HOW THE QUEENS OF THE PARASITIC AND SLAVE-MAKING ANTS ESTABLISH THEIR COLONIES.

By WILLIAM MORTON WHEELER.

(Reprinted from the *American Museum Journal*, Vol. V, No. 4, October, 1905.)

Date of issue, September 29, 1905.

HOW THE QUEENS OF THE PARASITIC AND SLAVE-MAKING ANTS ESTABLISH THEIR COLONIES.

A CONTINUATION of the author's study of temporary social parasitism among ants, briefly noticed a year ago in the AMERICAN MUSEUM JOURNAL (Vol. IV, p. 74), has brought to light some interesting facts concerning the establishment of formicaries in several of our species. It is now well known that an ant colony is started by a single fertilized female, or queen. This insect, after mating high in the air during her nuptial flight, descends, pulls off her wings, and proceeds to dig a tiny nest in the ground or in rotten wood. She closes the entrance behind her and remains secluded and without food for nine or ten months, while she lays a packet of eggs and cares for the larvæ when they hatch. Until the larvæ mature as workers, the queen feeds them with salivary secretion derived from her own fat-body and degenerating wing-muscles. These firstling workers are always small, because as larvæ they were insufficiently fed. They open the entrance to the nest, and go forth in search of food for their queen and themselves. The mother insect is now able to devote all her energies to assimilating nourishment and producing eggs, while the workers care for the brood and extend the galleries of the nest and give it whatever external architecture it may possess.

This method of colony formation, which is adopted by nearly all ants, may be called the typical method. There are, however, two other methods which are resorted to by the queens of certain species, one of a more complicated, or redundant, the other of a simpler, or defective type. The redundant type occurs among the leaf-cutting and fungus-growing ants (*Attii*) of tropical and subtropical America, in which the queen not only brings up a colony of workers by herself alone, but simultaneously keeps up a culture of the peculiar fungus which, so far as known, constitutes the only food of these ants. The defective type is found in certain ants whose queens, either because they are too small and infertile, or for some unknown reason, are unable to bring up a firstling brood without the assistance of workers of another

species. The latter method of colony formation appears under three aspects:

First, the queen may seek adoption in a moribund or queenless colony of another species and there have her young fed and reared by the alien workers. Later these die off and leave a pure colony of the parasitic species, which has now waxed sufficiently strong and independent, both in number and pugnacity, to hold its own in the struggle for existence. In the former note in the JOURNAL attention was first called to this type of temporary social parasitism in a Connecticut ant (*Formica difficilis* var. *consocians*) which, till its colony is established, lives with the common *F. schaufussi* var. *incerta*. During the past July the author was able to confirm and extend his observations on these insects. It was learned that queens of *F. consocians* were readily adopted by *incerta* workers, even when the latter had been isolated as pupæ and could not, therefore, have had any previous experience with the parasites. It was also discovered that workers of our common black ant (*Formica fusca* var. *subsericea*) could be induced to adopt solitary queens of the mound-building ant (*F. exsectoides*) and the fallow ant (*Formica rufa* subsp. *integra*). Hence it is probable that these species, which, of all our ants, develop the largest and most formidable colonies, start as humble temporary parasites in the nests of another species. Very recently Wasmann has shown that the author's conclusions are in all probability applicable also to the European ants of the *rufa* and *exsecta* groups.

The parasitic instincts of the queen ants belonging to the *rufa* and *exsecta* groups, which include *F. consocians*, *integra*, *exsectoides* and all the different forms of fallow ant (*F. rufa*) both of Europe and America, are probably traceable to a peculiarity of the adult colonies of these insects. It is known that these colonies sometimes consist of dozens of different nests, which have all been founded by young fertilized queens, accompanied by a number of workers of their own species, as offshoots from the original nest, that is, the one first established through temporary social parasitism. This habit of propagating a colony over several nests often many feet apart, has probably been the means of depriving the queens of the *rufa*

