Model selection analysis of temporal variation in benefit for an ant-tended treehopper

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Abstract. Recent studies of mutualism have emphasized both that the net benefit to participants depends on the ecological context and that the density-dependent pattern of benefit is key to understanding the population dynamics of mutualism. Indeed, changes in the ecological context are likely to drive changes in both the magnitude of benefit and the density-dependent pattern of benefit. Despite the close linkage between these two areas of research, however, few studies have addressed the factors underlying variation in the density-dependent pattern of benefit. Here I use model selection to evaluate how variation in the benefits of a mutualism drives temporal variation in the density-dependent pattern of net benefit for the ant-tended treehopper *Publilia concava*. In the interaction between ants and treehoppers in the genus *Publilia*, ants collect the sugary excretions of treehoppers as a food resource, and treehoppers benefit both directly (e.g., by feeding facilitation) and indirectly (e.g., by predator protection). Results presented here show that temporal changes in the relative magnitude of direct and indirect benefit components of ant tending, especially the effectiveness of predator protection by ants, qualitatively change the overall pattern of density-dependent benefit between years with maximum benefit shifting from treehoppers in small to large aggregations. These results emphasize the need for empirical studies that evaluate the long-term dynamics of mutualism and theoretical studies that consider the population dynamics consequences of variation in the density-dependent pattern of benefit.

Key words: context dependency; density dependence; functional form; mutualism; Publilia concava; *treehoppers.*

INTRODUCTION

A dominant focus of mutualism research over the past two decades has been on understanding the ecological causes of variation in the costs and benefits of this interaction (Thompson 1988, Bronstein 1994). This focus has resulted in a number of studies showing that the net benefit of mutualism is a complex function of community-level interactions (Stanton 2003, Strauss and Irwin 2004, Morris et al. 2007), and that the net benefit of mutualism can include multiple mechanisms of benefit or costs (Stachowicz and Whitlatch 2005, Giladi 2006).

Although identifying and quantifying variation in the benefits and costs of mutualism is an important first step, a key question is how net benefit translates to population or evolutionary dynamics. Despite significant attention paid to the presence and underlying causes of variation in the costs or benefits of mutualisms, it is unclear how this variation translates to population dynamic or evolutionary consequences. One potential exception is for studies that have focused on the density-dependent pattern of benefit. In general, the population dynamic consequences of species interactions depend on the density-dependent pattern of interaction strength (Abrams 2001). This link

between density-dependent interaction strength and population dynamics is especially well documented for predator–prey interactions. In particular, the density-dependent pattern of predation in the short term (i.e., the functional response) is used to model changes in predator and prey density over the long term. The availability of long-term data sets for predator–prey interactions has validated this approach with studies showing that the spatiotemporal dynamics of prey populations can be predicted from the functional response of predation (Turchin and Hanski 1997, Gilg et al. 2003).

Similar approaches have been advocated for mutualism. Indeed, the unrealistic result of unbounded population growth in early models of mutualism emerged from the assumption of density-independent benefit (May 1974). Later models that incorporated density-dependent effects of mutualism, including biologically realistic extensions of consumer-resource models (Soberon and Martinez del Rio 1981, Wells 1983, Wright 1989) eliminated the unrealistic result of unbounded growth (Wolin and Lawlor 1984). The realization that density-dependent benefit is key to understanding the population dynamics of mutualism has led to empirical studies that have quantified density-dependent patterns of net benefit (Breton and Addicott 1992, Morales 2000*b*, Anderson and Midgely 2007, Morris et al. 2010), and to theoretical studies that have explored the effect of the functional form of net benefit

for the population dynamics of mutualism (Holland et al. 2002). Despite the close linkage between studies of context-dependent variation in the costs and benefits of mutualism and density-dependent costs and benefit, however, the density-dependent pattern of net benefit is typically viewed as fixed for a given system (Morales et al. 2008, Morris et al. 2010). In reality, both the magnitude and density-dependent pattern of benefit is likely to vary as the ecological conditions change.

Ultimately, understanding the population dynamics of mutualism may require linking the short-term behavioral response of mutualists to density-dependent patterns of net benefit and finally to long-term changes in abundance. The consumer–resource basis of consumer–resource mutualisms (Holland et al. 2005), in which one partner provides a food reward in exchange for a non-food service, suggests that this approach should be especially effective in these cases. Notably, the services provided in consumer-resource mutualisms can include indirect effects, as in the case of protection from predators, or direct effects, as in the case of seed dispersal or pollination.

Ant–hemipteran interactions are one well-studied example of consumer–resource mutualism that can include both direct and indirect components of benefit. Ant–hemipteran mutualisms are categorized as "protection mutualisms" because ants protect hemipterans from their predators in exchange for sugary excretions called honeydew (Buckley 1987). However, hemipterans can also benefit directly in this mutualism (Stadler and Dixon 1999, Flatt and Weisser 2000, Morales 2000b, Morales and Beal 2006) because ant-tending increases feeding rates which can independently increase growth and survivorship (Way 1954). In other cases, the increased feeding rate associated with ant-tending causes a decrease in growth and survivorship such that hemipterans incur a cost from ant tending in the absence of predators (Stadler and Dixon 1998). Although the factors underlying this difference are not fully understood (Stadler and Dixon 1999), the density-dependent pattern of net benefit for hemipterans will nevertheless result from the indirect component of benefit (i.e., predation) combined with the direct component of benefit or cost as it relates to density (Holland and DeAngelis 2010).

