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PARASITOID COMPETITION AND THE DYNAMICS OF HOST-PARASITOID MODELS

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Both parasitoids and predators compete intraspecifically for prey or hosts. The nature of this competition, however, is potentially much more complex and varied for parasitoids than for predators. With predators, prey are generally consumed upon capture and thus cease to be bones of contention: competition is simply for discovery (or capture) of prey. In contrast, parasitoids do not consume hosts immediately upon discovery; the hosts remain available to be discovered—and possibly parasitized—again. An individual parasitoid's reproduction from a particular host generally depends, therefore, on whether the host has already been, or is subsequently, discovered by another female; that is, there is competition for exploitation of individual hosts (*within-host competition*) as well as for their discovery (*across-hosts competition*).

Parasitoid competition naturally is quite important in host-parasitoid dynamics. As shown below, it is necessary for stability in many host-parasitoid models. In addition, the various forms of heterogeneity that have been the focus of much current theory (e.g., Bailey et al. 1962; Hassell and May 1973, 1974; Beddington et al. 1978; May 1978; Hassell and Anderson 1984) all act largely by increasing the "discovery" component of competition (Taylor, MS). In contrast, the within-host aspect of competition and the potential difference it creates between predator and parasitoid dynamics have been almost totally ignored. The standard models all assume what is in essence an extreme form of contest competition: the number of (female) parasitoid progeny produced from each parasitized host is independent of the number of times that the host was encountered. Only two models with different within-host dynamics have been proposed previously, and in neither were overall dynamics studied. Thompson's (1929) model completely lacked not only parasitoid competition (i.e., every encounter produced the same number of progeny) but also any numerical response to host density; thus, no equilibrium or even persistence was possible. The model of Griffiths and Holling (1969), in contrast, was in many ways similar to those developed below (including the

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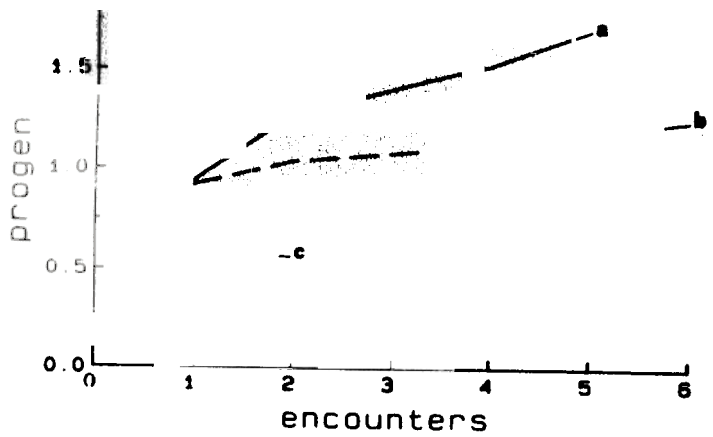


FIG. 1.—Estimated encounter-dependent yields of three solitary parasitoids: a, *Glypta fumiferanae*, McLeod 1977; b, *Apanteles fumiferanae*, McLeod 1977; c, *Diadromus collaris*, egg-distribution data from Lloyd 1940, larval survival data from Kalmes et al. 1983. The estimated proportion of multiple encounters resulting in superparasitism (table 1) was combined with density-dependent larval survival rates to obtain the predicted mean yields.

negative-binomial distribution of encounters), but they did not analyze its multigeneration dynamics.

The within-host dynamics of few parasitoids—that is, the relationship between the number of encounters and the level of parasitoid recruitment from a given host—are actually known under natural conditions. The available evidence does suggest, though, that the "constant-yield" assumption of standard theory is probably incorrect for some (though probably not for most) species. Failure of the assumption—that is, variation in the number of progeny from a host, depending on the number of times the host was encountered—requires that females at least sometimes oviposit in or on previously parasitized hosts (superparasitize, in the broad sense of Fiske 1910) and that larval competition does not nullify the effects of this superparasitism. I have been able to find data on both these aspects (fig. 1) for only three species (all solitary): of these, one shows a substantial increase in yield with increasing numbers of encounters. Evidence of one or the other of the requirements for variable yield, however, is available for many species. Superparasitism occurs at least occasionally, and in some cases frequently, in the solitary species in which it has been examined (table 1); it is not so clearly observable in gregarious species in the field, but it has been reported (Shiga and Nakanishi 1968; van Alphen and Nell 1982; Takagi 1987), and it is common in laboratory studies (reviews in van Lenteren 1981; Taylor 1984, 1988*b*). Larval competition has been studied extensively in gregarious species (see Taylor 1984, 1988*a*), and yield has been shown to increase continuously (e.g., Shiga and Nakanishi 1968), to rise to a plateau (e.g., Klomp and Teerink 1967), or first to increase and then to decrease as density rises (e.g., Takagi 1985); in no case was a

TABLE 1

FIELD EVIDENCE OF SUPERPARASITISM BY SOLITARY PARASITOIDS

PARASITOID	SOURCE	FREQUENCY OF SUPERPARASITISM* Mean	Range	*N*†
Diadromus collaris	Lloyd 1940	0.84		
Synomelix sp.	Carl 1976	0.83		
Eurytoma robusta	Varley 1941	0.79		1
Pimplopterus dubius	Jørgensen 1975	0.65	0.43–0.86	2
Lathrolestes luteolator	Carl 1976	0.50	0.0–1.0	2
Apanteles fumiferanae	McLeod 1977	0.49	0.0–1.0	15
Glypta fumiferanae	McLeod 1977	0.48	0.0–1.0	15
Exenterus amictorius	McLeod 1972	0.44	0.24–0.61	5
Ibalia leucospoides	Chrystal 1930‡	0.30	0.0–1.0	26
Collyria calcitrator	Salt 1932	0.28		
Angitia sp.	Lloyd 1940	0		1
Angitia sp.	Ullyett 1943	0.24	0.16–0.33	5
Exenterus diprionis	McLeod 1972	0.21		1
Aphelinus mali	Thompson 1934	0.19	0.02–1.0	9
Limnerium validum	Timberlake 1912§	0.17		1
Eurytoma curta	Varley 1941	0.01		1

