

# Natural History and Evolution of Paper-Wasps

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# The evolution of eusociality, including a review of the social status of *Ropalidia marginata*

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## What is eusociality?

Social insects, especially bees and wasps exhibit such a bewildering variety of social organizations that we would be quite lost without a sound classification and some technical terms with universally accepted definitions. A system of classification that is built along lines of progressively varying degrees of social organization and sophistication would be even more attractive. Michener (1969) has presented just such a system of classification that has been so popularized by Wilson (1971) that it has now the added virtue of being nearly universally acceptable. According to this system of classification, eusocial insects (the only truly social insects, by definition) are defined as those that possess all of the three fundamental traits of eusociality namely:

- (1) cooperative brood care;
- (2) differentiation of colony members into fertile reproductive castes (queens or kings as the case may be) and sterile non-reproductive castes (workers) (simply referred to hereafter as reproductive caste differentiation);
- (3) an overlap of generations such that offspring assist their parents in brood care and other tasks involved in colony maintenance.

The system explicitly recognizes equally well-defined groups that are not eusocial. Omit the criterion of overlap of generations and we have the semisocial. Omit also the criterion of reproductive caste differentiation and we have the quasisocial. Omit all three criteria and we have the subsocial, if there are aggregates of parents and immature offspring (where parents care for their offspring and not vice versa) or communal, if there are aggregates of individuals of the same generation and solitary, if there are no aggregates at all.

It is customary to recognize two further subdivisions of the eusocial—the primitively eusocial and the highly eusocial—although there is relatively less clarity and agreement about the definitions here. The most widely accepted criterion for separating the primitively and highly eusocial stages is that of morphologically differentiated reproductive and non-reproductive castes in the highly eusocial species and their absence in the primitively eusocial ones. But the criterion of morphologically differentiated castes is not easy to define. Reproductive and worker castes

may exhibit morphological differentiation ranging from minor statistical differences in body size all the way up to morphs that have completely different morphological and anatomical structures, so much so that they may be classified as different species by the unwary taxonomist (see Wheeler 1913, pp. 248–249).

The presence of morphologically differentiated castes in the highly eusocial species and their absence in the primitively eusocial species imply several other parallel phenomena. For example, if reproductive and worker castes are morphologically differentiated, it suggests that caste determination must take place in the pre-imaginal stages and be quite irreversible so that the adult insects should have little or no flexibility in the social roles they can adopt. Conversely, if the reproductive and worker castes are not morphologically differentiated, it is possible (though not necessary) that caste determination takes place in the imaginal stage and that there may therefore be considerable flexibility in the social roles that the adult insects may adopt and indeed, caste determination could in principle be reversible—at least there is no morphological barrier to reversibility. Although these parallel phenomena have been documented for several highly and primitively eusocial species respectively, they are not so obvious as to be available for appropriate classification of poorly studied species. It is therefore not surprising that there may be some ambiguity in classifying, some species (bumblebees for example) as either primitively or highly eusocial. Nevertheless, the distinction between the primitively and highly eusocial is a useful, indeed an essential one (as we shall see below) if we are to make any headway in understanding the evolution of eusociality.

### The distribution of eusociality

When the definitions given above were being formulated, known examples of eusociality were restricted to the class Insecta and even there to just two orders, namely Isoptera (termites) and Hymenoptera (ants, bees and wasps). While all known termites are eusocial, the distribution of eusociality in the Hymenoptera is curious. The suborder Symphyta, consisting of several families of free-living phytophagous species is devoid of eusociality. In the other suborder Apocrita, the sub-group Terebrantia consisting of several families of parasitoid species is also completely devoid of eusociality. It is only in the subgroup Aculeata that eusociality is seen. But even here, while all ants are eusocial, most bees and wasps are not eusocial. Nevertheless eusociality is believed to have originated at least eleven (Wilson 1971) or twelve times (Alexander 1987) independently within the Aculeata.

In recent times, eusociality has been demonstrated in three other orders of insects namely Homoptera (in the aphids) (Aoki 1977; Itô 1989; Benton and Foster 1992), Thysanoptera (thrips) (Crespi 1992) and Coleoptera (in an ambrosia beetle) (Kent and Simpson 1992). There is also a claim (though not as well substantiated) of a eusocial spider (Vollrath 1986) and a clear demonstration of eusociality in two mammals, the naked mole rat (*Heterocephalus glaber*) (Jarvis 1981; Sherman *et al.* 1991) and the Damaraland mole-rat (*Cryptomys damarensis*) (Bennett *et al.* 1988; Jarvis *et al.* 1994). The discovery of eusociality in any species of animal outside the

Isoptera and Hymenoptera has come to be regarded as sensational, usually warranting a report in *Nature* or *Science* (Matthews 1968; Jarvis 1981; Crespi 1992) but claims and counter-claims about whether something should be classified as eusocial continue (see, for example, Hölldobler and Wilson 1990, p.184; Benton and Foster 1992). All this has bestowed upon the definition of eusociality, a certain degree of sanctity which is arguably unjustified (see below).

### Problems with the definition of eusociality

In spite of the apparent soundness and wide acceptance of this system of classification, I think there are at least two quite serious problems with it. One has to do with the rather unfortunate inclusion of the criterion of overlap of generations in the definition of eusociality because of its relatively trivial importance for an 'evolutionary' classification of social life. For one thing, there is no less altruism in a semisocial group of sisters, so long as they show co-operative brood care and reproductive caste differentiation. The central problem of the evolution of eusociality is the evolution of altruism, and by leaving out the semisocial species we are unnecessarily excluding equally important and interesting model systems and especially model systems that might represent the crucial transition from the selfish to the altruistic.

Another problem with the definition of eusociality has to do with its most important criterion namely reproductive caste differentiation. The problem is how to define a sterile worker caste? Should we demand that sterility and worker roles be life-time properties or is it sufficient if they are only temporary? For instance Tsuji (1990) who discovered age polyethism in reproductive division of labour in the Japanese queenless ant *Pristomyrmex pungens* (where all individuals seem to begin adult life as egg layers inside the nest and later forage outside the nest) and labelled it as communal, has now been persuaded (by Furey 1992) to retract his classification and accept that *Pristomyrmex pungens* is not communal but has not been persuaded to call it eusocial; he insists that since there is no life-time sterility, the species cannot be called eusocial (Tsuji 1992). Now all this has two unfortunate consequences.

First, there are many species of 'primitively eusocial' wasps where sterility is not necessarily for life for many workers. Second, the insistence on life-time sterility has precluded the simultaneous consideration of the evolution of altruism in a number of co-operatively breeding birds (Stacey and König 1990) and mammals (Gittelman 1989) where individuals routinely stay on in the nests or territories of their parents or those of others and help in rearing one or more broods of chicks or pups. Only because many of these helpers will go on to raise their own brood (but so do many primitively eusocial wasps), we exclude them from the eusocial fold.

The real problem is that primitively eusocial species not only have a great deal in common with semisocial species, species that lack life-time sterility and co-operatively breeding birds and mammals, but also that have rather little in common with highly eusocial species. As we will see below, a *Ropalidia marginata* female is really much more like the helpers in the Florida scrub jay for instance than she is like a honey bee.

### **A possible solution**

The evolution of altruism is a major unsolved problem in evolutionary biology and it is most likely to be understood if we have a way of classifying together all species that show a substantial amount of altruism—species where individuals give up at least some personal reproduction for aiding conspecifics. I therefore suggest that we expand the scope of eusociality to include semisocial species, primitively eusocial species, highly eusocial species as well as those co-operatively breeding birds and mammals in which individuals give up personal reproduction for aiding conspecifics. There should be no requirement of overlap of generations or of life-time sterility. Tsuji (1992) has worried that by not insisting on life-time sterility, we would be throwing open the flood-gates to include 'a great many species, including our own' and therefore that 'the sterility criterion should be interpreted as a whole-life phenomenon, and not as an ontogenetic one'. I think that will not be a problem as long as we use the criterion of giving up personal reproduction in order to aid conspecifics and not merely of sterility being restricted to an ontogenetic stage. I also suggest that the distinction between primitively eusocial and highly eusocial should continue based on the presence and absence of morphologically differentiated castes (Gadagkar 1994a). The primitively eusocial species may then be used to study the origin of eusociality and the highly eusocial species to study the maintenance of eusociality (see below).

