter the nest at some moment when the resident wasps lower their vigil and start laying eggs. If she does that then the workers of the resident nest will have to care for the brood of an unrelated individual and this would yield them no evolutionary fitness. That the older workers among the non nestmates were not allowed to land on the nest was also not surprising as it was consistent with what we have observed in nature. That the young non nestmate wasps were accepted onto the alien nests was however rather surprising.



**Figure 6** A: Plastic box of dimension  $22 \times 11 \times 11$  cm, used to isolate individual wasps and conduct the triplet assay described in the text. B and C: Wood and wire mesh cages of dimension  $45 \times 45 \times 45$  cm used for rearing large colonies of *Ropalidia marginata*, and for conducting the experiments in semi-natural conditions described in the text. Reprinted with permission (Gadagkar, 2001).

To understand the factors affecting the acceptance of alien wasps we conducted additional experiments in which we introduced into cages containing nests, many non nestmates drawn from other nests; this time we deliberately chose non nestmates of different ages ranging from 0 to 29 days after their own emergence as adults on their nests (Venkataraman and Gadagkar, 1995). These experiments confirmed that young wasps equal to or less than eight days of age had a high probability of being accepted onto alien nests. This is likely to be related to the fact that younger wasps are expected to have poorly developed labels and templates compared to older wasps. But from an evolutionary point of view, what is the advantage for the resident wasps of accepting young non nestmates and of rejecting older non nestmates? In a new set of experiments we considered two possibilities. One is that young wasps have very poorly developed ovaries and older wasps, even though not the queens of their colonies, sometimes have partially developed ovaries. For the same reason that the non nestmate queens were killed, it may be best not to accept older non nestmates lest they also enter and start laying eggs at some future point in time. The other possibility is that it is age itself that matters and not differential ovarian development associated with age. In experiments designed to dissociate the tangled effects of age

and ovarian development, we showed that age is a more important predictor of acceptance than ovarian development (Arathi *et al.*, 1997a). We suspect that younger non nestmates are accepted more often because in addition to having poorly developed ovaries, they may also be more easily molded into working for their foster colonies. Conversely, older individuals may be accepted less often not only because they have partially developed ovaries but also because their behavior may be more difficult to mould in new directions. It must be pointed out that young wasps made more attempts to join the alien nest available to them in the experiment and also met with greater probability of success per attempt in being accepted, suggesting that both the joiners and the acceptors had an interest in their joining (Venkataraman and Gadagkar, 1995) (Figure 7). We do not know how often young non nestmates land on alien nest and provide opportunities for alien colonies to accept and mould them, but the possibility cannot be ruled out. In summary, social insects may occasionally wage war with other species that may be their prey or their predators but their real, day-to-day concern is the threat of colony invasion by other members of their own species. Hence they have developed an elaborate machinery of chemicals and behavior to maintain the integrity of their colonies.



**Figure 7** Young introduced wasps attempt to join alien nests and get accepted. The bars on the left represent the number of attempts per wasp, for wasps less than and equal to 8 days and for wasps greater than 8 days. The bars on the right represent the number of successful attempts/total attempts for wasps less than or equal to 8 days and wasps greater than 8 days. Wasps less than or equal to 8 days make significantly more attempts/individual than wasps greater than 8 days (Monte-carlo test,  $p < 0.02$ ) wasps less than or equal to 8 days also have a higher success rate per attempt than wasps greater than 8 days (Monte-Carlo test,  $p < 0.001$ ). Reprinted with permission (Venkataraman and Gadagkar, 1995).

