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THE DENSITY DEPENDENCE OF PARASITISM BY TEPHRITID FRUIT FLIES¹

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Abstract. The density dependence of parasitism in host–parasitoid systems has received considerable theoretical and experimental treatment recently, but usually at the intergenerational or interseasonal level. Here we study the density dependence of parasitism within a season, using tephritid fruit flies as a model system for parasites. Our work is motivated by conflicting observations that individual *Rhagoletis pomonella* flies foraged with direct density dependence (Roitberg et al. 1982), but that a population of flies of the sibling species *Rhagoletis cornivora* showed either no relationship between parasitism and host density (density vagueness) or inverse density dependence (Borowicz and Juliano 1986). Thus, we want to understand how a direct response to density at the individual level can be translated to a lack of response or to inverse density dependence at the population level. To do this, we employ behavior-rich simulations as well as individual-based state variable models. Our results resolve the apparent conflict: individual behaviors may not translate to the same population level patterns due to (1) a lack of defined patch boundaries (from the parasite's perspective), (2) repeated visits by parasites to patches, (3) uneven rates of host acceptance, and (4) egg limitation. Finally, we show the importance of relating the experimental region to the rest of the world of the parasite and propose that future studies of host–parasitoid systems should monitor both host and parasite populations.

Key words: density dependence; dynamic programming; fruit flies; foraging; simulation model; parasitism; population dynamics.

INTRODUCTION: DIRECT AND INVERSE DENSITY DEPENDENCE IN PARASITISM

The relationship between density of hosts and fraction of hosts attacked by parasites is key both to the development of appropriate pest control measures and to our basic understanding of the biology of host–parasite systems. The relationship can be density independent, in which case the fraction of hosts attacked is independent of host density. Alternatively, when the fraction of hosts attacked increases with increasing host density, the relationship is referred to as direct density dependence. Finally, when the fraction of hosts attacked decreases with increasing host density, then the relationship is called inverse density dependence. These within-generation patterns of parasitism have received considerable attention recently (e.g., Hassell and Waage 1984, Hassell et al. 1985, Lessells 1985, Hassell and

May 1986, May and Hassell 1988, Walde and Murdoch 1988). Most investigations focus on two major questions. (1) What generates the particular form of the density dependence? (2) What are the population consequences of density-dependent parasitism, particularly extinction, endemism, and cycles? In this paper, we will touch on both of these questions, but mainly concentrate on the form and mechanisms underlying density dependence. To do this, we begin with a broad review and discussion of the issues involved.

Most of the previous theoretical work on density dependence of parasitism has been based on intergenerational or interseasonal models. These models typically take the following form:

$$\begin{aligned} H_{t+1} &= H_t R[f(H_t, P_t)] \\ P_{t+1} &= H_t [1 - f(H_t, P_t)], \end{aligned} \quad (1.1)$$

where H_t and P_t are the respective host and parasite populations in generation t , R is the host fecundity, and

$$f(H_t, P_t) = \text{fraction of hosts escaping parasitism as a function of } H_t \text{ and } P_t. \quad (1.2)$$

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If we assume that

$$f(H, P) = \exp[-aP(n)], \quad (1.3)$$

where a is a parameter relating mean attack rate and parasitoid numbers, then the resulting model is the classical Nicholson-Bailey (e.g., Hassell 1978) model. This model is often called a "random encounters" model, since it is derived from the notion of random search (Mangel 1985).

An alternative is to assume that $f(h, p)$ is given by the zero term of the negative binomial distribution. The simplest form (Godfray and Hassell 1987) is

$$f(h, p) = [k/(k + ap)]^k, \quad (1.4)$$

where a is a parameter again relating the mean attack rate to parasitoid numbers and k is the "overdispersion parameter" of the negative binomial distribution. This model is often referred to as "nonrandom," but in fact it is still generated by a probability distribution with associated stochasticity. That is, use of the negative binomial term still assumes some kind of random allocation of individuals to hosts. In actual fact, individuals may be allocated to hosts in nonrandom ways.

Here we want to concentrate on questions of intragenerational or intraseasonal density dependence. In particular, we want to look at the ecological determinants of $f(h, p)$ within a single generation. Our ultimate objective is to replace phenomenological models such as Eqs. 1.3 or 1.4 by models generated from assumptions about the behavioral ecology and the individual decisions made by parasitoids. That is, throughout this paper we will employ a broad definition of density-dependent parasitism that describes the relationship between host density and percent parasitism and not necessarily the population dynamics consequences thereof. In this regard, our objective is similar to that of Bernstein et al. (1988), who modeled the behavior of predators searching in a variety of patches for prey. In the last section, we will compare our conclusions with theirs.

In this paper, we use tephritid flies as models for parasites (sensu Price 1977). These flies have life cycles that mimic many parasitoids. The adults are free living while the eggs and larvae spend their time in host fruit. (Since the larvae do not kill the host fruit, these flies are not true parasitoids.) Thus, we view tephritid flies as fruit parasites. One of the experimental advantages of using tephritids is that a considerable technology exists for observing, manipulating, and trapping such insects, and we are thus, in principle at least, able to monitor both host and parasite populations.

Our work is motivated by the following conflicting observations. As part of a general study of the foraging behavior of the apple maggot fly *Rhagoletis pomonella* Walsh, Roitberg et al. (1982) observed a positive relationship between fruit density and egg-laying rates by individual flies (Fig. 10 of their paper). Borowicz and Juliano (1986) recently conducted a study of the

density dependence of parasitism by a sibling fruit fly, *Rhagoletis cornivora*. This fly attacks fruit of the shrub-by dogwood (*Cornus amomum*) when the fruit is mature and healthy, and causes the fruit to turn soft and occasionally fall off the plant prematurely. Borowicz and Juliano (1986) found an "inverse-density dependence" or "density-vague dependence." In particular, they experimentally reduced the number of fruit on the dogwood bushes and found that when fruit was removed, a larger fraction of the remaining fruit was attacked by the fly than in cases in which there was no fruit removal, i.e., "low fruit density is associated with increased parasitism" (Borowicz and Juliano, 1986: 641). Thus, there appears to be conflict in that patterns observed at the individual level do not appear to be translated to the same patterns at the population level. In making a comparison such as this, we implicitly assume that many tephritid species have the same kinds of behavioral adaptations (see, e.g., Prokopy and Roitberg 1984) and will thus respond in a similar fashion to varying environmental conditions. Messina (1989) also uses this assumption in another interspecific comparison of two *Rhagoletis* flies.

The purpose of this paper is not to criticize the results or conclusions of Borowicz and Juliano (1986). In fact, our investigation lends support to their results. Rather, we wish to develop methods that can be used to understand the structure of $f(h, p)$ in a nonphenomenological way and the ecological conditions that will lead to a particular kind of density dependence. For example, we will show that both inverse and direct density dependence can be predicted to occur, depending upon host quality, number, and distribution (as perceived by the fly), and the individual response of the parasites to those ecological conditions. Our methods allow the identification of situations in which inverse density dependence will occur.

We apply a mixture of modeling techniques, including simulation of individual behavior using "rule-of-thumb" observation and dynamic, behavioral modeling (Mangel and Clark 1988). The simulation (Tourigny 1985) is based on extensive study of *Rhagoletis pomonella*, in natural and laboratory situations (see, e.g., Roitberg and Prokopy 1981, 1982, 1983, 1984, Roitberg et al. 1982, 1984, Prokopy and Roitberg 1984, Roitberg 1985). It provides a detailed mechanistic description of the behavior of the fruit fly, incorporating understanding of behavioral mechanisms obtained by field and laboratory studies. We call this a *behavior-rich* simulation, and we use it to vary the aforementioned host parameters and then observe the response of the parasite.