I see no problems in further sub-dividing eusociality into semisocial, subsocial, communal, etc., but the critical entity in the study of the evolution of altruism, which is now eusociality, should include all the sub-groups and not include some (such as polistine wasps and honey bees) and exclude others (such as semisocial insects and co-operatively breeding birds). It may also happen that different nests or even different individuals of the same species represent different sub-divisions of eusociality; the same may be true of given nests and individuals at different times in their life. Indeed, such variation may even cross the boundaries of the liberal definition of eusociality suggested here, to include completely selfish or solitary stages or individuals. All this variety could be usefully documented without forfeiting the advantage of having a single entity to include all groups showing altruism.

### **What do we mean by 'understanding the evolution of eusociality'?**

Grafen (1991) has called the philosophy of behavioural ecology a phenotypic gambit where we assume quite brazenly (for we know it cannot be literally true) (1) that phenotypic characters of interest are determined by the simplest genetic system—perhaps even a haploid locus, at which each allele produces a distinct phenotypic character and (2) that enough mutations occur to produce the required variations. Natural selection is then expected to act on this variation to favour or disfavour specific variants as appropriate to the environmental conditions at hand.

The phenotypes of interest to us now are (1) a selfish individual that rears his or her own offspring and (2) an altruistic worker that cares for somebody else's offspring rather than rear his or her own. The question we are interested in asking is,

under what conditions the selfish and the altruist respectively would be favoured by natural selection. Our first and most important distinction is that between the origin of eusociality and its maintenance.

By the maintenance of eusociality we mean the conditions under which a selfish mutation cannot spread in a population of altruists so that eusociality is stably maintained. It seems reasonable to turn to the highly eusocial species when we are dealing with stably maintained populations of altruists. Thus the question is, why don't honey bee, ant and termite workers become selfish, stop working for their colonies and revert to solitary life? I suspect that this question is virtually impossible to answer. The problem is not that we have reduced the underlying genetics to an unrealistic level but that the second assumption of the phenotypic gambit that enough mutations occur to produce the required variation in characters is probably false. Because the reproductive and worker castes are morphologically differentiated and because caste determination is essentially irreversible in highly eusocial species, a worker cannot revolt against the queen and either drive her away or leave to found a new nest of her own. It is true that the cape honey bee (Anderson 1963) and ants such as *Pristomyrmex pungens* (Tsuji 1990) have evolved thelytoky and manage to get along without their queens, and that in many ponerine ants, workers can mate and manage to survive without their queens (Peeters and Crewe 1985, 1986; Peeters 1987). These examples suggest that there has been some reversal from the highly eusocial to the primitively eusocial state but there is no evidence that any eusocial species has actually ever reverted to the solitary state.

We cannot therefore rule out the trivial alternative hypothesis that workers in highly eusocial species remain altruistic because they have irretrievably lost their reproductive options and have no choice but to work for their colonies, even if the worker strategy is potentially invadable by a selfish alternative. Given this caveat, it is perhaps rather uninteresting to try and ask what maintains eusociality in the highly eusocial species today.

Let us turn to the question of its origin: under what conditions can altruists invade a population of selfish, solitary individuals? To answer this we would ideally like to be able to trace the evolutionary past of the eusocial species. But that is not really possible because there are no fossils and even if there were, they would tell us precious little about behaviour, altruism and social organization! Our next best bet then lies in turning to the primitively eusocial species to see if they are any good for our purpose. Fortunately we are on much better ground here. The primitively eusocial species are certainly in no evolutionary *cul-de-sac*. As we have seen, caste differentiation is not morphological and workers have clear reproductive options; they can replace their queens or leave to start their own solitary foundress nests. Why then do they not always do so? Now that is a much more promising question because we can rule out the trivial alternative hypothesis that they have no option but to continue to work for their colonies. In other words we have some hope of understanding why eusociality is maintained in the primitively eusocial species today. But is that equivalent to understanding the origin of eusociality? I think the answer is yes, but a guarded and qualified yes. It is perhaps reasonable to assume that highly eusocial species have passed through stages that might have resembled

today's primitively eusocial species. If that is reasonable, we may explore the factors that maintain eusociality in the primitively eusocial species today and assume that similar factors may have been responsible for the origin of eusociality.

### Inclusive fitness theory as a unifying theme

Our central question then is, why do workers in primitively eusocial species not all become selfish and start single foundress nests of their own rather than behave altruistically in somebody else's nest and indeed why do some do so? Hamilton (1964*a, b*) argued that the paradox of altruism was no paradox since natural selection is dependent on changes in relative frequencies of alleles without regard as to the pathway by which these changes are brought about. It follows then that producing offspring is only one way to increase the representation of one's genes in the population. Aiding genetic relatives that also carry copies of one's genes, identical by descent, is an alternate equally legitimate way of doing so. The attractiveness of this proposition comes from the fact that, since the probability of occurrence of copies of one's genes, identical by descent, in any class of genetic relatives, including offspring, can be relatively easily calculated, one can now compute a composite quantity called the inclusive fitness. Inclusive fitness then is the sum of all genetic relatives (including offspring) for whose survival a given individual is responsible, after appropriately devaluing the number of relatives in each class by the probability of sharing genes identical by descent, by that class of relatives with the individual in question. Thus inclusive fitness has two components, a direct or selfish component gained through production and care of offspring and an indirect or social component gained through care of genetic relatives. From this Hamilton deduced an elegant rule, which has come to be known as Hamilton's rule. Hamilton's rule thus specifies the conditions under which an 'altruist' allele would spread in a population relative to an alternate selfish allele. The condition is usually represented algebraically as:

$$B/C > 1/r \quad (1)$$

Where  $B$  is the benefit to the recipient of the altruism,  $C$  is the cost to the altruist and  $r$  is the coefficient of genetic relatedness between altruist and recipient, the latter being the probability that genes present in the altruist are also present in the recipient, identical by descent. This expression can be conveniently rewritten as:

$$Br > 1 \cdot C \quad (2)$$

meaning that the benefit to the recipient, devalued by the genetic relatedness between altruist and recipient should be greater than the cost to the altruist. Even more conveniently for our purpose,

$$B/C > r_0/r_i \quad \text{or} \quad Br_i > Cr_0 \quad (3)$$

Where  $r_i$  is the genetic relatedness of the altruist to the recipient's offspring and  $r_0$  is the genetic relatedness of the altruist to his/her own offspring. Here  $B$  can be thought of as the additional numbers of offspring produced by the recipient as a

result of the help given by the altruist and  $C$  can be thought of as number of his own offspring given up by the altruist in order to help the recipient.