## Intra-colony Kin Recognition

As we have seen the wasps are very efficient at detecting and keeping outsiders away, but is there also strife within the colony, among relatively different insiders? Most social insect

colonies are family affairs consisting of the queen and her daughters. And yet there is plenty of scope for intra-colony heterogeneity in genetic relatedness. First, workers who are usually the queen's daughters are of course not clones of each other and share only 75% of their genes and should therefore be prone to some conflict. Here the genetic relatedness between two full sisters is not 50% as in diploid organisms but 75% because males are haploid and contribute an identical set of genes to each daughter. The females being diploid, contribute 50% of their genes to their daughters. Thus full-sisters on an average share 75%<sup>11</sup> of their genes with each other. Second, the queen can mate with two or more males and simultaneously produce half-sisters who are related to each other by only 0.25%<sup>12</sup>, providing even greater scope for intra-colony conflict. We investigated this phenomenon in *R. marginata* and showed that queens mate with from one to three different males and the average intra-colony relatedness thus drops from the theoretically expected 75% (for single partner mating) to nearly 50% (Muralidharan *et al.*, 1986). This should of course offer more scope for conflict. The value 50% for average intra-colony relatedness actually belies the extent of conflict that is possible because it obscures the fact the colony may contain up to three separate groups of half-sisters related among themselves by 75% but between each other by only 25%. In *R. marginata* we found evidence of even more genetic heterogeneity. Recall that our earliest experiments suggested wasps have the option of working for some time in their nest of birth and then replacing the original queen. It turns out that wasps really do exercise this option from time to time. In a long-term study of four colonies we found that queens maintained their status for variable periods of time, ranging from 7 to 219 days and were replaced at the end of their tenures by their daughters, sisters, nieces or their cousins. Since workers also have a highly variable life span ranging from 1 to 160 days and since they do not abandon the nest or stop working after a queen replacement, intra-colony relatedness can be even more highly variable. In this long-term study, we found to our great surprise that colonies could consist of mothers, daughters, sisters, nieces, cousins, cousin's offspring, mother's cousins, mother's cousin's offspring and even mother's cousin's grand-offspring (Gadagkar *et al.*, 1993). Thus there is almost unlimited scope for strife and conflict among the members of a colony.

We therefore set out to investigate this potential intra-colony conflict. Intra-colony conflict is only possible of course if variations in intra-colony genetic relatedness can be perceived by the members of the colony. Just as the wasps can most efficiently discriminate between nestmates and non nestmates, they should be able to tell apart their sisters, from their nieces, their nieces from their cousins and so on, even though they inhabit the same nest. There was no *prima facie* reason to suspect that, with such well developed nestmate discrimination abilities, the wasps might be incapable of intra-colony kin recognition. And yet what we had learned about the mechanism of their nestmate recognition raised some doubts. If recognition depended on labels and templates and if naïve wasps, without appropriate labels and templates could not discriminate nestmates from non nestmates, it suggested that either labels or templates or both were acquired from the environment, in adulthood, and thus may be similar in all colony members. We coined the terms "self-produced" for labels that do not need wasps to be exposed to their nests and

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<sup>11</sup> This is the average of 100% from fathers and 50% from mothers.

<sup>12</sup> This is the average of 100% from fathers and 50% from mothers.

“non self-produced” for labels that required such exposure. Similarly we coined the terms “self-based” for templates that do not require exposure of the wasps to their nests and “non self-based” for templates that require such exposure (Figure 8). If that was so then nestmates might be easily discriminated from non nestmates but no further discrimination of different members within a colony might be possible. In other words, all wasps could be classified as nestmates and non nestmates but once wasps mingled with each other inside a colony they would lose their identity precluding further subdivision. But of course we did not yet know for sure that both labels and templates were missing in naïve individuals.

We now set out to perform another set of experiments by recording one-way interactions between naïve and experienced wasps. For example, if experienced individuals, who should possess the appropriate labels and templates, behaved tolerantly toward naïve nestmates, then we would conclude that the naïve individuals possess the required labels and hence experience was not necessary for acquiring labels, i.e., labels are self-produced. Similarly, if naïve individuals behave tolerantly toward experienced nestmates then we would conclude that naïve individuals possessed the required templates and thus experience was not needed for acquiring templates, i.e., templates are self-based (Figure 9). In reality we found however that neither experienced individuals behaved tolerantly toward naïve nestmates nor naïve individuals behaved tolerantly toward experienced nestmates. Both interacting partners had to be experienced for tolerance to occur; even if one of them were naïve no recognition occurred. Thus we concluded that experience with one's nest in adulthood was required for the acquisition of labels as well as of templates, i.e., labels are not self-produced and templates are not self-based. This means that all individuals in a colony would have the same labels and templates and therefore no discrimination between individuals of different relatedness would be possible (Venkataraman *et al.*, 1988).

