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APPARENT COMPETITION AND ENEMY-FREE SPACE IN INSECT
HOST-PARASITOID COMMUNITIES

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Abstract.—Apparent competition is indirect competition between two or more victim species that share a natural enemy, caused by that enemy's numerical response. We review empirical examples of apparent competition in phytophagous insect hosts attacked by polyphagous parasitoids and develop models of apparent competition in host-parasitoid systems. Apparent competition is particularly likely in insect assemblages because parasitoids can limit their hosts to levels at which resource competition is unimportant. A consideration of both equilibrium and nonequilibrium models in which polyphagous parasitoids impose significant mortality on their hosts suggests that the most common outcome is the exclusion of all but one host species, which generates *dynamic monophagy* (i.e., a single host species persisting with a potentially polyphagous parasitoid). A crisp criterion for dominance in apparent competition is that the winning host supports the highest parasitoid density. We conclude that it is difficult for alternative hosts to coexist when the sole regulatory factor is a shared parasitoid. Yet in nature, coexisting hosts frequently do share parasitoids. We examine several mechanisms promoting host coexistence, including donor-controlled parasitoid dynamics, additional sources of host density dependence (e.g., resource limitation), spatial and temporal refuges, trophic web structure, and labile parasitoid behavior. Elucidating the mechanisms permitting the coexistence of host species confronted by effective polyphagous parasitoids deserves more attention from experimental field ecologists.

A recurring theme in insect community ecology is that many phytophagous insect species seem, on the average, to be considerably less abundant than ought be permitted by the availability of their food resources (Lawton and Strong 1981; Strong et al. 1984). One broad (but certainly not the only) explanation for this pattern is that natural enemies—predators, parasitoids, and pathogens—of phytophagous insects limit the population sizes of their prey. Parasitoids (primarily Hymenoptera, but also Diptera) comprise a particularly important and well-studied class of natural enemies on insect herbivores. Detailed studies of local assemblages reveal that the great majority of phytophagous species are attacked by one or more species of parasitoid (Hawkins and Lawton 1987; Hawkins 1988, 1990). The biological control literature is replete with examples in which the introduction of one or more parasitoid species has greatly depressed the population size of a host population to several orders of magnitude below prior, parasitoid-free levels (Beddington et al. 1978). Though direct evidence from natural communities is scarcer, it seems likely that parasitoid assemblages, acting in

conjunction with other predators and vagaries in the abiotic environment, are indeed able to keep many host insect populations rare, relative to the population sizes permitted by resources.

Over the last several decades, a considerable body of empirical and theoretical work has built up on the factors allowing parasitoids to limit and regulate populations of single host species (Hassell 1978; Hassell and Anderson 1989; Hassell and Pacala 1990). This work provides an excellent base for examining the impact of parasitoids at the community level. The theme we wish to develop in this article is that oligophagous and polyphagous parasitoids should play a potent role in structuring insect communities, particularly in constraining the number of host species that can co-occur in a local community. Previous work on multihost systems by Hassell and others (see, e.g., Comins and Hassell 1976, 1987) has largely emphasized how parasitoids can in some circumstances facilitate the coexistence of strongly competing host species. We, by contrast, will concentrate on the ways in which parasitoids might limit the species richness and govern the niche partitioning of local host communities (Lawton 1986). A full assessment of the role of parasitoids in determining host community structure will ultimately require considering their effects on both directly competing host species and species kept at densities too low for direct or resource competition to be significant.

Following a brief discussion of the incidence and biological interpretation of oligophagy and polyphagy among parasitoids, we present two field examples that strongly suggest that polyphagous parasitoids can lead to *apparent competition* between alternative hosts—defined as an indirect interaction in which some host species tend to be reduced in abundance and even excluded from the community by other host species because of a shared natural enemy (Holt 1984; Lawton 1986). We then develop both equilibrium and nonequilibrium models of host-parasitoid systems in which an effective parasitoid simultaneously attacks two or more host species, and we demonstrate that this leads to a problem in host species coexistence. This leads to a general question: What are the mechanisms permitting the coexistence of multiple host species, linked by one or more species of shared parasitoid? We conclude by examining some possible answers to this question, the ways in which the action of apparent competition is modified in complex food webs, and evidence for the impact of apparent competition in real host-parasitoid assemblages.

TWO KINDS OF MONOPHAGY

Though appropriate quantitative data are relatively scarce, oligophagy and polyphagy appear to be common in many natural parasitoid communities (for a particularly clear example, see Hawkins and Goeden 1984; see also Lawton 1986). For instance, a recent intensive study of 84 species of parasitoids attacking leaf-miner communities in Costa Rica revealed that 35 parasitoid species (about 42%) attacked two or more host species (J. Memmott, personal communication). It is, however, important to emphasize one inherent difficulty in using even the best

descriptive field data on host use in local communities to assess the relevance of our ideas.

A given parasitoid could be found to be host-specific in a particular local community for two quite different reasons. A parasitoid is a *biological monophage* if, out of an array of available potential prey, only a single host species is taken. In this case, monophagy clearly reflects some combination of (probably genetically fixed) behavioral selectivity by the parasitoid and escape strategies used by the other potential prey species.

By contrast, a parasitoid is a *dynamic monophage* if alternative prey are made unavailable by the parasitoid's own actions. If there are alternative, acceptable host species available at some spatial scale larger than that set by the lifetime foraging range and microhabitats used by individual parasitoids, these hosts may not be typically found in that parasitoid's host range (defined as those hosts from which this parasitoid is observed to emerge) because they are excluded by parasitism whenever they attempt to invade the local community. Observed patterns in monophagy and the degree of polyphagy thus reflect the dynamic outcome of interactions between parasitoids and hosts, including the exclusion of host species from local communities—and the diminution of the observed host range of resident parasitoids in those communities—as well as behavioral selectivity by parasitoids. Manipulative experiments are required to distinguish unequivocally biological from dynamic monophagy. If dynamic monophagy is at all common in nature, descriptive surveys of parasitoid host range may greatly underestimate the potential importance of generalist parasitoids in structuring insect assemblages.

APPARENT COMPETITION IS PARTICULARLY LIKELY IN HOST-PARASITOID SYSTEMS

A parasitoid that is a dynamic monophage by definition reduces local host species richness by excluding one or more species of hosts. To do so, this parasitoid must itself persist as a viable population in the absence of the excluded host species, as must the resident host species on which the parasitoid depends. Thus, the exclusion of host species by parasitoids from local communities seems logically to rest on the existence of an indirect interaction between alternative hosts, mediated through a shared parasitoid, that is, apparent competition (Holt 1977). Moreover, the resident host species must have one or more adaptive features that permit it to persist while supporting this parasitoid population, which in turn implies that it successfully occupies its own corner of enemy-free space (Jeffries and Lawton 1984; Lawton 1986). Elsewhere we have presented general conceptual and mathematical models (Holt 1977, 1984; Jeffries and Lawton 1984; Lawton 1986) dealing with apparent competition and enemy-free space. Here, we examine in greater detail these phenomena in host-parasitoid systems, where we expect these effects to be particularly pronounced.