A reasonable starting point for understanding the dynamics of ant–hemipteran mutualisms is to link density-dependent patterns of hemipteran survivorship to the short-term behavioral response of ants and predators. In ant–hemipteran and related mutualisms, ants and predators are typically generalists, even in cases where the ant-tended partners are obligately dependent on ant protection (Way 1963, Buckley 1987, DeVries 1991). Because ant-protected insects are characterized by limited mobility, they are usually tended in aggregations (defined as the offspring of one or more females that have oviposited on a given host plant; Axén and Pierce 1998, Dyck et al. 2000, Morales 2002). For these aggregations, the processes controlling local ant and predator densities are largely behavioral and operate on a much faster time scale than the dynamics of hemipteran abundance (Morales 2000a). In addition, the highly generalist nature of ants and hemipteran predators suggests that the long-term consequences of this mutualism will be much greater for the hemipteran partner. Thus, for interactions between ants and their tended hemipterans, the population dynamic consequences of the mutualism may be largely restricted to hemipterans as driven by short-term behavioral responses of ants and predators.

The interaction between *Publilia* treehoppers and ants has become a model system for the study of ant–hemipteran mutualisms, and we know a lot about the underlying mechanisms generating variation in the outcome of this interaction. Treehoppers benefit from ant tending both directly and indirectly (Morales 2000b) and studies have identified variation in the net benefit to treehoppers (measured as differential survivorship between ant-tended and untended treatments) as a function of temporal or spatial variation in background predator levels, the species of ant-tending partner, and density of treehoppers (McEvoy 1979, Bristow 1984, Cushman and Whitham 1989, 1991, Billick and Tonkel 2003, Morales and Beal 2006). Moreover, different studies have reported qualitatively different patterns of density-dependent benefit for *Publilia* treehoppers (i.e., maximum benefit at low, medium, or high treehopper density; McEvoy 1979, Cushman and Whitham 1989, Morales 2000b). Ultimately, the overall pattern of density-dependent benefit for *Publilia* treehoppers will depend on the underlying density-dependent pattern of direct and indirect benefit as mediated by the ecological context. In this paper, I evaluate the density-dependent pattern of, and temporal variation in, both ant recruitment and the benefits from ant tending. These results are combined to provide a mechanistic basis for understanding temporal variation in the pattern of density-dependent benefit and to provide a mechanistic framework for future studies modeling the population dynamics of mutualism.

METHODS

Natural history

Publilia concava is a univoltine phloem-feeding insect found primarily on tall goldenrod (*Solidago altissima*) for populations in northwestern Massachusetts, USA. *Publilia concava* adults overwinter in the leaf litter and emerge in early spring to mate. Adult females lay eggs in the spring, nymphs hatch out in early summer, and both adults and nymphs are tended by ants. Females produce one or two broods within a variable time period but usually not exceeding one month between broods. Two broods from a given female can be found on one or two host plants (Zink 2003) and multiple females often oviposit on a single host-plant. Nymphs and newly eclosed adults remain on their natal host plant so that aggregations from a few to over 1000 persist throughout

the period of summer development. Thus, the density-dependent pattern of benefit from ant tending can be estimated by comparing the survivorship of control aggregations to those with ants excluded. Additional life-history details of *P. concava* can be found in Morales (2000b), Zink (2003), and Morales and Beal (2006).

Treatments

Data used in these analyses come primarily from a set of experiments conducted over the summers 2003 and 2004. The study site in both years was an old field located in Hopkins Memorial Forest, Williamstown Massachusetts, USA (42°43′34″ N, 73°13′ 25″ W). Details of the site can be found in Morales and Beal (2006).

From late May to early June, aggregations were established on potted plants by confining mated pairs of adult treehoppers using mesh netting over wire cages. To facilitate estimating density-dependent effects, I generated a range of treehopper aggregation densities by establishing plants with equal numbers of either one, three, or five to six mated pairs. Pots were transferred to the field in late June to early July and arranged in circular arrays of six plants in 2003, and either one or six plants in 2004 at which time mesh bags were removed. All six-plant arrays consisted of two sets of each density level. Similarly, density treatments were evenly assigned for the single plant arrays in 2004. Arrays were separated by at least 10 m and within arrays, plants were separated by 0.5 m. Array size (one or six) had no effect on treehopper survivorship (M. Morales, *unpublished data*) and is not considered in the current analyses.

I established ant-exclusion treatments using Tanglefoot (Contech Enterprises, Victoria, British Columbia, Canada) applied to the base of stems for half of the plants beginning at the first census. A total of three censuses were conducted beginning on 20 July 2003 and 19 July 2004 with each census taking at most two days. Remaining censuses were spaced at approximately two-week intervals (±2 days). This timing allowed me to distinguish between early- (census 1 to 2) and late- (census 2 to 3) season dynamics; early-season dynamics include a mixture of egg hatching and nymph survivorship whereas late-season dynamics are dominated by nymph survivorship ending with adult eclosion. To reduce the effect of measurement error, each census included at least two counts of both ant and treehopper abundance for each plant, averaged prior to analysis. Ant counts were taken immediately prior to and following each census and identifications were made in the field to genus, species group, or species where possible.

After excluding counts where initial treehopper density was zero, a total of 247 and 250 counts (from 138 plants in 24 grids and 137 plants in 80 grids) in 2003 and 2004, respectively, were available for analysis (note that the aggregations were not followed across years). These data were analyzed using model selection to evaluate both the functional form of direct and indirect benefit and the pattern of temporal variation in density-dependent benefit to treehoppers.

Model selection

Model selection is a statistical framework based on translating hypotheses to a set of candidate models and then evaluating which of these candidate models is most supported by the data (Burnham and Anderson 1998, Johnson and Omland 2004). Model selection differs from traditional null hypothesis testing in that models are ranked but not rejected, per se. Rather, model selection evaluates the degree of support among a set of candidate models. Unlike statistical approaches based on significance tests, model selection can identify which of many biological factors dominate the dynamics of particular system. An additional advantage of model selection is that it facilitates the statistical comparison of biologically based models. Importantly, model selection using biologically-based models has higher power for hypothesis testing than traditional approaches that rely on phenomenological statistical models (de Valpine 2003). Finally, to the extent that model selection is based on biologically based models, it provides an explicit link between theory and data.