NOTE.—Included are all available studies reporting the distributions of eggs or progeny across hosts, excluding samples with parasitism of 100% or less than 5% and samples in which more than one egg is likely to have been laid on some encounters. Additional unquantified reports of superparasitism: *Ooencyrtus kuvanae*, Lloyd 1938; *Trioxys indicus*, Singh and Sinha 1982; *Ceratobaeus* sp., Austin 1984; *Diadromus pulchellus*, Labeyrie and Rojas-Rousse 1985.

* Proportion of encounters with previously parasitized hosts that result in superparasitism, calculated as in Rogers 1975.

† *N* is the number of separate samples reported.

‡ In Rogers 1975; original not consulted.

§ In Salt 1934; original not consulted.

constant yield independent of egg density observed. Yield apparently varies with egg density in a number of solitary species also (table 2), though in many others larval competition does produce a constant yield (fig. 1; Ryan 1971; Wylie 1971; Gerling 1972; Khalaf 1982; review in Salt 1961).

Almost certainly, then, parasitoids exhibit a wide range of within-host dynamics, many of which violate the constant-yield assumption of standard theory. What follows is an investigation of some of the consequences of this in simple modifications of standard host-parasitoid models.

A GENERAL MODEL FOR WITHIN-HOST COMPETITION

Within the standard framework of simple, deterministic discrete-time, discrete-generation host-parasitoid models (Hassell 1978), recruitment of parasitoid progeny into the next generation can be expressed in the following general form (Griffiths and Holling 1969):

$$P_{t+1} = H_t \sum_{i=1}^{\infty} p(i|H_t,P_t)h(i|H_t,P_t) \qquad (1)$$

TABLE 2

SOLITARY SPECIES IN WHICH YIELD VARIES WITH EGG DENSITY

Species	Source
QUANTIFIED DENSITY RESPONSES	
Trichogramma japonicum	Iyatomi 1958
Diadromus pulchellus	Labeyrie & Rojas-Rousse 1985
UNQUANTIFIED REPORTS	
Several spp.	Pierce 1910
Collyria calcitrator	Salt 1932
Trichogramma evanescens	Salt 1936
T. e. minutum	Narayanan & Chacko 1957; Chacko 1969
Nemeritis canescens	Simmonds 1943
Pimplopterus dubius	Jørgensen 1975
Caliroa cerasi	Carl 1976

where H_t and P_t are the densities of hosts and of female parasitoids in generation t; $p(i|H_t,P_t)$ is the proportion of hosts encountered i times, which may depend on the densities of both hosts and parasitoids; and $h(i|H_t,P_t)$ is the number of female progeny produced from each such host. In words, this classes hosts by how many times they are encountered, and then sums the parasitoid progeny from each such host class, weighted by its abundance. The set of p's represents the across-hosts component of parasitoid competition, and the h's the within-host component.

The corresponding recruitment of the host population depends on the proportion of hosts escaping parasitism, $p(0)$, and their per capita reproduction, $f(H_t)$:

$$H_{t+1} = H_t f(H_t) p(0|H_t,P_t). \quad (2)$$

In general, h might depend on the densities of the total populations (as written in eq. 1), as well as on i. The distribution of encounters across hosts (i.e., the $p(i)$'s) will also often depend on both parasitoid and host densities, and host reproduction (f) may be density-dependent as well. In order to isolate the effects of parasitoid competition from any density dependence in the host population, however, I assume that (1) h depends only on the "encounter density" (i) of a given host; (2) the distribution of encounters is independent of host density, and only its mean varies with parasitoid density; and (3) f is density-independent. The effect of relaxing assumption 2 and the relationship between the dynamics of the present models and those of Hassell et al. (1983) and Comins and Wellings (1985), which share assumptions 2 and 3 but in effect assume that h depends on P_t or H_t but not on i, are considered in the Discussion; the effects of density dependence in f and $h(i)$ are analyzed in a later paper.

Because of the interdependence of the within-host and encounter components of competition, the models will include heterogeneous parasitism: the distribution of encounters across hosts, the $p(i)$'s, are assumed to follow a negative-binomial distribution (Bailey et al. 1962; Griffiths and Holling 1969; May 1978). This is not meant to represent any particular form of heterogeneity (e.g., spatial density dependence), but rather the general phenomenon of variability among hosts in the

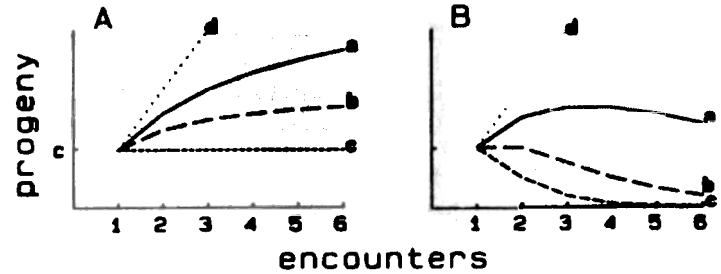


FIG. 2.—Within-host dynamics of the models used in this paper. *A*, Contest model (eq. 4): a, $d = 0.333$; b, $d = 1$; c, $d = \infty$, i.e., constant-yield model (eq. 6); d, $d = 0$, i.e., density-independent (eq. 3). *B*, Scramble model (eq. 5): a, $y = 0.25$ ($d = 0.2877$); b, $y = 0.5$ ($d = 0.6931$); c, $y = 0.75$ ($d = 1.386$); d, $y = 0$, i.e., density-independent (eq. 3).

risk of parasitism (Chesson and Murdoch 1986); some of the limitations of this model are addressed in the following section and the Discussion.

