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Selective Factors Associated with the Evolution of Membracid Sociality

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Membracids (treehoppers) exhibit a variety of social patterns which are consistent within generic and, in most cases, tribal lines. Solitary species may or may not interact with ants, while those which form nymphal and adult aggregations are usually associated with mutualistic ants. Aggregations may be composed of siblings or offspring from several females, but parent females are not involved in the maturation of offspring. In some species parent-offspring associations occur in which the parent female plays an active role in the maturation of offspring.

Parent-offspring interactions occur in at least 50 species of Membracids (Wood, Unpublished). Among these species female investment in offspring and their interaction with ants are variable. Females of some species desert offspring after they reach the 1st instar leaving ants to provide protection to offspring. In others, females remain with and protect offspring until they mature but do not interact with ants (Wood, 1974; 1976a, b; 1977a; 1978; 1979). Although parental care occurs in a number of orders including the Homoptera (Review by Eickwort, Unpublished; Wilson, 1971), only in the Membracidae does it involve ant mutualism. The influence of ant mutualism on Membracid life histories is poorly understood.

I propose here that the following interactive causal agents (Fig. 1) are responsible for the variety of social organization in the Membracidae: 1) predation, 2) ant mutualism, 3) host plant utilization, and 4) geography. These factors and predictions of how they influence Membracid life histories are presented below.

1. Predation - Egg mortality can be postulated as a primary factor influencing whether eggs are deposited singly or in clusters. A female which deposits eggs in small groups throughout a single host plant or among several plants may spread out the risk of predation for any single egg. This appears to be the case for many solitary species. Other Membracids deposit eggs into masses which contain a female's entire reproductive output. This behavior increases the consequences of predation unless there is some countering selective advantage in nymphal survival.

Active or passive egg guarding by parent females is mechanism to reduce predation on clusters of eggs (Wood, 1974; 1976a, 1977a, 1978, 1979) and may establish aggregations of nymphs which in turn

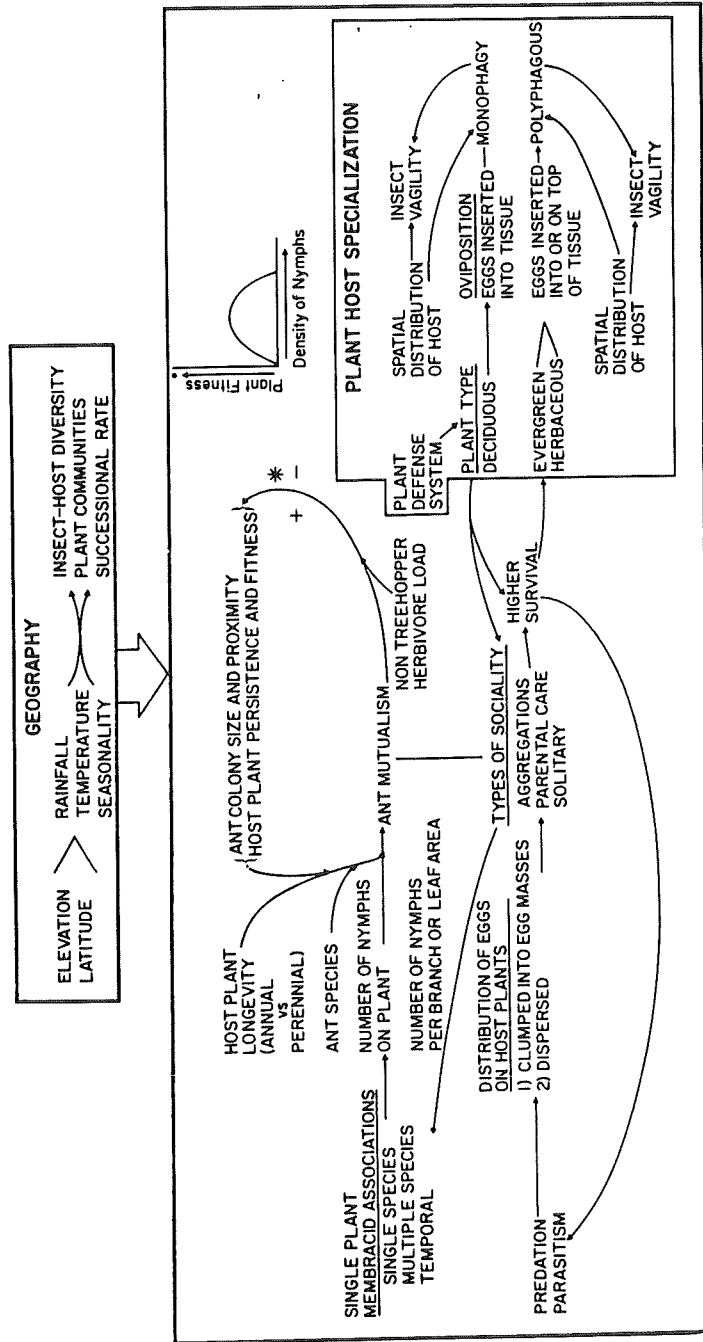


Fig.1-EVOLUTION OF MEMBRACID LIFE HISTORIES

attract mutualistic ants. In some tropical habitats predation by ants is heavy (Jeanne, 1979; Leston, 1973a, b) but Membracids which release honeydew to ants become an energy resource to these ants. In turn, ants are a resource to Membracids because they reduce predation to nymphs (Wood, 1977a).

