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SOCIALITY IN THE MEMBRACIDAE (HOMOPTERA)

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ABSTRACT

The treehoppers exhibit several forms of social behavior which can be categorized in terms of nymphal aggregating habits and the role of parent females in offspring maturation. These are: 1) nymphs occur solitarily without parental involvement; 2) nymphs occur gregariously and interact with attendant ants without parental care; 3) nymphs occur gregariously interacting with both parent females and attending ants; 4) nymphs occur gregariously with parental care until offspring mature. This paper describes these forms and suggests that predation is a major selective force guiding the development and maintenance of sociality and ant mutulism in these insects.

Insect sociality in the broad sense can be defined as associations of individuals which interact or communicate beyond the mating process (Wilson 1975). The apex of sociality in the insects is generally considered to have been reached by the eusocial Hymenoptera and Isoptera. Other insect groups have developed presocial behaviors which promote reproductive success or survival such as parental care which involves interaction between a parent and its offspring. Parental care has evolved in diversity of insect orders, but, until recently, has been a relatively unexplored aspect of insect biology (Wilson 1971, 1975; Eickwort, in press).

In the treehoppers (Homoptera: Membracidae), for example, Murtfeldt (1887) was the first to recognize parental care in *Entylia sinuata*. Subsequently, Haviland (1925) and Beamer (1930) found associations of what appeared to be parent females with offspring, but these observations were considered by Funkhouser (1917, 1951) to be incidental rather than indications of parental care.

The temperate and tropical membracids which I have studied exhibit several forms of sociality. These can be assigned to 4 categories in terms of the degree to which nymphs aggregate and the amount of time a parent female remains with her offspring: 1) nymphs occur solitarily (or in very small groups) without parental involvement; 2) nymphs occur gregariously and interact with attendant ants but without parental care; 3) nymphs occur gregariously with active parental care until offspring mature. In this paper I describe these categories of social behavior giving specific examples of each and discuss the significance of predation in the evolution of membracid sociality.

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Nymphs solitary - no parental care: Nymphs of *Sphongophorus* sp. occur solitarily or in groups of 2 or 3 individuals without parental care. Observations over several days indicated that while nymphs were attended by the ant, *Ectatomma ruidium* Oliver, the daily presence of these ants was sporadic. The intermittent nature of ant attendance on *Sphongophorus* sp. was likely due to the relatively small quantity of honeydew provided by one or a few nymphs and appeared to afford little protection to nymphs from predators.

Nymphs gregarious - no parental care: A 2nd form of sociality exhibited by the Membracidae is one in which the nymphs occur gregariously without direct parental care. *Enchenopa binotata* (Say) is a complex of 6 races (or species), each of which selectively feeds on one of 6 deciduous trees or shrubs in North America (Wood, in press). Social behavior in this species is characterized by aggregations of nymphs and teneral adults but without direct involvement of the parent female in offspring maturation. Eggs are deposited into twigs of the host plant in late summer and are then covered with a white, waxy material or egg froth. The lipid fraction of this egg froth contains an ovipositional attractant which draws other females that deposit their eggs on that branch. As more and more egg masses are deposited, more females are attracted, resulting in eggs being clustered on the plant. On some hosts, it is not unusual to find 100-150 egg masses on a given branch. Clustering of egg masses results in large clusters of 1st-stage nymphs at the ovipositional site the following spring. Such aggregations are probably more effective in attracting and maintaining attending ants by producing copious quantities of honeydew regularly. Small groups of nymphs suffer high mortalities in the field and are often not attended by ants. Nymphal survival is dependent on early location by ants shortly after egg hatch (Wood, unpublished).

The ovipositional habits of *E. binotata* favor the occurrence of nymphal aggregations which enhance survival. Gregarious nymphs provide a constant and copious source of honeydew which attracts and maintains continuous ant attendance.