Below, I develop a set of candidate models that differ in the density-dependent pattern of direct and indirect benefit and I evaluate which of these models is most consistent with the observed pattern of treehopper survivorship. Finally, I use this approach to quantify the extent to which temporal variation in the direct and indirect components of benefit drives variation in the density-dependent pattern of net benefit for treehoppers in this study.

Models

To analyze the survivorship of treehoppers during the period from nymph hatching to adult eclosion, I used an extension of the Ricker logistic growth model (Turchin 2003) that incorporated both direct and indirect benefits of ant tending:

$$\ln\left(\frac{N_{t+1}}{N_t}\right) = r_t + mN_t + f(.) - g(A_t). \quad (1)$$

The model includes five components: the baseline growth rate (r_t, typically negative) of treehoppers at time t (density N_t, where time t is census number); density-dependent self-regulation (m); the change in growth rate resulting from the direct effects of ants (f, where the symbol "." is used because the predictor variables in the different candidate models vary); and the effect of predators on growth rate (g) as mediated by ant (A_t) protection. Note that the natural log of N_{t+1}/N_t provides a discrete approximation of the realized per capita growth rate such that the model parameters can be interpreted as adjustments to the intrinsic growth rate, r_t (Turchin 2003). Because early season dynamics can include both births and deaths whereas late season dynamics are dominated by deaths, I allowed for the intrinsic growth rate to vary seasonally (each aggregation was censused three times over the summer

providing two survivorship intervals). Yearly variation in the intrinsic growth rate was not included because models with a yearly or seasonal by yearly interaction term in the intrinsic growth rate consistently underperformed those models without (M. Morales, *unpublished data*). For the same reason, temporal variation in density dependence was not included.

Functional forms of benefit

Initially, the base model (Eq. 1) was used to evaluate the density-dependent pattern of indirect and direct benefit. This was done by replacing specific functional forms for $f(.)$ and $g(A_t)$ in Eq. 1, estimating model parameters using non-linear mixed-effects methods (Pinheiro and Bates 2000), and by using AIC_c (AIC corrected for small sample size; Burnham and Anderson 1998) to evaluate which functional form best described the pattern of treehopper survivorship over time.

The functional forms considered for the direct benefit of ant tending (e.g., feeding facilitation) were based on the assumption that benefit is proportional to the rate of contact with ants. Because ants act as consumers in this interaction, the rate of contact between ants and treehoppers is determined by the consumption rate of honeydew. Consequently, my choice of functional forms for the direct benefit of ant-tending came from two commonly used functional responses in consumer-resource theory: linear (i.e., type I) and monotonically saturating (i.e., type II) (Turchin 2003).

The linear functional form for per capita benefit to treehoppers,

$$\alpha_D A_t \qquad (2)$$

is derived mechanistically from the law of mass action (Turchin 2003) assuming that at a given aggregation, ants and treehoppers encounter each other randomly. Phenomenologically, this functional form defines a regression model in which the per capita benefit to treehoppers is a linear function of ant density where α_D defines the slope of the relationship.

The monotonically saturating functional form for per capita benefit to treehoppers,

$$\alpha_D \frac{A_t}{N_t + b} \qquad (3)$$

can be derived mechansitically from the search and handling time of ants (Turchin 2003). At low treehopper density, ants spend most of their time searching for treehoppers. At high treehopper density, ants spend most of their time collecting honeydew (i.e., handling time). The maximum benefit to treehoppers, α_D, is inversely proportional to the handling time of ants (i.e., the maximum feeding rate) and b is a scaling constant that defines the density of treehoppers at which half the maximum feeding rate is reached. Phenomenologically, this functional form describes the case where per capita benefit to treehoppers decreases to zero as treehopper density increases.

A third functional form for the direct benefit to treehoppers was based on the observation that because treehoppers are highly clustered, the time spent searching for treehoppers by ants is very short. Therefore, a special case of Eq. 3 was considered in which search time was set to zero yielding the linear ratio-dependent functional form:

$$\alpha_D \frac{A_t}{N_t}. \qquad (4)$$

Phenomenologically, this describes the case where benefit to treehoppers depends on the ratio of ants to treehoppers.

Predation was modeled as in Morales et al. (2008) under the assumption that predators equilibrate rapidly to changes in treehopper and ant abundance. The predation rate was modeled mechanistically by assuming a constant immigration and attack rate for predators, and by allowing the rate at which predators leave aggregations to vary as a function of treehopper and ant density. Thus, predators are less likely to leave a treehopper aggregation as treehopper density increases, but are more likely to leave a treehopper aggregation as ant density increases. I evaluated three functional forms for the relationship between ant density and predator emigration (see Appendix A for derivation). Note that predator density or attack rate was not observed directly but was estimated from the pattern of survivorship between ant-tending treatments. Therefore, in the equations below, γ subsumes both the per capita attack rate of predators and predator density to give the per capita mortality of treehoppers due to predators.

The step functional form,

$$g(A_t = 0) = \gamma$$

$$g(A_t > 0) = 0 \qquad (5)$$

assumes that predators emigrate instantaneously from plants with any level of ant tending. It is consistent with the biological scenario in which predators are able to indirectly assess the presence of ants and immediately abandon defended aggregations (Oliver et al. 2008).

The linear functional form,

$$g(A_t) = \frac{\gamma}{(1 + \alpha_I A_t)} \qquad (6)$$

assumes that the emigration rate of predators increases linearly with the density of ants. It is consistent with the biological scenario in which ants and predators encounter each other at random and where predators abandon plants after encountering ants. Thus treehopper mortality due to predators (γ) declines to zero as ant density increases where α_I defines the rate of predator removal by ants (i.e., the increase in predator emigration).