Our motivation to conduct these experiments did not originally come from an interest in studying conflict and cooperation, such an interest was aroused after we found that conflict with outside was routine and that there were mechanisms to prevent conflict with insiders (more on this below). Our motivation for these experiments came from a desire to test a rather famous theory for the evolution of social behavior and altruism. On the face of it altruism seems difficult to evolve by natural selection because rather than maximizing their chances of survival and reproduction, altruists decrease their chances of survival and reproduction in favor of others; in extreme cases they sacrifice their lives to help others to survive and reproduce. Thus altruism was deemed as an evolutionary paradox. The theory was proposed by WD Hamilton who argued that self sacrificing altruism was no paradox if we consider the point of view of genes. If the bearer of an altruistic gene kills himself and aids the survival of more similarly altruistic individuals, then the act of sacrifice will actually result in the increase in the survival of altruistic genes, notwithstanding the loss of a few altruistic individuals. This has come to be known as inclusive fitness theory or kin selection theory. See Gadagkar (1995) for a review. It follows then that altruism should be observed to be preferentially directed toward close genetic relatives who have a high probability of sharing genes with the altruist. If an individual gives up reproduction, as sterile workers in insect societies do, then their sacrifice should aid in the spread of more copies of the altruistic gene than might have been the case if the altruist had herself reproduced. In diploid species (where everybody inherits two sets of genes, one from the father and another from their mother) this is a bit difficult because every individual is related to her offspring by  $\frac{1}{2}$  and by not more than  $\frac{1}{2}$  to her closest genetic relatives namely, her sisters.

	WASP A	RESULT OF BEHAVIORAL ASSAY	WASP B	CONCLUSION
I	Experienced 	Recognition ↔ Recognition	Experienced 	Behavioral assay is working
II	Naive 	No recognition ----- No recognition	Naive 	Either label not self-produced or Template non self-based or both
II	Experienced 	Recognition ----- No recognition	Naive 	Label self-produced but Template non self-based
IV	Experienced 	No recognition ----- Recognition	Naive 	Label not self-produced but Template self-based
V	Experienced 	No recognition ----- No recognition	Naive 	Label not self-produced and Template non self-based
VI	Naive 	Recognition ↔ Recognition	Naive 	Label self-produced and Template self-based

**Figure 8** An experimental approach to distinguish between the roles of labels and templates in kin recognition. A and B are two animals (say, wasps) who may or may not recognize each other as close genetic relatives depending on their rearing conditions. Based on this one can infer the ontogeny of the labels and the templates, i.e., whether labels are self-produced or not self-produced and whether templates are self-based or non self-based. See text for details. Reprinted with permission (Gadagkar, 1985).

The only way then to make more copies of their genes through altruism is to rear more siblings than offspring given up. This would require special conditions where altruists work harder or have greater success compared to selfish individuals. It is not easy to see why this should be so.

	A	B	
	Tolerance of “Isolated” nestmates and non-nestmates by “Exposed” wasps	Tolerance of “Exposed” nestmates and non-nestmates by “Isolated” wasps	
1	$T_b > T_d$	$T_b > T_d$	Labels self-produced and Templates self-based
2	$T_b > T_d$	$T_b = T_d$	Labels self-produced and Templates non self-based
3	$T_b = T_d$	$T_b > T_d$	Labels non self-produced and Templates self-based
4	$T_b = T_d$	$T_b = T_d$	Labels non self-produced and Templates non self-based

**Figure 9** Experimental design of mixed triplets aimed at distinguishing between self-produced and non self-produced labels and self-based and non-self-based templates. In part A the ability of an “Exposed” wasp to discriminate between a nestmate and a non-nestmate both of whom are “Isolated” is assessed. Conversely, in part B the ability of an “Isolated” wasp to discriminate between a nestmate and a non-nestmate both of whom are “Exposed” is assessed. The six possible types of interactions between the three animals in these triplets are similar to those in Figure 6, but only the relevant interactions, that is, b and d, are labeled. Discrimination is again assessed by comparison of tolerance indices calculated for b and d as in the previous set of experiments. See text for details. Reprinted with permission (Venkataraman *et al.*, 1988).

