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## WORKER REPRODUCTION IN THE HIGHER EUSOCIAL HYMENOPTERA

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### ABSTRACT

*Worker reproduction (i.e., the parthenogenetic production by workers of males and, more rarely, females) is very widespread in the higher eusocial Hymenoptera (bumble bees, stingless bees, honey bees, vespine wasps, higher ants). Examples are given in the text. The mutualistic theory ("hopeful reproductive" hypothesis) of hymenopteran eusociality (semisocial route) states that the first workers were reproductive because the possibility of future reproduction was the condition for their originally working. In Hamilton's kinship theory (subsocial route) workers produce males on account of their greater relatedness to sons than to brothers. Several recent models indicate that worker male production could have facilitated the evolution of eusociality. Queen control (queen inhibition of worker fertility) arises because queens are more closely related to their own than to workers' offspring, and explains why present-day workers are most reproductive in queenless conditions. Conversely worker reproduction in queenright colonies (i.e., colonies containing the maternal queen) reflects selection on workers to evade queen control. Optimization models predict that workers should produce all or none of a colony's males. Although workers in some species produce 100 per cent of the males, reproductive workers more usually produce an extremely variable proportion of males. When workers reproduce, the expected equilibrium sex ratios change; but the information needed to assess the importance for sex-ratio determination of worker male production is lacking. Kinship theory suggests that polygyny (multiple queens) and multiple mating both promote queenright worker reproduction by reducing intracolony genetic relatedness. The analysis of data assembled on 40 ant species reveals that workers in monogynous species (i.e., with one queen per colony) reproduce mostly in queenless conditions, whereas those in polygynous species reproduce in queenless and queenright conditions equally often, in agreement with kinship theory. Monogyny could favor a reproductive worker caste because the high probability of colony orphanage allows workers greater opportunity to reproduce free from queen control.*

*The ability of workers to reproduce has important consequences for colony organization and function. These include (1) the extent and nature of queen control of worker fertility, such control being viewed as the outcome of an "arms race" with workers over male parentage; (2) the occurrence of dominance behavior, egg cannibalism, brood destruction, and possibly even matricide in colonies with reproductive workers; (3) reduced colony efficiency and the system of temporal division of labor based on worker age and ovarian development; and (4) the rarity of physical castes among workers. For all these reasons, worker reproduction is crucial to our understanding of hymenopteran eusociality.*

### INTRODUCTION

**E**USOCIAL ANIMAL societies are characterized by cooperative care of young, overlap of generations within the society, and reproductive division of labor—meaning, in eusocial Hymenoptera, the differentiation of females into queen and worker

castes (Wilson, 1971). The higher eusocial Hymenoptera are those social bees, wasps, and ants in which queens and workers differ morphologically. Such differences extend to the reproductive system: workers are morphologically incapable of mating. If such workers retain ovaries they can still reproduce, however, because in all Hymenoptera males arise par-

thenogenetically from unfertilized eggs. Females may also develop without fertilization, but this is rare. This review describes the occurrence and significance of worker reproduction, a phenomenon defined here as parthenogenetic reproduction by workers, throughout the higher eusocial Hymenoptera. I deal exclusively with this group so as to emphasize the importance of worker reproduction even when the worker caste is, by definition, morphologically adapted for helper behavior.

Hymenopteran societies, often likened to multicellular organisms to emphasize their high degree of social integration (see Wilson, 1971, 1985a), also resemble such organisms in having achieved their advanced organization only after undergoing complex evolutionary histories (West-Eberhard, 1981). This review argues that worker reproduction was a major factor in this process. I synthesize recent ideas from the literature to conclude that, through its historical role, worker reproduction greatly influenced the development of many characteristic colony traits, including queen regulation of worker fertility (queen control), the temporal division of labor, and physical caste polymorphism among workers. I also argue that worker reproduction, in colonies of those species where it still occurs, remains a powerful influence on social cohesion, colony efficiency, and sex investment ratios. Worker reproduction is often underrated because of its present frequent association with queen death and colony decline. I therefore reassert the importance of worker reproduction in our understanding of hymenopteran societies (see also Lin and Michener, 1972; Evans, 1977; West-Eberhard, 1981, 1982).

The review begins by considering the theoretical basis of worker reproduction. This section discusses explanations for why members of a helper caste should also be reproductive. It then examines the probable involvement of worker reproduction in the evolution of eusociality, outlines the nature of queen-worker conflict over worker reproduction, and describes models predicting the optimum proportion of worker-produced males, and how sex investment ratios may consequently alter. Lastly, this section reviews links between worker reproduction and the social regime, in preparation for later tests of the relevant hypotheses.

The second section is a summary from the

literature of records of worker reproduction in the higher eusocial Hymenoptera, with systematic consideration of such important details as whether workers lay eggs in the presence or absence of queens, and the proportion of worker-produced males. The section therefore supplements previous compilations of cases of worker reproduction (e.g., in Wilson, 1971; Lin and Michener, 1972; Hamilton, 1972; Oster and Wilson, 1978; Brian, 1979, 1980, 1983; Fletcher and Ross, 1985).

In the third part of the review, data assembled on ants are used to test for the first time hypotheses (referred to above) that link worker reproduction with social variables such as queen number and hence, indirectly, the level of intracolony relatedness.

The final section describes features of contemporary eusocial colonies that are conceivably direct consequences of worker reproduction. Its main theme is West-Eberhard's (1981) hypothesis that for much of their history eusocial colonies have been evolutionary battlegrounds on which queens and workers have fought over worker reproduction. This idea gains extra support if worker reproduction was implicated in eusociality's early stages. Queen control of worker fertility can then be explained as a response to the threat to queen fitness posed by worker reproduction. Despite the prevalence of such control, workers in many species have evidently retained their reproductive ability, and consequently worker reproduction continues to provoke overt intracolony reproductive competition, as exemplified by worker dominance orders. Such orders are also discussed in this section. Further, evidence is presented that selection for worker reproduction has influenced the development of a common system of temporal division of labor in social Hymenoptera, and has constrained the proliferation of specialist physical castes among workers. My conclusion is, therefore, that worker reproduction deserves recognition as an integral feature of hymenopteran eusociality.

#### THEORETICAL BASIS OF WORKER REPRODUCTION

##### *Worker Reproduction and the Evolution of Eusociality*

The existence of sterile workers was the

evolutionary puzzle that prompted all the various theories of hymenopteran eusociality (reviewed by Starr, 1979; Brian, 1983; Brockmann, 1984; Andersson, 1984; Jaisson, 1985). But what needed explaining in many cases was a worker caste that managed to combine helper behavior with some degree of reproductive activity. A common strength of the two main theories of eusocial evolution is that each offered an explanation of this situation.

First, the mutualistic theory maintained that the earliest workers were individuals which joined semisocial (single generation) groups to gain the advantages of group living, then found it paid to defer reproduction and to work because all workers had some probability of reproducing later. Their work was therefore an investment in future offspring, although these were not guaranteed to all. The forerunners of the sterile caste were, in other words, "hopeful reproductives" (Lin and Michener, 1972; West-Eberhard, 1978; Ross, 1985; Fletcher and Ross, 1985).