SPECIFIC MODELS

Within-Host Recruitment

Three simple functions, encompassing a wide range of dynamics (fig. 2), are used for the $h(i)$. In the first, parasitoids do not compete, and progeny production per encounter is constant:

$$h_{d=0}(i) = ci; \quad (3)$$

these dynamics should not be confused with those of standard models (eq. 6, below) in which progeny production per host is constant. In equation (3) and in the following models, c represents the progeny produced from hosts encountered once, that is, in the absence of interclutch competition; Hassell (1978, eq. 1.1b) introduced this parameter in the context of a constant yield per host but then assumed that it equals one.

The two remaining h's incorporate monotonically increasing and hump-shaped density-yield models, which I refer to as "contest" and "scramble," respectively:

$$h_c(i) = ci(1 + d)/(1 + di); \quad (4)$$

$$h_s(i) = cie^{-d(i-1)} = ci(1 - y)^{i-1}. \quad (5)$$

The labels "contest" and "scramble," following Hassell (1975), are introduced solely for ease of reference and are not meant to imply mechanisms. In these models, d scales the density dependence, with larger values representing a more rapid decrease in progeny production with increasing i. If $d = 0$ in either of these models, equation (3) results. The term $1 + d$ appears in the numerator of equation (4), and the exponent in equation (5) is $i - 1$ rather than i, in order that $h(1)$ will equal c. The parameter $y = 1 - e^{-d}$ is introduced in equation (5) for notational convenience below.

The crucial distinction between these two models is that in the contest model the yield, $h(i)$, always increases with density, i, but the scramble model is overcompensating: yield initially increases with density but then decreases as density increases further. In particular, if y in the scramble model is greater than ½ (i.e., $d > \ln 2$), the number of progeny from a host encountered more than once will be less than that from a host encountered only once.

The model of Griffiths and Holling (1969), mentioned in the introduction, used

$$h(i) = ci, \quad i \le b,$$
$$h(i) = c(b - a), \quad i > b, \tag{6}$$

with b a maximum supportable density and a "the degree of scramble" (i.e., the decrease in yield caused by excess density). These within-host dynamics, with an abrupt, possibly even stepped, transition from density independence to perfect constancy, are somewhat peculiar. When combined with a negative-binomial distribution of encounters, though, they produce population-recruitment curves qualitatively similar to those of the models in the present paper (cf. their fig. 6 with fig. 3, below); the resulting population dynamics, which have not been analyzed, presumably would also be similar.

Most previous host-parasitoid models, the constant-yield models, imply the function

$$h(i) = c, \quad h(0) = 0, \tag{7}$$

where $i > 0$. Note that this model is the limiting case of the contest model (eq. 4) with d infinite.

Distribution of Encounters

As noted above, I assume that $p(i)$ follows the negative-binomial distribution (Bailey et al. 1962; Griffiths and Holling 1969; May 1978). I also assume that (1) the distribution is independent of host density (i.e., there is no handling time [Holling 1959] or any aggregative or other response to absolute host density); (2) the mean of the distribution is a constant multiple of the number of parasitoids, aP_t (e.g., there is no mutual interference; Hassell and Varley 1969); and (3) the aggregation of the distribution, defined by the parameter k, is constant.

Although they have not been investigated directly, the first two of these assumptions seem unlikely to have substantial qualitative effects, though mutual interference probably would somewhat weaken the effects of within-host competition. The negative-binomial model with k independent of densities has been criticized recently (Chesson and Murdoch 1986; Perry and Taylor 1986; cf. Griffiths and Holling 1969). For present purposes, however, a constant k is advantageous: it allows the effect of parasitoid density dependence to be analyzed in the absence of any host density dependence.

The Parasitoid Models

The density-independent model is extremely simple: every encounter yields c progeny, regardless of how many times a particular host is encountered. Recruitment therefore depends only on the number of encounters, not on their distribution. The model is

$$P_{t+1} = caP_tH_t. \tag{8}$$

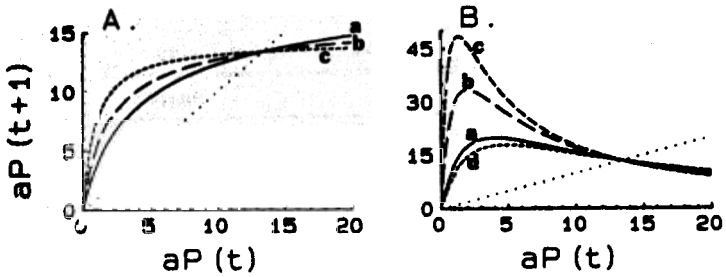


FIG. 3.—Parasitoid recruitment curves, with host densities (caH_t) for each curve fixed at equilibrium values, and $\ln f = 3$, $k = 1.20$. Dotted lines indicate exact replacement. *A*, Contest model (eq. 9): a, $d = 0.333$ ($caH^* = 4.90$); b, $d = 1$ ($caH^* = 8.14$); c, constant-yield model (eq. 11; $caH^* = 14.1$). *B*, Scramble model (eq. 10): a, $y = 0.25$ ($caH^* = 18.8$); b, $y = 0.5$ ($caH^* = 63.3$); c, $y = 0.75$ ($caH^* = 138$); d, $y = 0.2085$ (equivalent competition to constant-yield model; $caH^* = 14.1$).

