

Survivorship of an ant-tended membracid as a function of ant recruitment

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I used a host-visitor modeling framework to examine the interaction between the treehopper *Publilia concava* and ants in the genus *Formica*. In particular, I tested the functional relationship between ant tending, the spatial distribution of treehoppers, and treehopper density. The per-capita density of ants at each host plant was a decreasing function of treehopper density, distance from the ant nest and the neighborhood density of treehoppers. Treehopper survivorship was proportional to the per-capita density of ants and the duration of ant tending. Consequently, treehoppers in low-density aggregations on isolated host plants near the nest received maximum benefit from ant tending. Treehoppers tended by the ant *Formica integra* were abandoned as the summer progressed, although many of these treehoppers were re-colonized by other species of ants. While *F. integra* ultimately abandoned all treehoppers, treehoppers on host plants with fewer initial ants were abandoned first. Results from the present study are consistent with previous findings suggesting that patterns of density-dependent benefit for homopterans are a function of the recruitment response of ants. Additionally, results suggest a tradeoff between maximizing the persistence or probability of ant-tending and minimizing competition for ants when tended. In general, host-visitor models of mutualism may provide a theoretical framework for understanding conditional outcomes in ant-homopteran, and other host-visitor mutualisms.

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Recently, studies have highlighted variability in the degree of benefit for the participants of many mutualisms (Cushman and Addicott 1991, Breton and Addicott 1992a, Setälä et al. 1997). Although such variability is an expected consequence of interacting within a complex environment, its predictability remains unclear. Where variation in outcome is context dependent, the term conditionality has been used (Bronstein 1994). In general, conditionality in mutualism can result either from variation in the degree to which partners benefit, or from variation in the per-capita density of mutualist partners (Cushman and Addicott 1991, Bronstein 1994). In the current paper, I use a host-visitor modeling framework to explore the dynamics of conditionality in an ant-homopteran mutualism.

The interaction between ants and homopterans has become a model system for studies of conditionality in mutualism, and variation in outcome is especially well documented for this system (Bronstein 1994). In ant-homopteran mutualisms, ants collect the sugary excretions of homopterans. Homopterans benefit from ant tending because ants attack and remove predators from their host plants, increase their feeding rates, and prevent the buildup of uncollected honeydew (reviewed in Buckley 1987). Conditional outcomes in this interaction have been documented as the result of both variation in the per-capita density of ants (i.e., variation in the per-capita density of mutualist partners; e.g., McEvoy 1977, Cushman and Whitham 1991, Breton and Addicott 1992a, Morales 2000) and predator levels (i.e.,

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variation in the degree of benefit; e.g., Bristow 1984, Cushman and Whitham 1989, Morales 2000).

In host-visitor mutualisms, hosts such as homopterans provide some form of food resource (e.g., honeydew, nectar, fruit) in return for a variety of visitor, (e.g., ant) services, such as protection, pollination, or seed dispersal (Thompson 1982). Models of host-visitor mutualism may provide a theoretical basis for understanding conditionality in ant-homopteran mutualisms arising from variation in ant recruitment (Morales 1999). For example, in a model of host-visitor mutualism which I have developed, visitor recruitment is defined to be some function of host density, and host benefit is defined to be some function of visitor recruitment (Morales 1999).

Similarly, optimal foraging theory can be applied to understand patterns of visitor recruitment and corresponding patterns of host benefit (Cushman and Addicott 1991). For example, theory predicts that recruitment will decrease as foraging distance increases for central place foragers (Taylor 1978, Pyke 1984). This prediction is supported by studies from a variety of ant-resource mutualisms, which demonstrate that ant recruitment decreases as distance from the ant nest increases (Tilman 1978, Inouye and Taylor 1979, Sudd 1983, Pierce et al. 1991, Whittaker 1991).

In this study, I relate patterns of treehopper survivorship to patterns of ant recruitment within a host-visitor modeling framework. Ant recruitment is modeled as a function of treehopper density and the spatial distribution of treehoppers, and treehopper survivorship is modeled as a function of treehopper density and the per-capita density of tending ants. Results are applied to evaluating a host-visitor modeling framework as a possible basis for understanding conditionality in these interactions.