Second, Hamilton's (1964, 1972) kinship theory also provided an explanation for reproduction in the worker caste. In the Hymenoptera the haplodiploid sex determination system by which females usually develop from fertilized eggs and are diploid, whereas males develop from unfertilized eggs (arrhenotoky) and are haploid, leads to unusual asymmetries in genetic relatedness among colony members. Assuming a subsocial (matrifilial) route to eusociality, Hamilton argued that on the basis of their greater relatedness to their sisters (relatedness coefficient,  $r$ , = 0.75) compared to their daughters ( $r$  = 0.5), hymenopteran workers should rear sisters; by the same token, however, they should produce sons ( $r$  = 0.5) instead of rearing brothers ( $r$  = 0.25). Trivers and Hare (1976) pointed out that Hamilton's theory implied workers had two options, either to rear sisters and produce sons, or to forfeit personal reproduction and rear a female-biased brood of sisters and brothers. Only workers following the second option would be completely sterile. Workers following the first option would combine worker behavior with reproduction.

Interestingly, Aoki and Moody (1981) concluded from allele frequency models of (subsocial) eusocial evolution that if the first workers had taken the fertile rather than the sterile

option, worker behavior would have arisen more easily. This was because conditions for the fixation of a worker behavior allele were less restrictive if workers substituted sons for brothers than if they raised a brood biased in favor of sisters (single-locus model). Also, in a more realistic two-locus model (where one locus controlled worker behavior, and the other controlled the ability of workers to raise a brood biased in favor of sisters or to substitute sons for brothers), the worker allele was favored without having to assume tight linkage of the loci if workers were egg-layers, but was only favored given such linkage when workers were not egg-layers. Hence, together the models suggested that the laying-worker route to eusociality was more likely than the nonlaying route. Significantly, several other authors, each using a different modelling approach, have also recently concluded that male-producing workers would have facilitated the subsocial evolution of eusociality (Iwasa, 1981; Bartz, 1982; Pamilo, 1984)—for example, by removing the requirement for female-biased sex ratios to create average degrees of relatedness favorable to worker evolution (Bartz, 1982). These findings emphasize that total worker sterility arose late in eusocial evolution, and suggest, as noted by Aoki and Moody (1981), that queen control of worker reproduction is a secondary feature (see final section).

#### *Worker Reproduction in Present Day Colonies*

Even if it did facilitate the origin of eusociality, the persistence of worker reproduction in present-day colonies needs explaining, because the interests of queens and workers conflict over the parentage of males (Trivers and Hare, 1976; Oster, Eshel, and Cohen, 1977; Bulmer, 1981; Starr, 1984). A queen should prefer that the colony invest in her sons and daughters ( $r$  = 0.5) rather than in her less closely related grandsons ( $r$  = 0.25), and should therefore oppose the production of males by workers in her presence. This argument underlies the explanation for the evolution of queen control later in the review. If the queen dies, however, and there are no more of her offspring to be reared, queen and worker interests concur. Both parties favor male production by workers—in the case of the departed queen because, to her, posthumous grandson production is better than no reproduction at all (Alexander, 1974:

365; Owen and Plowright, 1982). Such reasoning is supported by the strong, observed association between worker reproduction and colony orphanage (see following sections).

Cases of workers continuing to lay in queen-right conditions (i.e., with the queen present) cannot be so simply explained. These have often been ascribed to accidental failures in queen control. However, this interpretation ignores selection on workers to pursue queen-right worker reproduction and hence actively to circumvent queen control. Such selection could arise for the reasons deriving from the mutualistic and kinship theories of eusociality already discussed, or because of low worker-brood relatedness, as explained later. In any event, such selection may be very strong (Charnov, 1978a). West-Eberhard (1981) calculated that a worker *Apis mellifera scutellata* (honey bee) could increase its inclusive fitness 25-fold by producing just a single son. Lin and Michener (1972) and Alexander (1974) suggested the interesting possibility that males themselves could also be influencing workers to reproduce. Hymenopteran arrhenotoky means a male is unrelated to his mate's sons, and so can only contribute to the next male generation through reproductive worker daughters. However, no evidence exists that males somehow manipulate their worker daughters into reproducing (see Starr, 1984, for further discussion of the possible role of male interests in queen-worker conflicts). Hence the best explanation for queenright worker reproduction is that in some circumstances, despite queen opposition, it is favored by selection on workers.

#### *The Proportion of Worker-Produced Males and Sex Ratio*

If workers are to be reproductive at all, what proportion of males should they produce? Oster, Eshel, and Cohen (1977) and Oster and Wilson (1978) developed optimization models from kinship theory which predicted that workers should produce all, or none, of a colony's males. Reproductive workers do produce all males in some species, but data in the next section indicate that more often they produce only a proportion. Oster and Wilson (1978) proposed three explanations of such mixed male parentages: (1) laying workers are subsidized by energetic surpluses in the colony; (2) queen control fails; (3) competitive group

selection permits a stable equilibrium of laying and nonlaying workers. Owen and Plowright (1982) tested the first two of these hypotheses with data from the bumble bee *Bombus melanopygus*, and rejected them in this case. However, Oster and Wilson (1978) themselves acknowledged the tentative nature of their proposals, and pointed out the striking variation among social Hymenoptera in the proportion of worker-produced males (documented in the next section). This variation still awaits explanation.

When workers produce males in a colony with a queen the expected equilibrium sex investment ratios of the queen and of the nonlaying workers change: relative male investment should increase (Trivers and Hare, 1976; Oster, Eshel, and Cohen, 1977; Charnov, 1978b; Benford, 1978). The precise sex ratio depends on the proportion of worker-produced males, the number of laying workers, and which party controls investment. For example, if all males arise from one or a few laying workers, the expected sex ratio in most models proposed by the above authors is 1:1 males:females (control of investment by the queen or nonlaying workers) or 4:3 males:females (control of investment by laying workers). Alternatively, workers might produce males only in orphaned colonies. Taylor (1981) presented a model showing that when workers reproduce only when orphaned (and assuming queen control of investment) queens heading unorphaned colonies should compensate for the extra males by producing a more female-biased brood than previously, but not so biased as to restore equal investment; the result would be a male-biased overall population sex ratio. Such sex-ratio compensation by queens has been reported in bumble bees (Owen, Rodd, and Plowright, 1980) and ants (Forsyth, 1981). Taylor's model was extended to cover worker control by Nonacs (1986). Worker male production has long been recognized as a likely influence on social hymenopteran sex ratios (Trivers and Hare, 1976; Alexander and Sherman, 1977; Nonacs, 1986). However, since lack of information has often led sex-ratio studies to assume that workers are totally sterile more data are needed to test thoroughly the influence of worker reproduction on sex ratios predicted by the above models (see Nonacs, 1986, for a recent review of these issues in ants).