In general predator-prey systems it is often reasonable to expect the following ordering of time scales: prey resources < prey populations < predator populations. The main circumstance leading to apparent competition (though not the

only one; see Connell 1990; Holt and Kotler 1987) is for a predator population to exhibit a numerical response to its prey (Holt 1977). Because of the nested time scales, short-term studies are more likely to detect interactions between prey (within or between species) mediated through their underlying resource base or through the predator's functional response than interactions via a numerical response by an entire predator population. Moreover, physical disturbances are more likely to interrupt indirect interactions acting over longer time scales. This tends to obscure the action of apparent competition, particularly in considering population dynamics over time scales exceeding a few generations.

These potential constraints on the action of apparent competition are greatly diminished in host-parasitoid systems. Parasitoids usually have a generation length comparable to that of their hosts, so that a numerical response by the parasitoid population occurs on roughly the same time scale as host recruitment. Moreover, there is abundant evidence, cited earlier, that parasitoids often do sharply reduce host densities well below the carrying capacity set by resources. This contrasts with more poorly documented evidence for pronounced predator limitation in other systems, such as many vertebrate predator-prey interactions. We thus might expect that apparent competition driven by the numerical response of parasitoids to their hosts could be particularly important in structuring assemblages of phytophagous insects.

ILLUSTRATIVE EXAMPLES

Empirical evidence is growing to show that polyphagous parasitoids can generate apparent competition that may limit the number of host species coexisting in local communities. We present two recent examples.

Larvae of the midge *Masakimyia pustulae* form galls on *Euonymus japonicus* in Japan. Sixteen populations studied by Sunose (1985) were attacked by a single species of parasitoid, an undescribed, apparently host-specific platygastriid. All 16 populations either were stable at low levels or showed outbreaks over a period of 10–14 yr; none became extinct. Three additional populations of the midge supported the platygastriid, plus a eulophid, *Chrysonotomyia* sp., which Sunose (1985) describes as likely to be polyphagous. He attributes the absence of *Chrysonotomyia* at most sites to an absence of alternative hosts. At two of the three sites where *Chrysonotomyia* was present, *Masakimyia* was exterminated by 100% parasitism from the eulophid and remained absent from both sites for several years, eventually reestablishing at one of them from a small number of immigrants. Unfortunately, the host(s) that must be present to sustain *Chrysonotomyia* at these sites, and that therefore enter into apparent competition with the gall midge, are unknown.

Details are better documented in our second example and suggest that shared parasitism may generate apparent competition not only locally but over large geographical regions. In the San Joaquin Valley, California, the endemic grape leafhopper *Erythroneura elegantula* is attacked by a polyphagous egg parasitoid, the mymarid *Anagrus epos*. In 1980, a second species of *Erythroneura*, *Erythroneura variabilis*, invaded the valley; the invasion was followed by a marked

reduction in the abundance of *E. elegantula*, although it has not yet declined to extinction (Settle and Wilson 1990). The decline in *E. elegantula* is not due to resource-based competition with *variabilis*, however; *elegantula* is more vulnerable to parasitism by *Anagrus* than is *variabilis*, and as the parasitoid builds up on the invading host, *elegantula* populations suffer much heavier levels of attack than they experienced in the absence of the invader (Settle and Wilson 1990). It remains to be seen whether *variabilis* will eventually cause the local extinction of *elegantula* via their shared, polyphagous parasitoid.

BASIC THEORY

Consistent with these empirical examples, simple host-parasitoid models suggest that dynamic monophagy is to be expected whenever a parasitoid attacks several host species and can depress each to abundances well below that set by limiting resources. Consider the following general model for the dynamics of two host species coupled with a parasitoid, where all three species have synchronized, discrete generations (Comins and Hassell 1987):

$$\text{host } i: N_{i,t+1} = N_{i,t} R_i g_i(N_1, N_2) f_i(P_t), \quad i = 1, 2; \quad (1a)$$

$$\text{parasitoid: } P_{t+1} = N_{1,t}[1 - f_1(P_t)] + N_{2,t}[1 - f_2(P_t)], \quad (1b)$$

where $N_{i,t}$ is the abundance of host i at the start of generation t ; R_i is its finite rate of increase in the absence of competition and parasitism; $f_i(P_t)$ is the fraction of hosts escaping parasitism ($f_i[0] = 1$ and f_i decreases with increasing P); and $g_i(N_1, N_2)$ measures the fractional degree to which the per capita growth rate of host i is depressed by intraspecific and interspecific density dependence ($g_i[0, 0] = 1$, and g_i decreases with increasing N_1 and N_2). The function $g_i(N_1, N_2)$ phenomenologically describes the effects of both direct interference and exploitative competition for limiting resources. For now, assume that the parasitoid is effective at reducing host densities to levels sufficiently low to preclude intra- or interspecific interactions among hosts such as competition for food or space. In other words, $g_i(N_1, N_2) \approx 1$, and the dynamics of host i are described by the simpler equation $N_{i,t+1} = N_{i,t} R_i f_i(P_t)$. Moreover, assume that the parasitoid can persist at a stable equilibrium with either host species alone. (We will relax both these assumptions below.)

The conditions for a locally stable equilibrium of a single host with the parasitoid are as follows: $R_i > 1$ (i.e., host i persists on its own); $1 > -R_i N_i^* f_i'(P^*)$ (i.e., the total productivity of host i at the equilibrium density determined by parasitism cannot be too great); $|f_i'(P^*)|$ must be sufficiently small (i.e., the marginal effect of the parasitoid on host survival cannot be too large; this is most easily achieved with a heterogeneous distribution of attacks, e.g., because some hosts are in refuges). Given that each host can on its own stably coexist with the parasitoid, can all three species coexist?

A Graphical Model of Host Exclusion by Apparent Competition

The two hosts cannot stably coexist in equilibrium with the parasitoid. For host species i to be in equilibrium, it must be the case that $1 = R_i f_i(P_i^*)$, where

P_i^* denotes the equilibril population size of the parasitoid when it subsists just on host i . In this one-host situation, the equilibril number of parasitoids is determined solely by the parameters associated with host i (its intrinsic rate of increase, etc.). Because f_i declines monotonically with P , if $P < P_i^*$, the population of host i grows, and if $P > P_i^*$, host i declines.

For two hosts to persist at a joint equilibrium, it must be the case that $P_1^* = P_2^*$, but this is exceedingly unlikely to occur without a delicate balancing of host parameters. Thus, in most circumstances, no three-species point equilibrium exists.

