BIOLOGICAL CONTROL IN THEORY AND PRACTICE

WILLIAM W. MURDOCH, JEAN CHESSON, AND PETER L. CHESSON

Department of Biological Sciences, University of California, Santa Barbara, California 93106;
Batelle Columbus Laboratories, 505 King Avenue, Columbus, Ohio 43201; Department of Zoology,
Ohio State University, 1735 Neil Avenue, Columbus, Ohio 43210

Biological control in practice is a tactical, empirical procedure. In classical biological control, typically various enemies from the pest's area of origin are released, together or in sequence, in the hope that one or more will prove successful. Pre-release screening concerns possible deleterious side effects or physiological tolerance, not the finer points of population dynamics. This has proved a quite successful procedure (Huffaker and Messenger 1976).

By contrast, the literature concerning the general strategy of biological control (e.g., Huffaker and Messenger 1976) and possible relevance of ecological theory (e.g., Murdoch 1973; Hassell 1978) has emphasized aspects of pest-enemy population dynamics. The theory derives mainly from the Nicholson-Bailey model (e.g., Beddington et al. 1978; May and Hassell 1981), and it and the conventional wisdom in general agree broadly on several basic issues. (1) Successful biological control is caused by the enemy imposing a low, stable host equilibrium. (2) Success is most likely when the enemy has the following features: (a) it is host-specific; (b) it is synchronous with the pest; (c) it can increase in density rapidly when the host does; (d) it needs few pest individuals (usually only one) to complete its life cycle (and hence can persist when the pest is at its low equilibrium density); and (e) it has a high searching ability. These features are more typical of parasitoids than predators. (3) General predators are considered poor candidates precisely because they are polyphagous, are not synchronized with the pest, and do not usually have a high potential for increase. (There is also the practical problem that general predators might eat beneficial insects.) Models of successful biological control, therefore, have been locally stable deterministic equations describing the dynamics of a single prey species and a single parasitoid or predator species.

The dissenting case in support of general predators has occasionally been made, especially for short-lived crops where polyphagy may help maintain the predator when the pest disappears (Murdoch 1973, 1975; Ehler 1977; Ehler and Miller 1978). The central role of a low stable pest equilibrium has only rarely been challenged (Murdoch 1979; Murdoch et al. 1984), however, and such stable

equilibria are considered the key to the control of pests in the particular case of long-lived crops (e.g., Hassell 1978).

Here we suggest that the conventional wisdom may be a poor guide to biological control even in persistent ecosystems, that local pest extinction rather than stable pest equilibrium may often be a more appropriate goal, and that general predators can be good control agents in these and other circumstances.

We first briefly review mathematical theory pertaining to biological control and discuss some of its limitations. Next we show that even very simple modifications to the assumptions underlying the models can provide a much greater variety of potentially satisfactory biological control situations. We then look at field examples. These include six cases of successful control that have been viewed as good examples of the equilibrium paradigm. We argue that most of these examples do not fit the existing theory, and we provide three additional examples that support the case that general predators and local extinctions deserve serious consideration as agents and mechanisms of biological control.

Mathematical Theory

The Question of Equilibrium

Mathematical theory, to the extent that it captures the important aspects of nature, perhaps can make general statements about the characteristics that a biological control agent should possess. Beddington et al. (1978) is a seminal contribution along these lines. Like other extensions of the Nicholson-Bailey equations aimed at this goal (e.g., Hassell 1978, 1980; May and Hassell 1981), that paper assumes that a low, stable-equilibrium pest population is the desirable outcome in pest control. Paradoxically, the factor that Beddington et al. concluded was important in achieving a stable equilibrium, namely aggregation of parasitoids in response to local host density, affords protection to the pest. Parasitoid aggregation has since been taken to be the major mechanism ensuring control (see references above and Hassell 1982; Waage 1983; Heads and Lawton 1983), and becomes an additional desirable property (2f) to add to the above list. Hassell (1980) points out that the amount of aggregation may depend on host density and that this complicates the relationship between aggregation and stability.

A brief review of the theory follows. Hassell and May (1973) showed that aggregation by parasitoids to patches initially containing a high fraction of the pest population can in some circumstances lead to a locally stable model. Free et al. (1977) showed that the stabilizing mechanism is "pseudointerference," which leads to decreased parasitoid efficiency as parasitoid density increases, as a result of parasitoids increasingly discovering already parasitized hosts. Comins and Hassell (1979) allowed parasitoids to move among patches in an optimal way within a generation and showed that this also leads to local stability under some narrower circumstances. The model is not globally stable.

May (1978) proposed a phenomenological model intended to capture the effects of aggregation to host density while omitting the mechanistic details that cause the

models mentioned above to be analytically awkward. The model is

$$H^* = \frac{\lambda}{\lambda - 1} \frac{k}{a} (\lambda^{1/k} - 1). \tag{1}$$

Here, H^* is the pest equilibrium; λ is its finite rate of increase taking into account all sources of mortality other than the parasitoid; a is the parasitoid's area of discovery; and k is the parameter of the negative binomial that is sensitive to the distribution of parasitoid attacks among hosts. As k decreases, clumping increases. Thus the parasitoids can lay many eggs in a single host and the distribution of eggs among hosts is negative binomial, though the model also applies to aggregating parasitoids that lay no more than one egg per host (Murdoch et al. 1984).

May's detail-free model was used by Beddington et al. (1978) to demonstrate their conclusion that parasitoid aggregation to local pest density in a heterogeneous environment is the key to successful control. The model has also served as the basis for more recent elaboration of the basic theory (e.g., May and Hassell 1981; Hogarth and Diamond 1984). A detailed examination of the possible derivations of this negative binomial model, however, shows that it arises most naturally when parasitoid attacks are clumped independently of local host density (P. L. Chesson and W. W. Murdoch, MS). Although it can also arise as a result of aggregation to areas of high host density, such aggregation is much more likely to produce different dynamical equations. (In these circumstances it can also arise when parasitoids, or more exactly risk of parasitism, are concentrated in patches with few hosts, rather than in patches with many hosts.) Additionally, P. L. Chesson and B. L. Kerans (in prep.) show that some kinds of aggregation lead not to stability, but to host extinction. In sum, aggregation independent of host density appears to be the most useful interpretation of the negative binomial model.

As a consequence of this assumption of what is essentially inefficient parasitoid behavior, there is a trade-off between stability and maintenance of a low pest density. Since the negative binomial distribution with finite k has a larger fraction of zero occurrences than the Poisson distribution with the same mean, a larger fraction of the pest population escapes than in the original Poisson version of the Nicholson-Bailey model. The smaller k is, the larger is this fraction. This relationship is discussed by Hassell (1978) and May and Hassell (1981).