The dynamic modeling approach that we employ uses state variables (e.g., egg complement or information) to characterize the current state of the foraging fly (Mangel and Clark 1986, 1988, Mangel 1987a, b). An important feature of the models is the assumption that the fly's behavior has evolved to maximize lifetime

fitness through oviposition decisions. This allows us to develop theory to predict optimal oviposition decisions as a function of ecological conditions and physiological state (e.g., host density and quality, egg availability, etc.).

The behavior-rich simulations and the dynamic modeling are tied together by incorporating the behavioral rules derived from the dynamic modeling approach into a further set of simulations where populations of flies forage for hosts under conditions faced by flies in the behavior-rich simulations. We can thus compare the detailed, mechanistic behaviors with the behaviors based on dynamic optimization.

In the next section we describe the behavior-rich simulation for *Rhagoletis pomonella* and its application to the experimental situation studied by Borowicz and Juliano. We choose this particular experiment, since for a simulation one must pick a detailed scenario, but believe that our insights are general. In the third section, we describe models for the behavior of individual parasites and how these models can be used to make predictions about density dependence. In the last section, we summarize our results and further discuss the general nature of density-dependent parasitism.

THE *RHAGOLETIS* BEHAVIOR-RICH SIMULATION

In this section, we employ simulation models of fruit fly behavior and decisions to study density-dependent parasitism in nature. The simulation model used here was developed by Tourigny (1985) to reproduce the foraging behavior of tephritids in general with particular reference to the apple maggot, *Rhagoletis pomonella*. This model was statistically validated against Roitberg et al.'s (1982) empirical results for *R. pomonella* foraging in trees containing varying densities of fruit clusters. It has recently been used to address questions regarding the evolutionary ecology of marking pheromones (Roitberg and Mangel 1988).

Our aim in this section is to employ the simulation model to provide insights into the seemingly conflicting density relationships observed at the individual and population levels. First, we provide a brief and general description of the model and then describe modifications that were implemented to reproduce Borowicz and Juliano's (1986) field experiments faithfully. Finally, the simulation results are presented and discussed in the light of more general models of density dependence.

Description of the model

The purpose of the model is to provide an accurate description of flies traversing through host plants in search of host fruit and, upon discovery of such fruit, to provide a further description of flies' oviposition-related behaviors. The model uses queuing techniques to track the flies' foraging behaviors in fixed units of time. Three types of events are considered: (1) within-

tree foraging (the exploration of a portion of the tree space, which may or may not lead to an encounter with a fruit cluster); (2) within-patch foraging (visit to host fruits within clusters once such clusters are found); and (3) oviposition and host marking (laying an egg by a fly once a host fruit is accepted for oviposition, followed by marking with a host-marking pheromone).

Fly search

In nature, flies hop from leaf to leaf, usually moving up-limb (i.e., toward the tip), until fruit clusters are visually located (Roitberg 1985) or until the flies emigrate from the tree. Occasionally, though, flies move randomly to other parts in the tree. The search behavior can be aptly categorized as a systematic search by flies that yields random encounters with fruit clusters.

The model representation of this search behavior consists of flies exploring a tree space. Fruit clusters were randomly assigned to the available positions, the total number of positions in the tree being a function of the actual tree volume, taken from field experiments.

Flies explore portions of the tree space by "hopping" from position to position, moving along randomly selected search path directions according to movement probability frequencies derived from empirical observation (Tourigny 1985). Search bouts are terminated by either the discovery of a cluster of fruit or by the total search distance exceeding a critical value. In the first case a fly is assumed always to see and approach any cluster that lies within some maximum distance of its search path. That maximum distance is determined from Roitberg's (1985) visual, reactive distance model. The tortuosity of the search path is a function of a fly's past oviposition history: a fly that recently oviposited searches the tree positions nearest to the position where she last found a cluster and oviposited, whereas a fly that has not recently oviposited searches farther away along straight paths. The lengths of these are random functions of the number of unsuccessful bouts since last oviposition. This representation of search behavior approximates search intensification following host encounter and oviposition and extensive search when no acceptable resource has been encountered for a certain period of time (cf. Tinbergen's [1960] "area restricted search").

When a fruit cluster is encountered the fly assesses a randomly selected fruit within that cluster for oviposition. The decision to oviposit in an uninfested host is a probability function of choosiness or host acceptance rate, empirically determined by Roitberg et al.'s (1982) field experiment. If oviposition occurs, the fly is arrested within that cluster and then set to visit the same or another fruit at random.

Within-cluster search persistence

Within-patch search persistence is determined by the probability that a fly remains in a fruit cluster following the n^{th} visit to a fruit and is a decreasing function of

number of visits to and rejections of marked and unmarked fruits within that cluster (see Tourigny 1985 for further details). Thus, flies show a marked tendency to remain in a patch for the first few visits, with this tendency rapidly dropping if oviposition does not occur (cf. Waage 1979).

Within-tree search persistence

In nature, two features of *R. pomonella* behavior determine how long a fly will remain in a tree: (i) increased search effort allotment after oviposition (Roitberg et al. 1982) and (ii) decreased search effort allotment following encounters with marked fruits (Roitberg and Prokopy 1984). The model employs rules of thumb derived from these observed behaviors to determine within-tree search persistence. The visitation sequence (history of successful and unsuccessful visits to host fruits) and an emigration threshold are used to determine when a fly should give up searching a tree. The fly's propensity to emigrate from a tree is a function of the number of unsuccessful visits, an unsuccessful visit being defined as (i) a visit to an empty patch, or (ii) a visit to and rejection of an unmarked fruit on the basis of sampling or improper chemical or physical stimuli, or (iii) a visit to a marked fruit. The latter always leads to host rejection and to decreased search effort. Decreased search effort is achieved by setting a visit to a marked fruit to be worth two or more unsuccessful visits, thereby increasing the fly's tendency to emigrate. A fly's emigration propensity is reset after each oviposition at some lower value that is a function of the oviposition sequence history. When the tendency to emigrate exceeds a set threshold (as determined from the validation of simulation results for Roitberg et al.'s [1982] experiment) the fly emigrates from the tree.

Modifications of the model

For the purpose of simulating Borowicz and Juliano's (1986) experiment we assume that, as sibling species, *R. cornivora* females foraging for *Cornus amomum* fruits behave in a manner similar to *R. pomonella* flies foraging for *Crataegus* fruits, so that: (1) *R. cornivora* encounters fruit clusters at random within trees; (2) *R. cornivora* employs hypothesized, simple rules of thumb for decreasing (following encounters with marked hosts) or increasing (following encounter and oviposition in a host upon arrival at the tree) search effort within trees; (3) parasitized fruits rapidly decrease in acceptability (and even rot and fall from the host plant) and become unattractive for further oviposition by the time a mark has decayed, and (4) *R. cornivora* chooses hosts according to the same host acceptance rate function found to hold for *R. pomonella* (Roitberg et al. 1982). We also assume that (1) *R. cornivora* flies have a fixed daily egg complement of 12 eggs/d, and that (2) effectively only one fly foraged for the 42 d Borowicz and Juliano's (1986) experiment lasted. (The figure of one fly was arrived at by taking

the value of 292 pupae that they collected, multiplying it by 2 to make up for the fact that only half the area was sampled, which yields 584 pupae, divided by 42 d divided by 12 eggs/d, which yields 1.16 flies average value, rounded to 1 fly.) In actual fact, whether we simulate one fly over 42 d or six flies each visiting the patch of trees for 1 wk doesn't matter for the results presented here because we assume no behavioral interactions among flies and no mortality.

