The Family Emotional System

An Integrative Concept for Theory, Science, and Practice

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Chapter 11

The Family System of a Social Wasp

Raghavendra Gadagkar

In many species of insects individuals organize themselves into societies that parallel, and in many respects surpass, our own societies. They live in colonies, which are essentially families, ranging from nuclear families to extended joint families and sometimes, even clans. The best examples of these are to be found in the insect orders Hymenoptera (ants, bees, and wasps) and Isoptera (termites). In the termites, both males and females are involved in family life. In the ants, bees and wasps however, only females participate in family life and they have therefore been dubbed 'feminine monarchies' (Sarton, 1943). We, as humans, cannot help but be curious about how these families function and perhaps dysfunction. How do insects that diverged from us hundreds of millions of years ago, deal with what must be very similar opportunities and challenges afforded by family life? (Wilson, 1971).

My students and I spend most of our time pondering over these questions and seeking answers through observation and experimentation. We have chosen the social wasp *Ropalidia marginata*, which occurs abundantly all over peninsular India and indeed, in and around our homes and offices, (Gadagkar, 2001). We study these wasps wherever they occur in nature but we have also learnt to bring them to our laboratory and keep them in cages of different sizes and stack them up in the vespiary (the house of wasps). Here I will attempt to describe our current understanding of the family system of *R. marginata*, deliberately using, to the extent possible, the same language that we normally use to describe human families and societies. I will deliberately use the terms colony and family interchangeably (Figure 11.1).

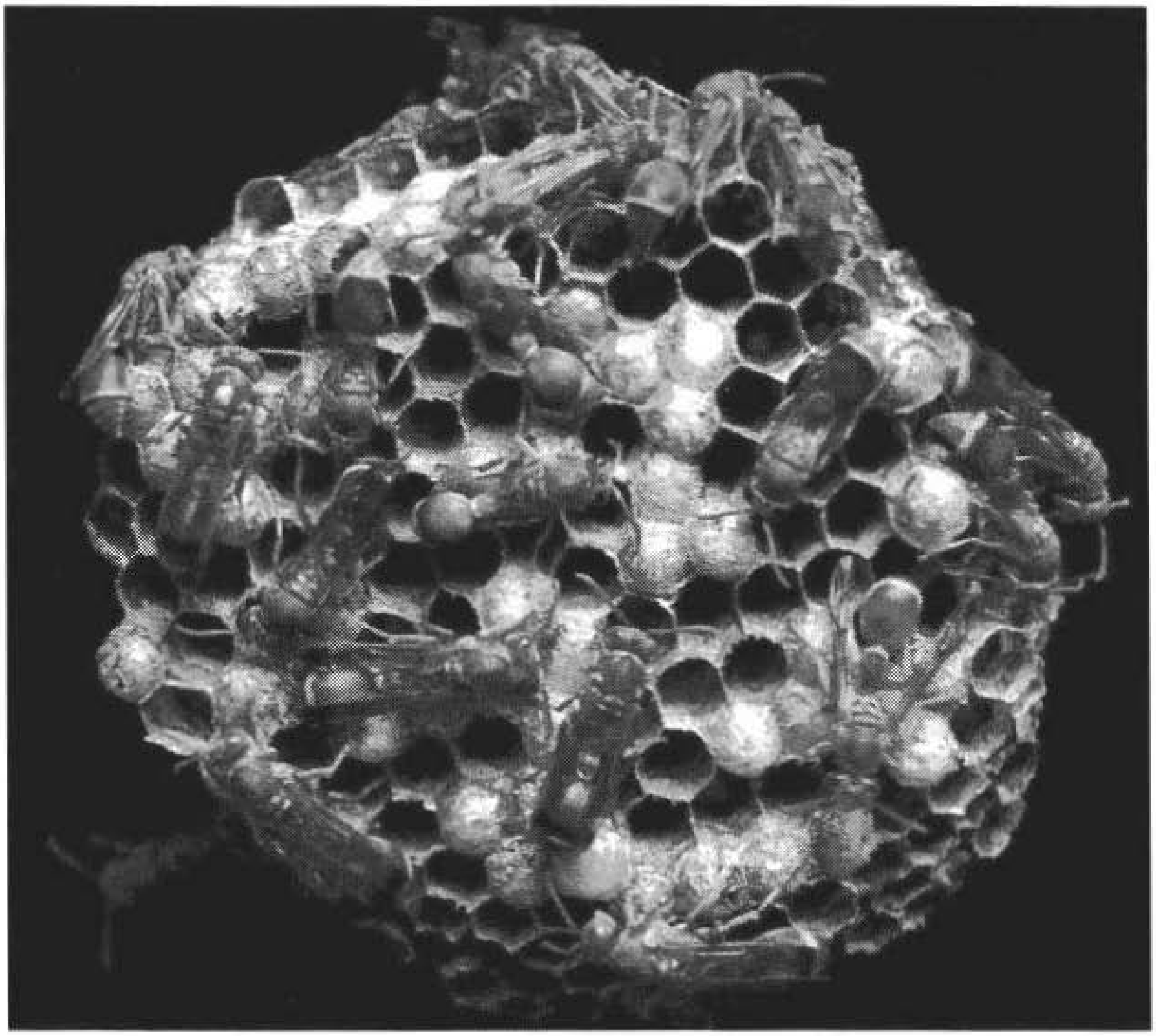

Figure 11.1 The Family System of the Social Wasp, *Ropalidia marginata*. A typical nest showing the nest, adult wasps, and brood. *Photo credits:* Dr. Thresiamma Varghese

THE FATHER

The father is always absent in any *R. marginata* family. He is only represented by his sperm, which now reside in and are nourished by his mate, inside of her body (in a gland called the "spermatheca"), to be used when needed. Adult males spend only about a week in the family of their birth and then leave to lead a nomadic life, never to return. They may mate with females (usually from other colonies) whom they may encounter while the latter are away from their own homes, in search of food. After thus donating sperm to one or more females in such chance encounters, they simply die. But as an evolutionary biologist would not fail to note, they have passed on their genes (through their sperm) for potential transmission to future generations, via the females they have mated with (Gadagkar, 2001).

There is also something peculiar about how they were born. Their mother produces them by laying unfertilized eggs, even though she may well have had a supply of sperm in her spermatheca. Those sperm she would reserve for producing daughters. Sons are always produced through the parthenogenetic development of unfertilized eggs. This, of course, means that the unfertilized eggs carry only one set of chromosomes, namely those of the mother. Thus the adult males also have only one set of chromosomes. This condition is referred to as "haploidy" as opposed to "diploidy," which is the normal condition (two sets of chromosomes) in all of us (males and females), as also in the females of *R. marginata*. An amusing consequence of this is that males in *R. marginata* (and of course also in all species of ants, bees and wasps) have neither fathers nor sons—they only have grandfathers and grandsons (Wilson, 1971).

THE MOTHER

The mother is obviously a pivotal figure in this feminine monarchy. Every family (which we usually call a 'colony'), is headed by a single adult reproducing female and we respectfully call her the 'queen'. I will call her mother and queen interchangeably. Unlike in the advanced insect societies such as those of honey bees, ants, and some wasps, the queen of *R. marginata* are morphologically indistinguishable from everybody else in the family. She is not consistently smaller, bigger, or shaped differently from anybody else. So we have to watch her in the act of laying eggs before we can identify her among all the other similar-looking females (Gadagkar, 2001). Of course if we dissect her abdomen we can see that she has very well-developed ovaries unlike any worker. Based on what was known in the literature from studies of other social wasps, we expected the mother queen to be an exceptionally active, interactive, and aggressive individual, preventing everyone else from reproducing and making them all work for the welfare of the family, by sheer physical harassment (Gamboa et al., 1990; Reeve & Gamboa, 1987). However, we were in for a big surprise. It turns out that an *R. marginata* queen is exceptionally meek and docile—inactive, noninteractive, and unaggressive (Premnath, Sinha, & Gadagkar, 1995). *R. marginata* families frequently lose their mother—she dies, is overthrown as the queen, or driven away. In our observations over the years we have seen queens with life spans as short as a week all the way to as long as almost a year. From long-term observations of many families, we have computed the life span of mothers to be about 80 ± 72 days (Gadagkar et al., 1993). Once they leave or are driven away from their family, as far as we know, they have no further life. But as long as they are healthy and in control, they are treated with respect—no one bites them or chases them around, as is the normal treatment for the rest of the family members.