Hamilton's inclusive fitness theory offers a unifying theme to evaluate a multitude of factors that might be responsible for this. Inclusive fitness theory predicts that workers do not become selfish and start their own solitary foundress nests if,

$$\Omega > W \quad (4)$$

where  $\Omega$  and  $W$  are the inclusive fitnesses of a worker and a solitary foundress respectively. The question then is, under what circumstances would the inclusive fitness of workers be greater than that of solitary foundresses? To understand this let us break up inclusive fitness into its constituent components and rewrite inequality (4). The inclusive fitness of workers and solitary foundress can be broken up into at least three components (Queller 1989; Gadagkar 1990*b*, 1991*b*) so that we have the prediction that

$$\beta \rho \sigma > b r s \quad (5)$$

where  $\beta$  is the intrinsic productivity of a worker, defined as the number of individuals she can rear to adulthood provided she survives for their entire developmental period,  $\rho$  is the coefficient of genetic relatedness of a worker to the brood she rears and  $\sigma$  is the demographic correction factor for a worker, defined as that factor by which a worker's intrinsic productivity should be devalued because of the probability of her dying before the brood under her care complete development.  $b$ ,  $r$  and  $s$  are the corresponding parameters for a solitary foundress. Clearly at least three classes of factors can contribute to inequality (5).

### Predispositions to eusociality

#### *Ecological or physiological predisposition: $\beta > b$*

One reason why the inclusive fitness of workers may be greater than that of solitary foundresses is that workers may be able to rear more brood per capita than solitary foundresses. This may happen because of better protection from parasites, predators and conspecific usurpers in a group nesting situation compared with a solitary nesting situation (see for example, Lin and Michener 1972; Gamboa 1978; West-Eberhard 1978*b*; Litte 1977, 1979, 1981; Suzuki and Murai 1980; Gadagkar 1985, 1991*c*; Itô 1986*c*; Strassmann *et al.* 1988) or because individuals that opt for worker roles may be subfertile whose  $b$  would be relatively small if they became solitary foundresses but whose  $\beta$  as workers would be relatively high (see for example, West-Eberhard 1975; Craig 1983; Gadagkar *et al.* 1988, 1990).

#### *Genetic predisposition: $\rho > r$*

Another reason why the inclusive fitness of workers may be greater than that of solitary foundresses is that workers may have access to brood that are more closely related to themselves than a solitary foundress is to her offspring. The haplodiploid genetic system in the Hymenoptera, coupled with an ability to bias investment in

favour of female brood can make this possible (see for example, Hamilton 1964*a, b*; Trivers and Hare 1976; Gadagkar 1990*c, 1991a*).

*Demographic predisposition:  $\sigma > s$*

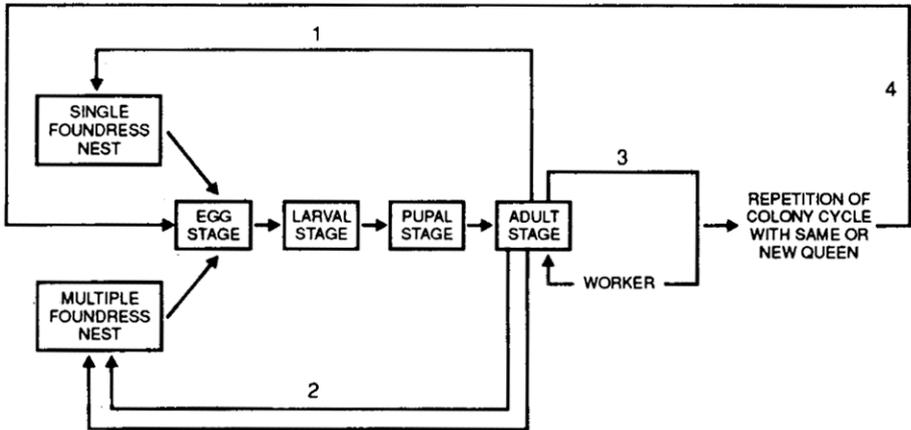
Yet another reason why the inclusive fitness of workers may be greater than that of solitary foundress is that workers may have lower mortality rates compared with solitary foundress but more importantly, the consequence of similar mortality rates may be quite different for workers who function in groups compared with a solitary foundress that works alone (see for example, Queller 1989, this volume; Strassmann and Queller 1989; Gadagkar 1990*b, 1991b*; Nonacs 1991).

The use of the word predisposition perhaps needs some justification. To predispose means to render susceptible or liable, beforehand. This connotation is perfectly valid in the case of genetic predisposition caused due to the genetic asymmetries created by haplodiploidy. Since nearly all known hymenopterans including the solitary groups most closely related to eusocial species are haplodiploid, haplodiploidy can be inferred to have preceded eusociality. Hymenopterans may thus be legitimately said to be potentially genetically predisposed to the evolution of eusociality.

The situation with ecological, physiological or demographic predisposition is somewhat different however. The kinds of factors mentioned above, as examples of these forms of predisposition to eusociality (such as variations in fertility, life spans, etc.) cannot really be said to be more primitive characters of the Hymenoptera compared with eusociality. We know almost nothing about the distribution of these factors among different groups in the Hymenoptera. Nevertheless I think we can justifiably use the term predisposition even for ecological, physiological and demographic factors as long as we are dealing with primitively eusocial species. Recall our formulation of what is meant by understanding the evolution of eusociality. Since we cannot really hope to retrace the actual events in the evolutionary progression towards eusociality, we have decided to look at primitively eusocial species, where workers behave altruistically in spite of having the option of direct reproduction, and equate the factors that maintain eusociality in primitively eusocial species today with those that might have been responsible for the origin of eusociality. Given this caveat, any ecological, physiological or demographic asymmetries that we may discover in today's primitively eusocial species may analogously be considered to constitute predispositions to the evolution of eusociality. As a model system for studying predispositions to eusociality, *Ropalidia marginata* has provided a rich source of new insights.

***Ropalidia marginata* as a model system**

*Ropalidia marginata* is an Old World, tropical, primitively eusocial polistine wasp abundantly distributed in peninsular India. The life cycle and many aspects of the biology of *Ropalidia marginata* are quite similar to those of *Polistes*, especially the tropical species (see Reeve 1991 for a review). New colonies may be founded throughout the year by one or a group of females wasps. In single foundress colonies, the lone female builds a nest, lays eggs, cares for her larvae by foraging



**Fig. 15.1** The perennial, indeterminate nesting cycle of *Ropalidia marginata*. Female wasps have at least four different options shown by numbers 1—4 namely, leave their natal nests to initiate single foundress nests, leave in a group to initiate multiple foundress nests where they may become queens or workers, stay back in their natal nests as workers and stay back in their natal nests to eventually take over as new queens. For schematic convenience, the egg, larval, and pupal stages are shown as being distinct. In reality, there is considerable overlap between them. 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.

for them as well as guarding the nest and brings them to adulthood, unaided by conspecifics, much like a solitary wasp. In a multiple foundress nest however, there is a dominance hierarchy, leading to division of labour such that only one individual functions as the queen and lays all eggs while the rest perform all the tasks involved in colony maintenance and brood care. Male offspring stay on their natal nests for about a week before leaving the nest. They lead a nomadic life near places likely to be visited by foraging female wasps and mate with them.

Daughters eclosing from single- as well as multiple-foundress colonies have a number of options open to them. They may either leave soon after eclosion to found their own single- or multiple-foundress colonies or join other newly initiated colonies, where they may act as queens or workers. They may stay on their natal nests and spend their entire life performing the role of a sterile worker. They may stay and work for some time and then leave to found new colonies or join other colonies or after some period of work, they may drive away the queen of their natal colony and take over the rôle of the queen. Colonies are initiated throughout the year, and the nesting cycle is indeterminate: there is no consistent natural end to the colonies, which may persist for years, with a gradual turnover of the individuals present. This is made possible by a number of factors. The tropical climate in peninsular India makes colony life and brood rearing possible through out the year, the cells in the nest are reused many times over and workers can replace old and weak queens from time to time (Fig. 15.1).