In ants, bees and wasps however only the females are diploid while the males are haploid. This makes a female wasp related to her full sister by  $\frac{3}{4}$  as compared to the usual relatedness of  $\frac{1}{2}$  with her daughter, as discussed above. Thus an altruistic sterile worker rearing sisters, needs to do less work as compared to a fertile individual who rears her own offspring, to get the same fitness. This so called haplodiploidy hypothesis can potentially explain why altruistically sterile workers are so common in ants, bees and wasps compared to other diploid organisms. However, we had shown that in *R. marginata* mating of the queen by more than one male and frequent queen replacements reduce the intra-colony relatedness so that workers were actually rearing brood related to them by less than  $\frac{1}{2}$ . This would be a problem for the theory unless of course we could show that workers do not dispense altruism indiscriminately toward everybody in the colony but discrimi-



nate effectively between low relatedness and high relatedness values within the colony and behave in a selectively nepotistic manner. Hence we were interested in studying the possibility that intra-colony kin discrimination was possible. As it happened, we showed that intra-colony kin recognition is not possible, knocking down the haplodiploidy hypothesis. It must be emphasized that we did not knock out Hamilton's original inclusive fitness theory but only its derivative, the haplodiploidy hypothesis (Gadagkar, 2001).

Nevertheless we decided to put the possibility of intra-colony kin discrimination and the resulting potential for conflict to a further direct test. We decided to directly look for conflict inside the colony. This is not easy to do because although there is plenty of intra-colony genetic heterogeneity, it is not easy for the experimenter to discriminate individuals based on their genetic relatedness; how then can he know whether the wasps discriminate each other based on genetic relatedness? Our observation that young foreigners are accepted into alien nests gave us the possibility of creating genetically mixed nests, allowing us to mark the wasps beforehand for our easy recognition. Thus we created 12 genetically mixed colonies by introducing young, non nestmates into observation colonies in the laboratory. We took several precautions in doing this experiment. First we ensured that the observation colonies, which served as foster colonies and the donor colonies that yielded the wasps for introduction, were originally collected from well separated localities so that wasps from the two sets of colonies were unrelated to each other. Second, we made observations on the foster colonies before introducing the non nestmate wasps so that we could compare the foster colonies before and after the introduction. Third, we matched introductions of unrelated wasps carefully with eclosion of new individuals in the foster colonies so that the unrelated wasps had age-matched partners among the resident wasps, which could be treated as controls while studying the behavior of introduced wasps. In all, eighty-five relatively young wasps were introduced and all were accepted into their foster colonies, without any aggression. Thus there was no evidence of intra-colony kin discrimination. We compared the behavioral profiles of pairs of introduced and resident wasps and failed to find any significant difference; nor was there any difference in the rates of behavioral interactions between kin and non-kin wasps. Social organization, division of labor and cooperation were unaffected in the genetically mixed colonies. Even more striking was the result that some of the manually introduced wasps went on to become queens of their foster colonies. We concluded from these experiments that the genetically unrelated intruder wasps were not only accepted into their foster colonies but became well integrated and behaviorally indistinguishable from the resident wasps, eventually becoming foragers and even having a fair chance of becoming replacement queens (Arathi *et al.*, 1997b).