*Social Correlates of Worker Reproduction*

Several authors have supposed that workers are more likely to reproduce in some social regimes than in others. For example, Hamilton (1972) argued for an association between worker reproduction and monogyny (single-queen colony), and worker sterility and polygyny (multi-queen colony). Trivers and Hare (1976), rejecting the hypothetical connection between polygyny and inbreeding upon which this argument was based, reversed Hamilton's predictions. They reasoned that in a monogynous colony the queen had an intrinsic advantage in the conflict with workers over male parentage. In any physical contest over worker laying, a worker killing the queen would greatly reduce its inclusive fitness by destroying the one source of new queens. But if the queen killed the worker her loss of fitness would be minimal. However, in the presence of several queens to which it was closely related, the worker would not be handicapped in this way. Therefore, Trivers and Hare argued, workers might lay more readily in polygynous than in monogynous colonies. Similarly, worker reproduction would be more likely in annual colonies, since a worker killing the queen of a perennial colony would have more to lose. However, evidence presented later suggests that workers of some monogynous (albeit annual) bees and wasps do kill their queen to reproduce, in apparent contradiction to Trivers and Hare's hypothesis.

A more important factor governing the amount of worker reproduction is almost certainly intracolony relatedness. The converse of Hamilton's (1964) original 3/4 relatedness hypothesis for worker sterility is that a worker should not rear broods less closely related to it (on the average) than any offspring it might bear). This again implies that polygyny (which reduces worker-brood relatedness) promotes worker reproduction, and monogyny (which raises worker-brood relatedness) promotes worker sterility although, as already described, kinship theory permits worker reproduction in monogynous colonies if workers substitute sons for brothers. Similar considerations suggest worker reproduction is promoted by multiple mating of queens, since multiple mating also reduces relatedness assuming simultaneous usage of sperm from different males (as confirmed by Ross, 1986, in vespine queens).

These effects of polygyny and multiple mating could be mitigated, however, if workers recognize and selectively rear the brood most closely related to them, a possibility now receiving much attention (e.g., Visscher, 1986; review of Gadagkar, 1985). At the end of the next section some of the relations predicted above between gyny levels and worker reproduction are tested with data from ants and it is tentatively concluded that, although most species with reproductive workers are monogynous, workers in those species tend to reproduce less in queenright and more in queenless conditions than workers of polygynous species. This conclusion is in keeping with the arguments from relatedness.

## THE OCCURRENCE OF WORKER REPRODUCTION

This section is a survey of records of worker reproduction in the higher eusocial Hymenoptera. These, as explained in the Introduction, constitute those groups where workers are morphologically distinct from queens (bumble bees, stingless bees, honey bees, vespine wasps, higher ants). Groups where workers are mainly behaviorally defined (halictine bees, polistine wasps, polybiine wasps, some primitive ants) are not included: aspects of reproduction by workers in these groups are reviewed by Fletcher and Ross (1985). The morphological-behavioral distinction is not clear-cut. I make it because I wish to consider reproduction only by workers unequivocally adapted for a helper role, as evidenced most convincingly by differences in morphology between queens and workers. Such differences include reduced worker body size, lack of wings (in worker ants) and, as already indicated, worker inability to mate and reproduce sexually (e.g., through loss of the spermatheca or through vaginal constriction). By concentrating on morphologically distinct workers, workers that could found their own colonies are excluded from consideration. Confusion of worker reproduction with male production by uniseminated queens is also avoided. Caste differences in social insect reproductive systems are reviewed by Brian (1979). Since workers incapable of mating are being considered, their offspring are nearly always parthenogenetically produced males (owing to hymenopteran arrhenotoky). However, cases of worker thelytoky—i.e., the partheno-

genetic production of females (see Crozier, 1975)—are also covered, since they hold a similar interest.

Where possible, particular attention is paid to (1) whether worker reproduction occurs in queenright or queenless conditions; (2) the proportion of all males that workers produce; (3) the frequency of egg-layers in the worker population; (4) whether fertile workers show dominance behavior.

#### *Bumble Bees (Bombinae)*

Worker reproduction is widespread in bumble bees, but the proportion of males that workers produce varies greatly. Zucchi (cited in Kerr, 1969: 158) found that workers of the perennial and polygynous *Bombus atratus* produced nearly all (up to 98%) of the males, apparently in the presence of queens. In a *B. terrestris* colony studied by van Honk, Röseler, Velthuis, and Hooegeven (1981), 82 per cent of males were worker-derived; laying began with the queen present, and eventually involved 25 of the colony's 99 workers. *B. melanopygus* workers produced 19 per cent of the males in queenright colonies, and accounted for 39 per cent of the males overall, since laying continued after the queen's death (Owen and Plowright, 1982). In fact, worker laying when the queen is dead occurs "in almost all bumble bee species" (Owen and Plowright, 1982: 92). In orphaned colonies of *B. terricola* reproductive workers were thought to account for the male-bias of the population sex ratio (Owen, Rodd, and Plowright, 1980). On the other hand, in several bumble bee species in Canada the percentage of males coming from workers was low, reaching zero in *B. polaris* (Richards, 1977).

Reproduction in worker bumble bees frequently involves aggressive dominance behavior among workers and between workers and the queen (*Bombus pratorum*, *B. agrorum*: Free, 1955; *B. ignitus*: Katayama, 1971; *B. hypocrita*: Katayama, 1974; *B. terrestris*: van Honk, Röseler, Velthuis, and Hooegeven, 1981; van Honk and Hogeweg, 1981; van Honk, 1982; Hogeweg and Hesper, 1983; van Doorn and Heringa, 1986; reviewed by Michener, 1974; Röseler and Röseler, 1977; Morse, 1982; Plowright and Laverty, 1984). This aggression often includes reciprocal oophagy (egg-cannibalism) by workers and queens (e.g., *Bombus lapidarius*:

Free, Weinberg, and Whiten, 1969; *B. ruderals*: Pomeroy, 1979).

#### *Stingless Bees (Meliponini)*

Egg-laying by workers in stingless bees is very common and has been reviewed by Sakagami (1982). When the queen is present workers of many species produce nonviable trophic (nutritional) eggs, which the queen eats during the complicated cell-provisioning and queen-oviposition process characteristic of these bees (see Wilson, 1971: 93). Workers frequently only lay reproductive eggs in queenless conditions (Sakagami, 1982). However, queenright worker reproduction occurs in some species. For example, in *Trigona postica* colonies, Beig (1972) reported that the queen laid one egg per cell, and that such cells nearly always yielded females. In 27 per cent of the cells, however, fertile workers (numbering an estimated 23 per colony) laid an extra egg. These two-egg cells always yielded males because, in each such cell, the worker-produced male larva killed the female larva or the egg produced by the queen (Beig, 1972; see also Beig, Bueno, da Cunha, and de Moreas, 1982). Therefore in queenright colonies of this species workers produce nearly all of the males, at the expense of 27 per cent of the queen's almost exclusively female offspring. Beig also found most males came from workers in three more stingless bee species (cited in Kerr, 1969: 169). In another species, *Melipona subnitida*, Contel and Kerr (1976) showed by electrophoretic analysis that queenright laying workers produced an average 39 per cent of the males. In *Melipona favosa* worker laying appeared to be associated with aggression among workers, at least in orphaned colonies (Sommeijer and Velthuis, 1977; Sommeijer, 1984).

