

phenazine decanoate to be slightly more potent in promoting orofacial dyskinesia than oral treatments. Several investigators recently noted that tardive dyskinesia may be significantly more common in patients who have received intramuscular fluphenazine decanoate than in those who had received oral treatments (18).

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Treehoppers Transfer Parental Care to Ants: A New Benefit of Mutualism

Abstract. *Female treehoppers (Publilia reticulata Van Duzee) modify their parental care behavior in the presence of ants. Females with untended young remain with their original brood, but females from ant-tended colonies readily desert their first brood and produce additional clutches. Care by female treehoppers, in the absence of ants, increases the probability that a colony will produce some survivors, but ant attendance greatly increases the number of surviving nymphs.*

Mutualisms between ants and honeydew-producing insects have generally been described in terms of benefits to insects that are directly associated with the ants (1). Females of some species of treehoppers (Homoptera: Membracidae), which remain with their young, change their behavior in the presence of ants—either abandoning broods earlier (2) or later than usual (3). I present evidence that females that abandon nymphs may be abdicating parental care to the ants; these females can then produce additional broods and thus increase their total fitness. Because females are apparently exploiting mutualists and benefiting from their activities without direct interaction, this response may provide a new class of mutualistic benefits. To determine whether treehoppers receive such indirect benefit, I examined the effects of ant attendance on female parental behavior and the consequences of ant attendance and parental care on juvenile survival in the North American treehopper, *Publilia reticulata*.

Publilia reticulata is a membracid which commonly feeds on ironweeds (*Vernonia* spp.) throughout the eastern and midwestern United States. In the spring, females, which have overwintered as adults, mate and oviposit a clutch of about 50 eggs into the midrib of a leaf. Although some females may produce additional clutches, there is only a single generation per year. Nymphs complete their 40- to 50-day development period feeding in aggregations on the natal plant. Both adult and immature forms produce honeydew, which is highly attractive to ants. At the study site in central New Jersey (4), seven species of ants were found tending colonies of *P. reticulata* (5). Females of *P. reticulata*, in common with some other species of treehoppers (6), exhibit parental care by remaining with egg masses and young nymphs. This behavior has been shown in other species to protect egg masses from parasitoids (7), maintain nymphal aggregations (8), and deter predators (9). In a field study in the summer of 1981,

Table 1. The effect of ant care and parental care on survival of *Publilia reticulata*. Results for mean colony size and mean number of survivors per clutch were analyzed by using the Newman-Keuls test, and results for colonies producing survivors were analyzed by Fisher's exact test; results with the same letter did not differ at the .05 level.

Treatment group	Colonies (N)	Colony size	Colonies with survivors		Total nymphs (N)	Nymphs surviving		Survivors per clutch	
			N	%		N	%		
No ants									
No females	8	48.8 ± 14.3 A	2	25 A	390	12	3.1	1.5 A	
Females	15	45.4 ± 6.5 A	10	67 A, B	681	73	10.7	4.9 A	
Ants present									
Brood 1	37	47.3 ± 7.4 A	29	78 B	1751	475	27.1	12.8 B	
Brood 2	12	32.8 ± 4.3	10	83 B	393	167	42.5	13.9 B	

answers to three questions were sought: Does the presence of ants affect female parental behavior? Do females that abandon broods subsequently produce other broods? Does the presence of ants or of females affect the survival of nymphs?

To assess the effect of ants on survivorship, 33 plants bearing 37 treehopper colonies (10) which were tended by ants were censused daily from mid-June through August. Twenty-five females from these colonies were marked (11) to determine tenure. A similar census was conducted on 20 plants bearing colonies from which ants were excluded (12). These 20 plants were divided into two groups. The first group consisted of six plants bearing eight colonies with no females present, and the second had 14 plants supporting 15 colonies with marked females guarding broods. Females had free access over the plants and could leave by flying. There was no statistically significant difference in the initial size of colonies in the three groups (Table 1). All suitable ironweed stems were examined weekly to relocate marked females that might have moved and to determine whether nymphs that had disappeared had simply moved to another plant. Since no nymphs were located on new plants, disappearance is probably a reliable estimate of mortality (13).

The effect of ants on female parental behavior. Normally *P. reticulata* females remained with their clutches until hatching, 13 to 17 days after oviposition. Beyond the first hatching, however, tenure with brood was strongly modified by the presence of ants. Ant-tended females abandoned nymphal aggregations significantly sooner (5.9 ± 1.8 days, mean $\pm$ standard error of mean) than did females from exclusion colonies (32.2 ± 7.5 days, $P < .001$, Mann-Whitney U test).

