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**The Ecological Consequences of Host Density-Dependence and Parasitoid
Fecundity for Host-Parasitoid Population Dynamics**

by

Stephen D. Lane

B.A. (University of California, Santa Cruz) 1992

**A dissertation submitted in partial satisfaction of the
requirements for the degree of**

Doctor of Philosophy

in

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in the

GRADUATE DIVISION

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Committee in charge:

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Abstract

The Ecological Consequences of Host Density-Dependence and Parasitoid Fecundity for Host-Parasitoid Population Dynamics

by

Stephen D. Lane

Doctor of Philosophy in Integrative Biology

University of California, Berkeley

Professor Wayne M. Getz, Chair

Theory predicts that parasitoids with a greater fecundity will provide better control of their hosts, and will be better biological control agents. A simple host-parasitoid model, incorporating the effects of parasitoid fecundity-limitation and host density-dependence, supports this prediction. A taxonomically diverse data set obtained from the biological control record failed to support this theoretical prediction, while at the same time indicating a strong effect of host taxon on the outcome of biological control. The hypothesis that the fecundity of parasitoids is correlated positively with their ability to suppress host populations is supported by data exclusively from the host order Lepidoptera.

An Ephestia kuehniella - Venturia canescens host-parasitoid laboratory system was used to study the influence of host and parasitoid density variation on host and parasitoid life-history parameters. *E. kuehniella* intraspecific competition is of scramble type, and is driven by reduced growth leading to pupal mortality, rather than by juvenile mortality. This system exhibits a density threshold effect

such that, at sufficiently high initial host densities, total (host plus parasitoid) survivorship to adulthood decreases due to the effects of juvenile host intraspecific competition, leading to weakened host larvae which are parasitized and killed, but which are subsequently unable to support parasitoid development to adulthood. Host self-limitation models with a density threshold provided the best fits to the data, with the generalized Beverton-Holt model providing the best fit. The Ricker model, with fewer free parameters, provided a poor fit to the data.

Theory predicts that competing species cannot coexist on a single, non-replaceable resource unless the resource is partitioned in some way. A simple one-host, two-parasitoid model indicates that stable three-species coexistence is possible under a wide range of conditions, and demonstrates that the R^* rule, the generalization that the stronger competitor will draw down the resource to the point of excluding the weaker, does not apply under these circumstances. For biological control purposes, this analysis shows the potential conflict between the properties of a one-host, two-parasitoid system that provide the maximal *absolute* host suppression, and those properties that provide the maximal *additional* host suppression resulting from the addition of a second parasitoid.

Chair

Date

For K

For Fern, Gloria and Ruby

And for Jasper & Lucy, Nicholas & Nora,

and all the others along the way:

Thank you for the enlightening natural science lessons.

“Nature abhors a vacuum

But not as much as cats do.”

-- Lee Entrekin

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1. INTRODUCTION

Science is, first and foremost, a human endeavor, and it is therefore subject to all the idiosyncrasies and surprises of any such endeavor. There is an art to the way in which “successful” science is conducted (e.g. science leading to elegant and/or useful results; Getz, 1998). On a simply semantic level, scientists speak of the “state-of-the-art” tools, techniques and status of their field (e.g. Lauenroth et al., 1983; Breckling & Mueller, 1994; Grossmann, 1994; Jorgensen, 1999).

The research done for this dissertation could have, and perhaps should have, been done some time ago. It follows, very naturally in some ways, from work that was done over 50 years ago (Thompson, 1922, 1924, 1929, 1939; Lotka, 1925, 1932; Volterra, 1928; Smith, 1929; Brindley, 1930; Nicholson, 1933; Norris, 1933; Gause, 1934; Nicholson & Bailey, 1935; Ahmad, 1936; Park, 1938; Simmonds, 1943; Ulliyett, 1945; Ulliyett & van der Merwe, 1947; Sang, 1949), and certainly from work that was done over 20 years ago (Takahashi, 1953, 1956, 1963, 1968; Utida, 1953; Andrewartha & Birch, 1954; Nicholson, 1954; Birch, 1957; Sweetman, 1958; Holling, 1959; Cole, 1960; Hardin, 1960; Andrewartha, 1961; Fisher, 1962; Salt, 1965, 1966, 1975, 1976; Corbet, 1968; Griffiths & Holling, 1969; Hassell & Huffaker, 1969; Hassell & Varley, 1969; Smith, 1969; White & Huffaker, 1969a, b; Zwölfer, 1971; Rogers, 1972; Benson, 1973; Stewart & Levin, 1973; Varley et al., 1973; Beddington, 1974; Force, 1974; Koch, 1974a, b; Podoler, 1974a, b; Price, 1974; Beddington et al., 1975, 1978; Hassell, 1975, 1978, 1980; Murdoch & Oaten, 1975;

Price, 1975; Bell, 1976; Huffaker et al., 1977; May, 1978; Armstrong & McGehee, 1980; Bellows, 1981, 1982; May & Hassell, 1981; May et al., 1981; Ehler & Hall, 1982; Münster-Swendsen, 1982; Tilman, 1982; Waage & Hassell, 1982). It is not surprising, however, that this work has not been done before now, given that science is done “in the real world”, and is nothing if not a slow process. Some problems and questions seem more interesting than others; one thing and not another grabs the attention of a particular individual. There is a great deal of art in picking out a potentially rewarding avenue of research. This body of work clearly demonstrates, however, that by whatever route, going back to the basics and asking fundamental questions that may have been overlooked or not fully pursued, for whatever reasons, by using simple models and simple systems, can reward such efforts by producing important new insights in both the pure and applied arenas (Slobodkin, 1986).

There is utility in building on previous work - for comparison purposes, and to make the research easier to begin and /or to make progress in it. If fruitful work was done in one way, perhaps more fruitful work may be done in the same way. This worker offers a caution, however: some areas of research come to their natural conclusion (i.e. “we’ve done all we can in this area for the time being”), so it may be fruitless to pursue these areas. On the other hand, it is sometimes the case that going back and pressing harder can lead to new results (“a conclusion is simply the place where someone got tired of thinking”). But, as with any learning experience, the only way to know for sure where you will

wind up is to start out, and see where you go. Or, as Carl Siegel put it, "One cannot guess the real difficulties of a problem before having solved it."

The purpose of this research was to examine some basic precepts of host-parasitoid population dynamics in a combined theoretical and empirical context. The following assumptions were made: (1) Simple dynamical models of host-parasitoid dynamics have useful things to say about these dynamics in the real world, particularly in the context of biological control; (2) the utility of these models is not diminished (i.e. they do not become overly complicated) by incorporating host self-limitation (density dependence) and parasitoid egg limitation, real-world phenomena which can be shown to have a significant impact in a real-world (laboratory) system; and (3) the *Ephesttia kuehniella* - *Venturia canescens* host-parasitoid laboratory system is ideal for examining the predictions of these models and/or for parameterizing them. In addition, the modeling and laboratory work was designed with the intention of facilitating straightforward comparisons with prior theoretical and empirical work.

Chapter 2 examines the commonly-accepted hypothesis that, all else being equal, a parasitoid species with a higher fecundity will be a better biological control agent because of its ability to kill a greater number of hosts over the course of its lifetime. This issue is addressed in both theoretical and empirical contexts, making use of both a simple dynamical model and the historical record of biological control introductions to test this hypothesis. Chapter 3 presents the results of two experiments designed to determine the effects of variation in host

and parasitoid density on both host and parasitoid life-history parameters. It makes use of the *Ephestia kuehniella* – *Venturia canescens* host-parasitoid laboratory system, both to provide data for statistical analysis to determine the above effects, and to parameterize the host self-limitation model laid out in Ch. 2. Chapter 4 extends the model from Ch. 2 to a system with two parasitoid populations, and focuses analytical attention on the form of the host-parasitoid encounter rate and the ways in which this encounter rate interacts with the host population's intrinsic growth rate, host density-dependence and parasitoid aggregation to affect the dynamical stability of the model and the host population's equilibrium density. These results are then compared to those obtained previously for multiple-parasitoid systems, for the purposes of understanding the ways in which competition between parasitoid populations can lead to resource partitioning, and in order to detail the conditions under which multiple parasitoid biological control introductions provide better (or worse) control of hosts than single-species introductions. Finally, the concluding remarks note some as-yet unanswered questions that resulted from this research, and point the way toward future work which would build on that presented here, thus (hopefully) artistically furthering the scientific discipline of host-parasitoid population dynamics.

2. THE EFFECTS OF HOST TAXON AND PARASITOID FECUNDITY ON THE BIOLOGICAL CONTROL OF INSECT PESTS

INTRODUCTION

The use of parasitoids for the classical biological control of insect pests (hereafter referred to simply as biological control) has a checkered history of success. Approximately 12% of all parasitoid introductions have led to significant sustained control, but the majority of introductions has failed to provide control of the pest (Greathead & Greathead, 1992), either because introduction did not lead to establishment or because establishment did not lead to control. Reasons proposed to account for the failure of parasitoid biological control include climatic mismatch, poor administration, lack of alternate hosts, and poor performance characteristics of the parasitoid relative to the host (Bierne, 1984; Hoy, 1985; Stiling, 1993). Where success has been achieved in biological control, the outcome has frequently been attributed to a single parasitoid species (Myers et al., 1989). As a result, there has been considerable interest in identifying those attributes of parasitoid performance that are or might be correlated with success (Waage & Hassell, 1982; Van Lenteren, 1986; Stiling, 1990, 1993; Jervis et al., 1996). The development and analysis of theoretical models that describe the population dynamics of host-parasitoid interactions has played, and continues to play, a large role in this investigation (Barlow et al., 1994; Mills & Getz, 1996; Murdoch & Briggs, 1996; Hochberg & Holt, 1999).

The lifetime fecundity or reproductive potential of a parasitoid (hereafter referred to simply as fecundity) has frequently been cited in the biological control literature as an important characteristic of successful biological control agents. High fecundity is considered necessary for parasitoids to be able to reproduce more rapidly than the pest population and to respond to changes in the abundance of the pest (Sweetman, 1958; Douthett & DeBach, 1964; Huffaker et al., 1977; Beddington et al., 1978; Waage & Hassell, 1982; Waage, 1990; Ehler, 1995). Furthermore, Stiling (1990) found that fecundity has a significant influence on the rate of establishment of parasitoids in biological control programs. Because of the importance of fecundity in this context, and because there has been considerable interest in the influence of egg limitation on parasitoid foraging behavior (Iwasa et al., 1984; Heimpel et al., 1996; Rosenheim, 1996; Van Alebeek et al., 1996), and on the dynamics of host-parasitoid interactions (Getz & Mills, 1996; Shea et al., 1996), it has become important to formalize the distinction, where appropriate, between fecundity limitation and egg-load limitation.

The egg load of a parasitoid is the number of mature eggs available for laying at any given point in time. In pro-ovigenic parasitoids, which emerge as adults with a full lifetime complement of mature eggs, the egg load is simply a decreasing function of eggs laid, and there is thus no distinction between egg-load limitation and fecundity limitation. In contrast, synovigenic parasitoids continue to mature eggs throughout their lifetime, often in conjunction with

host-feeding, and may thus experience short-term egg-load limitation without incurring lifetime fecundity limitation.

Getz and Mills (1996), using a discrete-time, Thompson-Nicholson-Bailey model, and Shea et al. (1996), using a continuous-time, stage-structured Lotka-Volterra model, analyzed the effects of parasitoid egg limitation on host-parasitoid dynamics. Getz and Mills (1996) presented a mean encounter rate function that combines the saturation effect of fecundity limitation with the more traditional concept of search limitation, to produce a Type II functional response (Holling, 1959; Van Alebeek et al., 1996). In the absence of host density dependence they found that there is a trade-off between fecundity and the degree of aggregation of parasitoid attack, such that as aggregation increases ($k \rightarrow 0$ in the negative binomial model; May, 1978; Getz & Mills, 1996), parasitoid fecundity must increase if the host-parasitoid equilibrium is to remain stable, or indeed exist at all.

Similarly, Shea et al. (1996) examined the interaction of egg-load limitation and host feeding, distinguishing between pro-ovigenic and synovigenic parasitoids. For pro-ovigenic parasitoids (no host feeding), egg-load limitation had no effect on the neutrally-stable equilibrium of the Lotka-Volterra model, although greater egg-load limitation led to an increase in host equilibrium density. For synovigenic parasitoids, the effects of egg limitation were in general destabilizing, or retained neutral stability in an otherwise neutrally stable model (see Briggs et al., 1995 for congruent results).

Jervis et al. (1996) recently examined the link between destructive host-feeding parasitoids and their success in biological control. Destructive host-feeding parasitoids tend to have a lower fecundity than non-destructive host-feeders and non-host-feeders, but Jervis et al. found that destructive host-feeding parasitoids, in contrast to theoretical predictions, were in general *better* biological control agents than other types of parasitoids. Furthermore, Yamada (1988) noted that many synovigenic parasitoids that have been successful in biological control have a low daily rate of egg maturation and experience egg-load limitation. These results contrast with the theoretical predictions outlined above, and highlight the importance of comparing theoretical predictions with field data.

This chapter examines the commonly-accepted hypothesis that, all else being equal, a parasitoid species with a higher fecundity will be a better biological control agent because of its ability to kill a greater number of hosts over the course of its lifetime. This issue is addressed initially in a theoretical context, extending the analysis of Getz and Mills (1996), to examine the influence of fecundity limitation on the stability and equilibrium abundance of a self-limited host population. Subsequently, following the approach of Jervis et al. (1996), the historical record of biological control introductions is examined to determine whether it supports the hypothesis that parasitoids with a higher fecundity have a greater frequency of success in biological control.

THE MODEL

The modelling approach used here is a simple unification of the standard Thompson and Nicholson-Bailey models (Thompson, 1929; Nicholson & Bailey, 1935; Hassell, 1978; Barlow & Wratten, 1996; Getz & Mills, 1996; Mills & Getz, 1996):

$$\begin{aligned} N_{t+1} &= N_t g(N_t) f(\varepsilon_t) \\ P_{t+1} &= c N_t [1 - f(\varepsilon_t)] \end{aligned} \quad (1)$$

where N_t and P_t are the densities of hosts and female parasitoids, respectively, at time t ; $g(N_t)$ is the *per-capita* population growth rate of the host (the host density-dependence or self-limitation function); $f(\varepsilon_t)$ is the escape function (the proportion of hosts that escape parasitism each generation); and c is the mean number of adult female parasitoids that emerge from a parasitized host individual.

Self-limited (i.e. density dependent) host *per-capita* population growth is incorporated into the model in the function g . The version of this function utilized here is the standard Ricker model (with density-independent growth rate parameter $r \equiv \ln \lambda$ and carrying capacity parameter K)

$$g(N) = \exp \left[r \left(1 - \frac{N}{K} \right) \right], \quad (2)$$

although the generalized Ricker form

$$g(N) = \exp \left\{ r \left[1 - \left(\frac{N}{K} \right)^r \right] \right\},$$

or the generalized Beverton and Holt form

$$g(N) = \frac{\lambda}{1 + \left(\frac{N}{K}\right)^\gamma}$$

(both forms having shape parameter $\gamma > 1$), probably represent more realistically the actual process of self-limitation (Bellows, 1981; Getz, 1996; Ch. 3). To facilitate ease of analysis and comparison with prior efforts, eqn 1 was analyzed using the Ricker form of host self-limitation (eqn 2).

Although there is no explicit stage-structure in this model, a sequence of events can be inferred by examining how the various functions in the model (f and g) depend on the modification of the population variables, most notably host density, N (May et al., 1981; Mills & Getz, 1996). Although May *et al.* (1981) have shown that this issue can have a substantial impact on the dynamics and equilibria of the system, and in spite of the fact that the convention in the literature appears to be moving slowly towards incorporating one or the other of the two more biologically appropriate formulations outlined by May *et al.* (1981; see Godfray & Waage, 1991; Hochberg & Holt, 1995; and Kean & Barlow, 2000, for examples), the historically conventional approach is followed here, once again, for the sake of comparison with prior results.

The form of the escape function used here is taken from May (1978), who introduced an escape function based on the zero term of a negative binomial distribution with mean ϵ , and aggregation parameter $k > 0$. This latter

parameter reflects the degree to which encounter rates are influenced by aggregation of hosts or parasitoids (smaller k corresponds to greater aggregation and $k \rightarrow \infty$ corresponds to the Poisson; May, 1978), and yields

$$f(\varepsilon) = \left(1 + \frac{\varepsilon}{k}\right)^{-k}. \quad (3)$$

The argument of the escape function, ε , is the mean host-parasitoid encounter rate. Thompson (1922, 1924, 1929), who was the first to analyze host-parasitoid systems in a significant way using the difference-equation approach of eqn 1 (Mills & Getz, 1996), assumed that parasitoid fecundity would primarily limit the parasitoid population's ability to successfully attack hosts in a single patch. He proposed the form of the encounter rate

$$\varepsilon(N, P) = \frac{\beta P}{N} \quad (4)$$

where the parameter β is interpreted as the average number of eggs (or clutches in the case of gregarious parasitoids) that each parasitoid will lay in her lifetime. This assumption about the parasitoid's ability to attack hosts is most realistic when host densities are high: parasitoids will be most limited in their ability to successfully attack hosts by their total egg laying capacity, or lifetime fecundity (hereafter simply referred to as fecundity). Alternatively, when host densities are low and fecundity is not limiting, this assumption breaks down, because it assumes that the parasitoid's ability to locate and attack hosts is independent of host density.

In contrast, Nicholson (1933) and Nicholson and Bailey (1935) assumed that the encounter rate in a single patch is search-limited, i.e.

$$\varepsilon(N, P) = aP \quad (5)$$

where a has the interpretation of an “area of discovery” or “area of search”, and is a measure of the proportion of the patch a single parasitoid is able to search in her lifetime (Hassell, 1978; Getz & Mills, 1996). This parameter is referred to here as a parasitoid’s *per-capita* searching efficiency parameter, or simply the search efficiency parameter. This assumption about the factor most strongly limiting the rate of host discovery is most realistic when host densities are low – thus, parasitoids will be most limited in their ability to attack hosts by their ability to *find* hosts. Alternatively, when host densities are high and hosts are easily located, *this* assumption breaks down, because it assumes that the parasitoid’s ability to locate hosts is linear with host density, and that there is no saturating effect.

There has been a recent flurry of interest in the influence of egg and/or fecundity limitation on parasitoid foraging behavior (Heimpel & Collier, 1996; Rosenheim, 1996; Van Alebeek et al., 1996), and on the dynamics of host-parasitoid interactions (Getz & Mills, 1996; Shea et al., 1996), as well as in the issue of host-feeding (Briggs et al., 1995; Heimpel & Collier, 1996; Jervis et al., 1996; Tokumaru & Takada, 1996; Krivan, 1997; McGregor, 1997; Veno, 1997) and its consequences for parasitoid egg load, fecundity and impact on the host population. In particular, Getz and Mills (1996) have promoted the concept of

egg-limited parasitoid encounter rates in the context of discrete-time dynamical models. As a general assumption they suggest that egg limitation is no less reasonable than search limitation on parasitoid encounter rates, although it is clear that each has its own domain of strongest influence at opposite ends of the host-density spectrum. In their analysis, Getz and Mills (1996) use the generalized encounter rate function

$$\varepsilon(N, P) = \frac{a\beta P}{\beta + aN} \quad (6)$$

which can also arise under the assumption that the time it takes for parasitoids to handle the hosts they attack is long enough to significantly impact the average time it takes to find and handle hosts (i.e. handling time is nontrivial). In this context, β is the ratio of the total time available for searching to the time it takes to handle each host. The parameter β sets the maximum number of individuals that can be handled by each parasitoid, while the parameter a controls how close to this maximum the parasitoids can come at different host densities (e.g. when $N = a$, the average number of attacks by each parasitoid is $\beta/2$) (Holling, 1959; Hochberg & Holt, 1995). In situations where neither search nor handling time is a constraint, but each parasitoid is limited either by the total number of eggs it can lay or by the rate at which it can lay eggs, then β has the interpretation of a fecundity parameter: either the fecundity of a solitary parasitoid, or the number of clutches (fecundity/average clutch size) of a gregarious parasitoid (Thompson, 1924, 1929; Getz & Mills, 1996). Note that when N is small, $\varepsilon \cong \frac{\beta}{a} P$

(so that β/a is equivalent to an area of discovery parameter) and that when N is large $\varepsilon \cong \frac{\beta P}{N}$. Thus at high host densities the parasitoid encounter rate is either fecundity- or handling time-limited, depending on the biology of the parasitoid, and at low host densities, the parasitoid encounter rate is search limited. This is mathematically equivalent to a Holling Type II functional response (Holling, 1959; Getz & Mills, 1996; Mills & Getz, 1996).

While the purely fecundity-limited and search-limited encounter rates (eqns 4 and 5) are extreme formulations of the more general mean encounter rate formulation given by eqn 6, one might expect that selection will act to mitigate whichever is the more severe limitation on the fitness of individuals. Even for eqn 6, however, it may or may not be reasonable to assume the parameters a and β are constant (thereby reflecting changes in the environment with time) or are wholly independent of host or parasitoid densities (thereby acknowledging a simplistic functional description), depending on whether eqn 6 provides a reasonable “first order” description of the mechanisms governing parasitoid encounter rates. If eqn 6 is a reasonable description then, although the equation may be a poor predictor of actual encounter rates at given parasitoid and host densities, it can still be useful in generating hypotheses about real host-parasitoid systems that can then be explored using information available in the literature.

Getz and Mills (1996) considered the dynamics of eqn 1 in the absence of host self-regulation [incorporating eqns 3 and 6 with $g(N) = N\lambda$, $\lambda \equiv \exp(r)$]. They

found that, when the parasitoid is search- and fecundity-limited at opposite ends of the host-density spectrum, eqn 1 admits a non-trivial equilibrium that is stable provided that, (a) the negative binomial aggregation parameter $k < 1$ (as is true for the purely search-limited case; May, 1978); and (b), that the following “fecundity limitation” constraint is satisfied:

$$\lambda^{\frac{k+1}{k}} - \left(\frac{\beta c}{k} + 1 \right) \lambda + \frac{\beta c}{k} < 0.$$

Note that the parasitoid’s search efficiency does not contribute at all to the stability or instability of the system (although it does influence the equilibrium densities; Getz & Mills, 1996).

Figure 1 illustrates the stability analysis of eqn 1 extended to include host density-dependence (incorporating eqns 2, 3 and 6). For each panel the abscissa is r , the density-independent growth rate of the host, and the ordinate is $q \equiv N^*/K$, the ratio of the equilibrium density of the host in the presence of the parasitoid to its equilibrium density in the absence of the parasitoid. The ratio q is thus a measure of the ability of the parasitoid to suppress the host population, and is therefore a quantitative measure of the outcome of biological control (Beddington et al., 1975; Hassell, 1978). Note that variation in q is achieved by systematic variation of the search parameter a , since $q = q(a)$ if β , c , K , k and r are fixed, as they are in each of the panels. The variable q is used to scale the ordinate axis because of its utility as a measure of host suppression, and because nonlinearities in the model prevent an analytical description of $q(a)$.

The relationship between q and r is illustrated for various combinations of the negative binomial aggregation parameter k and parasitoid fecundity β (Fig. 1). Shaded areas indicate regions of parameter space for which there is a non-trivial (i.e. non-zero), locally-stable host-parasitoid equilibrium. Regions marked A and B are areas where this equilibrium exists and is locally unstable (Hassell, 1978; May et al., 1981). The dynamics in region A are characterized by strong self-regulation of the host (large r) and low parasitoid search efficiency (a), so that the parasitoid is unable to maintain itself on the host and becomes extinct. The host then experiences limit-cycle or chaotic dynamics, depending on the exact value of r . In region B, the parasitoid has a very high search efficiency (a), overexploiting the host and driving the host and itself to extinction. As the degree of aggregation in the model increases ($k \rightarrow 0$), region B is replaced by locally stable equilibria (Hassell, 1978). Regions marked C are areas where no non-trivial host-parasitoid equilibrium exists. At the upper boundary of this region (illustrated by a dashed line in Fig. 1), a is infinite and the equilibrium mean encounter rate is determined by β , such that increasing β causes region C to move to the right, to correspondingly larger values of r .

When the distribution of parasitoid attacks is sufficiently aggregated to allow suppression of the host equilibrium density to zero under the assumption of a purely search-limited mean encounter rate ($k \leq 1$, $\beta \rightarrow \infty$), the addition of a fecundity-limitation constraint ($\beta < \infty$) prevents the existence of *any* host-parasitoid equilibrium, stable or unstable, for values of r above a threshold level

(i.e. region C becomes a significant fraction of the parameter space; Fig. 1).

Furthermore, as the level of aggregation in the distribution of parasitoid attacks increases (k decreases from one to zero, moving down the panels in Fig. 1), or the fecundity of the parasitoid decreases (β becomes smaller, moving from the right to the left panels in Fig. 1), or both, the region of stable coexistence also decreases. Thus, the model suggests that a parasitoid with greater fecundity should provide stable control of a host population over a wider range of parameter space.

The predicted effect of parasitoid fecundity on host suppression is illustrated in Fig. 2. When a , c , K , k and r are fixed, as they are for each of the curves in Fig. 2, $q = q(\beta)$ is a function of β alone. The rate of change of this function is used to identify fecundity limitation at two points. For values of parasitoid fecundity below β_{\min} (which has a value close to 5 in these examples, but which varies systematically with a and k), the parasitoid is unable to maintain itself in the system and host suppression is zero ($q = 1.0$). For $\beta_{\min} < \beta < \beta_c$ (where β_c is the value of β for which q achieves 95% of its maximum depression from unity, and also varies with a and k), the parasitoid is able to maintain itself in equilibrium with the host, but fecundity limitation is strong, so that small increases in β lead to comparatively large increases in the degree of host suppression. This pattern holds until $\beta > \beta_c$ where, by definition, a maximal increase in host suppression of only 5% occurs, even if β is taken to infinity (as is possible by considering the purely search-limited encounter-rate function of Nicholson and Bailey, 1935,

eqn 5). As a result, the model predicts that host equilibrium abundance is minimized when parasitoid fecundity and search efficiency are high, and the aggregation of attack is moderate rather than strong. Thus the prediction that fecundity limitation reduces control of the host is in agreement with the simple intuitive argument that higher parasitoid fecundity leads to greater suppression of the host population.

THE DATA

The discrete-time fecundity-limitation model analyzed in this chapter applies strictly to host-parasitoid systems in which the parasitoid generations are synchronized with those of the host, and the host generations are discrete and non-overlapping (Hassell, 1978). An appropriate test of the specific hypothesis of the model, that parasitoid fecundity limitation constrains the outcome of biological control introductions, is thus strictly applicable using only the subset of available biological control data satisfying these conditions. At a more general level, however, this hypothesis can be expected to hold for most host-parasitoid systems, including those that do not conform to the model assumptions outlined above, and can thus be evaluated in the context of the complete set of biological control introductions for which appropriate data are available. The data analysis here thus distinguishes between a specific test of the model, and a general test of the hypothesis suggested by the model. As there are insufficient data on the growth rates of pest populations in the biological control record (Hochberg &

Holt, 1999), this analysis simply examines the relationship between parasitoid fecundity and the outcome of biological control.

The BIOCAT database provides a compilation of biological control introductions (Greathead & Greathead, 1992), and has been used widely to test ecological hypotheses of host-parasitoid interactions (Greathead, 1986; Waage & Mills, 1992; Hawkins, 1994; Mills, 1994a; Jervis et al., 1996). Parasitoids, for which data on fecundity (solitary), number of clutches (gregarious) and development could be found in Sweetman (1958), Price (1975), and Clausen (1978), were linked to their success as biological control agents from the BIOCAT database. Following Waage (1990), the outcome of each biological control introduction was classified qualitatively as either success (including partial, substantial, and complete control) or failure (establishment only), due to inherent inaccuracies in the different ratings used in the biological control record. As many parasitoids have been subject to repeated introductions against the same pest in different geographic regions, it was also necessary to select only the single best outcome for each parasitoid species (after Mills, 1994a).

To insure the compatibility of gregarious parasitoids with the fecundity-limitation model presented here, fecundity is defined as the number of clutches a female parasitoid can lay (i.e. the number of hosts that can be attacked), which is the average number of eggs laid in a lifetime divided by the average clutch size. Defining fecundity in this way allows the partitioning of lifetime reproductive success into the average number of clutches laid (represented by β in the discrete

fecundity-limitation model), and the average production of female progeny from each clutch (represented by the parameter c ; Getz & Mills, 1996).

To provide an opportunity for a strict test of the model, each system in the database is classified into one of the following four mutually-exclusive categories: DS: fitting the Discrete (\leq two pest generations per year) and Synchronous (a single parasitoid generation per host generation) assumptions of the model; or, as failing to meet one or both of these assumptions, CA: Continuous ($>$ two pest generations per year) and Asynchronous ($>$ one parasitoid generation per host generation); CS: Continuous but Synchronous; or DA: Discrete but Asynchronous. The data were also classified according to the taxonomic order of the host insect. It is known that biological control succeeds better against some host taxa than others (Greathead & Greathead, 1992; Mills, 1994a), and for this reason it is important to consider the fecundity-limitation hypothesis in a phylogenetic context (Felsenstein, 1985; Harvey & Pagel, 1991), thereby ensuring that the effects of fecundity are not overwhelmed by stronger effects due to differences in life-history evolution.

Sufficient data on parasitoid fecundity and average clutch size were found for 76 established parasitoid species from the BIOCAT database of biological control introductions (Table 1). The success rate (as defined above) of this group is 57%, reasonably close to the overall success rate of 49% for all biological control introductions (Waage & Mills, 1992), suggesting that it is unlikely the assembled data are biased either for or against instances of successful control (Stiling, 1993).

Outcome is analyzed in relation to parasitoid fecundity (or clutches in the case of gregarious parasitoids), whether the system is DS or not (CA, CS, or DA), and taxonomic order of the host insect, via logistic regression, analysis of deviance, and a two-way test of independence (Sokal & Rohlf, 1981; Crawley, 1993; Neter et al., 1996).

The general hypothesis of a positive relationship between fecundity and outcome is rejected when tested against the complete data set (Fig. 3), as the goodness-of-fit of a logistic regression is almost significant and the null hypothesis of a non-positive (i.e. a zero or negative) slope could not be rejected [maximum likelihood logistic regression, $\text{logit}(\text{outcome}) = 1.65 - 0.69 \log_{10}(\text{fecundity})$, $n = 76$, $\chi^2 = 3.51$, d.f. = 1, $P = 0.06$; one-tailed test for positive slope, d.f. = 74, $t = -1.80$, $P = 0.96$]. When tested against the DS-only subset of the data, however, the more specific prediction of the model is not supported because the logistic regression does not provide a good fit to the data, indicating that parasitoid fecundity does not influence the outcome of biological control in this subset of the data [single-factor analysis of deviance for $\log_{10}(\text{fecundity})$, $n = 27$, $\chi^2 = 0.85$, d.f. = 1, $P = 0.36$].

The data set is, however, quite heterogeneous, and contains a readily identifiable source of confounding variation, the taxonomic order of the host. Host taxon has a highly significant effect on the outcome of biological control in the complete data set [7 x 2 contingency table, network algorithm (SPlus 4, 1997, program 'fisher.test'), $n = 76$, $P < 0.0001$]. The presence of this variation in the

data set requires that more appropriate tests of the fecundity-limitation hypothesis (both the general and specific cases) be conducted independently for the different host taxa. As biological control introductions against Homoptera and Lepidoptera account for 76% of the complete data set (Table 1), further analysis is restricted to these two host taxa.

For the Lepidoptera there is significant variation in biological control outcome due to parasitoid fecundity (Fig. 4), and the relationship is positive, thereby supporting the general hypothesis that there should be a positive relationship between parasitoid fecundity and the success of biological control [maximum likelihood logistic regression, $\text{logit}(\text{outcome}) = -6.10 + 2.0 \log_{10}(\text{fecundity})$, $n = 27$, $\chi^2 = 4.18$, d.f. = 1, $P = 0.04$; one-tailed test for positive slope, d.f. = 25, $t = 1.77$, $P = 0.04$]. The specific prediction of the model is not supported, however, for the DS-only subset of the Lepidoptera [single-factor analysis of deviance for $\log_{10}(\text{fecundity})$, $n = 13$, $\chi^2 = 2.48$, d.f. = 1, $P = 0.12$], and the general hypothesis is not supported for the Homoptera [single-factor analysis of deviance for $\log_{10}(\text{fecundity})$, $n = 24$, $\chi^2 = 0.80$, d.f. = 1, $P = 0.37$], due to an absence of significant variation in biological control outcome in relation to parasitoid fecundity. The DS-only subset of the Homoptera was not analyzed due to inadequate sample size ($n = 2$).

DISCUSSION

Two fundamental aspects of the biology of host-parasitoid systems are that the host population must experience self limitation and the attack rate of the parasitoid must be constrained by fecundity limitation. Incorporating these two components into a simple discrete-time model shows clearly that parasitoid fecundity has a strong influence on both the stability of the system and the equilibrium abundance of the host population. In addition, the model provides support for the traditional concept of biological control practitioners that parasitoids with greater fecundity are more likely to be successful in biological control. Although there are insufficient data to support the specific hypothesis of the model for discrete synchronized host-parasitoid systems, the available evidence suggests that when the effects of host taxa are ignored, fecundity-limited parasitoids are in general more successful in biological control than those with a greater fecundity. This result is at variance with the more general hypothesis of the model, as well as that of Shea et al. (1996) for pro-ovigenic parasitoids. When differences between host taxa are taken into account, however, there is a significant positive relationship between the outcome of biological control and parasitoid fecundity for the Lepidoptera, but no significant relationship for the Homoptera.

One possible explanation for the lack of support for the fecundity-limitation hypothesis in the complete data set is that a stable equilibrium is not a necessary condition for the success of biological control. Murdoch et al. (1985) argued that

biological control systems may not exhibit local stability, and that populations can even be characterized by local extinctions. The destabilizing influence of fecundity limitation in local populations could be counterbalanced by the stabilizing influence of the movement of both hosts and parasitoids between local patches at the metapopulation level (Comins & Hassell, 1996; Murdoch & Briggs, 1996). It is also worth noting that *success*, as defined in the biological control literature, often has a very different meaning from its use in the context of theoretical models. With respect to the discrete fecundity-limitation model, *success* means that the equilibrium density of the host is greatly reduced, potentially to (very close to) zero. While this is clearly the case in some instances of successful biological control (Beddington et al., 1978), in other instances a reduction in the mean density of the host of as little as 40% may be counted as successful, especially if this degree of control significantly reduces economic losses due to the pest problem (Waage, 1990). Therefore, the success rating for a biological control program is only a qualitative measure of host suppression, and may not be sufficient to provide an accurate reflection of the true relationship between success and parasitoid fecundity.

Another factor potentially contributing to the dichotomy between theory and practice is that constraints on the evolutionary process could lead to a trade-off between parasitoid fecundity and search efficiency (Sweetman, 1958; Price, 1975; Waage, 1990), where search efficiency is determined by an array of factors, such as longevity, mobility, sensory competence, and/or energy efficiency.

Parasitoids may be forced to sacrifice fecundity in order to achieve, for example, greater longevity (Ellers, 1996), creating the potential for increases in search efficiency. Alternatively, selection might act in favor of increased search efficiency at the expense of fecundity, perhaps because of the need for parasitoids to find food and/or mates as well as hosts (Guertin et al., 1996; Sirot & Bernstein, 1996; Sirot et al., 1997).

Waage (1990) has argued, following Price (1975), that individual attributes of a parasitoid, such as fecundity, should not be expected to relate to their impact on the host population. If parasitoids evolve a fecundity to match their lifetime expectancy of host encounters and subsequent survival within the host, then the ultimate impact (irreplaceable parasitoid-induced mortality) might be expected to be equivalent for all parasitoids irrespective of fecundity or host stage attacked. While true of natural systems, this argument may not be valid for biological control systems, as exotic pests typically suffer far less juvenile mortality, possibly allowing introduced parasitoids to achieve an impact that more closely matches their fecundity. Some supporting evidence for this is provided by Mills (1994a), who found that the later the host stage killed by the parasitoid the lower the rate of success in the biological control of Lepidoptera.

It is also possible that low-fecundity parasitoids exhibit more moderate levels of attack aggregation, or that such parasitoids are associated with pests that have lower density-independent growth rates. Unfortunately, it is impossible to test this last hypothesis at present, as the necessary data are lacking for the majority

of biological control systems, a shortcoming that led Hochberg and Holt (1999) to request that a concerted effort be made to collect data on the population growth rates of pest populations.

Clearly the strongest pattern to emerge from the data is that host taxonomy has the greatest influence on the success of biological control. It is well known, for example, that the Homoptera have been far more successful as targets for biological control introductions than the Lepidoptera (Greathead & Greathead, 1992; Mills, 1994a). The Homoptera are sedentary external plant feeders and have less of a refuge from parasitism than the Lepidoptera, which are either more mobile as external feeders or are protected as internal feeders within plant tissues (Stiling, 1990; Gross, 1991; Hawkins, 1994). In addition, parasitoids of the Lepidoptera can be classified into guilds that are characterized by distinct, and frequently short, windows of host vulnerability to attack (Mills, 1992, 1994b). In contrast, the Homoptera tend to be susceptible to parasitoid attack over a greater part of their life cycle. This difference in the duration of vulnerability to attack by a particular parasitoid may have led to the evolution of a greater range of fecundity among the parasitoids of the Lepidoptera, as appears to be the case for ichneumonid parasitoids in general, and for the parasitoids of the Swaine jack pine sawfly in particular (Price, 1974, 1975). Together with the greater likelihood that parasitoids can realize their potential fecundity as introductions against exotic pests, this may account for the positive relationship between parasitoid fecundity and the outcome of biological control against the Lepidoptera, in

contrast to the absence of a relationship for the Homoptera and the more general negative relationship seen for the combined data set. Thus in seeking a better explanation for success and failure in biological control it would seem prudent to pay greater attention to the characteristics of the host population, including windows of vulnerability to parasitism, growth rates and refuge characteristics.

The dichotomy between theory and data is not new to biological control. Jervis et al. (1996), for example, point out such a dichotomy with respect to the issue of host feeding. They note that population dynamics theory predicts that destructive host feeding parasitoids will be no more likely to become established, compared to other parasitoids, and that they should not be able to depress the host equilibria as strongly. Their analysis of the BIOCAT database, however, indicates that destructive host feeding parasitoids of the Homoptera are better at both establishment and control than other parasitoids. Jervis et al. (1996) concluded that while destructively host-feeding parasitoids probably provide better biological control than their alternative, it would be, "...imprudent to use destructive host feeding as the sole, or even primary, selection criterion when seeking agents for classical biological control...". Based on the results of this study, such a sentiment is also warranted with respect to fecundity. Low fecundity should not always be considered as a constraint in the selection of parasitoids for introduction in biological control programs, and under some circumstances may actually be desirable.

Table 1. Biological control introductions for which sufficient data exist in the biological control record to evaluate the effect of parasitoid fecundity on biological control success. Introduction and outcome records from BIOCAT, parasitoid and host biology from Sweetman (1958), Price (1975), and Clausen (1978). Unless otherwise noted, parasitoid fecundity represents the lifetime average number of eggs laid. DS: Discrete and Synchronous; CA: Continuous and Asynchronous; CS: Continuous but Synchronous; DA: Discrete but Asynchronous.