#### *Honey Bees (Apini)*

Even the worker honey bee, the epitome of the self-sacrificing worker social insect, has the capacity for personal reproduction. When worker honey bees are kept in queenless groups, some develop their ovaries and start to lay eggs, and aggression breaks out in the group (*Apis indica*: Sakagami, 1954; *A. cerana*: Sakagami, 1958; Bai and Reddy, 1975; *A. mellifera*: Sakagami, 1958; Jay, 1968, 1970, 1972, 1975; Jay and Jay, 1976; Velthuis, 1970; Hesse, 1979; Korst and Velthuis, 1982; reviewed by

Michener, 1974; Velthuis, 1977, 1985; Seeley, 1985). The aggression is frequently directed at the workers with ovarian development (Sakagami, 1954; Velthuis, 1970, 1977). Honey bee workers within a hive constitute patrines, because the single queen mates multiply (review by Seeley, 1985). Evers and Seeley (1986) recently found that in queenless groups half sisters were preferentially attacked over full sisters: this is the first evidence to suggest the existence of kin-defined factions among reproductive workers (see final section). Intriguingly, one laying worker in a queenless colony may start both to behave and to attract a retinue like a queen (Sakagami, 1958). Further, this "false queen" appears to inhibit ovarian development in the other workers (Sakagami, 1958). Velthuis, Verheijen, and Gottenbos (1965) found that extracts from ordinary laying workers could also restrict ovarian development in other bees (see also Jay and Nelson, 1973). In fact, in *Apis mellifera capensis*, both "false queens" and laying workers produce 9-ODA (9-oxo-trans-2-decenoic acid), a major component of honey bee queen substance, i.e., the pheromonal mix with which the hive queen suppresses worker ovarian growth (Ruttner, Koeniger, and Veith, 1976; Velthuis, 1985).

In natural colonies it might seem worker bees never experience the queenless conditions necessary for laying, since a new queen is always reared in preparation for swarming and the old queen's departure. Orphaning could occur, however, if the old queen died in winter when there was no brood to supply her replacement; or in the summer if a young queen failed to return from her nuptial flight having previously killed her royal sisters (J. B. Free, pers. commun.). Interestingly, Page and Metcalf (1984: 696) suggested that the frequency of orphaned nests in *A. mellifera* populations is "relatively high." One orphaned hive they studied produced over 6000 male bees. The proportion of worker-produced males in natural honey bee populations may therefore be significant. Further, Free and Williams (1974) showed that laying *A. mellifera* workers preferred to oviposit in drone cells rather than in the smaller worker cells (which would yield undersize males), unlike queens laying only unfertilized eggs, who displayed no such preference. This discrimination by laying workers is additional evidence for the impor-

ance of worker male production in orphaned hives (Page and Metcalf, 1984). In the giant honey bee, *A. dorsata*, male production by naturally occurring queenless workers has also been reported (Velthuis, Clement, Morse, and Laigo, 1971).

Laying by worker bees may not be confined to queenless nests. Taber (1980) reported that even in active queenright colonies about one in every hundred workers had ovaries in egg-laying condition. Although in honey bees (as in some ants) ovary-developed workers are not always layers (Ribbands, 1953; Sakagami, 1958; Velthuis, 1977), these workers were described as a "possible source of a few males" by Fletcher and Ross (1985: 328). Since a hive contains 20,000 to 80,000 workers (Wilson, 1971), one per cent represents many potential worker egg-layers. Even if unable to produce eggs in normal circumstances, such workers might take advantage of periods in the colony cycle (e.g., during swarming), when queen control is temporarily weak or absent, to start laying. On the other hand, they might still be prevented from this by the inhibitory effect queen-produced broods evidently have on worker ovarian development (Jay, 1970, 1972; Jay and Jay, 1976; Kropáčová and Haslbachová, 1971; Seeley, 1985). Despite this, however, Kropáčová and Haslbachová (1969, 1970) found worker ovarian development to be greatest shortly after swarming, and Velthuis (1985: 348) wrote "once swarming preparations are being made, workers often have well developed oocytes and may occasionally lay an egg." Also, Fletcher (in Fletcher and Ross, 1985) found that in emergency queen rearing, laying *A. m. adansonii* workers could arise rapidly enough to produce drone pupae before the new queen's appearance. In general, however, the extent of the production of males by workers in natural queenright colonies appears to be a little-explored area of honey bee biology.

The South African honey bee race *A. m. capensis* is exceptional in having workers that produce female offspring (both workers and queens) by thelytoky involving automictic parthenogenesis (Wilson, 1971; Ruttner, 1977; Verma and Ruttner, 1983). Moritz and Hillesheim (1985) presented evidence that the correlates of reproductive dominance in *A. m. capensis* workers are largely genetically determined, and thereby drew attention to the in-



fluence of selection for worker reproduction in *A. m. capensis* colonies. *A. m. capensis* workers also reportedly intrude into hives of other races and start egg-laying when the resident queen has gone (Anderson, cited in Kerr, 1969: 169; Ruttner, 1977). In wasps, Akre, Garnett, MacDonald, Greene, and Landolt (1976) described how a few *Vespula consobrina* workers entered a neighboring *V. atropilosa* nest and produced males there. These two cases may therefore represent an extremely intriguing phenomenon—worker reproduction by social parasitism.

#### *Vespine Wasps (Vespinae)*

Previous reviews of vespine worker reproduction include those of Richards (1971), Spradbery (1973), Jeanne (1980), and Akre (1982). Ishay (1964) found that workers of the oriental hornet *Vespa orientalis* laid eggs both in orphaned colonies (up to 40 to 50% of all colonies) and in queenright colonies at the season's end. He suggested that workers produced an "important percentage" of late-season males. The queen's death was accompanied by (1) fighting between workers, sometimes fatal; (2) partitioning of the nest into egg-laying territories; and (3) worker killing of queen-produced larvae. Often the queen herself was killed by the workers: she was literally licked to death by them (Ishay, 1964). In both *V. orientalis* and the European *Vespa crabro* small groups of workers can also reportedly found new nests in which they rear males (Hamilton, 1972, pers. commun.; Ishay, 1976, pers. commun.; Kugler, Motro, and Ishay, 1979). Workers of *Dolichovespula maculata* habitually lay in the queen's presence. She attacks them and eats their eggs, and workers also eat each other's eggs (Greene, 1979). A similar situation exists in *D. arenaria* (Greene, Akre, and Landolt, 1976).

