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Density-dependent foraging behaviors in a parasitoid lead to density-dependent parasitism of its host

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Abstract Empirical studies of spatial heterogeneity in parasitism by insect parasitoids have focused largely on patterns, while the many possible underlying mechanisms have been little studied in the field. We conducted experimental and observational studies on *Tachinomyia similis* (Diptera: Tachinidae) attacking western tussock moths (*Orgyia vetusta*; Lepidoptera: Lymantriidae) on lupine bushes at Bodega Bay, Calif., USA. We examined several foraging behaviors that have been hypothesized to create density-dependent variation in parasitism rates, including spatial aggregation of parasitoids to high host density, mutual interference among searching parasitoids and decelerating functional responses of the parasitoid. At the spatial scale of individual bushes, we detected both aggregation to a high density and a decelerating functional response. The resulting spatial pattern of parasitism was best fit by two models; one included an effect of parasitoid aggregation and the other included an effect of aggregation and a decelerating functional response. Most of the variation in parasitism was not correlated with density of *O. vetusta*.

Keywords Parasitoid aggregation · Functional response · Interference · Spatial heterogeneity

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Introduction

Understanding the causes and effects of spatial heterogeneity in ecological systems has been a central focus of ecological research over the past two decades. In particular, both theoretical and empirical research have focused on the effects of spatial heterogeneity on insect host-parasitoid interactions and population dynamics. While theoretical work has concluded that variability in the risk of parasitism can be an important stabilizing factor in these systems (Chesson and Murdoch 1986; Hassell et al. 1991), the source and importance of this variability in natural systems is an open question (Pacala and Hassell 1991; Jones et al. 1993; Murdoch and Briggs 1996; Gross and Ives 1999).

Historically, theoretical studies have examined how the movement behavior of parasitoids leads to either higher or lower parasitism in high-density host patches (Hassell and May 1973; Comins and Hassell 1979; Hassell et al. 1991). In nature, parasitoids display many movement behaviors that should lead to increased densities and higher parasitism levels in patches of high-density hosts (Waage 1983; Casas 1989; Connor and Cargain 1994). However, reviews of field data show that the relationship between host density and parasitism is frequently negative rather than positive (Stiling 1987; Walde and Murdoch 1988). Mechanisms that lead to inversely density-dependent patterns of parasitism include leaving patches at a constant rate to avoid self-superparasitism (Rosenheim and Mangel 1994), decelerating functional responses caused by behaviors such as handling time or group defenses (Hunter 2000), and interference among parasitoids (Walde and Murdoch 1988; Ives 1992).

While any one of these mechanisms falls within the general framework proposed by Chesson and Murdoch (1986) and Hassell et al. (1991), in which increasing variance in risk of parasitism stabilizes host-parasitoid systems, the presence of multiple factors can complicate results. One mechanism alone, which leads to a monotonic pattern of parasitism risk as a function of host density, will necessarily increase variability in risk of parasitism.

However, if two mechanisms produce counteracting impacts of host density, then the pattern of parasitism risk versus host density may not be monotonic and there may not be an increase in variability in the risk of parasitism. Ives (1992) examined such a model, where parasitoids exhibited both a type 2 functional response and movement behaviors that led to aggregation of parasitoids to high densities of their host. Either mechanism alone could stabilize dynamics, but unstable dynamics resulted when both mechanisms were strong (Ives 1992).

Although there is an abundance of data relating host density to parasitism rates, few studies have shown the relative importance of different behavioral mechanisms in the field, and fewer yet have tied these mechanisms to the observed patterns of parasitism. Decelerating functional responses, a large class of functional responses, defined by a decrease in the attack rate of the parasitoid with increasing host density, have frequently been posited as a cause of inverse density-dependent parasitism (Walde and Murdoch 1988; Ives 1992), but their importance in natural systems is still not well documented (but see Tillman 1996; Wang and Ferro 1998). While laboratory experiments have frequently demonstrated deceleration (e.g. Hassell 1978), the abnormally high host densities used in laboratory experiments can produce a decelerating parasitoid response that is not detectable in field experiments at lower, naturally occurring densities (O'Neil 1997). Similarly, parasitoid interference, where increasing numbers of parasitoids decrease the attack rate per parasitoid, has rarely been detected in field experiments (Godfray 1994). The few field studies that have examined the mechanisms underlying aggregated parasitism have shown that parasitoids have behaviors that increase the time spent in high-density host patches (Waage 1983; Casas 1989; Connor and Cargain 1994). Curiously, in two studies that examined the resulting pattern of parasitism (Waage 1983; Connor and Cargain 1994), parasitism was independent of host density. Waage (1983) demonstrated that the functional response was indeed decelerating; the deceleration of the functional response was thought to be strong enough to explain the pattern of density-independent parasitism.