By convention, let host species 1 be the host that sustains the higher equilibril density of the parasitoid (i.e., $P_1^* > P_2^*$). If a very small number of host 2 are now introduced into the equilibril community, there will be a negligible effect on parasitoid density. The rate of growth of host species 2 as it attempts to invade is $R_2 f_2(P_1^*) < R_1 f_1(P_1^*) = 1$. Hence, the invading propagule of host 2 will decline toward extinction, and the species thus is excluded from the community, directly by the parasitoid and indirectly by the host sustaining that parasitoid.

Conversely, if host 2 is at equilibrium with the parasitoid and a small propagule of host 1 is introduced into the community, then $R_1 f_1(P_2^*) > R_2 f_2(P_2^*) = 1$, so host 1 can increase when rare. The only stable point equilibrium is one in which the host that can withstand the higher parasitoid density is present, and the alternative host is excluded.

The above points are expressed in the simple graphical model depicted in figure 1. We plot f_i as a decreasing function of P . The value of P_i^* is given by the intersection of this function with a horizontal line $P = 1/R_i$; at the intersection, $1 = R_i f_i(P_i^*)$, and host i is in equilibrium. In figure 1a, parasitism affects the two host species in an even-handed manner (i.e., $f_1 = f_2$), but $R_1 > R_2$. Hence, $P_1^* > P_2^*$, and host 1 should exclude host 2. In figure 1b the two hosts have the same growth rate ($R_1 = R_2$), but host 1 suffers a lower intensity of parasitism at all parasitoid densities ($f_1 > f_2$). Once again, host 2 should be excluded. And finally, figure 1c shows for two hosts with equal growth rates that, if the relative intensity of parasitism varies with parasitoid density, the identity of the winning host is contingent on overall host growth rates.

Host Species Dominance in Equibril Communities

To make the above argument more concrete, consider a system in which the fraction of hosts escaping parasitism is described by the zero term of a negative binomial distribution:

$$f_i(P_t) = \left(1 + \frac{a_i P_t}{k_i}\right)^{-k_i} \quad (2)$$

The parameter a_i is the mean rate of parasitoid encounter and attack on hosts per unit search time, whereas k_i describes the degree of variation among hosts in rates of parasitism. For instance, lower values for k_i may correspond to greater spatial heterogeneity in parasitoid attacks (May 1978). Chesson and Murdoch (1986) showed that the negative binomial accurately describes the net result of

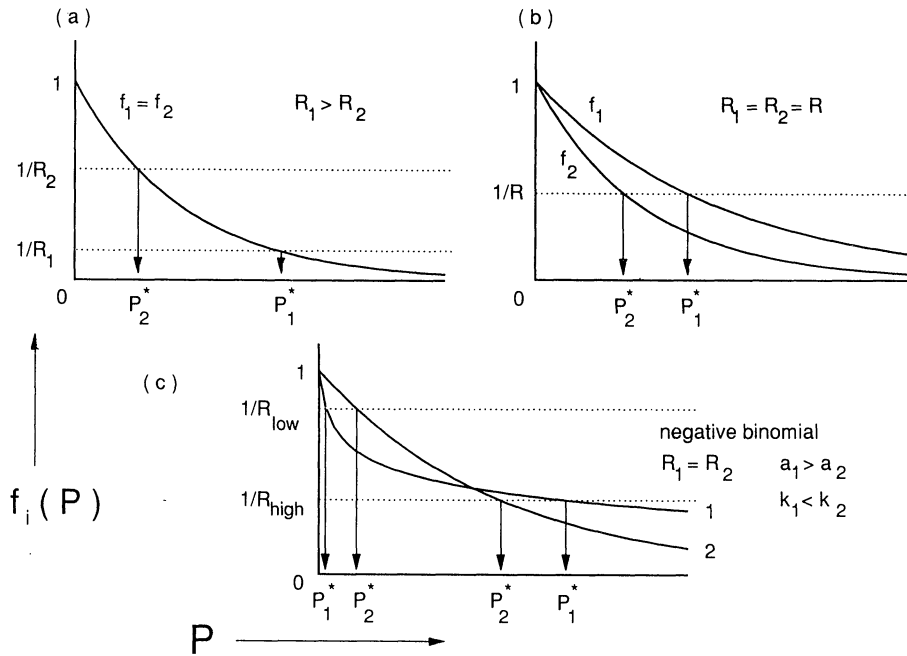


FIG. 1.—A graphical model of host exclusion by apparent competition. The *solid lines* are fractions of hosts escaping parasitism as functions of parasitoid density, P . The size of the parasitoid population sustained at equilibrium with host i (denoted by P_i^*) is the value of P that reduces the net growth rate of that host to unity: $1 = f_i(P_i^*)R_i$, or $f_i(P_i^*) = 1/R_i$. Graphically, this is found at the intersection of f_i and the horizontal line $1/R_i$. *a*, Both host species experience the same rate of parasitism (i.e., $f_1 = f_2$), but host 1 has a higher intrinsic rate of increase: host 1 sustains a higher density of parasitoids than can be tolerated by host 2. *b*, Host species 1 and 2 have the same intrinsic growth rate, but host 1 is less heavily parasitized at all P ; host 1 supports a parasitoid density sufficient to exclude host 2. *c*, The two hosts have equal intrinsic growth rates, but the host that is more heavily parasitized varies with P , as is possible in the negative binomial model. At low growth rates, the host with the lower attack coefficient (in the figure, host 2) supports more parasitoids. At high growth rates, the host experiencing more heterogeneous attacks (i.e., lower k_i) predominates.

parasitism when hosts are distributed in patches, and the attack rate varies among patches according to a gamma distribution with coefficient of variation $(1/k)^{0.5}$.

The single-host/parasitoid system is stable if $k_i < 1$ (May 1978); we assume this holds for each host species. Host species i is in equilibrium when the parasitoid is at density

$$P^* = \frac{k_i}{a_i} (R_i^{1/k_i} - 1). \tag{3}$$

The graphical analysis in figure 1 yields a simple rule-of-thumb about dominance in multihost/parasitoid interactions: The host species that persists is the one that withstands the higher density of parasitoids. Another, subtly different way of stating this rule is that the winner is the one that supports the higher

equilibrial parasitoid density. These rules are analogous to the rule of dominance in resource competition, in which the winning competitor is the one that can withstand the lowest resource level and also depress resources to these low levels (Tilman 1982). This parallel will be more fully explored elsewhere (R.D. Holt, J. Grover, and D. Tilman, unpublished manuscript).

