Translation of pp 150-53 of:

Roubaud, E. 1916. Recherches biologiques sur les guêpes solitaires et sociales d' Afrique. La genèse de la vie sociale et l'évolution de l'instinct maternel chez les vespides. Annales des Sciences Naturelles (Zoologie) (10) 1:1-160.

SUMMARY

COMPARISON OF SOCIAL EVOLUTION IN VESPID WASPS AND OTHER HYMENOPTERA

Social evolution in vespids appears to be conditioned entirely by the interests of the individual and by exchange of nutrients, or trophobiosis. As adult behaviour that fosters larval growth and development is increasingly focused and concentrated around the brood, larvae become a source of personal gain for females and are exploited as such.

Vespid colonies are trophobiotic societies in which the exploitation of larvae is key. They thus tend toward maximum production of brood primed by individual adult self-interest. The motherly love that manifests itself in the highly perfected care and nourishing of brood in the nursery -- so like that seen in birds -- is fundamentally no different from the solicitude of ants for the aphids and scale insects that they tend for their sugary secretions. In brief, the communion of wasps with their brood is a special case of those nutrition-driven social phenomena of which social insect life offers so many examples. Familial symbiosis of this kind is, however, sufficiently distinct that I shall give it a special term, *ecotrophobiosis*[1].

There is good reason to doubt that social organization under the influence of ecotrophobiotic effects is peculiar to social wasps. It would not be prudent to generalize the concepts arising from my studies of wasps to other social insects, as so many factors in the development of termite and ant colonies remain unknown. Nonetheless, it seems likely that in these other groups, too, individual self-interest of a trophic nature will be found to be a driving force. In ants, for example, the workers are continually licking the eggs and larvae. And Bugnion has found that in termites the eggs issuing from the queen are bathed in a thin fluid layer that is immediately licked up by workers. Without this licking, the eggs will not hatch. The termite queen, for her part, receives from the workers a considerable amount of salivary secretion which, along with fungal fragments[2], forms the main part of her food. In these various interactions we see manifestations of ecotrophobiotic phenomena comparable to those in wasps.

It is the view of leading authorities on bees, including Verhoeff and Buttel-Reepen, that sociality could have evolved from the grouping of adult females, whether for nesting (*Chalicodoma*, *Osmia*, *Anthophora*) or hibernation (*Xylocopa*, *Halictus*)[3]. The primary causes of such groups are not yet known. The best we can do is to note some of the advantages arising from them, which may in turn have favoured the later appearance of closer assocations.[4] In any event, trophobiotic brood rearing appears to be independent

of such social phenomena, as workers of the stingless meliponid bees studied in South America by Drury, Ihering and others provide no direct feeding of their larvae. Rather, eggs are sealed in their respective cells with a full set of provisions.

Combining what is known of behaviour and physical structure in the different groups of predatory and pollen-and-nectar-feeding, or melliferous hymenoptera, we can detect two evolutionary paths in the direction of sociality. These are determined by the feeding regimes to which larvae are adapted. Predatory and melliferous hymenoptera can be divided on morphological grounds into two distinct groups. Handlirsch unites the vespids and pompilids in one of these, the Vespiformia, while placing the bees and sphecids in the Sphegiformia. The phyletic relationship between the two groups is controversial, as is the nature of the common ancestor. Verhoeff, among others, regards this latter as related to present-day *Trypoxylon*.

With these two groups in mind, the two social-evolutionary directions taken by the hymenoptera can be conceived as in Fig. 34. The Vespiformia branch, in which Handlirsch unites the vespoids and pompilids on morphological grounds, is shown to have taken two directions, according to the feeding regime to which the larvae are subject and the use or disuse of venom in the course of brood care. One of these, the *melliferous regime* characterizes the evolution of non-predatory wasps (masarines), which have not passed the stage of mass provisioning and solitary life.

On the other hand, the pompilids and eumenines follow the *predatory regime*, characterized by the paralysis of prey through stinging. The eumenines have broken free of the limitations imposed by mass provisioning to evolve direct feeding of larvae and therefore trophobiosis. This in turn has opened the way to the evolution of sociality in vespids.

The Sphegiformia, which brings together the sphecids and bees, likewise manifest two evolutionary paths, although quite contradictory to those found in the Vespiformia. The predatory sphecids, which rear their brood on prey and have evolved toward paralysis as a way to subdue it, have not gone past the stage of mass provisioning and solitary life. It is only in the melliferous bees, which do not paralyse and feed their brood plant matter, that some species have gone beyond the way of solitary toward advanced forms of sociality.

We find, then, that in the Vespiformia the melliferous, non-paralysing sub-group has not reached the level of organized societies, while its counterpart in the Sphegiformia has shown just this sort of progress.

It would be premature at this time to set forth a formal explanation for these evolutionary tendencies. However, it seems logical to suggest that, if sociality has not arisen in the masarines because of a lack of trophobiosis, it is perhaps because the vegetarian feeding regime of both the adults and brood has not given rise to the development of abundant salivary secretions by the larvae and/or a need for such secretions by the adults.

In the Sphegiformia, on the other hand, such a line of reasoning

cannot apply. As we have seen, in this group social evolution has taken place through apparently quite different factors of individual self-interest. In general, the adaptation of larvae to a vegetarian regime in the melliferous sub-group originates above all from the venom apparatus's essential unfitness for effective paralysis of prey.

Many problems of insect social life are at best seen darkly. The study of living wasps in the tropics will undoubtedly throw a great deal of light onto these problems. It is hoped that this paper will stimulate future researches along similar lines, which will in turn provide many improvements on our present rudimentary understanding.

Translator's notes

1. Now known as *trophallaxis*. For a discussion of the history of these two terms, see Wilson's *The Insect Societies* pp 281-83.
2. Refers to fungus-gardening termites, Macrotermitinae.
3. At least some of these genera are today more narrowly defined.
4. This is a weak reflection of Roubaud's view, set forth earlier in the paper (pp 145-47), that the origins of hymenopteran sociality are to be sought in mother-daughter relationships ("filial associations") and not in adult aggregations.

C.K. Starr, 1996