In this study, we measure the behavioral response of the tachinid parasitoid, *Tachinomyia similis* Williston, to varying densities of its host, the western tussock moth (*Orgyia vetusta* Bdv. Lymantriidae). Until recently, the population of *O. vetusta* that we studied had been a spatially isolated outbreak for over a decade. Experiments and theoretical studies have demonstrated that the spatial spread of this outbreak is limited by widely dispersing parasitoids (Brodman et al. 1997; Hastings 1997; Maron and Harrison 1997; Wilson et al. 1998). However, models predict that for the spatial pattern in *O. vetusta* density to be stable, there must be either a decelerating functional response in parasitism or parasitoid interference. Here we ask whether *T. similis* aggregates to high-density patches of tussock moths, whether there is a decelerating functional response and whether there is interference among foraging parasitoids. Furthermore, we examine whether the presence or absence of these behavioral mechanisms results in any pattern in parasitism rates in response to varying host densities.

Materials and methods

Natural history

Much of the natural history of this system has been detailed previously (see Harrison 1994, 1997; Harrison and Maron 1995; Harrison and Wilcox 1995; Brodman et al. 1997) and we describe briefly the important details. The experiments were carried out at the University of California's Bodega Marine Reserve (BMR; Sonoma County, California) (Barbour et al. 1973). Bush lupine (*Lupinus arboreus* Sims.) is a short-lived evergreen perennial that is found in coastal dunes and grasslands from Ventura County to Sonoma County. At BMR it is the dominant shrub in grasslands; shrubs often grow in dense stands at many grassland site on BMR. *O. vetusta* is native to the California coast and feeds on lupines, willows, and other woody plants; at BMR it occurs only on *L. arboreus*. The moth is univoltine, and over-wintering eggs hatch between April and June. Larvae feed on lupine foliage and flowers and pupate between mid-June and early August. Eclosion and mating occur 1–2 weeks later, and the flightless females lay a single mass of 100–300 eggs on the undersides of bushes (Furniss and Knopf 1971).

T. similis is a parasitoid of several species of Lepidoptera. At BMR it specializes on *O. vetusta*. Females attach conspicuous white eggs to the cuticle of late instar larvae. The larvae of *T. similis* emerge from either larvae or pupae and then pupate and over-winter in the soil. There are several other important parasitoids of tussock moths at BMR: the scelionid wasp *Telenomus californicus* Ashmead parasitizes eggs; and two other tachinid flies, *Patelloa pluriseriata* or *fuscimacula* (Aldrich and Webber; we have been unable to get a definite species identification) and *Protodejeania echinata* Townsend, both attack larvae and emerge from pupae.

The experiments described here took place at Mussel Point in 1998. The western tussock moth had defoliated bush lupines at BMR every year from 1983 to 1997, but had been confined to a single 100×400 m stand at Mussel Point except in 1997 where it had spread to a stand of lupines 800m away. In 1998, the numbers at Mussel Point had declined significantly.

Fly aggregation and density-dependent parasitism

To determine how parasitoid behavior and levels of parasitism vary with host density, we created replicate experimental populations of tussock moth larvae of different densities. Populations were created by seeding large lupine bushes with tussock moth egg masses that we collected in late summer 1997. Egg masses were kept over the winter in plastic containers in outdoor cabinets. In February 1998 we selected and marked 48 adult lupine bushes to seed with tussock moth propagules. Twenty-four bushes were in grasslands and 24 grew in dunes. We started the experiments in both habitats to examine possible impacts of habitat on parasitism. However, survivorship of larvae on dune bushes was so low that we were unable to analyze any of the data from dune bushes and no data from those bushes are reported. Large bushes were chosen so that even the highest-density tussock moth treatment would not result in the complete defoliation of the bush. Bushes were pruned, where necessary, to ensure that caterpillars could not disperse to neighboring bushes by climbing across touching branches. We attached 10, 50, or 100 egg masses per bush (for grassland bushes). At Bodega Bay, natural densities of egg masses reach as much as 40 per bush (Harrison 1994). Up to 10 egg masses were grouped together in bridal veil bags that were tied to the underside of plants. We estimated that each tussock moth egg mass produces 100–200 first instar larvae that are subject to large amounts of density-

independent and density-dependent mortality (Harrison 1994). Tussock moth density treatments were randomly assigned to each bush, such that each density treatment was replicated eight times.