THE CHILDREN

The adult children of the family consist of the mother's sons and daughters. Sons and daughters can easily be distinguished from each other by the relatively paler faces of the sons. As mentioned already, the sons stay only for a week or so after birth and leave after that. Many fewer sons are produced than daughters. This must certainly have to do with the fact that daughters work as helpers (usually called 'workers') in addition to, or instead of, becoming future queens while sons never work as helpers. Sons are also produced mainly in the summer (although some sons may be produced in some nests at any given time) while daughters are produced throughout the year. We have also observed that mothers in newly founded colonies first produce at least one batch of daughters before producing sons, and many mothers may die before they ever produce any sons. On the other hand, mothers who have failed to mate can at least produce sons, by laying unfertilized eggs. So in most families, most of the time, we see only daughters and no sons. We have observed daughters to stay in the nests of their birth for very variable periods of time—from just a few days all the way to several months (mean ± S.D. = 27 ± 23 days; Gadagkar, 2001).

While sons have only one option open to them, namely to leave and lead a nomadic life, daughters have at least six options open to them (Figure 11.2). One option is to leave their mother's family and start their own new family, all by themselves, that is, to mate, gather sperm and become single mothers. Daughters taking this option build a nest, lay eggs, forage for food, feed their larvae, guard their nest and bring their offspring to adulthood, all by themselves, without the aid of any helpers. This, of course, is the typical lifestyle of most solitary insects and must have been the lifestyle of the evolutionary ancestors of *R. marginata*. It is remarkable that in spite of millions of years of evolutionary history as a social species, the solitary lifestyle has not been forgotten. A second option for the daughters is to leave as a small group and co-found a new family where only one of them reproduces (becomes the queen) while the rest act as helpers, at least in the beginning. A third option is to join a newly founded family as a nonreproducing helper. A fourth option is to invade a small family, drive away the existing queen, take charge as the new queen and start reproducing, with support of the helpers of the previous queen, who generally seem willing to help the new invading queen just as they did for the old queen. A fifth option, and by far the most commonly chosen option, is to stay back in their mother's nest, and spend their entire lives as nonreproductive helpers. As evident from the fourth option described above, such helpers will usually continue to work as helpers even when their mother dies and someone else takes the position of the queen of their colony. The sixth option is to stay back, work as

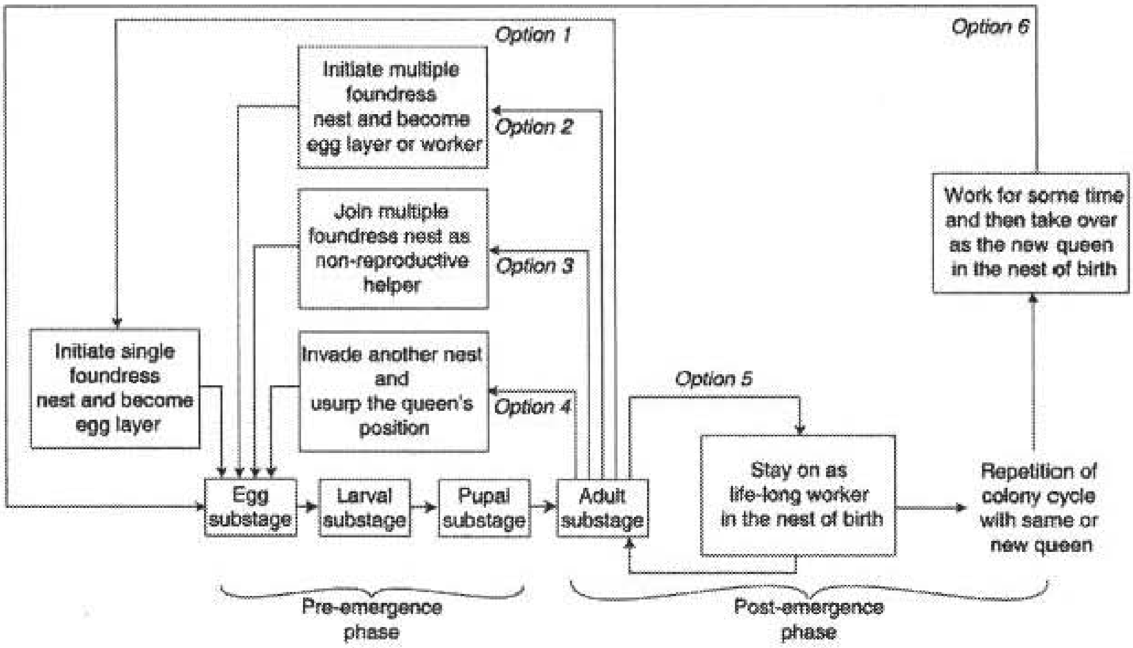

Figure 11.2 Diagrammatic Representation of the Life Cycle of the Colony showing the different options open to adult female wasps. Males are not shown. For schematic convenience, the egg, larval, and pupal stages are shown as being distinct. In reality, there is considerable overlap between them, especially when several colony cycles are repeated on the same nest. Similarly, change of queens can take place at any time of the colony cycle. Note also that new colonies may be initiated at any time of the year and may also be abandoned at any time of the year and at any stage in the colony cycle. *Source*: Redrawn from p. 256, Fig. 15.1 from ch. 15: "The evolution of eusociality, including a review of the social status of *Ropalidia marginata*" by Raghavendra Gadagkar from *Natural History and Evolution of PaperWasps* edited by Turillazzi, Stefano & West-Eberhard, Mary Jane (1996). By permission of Oxford University Press

helpers for some time and at an opportune moment, drive away their mother (or wait till their mother dies on her own) and take over as the new queen of the colony of their birth. It is perhaps not so surprising that the option of staying on as lifelong nonreproducing helpers is the most commonly adopted one, as it is the safest one. Starting a family on one's own is prone to failure, usurping the position of another queen in another family is risky, and to be able to drive away your mother or have her die on her own in your lifetime is a very rare chance (mother queens live much longer than helpers) (Gadagkar, 2001).

RELATIVES

Most *R. marginata* families consist not merely of a mother and her daughters and some occasional sons but also of many kinds of close and distant relatives, all living together and acting as helpers, assisting a single fertile queen to reproduce. By long-term observations of several colonies where every egg, larva, pupa, and adult wasp was tagged and censused three times a week, we have constructed pedigrees of queens in colonies of *R. marginata,* the most complex of which (Figure 11.3) shows that a queen may be replaced by her daughters, sisters, nieces, or cousins and that helpers may share their nests with their mother, brothers, sisters, nieces, nephews, cousins, mother's cousins, mother's cousin's children and even mother's cousin's grandchildren (Gadagkar et al., 1993). I am very fond of saying that an *R. marginata* family will put any Indian joint family to shame. There are reasons why the members of the family can be a mixture of close and distant relatives. When new colonies are founded, wasps from two or more different colonies may come together and jointly start a new colony (Shakarad & Gadagkar, 1995). Queens may mate with more than one