Nymphs gregarious - parental care by parent and ants: A 3rd category of social behavior in treehoppers involves a mutualistic relationship where both the parent female and ant attendants are involved in nymphal maturation. For *Entylia bactriana* Germar, parental care is restricted to the protection of eggs and 1st and 2nd stage offspring. Mutualistic ant associations provide protection to older nymphs upon desertion by females. In southern Ohio adults overwinter apparently in leaf litter and deposit eggs on giant ragweed, *Ambrosia trifida* L., or thistle, *Cirsium* spp., in the spring. The females from these eggs oviposit in late July or early August and their offspring mature in September and then overwinter (Wood 1977a).

Eggs are inserted into the midrib of the leaf undersurface. The female remains on top of and almost entirely covers the egg mass. Before eggs hatch,

the female makes incisions in the midrib above the egg mass near the petiole with her ovipositor. Within days, this tissue darkens and the midrib breaks. Observations in the field revealed that egg masses protected from predators by females suffered less mortality than unprotected egg masses. Dislodged females were able to relocate egg masses, but specific recognition of egg masses was not demonstrated (Wood 1977a).

Females in the laboratory remained on eggs until hatch, but in the field they sometimes deserted egg masses. In the field, females on eggs are often attended by ants which collect honeydew. Attendant ants have been observed attacking objects placed in front of females and preventing disturbed females from leaving their egg masses. The presence of ants appears to have a calming affect on disturbed females since they often remain on or return to egg masses. Daily observations of a large number of females on egg masses indicate that the more consistently a female is attended by ants, the more likely she is to remain on eggs until hatch. Conversely, females which are not consistently ant attended frequently desert their egg masses (Wood 1977a).

The presence of parent females during the 1st nymphal stage reduced nymphal mortality by predators. If females desert their offspring and nymphs are not ant attended, very few nymphs survive predation. When eggs hatch in the absence of a parent female but are subsequently located by ant attendants, nymphal survival is comparable to that if parent females were present. When females on egg masses are continuously ant attended, this almost insures that ants will be present at egg hatch to provide protection of nymphs (Wood 1977a).

Nymphs of *E. bactriana* contain alarm pheromones that are released when the body wall is ruptured. These pheromones trigger the immediate dispersal of the aggregation from the underside of the leaf to the petiole and main stem of the plant (Nault et al. 1974). Dispersed nymphs then reaggregate but not necessarily at the original site. Parent females with 1st stage offspring respond to introduced predators by assuming a position between offspring and predator. Staged encounters of this type were highly successful in preventing predation of nymphs. A crushed nymph placed on a leaf with a parent female elicited a similar defense response by the parent female (Wood 1977a).

Nymphal escape behavior is modified by both the presence of ants and parent females. Nymphs by themselves react almost immediately to crushed nymphs by walking off the leaf. When the parent female is present, dispersal is much slower. However, females do not physically stop nymphs from moving. When nymphal aggregates are presented a crushed parent female, nymphs respond initiall as if a female were present, but respond later as if a sibling were injured. This suggests females contain an arrestant pheromone that facilitates the maintenance of aggregations in the presence of minor disturbances. If the female's defensive movements fail and she is captured, an alarm pheromone is released from the female that triggers the nymphal escape response (Wood 1977a).

The presence of attendant ants also modified nymphal escape behavior. When

crushed nymphs are presented to ant attended nymphal aggregations, ants attack the source of the alarm chemicals, but also prevent nymphs from dispersing by antennating their abdomens. Upon prolonged exposure to the alarm pheromones, nymphs will disperse (Wood 1977a). It is highly likely that ants are actually attracted to the treehopper alarm pheromones as Nault et al. (1976) have demonstrated for aphid ant associations. The number and kinds of ants present appears to determine the degree of predator protection provided to treehopper nymphs (Wood unpublished).