Biological control outcome	Parasitoid fecundity (clutches)	Parasitoid	Host	System characteristics
Success				
	1.5 ^a	<i>Dahlbominus fuscipennis</i> (Pteromalidae)	<i>Gilpinia hercyniae</i> (Hymenoptera)	DS
	1.94 ^b	<i>Neodusmetia sangwani</i> (Encyrtidae)	<i>Antonina graminis</i> (Homoptera)	CA
	3.84 ^c	<i>Pediobius parvulus</i> (Eulophidae)	<i>Promecotheca coeruleipennis</i> (Coleoptera)	CA
	8 ^d	<i>Aphytis lepidosaphes</i> (Aphelinidae)	<i>Cornuaspis beckii</i> (Homoptera)	CA
	8 ^e	<i>Aphytis melinus</i> (Aphelinidae)	<i>Aonidiella aurantii</i> (Homoptera)	CA
	8.33 ^f	<i>Pseudaphycus malinus</i> (Encyrtidae)	<i>Pseudococcus comstocki</i> (Homoptera)	CA
	13.23 ^g	<i>Metaphycus timberlakei</i> (Encyrtidae)	<i>Parthenolecanium persicae</i> (Homoptera)	DA
	17 ^h	<i>Aphytis holoxanthus</i> (Aphelinidae)	<i>Chrysomphalus aonidum</i> (Homoptera)	CA
	20	<i>Anagrus armatus</i> (Mymaridae)	<i>Edwardsiana crataegi</i> (Homoptera)	DS
	24	<i>Rhyssa persuasoria</i> (Ichneumonidae)	<i>Sirex noctilio</i> (Hymenoptera)	DS
	25	<i>Anaphoidea nitens</i> (Mymaridae)	<i>Gonipterus scutellatus</i> (Coleoptera)	DA
	25	<i>Tiphia vernalis</i> (Tiphidae)	<i>Popilla japonica</i> (Coleoptera)	DS
	26	<i>Coccophagus utilis</i> (Aphelinidae)	<i>Parlatoria oleae</i> (Homoptera)	DS
	30	<i>Aphytis maculicornis</i> (Aphelinidae)	<i>Parlatoria oleae</i> (Homoptera)	DA
	34	<i>Comperiella bifasciata</i> (Encyrtidae)	<i>Aonidiella aurantii</i> (Homoptera)	CS
	50	<i>Tiphia popillivora</i> (Tiphidae)	<i>Popilla japonica</i> (Coleoptera)	DS
	51.36 ⁱ	<i>Allotropa burrelli</i> (Platygasteridae)	<i>Pseudococcus comstocki</i> (Homoptera)	CA
	60	<i>Exenterus abruptorius</i> (Ichneumonidae)	<i>Gilpinia hercyniae</i> (Hymenoptera)	DS
	69	<i>Trissolcus basalis</i> (Scelionidae)	<i>Nezara viridula</i> (Heteroptera)	CA
	85	<i>Apoanagyrus lopezi</i> (Encyrtidae)	<i>Phenacoccus manihoti</i> (Homoptera)	CA
	85	<i>Scelio pembedoni</i> (Scelionidae)	<i>Oxya chinensis</i> (Orthoptera)	DA
	88	<i>Campsomeris annulata</i> (Scoliidae)	<i>Anomala sulcatula</i> (Coleoptera)	DA
	100	<i>Aphelinus mali</i> (Aphelinidae)	<i>Eriosoma lanigerum</i> (Homoptera)	CS
	100	<i>Hypercreteina aldrichi</i> (Tachinidae)	<i>Popilla japonica</i> (Coleoptera)	DS
	125	<i>Coccophagus gurneyi</i> (Aphelinidae)	<i>Pseudococcus calceolariae</i> (Homoptera)	CA
	150	<i>Tetracnemoidea brevicornis</i> (Encyrtidae)	<i>Pseudococcus calceolariae</i> (Homoptera)	CA
	150	<i>Trioxys pallidus</i> (Aphidiidae)	<i>Chromaphis juglandicola</i> (Homoptera)	CS
	200	<i>Bracon gelechiae</i> (Braconidae)	<i>Phthorimaea operculella</i> (Lepidoptera)	CS
	200	<i>Clausenia purpurea</i> (Encyrtidae)	<i>Pseudococcus citriculus</i> (Homoptera)	CS
	200	<i>Eretmocerus serius</i> (Aphelinidae)	<i>Aleurocanthus woglumi</i> (Homoptera)	CA
	232	<i>Trichopoda pennipes</i> (Tachinidae)	<i>Anasa tristis</i> (Heteroptera)	DS
	237	<i>Trichopoda pennipes/pilipes</i> (Tachinidae)	<i>Nezara viridula</i> (Heteroptera)	CS
	250	<i>Leptomastix dactylopii</i> (Encyrtidae)	<i>Planococcus citri</i> (Homoptera)	CA
	250	<i>Macrocentrus grandii</i> (Braconidae)	<i>Ostrinia nubilalis</i> (Lepidoptera)	DS
	250	<i>Trioxys complanatus</i> (Aphidiidae)	<i>Therioaphis trifolii</i> (Homoptera)	CS
	300	<i>Metaphycus helvolus</i> (Encyrtidae)	<i>Saissetia oleae</i> (Homoptera)	DA
	450	<i>Anicetus beneficus</i> (Encyrtidae)	<i>Ceroplastes rubens</i> (Homoptera)	DA
	500	<i>Paratheresia claripalpis</i> (Tachinidae)	<i>Diatraea saccharalis</i> (Lepidoptera)	CS
	700	<i>Chelonus annulipes</i> (Braconidae)	<i>Ostrinia nubilalis</i> (Lepidoptera)	DS
	700	<i>Metagonistylum minese</i> (Tachinidae)	<i>Diatraea saccharalis</i> (Lepidoptera)	CS
	800	<i>Prosenia siberita</i> (Tachinidae)	<i>Popilla japonica</i> (Coleoptera)	DS
	1000	<i>Lydella thompsoni</i> (Tachinidae)	<i>Ostrinia nubilalis</i> (Lepidoptera)	DS
	1400	<i>Cyzenis albicans</i> (Tachinidae)	<i>Operophtera brumata</i> (Lepidoptera)	DS

Biological control outcome	Parasitoid fecundity (clutches)	Parasitoid	Host	System characteristics
Failure				
	8.33 ^f	<i>Oomyzus brevistigma</i> (Eulophidae)	<i>Xanthogaleruca luteola</i> (Coleoptera)	CS
	23.25 ^f	<i>Goniozus emigratus</i> (Bethyidae)	<i>Maruca testulalis</i> (Lepidoptera)	CA
	25 ^h	<i>Apanteles harrisinae</i> (Braconidae)	<i>Harrisina brillians</i> (Lepidoptera)	DS
	30.5 ^f	<i>Dibrachoides druso</i> (Pteromalidae)	<i>Hypera postica</i> (Coleoptera)	DS
	33.33 ^m	<i>Tetrastichus giffardianus</i> (Eulophidae)	<i>Ceratitis capitata</i> (Diptera)	CS
	42	<i>Pleolophus basizonas</i> (Ichneumonidae)	<i>Gilpinia hercyniae</i> (Hymenoptera)	DS
	58.82 ⁿ	<i>Cotesia glomerata</i> (Braconidae)	<i>Pieris rapae</i> (Lepidoptera)	CS
	60	<i>Paralitomastix pyralidis</i> (Encyrtidae)	<i>Anarsia lineatella</i> (Lepidoptera)	CS
	70	<i>Spalangia drosophilae</i> (Pteromalidae)	<i>Hippelates</i> spp. (Diptera)	CS
	75	<i>Alysia manducator</i> (Braconidae)	<i>Calliphora</i> spp. (Diptera)	CS
	80	<i>Trichogrammatoidea robusta</i> (Trichogrammatidae)	<i>Hypsipyla grandella</i> (Lepidoptera)	CA
	85	<i>Apoanagyrus diversicornis</i> (Encyrtidae)	<i>Phenacoccus manihoti</i> (Homoptera)	CA
	90	<i>Scolia ruficornis</i> (Scoliidae)	<i>Oryctes rhinoceros</i> (Coleoptera)	CA
	100	<i>Agrypon flaveolatum</i> (Ichneumonidae)	<i>Operophtera brumata</i> (Lepidoptera)	DS
	100	<i>Compsilura concinnata</i> (Tachinidae)	<i>Lymantria dispar</i> (Lepidoptera)	DS
	100	<i>Temelucha interruptor</i> (Ichneumonidae)	<i>Rhyacionia buoliana</i> (Lepidoptera)	DS
	175	<i>Orgilus obscurator</i> (Braconidae)	<i>Rhyacionia buoliana</i> (Lepidoptera)	DS
	178	<i>Leptomastidea abnormis</i> (Encyrtidae)	<i>Planococcus citri</i> (Homoptera)	CS
	200	<i>Biosteres tryoni</i> (Braconidae)	<i>Ceratitis capitata</i> (Diptera)	CS
	200	<i>Ooencyrtus kuvanae</i> (Encyrtidae)	<i>Lymantria dispar</i> (Lepidoptera)	DS
	200	<i>Opius humilis</i> (Braconidae)	<i>Ceratitis capitata</i> (Diptera)	CS
	250	<i>Brachymeria intermedia</i> (Chalcididae)	<i>Lymantria dispar</i> (Lepidoptera)	DS
	250	<i>Triarthria setipennis</i> (Tachinidae)	<i>Forficula auricularia</i> (Dermaptera)	DS
	300	<i>Ascogaster quadridentata</i> (Braconidae)	<i>Cydia pomonella</i> (Lepidoptera)	CS
	300	<i>Meteorus versicolor</i> (Braconidae)	<i>Euproctis chryorrhoea</i> (Lepidoptera)	DA
	350	<i>Phanerotoma flavitestacea</i> (Braconidae)	<i>Anarsia lineatella</i> (Lepidoptera)	CS
	350	<i>Phanerotoma flavitestacea</i> (Braconidae)	<i>Ectomyelois ceratoniae</i> (Lepidoptera)	CS
	600	<i>Dolichogenidea lacteicolor</i> (Braconidae)	<i>Euproctis chryorrhoea</i> (Lepidoptera)	DA
	600	<i>Macrocentrus ancyliivorus</i> (Braconidae)	<i>Cydia molesta</i> (Lepidoptera)	CS
	600	<i>Phobocampe disparis</i> (Ichneumonidae)	<i>Lymantria dispar</i> (Lepidoptera)	DS
	600	<i>Pholetesor pedias</i> (Braconidae)	<i>Phyllonorycter blancardella</i> (Lepidoptera)	CS
	650	<i>Ibalia leucospoides</i> (Ibaliidae)	<i>Sirex noctilio</i> (Hymenoptera)	DS
	5000	<i>Blepharipa scutellata</i> (Tachinidae)	<i>Lymantria dispar</i> (Lepidoptera)	DS

^a Lifetime average number of eggs laid / average clutch size = 45 / 30; ^b 35 / 18; ^c 73 / 19; ^d 32 / 4; ^e 24 / 3; ^f 100 / 12;

^g 172 / 13; ^h 34 / 2; ⁱ 565 / 11; ^j 186 / 8; ^k 500 / 20; ^l 122 / 4; ^m 300 / 9; ⁿ 2000 / 34.

FIGURE LEGENDS

Fig. 1. The local stability properties of eqn 1 under the assumptions of Ricker host density-dependence (eqn 2), negative binomial host escape (eqn 3), and a search-and-fecundity-limited encounter rate (eqn 6). See text for details. The upper boundary of regions marked C is demarcated by a dashed line. Results were generated via numerical simulation; in all cases $c = 0.2$, $K = 1000.0$.

Fig. 2. The relationship between parasitoid fecundity β and host equilibrium suppression q for four different combinations of the parasitoid search efficiency parameter a and the escape function aggregation parameter k . In all cases $c = 0.2$, $K = 1000.0$, $r = 2.0$.

Fig. 3. The logistic regression of parasitoid biological control outcome on parasitoid fecundity (clutches) for the complete data set.

Fig. 4. The logistic regression of parasitoid biological control outcome on parasitoid fecundity (clutches) for the Lepidoptera.

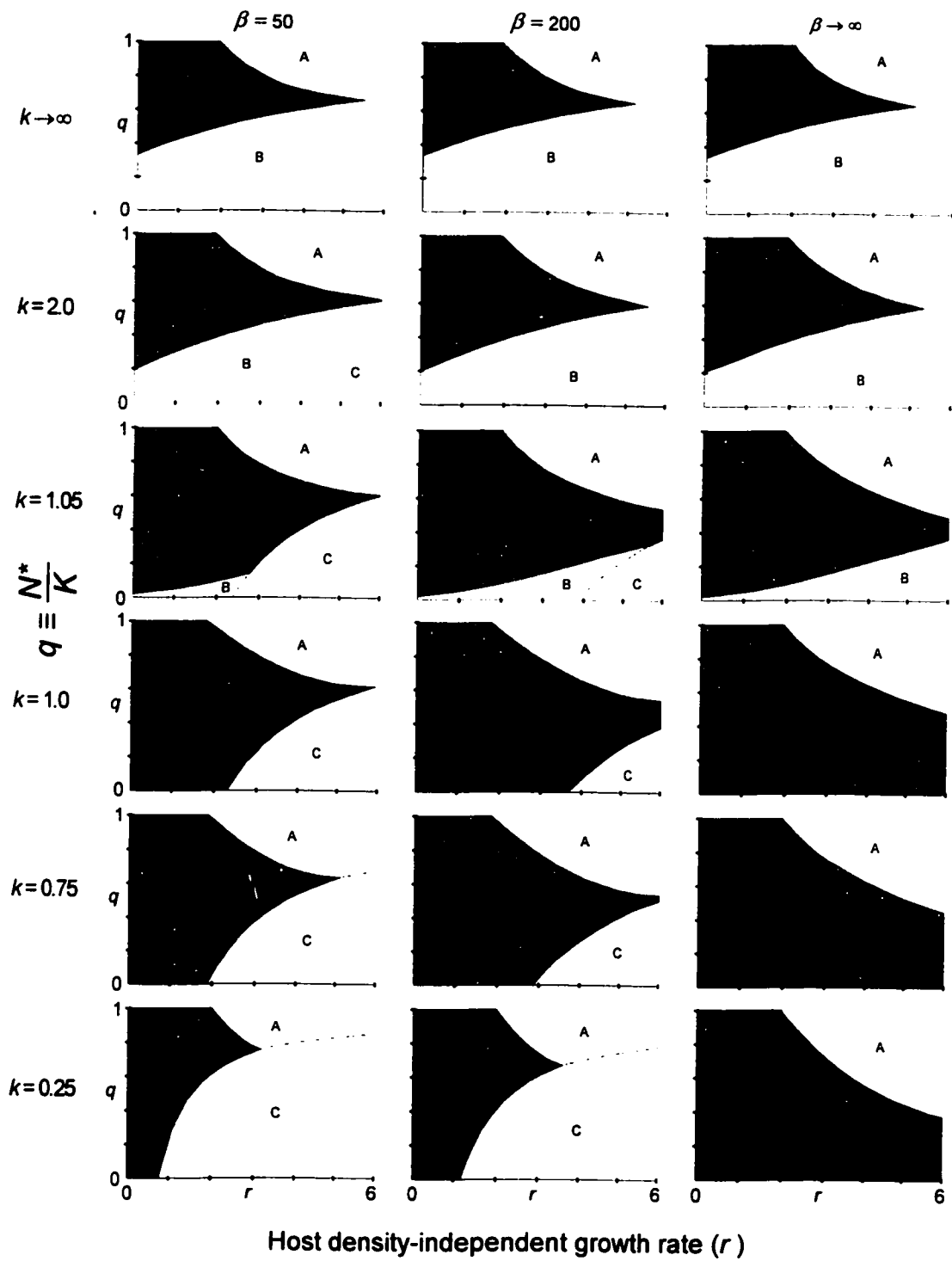


Figure 1

Figure 2

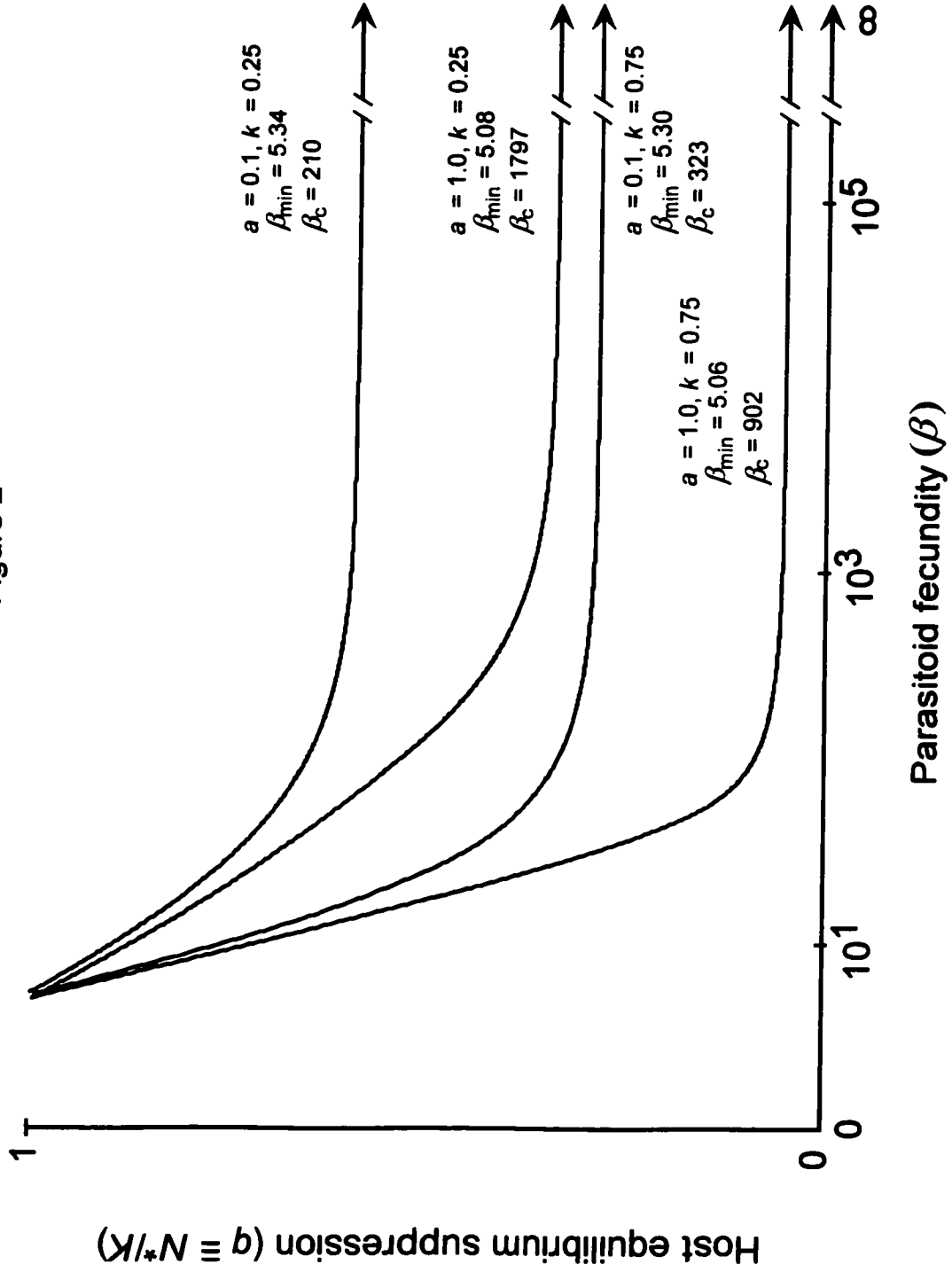


Figure 3

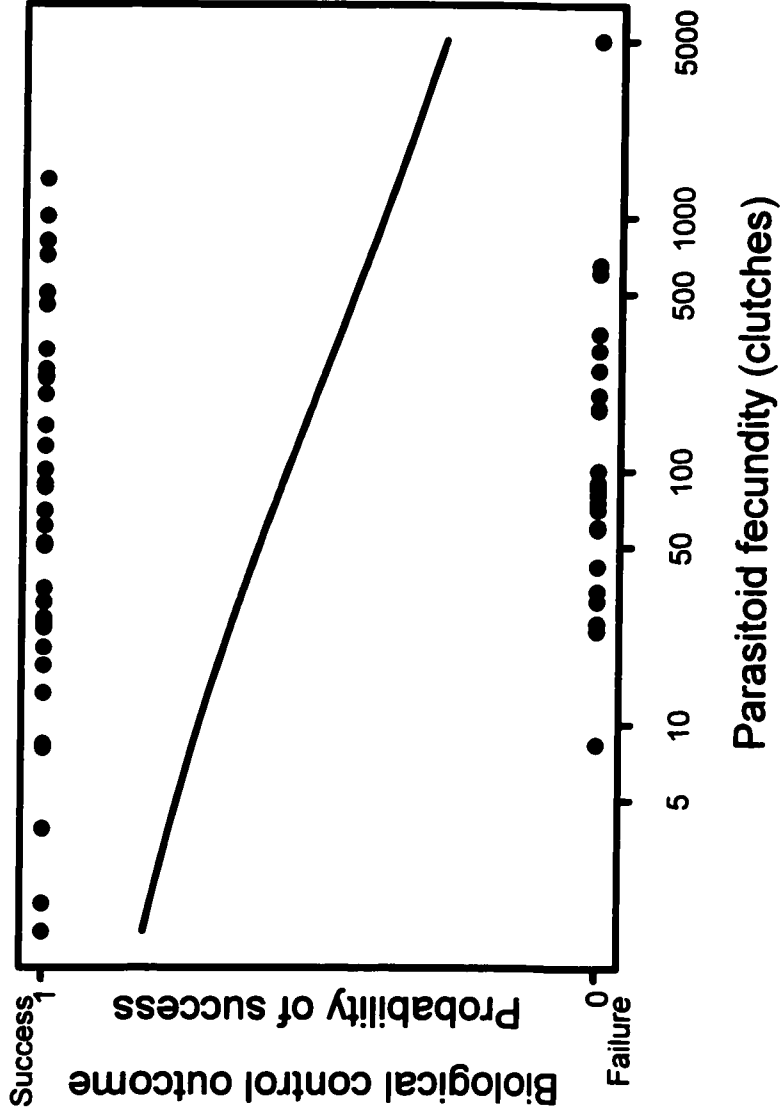
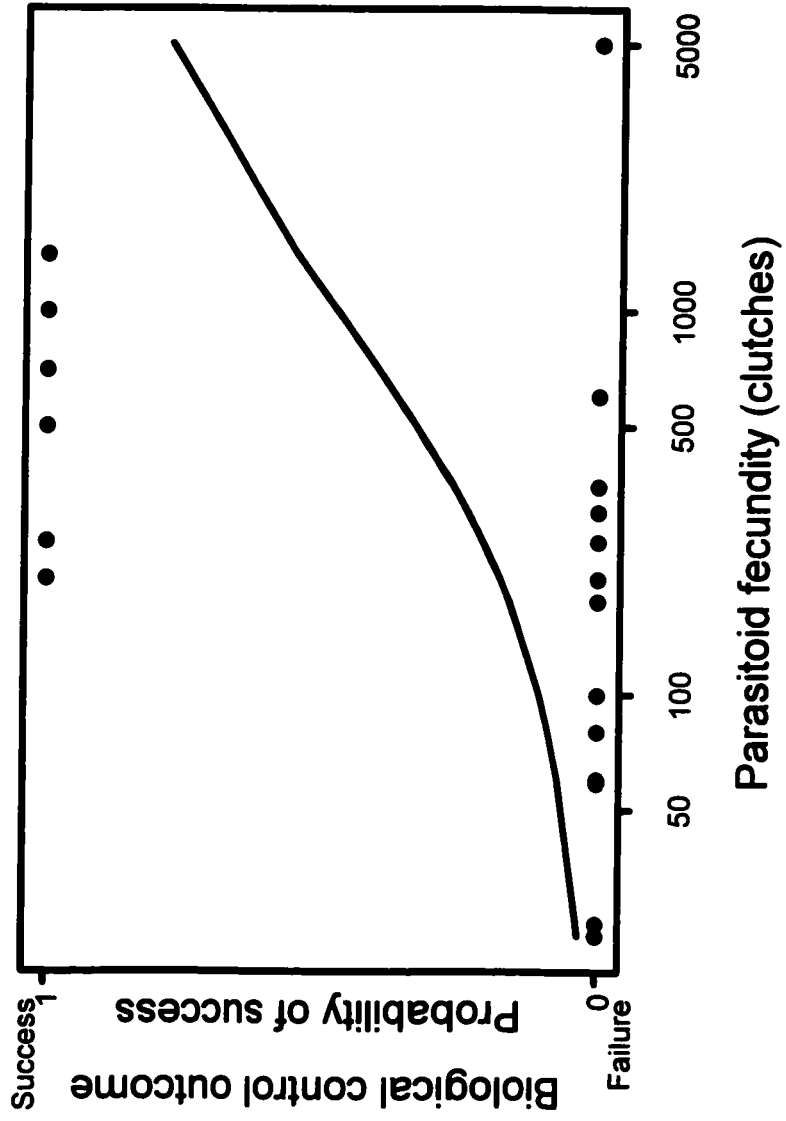


Figure 4



3. INTRASPECIFIC COMPETITION AND DENSITY DEPENDENCE IN AN *Ephestia kuehniella* – *Venturia canescens* LABORATORY SYSTEM

INTRODUCTION

The history of the study of population regulation has been characterized by a wide diversity of opinions about its presence, causes and consequences (Nicholson, 1933; Nicholson & Bailey, 1935; Andrewartha & Birch, 1954; Lidicker, 1965; Hanski, 1990; Murdoch, 1994; Turchin, 1995; den Boer & Reddingius, 1996; Getz, 1996; Uchmanski, 2000). While it is certainly true that density-independent mechanisms (primarily disturbance) can play a central role in the regulation of populations (Turchin, 1995; Ritchie, 1996; Huffaker et al., 1999), most of the focus of research on population regulation has been to elucidate density-dependent mechanisms operating on populations, internally (intraspecific competition) and/or externally (interspecific competition, density-dependent predation and/or parasitism) (den Boer, 1990; Latto & Bernstein, 1990; Hochberg, 1991; Floyd et al., 1996; Lynch et al., 1998; Bonsall et al., 1999; Huffaker et al., 1999). Since the world is populated by organisms, but not overrun by them, there must be mechanisms by which population growth rates are positive when population densities are low, and negative when they are high. The precise nature of how this occurs has been the subject of much debate.

In the realm of biological control, this inquiry takes on particular importance. In classical biological control introductions (hereafter referred to simply as

biological control), potential control agent(s) are introduced at low densities, with the intention that they will establish (i.e. initially experience positive population growth rates), control the pest (i.e. cause the pest's realized population growth rate to become negative), and then settle into a stable relationship with all populations persisting at very low densities. Much of the focus on why biological control works, or (more frequently) why it doesn't, has been on density-dependent processes operating within the pest population, the potential control agent population(s), and/or as a result of the interactions between these populations (Hassell, 1978, 2000a, b; Bellows, 1981; May et al., 1981; Barclay, 1986; Bernstein, 1986; Taylor, 1993a, b, 1996; Barlow & Wratten, 1996; Getz, 1996; Mills & Getz, 1996; Murdoch & Briggs, 1996; Reed et al., 1996; Briggs et al., 1999; Cavalieri & Koçak, 1999; Hochberg & Holt, 1999; Takagi, 1999; Kean & Barlow, 2000; Mills, 2000).

Parasitoids are the most frequently used group of control agents in biological control projects, due largely to their high level of target-pest specificity (Greathead & Greathead, 1992; Mills, 2000; but this could be a detriment in terms of control of the pest - Murdoch et al., 1985; Symondson et al., 2002). For this reason, some of the theory behind pest-parasitoid population dynamics is briefly considered here. Pest-parasitoid models often omit explicit density dependence in the pest population, for the purpose of focusing on density-dependent regulatory mechanisms inherent in the pest-parasitoid interaction (e.g. Briggs, 1993; Briggs et al., 1993; Getz & Mills, 1996; Murdoch et al., 1996; Shea et al.,

1996). It *must* be the case, however, that such intraspecific-competitive processes occur, because, as pest densities increase toward some threshold level, the rate of resource depletion becomes greater than the rate of resource renewal. The critical questions in this regard are: over what range of densities do such processes occur, and how are they relevant to the population dynamics of the pest-parasitoid interaction (Barlow & Wratten, 1996; Getz, 1996; Mills & Getz, 1996; Hochberg & Holt, 1999). Recently, Mills (2000), as part of a specification of minimum requirements for host-parasitoid models, included self-limitation (density dependence) for the host population as one of the fundamental features of these models if they are to be used for the purpose of examining biological control scenarios.

There has been a great deal of debate in the host-parasitoid theoretical literature over the last 30 years about the impact of variation in parasitoid density on host-parasitoid population dynamics (see reviews in Barlow & Wratten, 1996; Mills & Getz, 1996; Bernstein, 2000; Hassell, 2000a, b). This work has led to the " $CV^2 > 1$ " rule for the stability of the host-parasitoid interaction, where " CV " is the coefficient of variation of searching parasitoids per discrete patch of hosts (Taylor, 1993b). As both Mills and Getz (1996) and Hassell (2000a) point out, however, the generality of this result requires that the host population *not* experience self-limitation, and that the functional response of the parasitoid be linear. As the generality of both these assumptions is questionable (Barlow & Wratten, 1996; Getz, 1996; Getz & Mills, 1996; Mills & Getz, 1996; Chs. 2, 4), it

thus becomes even more important to understand at a mechanistic level how density dependence influences the dynamics of pest-parasitoid populations.

There is a substantial body of laboratory work on the biology of the Mediterranean flour moth, *Ephestia* (= *Anagasta*) *kuehniella* Zeller (Lepidoptera: Pyralidae); its solitary larval koinobiont thelytokous (i.e. parthenogenetic) endoparasitoid, *Venturia* (= *Nemeritis*) *canescens* Gravenhorst (Hymenoptera: Ichneumonidae); and their interactions (e.g. Fisher, 1962; Takahashi, 1963, 1968; Salt, 1965, 1966; Corbet, 1968; Hassell & Huffaker, 1969; White & Huffaker, 1969a, b; Rogers, 1972; Hassell, 1978; Amaral Filho, 1985). (*E. kuehniella* has been referred to in some literature as *E. sericarium* Scott, and the species name is sometimes spelled *kühniella*. *V. canescens* has been chronologically placed in the genera *Nemeritis*, *Idechthis*, *Exidechthis*, *Devorgilla* and *Venturia*; Salt, 1976.) Recent ecological work has addressed a wide variety of topics, from tests of ideal free distribution theory (Tregenza et al., 1996), to the examination of host suitability and the consequences of superparasitism (Hughes et al., 1994b; Harvey, 1996; Sirot, 1996; Harvey & Vet, 1997; Sait et al., 1997; Sirot et al., 1997), to the demonstration of apparent competition (Bonsall & Hassell, 1997, 1998, 1999, 2000), and builds on a tradition that dates to at least the 1930's and 40's (e.g. Brindley, 1930; Norris, 1933; Ahmad, 1936; Simmonds, 1943; Ulliyett, 1945; Ulliyett & van der Merwe, 1947). These organisms are frequently used in laboratory studies because *E. kuehniella* is a major stored-product pest in many parts of the world (Munro, 1966; Benson, 1973; Subramanyam & Hagstrum, 1996, 2000);

because both host and parasitoid are easily cultured (Corbet, 1968; Amaral Filho, 1985; Cerutti et al., 1992; Daumal & Boinel, 1994b); and because *E. kuehniella* readily provides a rearing substrate for *V. canescens*, as well as for *Trichogramma* egg parasitoids (Daumal & Boinel, 1994a) and other parasitoid species (Ullyett, 1945; Benson, 1973). In an effort to build further on this work, as well as for ease of methodology and for the ability to draw on previously collected data in the literature, these two organisms were used to examine the population consequences of variation in host and parasitoid density.

In general, laboratory population dynamics studies of these species have focused either on mass rearing (e.g. obtaining the maximum number of host eggs, larvae and/or parasitoids per square meter of shelf space; Brindley, 1930; Ullyett, 1945; Ullyett & van der Merwe, 1947; Smith, 1969; Bell, 1976; Cerutti et al., 1992); or on minimizing the pest's impact on stored products via a variety of control methods (e.g. Plarre et al., 1993, Bell and Savvidou, 1999, Nielsen, 2001). While significant exceptions to this general rule exist (mostly in the form of time series experiments; see Fisher, 1962; Hassell & Huffaker, 1969, and White & Huffaker, 1969a, b; and Bonsall & Hassell, 1997, 1998, 1999, 2000), and while many studies exist concerning the effects of density on insects in culture (see Benson, 1973, and Peters & Barbosa, 1977 for pertinent reviews), no studies to date have examined the effects of simultaneous variations of host and parasitoid density on the life-history parameters of these organisms (although see Ahmad, 1936, Simmonds, 1943).

This chapter presents the results of two experiments designed to determine the effects of variation in host and parasitoid density on both host and parasitoid life-history parameters. In the first experiment, *E. kuehniella* were reared at five initial densities to determine the effects of intraspecific competition on host survivorship, growth and fecundity. In the second, the same five initial host densities were exposed to two different densities of *V. canescens* to determine the effects of parasitoid density on host and parasitoid survivorship and growth, and on host fecundity. The data resulting from these experiments were then used to parameterize several different versions of the host self-limitation function (Ch. 2).

MATERIALS AND METHODS

REARING AND EXPERIMENTAL PROTOCOLS

E. kuehniella and *V. canescens* were obtained from a colony maintained by the College of Natural Resources insect rearing facility at the University of California, Berkeley. The *E. kuehniella* colony was mass-reared in plastic trays (47.0 x 36.8 x 3.8 cm) on a diet of semolina. *E. kuehniella* generally passes through five larval instars (Corbet, 1968; Harvey & Vet, 1997). The *V. canescens* colony was reared on 3rd - 5th instar *E. kuehniella* larvae in clear plastic boxes (17.8 x 12.7 x 6.7 cm). *E. kuehniella* and *V. canescens* used in experiments were maintained at 27.3 ± 0.1 °C (mean \pm SE), 72.5 ± 12.5 % RH (mean \pm range), and L14:D10. Naïve

V. canescens, with no access to hosts, were provided with honey prior to exposure to hosts, and females of ages 1-3 days were used in experiments.

Experiments were conducted in 0.47 L (one pint) unwaxed paper containers with clear plastic lids (obtained from AC Paper and Supply Co., Berkeley, CA), to which 5.00 ± 0.04 g semolina (mean \pm range) was added. A set of 32 containers was used for each of five initial densities of *E. kuehniella* eggs (IHD \equiv initial host density): 10, 45, 80, 115 or 150 eggs, as determined by direct count (for the IHD 10 treatment), or by weight. Mean \pm SE egg weight was 26.1 ± 0.5 μ g for both the *E. kuehniella*-only experiment ($n = 75$) and the *E. kuehniella* + *V. canescens* experiment ($n = 20$). This mean was used as the basis for weighing out 45, 80, 115 and 150 eggs.

Egg hatch failure of *E. kuehniella* (i.e. density-independent egg mortality) was assessed by placing 100 eggs into each of eight 0.47 L unwaxed paper containers with clear plastic lids. All hatching larvae were counted. For purposes of data analysis and presentation all hatching was assumed to have occurred on day three after egg laying. It is possible that some small but significant proportion of eggs in this assessment failed to hatch due to desiccation (no evidence of cannibalism in newly-hatched larvae was observed). This methodology, however, was the best available for determining hatching success via sampling as close to the time of hatch as possible (the very small newly-hatched larvae proved impossible to locate when eggs were placed in diet, which would have helped to prevent desiccation).

In the first experiment (parasitoids absent), populations were monitored in one of two ways. For juvenile stages, containers were destructively harvested as the experiment progressed, at the peaks of the mid-larval, late-larval and pupal stages. A single destructive harvest involved opening a random selection of 8 containers of each initial host density. All *E. kuehniella* larvae and/or pupae were removed, counted and fresh weighed. A further 8 containers of each initial host density were used to monitor adult *E. kuehniella*, which were collected on a daily basis from the day of first emergence until emergence ceased. Twenty adults from each initial host density were fresh weighed. Additionally, eight mating pairs from each initial host density were removed from the paper containers whilst *in copula* and kept in 150 x 25 mm glass test tubes capped with window screen mesh until both members of the pair died. The mesh size was large enough to allow passage of moth eggs but small enough to restrict the adult moths. Test tubes were inverted and the window-screen-covered open ends placed in small cups containing a thin layer of very fine-ground pastry flour, to cue female moths not to lay eggs elsewhere in the test tube (Daumal & Boinel, 1994b). Eggs from these mated pairs were collected daily via sifting the pastry flour, and the total fecundity and total fresh egg weight (used to determine mean fresh egg weight) was measured for each female moth. Hatching success of host eggs resulting from experimentally-obtained mated host pairs was not assessed (see Norris, 1933; Ahmad, 1936; Leather & Burnand, 1987; Cerutti et al., 1992; Awmack & Leather, 2002). Data from this experiment were used to examine host

survivorship and growth, in order to understand how intraspecific competition influenced the host population in the absence of parasitoids, as well as to parameterize several different versions of the host self-limitation function.

In the second experiment, one or three female *V. canescens* were exposed to *E. kuehniella* from the late-larval stage until the death of the parasitoid(s) ($n = 8$ for each initial-host-density x parasitoid-density combination.) Parasitoids were not given honey subsequent to host exposure, and typically lived for 4-6 days thereafter. Adult *E. kuehniella* counts, fresh weights, emergence times, mated pairs and eggs were collected as detailed above. In addition, adult *V. canescens* were collected on a daily basis, counted, and fresh weighed as outlined above for *E. kuehniella*. The fecundity of parasitoids resulting from experimental treatments was not assessed (see Trudeau & Gordon, 1989; Hughes et al., 1994a, b; Harvey & Thompson, 1995; Harvey & Vet, 1997; Harvey et al., 2001). In some cases, host and/or parasitoid mortality prevented collection of complete replicates for some experimental combinations; the details of these exceptions are listed in table footnotes where appropriate. Data from this experiment were used in conjunction with the data from the first experiment to examine the effects of parasitism on host intraspecific competition, as well as to examine the effects of variation in initial host density on the host-parasitoid interaction.

STATISTICAL ANALYSIS

All data were initially subjected to analysis of variance (ANOVA) (Underwood, 1997), and subsequently to linear regression and/or multiple comparison, as appropriate. Where ANOVA requirements necessitated transformation of the data (specific transformations are listed in table footnotes), the ANOVA was performed on, and the significance of any regression line(s) determined against, transformed data. Data presented *in figures*, however, are untransformed. For this reason, the slopes of regression lines are not presented, only their statistical significance in departure from zero. Error bars in figures are \pm standard error of the mean.

Where ANOVA indicates a significant interaction effect, *P*-values for the main effects are not presented - where subsequent linear regression results are presented, ANOVA significance on a per-treatment basis is indicated by the *P*-values for the main effects in each linear regression table (Sokal & Rohlf, 1981). In some cases where ANOVA did not indicate a significant interaction, linear regression, while not necessary to explain main effects, was computed for the purpose of plotting graphical linear fits in figures.

Linear regressions were computed using the residual sum-of-squares minimization approach for more than one value of *y* per value of *x*, the linear model being tested against the deviations from regression with no mean square pooling (Sokal & Rohlf, 1981; SPlus4, 1997). Where regression was not significant, the mean value of the data was plotted. When the slope of a linear

regression is significantly different from zero, but there are also significant deviations from the regression, the linear model represents a significant linear trend, but some caution is noted in that these are not strictly linear relationships.

Where linear regression did not provide a significant model of the data, simultaneous mean difference 99% confidence intervals were computed via simulation (Edwards & Berry, 1987; SPlus4, 1997). Multiple comparisons were used both vertically, between treatments at a given host stage or initial host density; and horizontally, between host stages or initial host densities for a given treatment. Correlations were computed using Pearson's product-moment correlation (Sokal & Rohlf, 1981; SPlus4, 1997). Analysis and presentation of emergence time data was performed on the median value for each container.

FITTING MODELS TO THE DATA

Data from the first experiment were used to parameterize the host self-limitation or density-dependence function, $g(N)$, which models the *per capita* population growth rate of the host in the absence of the parasitoid. In the equation for population growth $N_{t+1} = N_t g(N_t)$, (where N_t is the density of the population at time t), it is possible to decompose the function $g(N)$ into components for survivorship and fecundity, so that $g(N) = s(N) b(N)$, (where s and b are respectively the density-dependent survival and birth rates in the absence of parasitoids). This then allows models of $g(N)$ to be fit to data which are the product of survivorship and fecundity. For each initial host density in the first

experiment, the product of the means of host survivorship and fecundity ($n = 8$) was used as a single data point for the purpose of model fitting; this data set thus contained five data points corresponding to each of the five initial host densities. Asymmetric confidence intervals (CI) for these data points were computed via the delta-method (Schervish, 1997, T. Strounekov, *pers. comm.*):

$$CI_{\mu_x\mu_y} = [\mu_x\mu_y \exp(-r), \mu_x\mu_y \exp(r)],$$

$$r = z\sigma_{\log(\mu_x\mu_y)}, \quad \sigma_{\log(\mu_x\mu_y)} = \sqrt{\left[\frac{1}{n_x-1} \left(\frac{\sigma_x}{\mu_x} \right)^2 + \frac{1}{n_y-1} \left(\frac{\sigma_y}{\mu_y} \right)^2 \right]}, \quad (1)$$

where μ_x and μ_y are the means, σ_x and σ_y the standard deviations and n_x and n_y the sample sizes of the survivorship and fecundity distributions; r is the confidence radius; z is the critical value of Student's t -distribution with infinite degrees of freedom and the desired α -level; and $\sigma_{\log(\mu_x\mu_y)}$ is the standard error of the log of the product of the two means.

Gauss-Newton non-linear regression (residual sum-of-squares minimization; SPlus4, 1997) was used to fit four models of $g(N)$ to the *per capita* *E. kuehniella* population growth rate data (the linear, Ricker, generalized Ricker and generalized Beverton and Holt models; see Getz, 1996 for details). The goodness-of-fit criterion for each of the four models was a modification of the method described by Hilborn and Mangel (1997, eqn 5.11). This method makes use of the formula $SSQ_{adj} = SSQ_{res} / (n - 2m)$, where SSQ_{res} is the residual sum-of-squares of the regression, n is the number of data points, and m is the number of parameters in the model. Smaller SSQ_{adj} indicates a better fit of the model to the data.