We began monitoring *O. vetusta* larvae on experimental bushes on 9 June 1998 and continued with weekly censuses until 21 July, when most larvae had either died or pupated. At each census, we recorded the number of larvae remaining on the bush and the number of larvae with conspicuous white eggs of *T. similis* on their cuticles. Counts of larvae with parasitoid eggs do not provide an estimate of the total number of larvae that are parasitized at any census period because previously parasitized larvae lose the egg on their cuticle (the tell-tale sign of parasitism) when they molt or when *T. similis* eggs hatch. However, these counts do provide an index of parasitism that can be compared across density treatments. Actual parasitism levels are likely to be higher.

Late instar tussock moth larvae tend to disperse from defoliated bushes. To prevent this from occurring, we placed 10 cm tall plastic landscape edging around the outer perimeter of each bush on 3 July. Edging was held upright by plastic stakes and topped with Tanglefoot (Tanglefoot Co., Grand Rapids, Mich., USA).

Fly densities were monitored weekly from 17 June until 22 July. Each bush was sampled in the morning and afternoon on each sampling date. Fly sampling protocol consisted of two minutes of visual scanning while circling the target bush. The time period of sampling was selected as a minimum to search all branches of a bush while allowing minimal arrivals of new flies. Only female parasitoids were counted.

The effect of larval *O. vetusta* density on fly density was analyzed using Poisson regression. Preliminary analysis showed no effect of time of day, so counts for each day were added together prior to analysis. Because many observed discrete data have higher variance than expected from the Poisson assumption (see McCullagh and Nelder 1989), we standardized the variance of the model by the deviance.

Functional response and interference

To determine how parasitoid behavior was influenced by both intraspecific density and the density of their hosts, we initiated a factorial experiment by crossing two fly densities (two and eight flies per bush) with two *O. vetusta* larva densities (20 and 100 per bush). Density treatments were chosen from observed field densities for both species. For each treatment level, we randomly selected four lupines which we enclosed in 1 m^3 mesh cages constructed of PVC tubes covered with mesh fabric. We ran the experiment twice (on 31 July and 4 August) using the same bushes with treatments randomly selected on each date. Tussock moth larvae without visible parasitoid eggs were collected from bushes throughout our study site the day before and the day of the experiment. Similarly, female flies were collected over these two days. Flies collected the previous day were placed in the refrigerator to reduce mortality prior to the experiment. The afternoon of the experiment, larvae already on the bush were removed before both larvae and flies were placed on the bush. Cages were opened up two days later and the number of flies and unparasitized and parasitized larvae were counted.

A two-way nonparametric analysis of variance [the Scheirer-Ray-Hare extension of the Kruskal Wallis test (Sokal and Rohlf 1995)] was used to analyze the relationship between larva and fly density and parasitoid attack rate and to test for an interaction. In order to access parasitoid attack rates, the data were transformed by taking the log of the fraction unparasitized and then dividing by the number of flies added to the treatment. This transformation is derived from the basic assumption of multiplicative risk in the Nicholson-Bailey model, where the proportion escaping parasitism equals $\exp(-atP)$ where a is the attack rate, P is the parasitoid density and t is the time span over which foraging occurs. Because t was the same for all experiments, we incorporate it into the attack rate parameter so that we in fact estimate at.

Analysis of density-dependent parasitism

To test the influences of both aggregation and a decelerating functional response on the pattern of parasitism, we used an information criteria technique to select among models of increasing complexity. This technique compares the ability of different models to fit data, penalizing models with more parameters (Burnham and Anderson 1998; Strong et al. 1999). Likelihood functions were created assuming the distribution of parasitism was binomial and mean parasitism rate could be described as one of the four functions of host density listed below:

1. No effect of host density on parasitism.

$$p_{1i} = 1 - \exp(\alpha_i) \tag{1}$$

2. Weekly variability in parasitoid aggregation, no decelerating functional response.

$$p_{2ji} = 1 - \exp\left[\alpha_i \exp(h_{ji}\beta_i)\right] \tag{2}$$

3. Decelerating (type 2) functional response

$$p_{3ji} = 1 - \exp\left(\frac{\alpha_i}{1 + sh_{ji}}\right) \tag{3}$$

4. Decelerating functional response and weekly variability in parasitoid aggregation

$$p_{4ji} = 1 - \exp\left[\frac{\alpha_i \exp(h_{ji}\beta_i)}{1 + sh_{ji}}\right] \tag{4}$$

