

## MECHANISMS AND DENSITY DEPENDENCE OF BENEFIT IN AN ANT–MEMBRACID MUTUALISM

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**Abstract.** I examined mechanisms and patterns of benefit for the membracid (treehopper) *Publilia concava* tended by the ant *Formica obscuriventris* to test two hypotheses: that treehoppers benefit from ant attendance only by protection from predators, and that density-dependent benefit depends on the presence of predators. I used a factorial design, manipulating ants and predators in 1996, and ants and removal of uncollected honeydew in 1997. Results showed that treehoppers benefit from ant attendance by protection from predators. Additionally, results suggested that treehoppers benefit from ant attendance in ways other than protection from predators; tended treehoppers outperform untended treehoppers even with predators excluded. There was no support for the hypothesis that a proximate benefit of ant-tending includes removal of uncollected honeydew. A possible benefit (untested) of ant-tending is increased feeding rates. Treehoppers in small aggregations benefited more than treehoppers in large aggregations, indicating a density-dependent benefit in this mutualism, independent of predator level. Correspondingly, the number of ants per treehopper was highest for small aggregations. This study suggests that individuals can benefit from mutualisms in complex ways. Additionally, it adds to a growing number of studies that support the hypotheses that mutualisms may be stabilized by density-dependent benefit and that density-dependent benefit may be driven by the recruitment patterns of mutualists.

**Key words:** ants; ant–homopteran mutualism; density-dependent benefit; *Formica obscuriventris*; *Formicidae*; *Hemiptera*; *Hymenoptera*; *Membracidae*; mutualism; predation; *Publilia concava*; treehoppers.

### INTRODUCTION

Although ecologists have come to recognize mutualism as an important population- and community-level process, we are still relatively unaware of the dynamic and stability properties of these interactions (Bronstein 1994a). Studies manipulating the presence or density of mutualists have identified important features of mutualism, including ecologically based variation in outcome (e.g., Cushman and Addicott 1991) and patterns of density-dependent benefit (e.g., Breton and Addicott 1992a). However, the underlying mechanisms that generate these results remain largely untested. Currently, experiments are needed that manipulate proposed mechanisms of benefit in addition to the abundance of mutualists.

Ant–homopteran interactions are frequently studied mutualisms (see reviews by Way [1963], Boucher et al. [1982], Buckley [1987]). In these interactions, ants collect the carbohydrate-rich excretions (honeydew) of homopterans. Homopterans benefit from ant tending because ants attack and remove predators from their host plants (reviewed in Way 1963, Buckley 1987). Other benefits include removal of honeydew and fa-

cilitation of feeding. Facilitation of feeding may result in increased survivorship, fecundity, developmental rate, or size (El-Ziady and Kennedy 1956, Banks and Nixon 1958, Bristow 1984). Similarly, uncollected honeydew may trap nymphs (McEvoy 1977; *personal observation*) and can result in the formation of sooty molds (Fokkema et al. 1983), which might block excretion (Way 1954) and ultimately decrease photosynthesis in the host plant (Wood et al. 1988).

Studies of ant–homopteran mutualisms focus primarily on protection from predators as the critical means by which homopterans benefit (Buckley 1987). Although generally convincing, support for the predator protection hypothesis is nevertheless largely indirect (but see Bristow [1984] for an exception). Benefit to homopterans is tested by manipulating the presence or abundance of ants, and the density of predators is compared between treatment and control groups (e.g., Cushman and Whitham 1989, Itioka and Inoue 1996a).

The predator protection hypothesis has also been invoked to explain temporal variation in benefit to homopterans. Cushman and Whitham (1989) showed that yearly variation in the magnitude of mutualistic benefit to membracids was qualitatively correlated with the abundance of predators over a three-year period. Although the hypothesis was not tested directly, this study

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is cited as a strong example of predator-driven variation in mutualistic outcome (e.g., Bronstein 1994b).