Because SSQ_{adj} is intended *only* as a *relative* measure of the goodness-of-fit of these models (no *P*-values were calculated for these regression coefficients), *m* was modified to be the number of parameters in the fitted model less two (since $n = 5$). Thus, for the linear and Ricker models, $m = 0$; for the generalized Ricker and generalized Beverton and Holt models, $m = 1$.

As an additional goodness-of-fit criterion for the four models, 5000 data sets of $n = 5$ were generated via bootstrapping from the original data, using the same product-of-means method described above (Davison & Hinkley, 1997; Hilborn & Mangel, 1997). Again, for comparison purposes only, SSQ_{adj} were calculated for each of the models for each of these 5000 data sets, and the proportion of data sets for which each model provided the best fit (i.e. smallest SSQ_{adj}) was assessed (after Hilborn and Mangel, 1997, Ch. 6).

RESULTS

AGE-SPECIFIC HOST SURVIVORSHIP AND GROWTH IN THE ABSENCE OF PARASITOIDS

Egg hatch-success of *E. kuehniella* was 0.85 ± 0.09 , independent of initial host density (Fig. 1, Hatch). A pronounced effect of initial host density on host development rate required destructive sampling of higher initial host densities at increasingly later dates after experiment initiation in order to obtain samples from the appropriate juvenile stages (as determined via pilot studies; Table 1). A significant interaction was found between initial host density and host stage in

their effects on host survivorship in the absence of parasitoids (Table 2). A multiple comparison test (the approximated critical point is 3.78) indicates no differences in survivorship at the mid-larval stage, and that survivorship in all of the treatments except for IHD 10 was the same at the late-larval and pupal stages. Only at the adult stage was survivorship significantly less in the IHD 80, 115 and 150 treatments than in the IHD 10 and 45 treatments.

There was also a significant interaction between initial host density and host stage in their effects on host weight in the absence of parasitoids (Table 3; Fig. 2). A multiple comparison test (the approximated critical point is 3.69) indicates no differences between the IHD 10 and IHD 45 treatments at any host stage, nor between the IHD 115 and IHD 150 treatments. This test further indicates that the IHD 80 treatment is intermediate between these two extremes, grouping with the high initial host densities at the mid-larval stage, with the IHD 45 treatment at the late-larval stage, with the IHD 115 treatment at the pupal stage, and with the IHD 45 treatment at the adult stage.

In the absence of parasitoids, increasing initial host density resulted in decreasing host weight. This influence of competition on growth in *E. kuehniella* starts early in the life cycle, as there is already a significant effect by the mid-larval stage, but does not translate into severe mortality until the pupal stage, when undernourished individuals die prior to emerging as adults.

HOST MATURATION TIME, WEIGHT, FECUNDITY AND EGG WEIGHT

Median host maturation time was strongly non-linearly influenced by initial host density, and there was no significant interaction with parasitoid density (Table 4; Fig. 3). At densities beyond the threshold for resource competition (IHD 45; Figs. 1-3, 9-11), an increase in initial host density resulted in increased host maturation time, an effect that plateaued at the highest initial host density. (A multiple comparison test does not support a downturn in host maturation time with initial host density increasing from 115 to 150 for any parasitoid density; the approximated critical point is 3.58). In spite of a significant effect of parasitoid density indicated by the ANOVA (Table 4), and the suggestion from Fig. 3 that the presence of parasitoids may depress the development time of unattacked hosts with increasing initial host density, a multiple comparison test revealed no significant differences between parasitoid densities (the approximated critical point is 3.46). This is not particularly surprising, because parasitism took place late in host larval development, after the majority of competition for resources had occurred.

The interaction between initial host density and parasitoid density had a significant effect on host adult weight (Table 5A). Increasing host density resulted in decreased adult weight in the absence of parasitoids (Table 5B; Fig. 4). The presence of one parasitoid served to reduce adult weight for hosts surviving parasitism evenly across host densities (Table 5C). Low host emergence from the 3-parasitoid containers precluded linear analysis of the influence of host density,

but multiple comparison revealed no significant differences between the 1- and 3-parasitoid treatments at IHDs 115 and 150 (the approximated critical point is 3.21). This suggests that only the smallest hosts escaped parasitism to produce adults in each of the initial host density treatments.

Host fecundity was significantly affected by the interaction between initial host density and parasitoid density (Table 6A), in a manner similar to that seen for host adult weight. Egg production was highly correlated with host adult weight for all treatments for which data were available (two-sided test, $n = 11$, $t_9 = 6.625$, $P < 0.001$, $r = 0.91$). In the absence of parasitoids, increasing initial host density led to a linear decrease in egg production by surviving host females (Table 6B; Fig. 5). In the presence of parasitoids there was no significant influence of initial host density on the fecundity of surviving females (Tables 6C and 6D), and no difference in the level of fecundity reduction between the 1- and 3-parasitoid treatments except at IHD 150 (multiple comparison, the approximated critical point is 3.43). It is important to recognize that any conclusions about the effects of parasitoid density on host adult weight and/or fecundity in this study are somewhat tentative, because the combination of high parasitoid density and low host density resulted in almost complete suppression of the host and an absence of data for these density combinations.

ANOVA indicates that *E. kuehniella* egg weight was significantly influenced by the interaction between initial host density and parasitoid density (Table 7A). Linear regression, on the other hand, did not reveal a significant linear

relationship between host egg weight and initial host density for any parasitoid densities (Tables 7B-D). Host egg weight at IHD 10 in the absence of parasitoids was significantly greater than at higher initial host densities (multiple comparison test; the approximated critical point is 3.51). Host egg weight was also significantly depressed to an equal extent in the 1- and 3-parasitoid treatments (Table 7E; Fig. 6). This suggests an effect similar to that observed for host adult weight and fecundity. In the presence of parasitoids, smaller larvae avoid parasitism and survive to adulthood, resulting in smaller adults with smaller eggs.

PARASITOID MATURATION TIME AND WEIGHT

ANOVA indicates significant effects of initial host and parasitoid density on median parasitoid maturation time (defined as the time from parasitoid introduction into the containers to adult emergence), and no significant interaction (Table 8A). Regression analyses, however (Tables 8B and 8C), indicate that parasitoid maturation time is not linearly related to initial host density at either parasitoid density (Fig. 7). Multiple comparison tests indicate that only the 3-parasitoid, IHD 10 treatment is different from any of the others (between parasitoid densities the approximated critical point is 3.21; between initial host densities the approximated critical point is 3.61). Thus, no significant effect of initial host or parasitoid density on parasitoid maturation time appears to exist.

ANOVA indicates a strong effect of initial *E. kuehniella* density on parasitoid adult weight, a significant effect of *V. canescens* density, and no significant interaction (Table 9A). For both parasitoid densities a significant linear decrease in parasitoid adult weight occurred with increasing initial host density (Tables 9B and 9C; Fig. 8), although the significant deviations from regression for the 1-parasitoid treatment (Table 9B) suggest a declining relationship that is non-linear. A multiple comparison test between parasitoid densities at each initial host density indicates no differences (the approximated critical point is 3.13). In addition, parasitoid adult weight was highly correlated with host adult weight in the *absence* of parasitoids (two-sided test, $n = 10$, $t_8 = 5.734$, $P < 0.001$, $r = 0.90$). Thus, no effect of parasitoid density on parasitoid adult weight was detected, but interestingly, in contrast to host adult weight in the presence of parasitoids (Fig. 4), parasitoid adult weight decreased with initial host density, suggesting that parasitized hosts may have reduced competitive ability relative to unparasitized hosts.

FORM OF HOST INTRASPECIFIC COMPETITION

The influence of resource competition on the survivorship of both parasitized and unparasitized hosts was determined from total insect emergence. A significant interaction effect of initial host density and parasitoid density on total insect (host + parasitoid) emergence was evident (Table 10A; Fig. 9). In the absence of parasitoids, a saturating effect of initial host density on host

emergence was detected, such that adult emergence increased from the IHD 10 treatment to the IHD 45 treatment and remained constant as initial host density increased thereafter (multiple comparison test; the approximated critical point is 3.67). Although the presence of parasitoids had no effect on total insect emergence in the IHD 10 treatment, there were significant effects at other initial host densities (Table 10B). At lower initial host densities parasitism resulted in a replacement of hosts by parasitoids, but at the same time there was a trend toward reduced total emergence as parasitoid density increased (significant at IHD 45; Table 10B). Over-stinging by parasitoids at low initial host densities may have resulted in some additional mortality of parasitized hosts. In contrast, at high initial host densities an equivalent level of additional host mortality was evident at both parasitoid densities (Table 10B), suggesting that survivorship of parasitized hosts relative to healthy hosts was compromised under conditions of intense competition, either through reduced competitive ability relative to unparasitized hosts or via greater susceptibility to cannibalism.

The influence of resource competition on host population growth rate was determined by combining data for host survivorship and fecundity (Fig. 10; data for host survivorship in the absence of parasitoids and fecundity were obtained from Figs. 1 and 5 respectively; data for host survivorship in the presence of parasitoids not shown). In the absence of parasitoids the host's population growth rate rises sharply as initial host density increases from 10 to 45, and thereafter drops as initial host density increases above 45, clearly illustrating a

density threshold for intraspecific competition in *E. kuehniella*. In the presence of parasitoids this effect is completely removed – host recruitment into the next generation is independent of initial host density and relatively uninfluenced by parasitoid density, maintaining approximately the level of recruitment of the IHD 150 treatment in the absence of parasitoids.

FITTING HOST SELF-LIMITATION MODELS TO EXPERIMENTAL DATA

Non-linear regression analyses of four different models of $g(N)$, the density-dependent *per capita* population growth rate of the host in the absence of parasitoids, were conducted against data for host survivorship and fecundity in the absence of parasitoids (obtained from the data in Figs. 1 and 5). These analyses indicate that the best fit to the data is provided by the generalized Beverton and Holt model (Table 11; Fig. 11). This result further demonstrates the presence of a density threshold in *E. kuehniella* intraspecific competition, such that below this threshold there is little or no effect of density on survivorship or fecundity. The fact that the Ricker function occasionally provides the best fit to bootstrapped data sets is due to this model being the best fit to extreme “outlier” data sets generated by the bootstrap process. It is worth noting that the values obtained by regression for r , the host’s intrinsic rate of increase, are in reasonable agreement among the three non-linear models (Table 11), although r for the Ricker model is somewhat larger than for the others. Similarly, the values obtained by regression for γ , the threshold or abruptness parameter, are in

reasonable agreement for both the generalized Ricker and generalized Beverton and Holt models.

DISCUSSION

EFFECT OF COMPETITION AND PARASITISM ON HOST LIFE-HISTORY PARAMETERS

In the absence of parasitoids, an increase in initial host density led to a reduction in host growth and development rate, resulting in increased mortality in the pupal stage and reduced adult weight and fecundity (which are highly correlated). Thus, a notable delay is evident between the timing of competition for limiting resources (which occurs during the larval stages), and its consequences for the dynamics of *E. kuehniella* populations (i.e. mortality during the pupal stage and reduced fecundity). This combination of factors has determining consequences for the host's *per capita* population growth rate (Fig. 11) - a threshold effect exists such that below an initial host density of approximately 25 eggs/5 g semolina little to no effect of density on *per capita* population growth occurs, while above the threshold a significant reduction in population growth is evident, approaching a lower asymptote beyond 100 eggs/5 g semolina.

While this is the first study to explicitly demonstrate a threshold effect in *E. kuehniella*'s *per capita* population growth rate (but see Bellows, 1981), and to explain the mechanisms underlying this effect, similar consequences of density

(e.g. crowding, resource limitation) on individual life-history parameters for *E. kuehniella* (e.g. growth and maturation rates, survivorship and fecundity) have been found by other workers. Norris (1933) found similar levels of egg mortality and that fecundity was reduced rather than mortality increased under conditions of moderate larval competition. Ulliyett (1945) also found that *E. kuehniella* fecundity decreased sharply once host density reached a value approximately equivalent to IHD 45 in this study, and Ulliyett and van der Merwe (1947) found a precipitous increase in larval and pupal mortality once food availability fell below 0.1 g diet per larva.

Additional congruent results for effects of density on individual life-history parameters have been found for *E. kuehniella* (Ahmad, 1936; Smith, 1969; Bell, 1976; Cerutti et al., 1992; Daumal & Boinel, 1994b; Anderson & Löfqvist, 1996), and for a variety of other insects, including other Lepidoptera (Takahashi, 1953, 1956; Podoler, 1974b; Tripathi & Singh, 1989, 1990; Kazimirova, 1996); Coleoptera (Park, 1938; Tsuda & Yoshida, 1985); Diptera (Sang, 1949, 1959; Scheiring et al., 1984; Botella & Mensua, 1987; Cilek & Knapp, 1989; So & Dudgeon, 1989; Saunders & Bee, 1995; Tsuda et al., 1997; Gleiser et al., 2000); Odonata (Van Buskirk, 1993); and Hymenoptera (Olson & Andow, 1998). The density-threshold phenomenon seen in *E. kuehniella* is likely to occur among the insects in the studies listed above. In fact, a threshold effect has been demonstrated for the population growth rates of a wide variety of other insect species under both laboratory and field conditions, including *E. kuehniella* (Bellows, 1981).

In the presence of parasitoids, although host maturation time was not significantly altered, host adult weight and fecundity were consistently reduced, independent of initial host density, to levels equivalent to those of hosts reared at higher initial host densities in the absence of parasitoids (Figs. 4 and 5). Egg size in the presence of parasitoids was also consistently reduced (Fig. 6). These effects could conceivably occur for at least two separate reasons, operating either singly or in conjunction. First, the suggestion (not supported statistically) that the presence of parasitoids can depress the development time of unattacked hosts (Fig. 3) may indicate that only the smaller host larvae that matured earlier than larger individuals escaped parasitism. Small individuals may escape due to the parasitoids' inability to successfully parasitize small hosts, and/or because parasitoids preferentially attack larger hosts (Sait et al., 1997). Alternatively, some host species have the potential to survive parasitism by *V. canescens* via encapsulation (Salt, 1975), but parasitism survivors can incur fitness costs resulting, for example, from reduced competitive ability (Harvey et al., 1996). Various *Drosophila* studies indicate that host-fitness consequences are associated with the encapsulation of parasitoid eggs, namely reduced competitive ability, growth and fecundity (Fellowes et al., 1998, Fellowes et al., 1999a, b, Fellowes and Godfray, 2000). This latter possibility can be excluded, however, as Salt (1964; 1965) has shown that *E. kuehniella* never encapsulates the eggs or young larvae of *V. canescens*.

With the addition of parasitoids, the density threshold for survivorship of hosts plus parasitoids increased from IHD 45 to IHD 80 (Fig. 9), indicating that parasitized host larvae have lower demands for resources than unattacked larvae (Harvey, 1996). At initial host densities above this threshold, survivorship to adulthood decreased as a consequence of increasingly intense intraspecific competition. This may reflect that parasitized larvae are poor competitors in relation to unattacked hosts, and as a consequence are often unable to support complete parasitoid development to adulthood. In addition, cannibalism is common in *E. kuehniella*, and is most prevalent at all initial host densities in the late larval stage, when resources are most limiting (*pers. obs.*). Chapman et al. (1999) found that cannibalism in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) conferred a fitness benefit *only* under conditions of low food availability. Furthermore, parasitized larvae may also be more susceptible to cannibalism than unattacked larvae, increasing the rate of cannibalism for experiments with parasitoids present as resource competition becomes more intense. Reed et al. (1996) found that *Plodia interpunctella* (Lepidoptera: Pyralidae) parasitized by *V. canescens* were more likely to be cannibalized in individual encounters between parasitized and unattacked larvae.

EFFECT OF COMPETITION ON PARASITOID LIFE-HISTORY PARAMETERS

Little to no effect of either host or parasitoid density on parasitoid maturation time was evident, and no effect of parasitoid density on parasitoid adult weight

was observed. Parasitoid adult weight, however, was strongly influenced by initial host density, and was strongly correlated with host adult weight in the absence of parasitoids. Harvey et al. (1995) also found that 5th instar hosts of *P. interpunctella* reared at high density produced smaller *V. canescens* adults, and Harvey and Thompson (1995) showed that adult wasp size was positively correlated with the number of ovulated eggs in *V. canescens*, with consequent implications for the fecundity of the parasitoids in this study.

Essentially no effect of parasitoid competition on parasitoid life history parameters was evident in this system. Trudeau and Gordon (1989) showed that *V. canescens* reared on *Cadra cautella* (Lepidoptera: Phycitidae) has a fecundity of over 250, and that the daily rate of host attack was on the order of 16-22 per day. Thus, for purely numerical reasons, it is highly likely that superparasitism took place in all parasitoid treatments, though this was not measured directly. On the other hand, Harvey et al. (1993) found that superparasitism by *V. canescens* resulted in increased parasitoid development time, and also resulted in smaller parasitoids emerging from later-instar *P. interpunctella* hosts. No evidence of either of these effects was detected in this study, indicating either that superparasitism did not occur, or that it does not have the same effect in this system, with *E. kuehniella* being a larger host.

HOST INTRASPECIFIC COMPETITION: SCRAMBLE VS. CONTEST

E. kuehniella life-history exhibits little mortality early in the life cycle, and trades off growth (weight) versus mortality in response to crowding. Thus, a separation occurs in the host's life-cycle between the timing of the *action* of density dependence and the *effects* of density dependence. Determining the form of competition (scramble or contest; Nicholson, 1954; Birch, 1957; Hassell, 1975; Bellows, 1981; Bernstein, 1986; Lomnicki, 1988; Toquenaga & Fujii, 1990, 1991a, b; Getz, 1996; Henson & Cushing, 1996; Reeve et al., 1998; Tuda & Iwasa, 1998; Parker, 2000) is often based on examining plots of the number of individuals surviving to reproduction, or to the next generation, as a function of the number of individuals in the current generation (e.g. Benson, 1974; Podoler, 1974; Bellows, 1981, 1982; Lomnicki, 1988; Toquenaga & Fujii, 1990, 1991a, b; Reeve et al., 1998); or, more generally, by examining the population density before and after the mortality effects of density-dependent competition (i.e. *k*-factor analysis; Varley et al., 1973; Benson, 1974; Podoler, 1974a, b; Hassell, 1975; Bellows, 1981). A significant problem with this approach, however, is that scramble competition may be mistaken for contest, if the nature of the resource and the competitive mechanisms in question are not fully understood, or if the population densities over which competition is examined are sufficiently small to avoid demonstrating scramble competition.

Consider, for example, survivorship alone (Fig. 9). In the absence of parasitoids, the number of host adults emerging as a function of initial host density remains constant for IHDs above 45, the threshold for resource limitation. This would seem to indicate that host adult emergence becomes independent of initial host density, and that competition is of contest type (Bellows, 1982; Łomnicki, 1988; Parker, 2000). Alternatively, plotting N_{t+1} vs. N_t for this system (Fig. 10) leads to the conclusion that competition in the absence of parasitoids is of the scramble form, as this plot takes into account not only survivorship but also loss of fecundity due to reduced growth. In this study, *E. kuehniella* completely exhausted its resource (semolina) at higher initial host densities (*pers. obs.*). The importance of whether the resource was “shareable” or “unshareable” (Nicholson, 1954; Parker, 2000) cannot be overemphasized. “Gains to competitors in contests are all or nothing (individuals are either ‘winners’ or ‘losers’), whereas in scrambles, all individuals achieve some gains, if sometimes less than enough to survive and/or reproduce” (Parker, 2000).

The presence of parasitoids causes host recruitment into the next generation to be independent of initial host density (Fig. 10), and the form of host intraspecific competition to shift from scramble to contest (Łomnicki, 1988). In this system parasitism functions as a selective force (Tuda & Iwasa, 1998), changing the competitive regime for hosts from one in which superior scramble or exploitative competitors for food are most successful, to one in which contest

or interference competitors for enemy-free space are most successful. This effect does *not* occur due to parasitoids reducing host densities below the threshold for scramble competition (Holt & Lawton, 1993), since the effects of parasitoids do not occur until *after* the window of host exploitative competition. Scramble competition is still occurring prior to the action of parasitoids in the host's life-cycle, but, in the presence of parasitoids, contest competition occurs later in the host's life-cycle, and dominates the overall host competitive regime (see Reeve, et al., 1998 for a system in which contest competition is followed in the organism's life-cycle by scramble, the latter dominating the competitive regime).

HOST INTRASPECIFIC COMPETITION: MODELING THE DATA

The effect of host density-dependent mortality is extremely nonlinear with initial host density, contributing far more than the effects of initial host density on fecundity to the reverse sigmoid shape of the survivorship x fecundity data set used for nonlinear regression (Fig. 11). Models of density dependence incorporating sigmoid thresholds provide the best explanation of the data, with the generalized Beverton and Holt model providing the best fit. The Ricker model, with fewer free parameters, provided a poor fit to the data. Clearly, representing density dependence in this population with a model for which no threshold is present (e.g. the Ricker model) would be inappropriate. A threshold effect has been shown for a variety of insect populations (Bellows, 1981), and has

been reasonably argued on both theoretical (Bernstein, 1986; Getz, 1996) and empirical grounds (Hassell, 1975).

The inadequacy of the Ricker model as a description of density dependence in this population is noteworthy for two reasons. The use of the this model is common in host-parasitoid population dynamics models (Barlow & Wratten, 1996; Mills & Getz, 1996), while at the same time such models exhibit the phenomenologically unrealistic property that the *effect* (i.e. the strength) of density dependence is greatest at *low* densities (Getz, 1996; but see Jarosik & Dixon, 1999). Thus the generalized Beverton and Holt model should be used to capture the essence of host self-limitation in host-parasitoid models.

ORDERING OF EVENTS IN MODELS OF HOST-PARASITOID POPULATION DYNAMICS

In the *E. kuehniella* - *V. canescens* host-parasitoid system examined here, the mechanism of host self-limitation occurs in the host's life-cycle prior to the action of the parasitoid, though the effects occur after parasitism. May et al. (1981) emphasize the need for, and illustrate the dynamical consequences of, stage and/or age structure in even simple Thompson-Nicholson-Bailey models (see also Barclay, 1986; Bernstein, 1986; Hill, 1988; Godfray & Waage, 1991; Barlow et al., 1994; Cavalieri & Koçak, 1999). While some models of host-parasitoid dynamics incorporate these features (e.g. Hochberg & Holt, 1995, 1999; Tuda & Iwasa, 1998; Hochberg & Ives, 1999; Kean & Barlow, 2000; Mills, 2001), the results of the present study re-emphasize the need to account for any specific biological

features that may influence either the generality or specificity of predictions made on the basis of these models, particularly in the context of biological control (after Hassell, 1980). Certain advantages exist in keeping models simple. But when they are *too* simple, they lose any relevance to real systems (natural, biological control or laboratory; Hochberg and Holt, 1999), and become mere exercises in analysis.

Table 1. Relationship between host stage and median host age (days) for each initial host density.

Host stage	Initial host density [†]				
	10	45	80	115	150
Mid-Larval	22	22	22	22	22
Late-Larval	27	27	28	30	30
Pupal	32	32	34	39	39

[†] $n = 8$ for each Host stage x Initial host density combination.

Table 2. ANOVA of effects of initial host density and host stage on host survivorship[†] with parasitoids absent.

Source of variation	d.f.	MS	<i>F</i>	<i>P</i>
Initial host density	4	0.96	71.47	----
Host stage	4	0.63	47.03	----
Interaction	16	0.19	14.19	<0.001
Error	175	0.01		

[†] Survivorship data were arcsin transformed for ANOVA and multiple comparison.

Table 3. ANOVA of effects of initial host density and host stage on host weight with parasitoids absent.

Source of variation	d.f. [†]	MS	<i>F</i>	<i>P</i>
Initial host density	4	1550.0	193.7	----
Host stage	3	1593.7	199.2	----
Interaction	12	54.30	6.8	<0.001
Error	200	8.00		

† Weights for the egg stage (Fig. 2) were not included in this analysis, nor in the multiple comparison test (see text for results). For the juvenile treatments, each datum is the mean mass of all individuals from an experimental container, $n = 8$ containers. In the adult treatments, $n = 20$ individual weights.

Table 4. ANOVA of effects of initial *E. kuehniella* density and *V. canescens* density on *E. kuehniella* maturation time.

Source of variation	d.f. [†]	MS	F	P
Initial <i>E. kuehniella</i> density	4	476.78	103.19	<0.001
<i>V. canescens</i> density	2	32.78	7.09	0.001
Interaction	6	9.68	2.10	0.062
Error	86	4.62		

[†] Degrees of freedom are reduced due to the absence of any adult *E. kuehniella* emerging from the 10 x 3 initial *E. kuehniella* density x *V. canescens* density treatment, and inadequate sample size ($n = 3$) from the 10 x 1 treatment. For the 45 x 3 treatment $n = 5$ and for the 80 x 3 treatment $n = 6$. In all other cases $n = 8$.

Table 5A. ANOVA of effects of initial *E. kuehniella* density and *V. canescens* density on *E. kuehniella* adult weight.

Source of variation	d.f. [†]	MS	F	P
Initial <i>E. kuehniella</i> density	4	810.51	66.74	----
<i>V. canescens</i> density	2	226.59	18.66	----
Interaction	4	59.46	4.90	<0.001
Error	209	12.14		

† Degrees of freedom are reduced due to inadequate adult *E. kuehniella* sample size in the 10 x 1, 10 x 3, 45 x 3 and 80 x 3 initial *E. kuehniella* density x *V. canescens* density treatments. Sample size is $n = 20$ in all other cases.

Table 5B. Linear regression of effects of initial host density on host adult weight with 0 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	461.84	33.11	<0.001
Linear regression	1	1756.70	58.12	0.005
Deviations from regression	3	30.22	2.17	0.097
Error	95	13.95		

Table 5C. Linear regression of effects of initial host density on host adult weight with 1 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	3	64.69	5.69	0.001
Linear regression	1	140.78	5.28	0.148
Deviations from regression	2	26.65	2.34	0.103
Error	76	11.36		

Table 6A. ANOVA of effects of initial *E. kuehniella* density and *V. canescens* density on *E. kuehniella* fecundity[†].

Source of variation	d.f. [‡]	MS	F	P
Initial <i>E. kuehniella</i> density	4	253.92	25.26	---
<i>V. canescens</i> density	2	15.59	1.55	---
Interaction	5	39.59	3.94	0.003
Error	77	10.05		

[†] Fecundity data were square-root transformed for ANOVA and linear regression.

[‡] Degrees of freedom are reduced due to the absence of *E. kuehniella* mated pairs from the 10 x 1 initial *E. kuehniella* density x *V. canescens* density treatment, and due to inadequate sample size ($n < 4$) from the 10 x 3, and 45 x 3 treatments. For the 80 x 3 treatment, $n = 4$; for the 80 x 1, 115 x 1 and 115 x 3 treatments, $n = 7$; otherwise, $n = 8$.

Table 6B. Linear regression of effects of initial host density on host fecundity with 0 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	192.67	26.76	<0.001
Linear regression	1	763.32	310.21	<0.001
Deviations from regression	3	2.46	0.34	0.795
Error	35	7.20		

Table 6C. Linear regression of effects of initial host density on host fecundity with 1 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	3	12.00	0.92	0.443
Linear regression	1	19.53	2.37	0.264
Deviations from regression	2	8.24	0.63	0.538
Error	26	12.99		

Table 6D. Linear regression of effects of initial host density on host fecundity with 3 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	2	82.44	7.15	0.006
Linear regression	1	139.53	5.50	0.257
Deviations from regression	1	25.35	2.20	0.157
Error	16	11.52		

Table 7A. ANOVA of effects of initial *E. kuehniella* density and *V. canescens* density on *E. kuehniella* egg weight.

Source of variation	d.f. [†]	MS	F	P
Initial <i>E. kuehniella</i> density	4	57.86	14.48	----
<i>V. canescens</i> density	2	482.91	120.88	----
Interaction	7	49.32	12.34	<0.001
Error	206	4.00		

† Degrees of freedom are reduced due to the absence of *E. kuehniella* mated pairs from the 10 x 1 initial *E. kuehniella* density x *V. canescens* density treatment. For the treatments with 0 *V. canescens* each datum is the mean mass of all eggs from a mated pair, $n = 8$ mated pairs. In all other cases $n = 20$ individual egg weights.

Table 7B. Linear regression of effects of initial host density on host egg weight with 0 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	79.51	12.64	<0.001
Linear regression	1	140.98	2.39	0.220
Deviations from regression	3	59.02	9.38	<0.001
Error	35	6.29		

Table 7C. Linear regression of effects of initial host density on host egg weight with 1 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	8.84	2.08	0.090
Linear regression	1	14.42	2.06	0.246
Deviations from regression	3	6.98	1.64	0.185
Error	95	4.26		

Table 7D. Linear regression of effects of initial host density on host egg weight with 3 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	3	52.58	20.16	<0.001
Linear regression	1	14.36	0.20	0.698
Deviations from regression	2	71.69	27.48	<0.001
Error	76	2.61		

Table 7E. Simultaneous mean difference 99% confidence intervals[†] for host egg weight vs. *V. canescens* density at each initial host density for which data were available.

<i>V. canescens</i> densities	Initial <i>E. kuehniella</i> density			
	45	80	115	150
0 vs 1	-0.77, 4.71	3.65, 9.13*	1.69, 7.17*	1.52, 7.00*
0 vs 3	-1.57, 3.90	5.07, 10.60*	2.51, 7.98*	0.45, 5.93*
1 vs 3	-2.88, 1.27	-0.65, 3.49	-1.26, 2.89	-3.14, 1.00

[†] The approximated critical point is 3.39. Absolute differences significantly different from zero are indicated in **bold** and by an asterisk (*).

Table 8A. ANOVA of effects of initial *E. kuehniella* density and *V. canescens* density on *V. canescens* maturation time[†].

Source of variation	d.f. [‡]	MS	F	P
Initial <i>E. kuehniella</i> density	4	7.90	8.70	<0.001
<i>V. canescens</i> density	1	14.82	16.32	<0.001
Interaction	4	2.13	2.34	0.064
Error	67	0.91		

[†] Maturation time measured from the day of *V. canescens* introduction into containers.

[‡] Degrees of freedom are reduced due to $n = 7$ in the 10×1 , 45×1 and 115×1 initial *E. kuehniella* density \times *V. canescens* density treatments; $n = 8$ in all other cases.

Table 8B. Linear Regression of effects of initial host density on parasitoid maturation time with 1 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	1.14	1.58	0.204
Linear regression	1	2.16	2.69	0.200
Deviations from regression	3	0.80	1.11	0.359
Error	32	0.72		

Table 8C. Linear Regression of effects of initial host density on parasitoid maturation time with 3 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	8.68	8.06	<0.001
Linear regression	1	20.00	4.08	0.137
Deviations from regression	3	4.91	4.56	0.009
Error	35	1.08		

Table 9A. ANOVA of effects of initial *E. kuehniella* density and *V. canescens* density on *V. canescens* adult weight.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	68.81	52.10	<0.001
<i>V. canescens</i> density	1	6.30	4.77	0.030
Interaction	4	2.77	2.09	0.083
Error	190	1.32		

Table 9B. Linear regression of effects of initial host density on parasitoid adult weight with 1 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	28.63	22.24	<0.001
Linear regression	1	99.45	19.78	0.021†
Deviations from regression	3	5.03	3.91	0.011†
Error	95	1.29		

† Both the regression and the deviations are significant.

Table 9C. Linear regression of effects of initial host density on parasitoid adult weight with 3 *V. canescens* / container.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	42.94	31.72	<0.001
Linear regression	1	162.58	53.08	0.005
Deviations from regression	3	3.06	2.26	0.086
Error	95	1.35		

Table 10A. ANOVA of effects of initial *E. kuehniella* density and *V. canescens* density on total insect emergence†.

Source of variation	d.f.	MS	F	P
Initial <i>E. kuehniella</i> density	4	39.14	120.81	----
<i>V. canescens</i> density	2	4.80	14.80	----
Interaction	8	2.26	6.96	<0.001
Error	105	0.32		

† Emergence data were square-root transformed for ANOVA and multiple comparisons.

Table 10B. Simultaneous mean difference 99% confidence intervals† for total insect emergence vs. *V. canescens* density at each initial *E. kuehniella* density.

<i>V. canescens</i> densities	Initial <i>E. Kuehniella</i> density			
	10	45	80	150
0 vs 1	-0.83, 1.16	-0.41, 1.58	-1.68, 0.31	0.19, 2.18*
0 vs 3	-0.54, 1.45	0.08, 2.07*	-1.93, 0.06	0.31, 2.3*
1 vs 3	-0.68, 1.29	-0.51, 1.48	-1.25, 0.74	-0.88, 1.11

† The approximated critical point is 3.49. Absolute differences significantly different from zero are indicated in **bold** and by an asterisk (*).

Table 11. Linear and three nonlinear models of the host *per capita* population growth rate function $g(N)$, the fitted values of each model's parameters to the original dataset, the adjusted residual sums-of-squares describing each model's relative fit to the original dataset, and the proportion of bootstrapped datasets for which each model provides the best relative fit to each bootstrapped dataset (linear model provided for comparison purposes).

Model	Form of $g(N)$	m	b	$r = \ln(\lambda)$	λ	K^\dagger	γ	SSQadj	Proportion of Best Fits
Linear	$mN + b$	-2.22	299.9	--	--	--	--	1285.5	0.000
Ricker	$\exp[r(1 - N/K)]$	--	--	5.95	383.0 [‡]	317.7	--	725.6	0.004
Generalized Ricker	$\exp\{r[1 - (N/K)^\lambda]\}$	--	--	5.73	308.3 [‡]	145.8	2.28	124.9	0.085
Generalized Beverton-Holt	$\lambda / [1 + (N/K)^\lambda]$	--	--	5.72 [‡]	303.7	56.42	3.69	12.2	0.911

[†] In the Ricker and generalized Ricker models, $K > 0$ is the carrying capacity, the value of N for which $g(N) = 1$. In the generalized Beverton-Holt model, $K > 0$ is the value of N for which $g(N) = \lambda / 2$. See Getz (1996) for details.

[‡] $\exp(r)$ or $\ln(\lambda)$ of the corresponding estimated parameter value (λ or r), as appropriate, provided for comparison purposes.

FIGURE LEGENDS

Fig. 1: Effects of initial host density and host age on host survivorship in the absence of parasitoids. The data point for Hatch (Host Age 3 days) applies to all five initial host density treatments.

Fig. 2: Effects of initial host density and host age on host weight in the absence of parasitoids. The Host Age 0 datum is the mean egg weight, $26.1 \pm 0.5 \mu\text{g}$.

Fig. 3: Effects of initial *E. kuehniella* density and *V. canescens* density on median *E. kuehniella* maturation time.

Fig. 4: Effects of initial *E. kuehniella* density and *V. canescens* density on *E. kuehniella* adult weight. No line was fitted to the 3 *V. canescens* per container data due to inadequate degrees of freedom for regression analysis.

Fig. 5: Effects of initial *E. kuehniella* density and *V. canescens* density on *E. kuehniella* fecundity (\equiv lifetime *per capita* eggs laid). Lines for the 1- and 3-parasitoid treatments are the means of the data subsets for those treatments.

Fig. 6: Effects of initial *E. kuehniella* density and *V. canescens* density on *E. kuehniella* egg weight. Lines represent the means of the data subsets for the 0-, 1- and 3-parasitoid treatments.

Fig. 7: Effects of initial *E. kuehniella* density and *V. canescens* density on median *V. canescens* maturation time (from initial *V. canescens* introduction into containers). Lines for the 1- and 3-parasitoid treatments are the means of the data for those treatments.

Fig. 8: Effects of initial *E. kuehniella* density and *V. canescens* density on *V. canescens* adult weight.

Fig. 9: Effects of initial *E. kuehniella* density and *V. canescens* density on the total emergence of adults (*E. kuehniella* + *V. canescens*).

Fig. 10: *E. kuehniella* population growth rate (initial host density x survivorship x fecundity) as a function of initial *E. kuehniella* density.

Fig. 11: Comparison of linear and three nonlinear regression models of *E. kuehniella per capita* population growth rate (survivorship x fecundity) as a function of initial *E. kuehniella* density. Error bars represent 95% confidence intervals for the regression data set (e.g. $\alpha = 0.05$, so that $z = 1.96$ in eqn 1).