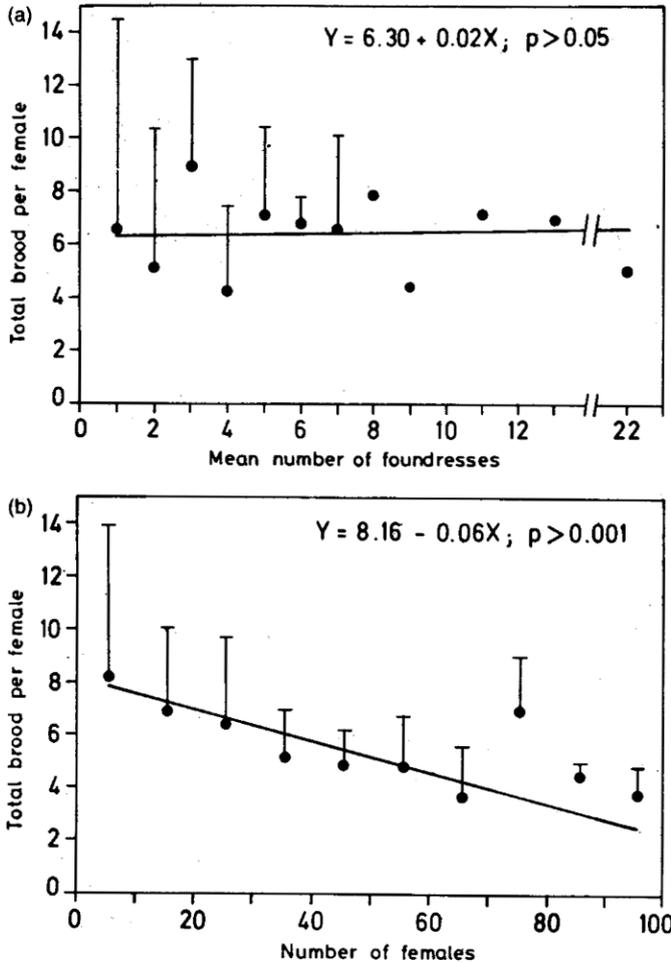
All of these features make *R. marginata* a particularly useful species to investigate the factors that favour the spread of eusociality. Its primitively eusocial status is only one of the reasons for this. Many well-studied species of *Polistes*, for example, occur in the temperate latitudes but where colony life is restricted to the few favourable months of the year (see Yamane this volume). All queens and workers die at the onset of winter and only females eclosing late in the season and which have not acted as workers usually mate and hibernate. These overwintered female wasps then initiate new nests more or less synchronously the following spring. Early initiation of nests can be so crucial to success in eventually producing reproductive offspring that subordinate wasps, which lose out in fights for the dominant, egg-laying status, seem not to have the option of then leaving and founding their own nests. (West-Eberhard 1969b; Gadagkar 1991c; Reeve 1991). However, this option is common in *R. marginata* just as in the case of *P. erythrocephalus* (West-Eberhard 1969b). Foundresses move from one nest to the other and seem to choose the appropriate set of co-foundresses to nest with and they have the freedom to do this as time is not that critical; colony success does not depend critically on the time of initiation. This difference in the importance of time of nest initiation automatically reduces the options open to different female wasps in temperate latitudes. Besides, females eclosing early in the year in temperate species, usually have no males to mate with and thus cannot produce female progeny. Even in the well-studied tropical polistine wasps such as *Mischocyttarus drewseni* the nesting cycles are determinate (Jeanne 1972), thus preventing these species from having as rich a milieu for co-operation and conflict among individuals as *R. marginata* does.

It is thus the combination of the primitively eusocial status, the tropical climate that guarantees nearly equal opportunities to wasps eclosing at all times of the year and the highly indeterminate and prolonged nesting cycle, that makes *R. marginata* especially suited for the study of the evolution of eusociality.

The evolution of eusociality is a complex problem and has almost certainly involved a multitude of factors. It is not surprising that the insights gained from studying different species are likely to be different and even contradictory, at least in the beginning. Presenting a unified picture therefore can be hazardous and there is merit in making explicit the picture that emerges from detailed studies of individual species before attempting a unifying picture. Here I will attempt to illustrate the evolution of eusociality by exploring potential ecological, physiological, genetic and demographic asymmetries between workers and solitary foundresses in *R. marginata*.

### **Ecological predisposition in *R. marginata***

Do ecological asymmetries contribute to the evolution of eusociality in *R. marginata*? Is  $\beta > b$  for ecological reasons? This is not easy to test empirically but at least one can ask if workers in multiple-foundress nests raise more brood than solitary foundresses manage to do. In a recent study, we surveyed two localities where *R. marginata* is known to nest regularly and discovered 145 pre-emergence nests in their early egg stage and monitored them until the eclosion of the first adult



**Fig. 15.2** (a) Per capita productivity (measured as the numbers of eggs+larvae+pupae per female, on the day of the eclosion of the first adult) does not increase as a function of number of foundresses in pre-emergence nests ( $n = 145$  nests) (after Shakarad and Gadagkar 1993). (b) For a random sample of pre- and post-emergence nests ( $n = 244$  nests) per capita productivity (measured as the numbers of eggs + larvae + pupae per female, on the day of collection of the nest) decreases with number of females. Thus larger nests do not produce more brood than smaller ones, and if they do it is only in proportion to the number of females present on the nest.

(Shakarad and Gadagkar 1993). As mentioned earlier, these nests are perennial with an indeterminate nesting cycle so that one cannot hope to monitor nests for their entire duration. We therefore chose the time of eclosion of the first adult offspring as a reasonable time to terminate monitoring because the number of adult wasps on the nest changes at that time. The number of foundresses per nest varied from one to 22 with a mean of 2.84. About 35% of newly initiated nests were single foundress

nests. Given the distribution of group sizes in multiple foundress nests, it turns out that about 35% of the founding population become egg layers and the remaining 65% become workers. There was a statistically significant increase in productivity (measured as eggs+larvae+pupae) with increase in group size but the per capita productivity did not vary with group size (Fig. 15.2; upper panel). This suggests that there is no particular advantage in being in a large group as the productivity of larger groups increases only in proportion to the number of individuals contributing to labour in these colonies. The probability of survival until the production of the first adult offspring was higher for larger groups but this was taken into consideration in computing the mean productivity for each group size.

Larger group sizes might conceivably have the advantage of making it possible for the brood to complete development earlier. We tested this hypothesis but it was not supported; the time taken from the hatching of the first larva to the eclosion of the first adult offspring did not vary as a function of group size. Another possibility is that while there may not be any effect of group size at the time of the eclosion of the first adult offspring but subsequently, there may be an increase in per capita productivity, with group size. To test this we used 244 nests that had been collected over the years for various experiments in our laboratory, and found that there was a significant negative correlation between per capita brood content and number of adult female wasps present on the nest at the time of collection (Fig. 15.2(b)). The nests used here represent the range of natural colony sizes in different stages of development. We realize that all the females present on a nest at all times of the nesting cycle may not be actually working for the colony but, at least, we can say that so far we have been unable to discover any per capita increase in productivity as a function of group size in *R. marginata*.

In these arguments we are making the assumption that all wasps are identical and that the workers would have been as productive as the observed solitary foundresses had they decided to found nests solitarily. This assumption may not be valid and there may be inherent differences between individuals that opt for solitary foundress roles and those that opt for worker roles, as I discuss below. Another potential problem with the foregoing analysis has to do with the possibility of direct pay off for successor queens. Because total productivity (as opposed to per capita productivity), increases as a function of group size, queens in multiple foundress colonies are better off than solitary foundresses. It follows then that if workers have some chance of becoming queens in their life time, they may gain more fitness than solitary foundresses. Workers in *R. marginata* are sometimes successful in driving away the queens in their colonies and taking their place. The hope of becoming a queen may thus be what selects for worker behaviour in *R. marginata* and those that realize this hope must compensate for those that die as workers (West-Eberhard 1978b; Gadagkar 1990d).

