

Queen Number and Sociality in Insects

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Reproductive structure and reproductive roles in colonies of eusocial insects

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Variation in the number of queens in colonies of social insects has become a subject of growing interest among sociobiologists. The increased concern with colony queen number is partly due to the discovery that multiple queen (polygynous) colonies are more common than previously recognized, especially among ants, in which polygyny may be the predominant social structure (Buschinger 1974; Rissing and Pollock 1988; Frumhoff and Ward 1992). More importantly, the mounting interest in polygyny stems from the realization that the origin and subsequent evolution of polygynous colonies from their presumed single-queen (monogynous) ancestors is an evolutionary enigma (Hölldobler and Wilson 1977; Nonacs 1988), presenting many of the same theoretical challenges as does the origin and maintenance of eusociality (see Ross 1988*a*, 1989). For this reason, Rosengren and Pamilo (1983) referred to the evolution of polygynous societies from monogynous ancestors as 'sociality evolving a second time'. Thus research into the origin and evolution of polygyny and eusociality are highly complementary, with insights gained into one situation likely to shed light on the other.

In this chapter we attempt to bring to light the complementary nature of research into these two issues. We do this by explicit reference to colony reproductive structure, defined as the manner in which reproduction is partitioned among colony members. We have broken down the reproductive structure of social insect colonies into its constituent parts as shown in Table 2.1. Of course the major component is the all-important reproductive division of labour into reproductive and worker castes. In addition to this fundamental partitioning of reproduction according to caste membership, there is further subdivision within each caste. There can be variation in the number of reproducing individuals in each caste, and when more than one caste member reproduces in a nest, there can be variation in the level of individual reproductive activity.

Among the components of reproductive structure, reproductive division of labour has been most thoroughly studied, in attempting to better understand the evolution of worker sterility. The primary focus of such studies

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Table 2.1 The components of the reproductive structure of eusocial insect colonies. The major distinction is the reproductive division of labour into reproductive and worker castes. Within each of these castes, variation exists in the number of reproducing individuals and in the reproductive output achieved by different individuals.

Individuals specialized in reproduction (reproductives)
Number of reproducing individuals
Variation in reproductive output
Individuals specialized in non-reproductive tasks (workers)
Number of reproducing individuals
Variation in reproductive output

is the extent to which workers are specialized in their role as non-reproductive helpers and the mechanisms responsible for determining this role. Although the other components have received some attention, there have been relatively few attempts to compare the separate components in order to see the degree to which the same or certain proximate and ultimate mechanisms are involved in determining different aspects of colony reproductive structure. It is our belief that such an approach will deepen our understanding of social insect reproductive roles and the selective forces that have shaped them. In this chapter we examine in some detail the proximate and ultimate mechanisms regulating the reproductive division of labour, the number of cohabiting queens, and variation in reproduction among cohabiting queens. In considering the reproductive division of labour we will be concerned with the prevalence of worker reproduction, i.e. the extent to which workers reproduce directly and the factors regulating their reproduction. The prevalence of worker reproduction as used here refers to reproduction by the worker caste as a whole and does not address the number of reproducing workers or the variance among workers in reproductive output. These latter two subjects comprise the remaining components of colony reproductive structure but to date have received too little attention to be included in this review.

In this analysis we find that because the different components of reproductive structure are subject to similar selective forces and are mediated by similar proximate mechanisms, study of any one component has relevance for the others, including the evolution of a sterile worker caste. It also appears that reproductive competition is a major force regulating reproductive roles, being largely mediated by aggressive interactions.

Variation in colony queen number is a major focus of this chapter. It is therefore important to point out here that there are two types of multiple queen colonies recognized for social insects (Hölldobler and Wilson 1977; Rissing and Pollock 1988). Several newly mated queens may associate

during colony founding, a condition called pleometrosis. Pleometrotic queen associations are generally temporary, since incipient colonies are usually reduced to monogyny either before or shortly after the emergence of the first workers (see Heinze this volume). Long-term, or permanent, polygyny occurs when there is stable coexistence of multiple queens in mature colonies. We largely confine our discussion to permanent polygyny, to which we refer simply as 'polygyny'. Recent discussions of pleometrosis are given in Rissing and Pollock (1988) and Heinze (this volume) for ants, Strassmann (1989) for wasps and ants, Packer (this volume) for bees, and Roisin (this volume) for termites.

The components of colony reproductive structure

The major components of reproductive structure are given for different social insect taxa in Table 2.2. As is evident from the table, there is a great deal of variation in all of the components of colony reproductive structure, providing rich material for comparative study. In this section we review the nature of the variation and point out trends among all the various taxa wherever possible. Although there is a continuum in all the traits characterizing the degree of social complexity of insect societies, the different species are frequently placed in one of two categories denoting the level of social organization: primitively and highly eusocial (Michener 1974; Fletcher and Ross 1985). The degree of social complexity is determined, in large measure, by reproductive structure, particularly the extent of reproductive division of labour, because much of the variation in reproductive structure is related to level of social complexity. We will therefore use the designations of primitively and highly eusocial as a basis for organizing this review.

Primitively eusocial insects usually have little or no morphological differences between reproductives and non-reproductives, colony size is generally small (not more than a few hundred individuals and often far less) and colonies are annual. The primitively eusocial species include the eusocial halictid bees, the eusocial carpenter bees, bumble bees (*Bombus*), the independent founding polistine wasps, the eusocial stenogastrine wasps, and *Microstigma comes*, the only known eusocial sphecid. The highly eusocial (sometimes called advanced eusocial) insects generally have clear morphological differences between queens and workers, form large colonies (often containing thousands of members) that are usually perennial, and trophallaxis among adults is extensive. Highly eusocial species include the termites, the ants, the honey bees, the stingless bees, the vespine wasps, and the swarm-founding polistine wasps.