The exponential function form,
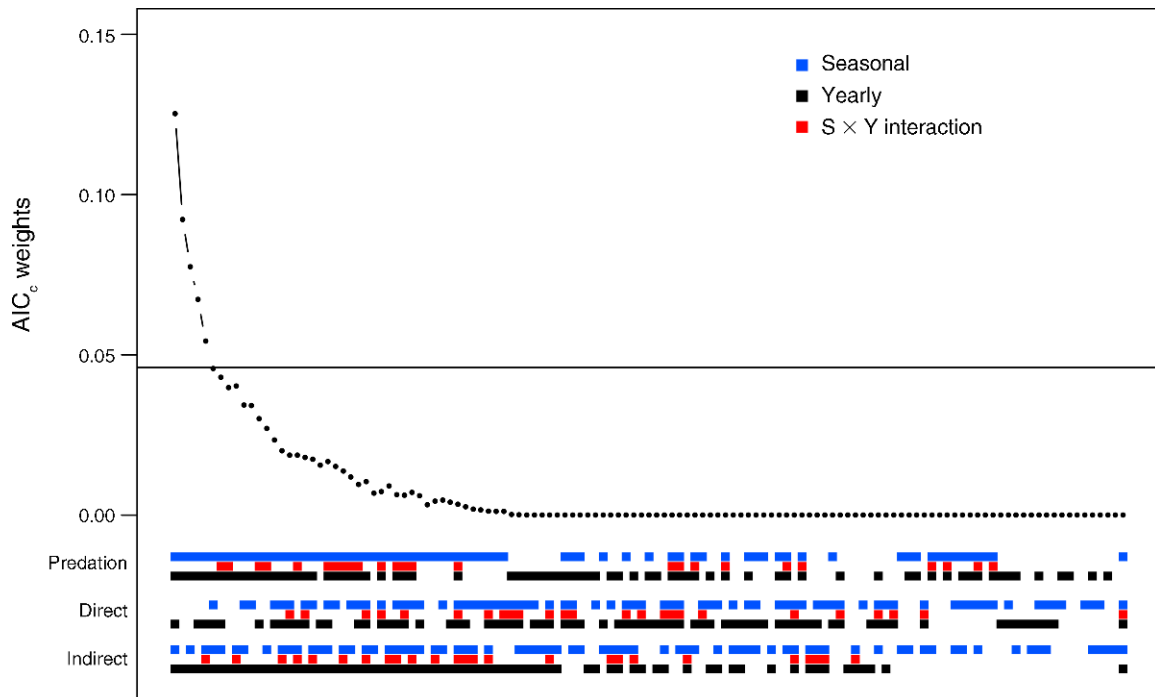
$$g(A_t) = \gamma \exp(-\alpha_I A_t) \qquad (7)$$

FIG. 1. AIC_c weights resulting from the model selection analysis of temporal variability. Each point represents a single model, and filled squares below identify for that model whether temporal variability is associated with direct benefit, indirect benefit, or the intensity of predation, and whether the pattern of variation is seasonal, yearly, or an interaction between the two. The solid horizontal line indicates the AIC_c weight equal to a ΔAIC_c value of 2.

is based on the assumption that the emigration rate of predators increases exponentially with the density of ants. It is consistent with the biological scenario in which predators are increasingly likely to abandon aggregations as their encounter rate with ants increases.

Because predation was not measured directly, I took advantage of a smaller data set collected during the summer of 2002 in which predators were excluded ($N = 54$ aggregations) to evaluate whether model selection using treehopper survivorship data could decompose direct and indirect components of benefit. Although details of the experimental design differ from that of the current study (Morales and Beal 2006), key features were shared: treehoppers were established on potted plants in the same field site with ants excluded from half of all plants. These data (predator-excluded) and those from 2003–2004 (primary data set) were analyzed using model selection with the set of functional forms above, but also including model combinations in which either or both the direct and indirect benefit components was set to zero. This analysis allowed a test of the prediction that a direct-benefits-only model would be selected for the predator-excluded data, and a combined-benefits model would be selected for the primary data set.

Temporal variation in benefit

After selecting the functional forms of benefit, I evaluated the pattern of seasonal and yearly variability in benefit by modifying Eq. 1 to allow parameters describing the direct and indirect components of benefit to vary temporally (see Appendix B for example R code). I considered all possible combinations of temporally variable year and season effects (including a year by season interaction) for the parameters associated with direct benefit, α_D, indirect benefit, α_I, and predation intensity γ (Fig. 1). To control for model selection uncertainty, relative importance of these terms was determined by summing the AIC_c weights for all models that contained either a year or season effect for each of the additive model parameters considered (Burnham and Anderson 1998).

Models were fit in the statistical environment R (R Development Core Team 2005) using non-linear mixed effects methods (Pinheiro and Bates 2000) to account for the repeated-measures design with grid and plant included as random effects. Errors of the log-transformed growth rates were normally distributed and maximum likelihood was used to estimate parameters. Finally, because untended aggregations typically have a higher variance in survivorship than tended aggregations (Morales and Beal 2006), variances were allowed to vary between ant treatments.

Density-dependent benefit

In the analyses above, I evaluated the functional form of benefit to treehoppers based on observed levels of ant and treehopper abundance (i.e., the functional response of ant tending: Turchin 2003). Because ant recruitment

TABLE 1. Model selection results for the analysis of treehopper survivorship based on the model in Eq. 1 using the functional form of direct and indirect components of benefit listed below.