Here we have assumed that the non-decelerating functional response is the type 1 and the decelerating functional response is the type 2 functional response (Holling 1959) and that the form of aggregation is the same type we fit in the aggregation section. In these equations, p_{lji} is the predicted proportion of larvae parasitized for bush j in week i for model l, and h_{ji} is the observed density of *O. vetusta* (in number of larvae/bush). The model fits several parameters that are used to test for the presence of different mechanisms. α_i is the weekly base parasitism risk (the parasitism risk predicted without any density-dependent effects) that integrates weekly changes in parasitoid density and parasitoid attack rate. α_i has no units, though it should be noted that there is an implicit rate of per week in this analysis. β_i is the weekly aggregative effect in units of (host density)$^{-1}$ and s is the strength of the functional response in units of (host density)$^{-1}$. Many authors use a slightly different form of the type 2 functional response: $\frac{a}{b+h}$. Our form is equivalent to this, but we have divided top and bottom by b, therefore s is equivalent to $1/b$. We chose the alternate form so that we could test for the presence of saturation by testing if s is significantly greater than 1. All these functions include weekly variability in base parasitism rate. Note that model 1 has density-independent parasitism rates, model 2 has positively density-dependent parasitism rates, model 3 has negatively density-dependent parasitism rates and model 4 can have positively, negatively or non-monotonic patterns of density dependence. From the above equation we can calculate a log likelihood:

$$\log\left[L_l(Y|\theta)\right] = \sum_{ji} \text{binomial}(h_{ji}, k_{ji}, p_{lji}) \tag{5}$$

where h_{ji} is the number of hosts on bush j in week i, k_{ji} is the number of hosts not parasitized on bush j in week i, p_{lji} is the predicted parasitism rate and is the vector of parameters for each model. The negative of this function was minimized using the simplex method of Nelder and Mead (Press et al. 1994) modified to not allow negative values for any of the parameters. Minimization was restarted 1000 times at random starting points for all modes. For the more complex models, an additional 1000 restarts were completed where all parameters but the is were randomly

initialized. In these cases the *i*s were initialized to the value determined by the maximization of the base model (Eq. 1). Overdispersion, which is variance greater than binomial, is common in biological systems (McCullagh and Nelder 1989). We scaled by the deviance function of the most complete model to account for this added variance. Finally, the relative ability of the different models to fit these data was tested by comparing information criteria. We used the quasi-likelihood Akaike information criterium (QAICc), which takes into account the amount of overdispersion in the data (Burnham and Anderson 1998). Differences in QAICc greater than 2 are generally considered significant at the P=0.05 level (Burnham and Anderson 1998).

Results

Aggregation

As expected, mortality of *O. vetusta* larvae was high. Maximal densities expected, given the number of egg masses and the number of eggs per egg mass would be nearly 20,000. However, the highest observed density was 1,086, which is at the upper edge of observed densities (Maron et al. 2001). The density of freely foraging *T. similis* was positively correlated with the density of hosts (Table 1, Fig. 1). There was also a significant effect of sampling date on the density of *T. similis* (Table 1) suggesting that the overall density of parasitoids changed throughout the experiment. Finally, there was a nearly significant (P=0.053) week by host density interaction, suggesting that the strength of aggregation varied throughout the season. Separate analysis of individual weeks found two weeks when there was not a significant relationship between larval density and fly density (Fig. 1). These two sampling dates had low overall fly densities, which appear to be related to cool and cloudy weather (J. Umbanhowar, personal observation) and don't appear to be part of a seasonal trend. Regression parameters for the remaining dates are quite similar (Fig. 1).