The most basic distinction in reproductive role is denoted by caste membership. However, there is some controversy over how to define the 'queen' and 'worker' castes in the Hymenoptera (see e.g. Buschinger 1987;

Table 2.2 The main characteristics of the social and reproductive structure of the major taxonomic groups of social insects.

Taxon	Form of colony	Degree of caste dimorphism	Type of reproductive inhibition	Effectiveness of reproductive inhibition	Number of queens per colony	Variance in reproduction among queens	References
Primitively eusocial wasps <i>Microstigma comes</i> (Sphecidae)	haplometrosis	very low	?	low	1-few	unknown	1,2
Hover wasps (Stenogastrinae)	haplometrosis	none-low	behavioural dominance, pheromonal?	low-medium	1-few	low?	3,4
Independent-founding Polistine	haplometrosis	none-low	behavioural dominance	medium-high	1-few	high, but sometimes low	5,6,7
Primitively eusocial bees Sweat bees (Halictini) and Augochlorini	haplometrosis	none-medium	behavioural dominance, pheromonal	low-high	1-several	?	8,9,10
Ceratinini	haplometrosis	none-low	behavioural dominance, pheromonal?	low	1-several	?	8,11
Bumble bees (Bombinae)	haplometrosis	medium	behavioural dominance, pheromonal?	medium	1		8,12,13

mating), and 'non-reproductive queens' if they have undergone those processes but are nevertheless reproductively inactive. Unless otherwise noted, the term 'queen', when unqualified, will apply only to mated individuals. 'Workers' are simply members of the worker caste; these can be reproductively active or inactive. The caste system in termites is complex and readers are referred to Noirot (1989) for a review of this topic.

Comparative studies of the variance in reproductive output between queens and workers and among cohabiting queens are crucial to understanding the evolution of reproductive roles in colonies of social insects and the forces that shape those roles. In order to make rigorous comparisons of the degree of reproductive activity among nestmate females, it is necessary to quantify the variance in reproduction they exhibit. Reeve and Keller (unpublished) have developed a conceptually simple way to do this (see also Reeve and Ratnieks this volume); their skew index is expressed as $(N_b v + N_n)/(N_b + N_n)$, where N_b is the number of breeders in the group, N_n is the number of non-breeders, and v represents the variation in reproduction among breeders. With a single breeder, $v = 1$; with multiple breeders, $v =$ the observed variance among breeders in the proportion of total reproductive offspring produced, divided by the maximum possible value for this variance. In the latter case v is equal to $N_b s^2$, where s^2 is the sample variance in the proportion of total offspring produced by breeders (i.e. $s^2 = [\sum(p_i - 1/N_b)^2]/(N_b - 1)$ where p_i is the proportion of all offspring produced by the i th breeder).

This skew index varies between zero and one. When a single individual produces all of the offspring, the skew is one; when reproduction is perfectly equitable among all group members, the skew is zero. Thus for a colony containing workers and several queens the skew decreases with greater prevalence of worker reproduction, higher number of queens, and lower variance in reproduction among queens. The magnitude of the skew has important implications for relatedness among individuals produced in a colony; the lower the skew, the lower the relatedness. Here we use it to describe intra- and interspecific variation in reproductive output among queens. A skew value is given whenever sufficient data are available to calculate it.

Prevalence of worker reproduction

Primitively eusocial species

The first brood of females produced consists of workers which are generally smaller than the foundresses. However, there are significant interspecific differences in the degree of size dimorphism even within a single genus; for example, there are no size differences between queens and workers in *LasioGLOSSUM (Evyllaenus) marginatum*, whereas there is complete non-overlap in *E. malachurum* (Michener 1974).

Because in most species workers are unmated, their contribution to reproduction is generally limited to males. In several species workers do not reproduce when queens are present (wasps: West-Eberhard 1969; Metcalf and Whitt 1977; bees: Richards 1977; Knerer 1983), whereas they commonly do so in others (wasps: Miyano 1980; bees: Batra 1964; Eickwort and Eickwort 1971; Michener *et al.* 1971; Michener 1974). That eggs laid by workers effectively develop into males has been conclusively shown only in a few species. Using allozyme markers Kukuk and May (1991) showed that workers were able to produce a substantial proportion (mean = 5 per cent) of the males in laboratory colonies, but there was considerable variation among colonies in the extent of worker parentage (range: 0–50 per cent). High intraspecific variation in the prevalence of worker reproduction has also been shown in other species. For example, Miyano (1980) monitored the number of eggs laid by queens and workers in two colonies of *P. chinensis*. The workers ($N = 31$ in both colonies) contributed only a small proportion of the eggs in one colony (skew = 0.96), whereas in the other the total reproductive output of the workers far exceeded that of the queen (skew = 0.36; mean of the minimum and maximum possible values depending on the partitioning of reproduction among workers for which individual data were not given; calculated from Miyano 1980). Although this study suggests that there can be high intraspecific variability in the prevalence of worker reproduction, it must be noted that the true extent of worker reproduction in the above *P. chinensis* colonies is uncertain, because only oviposition rates were monitored, and it is not known whether worker-laid eggs differed in viability (e.g. due to differential oophagy) from queen-laid eggs. Finally, prevalence of worker reproduction has been shown to vary during the colony life cycle for some species. For example, in the genus *Bombus* worker reproduction greatly increases late in the season (Röseler and Röseler 1977).