Functional form		Number of parameters	ΔAIC_c	
Direct, $f(.)$	Indirect, $g(A)$		Primary data	Predator-excluded data†
		7	148.9	6.3
Ratio (Eq. 4)		8	111.8	**0.0**
Type I (Eq. 2)		8	103.8	1
Type II (Eq. 3)		9	79.9	2.0
	step (Eq. 5)	8	15.5	1.8
	linear (Eq. 6)	9	5.5	1.8
	exponential (Eq. 7)	9	11.1	1.5
Ratio (Eq. 4)	step (Eq. 5)	9	8.5	1.5
Type I (Eq. 2)	step (Eq. 5)	9	10.5	2.1
Type II (Eq. 3)	step (Eq. 5)	10	4.8	3.8
Ratio (Eq. 4)	linear (Eq. 6)	10	**0.0**	3.9
Type I (Eq. 2)	linear (Eq. 6)	10	5.6	3.9
Type II (Eq. 3)	linear (Eq. 6)	11	1.0	‡
Ratio (Eq. 4)	exponential (Eq. 7)	10	5.3	3.7
Type I (Eq. 2)	exponential (Eq. 7)	10	8.1	4.9
Type II (Eq. 3)	exponential (Eq. 7)	11	5.0	6.6

Notes: Functional forms are: $f(.)$, direct effect of ants; $g(A)$, growth rate as mediated by ant protection. Boldface type highlights the most strongly supported model (the model with the lowest AIC).

† Data are from Morales and Beal (2006). See *Methods* for details.

‡ Model could not be fit.

is itself a function of treehopper density (i.e., the aggregation response; Turchin 2003), the overall pattern of density-dependent benefit to treehoppers also depends on the aggregation response of ants. To evaluate the density-dependent pattern of net benefit, I generated survivorship curves for ant-tended and untended aggregations as a function of treehopper density using the model selected from the survivorship analysis and the estimated aggregation response of ants to treehoppers.

A phenomenological, but statistically convenient, approach to modeling the aggregation response of ants to treehoppers is with a power function on a log-log scale to normalize the data and stabilize the variance (Morales 2000b). I used a mixed-effects linear model (Pinheiro and Bates 2000) with a log-log transformation of ant and treehopper density to estimate ant-recruitment. To account for temporal variation in ant recruitment, I evaluated a model that included all interactions with year and census. Grid and plant were included as grouping factors to account for the repeated measures design.

RESULTS

Functional forms of benefit

Model selection analysis provided strong support for a combined-benefits model when applied to the primary data set, and for a direct-benefit-only model when applied to the predator-excluded data (Table 1). More specifically, there was substantial support for a linear functional form for predator protection by ants, and for a ratio-dependent form for the direct benefit of ant tending. For the larger, primary data set, a reasonable alternative model ($\Delta AIC_c < 2$; Burnham and Anderson 1998) incorporated a type II functional form for the direct effect of ant tending, but this model had a lower

AICc score despite having one additional parameter. Moreover, a type II functional form (Eq. 3) becomes a ratio-dependent functional form (Eq. 4) as the half-saturation constant (b) approaches zero, in this case estimated at 0.22. The low estimate of b is consistent with the expectation that the search time of ants at an aggregation is much lower than the handling (tending) time. For these reasons, all analyses of temporal variability below are based on the combined benefits model that incorporates a linear functional form for predator protection and a ratio-dependent functional form for the direct effects of ant tending:

$$\ln \frac{N_{t+1}}{N_t} = r_t + mN_t + \alpha_D \frac{A_t}{N_t} - \frac{\gamma}{1 + \alpha_I A_t}. \qquad (8)$$

Temporal variation and density-dependent benefit

After accounting for model uncertainty by summing the AIC_c weights for the main effects in each of the models (Fig. 1), there is very strong support for both seasonal and yearly variation in the magnitude of predation (γ) and for yearly variation in the protection provided by ants (α_I) (Fig. 2). There is moderate support for the importance of seasonal variation in ant protection and for yearly variation in the direct effect of ant tending (α_D) (Fig. 2). Finally, there is only weak support for seasonal variation in the direct effect of ant tending (Fig. 2). Thus, in this study predator pressure changed both within and between years while the effectiveness of ant defense changed between years, yielding the following model:

$$\ln \frac{N_{t+1}}{N_t} = r_t + mN_t + \alpha_D \frac{A_t}{N_t} - \frac{\gamma_{(S,Y)}}{1 + \alpha_{I(Y)} A_t} \qquad (9)$$

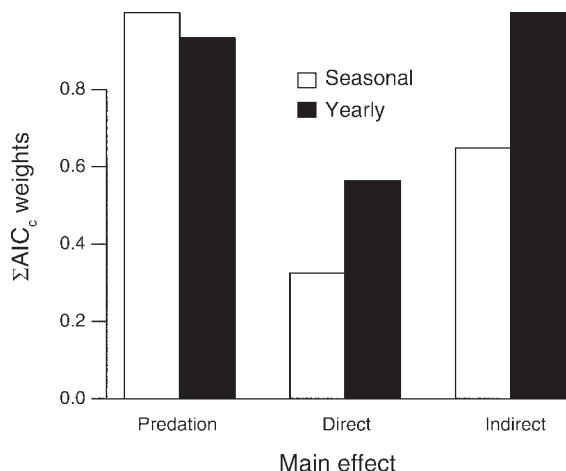where the subscripts S and Y denote seasonal or yearly

FIG. 2. Relative support (range 0–1) for seasonal or temporal variability in direct benefit, indirect benefit, or the intensity of predation. Values were obtained by summing the AIC_c weights for the main effects of all models that included a free parameter associated with seasonal or yearly variability.

variation in the parameter. Although this was the second best model overall (Fig. 1), the difference in AIC_c from the best model was small. Regardless, qualitative conclusions in the analyses below remain unchanged when using the top-ranking model or the one supported after accounting for model uncertainty (M. Morales, *unpublished data*)