The results of this experiment reinforced the idea that the advantage of altruistically working for a colony for some time and eventually taking over a reproductive role to fulfill selfish interests, may well be one of the factors that drive the evolution of altruistic worker behavior in this species. Be that as it may, the striking aggression toward non nestmates as long as they belonged to foreign colonies and the striking lack of aggression when former non nestmates joined one's own colony was a remarkable and quite an unexpected result – unexpected based on all the impressions we had thus far gathered about the wasps and unexpected based on the theory of kin selection that had been proposed to explain the evolution by natural selection, of social behavior and altruism in such insect societies.

## Queen succession

That the wasps were so ready to engage in war with outsiders and so unwilling to wage war with insiders was intriguing enough to motivate us to re-examine the issue in more detail. Perhaps we had been previously focusing on a situation where, despite the presence of genetic heterogeneity in the colony, there really was not that much scope for conflict. From an evolutionary point of view the main reason for conflict of course is unequal reproduction. Was it therefore possible that conflict erupts only at the time when the old queen is to be replaced by a new one? We now explored this most conflict-prone situation in natural colonies which as we saw above already have a great deal of genetic heterogeneity. To do so we designed a different kind of experiment. We studied normal colonies before any manipulation, identified the queen, experimentally removed her, studied the queen-less colonies and later studied the colonies again after returning the queen. The result of removing the queen was most spectacular. Within minutes of removing the queen the reasonably peaceful colony became a highly aggressive one. There was a several-fold increase in aggression compared to the time when the queen was present. Naturally we thought that we had solved the puzzle of intra-colony peace seen at times other than queen replacement. But the elevated aggression seen after queen removal turned out to be a red herring. All of the elevated aggression was shown only by one individual and it was all unidirectional. The aggressor was never challenged; she did not receive any aggression from any of the others. This was hardly an expression of conflict; it seemed more like take over by a pre-decided successor. That the aggressor was indeed the successor was easy to verify because if we did not return the original queen the aggressor went on to become the next queen within about a week. We therefore labeled the aggressor “potential queen” until she actually began to lay eggs when of course she would be properly entitled to the label queen. The result of returning the queen was equally interesting. The hitherto highly aggressive potential queen dropped her aggression and went back to being a normal worker as soon as we replaced the queen. The queen was unchallenged by the potential queen or by any other colony member. The potential queen, who clearly accepted the superior status of the queen was in turn unchallenged by any other wasp in the colony, irrespective of the presence of the queen (Premnath *et al.*, 1995; Premnath *et al.*, 1996; Sumana and Gadagkar, 2003). We seemed to be back to the idea of intra-colony peace and an orderly transfer of power without an overt expression of conflict.

This fascinating result deserved to be probed further. Every time we removed a queen we could identify a potential queen due to her hyper-aggressive behavior but we were unable to identify the potential queen before removing the queen. Naturally the identity of the queen's successor and the mechanism by which she is chosen is of great interest. We undertook a number of specific studies with the express goal of identifying the potential queen before removing the queen, but without success. We studied various properties of all the workers before removing the queen and attempted to identify some unique character of the individual who became the potential queen. But she was not unique in any way we could tell. The potential queen was not the largest or smallest, not the oldest or youngest, not the most aggressive or least aggressive, not even the one with the best developed ovaries. To this day we have been unable to predict the potential queen with any degree of accuracy and yet we can identify her without fail as soon we remove the queen (Deshpande *et al.*, 2006). The image of a society, which wages war with outsiders and

maintains peace with insiders at all costs, was only reinforced by these new experiments. Why the potential queen who was not challenged by anyone else, was herself so aggressive to others however was a bit of a mystery. We first thought that she might beat up everybody in the colony in order to pre-empt anyone else from attempting to become a potential queen. This was probably an unlikely hypothesis because if this were so I would expect the potential queen to have received some challenge. We have now solved this mystery. We have found evidence that the potential queen needs to show all that aggression in order to facilitate the rapid development of her own ovaries so that she could start laying eggs quickly. We have shown that a potential queen without the opportunity to show aggression takes longer to develop her eggs as compared to one that has such opportunities (Lamba *et al.*, 2007). We think of this in analogy with exercise physiology and suspect that expression of aggression results in physiological changes in the aggressor so as to permit her to develop her ovaries rapidly (Gadagkar, 2009a).