Highly eusocial insects

In species exhibiting well-developed caste dimorphism (i.e. broadly comprising the highly eusocial species except the swarm-founding Polistinae) morphological specialization of workers frequently includes reduction of the copulatory apparatus, which prevents mating and thereby the production of female offspring. Although workers of most highly eusocial wasp, bee, and ant species have functional ovaries, they are frequently inhibited from reproducing in queenright colonies (see Wilson 1971; Passera 1984; Fletcher and Ross 1985; Bourke 1988; Choe 1988). In the swarm-founding Polistinae workers have retained the ability to mate. If the queen(s) dies, young workers are able to undergo ovarian development, mate and become replacement queens (see Jeanne 1991). The prevalence of worker reproduction has been extensively reviewed by Bourke (1988). Generally, queens have a very strong inhibitory effect on worker reproduction. For instance, in

at least two species of *Vespa* (Ross 1986) and in *Apis mellifera* (Vischer 1989) worker reproduction is extremely low in the presence of the queen, in which case workers produce only about 0.1 per cent of the males. However, in other species worker reproduction in the presence of the queen can be extensive; for example, in *Melipona subnitida* electrophoretic analysis showed that workers produce 40 per cent or more of the males in queenright colonies (Contel and Kerr 1976). Within ants there is also a great deal of variation in the extent to which workers reproduce directly. In some species workers lack reproductive organs altogether or are totally inhibited from laying eggs in queenright colonies. Workers in other species lay only trophic (non viable) eggs when the queen is present, although in queenless colonies they may lay viable eggs that develop into males (Passera 1969; Brian and Rigby 1978). At the other extreme, there are some species, such as *Myrmica rubra*, in which workers probably produce most of the males even in queenright colonies (see Bourke 1988 and references therein).

Queen number

Primitively eusocial insects

Characterizing the number of queens in colonies of primitively eusocial species is difficult for two main reasons. First, colonies are generally started by varying numbers of mated foundresses (Table 2.2), and their numbers frequently change during colony ontogeny. For example, in the genus *Polistes* the proportion of multiple-foundress colonies varies between 0 and 100 per cent (with a maximum number of 36 cofoundresses) depending on the species and their geographic location (see Reeve 1991; Spradbery 1991). Similarly, this proportion varies between zero and 93 per cent in the other genera of independent founding wasps (Gadagkar 1991) with a maximum number of 22 cofoundresses in some species. However, in most species there is a sharp decrease in the number of cofoundresses by the time the first workers emerge (e.g. Pardi 1948; Gamboa *et al.* 1978; Hughes and Strassmann 1988; Gadagkar 1991; Reeve 1991), but this is not always true (Hughes and Strassmann 1988). Second, cofoundresses may differ greatly in their reproductive roles. In associations of most species dominance hierarchies are established very quickly resulting in one or a few individuals becoming dominant (queens) and producing most of the eggs in the colony (e.g. Pardi 1948; West-Eberhard 1969; Reeve 1991; Röseler and van Honk 1990). Additionally, differential oophagy (Gerret 1964; West-Eberhard 1969) may further increase differences in direct reproductive success (see next section). Subordinate cofoundresses become worker-like in their behaviour or they may become inactive or depart from the nest (West-Eberhard 1969).

As a result of the frequent sharp reduction in the number of cofoundresses and the ability of a few of them to monopolize reproduction, the effective number of queens in primitively eusocial insects is generally

low. This translates into high relatedness among nestmate females (see next section).

Highly eusocial insects

Although polygyny is widespread in the highly eusocial insects, its taxonomic distribution differs greatly among the major groups (Table 2.2 see Ross and Carpenter 1991a for a phylogenetic approach). Polygyny is the common state of most swarm-founding species, but queen number appears to fluctuate considerably during the colony life cycle of many species (West-Eberhard 1977; Jeanne 1991; Itô this volume; Hughes *et al.* this volume). In the Vespinae polygyny is sporadic and mainly confined to a single restricted taxon, the *Vespa vulgaris* species group. Highly eusocial bees (Meliponinae and Apinae) are typically monogynous with the exception of *Melipona nigra*, in which two or more queens may be present in a single nest (Michener 1974; Bego 1989; Engels and Imperatriz-Fonseca 1990).

In the ants the available data suggest extreme plasticity in this social trait at all levels. Virtually all subfamilies, and a great many genera and species groups, contain both typically monogynous and polygynous species (Wilson 1971; Hölldobler and Wilson 1977; Brian 1983; Rissing and Pollock 1988; Frumhoff and Ward 1992), and there is an increasing number of reports of intraspecific polymorphism as well (Pamilo and Rosengren 1984; Ross *et al.* 1987; Ward 1989; Elmes and Keller this volume; Rosengren *et al.* this volume). Nevertheless, some ant taxa appear rather invariant in their expression of queen number, e.g. monogyny in the army ants (subfamilies Ecitoninae and Dorylinae; Gotwald 1988) and in most fungus growing ants (tribe Attini; Brian 1983; Mintzer 1987).

Thus, in the highly eusocial Hymenoptera queen number is relatively invariant at the level of the genus or higher in highly eusocial bees and wasps, but this trait commonly varies within genera or even within species in ants.

Thorne (1985) reviews the data on polygyny in termites. Multiple supplementary or neotenic reproductives are relatively common in colonies of some termite species, particularly the lower termites. The occurrence of multiple alate-derived queens appears confined to the phylogenetically advanced family Termitidae. In this family multiple imaginal queens have been found coexisting in at least one colony in 38 species representing 15 genera scattered over all four subfamilies. As pointed out by Thorne (1985), this is no doubt a conservative estimate, because the royal compartment housing the primary reproductives is often difficult to access. In all termite species so far studied polygyny appears to be facultative, but in at least a few species, such as *Nasutitermes princeps*, *N. polygyus*, and *N. costalis* (Roisin and Pasteels 1985, 1986), it is the predominant state. The presence of multiple alate-derived queens in termites is generally

accompanied by the presence of multiple kings. Polygyny can also result from the differentiation of multiple nymphoid queens (neotronics coming from wing-budded nymphs) within the same colony. These nymphoid queens become physogastric, just as do alate-derived queens and, like them, they inhibit the differentiation of new queens (Roisin, personal communication). Associations of neotenic queens are common in several families, e.g. Termitidae (Emerson 1925; Noirot 1985; Roisin 1990, this volume), Rhinotermitidae (Buchli 1958; Renoux 1976; Lenz and Barrett 1982) and Hodotermitidae (Coaton 1958). In contrast to these families, supernumerary neotronics are usually eliminated until one pair is left in the Kalotermitidae (Lüscher 1952; review in Lenz 1985).