Regardless of the merit of particular models, it is clear that the existence of a stable equilibrium is neither necessary nor sufficient for satisfactory control in practice. From a practical point of view the aim of biological control is to keep pest density below some economic threshold level all or most of the time. The existence of an equilibrium, which is locally or globally stable in the mathematical sense, provides no assurance that the system will be at or near the equilibrium, but only that the system will tend to move toward the equilibrium state in the absence of an external perturbation. Furthermore, if the equilibrium is only locally stable (see, e.g., Comins and Hassell 1979), then the system has to be sufficiently close to the equilibrium values for such a move to occur. In this case one needs to know the size of the domain of attraction in order to make any useful prediction about the model's behavior (Beddington et al. 1976). Conversely, the

absence of a stable equilibrium does not preclude satisfactory control. Pest and/or natural enemy densities may fluctuate wildly without pest densities exceeding the economic threshold. Pest extinction, which need not necessarily imply natural enemy extinction, is also compatible with satisfactory control.

An alternative approach uses stochastic models and the concept of stochastic boundedness (Chesson 1978, 1982; Murdoch 1979). In this approach the disturbance functions are given probability distributions (they are the stochastic environment) and one can ask whether a population is driven extinct and, if it is not, estimate the upper stochastic bou:ids to indicate the maximum probability that the economic threshold is exceeded at any given time. As yet, no models of this sort have been developed for biological control.

<div align="center">THE QUESTION OF POLYPHAGY</div>

Results from mathematical models of host-parasitoid interactions have also been used to reinforce the belief that polyphagy is undesirable in a natural enemy in long-lived crop systems (Hassell 1978; Beddington et al. 1978). Existing models support this conclusion, however, because in general they include only a single prey species and ask what properties the natural enemy should possess to achieve a locally stable equilibrium with both predator and prey present and the prey at low density. In these models there is thus no opportunity for a polyphagous natural enemy to take advantage of the property that distinguishes it from a specialized one, namely the fact that its survival and reproduction are not dependent solely on the pest.

With a polyphagous natural enemy there is little justification for requiring a stable equilibrium that includes both predator and prey. Relaxation of this requirement allows a greater range of model parameter values to be compatible with successful biological control, as we will demonstrate in the examples below. (It must be stressed that we are not advocating these models as a suitable basis for practical decisions, but to illustrate how conclusions derived from models in the past have been biased against polyphagous natural enemies.)

Consider a model of a host-parasitoid or more generally a predator-prey interaction in which the predator (of density P_t) has unspecified other prey:

$$H_{t+1} = H_t f(H_t, P_t)$$
$$P_{t+1} = g(H_t, P_t)$$

(2)

where $f(H_t, P_t)$ is the proportion of pests not attacked by the predator and $g(H_t, P_t) > P_{min} = g(0, P_{min})$. This condition on g expresses the polyphagy of the predator, since other prey species are assumed to be sufficiently abundant to maintain the predator at the density P_{min} in the absence of the pest. The model has the equilibrium point $(0, P_{min})$ in which the pest is extinct and the predator is maintained entirely by other prey. This equilibrium point will be locally stable if $f(0, P_{min}) < 1$. Naturally, polyphagy is necessary for an equilibrium with zero pest numbers and positive predator numbers, and this makes it possible to have pest extinction as part of a locally stable equilibrium point.

Beddington et al. (1978), using a related model, look for conditions for a low, but positive, stable equilibrium via a type III functional response. They suggested that polyphagous predators do not respond numerically to the pest population. As a consequence, if pest density is perturbed above some threshold level (related to saturation of the functional response), the pests escape control by the predators and increase until checked by some other factor.

This sort of behavior could also occur in our model under certain conditions. In our model, information on the functional response is assumed to be incorporated in $f(H_t,P_t)$. If $g(H_t,P_t)$ is independent of H_t or increases only slowly with H_t, then saturation of the functional response could allow the pest to escape control if a large influx of pests occurred. However, if the predators are efficient and have short handling times for the pest, the threshold will be high, making highly unusual circumstances necessary for escape of control. Moreover, even a polyphagous predator is likely to respond numerically to the pest. Indeed if the pest becomes abundant, increasing the predator's food supply, then the predator may well increase in numbers and begin reducing the pest population, bringing it back under control.

A parasitoid with a numerical response to the pest can be modeled by having

$$P_{t+1} = g(H_t,P_t) = P_{min} + H_t[1 - f(H_t,P_t)]. \tag{3}$$

The difference between these equations and those of a specialized parasitoid is merely the presence of P_{min}. The polyphagous parasitoid has an advantage over the corresponding specialized parasitoid in that it starts at a higher density and its rate of increase is higher at all densities. Thus it may be able to increase more quickly to the level where it begins to stem a pest outbreak. These features in a general predator may more than make up for any lack of specialized abilities for hunting the pest.

Clearly, there are many factors involved other than those modeled; the purpose of this discussion is simply to demonstrate that, even within the restricted framework of a simple deterministic difference equation, the conclusion that a polyphagous natural enemy is necessarily inferior to a specialized one no longer holds if one recognizes that the polyphagous natural enemy can survive in the absence of the pest.

DETERMINISTIC VERSUS STOCHASTIC APPROACHES: THE IMPORTANCE OF SCALE

Among the features listed in the introduction that are thought to characterize successful control, the assumption of pest equilibrium is by far the most difficult to test using available data. The question of spatial scale is critical here. A probabilistic, and realistic, view leads us to expect that the degree of stability we observe will be a function of spatial scale. If we define our universe to be small enough—an individual in the extreme—we expect to see extinction in the short run, with probability close to one. As we increase the size of the universe this probability of extinction will decrease (fig. 1). This decrease results from the fact that population fluctuations and environmental events may show a degree of asynchrony or statistical independence in space (Crowley 1977), and as the area is

Fig. 1.—Expected relationships between probabilistic measures of population stability and area censused. Stability could be measured by degree of stochastic boundedness or probability of persistence during an ecologically relevant time interval.

increased the local fluctuations are added together and tend to cancel each other out to yield a much stabler situation for the population on a large area (Nicholson and Bailey 1935; Slatkin 1974; Zeigler 1977; Caswell 1978; Hastings 1980; P. L. Chesson 1981). If there are no long-distance correlations in population fluctuations, then at the largest spatial scale the population fluctuates very little and the probability of extinction in meaningful ecological time is close to 0. However it must be kept in mind that, even though the population may be almost constant on this large spatial scale, the actual value of population size may be critically dependent on the population fluctuations that occur on smaller spatial scales, as discussed below.

