The uniformity and density of pest exploitation as guides to success in biological control

MICHAEL E. HOCHBERG AND ROBERT D. HOLT

Introduction

Quantitative theory on biological control is usually so simple as to be justifiably criticized as 'unrealistic' and 'untestable'. The synthetic nature of parameters in simple models often leads to insurmountable difficulties in their accurate measurement. It is therefore hardly surprising that few field experiments (see Chapter 3), and only one relevant comparative analysis (Hawkins *et al.*, 1993) have been expressly designed to test biological control theory.

Difficulties in the precise interpretation and measurement of parameters are only part of the reason for a reticence in testing theory. A more chronic problem is that the large body of theoretical research on biological control lacks a conceptual synthesis. We believe that the synthesis developed here will be useful to biological control specialists, because population-specific parameters measurable in the field can be related to the two concepts we introduce below.

A survey

Insect parasitoids are without doubt the most commonly employed biological control agents both in practice and in theoretical developments. Table 4.1 presents a survey of modeling studies on insect parasitoids published since Hassell's seminal monograph on the subject (Hassell, 1978). This table provides a fairly complete catalog, reflecting how both topics and modeling approaches have evolved over the past 20 years. The criteria employed for selecting studies compiled in this list are the following:

1. The study must be published in a scientific journal.
2. The study must propose a new model structure, somehow extend previous models, or apply pre-existing models to a new biological problem.
3. One or more models must be explicitly presented.
4. The study must make explicit mention of insect parasitoids in relation to the model(s).
5. The model(s) must simulate or predict temporal population dynamics.

Two partially conflicting objectives of biological control

'Success' in biological control is ultimately assessed using economic criteria. An enemy highly effective at regulating a pest population to low densities may be a partial or complete failure if the economically permitted level of damage to the crop is low (Fig. 4.1). However, given no *a priori* reason for why there should be an association between realized depression of a pest population and economic objectives, it should be the case that greater depression of a pest population will be (on average) associated with attaining economic control objectives.

Unfortunately, cross-species comparisons of reduction in pest levels and economic gain have yet to be made, so we cannot say with certainty that population measures commonly gleaned from theoretical models are reliable enough indicators of the attainment of real economic targets. It is for these very reasons that one should be careful to distinguish population dynamic objectives from economic ones. In this chapter, we are interested in the former under the reasonable assumption that they are at least correlated with the attainment of the latter.

An incontestable indication of success in biological control programs is the local, or regional, eradication of a pest. Succinctly put, population dynamics theory says that to eradicate a population, a natural

Table 4.1. *Literature survey of parasitoid models*

Reference	Year	Generations	Spatial level	Subjects
Beddington et al.	1978	D	1	1,5
Hassell	1978	D	1,2	1,3,5,6
Hassell & Comins	1978	D	1	5
May	1978	D	1	1
Münster-Swendsen & Nachman	1978	D/C	1	1,2
Comins & Hassell	1979	D/C	2	1,5
Adams et al.	1980	C	1	5
Hassell	1980	D	1	1
Wang & Gutierrez	1980	D	1	2,3
May & Hassell	1981	D	1	1,5,6
May et al.	1981	D	1	1,2,5
Münster-Swendsen	1982	D	2,3	1
Reddingius et al.	1982	D	1	4
Hassell et al.	1983	D	1	1,3,6
Kidd & Mayer	1983	D	1,2	1
Gutierrez & Baumgaertner	1984	D/C	1	2,5,6
Hassell	1984a	D	2	1
Hassell	1984b	D	1	1,5
Hassell & Anderson	1984	D	1	1
Hogarth & Diamond	1984	D	1	1,2,6
Kakehashi et al.	1984	D	1	1,6
Murdoch et al.	1984	D	1	1,5
Barclay et al.	1985	D	1	1,3,5,6
Comins & Wellings	1985	D	1	3,5
Hassell	1985	D	1	1,4
Münster-Swendsen	1985	D	1	2,6
Murdoch et al.	1985	D	1	5,6
Shimada & Fujii	1985	D	1	2,6,7
Waage et al.	1985	D	1	5
Barclay	1986a	D	1	3,5
Barclay	1986b	D	1	1,3,5,6
Bernstein	1986	D	1	1,3,5
Chesson & Murdoch	1986	D	1,2	1
Dempster & Pollard	1986	D	1	1,4,5
Hassell & May	1986	D	1	1,5,6
Perry & Taylor	1986	D	1	1
Bernstein	1987	D	1	1
Comins & Hassell	1987	D	2	1,6
Godfray & Hassell	1987	C,D	1	1,2,5
Morrison & Barbosa	1987	D	1	1,4
Murdoch et al.	1987	C	1	2
Perry	1987	D	1	1
Ravlin & Haynes	1987	D/C	1	2,5,6
Bellows & Hassell	1988	C/D	1	2
Gutierrez et al.	1988	C	1	2,5,6

Table 4.1. (*cont.*)