Since crop reduction treatments in Borowicz and Juliano's (1986) experiment probably influenced fruit drop (which in turn probably influenced the amount of parasitized fruits collected in fruit traps beneath shrubs), and since it is easy to track the full state of the crop in a computer simulation experiment, we considered percentage fruit parasitism in relation to the standing crop only and chose to disregard fruit drop entirely in the simulations. We therefore assumed that fruit drop is unimportant, although it might have been important in the context of Borowicz and Juliano's field experiment, with unpredictable impact on their conclusions. We chose not to simulate fruit drop, but to allow marked fruits to remain marked for the duration of the simulations. The latter option probably did not alter the fly's behavior significantly since our simulation data showed that percent re-encounter with marked hosts was low (6, 11, 19, and 26% for the control, fruit, infructescence, and fruit-infructescence reduction treatments, respectively). More importantly, most re-encounters occurred when the flies were forced to visit fruits within the same cluster. This biased re-encounter rates upwards.

Model parameters

For most parameters, we used values identified by Tourigny (1985) for *Rhagoletis pomonella* (Table 1); only parameters not in Tourigny's original model or parameters whose values we altered are described here.

Borowicz and Juliano's (1986) factorial design involved 10 shrubs, two treatments (fruit and infructescence reductions), and two levels per treatment. These were: no reduction (control, which we denote by CTL), $\approx 50\%$ reduction of the fruit density (F), $\approx 75\%$ reduction of infructescence density (I) or $\approx 85\%$ reduction of fruit and infructescence density (FI); the actual values used by Borowicz and Juliano (1986) are shown in Table 1 of their paper. In order to reproduce their experiment, the model was modified to include 10 trees, with each tree divided into four randomly assigned treatment quarters. Tree size (number of positions in the tree) was determined on the basis of actual individual shrub volume and the volume of *R. pomonella*'s reactive envelope. For computational ease Borowicz and Juliano's shrubs were divided into two size classes: small and large. The small shrubs were allotted 216 positions (6^3 positions in "tree space") and large shrubs 512 positions (8^3 positions). These tree sizes approximated fairly closely the shrubs' real volumes (V. A.

Borowicz and S. A. Juliano, *personal communication*). The treatments that we assigned were either CTL (no reduction), F (50% reduction), I (75% reduction), or FI (85% reduction).

The model was designed to simulate a forest of trees, and the fly was free to move to any other tree or back to the same tree at random once it emigrated from a given tree. The distribution of the duration of intertree flight times is unknown for both fly species and was chosen, based on our field observations, to be uniform for the interval (1, 5) min. The fly's landing position upon arrival at the tree was uniformly selected from all available positions in the tree, thereby ensuring that flies landed in any treatment at random and with equal frequency for all treatments.

In the modified version of the model, host acceptance rate Y for a tree with X clusters is given by

$$Y = \max[\exp(-1.1801 - 0.0578X), 0.02]. \quad (2.1)$$

This relationship was empirically derived by Roitberg et al. (1982) for flies foraging in trees with either 2, 4, 8, or 16 clusters of four *Crataegus* fruit. Though we have not identified the mechanism that leads to such an effect, we offer the following parsimonious explanation. First, fruits vary in their ability to support individual larvae through to pupation (Averill and Prokopy 1987). Second, flies can evaluate this quality and rank those fruit accordingly. Finally, as flies perceive an increase in the quantity of hosts within trees, the flies raise their acceptance threshold so that fewer and fewer of the lower ranked fruit are accepted for oviposition. In latter portions of this paper we use the term "choosiness" to describe this purported change of acceptance threshold.

The use of Eq. 2.1 to determine acceptance rate means that flies accepted host fruits at a rate of 2% in trees or treatments harboring ≥ 47 clusters (computed from the formula given above) and at a rate determined by the parameter values of the exponential decay relationship when $X < 47$ clusters. For example, for a tree with one cluster, $Y = 29\%$ and with 16 clusters, $Y = 16\%$. (Running simulations with higher cutoff values did not change the outcome of the model.)

The number of clusters in each treatment was provided by V. A. Borowicz and S. A. Juliano (*personal communication*) and ranged from 19 to 136 in the no-reduction treatment and from 5 to 41 in the infructescence-reduction treatment. The simulated number of fruits per cluster followed the empirical distribution as per the data provided by V. A. Borowicz and S. A. Juliano (*personal communication*) for up to 10 clusters per treatment [$n = 176$ distributed on the interval (2, 54) for the no reduction treatment and $n = 166$ distributed on the interval (1, 27) for the fruit reduction treatment]. The distributions are skewed to the left. The number of fruits per infructescence was generated numerically. The mean values compared from simu-

TABLE 1. Attributes and parameter values employed in the behavior-rich model. See Tourigny (1985) for further details.

Attribute	Value
Shrub volume:	
Small	216 positions
Large	512 positions
Host assessment time	0.25 min
Oviposition duration	1.0 min
Marking event duration	0.25 min
Within-tree movements	0, 0.46, 0.54 for vertical, horizontal, and diagonal, respectively 0.87/0.13, 0.5/0.5, 0.5/0.5 for up/down, north/south, and east/west orientation, respectively 0.7 for probability of a distant move
Probability of remaining in cluster	$y = -0.12n + 1.3$, where n is number of rejections of fruits

lations very closely approximate Borowicz and Juliano's (1986) empirical values.

Ten replications were run for each simulation effectively yielding a $10 \times 10 \times 2 \times 2$ factorial design (10 replications \times 10 shrubs \times 2 fruit treatment levels \times 2 infructescence treatment levels). Simulation results were analyzed using BMDP's ANOVA statistical package for the analysis of variance and covariance including repeated measures (BMDP 1983).

Results and discussion

The simulation results shown in Fig. 1 match Borowicz and Juliano's (1986) empirical results for percent parasitism reasonably well. These simulation results were obtained without adjustment, i.e., those parameter values that were estimated from experience with other fruit fly systems or empirically estimated from Borowicz and Juliano's data were not altered to obtain the desired "fit." The purpose of this simulation is to understand why inverse relationships between host density and percent parasitism are obtained at the population level when individuals clearly forage in a density-dependent manner. Our simulations support Borowicz and Juliano's data and conclusions, and our objective is now to demonstrate how inverse density dependence at the field level can be obtained from density-dependent foraging behavior at the individual level.

First consider the foraging statistics generated by the simulations, namely the number of hosts parasitized, the time spent foraging, the number of visits to clusters, and the number of visits to fruits within each of the four treatments considered (Fig. 2). Although the number of hosts parasitized is statistically significantly different for all treatments, these numbers provide evidence that approximately the same number of eggs were laid in all treatments. This suggests that even in

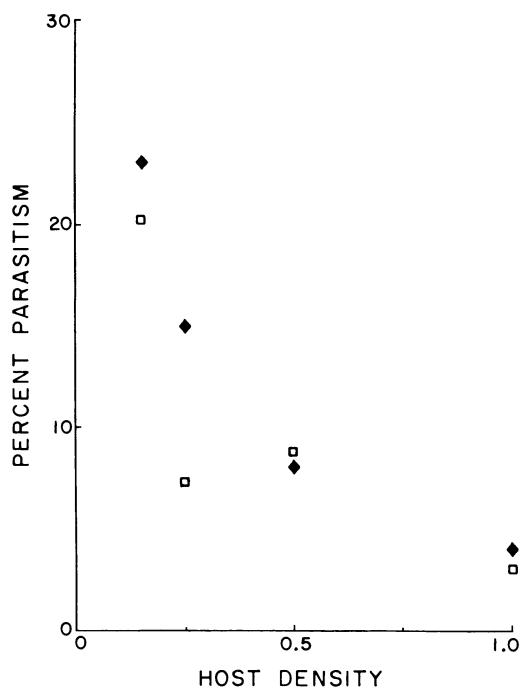


FIG. 1. Comparison of percent parasitism from Borowicz and Juliano's (1986) experiments vs. percent parasitism predicted from computer simulations for the four crop reduction treatments. Host density is measured relative to the control (CTL, host density = 1.0). The three reduction treatments give host densities of 0.5 (F, fruit reduction), 0.25 (I, infructescence reduction), and 0.15 (FI, fruit and infructescence reduction). □ empirical results, ◆ simulation.