Fate of marked females. Mark-recapture data suggest that females may benefit from abandonment of broods by being freed to produce additional clutches. Ten of the 25 marked females from ant-tended colonies were found with new egg masses on other parts of the same plant, but only one of 15 females from the colonies in which ants were excluded deserted the first brood to produce a second brood on the same stem ($P = .024$; Fisher's exact test). Ten of 24 marked females (14) from ant-tended colonies were relocated with additional broods on new plants; no females from colonies without ants were found on new plants ($P = .003$; Fisher's exact test).

Survivorship of tended and untended

broods. Results show that 27.1 percent of nymphs from ant-tended colonies survived to the adult stage, but only 10.7 percent of the female-guarded nymphs and 3.1 percent of untended nymphs successfully completed development. Although the total success of female-tended broods was not significantly different from that of untended broods, the proportion of colonies that produced survivors was considerably higher ($P = .070$; Fisher's exact test). Although the reasons for this differential success were not determined, protection from predators is probably important. Predators, including spiders, coccinellids, and chrysopid larvae, were observed on ant-tended plants only seven times, but on 42 occasions on plants without ants.

Second broods. In general, second broods were smaller than first broods, but in 1981 the overall success rate of second ones was somewhat greater than that of first broods (Table 1). The increased proportion of individuals surviving in the second groups may reflect the fact that the weather was warmer and more favorable during their development. In addition, all second broods were ant-tended, and ants became more active as the season progressed. However, such broods are more vulnerable to environmental extremes. In 1980, a drought caused all ironweed stems to die back by late August, leading to high mortality in late broods.

Female behavior with second broods followed the same pattern of abandonment as with first broods; however, females producing second clutches on the original plant tended to abandon these very rapidly (6.1 ± 1.6 days before hatching). Females producing second clutches on new plants behaved similarly to those producing first clutches on original plants, remaining 3 to 7 days beyond the date of the first hatching.

Publilia reticulata females thus seem to be able to assess the presence of ant mutualists and to modify their parental behavior accordingly. When ants are protecting broods, females incur no penalty for deserting them and may substantially increase their fitness by producing additional clutches. When no ants are present, however, abandonment results in lowered survival of nymphs. In the absence of ants, females remain with their original brood, providing some direct protection. Females may also serve to attract ants to the small nymphs (15), and this may be a major role of parental care in *P. reticulata*.

These results suggest that ant mutualisms act indirectly to benefit adult tree-

hoppers as well as directly to benefit immature forms. This new mechanism of benefits in mutualism highlights the potential importance of mutualisms in comparison with other biotic interactions like competition, predation, and parasitism.

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4. The study was conducted in the summer of 1981 at the New Lands Research Reserve, a 162-ha tract of undeveloped land maintained by the Stony Brook-Millstone Watershed District, near Pennington, N.J.
5. The following species of ants were observed tending *P. reticulata* at the study site: *Tapinoma sessile* Say, *Myrmica lobicornis fracticornis* Emery, *M. americana* Weber, *Dolichoderus pustulatus* Mayr, *Crematogaster lineolata* Say, *Leptothorax ambiguus* Emery, and a *Formica* sp. No significant difference in female tenure was found in response to the most common ant species (colonies tended by *T. sessile*, 6.2 ± 0.7 days, and *Myrmica*-tended colonies, 5.3 ± 0.4 days).
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10. Several plants in each group supported more than one colony. This aggregative response in ovipositing females has also been observed in the congener, *P. concava* [P. B. McEvoy, thesis, Cornell University, Ithaca, N.Y. (1977)]. Colonies were treated separately.
11. Marks of water-soluble pigments in different colors (White-Out correction fluid) were applied to the pronotum of each adult. Both tended and untended females were identified only by area and by treatment group. Some colonies in each group had been abandoned by females before marking and exclusion of ants. These were included in survivorship analysis.
12. Ants were excluded through the use of a sticky barrier, a 5- to 10-cm band of tanglefoot applied near the base of the stem.
13. Nymphs showed no tendency to leave aggregations and would return to their original brood if moved up to 1 m away, sometimes bypassing intervening suitable stems to do so.
14. One female on a second brood on the original plant was damaged and removed and was therefore excluded from the analysis of females leaving the original plant since her fate was known. The 14 females that left the first plant but were not relocated may have been overlooked, have died, or have emigrated from the area. The marking system used showed that no females that were recovered had moved more than a few meters. However, it did not allow absolute identification of females; thus it is possible that some of the females that produced a second clutch on a new plant had already produced two clutches on the original plants. None of the relocated females, however, had colonized a third plant.
15. P. B. McEvoy (10) has shown that *Publilia* individuals increase in attractiveness to ants with increasing size. Adults may thus serve to attract ants to colonies of small early instar nymphs.
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