As pointed out by Crowley (1977), in some cases there are large-scale correlations in environmental factors that may prevent nearly constant numbers being seen on a large spatial scale, but even then the probability of extinction on an ecological time scale can still be close to 0 for a large area (Chesson 1982), provided the population fluctuations are stochastically bounded (Chesson 1978; Murdoch 1979).

By contrast, existing deterministic models of population density (compared for example with those that model the number of occupied patches) do not include the possibility of extinction and are insensitive to questions of scale. The population's equilibrium density, being a continuous variable, is either stable or not, and no account is taken of the absolute spatial extent of the population. Thus, the idea in figure 1 is not one that emerges from a deterministic view. Instead, the stabilizing mechanisms are considered to occur uniformly throughout the environment. This is true even for models that appear to contain explicit spatial heterogeneity. For example, Hassell and May (1973) model a patchy environment in which the ith patch has a fraction (β_i) of the parasitoid population that increases with the fraction (α_i) it contains of the pest population, so that the overall fraction of hosts surviving in n patches is

$$f = \sum^{n} (\alpha_i e^{-a\beta_i P_i}). \tag{4}$$

However, an important feature of this model is that spatial variation in host density occurs on a small scale, a scale that is small enough to allow individual parasitoids to respond behaviorally to the variation in host density. A local

population, one that encompasses the range of a parasitoid during its activities of oviposition, contains many host patches on this scale of variation. Thus on the scale of these local populations, this model assumes spatial homogeneity. By contrast, we expect that such a local population will exhibit stochastic fluctuations and may even go extinct, and thus spatial heterogeneity should be found on this larger scale.

While the differences between equilibrium and nonequilibrium, or deterministic and stochastic, situations may be clear in theory, they are difficult to explore in real systems. As emphasized by Chesson (1985), deterministic and stochastic population regulatory mechanisms can lead to very similar population dynamics. A deterministic mechanism can operate in the presence of stochastic perturbing forces so that dynamics look stochastic, yet depend heavily on a deterministic mechanism. On the other hand, accurate deterministic phenomenological approximations can be found for situations that are intrinsically stochastic (P. L. Chesson 1981, 1984). For example, this can be so for the dynamics of the total population on a collection of patches, where the population density in each patch varies in a stochastic manner. In this situation the local population variance, not just its mean, is built into the deterministic approximation to the dynamics of the total population. Only the full stochastic model, however, portrays the mechanisms.

In the examples below we provide modest evidence on this issue: for example, on whether or not parasitoids wipe out pests in various-sized areas. The best example we know of, however, comes from a study of competition, and we mention it to illustrate the point. Sousa (1980) showed that several species of intertidal algae are able to co-occur on a boulder field because physical disturbance overturns boulders and drives to extinction patches of the species that tends to win in competition; the losers can reinvade faster than the winner, and occur temporarily on boulders that have been disturbed. On fixed substrates in the absence of disturbance, the winner wins and the losers are permanently excluded. On the boulder field as a whole, however, all species persist because disturbance on patches is a stochastic event, i.e., because local extinction tends to occur at different times on different patches. It would be possible to write a phenomenological deterministic model for the boulder field as a whole, specifying the equilibrium proportion of boulders containing a particular species, and for many purposes this might be adequate. Indeed Hasting's (1980) model has many of the elements of this field example and shows how the essential local stochasticity can be consistent with a phenomenological deterministic description for the whole boulder field. But the stochastic elements are essential for understanding how the mechanisms, i.e., local competition and random disturbance, lead to the large-scale picture of persistence.

Most field studies cannot yield such unambiguous definitions of patch size or unequivocal evidence for local extinction. Furthermore, local extinction is only the most extreme outcome predicted by stochastic models: stochastic events and nonequilibrium dynamics may be critical even though local extinction is rare or absent. Field studies of biological control, in particular, have not usually included measurements that would reveal parasitoid behavior, probability of pest extinction, local rates of movement, etc., on small spatial scales. That is, we do not

usually have observations on the spatial scale at which proposed mechanisms are thought to work. Furthermore "patches" are open and we expect immigration will frequently obscure the tendency to local extinction. Thus, existing data are not likely to settle these questions and can be expected to do little more than confirm that a nonequilibrium view may be appropriate in some circumstances.

In the present context the practical importance of these issues is that a deterministic approach suggests criteria for selecting natural enemies, as discussed in the introduction, that can be quite different from those suggested by a stochastic approach. Most obviously, several deterministic models recommend parasitoid behavior that stabilizes by inefficiently letting a portion of hosts escape parasitism, whereas stochastic models might emphasize the parasitoid's ability to drive the pest as low as possible in any area, including to extinction. Other aspects such as dispersal ability might also be important.

FIELD EXAMPLES

A. CLASSICAL EXAMPLES

We have chosen the following six examples because it is generally agreed that they are cases of successful biological control in perennial crops and because the important paper by Beddington et al. (1978) uses them to exemplify the appropriateness of standard Nicholson-Bailey type theory. In reviewing the examples we will look for consistency with the general structural features of the theory, rather than with particular details of particular models. The general features follow. (1) The parasitoid is highly specific. (2) The parasitoid has the same generation time as the pest; Beddington et al. modified their models to examine the effects of different generation times and concluded that shortening the parasitoid's generation time has a negligible effect on the minimum attainable stable pest equilibrium. (3) The introduced parasitoid drives the pest to a new low stable-equilibrium density. (4) The parasitoid aggregates at denser patches of the pest.

1. Winter Moth in Nova Scotia

Between 1954 and 1961 two parasitoids, *Cyzenis albicans* and *Agrypon flaveolatum*, were introduced to control the recently introduced European winter moth, *Operophtera brumata*, in hardwood forests in Nova Scotia (Embree 1965, 1966, 1971; Hassell 1978, 1980). By 1965 both species were widespread. The general pattern appears to be that *Cyzenis* quickly caused a drastic decline in winter moth numbers and that *Agrypon* appeared later and was more effective at driving the density of winter moth even lower (fig. 2).

A new virus invaded the winter moth population in 1961 and was widespread by 1964. The effect of this virus was not measured. Nor was it known if it was the same virus that, at this time, was beginning to control an outbreak of the Bruce spanworm (*Operophtera bruceata*).