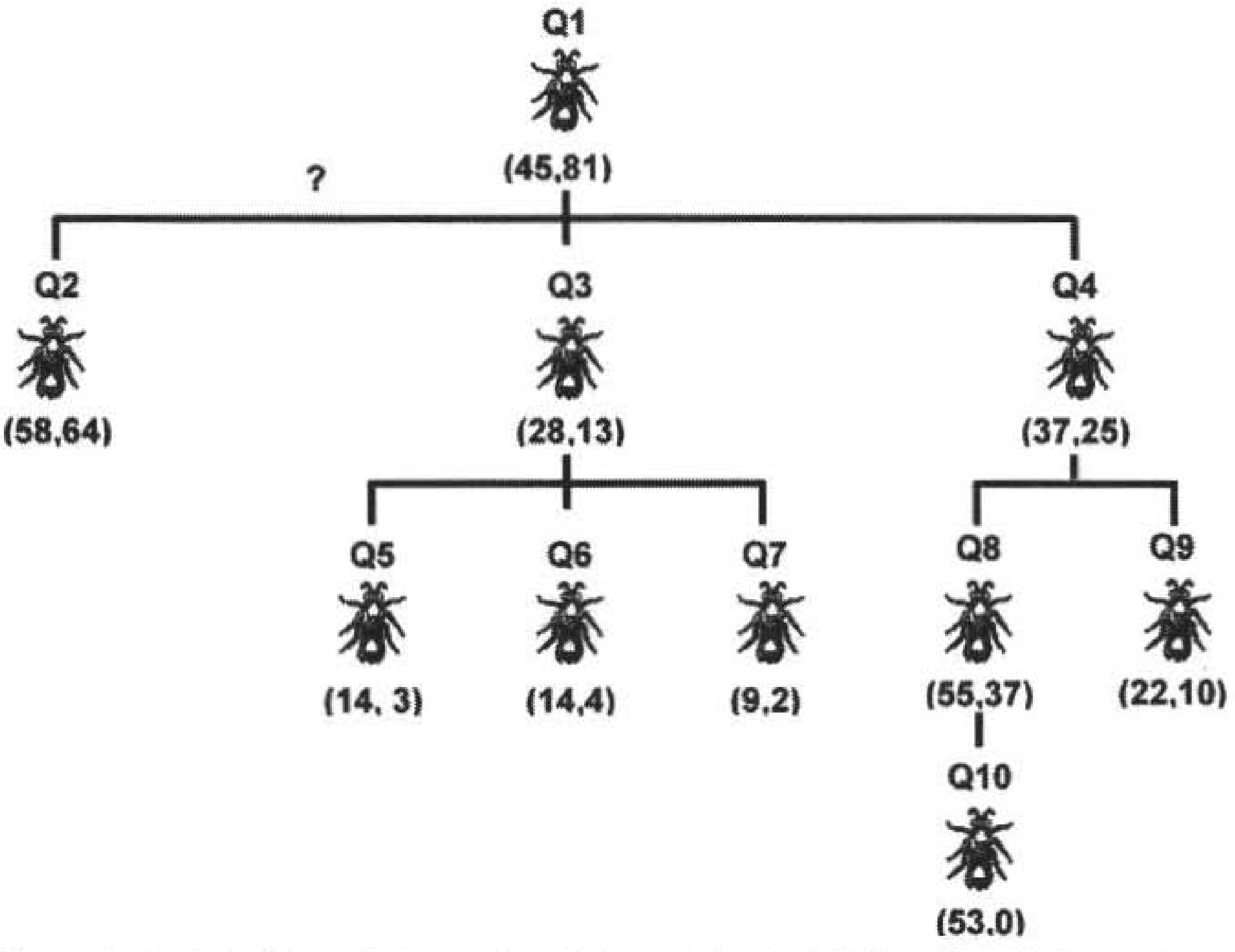

Figure 11.3 A Pedigree of Queens in a Colony of the Social Wasp, *Ropalidia marginata.* This means that Q2, Q3 and Q4 were daughters of Q1, and Q5, Q6 and Q7 were daughters Q3 and so on. The question mark indicates that the relationship of Q2 alone to Q1 was somewhat doubtful. Of the two numbers in parentheses 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. *Source*: Reprinted by permission of the publisher from *Survival Strategies: Cooperation and Conflict in Animal Societies*. "A pedigree of queens in a colony of the social wasp *Ropalidia marginata*", by Raghavendra Gadagkar, p. 117, Cambridge, Mass.: Harvard University Press, Copyright © 1997 by the President and Fellows of Harvard College

male, resulting in the queen's daughters sometimes being half-sisters (step-sisters) (Muralidharan, Shaila, & Gadagkar, 1986). And as discussed above, offspring of successive queens may coexist in a colony.

The obvious question that arises is whether the members of nuclear family treat the members of the extended family—the relatives—differently. We have spent a great deal of time investigating this question. And again we were in for a big surprise. First, we asked whether the wasps could tell their nestmates (family members and relatives living together) apart from any non-nestmates, when they possibly encounter each other outside the context of their nest. To answer this question we put three female wasps in a little plastic box and observed their interactions. Two of the three wasps were chosen such that they were nestmates and the third was a non-nestmate of the other two. We found that nestmate-nestmate interactions were more tolerant than nestmate-nonnestmate interactions. This was true not only when the nestmates were previously familiar with each other by virtue of having shared the same nest, but even when they had never previously encountered each other, by virtue of being born on two experimentally separated fragments of the same nest. They were unable to recognize their nestmates from their non-nestmates only when they were removed from their nests before birth and hatched in an incubator. We concluded from this that wasps carry, on their body and in their brains, a label and template respectively, of their nest identity. They then compare the label on the bodies of an encountered wasp (on or away from the nest) with the template stored in their brain and decide whether the encountered individual is a nestmate or non-nestmate. However wasps are not born with their colony-specific labels and templates; both labels and templates are acquired after birth, from their nest and/or nestmates. This explains why nestmates born on different fragments of the same nest can recognise each other while wasps born in an incubator cannot. Thus all wasps living together in the same family, including the mother and her offspring as well as any other relatives acquire the same labels and templates. Hence they have no way of telling apart close from distant relatives and no way therefore of treating anybody differently—they all live as one (happy?—see above) family (Venkataraman et al., 1988).

THE NURSERY

A typical family consists of many more immature stages than adults. The immature stages are comprised of eggs, larvae of five distinct stages of development (Figure 11.4), and pupae. The eggs and pupae need no care other than to be guarded against being eaten by predatory ants or other species of wasps. But the larvae need to be fed several times everyday for 3–4 weeks after