Figure 1

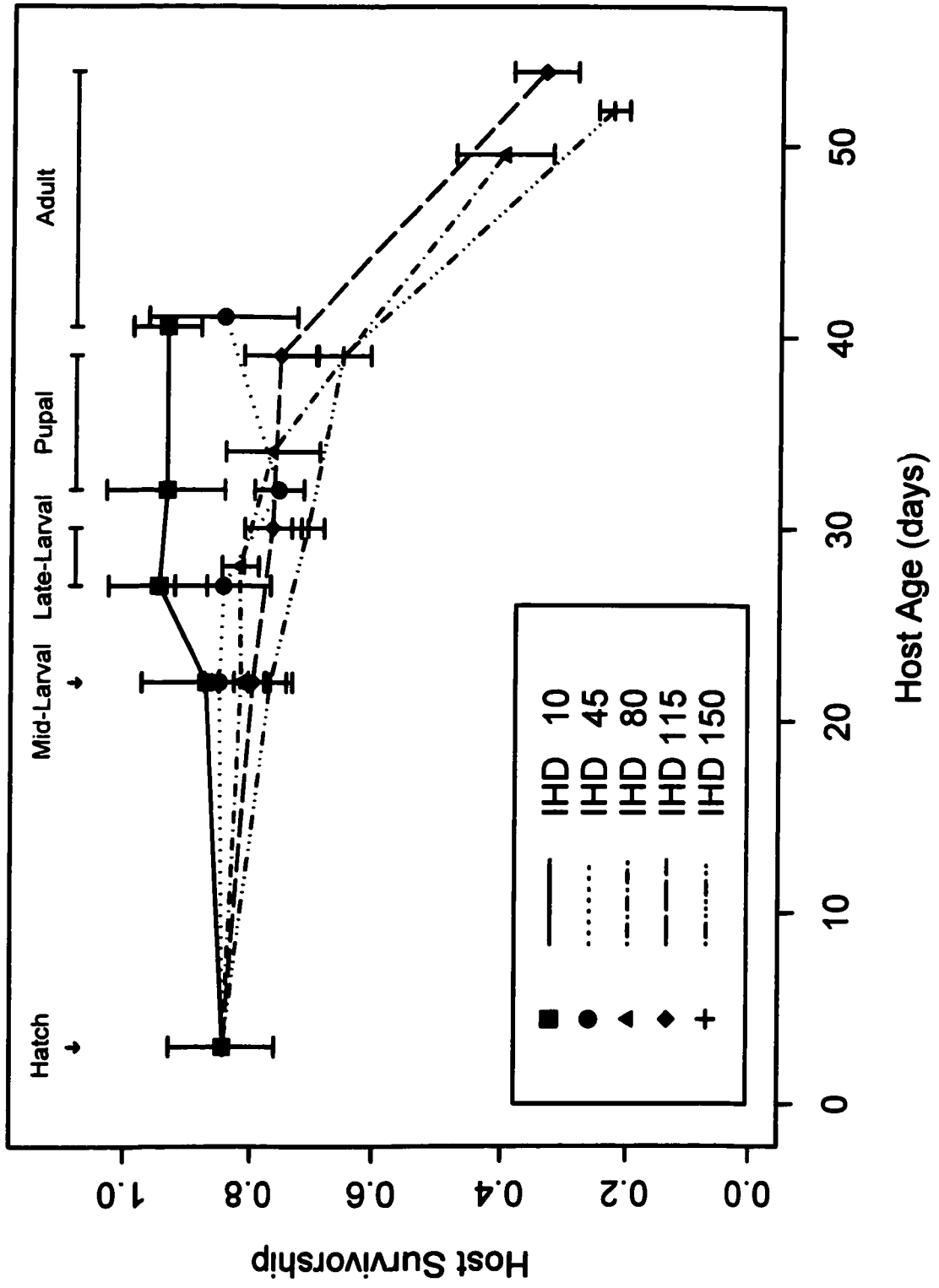


Figure 2

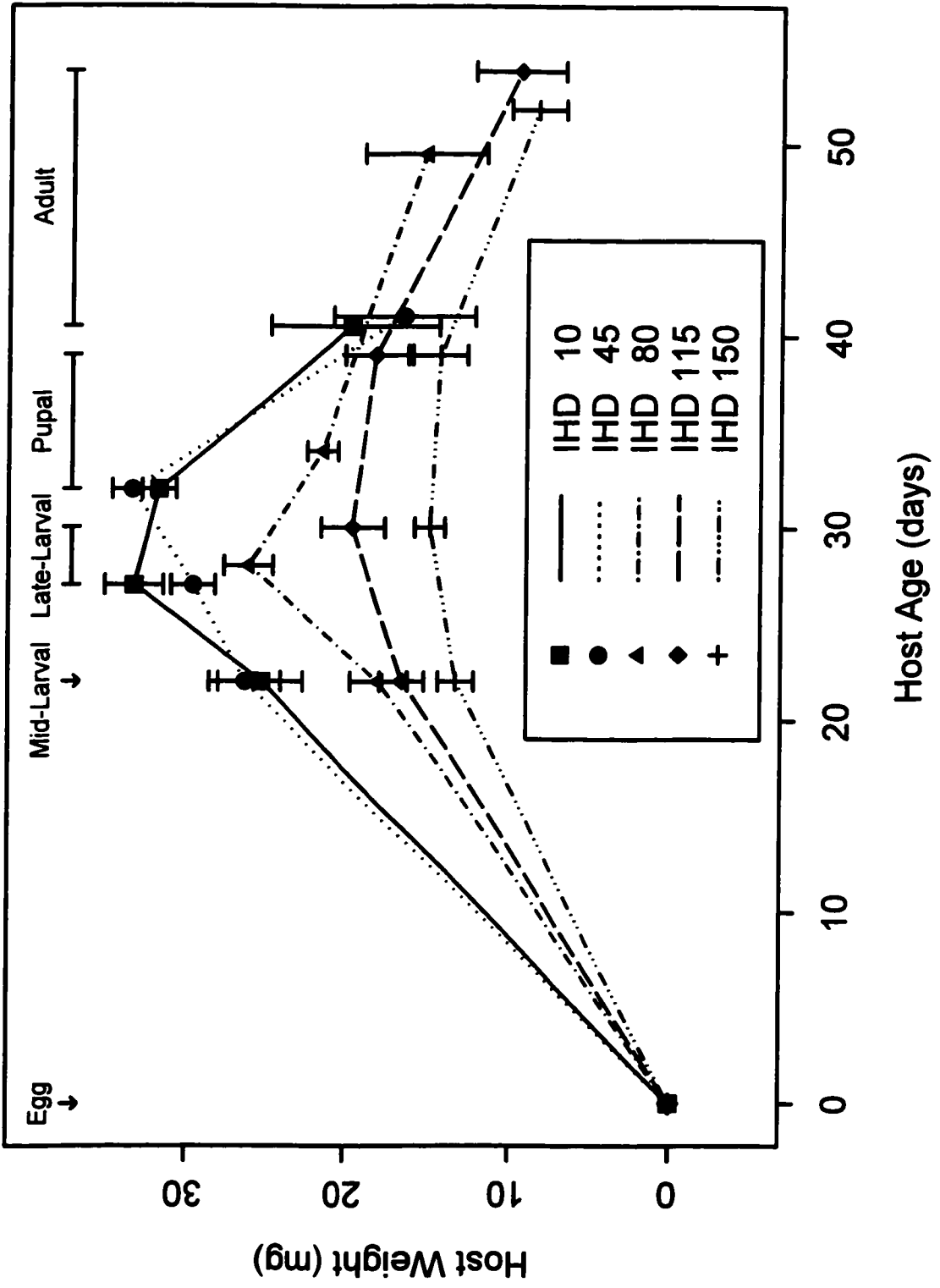


Figure 3

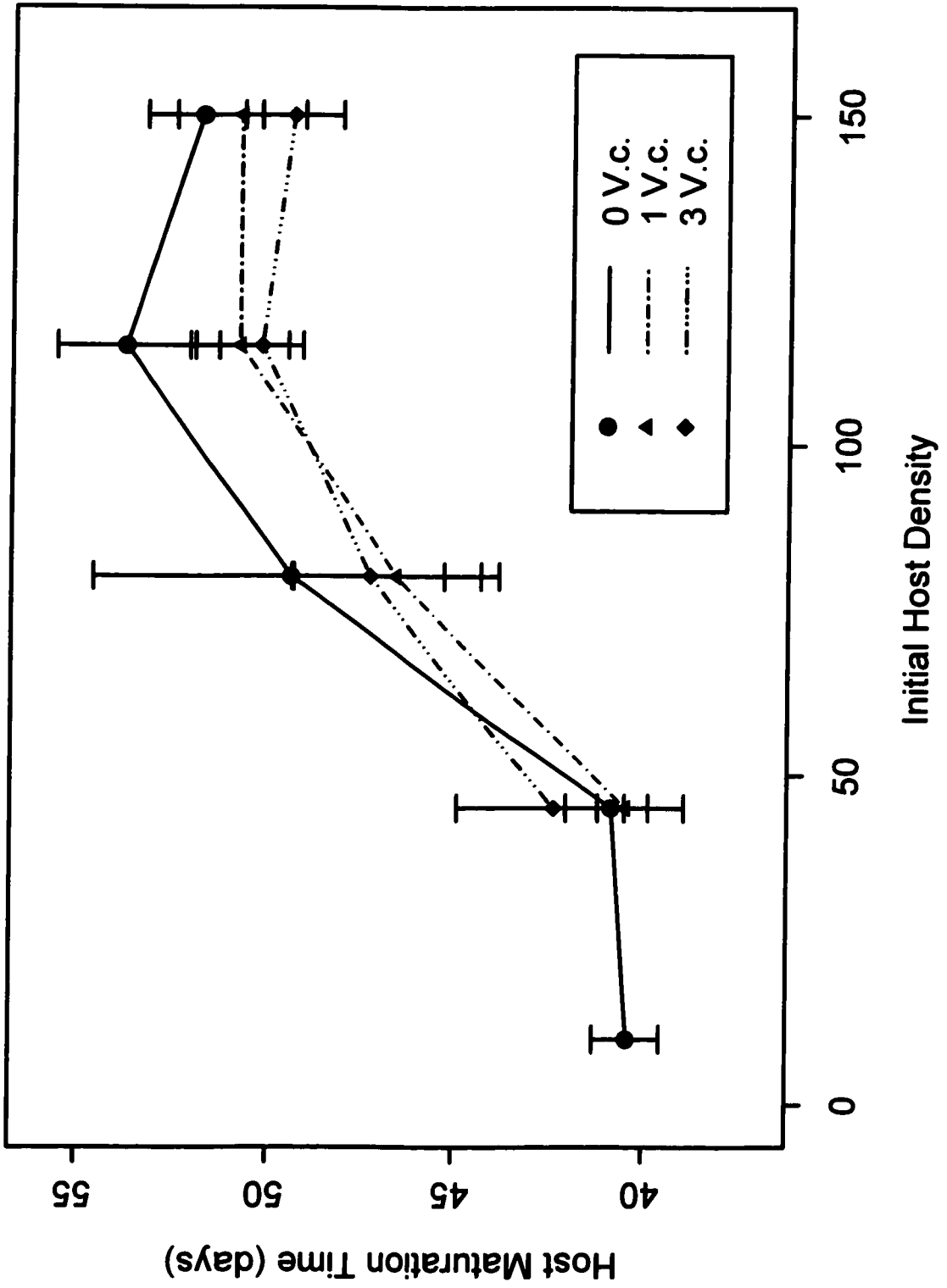


Figure 4

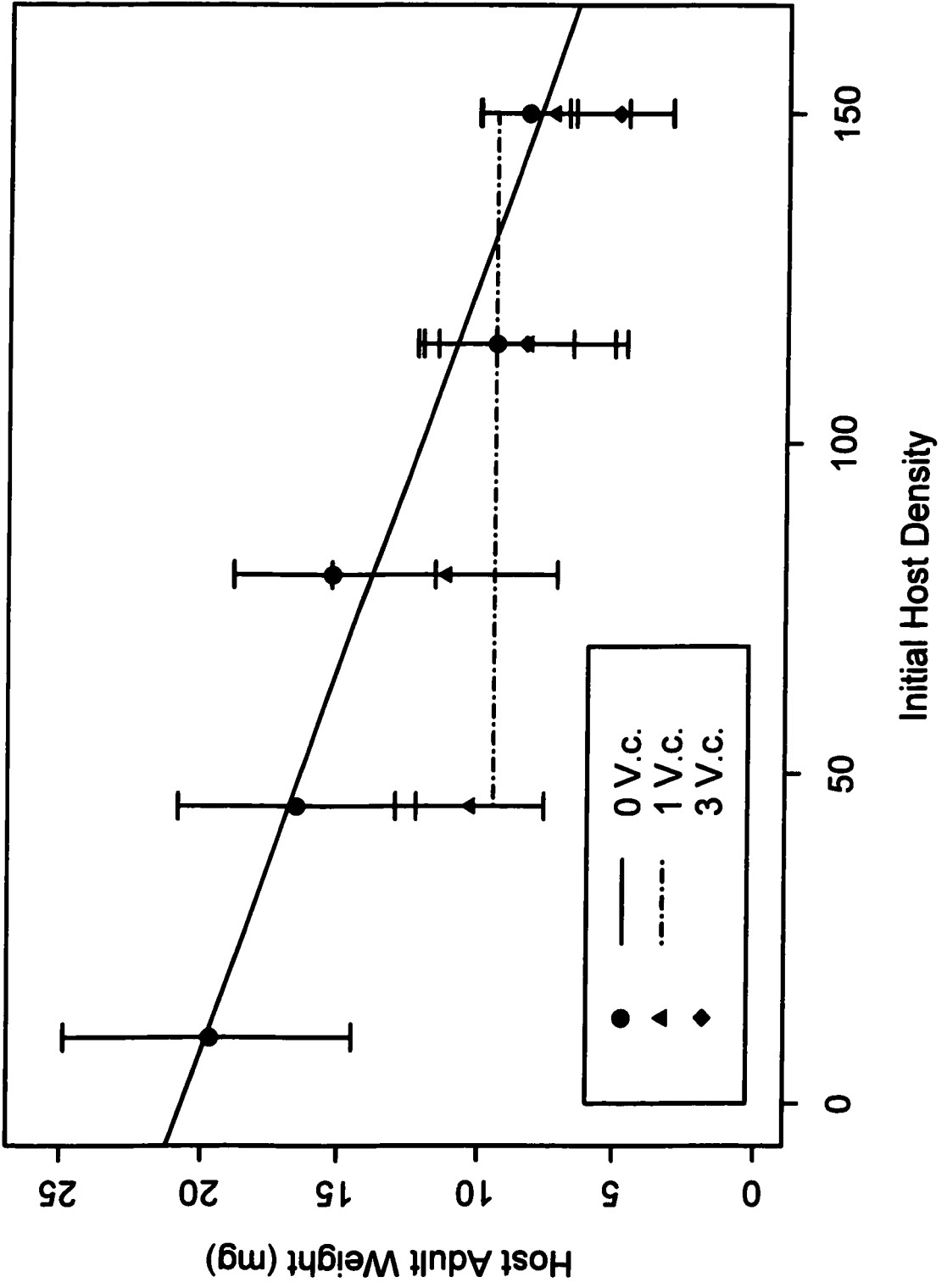


Figure 5

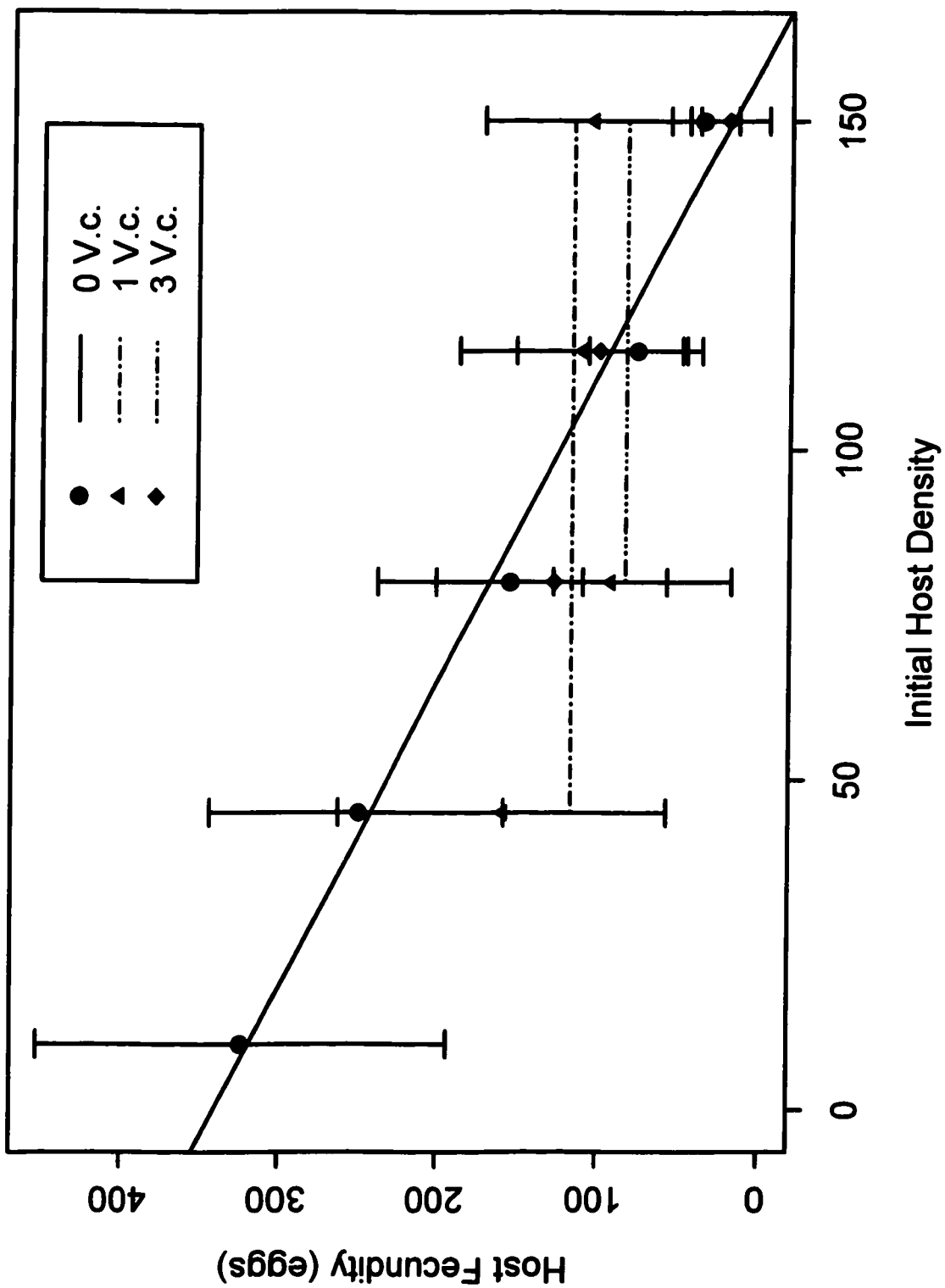


Figure 6

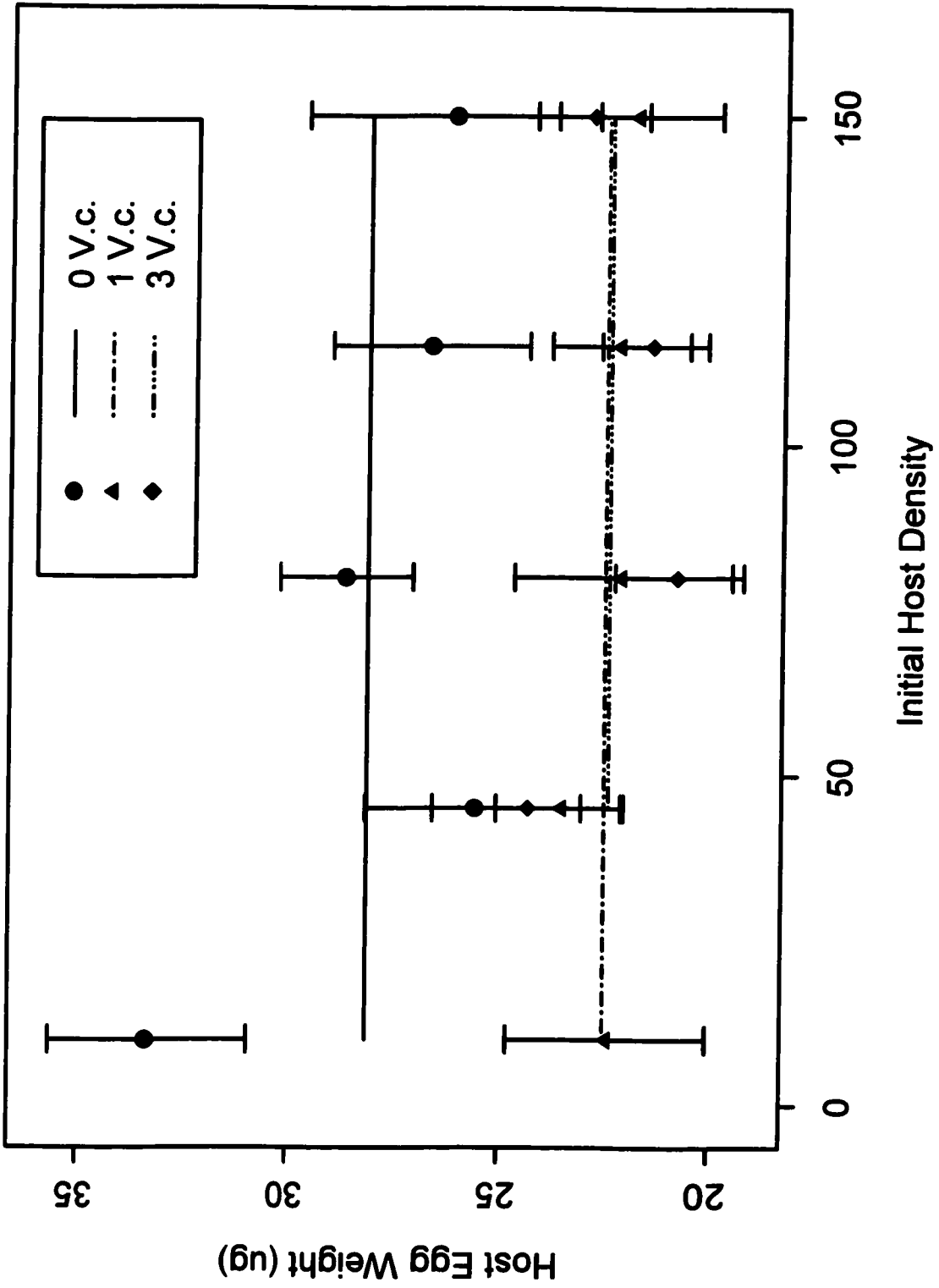


Figure 7

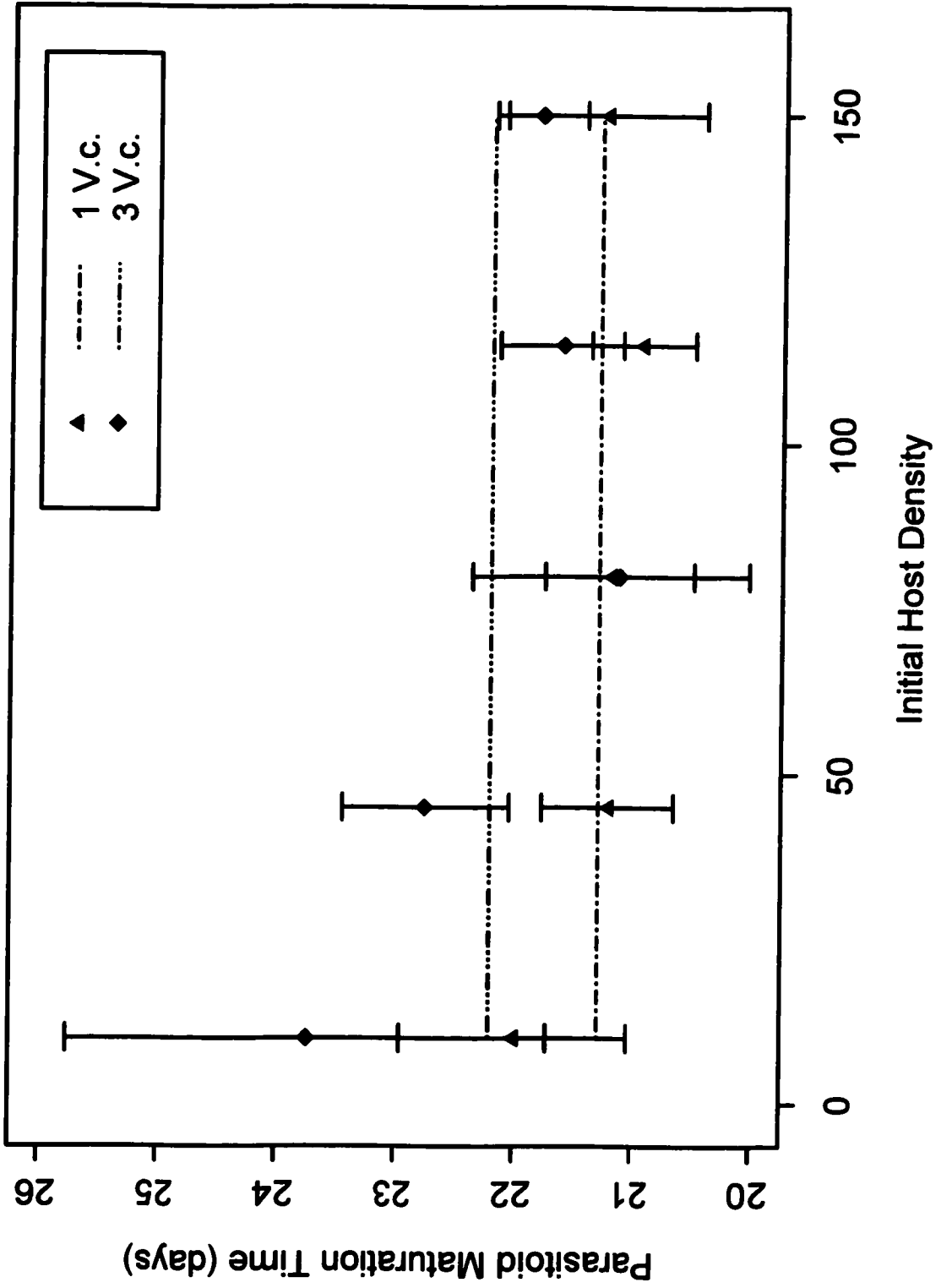


Figure 8

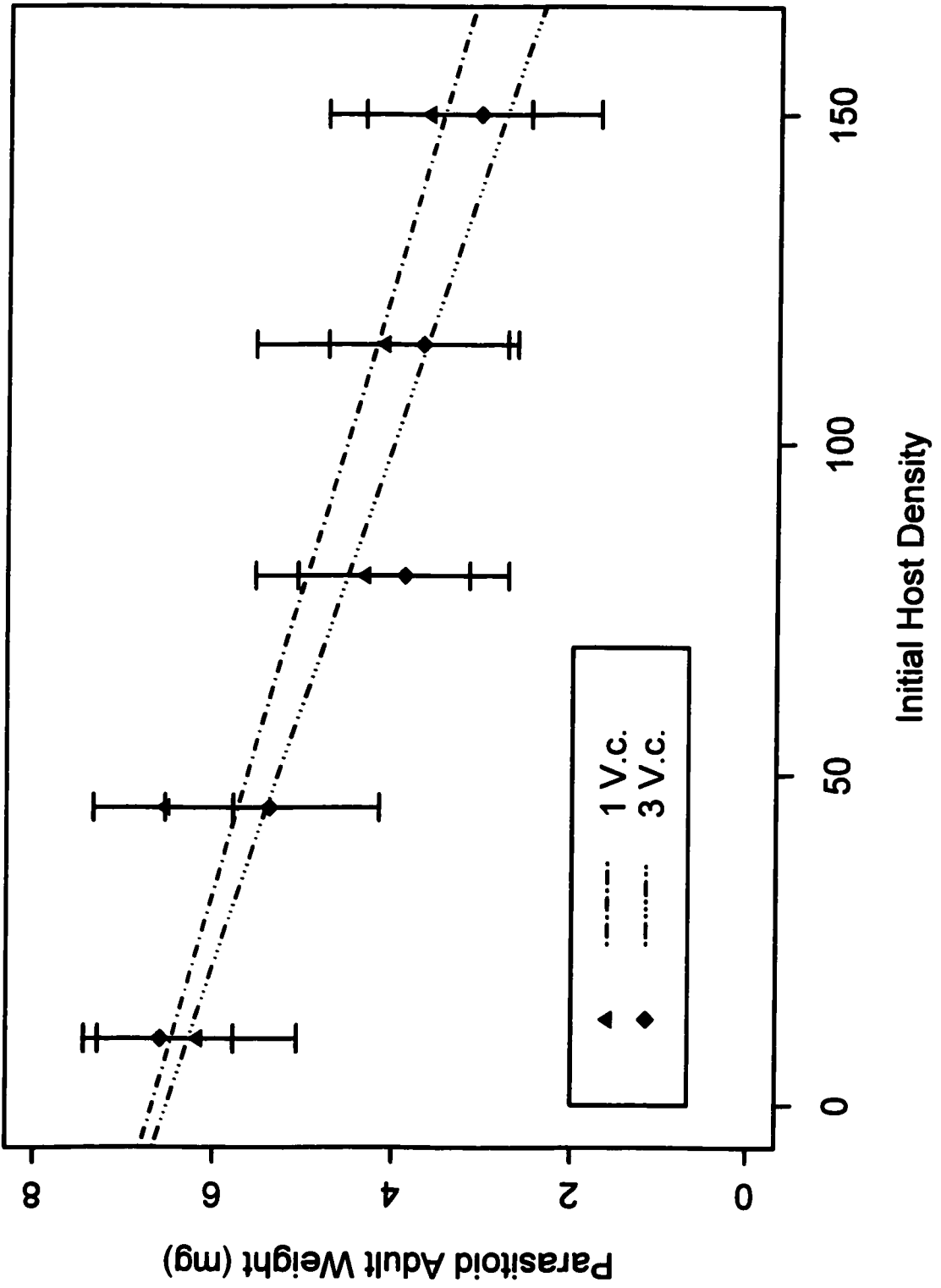


Figure 9

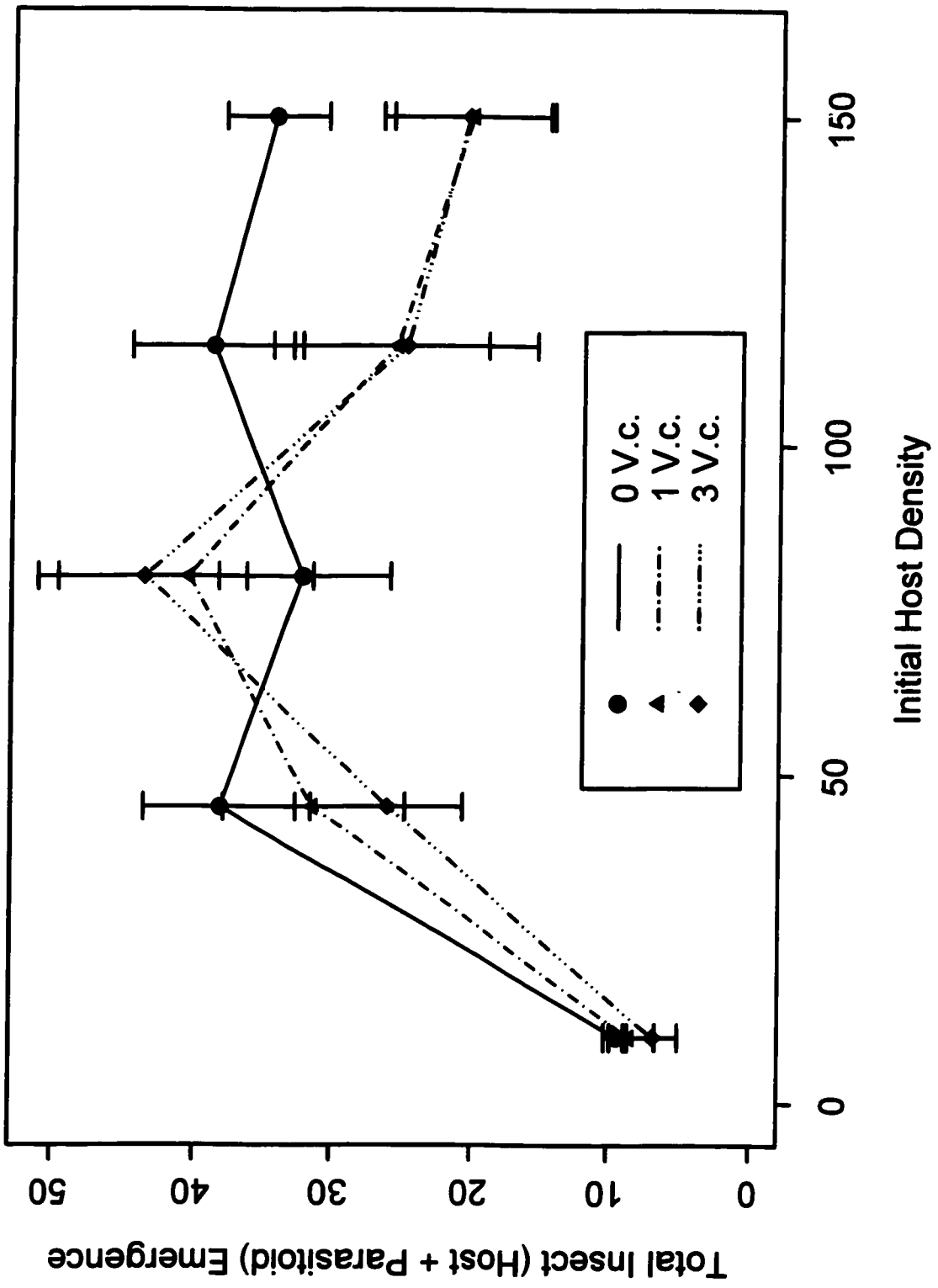


Figure 10

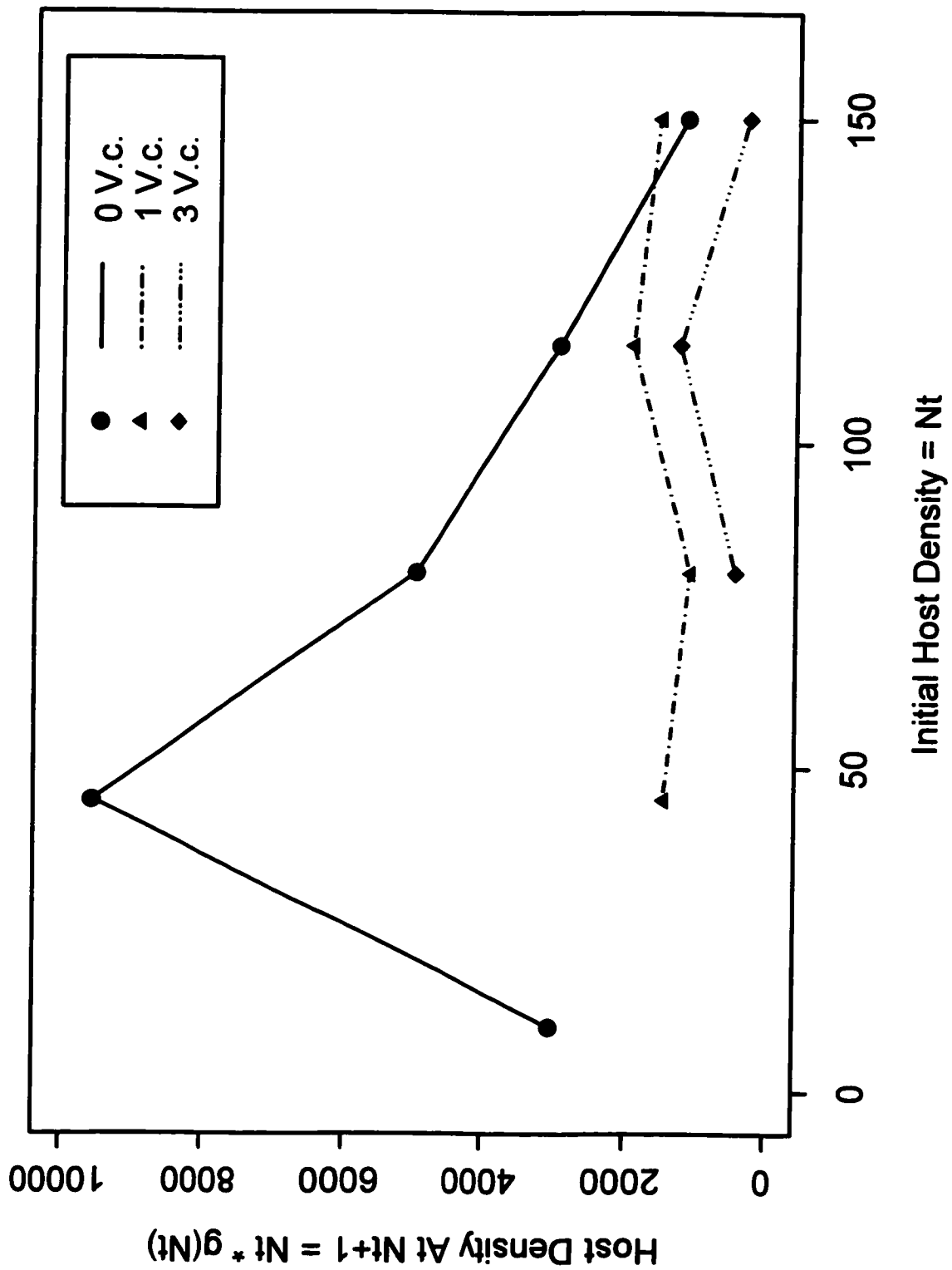
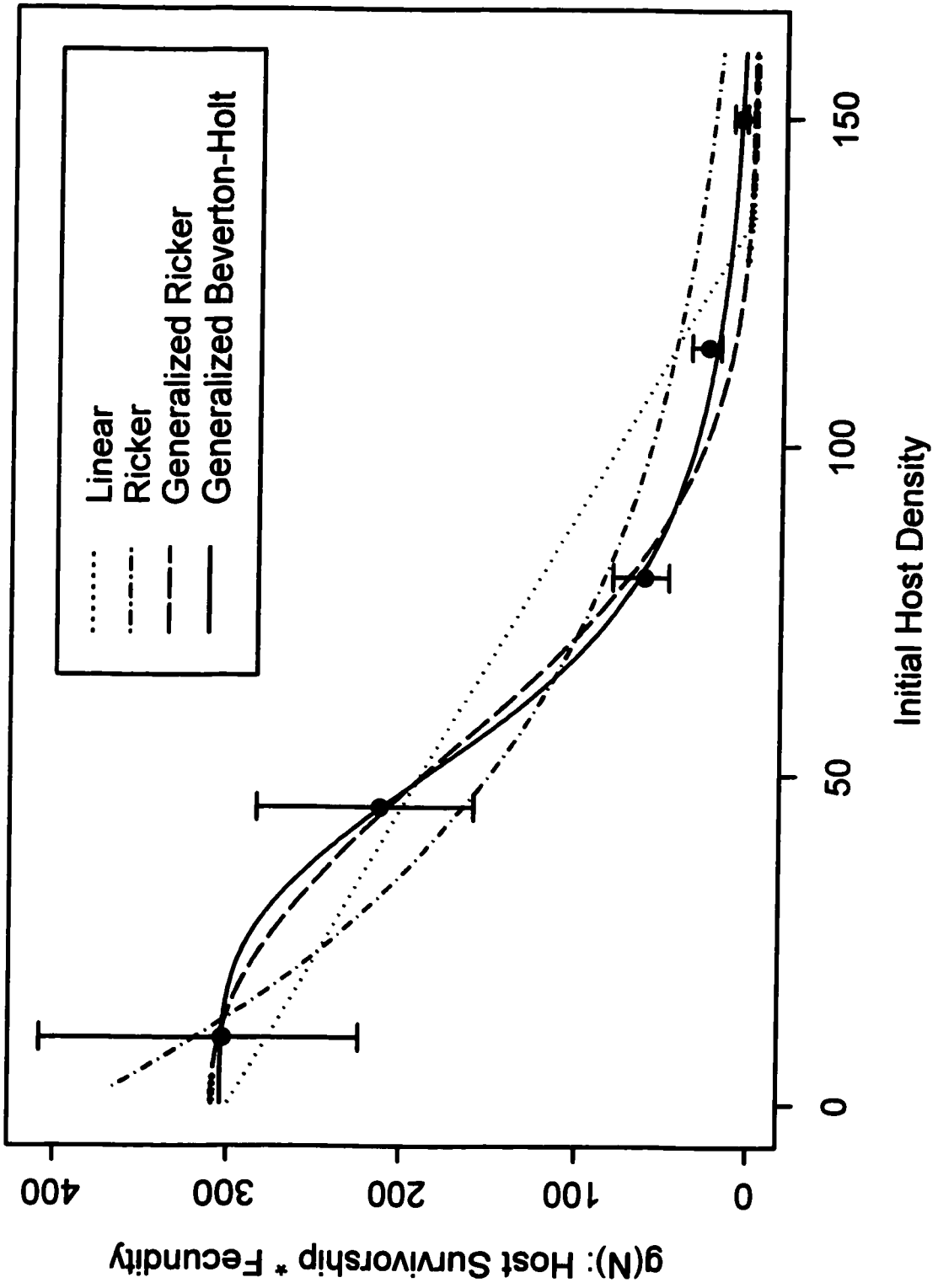


Figure 11



4. COMPETITIVE EXCLUSION AND RESOURCE PARTITIONING IN MULTIPARASITOID – HOST SYSTEMS

INTRODUCTION

A great deal of ecological theory suggests that competing species cannot coexist on a single, non-replaceable resource unless the resource is partitioned in some way (Grinnell, 1904; Volterra, 1928; Lotka, 1932; Udvardy, 1959; Hardin, 1960; Tilman, 1982, 1990; Holt et al. 1994). Thus, it might be expected that consumers competing for the same resource are either polyphagous or that they have evolved strategies to reduce competition through resource partitioning. Parasitic wasps, however, are often host specific, and their hosts are attacked by multiple parasitoid species (Zwölfer, 1971; Hochberg & Hawkins, 1994). The mechanisms that maintain multiparasitoid complexes on particular host species are not well understood, although such understanding is motivated by issues relating to the biological control of insect pests (Hassell, 1978; May & Hassell, 1988; Godfray, 1994; Mills & Getz, 1996; Murdoch & Briggs, 1996; Briggs et al., 1999; Mills, 2000), and by similarities to communities of helminth parasites (Sousa, 1994).

A long-standing debate exists concerning the potential benefits or liabilities of introducing multiple enemies in biological control introductions. Workers arguing the merits of this approach, often largely on theoretical grounds, have emphasized the potential benefits for host density reduction as a result of increased enemy presence, and have suggested that the enemies will sort

themselves out in the field, with the best competitor displacing all others and, by virtue of being the best competitor, provide maximal pest control and reduction (Smith, 1929; Thompson, 1939; Doult, 1961; van den Bosch, 1968; Hassell & Varley, 1969; Huffaker et al., 1971; Hassell, 1978; May & Hassell, 1981, 1988; Münster-Swendsen, 1982; Waage & Hassell, 1982; Hogarth & Diamond, 1984). These predictions are qualitatively identical to those obtained by Tilman (1982, 1990) in considering plants competing for a single limiting resource. He found that the best competitor is the one that can survive on the least amount of the resource, and, by drawing it down below the level needed for other competitors to persist, displace all other competitors (but see Getz & Schreiber, 1999).

Alternatively, researchers arguing against multiple enemy introductions have pointed out, often with the support of field data, that such introductions often result in higher pest densities and less effective pest control than can be obtained by the best enemy species alone (Pemberton & Willard, 1918; Utida, 1953; Turnbull & Chant, 1961; Zwölfer, 1963; Watt, 1965; Turnbull, 1967; Godfray & Waage, 1991; Briggs, 1993; Briggs et al., 1993). They have often emphasized the need to evaluate, prior to release, the efficacy of each individual enemy, and the subsequent release of only the most effective one. Furthermore, as Ehler and Hall (1982) have noted, sequential multiple introductions often result in species which are introduced later being unable to establish themselves due to reduced availability of pests. This can result in inferior pest suppression if those species introduced later would otherwise have provided better control. Because it has

become clear that the consequences of multiple introduction are highly situation- and biology-specific (e.g. Kakehashi et al., 1984), it is important to understand how such specifics influence the outcomes of this approach.

As alluded to above, much of the insight into the outcomes of multiple enemy introductions, and into the general issue of multiple parasitoid-species coexistence on a single host species, has come from theoretical modeling studies, dating back to those of Nicholson (1933) and Nicholson and Bailey (1935). Modern studies have focused on a variety of ecological aspects of such coexistence, including the effects of, and consequences for, spatial patterns (Münster-Swendsen, 1982; Hassell et al., 1994); whether or not the parasitoids are generalists or specialists (Hassell & May, 1986; Wilson et al., 1996); and the broader categories of invasion and competitive exclusion (Armstrong & McGehee, 1980; Crawley, 1986; Gutierrez et al., 1993), and generalized consumer-resource interactions (Koch, 1974a, b; Holt et al., 1994; see Barlow & Wratten, 1996; Mills & Getz, 1996; Murdoch & Briggs, 1996; Briggs et al., 1999; Hochberg & Holt, 1999 and Hassell, 2000a, b for recent reviews of host-parasitoid models). Additionally, there has been a great deal of work addressing the unequal exploitation of the host population by individuals in a single parasitoid population (Hochberg & Holt, 1995). None of these studies, however, have addressed the consequences of *explicit* limitations on the abilities of *multiple* parasitoid populations to attack their hosts, either due to the effects of explicit refugia, or to those of egg and/or fecundity limitation (see the Introduction to

Ch. 2 for the definition of fecundity limitation). It is worth noting that spatial and/or temporal heterogeneity has been incorporated in to many of these models in a variety of ways (e.g. May & Hassell, 1981; Briggs et al., 1993), and that such heterogeneity does provide a refuge effect due to attack aggregation and the consequently reduced probabilities of attack for some hosts (Mills & Getz, 1996) . But it is also clear that, in particular, an *explicit* constraint on the ability of parasitoids to successfully attack hosts (e.g. fecundity limitation), can have impacts on the dynamics of host-parasitoid interactions apart from, or in addition to, those of spatial and/or temporal heterogeneity (Getz & Mills, 1996; Ch. 2).