In the negative binomial model indirect dominance via apparent competition can happen in three ways, each encompassing a wealth of biological possibilities:

1. The winning host experiences the lower mean attack rate, a_i , for instance because it has more refuges, less overlap spatially or temporally with the parasitoid, better-developed escape tactics or morphological defenses, or is of low quality and preferentially (but not completely) ignored by the parasitoid.
2. The winning host has a higher intrinsic rate of increase, R_i , because its resources are more readily available, it is physiologically better adapted to abiotic factors and so has a higher fecundity or quicker developmental rate, or it is better able to withstand density-independent mortality factors that reduce R_i .
3. The winning host experiences attacks in a more heterogeneous aggregated fashion (i.e., lower k_i) than does the loser. This simultaneously permits the interaction between this single host and the parasitoid to be stable and increases the density of the parasitoid (May 1978), which can then more heavily attack an alternative host that experiences a more homogeneous pattern of parasitoid attacks.

It seems to us that differences among host species in the magnitude of heterogeneity in parasitism (as measured, say, by k_i) may be quite common in natural communities. The attack rate describes the rate of successful encounter between individual searching parasitoids and individual hosts (Hassell 1978), and this single parameter can be mechanistically influenced by a wealth of sources of local variability, including physical factors such as temperature, which influences movement rates; the sensory environment, encompassing all the manifold factors that influence the strength and reliability of the sensory cues used by parasitoids to detect their hosts; and the degree of overlap between the microhabitats occupied or between phenological emergence patterns. If one host species is found in a narrow range of microhabitats and a second host species occurs in a broad range of microhabitats differing in the above respects, the host with greater microhabitat breadth is likely to experience greater variability in parasitism.

The existence of differences between host species in the magnitude of parasitism they experience raises an interesting possibility: one host species may suffer higher parasitism at low parasitoid densities (because this host has a high a_i) but lower parasitism than the other host species at high parasitoid densities (because of a lower k_i , i.e., more heterogeneous attacks). Assume that both host species have the same R_i , but $a_1 > a_2$ and $k_1 < k_2$. Along an environmental gradient that influences both hosts equitably, at positions on the gradient at which both species have high values for R , species 1 should dominate, whereas at positions at which both species have low R values, species 2 should dominate (fig. 1c). As before,

the host that persists at the higher parasitoid density excludes the alternative host from the community. However, the specific identity of this dominant host may shift along an environmental gradient from low to high overall host growth rates.

Drawing these arguments together, invasion is easier the higher the growth rate of the invading host species and the lower the per capita rate of attack on it by resident parasitoids. A general criterion for the successful invasion of a species into a community with generalist predators is $r > aP^*$, where r is the instantaneous growth rate of the invader, a the per capita attack rate by predators on the invader, and P^* the equilibrium density of the resident generalist predators (Lawton 1986). What the above models clearly reveal is that the total rate of parasitism imposed on an invading host species (aP^*) is a *dependent* variable of the resident host community, because P^* is an emergent property of the host-parasitoid interaction and indeed of the entire community in which that interaction is embedded. In model (1) with the negative binomial attack term defined by equation (2), equilibrium parasitoid population size, P^* , increases with the productivity of the resident host and decreases with increasing average per capita attacks on that host (i.e., overexploitation) or increasing uniformity in attacks. These relationships, mechanistically, explain the indirect dominance of one host species over another.

The Importance of Trade-offs

Consider the evolutionary implications of these ideas. In the usual Nicholson-Bailey formulation, the phenotype of a given host species is described by two parameters, a_i and R_i , or equivalently $\ln(R_i)$ and $1/a_i$, and so can be represented as a point in a two-dimensional phenotype space (fig. 2) (analogous to the fitness set approach to phenotypic evolution developed by Levins [1986]). Each point in this space corresponds to a parasitoid density maintainable by a host with that phenotype. Combinations of host phenotypic values that support a particular equilibrium parasitoid density, P^* , are described in this phenotype space by hyperbolic curves ($\ln[R_i]$) ($1/a_i$) = P^* .

Now, assume that a trade-off exists between a host's ability to escape parasitism ($1/a_i$) and its rate of increase ($\ln[R_i]$). (Whether such trade-offs exist in phytophagous insects is an interesting, untested question.) The range of possible host phenotypes can be described by a set, the outer boundary of which has a negative slope. Along this boundary, an increased ability to escape the parasitoid comes at a cost in reduced population growth rates. The host species that dominates the local community is the one whose phenotype sustains the highest parasitoid density. This can be found graphically (see fig. 2) as that point on the phenotype boundary just tangent to a curve of constant parasitoid density. If the phenotype set is convex (fig. 2a), the dominant host has intermediate growth and attack rates (relative to the potential variation in the assemblage). If the phenotype set is concave (fig. 2b), the dominant host may be one with a relatively extreme phenotype.

Host Exclusion in Nonequilibrium Communities

In arguing that one host species can indirectly depress the abundance of another, even to the point of local extinction, via a parasitoid's numerical response,

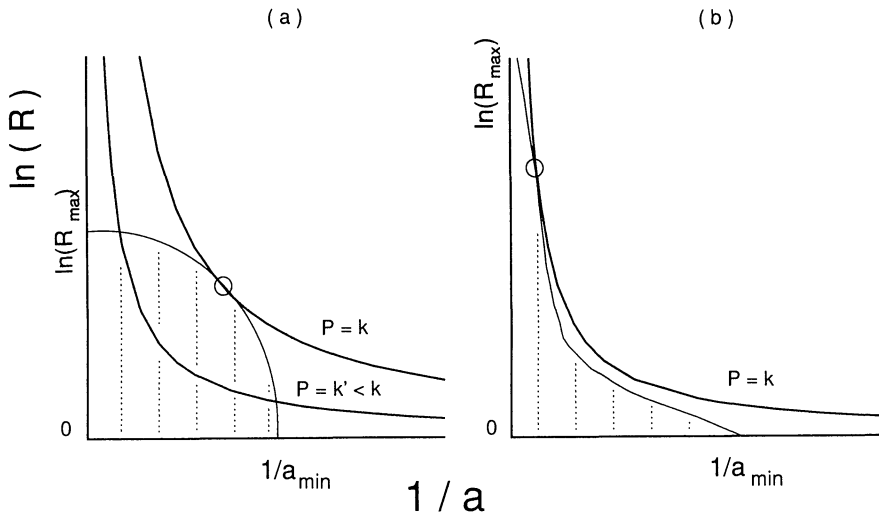


FIG. 2.—A fitness set approach to host dominance in apparent competition. The growth rate of host species i in the Nicholson-Bailey model is governed by two parameters: R_i and a_i or, equivalently, $\ln(R_i)$ and $1/a_i$. An array of potential host species can be described as a cloud of points in a two-dimensional space, within the axes given by these two transformed parameters; each point in this set (the *shaded areas* in *a* and *b*) represents a particular host species. For a host species to be present at all requires $\ln(R_i) > 0$. The maximum host growth rate in the host assemblage is R_{\max} , and the attack coefficients on hosts range from a_{\min} to a_{\max} . Some hosts may have both low growth rates and high attack rates and so will be represented as a point near the origin. If host species that are relatively more able to escape parasitism suffer a cost in their growth rate, the outer boundary of the phenotype set will have a negative slope. The parasitoid density sustained by host i is $P_i^* = \ln(R_i)/(1/a_i)$, so the combinations of host parameters that lead to a given parasitoid density, k , is described by a hyperbolic curve, $k = \ln(R_i)/(1/a_i)$. The host phenotype supporting the highest density of parasitoids (and hence dominant in the host community) is the one on the edge of the phenotype set tangent to the hyperbola of highest k (e.g., the *open circles* in *a* and *b*). In *a*, this phenotype has intermediate growth attack and rates; in *b*, this phenotype has high growth and attack rates.