Methods

Study system

The treehopper *Publilia concava* Say has a univoltine life cycle in the northeastern United States. Females oviposit beginning in late May to early June, usually on the midrib of *Solidago altissima* L. Several females lay their eggs on a given host plant, and aggregations of up to 1100 nymphs emerge by late July (pers. obs.). I define an aggregation as all treehoppers on a single host plant, and a patch as all aggregations tended by a given ant colony. Ants tend both nymphs and adults, and *Publilia* spp. have been shown to benefit from this interaction (McEvoy 1977, Bristow 1983, Cushman and Whitham 1989, Morales 2000).

I collected treehopper survivorship and ant recruitment data from two patches located within the Dennis

Hill Farm Preserve of the Nature Conservancy, Putnam, CT. One patch was tended by a colony of *Formica pergandei* Emery, and will be referred to as the “pergandei” patch. A second patch was tended by a colony of *Formica integra* Nylander and will be referred to as the “integra” patch. Both patches were located in an open field dominated by *S. altissima* and all aggregations were found on this host plant. Other *Solidago* spp. along with saplings of *Juniperus virginianus*, *Pinus strobus*, and *Elaeagnus* sp. were scattered throughout the field, while the forest edge was composed mainly of *Betula lenta* with scattered *Acer saccharum*, *Betula populifolia*, *Quercus rubra*, and *Pinus strobus* individuals.

Treehopper dynamics

A general model for mutualistic host dynamics is given below (Morales 1999):

$$\frac{dH}{dt} = rH - qH^2 + af(V, H) \quad (1)$$

In this model, H represents each host (treehopper), r defines its intrinsic growth rate, q defines the density-dependent change in its growth rate, $f(V, H)$ defines the recruitment response of visitors (ants) to hosts, and a converts encounters with visitors into hosts. For the purposes of this paper, the model is applied to individual aggregations. Because ant recruitment to aggregations can be directly measured, $f(V, H)$ can be replaced with R , explicitly defining the density of ants at a given aggregation. Dividing eq. 1 by H , and rewriting the result as a difference equation (Eq. 2), parameter estimates for r , q , and a , can be approximated using standard multiple regression techniques to analyze treehopper survivorship:

$$\ln \frac{H_{t+1}}{H_t} = r - qH_t + a \frac{R_t}{H_t} \quad (2)$$

Note that the above model assumes a type 0 functional form (aR) for the benefit function (Morales 1999). This assumption was tested by comparing the explanatory power of the basic model to one that included either a type I (aRH) or II ($aRH/[H + b]$) benefit function. For a type 0 functional form, benefit provided by each ant is independent of treehopper density, while benefit received by each treehopper is proportional to the per-capita density of ants. For a type I functional form, benefit provided by each ant is proportional to total treehopper density, while benefit received by each treehopper is proportional to total ant density. For a type II functional form, benefit provided by each ant is a saturating function of treehopper density, while benefit

received by each treehopper is proportional to the per-capita density of ants.

To assess the effectiveness of eq. 2 to describe treehopper dynamics, standard regression analyses (StatSoft 1999) were performed for survivorship data collected from the “*integra*” patch. Treehopper survivorship was estimated over two periods during the summer of 1998; from 31 July to 18 August (early summer census) and from 18 August to 14 September (late summer census). Similarly, ant recruitment was censused on 1 and 19 August and ant presence, predator density, and herbivore density were censused periodically throughout the summer. By the start of the early summer census, most egg masses had hatched, and analyses were restricted to aggregations which showed a growth rate of less than one ($N = 73$, three excluded from survivorship analysis due to damage to the host plant). This allowed an examination specifically of survivorship. Additionally, it ensured that ant tending levels did not change qualitatively after the initial census due to recruitment from previously unhatched eggs. Note that eq. 2 represents a discrete form of the continuous model presented in eq. 1. Log-transforming survivorship in part corrects for this discretization. Nevertheless, parameter estimates are to be taken as approximations of an underlying continuous process.