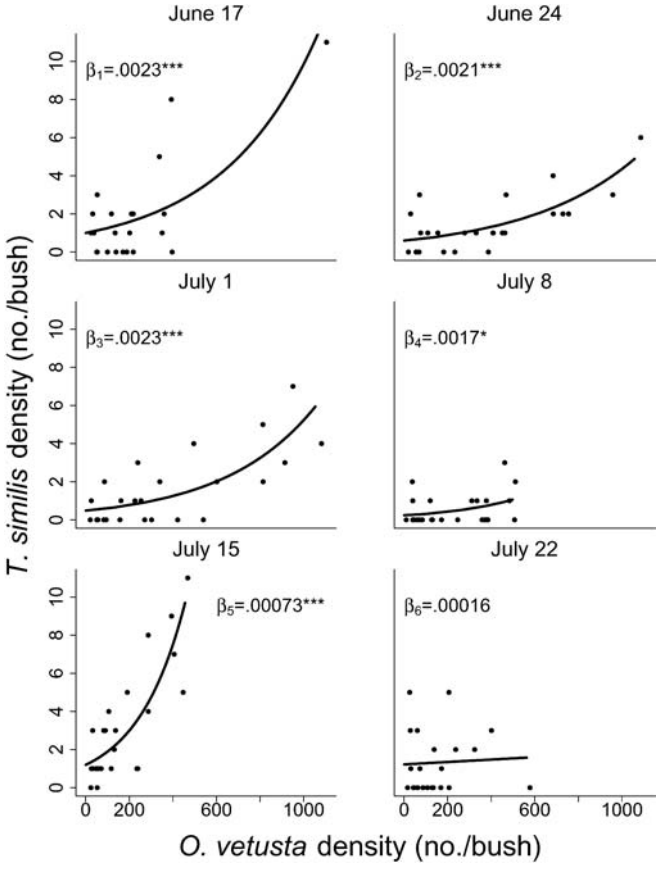

Fig. 1 Foraging *Tachinomyia similis* (fly) population response to variation in *Orgyia vetusta* (host) density. *O. vetusta* density is taken from counts of larvae either on that day or preceeding day. Densities of *T. similis* are combined counts for date shown. *Fitted lines* show the best fit for Poisson regression with log link. β_i values shown are the coefficient on the larval density for week *i*. Significance was tested by analysis of deviance with the ratio of deviances between the model with larval density and the model without, being χ^2 with 1 *df*; *** P<0.001; * P<0.1

Functional response

Higher larval densities resulted in lower attack rates (Kruskal-Wallis test, Scheirer-Ray-Hare extension: P<0.001), suggesting a decelerating functional response (Fig. 2). While there appeared to be a slight trend towards a lower risk per parasitoid (Fig. 2), statistical tests showed no significance of this relationship (Kruskal-Wallis test, Scheirer-Ray-Hare extension: P=0.73), leading us to conclude that there is no interference among parasitoids, at least at the densities observed in the field. Similarly, there was no interaction between larval density and parasitoid density on parasitism rate. An example of a mechanism that would create such an interaction is if interference were lessened at high larval densities because the time spent searching, and, consequently, the possibility of interacting with other searching parasitoids, was reduced as more time was spent handling prey at high larval densities.

Density-dependent parasitism

Parasitism levels increased throughout the season (Fig. 3). Models 2 and 4, which had almost the same QAICc value (QAICc = 243.0 and 242.5 respectively) were much better

Table 1 Analysis of deviance table for aggregation experiment. Terms are added sequentially and P value is (χ^2 statistic (difference of deviances) with *dDf* of term added

Term	Deviance	*df*	Residual deviance	Residual *df*	*P*
Null			348.10	141	
Larval density	67.89	1	280.21	140	<0.0001
Week	85.27	5	194.94	135	<0.0001
Week × larval density	10.94	5	184.00	135	0.053

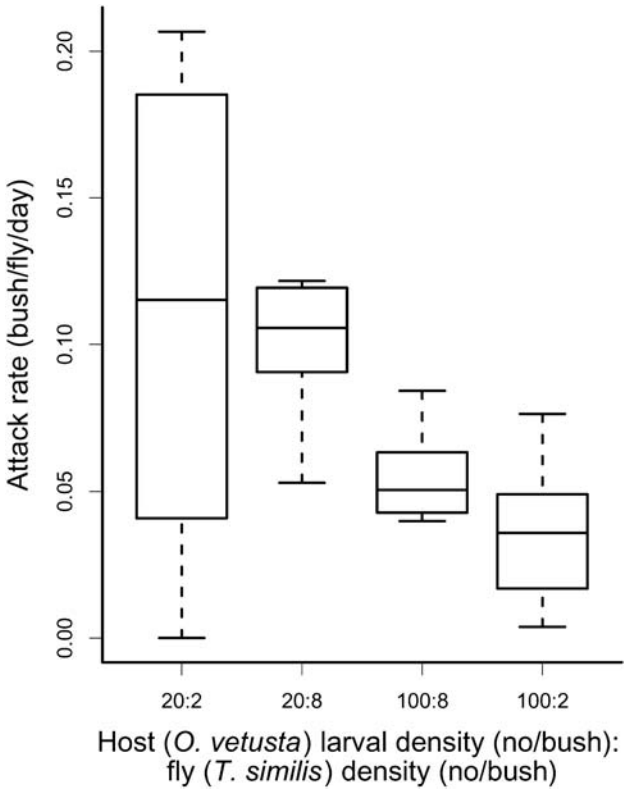

Fig. 2 Attack rates by *T. similis* in relation to experimentally manipulated density of *O. vetusta* and *T. similis*. *Center line* of box and whisker plot is median parasitism rate. The top and bottom of the box are the 75th and 25th percentiles respectively. Whiskers extend to 1.5 times the most extreme point. Statistical significance: host treatment Kruskal-Wallis test, Scheirer-Ray-Hare extension: χ^2=10.75, *df*=1, *P*<0.001; fly density Kruskal-Wallis test, Scheirer-Ray-Hare extension: χ^2=0.115, *df*=1, *P*=0.73