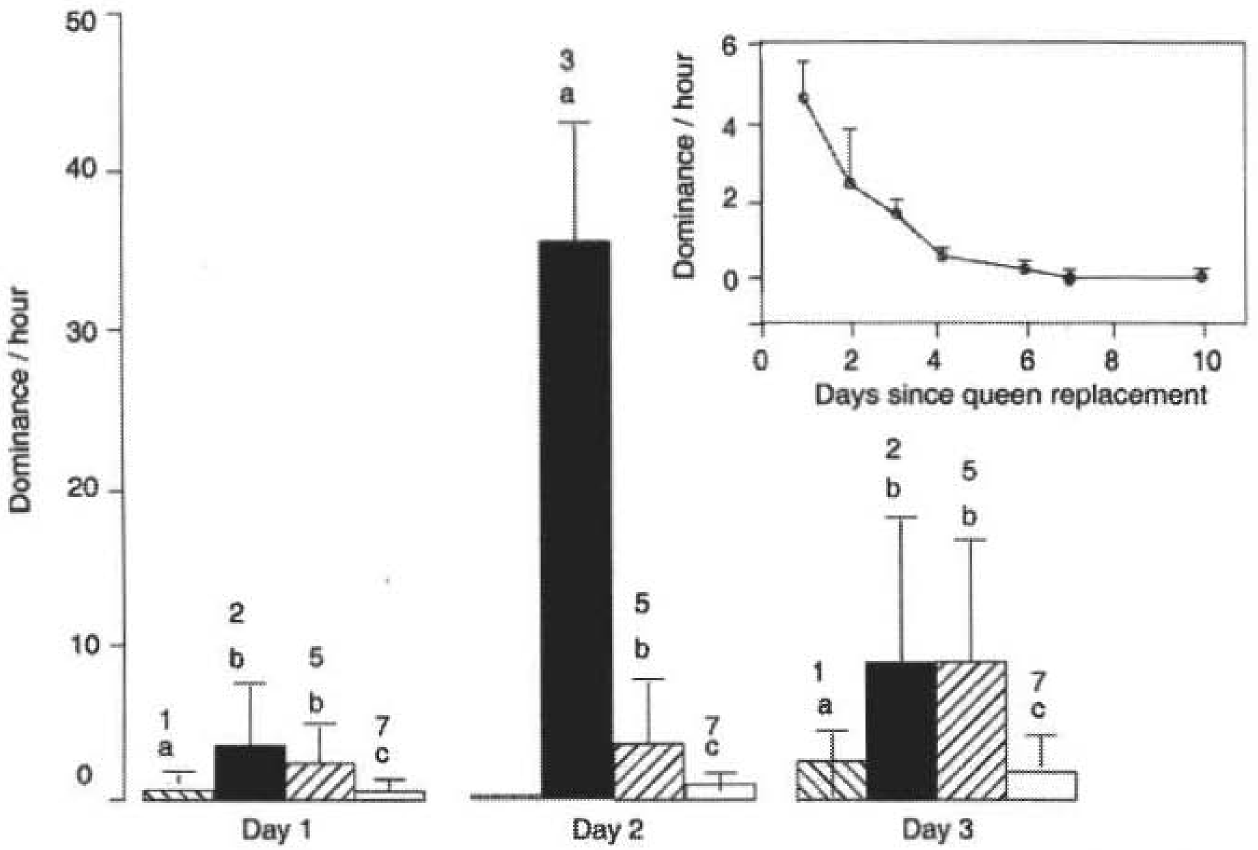

Figure 11.4 A typical Queen Removal Experiment showing the frequencies per hour of dominance behaviour shown by the queen (left hatched bars), potential queen (black bars), max worker (the individual who showed maximum behavioral dominance in the colony apart from the queen and the PQ) (right shaded), and mean worker (open bars) on days 1, 2 and 3. Inset: Dominance acts per nest-mate per hour shown by replacement queens from the day of takeover up to 10 days after queen replacement. Means and 1 S.D. are shown for nine nests for days 1–7 and six nests on day 10. *Source*: Redrawn with permission from Sudha Premnath, Anindya Sinha, Raghavendra Gadagkar, "Regulation of worker activity in a primitively eusocial wasp, *Ropalidia marginata*", *Behavioral Ecology*, 1995, 6, 2, by permission of Oxford University Press

which they pupate. This is a major task for the whole family, although the mother does very little of it. In a large active colony, there may be hundreds of hungry larvae being fed constantly by dozens of adults and this is fascinating to watch. Generally adults working outdoors bring food and hand it over to those working indoors who then feed the larvae. It makes you wonder how each of the hundreds of larvae of different ages and sizes and hunger levels are fed as per their need (and none forgotten), not to mention how those working outside know what, when, and how much to bring. It must be mentioned that when there is a real shortage of food, the adults will cannibalize the larvae before they themselves die of hunger. There is one fascinating quirk that I cannot help mentioning. One might imagine that the family must face serious problems associated with toilet training for the young ones. The adults conveniently defecate while hanging on to their nests and dangling their abdomens away from the surface of the nest, but what about the larvae that are essentially sedentary? No problem, because the larvae do not defecate. Their faecal matter accumulates at the end of the digestive tract and is finally removed once and for all, by the adults who chew a hole at the bottom of the larval chamber and extract it out of the bottom end of the fully grown larvae! (Gadagkar, 1991).

THE HOUSE

The wasp family constructs a house for itself. This is called a nest and it is an exquisitely elaborate structure made from paper—hence social wasps are often called paper wasps. And of course they manufacture their own paper by scraping cellulose fibres from plants, adding some secretions and chewing it up into pulp before spreading it into a thin layer. The nest is a two dimensional array of nearly perfect hexagonal cells with a depth of about 5–10 mm. One egg is laid in each cell and that individual stays in that cell through larval and pupal development. The nest surface is periodically cleaned and coated with some secretions making it both water proof and unsuitable for the growth of unwanted bacteria and fungi. The whole structure is attached to a rock, wall or leaf, by means of one or more pedicels. These pedicels are regularly coated with an ant-repellent dark substance also secreted by the adults. This secretion exudes from an opening in their abdomen making it easy for them to rub their abdomens around the pedicels. In the absence of this active defence, ants would quickly find the nest and consume the eggs, larvae, and pupae. And yet, this does not protect the brood from flying enemies. Tiny parasitic wasps (belonging to the Hymenopteran family Ichneumonidae) literally inject their eggs using long and thin ovipositors into the larvae of *R. marginata* wasps. Certain kinds of parasitic flies (belonging to the Dipteran family Tachinidae) "air-drop" their own tiny larvae onto the nest. In both cases the parasite larvae consume the host larvae and complete their development and fly away to attack other *R. marginata* nests. And finally and most devastatingly, adults of a large predatory wasp called *Vespa* alight on *R. marginata* nests and consume the larvae and pupae. Adult *R. marginata* wasps are entirely defenceless and watch helplessly while the predator feasts on the brood they have been ceaselessly caring for. *Vespa* never takes adult *R. marginata* and this may be the reason why the adults avoid the risk of injury of attempting to defend their brood and prefer instead to stay alive and produce more brood. The nest is a well-adapted dwelling place for the family, with the eggs, larvae and pupae being inside the cells and the adults sitting on the surface of the nests. The nest of a large colony, covered on the surface by adult wasps is surely a frightening sight for many other predators including humans (Gadagkar, 2001).

REPRODUCTION

As mentioned before, only one member of the family reproduces and we call her the queen. She is usually (but not always) the oldest member of the family and usually (but not always) the mother of the rest of the family. The rest of the family does not reproduce and labours instead to rear the queen's offspring. This is an act of altruism and a great evolutionary paradox. Why does evolution by natural selection not eliminate such altruism and promote only selfish behaviour. The phenomenon becomes even more paradoxical when we realize that most or all the members of the family are potentially capable of reproducing—they are merely suppressed in the presence of the queen. I shall return to the evolutionary paradox of altruism later. Here I wish to dwell on the mechanism of suppression of reproduction by the rest of the family. Since *R. marginata* queens are meek and docile, physical aggression cannot be the mechanism of suppression. We have found instead that the queen seems to suppress reproduction by the rest of the family by means of chemicals that she secretes from her body and rubs on the nest surface. Such chemicals are called pheromones but the exact mechanism of how they suppress ovarian development of the wasps is not understood (Sumana et al., 2008; Bhadra et al., 2010).

Whatever the mode of suppression, we know that it is reversible. If the queen dies or is experimentally removed by us, one of the hitherto non-reproducing individual becomes the next queen. When we had first discovered that the queen is a meek and docile individual, we had wondered why the rest of the family accepts her as their queen. In other species where the queen is active, interactive and aggressive, it is not so difficult to see that everybody else accepts her. Not so in this species. To solve this paradox, we conducted experiments in which we removed the queen and continued to observe the rest of the family. Incidentally, we mark all wasps uniquely with spots of coloured paints and can therefore follow changes in their behaviour over time. A great surprise awaited us when we first experimentally removed a queen from a colony. The *R. marginata* family is normally fairly peaceful with just an occasional act of aggression by some of the members toward others. These infrequent acts of aggression involve one wasp biting, pecking at, or chasing another, and are called dominance-subordinate interactions, the biter, pecker, or chaser being referred to as the dominant wasp and the bitten, pecked, or chased wasp being referred to as the subordinate wasp (Gadagkar, 2001). Upon removal of the queen, the normally peaceful colony immediately became extremely aggressive, increasing the normal low levels of dominance-subordinate behaviours manyfold. Even more surprisingly, all of the new aggression was shown by a single member of the family. We discovered later that this individual could be the daughter, sister, niece or cousin of the original removed queen. We also found out soon that if we replaced the original queen within 24 hours, the newly aggressive individual lost her aggression and went back to her normal behaviour. If we did not replace the original queen, the newly aggressive individual went on to become the next queen, but of course only after she lost her aggression, so that she could be a truly meek and docile queen. We labelled this hyperaggressive member of the family as 'potential queen' (PQ) (Figure 11.4). Thus we solved the problem of why the rest of the members of the family accept a meek and docile individual as their queen—the queen starts her career as a hyperaggressive individual and only after she is accepted does she become meek and docile (Premnath, Sinha, & Gadagkar, 1995; Sumana et al., 2008; Kardile & Gadagkar, 2002). Although this experiment helped solve one outstanding problem, it opened up several new problems, but then that is the joy of science.

