MATERNAL CARE IN A LACE BUG,
CORYTHUCHA HEWITTI (HEMIPTERA: TINGIDAE)*

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INTRODUCTION

Many species in at least 13 families of Hemiptera display parental care (Wilson, 1971). For the Tingidae (lacebugs), a relatively large family with member species that are often very abundant (Drake & Ruhoff, 1965), parental care has been described in detail for only a few species. Tallamy's (1982, 1984, 1985, 1986) and Tallamy & Denno's (1981a, b, 1982) extensive studies of the lace bug, *Gargaphia solani*, showed that maternal care of offspring is age specific, has a genetic basis, and greatly improves offspring survival by reducing predation. Maternal care, however, is costly in that tending females are less fecund (Tallamy, 1982,; Tallamy & Denno, 1981a, b, 1982). Three other lace bug species do not exhibit maternal care, but two of these are not subjected to intense predation and the third possesses other life history traits to avoid predation (Tallamy & Denno, 1981b).

In this paper, I describe the biology and parental care behaviors for *Corythucha hewitti* (Drake), a lace bug that has a wide distribution (Canada and northeastern through northcentral US (Drake and Ruhoff, 1965)), high densities, and causes extensive plant damage. Neither the biology nor behavior of this species has been previously described. To test the hypothesis that tending by female parents influences persistence of their broods, I experimentally removed female adults.

Maternal care can evolve and persist if increased inclusive fitness of adult females via increased survival of brood offspring outweighs assumed costs of tending or protecting offspring (Wilson, 1975; Tallamy 1982, 1986; Tallamy & Denno, 1981a, b, 1982). Fitness via increased brood survival may be further increased if kin discrimination occurs, so that related individuals are treated preferentially and

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energy and time are not wasted in caring for non-relatives (Waldman et al., 1988). For *Corythucha hewitti*, kin discrimination should be particularly important due to high densities; unrelated broods often co-occur on the same leaves and nymphs and adults probably often encounter unrelated conspecifics when broods move *en masse* to nearby leaves. In an initial test of kin discrimination, I experimentally removed maternal adults and replaced them with adult females from unrelated broods. I then compared persistence of these experimental broods and the adult females with control broods.

MATERIALS AND METHODS

The biology and behavior described here are based on observations and experiments from 14 June–July 2, 1987 and 30 June–July 18, 1988 at University of Minnesota, Lake Itasca Forestry and Biological Station, Lake Itasca, MN. The habitat is a mixed hardwood-conifer forest.

To test the hypothesis that presence of a female adult affects persistence of the brood, I removed adult lace bugs from their broods. Fifty pairs of leaves (a pair occurred on the same twig) on five *Prunus virginiana* (chokecherry) trees, each with a brood of first or second instars and an adult, were labelled with tape near the petiole. For each pair, an experimental and a control brood was assigned randomly by a coin flip. The adult female was removed from each experimental brood on 4 July 1988. Nymphs in each experimental and control brood were counted. I assumed that the adult present was indeed the mother. Although actual kinships were not determined, this assumption is reasonable since females were observed to remain near their broods from egg through nymphal stages. On July 7 1988, all experimental and control broods were re-censused. Seventeen of 50 pairs were not used in statistical analysis (Wilcoxon rank sum test comparing difference in fraction of nymphs remaining) either because one of the leaf pairs was missing or control broods had no adult present at the time of re-censusing. This experiment determines the effect of adult females on persistence of the nymphal brood; the actual fate of missing nymphs cannot be ascertained.

To test the hypothesis that kin discrimination or recognition occurs between a mother and her nymphs, I removed adult females and

replaced them with unrelated females. I assumed that females removed from broods were indeed mothers and that females used to replace these mothers were unrelated or at least not maternal to the nymphs. Twenty four pairs of leaves on two *Betula papyrifera* (paper birch) trees harboring at least one adult and a third to fourth instar nymphal brood were marked (as above) and one of each pair assigned randomly as experimental or control. On experimental leaves, the adult female was removed with forceps and replaced with a female from a brood on a different branch on 11 July 1988. At the same time, adults on control leaves were lifted from the leaf with forceps but then returned to the same leaf. Lifting was done to control for any effects caused by physically disturbing the females. Nymphs and adults on control and experimental leaves were censused four days later; 20 of 24 experimental leaves and 23 of 24 control leaves were recovered. A Wilcoxon rank sum test was used to statistically compare fraction of remaining nymphs between experimental and control leaves.

RESULTS

Biology and Behavior of the Lace Bug.