To evaluate whether changes in ant effectiveness were associated with changes in ant-species composition, I tested whether ant-species composition varied temporally. The pattern of temporal variation in ant-species composition shows significant yearly, but not seasonal, variation in ant-species composition (Fig. 3; species × year | species + census + year + species × census: $\chi^2_{df=5} =$ 63.0, $P < 0.001$; species × census | species + census + year + species × year: $\chi^2_{df=5} = 2.3$, $P = 0.81$). Thus, the pattern of variation in ant-species composition was consistent with the pattern of variation in the effectiveness of

predator-protection by ants. To further explore whether changes in ant-species composition were responsible for the decline in effectiveness of ant protection from 2003 to 2004, I restricted the data set to the three most abundant ant species and replaced the yearly term for predator protection in Eq. 9 (α_I) with one that explicitly accounts for the species-specific effect of ants. Results suggests that the most abundant ant genera in 2003, *Myrmica*, was also most effective on a per capita basis (mean $\alpha_I \pm$ SE: *Myrmica* = 4.04 $\pm$ 8.39, *F.* "fusca" = 1.06 $\pm$ 0.82, *Tapinoma sessile* = 0.56 $\pm$ 0.47) and this pattern holds even after accounting for mean ant abundance (*Myrmica* = 24.3 $\pm$ 2.5, *F.* "fusca" = 9.1 $\pm$ 1.1, *T. sessile* = 19.8 $\pm$ 2.6). Consequently, differences among ants in their effectiveness at removing predators are consistent with the hypothesis that variation in ant-species composition was responsible for variation in the effectiveness of ant protection. On the other hand, the model with species-specific effects in lieu of yearly variation for predator protection performs significantly worse ($\Delta AIC = 81$) consistent with the large confidence intervals for the species-specific estimates of α_I.

To evaluate the overall pattern of density-dependent survivorship and net benefit, I replaced empirical ant density in Eq. 9 (A_t) with the aggregation response of ants (i.e., ant density as a function of treehopper density). The aggregation response was modeled as a power function using a log-log transformation of ant and treehopper density (N_t; see *Methods*). Temporal variation in ant recruitment was incorporated by including year (Y) and census (S) terms and their interactions. Because no interaction terms were significant ($S \times Y + \ln(N_t) \times S + \ln(N_t) \times Y + \ln(N_t) \times S \times Y | \ln(N_t) + S + Y$; $\chi^2_{df=4} = 5.48$, $P = 0.24$), they were excluded from the final model (Appendix C: Table C1).

Incorporating the aggregation response of ants above into Eq. 9 shows that the density-dependent pattern of survivorship (Fig. 4) and net benefit (Fig. 5) varied quantitatively within years and qualitatively between
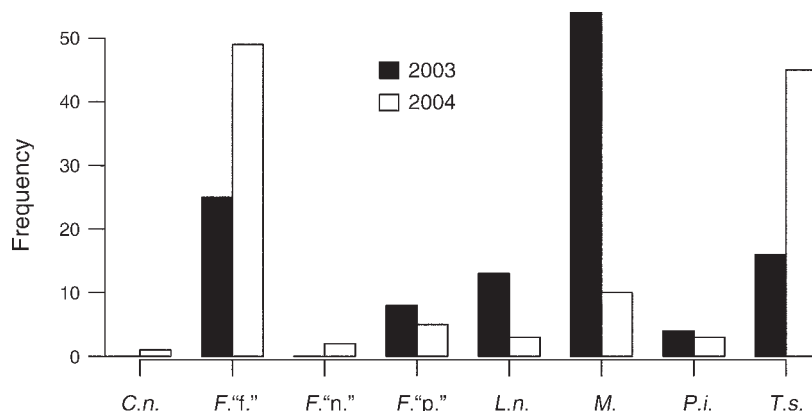