Perhaps the most important new question was which of the family members is chosen or allowed to become the potential queen and eventually the new queen. As humans this question is one of obvious interest to us but as evolutionary biologists, it was truly fundamental. Reproduction after all is the currency of evolutionary fitness—those who reproduce stay in the race and those who don't are eliminated by natural selection. So there must be a great deal of competition about which member of the family replaces the old queen and becomes the new queen of the colony. We have set ourselves the goal of predicting the queen's successor before removing the original queen. To achieve this goal we have tried every possible experimental strategy and worked very hard for many years but we have utterly failed. To this day we cannot predict the queen's successor before removing her. The potential queen seems not to be special in any way. She is not the biggest or smallest, oldest or youngest, laziest or most hardworking, the most dominant or least dominant, not even the one with the best or least developed ovaries (Deshpande et al., 2006). Although we did not achieve our goal, we discovered two other remarkable features about the working of the *R. marginata* family.

The first of these remarkable features is that there is not just one potential queen, but a whole series of them. Since the potential queen can be detected by her hyperaggressive behaviour, we asked what would happen if we also removed the hyperaggressive potential queen before she had the chance to drop her aggression and start laying eggs. Thus we removed the potential queen within an hour of removing the original queen. To our great surprise we found that upon removing the potential queen, another member of the family immediately became hyperaggressive and would go on to lose her aggression and lay eggs if neither the queen nor the previous potential queen was returned. This meant that there were two potential queens in waiting even before the loss of the queen. And it did not stop there. We could remove potential queen number two and get potential queen number three, remove number three and get potential queen number four, remove number four and get number five (Figures 11.5 and 11.6). Thus there appears to be a long queue of potential queens each waiting for their turn to succeed their predecessor queens (Bang & Gadagkar, 2012).

The second remarkable feature is that the entire family seems to know who their next queen is going to be. Remarkable as it is, it is made even more remarkable by the fact that we ourselves cannot predict the queen's successor, in spite of all our experimentation. We had a strong suspicion that the wasps may know their successor because in the long queue of PQs, each PQ seemed to know her place in the queue and did not break the queue. Put in another way, none of the potential queens were challenged when they became hyper-aggressive; two or more individuals did not appear to compete when there is a vacancy for the queen's position. We then conducted a more direct test of the hypothesis that the wasps know who their successor is, that is, that there is a previously decided heir designate.

The experiment involved cutting the nest in half, separating the two halves with a wire mesh screen so that the wasps cannot go through. We then randomly reintroduced all the wasps, including the queen, half of them on each side. This of course meant that there was a queen-right side (with queen) and a queen-less side (without queen). We already knew that in such a situation, the wasps on the queen-less side cannot detect the queen on the queen-right side and will therefore behave as if they have lost their queen, that is, a potential queen will become hyperaggressive (Sumana et al., 2008). Now we argued that if the heir designate happens by chance to be in the queen-less side, she will be the unchallenged PQ on her side and of course there will be no PQ on the queen-right side. Once we saw a PQ on the queen-less side, we swapped the positions of the queen and PQ. Now the PQ has been brought to the other side but since she is the heir designate for the whole colony she should not be challenged by the wasps on the new side either. However, only in half the experiments would the heir designate end up in the queen-less side by chance alone. In the other half of the experiments, the heir designate would be in the queen-right side where she will have no opportunity to take over. On the queen-less side however, there is no queen and we expect the 'best' individual in this side to become the PQ. We now swap the positions of this non-heir designate PQ and the queen. Here the outcome of the swapping should be different. The non-heir designate PQ may have been the 'best' in the queen-less side but not on the queen-right side. Here she comes face-to-face with the true heir designate of the whole colony and should be challenged, resulting in the true heir designate now becoming the PQ. Thus we predicted that the new heir designate PQ should be unchallenged on both sides. Thus in about half the experiments, the first individual to become PQ should be accepted on both sides, but in the remaining half of the experiments

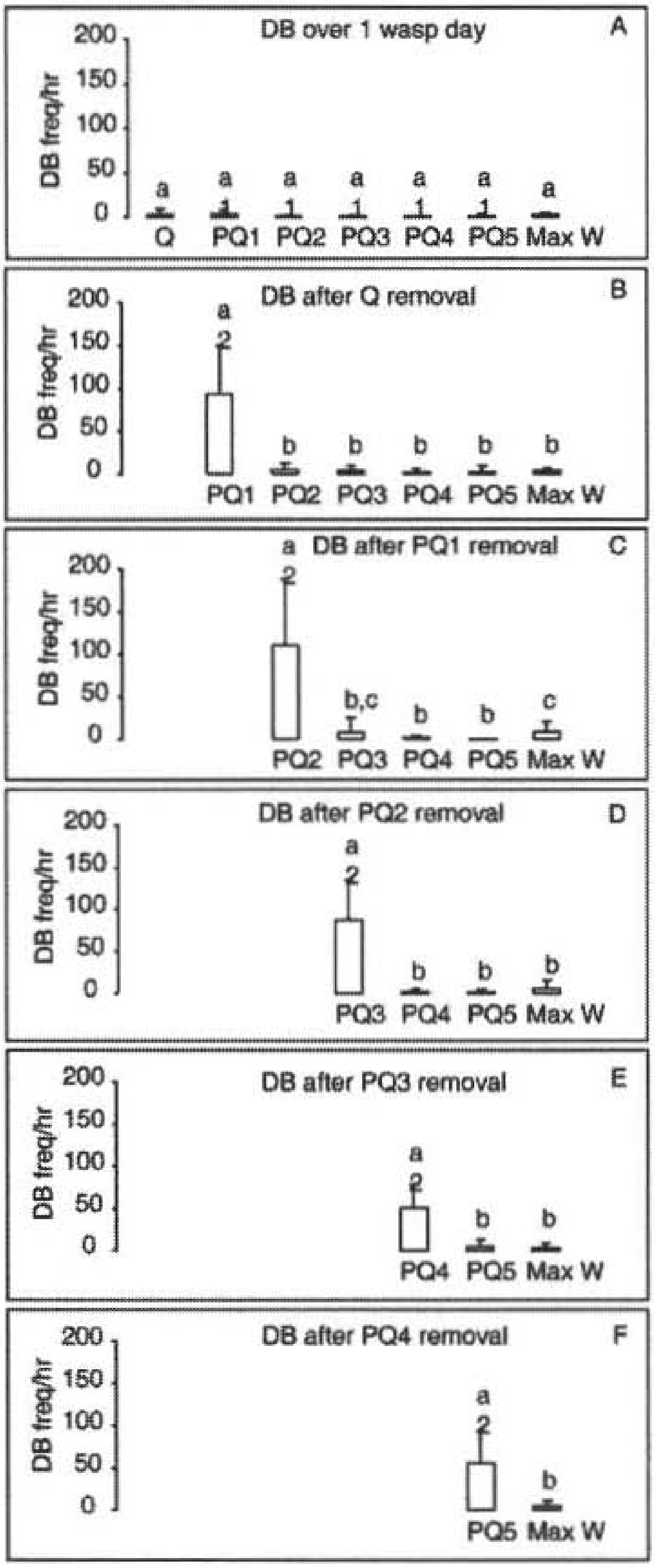

Figure 11.5 Evidence for a Reproductive Queue in *R. marginata*. Means and standard deviations of frequencies per hour of behavioral dominance of (A) the queen, five PQs and the max worker (the individual who showed maximum behavioral dominance in the colony apart from the queen and the five PQs) in normal queen-right colonies, and (B–F) the PQs and the max workers in the absence of the queen and the preceding PQs (n = 19 colonies). Note that each PQ showed higher aggression after the queen and the previous PQs were removed than what she showed in the queen-right colony and also compared to any other individual in the queen-less colony. DB = behavioral dominance; Q = queen; PQ1…PQ5 = potential queens 1–5; Max W = max worker. *Source*: Redrawn with permission from Bang and Gadagkar 2012