Cautioning against an exclusive concentration on the role of genetic relatedness in driving social evolution, Lin and Michener (1972) drew attention to a large number of insect species where sterility is absent or incomplete and suggested the possibility that individuals in such groups may be selected to come together for mutual benefit. This so called theory of Mutualism has sometimes been dismissed

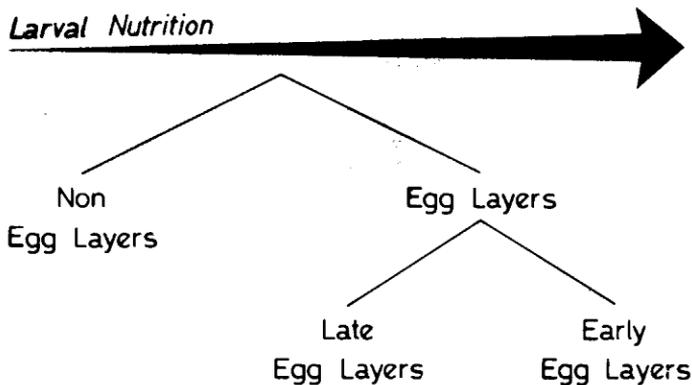
as incapable, by definition, of explaining the evolution of a sterile worker caste because the term mutualism suggests that both or all participants benefit but the sterile worker caste and the fertile queens are not usually thought of as benefiting equally from the associations (e.g. Itô 1989; Crozier 1977). This argument however deserves a second examination. Consider a situation where an individual that nests in a group may obtain more fitness, on the average, than it would as a solitary individual. If we replace the concept of alleles programming individuals into workers with alleles programming individuals to take the risk of being part of the group, then, under certain ecological conditions, the 'Gamblers' will be fitter than the risk-averse solitary individuals (West-Eberhard 1978b; Gadagkar 1991a). The losers in the 'Gamble' will leave behind no offspring and we will see them as 'sterile workers'. Nevertheless, it is a form of mutualism that has given rise to this situation. One advantage of such a model is that it requires no assumption of increased genetic relatedness or parental manipulation.

An important assumption of this so called 'Gambling Hypothesis' (also called the 'mutualistic loser' hypothesis in West-Eberhard 1978b) is that the productivity in the group mode is higher (or more reliable; see Wenzel and Pickering 1991) than in the solitary mode. In *R. marginata* a solitary foundress produces on the average no more than one or two offspring (Shakarad and Gadagkar 1993) whereas a queen of a multi-female colony produces on the average, 76 offspring (Gadagkar 1990a). I argue therefore that, although there appears to be no per capita increase in productivity as a function of group size, the opportunities for queen turn overs provide some ecological predisposition to the evolution of eusociality in *R. marginata*. We are not yet in a position to assess the magnitude of such asymmetry as we do not have good estimates of the probability with which workers become queens in their life time.

### Physiological predisposition in *R. marginata*

Do physiological asymmetries contribute to the eusociality of *R. marginata*? To test this one must know if there are physiological differences between individuals choosing solitary foundress roles and those choosing worker roles. Again it is not easy to test this directly but at least one can ask if all eclosing female wasps are capable of developing their ovaries and initiating single-foundress nests. We now have evidence that mating is not only unnecessary for the development of a female's ovaries but is also unnecessary for an individual to assume the role of the queen of a colony, prevent all other individuals from laying eggs and maintain normal social organization (Chandrashekara and Gadagkar 1991).

We therefore tested a large number of freshly eclosed virgin females for their ability to develop their ovaries and initiate single-foundress nests in laboratory cages with an *ad libitum* food supply. To our surprise we found that only 97 out of 197 wasps tested initiated nests and laid eggs whereas the remaining 100 wasps died without doing so, in spite of living, on average, longer than the time taken by the egg layers to lay their first eggs (Gadagkar *et al.* 1988). We repeated the experiment with an independent sample of 102 wasps and obtained essentially the same results;



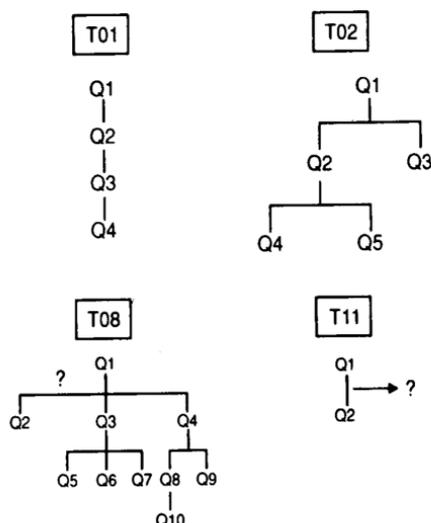
**Fig. 15.3** When virgin, freshly eclosed female *Ropalidia marginata* are isolated into laboratory cages, about 50% of them initiate single foundress nests and lay eggs while the remaining die without doing so. Among those that build nests and lay eggs, the time taken to do so varied from 14 to 191 days after eclosion. Larval nutrition influences these capabilities of the adults such that poorly nourished larvae develop into non-egg-layers, somewhat better nourished larvae develop into late reproducers while even better nourished individuals develop into early egg layers (Gadagkar *et al.* 1988, 1990, 1991a).

53 wasps initiated nests and laid eggs and the remaining 49 died without doing so (Gadagkar *et al.* 1990). With these results we postulated that there is at least some pre-imaginal biasing of caste leading to the production of potential egg layers and non-egg-layers.

In a subsequent study we were able to determine the mechanism of such pre-imaginal biasing of caste. Using six naturally occurring nests we measured the rates at which larvae were fed in them and then we tested individuals eclosing from these nests for their ability to lay eggs under laboratory conditions, as above. Once again only about 50% (47 out of 87) of the wasps initiated nests and laid eggs. But here we were able to show that the probability of becoming an egg layer was influenced by the rates at which larvae were fed in the nest from which these individuals eclosed. Thus larval nutrition seems to play a role in pre-imaginal biasing of caste such that better nourished larvae become potential egg layers whereas relatively poorly nourished larvae become potential non-egg-layers (Gadagkar *et al.* 1991a) (Fig. 15.3).

These experimental results suggest that indeed there are inherent differences between individuals and these differences might well influence their choice of roles. But how would the results of these laboratory experiments translate to natural conditions? Although, I do not believe that our results would apply quantitatively under more natural conditions, I think they would qualitatively. I tend to think of the egg layers in our experiment as individuals that would have a higher chance of capitalizing on an egg-laying opportunity under natural conditions and the non-egg-layers in our experiment as those that might have a smaller chance of doing so.

These observations suggest a substantial physiological predisposition to the evolution of eusociality in *R. marginata*. Individuals with a high probability of



**Fig. 15.4** Pedigrees of queens in four colonies of *Ropalidia marginata*. The relationship between queen 1 (Q1) and queen 2 (Q2) was unknown for colonies T08 and T11 because both queens 1 and 2 were among the animals present on the nests at the time of their collection and transplantation. Note the variety in the kind of pedigrees seen in different colonies. In colony T01 for example, new queens were always daughters of their predecessor queens. In colony T08 on the other hand, new queens were daughters, sisters, nieces or cousins of their immediate predecessor queens (Gadagkar *et al.* 1993).

capitalizing on egg-laying opportunities would have high intrinsic productivities as solitary foundresses and would thus be selected to choose that pathway; those with lower probabilities of seizing egg-laying opportunities would have relatively higher intrinsic productivities as workers than they would as solitary foundresses and would be selected to opt for worker roles. The possibility of pre-imaginal caste bias has not been explicitly investigated in *Polistes* and other polistine wasps. However, circumstantial evidence suggests that a similar phenomenon as that seen in *R. marginata* may well be occurring in other species (see Gadagkar *et al.* 1988 and Gadagkar 1991c for reviews).