To explore the effect of predator and herbivore density on treehopper dynamics, multiple partial F -statistics for treehopper survivorship were analyzed for the basic model compared to a model that included both predator and herbivore density. Predator density was defined as the sum of all spiders, coccinellid larvae and adults (Coleoptera: Coccinellidae), and green lacewing larvae (Neuroptera: Chrysopidae) observed on each host plant during each census. Herbivore density terms included both the number of leaves infested with tingid nymphs (Hemiptera: Tingidae) and the density of phytophagous insects.

F. integra ants abandoned aggregations as the summer progressed (see Results), and many of these abandoned aggregations were re-colonized by other species of ants. Abandoned aggregations ($N = 21$) were excluded from analysis for the first census period, even if tended by a different ant species. However, because all aggregations were abandoned by *F. integra* by the end of the second census period, the number of 4-d periods (range 0–4) during which aggregations were tended by any species of ant was included as the per-capita ant recruitment term in eq. 2 for analysis of data from this period.

Ant recruitment

If eq. 2 provides a reasonable model for host dynamics, conditionality resulting from variation in visitor

abundance will be predictable to the extent that visitor recruitment can be modeled. In the simplest case, $R = \alpha VH$, where α is some fraction of the total possible encounters between hosts and visitors which result in recruitment. This functional form for the recruitment response does not predict density-dependent benefit. For models derived from consumer-resource theory, visitor recruitment can be a monotonic (type II) or sigmoidal (type III) saturating function of host density, where α is a scaling factor which defines the maximum recruitment rate of visitors and β defines the density of hosts which attracts one half the maximum recruitment of visitors (Morales 1999):

$$R_{\text{typeII}} = \frac{\alpha VH}{H + \beta} \quad (3)$$

$$R_{\text{typeIII}} = \frac{\alpha VH^2}{H^2 + \beta^2}$$

These functional forms generate maximum benefit per host at low and intermediate host density for type II and III recruitment, respectively (Morales 1999). To examine the functional form of ant recruitment, the relationship between ant tending and treehopper density was examined using nonlinear estimation (quasi-newton and simplex algorithms) to parameterize eq. 3 (StatSoft 1999). Note that for this analysis, ant density (V) was set to one, so that α defines the maximum total ant recruitment at each aggregation.

To explore the effects of distance from the nest and neighborhood density on ant tending levels, all aggregations from both patches were mapped. The relative error remaining after fitting eq. 3 (defined as observed recruitment/predicted recruitment) was analyzed as a function of distance from the nest and neighborhood density using multiple regression analysis. Because relative error cannot be less than or equal to zero, values were log-transformed, providing an exponential decay function. Neighborhood density was defined as the sum of all treehoppers within a given radius. Radius length was chosen by the distance that minimized the total variance in ant density over the range of 10–500 cm \pm 1 cm). For data collected from the “*pergandei*” patch, aggregations ($N = 47$) were manipulated to a density of 20, 100, and 200 treehoppers \pm 10% beginning 5 August 1997, and the number of ants was censused one week after manipulation. Analysis followed the procedure used for analyzing spatial effects in the “*integra*” patch.

Finally, logistic regression analysis (StatSoft 1999) was used to explore possible factors influencing the probability of abandonment and re-colonization for aggregations at the “*integra*” patch.

Table 1. The effects of treehopper density and per-capita ant tending levels on treehopper survivorship. Degrees of freedom = 46 for the early summer census and 65 for the late summer census. Italicized letters correspond to parameters from eq. 2.