Nymphs gregarious - continuous parental care: Another form of sociality exemplified by several membracid species is one in which the parent female remains with her gregarious offspring throughout their development. Females of *Umbonia crassicornis* Amyot and Serville form an egg mass by inserting eggs into the branch of their host plants (*Calliandra*, *Lysiloma*, *Albizzia*). During egg maturation, females remain with them (Wood 1974) and do not leave even if physically disturbed by probing with a pencil. Dislodged females can relocate egg masses, but when given a choice between their own eggs and others, they do not differentiate (Wood unpublished). When females are removed in the field, egg masses suffer a higher mortality than those tended by females. Females tending egg masses are protected to some degree from certain vertebrate predators by behavioral and physical adaptations. During the egg maturation period, the female remains motionless, enhancing her dark green cryptic coloration. This behavior presumably reduced mortality by predators such as *Anolis* which primarily capture moving prey. A female is also protected by its highly sclerotized pronotum. Experimental removal of the pronotum renders a female more acceptable to *Anolis* (Wood 1975, 1977b).

Before eggs hatch, the female moves off the egg mass and makes a series of spiral slits in the bark below the egg mass with her ovipositor. At egg hatch the female positions herself about 4 cm below the egg mass and as 1st stage nymphs appear, they move off the egg mass and line up along the spiral in front of the female.

Parent females actively maintain nymphal aggregations. Nymphs walking down the branch are intercepted by the parent female who taps on their dorsum with her front legs. Nymphs respond by stopping and/or returning to the aggregation. As nymphs develop, the female moves farther down the branch but remains with her offspring until they mature. Removal of females from 1st instar aggregations results in higher dispersal and predation of nymphs than if females were present (Wood 1976a). Females respond aggressively to predators in particular, adult coccinellids, by walking directly toward the predator while fanning her wings. Such aggressive displays dislodge coccinellids from branches and thereby reduce predation of nymphs. Aggressive behavior is also evoked when an alarm pheromone(s) is apparently released from the body of a crushed nymph. Females attracted to the site of an injured nymph and presumably a potential predator initiate the same aggressive displays as if a predator were present (Wood 1974, 1976a). In contrast to

other aggregating species, nymphs of *U. crassicornis* do not respond to alarm pheromones from injured siblings.

Social behavior is not restricted to female-offspring interactions. Teneral adults also form aggregations that last 20 to 30 days. The pronota of teneral adults are aposematic with a light yellow ground color, contrasted with black stripes and red tip of the dorsal horn. At this stage the pronotum is soft and pliable, presenting no physical obstacle to a vertebrate predator such as the lizard, *Anolis*. When naive anoles are released at the base of trees with adult aggregations of *U. crassicornis*, anole movement on branches triggers a cataleptic response by the treehoppers. Anoles may walk over or even remain on top of treehoppers without disrupting the aggregation. When presented individually to caged anoles, teneral females are rejected. The basis for this rejection is a taste response since other treehoppers of this stage whose pronota had been removed were also rejected. As adults mature, the pronotum hardens, providing a physical defense and their behavior changes. The entire aggregation of mature adults, when disturbed, explosively disperse which may produce a startle response in a predator (Wood 1975, 1977b).

Platycotis vittata F. is the only other North American species in the same tribe as *U. crassicornis*. Parental care in this species (Wood 1976b) is very similar to that of *U. crassicornis*. The major difference is that *P. vittata* has only 2 generations a year, while *U. crassicornis* may have 4 or more. Of interest here is that *P. vittata* is the only north temperate membracid whose females remain with offspring until maturity. The range of *U. crassicornis* does not extend farther north than central Florida where killing frosts occur annually.

Guayaquila compressa Walker has been recorded only from Central America where I have collected it in lowland wet forests. Females deposit eggs on top of branches or leaves in clusters and surround them with a white secretion. Females then sit on top of the cluster, but leave some peripheral eggs exposed. In contrast to *U. crassicornis*, female *G. compressa* are extremely sensitive and readily desert eggs when disturbed. Disturbed females fly 3 meters or more from egg masses but return within an hour.