Thompson (1922, 1924, 1929) was the first researcher to examine the theoretical effects of egg limitation on host-parasitoid dynamics by utilizing simple mathematical models. Modern workers have largely discounted or ignored the importance of egg limitation in the context of such simple models, although studies utilizing more complex models have considered its effects (Griffiths & Holling, 1969; Münster-Swendsen & Nachman, 1978; Yamamura & Yano, 1988; Kidd & Jervis, 1989; Shea et al., 1996). This tendency to discount the importance of egg and/or fecundity limitation is probably in part due to the mathematical equivalence of egg-limitation submodels with those for the effects of handling time (Getz & Mills, 1996), which has been shown empirically *not* to be of significant importance to parasitoids (Hassell, 1978). Clearly, however, the two processes operate by different mechanisms, as evidenced by empirical

results, in spite of being modeled in mathematically similar ways. There has very recently been an increase in attention paid to this phenomenon (Getz & Mills, 1996; Shea et al., 1996; Ch. 2), doubtless due to the empirically demonstrated importance of egg and/or fecundity limitation to parasitoid behavioral ecology (Heimpel et al., 1996; Van Alebeek et al., 1996; Heimpel et al., 1998; Heimpel & Rosenheim, 1998; Rosenheim, 1999), and, consequently, to host-parasitoid population dynamics. Furthermore, it has been shown that parasitoid fecundity can be a significant determinant of the success or failure of biological control (Stiling, 1990). Thus, a stronger theoretical understanding of the effect of fecundity limitation on host-parasitoid population dynamics will enhance the understanding of basic consumer-resource dynamics, as well as improve the chances of successful biological control.

The model used here is based on the discrete-generation approach pioneered by Thompson (1929) and Nicholson and Bailey (1935), which has since been elaborated by many other workers (see Barlow & Wratten, 1996, and Mills & Getz, 1996 for reviews). The general mathematical structure of this model has been outlined elsewhere (Hassell, 1978; May, 1978; May & Hassell, 1981; Barlow & Wratten, 1996; Getz & Mills, 1996; Mills & Getz, 1996; Ch. 2), but is briefly reviewed in the following sections for the purpose of focusing the reader's attention on aspects of the approach which are potentially confusing or controversial. In particular, because this analysis considers a discrete-generation, synchronized host-parasitoid system, it is possible to simplify the modeling of

the dynamics by ignoring the effects of population structure within the host and/or parasitoid populations (Hassell, 1978). For this reason a purely discrete-time modeling formulation is adopted here. It has been argued elsewhere that the continuous-time, stage-structured Lotka-Volterra-based approach (Murdoch & Briggs, 1996), or the approach combining elements of discrete-time modeling for between-generation dynamics with continuous-time modeling for within-generation dynamics (Godfray et al., 1994; Rohani et al., 1994), are more appropriate and useful for understanding host-parasitoid dynamics than the more traditional approach utilized here. Such approaches, while leading to significant insights about the dynamics of host-parasitoid systems, are mathematically more complex than this standard discrete-time general model. By retaining a model with a simple basic structure it is possible to more closely focus on the biological questions at hand, and to effectively compare the results obtained using this approach with those already in the literature.

The majority of theoretical treatments of this topic (including this one) take an ecological, rather than evolutionary, modeling approach (see Rosenheim, 1996; Mangel & Heimpel, 1998; Sevenster et al., 1998 and Rosenheim, 1999 for exceptions). It is possible, however, to make generalized hypotheses about the patterns of evolution in parasitoids on the basis of these models. When such predictions are upheld, they provide support for the logic and the assumptions of the model. When they are not upheld, it calls into question the generality of the model, and potentially casts doubts on its underlying assumptions.

This chapter presents a dynamical analysis of a generalized two-parasitoid, one-host model which represents an extension of the one-parasitoid model (Ch. 2). Analytical attention is focused on the form of the host-parasitoid encounter rate (the discrete-time equivalent of the predator functional response, Getz & Mills, 1996), utilizing a submodel in which the parasitoids are search-limited when hosts are at low densities and fecundity-limited when hosts are at high densities (i.e. a Holling Type II saturating functional response; Holling, 1959). The ways in which this encounter rate interacts with the host population's intrinsic growth rate, host density-dependence and parasitoid aggregation to affect the dynamical stability of the model and the host population's equilibrium density are examined in detail. Finally, these results are then compared to those obtained previously for multiple-parasitoid systems, for the purposes of understanding the ways in which competition between parasitoid populations can lead to resource partitioning (in the absence of density-dependent parasitoid sex ratios – see the next section), and in order to detail the conditions under which multiple parasitoid biological control introductions provide better (or worse) control of hosts than single-species introductions. These comparisons are part of a general discussion of the utility of analyses such as the one outlined in this chapter for practitioners of biological control.

THE MODEL

The dynamical properties of a synchronized two-parasitoid, one-host system where the parasitoids have Holling Type II functional responses have not been previously described (but see Godfray et al., 1994). The model used here for this purpose is structurally identical to that used by May and Hassell (1981), with the distinction that the form of the parasitoid encounter rate submodel for each parasitoid is that proposed by Getz and Mills (1996) and utilized in the one-parasitoid case presented in Ch. 2. Here, N_t denotes the host density, and P_t and Q_t the density of parasitoid females of two distinct populations, at time t . Parasitoid populations P and Q both attack N , and are thus in direct exploitation competition for their host resource. P and Q may represent either separate species or two reproductively isolated phenotypes of the same species, where each phenotype has a different strategy for attacking host individuals.

As in Ch. 2, for clarity of presentation, the model is written here in a form that explicitly identifies the functions $\varepsilon_t^P = \varepsilon(N_t, P_t)$ and $\varepsilon_t^Q = \varepsilon(N_t, Q_t)$ (Getz & Mills, 1996; Mills & Getz, 1996), which represent the mean number of hosts encountered per parasitoid per unit area (per generation) for parasitoid populations P and Q respectively, and which are referred to as the encounter rate for P and Q . Further, allowing the functions $f_P = f_P(\varepsilon_t^P)$ and $f_Q = f_Q(\varepsilon_t^Q)$ to represent the proportion of hosts escaping attack by the parasitoid populations P and Q respectively, the function $g(N_t)$ to represent the *per-capita* growth rate of

the host population from one generation (time period) to the next in the absence of parasitoids, and the constants c_P and c_Q to be the average number of adult female parasitoids of populations P and Q respectively that emerge from an attacked host, results in the model used here taking the following form:

$$\begin{aligned} N_{t+1} &= N_t g(N_t) f_P(\varepsilon_t^P) f_Q(\varepsilon_t^Q) \\ P_{t+1} &= c_P N_t [1 - f_P(\varepsilon_t^P)] \\ Q_{t+1} &= c_Q N_t f_P(\varepsilon_t^P) [1 - f_Q(\varepsilon_t^Q)] \end{aligned} \quad (1)$$

Note that the parasitoid sex ratio, reflected in the values of c_P and c_Q for parasitoid populations P and Q respectively, is assumed to be independent of population density, even though it is known that parasitoid sex ratios can, to some extent, be influenced by population density (Hassell et al., 1983; Comins & Wellings, 1985), and can, in turn, influence ecological stability and parasitoid competitive ability (Kaitala & Getz, 1992).

In this analysis, the host *per-capita* population-growth-rate function g is either a constant function, independent of N ,

$$g(N) = \lambda \quad (2)$$

where $\lambda > 1$ is a constant *per-capita* rate of increase (representing the density-independent host, or DI, case); or g is an appropriate density-dependent function (the DD case), where the Ricker form (with density-independent growth rate parameter $r \equiv \ln \lambda$ and carrying capacity parameter K)

$$g(N) = \exp \left[r \left(1 - \frac{N}{K} \right) \right] \quad (3)$$

is used here to facilitate ease of analysis and comparison with prior efforts, although other forms of the function $g(N)$ may more accurately depict the actual processes of density dependence (Bellows, 1981; Getz, 1996; Ch. 3).

As in Ch. 2, the form for f used here is that taken from May (1978), who introduced an escape function based on the zero term of a negative binomial distribution with mean ε_i^P , and aggregation parameter $k_P > 0$. This approach yields

$$f_P(\varepsilon_{P,i}) = \left(1 + \frac{\varepsilon_{P,i}}{k_P}\right)^{-k_P} \quad \text{and} \quad f_Q(\varepsilon_{Q,i}) = \left(1 + \frac{\varepsilon_{Q,i}}{k_Q}\right)^{-k_Q} \quad (4)$$

as the proportion of hosts escaping attack for parasitoid populations P and Q respectively.

Finally, and again as in Ch. 2, the form of the mean encounter rate for each parasitoid is that used by Getz and Mills (1996), which embodies a Holling Type II saturating functional response in the parasitoids (Holling, 1959; Getz & Mills, 1996; Mills & Getz, 1996), and which gives

$$\varepsilon^P = \frac{a_P \beta_P P}{\beta_P + a_P N} \quad \text{and} \quad \varepsilon^Q = \frac{a_Q \beta_Q Q}{\beta_Q + a_Q N}. \quad (5)$$

It should be noted here that the general model (eqns 1) contains a structural distinction between the two parasitoid populations, which may be interpreted in one of two ways (May & Hassell, 1981). This structure can represent an order of attack during the host's life-cycle, such that hosts attacked by parasitoid P are unavailable for attack by parasitoid Q . Alternatively, this structure can be seen

as a deterministic outcome to parasitoid larval competition within the host, where such competition exists, such that parasitoid P always emerges from any host parasitized by both P and Q . These interpretations are mathematically equivalent, and without loss of generality it can be simply stated that P attacks first, and that hosts attacked by P are unavailable for attack by Q . This assumption can be relaxed, and a model formulated that is symmetric with respect to the timing of the attack strategies of individuals in populations P and Q , under the assumption that the “first attacker wins” (Takehashi et al., 1984; Schreiber et al., 2000). In such a model, however, the relative advantage of being the first to attack cannot be evaluated, as is done in this chapter. Thus, the difference in parasitoid strategies (described below) may be purely the difference in the timing of attack during the host's life-cycle, or could include a difference in attack efficiency and/or lifetime fecundity.

The behavior of the system described by eqns 1 with mean encounter rates given by eqns 5 is a direct generalization of May and Hassell's (Hassell, 1978; May & Hassell, 1981) analysis of eqns 1 under the assumption of purely search-limited encounter rates, and thus their analysis serves as a baseline for understanding the effects of fecundity limitation and density dependence in the more general formulation of an encounter rate given by eqns 5.

This model was examined under the assumptions of linear and density-dependent host-population growth (the density-independent and density-dependent, or DI and DD, scenarios, incorporating eqns 2 and 3 respectively).

Despite the relative simplicity of this model, the forms of the functions f and ε prevent obtaining closed-form expressions for the host and parasitoid equilibrium densities (see the Appendix). Thus, stability and host-suppression results were obtained numerically (see the Appendix sections *the equilibrium conservation equation* and *numerical analysis and simulation*), which required assumptions about appropriate simulation initial conditions (see the next subsection and the Appendix section *parameter values*).

INITIAL CONDITIONS

The need to analyze the 3D systems resulting from eqns 1 via simulation requires choosing simulation initial conditions. The focus here on the dynamics of invasion and coexistence leads naturally to two different initial condition scenarios. Under either scenario, the equilibrium densities of a system consisting of a host and a single resident parasitoid species (or phenotype) are first determined. The other parasitoid is then introduced to this system. Note that all scenarios are considered in pairs, with each parasitoid in turn serving as the resident, to avoid introducing a bias due to the relative timing of attack by the two parasitoids in the host's life-cycle. This can cause the parameter values of the resident to change if they differ between the two parasitoids, which influences the amount of host suppression provided by the addition of the second parasitoid (see the subsection *consequences for host suppression*).

After determining the host and resident equilibrium densities, the two parasitoids are brought together with the host in one of two ways. In the invasion scenario, the host and the resident parasitoid are at their equilibrium densities as described above, and the other parasitoid species or phenotype is introduced into the system at a density $1/1000^{\text{th}}$ that of the resident's equilibrium density (i.e. $1/1000^{\text{th}}$ that of the other parasitoid's initial density). Note that for some combinations of parameter values the only difference between the two parasitoids is that they attack at different times in the host's life-cycle, and that they have different initial densities. In the coexistence scenario this last distinction is removed. Having first determined the host and resident parasitoid equilibrium densities in the absence of the introduced parasitoid, the two parasitoid species (or phenotypes) are brought together with the host species, each parasitoid's initial density being half that of the resident's equilibrium density in the absence of the second parasitoid. These two cases thus represent extremes on a continuum of "resident : introduced" parasitoid initial density ratios: 1000 : 1 versus 1 : 1.

It is important to emphasize that the host and resident parasitoid parameter values for the initial 2D (\equiv one-host, resident-parasitoid) system, were chosen such that the system was *insured* to have a *stable* equilibrium. Because of this it was not possible to explore the equilibrium dynamics of systems in which *both* one-host, one-parasitoid systems were unable to achieve equilibrium. Such systems include those in which $k_R > 1$ and the host is not self-limiting (the "R"

subscript indicates the resident; the subscript “*I*” is used where appropriate to indicate the introduced parasitoid). Furthermore, the values of λ were kept low enough to insure coexistence for the values of β_R used (Getz & Mills, 1996; Ch. 2). To allow effective comparisons between the coexistence and invasion initial condition scenarios, and between the DI and DD cases, these restrictions were carried over into systems for which it was not strictly necessary for the sake of 2D stability (e.g. the coexistence scenarios, which conceptually do not require a stable 2D system to be present prior to parasitoid introduction; or systems in which the host was self-limiting).

The invasion and coexistence scenarios correspond to two different biological control scenarios. In the invasion case, the pest (host) is maintained at some equilibrium density by the resident parasitoid, and a second parasitoid is introduced at low density, with the hope of improving control of the pest. The coexistence case represents a simultaneous biological control introduction of two parasitoids (at high densities) into a system consisting of only the pest (host), and represents an example of a multiple-parasitoid classical biological control introduction.

While the invasion and the coexistence scenarios, by virtue of their differing initial conditions, had the possibility of leading to different dynamical outcomes, this did not prove to be the case. Simulations show that the three-species equilibria exhibit only local stability, but they also reveal that the domains of attraction are fairly large, in particular encompassing both sets of initial

conditions. Because they provided identical outcomes, the arbitrary choice was made to present only the coexistence scenario outcomes in the dynamical analysis. It is important to note, however, that it is nonetheless possible to apply an invasion criteria to these systems. The appropriate criteria is that successful invasion requires the invading (or introduced) parasitoid to have a positive growth rate when its density is low (Murdoch & Briggs, 1996). It is thus possible to discuss the success or failure of an invasion attempt, and whether or not the successful invader subsequently displaces the resident, even though there is no distinction between the outcomes resulting from the two sets of initial conditions.

RESULTS

SEARCH EFFICIENCY AND FECUNDITY: THE BASIC RESULT

In spite of a wide range of initial condition and parameter value combinations, the outcomes of these simulations fell into a very small number of distinct categories. With respect to the relationship between the search efficiencies and fecundities of the two parasitoids, a single structure repeatedly emerged. Fig. 1 illustrates this basic equilibrium stability result for eqns 1; all the other dynamical results (Figs. 2-9) are variations on the theme laid out in Fig. 1.

For each simulation one of five outcomes is possible: the host can coexist with P in the absence of Q ; the host can coexist with Q in the absence of P ; the

host can coexist with both P and Q , with all three species at mathematically stable equilibrium densities (indicated by light shading in the figures); the host can coexist with both P and Q with all three species experiencing bounded but varying densities through time (unstable equilibrium or oscillatory coexistence, indicated by dark shading in the figures); and finally the host population can grow unbounded with either or both of the parasitoid populations going extinct, or growing without bound but at a slower rate than the host population growth rate (indicated by black shading in the figures; Fig. 1). Note that this last outcome is possible only when the host is not self-limiting – host density-dependence is thus always a stabilizing feature of the model, as is expected and intended. Note also that there exist regions (very near the origin and as the values on both axes go to infinity) where one-host, one-parasitoid systems exhibit characteristic dynamics for such systems (e.g. the parasitoid over-exploits the host and drives the system to extinction, or where highly chaotic systems would eventually result in biological extinction). Such regions are not detailed in these figures – see Ch. 2 for a summary of such dynamics.

The general pattern of coexistence and stability for eqns 1 is demonstrated in each of the panes in Fig. 1. Proceeding outward from the origin into the interior of the first quadrant, a region exists where one of the parasitoids is able to exclude the other and to coexist with the host (P in the cases where Q is the resident, so that P 's search efficiency and fecundity are the denominators of the ratios on the axes; see the Appendix section *parameter values*, and the subsection

reversing the attack timing of resident and introduced parasitoid below). This region is bounded against the axes by a region of three-species coexistence (the shaded region, which is almost entirely stable in the cases illustrated in Fig. 1), and which in turn is bounded by a region where the other parasitoid is able to exclude the first and coexist with the host. Because variation on the axes is accomplished by varying the denominator of a ratio, decreasing the value of P 's search efficiency or fecundity leads to increases in the value obtained on the abscissa or ordinate, respectively. Thus the clear cause of this pattern is that, when both of P 's encounter rate and fecundity are high relative to those of Q , P excludes Q . As one or the other or both of P 's encounter rate and fecundity diminish relative to those of Q , three-species coexistence is permitted, and when one or the other or both drop too low to permit coexistence, P is excluded. Variations on this pattern are seen over the complete range of parameter combinations examined in this chapter (see the Appendix section *parameter values*).

For the parameter value combinations used to generate Fig. 1, three-species coexistence is not an uncommon occurrence. As will be seen, the relative abundance of coexistence parameter-space can change significantly with changes in the parameter values, particularly the host's population growth rate (see the subsection *host strategies: population growth rate and self-limitation below*).

Furthermore, in Fig. 1 almost all of the coexistence region is stable, three-species equilibrium coexistence. This too is subject to significant change as a result of

changes in parameter values, particularly parasitoid attack aggregation (see the subsection *parasitoid strategies: attack aggregation* below). But the relative positions of the two- and three-species coexistence regions are invariant across changes in parameter values.

Because the region of three-species coexistence is determined by the ratios of the parasitoid's fecundities and search efficiencies, the relative values of these parameters are more significant for parasitoid coexistence than their absolute values. It is possible to trade-off fecundity and search efficiency to allow three-species coexistence, and it is possible for two parasitoids with high or low fecundities and/or search efficiencies to coexist. The consequences for host suppression are much more strongly influenced by the absolute values of these parameters (see the subsection *consequences for host suppression* below).

The point (1, 1) on the panes of Fig. 1 is worthy of particular attention. This is the point where the search efficiencies and fecundities of the two parasitoids are identical, such that $a_P = a_Q \equiv a$ and $\beta_P = \beta_Q \equiv \beta$. Because the c 's and k 's of both parasitoids are also identical in this figure, this point indicates the scenario in which both parasitoids are identical in their strategies except for their order of attack [a *strict* (1, 1) scenario]. One might expect a competitive exclusion principle to operate and for the clearly inferior competitor Q , which always loses when superparasitism occurs, to be excluded by P . Yet this is not the case. In Fig. 1 the strict (1, 1) scenario always leads to stable three-species coexistence, meaning that such coexistence is possible even when one of the parasitoids has a

clear competitive disadvantage (see the subsection *reversing the attack timing of resident and introduced parasitoid*, below).

It is important to note that the (1, 1) scenario does not always lead to a stable three-species equilibrium, particularly when the values of the parasitoid aggregation parameters (k_P and k_Q) create an additional distinction between the two parasitoid populations, as will be shown in the following sections. In general, when parasitoid aggregation is not high (e.g. $k_P, k_Q \geq 0.75$, unlike the situation depicted in Fig. 1), increasing a or β or both is destabilizing under the (1, 1) scenario. This effect can potentially be offset if the host's intrinsic rate of increase (λ) is increased (under some circumstances by even as little as 10% or less), and/or if the strength of host density dependence is increased (K reduced), but the ability of these alterations to offset destabilization in this way depends on the values of the other parameters. Note, however, that under some circumstances increases in the host's intrinsic growth rate and/or strength of density dependence can act to *destabilize* the three-species equilibrium under the (1, 1) scenario, in favor of two-species coexistence (which can be stable or unstable), or the extinction of both parasitoids. Also bear in mind that these generalizations apply only to the (1, 1) scenario. But it is worth reemphasizing that, over the range of parameter values examined here, it is often the case that the (1, 1) scenario leads to (sometimes oscillatory) coexistence, indicating that, while attacking last does incur a competitive disadvantage, it is not always a fatal

one, and that it can often be offset by other factors. These ideas will be explored further in the Discussion.

For the parameter values considered in Fig. 1, changes in the value of the search efficiency of the resident parasitoid (Q in this case) do not affect the location of the coexistence region on the abscissa, but do directly affect its location on the ordinate. From Fig. 1 it is apparent that increasing β_Q by a factor of 4 has only a small effect on the shape and relative size of the stability region, other than moving and scaling the coexistence region on the ordinate as described above, although the small region of instability that exists when $\beta_Q = 50$ disappears when $\beta_Q = 200$. Although the basic character of the coexistence region is always maintained (a diagonal band from the ordinate to the abscissa, dividing the first quadrant into three separate regions), the absolute and relative size of this region, the relative amounts of stable and oscillatory coexistence, and whether or not it forms a continuous band can all change radically as a function of changes in some of the other parameter values of the model (as will be seen below).

Finally, note the location of the areas of oscillatory coexistence and (in the case of Fig. 1A) uncontrolled host growth, abutting the ordinate axis. Values on the axes correspond to one of two scenarios: on the abscissa, the value of β_P is infinite, so that P 's encounter rate is actually represented by $\varepsilon_P = a_P P$ (see Ch. 2); on the ordinate, the value of a_P is infinite, so that P 's encounter rate is actually represented by $\varepsilon_P = \beta_P P/N$ (see Ch. 2 and the Appendix section *parameter*

values). An encounter rate of the form $\varepsilon_p = \beta_p P/N$ is extremely destabilizing, and in one-parasitoid systems often leads to uncontrolled host growth (Getz & Mills, 1996). Thus it is to be expected that, in regions where P 's search efficiency and fecundity are high relative to Q 's, so that Q is close to being unable to maintain itself in the system, and where the effect of P 's search efficiency on stability diminishes ($a_p \rightarrow \infty$), the stability of the three-species system would be diminished, leading even to uncontrolled host growth under some circumstances (e.g. Fig. 1A). The size of such regions in parameter space increases with increasing instability due to decreased parasitoid aggregation, and decreases with increasing stability due to host density dependence, as will be illustrated below. Note that, on the ordinate axis itself, where P 's search efficiency is never limiting, 2D systems containing only P are often unstable (Getz & Mills, 1996).

HOST STRATEGIES: POPULATION GROWTH RATE AND SELF-LIMITATION

Figs. 2-4 illustrate the basic consequences of changes in the life-history strategy of the host for the stability of eqns 1. In Fig. 2 the host's population growth rate has been increased from 1.1 to 2.0 (compare with Figs. 1C and 1D), producing a huge increase in the amount of parameter space occupied by simulations exhibiting three-species stable coexistence (note the abscissa scale). Also, the small area of oscillatory coexistence has been eliminated in favor of equilibrium coexistence (see the Appendix section *numerical analysis and simulation*). In addition, there is now a large difference in the proportion of coexistence parameter space as a

function of Q 's fecundity, unlike for the smaller value of λ . These two panes are essentially identical to those produced for $a_Q = 0.01$ (data not shown).

Fig. 3 illustrates the stability consequences after the host has gone from density-independent population growth to self-regulated population growth (compare with Figs. 1A and 1C). The qualitative change in the size and shape of the coexistence region is much smaller than that obtained in increasing the host's population growth rate (Fig. 2). Once again, the small area of oscillatory coexistence has been given over to equilibrium coexistence, because of the stabilizing effects of host self-limitation. And, again, there is an interaction effect between the host's life-history strategy and the parasitoid's, although in the case of host self-limitation, the interaction is with Q 's search efficiency rather than fecundity. A decrease in a_Q leads to a small but significant decrease in coexistence parameter space (Fig. 3A). These two panes are essentially identical to those produced for $\beta_Q = 200.0$ (data not shown).

Finally, both of these changes in host life-history strategy are combined in Fig. 4, where their interaction can be observed. There is still an increase in stable parameter space due to the increase in the host's population growth rate (compare Fig. 4A with Fig. 1C), but it is diminished by the effect of density dependence (compare Fig. 4A with Fig. 2A). This diminishing effect is not complete, however, as can be observed by comparing Fig. 4B ($K = 80.0$) with Fig. 1C. The two regions of stable coexistence coincide, but the increase in the

strength of density dependence is unable to completely remove the widening effect of the increased host population growth rate on the coexistence region.

Thus, increasing the strength of host density dependence leads to *decreasing* the absolute size of the coexistence region, and this effect is more pronounced for larger host-population growth rates. The compliment to this phenomenon is that increasing the host population-growth-rate *increases* the absolute size of the coexistence region, although this effect is less pronounced as the strength of host density dependence increases.

PARASITOID STRATEGIES: ATTACK AGGREGATION

Figs. 5-7 illustrate the basic consequences of changes in attack aggregation for the stability of eqns 1. Figs. 5 and 6 represent the density-independent host-growth scenario, and Fig. 7, the self-regulated host-growth case. In Fig. 5A the parasitoid which attacks first, P , the introduced parasitoid in this case, has its attack aggregation reduced ($k_P: 0.25 \rightarrow 0.75$, compare with Fig. 2A; note that $\lambda = 2.0$ for all panes in Fig. 5). This change results in destabilization: the total area of parameter space taken up by coexistence decreases slightly, and the proportion of coexistence parameter space given over to oscillatory coexistence increases. Furthermore, this destabilizing effect is asymmetrical with respect to the two parasitoids in at least three ways. First, in comparing Fig. 5A with Fig. 2A, it should be noted that all of the loss of coexistence parameter space occurs on the side closest to the origin, thus representing an increase in the area of parameter

space in which P is able to exclude Q . Recall that, in considering the two-species system, it was determined that increasing k_P from zero to unity led to an increase in stable parameter space, and that the system was stable for increasingly large values of λ (Ch. 2). The consequences of these facts are seen here. Decreasing aggregation ($k_P: 0.25 \rightarrow 0.75$) and decreasing fecundity limitation (increasing β_P) serve to stabilize the N - P system relative to the N - Q system, and thus P is able to exclude Q from the three-species coexistence system for lower values of a_P and β_P .

Second, it should be noted that, while the size of the coexistence region shrinks in favor of N - P systems, three-species systems with higher values of a_P and β_P become unstable, as equilibrium coexistence is converted to oscillatory coexistence. This is because, although the size of the 2D region of coexistence does not change as aggregation increases when $k_P < 1$, the composition of the coexistence region does change, as more of the region goes from being exponentially damped to being oscillatory damped (see Fig. 4.10 in Hassell, 1978 for an example in the unlimited fecundity case), so that lower values of a_P lead to increasingly oscillatory (although still damped) trajectories. Destabilization of one of the underlying one-parasitoid systems thus leads to destabilization of the two-parasitoid system.

Third, the magnitudes of these effects are asymmetrical with respect to the two parasitoids, as can be seen in Fig. 5B, where k_Q is increased to 0.75. The proportion of parameter space given over to coexistence is dramatically reduced

in favor of N - Q systems (note the abscissa scale), and the proportion of coexistence parameter space given over to oscillatory coexistence dramatically increases.

When both parasitoids have their attack aggregation reduced ($k_P = k_Q = 0.75$) the destabilizing effect is extreme (Fig. 5C). Coexistence parameter space is greatly reduced in favor of both N - P and N - Q systems. Furthermore, the stable proportion of coexistence parameter space is also dramatically reduced, due mainly to the reduction in attack aggregation of parasitoid Q . Additionally, however, a large proportion of parameter space is now given over to uncontrolled host growth, because increasingly oscillatory solutions lead to systems wherein both parasitoids together are unable to control the host.

The previous analysis has focused on the question of coexistence. In a one-parasitoid system coexistence is not possible if the aggregation parameter $k > 1$ unless the host exhibits density dependence. It makes sense, however, to ask if a parasitoid that exhibits little aggregation ($k > 1$) can invade a coexisting host-parasitoid system that does not include host density dependence (i.e. a system in which the resident parasitoid population's $k < 1$; see the Appendix section *parameter values*).

Fig. 6 illustrates the effects of values of $k > 1$ for an invading (\equiv introduced) parasitoid on the coexistence region. For values of k_P greater than unity the region of parameter space in which Q is excluded by P is greatly increased over its size for lower k_P values, and the size of the P - Q oscillatory coexistence region

is increased and its position is on the side of the coexistence region adjacent to the *N-P* system region, as was discussed previously (compare Fig. 6A with Fig. 5A, and with Fig. 2A). Additionally, the region of coexistence parameter space is modified as a result of changes in *Q*'s fecundity (compare Fig. 6B with Fig. 2B). The absolute size of the *P-Q* coexistence region shrinks, and the relative proportion of oscillatory coexistence parameter space to total coexistence parameter space is increased. No such modifications occur as a result of changes in *Q*'s search efficiency (data not shown). It is worth emphasizing, however, that there is a large region of stable three-species coexistence, thus indicating that attack aggregation sufficient to stabilize a one-parasitoid system is also sufficient to stabilize a two-parasitoid system that would otherwise be unstable if the more aggregated parasitoid is removed.

Finally, Fig. 7 illustrates the interaction between density dependence and reduced parasitoid aggregation. In comparing Fig. 7A with Fig. 5B, it can be seen that density dependence reduces both the absolute size of the coexistence region and the oscillatory proportion when only *Q* has its aggregation reduced. (Note that $k_Q = 0.75$ for all panes in Fig. 7; when only *P* has its aggregation reduced in the density-dependent case the reduction in coexistence parameter space is quite significant, but there is essentially no change in the proportion of the coexistence region which is composed of oscillatory coexistence - data not shown.) The comparison between Fig. 7B and Fig. 5C illustrates that when both parasitoids have their attack aggregation reduced, the oscillatory proportion of the

coexistence region is decreased, the uncontrolled host-growth portion is eliminated entirely, and the total size of the coexistence region decreases. Furthermore, when Q 's search efficiency is reduced (Fig. 7C) the coexistence region is overall reduced, but the oscillatory part is eliminated completely. No such change takes place in the density-independent case, and there are essentially no changes to the outcomes shown in Fig. 7 resulting from changes to Q 's fecundity (data not shown). Thus, when the aggregation of both parasitoids is reduced and the host is not self-limited, the effect is generally destabilizing. In other words, three-species coexistence is enhanced if one of the parasitoids has high aggregation, compared to the situation wherein both parasitoids have moderate aggregation. Under those circumstances the addition of host self-limitation leads to increased stabilization of the coexistence region, but the overall size of the region shrinks, as was shown previously for the case with high parasitoid aggregation.

REVERSING THE ATTACK TIMING OF RESIDENT AND INTRODUCED PARASITOID

The original intention in setting up the axes as ratios of the parasitoid's search efficiencies and fecundities was to evaluate the introduced parasitoid's ability to successfully colonize the one-host, one-parasitoid system over a wide range of invasion strategies (\equiv parameter combinations). Thus, the invader's search efficiency and fecundity, which are the denominators of the axis ratios, are varied to provide variation on the axes, while the resident's search efficiency and

fecundity remain fixed in each pane of the figures. There is no obvious reason for making the parasitoid attacking second the resident, as has been the case up to now, and in fact making the parasitoid attacking first the resident leads to several interesting insights. In Figs. 8 and 9 the ratios on the abscissae and ordinates have been inverted, so that variation on the axes is accomplished by variation in the search efficiency (in the case of the abscissae) or fecundity (in the case of the ordinates), of Q , the parasitoid attacking second in the host's life-cycle.

Fig. 8 clearly demonstrates the disadvantage to attacking second. Individuals in population Q require a higher search efficiency, fecundity or both to successfully invade a stable N - P system than individuals in population P do to successfully invade a stable N - Q system. This is seen in the movement of the upper boundary of the coexistence region toward the origin (compare Fig. 8A with Fig. 1C). This effect is increasingly pronounced with increases in host population growth rate (compare Fig. 8B with Fig. 2A).

In addition to demonstrating the disadvantage of attacking second, reversing the attack timing of resident and introduced parasitoids eliminates the small regions of oscillatory coexistence in the cases where the host population growth rate is low. The consequences of changes in P 's search efficiency and fecundity for the coexistence region (data not shown) are essentially identical to those in the $k_P = k_Q = 0.25$ cases previously considered.

It should be pointed out that, in switching the roles of the resident and introduced parasitoids, if the values of the non-axial parameters are preserved (e.g. model parameters other than those used to obtain variation on the axes, namely those other than a_i , and β_i), then the only distinction between the two scenarios becomes the ordering of attack within the host's life-cycle. Thus, Fig. 8A, in which Q is the resident, so that $a_Q = a_R = 0.1$ and $\beta_Q = \beta_R = 50.0$, and in which the c 's and k 's of both parasitoids are identical, has a complement in Fig. 1C, in which P is the resident, so that $a_P = a_R = 0.1$ and $\beta_P = \beta_R = 50.0$. In comparing these panes in the two figures, the distinction between them is that in Fig. 1C the parasitoid with fixed a and β attacks first, and in Fig. 8A this parasitoid attacks second. It is thus possible to distinguish between the effects of changes to the life-history strategy of the introduced or the resident parasitoid, in addition to changes to the life-history strategy of the parasitoid attacking first or second. It is *also* important to note, however, that if the parameter values of the two parasitoids are *at all* different, then the equilibrium density obtained for the 2D system will change when the roles of resident and introduced parasitoid are reversed. Although this fact does not have consequences for equilibrium stability, it *does* influence host suppression subsequent to the introduction of the second parasitoid (see the subsection *consequences for host suppression* below).

Fig. 9 illustrates the changes to the coexistence region which result from changes in parasitoid aggregation and the addition of host self-regulation. In Fig. 9A the resident, P , has its aggregation decreased ($k_P = 0.75$), while Q 's

aggregation remains high. Comparing Fig. 9A with Fig. 8B shows that the most significant effect of decreased aggregation in this case is identical to that seen when Q is the resident (compare Fig. 2A with Fig. 5B): a reduction in coexistence parameter space. Comparing Fig. 9A directly with Fig. 5B illustrates again the asymmetrical effect of the attack ordering: the coexistence region is greatly reduced, but the region of oscillatory coexistence is almost eliminated (the dashed-line box in Fig. 9A highlights the small remaining bit). In other words, decreasing the resident's aggregation has a much greater destabilizing effect on the coexistence region when the resident attacks second, although the coexistence region as a whole is larger. Note that coexistence parameter space is also reduced when it is the introduced parasitoid's aggregation that is decreased (data not shown), but that there is no corresponding change in oscillatory coexistence - all coexistence is equilibrial under these circumstances, irrespective of the identity of the resident.

Fig. 9B shows that reducing parasitoid aggregation in both parasitoids is extremely destabilizing irrespective of which parasitoid is the invader (compare with Fig. 5C). The addition of host self-regulation acts as a stabilizing influence with respect to uncontrolled host growth, but has less of an impact on oscillatory coexistence (Fig. 9C: compare with Fig. 7B for the consequences of reversing the attack timing of resident and invader; compare with Fig. 9B for the effects on uncontrolled host growth and oscillatory coexistence). Finally, reducing the resident's search efficiency when hosts are self-limiting eliminates oscillatory

coexistence and modifies the relationships between parasitoid fecundities and search efficiencies which permit three-species coexistence (Fig. 9D: compare with Fig. 7C for the consequences of reversing the attack timing of resident and invader; compare with Fig. 9C for the effects on uncontrolled host growth and oscillatory coexistence).

CONSEQUENCES FOR HOST SUPPRESSION

For simulations resulting in stable three-species equilibria it is possible to measure the increase in host suppression resulting from the addition of a second parasitoid to a one-host, one-parasitoid system at equilibrium. Because this one-parasitoid system provides the initial conditions for all the three-species simulations (see the subsection *initial conditions*), this is a natural approach for comparing the effect of two parasitoids on host suppression to that of one alone. This approach is almost completely analogous to that first suggested by Beddington et al. (1975; Hassell, 1978) for measuring the degree of host suppression by a parasitoid introduced into a system with the host at its equilibrium carrying capacity, K . Their approach utilized the variable $q = N^*/K$, where N^* is the host's equilibrium density in the presence of the parasitoid (see Ch. 2). It is important to understand, however, that the reference value used here, the host equilibrium density in the presence of one parasitoid alone, changes as a function of changes in the host and/or resident parasitoid parameter values. Thus, this situation is distinctly different from that comparing

the host equilibrium density in the presence of one parasitoid to the host equilibrium density in the absence of any parasitoids (which is fixed at K , and only changes if K changes). The variable $q^{PQ} = N^{*PQ}/N^*$ is therefore utilized to examine the effects of a second parasitoid on host equilibrium suppression, where N^{*PQ} is the host population's equilibrium density in the presence of both parasitoids, and N^* is the host's equilibrium density in the presence of the resident parasitoid only. Note that this ratio, as with the original q of Beddington et al. (1975), can in theory take any values from zero to infinity, with zero representing complete host suppression relative to the reference value (e.g. relative to the denominator - the host's carrying capacity K in the q used by Beddington et al., 1975, and the one-host, one-parasitoid equilibrium in the q^{PQ} used here), unity representing no effect of the additional parasitoid on host equilibrium density, and values greater than unity representing a *release* of the host from parasitism. Note also that, because it is possible to have a one-parasitoid, host system with a stable equilibrium without the need for the host to be self-limited, this analysis offers the possibility of considering cases where such self-limitation does not exist, unlike the situations considered by Beddington et al. (1975).

One significant consequence of the change in N^* as a function of changes in the resident parasitoid's parameter values is that, as the resident's fecundity increases, the amount of additional suppression provided by a second parasitoid *decreases* (i.e. q^{PQ} goes from zero toward unity; Fig. 10A). This is because

increases in the resident's fecundity lead to increased host suppression by this parasitoid alone (i.e. lead to decreases in N^*), so that the ability of a second parasitoid of a given fecundity to further reduce the host equilibrium decreases (i.e. q^{PQ} increases with β_R). When the fecundity of the *resident* remains fixed, increases in the *introduced* parasitoid's fecundity lead to increases in host suppression (Fig. 10B). These relationships also hold true for the search efficiency and attack aggregation parameters of the parasitoids (data not shown). Increases in the value of either parameter in the resident result in decreasing the amount of additional host suppression provided by the introduced parasitoid; increases in the value of either parameter in the introduced parasitoid result in increasing the amount of additional host suppression provided by the introduced parasitoid.

There is a small asymmetry to the above effect as a function of whether the resident attacks first or second in the host's life-cycle. This is because of the relationship between the fecundities of the two parasitoids and the timing of their attacks in the host's life-cycle, the basic nature of which is altered by the relative values of the parasitoid's search efficiencies and degree of attack aggregation. Consider the situation where all the parameter values of the two parasitoids except for their fecundities are equal, so that the only differences between them are their fecundities and timing of attack in the host's life-cycle. Under these circumstances, if the introduced parasitoid attacks later than the resident in the host's life-cycle and has a higher fecundity than the resident, there

will be slightly greater marginal host suppression (i.e. the difference between the host's equilibrium densities in the presence of one versus two parasitoids will be greater) than if the introduced parasitoid attacks earlier than the resident. The converse also holds: if the introduced parasitoid attacks later and has a lower fecundity than the resident, there will be less marginal host suppression than if the introduced parasitoid attacks earlier (Fig. 11A). Thus, all else being equal, if a second parasitoid is to be introduced, and it attacks after the resident, it should have a higher fecundity than the resident to achieve greater additional host suppression. If it attacks earlier, it should have a lower fecundity than the resident. This is essentially a manifestation of the disadvantage of attacking second, and it should be noted that in general the amount of this asymmetry is relatively small. It can be magnified, and the difference in degree of additional suppression increases, as the fecundity of the resident decreases, as the amount of attack aggregation in *both* parasitoids decreases (i.e. k_P and k_Q get larger), and/or as the host's intrinsic growth rate increases. The strength of host self-limitation does not alter the relative nature of this asymmetry, nor does changing the search efficiencies of *both* parasitoids together (i.e. a_P and a_Q *both* increase or *both* decrease). The asymmetry can be *reversed*, however, if the parasitoid attacking second has a search efficiency sufficiently less than that of the parasitoid attacking first (i.e. $a_Q < a_P$). It can also be reversed if the degree of attack aggregation of the parasitoid attacking second is sufficiently greater than that of the parasitoid attacking first (i.e. $k_Q < k_P$, recall that larger k means less

aggregation), where in both cases “sufficiently” depends on the values of the other parameters. Under these last two sets of circumstances, if the introduced parasitoid attacks later than the resident in the host’s life-cycle, and has a higher fecundity than the resident, there will be less marginal host suppression than if the introduced parasitoid attacks earlier than the resident (Fig. 11B). The converse also holds. Note that these last two features can compensate for each other. If $a_Q < a_P$ but $k_Q > k_P$, or vice versa, again by sufficient amounts, then the asymmetry will be maintained as described initially (e.g. as in Fig. 11A).