In general, both biotic and abiotic factors have been suggested as important sources for variation in mutualistic outcomes (Thompson 1988, Cushman and Addicott 1991), but there have been few experimental tests of the specific mechanisms that contribute to this variation (see Setälä et al. 1997). Where variation in outcome results from context-dependent benefit and partners benefit in complex ways, presence-absence manipulations may be unable to isolate the particular factors that contribute to these conditional outcomes. Mechanistic studies will not only provide this basic information, but also can be applied to test hypotheses regarding the possible factors that may stabilize mutualism. For example, theoretical studies have shown that mutualisms will be stabilized if benefit decreases as recipient density increases (Addicott 1981, Dean 1983, Wolin and Lawlor 1984), regardless of mechanism. Although a few studies of ant-homopteran mutualisms have reported patterns of density-dependent benefit to homopterans (McEvoy 1977, Cushman and Whitham 1989, Breton and Addicott 1992a), no studies have experimentally addressed the role of predators or competitors in generating these patterns. Because ant-homopteran mutualisms are a tri-trophic system (ants  $\rightleftharpoons$  homopterans  $\rightarrow$  predators), they provide an excellent opportunity to test whether decreases in per capita benefit depend on interaction with a third participant.

In this study, I tested the hypotheses that treehoppers benefit from ant attendance only by protection from predators, and that density-dependent benefit depends on the presence of predators. Finally, I examined whether patterns of ant recruitment could explain patterns of density-dependent benefit.

## METHODS

### *Study system*

I examined the mutualism involving the ant *Formica obscuriventris* Mayr and the treehopper *Publilia concava* Say during the summers of 1996 and 1997. The study site was located within an old field bordering a recreational park in Ashford, Connecticut, USA. The vegetation was dominated by *Solidago* spp., with *Rosa multiflora* and *Populus tremuloides* saplings interspersed throughout. The forest edge included *P. tremuloides* and *Quercus rubra*. Other tended homopterans consisted of a small colony of aphids feeding on *P. tremuloides* (aphids were removed prior to the experiment). All treehopper aggregations for both years were found on a ~15 m diameter patch of *Solidago altissima* L. Common predators of *P. concava* nymphs at this study site included spiders, coccinellid beetles, and lacewing larvae. The only predators observed to feed on *P. concava* adults were salticid spiders (*unpublished data*).

*P. concava* has a single generation per year in the

northeastern United States. Adults of *P. concava* overwinter and emerge in May, when mating occurs (McEvoy 1977). Females then oviposit, most commonly on the midrib of *Solidago* and *Eupatorium* spp. (*personal observation*). Several females (up to a maximum of 13 observed; *unpublished data*) lay their eggs on a given host plant, and aggregations of up to 1100 nymphs emerge by late July. An aggregation is defined as all the treehoppers on a single host plant. Ants tend both nymphs and adults, and *Publilia* has been shown to benefit from this interaction (McEvoy 1979, Bristow 1983, 1984, Cushman and Whitham 1989).

Colonies of *Formica obscuriventris*, which commonly tend treehoppers in this region (Funkhouser 1923), are often located near forest edges. The nests are very diffuse compared to those of other species in the genus, and can occupy up to 55 m<sup>2</sup>, with covered runways and brood chambers (Talbot 1964). In the study site, one nest nearly circumscribed the region of tended treehoppers, with the important effect of minimizing variation in ant recruitment associated with distance from the ant nest.

### *Predator-replacement experiment*

To test the effect of ant-tending behavior and predator exclusions on the success of *Publilia concava* individuals in aggregations of varying size, I selected 60 *Solidago altissima* plants sustaining ant-tended aggregations of *P. concava*. Initially, treehopper predators were removed by hand and were subsequently excluded from all host plants for all treatments, using net bags made from green 24 × 20/inch mesh polyester (Bioquip, Gardena, California, USA). Net bags (~1 × 0.5 m) were draped over each plant and a supporting stake located immediately adjacent to host plants. Bags were fastened to the supporting stakes at a height of 0.25–0.50 m from the base of the stem, leaving a small opening (~5 cm diameter) such that ants could crawl up the stem to access aggregations. The setup of net bags was identical among treatments. Similar protocols have been used in other studies to exclude predators while allowing access to ants (e.g., Breton and Addicott 1992b). Because herbivores may indirectly influence *P. concava* survivorship (Messina 1981), these insects were also removed.

A two-by-two experimental design was used, with ants excluded and predators replaced for appropriate treatments. Experimental predators were late second-instar and early third-instar lacewing larvae (*Chrysopa oculata*, Neuroptera: Chrysopidae), which possess several ant defenses (Spiegler 1962, LaMunyon and Adams 1987) and feed on treehoppers and other soft-bodied homopterans (*personal observation*). Treatments, randomly assigned, consisted of: ants and predators, ants only, predators only, and neither ants nor predators.