Combining the two density-dependent $h(i)$'s of equations (4) and (5) with the negative-binomial distribution of encounters (following Ives and May 1985) yields the following parasitoid recursion equations for the contest and scramble models, respectively:

$$P_{t+1} = caP_tH_t\frac{1 + d}{d}\int_0^1 u^{1/d}[1 + (1 - u)aP_t/k]^{-(k+1)}du; \tag{9}$$

$$P_{t+1} = caP_tH_t(1 + yaP_t/k)^{-(k+1)}. \tag{10}$$

The comparable constant-yield model is that of May (1978):

$$P_{t+1} = cH_t[1 - (1 + aP_t/k)^{-k}]. \tag{11}$$

Typical recruitment curves for these models are shown in figure 3. The differences in the forms of these curves directly reflect the differences in the within-host competition (fig. 2); the scramble model usually has overcompensating competition (humped recruitment curves) in the population as a whole, as well as within hosts, and both the contest model and its limiting case, the constant-yield model, are never overcompensating.

The Host Model

The dynamics of the host population from one generation to the next do not depend on how the parasitized individuals are used by the parasitoids. Assuming that no density dependence acts directly on the host's rate of increase, the usual model is

$$H_{t+1} = fH_t(1 + aP_t/k)^{-k}, \tag{12}$$

where f is the constant finite rate of increase for the host.

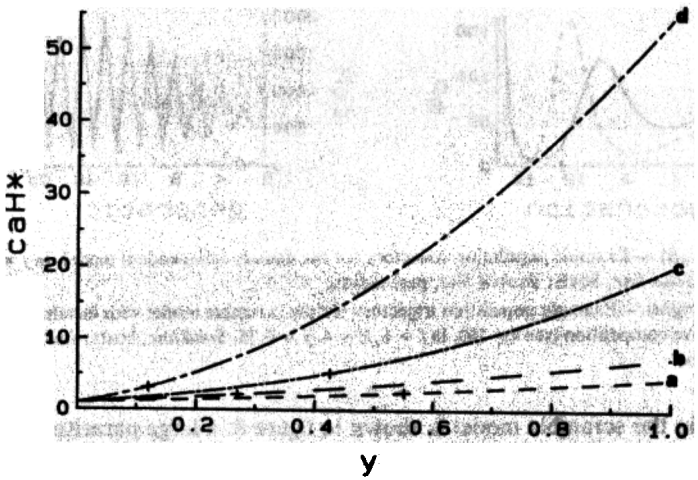


FIG. 4.—Host equilibria in the scramble model (eq. 16), as a function of the intensity of within-host competition. Minimum stable y is indicated by +. a, $\ln f = 1$, $k = 2$; b, $\ln f = 1$, $k = 1$; c, $\ln f = 2$, $k = 2$; d, $\ln f = 2$, $k = 1$.

ANALYSIS

Equilibria

The parasitoid equilibrium, P^*, is entirely independent of the $h(i)$'s:

$$P^* = k(f^{1/k} - 1)/a. \tag{13}$$

The host equilibrium, H^*, however, increases with increasingly intense within-host parasitoid competition:

density-independent,

$$H^* = 1/ca; \tag{14}$$

contest,

$$H^* = d\Big/\left\{ca(1+d)\int_0^1 u^{1/d}[1+(1-u)(f^{1/k}-1)]^{-(k+1)}du\right\}; \tag{15}$$

scramble,

$$H^* = [1 + y(f^{1/k} - 1)]^{k+1}/ca; \tag{16}$$

constant-yield,

$$H^* = kf(f^{1/k} - 1)/ca(f - 1). \tag{17}$$

This increase in the host equilibrium with increasing parasitoid competition is shown, for the scramble model, in figure 4. The parasitoid equilibrium, P^*, and thus net parasitoid competition and ultimately H^* all increase with f and aggregation (i.e., decreased k); aggregation also increases parasitoid competition and H^* by increasing the overlap, the across-hosts component of competition, among any given number of parasitoids. Host equilibrium, H^*, also increases with a decrease in either a (and thus the number of encounters per parasitoid) or c (the parasitoid "intrinsic" rate of increase per encounter).

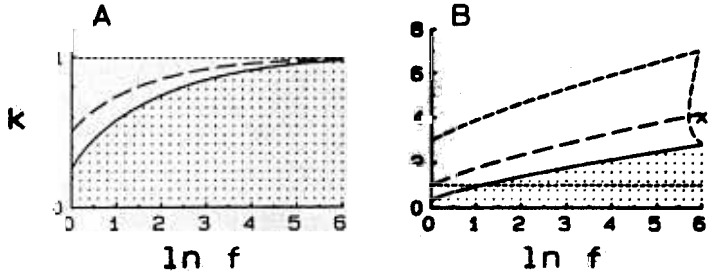


FIG. 5.—Local stability boundaries for the contest and scramble models (with eq. 12), with values of d as in figures 2 and 3; the regions below the curves are stable. *A*, Contest model (eq. 9); *B*, scramble model (eq. 10). Point X is illustrated in figure 8.

Local Stability

The effect of $h(i)$ on the local stability of these equilibria is straightforward: it acts solely through the density dependence within the parasitoid population at the equilibrium (i.e., $\delta = \partial P_{t+1}/\partial P_t$, evaluated at equilibrium; see the Appendix).

When within-host competition does not occur, such that equations (3) and (8) apply, there is no density dependence in the parasitoid dynamics (δ is 1); given the additional assumption of no direct density dependence in the host population, stability is impossible (Appendix).

The within-host competition in the other models, however, allows stability for some parameter values (fig. 5), and all else being equal, more-intense within-host competition (greater d and thus lower mean $h(i)$) generally enhances stability by increasing net parasitoid density dependence (reducing δ; fig. 3). Specifically, stability generally is possible with larger k as d increases (fig. 5).