In the genus *Vespula* workers removed from the queen's influence also laid eggs, fought, and ate the eggs of rivals (Landolt, Akre, and Greene, 1977). Queenright laying has been reported, too, in *V. vulgaris*, *V. germanica* (Montagner, 1966; Spradbery, 1971) and *V. consobrina* (Akre, 1982). Montagner estimated that in half of his colonies workers produced 75 to 100 per cent of the males. Worker laying was associated with occasionally fatal aggression among workers and between workers and the queen (Montagner, 1966). Further, Archer (1981) found

field evidence suggesting laying *V. vulgaris* workers destroyed the queen's male brood while sparing their own. After finding only 4 per cent of workers in natural *V. vulgaris* populations had developed ovaries, however, Spradbery (1971: 513) concluded that such workers "would be unlikely to make a significant contribution to male production." Similar conclusions have recently been reached in other *Vespula* studies. Akre et al. (1976), in prolonged observations of *V. pennsylvanica* and *V. atropilosa*, never witnessed worker oviposition. Ross (1985), investigating several North American species, discovered that only 1.6 per cent of the workers had ovarian development in queenright colonies, a figure rising to 30 to 45 per cent in colonies lacking a queen. He considered the proportion of worker-produced males "insignificant" (Ross, 1985: 420). In addition, he questioned the reproductive success of worker-produced males, which would have emerged late in the season when mates are few (Ross, 1985; Fletcher and Ross, 1985). Montagner's findings may have resulted from artificial weakening of queen control, since his experimental techniques involved temporarily removing and radio-labelling the queen (Hamilton, 1972; Ross, 1985). In the first electrophoretic investigation of vespine male parentage, Ross (1986) also showed that in queenright *V. maculifrons* and *V. squamosa* colonies in the field, males almost certainly originated exclusively from the queen. However, workers did produce males when queenless. Hence, overall, vespine workers appear to be reproductive mostly in queenless conditions, suggesting that future research on vespine worker male production should concentrate on the natural frequency and productivity of orphaned colonies, and on the reproductive success of their progeny.

#### *Ants (Formicidae)*

As pointed out by Cole (1986), ants present a variety of worker reproductive systems. They include species in which workers possess both ovaries and a spermatheca, species in which they have ovaries only, and species in which the complete reproductive apparatus has been lost.

Workers with ovaries and a spermatheca occur in primitive ant species—e.g., *Nothomyrmecia macrops* (Hölldobler and Taylor, 1983), and the ponerines (Brian, 1979; Ward, 1983;

Peeters and Crewe, 1985). Their potential to mate and reproduce sexually, however, excludes them from this review. Table 1 lists species where workers have ovaries but no spermatheca in which either (1) male production by workers occurs, or (2) worker laying of reproductive eggs has been reported. Table 1 therefore groups together examples of worker reproduction of widely varying quality, depending on the method of determining worker reproduction (specified in the table). The interpretation of egg-laying and ovarian development in ants is complicated by the following pair of widespread phenomena: (1) As in stingless bees, in many ants workers produce nonviable trophic eggs as food for other colony members (Wilson, 1971: 281) (cases of trophic egg-laying alone are therefore not included in Table 1). (2) In some species workers' ovaries undergo a cycle of growth and resorption correlated with the temporal division of labor, without eggs being laid (e.g., *Formica* spp., Dumpert, 1981: 117; also see final section below). Therefore ovarian dissections alone provide the weakest evidence for worker reproduction. Discussion of the data from Table 1 is reserved until the next section.

Workers entirely lacking reproductive organs, or with vestigial ovaries, occur in species of the ant genera *Solenopsis*, *Monomorium*, *Pheidole*, *Tetramorium*, and *Eciton* (Wilson, 1971; Oster and Wilson, 1978; Fletcher and Ross, 1985). Here worker reproduction is obviously impossible.

Asexual production of female offspring (thelytoky) occurs in the workers of a small but growing number of ant species (Table 2; see also the reviews of Wilson, 1971: 325; and Crozier, 1975). In some species—e.g., *Lasius niger*—the prevalence of worker thelytoky in natural populations seems unknown. In others—e.g., *Crematogaster* spp. (Soulié, 1960) and *Pristomyrmex pungens* (Itow et al., 1984)—worker thelytoky is part of an unusual life cycle. Thelytokous workers can often also produce males (Table 2). The conditions favoring the evolution of worker thelytoky appear poorly understood.

#### WORKER REPRODUCTION AND GYNY LEVELS: COMPARATIVE TEST OF THE HYPOTHESES

In this section the data on ants in Table 1 are used to test the hypotheses described earlier that predict whether worker reproduction

should be associated with monogyny or polygyny (see Social Correlates of Worker Reproduction, above).

Of 40 species in Table 1 whose gyny is known, 29 are monogynous and 11 are polygynous. Buschinger (1974) found in a survey of European ants that the ratio of monogynous to polygynous species is 50:50. Hence, if this ratio is universal, a significantly greater number of species with reproductive workers are monogynous than expected by chance ( $\chi^2$  test,  $\chi^2 = 8.1$ , d.f. = 1,  $p < 0.01$ ), suggesting an association between worker reproduction and monogyny. This conclusion is tentative because (1) some authorities (e.g., Hölldobler and Wilson, 1977) state that most ant species are monogynous; (2) the analysis ignores the influence of multiple mating by queens, since present data are too scant (Table 1). In addition, a more refined comparative method would replace individual species with separately evolved lineages as the unit of test of the null hypothesis (that worker reproduction is equally likely to be associated with monogyny as with polygyny). This is because closely related species are less likely to constitute independent tests due to their common descent (Ridley, 1983). However, ant phylogeny is too poorly known for such a procedure to be followed here. The use of individual species was arguably justified anyhow, since gyny levels are not uniform within ant taxa (Table 1).

Despite the above reservations, the finding that worker reproduction is associated with monogyny could be informative when coupled with further analysis of Table 1. Data in the table also indicate that in monogynous species worker reproduction occurs mostly in queenless conditions, whereas in polygynous species it occurs in queenless and queenright conditions equally often. Of 29 monogynous species, workers reportedly reproduce in the absence of the queen in 21 and in her presence in 8; of 11 polygynous species, however, workers reproduce with queens absent in 6 and with queens present in 5 (Table 1). The apparent association between monogyny and queenless worker reproduction, however, is not statistically significant ( $\chi^2$  test for association,  $\chi^2$  corr. = 0.49, d.f. = 1,  $p > 0.1$ ), although this could be the fault of small sample sizes. In addition, the data in Table 1 concerning whether workers reproduce in the presence or absence of queens may simply reflect the