Variance in reproductive output among nestmate queens

Primitively eusocial species

There is considerable interspecific variation in the reproductive output of cofoundresses (see Gadagkar 1991; Reeve 1991; Itô this volume). For example, the non-reproductive skew varied between 0.10 to 1.00 in associations of two foundresses in four species of *Polistes* (*P. biglumis* = 0.10, Makino and Aoki 1982; *P. fuscatus* = 0.77, Noonan 1981; *P. exclamans* = 1.00, Hughes and Strassmann 1988; for all of these species, the reproductive output of foundresses is estimated from the number of eggs laid corrected for differential oophagy (when observed)). Metcalf and Whitt (1977) used genetic markers to track the production of sexuals in colonies of *P. metricus*. The reproductive skew for this species was 0.44 (based on the assumption that males and females have the same reproductive value).

Another way to determine the number of cofoundresses which effectively reproduce in a colony is to look at the genetic relatedness among the females produced. Such data exist for 18 primitively eusocial wasps (mean relatedness: 0.54; range: 0.3–0.77, mean values were used when several values per species were given; from Ross and Carpenter 1991b). As mentioned earlier, apart from the number of reproductives, colony genetic structure is also influenced by other factors, such as the genetic relatedness among reproducing individuals, number of matings, and reproductive skew (see also Queller this volume, Hughes *et al.* this volume). However, even if cofoundresses are highly related (which frequently is the case), the very high genetic relatedness among the females produced suggest that only a few of them reproduce, or alternatively that there is high variance in their reproductive output. Unfortunately, for the vast majority of nests studied there is no detailed information on their history (i.e. number of cofoundresses, number of matings, and possible temporal variation in the number and identity of the queens reproducing). A detailed analysis of the role of frequent queen changes within a colony (serial polygyny) on genetic structure is given by Gadagkar *et al.* (this volume).

There have been very few studies of the degree to which the skew may vary among nests of a single species, but it appears that in some cases there may be considerable intraspecific variation. Two colonies each containing two foundresses were studied in *Polistes biglumis* (Makino and Aoki 1982). The dominant secured 70 per cent of egg-laying in one colony and 60 per cent in the other (non-reproductive skew = 0.16 and 0.04, respectively); however, some caution should be used in drawing conclusions from these data, as the queens were observed only for a short period of time: 13 and 28 hours per colony, during less than one month.

Highly eusocial species

Species of highly eusocial insects can vary tremendously in the degree to which reproductive effort is distributed among nestmate queens. In the swarm-founding Polistinae it seems that queens have relatively equivalent rates of oviposition and ovary development, suggesting that the variance in their reproductive output may be low (Jeanne 1980; Hughes *et al.* this volume). In the vespine *Vespa affinis* Spradbery (1986) recorded the behaviour of five queens in a polygynous nest for a total of 10 hours. One of them was more active in foraging, larval feeding, nest building and cell inspection, and only this queen was observed to lay eggs (2). This raises the possibility that queens may differ in their total activity and reproductive success, but obviously more data are needed. Among the few polygynous stingless bees, interactions among queens have been studied in *Melipona bicolor*, and nestmate queens appeared to share equally in reproduction (Bego 1989).

Heinze (this volume) provides an extensive review of the variation in reproduction among nestmate queens in ants, wherein it appears that it can be quite large. In some species queens seem to share reproduction relatively equally (Keller 1988; Ross 1988b), whereas in others a single queen is able to monopolize reproduction. This latter condition, called functional monogyny, occurs when several mated queens coexist in the same nest, but only one is reproductively active (Buschinger 1968; Heinze this volume). Large intraspecific variation has also been reported in some species, e.g. *Leptothorax acervorum*, in which colonies are facultatively polygynous in Europe (Buschinger 1968) but are functionally monogynous in Japan (Itô 1990).

Variance in reproductive success among nestmate queens depends not only on their relative fecundity, but on the ability of their eggs to develop into sexuals. Ross (1988b) showed that in the polygynous form of *Solenopsis invicta* nestmate queens differed significantly in their contribution to the maternity of workers and female sexuals. Queens contributed more equally to worker offspring than to female sexuals, with a non-reproductive skew of 0.09 for worker production (based on data from colony C1, the colony with the most samples), and a skew of 0.24 for queen production

(Ross 1988*b*). However, although Ross tracked the relative contribution of queens for over a year, it is not certain that this short-term variability would translate into significant long-term differences in reproductive success, because the queens probably live for six to seven years (inferred from life-span of queens from monogynous colonies, Tschinkel 1988). It is possible that variability in apportionment of maternity of female sexuals is age-related, in which case life time reproductive skew could be lower.

Very few data exist on direct reproduction by termite queens in polygynous colonies. Thorne (1985) reviewed the data on relative weights of queens and found that in most cases nestmate queens were approximately the same weight. Because queen weight is highly correlated with fecundity in this group, these findings suggest that all females contribute to a similar extent to reproduction.

Proximate mechanisms regulating reproduction

Differential participation among queens as well as between queens and workers in the production of reproductives can arise by one or more of the following means: (i) differential fecundity, (ii) differential viability of eggs, (iii) differential probability of eggs developing into sexuals, (iv) differential oophagy, and (v) differential survivorship of egg-layers (e.g. Keller, in press; Keller and Ross, in press). The available evidence suggests that all of these mechanisms contribute to differential reproductive success among nestmate queens and between the queen and worker castes (see below).