The contest model always has less competition than does the constant-yield model. Accordingly, the maximum k allowing stability in the contest model is always less than one (the value for the constant-yield model), asymptotically approaching one as f or d becomes infinite (fig. 5*A*). In contrast, density dependence is generally greater in the scramble model than in the other models: δ generally is negative. As a result, at all but small f and d, stability is possible with k larger than one (fig. 5*B*). When reproduction per host is a strictly decreasing function of the number of encounters (i.e., when $y > \frac{1}{2}$), competition is always more intense than in the constant-yield model, and the stability boundary (fig. 5*B*) is always at k larger than one. Stability is possible, in fact, for any finite k in the scramble model, given sufficiently intense competition; with random encounters ($k = \infty$), it is not quite possible (Appendix).

A novel feature of the scramble model is that stability can actually be lost as the

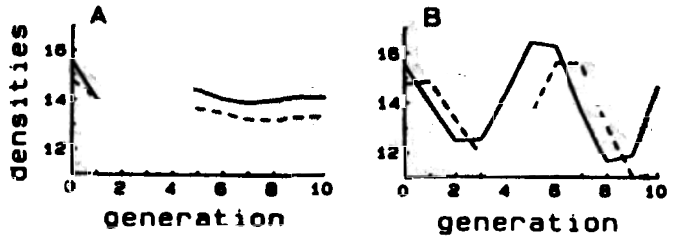


FIG. 6.—Example population trajectories for the scramble and constant-yield models, with y for the scramble model chosen such that the mean recruitment per host, and thus caH^*, is the same in the two models. $\ln f = 3$, $k = 1.2$. *Solid lines*, hosts; *dashed lines*, parasitoids. *A*, Scramble model, $y = 0.208524$; *B*, constant-yield model.

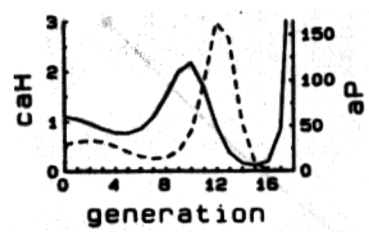
result of increases in any of the factors that generally favor stability, that is, f, d, or aggregation (low k). Although this occurs only with very large f (extreme right of fig. 5*B*) in the present model, it occurs at lower f if host density dependence is also overcompensating (Taylor, MS); it cannot occur in the contest or constant-yield models.

As figure 5 shows, stability is also generally favored by increasing f or decreasing k (except in the constant-yield model; May 1978). This effect of f is indirect, by increasing P^* and thereby increasing across-hosts competition. Aggregation (smaller k) also acts on across-hosts competition, both indirectly by increasing P^* and directly by increasing the overlap among the parasitoids.

The possibility of parasitoid recruitment curves with different shapes has an important consequence: two models of different form may have the same average recruitment per parasitized host (average h) at equilibrium but very different sensitivity to variation in density (δ). They could thus have the same equilibria but differ in stability. Specifically, y in the scramble model can be chosen (for given f and k) such that equilibria are the same as in the constant-yield model, but the marginal density dependence (δ; fig. 3) and stability (fig. 5) of the scramble model will always be greater.

The population trajectories in figures 6–8 illustrate these effects of parasitoid density dependence (δ) on stability. Figure 6 compares stable dynamics resulting from strong parasitoid competition with unstable dynamics resulting from weaker density dependence. Strong competition causes the parasitoids, when abundant, to decrease rapidly, at the same time that the hosts are decreasing because of intense parasitism; similarly, relaxation of this strong competition at low density allows the parasitoid population to increase and keep up with the now-increasing host population. In contrast, weak (fig. 6, unstable trajectory) or absent (fig. 7) parasitoid competition allows large parasitoid populations to continue increasing even while the hosts are decreasing and, conversely, to continue crashing even after the hosts have started to recover. In essence, damping the fluctuations of the parasitoid population decreases the lag between its cycling and that of the hosts; with less parasitoid competition, the parasitoids do not track the hosts as closely, and diverging oscillations result.

The instability resulting from overly strong parasitoid density dependence (very



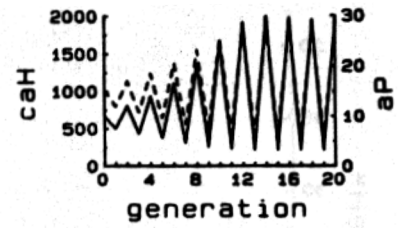


FIG. 7 (*left*).—Example population trajectory for the density-independent model. $\ln f = 2$, $k = 0.5$. *Solid line*, hosts; *dashed line*, parasitoids.

FIG. 8 (*right*).—Example population trajectory for the scramble model with instability due to excessive competition (see fig. 5*B*). $\ln f = 6$, $k = 4$, $y = 0.75$. *Solid line*, hosts; *dashed line*, parasitoids.

negative δ) in the scramble model is shown in figure 8: a large parasitoid population crashes because of intense competition, which then allows both parasitoids (now released from competition) and hosts (with their huge reproductive rate and now little parasitism) to rebound to even greater levels, and so on. The cycles of the two populations (of period two) are now exactly in phase, and they are similar to the cycles caused by overcompensating competition in single-species models.

DISCUSSION

These results show that this previously ignored aspect of parasitoid biology—the opportunity for competition arising from the possibility of a host's being discovered and exploited more than once—can indeed substantially affect host-parasitoid dynamics. On the one hand, quantitative conclusions from such simple models should not be taken literally. On the other hand, the qualitative effects of within-host competition on the rate and density dependence of parasitoid reproduction, and thus on abundances and stability, seem likely to be robust; whether they are important in nature is an empirical question depending on which "within-host" dynamics actually occur and on whether other factors swamp their effects.