TABLE 1  
*Reproduction (male production) in worker ants*

Species	Gyny <sup>a</sup> Method <sup>b</sup>		Remarks <sup>c,d</sup>	References <sup>e,f</sup>
<b>Myrmeciinae</b>				
<i>Myrmecia</i> and <i>Promyrmecia</i> spp.	M	OM	QA	Haskins and Haskins, 1950
<i>M. gulosa</i>	M	OM	QA	Freeland, 1958
<b>Ponerinae</b>				
<i>Odontomachus haematodes</i>	P	OL,OM	QP	Colombel, 1971, 1972
<i>Neoponera obscuricornis</i>	M(P)	D,OL	QP	Fresneau, 1984
<b>Dorylinae</b>				
<i>Anomma</i> spp.	M	OM	QA; but worker-produced male larvae reportedly fail to reach adulthood	Raignier, 1972
<b>Myrmicinae</b>				
<i>Myrmica rubra</i>	P	D,OL, OM,R,V	QP; all males possibly from workers	Weir, 1959; Brian, 1953, 1969; Brian and Rigby, 1978; Smeeton, 1981, 1982a,b,c
<i>M. sulcinodis</i>	M(P)	C	QA; orphaned colonies produced 45% of males	Elmes, 1974
<i>Aphaenogaster rudis</i>	M	E	QA	Crozier, 1974
<i>A. subterranea</i>		OM	QA	Bruniquel, 1972
<i>A. senilis</i>	M	OM	QA	Ledoux and Dargagnon, 1973
<i>Stenammina fulvum</i>		OM	QA	Fielde, 1905
<i>Leptothorax tuberosus unifasciatus</i>	M	OL	QA	Bier, 1954
<i>L. nylanderii</i>	M	D,G,OL	QP; all males from workers?	Plateaux, 1970, 1981
<i>L. ambiguus</i>	P	D	QA	Alloway et al., 1982
<i>L. curvispinosus</i>	P	D	QA	Alloway et al., 1982
<i>L. longispinosus</i>	P	D,U	QP	Alloway et al., 1982; Herbers, 1984
<i>L. allardycei</i>	M	D,OM,V	QP; workers form dominance hierarchy and lay 22% of eggs	Cole, 1981, 1986
<i>Temnothorax recedens</i>	M	OL,U	QP	Dejean and Passera, 1974
<i>Harpagoxenus americanus</i>	M	C,D	QP; workers form dominance hierarchy	Buschinger and Alloway, 1977; Franks and Scovell, 1983
<i>H. sublaevis</i>	M	C,D,E, OL,OM	QA, possibly QP; workers form dominance hierarchy; orphaned colonies produced up to 22% of males	Buschinger and Winter, 1978; Bourke, in press; Bourke, van der Have, and Franks, in press
<i>H. canadensis</i>	M	D	QP	Buschinger and Alloway, 1978
<i>Epimyrma ravouxi</i>	M	C	QA; orphaned colonies produced 27% of males	Buschinger and Winter, 1983; Winter and Buschinger, 1983
<i>Messor capitatus</i>	M	OL	QA	Delage, 1968
<i>Novomessor cockerelli</i>	M	OM	QA; worker aggression	Hölldobler and Bartz, 1985, p. 248
<i>Aptostigma dentigerum</i>	M	C,D	QA; orphaned colonies produced 43% of males	Forsyth, 1981
<i>Crematogaster impressa</i>	M(P)	C	QA	Delage-Darchen, 1974
<i>Zacryptocerus varians</i>	M	OM	QA	Wilson, 1976
<b>Dolichoderinae</b>				
<i>Dolichoderus quadripunctatus</i>	M	OL,OM	QA; all males from workers?	Torossian, 1968

TABLE 1 (continued)

Reproduction (male production) in worker ants

Species	Gyny <sup>a</sup>	Method <sup>b</sup>	Remarks <sup>c,d</sup>	References <sup>e,f</sup>
Formicinae				
<i>Plagiolepis pygmaea</i>	P	OL,U	QA	Passera, 1966
<i>Lasius niger</i>	M	E,OM	QP; possibly also thelytokous (see Table 2)	Lubbock, 1885; van der Have, Boomsma, and Menken, 1988.
<i>Formica polyctena</i>	P	OL,OM	QP	Ehrhardt, 1962; but see Schmidt, 1982
<i>F. sanguinea</i>	P	E	QP	Pamilo and Varvio-Aho, 1979; Pamilo, 1982
<i>F. exsecta</i>	P,M	E,OM	QA	Pamilo and Rosengren, 1983
<i>F. fusca</i>	P,M	OM	QA	Lubbock, 1885
<i>F. cinerea</i>	P,M	OM	QA	Lubbock, 1885
<i>F. pergandei</i>		OL,OM	QA	Hung, 1973
<i>F. canadensis</i>		D,OM	QA	Hung, 1973
<i>F. argentata</i>		OM	QA	Fielde, 1905
<i>Polyergus rufescens</i>	M	OM	QA	Lubbock, 1885
<i>P. breviceps</i>	M	OM	QA	Hung, 1973
<i>Campanotus herculeanus</i>	M	OM	QA	Fielde, 1905
<i>C. aethiops</i>	M	D,OL,OM	QA	Dartigues and Passera, 1979
<i>Oecophylla longinoda</i>	M	OL,OM	QA; allegedly also thelytokous (but see Table 2)	Hölldobler and Wilson, 1983
<i>O. smaragdina</i>	M	OL,OM	QA	Hölldobler and Wilson, 1983

<sup>a</sup> Gyny levels (where known): M = monogynous; M(P) = almost all colonies monogynous; P = polygynous; P,M = gyny levels reportedly differ between populations. Information on gyny comes from references in far right column and Buschinger, 1968, 1974; Collingwood, 1979. For comparisons in the text, M and M(P) species were classified together, P with P,M species. Buschinger (1974) discusses fully the classification of gyny levels.

<sup>b</sup> Method specified in references for determining worker male-production or worker laying of reproductive eggs: C = census of production from queenless colonies; D = ovarian dissection; E = electrophoretic allozyme analysis; G = analysis of visible genetic markers; OL = worker egg-laying observed; OM = worker male-production observed (e.g., in captive worker-only groups); R = worker egg-laying indicated by radio-labelling; V = worker egg-laying indicated with vital dyes; U = reference asserts worker male-production but evidence unspecified.

<sup>c</sup> QA = worker reproduction reported in absence of queen(s); QP = worker reproduction reported with queen(s) present.

<sup>d</sup> The number of queen matings is known for 9 species in the table: *Aphaenogaster rudis*, *Harpagoxenus sublaevis*, *H. canadensis* (1 mating); *Lasius niger*, *Formica polyctena*, *F. sanguinea*, *F. pergandei* (>1); *F. exsecta* (1-2); *Myrmica rubra* (5-6). Sources: Cole, (1983), Starr (1984), Page (1986), and contained references.

<sup>e</sup> In over 60 species of leptothoracine (Myrmicinae) kept by A. Buschinger (pers. commun.) queenless workers produced males.

<sup>f</sup> Bier (1953) reported egg-laying by queenless workers in several additional formicine and myrmicine species.

greater ease with which worker reproduction is detectable in worker-only groups, rather than the natural situation.

The suggestion that workers in monogynous ant species, if reproductive, reproduce mostly in queenless conditions is nevertheless interesting for several reasons. First, it removes the apparent contradiction between the prediction that workers in monogynous species should tend to be nonreproductive owing to high worker-brood relatedness, and the previous re-

sult suggesting that most ant species with reproductive workers are monogynous. This is because, as earlier described, this prediction does not apply following the death of the queen and the rearing of her remaining brood, when — as confirmed by the current findings — worker reproduction is expected. Second, given the alternative view in kinship theory that workers in monogynous species should be reproductive even in queenright conditions provided they substitute sons for brothers, the

TABLE 2  
*Thelytoky in workers ants*

Species	Caste(s) workers produce	References
Myrmicinae		
<i>Pristomyrmex pungens</i>	Workers (queens and males rare: all reproduction is by workers)	Itow et al., 1984
<i>Crematogaster</i> spp.	Queens	Soulié, 1960
Formicinae		
<i>Oecophylla longinoda</i>	Workers, queens, males	Ledoux, 1950; but Hölldobler and Wilson (1983) could not confirm thelytoky here
<i>Lasius niger</i>	Workers, males	Crawley, 1911
<i>Cataglyphis cursor</i>	Workers, queens, males	Cagniant, 1979, 1982

above result suggests that queen inhibition of worker fertility has been important in the queen-worker conflict over worker reproduction (see following section). Third, the suspected link in monogynous species between worker reproduction and queenlessness could partially explain the tentative association between worker reproduction and monogyny itself. The greater probability of worker-only groups arising as a result of queen mortality in monogynous species than in polygynous ones could mean that there has been greater selection on workers in monogynous species to retain their reproductive capability, by virtue of their having more opportunity to exercise it unhindered by queens. Evidence for the effectiveness of reproduction by orphaned workers in monogynous species comes from three such species (Table 1), *Myrmica sulcinodis*, *Epimyrma ravouxi*, and *Apterostigma dentigerum*, in which queenless colonies produce a substantial proportion of the males. Clearly, however, better data on worker reproduction in nature, gyny levels, number of queen matings, and frequency of orphanage are necessary to confirm or refute these conclusions.