### Genetic predisposition in *R. marginata*

Is *R. marginata* genetically predisposed to the evolution of eusociality? Do workers have opportunities to rear brood more closely related to them than a solitary foundress would? In principle this is possible if, in addition to genetic asymmetries created by haplodiploidy, workers have an ability to skew investment in favour of female brood. But much would depend on whether queens are singly mated and whether colonies are monogynous with daughters working to rear the queen's

**Table 15.1** Genetic relationships between successive queens and between workers and brood observed in the four colonies (Gadagkar *et al.* 1993).

Observed genetic relationships	
Relationship between queens and their immediate predecessors	Relationship between workers and brood*
a. Daughters	1. Sisters (0.75 or 0.53)
b. Sisters	2. Brothers (0.25)
c. Nieces	3. Nieces and Nephews (0.375 or 0.265)
d. Cousins	4. Cousins (0.1875 or 0.1325)
	5. Cousins' offspring (0.0938 or 0.0663)
	6. Mother's cousins (0.0938 or 0.0663)
	7. Mother's cousins' offspring (0.0469 or 0.0331)
	8. Mother's cousins' grand-offspring (0.0234 or 0.0165)

\* Brood were sisters, brothers etc. of the workers. Values of relatedness given average  $r$  for sisters = 0.53, based on electrophoretic data from Muralidharan *et al.* (1986) and Gadagkar (1990d).

brood. This is of course not possible in pre-emergence colonies as these are likely to be initiated by groups of sisters where the workers rear their nieces and nephews rather than their siblings. More importantly, there is considerable drifting of females during colony foundation so that cofoundresses are probably not always sisters (Shakarad and Gadagkar 1993). To test if queens mate singly, we analyzed isozyme polymorphism at the *esterase* locus of the egg layers and their daughters from four colonies. Our results showed that queens mate with at least 1–3 males and use sperm simultaneously from different males to produce mixtures of full and half sisters. Our data yielded an average coefficient of genetic relatedness among sisters of 0.52, a value not very different from a solitary foundress's relatedness to her offspring (Muralidharan *et al.* 1986; Gadagkar 1990c).

Even more important, there is frequent queen turnover leading to a system of serial polygyny. Long-term studies of another sample of four colonies have shown that new queens may be daughters, sisters or cousins of their immediate predecessor queens and there is sufficient overlap between offspring of different queens so that workers care for a complex mixture of their full and half siblings, nieces and nephews, cousins, cousin's offspring, mother's cousins, mother's cousin's offspring and even mother's cousin's grand-offspring (Fig. 15.4; Table 15.1). Our data yield values of genetic relatedness among female wasps in a colony ranging from 0.22 to 0.46 as a combined effect of polyandry and serial polygyny (Table 15.2). A computer simulation model of serial polygyny suggests that in *R. marginata* eusociality is not associated with asymmetries in genetic relatedness (Gadagkar *et al.* 1991b, 1993) (Fig. 15.5).

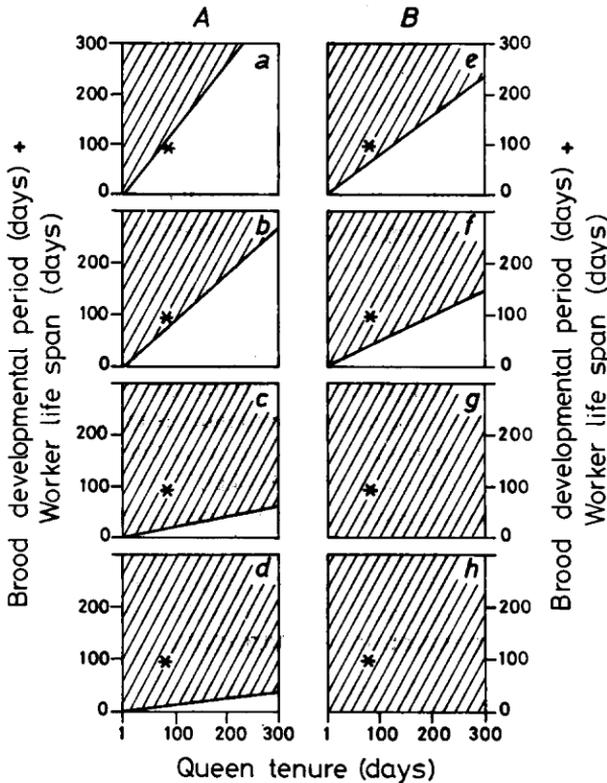
In spite of such low values of genetic relatedness brought about by polyandry and serial polygyny, the genetic asymmetries created by haplodiploidy may be effectively restored if the workers have an efficient mechanism of intra-colony kin recognition. We investigated this possibility by an indirect method and came to the

**Table 15.2** Effects of serial polygyny in *R. marginata* on worker-brood genetic relatedness (Gadagkar *et al.* 1993).

Colony	Number of Queens	Relationship between successive queens	Single mating			Multiple mating (Relatedness between sisters = 0.53) (a)		
			Grand mean genetic relatedness of workers to:		Weighted mean relatedness of workers to brood (b)	Grand mean genetic relatedness of workers to:		Weighted mean relatedness of workers to brood (b)
			Female Brood	Male Brood		Female Brood	Male Brood	
T01	4	Known	0.65	0.28	0.54	0.46	0.25	0.38
T02	5	Known	0.53	0.28	0.44	0.38	0.24	0.32
T08	10	All but one known; one unknown relationship, assumed daughters	0.35	0.28	0.32	0.25	0.20	0.23
		All but one known; one unknown relationship, assumed sisters	0.32	0.24	0.29	0.22	0.18	0.20
T11	2	Assumed daughters	0.63	0.29	0.52	0.45	0.26	0.38
		Assumed sisters	0.57	0.23	0.47	0.40	0.21	0.34

(a) Data from Muralidharan *et al.* (1986); Gadagkar (1990d).

(b) Weighted mean relatedness to brood obtained if worker skew investment in sisters and brothers in the ratio of their relatedness to them (Gadagkar 1990c, 1991a).



**Fig. 15.5** A computer simulation model explores regions in the queen tenure and brood developmental period plus worker life span parameter space where haplodiploidy cannot (hatched region) and can (unhatched region) lead to genetic predisposition for the evolution of worker behaviour. In panel A, the condition for genetic predisposition is that the relatedness of workers to female brood is greater than 0.5. In panel B, the corresponding condition is that workers should obtain a weighted mean relatedness to brood of the two sexes of at least 0.5 after they bias investment in female and male brood in the ratio of their relatedness to them. (a) and (e): queens mate singly and new queens are daughters of their predecessors. (b) and (f): queens mate singly and new queens are sisters of their predecessors. (c) and (g): queens mate multiply and new queens are daughters of their predecessors. (d) and (h): queens mate multiply and new queens are sisters of their predecessors. The lines separating the hatched and unhatched regions are given by the equations: (a),  $Q \times 1.33 = B + W$ ; (b),  $Q \times 0.9 = B + W$ ; (c),  $Q \times 0.2 = B + W$ ; (d),  $Q \times 0.13 = B + W$ ; (e),  $Q \times 0.8 = B + W$ ; and (f),  $Q \times 0.5 = B + W$  where,  $Q$  is the queen tenure,  $B$  is the brood development period and  $W$  is the worker life span. The position of *R. marginata* is shown in each part by an asterisk to illustrate that haplodiploidy does not lead to genetic predisposition for the evolution of worker behaviour in this species except in case (a) (Gadagkar *et al.* 1993).

conclusion that the labels and templates used by *R. marginata* workers in nestmate recognition are acquired by all individuals from a common external source such as the nest. Thus the possibility of wasps discriminating between different classes of relatives within a colony seems remote (Venkataraman *et al.* 1988). This conclusion is supported by more recent experiments showing that unrelated conspecifics, if introduced early in life, are not only accepted by alien colonies but become well integrated into their foster colonies and even become replacement queens (Arathi and Gadagkar 1993). In addition, there is a wealth of evidence from other species of primitively eusocial wasps suggesting that intra-colony variations in genetic relatedness are unlikely to be detected by the workers (Gamboa *et al.* 1986a and this volume; Queller *et al.* 1990). Nonetheless, all experiments so far have been indirect; no one has actually measured whether workers in primitively eusocial species feed larvae differentially, based on their relatedness to them. Besides, we have recently obtained the tantalizing result that queens are more productive when the worker-brood genetic relatedness during their tenure is relatively high (Gadagkar *et al.* 1993). Nevertheless, our tentative conclusion is that the genetic asymmetries potentially created by haplodiploidy are so broken down in *R. marginata* that there is not much scope for the existence of a strong genetic predisposition to the evolution of eusociality.