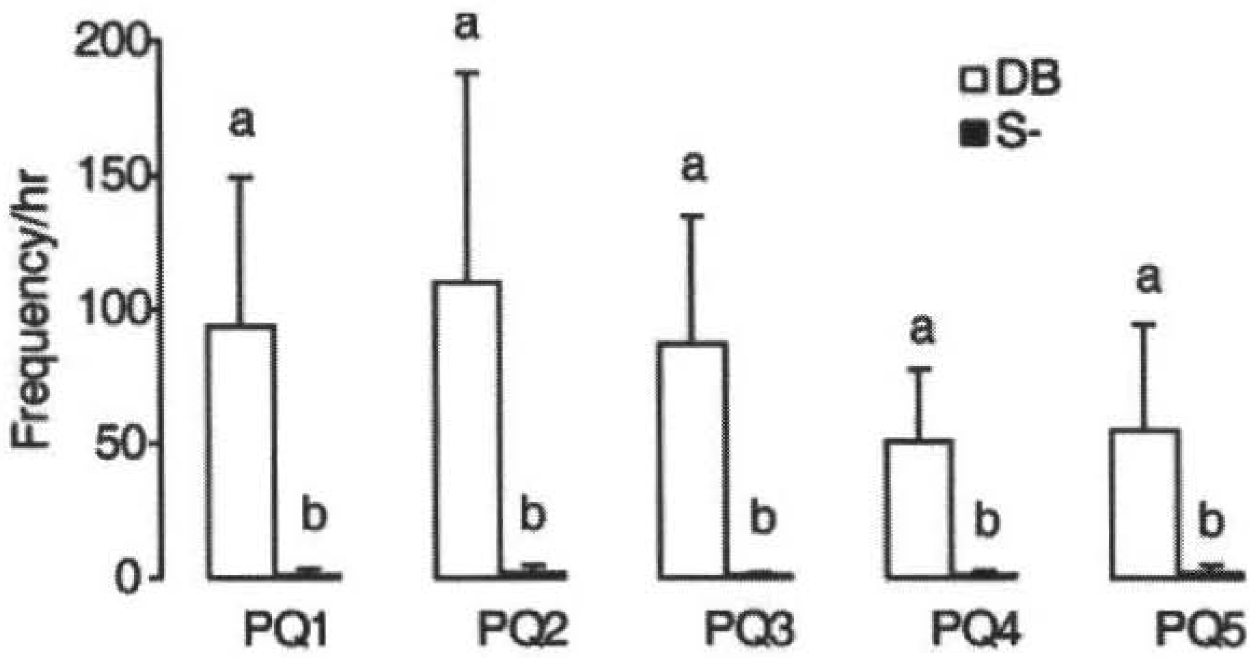

Figure 11.6 Behavioural Dominance Shown and Received (mean ± s.d.) by different PQs in the absence of the queen and previous PQs. Note that each PQ showed significantly higher behavioural dominance than what she received. On an average, dominance shown by each PQ was ~40–180 fold higher than the dominance she received. DB = behavioural dominance shown; S- = behavioural dominance received; PQ1...PQ5 = potential queens 1–5. *Source*: Redrawn with permission from Bang and Gadagkar 2012

the first individual to become PQ should be unacceptable on the opposite side and a new PQ acceptable to both sides should emerge. This is exactly what we found (Figure 11.7), but with one unexpected twist. When the PQ was unacceptable on the opposite side, she was not challenged. Instead she on her own dropped her aggression, as if she knew that it was not her turn yet. And she did not challenge the second individual (the true heir designate) when the latter became hyperaggressive. Hence we concluded that all the wasps knew who their next successor would be, and let it not be forgotten, even though we ourselves could not identify her. In other words, there was a heir designate but she was cryptic to us (Bhadra & Gadagkar, 2008).

THE ORGANIZATION OF WORK

Another new question arose in our minds when we found that the new queen is aggressive only for about a week and then becomes meek and docile. How does a meek and docile queen ensure that the rest of the family worked hard to care for her brood? In other species where the queen is aggressive throughout her career, she is known to use physical aggression (dominance-subordinate interactions) to ensure that everybody does their respective jobs. For instance, if a worker (all non-reproducing female members of the colony

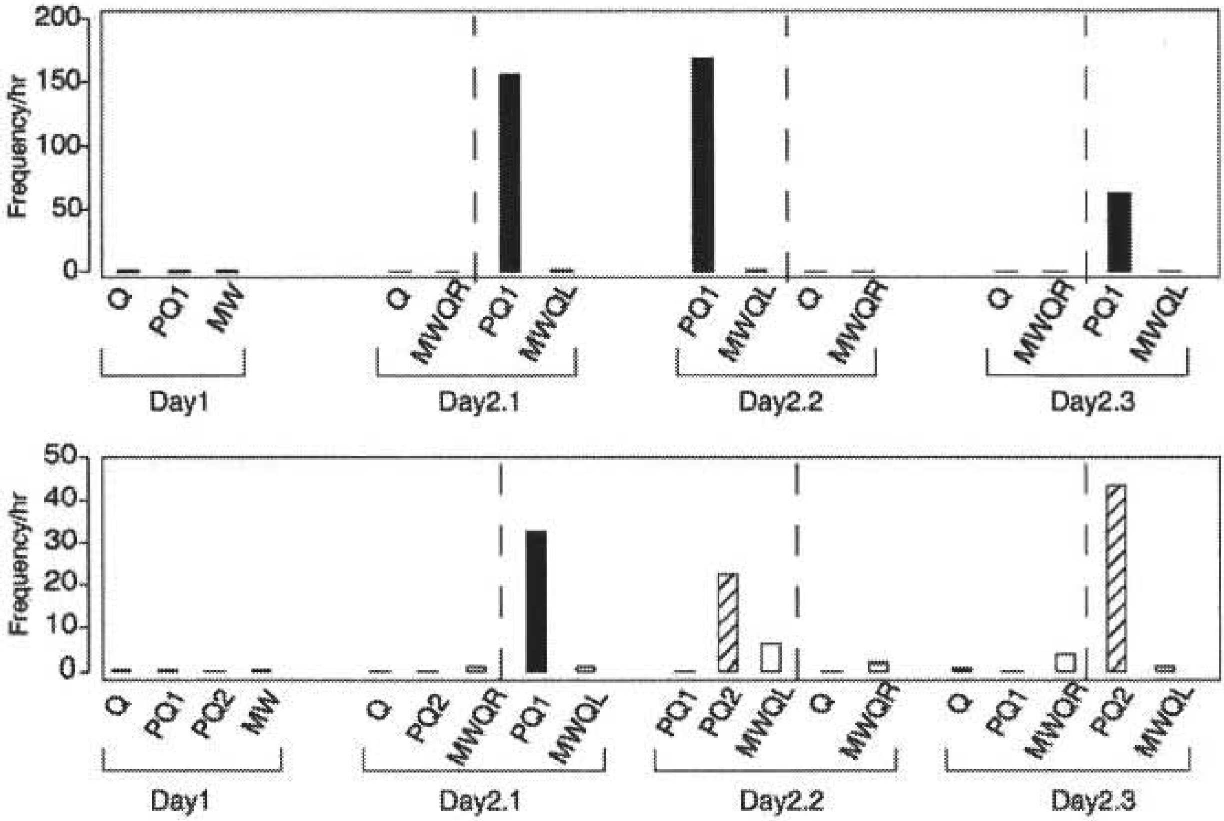

Figure 11.7 The Q-PQ Exchange Experiment. Upper panel: A typical experiment in which the PQ1 was the cryptic successor. The frequency per hour of dominance behavior exhibited by the Queen, PQ1 and Max worker (defined as the worker showing maximum aggression) on day 1 in the normal colony, and on the 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 behaviour 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. *Source*: Redrawn with permission from (Bhadra & Gadagkar 2008)

are referred to as workers) began to rest after she brought some food and distributed it, the queen in other species would go and bite, peck or chase the lazy member of her family (show dominance behaviour) as a result of which the latter would leave to work again. But how does the queen ensure that her workers work hard in *R. marginata*? In an attempt to answer this question, we conducted another experiment. We compared the working habits of all family members before and after removal of the queen, that is, in a queen-right and a queen-less colony. We chose two important kinds of work for our study, namely, bringing food and feeding the larvae. We found to our surprise that the presence or absence of the queen made no difference to the workers—they worked anyway. There was no difference between the queen-right and queen-less conditions in the rates at which food was brought to the colony and the rates at which the larvae were fed. In other words, the queen does not regulate the work of the rest of the family and can therefore afford to be meek and docile, especially since she uses pheromones (and not aggression) to maintain her reproductive monopoly in the family (Premnath, Sinha, & Gadagkar ,1996).