In addition to the above results, the combinations of parameter values examined for equilibrium stability resulted in almost 600,000 simulations with stable three-species equilibria. Of these, 7,206 provided more than an 80% improvement in host suppression with the addition of the introduced parasitoid (68,413 provided more than a 25% improvement in suppression). This 80% host-suppression boundary was used to assess the general characteristics of host and parasitoid populations which result in maximal stable host suppression resulting from the introduction of a second parasitoid. Two things of importance about this assessment should be noted. First, because the simulation parameters were not selected at random, the ratios $7,206/600,000$ and $68,413/600,000$, and the fractions given below, have no statistical significance. Second, in reference to biological control introductions, even 80% suppression of a pest population does not guarantee that the pest has been reduced below the economic threshold of crop damage.

Of the simulations in which the additional parasitoid provided at least an 80% improvement in suppression of the host equilibrium density, all of them occurred in systems with a high host population-growth-rate, and all but thirty of them in systems without host self-regulation. The simulation initial conditions had no effect on host suppression (indicating that the size of the initial-condition region influenced by the locally-stable equilibria is relatively large). In all of these systems, the resident parasitoid population had high aggregation ($k_R = 0.25$), but the same was not true for the introduced parasitoid. One-third of these systems had $k_I = 0.25$; almost 60% of them had $k_I = 0.75$, and the rest had $k_I = 2.0$. In addition, these systems uniformly had the highest values of search efficiency and fecundity for the introduced parasitoid which permitted stable three-species coexistence.

It is important to recognize that there can be a conflict between the properties of a one-host, two-parasitoid system that provide the maximal *absolute* host suppression, and those properties that provide the maximal *additional* host suppression resulting from the presence of the second parasitoid. Thus, the addition of a second parasitoid to a one-host, one-parasitoid system *at equilibrium* for purposes of a strong increase in host suppression can be justified under several sets of circumstances. In general, systems with high host population-growth-rates and low host self-regulation will allow a second parasitoid to substantially increase host suppression. Furthermore, high attack aggregation in the resident allows the opportunity for an introduced parasitoid to greatly

improve host suppression. The degree of aggregation in the introduced parasitoid is less important.

DISCUSSION

The ecological analysis of multiparasitoid systems has been motivated by two considerations. The first is that such systems are widely found in nature. Many, perhaps most, hosts of parasitoids support more than one parasitoid species, a significant fraction of which are specialists on that host. The second concerns biological control. The benefit and detriment of introducing more than one enemy species in classical biological control has been argued extensively. Thus, it is important to understand how multiparasitoid complexes can be supported, and to determine the effects of multiparasitoid biological control introductions, as opposed to those of a single parasitoid, on host densities.

With respect to the first issue, it is certainly worth emphasizing the finding that three-species coexistence, and in particular *stable* three-species coexistence, is possible under a wide range of conditions. Equilibrial three-species coexistence is *almost always* possible for *some* combinations of search efficiencies and fecundities of the two parasitoid populations, provided at least one of the parasitoids has sufficient attack aggregation ($k < 1$). When the search efficiency *and* fecundity of one of the parasitoid populations is much larger than those of the other, the parasitoid population with the lower values will invariably be excluded. But, when the aggregation parameters k_P and k_Q are both less than

unity, coexistence is *always* possible for some combinations of a_P , a_Q , β_P and β_Q . Even when one of the parasitoid populations has $k > 1$, stable coexistence is curtailed but not eliminated.

Such coexistence regions exist even when the search efficiencies or fecundities of the two parasitoid populations are widely (i.e. orders of magnitude) different. This can be seen in the general structure of the equilibrium coexistence region as a diagonal band from one axis to the other, and the fact that the axes represent ratios. The absolute values of the search efficiencies and fecundities influence the particular makeup of the coexistence region (i.e. width, proportion of oscillatory coexistence, etc.), but its general structure remains invariant. These results are in agreement with those of May and Hassell (1981), indicating that the presence of fecundity limitation does not adversely affect the potential for stable coexistence. These sorts of results may explain why multiparasitoid complexes are so common: the conditions for their existence may be very permissive (Hutson & Law, 1985).

While it is clear that there is a disadvantage to attacking second in the host population's life-cycle, this disadvantage is not insurmountable, and, as evidenced by the previous point, often does not significantly affect the possibility of stable coexistence. When parasitoid heterogeneity is sufficiently high (i.e. $k_P, k_Q < 1$), the disadvantage of attacking second, even by a parasitoid with lower search efficiency *and* fecundity than the parasitoid attacking first, *can* be offset. This can happen even when only one of the parasitoids has high attack

heterogeneity. One might expect a competitive exclusion principle to hold under these circumstances, particularly since this is clearly a case of competitors coexisting on a single, non-substitutable resource (Tilman, 1990; Briggs, 1993). It has been demonstrated, however, that there are several circumstances under which such a principle would *not* in general be expected to hold (Armstrong & McGehee, 1980; Getz & Schreiber, 1999). In particular, coexistence can in general occur when the two predator or parasitoid populations utilize different stages of the host population's life-cycle (Haigh & Maynard Smith, 1972; Briggs, 1993; Briggs et al., 1993), as is the case under the interpretation of eqns 1's structural distinction between the two parasitoid populations. In addition, coexistence may be expected when there are time-lags in the dynamics (Hutchinson, 1961; Stewart & Levin, 1973; Koch, 1974a), as is the case in discrete-time models representing synchronized host-parasitoid generations (Mills & Getz, 1996). As Briggs et al. (1993) note, even Tilman's R^* concept (1982, 1990) allows for multispecies coexistence in a patchy environment, although it requires multiple resources, each species having a different limiting resource-ratio. Under the circumstances described by eqns 1, if the parameters of P and Q are the same, then R^* is the same for both parasitoids, but coexistence nonetheless occurs (i.e. the 1, 1 scenario). Even if the parasitoid parameters are perturbed slightly, thus changing the R^* of one or the other of the parasitoids, coexistence will still occur in general. Thus, the generalization that the stronger competitor will draw down

the resource to the point of excluding the weaker (i.e. the R^* rule) does not apply under these circumstances.

One general way in which coexistence is enhanced is through the presence of stabilizing features in the model (Armstrong & McGehee, 1980; May & Hassell, 1981; Briggs, 1993; Mills & Getz, 1996). In particular, the introduction of nonlinearities in the growth rate of the prey (self-limitation) and/or the parasitoids (attack aggregation) increase the amount of parameter space given over to coexistence, and decrease the proportion of the coexistence region given over to oscillatory coexistence in favor of equilibrial coexistence. It is important to recall, however, that host density dependence, while eliminating oscillatory coexistence in favor of equilibrial coexistence, decreases the range of parasitoid search efficiency and fecundity ratios which permit coexistence at all. This effect is more pronounced with increases in the host population's intrinsic growth rate, and it occurs regardless of the degree of attack aggregation in either parasitoid, although it is mitigated by increased parasitoid attack aggregation. Increasing host self-limitation, especially in combination with an increased host population growth rate, leads to chaos in discrete-time systems (May, 1974). The consequences for three-species systems are that at the boundaries of the coexistence region, where the differences between the parasitoid's search efficiencies and fecundities are the largest such differences which still permit coexistence, underlying oscillatory or chaotic dynamics in the host population

force the disadvantaged parasitoid out of the system, or, alternatively, prevent it from successfully invading.

As has been observed previously (Hochberg & Lawton, 1990; Taylor, 1993a; Getz & Mills, 1996), in the one-parasitoid population case increasing aggregation does not always lead to increased stability. Hochberg and Lawton (1990) found that, in one-parasitoid population systems, as the strength of host density-dependence increased, the importance of increased parasitoid aggregation for stability decreased. In fact, they found that in systems where the strength of host density-dependence leads to chaotic dynamics, *decreased* levels of parasitoid aggregation were necessary to stabilize the interaction. In the two-parasitoid population case, however, over the range of aggregations (k -values) examined in this chapter, this is not the case. Increased parasitoid aggregation in one or both parasitoids (but somewhat more-so in the parasitoid attacking first) always leads to increased coexistence parameter space overall, and to an increased proportion of equilibrial coexistence parameter space. As can be seen clearly from the one-parasitoid cases (Getz & Mills, 1996; Ch. 2), fecundity-limitation is generally a destabilizing feature for host-parasitoid model dynamics, because the proportion of hosts parasitoids are able to attack decreases as host density increases (a feature of Holling Type II functional responses; Murdoch & Oaten, 1975). The nonlinearities in host and parasitoid population growth rates are stabilizing because they provide negative feedback to the population growth rates in response to changes in population density. Fecundity limitation serves to reduce

the strength of this negative-feedback linkage for each parasitoid, so that when more than one parasitoid is present in the system, it appears that increased aggregation offsets the fecundity limitation's destabilizing effects.

Much of the work modeling host-parasitoid interactions has focused on the need and potential for stable coexistence equilibria (Barlow & Wratten, 1996; Mills & Getz, 1996). This emphasis stems from the perceived need for these systems to respond in a density-dependent fashion to externally-induced perturbations. If this does not occur (i.e. if there are no negative feedbacks), all populations will eventually achieve zero density via stochastic random walk (Cole, 1960). The need for a stable equilibrium to provide continued coexistence is no longer accepted *a priori*. Many workers have clearly demonstrated theoretically that oscillatory but bounded population-density trajectories can occur as a result of spatial and/or temporal variability (Koch, 1974a; Armstrong & McGehee, 1980; Briggs, 1993; Briggs et al., 1993). It has also been argued that biological control systems in particular need not necessarily exhibit stable equilibria for persistence and may in many cases be characterized by local extinctions and subsequent recolonizations from source populations (Murdoch et al., 1985; Comins & Hassell, 1996; Murdoch & Briggs, 1996). As the analysis in this chapter demonstrates, there are a variety of conditions under which persistent but oscillatory three-species coexistence occurs. Such coexistence occupies an increasing proportion of the total coexistence parameter space as stabilizing features of the dynamics are weakened (i.e. aggregation decreases or

host density-dependence is absent). It is also the case, however, that in a non-spatially-structured environment with no source populations, as is represented by the model analyzed here and as is the case in classical biological control introductions, oscillatory populations would be more vulnerable to extinction as a result of stochastic factors (e.g. environmental perturbations). Thus, while it is clear that non-equilibrial coexistence is possible, it is also clear that, given the possibility of equilibrial coexistence, the latter will enhance the probability of continued three-species coexistence. This is a particular consideration in classical biological control, which is examined next.

This analysis supports May and Hassell's (1981) finding that, when it comes to host suppression, more parasitoids are in general better. While it has been clearly shown that this prediction is robust with respect to discrete-time models, it often fails to hold up when systems with overlapping generations are modeled, particularly when age or stage structure in the host population is incorporated into the model (Briggs, 1993; Briggs et al., 1993). Thus, the generality of this prediction should remain confined to systems in which the host and parasitoid populations are synchronized.

May and Hassell (1981) found that increasing the host population's growth rate led to decreased host suppression. This analysis supports exactly the opposite contention: increasing the host population's growth rate leads to increased host suppression. Clearly when parasitoids are fecundity limited, increasing the reproductive rate of the pest permits an increased numerical

response in the parasitoids. In the case of eqns 1, this increase more than compensates for the host increase, which is ultimately limited by environmental factors, thereby resulting in the host's equilibrium density decreasing with increasing λ in the presence of the parasitoids. This is in clear contrast to the situation when fecundity is not limiting (May & Hassell, 1981; Hochberg & Lawton, 1990; but see Ives & Settle, 1996), in which case increases in the pest's reproductive rate lead to *decreases* in the ability of the parasitoids to suppress the host (i.e. the host's equilibrium density increasing with increasing λ in the presence of the parasitoids).

Decreased host equilibrium density results from decreased host self-regulation, and from increased parasitoid search efficiency in the invading parasitoid. It is also worth pointing out, however, that the same does not apply with respect to parasitoid fecundity. In the one parasitoid case, decreased parasitoid fecundity can lead to an increase in host equilibrium density (Ch. 2). In the two parasitoid case, increased host equilibrium densities result from decreased fecundity in the invading parasitoid, but from *increased* fecundity in the resident parasitoid. In other words, as the resident parasitoid's fecundity goes down, so does the host equilibrium density. This may be due to the ability of the invading parasitoid to better control the host on its own due to its extremely high search efficiency and fecundity. Under such circumstances, low fecundity in the resident parasitoid may be desirable because it prevents the resident parasitoid from interfering (i.e. through multiparasitism) with the more

effective control provided by the invader, and/or allows the control provided by the resident to more effectively compliment that of the invader. Godfray and Waage (1991), however, have shown that density dependence in both parasitoid populations (in the form of mutual interference) can allow two parasitoid populations to more effectively reduce the density of the host population than either parasitoid by itself. Higher fecundity in the parasitoid populations increases the degree of mutual interference (intraspecific competition) via superparasitism. The current result is thus at odds with that of Godfray and Waage (1991). This discrepancy will require further investigation to resolve.

APPENDIX

THE EQUILIBRIUM CONSERVATION EQUATION

Consider the one-parasitoid model (Ch. 2) with no host density dependence (i.e. incorporating eqn 2). It can easily be seen that there is a simple relationship between \hat{N} and \hat{P} (where the hats denote equilibrium values; Getz & Mills, 1996):

$$\hat{N} = \frac{\lambda \hat{P}}{c_p(\lambda - 1)} \quad (\text{A1})$$

Note that this relationship is independent of the function f_P or its parameters.

Eqn A1 by itself does not allow the determination of \hat{N} independently of \hat{P} or vice versa, but because the one-parasitoid model contains only a single

function f , it is possible to find explicit values for the equilibrium solutions (\hat{N}, \hat{P}) in terms of the independent parameters. This is because the identity $f_p^{-1}(1/\lambda) = \hat{\varepsilon}_p$, where $\hat{\varepsilon}_p = \varepsilon(\hat{N}, \hat{P})$, results in a representation of either \hat{P} in terms of the independent parameters, or of \hat{P} in terms of \hat{N} (depending on the form of ε), which can then be substituted into eqn A1, resulting in a representation of \hat{N} (and thus \hat{P}) in terms of the independent parameters (see Getz & Mills, 1996).

As has been shown, this approach is easily extended to encompass systems with two parasitoids (eqns 1; Hassell, 1978; May & Hassell, 1981). Consider eqns 1 at equilibrium, so that the system is transformed into the following:

$$\frac{1}{\lambda} = \hat{f}_1 \hat{f}_2 \quad (\text{A2})$$

$$\frac{\hat{P}}{c_p \hat{N}} = 1 - \hat{f}_p \quad (\text{A3})$$

$$\frac{\hat{Q}}{c_Q \hat{N}} = \hat{f}_p (1 - \hat{f}_Q) \quad (\text{A4})$$

By adding together equations A3 and A4, substituting in eqn A2 and rearranging the result, the following identity is obtained:

$$\hat{N} = \frac{\lambda(c_Q \hat{P} + c_p \hat{Q})}{c_p c_Q (\lambda - 1)}$$

Thus, the value of \hat{N} is a function only of P and Q , c_P and c_Q and λ ; the functions f and their parameters have no effect on the equilibrium densities (this is the two

parasitoid case of the identity obtained for one parasitoid in eqn A1). This relationship is an invariant, or conservation equation, for the equilibrium population densities. Once again, it is not possible to use such an equation by itself to determine the value of one of the dependent variables independently of the others. Unfortunately, in the cases with more than one parasitoid (and thus more than one f) it may not in general be possible to find explicit expressions for the equilibrium population densities, because it is not possible to rearrange equations A2-A4 so that back substitution for dependent variables can occur (i.e. $f_p^{-1} = F(f_Q)$ and $f_Q^{-1} = G(f_p)$, so that it is not possible to determine the inverse of one of the functions f independent of the dependent variables). This is in particular the case when the functions f are of the negative binomial form (eqns 4) with aggregation parameters $k_P, k_Q < \infty$, with $k_P, k_Q \neq 1$, and with the arguments to the functions f of the form in eqns 5 (note that when $k_P = k_Q = 1$ it is possible to obtain closed-form expressions for the equilibria, but that the linear stability analysis of these solutions simply indicates that $k_P = k_Q = 1$ represents either a transition between stable and unstable solutions, or is always unstable, depending on the values of the other parameters, as has been shown previously; see May, 1978; May & Hassell, 1981; Getz & Mills, 1996).

In the case with host density dependence considered here (eqn 3), there is again a conservation relationship between the equilibria, which is independent of the functions f and their parameters, but which has no analytical solution. The system is reduced to

$$c_Q \hat{P} + c_P \hat{Q} = c_P c_Q \hat{N} \left\{ 1 - \exp \left[r \left(\frac{\hat{N}}{K} - 1 \right) \right] \right\}$$

which has no analytical solution - it is not possible to find \hat{N} analytically, even if all the parasitoid equilibrium densities and model parameters are known. (Note that the Lambert W-function can provide an infinite family of solutions to an equation of the form $y = x \exp(x)$, but does not provide solutions to equations of the form $y = x [1 - \exp(x)]$, Maple, 1994; see Rosenheim, 1996, Appendix A for a similar problem with a graphical solution.) For this reason it is also impossible to determine \hat{N} analytically when eqns 1 incorporates the modified Ricker function (Getz, 1996) for $g(N)$. It may, however, be possible to do so when eqns 1 incorporates the modified Beverton and Holt function for $g(N)$ (Getz, 1996), again, provided P and Q can be determined.

NUMERICAL ANALYSIS AND SIMULATION

Computational algebra was performed using 64-bit Maple V Release 3 computational mathematics software (Maple, 1994), running on a Digital Equipment Corp. AlphaStation under Digital UNIX 4.0. Numerical results were obtained by solving two- and three-dimensional equilibrium and eigenvalue problems at points of interest in the parameter space, and by direct numerical simulation, using the Maple computational mathematics package and C code written by the author, running on the above machine. The results of the

eigenvalue solutions were checked by direct simulation of eqns 1 at various representative points in the parameter space.

Initially, attempts were made to find equilibrium solutions to eqns 1 via computational algebra and/or numerical analysis (Newton's method), and then to determine the stability of these solutions via analysis of the Jacobian matrix. This approach proved unsatisfactory, due to the inability of the algebraic and numerical solvers to determine equilibrium solutions and/or the slow rate at which such solutions were located (see the Appendix section *the equilibrium conservation equation* above). Direct simulation was thus employed, using an approach nearly identical to that employed by Hochberg and Holt (1995) to analyze two-dimensional systems. Simulations were run for 10^6 generations (time-steps) or until one or more of the following stopping criteria were met : $N_t > 10^{20}$ (uncontrolled host growth); N_t , P_t or $Q_t < 10^{-10}$ (host and/or parasitoid extinction); N_t , P_t and Q_t all greater than 10^{-10} , less than 10^{20} and no species density varied more than 10^{-10} for 25 consecutive generations (three-species equilibrium). Simulations extending to 10^6 generations (i.e. not blowing up, crashing or reaching equilibrium) were considered oscillatory coexistence systems; note that this analysis does not distinguish between cyclic (periodic) and acyclic (chaotic) oscillatory coexistence. In some individual simulation cases which reached the 10^6 time-step boundary and were still oscillating it was indeterminate whether the amplitude of the oscillations was still decreasing or not, i.e. whether the trajectory was oscillating towards equilibrium extremely

slowly, or if it exhibited oscillatory coexistence with an extremely small amplitude. In all cases such simulation results accounted for less than 0.1% of the total number of simulations for any given combination of non-axial parameters (i.e. any given combination of all parameters except the two varied to obtain variation on the axes), and, as such results were distributed more-or-less at random throughout the region of equilibrium coexistence, they were considered anomalous. For information on simulation initial conditions and parameter values see the description of the analysis in the text section *The Model* and the Appendix section *parameter values* below.

PARAMETER VALUES

One goal of this chapter was to examine the potential interactions and trade-offs between parasitoid fecundity and search efficiency. Thus, the graphs of parameter space were laid out in terms of the following two ratios: the two parasitoid's fecundities on the ordinates, and the two search efficiencies on the abscissae. The search efficiency and fecundity of one of the parasitoids is fixed for any given simulation. This is the resident parasitoid from which the initial conditions for the 3D simulations are obtained; the other parasitoid is the invading or introduced parasitoid. The axis ratios are the parameter value of the resident to that of the invader, so that values *on* the axes themselves represent limiting cases for the invader. In the case of the abscissa, the introduced parasitoid's fecundity is infinite and its encounter rate is actually represented by

a search-limited encounter rate; in the case of the ordinate, the introduced parasitoid's search efficiency is infinite and its encounter rate is actually represented by a fecundity-limited encounter rate (see the text section *The Model*).

Thus, each of the panes of the dynamical results (e.g. each individual pane in Figs. 1-9) represents the outcomes of a set of simulations in which all parameters except the search efficiency and fecundity of the parasitoid chosen as the invader are fixed. This parasitoid's search efficiency and fecundity are referred to as the axial parameters, and all the other parameters, including the resident's search efficiency and fecundity, as the non-axial parameters. Because eqns 1 determine that one of the parasitoids attacks first in the host's life-cycle, it was necessary to conduct analyses in which both parasitoids had the opportunity to play the role of the resident for each of the two sets of initial conditions.

The three-dimensional system examined here contains a sufficient number of parameters to make exploration of its parameter space nontrivial. In the case of the DI scenarios, there are 8 actual free parameters: λ , a_P , β_P , k_P , a_Q , β_Q , c_Q and k_Q ; the DD scenario adds an additional free parameter, c_P (note that $r \equiv \ln \lambda$; in the case of the DI scenario, eliminate c_P from eqns 1 incorporating eqns 2, 4 and 5 by substituting N_t/c_P for N_t and see that $\beta_P \rightarrow \beta_P c_P$, $\beta_Q \rightarrow \beta_Q c_P$, and $c_Q \rightarrow c_Q/c_P$; in the DD scenario, eliminate K from eqns 1 incorporating eqns 3, 4 and 5 by substituting $N_t K$ for N_t and see that $\beta_P \rightarrow \beta_P/K$, $\beta_Q \rightarrow \beta_Q/K$, $c_P \rightarrow c_P K$ and $c_Q \rightarrow c_Q K$; note that these substitutions can also be appropriately applied to the two-dimensional system analyzed in Ch. 2). Although there are published values for

some of these parameters for some biological systems (including those in Beddington et al., 1978; Hassell, 1978; Hochberg & Holt, 1995 and references within these; Ch. 2), in many cases no such reliable values exist (particularly for λ ; Hochberg & Holt, 1999). In order to provide a wide yet biologically reasonable range of parameter values, to facilitate comparisons of these results with those made prior in the literature, and to avoid being overwhelmed with parameter value combinations, this analysis combined guidance from published values with an understanding of appropriate values, both from biological and mathematical perspectives. The following parameter values were explored in all possible combinations: λ : 1.1, 2.0; a_R : 0.01, 0.1; β_R : 50.0, 200.0; $c_P = c_Q = 0.2$; K : ∞ (the DI scenarios), 1000.0 (the DD scenarios, except in one case noted in the text where $K = 80.0$); k_R : 0.25, 0.75; k_I : 0.25, 0.75, 2.0.

It is worth noting at this point that the same value was used for both c_P and c_Q , and was fixed across all simulations, because of the desire to focus on the fecundity versus search-efficiency relationship, and thus to focus on parasitoid life-history strategies from egg-laying to adult emergence (as represented by β_P and β_Q) while setting constant the parasitoid life-history strategies from adult emergence to egg-laying (as represented by c_P and c_Q).

Additionally, the above values of λ were used for three reasons. First, as Hochberg and Holt (1999) point out, actual field values for λ are not well known, and these two values encompass two plausible scenarios. In one, the population is growing at 10% per generation; in the other, it is doubling each generation

(both in the absence of parasitoids and host self-limitation). Second, the interpretation of what λ is and actually measures changes under the density-independent (DI) and density-dependant (DD) scenarios. Under the DI scenario, λ will be forced very close to unity over evolutionary time scales because there is nothing else intrinsic to the population dynamics (in the absence of external factors, such as parasitoids) to prevent the world from becoming overrun with hosts ($\lambda > 1$), or to prevent the hosts from becoming extinct ($\lambda < 1$) (Hassell, 1978). It is certainly true that insect populations, particularly during outbreaks, can increase by several orders of magnitude within a generation or two, but in the absence of resource limitation or other mortality factors such levels of growth *cannot* be maintained over many generations, and uncontrolled outbreaking insect populations often crash as a result of resource overexploitation (Barbosa & Schultz, 1987; Huffaker et al., 1999). Thus, under the DD scenario evolutionary restrictions on the value of λ are removed, and it is possible for it to take larger values. Finally, however, these values are very close to those used by May and Hassell (Hassell, 1978; May & Hassell, 1981) in their analysis (1.2 and 2.0), thus facilitating comparisons between that work and this.

Variation on the abscissae of each pane was obtained by variation in a_i , and variation on the ordinates was obtained by variation in β_i . The desire to capture the three-species coexistence regions of parameter space in spite of changes in the values of other parameters (particularly λ and β_R) led to small changes in the ranges for a_i and β_i as a function of other parameter values. Representative

ranges are: $a_i: 0.003 \rightarrow \infty$; $\beta_i: 4.2 \rightarrow \infty$. Each axis was partitioned into 150 subsections, resulting in a 150 x 150 grid for each pane (22,499 simulations; the origin was excluded). Two sets of initial conditions for each parasitoid acting as the resident resulted in a total of 8,639,616 simulations available for analysis and comparison.

FIGURE LEGENDS

Fig. 1. Equilibrium stability diagrams for eqns 1 as described in the text (incorporating eqns 2, 4 and 5, the DI scenario). The axes in each of the panes in Fig. 1 are identical, and each axis represents a ratio. (The axes are the same in all panels of Figs. 2-9, with the exception that in Figs. 8 and 9 the ratios are inverted as a consequence of switching the identities of the resident and the invader.) The abscissae are the ratio of Q 's search efficiency to P 's search efficiency ($= a_Q/a_P$; recall that in this case P attacks first), and the ordinates are the ratio of Q 's fecundity to P 's fecundity ($= \beta_Q/\beta_P$). In Fig. 1 all of the model parameter values except for the search efficiencies and fecundities are fixed: the host's density-independent growth rate $\lambda = 1.1$, the host is not self-limited (DI scenario), the parasitoid survival-and-sex-ratio parameters $c_P = c_Q = 0.2$, and the parasitoid aggregation parameters $k_P = k_Q = 0.25$. Furthermore, for each pane in Fig. 1 the value of Q 's search efficiency and fecundity is fixed as illustrated in the figure. Thus, variation on the abscissa and ordinate of each pane is obtained by varying P 's search efficiency and fecundity, respectively, so that each point in a given pane represents the qualitative outcome of a dynamical simulation of eqns 1 with fixed parameters and with the coexistence set of initial conditions (see the description of the two-parasitoid analysis in the text section *The Model* and the Appendix section *parameter values*). Light gray regions indicate stable (equilibrium) three-species coexistence, dark gray regions indicate unstable (oscillatory) three-species coexistence, and black regions indicate uncontrolled

host growth. Note particularly that variation on the axes is achieved by variation in the denominator of these ratios – increasing the parameter in the denominator moves the axis value closer to the origin and vice versa. The symbol “x” marks the point (1, 1) on each pane. See text and the Appendix for further details.

Fig. 2. Equilibrium stability diagrams for eqns 1 as in Fig. 1, but with $\lambda = 2.0$.

Fig. 3. Equilibrium stability diagrams for eqns 1 as in Fig. 1, but incorporating eqn 3 (the DD scenario); $K = 1000.0$.

Fig. 4. Equilibrium stability diagrams for eqns 1 as in Fig. 1, but with $\lambda = 2.0$ and incorporating eqn 3 (the DD scenario).

Fig. 5. Equilibrium stability diagrams for eqns 1 as in Fig. 2 ($\lambda = 2.0$ and the DI scenario), but with changes in k_P and k_Q as indicated in the figure; $a_Q = 0.1$, $\beta_Q = 50.0$. Compare all panes in this figure with Fig. 2A.

Fig. 6. Equilibrium stability diagrams for eqns 1 as in Fig. 2 ($\lambda = 2.0$ and the DI scenario), but with $k_P = 2.0$ and $k_Q = 0.25$.

Fig. 7. Equilibrium stability diagrams for eqns 1 as in Fig. 4A ($\lambda = 2.0$ and the DD scenario), but with $k_Q = 0.75$; values for k_P and a_Q indicated in the figure; $\beta_Q = 50.0$. Compare panes A and B with Figs. 5B and 5C, respectively.

Fig. 8. Equilibrium stability diagrams for eqns 1. Pane A: Conditions as in Fig. 1C (Pane A), and Fig. 2A (Pane B), but with the identities of the resident and invader parasitoids reversed. The fixed parameter values are reversed between the two parasitoids from those in Figs. 1C and 2A; in particular, $a_Q = a_R = 0.1$. See text for details.

Fig. 9. Equilibrium stability diagrams for eqns 1. Identities of the resident and invader parasitoids reversed (e.g. parasitoid Q is the resident, as in Fig. 8; see text for details). In all cases $\lambda = 2.0$, $\beta_P = 50.0$, $c_P = c_Q = 0.2$, $k_P = 0.75$; other parameters as given in the figure. See text for details and for suggested figure comparisons.

Fig. 10. The relationship between parasitoid fecundity, β_P (pane A), and β_Q (pane B), and q^{PQ} , the degree of additional host equilibrium suppression provided by the introduction of a second parasitoid population, for three different values of the fecundity of the other parasitoid, β_Q (pane A), and β_P (pane B). Values of q^{PQ} less than unity indicate additional host equilibrium suppression due to the presence of the second parasitoid population in the system. In all cases $a_P = a_Q = 0.1$, $c_P = c_Q = 0.2$, $k_P = k_Q = 0.25$, $K = 1000.0$, $r = 2.0$. See text for details.

Fig. 11. The relationship between the ratio of the two parasitoids fecundities and the consequences of changes in this ratio for host equilibrium suppression. Pane A: Increases in the fecundity of the introduced parasitoid relative to that of the resident produce more marginal host suppression if the introduced parasitoid attacks later ($a_P = a_Q = 0.1$, $c_P = c_Q = 0.2$, $k_P = k_Q = 0.25$, $K = 1000.0$, $r = 2.0$). Pane B: The situation is reversed, and increases in the fecundity of the introduced parasitoid relative to that of the resident produce more marginal host suppression if the introduced parasitoid attacks earlier, when $a_Q < a_P$ ($a_P = 0.1$, $a_Q = 0.01$, $c_P = c_Q = 0.2$, $k_P = k_Q = 0.25$, $K = 1000.0$, $r = 2.0$). See text for details.

Figure 1

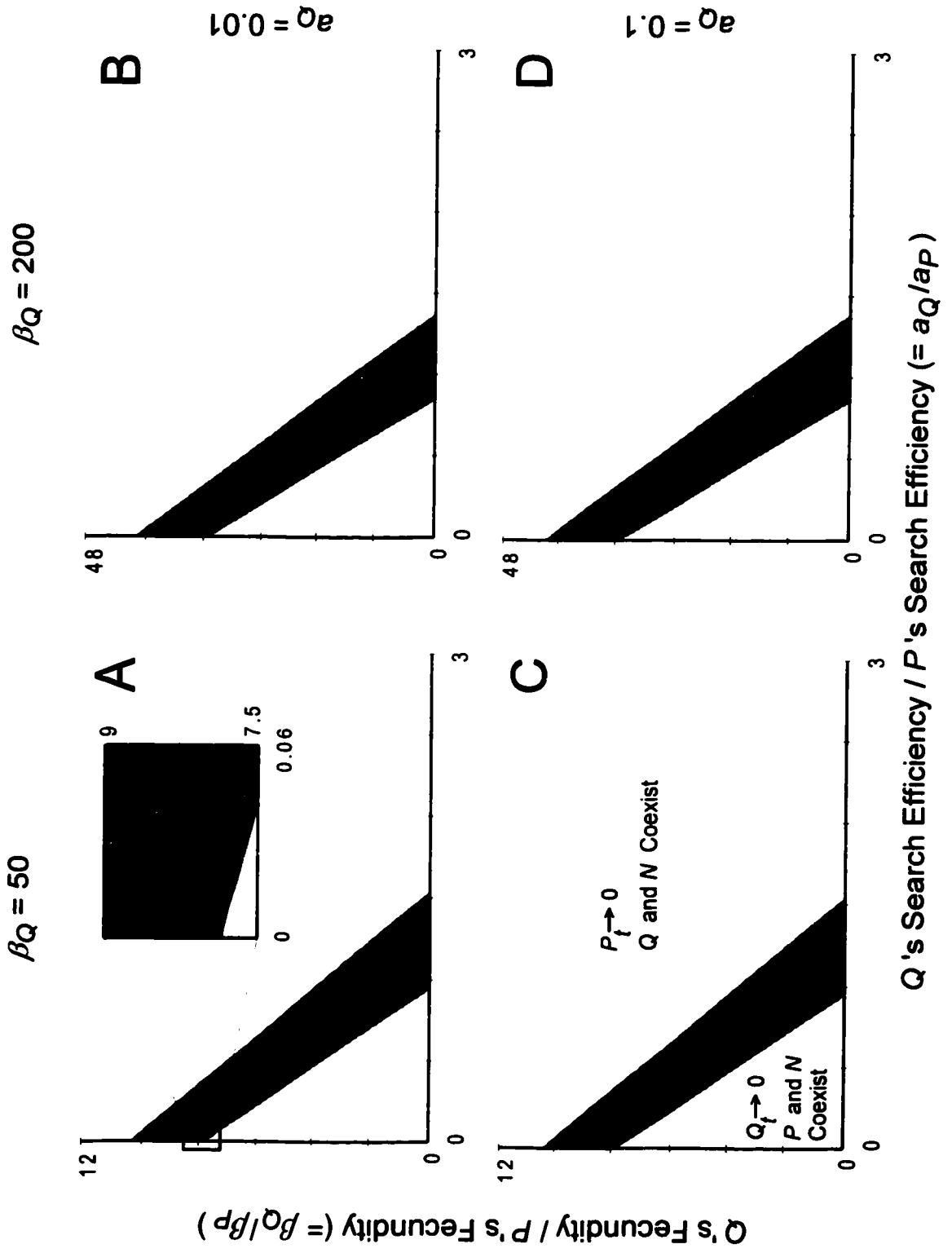


Figure 2

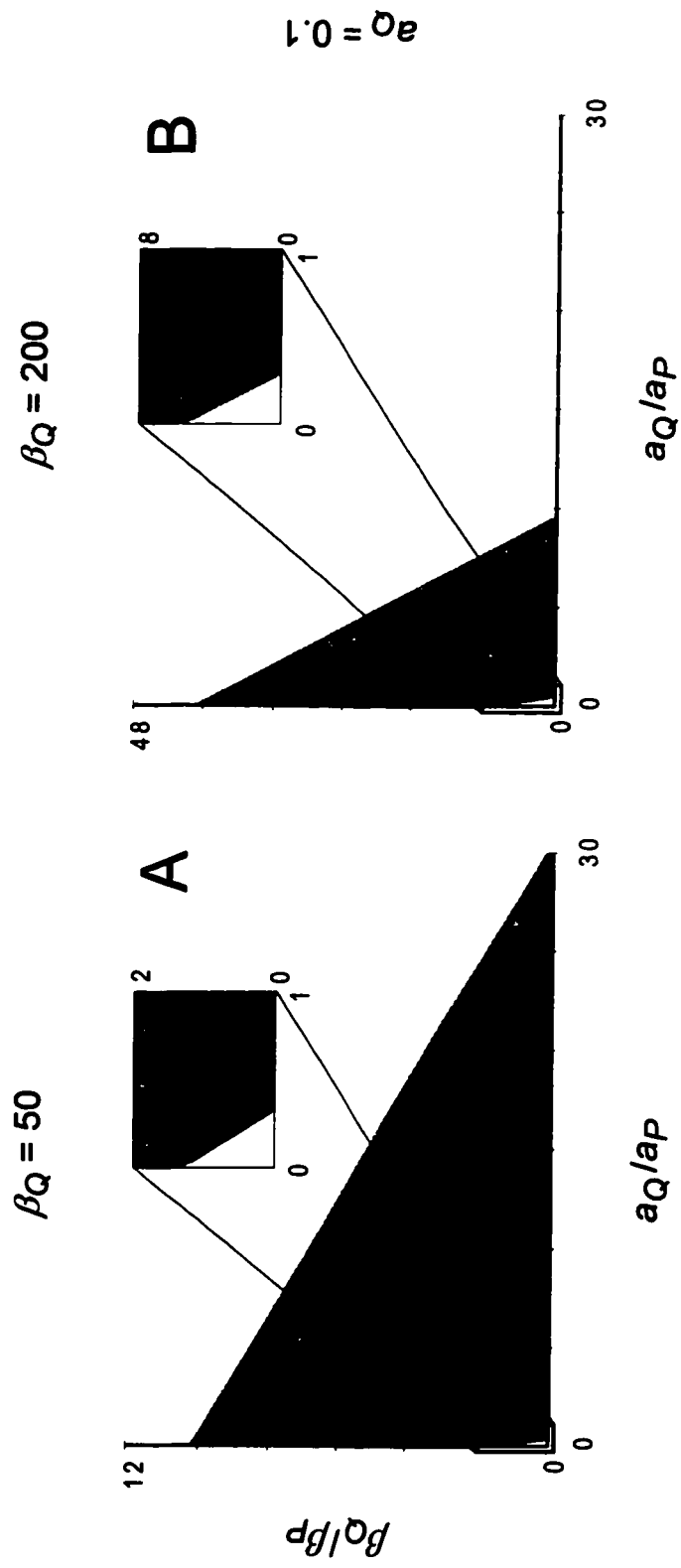


Figure 3

$$\beta_Q = 50$$

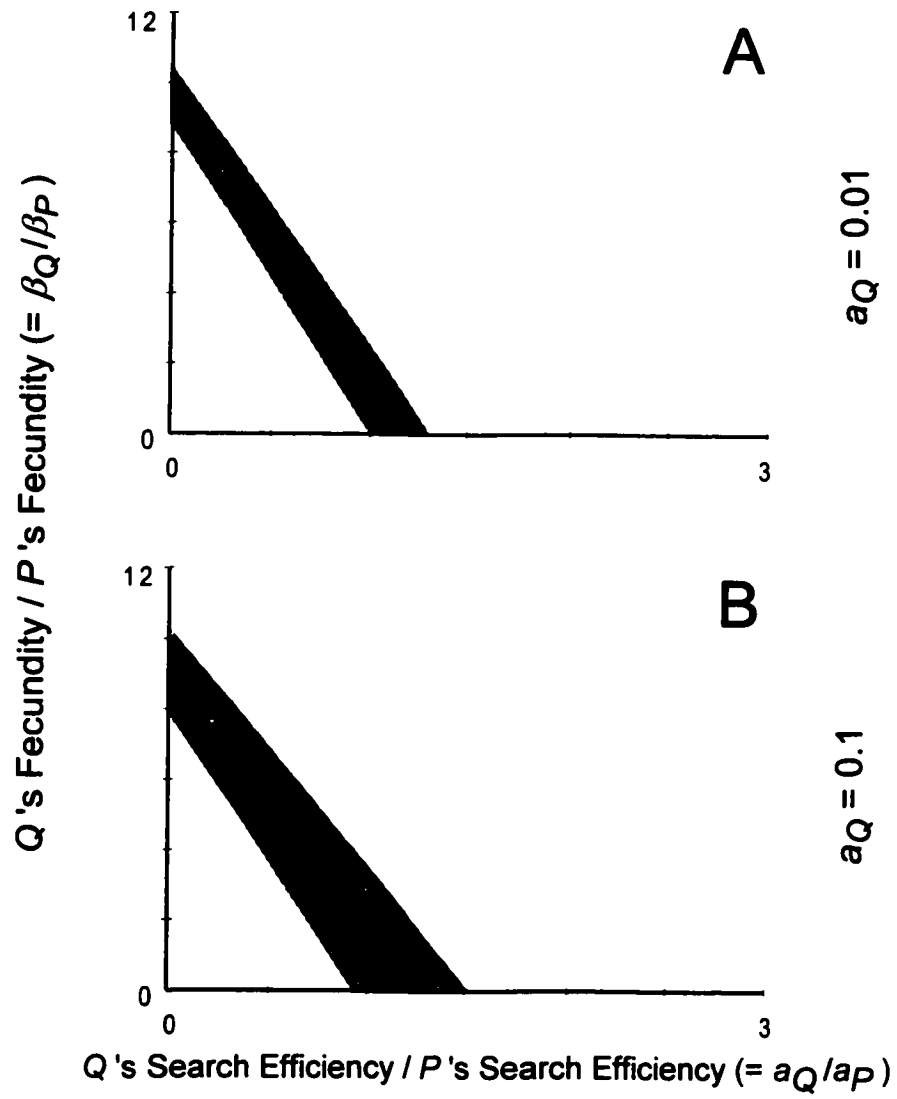
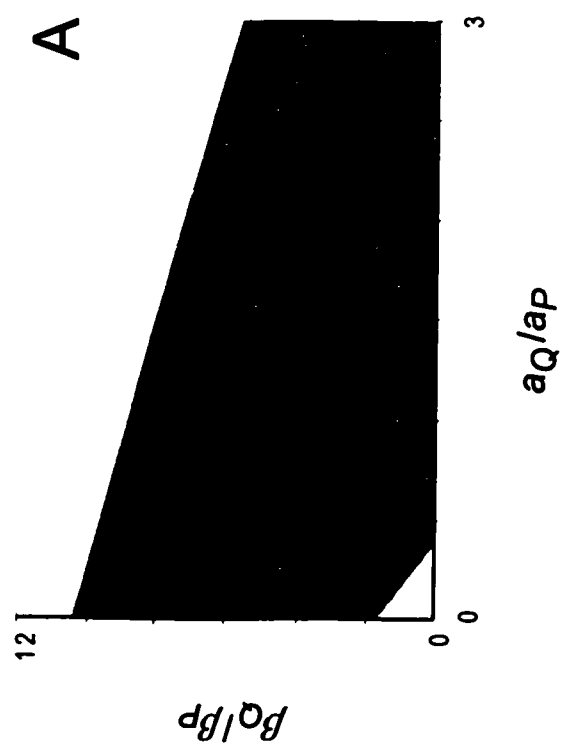