Workers in three species in Table 1 are suspected of producing all or nearly all the males. Two species are monogynous (number of queen matings unknown) and the third, *Myrmica rubra*, is polygynous with multiply mated queens. Hence, *M. rubra* exhibits extremely low intracolony relatedness, as confirmed electrophoretically by Pearson (1983). *M. rubra* workers reproduce in queenright conditions. Therefore, taken together with the relatively

high proportion of polygynous species with queenright laying workers (Table 1 and above), the scale of worker reproduction in *M. rubra* supports the hypothesis that queenright worker reproduction is favored by low worker-brood relatedness.

#### CONSEQUENCES OF WORKER REPRODUCTION

This section argues that, in the past and continuing in the present, the ability of workers to reproduce has had important consequences for other members of the colony and for colony organization. One such consequence, the effect that worker-produced males have on sex ratios, has already been discussed. The role of the production of males by workers in hymenopteran population genetics has been researched by Owen (1980, 1985, 1986).

#### *The Evolution of Queen Control*

Queen suppression of worker reproduction (queen control), both pheromonal and behavioral, is very common in social Hymenoptera (reviewed by Brian, 1979, 1980; Fletcher and Ross, 1985; Hölldobler and Bartz, 1985). One explanation for this is the theory that parental manipulation of worker reproductive behavior was itself primarily responsible for the evolution of worker sterility (Alexander, 1974; Michener and Brothers, 1974). However, since worker reproduction could have been implicated in eusociality's early stages (see Worker Reproduction and the Evolution of Eusociality, above) and clearly persists in eusocial colonies, it is also arguable that queen control evolved secondarily, over an extended period,

as a response to worker reproduction. Faced with reproductive workers, queens would have been selected (because of the greater relatedness of queens to their own offspring) to compel the workforce to rear queen-produced brood exclusively. Workers could then have been counterselected to resist reproductive inhibition and cling to their egg-laying ability, thus provoking repeated escalations in queen control. Evidence exists to support this dynamic view of the evolution of queen control, for in numerous lineages there appears to have been what amounts to an intraspecific evolutionary "arms race" (Dawkins and Krebs, 1979) between the queen and worker castes over worker reproduction (West-Eberhard, 1981). Supporting examples include the "multiplicity of queen control substances and the fact that each is only partially effective" in honey bees (West-Eberhard, 1981: 14), and the complex queen egg-laying ritual of stingless bees, which appears to be a relic of former dominance struggles with workers over egg-laying and oophagy (Hamilton, 1972; West-Eberhard, 1981; Sommeijer, Houtekamer, and Bos, 1984). Queen control as it now exists could therefore be largely a consequence of worker reproduction.

According to this view, queens of many species have evidently achieved total control of worker fertility in their lifetimes; for, though the workers possess ovaries, they only reproduce in queenless conditions (see Table 1 and previous section). In ants where such workers lay trophic eggs in the queen's presence (e.g., *Plagiolepis pygmaea* — Passera, 1966), this could be a contrivance for investing in the colony when the queen is alive, while keeping the ovaries active in preparation for her death (West-Eberhard, 1981). Ants in which the workers' ovaries are absent or nonfunctional may provide examples of absolute queen control. In these species queens may have permanently sterilized the workers by influencing their larval development, thereby avoiding the costs of continually having to inhibit reproduction by adult workers (Fletcher and Ross, 1985). If such a process has occurred, total worker sterility has indeed resulted from parental manipulation, but only after a prolonged queen-worker arms race over worker reproduction. In addition, queens may only have secured their victory where workers have eventually

consented — i.e., where selection on workers to resist manipulation has been weak (Anderson, 1984). It seems very likely that workers under monogyny would acquiesce more readily to sterility than workers in polygynous species, because of the high relatedness levels associated with monogyny. This would explain why monogynous ants, as well as including species characterized by queenless worker reproduction (see previous section) also include other species with totally sterile workers, the greatest queen-worker dimorphism, and the most powerful queen control (West-Eberhard, 1982; Hölldobler and Bartz, 1985). By contrast, in those species, whether monogynous or polygynous, where workers remain fertile and regularly lay eggs in queenright conditions, the queen-worker arms race must have had a fundamentally different outcome or be at an earlier stage, compared to the situation in species in which queen control is absolute.

In some species potentially fertile workers apparently escape the queen's influence in order to reproduce by simply distancing themselves from her. They do this either by occupying the periphery of large nests, as may occur in *Odontomachus haematodes* (Colombel, 1972), or by establishing satellite colonies (e.g., *Harpagoxenus americanus*, Franks and Scovell, 1983). It has been suggested that such behavior accounts for many of the cases of polydomy (multiple nests) in ants (Fletcher and Ross, 1985), although this cannot be true in the polydomous species *Leptothorax longispinosus*, in which queenless colony fragments raised female-biased broods (Herbers, 1984).

#### *Physical Conflicts between Colony Members*

In every group considered in this review, worker reproduction was associated with aggression among worker nestmates. This behavior undoubtedly stems from reproductive competition. Worker reproductives are evidently selected for attacking their fellows so as to inhibit rival reproductive activity, thereby safeguarding their own genetic representation among worker-produced males. This can lead to worker dominance hierarchies in which rank correlates with ovarian development, notably in bumble bees (and only recently detected in ants: Cole, 1981; Franks and Scovell, 1983; Bourke, in press). In addition, as novel con-

firmation of the importance of kinship in insect societies, there is evidence that when not full sisters, reproductive workers form rival, kin-defined factions (Evers and Seeley, 1986; see also Hölldobler, 1984: 360; Carlin and Hölldobler, 1987). In honey bees, workers have the queen-like ability to inhibit other egg-layers pheromonally as well as physically (Velthuis, 1985).