Ants were excluded by placing Tanglefoot (Tanglefoot, Grand Rapids, Michigan, USA) around a tape and

wax-paper sleeve at the base of the plant, and by clipping the surrounding vegetation. Control treatments were handled similarly, except that Tanglefoot was not used. Predator treatments involved adding one lacewing larva to appropriate aggregations, beginning 26 July and every 5 d thereafter for those treatments that had lost their predator. The number of predators used in this experiment was based on data collected in 1995 from 10 plants over four censuses. Results from this preliminary experiment showed that, for aggregations with ants excluded, there was  $1.0 \pm 0.27$  predator per plant ( $\bar{X} \pm 1 \text{ SE}$ ), and this did not vary with treehopper aggregation size (Spearman  $R = 0.417$ ;  $P = 0.304$ ). Additional support for the contention that one predator per plant is a realistic value of naturally occurring predator densities for untended aggregations comes from a study of *P. concava* in New York, where the mean density was  $\sim 1.25$  predators per plant for treehopper aggregations on plants without ants (McEvoy 1977). Similarly, studies on the closely related species *Pubillia reticulata* and *P. modesta* show a mean density of  $< 1$  predator per plant for untended treehopper aggregations (Bristow 1984, Cushman and Whitham 1989, 1991).

Treatments began on 22 July 1996, when an initial census of treehopper abundance (nymphs and adults) was taken. Treatments began then, because the majority of egg masses had hatched. Therefore, any subsequent difference in treehopper abundance among treatments could be ascribed to differential survivorship (dispersal is uncommon in this system; see *Discussion: Mechanisms of benefit*). Post-treatment censuses recorded the abundance of nymphs and adults on all host plants over a 4-d period for each of the following census starting dates: 10 August, 22 August, and 10 September, for a total of four censuses (including the pretreatment census).

#### *Honeydew-removal experiment*

To test whether benefits to treehoppers result from removal of uncollected honeydew, I conducted a second experiment during the summer of 1997. I selected 54 *Solidago altissima* plants and excluded treehopper predators and herbivores, as in the predator-replacement experiment. To remove honeydew, I washed treehopper aggregations on treatment plants with a fine spray, using an applicator designed for pesticides (MAX II, D. B. Smith, Utica, New York, USA). A two-by-two experimental design was used, with ants excluded and treehopper aggregations sprayed for appropriate treatments. Treatments, randomly assigned, consisted of: ants and washings, ants only, washings only, and neither ants nor washings.

Treatments began on 28 July, later than in the 1996 experiment because nymphal hatching was delayed (probably a result of an exceptionally cold spring). Spray treatments were applied every other day and consisted of water or a dilute fungicide solution of Daconil

2787 (Ortho, San Ramon, California, USA) at  $\sim 1 \text{ mL/L}$  to inhibit the growth of sooty molds, used on an alternating basis. A plastic sheet was positioned around treatment plants at the time of application to ensure that treatments affected only the designated treehopper aggregation. Control plants were sprayed with the identical solution at the base of the plant to eliminate indirect effects mediated by water availability to the plant.

Post-treatment censuses were conducted on 11 August, 25 August, and 10 September using the methods from the predator-manipulation experiment.

#### *Analysis*

Statistical analyses were conducted using STATISTICA version 5.1 (StatSoft 1997). Multiple regression analysis with dummy variables was used to investigate the number of treehoppers at census four as a function of initial treehopper aggregation size across treatments. Analyses were performed by analyzing multiple partial  $F$  statistics for reduced vs. full models. Models were compared hierarchically:  $H_0$ , equal intercept and equal slopes was tested first; then  $H_0$ , equal slopes; then  $H_0$ , equal intercepts. Terms were removed from the model when not significant.

Ant recruitment as a function of treehopper aggregation size was analyzed for the census dates 10 August 1996 and 25 August 1997. The number of ants recruiting to a given aggregation was calculated as the average of two values recorded over a 5-min interval on the last day of each census. These census dates were chosen for the recruitment analysis because almost no adult treehoppers were present at those times (0.13% and 0.41% adults, respectively), providing a clear interpretation of ant recruitment as a function of treehopper aggregation size. (Ants recruit differently to treehopper adults vs. nymphs [McEvoy 1977, Fritz 1982].) These data were used to test the hypothesis that patterns of density-dependent benefit were consistent with patterns of ant recruitment.