Parent females are found with offspring at egg hatch, but apparently do not modify the plant tissue in preparation for nymphal feeding as in *U. crassicornis*. Both parent female and offspring together may walk more than a meter away from the ovipositional site shortly after egg hatch. Such movements may occur several times during a 5 to 6 day period. This behavior is unlike that of *U. crassicornis* where both female and offspring remain on or near the branch where eggs were deposited.

Alarm or escape behavior in response to artificial disturbance in *G. compressa* involves both adult females and offspring. When disturbed,

females may fan their wings, produce a buzzing sound, and then rapidly fly off to nearby vegetation. During this interval, nymphs often disperse in different directions away from the disturbance and may travel more than a meter before they reaggregate or return to the original site. Females relocate offspring through a series of short flights back to the host, followed by walking up and down the plant until finding nymphs. Rapid dispersal or escape of parent females may produce a startle response in a predator and provide time for offspring to disperse.

Typically, there is only one aggregation of *G. compressa* per host plant. However, on one plant with 2 females and their offspring, I made observations over a 9 day period to determine if there was any cooperation between females in brood care. Egg masses were deposited about 0.9 m from each other and hatched several days apart. During a 2 day period, both females and their offspring merged into one aggregation and remained together for 6 days. When nymphs were disturbed, the combined activity of the 2 females appeared to facilitate the maintenance of the aggregation. When both parent females and nymphs were disturbed sufficiently to trigger dispersal, both females flew from the plant while nymphs walked to a branch 0.75 m away where they reaggregated. Nymphs did not regroup into 2 aggregations but into one. Both females relocated the nymphs but not at the same time. This is the first indirect evidence of female cooperation in brood care (Wood 1978a).

DISCUSSION

At least 50 membracid species exhibit some form of parental involvement in egg or nymphal maturation (Hinton 1977; Wood unpublished). Of these, only 3 extend to temperate North America and only in *P. vittata* does the parent female continuously care for her young. Cursory examination of the North American membracid fauna suggests that the majority of species fit the solitary category (Wood unpublished). This evidence suggests that sociality in treehoppers likely evolved in the tropics, which is consistent with Funkhouser's (1951) ideas on the origin of the membracids. Moderate tropical climates certainly could provide the basis for the evolution of parental care through increased female longevity (Wilson 1975). Tropical members of other families closely related to the Membracidae such as the Aethalionidae have also developed parental care (Brown 1976).

Wilson (1975) discusses a number of ecological factors which he postulates form a "web of causation" leading to the evolution of parental care. My observations strongly implicate predation as one major selective force guiding the evolution of sociality in the Membracidae. Each of the 4 forms of sociality exhibited by treehoppers represent behavioral adaptations to avoid predation. At one extreme *Sphongophorus* sp. has adopted a nearly solitary life style which

appears to reduce the likelihood of a parent's offspring incurring mortality from predation. By contrast, *E. bactriana* has adopted a life style where nymphal survival depends on both the parent female and ant mutualism. The role of the parent female in the care of her offspring is particularly evident in *U. crassicornis*, *P. vittata* and *G. compressa* where visual and chemical cues elicit behavioral responses to thwart predators. Females of *E. binotata*, although not actively involved in the maturation of offspring, through their ovipositional habits, establish nymphal aggregations. Large aggregates of nymphs produce more honeydew than smaller groups which increases their chances of being located and attended by ants.

Although further detailed quantitative studies of treehopper predation are needed, Funkhouser's statements (1917, 1951) that membracids have few natural enemies are not supported by my field observations. Anoles, Coccinellidae, spiders, wasps, Pentatomidae, and Reduviidae have all been observed in the field to feed on treehopper nymphs or adults, while Anthocoridae and mites have been observed eating eggs. The relationship of parent females with offspring or the interaction of nymphs with attendant ants suggests such behaviors have been in response to significant selection pressures. My studies which are summarized here show that significant mortality occurs when nymphs are unprotected and indicate that predation provides a strong selective force in the development of sociality in the Membracidae.

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