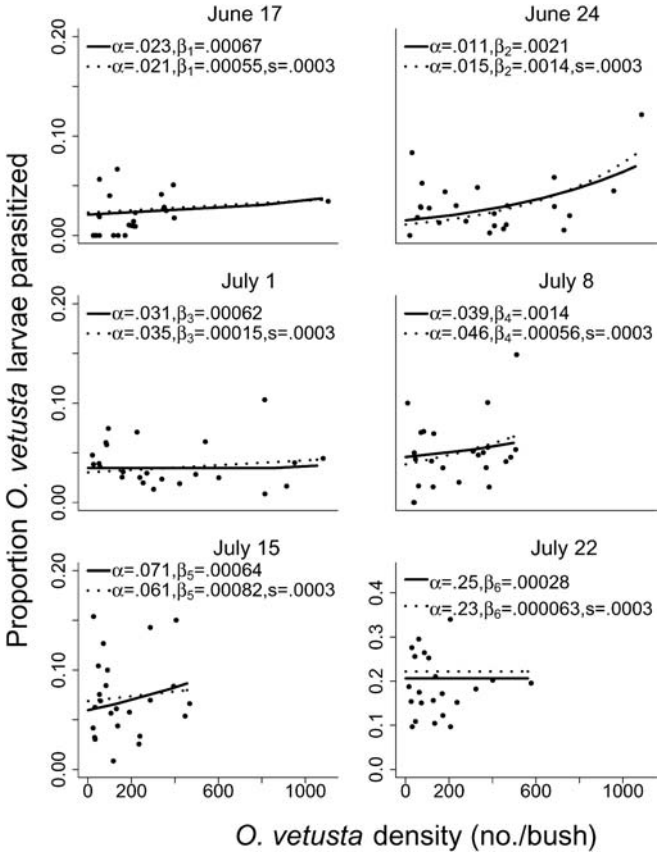

Fig. 3 Observed parasitism rates by *T. similis* (fly) throughout the season in relation to densities of larval *O. vetusta* (host). *Fitted lines* are from model 2 (*dashed*) which includes an effect of parasitoid aggregation and model 4 (*solid*) which includes an effect of both parasitoid aggregation and saturating functional response. Parameter values are for the respective models, with α being the base parasitism rate, β the increase in fly density expected with increases in host density, and *s* the strength of saturation in the functional response. Note the change in y-axis scale for 22 July

models than either model 1 or 3 (QAICc = 249.2 and 251.1 respectively). The similarity in the QAICc values of models 2 and 4 suggests that the addition of a new parameter in model 4 improves the fit enough to just overcome the penalty of adding a new parameter. Both of these models included an effect of host density suggesting that the observed aggregation of *T. similis* had an impact on parasitism. Model 4 included a saturating functional response, which, if strong, could lead to a negative relationship between host density and parasitism over a certain range of density. However, in this case, the aggregative effect appears to be strong enough to make the observed pattern monotonic and positively density dependent. Indeed, comparison of the two fits (Fig. 3) show that the difference between these two models over the range of host densities in the experiment is quite small in comparison to the variation in the parasitism data and no negative relationship between host density and parasitism. This fact is borne out by the large value of the overdispersion parameter (*m*=5.6). Burnham and Anderson (1998) recommend that if the overdispersion parameter of the model is greater than six, that the model is inadequate.

Discussion

Aggregation

We found more foraging parasitoids on bushes containing a higher density of tussock moth hosts. This result, while predicted by theoretical work, is rarely demonstrated in the field (Godfray 1994). Unfortunately, our data cannot be used to distinguish between different behavioral mechanisms of parasitoid aggregation. In fact, the model that best fits our data is biologically unrealistic, because it predicts ever increasing parasitoid densities with increasing host densities. A more realistic model would take into account the relationships among different host patches and would predict saturating parasitoid numbers at high host densities due to the finite population size of the parasitoid. However, given that the densities of tussock moths on bushes were quite low in comparison to probable total densities of flies, our model is likely to be valid over the range of host density we observed.