The number of reproductive females and variation in their direct reproductive output may be mediated through aggressive interactions among females and/or pheromones (Wilson 1971; Fletcher and Ross 1985). This section compares the importance of these two mechanisms for each of the components of reproduction. The possible modes of action of pheromones will be discussed in the next section (see also Keller and Nonacs 1993).

Prevalence of worker reproduction

There is a clear trend in both the nature and effectiveness of reproductive inhibition in relation to degree of social complexity (Wilson 1971; see also Table 2.2). In most primitively eusocial species worker reproduction is generally inhibited by physical domination by the queen (Wilson 1971; Fletcher and Ross 1985; see also Table 2.2), and indeed the queen's aggression is primarily directed at the workers with the greatest ovarian development. Furthermore, in several species worker reproduction is also inhibited by queen pheromones (Table 2.2; see also Fletcher and Ross 1985). Worker reproduction is more prevalent in these species than in highly eusocial species, indicating that reproductive inhibition is less effective.

Queen aggressive behaviour directed toward workers is much less frequent in highly eusocial species and seems to be restricted to some wasps in which queens attack workers with developed ovaries (see Greene 1991; Jeanne 1991). The rarity of direct dominance and the convincing demonstrations of chemical queen recognition have been used as evidence that the inhibition of worker reproduction is pheromonal (see Wilson 1971; Fletcher and Ross 1985; Bourke 1988; see also Table 2.2).

Number of queens

The number of queens in primitively eusocial species is regulated by aggressive interactions among dominant and subordinate females. As mentioned earlier, the number of cofoundresses frequently decreases when workers first emerge, at which time the level of intracolony aggression is high (see Reeve 1991 and references). Workers of these species generally behave aggressively toward non-nestmates thus preventing usurpation by foreign females (Gamboia *et al.* 1986).

In highly eusocial species workers seem to play a chief role in regulating queen number. For example, in the ant *Iridomyrmex humilis* workers execute c. 90 per cent of the queens just before the period of sexual production in spring (Keller *et al.* 1989). It is not yet known whether queen execution by workers is nepotistic in this and other species. Similarly, in most species workers behave very aggressively toward non-nestmate queens trying to enter the colony (e.g. Fletcher and Blum 1983).

Queens also actively contribute to the regulation of queen number in some species. In the swarm-founding vespine *Mesopolybia aztecoides*, queen reduction, which occurs after swarming, results from queens engaging in dominance interactions coupled with high aggressivity by workers toward subordinate queens (West-Eberhard 1977). As a result, all but one of the queens disappear from the nest or start behaving like workers. Reduction of queen number in pleometrotic ant associations is mediated by aggressive interactions among queens in some species, whereas in others workers are responsible for killing or expelling supernumerary queens (see Heinze this volume).

In many termite species the loss of the primary reproductives results in the production of numerous neotenic. However, the number of neotenic is reduced following their production. In a manner very similar to some hymenopteran species, supernumerary neotenic are eliminated through the combined activity of dominant neotenic and members of other castes (Lüscher 1952; Lenz 1985).

Variance in reproductive output among nestmate queens

Aggressive interaction is the chief mechanism regulating reproductive output by cofoundresses in primitively eusocial insects (see previous section). Greater disparity in reproduction among cofoundresses appears to be

frequently correlated with higher aggression levels. In the genus *Polistes* species with moderate or frequent dominance-related aggression exhibit a higher reproductive skew than those with relatively infrequent aggression (Reeve 1991). For example, four of the five *Polistes* species for which the reproductive skew index was given above (see previous section) exhibit moderate or frequent aggression (*P. metricus*, Metcalf and Whitt 1977; *P. fuscatus*, Noonan 1981; *P. exclamans*, Hughes and Strassmann 1988). The other species, *P. biglumis*, exhibits aggression infrequently (Makino and Aoki 1982). For the four species with high aggression levels the reproductive skew ranged between 0.44 and 1.00, whereas the skew value was only 0.10 for the species in which aggression is infrequent, supporting the notion that there is a significant association between the reproductive skew and level of aggressivity (Reeve 1991). Pheromones have been suggested to play a role in mediating differential reproduction among co-foundresses in several species, but as suggested by West-Eberhard (1977) they may possibly act as 'warning signals' indicating the presence of an individual with high fighting abilities (see also Keller and Nonacs 1993).

In many highly eusocial species aggressive interactions among queens are rare or do not occur at all. For example, no overt dominance interactions among queens have been observed in swarm-founding wasps (except during the time when queens are eliminated; Jeanne 1980), in the polygynous bee *M. bicolor* (Bego 1989) and in many ant species. Interestingly, ant species in which aggressive interactions do occur seem to be those exhibiting large reproductive variance among queens (see Heinze this volume). In some species, such as *I. humilis* (Keller, unpublished) and *S. invicta* (K. G. Ross, E. L. Vargo, and L. Keller, unpublished), there are apparently no aggressive interactions among queens, and all queens seem to participate to a significant degree in reproduction (Keller 1988; Ross 1988b). In contrast, high levels of aggression are frequent in species, such as several *Leptothorax* species, that are functionally monogynous (see Heinze this volume). In a few species, e.g. *Leptothorax curvispinosus*, differences in direct reproductive success among queens also appear to occur via differential oophagy (Wilson 1974a,b).