we have assumed that the system exists in a stable point equilibrium. However, we suspect that this conclusion is robust, as long as the parasitoid can persist (i.e., fluctuate within upper and lower limits, bounded away from zero) with one host species, and the parasitoid effectively depresses its hosts to levels too low for strong direct, density-dependent interactions among hosts.

There are three distinct kinds of nonequilibrium conditions that might, in principle, influence the structure of host assemblages. First, even if the external environment is constant, persistent host-parasitoid interactions may lead to sustained cycles or chaotic dynamics. Second, even if the interaction intrinsically tends toward a stable equilibrium, fluctuations in the external environment may induce population fluctuations. And finally, a given host-parasitoid interaction may be unstable, so that local populations of both species are driven to extinction; yet the interaction may nonetheless persist regionally because of a balance between such local extinctions and recolonizations.

Temporally fluctuating environments and chaotic dynamics.—To illustrate the effects of the first two kinds of nonequilibria, imagine that there is recurrent immigration by the parasitoid from outside the local community. In a single-host/parasitoid system such immigration is broadly stabilizing (May and Hassell 1988). Extending this model to incorporate two host species and temporal variation in host intrinsic growth rates and parasitoid immigration rates leads to

$$N_1(t + 1) = N_1(t)R_1(t)\exp[-a_1P(t)], \tag{4a}$$

$$N_2(t + 1) = N_2(t)R_2(t)\exp[-a_2P(t)], \tag{4b}$$

and

$$P(t + 1) = N_1(t)\{1 - \exp[-a_1P(t)]\} + N_2(t)\{1 - \exp[-a_2P(t)]\} + I(t), \tag{4c}$$

where $I(t)$ describes parasitoid immigration in generation t .

Consider first the system with just host species 1 and constant immigration and host vital rates. At equilibrium,

$$P^* = \frac{\ln(R_1)}{a_1}$$

and

(5)

$$N^* = \frac{P^* - I}{1 - 1/R_1}.$$

Parasitoid immigration depresses host density but does not increase local parasitoid density, which instead is determined by local host productivity and attack rates. If $I > P^*$, the parasitoid eliminates the local population of this host. If $\ln(R_1) - 1 + (1/R_1) < a_1I < a_1P^*$, the host persists and the equilibrium is locally stable. At lower immigration rates, the system exhibits sustained bounded oscillations, including limit cycles and chaos (May and Hassell 1988). The criterion for persistence of the host is $I < P^*$; when this holds, the host can always increase when rare. Therefore, the system is globally persistent if $0 < I < P^*$.

Now let host vital rates and parasitoid immigration vary among generations, with an initial density of $N_1(0)$ hosts and $P_1(0)$ parasitoids. We use a time-averaging approach (Levins 1979) to ascertain the potential for coexistence in the above model. Analogous approaches have been used to analyze density-dependent evolution in fluctuating environments (Holt 1983; J. A. J. Metz and H. C. J. Godfray, personal communication). At generation T we have the following number of hosts (the subscript on $P_1[t]$ denotes that just host 1 is present):

$$N_1(T) = N_1(0) \prod_{t=0}^{T-1} R_1(t)\exp[-a_1P_1(t)]. \tag{6}$$

Taking logs and rearranging,

$$\frac{\ln[N_1(T)] - \ln[N_1(0)]}{T} = \frac{1}{T} \sum_{t=0}^{T-1} \{\ln[R_1(t)] - a_1P_1(t)\} = \langle \ln(R_1) \rangle - a_1\langle P_1 \rangle, \tag{7}$$

where $\langle \ln(R_1) \rangle$ is the time-averaged logarithmic host growth rate, and $\langle P_1 \rangle$ is the time-averaged abundance of parasitoids. When T is large, if $N_1(t)$ fluctuates between upper and lower values bounded away from zero, the left side approaches zero. This leads to the following simple expression for the average parasitoid abundance in a fluctuating environment:

$$\langle P_1 \rangle = \langle \ln(R_1) \rangle / a_1. \quad (8)$$

So, in a fluctuating environment the long-term average parasitoid density is proportional to the long-term average logarithmic host growth rate. Because for any variable x , $\langle \ln(x) \rangle < \ln(\langle x \rangle)$, for a given mean host growth rate environmental fluctuations tend to depress parasitoid numbers.

Can host species 2 invade this temporally varying system? We use a variant of standard procedures for studying invasion in fluctuating environments (see, e.g., Chesson and Ellner 1989) to address this question. When host 2 is sufficiently rare, the dynamics of the parasitoid will be dominated by its interaction with the resident host, species 1. Species 2 will successfully invade only if its average growth rate more than compensates for the parasitism it experiences from the resident parasitoid. The intensity of parasitism is determined by the numbers of parasitoids present, which in turn reflects the productivity of the resident hosts. More formally, over a period of T generations, host 2 increases if

$$\left(\prod_{t=0}^{T-1} R_2(t) \right) \left(\prod_{t=0}^{T-1} \exp[-a_2 P_1(t)] \right) > 1. \quad (9)$$

Taking logarithms and letting T be large, as before, we find that host species 2 can invade if $\langle \ln(R_2) \rangle / a_2 > \langle P_1 \rangle$. But the quantity on the left is simply $\langle P_2 \rangle$, the average number of parasitoids that could be sustained by host 2 were it alone with the parasitoid. Hence, if $\langle P_2 \rangle < \langle P_1 \rangle$, host 2 cannot invade if it is rare and host 1 is persistently present. Similarly, if $\langle P_2 \rangle > \langle P_1 \rangle$, host 2 tends to increase when rare and when resident can in turn exclude species 1. In the exceedingly unlikely situation that $\langle P_2 \rangle = \langle P_1 \rangle$, the above invasion analysis is inadequate, and the interaction between the two host species will be dominated by fluctuations.