Predation by vertebrates was not studied thoroughly, but appeared to be important, both on winter moth larvae in trees and on pupae in the soil. There was
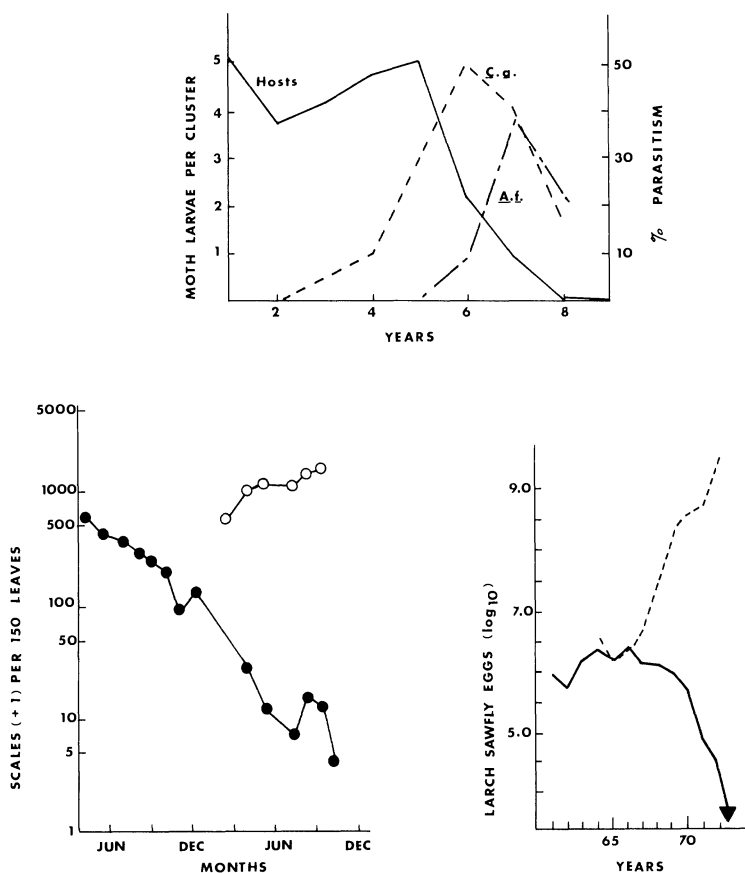
FIG. 2.—Three examples of biological control. Top: winter moth in Nova Scotia; broken lines = % parasitism by *Cyzenis albicans* (*C.a.*) and *Agrypon flaveolatum* (*A.f.*) (Embree 1966). Bottom left: red scale in Australia; open circles indicate absence of parasitoid (Campbell 1976). Bottom right: larch sawfly in Manitoba; dashed line = expected density in the absence of the parasitoid (Ives 1976).

evidence of density dependence in the pupal predation, and perhaps also in the predation on large larvae, although the latter relationship is unclear (Embree 1965).

Records were taken over 12 yr at one study site (Oak Hill). The winter moth maintained very high densities until 1961, but parasitism by *Cyzenis* apparently drove the winter moth to a very low density by 1963. In the four generations of declining and low winter moth density, parasitism by *Agrypon* exceeded that by *Cyzenis*. According to Embree (1966), this might have been caused, in part, by the fact that other defoliators increased in density as the winter moth declined, and drew off *Cyzenis* attacks from the winter moth. (*Cyzenis* simply lays eggs on leaves, and the eggs are eaten by insect larvae.) These alternative species are immune to this parasitism, so that *Cyzenis* wasted an increasing fraction of its

attacks. *Cyzenis* also has become established in spanworm populations, and Embree believes this will help maintain the parasitoid, which may in turn increase its usefulness for the winter moth. *Agrypon* appears to have played a critical role in driving the winter moth to very low densities. The role of the virus is unclear.

The field data do not provide much evidence on whether or not the pest has been maintained around equilibrium. No fieldwork has been done on the winter moth in Nova Scotia since 1965. D. G. Embree (personal communication) states that there has been no sign of the pest in the hardwood forests since 1965, suggesting the possibility of local extinctions. However, no intensive effort has been made to find the moth. The moth has persisted, with its parasitoids, in apple orchards and shade trees in towns, and these situations may provide a source of reinvasion.

Hassell (1980) fitted the average pre-control moth density, and the four data points in the decline phase, with a simulation model based on model 1 but with additional parameters, including the assumption that k increased linearly with host density. The model is unstable with the proposed Nova Scotia parameters, but it becomes stable when a term is added that causes parasitoids to waste time through direct interference. It is not possible to tell whether this behavior occurs in the field, and the parameter value chosen for time wasted is arbitrary. The model predicts an equilibrium moth density of 9.4 m^{-2}, and while long-term moth densities have not been estimated, this appears much too high given Embree's statement that there has been no sign of the moth in the forests. Finally, as noted by Hassell, the role of the parasitoid *Agrypon* is uncertain, but it does seem to have been critical in the process of bringing the moth under control, and is omitted from the model. Thus, overall the model does not strongly support the claim that *Cyzenis* controls winter moth in Nova Scotia at a stable equilibrium via the mechanisms embodied in the model.

In short, there is no good evidence that the winter moth is being held at a low stable equilibrium in hardwoods. The observations are sparse, they are consistent with local extinction of the pest, but do not by any means establish this; two, and perhaps three, enemy species played a critical role in control, and a major enemy species, *Cyzenis*, was not host-specific.

2. Olive Scale in California

This is one of the most intensively studied cases of successful biological control (Huffaker and Kennett 1966). Between 1952 and 1960 the Iranian strain of the wasp *Aphytis paramaculicornis* was introduced to attack the olive scale *Parlatoria oleae* in olive groves over a wide area of California. A second parasitoid, *Coccophagoides utilis*, was also released. *Aphytis* alone caused dramatic reductions in olive scale densities, but economic control requires both parasitoids, which act in a complementary way.

The scale has two generations per year, having breeding adult populations in late April and early May, and again in July and August. *Aphytis* can have six to eight generations per year. During winter it develops slowly on the host scale, but then undergoes rapid population growth, passing through three generations by

May, when parasitism may reach 100% of the hosts. The adult parasitoid is ill-adapted to the summer heat and, as a result, *Aphytis* parasitizes a very small percentage of the breeding scale population in August. *Aphytis* alone is not an adequate control agent and is unable to suppress outbreaks (Huffaker and Kennett 1966).

Coccophagoides utilis develops slowly inside the host and essentially produces two generations matching those of the host. *Coccophagoides utilis* usually does not parasitize more than about 50%–60% of the scales, but its crucial characteristic is that it does parasitize the August population at these rates, precisely when *Aphytis* is ineffective.

The data of Huffaker and Kennett have recently been reanalyzed (Murdoch et al. 1984). This analysis showed that parasitism rate was unrelated to local host density, nor was parasitism aggregated among hosts, independently of host density, to the degree required for stability in a model of the system. In fact, there is evidence for a rather even distribution of parasitism. In addition, there was evidence for frequent extinction of local patches of scale, and even for a tendency to extinction on trees or entire groves. By the end of the season, total parasitism in a grove frequently reached 100%. The percent parasitism fluctuated strongly through time, suggesting populations in a grove never approached equilibrium.