the most severe crop reduction treatments, host densities were still high enough to provide an ample resource, i.e., flies did not experience a shortage of host fruits and eventually managed to lay most or all of their eggs. Parasitism, then, appears to be inversely related to host density when considered on a percentage basis, simply because the numerator (number of parasitized fruits) remains the same while the denominator (total number of fruits available) varies with each treatment. Similarly, the other foraging parameters suggest that flies spent more time, visited more clusters, and visited more fruits in the higher host density treatments. In other words, individual flies were displaying the kinds of positive responses to host density that were observed by Roitberg et al. (1982) to lead to increases in percent parasitism.

These results suggest to us that host density, across all treatments, is high enough to mask any effects of individual behaviors and may thus be responsible for the conflict between individual and population patterns of parasitism.

We used the next set of computer simulations to test the following hypothesis. By reducing overall host densities in all treatments to much lower levels, a direct density-dependent rate of parasitism should result. The premise is that, if egg limitation confounds percent

parasitism patterns at high host densities, then, at very low host densities, direct density dependence should be obtained, soon leveling off to a plateau, beyond which inverse density dependence is observed (see, e.g., Fig. 6 in van Alphen and Vet 1987 or Lessells 1985). Borowicz and Juliano suggest that the reason they did not observe direct density dependence in their experiment while Roitberg et al. (1982) did was perhaps because the latter used much lower host densities. That is, the idea is that the number of fruits in the experiments of Borowicz and Juliano (1986) was simply so large that the flies were unable to attack all of the fruit.

To test this hypothesis we modified the model design to vary the initial host density by varying both the number of infructescences per treatment and the number of fruits per infructescence. We then applied the four protocols (CTL, F, I, or FI) to the shrubs with modified initial host density. The initial infructescence densities were: Borowicz and Juliano's original infructescence density, and, $\frac{1}{2}$, $\frac{1}{4}$, $\frac{1}{8}$, $\frac{1}{16}$, and $\frac{1}{32}$ of the original infructescence density. The initial fruit densities were Borowicz and Juliano's original fruit density and $\frac{1}{2}$ or $\frac{1}{4}$ of the original fruit density. Each fruit load reduction was applied in combination with each infructescence reduction setup (Fig. 3, Table 2). Each initial host density in Figure 3 (and Figs. 4, 5) should be viewed as a separate experiment.

At all levels of initial host density, even with much lower fruit and infructescence densities, percent parasitism figures continued to show a pattern of inverse density dependence, despite the fact that the number of hosts parasitized shows a definite and sharp increase with host density. In order to provide further insight into the determinants of density-dependent rates of parasitism we redesigned our system to remove other factors that might limit our analysis.

One factor that might limit analysis is Borowicz and Juliano's (1986) experimental design itself. In particular, by assigning all four treatments within individual shrubs, one assumes that flies recognize treatment "boundaries." However, in reality we suspect that treatment boundaries are likely to be crossed as flies go about foraging within the shrub boundaries (Roitberg 1985). Thus, flies may emigrate prematurely from the shrub while moving from a high to a low host density treatment, or conversely, remain longer than expected by going from a low to a high host density treatment. On the other hand, Roitberg and Prokopy (1982) and Roitberg (1989) showed that flies do treat trees as individual patches. Thus, we repeated the simulation experiment but this time with treatments assigned to single shrubs (Fig. 4 and Table 3). We modeled 40 shrubs, 10 shrubs assigned to each treatment, and each shrub retaining its original specifications such as size and treatment-related fruit densities. The same pattern emerges: percent parasitism exhibits an inverse density-dependence relationship. However, the numerical response changed. In particular, the number

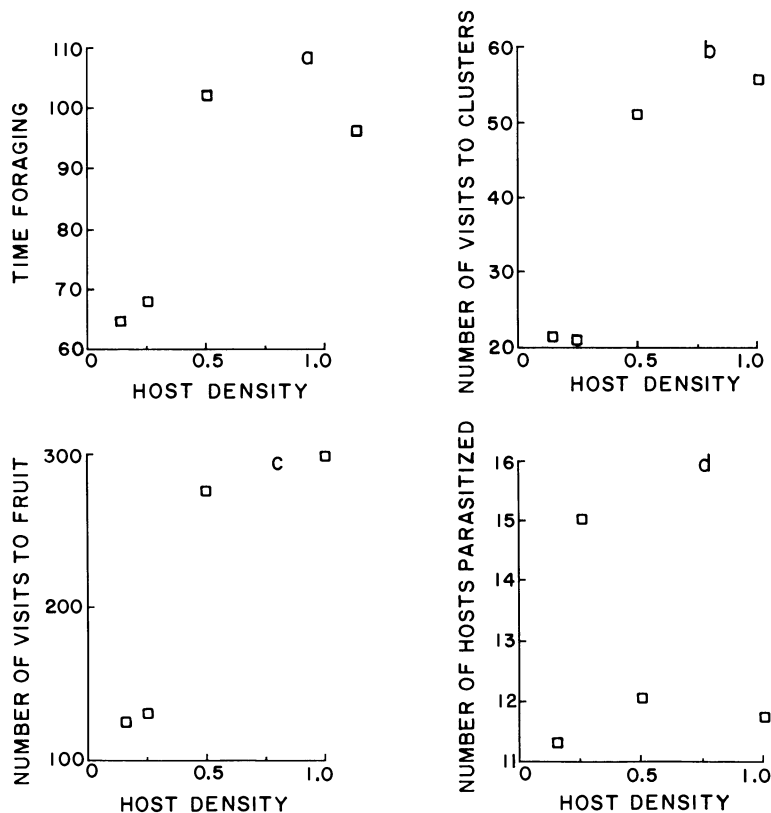


FIG. 2. Comparison of foraging parameters (a) time spent foraging, (b) number of visits to fruit clusters, (c) number of visits to fruits, and (d) number of hosts parasitized for simulated flies in the four fruit reduction treatments. Host densities are as in Fig. 1.

of hosts parasitized shifted to direct proportionality with decreasing host density.

In the previous simulations, shrubs could be visited more than once by the same or different flies. Such multiple visits to a shrub might obscure the effect of an individual's foraging on a single visit to an unexploited shrub. Indeed, examination of previous simulation results shows that not all shrubs are visited with equal frequency, with some shrubs being visited very few times or not at all, and others being visited more frequently than average. In the simulation, the destination of each visit is independently and randomly drawn from a uniform distribution. This may be one of the reasons why ANOVA analyses on the previous simulation data always show the interaction factor fruit \times infructescence reduction to be significant.

Our third set of simulations (Fig. 5, Table 4) involved single flies making a single visit to each of the 40 shrubs receiving single treatments. Though such occurrences may be rare in nature our goal is not to match any experimental results (we already achieved this), but rather to investigate those factors that generate patterns observed in the field. The interaction term in the ANOVA tables is now almost always non-significant as opposed to the previous system designs.