The effectiveness of a parasitoid in suppressing its hosts is often thought to depend primarily on its search rate, the mortality it inflicts on its hosts in a generation. The above models, however, emphasize that parasitoid reproduction is equally important. The parasitoid equilibrium—the density of parasitoids that will kill enough hosts to balance their reproductive rate—depends directly on searching effectiveness. The host equilibrium, however, is the density required to maintain the parasitoid population, and this obviously depends not only on how many hosts are attacked but also on how much parasitoid reproduction results (Hassell and Moran 1976) and thus on both the density-independent (c) and density-dependent aspects of per-host recruitment. Similarly, the product ca (in essence, the per-host intrinsic rate of increase of the parasitoid) sets the natural scaling for refuges and carrying capacities (Taylor, MS), and the ratio of these reproductive rates—not the ratio of the a's alone (May and Hassell 1981)—determines whether parasitoid species can coexist (Taylor, MS). (Note that these

points apply also to continuous-time predator-prey models, in which c is the rate of conversion of captured prey into predators.)

Within-host competition of course not only affects the net reproductive rate but also contributes to overall parasitoid density dependence. It is not surprising, then, that it helps determine stability, and indeed it may be the only source of stability, as shown by the density-independent model above. A less obvious point is that the instability in coupled consumer-resource models such as these has a different cause, and thus is affected differently by competition, than the instability in single-species competition models. In the latter models, any density dependence at all is sufficient for stability, with instability resulting only from excess overcompensation and thus only in scramble models. When the future abundance of the resource is affected by consumption (as in the models above), however, the density dependence must compensate for the destabilizing effect of the time lag in the interaction (Appendix). As a result, stability in such coupled models requires greater competition than in single-species models, and greater overcompensation can be tolerated before stability is lost (Taylor, MS). This explains both the stabilizing effect of d and the greater stability of the scramble model, when compared with the contest model in the host-parasitoid models above.

Most other sources of stability, and in particular those affecting the across-hosts component of parasitoid competition, reduce parasitoid reproduction and thus create a trade-off between stability and host suppression. In contrast, a difference in the form of parasitoid competition can affect stability without affecting equilibria, or indeed could simultaneously lower the host equilibrium and increase stability. This important new possibility implies, among other things, that superparasitism (without which variation in per-host yield cannot occur) can be beneficial to control of the host, contrary to the opinion of some biological-control workers (e.g., Ullyett 1943; McLeod 1972; Vinson 1977; Propp and Morgan 1984); even if, as implicitly assumed by these authors, parasitism is limited by the parasitoids' egg supply, the cost of superparasitism is primarily in parasitoid reproduction (Thompson 1929).

Other Forms of Parasitoid Density Dependence

Heterogeneous parasitism.—A major point throughout this paper has been that both heterogeneous parasitism (across-hosts competition) and within-host competition contribute to parasitoid density dependence, such that an increase in one can compensate for a decrease in the other. Indeed, the effect of each depends on the other: the effect of within-host competition depends on how much it is brought into play by multiple encounters, and the consequences of how often hosts are re-encountered depend on the within-host competition. As a result, the amount of heterogeneity necessary for stability can be quite different from what previous models had indicated, depending on the strength of within-host competition (for similar results concerning true parasites, see Anderson and May 1978).

The relationship between heterogeneity and within-host dynamics may often be more complex than in the preceding models. For many forms of heterogeneous

parasitism, the assumption that the distribution of encounters does not depend on host density may not be valid (Hassell 1980; Chesson and Murdoch 1986; Perry and Taylor 1986). If it is eliminated, an increase in within-host competition, by increasing H^*, will change the $p(i)$'s as well. If this change is toward less aggregation of encounters, as seems reasonable, the proportion of hosts escaping parasitism (for a given parasitoid density) decreases, and with it the equilibrium parasitoid density. These decreases in both aggregation and abundance decrease the across-hosts component of competition and oppose the effect of the increase in the within-host component. A decrease in aggregation with increasing d may also reduce density dependence in the host population. As an extreme example of these effects of inversely density-dependent aggregation, stability can actually decrease with increasing d in a model with a constant-number host refuge (Taylor, MS). This occurs partly because in this model, as the host equilibrium increases (as it does with increasing d), the host density dependence decreases (because the refuge has proportionately less effect). In nature this effect would probably be offset by an increase in host competition; thus, larger d might never actually be destabilizing. This example does suggest, though, that the stabilizing effect of within-host competition may often be somewhat weaker, as well as more complex, than in the models presented in this paper.

Per-host recruitment dependent on overall densities.—As well as, or instead of, varying with the number of times a given host is encountered, parasitoid reproduction per attacked host could vary with overall parasitoid or host densities, as in the models of Hassell et al. (1983) and Comins and Wellings (1985); in the notation of this paper, c could vary with P_t (and perhaps H_t). The two forms of density dependence have similar effects for the most part. An important difference, though, is that encounter-dependent within-host competition combines with across-hosts competition in an interactive way, as discussed above, whereas per-host reproduction that depends on total population density is independent of encounter densities and thus of the across-hosts competition. As a result, its stabilizing effect can be strong even with little overlap of encounters, and indeed, stability is possible even with random encounters (Hassell et al. 1983).

Hassell et al. (1983) and Comins and Wellings (1985) intended to model density-dependent sex ratios, arising from either differential competitive mortality or maternal manipulation of primary sex ratios. Both mechanisms, though, depend on variation in the number of clutches laid in or on an individual host (or at most a local patch of hosts; for the sex-ratio predictions, see, e.g., Charnov 1982) so that they would be better modeled as encounter-density-dependent. Clutch size might vary with overall densities, but it would increase, not decrease, with increasing density (Charnov and Skinner 1984, 1985; Parker and Courtney 1984), creating destabilizing positive feedback rather than regulation. It appears that the stabilizing per-host recruitment that varies only with overall densities, as modeled by Hassell et al. (1983) and Comins and Wellings (1985), would arise primarily from sources extrinsic to the host-parasitoid interaction per se, such as predation (e.g., Hassell 1969), whereas intrinsic factors would primarily produce encounter-dependent variation.