## RESULTS

### *Type of benefit*

Overall, tending by ants significantly increased the number of treehoppers surviving to census four for both 1996 and 1997 (Fig. 1, Table 1). In 1996, tended aggregations experienced significantly higher survivorship than did untended aggregations, even in the absence of predators (Fig. 1, Table 1). This indicated that treehoppers benefit from ants in ways other than receiving protection from predators. Across treehopper densities, ant tending increased survivorship of treehoppers by 8.8 and 2.3 times that of untended treehoppers in the presence and absence of predators, respectively. Predators had a disproportionate effect on the number of treehoppers surviving over 7 wk for untended vs. tended aggregations: predators reduced

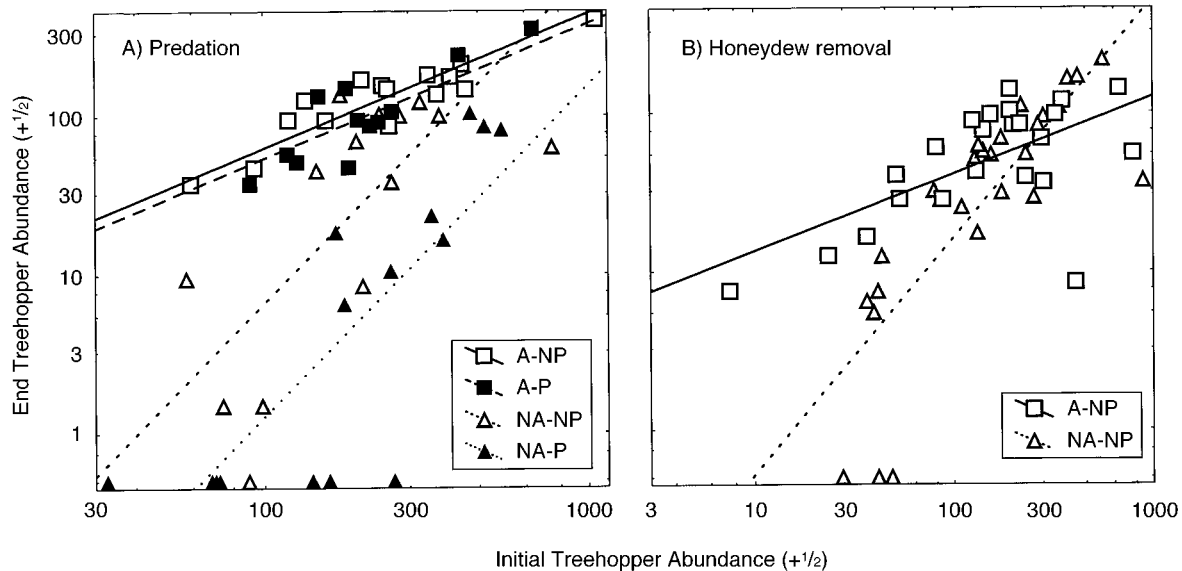


FIG. 1. The number of treehoppers surviving to census 4 (end treehopper abundance;  $S$ ) among treatments as a function of the number of treehoppers at census 1 (initial aggregation size;  $I$ ). Note log scales. (A) Treatments for the predator manipulation experiment were: A-NP, ants and no predators ( $S = 0.12 + 0.84I$ ); A-P, ants and predators ( $S = 0.06 + 0.84I$ ); NA-NP, no ants and no predators ( $S = -3.34 + 2.08I$ ); and NA-P, no ants and predators ( $S = -4.05 + 2.08I$ ). The overall model for the predator manipulation experiment (1996) is given by  $\text{Survivors} = \text{Ant} + \text{Predator} + \text{Density} + \text{Ant} \times \text{Predator} + \text{Ant} \times \text{Density}$  ( $R^2 = 0.79$ ,  $F_{5,50} = 36.98$ ,  $P < 0.0001$ ). (B) In the honeydew-removal experiment (1997), predators were excluded from all treehopper aggregations, and washing treatments were pooled, resulting in the treatments A-NP ( $S = 0.65 + 0.48I$ ) and NA-NP ( $S = -1.78 + 1.49I$ ). The overall model for the honeydew-removal experiment (1997) is defined by  $\text{Survivors} = \text{Ant} + \text{Density} + \text{Ant} \times \text{Density}$  ( $R^2 = 0.62$ ,  $F_{3,46} = 25.36$ ,  $P < 0.0001$ ). Models were determined as described in *Methods: Analysis* (see also Table 1). Survivors and density were  $\log_{10}(x + 1/2)$ -transformed for analysis.