FIG. 3. Frequency of ant species tending treehopper aggregations across years. Key to abbreviations: *C.n.*, *Camponotus noveboracensis*; *F.*"f.", *Formica* "fusca" group; *F.*"n.", *Formica* "neogagates" group; *F.*"p.", *Formica* "pallidefulva" group; *L.n.*, *Lasius neoniger*; *M.*, *Myrmica* spp.; *P.i.*, *Prenolepis imparis*; *T.s.*, *Tapinoma sessile*. Because of low frequency, *C.n.* and *F.*"n." were excluded from analysis.
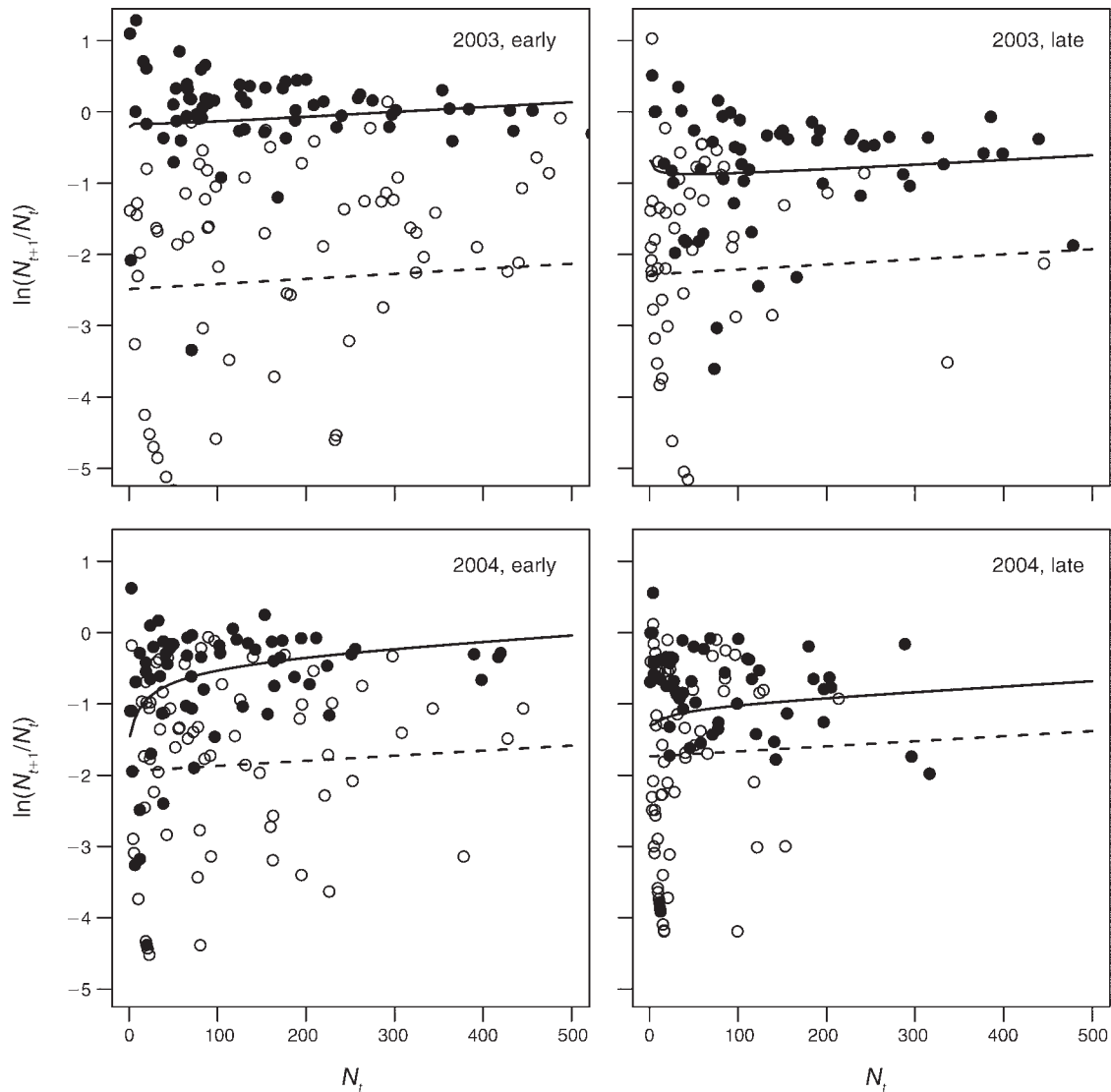
Fig. 4. Density-dependent survivorship of treehoppers with survivorship curves generated from Eq. 9 (for which parameters showed relative support > 95%; second-best AIC_c model overall); median treehopper density (median density N_t, where time t is census number) = 72.5.

years. Within years, the benefit of ant tending was highest earlier in the season. Between years, overall benefit (averaged across density) was higher in 2003 than in 2004, while maximum benefit to treehoppers was at low density in 2003 and at high density in 2004. This difference in the density-dependent pattern of net benefit was driven primarily by changes in the density-dependent pattern of ant protection (Fig. 5). In particular, the switch from negative to positive density-dependent benefit is driven by a reduction in the effectiveness of predator removal by ants ($\alpha_I = 7.82$ in 2003 and 0.39 in 2004; Appendix C: Table C2).

DISCUSSION

A number of studies have demonstrated that the net benefit of mutualism varies with the ecological context

(Bronstein 1994). Other studies have stressed the importance of the functional form of benefit for understanding the population dynamics of mutualism (Morales 2000a, Holland et al. 2002). This study integrates these two approaches by explicitly evaluating how temporal variation in the benefits of a mutualism drives temporal variation in the density-dependent pattern of net benefit. Results show that temporal changes in the relative importance of the direct and indirect benefit components of ant tending qualitatively change the overall pattern of density-dependent benefit between years. In particular, a decline in the effectiveness of predator removal by ants in the second year of this study caused maximum benefit to shift from treehoppers in small to large aggregations. Note that this change in overall pattern of net benefit results
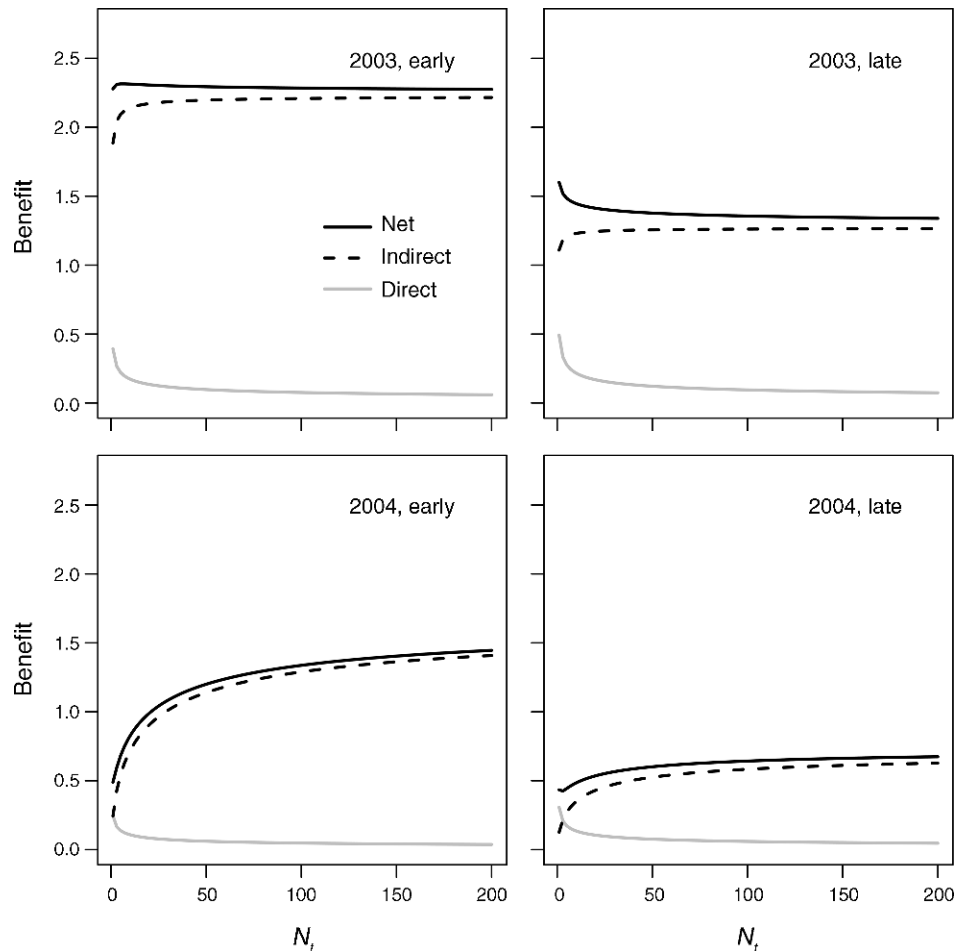
FIG. 5. Density-dependent pattern of benefit to treehoppers decomposed into indirect, direct, and combined (net) benefit components. Based on parameter estimates (Appendix A: Table A1) from Eq. 9 (for which parameters showed relative support > 95%; second-best AIC_c model overall).