But somebody should regulate the work of the family. Even if the wasps are intrinsically hardworking, somebody should tell when to bring more food and when to stop. In particular, those members of the family working outside should be told about the hunger levels of the family. We have investigated this question and found that the workers self-organize their work in a decentralized, bottom-up manner without the need for centralized, top-down control. How do they manage to do this? We hypothesized that workers use the low levels of dominance-subordinate behaviour seen in normal queen-right colonies to regulate each other's work. More specifically, we hypothesized that dominance behaviour shown to workers signalled the need for work. Thus family members working inside and who have information about the hunger levels of the colony can communicate this information to those working outside by means of dominance behaviour. We obtained three lines of evidence in support of this hypothesis. First, we found a positive correlation between the amounts of dominance behaviour a member of the family receives and her relative contribution to the family's foraging effort (Premnath, Sinha, & Gadagkar, 1995). Second, we found that giving excess food to the whole family reduced not only the levels of dominance-subordinate behaviour in the family as a whole, but also the levels of dominance behaviour received by habitual foragers (Bruyndonckx, Kardile, & Gadagkar, 2006). Conversely, by starving a colony we were able to increase the rates of dominance-subordinate behaviour in the colony. This increase was not simply an expression of general stress or unrest. Habitual foragers were the specific targets of such increased dominance behaviour (Lamba, Chandrasekhar, & Gadagkar, 2008).

There are two other aspects of division of labour within the family that I should mention. One has to do with the fact that the wasps gradually change their behavioural profiles as they age. This phenomenon is called age polyethism. Typically wasps first work inside, beginning with feeding the larvae and graduate to building the nest as they get a bit older, and then they work outside the nest, beginning with bringing fibre and finally becoming food foragers (Figures 11.8 and 11.9) (Naug & Gadagkar, 1998). The other has to be the fact that males do not do any work in the family. This is true for all ants, bees and wasps and is a curiosity that is not fully understood. In our species, males, of course, leave their family of birth and lead a nomadic life. But even their laziness during the week they live with the family is striking because females of that age begin to work. We have specifically focused some of our studies on male laziness. Using feeding of the larvae as an example of work, we reasoned that the males might not work for one or more of the following three reasons. One, they do not know how to feed the larvae. Two, they do not forage by themselves and depend on the females to supply even the food

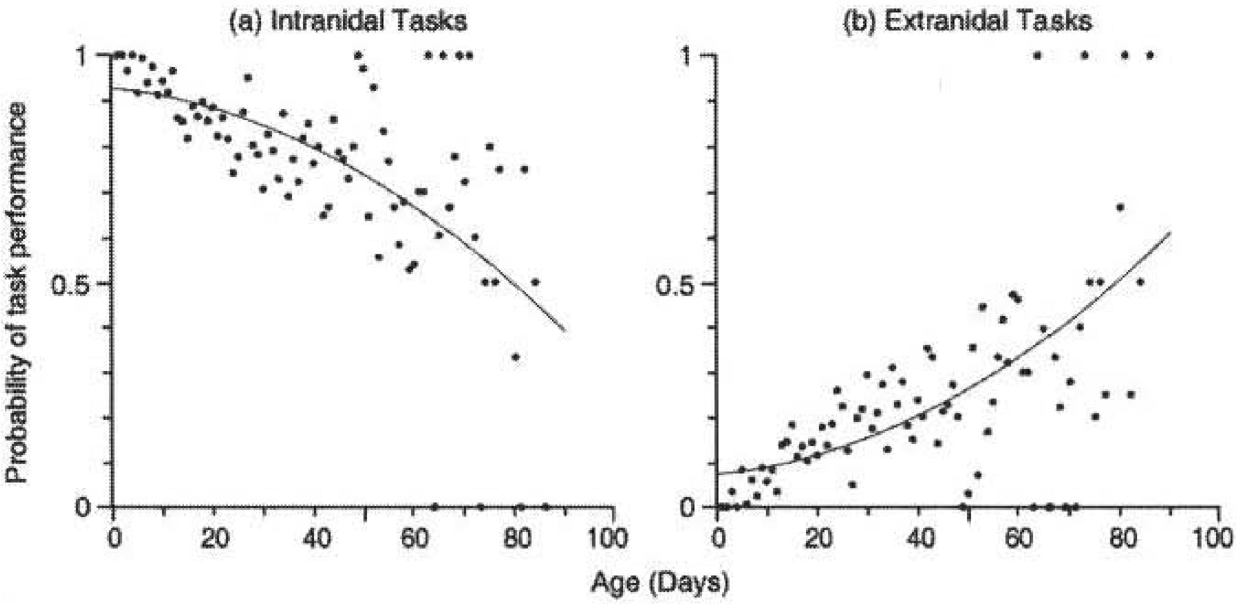

Figure 11.8 Young Wasps Work inside the Nest (intranidal work) and older wasps work outside the nest (extranidal work). Probability of task performance is plotted as a function of the age of the wasps fitted with 2-degree polynomial regression lines. Data points represent the mean value for all individuals in that age class in five colonies. (a) Intranidal tasks and (b) Extranidal tasks. *Source*: With kind permission from Springer Science+Business Media: *Behavioral Ecology and Sociobiology*, 42, 1998, page 39, Dhruba Naug and Raghavendra Gadagkar, figure number 2

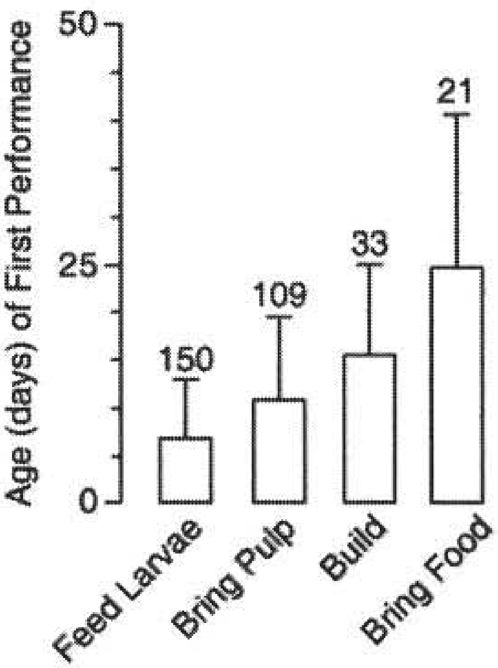

Figure 11.9 Age Dependent Changes in the Behavior of the Adult Female Wasps. Mean (± s.d.) of age of first performance of feed larva, build nest, bring pulp [for building the nest] and bring food. Number of wasps observed is given above the respective bars. *Source*: With kind permission from Springer Science+Business Media: *Behavioral Ecology and Sociobiology*, 42, 1998, page 39, Dhruba Naug and Raghavendra Gadagkar, figure number 3

they need for themselves; therefore they never have any leftover food to offer to the larvae. Three, because the females do a good and adequate job of feeding the larvae, they see no scope for them to add to the labour of the females, especially since they have to depend entirely on the females to get the food in the first place. To test these hypotheses, we first hand-fed the males to satiation and offered them even more food. Sure enough they began to feed the larvae showing that they were not incapable of doing so. However, they did rather too little of it. Then we hand-fed the males to satiation and simultaneously removed all the females and thus left the hungry larvae entirely under the care of well-fed males. Now the males indeed began to feed the larvae at rates comparable to those of the females. Thus males can and do feed larvae given an opportunity. In fairness to the females, it must be said however that the larvae did not do very well under the care of the males! (Sen & Gadagkar, 2006).