survivorship of tended treehoppers by 18.7%, but only by 6.4% for tended aggregations. This result is confirmed statistically by a significant ant  $\times$  predator interaction term (Table 1). For data from 1996, protection from predators explains 40.5% of the residual variation in survivorship (predator and ant  $\times$  predator terms in model of Fig. 1), whereas benefits other than protection account for 45.3% of the residual variance (ant and ant  $\times$  density terms in the Fig. 1 model).

For 1997, there was also a significant effect of ant tending on treehopper survivorship (Table 1). Because all treatments in 1997 were tested in the absence of predators, this finding is consistent with the hypothesis that treehoppers benefit in ways other than predator protection. There was no significant effect on treehopper survivorship of the washing treatments for removal of uncollected honeydew and inhibition of sooty molds (Table 1).

Although crawling predators, such as spiders, were occasionally able to enter predator enclosures through "ant entrances," net bags were nevertheless very effective at excluding predators. There was no significant difference in the mean density of nontreatment predators for ant vs. no-ant treatments ( $0.15 \pm 0.05$  predators per plant in ant treatments vs.  $0.13 \pm 0.04$  predators per plant in no-ant treatments,  $\bar{X} \pm 1 \text{ SE}$ ; Mann-Whitney  $U$  test:  $U = 1821$ , adjusted  $Z = -0.333$ , adjusted  $P = 0.739$ ). Because nontreatment predators

were removed within 24 h, these densities represent a conservative estimate of the true effectiveness of predator exclusions in reducing predator numbers over time. In comparison, the natural density of predators in ant-tended aggregations without predator exclusions, based on data collected from the present study site during 1995 and 1998, was  $0.43 \pm 0.12$  and  $0.48 \pm 0.15$  predators per plant ( $\bar{X} \pm 1 \text{ SE}$ ), respectively (see *Methods: Predator-replacement experiment* for naturally occurring predator densities of untended treehoppers).

#### Patterns of density dependence

The difference in number of survivors between tended vs. untended treehoppers was highest in small aggregations and decreased significantly as aggregation size increased for both 1996 and 1997 (Fig. 1, Table 1). In 1996, the ant  $\times$  density interaction was independent of predator presence (i.e., there was no significant ant  $\times$  predator  $\times$  density interaction), indicating that the density-dependent effect of ants on treehoppers does not depend on the presence of predators. This is consistent with a significant ant  $\times$  density interaction in 1997 in the absence of predators (note that washing treatments had no effect on any component of survivorship for 1997; Table 1).

#### Patterns of ant recruitment

The total number of ants tending treehoppers increased as aggregation size increased on a log-log scale

TABLE 1. Regression summary statistics for the effects of ant tending and experimental treatments (P, predators in 1996; H, removal of uncollected honeydew in 1997) on the relationship between treehopper abundance [ $\log_{10}(x + 1/2)$  transformed] at initial and final censuses.