In California the two parasitoids probably are quite host specific. Only *Coccophagoides* is synchronized with the scale, however, and this species is the less effective one. By contrast, it is precisely because *Aphytis* is not closely synchronized with the scale that it is able to parasitize so intensively in the spring. Parasitism by the first generation in the fall is only about 10% and increases rapidly with the successive *Aphytis* generations. Thus the multiple generations of *Aphytis* are a key to its success.

In summary, *Aphytis* alone did not produce a stable pest equilibrium; there is no good evidence for a pest equilibrium when both parasitoids are present, and the data are suggestive of nonequilibrium interpretations; and the parasitoids are not spatially aggregated.

3. Larch Sawfly in Manitoba

Larch sawfly, perhaps an introduced pest, caused enormous destruction, especially of tamarack, in the late nineteenth and early twentieth centuries (Ives 1976). In the early 1960s a strain of the parasitoid *Mesoleius tenthredinus* was introduced together with another parasitoid, *Olesicampe benefactor*, which is attacked by a hyperparasitoid, *Mesochorus dimidiatus*. Ives reports life-table data from five study plots in southeastern Manitoba that were established in 1955–1963 and were sampled until 1970. Data from three plots were collected until 1973.

Several factors kill sawflies in addition to parasitism, including flooding and predation by small mammals, birds and invertebrates. A third parasitoid, *Bessa harveyi*, is less important. Flooding and adult mortality from various sources were the main determinants of sawfly population trends before the parasitoids were introduced.

The first issue is the extent to which *O. benefactor* (and to a lesser extent *M.*

tenthredinus) actually controlled the sawfly. Ives (personal communication) feels that there is no clear answer, particularly because sawfly populations were already declining even where *O. benefactor* was not yet abundant. *Olesicampe benefactor* may have been maintaining the low sawfly density of the early 1970s.

Evidence on the efficacy of the parasitoids varied from plot to plot. Extensive data on percent parasitism were available only for one plot (Pine Falls), where *O. benefactor* parasitism of the susceptible stage eventually reached about 90% and remained at this level for 5 yr. (Actually the rate was probably close to 100%, the 90% figure involving a bias in the estimate.) In the last 2 yr of the study, however, the hyperparasitoid *M. dimidiatus* parasitized about 90% of the *O. benefactor*. This plot provides the best evidence that *O. benefactor* played a crucial role in ending the sawfly outbreak (fig. 2).

The evidence is generally against the hypothesis that *O. benefactor* created a new low equilibrium, and is suggestive of nonequilibrium behavior and even of local extinction. The population trends up to 1970–1973 (Ives 1976, fig. 14) show either no reduction caused by the parasitoids or a continuous downward trend in sawfly density; in two plots the populations appear to be headed for extinction. This was the case at Pine Falls, the plot that provided the best information and the best evidence for parasitoids' effectiveness (fig. 2).

Ives and his coworkers have collected some additional information on sawfly density and percent parasitism since 1973 (W. G. H. Ives, personal communication; Ives and Muldrew 1984), and these data strongly support a nonequilibrium interpretation. The sawfly has become very rare in southeastern Manitoba. Previously, one could always find sawfly larvae if one looked long enough and hard enough, but this was no longer true in many places in the mid–late 1970s. At Pine Falls, no larvae or cocoons could be found in 1973 and 1974 in spite of intensive sampling, and none was found at Seddon's Corner in 1974. The sawfly reappeared in some places during subsequent collecting visits.

The parasitoid may also have become extinct locally, and certainly a massive reduction in percent parasitism occurred: at Pine Falls in 1977 none of a collection of 72 sawfly larvae was parasitized, while parasitism in 1,730 cocoons collected at Pine Falls in 1978 was only 1.5%. In 1978 the sawfly was still extremely rare at Pine Falls, and there was no sign of it at Seddon's Corner and Rennie (another plot). In that same year there was zero parasitism at a site 8 km north of Pine Falls (in 237 larvae collected) but 15% at this same site in 1980. In 1980 at Seddon's Corner, some 70 km south of Pine Falls, there was zero parasitism among 150 sawfly cocoons. The data are thus consistent with the hypothesis that the parasitoid drove the sawfly to extinction in some areas, but that reinvasions occurred and, further, that the parasitoid itself became extinct locally but reinvaded.

In summary, the evidence that the parasitoids were responsible in general for reducing the sawfly to low levels is equivocal; the evidence is against the hypothesis that a stable equilibrium has been achieved and is consistent with local extinctions and nonequilibrium dynamics; and in general two parasitoids have been important.

4. Walnut Aphid in California

A strain of the wasp *Trioxys pallidus* from Iran was introduced into California to control the walnut aphid *Chromaphis juglandicola* in 1968 and 1969 (van den Bosch et al. 1979). In the study referred to by Beddington et al. (1978) one plot was monitored in 1969 and 1970. The wasp was rare in 1969 and had no measurable effect. It increased throughout that year, and by mid-May 1970 the aphid density was very low compared with May 1969. The Argentine ant strongly affected the interaction in 1970, and the aphids increased rapidly. These data are inadequate for reaching a judgment about a possible low pest equilibrium.

Additional information has become available from van den Bosch et al. (1979). By 1970 the parasitoid had spread to all the major walnut-growing areas of California. Two groves were studied in some detail during 1971 to 1974 (a period covering about 40 generations). In both situations in summer there was a tendency for the aphid to escape temporarily from the parasitoid's control. In the Reliez Valley grove this tendency was quickly checked, but in the Hanford grove the oscillations were marked: seasonal highs were several orders of magnitude greater than seasonal lows, and the largest peak density was 10 times greater than the smallest peak (van den Bosch et al. 1979, fig. 2). The peak density in one year (1973) amounted to an outbreak, which occurred, however, out of the economically critical season. The outbreak resulted from the low density of the parasitoid and its failure to catch up with the aphid.

According to van den Bosch et al. (1979), *Trioxys* is a highly successful control agent and has virtually removed the aphid from the list of economic pests of walnut. The evidence is not strong, however, that it achieves this control by establishing a stable low equilibrium density.

5. The Red Scale in California

Parasitoids of the genus *Aphytis* have successfully controlled red scale on citrus in many areas of California. The example of *Aphytis melinus* on *Aonidiella aurantii*, chosen by Beddington et al. (1978), is perhaps the most convincing of the six cases discussed here. DeBach et al. (1971, fig. 7) present semiquantitative data showing the scale undergoing quite narrow fluctuations over 8 yr in a citrus grove in California. Furthermore, the percent parasitism has stayed close to a constant level (15%–20%). This parasitoid apparently is alone responsible for control. It is highly specific.