The model allows for two possible causes for temporal fluctuations in parasitism. Even in a physically constant environment, at low immigration rates the system can exhibit cycles or chaotic dynamics. Moreover, variation in parasitoid numbers may be generated directly by variation in parasitoid immigration or indirectly by variation in host growth rates. The above argument suggests that, regardless of the exact cause of the fluctuations, the outcome should be no different than that expected in a constant environment with stable populations: one host tends to displace alternative hosts from the assemblage, and the winner is the host sustaining the highest average parasitoid density.

This model also suggests an additional mechanism for dominance in apparent competition in host-parasitoid communities. Assume for simplicity that host species 1 and 2 have the same average growth rate in a fluctuating environment, but species 2 has a constant growth rate and is more sensitive to the "noise" than is species 1 (i.e., to fluctuations in the weather or food supply). As is well known,

to a first approximation

$$\langle \ln(R_i) \rangle = \log(\langle R_i \rangle) - \frac{\text{var}(R_i)}{2\langle R_i \rangle}, \quad (10)$$

where $\text{var}(R_i)$ is the variance in the growth rate of species i . Hence, if two host species have the same arithmetic mean growth rate, the dominant species should be the one with lower variance.

In developing the above time-averaging argument, we have doubtless ignored subtleties in specifying how the parameters must be constrained in their temporal evolution, so that densities are ensured to be bounded away from zero. Numerical simulations suggest that our conclusions hold for reasonable patterns of temporal variability. Moreover, if the demographic rates and immigration are constant, there is a range of immigration rates generating stable cycles, in which for some T , $P(0) = P(T)$. In this case, expression (8) exactly describes the average parasitoid abundance over a single cycle, and expression (9) the precise criterion for a small propagule of host 2 to increase over a single cycle. For the invasion of host 2 to fail, its geometrical mean growth rate over the cycle must be <1 , and this is guaranteed if $\langle P_2 \rangle < \langle P_1 \rangle$.

In the above model, the system comprised of a dominant host species and the parasitoid persists because the parasitoid population is open, receiving immigrants regularly or episodically. However, the rate of parasitism is described by a simple, Nicholson-Bailey expression. An interesting avenue for future work would be to examine more complex functional forms for parasitism and determine the potential for the nonequilibrium coexistence of alternative hosts in fluctuating environments (analogous to the results of Armstrong and McGehee [1980] in nonequilibrium one-resource, two-consumer systems).

Exclusion in metapopulations.—If local host-parasitoid interactions are dynamically unstable, such that parasitoids routinely overexploit their prey to the point of local extinction (Washburn and Cornell 1981), the system as a whole may nonetheless persist because of an overall balance between local colonization and extinctions (Murdoch et al. 1985; Hassell et al. 1991). In such a metapopulation, alternative host species may indirectly interact even if they never co-occur in a patch, simply because the colonization rate of parasitoids will reflect the combined output of dispersers from all patches containing that parasitoid, regardless of which host species is present in which patch. It is conceivable that at high rates of parasitoid dispersal, one might observe exclusion via apparent competition between two host species that are completely segregated in space (although we have not investigated this possibility in detail). Examples certainly exist of alternative host species that live in physically separate locations but that are nevertheless indirectly coupled by the dispersal of shared parasitoids (Zwölfer 1961; Parnell 1964).

HOW, THEN, DO ALTERNATIVE HOSTS COEXIST?

We conclude that it is difficult for alternative host species to coexist when the sole regulatory factor impinging on them is a shared parasitoid. Yet clearly in

nature many parasitoids do manage to cohabit with multiple host species. There is a puzzle waiting to be solved, we suggest, each time one observes the sustained coexistence of alternative host species with one or more species of shared parasitoids.

Mechanisms of Coexistence

Here we outline a number of factors that act to promote coexistence. Several will be treated briefly, inasmuch as they involve the application to host-parasitoid systems of the mechanisms promoting coexistence in general predator-prey interactions (Holt 1977, 1984, 1987; Jeffries and Lawton 1984).

Donor-controlled systems.—Polyphagous parasitoids may not, in fact, act as regulatory agents; that is, they may not depress host numbers in a (delayed) density-dependent manner. In the absence of a density-dependent response, polyphagous parasitoids will not drive the system toward dynamic monophagy, which thereby relaxes one constraint on host coexistence. Such parasitoids may, nevertheless, still prevent some nonresident host species from invading the community, because of the exclusion criterion $r_i < a_i P^*$ discussed above.

Resource limitation of dominant hosts.—Donor-controlled systems are a limiting case of a less extreme possibility, in which generalist parasitoids are regulatory but not sufficiently so to prevent other sources of population regulation from being significant. There is some (admittedly equivocal) evidence to suggest that polyphagous parasitoids have lower attack rates than monophagous parasitoids (Rogers and Hubbard 1974), which would tend to make polyphagous parasitoids weaker regulatory agents. A useful gauge of the impact of parasitoids on host abundance is the quantity $q = N^*/K$ (Beddington et al. 1978), which measures the degree to which the equilibrium host population in the presence of the parasitoid, N^* , is depressed by parasitism below its resource-dependent carrying capacity, K . One obvious alternative source for regulation is competition for resources, for instance, food. If the parasitoid is relatively ineffective at reducing host numbers (i.e., low a_i), resource-based density dependence will persist even at those equilibrium host densities maintained by the parasitoid. Very roughly, this might occur for $1 > q > 0.1$. At higher attack rates (i.e., giving $q < 0.1$) resource-based density dependence becomes increasingly unlikely for the host.

Resource-based competition acting on the host reduces the average number of parasitoids that can be sustained by a given host population and hence relaxes apparent competition with other host species. For example, in model (1) assume that host growth in the absence of parasitism is described by the exponential logistic, $R_i g_i = \exp[r_i(1 - N_i/K_i)]$ and that parasitoid attacks are not clumped, so that $f_i = \exp(-a_i P)$. Figure 3 shows the equilibrium parasitoid abundance, P^* , as a function of the attack coefficient, a , when the parasitoid is supported by just a single species of resident host. Recall that apparent competition is mediated by the abundance of parasitoids supportable by a resident host population. At low attack rates, the parasitoid itself cannot persist when the resident host is at the carrying capacity set by resources. Above some threshold attack rate, the parasitoid persists, and increased attack rates increase parasitoid density. But there comes a point at which further increase in attack rates depresses equilibrium para-