Treatment	Source†	df	F	P
A) Predation experiment (1996)				
Equal slope (i.e., no treatment × density interactions)				
All treatments				
A × D, P × D, A × P × D	$b_5, b_6, b_7   b_1, b_2, b_3, b_4$	3, 48	3.301	0.028
Ant (within predator)				
A × D, A × P × D	$b_5, b_7   b_1, b_2, b_3, b_4, b_6$	2, 48	3.826	0.029
Predator (within ant)				
P × D, A × P × D	$b_6, b_7   b_1, b_2, b_3, b_4, b_5$	2, 48	0.207	0.813
Equal intercept (i.e., no treatment effects)				
Ant (within predator)				
A	$b_2   b_1, b_3, b_4, b_5$	1, 50	13.696	0.001
Predator (within ant)				
P	$b_3   b_1, b_2, b_4, b_5$	1, 50	20.087	<0.001
Ant × Predator				
A × P	$b_4   b_1, b_2, b_3, b_5$	1, 50	7.926	0.007
B) Honeydew-removal experiment (1997)				
Equal intercept and slope (i.e., no treatment effects or treatment by density interaction)				
All treatments				
A, H, A × H, A × D, H × D, A × H × D	$b_2, b_3, b_4, b_5, b_6, b_7   b_1$	6, 43	3.994	0.003
Ant (within honeydew removal)				
A, A × H, A × D, A × H × D	$b_2, b_4, b_5, b_7   b_1, b_3, b_6$	4, 43	5.6	0.001
Honeydew removal (within ant)				
H, A × H, H × D, A × H × D	$b_3, b_4, b_6, b_7   b_1, b_2, b_5$	4, 43	0.863	0.494
Equal slope (i.e., no treatment by density interaction)				
Ant				
A × D	$b_5   b_1, b_2$	1, 47	15.292	<0.001
Equal intercept (i.e., no treatment effect)				
Ant				
A	$b_2   b_1, b_5$	1, 47	18.421	<0.001

Notes: Analyses were conducted by analyzing multiple partial *F* statistics for the reduced vs. full model. Models were compared hierarchically:  $H_0$ , equal intercept and equal slope was tested first; then  $H_0$ , equal slope; then  $H_0$ , equal intercept. The  $H_0$  of equal intercept and equal slope is the null hypothesis that there are no differences among treatments in survivorship as density approaches zero, or in density-dependent survivorship. The  $H_0$  of equal slope is the null hypothesis that there are no differences among treatments in density-dependent survivorship. The  $H_0$  of equal intercept is the null hypothesis that there are no differences among treatments in survivorship as density approaches zero (this is equal to an ANCOVA when comparing treatments with identical slopes). Terms were removed from the model when not significant. The full model is generalized between years as: final aggregation density =  $\beta_0 + \beta_1D + \beta_2A + \beta_3T + \beta_4AT + \beta_5AD + \beta_6TD + \beta_7ATD$  where D is initial aggregation density, A is ant-tending level, and T is treatment. Tests of coincidence (equal intercept and slope) are not shown for 1996, because all comparisons were significantly different with respect to either slope or intercept.

† Regression coefficients (*b*) correspond to the  $\beta$  parameters in the Notes above.

(Fig. 2). However, the number of ants per treehopper was highest in small aggregations and decreased significantly as treehopper aggregation size increased, because the slope of the relationship between total ants and treehopper aggregation size on a log–log scale is significantly less than 1;  $t_{53} = 4.77, P < 0.0001$ . This relationship was consistent across years, with respect to both the magnitude (intercept) and pattern (slope) of recruitment (Fig. 2).

DISCUSSION

*Mechanisms of benefit*

The current study provides clear experimental support for the hypothesis that treehoppers benefit from

ant tending by protection from their predators. Additionally, results support the hypothesis that treehoppers benefit in ways other than predator protection; tended treehoppers experienced higher survivorship relative to untended treehoppers, even when predators were excluded, for both years of this experiment. For 1996, predator protection and other benefits of ant tending explained approximately equal components of the residual variation in treehopper survivorship (see *Results*). Although the specific contribution of protection vs. benefits other than protection will depend on the predation pressures of a given system, ants clearly can have important positive effects on treehopper survivorship in addition to the protection from predators that they provide.

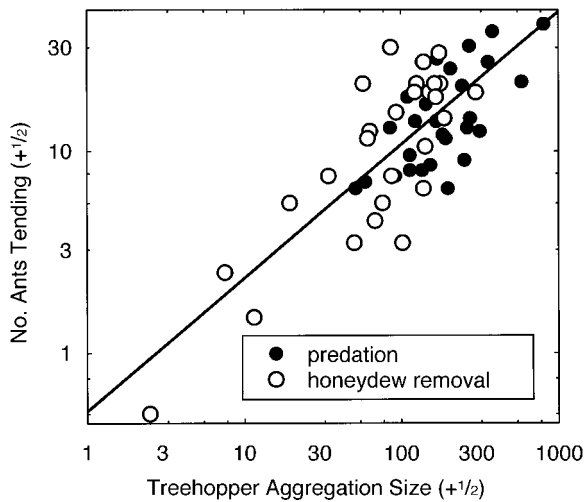


FIG. 2. Ant recruitment to treehopper aggregations as a function of treehopper aggregation size. Because treatment within years and year effects do not influence the relationship (slope and intercept) between ant-tending level and treehopper aggregation size ( $F_{6,47} = 1.49$ ,  $P = 0.202$ ), all data are pooled. The relationship between ant recruitment and treehopper aggregation size is defined as: ants =  $-0.29 + 0.66$  (treehoppers) ( $R^2 = 0.62$ ,  $F_{1,53} = 85.02$ ,  $P < 0.0001$ ). Numbers of ants and treehopper aggregation size were  $\log_{10}(x + 1/2)$ -transformed for analysis.

