Influences of parthenogenesis-inducing *Wolbachia* on its parasitic-wasp hosts

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By

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ABSTRACT

Thelytoky, a reproductive strategy by which females produce female offspring without fertilization, has been observed among 2.5% of the parasitic Hymenoptera. The mechanisms behind thelytokous reproduction have been studied in many wasp species, and in recent years the presence of bacterial endosymbionts in the ovaries and eggs of wasps has been found to induce this type of reproduction. Symbiont-host relationships can range on the parasitism-mutualism spectrum with regard to their effect upon host fitness; cytoplasmically inherited symbionts benefit from the induction of thelytokous reproduction, as all individuals in the host population have the ability to reproduce and propagate the endosymbiont.

This study was directed at two organisms, *Wolbachia* spp., a group of closely related, vertically transmitted endosymbiotic bacteria, and its host, parasitic wasps of the genus *Muscidifurax*. These thelytokous wasps are economically important natural enemies of houseflies.

The first part of the research deals with the immediate influence of the bacterium on its host's mode of reproduction. Previous work has shown *Wolbachia* to be responsible for thelytokous reproduction in *Muscidifurax*. The mechanism by which diploidy is restored to unfertilized haploid eggs, which then develop into diploid females, is described here. Using DNA fluorescence dye, and confocal and digital imaging microscopy, the mechanism of diploidy restoration was shown to be gamete duplication –

failure of the first mitotic division to complete normal division into two haploid daughter nuclei.

The density of *Wolbachia* in *M. uniraptor* eggs was regulated using various doses of antibiotics, making it possible to test the effect of bacterial load on the sex ratio of the host's offspring. The sex ratio of offspring produced by treated females was positively correlated with the number of *Wolbachia* found in the eggs of those females, indicating that the *Wolbachia* effect is density-dependent.

The second part of the study focuses on the long-term effects of the symbiont on its host. The effects of different titers of the bacterium on the fecundity, reproductive rate, longevity, and survival rate of the host were measured. No significant effects were detected with respect to these fitness components.

Attempts to establish an arrhenotokous line of *M. uniraptor* for further studies were unsuccessful, and revealed the existence of three irreversible reproductive barriers between antibiotic-induced *M. uniraptor* males and conspecific females: 1) males do not produce mature sperm; 2) females are reluctant to mate; and 3) a major muscle is absent from the spermatheca, rendering it incapable of conveying sperm. These barriers make sexual reproduction impossible, and probably contribute to the stability of the symbiont-host relationship, since *Wolbachia* is indispensable for host reproduction.

A search for additional bacterially-induced thelytokous species revealed that *Galeopsomiya fausta*, while not infected with *Wolbachia*, is nonetheless dependent on

bacteria for its thelytokous mode of reproduction. The reproductive barrier between antibiotic-induced *G. fausta* males and conspecific females appears to be based on non-receptivity of females.

The introduction of thelytoky by gamete duplication results in homozygosity at all wasp loci, a condition which would be expected to cause rapid accumulation of mutations. Since selection on sex is relaxed in the presence of thelytoky, and mutations influencing sex-related traits are no longer deleterious, reproductive barriers can develop which cause the host to become *dependent* upon the symbiont for reproduction. In such a system, therefore, *Wolbachia* can be considered a mutualistic symbiont. The finding that elimination of *Wolbachia* from the host has no effect on fitness components is consistent with this interpretation of the results: the genome-cytoplasmic gene conflict no longer exists, and the two partners are cooperating for mutual benefit.