I have since got over the initial frustration at not being able to predict the potential queen and now I find that inability quite charming; being intellectually defeated by the wasp is somehow pleasing. I will describe one more set of experiments that have given a new, even more charming twist to this tale. Some years ago we wondered whether the wasps knew who the successor would be even though we did not. Although we cannot predict the identity of the potential queen (hereafter, PQ), the facts that (i) only one individual steps up her aggression after queen removal, (ii) the swiftness with which she does so, and (iii) she is unanimously accepted by the rest of the workers, led us to suspect that there might be a pre-designated successor to the queen who may be “cryptic” to us in the presence of the queen but known to the wasps. At first, whether the wasps knew the identity of the successor seemed like a question that cannot be answered, for how would we know the mind of a wasp? We have now performed a most intricate experiment that does in fact permit us to answer this question. Some years ago and for a different reason, we had designed a so-called mesh experiment. Instead of removing the queen altogether we had found a way of separating some of the workers from the queen. We moved a colony into a cage, cut the nest in half and separated the two halves with a wire mesh screen and released the queen on one side – the queen-right side. We then randomly introduced half the workers on the queen-right side and the remaining half on the queen-less side. The wasps in the two sides could not interact with each other although any chemicals could flow through. We had reason to believe that the queen used a pheromone to signal her presence to the workers so that no potential queen emerged in her presence and we wanted to determine whether the queen pheromone was volatile or not. We found that the queen pheromone was non-volatile because while the queen-right side remained peaceful, the queen-less side became hyper-aggressive with a potential queen who also went on to become a queen on her side, if the wire mesh partition was not removed (Sumana *et al.*, 2008). Later we found this experimental set-up and its result very handy.

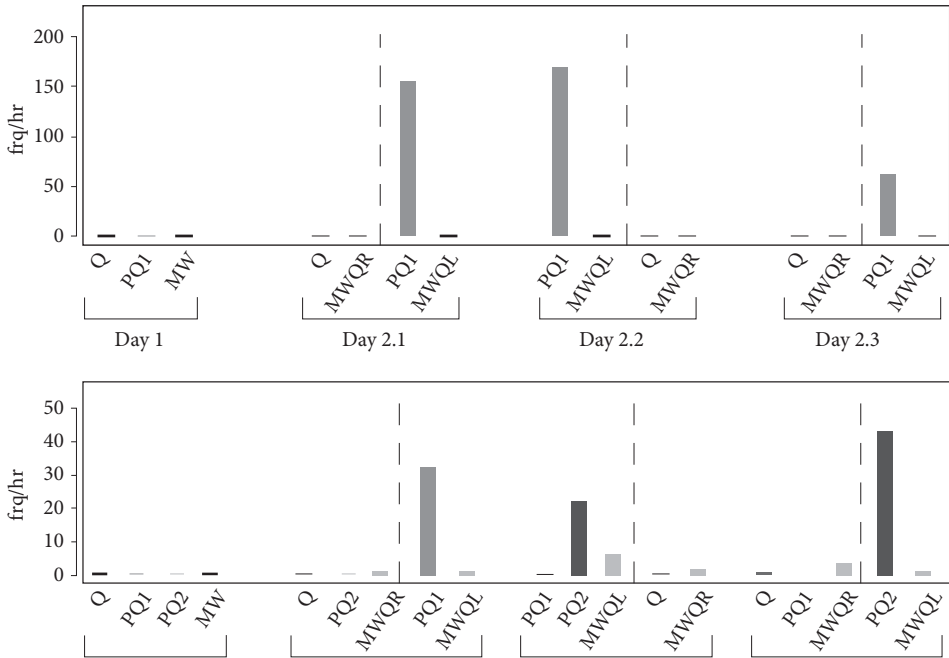
A modification of the mesh experiment permitted us to design an experiment to test the “cryptic successor, known to the wasps” hypothesis. The modification was that after a PQ became evident on the queen-less side of the wire mesh, we exchanged the PQ and the queen from side to side, leaving the workers undisturbed. The logic of this queen-PQ exchange experiment is as follows. Because the workers are randomly distributed between the 2 sides, the primary cryptic successor, if there is indeed one, has a 50% chance of being

on the queen-right and 50% chance of being on the queen-less side. In those experiments where the cryptic successor happened to be in the queen-less side, she would become a PQ (we call her PQ1) and, being the true successor, she should be acceptable to the workers on both sides even when she is moved from side to side.

