Sex...Only If Really Necessary
in a Feminine Monarchy

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The honey bee society was famously described as “The Feminine Monarchy” by the cleric Charles Butler in 1634. Honey bees and their relatives—including all hymenopteran societies—qualify for this label because their colonies are headed by one or a small number of fertile queens. These queens produce a large number of sterile or nearly sterile daughter workers and, later, with their assistance, produce a smaller number of fertile sons and daughter queens (1). The complex and diverse life cycles and social organization of the feminine monarchies are matched by their equally complex and diverse strategies for sexual and asexual reproduction (2). On page 1780 of this issue, Pearcy et al. (3) uncover a new dimension in the complexity of hymenopteran reproduction.

In the Hymenoptera, males are typically haploid and females are diploid (see the figure). It has been shown that sex is determined by a highly variable sex determination locus such that homozygosity (a very rare possibility, given the low probability of a female mating with a male having the same allele as herself) or hemizygosity (expected in all haploid individuals) results in male development, whereas heterozygosity results in female development (4). In social Hymenoptera, virgin queens make nuptial flights during which they acquire sperm from one or more males and store and nurture the sperm in their spermatheca—a tiny gland that opens into the oviduct. Queens have perfect control over the sex of their offspring. To produce daughters, a queen lets sperm flow from the spermatheca into her oviduct and then lays fertilized diploid eggs. Whether the diploid eggs develop into sterile workers or fertile queens depends on the nutritional environment of the young larvae. To produce sons, however, a queen prevents the flow of sperm into the oviduct and lays unfertilized haploid eggs. Such parthenogenetic development of males—known as arrhenotoky—is a universal and well-known feature of the Hymenoptera. Less widely known (and apparently rather infrequent) is another form of
Parthenogenesis known as thelytoky, which permits the production of diploid daughters without the need for a paternal genome (1).

Thelytoky (of the kind referred to as automictic) involves the secondary fusion of two non sister haploid nuclei after the meiotic second division. Automictic thelytoky restores diploidy and yet has the potential for maintaining heterozygosity at the sex determination locus, so that the sex of the resulting adult is female. Although thelytoky has been suspected as a minor form of reproduction in many species, it has been unequivocally demonstrated in one honey bee species (Apis mellifera capensis) and five phylogenetically distant species of ants. In all of these six cases, workers use thelytoky to produce diploid female offspring, even though they cannot mate. Thelytoky thus gives workers a degree of freedom from their queens, insomuch as they themselves can produce both male and female offspring. For this reason, thelytoky may also be interpreted as an attempt by the workers to revolt against the hegemony of the queen, and as a potential early step in the eventual loss of sociality (5).

But what Pearcy et al. (3) have found in the European formicine ant, Cataglyphis cursor, is radically different. In this species, workers in orphaned colonies were already known to produce diploid female offspring (both workers and queens). Now it appears that queens themselves use thelytoky to produce daughter queens. The authors genotyped workers and queens collected from field colonies as well as laboratory-raised workers and gynes (queens) at four highly polymorphic microsatellite loci. Their results provide unambiguous evidence that perhaps a small fraction of the workers but certainly the large majority of laboratory-raised gynes (54 of 56 gynes studied) were produced by the queens through thelytoky. Confidence in thelytoky as the mode of production of the gynes arises from the fact that all of them only carried alleles that could be attributed to the mother queen. The probability that this could be the result of a chance mating of the queens with males carrying alleles identical to their own is estimated at less than 10⁻²⁸!

Apparently, then, C. cursor queens use arrenotok to produce male offspring, normal sexual reproduction to produce worker progeny, and thelytoky to produce daughter queens (see the figure). The most striking consequence of this complex strategy, which the authors emphasize, is in the context of the cost of sex. Sexual reproduction involves a twofold cost because, relative to a parthenogenetic mother, a sexually reproducing mother transmits only half the number of her genes to each offspring (6). This genetic cost is thought (more precisely, hoped!) to be offset by the advantages of sexual reproduction in terms of enhanced genetic variability of the offspring. Such genetic variability is expected to be useful in dealing with variable environments—the physical environment to some extent, but biological environments such as rapidly adapting parasites in particular (7). C. cursor queens appear to forgo this benefit and save on the cost of sex while producing daughter queens, but reap the benefits of sex while producing daughter workers. Because workers are generally sterile and do not constitute a way for the queens to transmit their genes to future generations, the twofold cost of sex is irrelevant during their production. On the other hand, the benefits of sexual reproduction are expected to be profound. Workers are much more exposed than queens to different physical and biological environments. More important, genetic diversity among workers is known to facilitate efficient division of labor, driven by a genetic predisposition for task specialization (8). Daughter queens, by contrast, are the mode for transmitting genes to future generations, making the twofold cost of sex entirely relevant during their production. Pearcy et al. (3) make the reasonable argument that queens are relatively protected from the environment, so that the lack of genetic variability may not be as serious a problem for them. In short, C. cursor queens seem to have the best of both worlds—they reap the benefits of sex where it is most needed and the benefit of thelytoky where it is most affordable.

If C. cursor uses such a wonderful strategy, why don’t other social Hymenoptera do so? One possibility is that too few species have been studied in sufficient detail to conclude that this strategy is not more widespread (1). Alternatively, this may be an artifact of gyn production in the laboratory—an unlikely possibility but one that has not yet been ruled out. Perhaps the most interesting possibility is that the luxury of mixing sex and nonsex in this way is not available to all. What then is special about C. cursor?

Do their queens not need genetic variability, or do they mix sex and nonsex even while producing queens in nature? Genetic variability may, of course, be more important in some environments than others and more important for some species than others. There is also the intriguing possibility that the advantage of thelytoky for queens may be offset by the danger of such a powerful tool falling into the clutches of the workers, who could then use it for subversive purposes. Clearly, the time is ripe for theoretical and empirical investigations of a new paradigm: sex versus nonsex in the service of queens and workers.

References