It is well-established that in many social insects there is an inverse relationship between queen number per colony and the fecundity of individual queens (wasps: Richards and Richards 1951; Jeanne 1975; bees: Michener 1964; but see Packer this volume; ants: Passera 1969; Fletcher *et al.* 1980; Herbers 1984; Keller 1988; Vargo and Fletcher 1989; and termites: Thorne 1985; Roisin and Pasteels 1985). Queen produced inhibitory pheromones have been suggested as the responsible mechanism in some species (Mercier *et al.* 1985; Vargo and Fletcher 1989). The existence of such pheromones has recently been demonstrated (Vargo 1992) in the polygynous form of *S. invicta*, where mutual pheromonal inhibition among queens results in lower fecundity. It is not yet known whether such pheromones may act

directly on the physiology of the queens or whether differential pheromone levels in the colony are used by workers to regulate queen fecundity (e.g., through the amount of food they provide them). There is no way of knowing at present how widespread mutual pheromonal inhibition among queens might be in ants, but Bourke (1993) recently reported finding no evidence for pheromonal inhibition among cohabiting queens in polygynous colonies of *Leptothorax acervorum*.

Ultimate mechanisms regulating reproduction

From the above survey it is clear that there is considerable variation both within and among taxa in the three components of reproductive structure. In this section we examine the ultimate factors responsible for this variation as well as the possible interplay between the different components (e.g. how queen number may affect worker reproduction).

Prevalence of worker reproduction

The competing hypotheses for the evolution of a worker caste have been extensively discussed (Hamilton 1964a,b, 1972; West-Eberhard 1975, 1977, 1981; Starr 1979; Andersson 1984), and the reader is referred to these articles for more detail. The major theories are kin selection, parental manipulation, and mutualism. Mutualism may have been important in establishing nesting associations of female Hymenoptera, but kin selection, parental manipulation, or some combination of the two appear necessary for the evolution of worker sterility (Crozier 1979).

The ultimate reasons for why hymenopteran workers generally do not produce males has been the subject of much theoretical work recently. Worker reproductive output can be limited for one of the three following reasons. (i) Queens physically inhibit worker reproduction (queen policing: Oster and Wilson 1978); this is common in primitively and also occurs in some highly eusocial insects (Fletcher and Ross 1985; see previous section). (ii) Workers refrain from egg-laying (self policing), because worker reproduction sufficiently diminishes colony productivity (Cole 1986; see Ratnieks and Reeve 1992 for a review). (iii) Workers suppress the reproduction of other workers (worker policing: Starr 1984; Wojciechowski and Lomnicki 1987; Ratnieks 1988), a mechanism that may be selected for if workers are on average less related to the offspring of nestmate workers than to the offspring of the queen(s). The average relatedness of workers to the sons of the queens and workers depends on both the number of reproducing queens within the colony and queen mating frequency. Taking these two factors into account in an inclusive fitness model, Nonacs (1992) showed that worker reproduction should be more common under monogynous-monoandrous and polygynous-polyandrous conditions than under monogynous-polyandrous and polygynous-monoandrous conditions.

The only empirical test of a possible association between worker reproduction and colony reproductive structure found that worker-laying is less inhibited by queen presence in polygynous, as compared to monogynous species (Bourke 1988). However, mating frequency by queens was not considered in this study, and at present insufficient data exist to test Nonacs' (1992) prediction. Additionally, the degree of relatedness among queens and the numerical sex ratio influence worker inclusive fitness (Pamilo 1991), and therefore influence the extent of direct reproduction by workers. Interspecific variation in these two attributes are reviewed for ants in this volume by Herbers. Genetic relatedness among queens appears to be frequently low (Herbers this volume), and colony sex ratio appears to be highly variable and probably associated with queen number, queen mating frequency, and queen relatedness (Boomsma this volume; Nonacs this volume). Thus worker reproduction can be influenced by many factors, all of which are likely to influence each other. More detailed studies are needed in order to assess the relative roles of these different factors in influencing the reproductive activity of workers.

Evidence to date suggests that worker reproduction is less frequent than expected (Nonacs 1992), a situation that could arise if queen-produced males hide their sexual identity long enough during development to make it unprofitable for workers to replace the queen's (s') sons with their own (sexual deception, see Nonacs 1992). That workers might be unable to discriminate the sex of queens' offspring as late as the pupal stage has recently been reported in the ant *Camponotus floridanus*, a finding consistent with the 'sexual deception' hypothesis (Nonacs and Carlin 1990).

Overall, it appears that queen-worker conflict over male parentage is governed by genetic interests, but these interests are constrained by the cost of manipulation, e.g. reduced colony productivity (see also Schmid-Hempel 1990; Ratnieks and Reeve 1992), and effectiveness of communication, e.g. errors in assessing sex and relatedness of nestmates.

With regard to the problem of queen-worker conflict an important issue relates to the question of the role of queen pheromones in regulating reproductive activity in workers and other nestmates. Although queen inhibitory pheromones have frequently been viewed as a means by which queens establish and maintain their reproductive dominance, it is more likely that they serve as a means for other colony members to monitor the presence of the queen and her reproductive performance in order to adjust their own reproductive activity in a way that maximizes their inclusive fitness (see Keller and Nonacs 1993).

Queen number

The evolutionary explanations of polygyny are largely the same as those proposed for the evolution of eusociality. For reviews, see West-Eberhard (1981), Nonacs (1988), Herbers (this volume) and Rosengren *et al.* (this

volume). Kin selection and mutualism are the most commonly invoked explanations. An additional hypothesis to explain the evolution of polygyny has been proposed by Eilmes (1973), who suggested that polygyny may be the result of parasitism by queens. Under this hypothesis, newly mated queens invade existing colonies to the detriment of the current residents (see Herbers this volume; Rosengren *et al.* this volume).

Although we still have much to learn about the adaptive regimes promoting the reproductive division of labour between the queen and worker castes and those promoting polygyny, it appears that similar selective forces are at work in both cases. Thus, the number of queens and the partitioning of reproductive effort among them in polygynous colonies provides an alternative system for testing the roles of kin selection, mutualism and parental manipulation in regulating reproductive roles. It is worth considering some of the advantages and disadvantages of these two systems for testing the relative importance of various selective forces in shaping the reproductive structure of insect societies.