This suggests that we eliminated the variability introduced by uneven visitation frequencies to shrubs (and therefore treatments) or any other uncontrolled variable. However, the important result is that the model outcome remains unchanged: an inverse relationship between host density and percent parasitism at the original, unreduced crop densities. At reduced crop loads, mixed results are obtained. For instance, the fruit reduction treatment loses significance when the fruit load per infructescence is first halved and quartered at the original infructescence densities. Thereafter, with further reductions, significance is variably regained or lost.

The parasitism rate from infructescence reduction (I) is always highly significant until the initial host density is $\frac{1}{32}$ of the original host density, at which point percent parasitism is no longer significant across treatments. In addition, parasitism is not significant from fruit reduction (F) at host densities $\frac{1}{2}$ or $\frac{1}{4}$ of the initial host density. Percent parasitism figures at host densities $\frac{1}{16}$ and $\frac{1}{32}$ of the initial host density show a direct density-dependent trend. These results are consistent with the following picture: at low host densities percent parasitism is proportional to host density. As host density increases there is a "flat" region in which percent

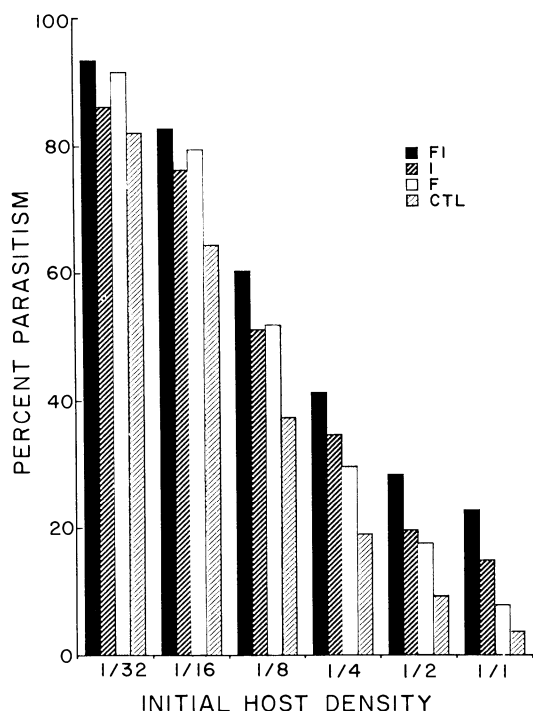


FIG. 3. Simulated percent parasitism for the four crop reduction treatments at six different initial host densities. The initial host density varies between the density used by Borowicz and Juliano (1/1) and $\frac{1}{32}$ of that density. The shading key is given at the upper right of the figure, with FI = fruit and infructescence reduction (85% host reduction), I = infructescence reduction (75% host reduction), F = fruit reduction (50% host reduction), and CTL = no reduction of initial host density. Each set of four columns, corresponding to a different initial host density, should be viewed separately. Note that at every level of initial host density, inverse density dependence occurs.

parasitism does not change markedly with host density. Finally, as host density increases even further, percent parasitism decreases with host density.

Several other features of fly behavior might suppress direct density dependence of parasitism at the population level when there are direct density-dependent rates of parasitism at the individual level: (i) choosiness (rate of host acceptance) as a function of host density, (ii) limited foraging time, and (iii) limited egg supply (Hassell 1982, Lessells 1985, Walde and Murdoch 1988).

Choosiness is a factor that is not constant from treatment to treatment. Indeed, in treatments with a lower host density, flies are correspondingly less choosy, i.e., overall, they accept hosts more frequently than when foraging in a higher host density treatment. To study the effect of choosiness on the pattern of parasitism, we raised the cutoff acceptance rate parameter from 2 to 10%. This ensures, given Borowicz and Juliano's (1986) empirical infructescence densities, that hosts will be evenly accepted at a rate of 10% across all shrubs and treatments. We modeled 40 trees and all possible

TABLE 2. Effects of further fruit (F) and infructescence (I) reduction relative to Borowicz and Juliano's host densities on the simulated parasitism rates by *Rhagoletis cornivora* on *Cornus amomum* fruit.

Infructescence reduction	Fruit reduction	Trend*	Treatments†			
			F	I	F × I	CTL
1/1	1/1	V	+	+	+	+
1/1	1/2	V	+	+	—	+
1/1	1/4	V	+	+	—	+
1/2	1/1	V	+	+	—	+
1/2	1/2	V	+	+	—	+
1/2	1/4	V	+	+	+	+
1/4	1/1	V	+	+	—	+
1/4	1/2	V	+	+	—	+
1/4	1/4	V	+	+	+	+
1/8	1/1	V	+	+	—	+
1/8	1/2	V	+	+	+	+
1/8	1/4	V	—	+	+	+
1/16	1/1	V	+	+	+	+
1/16	1/2	V	+	+	—	+
1/16	1/4	N	—	—	+	—
1/32	1/1	V	+	+	—	+
1/32	1/2	V	+	+	—	+
1/32	1/4	N	+	—	+	—

* Trend indicates density independence (N) or inverse density dependence (V) in percent parasitism. There were no cases of direct density dependence.

† Sign indicates whether a statistically significant effect of treatment on percent parasitism was (+) or was not (—) demonstrated at $P < .05$ (ANOVA).

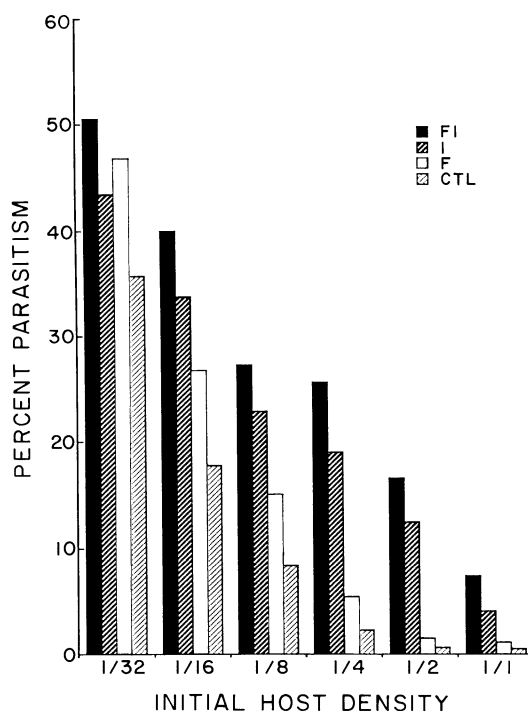


FIG. 4. Results of simulations analogous to those shown in Fig. 3, except that each tree receives a single treatment (CTL, F, I, or FI) and flies are permitted to visit a tree more than once. Each set of four columns, corresponding to a different initial host density, should be viewed separately. Note that at every level of initial host density, inverse density dependence occurs.

TABLE 3. Effects of further fruit (F) and infructescence (I) reduction on the simulated parasitism rates by *Rhagoletis cornivora* on *Cornus amomum* fruit when individual shrubs harbor a single treatment and flies are permitted to revisit shrubs.

Infructescence reduction	Fruit reduction	Trend*	Treatments†			
			F	I	F × I	CTL
1/1	1/1	V	+	+	+	+
1/1	1/2	V	+	+	+	+
1/1	1/4	V	+	+	-	+
1/2	1/1	V	+	+	-	+
1/2	1/2	V	+	+	-	+
1/2	1/4	V	+	+	-	+
1/4	1/1	V	+	+	-	+
1/4	1/2	V	+	+	-	+
1/4	1/4	V	+	+	+	+
1/8	1/1	V	+	+	-	+
1/8	1/2	V	+	+	-	+
1/8	1/4	V	+	+	+	+
1/16	1/1	V	+	+	-	+
1/16	1/2	V	+	+	-	+
1/16	1/4	V	+	+	+	+
1/32	1/1	V	+	+	-	+
1/32	1/2	V	+	+	+	+
1/32	1/4	V	+	+	-	+

* Trend indicates inverse density dependence (V) in percent parasitism. There were no cases of direct density dependence or density independence.