Reference	Year	Generations	Spatial level	Subjects
Hassell & May	1988	D	2	1
May & Hassell	1988	D	1	1,5,6
Reeve	1988	D	2	1,4,5
Taylor	1988	D	1	1,3
Yamamura & Yano	1988	C	1	2,5,7
Godfray & Hassell	1989	D,C	1	1,2,5
Kidd & Jervis	1989	D,C	1	1,2,4,8
Murdoch & Stewart-Oaten	1989	C	1,2	1
Reeve *et al.*	1989	D	2	1
Yano	1989	C/D	1	2,5
Godfray & Chan	1990	C	1	1,5
Hassell & Pacala	1990	D,C	1,2	1
Hochberg *et al.*	1990	D/C	1	1,5,6
Hochberg & Lawton	1990	D	1	1,5
Pacala *et al.*	1990	D	1	1
Reeve	1990	D	2	1,4
Barclay	1991	D	1	2,3,5
Godfray & Waage	1991	C	1	1,2,5,6
Gordon *et al.*	1991	C	1	1,2
Hassell *et al.*	1991a	D	3	1
Hassell *et al.*	1991b	D	1,2	1
Baveco & Lingeman	1992	D/C	3	4,8
Comins *et al.*	1992	D	3	1
Godfray & Pacala	1992	C	2	1
Hochberg & Hawkins	1992	D	1	1,6
Ives	1992a	C	2	1,2,4
Ives	1992b	D	1	1,5
Mangel & Roitberg	1992	D/C	1	1,7,8
Murdoch *et al.*	1992a	C	1,2	1,4
Murdoch *et al.*	1992b	C	1	2,3
Solé *et al.*	1992	D	3	
Taylor	1992	D	1	1,4
Adler	1993	D	2	1,4
Barlow & Goldson	1993	D/C	1	2,3,5
Boerlijst *et al.*	1993	D	3	7
Briggs	1993	C	1	2,6
Briggs *et al.*	1993	C	1	1,2,6
Gutierrez *et al.*	1993	C	1	2,3,5,6
Heinz *et al.*	1993	C/D	1	2,5
Hochberg & Hawkins	1993	D	1	1,5,6
Holt & Hassell	1993	D	1,2	1,4
Holt & Lawton	1993	D	1	1,6
Hopper & Roush	1993	C	3	5
Jones *et al.*	1993	D	1	1,6
Taylor	1993b	D	1	1,3

Table 4.1. (*cont.*)

Reference	Year	Generations	Spatial level	Subjects
Axelsen	1994	D/C	1	1,2,5
DeGrandi-Hoffman *et al.*	1994	C/D	1	2–6
Godfray *et al.*	1994	D/C	1	1,2
Gutierrez *et al.*	1994	C	1	3,5,6
Hassell *et al.*	1994	D	3	6
Hearne *et al.*	1994	C	1	1,2,5
Lampo	1994	D	1	1,2
Meier *et al.*	1994	D	1	1
Reeve *et al.*	1994b	C	1	1–3
Rohani *et al.*	1994a	D/C	2	1,2
Rohani *et al.*	1994b	D	2	1,3
Briggs *et al.*	1995	C	1	2,3
Flinn & Hagstrum	1995	C/D	1	2,5
Hochberg & Holt	1995	D	1	1,5,7
Barlow *et al.*	1996	D	1	1,2,5,6
Briggs & Latto	1996	C	1	2,6
Getz & Mills	1996	D	1	1,5
Hochberg	1996a	D	1	5,6
Hochberg *et al.*	1996	D/C	2	1,4,6,8
Mills & Gutierrez	1996	C	1	2,4,5,6
Murdoch *et al.*	1996	C	1	1,2,3,6
Reed *et al.*	1996	C	1	5
Rohani *et al.*	1996	D	2	1
Ruxton & Rohani	1996	D	3	4,6
Weisser & Hassell	1996	C	2	1
Wilson *et al.*	1996	D	1	1,6
Hochberg	1997	D	1	2,7
van Roermund *et al.*	1997	C	3	2,4,5,8
Wilson & Rand	1997	D	3	4

Notes:

Generations: D/C, discrete generations with within generation dynamics; C/D, continuous generations with discrete time steps.

Spatial level: 1, none or non-discrete; 2, discrete patches; 3, spatially explicit (>2 patches).

Subjects: 1, non-behavioral parasitoid interference; 2, age or size structure; 3, explicit parasitoid intraspecific competition; 4, stochastics or temporal variability; 5, contribution of parasitoid to control; 6, multispecies systems; 7, evolution; 8, individual based.

The first author of this chapter would appreciate being notified of any omissions to this table.

enemy must either reduce the pest population to the point that stochastic processes mediate its local extinction, or lower the long-term population growth rate of the pest to a level such that it can no longer sustain itself. When eradication is not attain-able in either of its forms, a logical alternative is to reduce pest population densities to the lowest, and most constant, levels possible in both time and space. The goal of low, constant densities is incidentally concordant with one of the central aims of more
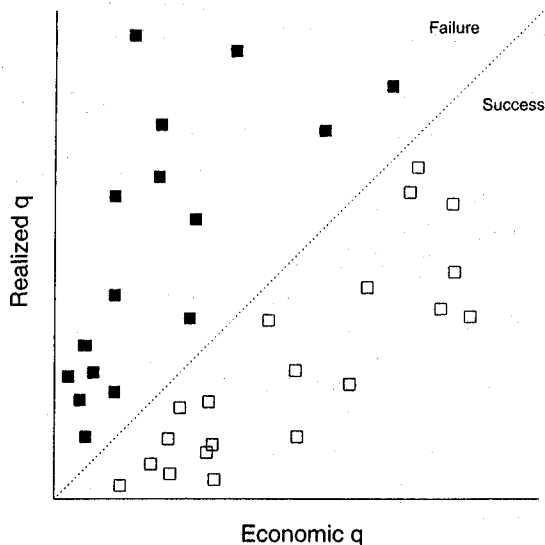
Figure 4.1. Hypothetical plot of outcomes of biological control programs in terms of realized level of pest suppression and the threshold level required for the program to be an economic success. *q* refers to the Beddington *et al.* (1975) index of equilibrium pest density after a biological control introduction, divided by equilibrium pest density prior to introduction.