Invasion by nontreatment predators is an unlikely explanation for the difference in survivorship observed between treatments. Predator exclosures caused a strong reduction in nontreatment predator levels, with no difference in abundance between treatments (see *Results*). Studies of the closely related treehopper *Publilia modesta* have demonstrated no effect of ant tending when predator levels did not differ between tended and untended aggregations (Cushman and Whitham 1989).

Similarly, removal of uncollected honeydew is an unlikely explanation for benefits other than predation observed in this study: experimental washing failed to show any effect of honeydew removal on treehopper survivorship. Although it is possible that the washing treatment caused other sources of mortality or had indirect effects on some aspect of membracid development, there is no reason to expect that washings would have a differential effect on ant vs. no-ant treatments. Alternatively, it is possible that washings in the present study were ineffective at removing honeydew, but this did not appear to be the case (*personal observation*). It is worth noting that other studies have provided some evidence that removal of uncollected honeydew via water spraying increased the growth of scale colonies (Way 1954).

Although not tested in the present study, facilitation of feeding could provide an important benefit from ant tending that is also related to sanitation. In this view, membracids decrease their feeding rates in the absence of ants to prevent honeydew contamination of them-

selves and their host plants (Way 1963). Although increased uptake of phloem would allow the selective assimilation of amino acids (Kennedy and Stroyan 1959), uncollected honeydew can result in the formation of sooty molds (Fokkema et al. 1983), which might block excretion (Way 1954) and can ultimately decrease photosynthesis in the host plant (Wood et al. 1988). Experimental support for the hypothesis that ants facilitate feeding in *Publilia concava* comes from a study of its congener, *P. reticulata*, in which ants were shown to have a positive effect on adult size and developmental rate of their tended treehoppers (Bristow 1984). Facilitation of feeding could be especially important for homopterans such as *Publilia* that have a well-developed trophobiotic organ, a cirlet of hairs around the anal tube that retains honeydew until it is collected by ants. It has been suggested that the trophobiotic organ is an adaptation that increases the attractiveness of homopterans to ants (Sudd 1987), but it probably reduces the membracid's ability to freely eject honeydew in the absence of ants, and represents a possible evolutionary cost of ant attendance.

If treehoppers modify feeding rates in response to ant abundance rather than to buildup of uncollected honeydew, the feeding facilitation hypothesis would explain why survivorship was associated with the per capita rate of ant attendance, but not with experimental washings. Experimental tests have confirmed that aphids will decrease feeding rates when not tended by ants (Banks and Nixon 1958). Nevertheless, it has been difficult to show that reduced survivorship results from decreased feeding rate in aphids, because excluding ants also increases the probability of aphid dispersal, which could result in spurious decreases in survivorship, i.e., not related to births and deaths (Banks and Nixon 1958, Way 1963; but see El-Ziady 1960).

For several reasons, differential dispersal in the present study is not likely to explain the higher survivorship of ant-tended treehoppers in the absence of predators. First, nymphs of *Publilia* show high fidelity to their natal plant, with only  $\sim 1\%$  of all nymphs dispersing (McEvoy 1977) and some nymphs returning to their natal plant if experimentally removed (Bristow 1983). Second, although adults will disperse when disturbed, a reanalysis of the data using total treehopper abundance at census three shows qualitatively identical patterns, with no significant change in any statistical results. At these dates for 1996 and 1997, 93.4% and 99.5%, respectively, of all treehoppers were present as nymphs, such that adult dispersal could not account for the variation observed between treatments. Third, there was no difference in the percentage of treehoppers as nymphs between treatments at census three (Kruskal-Wallis: 1996  $H_{3,52} = 0.50$ ,  $P = 0.92$ ; 1997  $H_{3,47} = 3.49$ ,  $P = 0.32$ ) and census four (Kruskal-Wallis: 1996  $H_{3,48} = 0.34$ ,  $P = 0.95$ ; 1997  $H_{3,47} = 1.09$ ,  $P = 0.78$ ), suggesting that if there was adult dispersal, it was unbiased among treatments.