Implications for Empirical Research

To determine the role of within-host competition in the dynamics of a real system, the seemingly straightforward approach would be to describe the $h(i)$'s of this paper: to determine that the standard constant-yield assumption is valid or to describe parasitoid reproduction explicitly. It is also clear, however, that describing the within-host component of competition not only may be difficult (see above), but also will be insufficient: the distribution of encounters over hosts, and its dependence on densities, must also be described. This too will be generally difficult.

One way around these difficulties would be to predict within-host dynamics from a parasitoid's general biology. For example, the mechanisms of larval competition differ, in general, between solitary and gregarious species (Salt 1961); gregarious species may also superparasitize more readily. Weak within-host competition, leading to low unstable host abundances, may thus be typical of gregarious parasitoids, whereas a constant or decreasing yield, giving higher but more-stable equilibria, may typify solitary species. It would be unwise, however, to apply such a generalization in a specific case without verification: the literal distinction between gregarious and solitary species is not in $h(i)$ but in c, which affects equilibria but not stability.

A more concrete approach would be to describe parasitoid recruitment curves analogous to those in figure 3. To do this directly would require, however, that the host density be kept constant while the parasitoid density is varied, which might be difficult. If one simply plots parasitoid recruitment over successive generations of a host-parasitoid interaction, the correlation between host and parasitoid densities totally distorts the relationship (fig. 9*A*).

Alternatively, the correlation between host and parasitoid densities might actually be taken advantage of: one of the features of the simulations in figures 6–8 is that tighter density-dependent regulation of the parasitoids reduces the lag between the populations' cycles. Time-series analysis, or even simple correlation, might detect this effect. It also shows up as a stronger correlation between parasitism and host density (fig. 9*B*), though this might be difficult to distinguish in noisy real data (it is unclear whether the slope of this relationship, which is what is usually looked at, provides information about parasitoid density dependence).

Probably the most useful method for studying within-host dynamics is to examine the mean yield per parasitized host, as a function of either parasitoid density (fig. 9*C*) or the density of attacked hosts (fig. 9*D*; Hassell and Huffaker 1969). Overcompensating, and thus (generally) stabilizing, competition will produce a negative correlation between mean yield and density (figs. 9*C*,*D*). Weaker, and therefore less stabilizing, competition, such as in the contest models above, conversely produces a positive slope. This approach might not reveal the specific cause of the density dependence (though censuses at several stages might allow this; e.g., Hassell 1969) and would not distinguish yield dependent on encounter densities (as in the models of this paper) from yield dependent on overall densities (as in Hassell et al. 1983; Comins and Wellings 1985). Even in noisy data, however, this approach should reveal any substantial density dependence in yield. This relationship, combined with the relationship between densities and the number of hosts attacked, could then be used to construct a recruitment curve. Comparisons of such descriptions of parasitoid density dependence should then be useful in predicting the differences in dynamics between otherwise similar systems, for example, a parasitoid attacking one or the other of two similar hosts, or a single host-parasitoid pair in different environments.

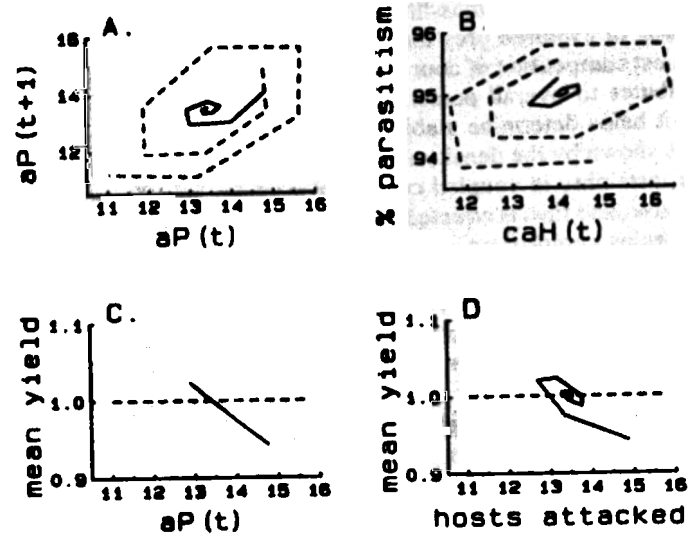


FIG. 9.—Possible indicators of stabilizing parasitoid density dependence. Data are from figure 6. *Solid lines*, the stable scramble model; *dashed lines*, the unstable constant-yield model. *A*, Total parasitoid recruitment; *B*, parasitism rate as a function of host density; *C*, mean recruitment per attacked host ("yield") as a function of parasitoid density; *D*, mean recruitment per attacked host ("yield") as a function of the density of attacked hosts.

SUMMARY

The standard host-parasitoid models assume that each parasitized host yields the same number of parasitoid progeny; but in many parasitoid species, the number of progeny per host depends on the number of times that host was encountered. I present a family of new host-parasitoid models incorporating this encounter-density-dependent variability in parasitoid reproduction per host.

Such within-host competition (which could be between ovipositing females, between larvae, or both) interacts with the distribution of encounters (i.e., aggregation) to determine the net parasitoid density dependence. Greater density dependence increases host equilibrium abundances while generally increasing the stability of the interaction. Overcompensating scramble-like parasitoid competition can be more stabilizing than contest-like competition, especially when the host has a moderate to high intrinsic rate of increase and encounters are moderately aggregated; overcompensation is destabilizing only at very high host reproductive rates.