† Sign indicates whether a statistically significant effect of treatment on percent parasitism was (+) or was not (-) demonstrated at $P < .05$ (ANOVA).

combinations of the following factors: multiple vs. single visits to shrubs, limited vs. unlimited egg supply, and limited vs. unlimited foraging time. The choosiness factor is set constant. The possible combinations are: (a) multiple visits; (b) multiple visits and an unlimited egg supply; (c) single visits or single visits and an unlimited foraging time; (d) single visits and an unlimited egg supply; (e) single visits and an unlimited egg supply and unlimited foraging time. (Letters in this list correspond to figure letters in Fig. 6, Table 5.) The possible combinations not shown (e.g., multiple visits and unlimited time) could not be run because they create an infinite loop, i.e., they do not provide an end condition to terminate the simulation. Finally, as in the previous modification, each shrub received a single reduction treatment.

Fig. 6a shows the simulation results for multiple visits (which thus represent the effect of the higher equal acceptance rate across all treatments). It has the effect of making the fruit reduction treatment nonsignificant compared to Borowicz and Juliano's (1986) experimental setup. However, with the infructescence treatment still highly significant, the evidence for an inverse density-dependent relationship is still apparent. Providing an unlimited egg supply to flies makes both reduction treatments statistically significant and retains the same inverse relationship (Fig. 6b).

Single visits and single visits with an unlimited foraging time yielded the same results (Fig. 6c). Together

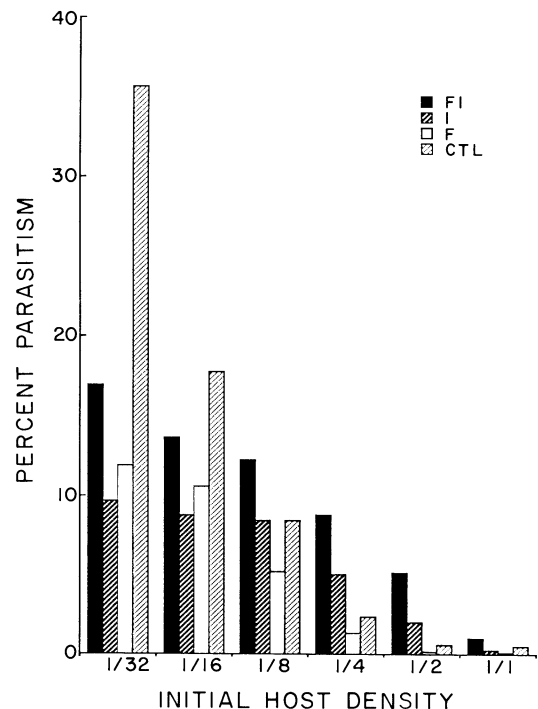


FIG. 5. Results of simulations analogous to those shown in Fig. 3 except that each tree receives a single treatment (CTL, F, I, or FI) and flies are permitted to visit a tree only once. Each set of four columns, corresponding to a different initial host density, should be viewed separately.

TABLE 4. Effects of further fruit (F) and infructescence (I) reduction on the simulated parasitism rates by *Rhagoletis cornivora* on *Cornus amomum* fruit when individual shrubs harbor a single treatment and flies are permitted only single visits to shrubs.

Infructescence reduction	Fruit reduction	Trend*	Treatments†			
			F	I	F × I	CTL
1/1	1/1	V	+	+	+	+
1/1	1/2	V	-	+	-	+
1/1	1/4	V	-	+	-	+
1/2	1/1	V	+	+	+	+
1/2	1/2	V	+	+	+	+
1/2	1/4	V	-	+	-	+
1/4	1/1	V	+	+	+	+
1/4	1/2	V	+	+	-	+
1/4	1/4	V	-	+	+	+
1/8	1/1	V	+	+	-	+
1/8	1/2	V	+	+	-	+
1/8	1/4	V	+	+	-	+
1/16	1/1	N	+	+	-	+
1/16	1/2	N	-	+	-	+
1/16	1/4	N	-	+	-	+
1/32	1/1	N	+	-	-	+
1/32	1/2	N	-	-	-	+
1/32	1/4	N	-	-	-	+

* Trend indicates density independence (N) or inverse density dependence (V) in percent parasitism. There were no cases of direct density dependence.

† Sign indicates whether a statistically significant effect of treatment on percent parasitism was (+) or was not (-) demonstrated at $P < .05$ (ANOVA).