And in those experiments where the primary cryptic successor happened to be on the queen-right side just by chance, a different individual should become the PQ1 on the queen-less side because of the absence of the legitimate successor on her side. But this PQ1 should be unacceptable to the workers on the opposite side when she is moved to there. Instead, the real cryptic successor should now become the new PQ (we call her PQ2). Finally, the PQ2 should remain unchallenged on both sides when she is moved from side to side. Thus, the PQ1 should be acceptable to the workers on both sides in about half the experiments and the PQ2 but not the PQ1 should be acceptable to workers on both sides in the remaining half of the experiments.

Clever as it is, this is a very difficult experiment to perform. With much difficulty, we have now managed to perform it 8 times. In 3 of these experiments the first PQ was accepted on both sides and in the remaining 5 experiments, only the second PQ was accepted on both sides (Figure 10). We therefore conclude that there is indeed a designated successor to the queen. But we refer to her as a cryptic successor because we cannot identify her in the presence of the queen. An important feature of our results was that neither PQ1 nor PQ2 ever received a single act of aggression from any individual, although they themselves showed high levels of aggression. Thus, when we say PQ1 was unacceptable when we moved her to the opposite side, we simply mean that she, on her own, stopped being aggressive and went back to work although she was never challenged by any wasp, not even by the PQ2. Hence we argue that the cryptic successor is “known” to the wasps even though we cannot identify her in the presence of the original queen (Bhadra and Gadagkar, 2008). I must confess that we have no idea how the decision about who should be the successor to the queen is made. But the point I wish to emphasize here is that the decision is made before the loss of the original queen so that there is no overt conflict when the queen dies. That all the wasps know who the successor would be in the event of the queen’s death, helps to ensure that power is transferred from one queen to the next without a breakout of internal conflict. Furthermore the decision appears to be made peacefully at whatever time it is made because we see no overt aggression before removing the queen. It is most remarkable that the wasps do not display intra-colony aggression and conflict, even in the context of queen succession. Indeed, we would like to create and study situations where there is conflict within a colony but have so far failed. War with outsiders and peace with insiders appears to be the invariant strategy of the wasps. I must mention that the strong nestmate discrimination abilities we have documented in *R. marginata* are not unusual; the same is true of most insect societies that have been studied (Hölldober and Wilson, 2009). But *R. marginata* is perhaps most extreme in the striking lack of intra-colony conflict and especially in the peaceful transfer of power from one queen to the next.

In retrospect, the propensity to make war with outsiders and maintain peace with insiders should not be so surprising after all. I believe that it is this dual strategy, this ability to tread a fine balance between conflict and cooperation, that accounts for the success of insect societies. Of course the war with outsiders is easier to explain than the peace



**Figure 10** The Q-PQ exchange experiment designed to check if the wasps know the identity of the successor to the queen. Upper panel: A typical experiment in which the PQ1 was the cryptic successor. The frequency per hour of dominance behavior exhibited by the Queen, PQ1 and Max worker (defined as the worker showing maximum aggression) on day 1 in the normal colony, and on the queen-right and queen-less fragments in the three sessions on day 2 are shown. Lower panel: A typical experiment in which the PQ2 was the cryptic successor. The frequency per hour of dominance behavior exhibited by the Queen, PQ1, PQ2 and Max worker on day 1 in the normal colony, and on the queen-right and queen-less fragments in the three sessions on day 2 are shown. See text for details. Reprinted with permission (Bhadra and Gadagkar, 2008).

with insiders. But war with outsiders is not of much use unless one can combine it with peace with insiders. Besides, the relative lack of intra-colony conflict is consistent with the recently resurrected fashion of treating insect colonies as super-organisms. It is also not really inconsistent with old fashioned individual and kin selection either, if one remembers that Hamilton's inclusive fitness theory, more precisely referred to as Hamilton's Rule, see (Gadagkar, 1997), postulated that the evolution of altruism is modulated by a balance between cost, benefit and relatedness, rather than merely by relatedness (Gadagkar, 2001).