fundamental modeling studies on host–parasitoid associations (Table 4.1): the search for conditions under which a natural enemy dominates the regulation of its host or prey population. In this chapter, we use the terms 'host' and 'pest' interchangeably.

As we shall see below, the theoretical properties of a parasitoid capable of eradicating its host do not quite border those for regulating parasitoids. Unless the objectives and constraints in biological control programs are carefully worked out, the differing attributes of what may be termed 'eradicators' and 'regulators' can lead biological control workers to introduce suboptimal enemies, or even worsen existing control (see Discussion, below).

Towards a unifying concept

Virtually all the studies presented in Table 4.1 either implicitly or explicitly model heterogeneous exploitation of hosts, and many consider in detail

how this phenomenon affects temporal population dynamics. This is not surprising since (following the seminal work of Nicholson & Bailey, 1935) many authors have shown that without recourse to other forms of density dependence, heterogeneity in host or prey exploitation by natural enemies generally promotes system persistence (Bailey *et al.*, 1962; Hassell & May, 1973; May, 1978; Chesson & Murdoch, 1986; Hassell *et al.*, 1991b; Ives, 1992a,b; Holt & Hassell, 1993; Rohani *et al.*, 1994a). Depending on the details of the model, heterogeneity may either stabilize (e.g., Hassell & May, 1973; Hassell *et al.*, 1991b) or destabilize dynamics (e.g., Murdoch & Stewart-Oaten, 1989; Murdoch, 1990; Taylor, 1993a,b), or bring other forms of density dependence into dynamic play (Hochberg & Lawton, 1990; Hochberg *et al.*, 1996).

The properties of the models surveyed in Table 4.1 converge to two major notions that encompass the many and varied population parameters often predicted to drive the outcomes of biological control. These notions are the *uniformity* and *density* of pest exploitation by the natural enemy.

Exploitation uniformity is the propensity for all individual hosts to be equally susceptible to parasitism. Exploitation uniformity is determined by spatial, temporal, and phenotypic components in (i) the capacity of parasitoid adults to locate and attack hosts, and in the ability of parasitoid larvae to develop within hosts, and (ii) in the capacity of host larvae to escape detection and attack, and to resist the development of parasitoid larvae. The complexity of the mechanisms determining exploitation distributions is largely what has fueled theoretical research on topics such as aggregation, spatial heterogeneity, and refuges in host–parasitoid systems (Table 4.1).

Exploitation density is the potential number of hosts an averagely fecund parasitoid female can parasitize and kill in the absence of competition with conspecifics. This quantity will notably be a function of the parasitoid's egg availability, the time and energy it takes to search for and to subdue hosts, and the density of the host population. Numerical (Hochberg & Lawton, 1990) and analytical (Getz & Mills, 1996) studies have shown that sufficient exploitation density is necessary for exploitation

uniformity to affect the dynamics of host–parasitoid systems.

The important conceptual message we wish to convey below is that the parasitoid must enforce itself (*via* exploitation density) in order to obtain either pest eradication or regulation to low densities. In a nutshell: the parasitoid's imposition must be more uniform for eradication than for regulation, and if it is too heterogeneous, then other density dependent effects (such as other natural enemies) will contribute to, or even dominate, pest dynamics. Before illustrating these points with a simple mathematical model, we briefly discuss measures of these two important quantities.

Correlative measures of exploitation uniformity and density

Given the likely complexity of processes underlying exploitation uniformity and density, we suggest that their precise measurements will generally be unattainable. We argue for the use of two correlative quantities, both of which can be estimated in the field and easily incorporated into simple population dynamic models.

The simplest way to model exploitation uniformity is to assume that pest individuals are simply either vulnerable to, or protected from, parasitism. Protected hosts are said to have (or be in) *absolute refuges* to parasitism. (The term 'refuge' should not be taken in the strict sense of a physical hiding place. Our usage includes any form of protection whatsoever that reduces the likelihood that a subset of the host population will be parasitized as compared to the most susceptible individuals.) Absolute refuges are at best approximate measures of exploitation uniformity because they reflect both the distribution and density of parasitism.