Worker reproduction also underlies other kinds of violent behavior found in hymenopteran colonies, such as oophagy and brood destruction. A remarkable example in the stingless bee *Trigona postica* was described earlier; here, male worker-produced larvae killed female larvae produced by the queen (Beig, 1972). In *Vespa orientalis* (Ishay, 1964), and possibly *Vespula vulgaris* (Archer, 1981), laying workers ejected queen-produced brood. In *V. vulgaris* it seems that male brood was selectively destroyed. Kinship theory predicts such selectivity as a consequence of worker laying. In bumble bees, however, brood destruction does not always appear linked with worker laying (Pomeroy, 1979; Plowright and Lavery, 1984). Fisher (1987), however, concluded that in *Bombus affinis*, the ejection of larvae, which occurred almost exclusively after the queen lost dominance, did stem from kin-selected queen-worker conflict. Alternative explanations for such behavior include such ecological factors as protein shortage (Wilson, 1971).

Finally, evidence exists that selection on workers to reproduce free from queen control may even provoke matricide. *Vespa orientalis* workers, prior to reproducing, killed their queen (Ishay, 1964); and in colonies of *Bombus ignitus* (Katayama, 1971) and *B. terrestris* (van Honk, Röseler, Velthuis, and Hoogeveen, 1981), the queen died after being expelled by laying workers. Because these are monogynous species, such behavior patterns are especially striking; and they are quite distinct from the phenomenon of worker culling of supernumerary queens found in some ants, which ends in monogyny—i.e., with one surviving queen (Forsyth, 1980). Further, these examples apparently contradict Trivers and Hare's (1976) argument described earlier (see Social Correlates of Worker Reproduction, above), that workers in monogynous colonies should avoid mortal conflict with the queen over reproduction. However, this conclusion requires qualifi-

cation. Montagner (1966) found that *Vespula* workers killed their single queen if, following radioactive treatment, she laid only male eggs. This suggests that in *Vespa* and *Bombus* matricide occurred because the queen had exhausted her sperm store and hence was producing solely haploid, male brood. This would not refute Trivers and Hare's hypothesis, which predicted that workers should not attack queens who might in future yield new queens. However, the sperm depletion argument emphasizes the severity of queen-worker conflict over male parentage, if it implies that workers kill their queen to reproduce only when she can produce nothing but males.

#### *Colony Efficiency and the Temporal Division of Labor*

The economic efficiency of the colony will tend to be reduced when workers are reproductive. For example, Cole (1986) estimated that in colonies of the ant *Leptothorax allardycei*, worker dominance activity reduced the time spent on brood care by 15 per cent. Worker reproduction may also damage colony efficiency indirectly. Laying workers could be reluctant to forage or participate in colony defence, because these risky tasks would jeopardize their reproductive futures (Franks and Scovell, 1983) (but see below). Furthermore, since the longevity of workers will be partially under individual-level selection if they are reproductive (Oster and Wilson, 1978), laying workers may render a colony unlikely to exhibit an "adaptive demography"—i.e., the worker age-frequency distribution best adapted to the colony's economic needs (Oster and Wilson, 1978; Wilson, 1985a,b).

In its lifetime an individual reproductive worker could both engage in personal reproduction and help raise kin. This is implicit in the idea that workers may have been selected to produce sons and rear sisters. To maximize its fitness, such a worker should remain in the nest and lay eggs when young and switch to colony-beneficial tasks outside the nest when old, since these include risky activities such as foraging. Intriguingly, it has been proposed that a mixed strategy of this sort for worker reproductives was the basis for a system of temporal division of labor commonly found in social insects (West-Eberhard, 1979, 1981; Wilson, 1985a). This is the "centrifugal"

system (Wilson, 1985a), in which young workers perform brood nursing and other tasks inside the nest, whereas external tasks such as foraging are performed by older workers. This system promotes colony efficiency because it maximizes the numbers of available nurses and foragers.

Evidence exists, however, that former selection on young workers to reproduce helped shape this system of temporal division of labor. This is the finding that in various species that now almost certainly lack queenright worker reproduction, the behavioral changes workers undergo with age are paralleled by changes in their ovarian development. Young workers inside the nest are ovary-developed, older foraging workers have degenerated ovaries (Wilson, 1985a). Among ants, early ovarian development cannot be explained by trophic egg-laying in every case. For remarkably, in *Formica* species, young nest workers apparently never lay but resorb all of the eggs they form (Wilson, 1971: 163; Dumpert, 1981: 118). Hence it is possible that as in some species queen control suppressed reproduction by young workers pursuing the mixed strategy, the difference in ovarian development among the worker age-classes (or the associated hormonal system) evolved to serve a new purpose, namely, to act as a mechanism for dividing the labor. Otherwise, the correlation between worker behavior and ovarian development remains unexplained. Therefore, what is now an adaptation that promotes colony efficiency very probably originated in previous intracolony reproductive competition (West-Eberhard, 1979, 1982).

#### *Caste Proliferation*

A final example of the evolutionary consequences of worker reproduction involves physical worker castes. Such castes frequently exhibit bizarre body forms clearly adapted for specialist colony-beneficial purposes such as defence. Oster and Wilson (1978) therefore suggested that physical castes would only arise and proliferate in conditions of worker sterility, since selection on reproductive workers to maximize the personal component of their fitness would counter the evolution of worker adaptations detrimental to their personal welfare. Oster and Wilson confirmed their hypothesis by demonstrating a significant statisti-

cal association between monomorphism (a single worker caste) and the presence of ovaries in ant workers, on the one hand, and polymorphism (two or more castes) and a lack of ovaries, on the other. Oster and Wilson also pointed out that polymorphism is uncommon in social Hymenoptera: it is "virtually absent" in bees and wasps, and only 17 per cent of ant genera have polymorphic species; a mere 2 per cent have species with three or more castes. Although other factors — e.g., ergonomic (Oster and Wilson, 1978) or developmental (Wheeler, 1986; Franks and Norris, 1987) ones — were almost certainly also influential, these findings suggest that worker reproduction has been a major constraint on the proliferation of physical castes, especially in bees and wasps.

#### CONCLUDING REMARKS

The essence of eusociality is reproductive division of labor among members of the society (Wilson, 1971). An extraordinary feature of hymenopteran eusociality is that this division of labor can involve the existence of a morphological worker caste that furnishes both helper and (parthenogenetically) reproductive individuals, which in some species produce all males. I propose that greater emphasis on the reproductive side of the hymenopteran worker condition, and greater appreciation of hymenopteran colonies as products of evolutionary history, could enrich our understanding of queen-worker conflict and the emergence of a totally sterile worker caste: totally sterile workers might only evolve after a prolonged queen-worker "arms race" fought over worker reproduction. The enormous variation in the prevalence of worker reproduction and the proportion of males produced by workers remains to be explained. A comparative approach to this problem that invokes social structures, relatedness levels, degrees of queen-worker conflict and, conceivably, ecological factors may prove possible as individual species are studied in ever-increasing detail. As shown in this review, among ants such an approach utilizing current data on gyny levels (and by inference relatedness levels), may yield coherent results. A suggestion emerging from this analysis is that worker reproduction may be associated with monogyny because of the high probability of orphanage in monogynous



colonies. More information is also needed to assess the influence on sex investment ratios of the production of males by workers. In addition, a search for further evidence of kin-defined factions among reproductive workers seems likely to be fruitful. Whatever the outcome of such enquiries and whatever the reasons behind the diversity in workers' ability to reproduce, it is clear that this ability has had and continues to have far-reaching effects on many characteristic features of hymenopteran eusociality.

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