### Demographic predisposition in *R. marginata*

Is there an asymmetry in *R. marginata* between workers and solitary nest foundresses in the values of the demographic correction factor in inequality (5)? I have developed a hierarchy of models to test this possibility (Gadagkar 1991b).

#### *Delayed reproductive maturation*

The first model shows how any delay in the time taken to attain reproductive maturity will affect solitary foundresses more than it will affect workers because workers are provided eggs by the queen and do not have to wait for their own reproductive maturity. Under laboratory conditions, the time required to attain reproductive maturity by isolated *R. marginata* females varies from 14 to 191 days after eclosion, with a mean and standard deviation of  $48 \pm 31$  days. Using the mean delay of 48 days, and a value of 62 days for the brood developmental period (Gadagkar 1990b) and survivorship data from natural colonies, I have computed the demographic correction factors for workers and solitary foundresses. The demographic correction factor  $s$  for a solitary foundress is the probability of survival for 48 days (time taken to attain reproductive maturity) + 62 days (brood developmental period) = 110 days, which is 0.015 (Gadagkar 1991b). The demographic correction factor  $\sigma$  for workers is simply the probability of survival for 62 days (as workers do not have to wait for their own reproductive maturity), which is 0.12. These different values for the demographic correction factors obtained for a solitary nesting female on the one hand, and a worker on the other, illustrate the disadvantage of delayed reproductive maturation for a solitary foundress compared with a worker. Assuming  $b = \beta$ , and

because  $r$  is expected to be 0.5, the threshold  $\rho$  value required for satisfying inequality (5) is given by the equation:

$$\text{threshold } \rho = s/2 \quad \sigma = 0.06 \quad (6)$$

Alternatively, assuming that  $\rho = r = 0.5$ , the threshold  $b/\beta$  value required for satisfying inequality (5) is given by the equation:

$$\text{threshold } b/\beta = \sigma/s = 8.0 \quad (7)$$

This means that other things being equal, workers would break even with solitary foundresses in spite of rearing brood related to them by a mere 0.06, or if  $\rho = r$ , then they would do so in spite of solitary foundresses being capable of performing eight times more work per unit time. Compared with the maximum threshold  $b/\beta$  of 1.5 obtained under haplodiploidy (when the brood consists entirely of full sisters), delayed reproductive maturation is thus 5.3 times more effective than haplodiploidy in promoting the evolution of a worker caste.

#### *Variation in age at reproductive maturity*

The delayed reproductive maturation model suggests a substantial advantage to workers over their solitary nesting counterparts but it does not explain why a mixture of single-foundress and multiple-foundress nests is common in a variety of primitively eusocial species (Michener 1974; Gadagkar 1991b; Reeve 1991). However, the variation in age at reproductive maturity may provide just such an expectation. With increasing delay in reproductive maturation, the disadvantage for solitary foundresses increases, thus favouring early reproducers to take up the solitary founding strategy and late reproducers to take up the worker strategy. In effect, a polymorphism with single-foundress and multiple-foundress associations will be favoured by natural selection.

#### *Mixed reproductive strategies*

The models and data considered above also suggest the possibility of selection for an individual to adopt a mixture of queen and worker strategies. If there is likely to be a delay in attaining reproductive maturity, then such an individual would maximize her inclusive fitness by first being a worker and then, approximately at the time of attaining reproductive maturity, changing over to the role of foundress or queen. Our data show that about 28% of the wasps could complete rearing one entire brood (by working for 62 days) before they become reproductively mature. Indeed, we have often seen *R. marginata* females adopt such mixed strategies, i.e. first be a worker and later take-over the colony as the next queen or leave to found or join other colonies.

#### *Assured fitness returns*

The asymmetry in the demographic correction factors for solitary foundresses and workers seen so far was due to the requirement that solitary foundresses have to survive longer than workers to rear the same number of brood. I have also developed a model that shows how there will be a difference in the demographic

correction factor even if solitary foundresses and workers survive for the same period of time. While solitary foundresses have necessarily to survive until the end of the developmental period of their brood, failing which they will lose all their investment in it, workers have a special advantage. If a worker cares for some brood for a part of its developmental period and dies before bringing the brood to independence, there is a good chance that another worker from that colony will continue to care for the same brood. Thus workers in multi-female nests are assured of some fitness returns for their labour even if they work only for a fraction of the brood developmental period. The demographic correction factor for solitary foundresses,  $s$ , once again is the probability of survival up to end of the brood developmental period of 62 days, which is 0.12. To allow for the fact that workers can get fitness returns in proportion to the fraction of the brood developmental period for which they survive, I have computed the demographic correction factor for a worker  $\sigma$  as,

$$\sigma = \sum_{i=1}^{n-1} \rho_i(i/n) + \sum_{i=n}^{\infty} \rho_i = 0.43 \quad (8)$$

where  $p_i$  is the proportion of workers that have a life span of  $i$  days. Using equations (6) and (7), the threshold  $\rho$  and  $b/\beta$  required for satisfying inequality (5) are 0.14 and 3.6 respectively (Gadagkar 1990c). Thus assured fitness returns can by itself make the worker strategy more advantageous than a solitary founding strategy. Its relative strength compared with haplodiploidy is 2.4 (Gadagkar 1991b).

In concert with the first three models considered above, Assured Fitness Returns provides an even more powerful force in selecting for worker behaviour. For example, when Assured Fitness Returns and Delayed Reproductive Maturation act in concert, the demographic correction factor  $s$  for a solitary foundress is 0.015 (because a solitary foundress has no Assured Fitness Returns) but the corresponding value of  $\sigma$  for a worker is 0.43. Now equations (6) and (7) yield values of 0.017 and 28.7 respectively showing that in concert, these two factors have a relative strength compared with haplodiploidy of 19.1. Just as Assured Fitness Returns and Delayed Reproductive Maturation can act in concert, Assured Fitness Returns and Variation in Age at Reproductive Maturity can also act in concert and provide, for any given age, a more powerful selective advantage for the worker strategy. In the absence of Assured Fitness Returns, the advantage of Mixed Reproductive Strategies can be exploited only by individuals that have a delay of 62 or more days in attaining reproductive maturity. When Assured Fitness Returns and Mixed Reproductive Strategies act in concert however, the advantage of mixed reproductive strategies become available to individuals with a variety of values of age at reproductive maturity. Their labour is not wasted even if they leave their natal nests to become solitary foundresses or queens, because Assured Fitness Returns will give them fitness returns in proportion to the fraction of the brood developmental period that they have worked.