When the absolute refuge is *proportional*, a constant fraction of the host population is protected from parasitism in each generation, whereas in a *constant number* refuge, a certain density of the host population is immune from parasitism, with the upper limit determined by the number of refuges in the environment. The major distinction between the two types is that in constant number refuges the proportion of hosts in the refuge is 100% at low host densities, decreasing to 0% as the host population becomes very large, whereas this proportion (obviously) remains constant for proportional refuges. Proportional refuges are generally thought to be more realistic approximations of variation in risk to parasitism than constant number refuges (Hassell, 1978; Holt and Hassell, 1993), and proportional refuges are more straightforward to estimate for most systems. In order of increasing precision, the proportional refuge is estimated from (i) the maximum observed level of parasitism, (ii) the estimated asymptotic maximum level of parasitism in a large group of independent samples, or (iii) the mean level of parasitism attainable (from a large number of independent samples) when parasitoids are super-abundant compared to their host. The crudest of these measures (i.e., maximum observed parasitism) suggests that proportional refuges are widespread in natural communities (Hochberg & Holt, 1995).

Exploitation density is most straightforwardly modeled as the maximum number of hosts a parasitoid can parasitize over its lifetime. This will be a function of a number of factors, such as egg load and/or rate of egg maturity, adult parasitoid lifespan, time taken in handling the host, and diverse adaptations to locate, subdue and develop within the host. Exploitation density can be estimated in three ways in order of increasing precision: (i) the maximum observed level of parasitoid population growth from one generation to the next, (ii) the estimated asymptotic maximum population growth based on a large number of independent samples, or (iii) the mean number of female parasitoid offspring produced (from a large number of independent samples) when a single, fecund parasitoid female is released into a previously unexposed host population. Data do exist on the first and second of these measures, but they are yet to be collated. Measures based on single parameters such as egg load, adult lifespan, etc., are bound to be poor descriptors on their own, due to the biological complexity of exploitation density.

An illustrative model

Consider a synchronous host–parasitoid system with discrete, non-overlapping generations, as would be

the case for many temperate insect pests and their parasitoids. The host is at density N_t adult females at the beginning of generation t and they produce λN_t female offspring. A fraction, $1 - \alpha$ of these hosts are exposed to attack by a monophagous parasitoid species at adult female density P_t.

The antecedents of the mathematical model are numerous (e.g., Thompson, 1924; Nicholson & Bailey, 1935; Hassell, 1978). It takes the general form:

$$N_{t+1} = \lambda N_t g(\alpha + (1 - \alpha)f) \qquad (4.1)$$

$$P_{t+1} = c\lambda N_t g(1 - \alpha)(1 - f) \qquad (4.2)$$

where λ is the maximum population growth rate of the host (the number of female offspring surviving to maturity per female adult in the absence of density dependence), and c is the average number of female parasitoids produced per host attacked (assumed equal to 0.5). Finally, α is the proportion of hosts protected from parasitoid attack, that is, in the proportional refuge (see above). We will employ the quantity $1 - \alpha$ (the fraction of hosts exposed to parasitism) as a measure of the exploitation uniformity of the parasitoid population on the host population.

Equations (4.1) and (4.2) are characterized by two forms of density dependence, each modeled using a simple mathematical expression.

First, g is the proportion of hosts surviving nonexplicit forms of density dependence (e.g., intraspecific competition, other natural enemies). Such 'self-limitation' can be modeled in a number of different ways, and its functional form (e.g., Hassell, 1978) and position in the host's life cycle with respect to other density-dependent mortalities (Wang & Gutierrez, 1980; May *et al.*, 1981) can have important ramifications for temporal population dynamics. For the sake of simplicity, we assume that self-limitation acts before parasitism, and that it renders host populations constant over time when the parasitoid is absent from the system.

The function employed is:

$$g = \left[1 + \frac{(\lambda - 1)}{K}N_t\right]^{-1} \qquad (4.3)$$

where K is the carrying capacity of the host population. This model reflects compensatory, stabilizing density dependence (Maynard-Smith & Slatkin, 1973; Hassell, 1978). To ensure host persistence in the absence of parasitism, we take $\lambda > 1$ and $K > 0$.

Second, the function for the proportion of exposed hosts escaping parasitoid attack, f, assumes the parasitoid searches at random over exposed hosts, and does not waste reproductive effort on protected hosts (either because they are simply never encountered, or because the parasitoid can discriminate them when encountered). f is given by

$$f = e^{(-XP_t/\zeta\{N_t\})} \qquad (4.4)$$

where X is the functional response. We assume that parasitism comes at a cost to the parasitoid, either in terms of limited egg supply or in terms of limited time for host encounters. The Holling Type II function is the most widely applied to approximate costs to parasitism, particularly those associated with limited encounter rates. It is:

$$X = \frac{a\zeta\{N_t\}}{1 + a\zeta\{N_t\}/\eta} \qquad (4.5)$$

a is a measure of parasitoid searching efficiency (assumed hereafter to equal 1). The function $\zeta\{N_t\}$ is the density of hosts over which the parasitoid expends reproductive effort (i.e., $\zeta\{N_t\} = \lambda N_t g(1 - \alpha)$), and η is the number of hosts a single adult female encounters and potentially parasitizes when hosts are not limiting (i.e., when $\zeta \gg \eta/a$). Because the function for ζ assumes that the parasitoid only expends reproductive effort on exposed hosts, this enables us to partially segregate the effects of exploitation uniformity and density in the discussion to follow. It should be stressed that the biological control models in which parasitoids waste reproductive effort on protected hosts are also interpretable in terms of these two conceptual measures.