Variable	$\bar{X} \pm SE$	<i>t</i>	<i>P</i>
Early summer census			
Intercept (<i>r</i>)	-0.78 ± 0.14	-5.40	<0.001
Treehopper density (<i>q</i>)	-0.001 ± 0.0004	-2.80	0.007
Ants per membracid (<i>a</i>)	1.25 ± 0.0005	1.25	0.002
Late summer census			
Intercept (<i>r</i>)	-4.62 ± 0.37	-12.49	<0.001
Treehopper density (<i>q</i>)	-0.01 ± 0.005	-2.19	0.032
Ant persistence (<i>a</i>)	0.93 ± 0.16	5.72	<0.001

Results

Treehopper dynamics

The model for host dynamics (eq. 2) explains a significant amount of the variance in treehopper survivorship for data collected from the “*integra*” patch during the early summer census period (adj. $R^2 = 0.38$, $F_{2,46} = 15.48$, $P < 0.0001$). Survivorship was negatively correlated with treehopper density and positively correlated with the per-capita density of ants (Table 1, Fig. 1). Neither a type I nor type II benefit response significantly improved model fit (adj. $R^2 = 0.36$ for a type I benefit response, while parameter estimates for a type II benefit response were biologically unreasonable), supporting eq. 2 as an appropriate model for treehopper dynamics.

Similarly, for data from the same patch collected over the late summer census period, density-dependent factors and persistence of ant tending combined explain a significant amount of the variation in treehopper survivorship (adj. $R^2 = 0.32$, $F_{2,65} = 16.56$, $P < 0.0001$).

Consistent with results from the early summer census, survivorship was negatively correlated with treehopper density and positively correlated with the persistence of ant tending (Table 1, Fig. 1).

Including predator or herbivore densities in the basic model of treehopper dynamics did not significantly improve model fit for either the early or late summer census periods (model = predators, tingids, herbivores | density, ants: $F_{3,43} = 1.703$, $P = 0.18$; $F_{3,65} = 0.294$, $P = 0.83$, respectively). This result was supported by a best subsets fitting procedure using Akaike’s Information Criterion, in which treehopper density and ant tending alone provided the best fit to the data for both census periods.

Aggregations that were abandoned by their original *F. integra* ants during the early summer census period were not included in that analysis. Abandoned aggregations showed reduced survivorship over this period relative to those aggregations that had not been abandoned ($\bar{X} \pm [SE] = 0.64 [0.02]$ vs $0.38 [0.05]$, Mann-Whitney $U = 247.5$, $Z = 4.31$, $P < 0.0001$).

Ant recruitment

To choose between a type II or type III recruitment response for data collected from the “*integra*” patch, nonlinear estimation was used letting the power constant from eq. 3 vary freely (a power constant of one defines type II recruitment, whereas a power constant of two defines type III recruitment). Results showed that a type II recruitment response (monotonic saturation) provided the best fit to the data for both the “*integra*” and “*pergandei*” patches (power constant of 1 and 0.88, respectively). Similarly, a second-order regression was selected as providing a better fit than a straight line regression using a best subsets fitting procedure based on Akaike’s Information Criterion. For a type II recruitment response, treehopper density ex-

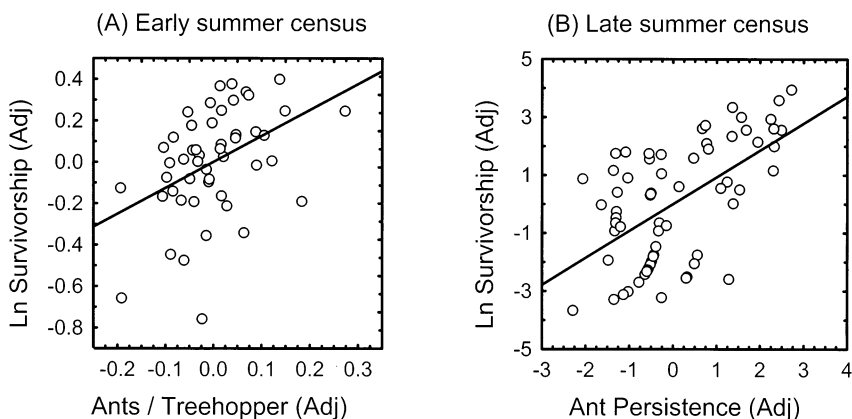
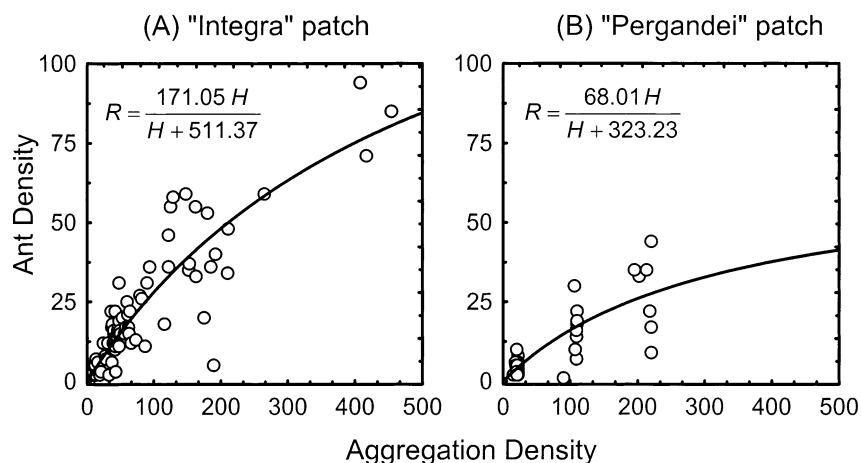