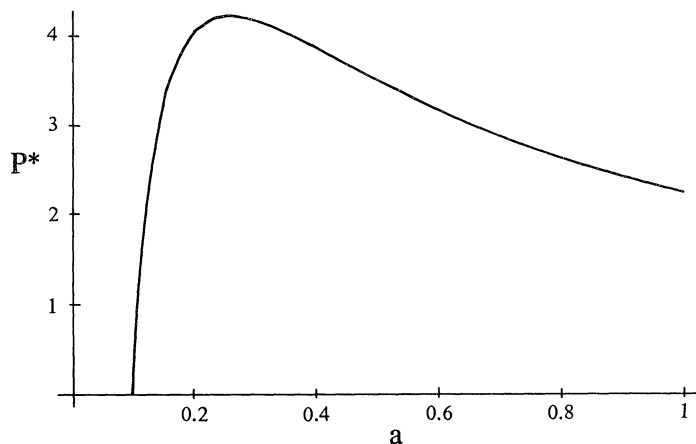


FIG. 3.—Equilibrial parasitoid density as a function of the attack rate. The model assumes that the host grows according to the exponential logistic and that attacks follow the usual Nicholson-Bailey formulation (see text).

sitoid abundance, in essence because the parasitoid overexploits its host. This suggests that, all else being equal, those host species that have the greatest indirect impact on other host species via apparent competition should be those that experience moderate attack rates from polyphagous predators.

How easy is it for a second host species to invade such a system? Let the resident (species 1) have the higher value for r/a , which implies that it is dominant in the absence of resource limitation. Host 2 invades if $r_2/a_2 > P_1^*$ (fig. 4). At high values for q ($q \rightarrow 1$, i.e., substantial resource limitation), there is essentially no constraint on invasion, and both species coexist in the presence of the parasitoid. But as q declines toward zero (i.e., weak to negligible intraspecific competition in the dominant host), the conditions for invasion by species 2 become increasingly stringent, and in the limit $q \rightarrow 0$ any alternative host with a lower value for r/a is excluded. Moreover, it can be shown that each successful invasion ultimately increases the abundance of the parasitoid, which makes further invasion by species 3, species 4, . . . , species n progressively less likely. In other words, even with low attack rates, there may be loose limits on the number of host species able to coexist with a polyphagous parasitoid.

Host switching.—An interesting complication that received considerable attention in earlier theoretical literature is the impact of switching (Murdoch 1969) by polyphagous enemies on the coexistence of two or more victim species competing for resources (see, e.g., Roughgarden and Feldman 1975; Comins and Hassell 1976; May 1977; Teramoto et al. 1978). Switching has been reported in at least two host-parasitoid systems (Harper and Whittaker 1976; Cornell and Pimentel 1978) but not in others (see, e.g., Dransfield 1979). Its role in promoting coexistence of multiple host species attacked by polyphagous parasitoids under field conditions thus remains unclear, although theoretically it is a general mechanism facilitating host species coexistence.

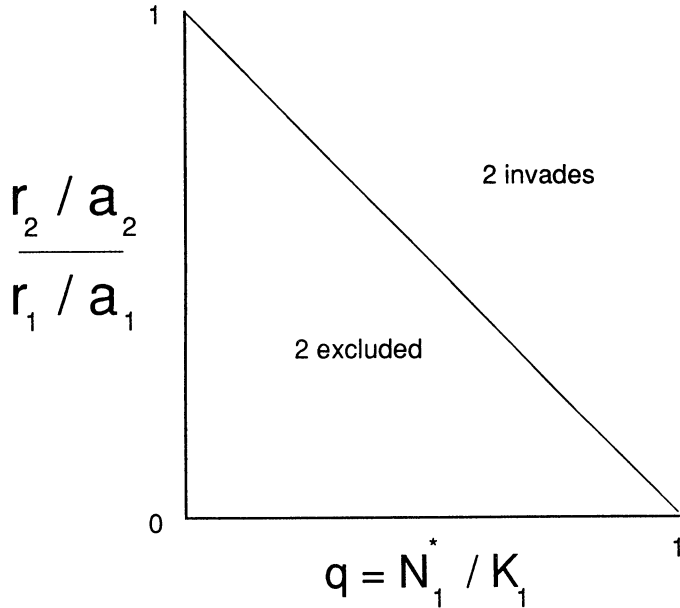


FIG. 4.—Conditions for host species coexistence. Host species 1 is dominant in apparent competition (i.e., has the higher value for r_i/a_i). The quantity q measures the degree to which the parasitoid depresses this host below its carrying capacity. The interaction is asymmetrical; host 2 cannot exclude host 1.

Spatial refuges.—If each host species has its own refuge in which it is free from parasitism, it might seem that this would permit the sustained coexistence of alternative host species. This is not necessarily the case. One can usefully distinguish between two sorts of refuges (Hassell 1978): those in which a constant *proportion* of hosts escape parasitism each generation and those in which a constant *number* of hosts escape attack. These two kinds of refuges have quite different effects on host species coexistence; only the latter allows coexistence.

A proportional refuge is incorporated into model 1 by assuming that a fraction e_i of hosts is exposed to attack each generation. Equation (1a) for host i is modified to become

$$N_{i,t+1} = N_{i,t}[R_i e_i f_i(P_t) + (1 - e_i)R_i].$$

Host i is in equilibrium with the parasitoid when

$$f_i(P^*) = \frac{1}{R_i e_i} [1 - (1 - e_i)R_i].$$

We assume that $(1 - e_i)R_i < 1$, which ensures that the parasitoid can regulate each host.

The graphical analysis of figure 1 still applies (albeit with the reciprocal of the host growth rate being replaced by a more complicated term). Once again, the host that supports the higher density of parasitoid will exclude the alternative

host from the community. In other words, proportional refuges do not promote the coexistence of alternative host species. Allowing host growth rates to vary between protected and exposed hosts (along the lines explored in Holt and Hassell 1993) does not change this basic conclusion.

In an absolute- or constant-number refuge model, one imagines that each host species has a fixed number of individuals who can live in an exclusive refuge each generation. If there is an absolute refuge for each host species, the host equation becomes

$$N_{i,t+1} = (N_{i,t} - Q_i)R_i f_i(P_t) + Q_i R_i,$$

where Q_i is the number of host i in a refuge each generation. Such refuges are both strongly stabilizing and, unlike proportional refuges, promote coexistence, because it is impossible for the parasitoid to eliminate a host species with an absolute refuge from the community. The important feature of the above model is that *each* host species has its own exclusive refuge, so that there is implicitly intraspecific but not interspecific competition for these refuges; if hosts instead overlap in the refuges they use, this may introduce an additional mode of interspecific competition leading to exclusion (Holt 1987). If alternative hosts do have distinct absolute refuges, they in effect exhibit a form of niche differentiation along axes relevant to predator escape (see Jeffries and Lawton 1984). The importance of this mechanism of coexistence cannot as yet be judged, however, because it is unclear whether constant number refuges are at all common in nature (B. A. Hawkins, personal communication).