An important problem in studies attempting to elucidate the origin of eusociality is that colony genetic and reproductive structure of most extant eusocial taxa may be far removed from that of the stem groups having given rise to the eusocial forms. As a result, only a few primitively eusocial species are appropriate foci for questions of social origin and only a few studies have considered the social and genetic structure of such species (see Ross and Matthews 1989*a, b*). In contrast, queen number and variance in reproduction among nestmate queens in polygynous colonies appear to be highly variable within some taxa and even within some species, thus providing good comparative systems for investigating the factors maintaining colony reproductive structure.

In order to assess the relative roles of candidate selective forces in shaping reproductive patterns, we have to understand the inclusive fitness costs and benefits for the different parties involved. In the case of facultative worker behaviour, it is necessary to compare the expected fitness of a female nesting alone to that expected by forgoing reproduction and helping raise offspring of her mother or other related individuals. A major hurdle in these studies is that it is difficult, if not impossible, to assess the probability that a female will succeed in starting her own colony independently. The problem is confounded by the fact that this probability may vary in relation to various factors such as inter-individual differences in size or timing of emergence. It is also very difficult to quantify the degree to which helpers can aid relatives and the mutualistic advantages of co-operation (see Strassmann 1989; Reeve 1991). As a result, establishing the relative roles of the different selective forces favouring co-operation is problematic (for other problems in comparing the inclusive fitness of solitary versus helper females see Queller 1989; Gadagkar 1990; Nonacs 1991).

In the case of polygyny in highly eusocial insects the problem is different; because queens are so specialized for reproduction and colonies contain many workers, each additional queen provides only an insignificant advantage (in terms of overall production) to the colony (e.g. Vargo and Fletcher 1989). Therefore, assessing the inclusive fitness of queens is somewhat simplified, because small variation in queen number does not significantly affect colony productivity (but see Sherman *et al.* 1988; Shykoff and Schmid-Hempel 1991 for a possible effect of increased genetic variability). However, a problem arising while studying the reproductive structure of polygynous colonies is that they are long-lived, requiring demographic data for assessing the inclusive fitness of queens on a lifetime basis. Specifically, two important problems are that (i) queen reproductive success (number of offspring produced and proportion developing into sexuals) may vary with age, and (ii) queen number and relatedness may vary during colony ontogeny. To date there is little information on these two parameters; in future studies a better understanding of the temporal dynamics of reproductive output and kinship in polygynous colonies will be of primary importance. New genetic techniques (e.g. DNA fingerprinting, mDNA sequencing) will undoubtedly help in assessing age-related differences.

In short, comparative study of queen number has some important advantages over studies of worker sterility for examining the role of various selective forces in shaping social insect reproductive structure. Further, because queen number and variance in reproductive output are highly variable within some taxa, and even within some species, there is ample opportunity for interspecific comparative studies and intra-populational analyses of ecological and other factors influencing reproductive roles.

Variance in reproductive output among nestmate queens

As we have seen, nestmate queens in polygynous colonies of some species share relatively equally in reproduction, whereas in other species there is large variation in reproductive output. In this section we examine the ultimate factors that might select for and against unequal reproduction among cohabiting queens.

Reeve and Ratnieks (this volume) modelled how reproductive skew among mated queens may be affected by ecological, genetic, and social factors. The outcome is that higher skew is favoured by (i) strong ecological constraints (i.e. low probability of succeeding in solitary founding), (ii) larger differences in fighting abilities among the females, and (iii) higher genetic relatedness among the females. On the other hand, it appears that the advantage of engaging in lethal fighting decreases with larger numbers of associating individuals; this is because a greater number of rivals must be defeated in order to achieve a given gain in reproduction in larger associations (but see Heinze this volume). An extensive discussion is provided by Reeve and Ratnieks on how these predictions correlate with the available

data in primitively eusocial insects and colony founding in highly eusocial species. Here we focus on how their model applies to mature colonies of highly eusocial species with regard to the existence of specialized reproductive castes, particularly ecological constraints on solitary founding and the role of workers in regulating queen number and queen reproductive output.

Reproductive strategies of highly eusocial species have evolved in such a way that queens have lost the ability to establish colonies on their own, or they can do so only during a very short period of their life. Ant and termite queens of independent founding species rapidly deplete and metabolize their energy reserves after mating (Wilson 1971; Keller and Passera 1989). Independent founding therefore becomes impossible within a few days after joining an existing colony. Dependent founding ant queens have lost the ability to store the energy reserves needed to undergo mating flights and independent founding (Keller and Passera 1989, 1990; Passera and Keller 1990); consequently, their only chance to survive and reproduce is to remain in the natal nest or join another established nest. The same holds true for swarm-founding queens which cannot survive without workers. The loss of the ability by these queens to start colonies probably evolved because joining yielded higher reproductive success to queens as compared to independent colony founding (see Nonacs this volume; Rosengren *et al.* this volume). Such species are interesting because they exemplify extreme cases of ecological constraints on independent colony founding (i.e. the probability of a queen starting a colony independently is 0), thereby providing one end of a comparative spectrum for investigating the influence of ecological constraints on reproductive skew.

The second particularity of highly eusocial insects is that workers are often involved in regulating the number of queens, and may possibly play a role in controlling their reproductive output (see above). Workers could increase their inclusive fitness by increasing the production of sexual offspring of the queens to which they are the more related. To do so they could either preferentially feed the queens or favour sexualization of their brood. However, to date there is no evidence that workers in polygynous colonies exhibit differential treatment toward queens, or their offspring, in relation to relatedness asymmetries (see Carlin *et al.* this volume). This, together with the fact that functional monogyny in ants always results from physical aggression among queens suggests that the number of queens and their overall reproductive output might be primarily under worker control, but that the variance in their reproductive output might be largely the result of interactions among them.