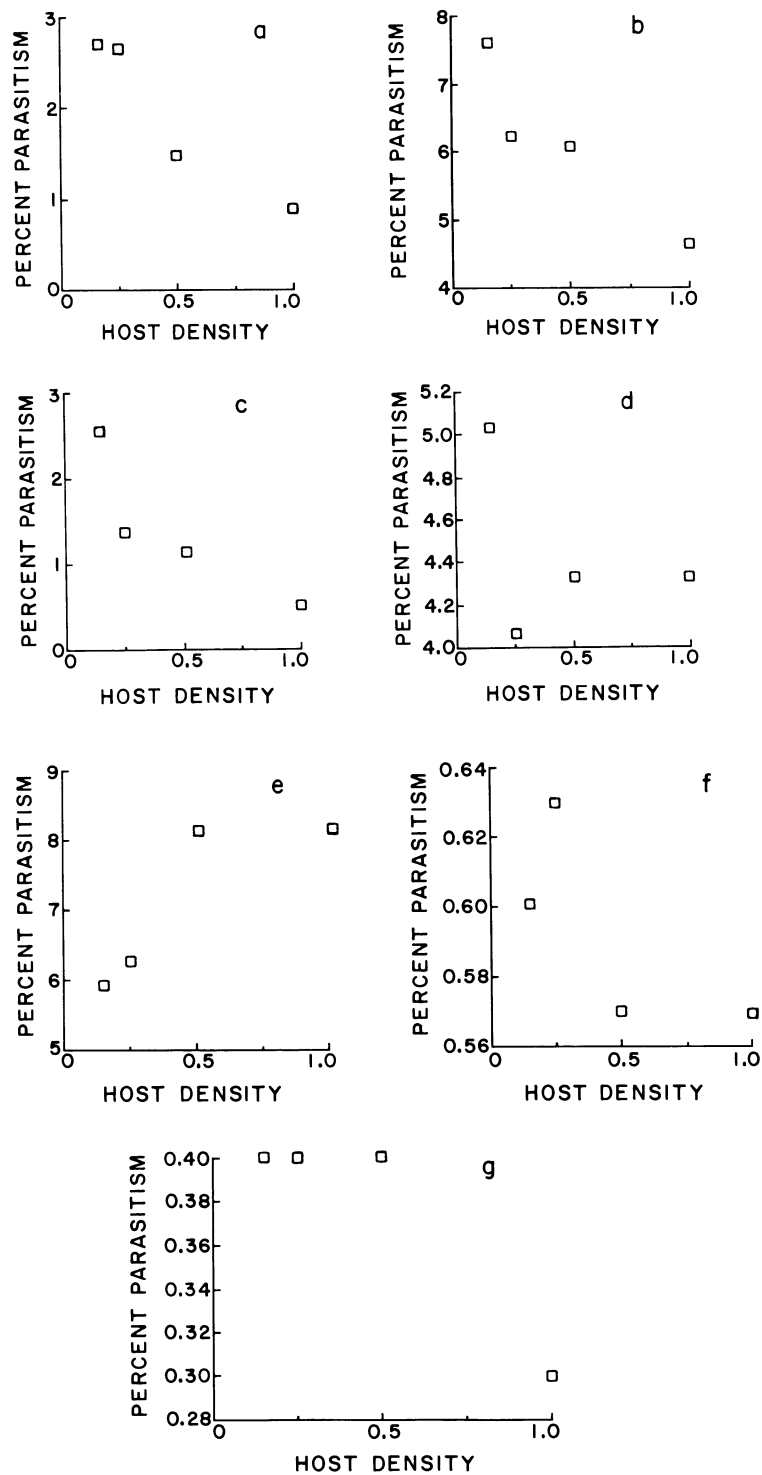


FIG. 6. Comparison of simulated percent parasitism under various system design modifications: (a) multiple visits, (b) multiple visits and unlimited egg supply, (c) single visits and unlimited foraging time, (d) single visits and unlimited egg supply, (e) single visits, unlimited egg supply, and unlimited time, (f) natural density and multiple visits, and (g) natural density and single visits. Host densities are as in Fig. 1.

with the single visits and unlimited egg supply combination, they produce, once again, the same outcome: an inverse density-dependent relationship that is highly significant statistically.

However, when both an unlimited egg supply and an unlimited foraging time are provided, the outcome is completely reversed (Fig. 6e): direct density dependence is obtained, and it is also highly significant statistically. What is more, the effect of shrubs on parasitism is no longer significant. This is evidence that the simulated flies consistently foraged in a density-dependent manner on the basis of their search and foraging behaviors only, regardless of tree size or status. We interpret the factors of unlimited eggs or times as typical of open systems in which flies may move in and out of patches of trees.

It is difficult to interpret the significance of the direct relationship between fruit density and percent parasitism that we obtained with single visits, unlimited egg supply, and unlimited foraging time. It is only by comparison with the other "unsuccessful" designs that we can conclude that a particular suite of features determines when there may or may not be correspondence between foraging performance at the individual and population levels. To summarize, our simulations suggest that the following combination of factors can mask such a correspondence: (1) the assignment of all four treatments to patch levels that may not correspond to levels at which the parasites respond (see Rosenheim et al. 1989); (2) repeated visits to the same or different shrubs by the same or different flies, with limited foraging time, in the course of the experimental season; (3) the uneven rates of host acceptance because of widely varying, although relatively high host densities; (4) limited egg supply; (5) and limited foraging time.

DYNAMIC STATE VARIABLE MODELS FOR INDIVIDUAL BEHAVIOR

Mangel and Clark (1988) recently developed a state variable model for the experiments of Borowicz and Juliano. Here we summarize their approach and results and show how it can be connected to the behavior-rich models developed in the previous section.

In the state variable model, the following assumptions are used. (1) The fly begins each day with a finite number of eggs. New eggs are matured when abdominal space permits (see Mangel 1987a); typically this is overnight so that there is no egg production during foraging. The state of the fly can be characterized by egg complement at time t , $X(t)$. This changes according to oviposition decisions. In particular, if time intervals are sufficiently small so that at most one host is encountered during a single period, then $X(t + 1)$ either equals $X(t)$ or $X(t) - 1$. (2) The environment harbors hosts of varying quality, and it is that quality that determines survivorship and fecundity of offspring deposited in each of those hosts. (3) Host qualities and densities change over time, as the flies oviposit in dif-

TABLE 5. Effects of different system designs on the simulated parasitism rates by *Rhagoletis cornivora* on *Cornus amomum* fruit.

System design	Treatment	F	P
Multiple visits	F	1.2	.28
	I	27.0	.0
	FI	1.0	.33
	Shrub	2.4	.01
Multiple visits, unlimited eggs	F	4.8	.03
	I	5.8	.02
	FI	0.0	.96
	Shrub	4.6	.00
Single visit, unlimited time	F	37.3	.00
	I	60.5	.00
	FI	3.3	.08
	Shrub	6.5	.00
Single visit, unlimited eggs	F	12.5	.00
	I	8.7	.00
	FI	1.6	.21
	Shrub	5.8	.00
Single visit, unlimited time, unlimited eggs	F	13.8	.00
	I	35.2	.00
	FI	10.8	.00
	Shrub	1.5	.14
Natural density, multiple visits	F	1.1	.3
	I	0.5	.50
	FI	0.02	.88
	Shrub	22.0	.0
Natural density, single visit	F	0.2	.66
	I	1.7	.19
	FI	0.96	.33
	Shrub	2.12	.03

ferent fruit types. (4) Acceptance (fly "choosiness") of a host of given quality is determined by the premise that the flies behave in a way that maximizes accumulated lifetime fitness from ovipositions in hosts. That is, when a host is encountered, the decision to oviposit or not depends upon the balance between the immediate increment in fitness gained through oviposition and the loss of expected future fitness since an egg used now will not be available for a later oviposition. (5) Flies are able to instantaneously assess the density of the different quality hosts in the portion of the environment in which they are foraging.

For the experiments of Borowicz and Juliano, Mangel and Clark (1988) used four host types: unparasitized mature and immature fruit and previously parasitized (and thus pheromone-marked) mature and immature fruit. The theory leads to a set of decision rules [$d_i^*(x, t)$] that indicate whether a fly with egg complement x at time t should oviposit in a host of type i . These decision rules thus provide an evolutionary interpretation to the fly choosiness described in the previous section. The decision rules are simple binary rules. When a host of type i is encountered during period t when the egg complement of the fly is x , then the host is either accepted [$d_i^*(x, t) = 1$] or rejected [$d_i^*(x, t) = 0$].

To study the density dependence of parasitism, Mangel and Clark used Monte Carlo methods to simulate

the behavior of a set of parasites using the decision rules $[d_i^*(x, t)]$ in patches with hosts of various densities. In order to do such a simulation, certain conventions about the relationship between the world of the fly and the experimental region must be implicitly assumed. For example, flies may move in and out of the experimental region through dispersal, which we characterize by the parameter s and may also exit the experimental region through mortality, characterized by the parameter m . Mangel and Clark (1988) finesse the difficulty of patch exit decisions by assuming a single patch (tree) containing a population of noninteracting flies each encountering host types randomly and ovipositing according to the optimal oviposition decisions; they then study two extremes of mobility of the parasites.

First, assume that dispersal is small, i.e., that flies are forced to remain in the patch of hosts. In such a case, it does not matter if the experimental region and the world differ since the parasites are essentially confined to the experimental region. In this situation, we find inverse density dependence. That is, as the number of hosts is decreased, the percentage of parasitism increases (Mangel and Clark 1988, Fig. 4.3a). It is now easy to understand the origin of this result. The number of flies is essentially fixed, but the number of hosts is decreasing so that fewer hosts are available for the same number of parasites. The ultimate effect is an increase in the percentage of hosts parasitized. We can relate this result directly to the choosiness criteria described in the previous sections though in this case "choosiness" is more explicit and is an output, rather than an input, of the model. When host density is high and fly numbers are constant, flies encounter more and more inferior fruit and become less choosy as time goes on. A fly always will oviposit in a mature, unparasitized fruit and with increasing time will be more likely to oviposit in immature or previously parasitized fruit. The net effect of the acceptance of immature or previously parasitized fruit is inverse density dependence. (If flies did not become less choosy at low host densities, percent parasitism would level off at low densities.) We thus see a result similar to that observed in the previous section: egg limitation (a bounded state variable $X(t)$), changing host densities, and changing acceptance decisions lead to inverse density dependence at the population level.