In the context of this basic model, the exploitation density of the parasitoid is equivalent to its maximum population growth rate, R. R can be estimated from the partial derivative of eqn (4.2) with respect to adult parasitoid density, which gives:

$$R = \frac{ac\eta(1-\alpha)K}{\eta + aK(1-\alpha)} \qquad (4.6)$$

R increases with host carrying capacity (K), parasitoid searching efficiency (a), parasitoid reproductive capacity (η), and juvenile parasitoid survival (c). R also increases with increasing exploitation uniformity ($1-\alpha$), but the association between the two is only pronounced as host carrying capacity becomes very small (i.e., $K \to \eta/\alpha(1-\alpha)$).

In highly productive environments (i.e., when $K \gg \eta/\alpha(1-\alpha)$), that is those which tend to define the host as a pest species, R simplifies to:

$$R \cong c\eta \qquad (4.7)$$

Note that the searching efficiency (a) of the parasitoid no longer influences its invasibility. This makes sense because searching area (a) scales how much of the K hosts can be encountered by the parasitoid.

Simulation methods

The patterns presented below are based on numerical simulations. We considered a system to have equilibrated if adult host density changed by no more than 10^{-7} between any two of a continuous string of 100 generations. Systems not meeting this criterion after 5000 generations were deemed non-equilibrated. We employ the q value of Beddington *et al.* (1975) to measure the ability of the introduced parasitoid species to depress or inflate the host population, relative to pre-introduction levels. q is defined as N^*/K, where N^* is the equilibrium level of hosts when the parasitoid is present in the system.

Model properties

The propensity for the parasitoid to reduce pest populations to extinction-menacing levels is clearly related to exploitation density and uniformity (Fig. 4.2). The effects of marginal changes in either or both of these quantities can have important consequences for q-levels, especially when exploitation density is low and uniformity high. For instance, when uniformity is near maximal (i.e., $\alpha \to 0$),
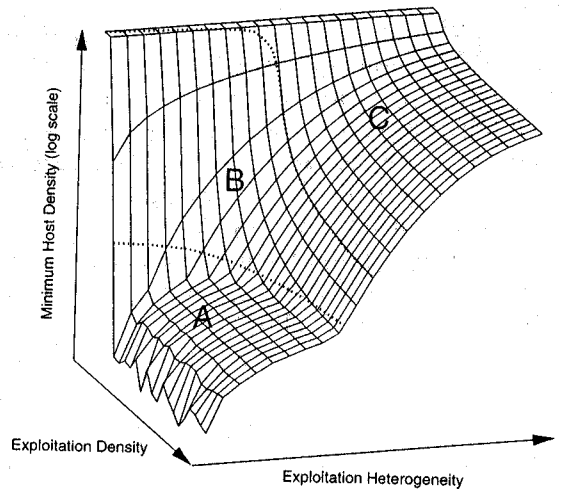

Figure 4.2. Minimum host population levels observed over the first 20 generations after the introduction of a single parasitoid into the host population at its carrying capacity. Region A, population dips below a density of 1 at least once. Region B, populations do not meet equilibrium criterion. Region C, populations meet equilibrium criterion. Other parameters: $\lambda = 2$, $c = 0.5$, $a = 1$, and $K = 100\,000$.

exploitation densities approximately greater than the pest's maximal population growth rate (λ) ensure the eventual extinction of the pest (Fig. 4.2: region A). If either or both exploitation types are not sufficiently pronounced, then long-term cycles may ensue (Fig. 4.2: region B). This is generally an undesirable result in biological control, because excursions of the pest population above the damage threshold may occur more or less predictably. Finally, insufficient uniformity will mean that although the parasitoid is able to depress the host population (perhaps below economically damaging levels), the parasitoid is not necessarily the dominating factor in host regulation (Fig. 4.2: region C).