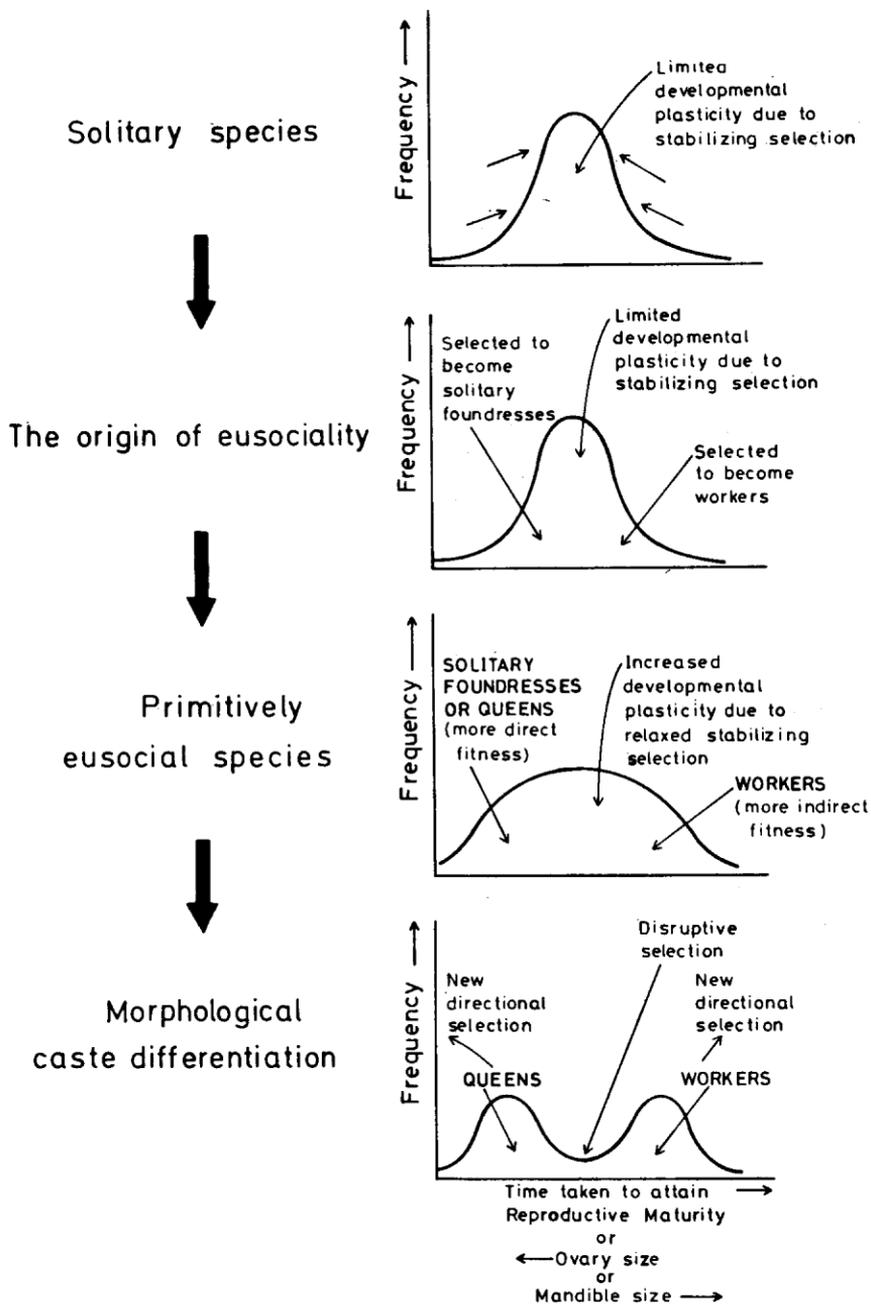
We have good reason to believe therefore that *R. marginata* is strongly demographically predisposed to the evolution of eusociality.

### The role of developmental plasticity

I have argued above (see also Gadagkar 1991*b*) that demographic factors such as initial variations in time taken to attain reproductive maturity will make it worthwhile for some individuals to adopt worker-like roles and for others to assume queen-like roles, leading to the establishment of eusociality. I have also suggested (Gadagkar 1991*b*) that such demographic factors will co-evolve with eusociality and become more pronounced because late reproducers will, for example, have a smaller selective disadvantage in a eusocial species compared with a solitary species because of the possibility of gaining indirect fitness in the former.

I argue that we can also envisage the evolution of highly eusocial species starting from completely solitary ancestors through selection for developmental plasticity. In solitary species, any character such as time taken to attain reproductive maturity, ovary size, mandible size, etc., would have limited developmental plasticity on account of stabilizing selection, because, both queen and worker functions would have to be optimized under a single developmental program. But even here, under the right ecological, genetic or demographic conditions (Gadagkar 1991*b*), individuals at the extremes of the distribution of values for these characters would be selected to take up predominantly or exclusively queen-like or worker-like roles. For example, individuals that have to wait only a short time before attaining reproductive maturity or have larger than average ovaries would be fitter as queens compared with individuals at the opposite ends of the distributions. Conversely, individuals with delayed attainment of reproductive maturity, smaller than average ovaries or larger than average mandibles (useful say, in transporting food back to the nest) would be fitter as workers than individuals at the opposite ends of the distributions. This stage may thus be thought of as the origin of eusociality. As the worker-like individuals begin to rely increasingly on the social component of inclusive fitness and queen-like individuals continue to depend on individual component, there would begin a quite different regime of selection.

First there would be a relaxation of stabilizing selection on genes that regulate the making, in workers, of structures needed for mating and reproduction and in queens, of structures needed for foraging, nest building and brood care. Such relaxed stabilizing selection would lead to divergence of queens and workers. In the next step such relaxed stabilizing selection would make previously impossible levels of directional selection on genes that regulate the making of structures needed for mating and reproduction in queens and structures required for foraging, nest building and brood care in workers. This is because the two kinds of structures, those needed for mating and reproduction on the one hand and those needed for foraging, nest building and brood care on the other hand, would no longer need to be optimized in the same individual. In a process analogous to evolution by gene duplication (Gadagkar 1994*b*), genes involved in making caste-specific structures (or behaviours) can evolve to new and extreme levels. As West-Eberhard (1979) has argued, this process can go far enough to make intermediate individuals to be good neither at being queens nor at being workers, thus leading to disruptive selection to reinforce the process of morphological caste differentiation (Fig. 15.6).



**Fig. 15.6** The origin and evolution of eusociality through selection for developmental plasticity (see text for details).

The ideas in this section are not all new. They are intimately related to West-Eberhard's discussion (1979, 1987*b*, 1988*b*, 1989, 1992) of the general role of 'alternate' phenotypes in evolution. I do believe however that the 'gene duplication' model suggested here, which is linked to the fact that some individuals in a species begin to rely on the social component of inclusive fitness while others, in the same species, continue to rely on the individual component, is different from (and, of course, in my opinion, simpler and superior!) to West-Eberhard's 'epigenetic' model.

## Conclusion

In conclusion, our present state of knowledge, suggests that *R. marginata* is not genetically predisposed to the evolution of eusociality but potential ecological, physiological and demographic asymmetries between solitary foundresses and workers can provide a strong selective advantage for the worker strategy while at the same time permitting the coexistence of single-foundress and multiple-foundress colonies. All of this should be viewed as no more than a first approximation of the shape of one piece in the jig-saw puzzle of the evolution of eusociality. Needless to say, much more detailed investigations of many more species are needed.

## Acknowledgements

Some paragraphs in this review have been taken with slight modifications from Gadagkar (1994*a,b*). My research reported here was largely supported by the Department of Science and Technology, and Ministry of Environment and Forests, Government of India and the Homi Bhabha Fellowship. This paper was largely written while I was visiting the University of Würzburg. I thank Bert Hölldobler for the invitation and financial support through the Leibnitz Award of the German Research Council DFG. I thank C. D. Michener, D. C. Queller, M. J. West-Eberhard and S. Turillazzi for many helpful comments on a previous version of this chapter. I also thank Barbara König and Wolfgang Kirchner for many stimulating discussion of the ideas discussed here.

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