Parasitoid aggregation is likely driven by the flies' behavior, and not by a reproductive response, i.e. the emergence of new adults in areas of high density as a result of high reproductive success. A reproductive response to varying densities is ruled out because *T. similis* did not reproduce in the period of the experiment—flies emerge from the pupae of *O. vetusta* and then pupariate. Our interpretation is consistent with previous field studies that have shown that density-dependent patch leaving and arrival behaviors can result in aggregation (Waage 1983; Casas 1989; Connor and Cargain 1994). The cause of these density-dependent behaviors will probably be related to the state of the searching parasitoid, such as egg load, age, and the amount of energy stores (Godfray 1994). More detailed information on *T. similis* behavior might provide insight into the correct spatial scale of aggregation, which for our study we can only assume to occur at the spatial scale of the lupine bush. This scale is probably biologically relevant because lupine bushes are discrete units on which egg masses are laid. The movement of *T. similis* larvae within bushes is probably much more common than movement between bushes, thus the heterogeneity at the bush scale is probably much more constant than that at a smaller scale, which probably changes rapidly through out the season.

Decelerating functional response and interference

Like aggregation, parasitoid interference and decelerating functional responses have long been viewed as important influences on host-parasitoid dynamics. However, because these processes are often studied in the laboratory, their strength and importance in the field is often unclear (though see Waage 1983; Tillman 1996; Wang and Ferro 1998). Laboratory studies often use inflated host and parasitoid densities; in contrast, our field experiments were conducted using host densities commonly observed in the field. The relatively low density of parasitoids we observed in the field may explain our inability to detect foraging interference, in contrast to that which is often found in laboratory experiments (Hassell 1978).

It should be noted that our experimental design was factorial and therefore not usable to fit specific functional responses, i.e. we could not detect the differences between type 2 and type 3 functional responses. However, the important part of the design is that it allows us to examine the slope of the per capita parasitism rates at high densities. Hence, we can safely state that the functional response is decelerating at realistic densities, as is the case in both type 2 and type 3, but not type 1, functional responses [though note that many authors (e.g. Hassell 1978) use type 1 functional responses with a threshold in them that are, strictly speaking, decelerating].

The fact that we detected a strong decelerating functional response is interesting, given that parasitoids are typically not thought to have long handling times, which can cause decelerating functional responses. In the case of *T. similis*, females can lay an egg in approximately 10 seconds (J. Umbanhowar, personal observation), which hardly seems long enough to explain the difference in parasitism rates between high and low host density treatments. Similarly, egg limitation also seems unlikely to explain the pattern we observed. Egg loads of *T. similis* typically range between 30 and 50 (J. Umbanhowar, personal observation), while the average number of hosts parasitized per parasitoid in our experiment was approximately 8. One possibility is that there is a limitation on how quickly parasitoids can prepare eggs for laying (Rosenheim et al. 2000). Another possibility is that handling time may include time spent investigating the suitability of hosts for parasitism.

Aggregation of parasitism

Our statistical method of determining the effect of host density on parasitism rates differs from previously used methods. Most early studies (see Stiling 1987; Walde and Murdoch 1988) used a simple regression, with a transformation to give frequency data the correct distributional form. The technique of Pacala and Hassell (1991) is similar to ours, allowing for non-linear functional forms in the relationship between host density and parasitism. It differs from our method in that it assumes a specific functional form of the overdispersion, which enabled them to relate the data to a model of dynamics (Hassell et al. 1991). Our use of a simple overdispersion parameter, however, has the advantage of being more robust in model fitting than are parameters that specify a specific functional form (McCullagh and Nelder 1989; Burnham and Anderson 1998).

Our analysis necessarily used specific functional forms for both the functional response and the aggregative response of the parasitoid. The functional responses we used were the commonly used and simple type 1 and type 2 responses, but our technique would be adaptable to other types of functional responses. Similarly, different models of the aggregative response of parasitoids could be incorporated into the technique. Indeed, the statistical method demonstrated here could be easily adapted to other situations, where the proportion parasitized and host density are known, by maximizing Eq. 5 where the expected percent parasitism, pj, is described by the general form $1-\exp[-F(\mathrm{H,P})A(\mathrm{H,P})t]$ where $F(\mathrm{H,P})$ is the functional response of the predator in units of (parasitoid density × time)$^{-1}$ and $A(\mathrm{H,P})$ is the aggregative response of the predator in units of parasitoid density and t is the length of the experiment. Additionally, we, or others, could use estimates of parasitoid density explicitly instead of estimating $A(\mathrm{H,P})$ in the fitting procedure. We chose not to do this so that we could explicitly test whether there was a positive impact of host density on parasitism.

Previous studies have classified the resulting correlation between host density and parasitism into three categories: positively density dependent, density independent, and inversely density dependent (positive, no, and negative correlation) (Stiling 1987; Walde and

Murdoch 1988). Within these three categories, our results would be classified as density dependent. However, it is important to note that one of the functions we examined (Eq. 4) allows for patterns that would not fall into these three categories, i.e., the correlation could be negative at low host densities due to deceleration and positive at high densities due to aggregation. Most important in this experiment is that there is much greater variability among bushes that is independent of host density than can be explained as a function of density. This result is consistent with previous studies of heterogeneity in parasitism (Stiling 1987; Walde and Murdoch 1988; Pacala and Hassell 1991). Our understanding of *T. similis* behavior is insufficient to explain this additional variation.