because the direct and indirect components of benefit show different density-dependent patterns (Fig. 5).

These results have significant implications for understanding the population dynamics of mutualism. For models of mutualism in general, negative density-dependent benefit is stabilizing whereas positive density-dependent benefit (including over a range of density as in an Allee effect), is destabilizing. In particular, positive density-dependent-benefit decreases the return-time stability (i.e., elasticity) of mutualism (Addicott 1981, Wolin and Lawlor 1984) and can generate limit cycles (Morales et al. 2008). Thus, the shift in functional form of benefit seen in this study may be associated with a temporal shift from stabilizing to destabilizing dynamics.

The focus of this study is on the density-dependent benefit of ant-tending for the period of treehopper development from nymphs to adults. Because the benefit of ant-tending in this system is not moderated by a compensatory response during the period of adult overwintering or oviposition (Morales and Beal 2006),

the effect of ant-tending seen in this study likely translates to yearly variation in overall population growth rates. These results emphasize the need for empirical studies that evaluate the long-term dynamics of mutualism, and theoretical studies that consider the population dynamics consequences of variation in the functional form of benefit.

Mechanisms underlying temporal variability

Despite strong evidence from a variety of study systems that the benefit of mutualism varies temporally (Bronstein 1994), it has not always been possible to relate variation in benefit to underlying biological mechanisms (Billick and Tonkel 2003, Kaplan and Eubanks 2005). In the interaction between *Publilia* treehoppers and ants, the relative abundance of predators has been correlated with temporal variation between years in one study (Cushman and Whitham 1989), but not in another (Billick and Tonkel 2003). Part of the difficulty may be that predator protection depends on both the abundance and attack rate of predators in

addition to the effectiveness of ants as protectors. As indicated by the results of the current study, the ability to parse these effects out using biologically-based models potentially increases statistical power (de Valpine 2003) and can provide insight into the mechanisms generating variation in outcome. For example, this study highlights scale dependence in the mechanisms driving variation in benefit: between years, variation in benefit was caused both by changes in predation intensity and the effectiveness of ant defense whereas within years, variation in benefit was caused only by changes in predation intensity.

The current analysis evaluates the mechanisms driving temporal variation in benefit at the level defined by the model parameters (i.e., direct benefit, predator protection, or predation intensity) but does not address the underlying mechanisms generating variation in these parameters. For example, results indicate that the seasonal variation in net benefit seen in this study is driven by variation in predation intensity, but does not address why predation intensity varies seasonally. By isolating variation in predation intensity as the cause of seasonal variation in net benefit, however, this analysis restricts the set of potential mechanisms at increasingly finer scales. For example, it seems likely that seasonal variation in predation intensity is associated with the increased difficulty of preying on larger nymphs (M. Morales, *personal observation*) or adults (Cushman and Whitham 1989) whereas yearly variation in predation intensity may be associated with changes in the density or species composition of predators. Similarly, variation in ant-species composition is consistent with, but does not unequivocally explain, the change in effectiveness of predator protection by ants between years (Fig. 5, see also *Results*). Thus, variation in predator-species composition, and corresponding changes in their ability to avoid removal by ants, remains a viable mechanism contributing to the difference in ant protection between years.

Conclusions

Quantitative methods that facilitate the analysis of complex dynamics over spatial and temporal scales are an important priority for future ecological research (Agrawal et al. 2007) and results presented here suggest that model-selection analyses may be one effective way of achieving this goal. In this study, model selection was used to identify the temporal pattern and functional form of indirect and direct mechanisms of benefit for an ant-tended treehopper thereby linking two focal areas of mutualism research: density-dependent benefit and variation in the costs and benefits of mutualism. Results highlight that the mechanisms driving temporal variation in benefit can be scale dependent and that this scale dependency can generate qualitative shifts in the pattern of density-dependent benefit. In general, model selection shows excellent promise for linking theoretical and empirical areas of research in ecology.

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APPENDIX A

Derivation of models for indirect benefit (*Ecological Archives* E092-059-A1).

APPENDIX B

Example code for fitting models in R (*Ecological Archives* E092-059-A2).

APPENDIX C

ANOVA table of the natural log of ant-tending as a function of the natural log of treehopper density, year, and season; and a table showing model parameters for Eq. 9 estimated from survivorship data (*Ecological Archives* E092-059-A3).