J. D. Reeve and W. W. Murdoch (in prep.) have been studying the system in a lemon grove in Ventura County in California. They find that the populations and percent parasitism are remarkably constant, and that live scale can almost always be found on even the smallest twig samples, suggesting that local extinction is rare and supporting DeBach's evidence that the parasitoid is actually regulating the scale in a stable manner. Parasitism, however, is typically density independent (occasionally inversely density dependent) in space over a very wide range of spatial scales, from single fruits to entire trees, so spatial aggregation to areas of

high host density by the parasitoid is not the stabilizing mechanism. There is also insufficient aggregation of parasitism independent of host density.

It can always be argued that spatial density dependence does occur in the olive and red scale and that the studies above have simply failed to detect it. Indeed, Heads and Lawton (1983) propose that patch size should be defined as that spatial scale at which spatial density dependence is detected. It then follows, by definition, that any study that fails to find spatial density dependence has looked at the wrong spatial scale. While this is an interesting approach for situations where aggregation is known to occur, it makes it impossible even to entertain our alternative hypothesis that aggregation does not occur.

Like *Aphytis* on olive scale, *Aphytis melinus* has several (3) generations for each host generation. A further complication is also important. *Aphytis melinus* feeds extensively on hosts it does not parasitize, so host mortality caused by the parasitoid is greater than the parasitism rate. In this respect adult *Aphytis* act like a predator.

6. California Red Scale in Australia

In 1969 the parasitoid *Aphytis melinus* was imported to South Australia to attack the California red scale, *Aonidiella aurantii*, which attacks citrus orchards (Campbell 1976). The wasp was introduced onto some trees in one infested orchard during 1969 and 1970. A control tree with no wasps was monitored, and five trees with wasps were infested with the scale. The numbers of scale declined steadily on the trees with the wasp (fig. 2). The experiment ended in late 1970. The numbers on the control tree increased. There was no evidence relevant to the existence of a stable, low pest equilibrium.

B. OTHER EXAMPLES

We now present three additional examples which support some of the arguments we have made concerning the usefulness of general predators and the occurrence of local pest extinctions.

7. Control of Mosquitoes by Notonecta

Several mosquito species (e.g., *Culex peus*, *Culiseta incidens*) occur in temporary and permanent ponds and other bodies of water in southern California, particularly where the backswimming bug *Notonecta* and the mosquitofish *Gambusia* are absent. Mosquito larvae can occur throughout the year, although development is greatly reduced during winter. Even during periods of high activity their appearance is sometimes sporadic.

We have studied the interaction between *Notonecta* and mosquitoes in stock tanks on ranches in Santa Barbara County. The results are described in detail in J. Chesson (1984) and Murdoch, Scott, and Ebsworth (1984) and here we present only a brief summary.

Figure 3 shows typical results of manipulating *Notonecta* densities in two tanks.
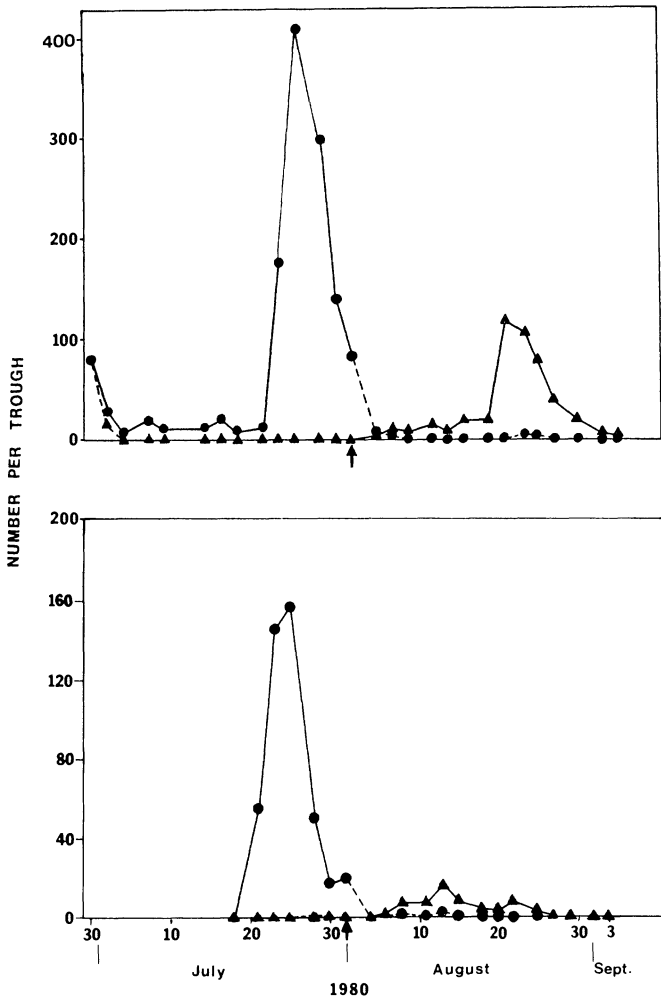
FIG. 3.—Effect of the predator *Notonecta* on the number of large mosquito larvae in 2 stock troughs. Each trough was divided in half and predators were confined to the right side (triangles) of the trough. The vertical arrow marks the point at which predators were moved to the left side (circles) to ensure that the results were not merely the result of fortuitous selection of treatment and control sides. Solid line joins mosquito numbers in the absence of predators; dotted line (coincidental with the horizontal axis for much of the time) joins mosquito numbers in the presence of predators. See J. Chesson (1984) for details.

Each tank was divided in half by a partition that prevented movement of *Notonecta* and mosquito larvae from one side of the tank to the other but allowed water exchange between the two sides. A summary of conclusions from our studies follows.

a) *Notonecta* typically reduced the density of large mosquito larvae plus pupae by tenfold to several hundredfold. The abundance of mosquito egg rafts was also

reduced in the presence of *Notonecta*, probably because mosquitoes avoided ovipositing there (J. Chesson 1984).

b) In some tanks, at some periods, no mosquitoes survived to the large larval or pupal stage in the presence of *Notonecta*, but were common in the control side of the tank. That is, local pest extinctions occurred. This, however, may have been a consequence of the simplicity and small size of these environments.

c) Pest extinction was not certain; rather, it was a probabilistic event.

d) There appeared to be permanent absolute refuges for mosquitoes in tanks that were not suitable for *Notonecta*. Temporary refuges also existed, however: *Notonecta* sometimes became extinct in some tanks, and mosquitoes sometimes survived and emerged even when *Notonecta* was present in the tank. Thus, although the absolute refuges may be important, it is likely that mosquitoes would survive in the system of stock tanks, even in the absence of these refuges, because local extinction is not certain.

e) Our analyses of the components of *Notonecta* predation all lead to the expectation that *Notonecta* will be a destabilizing force on its prey populations (J. Chesson 1981; Murdoch and Scott 1984).