Implications for dynamics

From the results of the parasitism experiment, it appears that, in this year, variation in host density over small spatial scales had relatively little effect on the amount of parasitism from *T. similis*, especially compared to variability unrelated to host density. Clearly, in terms of stability in the dynamics, the density-independent variation will be more important. However, the density-dependent variation may still have an impact on long term population dynamics. Our results from both the aggregation and functional response experiments suggest that host density has strong effects on key foraging behaviors that affect parasitism rates. Comparing two years with the same distribution of relative host densities, but different absolute densities, can show different patterns of parasitism: at lower host densities, where deceleration is generally not thought to be as important (Hassell 1978), the trend towards inverse density dependence will be weaker. Similarly, the aggregative response could change, especially if patterns of spatial variability change with changes in density (Jones et al. 1993). One of the few studies that examined the temporal pattern in the heterogeneity of parasitism showed that there was much variation between years (Jones et al. 1993). Ives et al. (1999) present an alternative, suggesting that the presence of large amounts of variability reduce the importance of aggregating and functional responses that occur over small spatial scales. We would need parasitism data for several years or a functional response experiment over a wide variety of densities to fully predict the long term impact of density-dependent parasitism on the stability of the system.

The method of Pacala and Hassell (1991) for determining the amount of variability in parasitism risk and partitioning the variability between density-dependent and density-independent types does not necessarily assume a monotonic relationship between host density and risk. However, all the specific models they fit did. If fit with a monotonic function, the data may show higher rates of density-independent variation, which might actually be the result of the interaction of two different mechanisms. This study suggests that more complex relationships between host density and parasitism may be more appropriate. Ives (1992) considered such a model which included both aggregation and a decelerating functional response. His results suggest that the presence of either mechanism alone led to stabilizing dynamics, while the presence of both in moderate amounts could lead to unstable dynamics. This is probably because each mechanism reduces the amount of variability in parasitism risk caused by the other. Variation in parasitism independent of density generally leads to stability of the interaction (Chesson and Murdoch 1986; Hassell et al. 1991). Unlike the model fitting method of Pacala and Hassell (1991), our method does not produce a parameter that can be used as a quantitative estimate of how stable the interaction is. While it may appear to be a weakness in our method, we chose it mainly because our method of dealing with extrabinomial variation is statistically robust (Burnham and Anderson 1998) and requires no additional, frequently untestable, assumptions. Although our method does not quantitatively predict the impact of either density-dependent or density-independent variation in dynamics, proper interpretation of the method of Pacala and Hassell (1991) requires that the populations be at equilibrium. This assumption may not hold for many populations and, in particular, does not appear to apply for the interaction between *T. similis* and *O. vetusta* at BMR (Maron et al. 2001). Additionally, Gross and Ives (1999) have shown how the measured density-independent variation in parasitism may actually be an overestimate in the variation in risk of parasitism.

Foraging behaviors such as those leading to spatial aggregation and decelerating functional responses play important roles in determining the presence and type of spatial patterns of abundance (Kareiva and Odell 1987; Turchin 1987; McCann et al. 2000). In this system, the persistence of spatial patterning is hypothesized to be enabled by the presence of interference or a decelerating functional response (Maron and Harrison 1997). The assumption of decelerating functional response is confirmed by our results. Large amounts of aggregation at a large spatial scale can lower the likelihood of spatial pattern emerging (McCann et al. 2000). However, as noted above, we cannot comment on whether the aggregation we observed over the small (individual lupine bush) scale would result at the larger (outbreak) scale. Previous experiments suggest that, at least for parasitism, there is no significant difference in parasitism levels inside the outbreak as compared to areas near the outbreak with low densities of *O. vetusta* (Brodman et al. 1997; Maron and Harrison 1997).

While many mathematical models of host-parasitoid dynamics have focused on the factors leading to stable dynamics, and the assumptions that allow for stability, the recent collapse of the outbreak at this site (Maron et al. 2001) and the presence of other outbreaks along the coast (Harrison 1997) suggest that the dynamics of *O. vetusta* are not stable. At BMR, overexploitation by *T. similis* appears, at least partly, to explain the collapse (Maron et al. 2001). The experiments here are at least suggestive that, despite the presence of strong density-dependent

behaviors, the parasitism by *T. similis* will not lead to stable dynamics due to the counteracting effects of these behaviors.

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