Fig. 1. The relationship between ant abundance and treehopper survivorship after correcting for treehopper density (i.e., adjusted variable plot, Chambers et al. 1983). For data from the early summer census, ant abundance is defined as the per-capita density of tending ants. For data from the late summer census, ant abundance is defined as the sum of observation periods during which aggregations were observed with ants (i.e., ant persistence, range 0–4). The slope of the relationships presented here correspond to parameter estimates from Table 1; however, intercepts are set to zero.

Fig. 2. Ant recruitment as a function of treehopper density. Data are fit to the model $R = \alpha H / (\beta + H)$ (see text for description of parameters). Note that data for both ant species are plotted on the same scale. Ant recruitment data for *F. pergandei* were collected from a patch where the density of treehopper aggregations was manipulated. The model explains 76 and 66% of the variance for data from the "integra" and "pergandei" patches, respectively.



plained 76% of the variance in ant density for data collected from the "integra" patch, and 66% of the variance for data collected from the "pergandei" patch (Fig. 2).

Based on regression analysis, ant-tending levels of *F. integra* responded most strongly to the total density of treehoppers within a neighborhood radius of 32 cm (Fig. 3). Ant density was negatively correlated with both distance from the nest and the neighborhood density of treehoppers (Table 2). For data from the "pergandei" patch, a neighborhood radius of 25 cm was found to minimize the variance in ant tending levels (Fig. 3). Consistent with results from the "integra" patch, ant tending was negatively correlated with both distance from the nest and the neighborhood density of treehoppers (Table 2).

The probability that ants abandoned aggregations (early summer census period, "integra" patch) was a decreasing function of initial ant density, and ant density was the only significant predictor of abandonment (Fig. 4, Table 3). Aggregations were completely abandoned by *F. integra* by 2 September. Many abandoned aggregations were re-colonized by this time, primarily by *Prenolepis imparis* and less commonly by *Tapinoma sessile* or *Myrmica* spp. ants. Excluding aggregations with zero density, the probability of re-colonization was not significantly related to treehopper density, predator density, herbivore density, distance from the *Formica* mound, or the neighborhood density of aggregations (logistic regression, $\chi^2 = 5.86$, $P = 0.32$).

Discussion

A number of studies have suggested that variation in the intensity of ant tending is responsible for generating patterns of density-dependent benefit to homopterans (McEvoy 1977, Cushman and Whitham 1991, Breton and Addicott 1992a, Morales 2000). However, the func-

tional form of this relationship had not been assessed before this study. Results here suggest that per-capita benefit to treehoppers is proportional to the per-capita density of tending ants, for treehoppers with continuous ant attendance. This study supports the hypothesis that patterns of density-dependent benefit for ant-tended treehoppers are driven in part by the recruitment response of ants, as suggested by models of host-visitor mutualism (Morales 1999).