The important and intriguing message conveyed in Fig. 4.2 is that an undesirable result (region B) divides two highly desirable alternatives (region A and parts of region C adjacent to region B). If our model were an accurate descriptor of real biological control, and if one could estimate the key parameters with sufficient precision, then the cyclic parameter space would be duly avoided. But this ideal is proba-
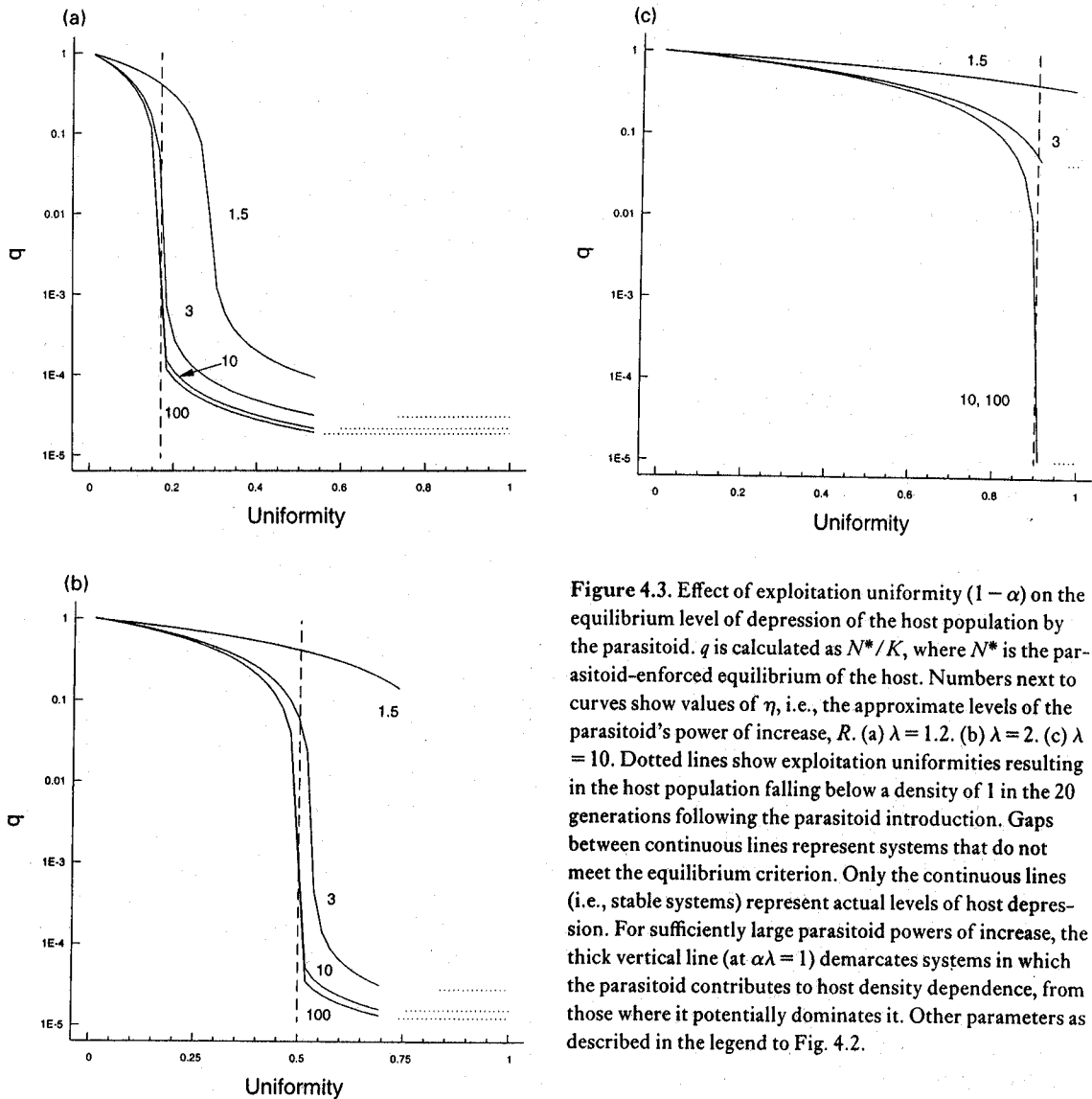
(a)

(b)

(c)

Figure 4.3. Effect of exploitation uniformity $(1 - \alpha)$ on the equilibrium level of depression of the host population by the parasitoid. q is calculated as N^*/K, where N^* is the parasitoid-enforced equilibrium of the host. Numbers next to curves show values of η, i.e., the approximate levels of the parasitoid's power of increase, R. (a) $\lambda = 1.2$. (b) $\lambda = 2$. (c) $\lambda = 10$. Dotted lines show exploitation uniformities resulting in the host population falling below a density of 1 in the 20 generations following the parasitoid introduction. Gaps between continuous lines represent systems that do not meet the equilibrium criterion. Only the continuous lines (i.e., stable systems) represent actual levels of host depression. For sufficiently large parasitoid powers of increase, the thick vertical line (at $\alpha\lambda = 1$) demarcates systems in which the parasitoid contributes to host density dependence, from those where it potentially dominates it. Other parameters as described in the legend to Fig. 4.2.

bly illusory for most systems. We suggest that ambitious aims of pest extinction or regulation to very low densities may require somewhat precise conditions (see below), and that model misspecification may lead one to chose an enemy that induces undesirable outbreaks in the pest (region B adjacent to region A). Such outbreaks are most likely when the exploitation density of the parasitoid approaches or exceeds the maximum productivity of the pest, or $R > \lambda$ and when exploitation uniformity is high.

Figure 4.3 considers these arguments in more detail. The target area for maximal depression under the host regulation scenario is delimited by a threshold at $1 - \alpha \approx 1 - 1/\lambda$. This means that if we know the productivity of the pest, then we can predict the level of uniformity necessary to obtain the lowest q-values.

The range of $1 - \alpha$ beyond the threshold yielding maximal depression increases with decreases in pest productivity, λ. This indicates that low productivity systems are the most likely to be amenable to the strong top-down regulation paradigm (compare Figs. 4.3(a)–(c)). It is also notable from Fig. 4.3 that the potential for maximal depression is only realised as $R > \lambda$, meaning again that pests with small productivities are easier to control.

In sum, the pest's maximum population growth rate, λ, emerges as a central parameter to predicting the success of biological control. The approximate conditions for exploitation uniformity and exploitation density to be sufficient for spectacular depression or induced extinction of the pest are $\lambda < 1/\alpha$ and $\lambda < R$, respectively. This means that the levels of exploitation uniformity and density leading to spectacular success will be contingent on the pest's maximum growth rate, λ.

