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## Sympatric speciation and radiative evolution of socially parasitic ants – Heretic hypotheses and their factual background

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### Abstract

According to current hypotheses the main types of social parasitism among ants, namely slavery, temporary parasitism, and inquilinism, arose from such features as predation on other ants, or territorial behavior, both presumed precursors of slavemaking, and polygyny, a presumed precursor of temporary parasitism and inquilinism. The latter is believed also to represent a final instar in several evolutionary pathways leading from slavery, temporary parasitism, and xenobiosis to this permanently parasitic, workerless condition. Speciation, the origin of parasitic species from their usually closely related host species, is suggested to occur due to temporary geographic isolation and subsequent transition of one of the newly formed daughter species to parasitism in the nests of the other.

Evidence is presented suggesting that the main types of social parasitism originated independently of each other. 15 ant genera are parasitized exclusively by inquilines, five other genera exclusively by temporary parasites. Only four groups of non-parasitic ant species (*Formica*, *Tetramorium*, *Leptothorax* subgenera *Leptothorax* and *Myrafant*) have parasites of several types each. Within these groups, however, there is little evidence of evolutionary transitions from one type to another. The few exceptions, mainly workerless species of the genera *Epimyrma* and *Chalepoxenus*, represent parasites which clearly derive from slave-making congeners, but differ from ordinary inquilines in that they eliminate the host colony queens like their actively dulotic ancestors.

The new hypothesis suggests that all forms of interspecific true social parasitism (excluding xenobiosis) originated from a common "preparasitic" stage, a subpopulation of reproductives in polygynous colonies and species, with diverging sexual behavior (near-nest mating vs. swarming) and caste ratios (production of more sexuals vs. workers). Arguments for sympatric speciation are compiled. Various features of the ancestral, and then host species (colony sizes, population density and structure, transition from polygyny to monogyny, etc.), and of the "preparasite" (production of few, or no workers, etc.) may shape the developing parasite to become a slave-maker, inquiline, or temporary parasite. These features usually leave open only one, or in a few genera, several options. The different types of parasitism within one host species group thus may have developed in a radiative manner from the common, preparasitic stage, which explains that independent colony foundation is a common feature of all true social parasites among ants.

**Key words:** Formicidae – Social parasitism – Evolution – Sympatric speciation

### Introduction

Since DARWIN (1859) presented a first hypothesis on the origin of slavery in ants, the evolution of dulosis and other forms of social parasitism between ant species has been discussed by numerous authors. For a recent review of the hypotheses hitherto published see BUSCHINGER (1986). Territorial raiding of conspecific, and later also heterospecific colonies as the basic behavior developing into slave-raiding, is the presently most favored idea, put forward by WILSON (1971, 1975), ALLOWAY (1980) and STUART and ALLOWAY (1982, 1983), whereas DARWIN (1859) had suggested that predation on other ants' brood be the first step leading to slave-making behavior. Both hypotheses, however, provide no explanation for the well-known fact that all true slavemaker species (i. e. those enslaving