Host-visitor models of mutualism provide a theoretical framework for understanding conditionality in mutualism arising from variation in mutualist abundance. The model of host-visitor mutualism used in the current paper predicts maximum host benefit at low host density for type II visitor recruitment, and maximum

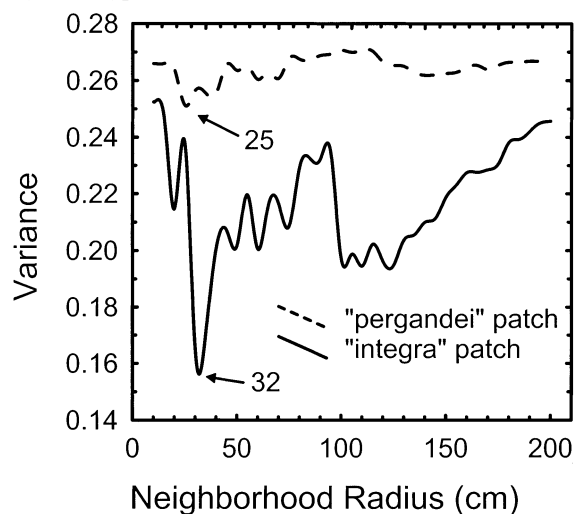


Fig. 3. Variance in ant recruitment as a function of neighborhood radius. Variance is based on the model, $\ln(\text{relative error}) = \beta_0 + \beta_1 \times \text{distance} + \beta_2 \times \text{neighborhood density}$, where relative error equals observed ant recruitment divided by predicted ant recruitment (Fig. 2), and neighborhood density is defined as the sum of all treehoppers within the designated radius. Arrows indicate the radius which minimizes the variance in ant-recruitment.

Table 2. The effects of distance from the ant nest and neighborhood density on ant tending levels. Analysis is based on data defined by the relative error ($\ln[\text{observed}/\text{predicted}]$) remaining after fitting a type II functional form (Eq. 3) to the relationship between ant recruitment and treehopper density (Fig. 2). Degrees of freedom = 70 for the “integra” patch and 44 for the “pergandei” patch.

Variable	$\bar{X} \pm \text{SE}$	t	P
“integra” patch			
Intercept	0.428 ± 0.161	2.66	0.0097
Distance (m)	-0.026 ± 0.012	-2.15	0.035
Neighborhood density	-0.0038 ± 0.0005	-7.01	<0.0001
“pergandei” patch			
Intercept	0.655 ± 0.169	3.88	0.0003
Distance (m)	-0.111 ± 0.024	-4.56	<0.0001
Neighborhood density	-0.0018 ± 0.0009	-2.08	0.043

benefit at intermediate density for type III visitor recruitment (Morales 1999). These predictions are supported by studies that have concurrently examined patterns of density-dependent benefit and ant recruitment, for both type II (Breton and Addicott 1992a, b, Morales 2000) and type III (McEvoy 1977) visitor recruitment.

Net benefit to hosts will be a combined function of the benefit provided by each visitor and the density of visitors as a function of host density (for an analogous example from a predator-prey interaction, see Turchin and Kareiva 1989). Because ant recruitment in the current study was described by a type II recruitment response, and per-capita benefit to treehoppers was proportional to per-capita tending levels, benefit from ant tending for each treehopper was highest in small

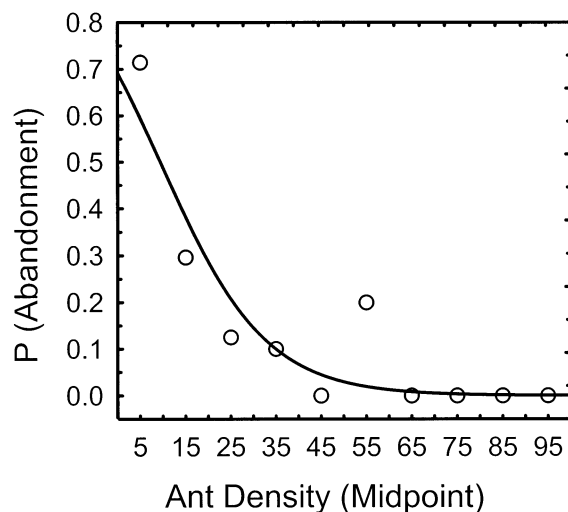


Fig. 4. The probability that aggregations were abandoned by *F. integra* during the early summer census period as a function of initial ant densities. $P(\text{abandonment}) = \text{Exp}(0.81 - 0.086 \text{ initial ant density}) / (1 + \text{Exp}[0.81 - 0.086 \times \text{initial ant density}])$.