Figure 4

$\beta_Q = 50 \quad K = 1000$



$\beta_Q = 50 \quad K = 80$

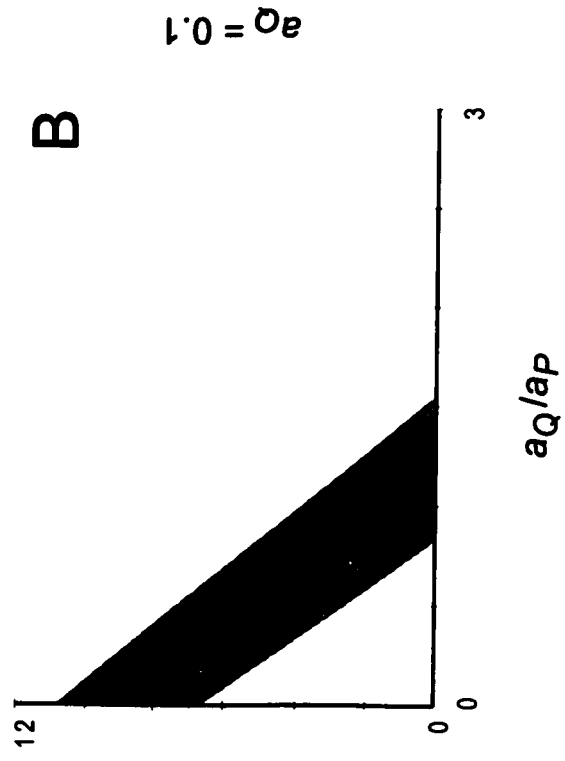


Figure 5

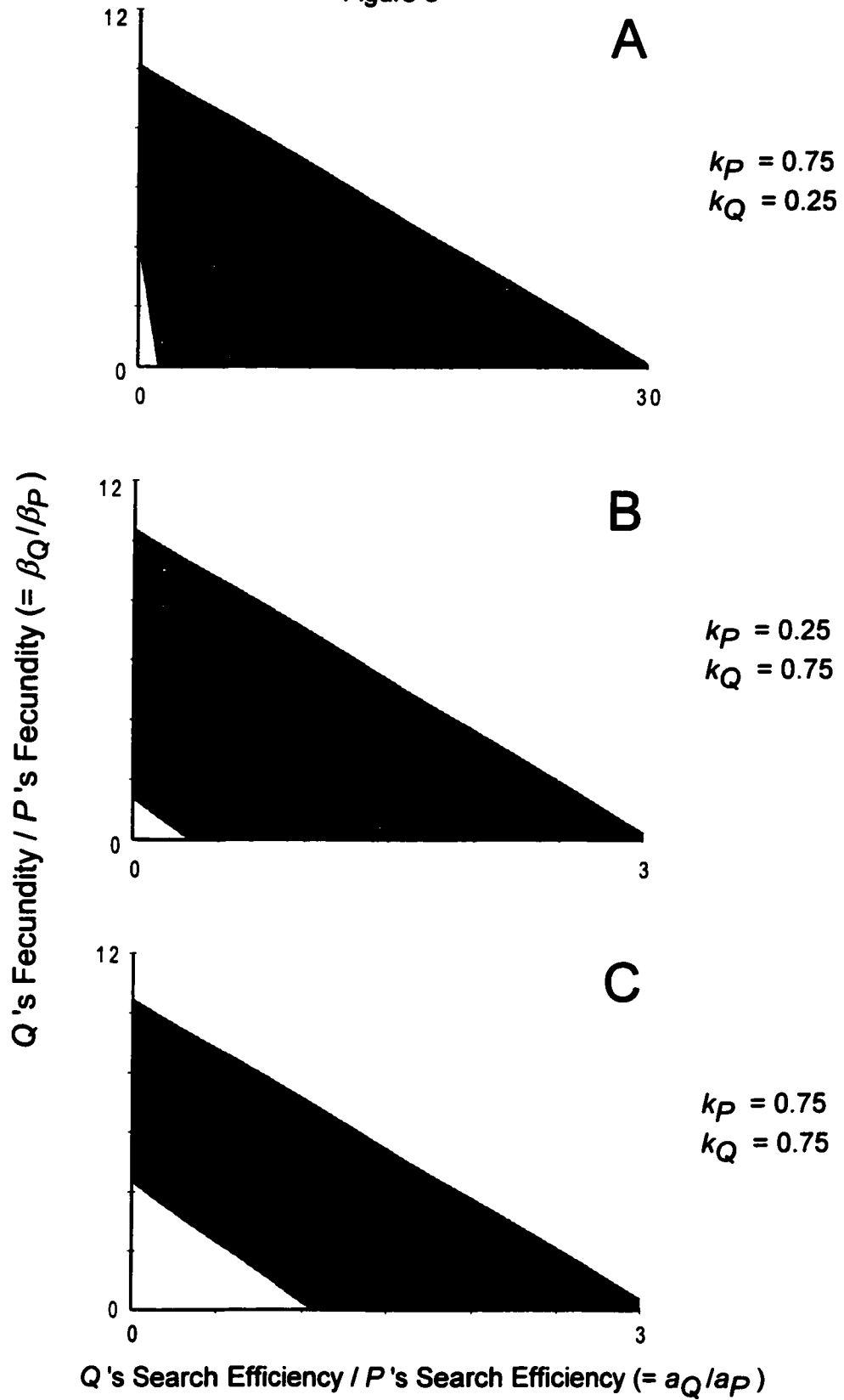


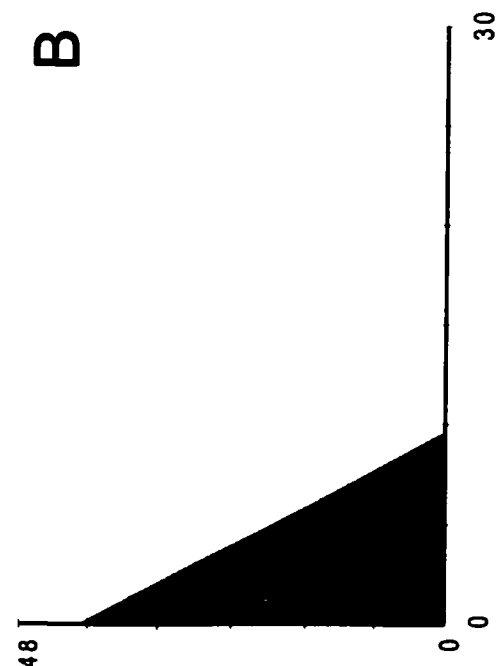
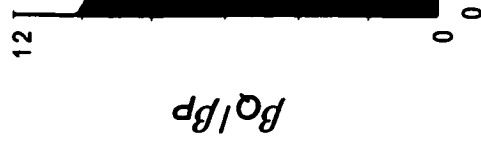
Figure 6

$\beta_Q = 50$

$\beta_Q = 200$

12

48



β_Q/β_P

$a_Q = 0.1$

a_Q/a_P

a_Q/a_P

Figure 7

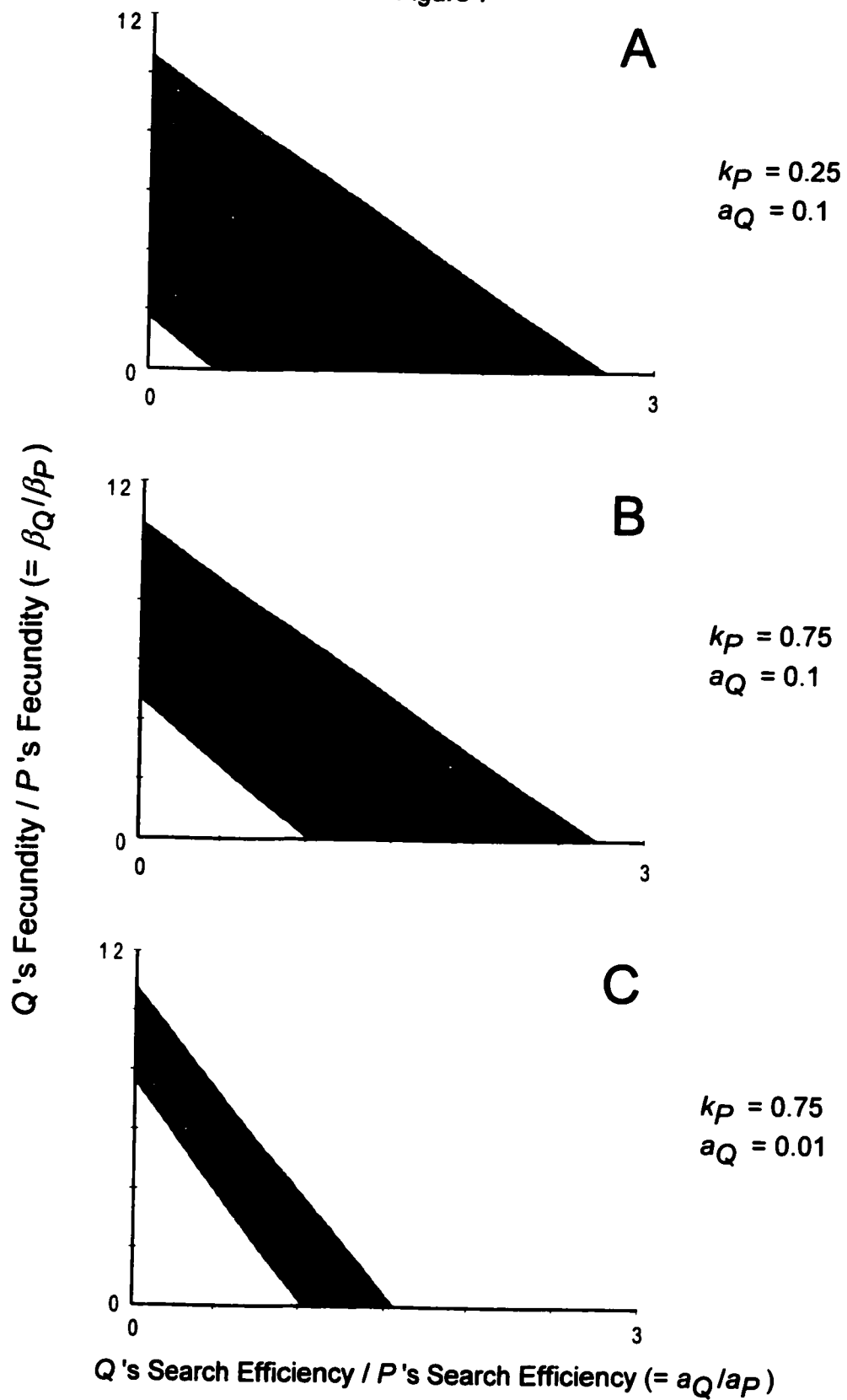


Figure 8

$$\beta_P = 50$$

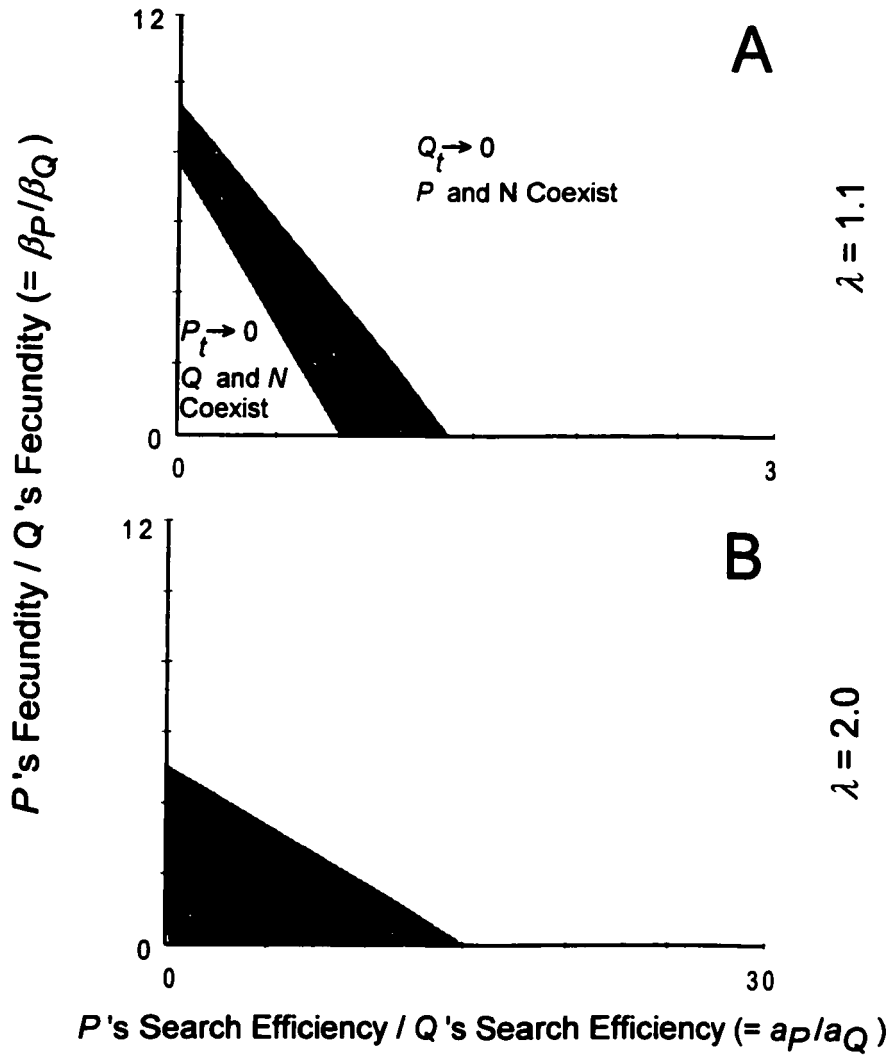


Figure 9

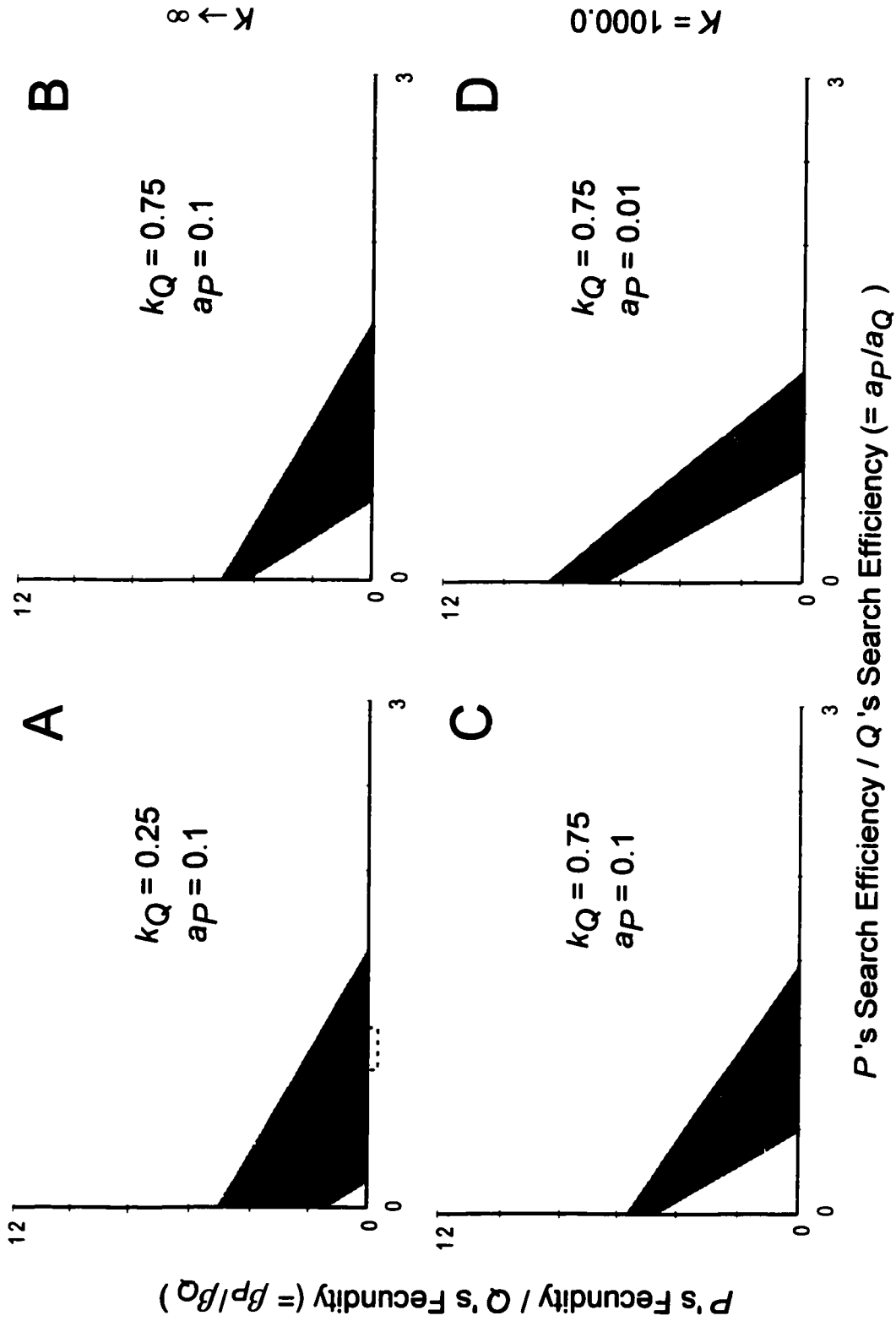


Figure 10

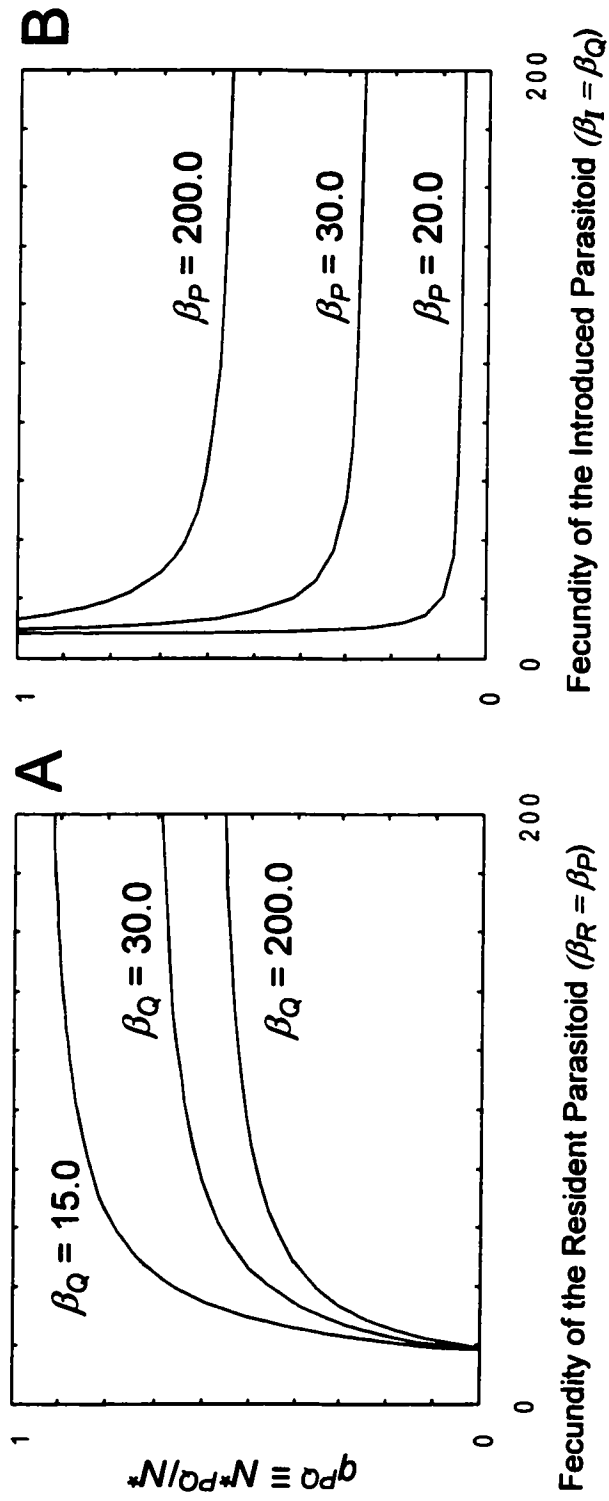
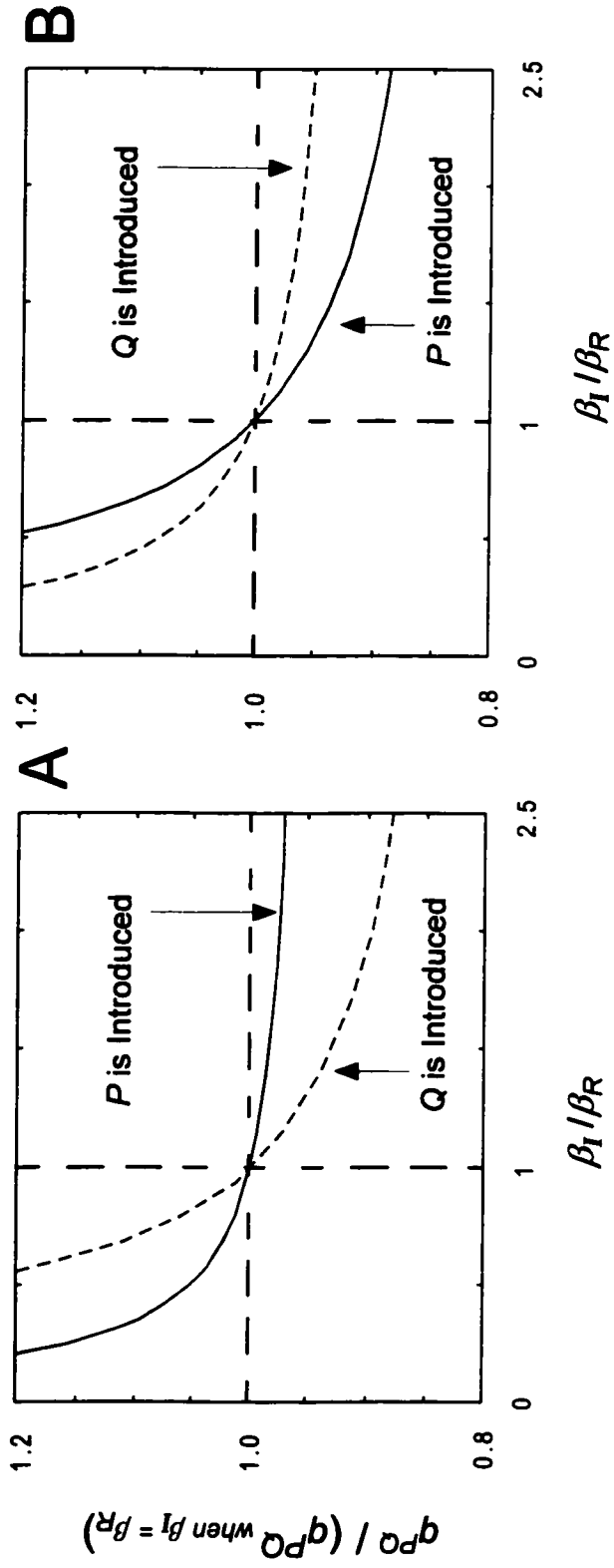


Figure 11



5. CONCLUSIONS AND DIRECTIONS FOR FUTURE RESEARCH

From the results obtained in the studies reported here, it is obvious that several areas of host-parasitoid population dynamics research, both theoretical and empirical, still await exploration. In particular, a great deal of basic biological data on these organisms is currently unavailable in the literature, data fundamental to anyone considering the biological control of *Ephestia kuehniella*, or the use of *Venturia canescens* as a biological control agent. The experiments conducted for Ch. 3 of this dissertation were in part performed because much of the information obtained from them was previously unavailable. This is not particularly surprising, as was detailed in the Introduction to this thesis, but that does not imply that matters should be allowed to stand as they are, and so these concluding remarks are an effort to provide future workers in this field with some hard-won insight into several avenues of research.

One outcome of the research reported in Ch. 2 is the recognition that information about the population growth rates of insect pests is unavailable in the literature. This has been made clear by Hochberg and Holt (1999), who called for a concerted effort to collect this data. In addition, at one point in the development of Ch. 4, the comparative method (Felsenstein, 1985; Harvey & Pagel, 1991) was to be used to evaluate whether the natural pattern of radiation in an appropriate lineage supported predictions derived from the analysis of the model. (An appropriate lineage is one for which there is a fairly well supported

phylogenetic hypothesis available, and in which the members are solitary parasitoids.) The Ophionine, a subfamily in the Ichneumonidae, was determined to be such a lineage: the members of this group are solitary larval parasitoids on macrolepidoptera, and a strong phylogenetic hypothesis is provided by Gauld (1985). Unfortunately, as appears to be characteristic of reasonably large lineages of parasitoids, only scant and sparse biological information is available for members of this lineage. In most cases, even the hosts of these parasitoids are as yet unknown, and when that information is available it is the result of larval rearings and therefore is rarely accompanied by details about when the larvae was initially attacked by the parasitoid, or what within-host competition may have taken place (C. M. St. Mary, *pers. comm.*). Thus, the organized assembly of as much biological information about as many parasitoid species as possible will help to allow better generalizations about these interesting and economically important insects, as well as to allow the evaluation of the theoretical work generated here and elsewhere (Hochberg & Lawton, 1990; Hochberg & Holt, 1999).

Along these lines, two of the effects of the host x parasitoid factorial experiment of Ch. 3 that were *not* measured directly were those on parasitoid egg load and those on host egg hatching success. Both of these data sets would be relatively straightforward to collect if proper resources were available. Parasitoid egg load data (e.g. the parameter β in the model of Chs. 2 and 4), could be evaluated directly by parasitoid dissections, and/or indirectly by

allowing parasitoids to parasitize a superabundance of hosts; the effects on host egg hatching success could be evaluated via the protocol used to examine hatching success described in this thesis. Further information about the fitness of the host and parasitoid offspring resulting from the experiments described in Ch. 3 could be obtained by essentially conducting the experiment twice in sequence, using the offspring from the first experiment in the sequence as the founding population for the second, in a full factorial design (see Jann & Ward, 1999 for some considerations of this type of experiment). In addition, the question of whether host maturation time actually *decreases* with IHDs above 150 could be examined via the simple expedient of higher IHD treatments (185 and 220 IHD/container). Finally, the addition of more parasitoid density treatments (2/container, 4/container and/or 5/container), would allow better discrimination of the parasitoid effects, as well as to examine the effects of over-stinging on population dynamics, and to allow formulations of the escape function which do not depend on host density to be used as regression models. Further examination of density consequences for host *and* parasitoid fecundity will help provide necessary information for evaluating the real-world utility of the fecundity-limitation model.

With respect to the theory of host-parasitoid population dynamics, at least two developments in the structure of the Thompson-Nicholson-Bailey model were not fully incorporated into this research, or indeed, have not yet been fully incorporated into the research literature at large. Both of these developments

have to do with the way host self-limitation is included in the model: the first with how the self-limitation function relates to the timing of events in the host life-cycle (May et al., 1981); and the second with the form that the self-limitation function takes (Getz, 1996). There are certainly examples of modeling efforts which have taken note of the issues relating to the timing of events in the host life-cycle (e.g. Godfray & Waage, 1991; Hochberg & Holt, 1995; Kean & Barlow, 2000), and efforts prior to now to examine which forms of density dependence functions best model the phenomenon (e.g. Bellows, 1981), but it is also clear that more work in this area would be beneficial. In particular, a thorough reexamination of the sequence of events in the host life-cycle, especially in the case where the host is parasitized by more than one parasitoid species, is almost certain to yield useful insights into the dynamics of multiparasitoid-host systems.

6. REFERENCES

- Ahmad, T. (1936) The influence of ecological factors on the Mediterranean flour moth, *Ephestia kuhniella*, and its parasite, *Nemeritis canescens*. *J. Anim. Ecol.*, **5**, 67-93.
- Amaral Filho, B. F. D. (1985) Contribution to the knowledge of the life cycle of *Venturia canescens* (Hymenoptera, Ichneumonidae) under laboratory conditions. *An. Soc. Entomol. Brasil*, **14**, 17-22.
- Anderson, P. & Löfqvist, J. (1996) Asymmetric oviposition behaviour and the influence of larval competition in the two pyralid moths *Ephestia kuehniella* and *Plodia interpunctella*. *Oikos*, **76**, 47-56.
- Andrewartha, H. G. & Birch, L. C. (1954) *The Distribution and Abundance of Animals*. University of Chicago Press, Chicago.
- Andrewartha, H. G. (1961) *Introduction to the study of animal populations*. University of Chicago Press, Chicago.
- Armstrong, R. A. & McGehee, R. (1980) Competitive exclusion. *Am. Nat.*, **115**, 151-170.
- Awmack, C. S. & Leather, S. R. (2002) Host plant quality and fecundity in herbivorous insects. *Ann. Rev. Entomol.*, **47**, 817-844.
- Barbosa, P. & Schultz, J. C., Eds. (1987). *Insect Outbreaks*. Academic Press, San Diego, CA.
- Barclay, H. J. (1986) Host-parasitoid dynamics: Effects of the position of density dependence. *Ecol. Model.*, **32**, 291-299.
- Barlow, N. D., Goldson, S. L. & McNeill, M. R. (1994) A prospective model for the phenology of *Microctonus hyperodae* (Hymenoptera, Braconidae), a potential biological-control agent of Argentine stem weevil in New Zealand. *Biocontrol Sci. Tech.*, **4**, 375-386.
- Barlow, N. D. & Wratten, S. D. (1996) Ecology of predator-prey and parasitoid-host systems: Progress since Nicholson. In *Frontiers of Population Ecology* (ed. by R. B. Floyd, A. W. Sheppard & P. J. De Barro), pp. 217-243. CSIRO, Collingwood, VIC, Australia.
- Beddington, J. R. (1974) Age distribution and the stability of simple discrete time population models. *J. Theor. Biol.*, **47**, 65-74.
- Beddington, J. R., Free, C. A. & Lawton, J. H. (1975) Dynamic complexity in predator-prey models framed in difference equations. *Nature*, **225**, 58-60.
- Beddington, J. R., Free, C. A. & Lawton, J. H. (1978) Characteristics of successful natural enemies in models of biological control of insect pests. *Nature*, **273**, 513-519.
- Bell, C. H. (1976) Effect of cultural factors on the development of four stored-product moths. *J. Stor. Prod. Res.*, **12**, 185-193.

- Bell, C. H. & Savvidou, N. (1999) The toxicity of Vikane (sulfuryl fluoride) to age groups of eggs of the Mediterranean flour moth (*Ephestia kuehniella*). *J. Stor. Prod. Res.*, **35**, 233-247.
- Bellows, T. S. (1981) The descriptive properties of some models for density dependence. *J. Anim. Ecol.*, **50**, 139-156.
- Bellows, T. S. (1982) Analytical models for laboratory populations of *Callosobruchus chinensis* and *C. maculatus* (Coleoptera, Bruchidae). *J. Anim. Ecol.*, **51**, 263-287.
- Benson, J. F. (1973) The biology of Lepidoptera infesting stored products, with special reference to population dynamics. *Biol. Rev.*, **48**, 1-26.
- Benson, J. F. (1974) Population dynamics of *Bracon hebetor* Say (Hymenoptera: Braconidae) and *Ephestia cautella* (Walker) (Lepidoptera: Phycitidae) in a laboratory ecosystem. *J. Anim. Ecol.*, **43**, 71-86.
- Bernstein, C. (1986) Density dependence and the stability of host-parasitoid systems. *Oikos*, **47**, 176-180.
- Bernstein, C. (2000) Host-parasitoid models: The story of a successful failure. In *Parasitoid Population Biology* (ed. by M. E. Hochberg & A. R. Ives), pp. 41-57. Princeton University Press, Princeton, New Jersey.
- Bierne, B. P. (1984) Avoiding obstacles to colonization in classical biological control of insects. *Can. J. Zool.*, **63**, 743-747.
- Birch, L. C. (1957) The meanings of competition. *Am. Nat.*, **91**, 5-18.
- Bonsall, M. B., Godfray, H. C. J., Briggs, C. J. & Hassell, M. P. (1999) Does host self-regulation increase the likelihood of insect-pathogen population cycles? *Am. Nat.*, **153**, 228-235.
- Bonsall, M. B. & Hassell, M. P. (1997) Apparent competition structures ecological assemblages. *Nature*, **388**, 371-373.
- Bonsall, M. B. & Hassell, M. P. (1998) Population dynamics of apparent competition in a host-parasitoid assemblage. *J. Anim. Ecol.*, **67**, 918-929.
- Bonsall, M. B. & Hassell, M. P. (1999) Parasitoid-mediated effects: Apparent competition and the persistence of host-parasitoid assemblages. *Res. Popul. Ecol.*, **41**, 59-68.
- Bonsall, M. B. & Hassell, M. P. (2000) The effects of metapopulation structure on indirect interactions in host-parasitoid assemblages. *Proc. Roy. Soc. Lond. B*, **267**, 2207-2212.
- Botella, L. & Mensua, J. L. (1987) Larval diapause induced by crowding in *Chymomyza costata* (Diptera: Drosophilidae). *Ann. Entomol. Fen.*, **53**, 41-47.
- Breckling, B. & Mueller, F. (1994) Current trends in ecological modelling and the 8th ISEM conference on the state-of-the-art. *Ecol. Model.*, **75-76**, 667-675.
- Briggs, C. J. (1993) Competition among parasitoid species on a stage-structured host and its effect on host suppression. *Am. Nat.*, **141**, 372-397.
- Briggs, C. J., Murdoch, W. W. & Nisbet, R. M. (1999) Recent developments in theory for biological control of insect pests by parasitoids. In *The Theory of*

- Biological Control* (ed. by B. A. Hawkins & H. V. Cornell), pp. 22-42.
Cambridge University Press, Cambridge.
- Briggs, C. J., Nisbet, R. M. & Murdoch, W. W. (1993) Coexistence of competing parasitoid species on a host with a variable life cycle. *Theor. Pop. Biol.*, **44**, 341-373.
- Briggs, C. J., Nisbet, R. M., Murdoch, W. W., Collier, T. R. & Metz, J. A. J. (1995) Dynamical effects of host-feeding in parasitoids. *J. Anim. Ecol.*, **64**, 403-416.
- Brindley, T. A. (1930) The growth and development of *Ephestia kuehniella* Zeller (Lepidoptera) and *Tribolium confusum* Duval (Coleoptera) under controlled conditions of temperature and relative humidity. *Ann. Entomol. Soc. Am.*, **23**, 741-757.
- Cavaleri, L. F. & Koçak, H. (1999) Comparative dynamics of three models for host-parasitoid interactions in a patchy environment. *Bull. Math. Biol.*, **61**, 141-155.
- Cerutti, F., Bigler, F., Eden, G. & Bosshart, S. (1992) Optimal larval density and quality control aspects in mass rearing of the Mediterranean flour moth, *Ephestia kuehniella* Zell. (Lep., Phycitidae). *J. Appl. Entomol.*, **114**, 353-361.
- Chapman, J. W. et al. (1999) Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. *Behav. Ecol.*, **10**, 298-303.
- Cilek, J. E. & Knapp, F. W. (1989) Influence of larval crowding on the adult life history of *Musca autumnalis* (Diptera: Muscidae). *Ann. Entomol. Soc. Am.*, **82**, 346-349.
- Clausen, C. P. (1978) *Introduced Parasites and Predators of Arthropod Pests and Weeds: A World Review*. USDA Handbook No. 480, Washington, DC.
- Cole, L. C. (1960) Competitive Exclusion. *Science*, **132**, 348-349.
- Comins, H. N. & Hassell, M. P. (1996) Persistence of multispecies host-parasitoid interactions in spatially distributed models with local dispersal. *J. Theor. Biol.*, **183**, 19-28.
- Comins, H. N. & Wellings, P. W. (1985) Density-related parasitoid sex-ratio: Influence on host-parasitoid dynamics. *J. Anim. Ecol.*, **54**, 583-603.
- Corbet, S. H. (1968) The influence of *Ephestia kuehniella* on the development of its parasite *Nemeritis canescens*. *J. Exp. Biol.*, **48**, 291-304.
- Crawley, M. J. (1986) The population biology of invaders. *Phil. Trans. R. Soc. Lond. B*, **314**, 711-731.
- Crawley, M. J. (1993) *GLIM for Ecologists*. Blackwell Scientific Publications, Oxford.
- Daumal, J. & Boinel, H. (1994a) Trophic quality of eggs of *Ephestia kuehniella* Zell. after freezing treatment for the rearing of *Trichogramma* species. *Mitt. Schweiz. Entomol. Ges.*, **67**, 373-383.
- Daumal, J. & Boinel, H. (1994b) Variability in fecundity and plasticity of oviposition behavior in *Anagasta kuehniella* (Lepidoptera: Pyralidae). *Ann. Entomol. Soc. Am.*, **87**, 250-256.

- Davison, A. C. & Hinkley, D. V. (1997) *Bootstrap Methods and Their Application*. Cambridge University Press, Cambridge.
- den Boer, P. J. (1990) Reaction to J. Latto and C. Bernstein - Regulation in natural insect populations: Reality or illusion? *Acta Oecol.*, **11**, 131-133.
- den Boer, P. J. & Reddingius, J. (1996) *Regulation and Stabilization Paradigms in Population Ecology*. Chapman and Hall, London.
- Doutt, R. L. (1961) The dimensions of endemism. *Ann. Entomol. Soc. Am.*, **54**, 46-53.
- Doutt, R. L. & DeBach, P. (1964) Some biological control concepts and questions. In *Biological Control of Insect Pests and Weeds* (ed. by P. DeBach), pp. 118-142. Chapman and Hall, London.
- Edwards, D. & Berry, J. J. (1987) The efficiency of simulation-based multiple comparisons. *Biometrics*, **43**, 913-928.
- Ehler, L. E. (1995) Biological control of obscure scale (Homoptera: Diaspididae) in California: An experimental approach. *Environ. Entomol.*, **24**, 779-795.
- Ehler, L. E. & Hall, R. W. (1982) Evidence for competitive exclusion of introduced natural enemies in biological control. *Environ. Entomol.*, **11**, 1-4.
- Ellers, J. (1996) Fat and eggs: An alternative method to measure the trade-off between survival and reproduction in insect parasitoids. *Nether. J. Zool.*, **46**, 227-235.
- Fellowes, M. D. E. & Godfray, H. C. J. (2000) The evolutionary ecology of resistance to parasitoids by *Drosophila*. *Heredity*, **84**, 1-8.
- Fellowes, M. D. E., Kraaijeveld, A. R. & Godfray, H. C. J. (1999a) Association between feeding rate and parasitoid resistance in *Drosophila melanogaster*. *Evolution*, **53**, 1302-1305.
- Fellowes, M. D. E., Kraaijeveld, A. R. & Godfray, H. C. J. (1999b) The relative fitness of *Drosophila melanogaster* (Diptera, Drosophilidae) that have successfully defended themselves against the parasitoid *Asobara tabida* (Hymenoptera, Braconidae). *J. Evol. Biol.*, **12**, 123-128.
- Fellowes, M. D. E., Masnatta, P., Kraaijeveld, A. R. & Godfray, H. C. J. (1998) Pupal parasitoid attack influences the relative fitness of *Drosophila* that have encapsulated larval parasitoids. *Ecol. Entomol.*, **23**, 281-284.
- Felsenstein, J. (1985) Phylogenies and the comparative method. *Am. Nat.*, **125**, 1-15.
- Fisher, R. C. (1962) The effect of multiparasitism on populations of two parasites and their host. *Ecology*, **43**, 314-316.
- Floyd, R. B., Sheppard, A. W. & De Barro, P. J., Eds. (1996). *Frontiers of Population Ecology*. CSIRO, Collingwood, VIC, Australia.
- Force, D. C. (1974) Ecology of insect host-parasitoid communities. *Science*, **184**, 624-632.
- Gauld, I. D. (1985) The phylogeny, classification and evolution of parasitic wasps of the subfamily Ophioninae (Ichneumonidae). *Bull. Brit. Mus. Nat. Hist. (Ent.)*, **51**, 1-185.