These results suggest that we must study parasitoid density dependence directly, both within a host and between generations within a population, in order to understand the dynamics of any actual host-parasitoid system. The most practical method appears to be to (1) describe the mean yield (parasitoid recruitment) per parasitized host as a function of the density of either parasitoids or parasitized hosts; and (2) relate the number (not the percentage) of parasitized hosts to parasitoid (and perhaps host) densities.

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APPENDIX

Stability Analyses

General Effects of Parasitoid Competition

Models like those in the text, which assume that the proportion of hosts parasitized, the reproductive rate of surviving hosts, and parasitoid reproduction per host are all independent of host density, can be represented generally by the equations

$$\begin{aligned} H_{t+1} &= fH_t g_H(P_t), \\ P_{t+1} &= H_t g_P(P_t), \end{aligned} \tag{A1}$$

where f is a constant (the host per capita reproductive rate), and g_H and g_P are functions of P_t defining, respectively, the proportion of hosts escaping parasitism and the production of parasitoid progeny per host.

The equilibria for this general model are

$$\begin{aligned} H^* &= P^*/g_P(P^*), \\ P^* &= g_H^{-1}(1/f), \end{aligned} \tag{A2}$$

where g_H^{-1} is the inverse function of g_H. The host equilibrium, H^*, depends on parasitoid reproduction and competition, but P^* does not. For the negative-binomial models in the text, g_H is defined by equation (11) and

$$P^* = k(f^{1/k} - 1)/a. \tag{A3}$$

Local stability in discrete-time two-species models, including the host-parasitoid models developed in this paper, requires (May 1974) that

$$2 > 1 + \alpha\delta - \beta\gamma > |\alpha + \delta|, \tag{A4}$$

where

$$\alpha = \frac{\partial H_{t+1}}{\partial H_t}, \quad \beta = \frac{\partial H_{t+1}}{\partial P_t}, \quad \gamma = \frac{\partial P_{t+1}}{\partial H_t}, \quad \text{and} \quad \delta = \frac{\partial P_{t+1}}{\partial P_t},$$

all derivatives evaluated at $H_t = H^*$ and $P_t = P^*$.

In models with the general form of equations (A1), the only affect of parasitoid reproduction (g_P) on stability is the direct one through δ. The host density dependence, α, will always be exactly 1:

$$\alpha = fg_H(P^*) = f(1/f) = 1. \tag{A5}$$

The cross-dependences β and γ each do depend on g_P (or on H^*, which depends on g_P), but these appear in the stability conditions (A4) only as the product $\beta\gamma$, in which the dependences on g_P cancel each other:

$$\beta\gamma = fH^* g_H'(P^*) g_P(P^*) = f[P^*/g_P(P^*)] g_H'(P^*) g_P(P^*) = fP^* g_H'(P^*), \tag{A6}$$

where g_H' is the derivative of g_H with respect to P_t (which is independent of g_P).

The effect of the dependence of parasitoid reproduction on parasitoid density, then, is simply δ:

$$\delta = H^* g_P'(P^*), \tag{A7}$$

where g_P' is the derivative of g_P with respect to P_t.

No Direct Density Dependence

When there is no direct host density dependence (i.e., $\alpha = 1$), the first inequality of condition (A4) becomes

$$\delta < 1 + \beta\gamma. \tag{A8}$$

In a host-parasitoid interaction, or any other victim-consumer interaction, β is almost always negative, and γ positive; stability thus requires that δ be less than 1, that there be some density dependence in the parasitoid's dynamics to counteract the destabilizing effect of $\beta\gamma$.

In the model of density-independent parasitoid recruitment (eq. 8), however, δ is exactly 1: g_P is simply the constant ca, and H^* is the reciprocal of this quantity (eq. 14); therefore,

$$\delta = caH^* = ca/ca = 1. \tag{A9}$$

Thus, when the reproduction of both the hosts and the parasitoids lack direct dependence on their own densities, stability is not possible.

The Scramble Model

With the scramble parasitoid model (eq. 10),

$$\delta = 1 - (k + 1)y(f^{1/k} - 1)/[1 + y(f^{1/k} - 1)]. \tag{A10}$$

Given this relationship, (A10), the conditions (A4), expressed in terms of the strength of the parasitoid density dependence ($y = 1 - e^{-a}$), are

$$y > k/(k + f^{1/k}) \tag{A11}$$

and one of the following:

$$k \le 1, \tag{A12a}$$

$$y < 2/(k - 1)(f^{1/k} - 1), \tag{A12b}$$

$$y < \frac{k(f^{1/k} - 1) + 4f^{1/k}}{[(k - 2)f^{1/k} + k](f^{1/k} - 1)}. \tag{A12c}$$

Condition (A11), arising from the first inequality of (A4), is a requirement for sufficient density dependence to counteract $\beta\gamma$. The second set of conditions (A12), from the second inequality in (A4), prohibits excessive overcompensation: it is violated when y is too large (and thus δ too negative), and it limits stability with f and y large and k moderate (i.e., the upper right corner of fig. 5*B*).

For $k \le 1$ and any f, stability is always possible: (A12a) is always met, and some valid y's (i.e., between 0 and 1) can be found to satisfy (A11). For finite $k \ge 1$, there exist some valid

y's that simultaneously satisfy conditions (A11) and (A12b), thus giving stability, so long as

$$f < [k(k + 3)/[k(k + 1) - 2]]^k. \quad \text{(A13)}$$

If, however, k is infinite (i.e., the distribution of encounters is random (Poisson)), the right-hand side of (A11) becomes 1, and the maximum value of y is 1; condition (A11) cannot then be satisfied, and stability is impossible.

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