THE BALANCE BETWEEN COOPERATION AND CONFLICT

Perhaps the most striking feature of the wasp family is the extreme cooperation within the family. As we have seen, only one member of the family, the queen, reproduces and the rest of the family labours for her reproductive success. Besides, the rest of the family need no top-down orders from the queen—they work whether or not she is present and self-regulate their work in a decentralized manner. Even more impressively, they deal with the death or loss of their queen, in what we humans would consider a most civilized manner. The members of the family seem to queue up in an orderly manner to replace the queen, even before the death of the queen and implement the queue without overt conflict upon the actual loss of the queen. As far as we can tell, there is little overt conflict even when the queue is being established in the presence of the queen. Why should there be so much cooperation, so much peace? And, is there no conflict at all in their lives? It turns out that the extreme cooperation within a family is matched by extreme conflict between families. I have already mentioned that the wasps have a well-developed ability for nestmate discrimination. So far I have pointed out how this helps maintain peace inside the family, because all family members carry the same labels and templates used in nestmate discrimination. The flip side of this is of course that it also makes possible and indeed promotes war with outsiders. We have seen direct evidence of this.

In one experiment, we introduced all the members of one nest, without their nest and brood, into another cage containing a different resident colony. The resident wasps showed a very nuanced response to the 'invading' aliens. The very young aliens were permitted to join the resident nest. The older workers (nonreproductives) were permitted to live in the cage but were not permitted to get close to the resident nest. The alien queen, who obviously constitutes the greatest reproductive threat to the resident colony, was attacked and torn to pieces, even when she was away from the resident nest (Venkataraman & Gadagkar, 1992). We seldom see non-nestmates land on natural colonies but when they do, they are usually (though not always) repelled. Thus the wasps display both cooperation and conflict, but which of the two they show depends very much on the context and not so much on the identity of the wasps. Now their great propensity to make peace with insiders, even though they may be distantly related begins to make sense—it is to successfully make war with outsiders and protect their brood and their resources. Only by putting up a united front can they face outsiders. And the threat of outside invasion is ever present. A united front within the nest may not be very useful to deal with ants, ichneumonid wasps who inject their eggs into the wasp larvae, Tachinid flies who air-drop their larvae onto the nest or vespine wasps who eat up their larvae and pupae. But it must be useful when the enemy is an alien *R. marginata* wasp trying to sneak into the colony and usurp the queen's position. We have evidence that usurpers take their chances whenever there is some hope of success. Such conspecific usurpation is one of the most important causes of failure for queens of small colonies (Shakarad & Gadagkar, 1995). Indeed, that such usurpation is rarely seen in large colonies is testimony to the effectiveness of a united peaceful colony in thwarting the efforts of potential usurpers.

THE EVOLUTION OF ALTRUISM

As already mentioned the altruistic behaviour of members of a wasp family toward the queen and her offspring is an evolutionary paradox. What's in it for the workers? Why should they sacrifice their own chances of reproduction and help another individual to reproduce? In more technical language this conundrum may be re-stated as follows: how does evolution by natural selection promote genes that make their bearers behave in such an altruistic manner; why do such genes not disappear from the population, since they cannot multiply as fast their counterpart 'selfish' genes that make their bearers reproduce as fast as possible, without wasting time and energy helping someone else. A prominent theory that attempts to explain this paradox is called kin selection. It argues (and shows mathematically) that altruism may be favoured by natural selection if it is directed toward genetic relatives. This is because genetic relatives of the altruists are also likely to carry the same altruistic genes. Thus from a gene's point of view, altruistic genes are helping each other when altruists help their genetic relatives. Under certain conditions the loss of personal reproduction for the altruist may be more than compensated by the multiplication of altruistic genes through the reproduction of the recipients of altruism (Hamilton, 1964a,b). We have found that this theoretical framework provides a satisfactory explanation of the altruistic behaviour in the *R. marginata* family. Using a model based on kin selection, we have correctly predicted that only a small proportion of the wasps (~5%) should opt for the selfish solitary nest founding strategy while the vast majority (~95%) should prefer to live in groups, even though it might mean loss of personal reproduction for them. Even though distant relatives live in extended families and altruism is sometimes directed toward not-so-close relatives, because the cost of helping is very low, the benefits of helping are very high and the prospects of selfish solitary nesting are very low, we find that kin selection does a good job of predicting the behaviour of these wasps (Gadagkar, 2001).

Kin selection, however, may not provide an adequate explanation for some of the observed behaviours. For example, why should wasps mate with multiple males and thereby lower intra-colony relatedness; why should they found new nests with non-nestmates; why should they admit young alien wasps into their colonies; why should they not discriminate between close and distant relatives in the family and dispense altruism preferentially to close relatives; why should the workers continue to work in the absence of the queen and in the absence of orders from the queen; why should they line up in orderly queues and await their turn for direct reproduction as future queens; why should they honour previous decisions and implement the reproductive queue without conflict; why is there so much peace with insiders in the family in spite of it being an extended family of close and distant relatives; why should war be reserved for dealing only with outsiders, even though relatedness to outsiders may sometimes not be very much less than relatedness to some family members? Kin selection may work in spite of all these apparently paradoxical behaviours, but what selects for these patterns of behaviour in the first place? Perhaps there are other, better explanations, or other competing selection pressures involved in the evolution of the *R. marginata* family system. This is the reason why I have argued that attempts to criticize kin selection and propose alternate theories (Nowak, Tarnita, & Wilson, 2010) should not be nipped in the bud (Gadagkar, 2010). In summary the evolution by natural selection of the *R. marginata*-like family systems is far from being understood. Much more new empirical and theoretical work is needed.

WHAT CAN WE LEARN BY STUDYING THE WASP FAMILY SYSTEM?

Insect societies are being studied with many different motivations. They make good model systems (proxies) for understanding biochemistry, development and diseases of higher animals including humans. Their mechanisms of division of labour, task specialization, and self-organization provide inspiration and clues for organizing our own societies and institutions. Their systems of communication have inspired highly efficient algorithms in computer science, telecommunication and the internet, accounting for profits running into millions of dollars (for a review, see Gadagkar, 2009). Nevertheless my personal motivation is more modest. I study the *R. marginata* system for the same kinds of reasons that anthropologists study human societies. Anthropologists can inform us about the lives and mores of "primitive" and exotic human societies with thousands of years of experience independent of contemporary human societies. I will argue that biologists can teach us about social animals of all kinds with millions of years of independent evolutionary history. And those of us who study social insects can be privy to "wisdom" from an altogether different sub-kingdom of life on this planet. I would not for a moment suggest that we should blindly imitate a wasp family, but I am convinced that the wasps hold a mirror to us, and help us better understand ourselves (Gadagkar, 2011). And that is arguably worth more than millions of dollars.

I will end with two general remarks.

First, I am conscious of the fact that I have not used the word emotion, a word which appears in the subtitle of the book in which this essay is included, thanks to the intellectual generosity of the editors. Do the wasps feel any emotions when they choose to be solitary or social, when they accept the role of a sterile helper, when they mate, when they succeed in becoming queens, when they feed a hungry larva, when they cannibalize a larva, when they build a perfect hexagon, when they watch their brood being eaten by a predator, when they admit young aliens into their fold or when they aggressively dismember an invading alien queen? Of course we do not know and we will probably never know (Gadagkar, 1997). Needless to say the neural, hormonal and other biological machinery of the wasps is rather primitive in comparison to our own. If they nevertheless feel emotions similar to our own it would be remarkable indeed. On the other hand, if they can manage to do all that they do without emotions, it would be even more remarkable.

Second, as I have said in the beginning, here I have deliberately attempted to describe colonies of the social wasp *R. marginata*, using the language normally used to describe human families. This has been amusing no doubt, but also surprisingly instructive. It has allowed me to look at the wasps in a new light and revealed gap in our knowledge of the wasps. Although we often decry the use of anthropomorphism in describing animals, I certainly found the attempt to anthropomorphise the wasp colony very instructive. I would therefore argue that anthropomorphism might be a good tool to generate questions or hypotheses about animals, hypotheses that can then be tested using more rigorous scientific methods.

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