- Gause, G. F. (1934) *The Struggle for Existence*. Williams and Wilkins Co., Baltimore.
- Getz, W. M. (1996) A hypothesis regarding the abruptness of density dependence and the growth rate of populations. *Ecology*, **77**, 2014-2026.
- Getz, W. M. (1998) An introspection on the art of modeling in population ecology. *Bioscience*, **48**, 540-552.
- Getz, W. M. & Mills, N. J. (1996) Host-parasitoid coexistence and egg-limited encounter rates. *Am. Nat.*, **148**, 333-347.
- Getz, W. M. & Schreiber, S. J. (1999) Multiple time scales in consumer-resource interactions. *Annales Zoologici Fennici*, **36**, 11-20.
- Gleiser, R. M., Urrutia, J. & Gorla, D. E. (2000) Effects of crowding on populations of *Aedes albifasciatus* larvae under laboratory conditions. *Entomol. Exp. Appl.*, **95**, 135-140.
- Godfray, H. C. J. (1994) *Parasitoids: Behavioral and Evolutionary Ecology*. Princeton University Press, Princeton, New Jersey.
- Godfray, H. C. J., Hassell, M. P. & Holt, R. D. (1994) The population dynamic consequences of phenological asynchrony between parasitoids and their hosts. *J. Anim. Ecol.*, **63**, 1-10.
- Godfray, H. J. C. & Waage, J. K. (1991) Predictive modelling in biological control: The mango mealy bug (*Rastrococcus invadens*) and its parasitoids. *J. Appl. Ecol.*, **28**, 434-453.
- Greathead, D. (1986) Parasitoids in classical biological control. In *Insect Parasitoids* (ed. by J. Waage & D. Greathead), pp. 289-318. Academic Press, New York.
- Greathead, D. & Greathead, A. H. (1992) Biological control of insect pests by parasitoids and predators: The BIOCAT database. *Biocontrol News & Info*, **13**, 61N-68N.
- Griffiths, K. J. & Holling, C. S. (1969) A competition submodel for parasites and predators. *Can. Ent.*, **101**, 785-818.
- Grinnell, J. (1904) The origin and distribution of the chestnut-backed chickadee. *Auk*, **21**, 364-382.
- Gross, P. (1991) Influence of target pest feeding niche on success rates in classical biological control. *Environ. Entomol.*, **20**, 1217-1227.
- Grossmann, W. D. (1994) Socio-economic ecological models: Criteria for evaluation of state-of-the-art models shown on four case studies. *Ecol. Model.*, **75-76**, 21-36.
- Guertin, D. S., Ode, P. J., Strand, M. R. & Antolin, M. F. (1996) Host-searching and mating in an outbreeding parasitoid wasp. *Ecol. Entomol.*, **21**, 27-33.
- Gutierrez, A. P., Neuenschwander, P. & Van Alphen, J. J. M. (1993) Factors affecting biological control of cassava mealybug by exotic parasitoids: A ratio-dependent supply-demand driven model. *J. Appl. Ecol.*, **30**, 706-721.
- Haigh, J. & Maynard Smith, J. (1972) Can there be more predators than prey? *Theor. Pop. Biol.*, **3**, 290-299.

- Hanski, I. (1990) Density dependence, regulation and variability in animal populations. *Phil. Trans. R. Soc. Lond. B*, **330**, 141-150.
- Hardin, G. (1960) The competitive exclusion principle. *Science*, **131**, 1292-1297.
- Harvey, J. A. (1996) *Venturia canescens* parasitizing *Galleria mellonella* and *Anagasta kuehniella*: Is the parasitoid a conformer or regulator? *J. Ins. Physiol.*, **42**, 1017-1025.
- Harvey, J. A., Harvey, I. F. & Thompson, D. J. (1993) The effect of superparasitism on development of the solitary parasitoid wasp, *Venturia canescens* (Hymenoptera: Ichneumonidae). *Ecol. Entomol.*, **18**, 203-208.
- Harvey, J. A., Harvey, I. F. & Thompson, D. J. (1995) The effect of host nutrition on growth and development of the parasitoid wasp *Venturia canescens*. *Entomol. Exp. Appl.*, **75**, 213-220.
- Harvey, J. A., Harvey, I. F. & Thompson, D. J. (2001) Lifetime reproductive success in the solitary endoparasitoid, *Venturia canescens*. *J. Ins. Behav.*, **14**, 573-593.
- Harvey, J. A. & Thompson, D. J. (1995) Developmental interactions between the solitary endoparasitoid *Venturia canescens* (Hymenoptera: Ichneumonidae), and two of its hosts, *Plodia interpunctella* and *Corcyra cephalonica* (Lepidoptera: Pyralidae). *Euro. J. Entomol.*, **92**, 427-435.
- Harvey, J. A., Thompson, D. J. & Heyes, T. J. (1996) Reciprocal influences and costs of parasitism on the development of *Corcyra cephalonica* and its endoparasitoid *Venturia canescens*. *Entomol. Exp. Appl.*, **81**, 39-45.
- Harvey, J. A. & Vet, L. E. M. (1997) *Venturia canescens* parasitizing *Galleria mellonella* and *Anagasta kuehniella*: Differing suitability of two hosts with highly variable growth potential. *Entomol. Exp. Appl.*, **84**, 93-100.
- Harvey, P. H. & Pagel, M. D. (1991) *The Comparative Method in Evolutionary Biology*. Oxford University Press, Oxford.
- Hassell, M. P. (1975) Density dependence in single species populations. *J. Anim. Ecol.*, **44**, 283-295.
- Hassell, M. P. (1978) *The Dynamics of Arthropod Predator-Prey Systems*. Princeton University Press, Princeton, New Jersey.
- Hassell, M. P. (1980) Foraging strategies, population models and biological control: A case study. *J. Anim. Ecol.*, **49**, 603-628.
- Hassell, M. P. (2000a) Host-parasitoid population dynamics. *J. Anim. Ecol.*, **69**, 543-566.
- Hassell, M. P. (2000b) *The Spatial and Temporal Dynamics of Host-Parasitoid Interactions*. Oxford University Press, Oxford.
- Hassell, M. P., Comins, H. N. & May, R. M. (1994) Species coexistence and self-organizing spatial dynamics. *Nature*, **370**, 290-292.
- Hassell, M. P. & Huffaker, C. B. (1969) Regulatory processes and population cyclicity in laboratory populations of *Anagasta kuehniella* (Zeller) (Lepidoptera: Phycitidae). III. The development of population models. *Res. Popul. Ecol.*, **11**, 186-210.

- Hassell, M. P. & May, R. M. (1986) Generalist and specialist natural enemies in insect predator-prey interactions. *J. Anim. Ecol.*, **55**, 923-940.
- Hassell, M. P. & Varley, G. C. (1969) New inductive population model for insect parasites and its bearing on biological control. *Nature*, **223**, 1133-1136.
- Hassell, M. P., Waage, J. & May, R. M. (1983) Variable parasitoid sex ratios and their effect on host-parasitoid dynamics. *J. Anim. Ecol.*, **52**, 889-904.
- Hawkins, B. A. (1994) *Pattern and Process in Host-Parasitoid Interactions*. Cambridge University Press, Cambridge.
- Heimpel, G. E. & Collier, T. R. (1996) The evolution of host-feeding behaviour in insect parasitoids. *Biol. Rev.*, **71**, 373-400.
- Heimpel, G. E., Mangel, M. & Rosenheim, J. A. (1998) Effects of time limitation and egg limitation on lifetime reproductive success of a parasitoid in the field. *Am. Nat.*, **152**, 273-289.
- Heimpel, G. E. & Rosenheim, J. A. (1998) Egg limitation in parasitoids: A review of the evidence and a case study. *Biol. Cont.*, **11**, 160-168.
- Heimpel, G. E., Rosenheim, J. A. & Mangel, M. (1996) Egg limitation, host quality, and dynamic behavior by a parasitoid in the field. *Ecology*, **77**, 2410-2420.
- Henson, S. M. & Cushing, J. M. (1996) Hierarchical models of intra-specific competition: Scramble versus contest. *J. Math. Biol.*, **34**, 755-772.
- Hilborn, R. & Mangel, M. (1997) *The Ecological Detective: Confronting Models with Data*. Princeton University Press, Princeton, New Jersey.
- Hill, M. G. (1988) Analysis of the biological control of *Mythimna separata* (Lepidoptera, Noctuidae) by *Apanteles ruficrus* (Braconidae, Hymenoptera) in New Zealand. *J. Appl. Ecol.*, **25**, 197-208.
- Hochberg, M. E. (1991) Population dynamic consequences of the interplay between parasitism and intraspecific competition for host-parasite systems. *Oikos*, **61**, 297-306.
- Hochberg, M. E. & Hawkins, B. A. (1994) The implications of population dynamics theory to parasitoid diversity and biological control. In *Parasitoid Community Ecology* (ed. by B. A. Hawkins & W. Sheehan), pp. 451-471. Oxford University Press, Oxford.
- Hochberg, M. E. & Holt, R. D. (1995) Refuge evolution and the population dynamics of coupled host-parasitoid associations. *Evol. Ecol.*, **9**, 633-661.
- Hochberg, M. E. & Holt, R. D. (1999) The uniformity and density of pest exploitation as guides to success in biological control. In *Theoretical Approaches to Biological Control* (ed. by B. A. Hawkins & H. V. Cornell), pp. 71-88. Cambridge University Press, Cambridge.
- Hochberg, M. E. & Ives, A. R. (1999) Can natural enemies enforce geographical range limits? *Ecography*, **22**, 268-276.
- Hochberg, M. E. & Lawton, J. H. (1990) Spatial heterogeneities in parasitism and population dynamics. *Oikos*, **59**, 9-14.

- Hogarth, W. L. & Diamond, P. (1984) Interspecific competition in larvae between entomophagous parasitoids. *Am. Nat.*, **124**, 552-560.
- Holling, C. S. (1959) The components of predation as revealed by a study of small mammal predation of the European pine sawfly. *Can. Ent.*, **91**, 293-320.
- Holt, R. D. & Lawton, J. H. (1993) Apparent competition and enemy-free space in insect host-parasitoid communities. *Am. Nat.*, **142**, 623-645.
- Holt, R. D., Grover, J. & Tilman, D. (1994) Simple rules for interspecific dominance in systems with exploitative and apparent competition. *Am. Nat.*, **144**, 741-771.
- Hoy, M. A. (1985) Improving establishment of arthropod natural enemies. In *Biological Control in Agricultural IPM Systems* (ed. by M. A. Hoy & D. C. Herzog), pp. 151-166. Academic Press, New York.
- Huffaker, C. B., Berryman, A. & Turchin, P. (1999) Dynamics and regulation of insect populations. In *Ecological Entomology* (ed. by C. B. Huffaker & A. P. Gutierrez), pp. 269-312. Wiley, New York.
- Huffaker, C. B., Luck, R. F. & Messenger, P. S. (1977) The ecological basis of biological control. In *Proceedings of XV International Congress of Entomology, Washington, DC, 19-27 August 1976* (ed. by D. White), pp. 560-586. The Entomological Society of America, College Park, Maryland, U.S.A.
- Huffaker, C. B., Messenger, P. S. & De Bach, P. (1971) The natural enemy component in natural control and the theory of biological control. In *Biological control* (ed. by C. B. Huffaker), pp. 16-67. Plenum, New York.
- Hughes, J. P., Harvey, I. F. & Hubbard, S. F. (1994a) Host-searching behavior of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): Interference-the effect of mature egg load and prior behavior. *J. Ins. Behav.*, **7**, 433-454.
- Hughes, J. P., Harvey, I. F. & Hubbard, S. F. (1994b) Host-searching behavior of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): Superparasitism. *J. Ins. Behav.*, **7**, 455-464.
- Hutchinson, G. E. (1961) The paradox of the plankton. *Am. Nat.*, **95**, 137-145.
- Hutson, V. & Law, R. (1985) Permanent coexistence in general models of 3 interacting species. *J. Math. Biol.*, **21**, 285-298.
- Ives, A. R. & Settle, W. H. (1996) The failure of a parasitoid to persist with a superabundant host: The importance of the numerical response. *Oikos*, **75**, 269-278.
- Iwasa, Y., Suzuki, Y. & Matsuda, H. (1984) Theory of oviposition strategy of parasitoids. I. Effect of mortality and egg number. *Theor. Pop. Biol.*, **26**, 205-227.
- Jann, P. & Ward, P. I. (1999) Maternal effects and their consequences for offspring fitness in the yellow dung fly. *Func. Ecol.*, **13**, 51-58.
- Jarosik, V. & Dixon, A. F. G. (1999) Population dynamics of a tree-dwelling aphid: Regulation and density-independent processes. *J. Anim. Ecol.*, **68**, 726-732.

- Jervis, M. A., Hawkins, B. A. & Kidd, N. A. C. (1996) The usefulness of destructive host feeding parasitoids in classical biological control: Theory and observation conflict. *Ecol. Entomol.*, **21**, 41-46.
- Jorgensen, S. E. (1999) State-of-the-art of ecological modelling with emphasis on development of structural dynamic models. *Ecol. Model.*, **120**, 75-96.
- Kaitala, V. & Getz, W. M. (1992) Sex ratio genetics and the competitiveness of parasitic wasps. *Bull. Math. Biol.*, **54**, 295-311.
- Takehashi, N., Suzuki, Y. & Iwasa, Y. (1984) Niche overlap of parasitoids in host-parasitoid systems: Its consequence to single versus multiple introduction controversy in biological control. *J. Appl. Ecol.*, **21**, 115-131.
- Kazimirova, M. (1996) Influence of larval crowding and mating on lifespan and fecundity of *Mamestra brassicae* (Lepidoptera: Noctuidae). *Euro. J. Entomol.*, **93**, 45-52.
- Kean, J. M. & Barlow, N. D. (2000) Can host-parasitoid metapopulations explain successful biological control? *Ecology*, **81**, 2188-2197.
- Kidd, N. A. C. & Jervis, M. A. (1989) The effects of host-feeding behaviour on the dynamics of parasitoid-host interactions, and the implications for biological control. *Res. Popul. Ecol.*, **31**, 235-274.
- Koch, A. L. (1974a) Coexistence resulting from an alternation of density dependent and density independent growth. *J. Theor. Biol.*, **44**, 373-386.
- Koch, A. L. (1974b) Competitive coexistence of two predators utilizing the same prey under constant environmental conditions. *J. Theor. Biol.*, **44**, 387-395.
- Krivan, V. (1997) Dynamical consequences of optimal host feeding on host-parasitoid population dynamics. *Bull. Math. Biol.*, **59**, 809-831.
- Lane, S. D., Mills, N. J. & Getz, W. M. (1999) The effects of parasitoid fecundity and host taxon on the biological control of insect pests: The relationship between theory and data. *Ecol. Entomol.*, **24**, 181-190.
- Latto, J. & Bernstein, C. (1990) Regulation in natural insect populations: Reality or illusion? *Acta Oecol.*, **11**, 121-130.
- Lauenroth, W. K., Skogerboe, G. V. & Flug, M., Eds. (1983). *Analysis of ecological systems: State-of-the-art in ecological modelling*. Developments in environmental modelling. Elsevier, New York.
- Leather, S. R. & Burnand, A. C. (1987) Factors affecting life-history parameters of the pine beauty moth, *Panolis flammea* (D and S): The hidden costs of reproduction. *Func. Ecol.*, **1**, 331-338.
- Lidicker, W. Z. (1965) Comparative study of density regulation in confined populations of four species of rodents. *Res. Popul. Ecol.*, **7**, 57-72.
- Łomnicki, A. (1988) *Population Ecology of Individuals*. Princeton University Press, Princeton, New Jersey.
- Lotka, A. J. (1925) *Elements of Physical Biology*. Williams and Wilkins Co., Baltimore.
- Lotka, A. J. (1932) The growth of mixed populations: Two species competing for a common food supply. *J. Wash. Acad. Sci.*, **22**, 461-469.

- Lynch, L. D., Bowers, R. G., Begon, M. & Thompson, D. J. (1998) A dynamic refuge model and population regulation by insect parasitoids. *J. Anim. Ecol.*, **67**, 270-279.
- Mangel, M. & Heimpel, G. E. (1998) Reproductive senescence and dynamic oviposition behaviour in insects. *Evol. Ecol.*, **12**, 871-879.
- Maple V Release 3 (1994). Waterloo Maple Software, Waterloo, Canada.
- May, R. M. (1974) Biological populations with nonoverlapping generations: Stable points, stable cycles, and chaos. *Science*, **186**, 645-647.
- May, R. M. (1978) Host-parasitoid systems in patchy environments: A phenomenological model. *J. Anim. Ecol.*, **47**, 833-843.
- May, R. M. & Hassell, M. P. (1981) The dynamics of multiparasitoid-host interactions. *Am. Nat.*, **117**, 234-261.
- May, R. M. & Hassell, M. P. (1988) Population dynamics and biological control. *Phil. Trans. R. Soc. Lond. B*, **318**, 129-169.
- May, R. M., Hassell, M. P., Anderson, R. M. & Tonkyn, D. W. (1981) Density dependence in host-parasitoid models. *J. Anim. Ecol.*, **50**, 855-865.
- McGregor, R. (1997) Host-feeding and oviposition by parasitoids on hosts of different fitness value: Influences of egg load and encounter rate. *J. Ins. Behav.*, **10**, 451-462.
- Mills, N. J. (1992) Parasitoid guilds, life-styles, and host ranges in the parasitoid complexes of tortricoid hosts (Lepidoptera: Tortricidae). *Environ. Entomol.*, **21**, 320-329.
- Mills, N. J. (1994a) Biological control: Some emerging trends. In *Individuals, Populations and Patterns in Ecology* (ed. by S. R. Leather, A. D. Watt, N. J. Mills & K. F. A. Walters), pp. 213-222. Intercept, Andover, U.K.
- Mills, N. J. (1994b) Parasitoid guilds: Defining the structure of the parasitoid communities of endopterygote insect hosts. *Environ. Entomol.*, **23**, 1066-1083.
- Mills, N. J. (2000) Biological control: The need for realistic models and experimental approaches to parasitoid introductions. In *Parasitoid Population Biology* (ed. by M. E. Hochberg & A. R. Ives), pp. 217-234. Princeton University Press, Princeton, New Jersey.
- Mills, N. J. (2001) Factors influencing top-down control of insect pest populations in biological control systems. *Basic Appl. Ecol.*, **2**, 323-332.
- Mills, N. J. & Getz, W. M. (1996) Modelling the biological control of insect pests: A review of host-parasitoid models. *Ecol. Model.*, **92**, 121-143.
- Munro, J. W. (1966) *Pests of Stored Products*. Hutchinson, London.
- Münster-Swendsen, M. (1982) Interactions within a one-host-two-parasitoids system, studied by simulations of spatial patterning. *J. Anim. Ecol.*, **51**, 97-110.
- Münster-Swendsen, M. & Nachman, G. (1978) Asynchrony in insect host-parasite interaction and its effects on stability, studied by a simulation model. *J. Anim. Ecol.*, **47**, 159-171.
- Murdoch, W. W. (1994) Population regulation in theory and practice. *Ecology*, **75**, 271-287.

- Murdoch, W. W. & Briggs, C. J. (1996) Theory for biological control: Recent developments. *Ecology*, **77**, 2001-2013.
- Murdoch, W. W., Briggs, C. J. & Nisbet, R. M. (1996) Competitive displacement and biological control in parasitoids: A model. *Am. Nat.*, **148**, 807-826.
- Murdoch, W. W., Chesson, J. & Chesson, P. L. (1985) Biological control in theory and practice. *Am. Nat.*, **125**, 344-366.
- Murdoch, W. W. & Oaten, A. (1975) Predation and population stability. *Adv. Ecol. Res.*, **9**, 1-131.
- Myers, J. H., Higgins, C. & Kovacs, E. (1989) How many insect species are necessary for the biological control of insects. *Environ. Entomol.*, **18**, 541-547.
- Neter, J., Kutner, M. H., Nachtsheim, C. J. & Wasserman, W. (1996) *Applied Linear Statistical Models*, 4th edn. Irwin, Chicago, Illinois.
- Nicholson, A. J. (1933) The balance of animal populations. *J. Anim. Ecol.*, **2**, 132-178.
- Nicholson, A. J. (1954) An outline of the dynamics of animal populations. *Aus. J. Zool.*, **2**, 9-65.
- Nicholson, A. J. & Bailey, V. A. (1935) The balance of animal populations, Part 1. *Proc. Zool. Soc. Lond.*, **3**, 551-598.
- Nielsen, P. S. (2001) The effect of carbon dioxide under pressure against eggs of *Ephestia kuehniella* Zeller and adults of *Stegobium paniceum* (L.) and *Oryzaephilus surinamensis* (L.). *Anz. Schaedlingskd.*, **74**, 85-88.
- Norris, M. J. (1933) Contributions towards the study of insect fertility.--II. Experiments on the factors influencing fertility in *Ephestia kuhniella* Z. (Lepidoptera, Phycitidae). *Proc. Zool. Soc. Lond.*, 903-934.
- Olson, D. M. & Andow, D. A. (1998) Larval crowding and adult nutrition effects on longevity and fecundity of female *Trichogramma nubilale* Ertle and Davis (Hymenoptera: Trichogrammatidae). *Environ. Entomol.*, **27**, 508-514.
- Park, T. (1938) Studies in population physiology: VIII. The effects of larval population density on the post-embryonic development of the flour beetle. *J. Exp. Zool.*, **79**, 51-70.
- Parker, G. A. (2000) Scramble in behaviour and ecology. *Phil. Trans. R. Soc. Lond. B*, **355**, 1637-1645.
- Pemberton, C. E. & Willard, H. F. (1918) Interrelations of fruit fly parasites in Hawaii. *J. Ag. Res.*, **12**, 285-295.
- Peters, T. M. & Barbosa, P. (1977) Influence of population density on size, fecundity, and developmental rate of insects in culture. *Ann. Rev. Entomol.*, **22**, 431-50.
- Plarre, R., Rassmann, W. & Wohlgemuth, R. (1993) Use of impact machines to control the Mediterranean flour moth *Ephestia kuehniella* (Lepidoptera: Pyralidae) in flour and semolina. *Anz. Schaedlingskd. Pfl.*, **66**, 15-18.
- Podoler, H. (1974a) Analysis of life tables for a host and parasite (*Plodia-Nemeritis*) ecosystem. *J. Anim. Ecol.*, **43**, 653-670.

- Podoler, H. (1974b) Effects of intraspecific competition in the Indian meal-moth (*Plodia interpunctella* Hübner) (Lepidoptera: Phycitidae) on populations of the moth and its parasite *Nemeritis canescens* (Gravenhorst) (Hymenoptera: Ichneumonidae). *J. Anim. Ecol.*, **43**, 641-651.
- Price, P. W. (1974) Strategies for egg production. *Evolution*, **28**, 76-84.
- Price, P. W. (1975) Reproductive strategies of parasitoids. In *Evolutionary Strategies of Parasitic Insects and Mites* (ed. by P. W. Price), pp. 87-111. Plenum Press, New York.
- Reed, D. J., Begon, M. & Thompson, D. J. (1996) Differential cannibalism and population dynamics in a host-parasitoid system. *Oecologia*, **105**, 189-193.
- Reeve, J. D., Rhodes, D. J. & Turchin, P. (1998) Scramble competition in the southern pine beetle, *Dendroctonus frontalis*. *Ecol. Entomol.*, **23**, 433-443.
- Ritchie, M. E. (1996) Interaction of temperature and resources in population dynamics: An experimental test of theory. In *Frontiers of Population Ecology* (ed. by R. B. Floyd, A. W. Sheppard & P. J. De Barro), pp. 79-92. CSIRO, Collingwood, VIC, Australia.
- Rogers, D. (1972) The ichneumon wasp *Venturia canescens*: Oviposition and avoidance of superparasitism. *Entomol. Exp. Appl.*, **15**, 190-194.
- Rohani, P., Godfray, C. J. & Hassell, M. P. (1994) Aggregation and the dynamics of host-parasitoid systems: A discrete-generation model with within-generation redistribution. *Am. Nat.*, **144**, 491-509.
- Rosenheim, J. A. (1996) An evolutionary argument for egg limitation. *Evolution*, **50**, 2089-2094.
- Rosenheim, J. A. (1999) Characterizing the cost of oviposition in insects: A dynamic model. *Evol. Ecol.*, **13**, 141-165.
- Sait, S. M., Begon, M., Thompson, D. J., Harvey, J. A. & Hails, R. S. (1997) Factors affecting host selection in an insect host-parasitoid interaction. *Ecol. Entomol.*, **22**, 225-230.
- Salt, G. (1964) The ichneumonid parasite *Nemeritis canescens* (Gravenhorst) in relation to the wax moth *Galleria mellonella*(L.). *Trans. R. Ent. Soc. Lond.*, **116**, 1-14.
- Salt, G. (1965) Experimental studies in insect parasitism. XII. The haemocytic reaction of a caterpillar to eggs of its habitual parasite. *Proc. Roy. Soc. Lond. B*, **162**, 303-318.
- Salt, G. (1966) Experimental studies in insect parasitism. XIV. The haemocytic reaction of a caterpillar to larvae of its habitual parasite. *Proc. Roy. Soc. Lond. B*, **165**, 155-178.
- Salt, G. (1975) The fate of an internal parasitoid, *Nemeritis canescens*, in a variety of insects. *Proc. Roy. Soc. Lond. B*, **127**, 141-161.
- Salt, G. (1976) The hosts of *Nemeritis canescens*, a problem in host specificity of insect parasitoids. *Ecol. Entomol.*, **1**, 63-67.
- Sang, J. H. (1949) The ecological determinants of population growth in a *Drosophila* culture: III. Larval and pupal survival. *Physiol. Zool.*, **22**, 183-202.

- Sang, J. H. (1959) Circumstances affecting the nutritional requirements of *Drosophila melanogaster*. *Ann. N. Y. Acad. Sci.*, **77**, 352-365.
- Saunders, D. S. & Bee, A. (1995) Effects of larval crowding on size and fecundity of the blow fly, *Calliphora vicina* (Diptera: Calliphoridae). *Euro. J. Entomol.*, **92**, 615-622.
- Scheiring, J. F., Davis, D. G., Ranasinghe, A. & Teare, C. A. (1984) Effects of larval crowding on life history parameters in *Drosophila melanogaster* (Diptera: Drosophilidae). *Ann. Entomol. Soc. Am.*, **77**, 329-332.
- Schervish, M. J. (1997) *Theory of Statistics*. Springer-Verlag, New York.
- Schreiber, S. J., Fox, L. R. & Getz, W. M. (2000) Coevolution of contrary choices in host-parasitoid systems. *Am. Nat.*, **155**, 637-648.
- Sevenster, J. G., Ellers, J. & Driessen, G. (1998) An evolutionary argument for time limitation. *Evolution*, **52**, 1241-1244.
- Shea, K., Nisbet, R. M., Murdoch, W. W. & Yoo, H. J. S. (1996) The effect of egg limitation on stability in insect host-parasitoid population models. *J. Anim. Ecol.*, **65**, 743-755.
- Simmonds, F. J. (1943) The occurrence of superparasitism in *Nemeritis canescens* Grav. *Rev. Can. Biol.*, **2**, 15-58.
- Sirot, E. (1996) The pay-off from superparasitism in the solitary parasitoid *Venturia canescens*. *Ecol. Entomol.*, **21**, 305-307.
- Sirot, E. & Bernstein, C. (1996) Time sharing between host searching and food searching in parasitoids: State-dependent optimal strategies. *Behav. Ecol.*, **7**, 189-194.
- Sirot, E., Ploye, H. & Bernstein, C. (1997) State dependent superparasitism in a solitary parasitoid: Egg load and survival. *Behav. Ecol.*, **8**, 226-232.
- Slobodkin, L. B. (1986) The role of minimalism in art and science. *Am. Nat.*, **127**, 257-265.
- Smith, H. S. (1929) Multiple parasitism: Its relation to the biological control of insect pests. *Bull. Entomol. Res.*, **20**, 141-149.
- Smith, S. (1969) The effect of crowding on larvae of the meal moth, *Ephestia kuehniella*. *J. Exp. Zool.*, **170**, 193-204.
- So, P.-M. & Dudgeon, D. (1989) Larval growth dynamics of *Hemipyrellia ligurriens* (Calliphoridae) and *Boettcherisca formosensis* (Sarcophagidae) in crowded and uncrowded cultures. *Res. Popul. Ecol.*, **31**, 113-122.
- Sokal, R. R. & Rohlf, F. J. (1981) *Biometry*, 2nd edn. Freeman, New York.
- Sousa, W. P. (1994) Patterns and processes in communities of helminth parasites. *TREE*, **9**, 52-57.
- SPlus 4 (1997). MathSoft, Inc., Seattle, Washington.
- Stewart, F. M. & Levin, B. R. (1973) Partitioning of resources and the outcome of interspecific competition: A model and some general considerations. *Am. Nat.*, **107**, 171-198.
- Stiling, P. (1990) Calculating the establishment rates of parasitoids in classical biological control. *Am. Entomol.*, **36**, 225-230.

- Stiling, P. (1993) Why do natural enemies fail in classical biological control programs. *Am. Entomol.*, **39**, 31-37.
- Subramanyam, B. & Hagstrum, D. W., Eds. (1996). *Integrated Management of Insects in Stored Products*. Marcel Dekker, New York.
- Subramanyam, B. & Hagstrum, D. W., Eds. (2000). *Alternatives to Pesticides in Stored-Product IPM*. Kluwer Academic, Boston.
- Sweetman, H. L. (1958) *The Principles of Biological Control; Interrelation of Hosts and Pests and Utilization in Regulation of Animal and Plant Populations*. W. C. Brown Co., Dubuque, Iowa.
- Symondson, W. O. C., Sunderland, K. D. & Greenstone, M. H. (2002) Can generalist predators be effective biocontrol agents? *Ann. Rev. Entomol.*, **47**, 561-594.
- Takagi, M. (1999) Perspective of practical biological control and population theories. *Res. Popul. Ecol.*, **41**, 121-126.
- Takahashi, F. (1953) On the action of population density in the population fluctuation of the flour moth, *Ephestia cautella*. *Res. Popul. Ecol.*, **2**, 55-64.
- Takahashi, F. (1956) On the effect of population density on the power of the reproduction of the almond moth, *Ephestia cautella*: 3. The maximum reproduction of population and the larval density. *Res. Popul. Ecol.*, **3**, 27-35.
- Takahashi, F. (1963) Changes in some ecological characters of the almond moth caused by the selective action of an Ichneumon wasp in their interacting system. *Res. Popul. Ecol.*, **5**, 117-129.
- Takahashi, F. (1968) Functional response to host density in a parasitic wasp, with reference to population regulation. *Res. Popul. Ecol.*, **10**, 54-68.
- Taylor, A. D. (1993a) Aggregation, competition, and host-parasitoid dynamics: Stability conditions don't tell it all. *Am. Nat.*, **141**, 501-506.
- Taylor, A. D. (1993b) Heterogeneity in host-parasitoid interactions: 'Aggregation of risk' and the ' $CV^2 > 1$ rule'. *TREE*, **8**, 400-405.
- Taylor, A. D. (1996) Sources of stability in host-parasitoid dynamics. In *Frontiers of Population Ecology* (ed. by R. B. Floyd, A. W. Sheppard & P. J. De Barro), pp. 257-267. CSIRO, Collingwood, VIC, Australia.
- Thompson, W. R. (1922) Biologie-Théorie de l'action des parasites entomophages. Les formules mathématiques du parasitisme cyclique. *C. R. Acad. Sci., Paris*, **174**, 1201-1204.
- Thompson, W. R. (1924) La théorie mathématique de l'action des parasites entomophages et le facteur du hasard. *Ann. Fac. Sci. Marseille*, **2**, 69-89.
- Thompson, W. R. (1929) On the effect of random oviposition on the action of entomophagous parasites as agents of natural control. *Parasitology*, **21**, 180-188.
- Thompson, W. R. (1939) Biological control and the theories of interaction of populations. *Parasitology*, **31**, 299-388.
- Tilman, D. (1982) *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.

- Tilman, D. (1990) Mechanisms of plant competition for nutrients: The elements of a predictive theory of competition. In *Perspectives on Plant Competition* (ed. by J. B. Grace & D. Tilman), pp. 117-141. Academic Press, San Diego, CA.
- Tokumaru, S. & Takada, H. (1996) Numbers of eggs deposited and host feeding in *Aphelinus gossypii* Timberlake (Hymenoptera: Aphelinidae), a parasitoid of *Aphis gossypii* Glover (Homoptera: Aphididae). *Jap. J. Appl. Entomol. Zool.*, **40**, 242-244.
- Toquenaga, Y. & Fujii, K. (1990) Contest and scramble competitions in two bruchid species, *Callosobruchus analis* and *C. phaseoli* (Coleoptera: Bruchidae): I. larval competition curves and interference mechanisms. *Res. Popul. Ecol.*, **32**, 349-364.
- Toquenaga, Y. & Fujii, K. (1991a) Contest and scramble competitions in *Callosobruchus maculatus* (Coleoptera: Bruchidae): I. larval competition curves and resource sharing patterns. *Res. Popul. Ecol.*, **33**, 199-211.
- Toquenaga, Y. & Fujii, K. (1991b) Contest and scramble competitions in two bruchid species, *Callosobruchus analis* and *C. phaseoli* (Coleoptera: Bruchidae): II. Larval competition experiment. *Res. Popul. Ecol.*, **33**, 129-139.
- Tregenza, T., Thompson, D. J. & Parker, G. A. (1996) Interference and the ideal free distribution: Oviposition in a parasitoid wasp. *Behav. Ecol.*, **7**, 387-394.
- Tripathi, S. R. & Singh, A. (1990) Effect of larval crowding on development, growth and reproduction of *Earias vittella* (F.) (Lepidoptera: Noctuidae). *Mitt. Zool. Mus. Berlin*, **66**, 375-379.
- Tripathi, S. R. & Singh, R. (1989) Effects of larval crowding on development, growth and reproduction of *Heliothis armigera* (Hubner) (Lepidoptera: Noctuidae). *Zeit. Ang. Zool.*, **76**, 247-253.
- Trudeau, D. & Gordon, D. M. (1989) Factors determining the functional response of the parasitoid *Venturia canescens*. *Entomol. Exp. Appl.*, **50**, 3-6.
- Tsuda, Y., Suzuki, A., Takagi, M. & Wada, Y. (1997) Different responses to larval crowding between 2 strains of *Aedes albopictus* (Diptera: Culicidae) from Japan and Thailand. *Med. Ent. Zool.*, **48**, 19-24.
- Tsuda, Y. & Yoshida, T. (1985) Population biology of the broad-horned flour beetle, *Gnathocerus cornutus*: II. Crowding effects of larvae on their survival and development. *Res. Popul. Ecol.*, **27**, 77-86.
- Tuda, M. & Iwasa, Y. (1998) Evolution of contest competition and its effect on host-parasitoid dynamics. *Evol. Ecol.*, **12**, 855-870.
- Turchin, P. (1995) Population regulation: Old arguments and a new synthesis. In *Population Dynamics: New Approaches and Synthesis* (ed. by N. Cappuccino & P. W. Price), pp. 19-40. Academic Press, San Diego, CA.
- Turnbull, A. L. (1967) Population dynamics of exotic insects. *Bull. Ent. Soc. Am.*, **13**, 333-337.
- Turnbull, A. L. & Chant, D. A. (1961) The practice and theory of biological control in Canada. *Can. J. Zool.*, **39**, 697-753.

- Uchmanski, J. (2000) Individual variability and population regulation: An individual-based model. *Oikos*, **90**, 539-548.
- Udvardy, M. F. D. (1959) Notes on the ecological concepts of habitat, biotope and niche. *Ecology*, **40**, 725-728.
- Ulliyett, G. C. (1945) Oviposition by *Ephestia kuhniella* Zell. *J. Entomol. Soc. Sth. Afr.*, **8**, 53-59.
- Ulliyett, G. C. & van der Merwe, J. S. (1947) Some factors influencing population growth of *Ephestia kuhniella* Zell. (Lep., Phycitid). *J. Entomol. Soc. Sth. Afr.*, **10**, 46-63.
- Underwood, A. J. (1997) *Experiments in Ecology*. Cambridge University Press, Cambridge.
- Utida, S. (1953) Effect of host density upon the population growth of interacting two species of parasite. Experimental studies on synparasitism. Second report. *Oyo-Kontyu*, **9**, 102-107.
- Van Alebeek, F. A. N., Koning, C. M., De Korte, E. A. P. & Van Huis, A. (1996) Egg-limited functional response of *Uscana lariophaga*, egg parasitoid of bruchid beetle pests in stored cowpea. *Entomol. Exp. Appl.*, **81**, 215-225.
- Van Buskirk, J. (1993) Population consequences of larval crowding in the dragonfly *Aeshna juncea*. *Ecology*, **74**, 1950-1958.
- van den Bosch, R. (1968) Comments on population dynamics of exotic insects. *Bull. Ent. Soc. Am.*, **14**, 112-115.
- Van Lenteren, J. C. (1986) Parasitoids in the greenhouse: Successes with seasonal inoculative release systems. In *Insect Parasitoids* (ed. by J. K. Waage & D. Greathead), pp. 341-374. Academic Press, New York.
- Varley, C., Gradwell, G. R. & Hassell, M. P. (1973) *Insect Population Ecology: An Analytical Approach*. University of California Press, Berkeley, California.
- Veno, T. (1997) Effects of superparasitism, larval competition, and host feeding on offspring fitness in the parasitoid *Pimpla nipponica* (Hymenoptera: Ichneumonidae). *Ann. Entomol. Soc. Am.*, **90**, 682-688.
- Volterra, V. (1928) Variations and fluctuations of the number of individuals in animal species living together. *Journal du conseil/Conseil International pour l'exploration de la mer*, **3**, 3-51.
- Waage, J. K. (1990) Ecological theory and the selection of biological control agents. In *Critical Issues in Biological Control* (ed. by M. Mackauer, L. E. Ehler & J. Roland), pp. 135-157. Intercept, Andover, U.K.
- Waage, J. K. & Hassell, M. P. (1982) Parasitoids as biological control agents - a fundamental approach. *Parasitology*, **84**, 241-268.
- Waage, J. K. & Mills, N. J. (1992) Biological control. In *Natural Enemies* (ed. by M. J. Crawley), pp. 412-430. Blackwell, Oxford.
- Watt, K. E. F. (1965) Community stability and the strategy of biological control. *Can. Ent.*, **97**, 887-895.
- White, E. G. & Huffaker, C. B. (1969a) Regulatory processes and population cyclicity in laboratory populations of *Anagasta kuehniella* (Zeller)

- (Lepidoptera: Phycitidae). I. Competition for food and predation. *Res. Popul. Ecol.*, **11**, 57-83.
- White, E. G. & Huffaker, C. B. (1969b) Regulatory processes and population cyclicity in laboratory populations of *Anagasta kuehniella* (Zeller) (Lepidoptera: Phycitidae). II. Parasitism, predation, competition and protective cover. *Res. Popul. Ecol.*, **11**, 150-185.
- Wilson, H. B., Hassell, M. P. & Godfray, H. C. J. (1996) Host-parasitoid food webs: Dynamics, persistence and invasion. *Am. Nat.*, **148**, 787-806.
- Yamada, Y. (1988) Optimal use of patches by parasitoids with a limited fecundity. *Res. Popul. Ecol.*, **30**, 235-250.
- Yamamura, N. & Yano, E. (1988) A simple model of host-parasitoid interaction with host-feeding. *Res. Popul. Ecol.*, **30**, 353-369.
- Zwölfer, H. (1963) Untersuchungen über die struktur von parasitenkomplexen bei einigen Lepidoptera. *Zeitschrift für Angewandte Entomologie*, **51**, 346-357.
- Zwölfer, H. (1971) The structure and effect of parasite complexes attacking phytophagous host insects. In *Dynamics of Populations* (ed. by P. J. den Boer & G. R. Gradwell), pp. 405-418. PUDOC, Wageningen.