### Density-dependent benefit

Analyses of early models of mutualisms showed that local stability for interacting mutualists will be lower than for non-interacting, but otherwise identical, participants (May 1981). Several models followed, showing that mutualism could be stabilized if (1) complexity is added by including participant predators and/or competitors (Heithaus et al. 1980, Ringel et al. 1996), or (2) the per capita effect of mutualistic benefit decreases as population size increases (Addicott 1981, Dean 1983, Wolin and Lawlor 1984).

Support for the second class of model comes from this and other studies that have demonstrated decreasing per capita benefit as recipient density increases (McEvoy 1977, Cushman and Whitham 1991, Breton and Addicott 1992a). However, no previous studies have used experimental manipulations to consider the possible factors that result in density-dependent benefit in mutualisms, reflecting a general gap between theory and experimental work for studies of mutualism as a whole (Bronstein 1994a). Studies addressing the importance of predators or competitors in generating patterns of density-dependent benefit will provide key insight into the specific mechanisms that contribute to stability, and will allow for the development of mechanistic models of mutualism.

In both years of this experiment, benefit to treehoppers from ant tending was greatest at low treehopper density and decreased as treehopper density increased, independent of predator presence. At least one other study has shown a decrease in mutualistic benefit for homopterans as density increases, with no corresponding difference in predator abundance between treatments.

### Mechanisms of conditionality

It seems likely that the density-dependent decrease in mutualistic benefit observed in the present study derives from the recruitment behavior of ants. As aggregation size increased, the number of ants per treehopper and the benefit of ant tending to treehoppers decreased. Other studies have shown similar association between ant tending level and homopteran survivorship (Cushman and Whitham 1991, Breton and Addicott 1992a). Because it is unclear how to independently manipulate only the number of ants recruiting to an aggregation, it will be difficult to test this hypothesis experimentally. However, a mechanistic model of mutualism that incorporates a type II recruitment response (e.g., recruitment of ants to treehoppers increases and then levels off) makes similar predictions (M. A. Morales, *unpublished manuscript*).

Other studies have shown that the treehoppers *Publilia concava* and the closely related species *P. modesta* experience maximum benefit from ant attendance at intermediate and large aggregation densities, respectively (McEvoy 1977, 1979, Cushman and Whitham

1989). Maximum benefit from ant tending at intermediate densities is expected if the recruitment of ants to treehopper aggregations is modeled as a type III curve (sigmoidal recruitment) (M. A. Morales, *unpublished manuscript*), in support of empirical results (McEvoy 1977). Sigmoidal recruitment of ants to treehoppers could also result in large aggregations showing highest per capita benefit if the aggregations examined are in the relatively low range of relevant densities. This suggests that species-specific or context-dependent ant recruitment patterns may contribute to differences in the patterns of density dependence observed among studies.

The conclusions of the present study are based on data from a single ant colony. If, as previously argued, patterns of benefit depend strongly on the particular recruitment response of ants, lumping colonies would be appropriate only where recruitment response curves are approximately identical among colonies. Because ant colonies vary in size and because homopteran aggregation size is often confounded with distance from ant nests, which independently influences patterns of recruitment (e.g., Taylor 1977, 1978; note that distance was not a factor in the present study), it is unlikely that this assumption will often be met. Rather, more studies are needed that relate patterns of benefit to the recruitment response of ants.

Although there was no predator  $\times$  density interaction in this experiment, the relative magnitude of predator vs. ant effects on survivorship varied with population density (because the magnitude of ant effects varied with density). In this experiment, only one predator was added regardless of aggregation size; in some homopteran systems, however, predators exhibit a functional response such that predator attack rates vary with prey densities (Turchin and Kareiva 1989). Furthermore, it has been suggested that efficacy of protection by ants should be proportional to total ant abundance rather than to the number of ants per membracid (Itioka and Inoue 1996b). The pattern of density-dependent benefit observed for a particular system may be a combined function of the recruitment response of ants, mediated by the functional response of predators, as homopteran aggregation size varies.

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