Discussion

It is hardly surprising that the degree of success in biological control should be so dependent on the pest's power of increase, λ. But, without the aid of mathematical theory, it is not easy to see precisely why. Our conclusion is that population dynamic influences on the outcome of biological control employing a specialized natural enemy boil-down to levels in the mean and variance of the intensity of parasitism on the host population. This is the first time to our knowledge that theoretical models have been so simply interpreted in a conceptual framework for biological control.

The risk of introducing a natural enemy that induces pest outbreaks will depend importantly on the spatial scale of the interaction. This is because the arbitrary densities demarcating stochastic extinction from persistent cycles will be inversely related to the size of the system. In other words, systems become more and more invulnerable to stochastic extinctions as their spatial scale increases. At very small spatial scales, much of the parameter space denoted as 'cyclic' will in fact correspond to the extermination of the pest. At very large scales, the opposite will be the case: much of what was 'extinction' will become 'cyclic'.

With knowledge about the pest's power of increase, a biological control practitioner can gauge to what extent it is useful (or even necessary) to estimate population parameters associated with candidate natural enemies. First consider pests with low levels of population increase, $\lambda \to 1$. It would at first sight appear unnecessary to be preoccupied with the exploitation uniformity and density of the enemy, simply because almost any level of each should lead to domination of host density dependence by the introduced parasitoid. However, our simple model indicates that such complacency can be dangerous because temporally variable populations may transpire; temporal variation will be a contingency especially if the exploitation density of the parasitoid is relatively low (see Fig. 4.3(a)). Now consider high levels of λ. Even the most extensive program may not identify candidate natural enemies that can effect a spectacular control of the host (see Fig. 4.3(c)). In contrast, there is relatively little danger of the parasitoid inducing persistent outbreaks in such pest species.

What little data there are on λ suggests values greater than 2 to be commonplace. For example, data from Hassell *et al.* (1976) show 9 out of a sample of 11 lepidopterans to have $\lambda > 2$. Although this is not necessarily a representative sample of targets for biological control, it does indicate that for some cases spectacular control or extermination will be a possibility, whereas in others the level of depression by the parasitoid will keenly depend on the uniformity and/or density of its exploitation of the pest. Amassing estimates of λ for insect pests should be a worthwhile endeavor.

Theoretical antecedents

Our theoretical synthesis has a rich pedigree, some of the main points of which are recounted below (see also Hochberg, 1996b).

Natural enemies as regulators

This is the interface of regions B and C of Fig. 4.2. Beddington *et al.* (1978) presented six case studies of biological control releases resulting in pest

population depression to extremely low levels. They examined the behavior of a series of mathematical models with the goal of discriminating the factors potentially responsible for intense population depression. They concluded that spatial heterogeneity in parasitism was the most likely explanation for host regulation dominated by a single natural enemy. Although spatial heterogeneity was already known to be a key parameter in top-down regulation (Bailey *et al.*, 1962; Hassell & May, 1973; Murdoch & Oaten, 1975), it was only Beddington *et al.*'s comparison and the concurrent works of Hassell (1978) and May (1978), that brought the applied importance of spatial heterogeneity in parasitism to the fore.

Much of the recent research on the impact of heterogeneity has concentrated on distinguishing components of this variation, notably spatial density dependence and density independent heterogeneity (Chesson & Murdoch, 1986; Pacala *et al.*, 1990; Hassell & Pacala, 1990; Hassell *et al.*, 1991b). Studies combining theory and data have since followed, examining the potential influence of heterogeneities in parasitism on population dynamics (Driessen & Hemerik, 1991; Pacala & Hassell, 1991; Jones *et al.*, 1993; Lampo, 1994; Reeve *et al.*, 1994a; Hochberg *et al.*, 1996).

Natural enemies as contributors

This is region C of Fig. 4.2. A separate body of theory has shown how parasitoids may contribute to host depression, but not be singly responsible for system dynamics. Two broad factors have been cited. First, density dependence acting on the host may lessen the regulatory impact of the parasitoid, and even be necessary for the parasitoid's persistence. Such density dependence may be produced by intraspecific competition (Beddington *et al.*, 1978; May *et al.*, 1981; Bernstein, 1986; Hochberg & Lawton, 1990; Ives, 1992b), host-feeding (Jervis & Kidd, 1986; Briggs *et al.*, 1995) or through the actions of other natural enemies (May & Hassell, 1981; Hassell & May, 1986; Hochberg *et al.*, 1990; Briggs, 1993; Hochberg, 1996a). Second, density dependence affecting the parasitoid itself can compromise its

influence on its host. Examples include mutual interference between parasitoid adults (e.g., Hassell, 1978), within-host competition between parasitoid larvae (Taylor, 1988), and density-dependent sex ratios (e.g., Comins & Wellings, 1985).

Numerous determinants of exploitation density and uniformity are already known to mediate the potential impact of the parasitoid on its host population. Both Hochberg & Lawton (1990) and Getz & Mills (1996) have shown how different forms of parasitoid exploitation affect the pertinence of spatial heterogeneity on system dynamics. In particular, Getz & Mills (1996) have elegantly shown how the potential population growth rate of the parasitoid must exceed that of the host for spatial heterogeneity to be of relevance to regulation. They identify egg limitation as an important constraint to the potential growth rate of the parasitoid. More generally, a diverse literature has identified how probabilistic host refuges (e.g., Hassell & May, 1973; Beddington *et al.*, 1978; Hassell, 1978; May, 1978; Perry & Taylor, 1986; Reeve *et al.*, 1989), and absolute host refuges (Hassell & May, 1973; Hassell, 1978; Murdoch *et al.*, 1987; Holt & Hassell, 1993; Hochberg & Holt, 1995) may lessen the impact of parasitoids on their hosts.

