Mycocepurus smithii

A Sex-less, Male-less Society

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In the insect order Hymenoptera (ants, wasps and bees), gender of individuals is typically determined by a genetic mechanism called haplodiploidy, whereby males develop from unfertilized haploid eggs and females develop from fertilized diploid eggs (*Figure* 1). Typical hymenopteran females acquire sperm from one or more males early in life and store sperm in a structure called spermatheca. Sperm can be released from spermatheca to flow into the oviduct and fertilize eggs. The ovipositing mother can choose not to use some of this stored sperm and lay haploid eggs which develop into males, or she can choose to fertilize the eggs with sperm and lay diploid eggs, which develop into females. Thus the mother has precise control over the gender of her offspring. This mechanism of sex determination results in the unique fact that males neither have fathers nor do they sire sons! Many hymenopteran insects are social, they live in colonies of a few to millions of members. Only a few of the females of such societies take part in reproduction, whereas other females function as temporarily or permanently sterile workers and attend to the chores of brood rearing and colony maintenance. Males however, do not assume worker roles in these societies, and because of their sole function of reproduction, they are often referred to as sperm packets. Therefore, from the social perspective of colony, the males are disposable, yet they are indispensible for producing future female progeny (1).

Key words: Hymenoptera, fungus growing ants, sexual reproduction, arrhenotoky, thelytoky.

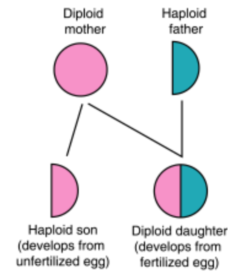

Figure 1. Haplodiploidy sex determination mechanism of hymenopteran insects. The sons are produced by arrhenotokous parthenogenesis. The daughters are developed from fertilized eggs. Both sons and daughters carry 50% of the diploid mother's genetic information and the daughters carry 100% of the haploid father's genetic information.

In a very few species of social Hymenoptera, the females have evolved mechanisms to produce fertile diploid females asexually (by parthenogenesis) in addition to regular sexual reproduction. This parthenogenesis is better known as thelytoky, in contrast to arrhenotoky, the parthenogenetic mechanism used to produce haploid males (*Box* 1). For example, workers of Cape honey bees (*Apis mellifera capensis*) [2] and a handful of ant species (eg. *Cerapachys biroi, Messor capitatus Pristomyrmex punctatus and Platythyria punctata*) can produce diploid females by thelytoky. The queens of the ants *Cataglyphis cursor*, *Wasmannia auropunctata and Vollenhovia emeryi* lay fertilized eggs to produce sterile workers, but use thelytoky to generate offspring queens (reviewed in [3]). In all these species, males are produced either occasionally or frequently and sexual reproduction is as important as asexual reproduction.

Box 1.

Parthenogenesis in Hymenoptera: Parthenogenesis is an asexual mode of reproduction whereby individuals develop from unfertilized eggs. In the insect order Hymenoptera, both males and females can be produced through parthenogenesis. Males are almost always produced through parthenogenesis but this mode of reproduction is rarely used to produce females. The parthenogenetic mechanism that produces males from haploid unfertilized eggs is known as arrhenotoky. Females are usually produced by fertilization of such haploid eggs with sperm. However, fusion of two haploid eggs (products of second meiotic division) can give rise to a diploid ovum, from which a female can develop. A diploid ovum can also be produced by mitosis (instead of meiosis) of primary oocyte, and give rise to a female. The developmental mechanism of diploid females from diploid ova is known as thelytoky. Although arrhenotoky is the main mechanism for producing males in Hymenoptera, thelytoky is very rare and has evolved only in a very few species.

Mycocepurus smithii females are unique among all social insects in that they have gone one step further and ceased producing males entirely. They solely depend on thelytokous parthenogenesis to produce sterile workers as well as reproductive females [3, 4, 5]. *M. smithii* is a fungus-growing ant, i.e., it cultivates fungus for food in small gardens made of vegetative materials (*Figure* 2). Like many other species of fungus-growing ants, this species is abundant throughout South and Central America. In over 100 years of collection and some intensive searches in the past decade, only females have been found in this species. Careful searches not only failed to find males in *M. smithii* nests, but also failed to find sperm in the spermathecae of reproductive *M. smithii* females. DNA fingerprinting analysis revealed that all workers in a colony are genotypically identical to each other and to their mother, thus ruling out sexual reproduction, which would generate genetic differences between offspring. In some insects, endosymbiont bacteria (e.g., *Wolbachia,* see *Box* 2) are known to switch the sex of their hosts [6]; *M. smithii* does not carry such

Figure 2. Mycocepurus smithii ants on their garden. The mother queen (the bigger individual) and her daughter workers (smaller individuals) are genetically identical.

Box 2

Endosymbiont: Endosymbionts are organisms that reside in cells or bodies of other organisms (hosts) and are generally transmitted to offspring during the host's reproduction. *Wolbachia* is one of the common bacterial endosymbionts found in reproductive tissues of many arthropods. Some *Wolbachia* manipulate reproduction of its host, for example by switching sexual females into asexual females or by switching male development into female development (feminization) [6].

endosymbionts and absence of males therefore cannot be attributed to such endosymbiotic infections. To test if different food could reinstate male production, *M. smithii* ants were offered foreign fungus (fungus cultured by a different species of ant) to cultivate as their food. Still no males were produced in these experimental lab colonies, indicating that absence of males was not dependent on *M. smithii*'s species-specific fungus. Thus absence of any apparent environmental or intrinsic factor that can induce loss of males shows that this species appears to have completely abandoned sexual reproduction.

This striking discovery challenges current evolutionary understanding of reproduction. The most important advantage of sexual reproduction is that it combines genetic materials from two parents and generates genetic variability among offspring, which in turn can accelerate adaptation to changing environments, such as coevolving diseases. How do *M. smithii* ants overcome the need for genetic variability? Since all individuals in a colony are genetically identical, what kind of environmental or maternal factors induce development of an individual into a worker and another into a morphologically distinct reproductive (*Figure* 2). The workers lack spermathecae but they have ovarioles. Given that sperm is not required for reproduction (and spermatheca may also be redundant) to produce females in this species, it is intriguing why the workers do not oviposit to produce females and rather consent to reproductive monopoly to the queens. Are the smaller workers inherently less efficient at reproduction? We can ask and possibly answer diverse questions regarding how sociality is maintained in such a species. Although *Mycocepurus smithii* relies on an exceptionally unusual system of reproduction, probably this males-less, sex-less ant will help us understand the importance of males and sexuality more clearly in hymenopteran eusocial societies.

Acknowledgements: The authors thank H D Ishak, C Rabeling and R Raychoudhury for their comments on the manuscript.

Suggested Reading

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