Table 3. Significance of predictors for aggregation abandonment by the ant *F. integra*. Analysis is based on logistic regression.

Variable	Estimate \pm SE	Wald stat.	P
Treehopper density	0.014 ± 0.012	1.234	0.267
Ant density	-0.143 ± 0.058	6.106	0.013
Predator density	-0.183 ± 0.449	0.167	0.683
Herbivore density	-0.146 ± 0.648	0.051	0.822
Tingid density	-0.108 ± 0.123	0.777	0.378
Distance from nest (m)	-0.272 ± 0.146	3.476	0.062
Neighborhood density	-0.013 ± 0.009	2.194	0.139
Distance \times Neighborhood	0.001 ± 0.001	2.385	0.122

aggregations and decreased as aggregation size increased. Per-capita ant tending levels were also shown to vary both with distance from the nest and with the neighborhood density of treehoppers, indicating that variation in the outcome of this interaction is in part a function of the spatial distribution of treehoppers.

Both *F. integra* and *F. pergandei* ants show decreasing recruitment as distance from the nest and neighborhood density increases. Studies have shown experimentally that aggregations of *Publilia modesta* compete for the service of *Formica altipetens* ants (Cushman and Whitham 1991). In the current study, aggregations that were located closest to the nest were also more clumped, so that the increase in ant tending for aggregations closest to the nest was partly offset by competition among those aggregations. For example, parameter estimates for b and c (i.e., the increase in ant tending for treehoppers closest to the nest and the decrease in ant tending as distance from the nest increases) are 0.454 and -0.102 , respectively, for data from the “pergandei” patch ignoring the effect of neighborhood density, compared to 0.655 and -0.111 when the effect of neighborhood density is included (Table 2).

Interestingly, the radius of maximum influence (i.e., the radius defining the neighborhood that explains the greatest variation in ant recruitment) was similar between patches (0.25 m for the “pergandei” patch vs 0.32 m for the “integra” patch). This result is probably not due to similar spacing patterns between patches. On average, the distance between an aggregation and its nearest neighboring aggregation was 0.53 m for the “integra” patch (total treehopper density of ~ 7664) compared to 0.94 m for the “pergandei” patch (total treehopper density of ~ 3166). It should be noted that only two patches were considered, each consisting of a distinct species of ant, so quantitative comparisons cannot be made. Nevertheless, these results add to a growing number of studies suggesting that homopterans compete with their neighbors for the services of ants at a variety of spatial scales (Addicott 1978, Cushman and Addicott 1989, Cushman and Whitham 1991).

Unexpectedly, *F. integra* abandoned aggregations as the summer progressed. The probability of abandonment significantly increased as ant density decreased, suggesting that abandonment was a stochastic process resulting from the serial loss of individual ants. Optimal foraging theory predicts that aggregations will be abandoned first in rank order of their value, where value is a function of resource concentration (i.e., treehopper density), interference (i.e., saturation in ant recruitment) and distance from the nest (Taylor 1978). Because ant density is a proximate measure of value, these results are consistent with theoretical predictions of ant foraging.

Many abandoned aggregations were re-colonized by other species of ants, and treehopper survivorship was strongly influenced by the persistence of ant tending. Because ants abandon (or fail to re-colonize) aggregations that go extinct, treehopper survivorship over the late summer census period may be spuriously correlated with ant persistence. A re-analysis of the data excluding aggregations where survivorship equals zero provides qualitatively identical results for the effects of ant persistence, with no change in conclusions of statistical significance.