During the summers of 1987 and 1988, the lace bug was at high densities (>10 per leaf; $N = 1000$ haphazardly-selected leaves per tree species) on *P. virginiana* (common chokecherry), *Tilia americana* (basswood or linden), and *B. papyrifera* (paper birch). The lace bug was also noted on *Prunus pennsylvanica* (pin cherry), *P. serotina* (black cherry), and *Quercus macrocarpa* (bur oak), although less so than the former three tree species. All of these represent new host records as this species has been recorded from only species of *Corylus* (Drake and Ruhoff, 1965). Some trees were damaged extensively; i.e., most leaves showed evidence of the distinctive discoloration and senescence caused by lace bug feeding.

Eggs are laid in clusters of usually 20–50 attached to the underside of a leaf and can be found in late June, although by this time most nymphs are in the first instar. Presence of some first instar broods in mid July suggests more than one generation per season. Mean size of first instar broods on chokecherry was 25.2 ± 18.0 (range = 5 – 102, $n = 100$ broods). The larger of these broods, however, may be the result of coalescing broods from different females on the same leaf or from egg dumping (Tallamy, 1985).

First instar nymphs begin feeding gregariously on the underside of the leaf near the base by puncturing the leaf with their beaks. The attending adult female remains near the leaf edge usually with her head pointed toward the brood (Fig. 1). On several occasions, I observed females that wandered from the leaf with the brood, but these eventually returned to the brood. Nymphs complete five instars in 20–30 days, while typically remaining within the brood. Apparently, broods can complete development on a single large leaf like basswood but may move to other leaves on trees like chokecherry, where leaves are relatively small. When moving to another leaf, adult females lead the way, rapidly vibrating the abdomen in a vertical plane. It is not known if an aggregation pheromone is involved in movement from leaf to leaf, although such has been suggested for other lace bugs (Kearns & Yamamoto, 1981). After completion of nymphal stages, eclosed adults tend to remain feeding in broods. In later stages, many broods are observed with more than one adult (range = 0 – 8 adults/brood, $\bar{x} = 1.76 \pm 1.68$, $n = 100$ broods), although I cannot be certain that additional adults are from the same brood. Adults likely overwinter in leaf litter and emerge in early June as do other species in this genus (Bailey, 1951).

Adult females do not display aggressive behaviors when either they or their nymphs are disturbed (i.e., prodded slightly with a pencil point in the field ($n = 20$) or in the laboratory on removed twigs ($n = 20$)). *Gargaphia solani*, on the other hand, aggressively defends nymphs against predators and inanimate objects (Tallamy & Denno, 1981a). When a nymph of *C. hewitti* was disturbed, it removed its beak from the plant tissues and began to move toward and then down the midrib, occasionally stopping and vibrating its abdomen in a vertical plane. Other nymphs in the brood followed. The adult female scurried down the leaf and arrested the nymphal column by stopping on the midrib, rapidly vibrating her abdomen and occasionally turning to face the nymphs. In this manner, the nymphs ceased moving and began to feed where the adult had perched. When adult females were disturbed, they moved down the midrib, stopped to vibrate the abdomen, and either stopped on the same leaf or moved to another leaf. Her nymphs usually followed (12 of 20 observations) and settled to feed wherever the adult eventually stopped. Occasionally, nymphs moved past a female perched on a twig but in 4 of 8 cases, the female re-located the brood on a

Figure 1. Photograph of female adult *Corythucha hewitti* and her brood (third and fourth instar nymphs) on a leaf of *Prunus virginiana*. Nymphs feed gregariously throughout their development. A lace bug mother usually remains near her offspring from egg stage through adulthood.

leaf within one hour. Fluttering of wings by adults was reported for *G. solani* and suggested as a predator defense by increasing apparent size of lace bugs (Tallamy & Denno, 1981a) or as way of directing nymphal movements (Kearns & Yamamoto, 1981). However, I observed only abdominal vibrations. Furthermore, nymphs with reduced wings performed the same vibrating behavior. It thus appears that maternal care consists of keeping the brood together by leading and "herding" rather than actively defending against natural enemies.

Field Experiments on Brood Persistence

Proportion of nymphs remaining in broods after adult females were removed was significantly less than broods where females were present (control $\bar{x} = .453$, $SD = .305$, $n = 33$; experimental $\bar{x} = .117$, $SD = .197$, $n = 33$; Wilcoxon rank sum test, large sample approximation, $W^* = 5.07$, $p < .001$).

When maternal females were replaced with unrelated adult females, proportion of remaining nymphs was significantly less than proportion remaining on control leaves where adult females were disturbed but not replaced (control $\bar{x} = .296$, $SD = .355$; experimental $\bar{x} = .086$, $SD = .240$; Wilcoxon rank sum test, large sample approximation, $W^* = 2.29$, $p < .05$). Percent of experimental leaves (mothers replaced with unrelated females) with adults remaining was 12.5% (3 of 20) compared to 39.1% (9 of 23) for control leaves (mothers disturbed but not replaced). During the course of this experiment, a severe thunderstorm occurred and, coupled with physical disturbance of lifting, may account for the low proportion of remaining nymphs and adults on the control leaves. However, the storm should have affected control and experimental broods equally.