Notonecta dynamics and feeding behavior are important in explaining this predator's effects on mosquitoes. The predator's generation time (roughly 4 to 6 mo) is about 8–12 times longer than that of mosquitoes. *Notonecta* are polyphagous and feed mainly on zooplankton and terrestrial insects trapped on the water surface; they are also cannibalistic. Although *Notonecta* powerfully influenced mosquito dynamics, mosquitoes played only a minor role in *Notonecta* dynamics.

Two features of this interaction are particularly salient to our general discussion. First, although *Notonecta* provides good control of mosquitoes, it fails singularly to meet the standard criteria for a successful control agent. In particular, *Notonecta* is polyphagous; it has a low rate of increase relative to the pest; and its life history is not synchronized with the pest's. Second, the pest is not controlled by being maintained around a low stable equilibrium. Instead, local extinction occurs at least some of the time, and pest dynamics appear to have irreducible stochastic aspects.

8. Control of Mosquitoes by Gambusia

The mosquitofish *Gambusia* is in general a highly successful control agent for mosquitoes in rice fields, irrigation ditches, permanent and temporary ponds, and stock ponds in many parts of the world (Krumholz 1948; Hoy et al. 1972). *Gambusia* shares some features with *Notonecta*: its generation time is longer and its rate of increase much lower than those of mosquitoes, and it is a very general predator (Washino and Hokama 1967). Mosquitoes are in general rare in the diet (since they are controlled so well), and indeed *Gambusia* may not be able to survive on a pure diet of mosquitoes, which are not strongly preferred (Reddy and Pandian 1972). As with *Notonecta*, *Gambusia*'s population dynamics are largely independent of those of the mosquitoes.

Unfortunately, there are very few well-documented, detailed and published studies of the mechanisms by which *Gambusia* controls mosquitoes. However, a

great deal is known about this action by Mosquito Abatement District (MAD) personnel in California, and the following account is based partly on that information (see also Bence and Murdoch 1982). It appears that *Gambusia* frequently drives mosquitoes to extinction or at least to such low densities that they cannot be found by sampling (MAD; J. R. Bence, in prep.; Green and Imber 1977). Many of the environments where this occurs are temporary, and the fish have to be restocked each season; however, *Gambusia* populations are able to persist indefinitely in some environments (e.g., large stock ponds) in southern California and in these habitats, again according to local MAD personnel, mosquito populations are driven to extinction but reinvade sporadically.

9. Cottony-Cushion Scale in California

There is now a sizeable literature dealing with models of predator-prey and other systems that can become extinct locally but that persist globally because the system contains many patches linked by migration (e.g., Caswell 1978; Hastings 1977; P. L. Chesson 1981). Furthermore, there are now some examples of natural populations that exemplify these processes (Connell 1978; Sousa 1980). It is possible that the cottony-cushion scale (*Icerya purchasi*) and its predatory beetle (*Rodolia cardinalis*) exemplify this process (Quezada 1969).

According to Quezada, isolated scale colonies can persist for quite long periods before being found by the beetle. The colony is then driven close to extinction, often from several thousand to a few individuals, and to complete extinction in some cases. The beetle apparently suffers local extinction quite frequently and disappears once local colonies have been heavily attacked. The scale has a refuge outside "the system" on at least one plant species that is largely immune from attack by the beetle. Whether this refuge is necessary for the persistence of the system is not clear, but since scales on citrus sometimes persist for longer than one generation before they are found by the fly or beetle, it appears that they are not. Unpublished observations of this system in northern California by L. Ehler confirm that local extinction is common in that area.

DISCUSSION

There is as yet no theory that provides a satisfactory general explanation for the successes of biological control of pests of perennial crops and permanent habitats. In particular, with the exception of red scale in lemon groves, the cases examined provide no good field evidence to support the standard view that control is achieved through the establishment of a low stable pest-enemy equilibrium. This is not to say that density-dependent pest mortality never occurs, or to deny that it may sometimes be important in preventing or reducing outbreaks; obviously, the existence of density dependence does not ensure stable equilibrium. Nor do we claim that equilibrium-centered models are never useful in explaining natural control; to the contrary they may be needed, for example, to explain control (or at least stability) of red scale in California. But we do believe there is as yet no adequate evidence that they describe the features that are important in successful control.

The field data also fail to confirm that certain characteristics are essential in successful control agents. These features include (1) a high degree of specificity for the pest, (2) a high degree of synchrony with the pest, (3) an enemy that requires only one or a few pest individuals in its lifetime, (4) a rapid numerical response to increases in pest density, and (5) a strong tendency for the enemy to aggregate either independently of pest distribution or preferentially in patches of high pest density. On the contrary, successful control agents have collectively violated all of these conditions, and violation of features 1–3 appears to have been central to success in several circumstances. In some situations it also appears that the joint operation of two or more natural enemies has been essential.

The question of spatial aggregation of the parasitoid is particularly interesting. Although such behavior probably would be adaptive some of the time (Comins and Hassell 1979), there is little field evidence that parasitoids actually do aggregate at high host densities in the situations where biological control is known to be occurring (see also Morrison and Strong 1980; Murdoch et al. 1984). Some positive examples are provided by Hassell (1982) and Heads and Lawton (1983).

Possible alternatives to conventional host-parasitoid models range from stable deterministic models of polyphagous enemies, to mixed models in which the enemy, but not the pest, is at equilibrium, to wholly stochastic models of specific or general enemies, in which populations exist in patches and local extinction is possible. The classical argument in favor of stable equilibrium models and against stochastic models (aside from analytic tractability) has been that the former allow the persistence of the pest and hence of the enemy. Indeed, as we have noted, the modern developments of the Nicholson-Bailey theory in relation to pest control have centered around keeping the pest in existence (i.e., keeping the equilibrium stable) by allowing a fraction to escape the enemy in each generation. It seems to us, however, that the danger of pest extinction (and hence, in a specific parasitoid, of enemy extinction) is a non-problem. Field situations are heterogeneous in time and space, and pest eradication by any means is recognized as an unrealistic goal in all but the most unusual circumstances. Pests will persist either because absolute spatial or temporal refuges exist (this may be the case in several of our examples), because there are invulnerable stages, or because the enemy cannot wipe out the pest everywhere simultaneously (the "hide-and-seek" mechanism). There is now an abundance of stochastic theory illustrating how such global persistence can occur in the face of local extinction (e.g., Hastings 1977; Caswell 1978).