In the second case, Mangel and Clark (1988) assumed that dispersal is large enough that flies adjust their numbers according to host densities. Thus, throughout the world and experimental region we assume that the ratio of hosts to flies is constant. This is essentially an assumption that the flies rapidly distribute themselves according to an "ideal-free" distribution. In this case (Mangel and Clark 1988, Fig. 4.3b) the density dependence of parasitism varies from direct density dependence (when the host density is low) to no dependence (i.e., a flat curve when host density is

high). At low host densities, most flies exit the patch and the remaining few have difficulty in finding hosts, hence the direct density dependence. As the host density increases, egg limitation prohibits the flies from attacking more than a fixed number of hosts and thus the density dependence levels off.

Our results suggest that patch exit represents a kind of choosiness. In the first case, we force the flies to remain in the patch, and they thus accept inferior fruit as time proceeds. In the second case, instead of accepting inferior fruit, flies exit from the patch in search of better patches.

We thus conclude that it is the interplay of egg complement, mortality, dispersal, and the structure of the experimental or observational region and the rest of the world, molded by natural selection into host acceptance rates, that will determine the density dependence of parasitism. A priori it is difficult, if not impossible, to predict the form of density dependence without tracking the behavior of the flies, as well as the hosts.

Extending the framework

Let us now try to connect the behavior-rich simulations and the individual state variable model described above. The density of clusters of fruit determine the encounter rates used in the behavior-rich models. The "trees" in the behavior-rich simulation play the role of the "world" as described above. Note that in the behavior-rich simulation we assumed that the entire world of the flies consisted of the trees in the simulation, thus suggesting that we should expect inverse density dependence. It is not difficult to conceive of a multitree extension of the model described in this section. In such an extension, we would index trees as well as host types. The results would be a more complicated set of decision rules: $(d_{ij}^*) =$ optimal oviposition decision when a host of type i is encountered on tree type j . In addition, we would need to explicitly model the patch exit decision from each tree. This is done in the behavior-rich models, but we have not done it for the individual state variable models because it is very clear that the main qualitative effects would still occur. Unlimited eggs or foraging time (equivalent to open experimental systems that have continual change with the outside world) would lead to direct density dependence in both models.

DISCUSSION AND CONCLUSIONS

Spatial patterns of parasitism have been examined in numerous different biological systems, and the conclusion from many of these studies is that it is difficult to generalize patterns of parasitism (Lessells 1985, Stiling 1988, Walde and Murdoch 1988). Walde and Murdoch (1988) showed that all three forms of density dependence of percent parasitism (direct, inverse, and vague) are likely to be found when one conducts surveys of spatial patterns of parasitism. Although differ-

ent mechanisms have been previously invoked to explain how each of these patterns might occur (Lessells 1985), we believe that our paper contains a comprehensive theory, built from individual behavior that can explain the origin of all three patterns of density dependence. Moreover, we conclude that in order to explain rather than just describe patterns, one must think about what the fly or parasite is doing as well as what happens to the host. For example, a thorough study of parasitism should sample parasite populations as well as host densities and populations. In the past this had rarely been done (e.g., Taylor 1988); this is one of the reasons that tephritids, which are easily sampled, provide good model systems.

A second result of our paper (as well as of Lessells 1985) is that intragenerational phenomena are important. The kinds of dynamic models developed here are more likely to reflect "real world" events than do models that consider only intergenerational parameters. Consideration of intragenerational effects may also lead to explanations of apparently paradoxical results. For example, Morrison (1986) showed that models of parasite foraging that consider variation in the allocation of patch search time between parasitoids can produce patterns not generated by the deterministic analogues. Our state variable approaches have shown how such variation can arise and how different levels of "choosiness" that result can lead to variation among individuals in egg-laying rates. Variation in such rates is analogous to the variable search time allocation used by Morrison.

Lessells (1985) developed a series of models that are similar to ours in that the models are dynamic, and parasites modify their behavior to maximize oviposition rates. Our approach differs from that of Lessells, however, in that the parasitoids we model are "designed" to maximize reproductive fitness (i.e., a function of offspring number and fecundity). For this reason, no hosts are a priori immune from superparasitism, but rather the probability of being attacked depends upon the life history of the parasitoid, its physiological state, and the relative and absolute number of the different host types available within and among patches. When such processes occur, variable parasite choosiness can drive the kind of spatial parasitism patterns often observed in nature.

From our behavior-rich simulations we also conclude that it is difficult to generate direct density-dependent rates of parasitism at the population level, in spite of the absence of environmental variation that would surely further obscure density-dependent patterns in "real" as opposed to "computer" worlds. The difficulty we had finding direct density dependence is discouraging news for those interested in pursuing field experiments on density dependence (e.g., Hassell 1982, Messina 1989).

Few studies have considered the effects of individual parasites altering their foraging behavior under differ-

ent environmental conditions (e.g., Comins and Hassell 1979), even though there is considerable evidence for such changes in behavior (e.g., Waage 1983). Recently, Walde and Murdoch (1988) suggested that more studies on within-generation dynamics are necessary to understand parasite-host population processes. Hassell and May (1985), however, have argued that a consideration of individual intragenerational behavior is likely to have little effect on overall population dynamics. In contrast, our study shows that a consideration of the behavior of individuals can have a profound effect on patterns of parasitism. In a study of the dynamics of host-parasitoid systems, it may be sufficient to treat the patterns of parasitism as given. Here, however, we are trying to understand the origin of such patterns.

Our results are similar in spirit to the results of Bernstein et al. (1988) who simulated predators searching for prey in a patchy environment in which prey encounter rates had to be learned. They conclude (C. Bernstein et al., *unpublished manuscript*) that the form of density dependence depends upon (i) learning rates, (ii) consumption rate, and (iii) cost of migration. We can identify the analogy between those variables and ours. First, learning is analogous to choosiness in the sense that both affect decisions about host or prey acceptance. Second, consumption is analogous to encounter rate, since both decrease the density of prey or hosts. Third, the cost of migration is analogous to the relation between the world and the experimental region since the latter determine survival costs.

Let us now explicitly consider the results of Borowicz and Juliano (1986), who concluded that the pattern of parasitism by the fruit parasite they studied tended towards either inverse density dependence or density-vague dependence. Their results were somewhat unexpected given those of Roitberg et al. (1982), who found direct density-dependent rates of oviposition in a sibling species. It turns out that these apparently conflicting results are not as contradictory as they first appear. In particular, the cause of differences between population-level and individual-level responses is a combination of fly choosiness, tendency to leave shrubs, and changing host states. Unfortunately, each of these factors and their interactions with the others would be difficult, if not impossible, to assess through a survey approach.

Our behavior-rich simulations point to the difficulty of performing static manipulation experiments or surveys in nature. Such approaches lead one to disregard key factors. Morrison (1986) correctly pointed out that the random attack model upon which most inferences about patterns of parasitism are drawn assumes that host number and quality do not change over the course of the observation period. Violations of this assumption can lead to a spurious detection of density vagueness or inverse density dependence. In the *R. cornivora*-*C. amomum* experiments, both host quantity and

quality are likely to have varied over the course of the season.

Finally, our results also reinforce the importance of habitat structure and scale to parasite foraging and density dependence. Heads and Lawton (1983) showed how the definition of patch unit can affect inferences about patterns of density dependence. Similarly, our simulations suggest that whether or not flies treat tree quadrats as discrete patches has important consequences for population-level spatial patterns of parasitism. Thus, if we are to construct generalizations about population-level phenomena, we are more likely to succeed when experimental designs incorporate habitat scale and structure from the perspective of the insect (Wellington 1977).

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