Concluding remarks

We have tried to show the degree of similarity in both the nature of inter-individual conflicts that exists at the different levels of social insect

reproductive structure and the proximate mechanisms used to resolve the conflicts. From this survey it appears that reproductive competition is a major force regulating reproductive roles. Evidently, females usually do not forgo reproduction simply because they are more related to the brood of the other female(s) than to their own, but, instead, they are actively prevented from doing so by other colony members.

Physical aggression is the primary proximate factor governing the three components of reproductive structure. The number of queens, their relative share of reproduction and the prevalence of worker egg-laying are regulated through dominance interactions which may occur among queens, among workers, and between queens and workers. In the case of primitively eusocial insects, direct aggressive interactions primarily occur among potential breeders, whereas in highly eusocial species workers seem to play a pivotal role in controlling the three components of reproductive structure. Frequently, workers can increase their own inclusive fitness by behaving differently in colonies with queens present than in queenless colonies. When queen presence results in workers favouring colony level reproductive strategies that also increase queen(s) inclusive fitness, both parties benefit from an effective communication system that signals the queen's presence. To a large extent, queen 'inhibitory' pheromones probably serve this function (see Keller and Nonacs 1993)

One common way to investigate the selective forces shaping reproductive structure of social insects is by comparing the inclusive fitness of nestmate females that differ in their reproductive roles (with the aim of testing whether a female can increase her inclusive fitness by helping raise the brood of other females). A major hurdle in such studies results from the difficulty of assessing the reproductive strategies (e.g. joining an association or not, forgoing reproduction in an association or not) available to different individuals in relation to size, fighting ability, and time of season they eclose, etc. and their expected fitness return.

An alternative way to study the selective forces acting within colonies of social insects is by correlating variation in reproductive structure with ecological factors and examining how changes in one of the components of reproduction affect the others. For example, queen number (or size of foundress association) and variation in reproductive output are most likely influenced by ecological factors such as the probability of succeeding in solitary founding and/or increased colony survivorship with higher queen number. Changes in these two components directly influence the colony generic structure, with higher queen number and lower variance in their reproductive output resulting in decreased mean relatedness among colony members. This, in turn, is likely to influence the prevalence of worker reproduction.

For each of the reproductive components there is considerable inter-specific variation. Only recently have students of social insects started to

focus on intraspecific variability in the reproductive structure, and the available data suggest that, for some species, this variability might be greater than previously suspected. Both intra- and interspecific variability provide suitable material for investigating the effects of ecological factors on the different components of reproductive structure as well as the interconnection among components. In this context, the high intra- and interspecific lability in queen number is ideal for comparative studies, especially in relation to the role of various ecological factors in shaping queen number and in assessing how worker reproduction and colony sex ratio are influenced by changes in queen number.

In conclusion we would like to stress that, although the components underlying reproductive division of labour in eusocial insect colonies have frequently been considered separately, they raise very similar evolutionary questions and are under the control of similar proximate mechanisms. Taking into account all of these components should therefore deepen our understanding of reproductive partitioning among colony members. Having a firm handle on the various factors promoting reproductive partitioning among colony members is one of the keys to solving the related evolutionary mysteries of polygyny and the existence of sterile castes.

Summary

Several previous authors have noted that the existence of stable queen associations (polygyny) in social insect colonies poses similar challenges to evolutionary theory as does the existence of eusocial organization. The similarity in these two phenomena is examined in detail by viewing both in the broader context of colony reproductive structure. We identify the major components of colony reproductive structure as (i) the reproductive division of labour (worker sterility), (ii) the number of reproducing individuals, and (iii) the variance in reproduction among cohabiting reproduceres. The characteristics of each of these components is reviewed, and the proximate and ultimate mechanisms determining these characteristics are discussed. Reinforcing the notion that the different components of reproductive structure pose similar evolutionary questions, we find that they are controlled by similar proximate mechanisms and that similar ultimate explanations apply to each. Thus comparative study of any one of these components should shed light on the others and lead to a deeper understanding of reproductive roles and reproductive partitioning in social insect colonies.

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3

Queen-queen conflicts in polygynous societies: mutual tolerance and reproductive skew

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In the years since Williams (1966) argued for an individual-selectionist approach to phenotypic evolution, theorists have steadily lengthened the list of potential conflicts within insect societies, even societies characterized by a high average genetic relatedness. Whenever any genetic heterogeneity exists within colonies, asymmetries occur among colony members in their relatednesses to potential colony propagules (Hamilton 1964). These relatedness asymmetries generate potential conflicts among colony members over who should reproduce and how colony resources should be allocated. Such potential conflicts promote the evolution of manipulative and counter-manipulative reproductive strategies by the parties in conflict.

However, potential conflict does not always translate into actual conflict, i.e. the actual expression of manipulative (and counter-manipulative) strategies. At least three mechanisms can limit the degree of actual conflict (Ratnieks and Reeve 1992). First, counter-manipulation can nullify the gain for manipulation so that neither is frequently expressed, as when worker policing inhibits attempted male-production by workers (Ratnieks 1988). Second, manipulation may be disfavoured by the negative effects it has on overall colony efficiency and productivity, as when selfish dominance behaviour reduces the time allocated to performance of colony-maintenance tasks (Cole 1986). Third, the initial spread or enhancement of manipulation may be prevented because of unavoidable errors in its execution, as when discrimination errors (i) prevent the invasion of queen-rearing nepotism (Ratnieks and Reeve 1991) or establish highly permissive discrimination thresholds for nepotists because of the risk of rejecting full-sisters (Reeve 1989) and (ii) prevent attempted worker manipulation of the sex ratio or parentage of the colony's males because of the risk of rejecting sisters (Nonacs 1992).

Even in monogynous insect societies, in which overlap of genetic interests is extensive because production of future queens is funnelled through a single breeding female, potential conflicts can arise over male parentage (Woyciechowski and Lomnicki 1987; Ratnieks 1988; Nonacs 1992), sex

