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Trophallaxis and the Evolution of Eusocial Hymenoptera

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The exchange of alimentary liquid among individuals of a social species has been recognized for more than two centuries as a prominent aspect of hymenopteran biology. Wheeler (1918) coined the term trophallaxis, which is now widely and generally used in reference to this behavior. Wilson (1971), Spradbery (1973), and Jeanne (1980) have given recent and useful reviews of it. The term trophallaxis is at present usually applied to two patterns of liquid food exchange; in one, larval saliva is imbibed by attendant adults, and in the second, ingluvial liquid is passed between adults. The first of these, adult ingestion of larval saliva, has figured prominently in writings on origins of social behavior. Roubaud (1916) presented the extreme position that the behavior is the cornerstone of vespid sociality. West-Eberhard (1978) has taken the opposite position that this form of trophallaxis need not be invoked at all to explain group life in wasps. My own position, to be presented here, is intermediate between these poles. I will argue that trophallaxis may be the key to our understanding of a more basic and more general phenomenon that has been central to the evolution of hymenopteran sociality.

The distinction between the two patterns of trophallaxis needs to be clearly drawn. The two habits have probably evolved independently, and each is probably polyphyletic. Both patterns of trophallaxis, however, exemplify the more general phenomenon to be presented in this paper.

LARVA-ADULT TROPHALLAXIS

Roubaud (1916) discussed this behavior in the context of a reciprocal food exchange, with larval provisioning as the complementary behavior. Other functions ascribed to the larval saliva include a role in regulation of nest temperature and humidity (Weyrauch, 1936), larval excretion (Brian and Brian, 1952), and as an aid in the ingestion and digestion of solid foods (Spradbery, 1965). The weight of recent evidence and opinion heavily favors a nutritional role in adults for the larval saliva that they ingest (Wilson, 1971; Spradbery, 1973; Jeanne, 1980).

Hunt, Baker and Baker (in press) have argued that though the production of a larval salivary exudate might have originated for any of the above three non-trophic functions (or for another as yet

unidentified function), its evolution and full expression as a pathway of adult nourishment may be reasonably explained. Hunt, Baker and Baker analyzed the free amino acid content of wasp larval saliva, and they noted a strong similarity between the nutrient composition of larval saliva and of floral nectars, which are the typical food for most adult aculeate solitary Hymenoptera. This similarity, they argue, reflects selection for a nutritional role for larval saliva, in those species having larva-adult trophallaxis, that is analogous to the role played by floral nectars in non-social Aculeata. Furthermore, they argue, the larval saliva may have facilitated the evolution of sociality in any or all of three ways: 1) by fostering more efficient foraging in social vs. solitary wasps; 2) by facilitating reproductive longevity in social vs. solitary wasps; and 3) by contributing to a trophic mechanism for the production of individuals with reduced fecundity.

The behavior of larva-adult trophallaxis has evolved at least twice. It is present in at least some subfamilies of Formicidae (Wilson, 1971, p.289) and in most if not all eusocial Vespidae.

ADULT-ADULT TROPHALLAXIS

The exchange by adults of liquids regurgitated from the crop is a conspicuous behavior in many social Hymenoptera. Such trophallaxis in honeybees is especially well documented, and this pattern of food exchange serves many integrative functions in advanced social species, including the efficient and equitable distribution of food among colony members. In primitively social species a major role for such trophallaxis, which I feel is not fully appreciated by most researchers, is that an unequal distribution of food is achieved. Pardi (1948) described dominance hierarchies in primitively eusocial Polistes wasps, and he noted trophic advantage to dominant individuals as an important result of the dominance order. Though ingluvial exchange is rarely, if ever, unidirectional in Polistes, dominant individuals receive liquids more often than they are donors. Such inequitable food distribution could serve to foster social evolution in varied ways analogous to those suggested in the preceding section: 1) dominant individuals could sustain their nourishment yet forage very little, with consequent low risk of predation or accidental death; 2) dominant individuals could be sufficiently well nourished to engender sustained reproduction as compared to otherwise equivalent species that lack such nourishment; and 3) sub-dominant individuals could experience a diminishment of their own nourishment sufficient to contribute to lessened reproductive capacity.

Adult-adult trophallaxis is polyphyletic. It is probably present in all social Vespidae, and it is variably present in both Formicidae and in social bees (Wilson, 1971).

ENHANCED PROTEINACEOUS NOURISHMENT AS A GENERAL PHENOMENON

I believe that the two patterns of trophallaxis just described are significant components of social evolution in those Hymenoptera that exhibit the behaviors. The most significant aspect of trophallaxis, in my opinion, is that reproductive individuals are

supplied with proteinaceous nourishment that is adequate and appropriate to support relatively high levels of egg laying as compared to nestmates, be they co-foundresses or offspring. Many social Hymenoptera, however, do not exhibit trophallaxis at all; others show one form but not the other. Clearly, trophallaxis *per se* cannot be essential to the evolution of sociality. It is my position that the underlying phenomenon, i.e. a pathway of reliable and relatively abundant proteinaceous nourishment to reproductive females, is a basic aspect of social evolution in Hymenoptera. In those species lacking trophallaxis, other behaviors may serve this purpose. Examples of alternative behaviors that may serve the same ultimate function include (but are not necessarily limited to) ingestion of liquids from malaxated larval provision loads, oophagy, and feeding on pollen.

1. Ingestion of liquids from malaxated larval provision loads

Several workers have shown that social vespids take liquid from malaxated provision loads into their crop. In a series of studies on *Polistes metricus* I have used radiotracers to show that the ingested liquids are typically regurgitated to larvae but that a variable quantity may be retained and so may be utilized as adult nourishment (Hunt, MS). The potential significance of this nutritional pathway is suggested by Evans' (1958) analysis of vespid social evolution, where prey malaxation is the penultimate adaptation preceding eusociality.

2. Oophagy

Oophagy has been reviewed by Wilson (1971) and reported to occur in varied patterns and at varied frequencies in many taxa of social Hymenoptera. The potential nutritional significance of oophagy is intimated by Wilson's (1971, p.281) observation that oophagy and adult-adult trophallaxis are largely complementary behaviors; i.e., when a social species conspicuously exhibits one of these behaviors the other is usually infrequent.

3. Pollen feeding

The nutritional value of pollen has been widely reported and is well known. Pollen is the primary larval provision of most bee taxa, and most adult bees ingest pollen together with nectar. Grogan and Hunt (1979) have shown in addition that pollens contain proteases of appropriate activity and adequate quantity for *in vivo* digestion. My opinion at present is that pollen in nectar may in general provide to bees a suitably rich nourishment source for sustained egg laying, with ecological variables (e.g., degree of polylecty) being primary determinants of potential reproductive longevity.

ESSENTIAL EXTRINSIC FACTORS IN EUSOCIAL EVOLUTION

Evans (1977) has drawn an important distinction between extrinsic and intrinsic factors that may be significant effectors of eusocial evolution. One extrinsic factor that has been effectively shown to be requisite to eusocial evolution is complex nesting habits. No hymenopteran is social in the absence of a nesting habit that

directly facilitates the conmingling of conspecifics. Though complete supporting evidence remains to be assembled, I would like to propose here that a pathway of proteinaceous nourishment that can augment, supplement, or replace entirely the nourishment pathways of solitary species be viewed as a second extrinsic factor that is requisite to hymenopteran eusocial evolution and equal in importance to complex nesting habits. Such pathways of proteinaceous nourishment are, like complex nesting, varied in expression and evolutionary history in Hymenoptera. Trophallaxis encompasses only two specific nourishment patterns that exemplify this more basic and general phenomenon.

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