Because ant recruitment was a saturating function of treehopper density, per-capita tending levels were highest for low-density aggregations, while total ant density was highest for high-density aggregations. Consequently, low-density aggregations showed increased survivorship relative to high-density aggregations when tended. However, because fewer total ants tended low-density aggregations, low-density aggregations were abandoned by *F. integra* earlier than high-density aggregations (note that treehopper density does not add any predictive power to abandonment after including ant density – see Table 3). Although total abandonment by ants is relatively uncommon for the treehopper *P. concava* (pers. obs.), McEvoy (1977) reported for the same system that constancy of ant tending (defined as the number of days where ants were observed tending) increased with increasing aggregation size. Similarly, Wood (1982) reports that the treehopper *Enchenopa binotata* is more likely to be tended as aggregation size increases. In general, the evolution of optimal aggregation size for tended homopterans may respond to a tradeoff between maximizing the probability of tending (by maximizing total treehopper density) and minimizing competition for ant services when tended (by minimizing total treehopper density, for a type II recruitment response). This tradeoff may explain differences in patterns of density-dependent benefit seen at different spatial scales (e.g., Cushman and Whitham 1989, 1991).

In many systems, the relative importance of attracting ants vs minimizing competition for ants when tended is probably quite variable. For example, ant tending has been shown to respond to honeydew and

host-plant quality (Volkl et al. 1999), and attracting ants may be especially important in nutrient poor sites, or for homopterans which feed on “low-quality” host plants. In general, maximizing attractiveness to ants may increase in importance as homopteran partners become increasingly dependent on ant tending.

Previous studies have suggested that the degree of benefit to homopterans is in part a function of predator densities (Bristow 1984, Cushman and Whitham 1989, Morales 2000). There was no effect of predator densities on survivorship patterns of ant-tended treehoppers in the current study. In a manipulative experiment of the effects of predator and ant tending levels on treehopper survivorship, predator levels had little effect on treehopper survivorship for ant-tended aggregations (Morales 2000). Furthermore, predators had no effect on patterns of density-dependent benefit (Morales 2000). Under natural conditions, predator levels may have their main effect on how poorly untended aggregations perform. As such, patterns of density-dependent benefit may be derived largely from benefits other than predator protection, such as facilitation of feeding. Support for this hypothesis comes from studies of *P. concava* documenting increases in growth rate and adult size for tended treehoppers (Bristow 1984).

Although studies of ant resource mutualism have traditionally focused on the role of top-down effects (i.e., predators), there has been a growing recognition that bottom-up effects may be important (Cushman 1991, Breton and Addicott 1992b). While bottom-up effects were not considered in the present study, strong evidence that host-plant quality may play an important role in the interaction between treehoppers in the genus *Publilia* and ants in the genus *Formica* comes from a study of *Publilia modesta* on *Artemisia ludoviciana* (Strauss 1987). Strauss (1987) found that fertilization had a strong positive influence on the density of both the treehopper *P. modesta*, and its tending partner, *Formica obscuripes*. Unfortunately, that study was not designed to partition the effects of host-plant quality among treehopper survivorship, ant-tending levels, and their interaction. Studies are needed which examine the influence of bottom-up factors on the dynamics of ant-homopteran, and other host-visitor mutualisms. While most studies of ant-homopteran mutualisms have focused on top-down factors, bottom-up forces may play an important, although largely unexplored role in the dynamics of these interactions.

Results from the present study are consistent with previous findings suggesting that patterns of density-dependent benefit for homopterans are a function of the recruitment response of ants. In addition, results suggest a tradeoff between maximizing the persistence or probability of ant-tending and minimizing competition for ants when tended. This adds to a growing number of studies that support the hypothesis that conditionality in ant-homopteran mutualisms can be understood in

part by modeling the recruitment response of ants. In general, host-visitor models of mutualism may provide a theoretical framework for understanding conditional outcomes in host-visitor mutualisms. Future studies are needed that consider the dynamics of host-visitor mutualisms within a host-visitor modeling framework.

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