Natural enemies as exterminators

This is region A of Fig. 4.2. Nicholson (1933: conclusion 40) was the first to suggest that a host-parasitoid link could persist regionally, even if confronted with extinctions locally. Empirical arguments for why extinction/colonization dynamics could be a prevalent phenomenon were first made by Murdoch and colleagues (Murdoch *et al.*, 1984, 1985). They maintained that five of the six case studies employed by Beddington *et al.* (1978) are characterized by unstable population dynamics at local spatial scales. That locally doomed systems could persist regionally was explored in the context of parasitoids by Allen (1975) and then Münster-Swendsen (1982), and more recently by Hassell & May (1988), Reeve (1988), Murdoch *et al.* (1992a), Holt & Hassell (1993), Hassell *et al.* (1991a), Comins *et al.* (1992), Solé *et al.* (1992), and Hassell *et al.* (1994). So far, the implications of large-scale spatial

structure have not been investigated in an explicit biological control context.

Evidence for our synthesis?

There is mounting evidence in support of the centrality of the two parasitoid exploitation potentials.

Comparative analyses in native and introduced systems

Hawkins et al. (1993) estimated host refuges from parasitism (which is the inverse of what we have called here 'exploitation uniformity') for a set of 74 biological control attempts. They employed the maximum observed level of parasitism by the introduced parasitoid as a measure of $1 - \alpha$. This measure, though potentially fraught with errors in its estimation (van Driesche et al. 1991), showed a highly statistically significant relationship with economic success in biological control programs. Hawkins and colleagues' analysis did not indicate that maximum parasitism could be employed as a precise estimator of population depression, but rather that as a proxy variable for the uniformity of exposure. Our synthesis lends theoretical support to their findings.

It could be argued that Hawkins et al.'s analysis is invalid, because maximum parasitism was estimated from the very control programs it was supposed to predict (Myers et al., 1994; Hawkins et al., 1994). To counter this criticism, Hawkins & Cornell (1994) compared maximum parasitism rates of natural enemies in their native habitats to economic success in biological control in target areas and found a highly significant relationship between the two. Together with the earlier analysis (Hawkins et al., 1993) this indicates that maximum parasitism is an approximate predictor of success in biological control, based either on *a priori* information from native habitats or *a posteriori* data in the control arena. Intriguingly, in both the exotic data set (Hawkins & Cornell, 1994) and the control-site data set (Hawkins et al., 1993), a cut-off exists in control outcomes at maximum parasitism rates (i.e., exploitation uniformity) of approximately 35%.

Below this level biological control very rarely achieves economic success. A challenge will be to explain this empirical phenomenon.

Host–parasitoid–pathogen interactions in experimental boxes

Recently, Begon et al. (1996) employed laboratory experiments to investigate the population dynamics of two and three species systems involving the Indian meal moth (*Plodia interpunctella*), a parasitoid (*Venturia canescens*) and a granulosis virus (PiGV). When the host is kept alone in experimental boxes with either the parasitoid or the virus, it exhibits cycles in adult moth numbers of approximately one generation interval. It would be misleading to call the populations 'unstable', since they are very regular in shape and amplitude from generation to generation, indicating that single natural enemy dynamics are relatively constant in time.

Consistent with our arguments for how such dynamics should arise, Begon and colleagues have shown limitations to what we call exploitation uniformity. For the virus, pathogen loads differ over the experimental arena (Sait et al., 1994), meaning that larvae feeding in sparsely contaminated areas will be less prone to infection than those encountering pathogen-rich areas. As for the parasitoid, deeply feeding hosts are less likely to be found and parasitized by searching parasitoid females than are surface-feeders (Begon et al., 1995). The major dynamic difference between the virus and parasitoid is that the former has very little impact on the amplitude of the host population cycles, whereas the latter's effect is intense. This is suggestive of high exploitation densities associated with the parasitoid.

Because of the spatial and temporal differences in exploitation tactics by the two natural enemies, total exploitation uniformity in the three-species system is greater than either of its two parts alone (see Hochberg, 1996c). Begon et al. (1996) found that these three-species systems ultimately went extinct. We suggest that the total exploitation uniformity and density were sufficient to generate either persistent cycles in the system as a transient phenomenon to

extinction (region A in Fig. 4.2), or as a final state (region B), which terminated in stochastic extinction due to small population numbers in the troughs of the cycles. In other words, adding a second natural enemy takes the system from either 'contribution' by the pathogen, or 'regulation' by the parasitoid, to 'cycles' or 'extinction' by both natural enemies acting together.

Additional concerns

In debating whether contribution, regulation or eradication is the most attainable option, an additional, important concern is the repercussion of control for the community surrounding the pest. We do not advocate the use of the theory discussed above without the thorough study of possible adverse effects on the interacting community. It is important that the conservation of other species be respected, and that no new pest species should emerge as a result of any control measure.

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