Many tropical Membracids in wet, lowland forests interact with ants. Females of some species deposit a clutch of eggs and then leave so that location of nymphs by ants is a fortuitous event. In some species the duration of egg guarding by females is increased by ant attendance. When ant attended the survival of both females and eggs is greater in addition to increasing the chance offspring will be attended by ants (Wood, 1977). In other species females cover eggs with a frothy substance which not only protects eggs but also serves as an attractant to other ovipositing females. The resulting clumping of eggs produces a large aggregation of nymphs at egg hatch which facilitates attraction of ants but does not involve parental care (Wood, Unpublished).

2. Ant mutualism - How effective ant mutualists are in promoting Membracid survival appears to depend on a number of factors. Early location and consistent ant attendance appears to depend upon: a) the overall number of nymphs on a plant, b) the number of nymphs on a branch or leaf, c) the proximity of the ant colony and its size, and d) the ant species. Longevity of the host plant also influences ant mutualism. Annual herbaceous plants may be less predictable to Membracids in terms of their distribution over time as compared to relatively long lived woody perennials. Ant attendance on annuals may also be more variable from year to year since ants may have to forage longer distances from nests before locating nymphs. Long lived perennials provide predictable oviposition sites to Membracid females and the resulting nymphal aggregation an energy resource to ants. The establishment of ant colonies close to such Membracid host plants would not only promote nymphal survival but also the fitness of the ant colony. Location of nymphs by ants does not necessarily enhance nymphal survival. Some ant species are more aggressive and thus more effective in protecting nymphs.

Membracids may benefit the host in a manner analogous to extrafloral nectaries (Messina, 1981). Ants attending extrafloral nectaries or associated with trees (Janzen, 1966; Bentley, 1976, 1977; Inouye and Taylor, 1979) appear to reduce herbivore damage particularly those eating leaves or interfering with seed set. Nymphs which attract ants may not stress a plant at low densities but rather reduce herbivore damage through the action of ants. At high treehopper densities predation on nymphs may be high because of the inability of ants to protect all aggregations.

3. Host plant utilization - The degree of host specialization, the predictability of the resource in space and time, and resource quality appear to influence Membracid life histories (Wood, 1980; Wood and Guttman, 1982). Some treehopper species on long lived evergreen legumes have low vagility because of host predictability which results in a high degree of relatedness on individual trees. The quality of the host resource changes as treehopper population density increases, which in turn appears to have a profound influence on female vagility, sex ratios of offspring, and body size of

offspring (Wood and Dowell, Unpublished). Whether host plants are herbaceous or woody, annual or perennial, deciduous or evergreen appears to influence the degree of resource specialization and the life histories of Membracids.

4. Geography - The influence of predation, ant mutualism and host plant specialization is modified by constraints imposed by geography. Elevation and latitude influence rainfall, temperature, and seasonality which in turn affect insect and host plant diversity as well as community structure. In view of these geographical considerations, different types of Membracid life histories are predicted in varying geographical regions and habitats.

In the tropics, there may be considerable differences in life histories, ant mutualism, and host specialization among diverse habitats. In lowland wet forests with high ant and plant diversity, the majority of Membracid species appear to interact with ants and are polyphagous. In higher elevations ant diversity and abundance is reduced and hosts are evergreen. I expect fewer treehoppers which are ant attended, solitary species more common and parental care which is not dependent on ant mutualism. In contrast seasonality is pronounced in deciduous dry forests and imposes limitations on life history. I expect Membracids to be seasonally abundant and show some degree of host plant specificity as a result of coordination of life history to host phenology. Seasonal ant activity should affect the number of species which are ant attended. Membracids with parental care should be on evergreen hosts and be polyphagous with restricted dependence on ants.

In North temperate regions such as the northeast United States, the majority of species deposit eggs on deciduous woody hosts. Thus there is a high degree of host plant specialization leading to monophagy (Wood, 1980; Wood, Unpublished; Wood and Guttman, 1982; Guttman et al 1981). Polyphagous species appear to feed on herbaceous plants. Some species interact with ants but not as commonly as in the tropics. Solitary life histories are common although on some host plants such as oak, multiple species associations may be formed to attract ants. Parental care is rare or highly modified.

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