group of their primitive ability to establish colonies exclusively through their own initiative. Hence when, during their nuptial flight, they drift too far away to find workers of their own colony or species at hand to assist them, they are compelled to solicit the aid of workers of another species. The extremely common, widely distributed, and very cowardly ants of the *fusca* and *schaufussi* groups are the ones naturally exploited for this purpose. In the species of the *rufa* group with large queens we probably still have the earlier phylogenetic stages of this development: the parasitic instinct is highly developed, but the stature of the ants has as yet undergone little or no diminution. In the species with diminutive queens, however, like *F. neppticula*, *microgyna* and *consocians*, we have the last stages in this retrogressive development, since the inability of the queen to establish a colony unaided is manifested not only in her parasitic instincts, but also in her diminutive size and frail structure.

Second, the queen may not only seek adoption among alien workers, but she and her progeny may continue to live with their hosts as permanent parasites. This seems to be the case in some of the European ants of the genus *Strongylognathus* and in the workerless species of *Anergates*, *Epœcus*, *Epipheidole* and *Sympheidole*.

Third, the queen may compel her own adoption or may snatch away the pupæ of an alien species and leave to the workers that hatch from them the care of bringing up her own offspring. These may, in turn, take to robbing the worker pupæ from other colonies of the host species and in this manner keep up a permanent mixed colony. This is slavery, or "dulosis," as practiced by the sanguinary ants (*Formica sanguinea*) and the amazon ants (*Polyergus rufescens*) of Europe and their American subspecies and varieties.

Experiments on artificial colonies of *F. sanguinea* subsp. *rubicunda* Emery have given an insight into the method in all probability adopted by this insect while founding its colonies under natural conditions. A detailed account of these experiments will be published in the near future, but the results may be here briefly stated. When a female *rubicunda* from which the wings have been removed is confined in an artificial nest

with as many as twenty workers of *F. fusca* var. *subsericea* and their brood, she is received with great hostility. At first her conduct is patient and insinuating, or even somewhat timid, but the persistent pulling and tweaking to which she is subjected by the workers soon throws her into a frenzy of rage. She falls upon her tormentors, drives them from their brood and, when they persevere in returning, kills them one by one. With feverish haste she then appropriates the pupæ, secretes them in some corner and carefully guards them, ever on the alert with open mandibles to attack an intruder, till the workers are ready to hatch. She deftly frees the pale drab callow young from their pupal envelopes, and immediately adopts them, thus quickly surrounding herself with the means of nourishing both herself and her own progeny as soon as the latter are brought forth. The immediate result of these tactics is to produce a small mixed colony consisting of a female of one species of *Formica* and a number of workers of another, exactly as in the *consocians-incerta* colony, but with the interesting and important difference that in this case the *incerta* workers are effete or moribund, or at any rate older than the queen, whereas the *subsericea* workers in the case of *rubicunda* are younger than the queen and have before them a lease of life amounting to three or four years. The result, moreover, in the case of *rubicunda* is not achieved passively, by adoption of the queen, as in *consocians*, but actively, by conquest and abduction. Of course, none of these differences is apparent from mere inspection of an incipient mixed colony of *consocians* or *rubicunda*, but can be ascertained only through studying the behavior of the queen during the period that elapses between the nuptial flight and the establishment of her colony.

The author's experiments with queens of our shining amazon (*Polyergus rufescens* subsp. *lucidus*) and workers of the species which it enslaves (*Formica schaufussi*) have, up to the present time, given contradictory results. All of these queens, when introduced into artificial nests containing *schaufussi* workers, were violently attacked. Some of them retaliated by ruthlessly killing all the latter, but remained perfectly indifferent to their larvæ and pupæ. Other queens, however, were more insinuating and far less bloodthirsty and, though equally indifferent

to the *schaufussi* young, seemed to be seeking adoption. Perhaps the method of colony formation resorted to by these insects may vary according to circumstances. It is certain, however, that the establishment of a colony must be attended with great difficulties or be possible only under unusual conditions, since the amazon ants are very rare and local in their occurrence.

WILLIAM MORTON WHEELER.