DISCUSSION

The evolution of parental care assumes that the costs of caring (e.g., time and energy investments, risk of predation, reduced fecundity) are outweighed by the gains (e.g., increased survival and reproduction of offspring) (Wilson, 1975; Tallamy & Wood, 1986). Results from this study suggest potential gains in fitness by maternal females. Without the mother, nymphs in the brood disappear, and probably wander to other leaves. This study did not determine their

fate, but it is likely that increased movement increases mortality from natural enemies, desiccation, or failure to find a suitable feeding site. Further, feeding in groups may enhance survival of nymphs. Aggregated nymphs may be able to use a wider array of leaf types, or groups of nymphs may create nutrient "sinks" (Tallamy & Denno, 1981a). Additional experiments examining the growth, survival, and reproduction of solitary versus group nymphs of *C. hewitti* should be productive.

The female replacement experiment suggests that some degree of kin recognition or discrimination (*sensu* Waldman et al., 1988) occurs. The direction of recognition (whether mothers recognize their nymphs or nymphs recognize mothers or both) is not clear since it was not possible from the maternal replacement experiment to determine if adult females deserted unrelated nymphs or vice-versa. Nevertheless, kin recognition should be advantageous in this system because high densities, multiple broods per leaf, and movement of entire broods from leaf to leaf via petioles and stems increase the likelihood of encountering unrelated conspecifics. Other subsocial hemipterans and homopterans display varying degrees of kin recognition. *Elasmucha grisea* and *Antiteuchus tripterus* females do not distinguish between their own eggs and conspecifics when guarding them (Melber and Schmidt, 1977; Maschwitz and Gutmann, 1979 cited in Eickwort, 1981), but female *Pisilus tipuliformis* recognize and prefer to guard their own eggs (Parker, 1965). Membracid females accept and protect eggs of conspecifics, but unlike *Corythucha hewitti*, are unlikely to encounter conspecifics in nature (Hinton, 1977). In the tingids, female *G. solani* orient to their own eggs and nymphs more so than unrelated ones but will also guard unrelated eggs (Tallamy, 1985, 1986; Tallamy & Denno, 1981a).

Maternal adults of *C. hewitti* appear to care for their nymphal brood by maintaining the feeding aggregation through "herding" and leading the brood to new leaves when disturbed or perhaps when the resources of a leaf are depleted. Adult females appear non-aggressive, at least when confronted with an inanimate object. Tallamy and Denno (1981a) found, however, that live predators and inanimate objects produced defensive responses in the tingid *G. solani*. Despite the lack of aggressiveness of *C. hewitti*, female parents could indirectly protect nymphs by maintaining the integrity of

the brood if rate of attack by natural enemies is less on individuals in groups or if increased movement by nymphs attracts natural enemies. Further, female parents may indirectly protect nymphs by releasing alarm pheromones that cause nymphs to scatter in the presence of predators as Kearns & Yamamoto (1981) suggested for *G. solani*. Although I observed no predation or parasitism of nymphs, I did observe egg broods that were heavily parasitized by wasps and I cannot exclude the possibility that mothers actively protect eggs or other life stages.

Adult female *G. solani* care for eggs and nymphs by actively defending them against predators (Tallamy, 1982, 1984, 1985, 1986; Tallamy & Denno 1981a, b). *Gargaphia solani* feeds mostly on horsenettle in old fields where predation is intense and probably a strong selective force in maintaining maternal care (Tallamy & Denno, 1981a, b). Tallamy & Denno (1981b) showed that predation was less severe on two *Corythucha* species that feed on forest trees, and these species did not display parental care. *Corythucha hewitti* feeds in similar forest habitats as do these species (in one case, on the same host tree) and thus predation may not be severe and maternal care is instead maintained by other selective pressures.

SUMMARY

Adult female lace bugs (*Corythucha hewitti*) remain in close proximity to their broods from egg stage, through five nymphal instars, to adulthood. Such subsocial is relatively common in the Hemiptera but few have examined experimentally the nature and consequences of such behavior. I tested the hypotheses that presence of mothers affects the persistence of the nymphal brood and that the presence of the mother as compared to an unrelated female promotes persistence of nymphal broods. In broods where mothers were removed, brood size was significantly less than control broods. When unrelated females were exchanged with mothers, brood size and number of adults also declined relative to controls. These results suggest that the presence of mothers increases persistence and probably survival of offspring nymphs and that either nymphs recognize their mothers, or vice-versa. Behavioral observations suggest that mothers do not actively protect offspring, but rather keep broods intact by "herding" or leading nymphs to new feeding sites.

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