

colony, kills or replaces by other means the host species queen, and is accepted by the host workers. From the parasitic queens' eggs a workforce of this species is reared, the host workers die out, and an independent, pure colony of the parasitic species is formed. This kind of parasitism has evolved, certainly convergently, in the subfamily Dolichoderinae, the Myrmicinae, and it is most frequent among the Formicinae. In the *Formica* group temporary parasitism in most species is combined with polygyny and polydomy.

For clarity I do not follow GAULD and BOLTON (1988), who define "temporary parasitism is where the worker caste is retained"; hereby the slave-makers are included within this group, though by far most of them are permanently dependent upon their host or slave species.

Dulosis or slavery

Together with the following group, the slave-making ants are parasitic during all their lifetime. With the exception of one group, *Raptiformica* spp., they are unable to survive without slaves. Typically the – often morphologically specialized – slavemaker workers raid upon neighboring nests of their hosts species, capture brood stages and carry them back to the own nest. From the foreign pupae, host- or slave-workers emerge which then care for their "masters", forage, feed the slavemakers' brood and so on. It is important to note that all slave-making species establish their colonies in a similar way as the temporary parasites, i. e. the young queens penetrate a slave species nest, kill or drive off the queen(s) and often also the adult workers, and obtain their first slaves from workers emerging from the brood of that nest.

Dulosis, like temporary parasitism, has evolved several times independently, at least once among the Formicinae and polyphyletically 5 to 6 times in the Myrmicinae (ALLOWAY 1980).

Permanent parasitism without dulosis

This group sometimes is also termed the "inquilines", however, it evidently comprises a variety of life habits which may have different phylogenetic origins. Clearly this inquilinism is the most frequent form of social parasitism. In the list of HÖLLDOBLER and WILSON (1990) about 80 inquiline species are noted, ca. 65 temporary parasites, 55 slavemakers, and 10 xenobiotic species. Exact numbers cannot be provided since in some cases the type of parasitism is not yet clearly documented, and in several groups a number of species will certainly fall into synonymy when carefully examined.

Characteristic for nearly all of the inquilines is their coexistence with the host species queens. Usually they also have the worker caste reduced, most species being workerless. Inquilinism is found in the primitive subfamily Myrmeciinae, in several genera of Myrmicinae, and in the Formicinae.

Current hypotheses on the origin of slavery and social parasitism

An important trait of practically all temporary and permanent parasites including the slave-makers is their always close relationship to the respective host species. There are a few exceptions, such as *Rhoptromyrmex mayri*, a tetramoriine once found in a *Pheidole* nest (*Pheidolini*), and *R. schmitzi*, one female found in a *Tapinoma* colony (*Dolichoderinae*) (BOLTON 1986a). Both are supposed to be inquilines, but this appears quite questionable. EMERY (1909) formulated what was later (LE MASNE 1956) termed "Emery's rule": The dulotic and the temporarily as well as the permanently parasitic ants all descended from closely related forms which serve them as slaves or host species". This rule is not strictly applicable, particularly in such instances where a number of parasitic species evidently from a monophyletic genus, or where one dulotic species enslaves two or three