Beddington et al. (1978) suggested absolute prey refuges as a possible alternative explanation for successful biological control at a stable equilibrium. In some of the examples discussed here there is anecdotal evidence that refuges are a factor in explaining the persistence of the pest; for example, other plant species in gardens may be a source of reinfestation of the olive scale in olive groves. In the examples, the refuges are outside the crop areas of interest; thus, the interaction within the crop system appears to be intrinsically unstable, whereas the global spatial system may be stable, or at least persistent.

Almost no literature exists on stochastic models that might give insight into pest control. P. L. Chesson and B. L. Kerans (in prep.) have shown in a parasitoid-host model that some kinds of parasitoid aggregation to local host density in fact

leads to host extinction. Given the difficulties mentioned above in achieving global eradication, this tendency to local extinction would seem to be a desirable feature and one that is perhaps worth aiming for in both models and real life. Extinction of the parasitoid opens up the possibility of pest outbreaks, but if host extinction is only local in space, the parasitoid can also persist globally and severe pest outbreaks are less likely.

Does it make any practical difference whether one believes biological control results in stable equilibria or is a stochastic or nonequilibrium process? After all, on the one hand we can interpret a very low stable equilibrium in a deterministic model as implying extinction, and on the other hand stochastic models of large collections of small population units are likely to have deterministic analogues.

We believe the distinction does matter, because different modeling approaches lead us to look for different properties to explain successful control. Equilibrium models force us to seek as key features those mechanisms that yield local stability. Indeed, in several models the stabilizing mechanisms operate to increase pest density. Once we discard the notion that stability is essential to control, such mechanisms lose their significance and other factors may become critical. In fact, we would argue that even when a pest-enemy system is apparently stable, the features that explain stability may not be critical to the enemy's ability to control the pest; instead, control may be successful in spite of factors that operate to save the pest from local extinction and hence lead to stability.

If local extinction of the pest is both a possible way to control pests and perhaps a desirable goal, what characteristics of natural enemies are either consistent with or promote local pest extinction? Two strategies are apparent, given that most of the time during successful biological control the predator or parasitoid is preventing outbreaks rather than reducing outbreak populations. The first strategy we might term "lying-in-wait," the second "search-and-destroy."

The lying-in-wait strategy requires the more or less continuous presence of the predator in local areas subject to pest infestation, combined with an adequate attack on the pest when it reinvades or begins to increase. An obvious set of desirable characteristics for this strategy is exemplified by *Notonecta* and other general predators, and by the models of equations (2) and (3). These characteristics include polyphagy (enhanced in many insect predators by cannibalism in response to food shortage [Fox 1975]) and resistance to brief periods of starvation. The type and abundance of alternative prey will be important in determining the predator's response to the prey but the pest need not be highly preferred relative to the other prey (J. Chesson 1981). The presence of polyphagy and resistance to starvation will not of course guarantee success, but they probably are necessary. In addition to the examples of this strategy discussed above, others from temporary crops may include the general predators in cotton (Ehler and Miller 1978) and alfalfa (Bisabri-Ershadi and Ehler 1981) in California.

The search-and-destroy strategy assumes that the predator or parasitoid is monophagous on the pest, or almost so, and is highly adapted to finding and attacking it. Here the control agent persists globally in the face of local extermination of its food because the pest survives globally; that is, spatial patchiness, heterogeneity and migration allow the pest (and hence the predator) to survive.

This strategy requires some of those characteristics long thought to be desirable in biological control agents: a powerful ability to detect and find the pest (high search rate) and a high rate of numerical increase. The latter feature is enhanced in pest enemies that have generation times shorter than those of the pest, and these occur in some of the successful agents discussed in this paper (the two *Aphytis* species and *Rodolia*). A high rate of dispersal relative to the pest is an additional requirement that arises from the hide-and-seek nature of the interaction.

The desirability of two other features, spatial aggregation and gregarious parasitism, is less clear. (In gregarious parasitism several parasitoid larvae can complete their development within a single host individual.) At first sight, aggregation to areas of high host density would seem a desirable feature, because it could increase the enemy's efficiency. Furthermore, P. L. Chesson and B. L. Kerans (in prep.) show that this behavior can lead to local extinction of the pest if the ratio of parasitoids to pests is high. This strategy, however, could also lead to pest refuges unless the parasitoid leaves patches where the prey are already parasitized. Avoidance of gregarious parasitism would also appear to be desirable because it saves ammunition, so to speak. On the other hand, gregarious parasitism is likely to lead to a high ratio of adult parasitoids to pests when pest density is low, as required for pest extinction by P. L. Chesson and B. L. Kerans (in prep.).

In practice, we found no evidence for aggregation in the successful control of scale insects. Aggregation of the parasitoid independent of pest density (as in May's negative binomial model [May 1978; P. L. Chesson and W. W. Murdoch, MS]) is probably undesirable because dense as well as sparse patches of the pest are missed and the overall parasitism rate declines. There seems to be no general rule about gregarious parasitism; it is rare in the successful *A. paramaculicoris* on olive scale, but is common in *A. melinus*, the successful parasitoid of red scale, where a large scale can produce up to four parasitoids (Luck and Podoler 1984).

The practitioners of pest control fortunately have not waited, before succeeding, either for the development of useful theory, or for ecologists to establish the crucial characteristics of a good biological agent. Yet such models and information might improve biological control and are worth searching for. Our comparison of cases suggests that there may be more than one formula for success. We have also shown that different types of theory might easily produce very different, or even conflicting, advice for the practitioner seeking a good natural enemy. The existing field evidence does not yet support any single theoretical framework.

Summary

The conventional wisdom of biological control of insect pests, and its related ecological theory, is that successful natural enemies in long-lived ecosystems (1) impose a low, stable pest equilibrium, and (2) share the following properties: (a) host-specific; (b) synchronous with the pest; (c) can increase in density rapidly when the pest does; (d) need only one pest individual to complete their life cycle; (e) have a high search rate for the pest; (f) aggregate at areas of high pest density, which is thought to stabilize the interaction. These features are more characteristic of parasitoids than predators.

We suggest that a stable pest equilibrium is neither a necessary nor a sufficient condition for control. We show that satisfactory control in model systems is compatible with both local extinction of the pest and polyphagy in the natural enemy. Only one of nine real examples of successful control is convincingly a stable interaction; the remainder show either strong evidence for instability and local extinction of the pest or are consistent with this interpretation. Successful natural enemies have collectively violated all of features 1 and 2 above, and violations of features 1 and 2a, 2b, and 2d appear to have been central to success in several situations. Two strategies by which a natural enemy may control a pest in a nonequilibrium state, termed here "lying-in-wait" and "search-and-destroy," are distinguished.

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