## Concluding Remarks

I am often asked why I study insect societies. It is not difficult to justify on several levels. Social insects provide excellent model systems for understanding animal physiology, pharmacology, genetics, development and above all, evolution. Some social insects such as honeybees and their relatives are of great economic importance on account of their pollination services and are the backbone of multi-billion dollar fruit industries.

Other social insects such as fire ants and leafcutter ants are serious pests of agriculture and other human activities leading to losses of like amounts of money. In recent times the study of communication and division of labor in insect societies have found profound practical applications by providing novel algorithms useful in computer science, telecommunication and work organization in industry (Gadagkar, 2009b). And yet my own motivation for studying insect societies is rather different. My motivation is similar to that of an anthropologist. As social beings we are conscious of the enormous benefits we derive from cooperation and division of labor, but we are also justifiably obsessed with the problems that social life inevitably brings with it, the potential for selfishness and conflict. A reasonable way to reflect on these issues, and indeed to understand why we behave as we do, is to turn to other societies. Anthropologists can offer us a glimpse into the lives and mores of “primitive” and “exotic” human societies. Biologists can do much more; they can offer us insights from a whole range of animal societies with millions of years of evolutionary history. And those of us who study insect societies can hope to harness wisdom from an altogether different sub-kingdom of animal life. I certainly do not think we should imitate insect societies blindly, but I do think that they can hold a mirror to us and offer us a means to reflect on our own society and learn more about ourselves (Gadagkar, 2009a). Just as we often see the way we have arranged the furniture in our house in a new light after visiting a neighbor, or see our culture in a new perspective after visiting a foreign country, a knowledge of how other social beings conduct themselves in situations that we often find ourselves in, provides new opportunities for understanding ourselves. With the message of this chapter that the wasps readily wage war with strangers and bend over backwards to avoid conflict with those with whom they live, who can escape reflecting on how we humans manage our dual proclivities for cooperation and conflict?

As school children in India we most passionately sang a song entitled “Taraanaa-e-hindi” (song of the Indians) whose opening lines were “Saare Jahan Se Achcha” (better than all lands) and which had the thumping words “Hindi hain hum, vatan hain hindostaan hamaara” (we are Indians, India is our homeland). I knew that this song was written by Sir Muhammad Iqbal, the great Urdu poet philosopher of the sub-continent who is now officially recognized as Pakistan’s national poet and who continues to be much admired in India. What I did not know until recently was that the same poet later wrote another very similar song entitled “Taraanaa-e-millee” (song of the Muslim community), now sung in Pakistan, with the corresponding thumping words “Muslim hain hum vatan hain saara jahan hamaara” (we are Muslims, the whole world is our homeland). Our reference points may change and the “insiders” and “outsiders” may change but much the same song seems to be sufficient to elicit the passion of patriotism! More reflections such as these are best left to the readers for each will have his or her own unique perspective. That is the purpose of this chapter and indeed one of the purposes of such studies. Just so that we don’t get completely lost in all the fascinating details of the insect world, I have attempted to prime the reader toward such reflection with the opening quotation by the 18<sup>th</sup> century French enlightenment writer of the pen name Voltaire: “It is lamentable, that to be a good patriot one must become the enemy of the rest of mankind”. I specifically chose the quotation among many possibilities because I sometimes think that it is not so much how we behave, but how we lament about how we behave, that gives a deep insight into ourselves. We do not know if the wasps lament about how they behave, but we must

acknowledge that they know a thing or two about cooperation and conflict and I think it is worth our while to reflect on these issues in relation to ourselves.

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