Temporal refuges.—Another form of refuge is escape through time, for instance via diapause. If temporal refuges are expressed within each generation (e.g., early-emergent hosts may escape parasitism) (Lawton 1986), this is in no important respect different from the proportional refuge model and does not promote host species coexistence. However, if a constant fraction of hosts born in generation t stay dormant and resistant to parasitoid attack through generation $t + 1$ before reentering the vulnerable population in generation $t + 2$, it is plausible that good years of recruitment will be “stored” in persistent invulnerable stages, analogous to the “storage effects” identified by Chesson (1985) and Chesson and Huntly (1989) in competition models. Although we have not explored this possibility in detail, a similar effect might permit alternative hosts to coexist in a fluctuating environment.

Regional coexistence.—All the models explored to this point consider a single local community. A number of different possibilities arise in an ensemble of local assemblages loosely coupled by dispersal. If there is spatial heterogeneity in this ensemble, a given host species may be superior in apparent competition in one community, but inferior elsewhere. For instance, a given species of host insect may have different intrinsic growth rates or suffer markedly different levels of attack from parasitoids on different species of host plants or at different points along a habitat gradient (Randall 1982; Clancy and Price 1986; Lawton 1986). If different host species are dominant in different communities, one may observe regional coexistence even if there is no within-community mechanism permitting coexistence. A small rate of dispersal may then lead to host species being found

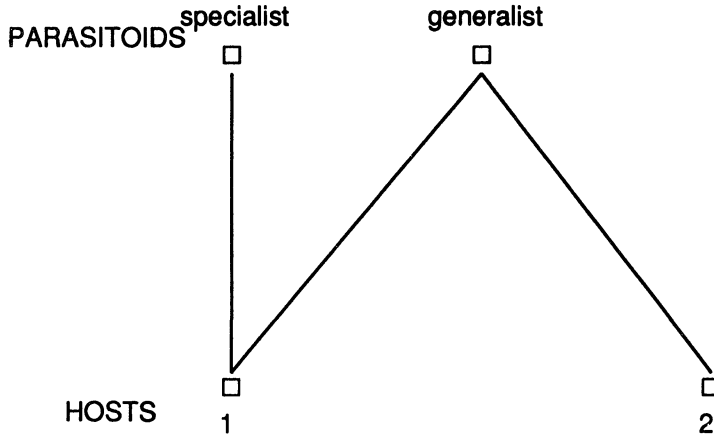


FIG. 5.—A mixture of specialist and generalist parasitoids. As discussed in the text, the presence of the specialist modifies the indirect impact of hosts 1 and 2 mediated through their shared generalist parasitoid.

in communities where they would be excluded in the absence of dispersal. We suspect that this is an important mechanism enriching the host species assemblages found in many local communities.

Complications Arising in Multispecies Communities

To this point we have considered a single species of parasitoid attacking two or more species of hosts. In the real world, things may be more complicated because hyperparasitoids or mixtures of specialist and generalist parasitoids coexist in local ensembles. How do these two complications influence the coexistence of host species?

Hyperparasitism.—May and Hassell (1981) have developed a host-parasitoid-hyperparasitoid model, in which each trophic link is described by a negative binomial submodel for parasitism, and the host density is so low that there is no direct density dependence (i.e., $q \ll 1$). In general predator-prey models, adding a third trophic level typically vitiates apparent competition among prey species (Holt 1977). Interestingly, this does not occur in parasitoid systems (at least in this model). The equilibrium density of the intermediate parasitoid in the full three-species system is $\ln(R_i)/a_i$, even when the hyperparasitoid is present and all three species are at their respective equilibrium abundances. Hence, if there are two host species present, whichever can sustain the higher density of the primary parasitoid again excludes the other, irrespective of the presence of a hyperparasitoid.

Specialist and generalist parasitoids.—Most natural host-parasitoid ensembles include a mixture of specialist and generalist parasitoids (Hassell and May 1986; Lawton 1986 and references therein). Consider the particular case shown in figure 5, in which a generalist feeds on two host species, one of which is also attacked by a specialist parasitoid. There is a twofold species coexistence problem here: the dynamical properties of the system must be such that the two parasitoid species can coexist (Hassell and May 1986), as well as the two host species.

Do the two hosts in figure 5 exhibit apparent competition? They do, but its magnitude should be reduced in impact by the specialist. For instance, an increase in the productivity of the nonshared host increases the abundance of the generalist, which should reduce the abundance of the alternative, shared host. But this is partially absorbed in a reduced density of the specialist parasitoid. This moderates the impact of the alternative host via the shared generalist predator. If the nonshared host is sufficiently productive, however, both the shared host and its specialist parasitoid may be excluded from the local community. Specialist parasitoids could play a particularly important role in maintaining host species richness if they attack hosts that otherwise would be dominant in the generalist parasitoid's array of hosts. It would be interesting to know whether specialist parasitoids differentially occur on hosts with high relative intrinsic growth rates.

CODA

Many of the detailed theoretical arguments developed here lack direct empirical support. We finish by drawing attention to some potential pitfalls in testing for these effects in the field and by drawing together a number of additional examples of apparent competition between phytophagous insects via shared parasitoids, to buttress our case that there are important phenomena here that warrant further attention by field ecologists.

Consider, first, the problem of experimental tests of apparent competition. Paradoxically, the more host species coexist with one or more shared parasitoids, the more difficult it may be to detect apparent competition by experimental manipulation of specific pairs of host species. To understand this, imagine that an idealized host assemblage contains n species present with identical intrinsic growth rates and attack coefficients. The shared parasitoid reduces the total abundance of the host community at equilibrium to N_T , so the average abundance per host species is N_T/n . If a single host species is removed, and the system settles to a new equilibrium, the average abundance per host species will increase to $N_T/(n - 1)$. The proportional increase in a particular host species' abundance following the removal of a given other host species is thus $1/(n - 1)$, which decreases with increasing n . In effect, an increase in host species richness dilutes the magnitude of pairwise effects. In detailed studies of local communities, it will be inherently difficult to detect pairwise interactions between host species in the diet of highly polyphagous predators, even if apparent competition from the entire suite of hosts collectively depresses any given host species by a large amount.

Nevertheless, there are a growing number of unintentional or deliberate manipulations of hosts and/or parasitoid populations, which suggest that apparent competition does occur in the field. For example H. Zwölfer (reported in Schulmreicht 1989; see also Lawton 1986) created experimental populations of the gall-forming tephritid *Urophora cardui*, beyond the limits of the species' normal geographical range in Germany. Several colonies appear to have been exterminated by very high levels of parasitism by *Eurytoma robusta*, a polyphagous parasitoid that attacks many other species of *Urophora*.

Other examples come from the biological control literature, where polyphagous parasitoids have been released to control insect pests, or exotic herbivorous

insects have been released to control exotic weeds, and they have in turn been attacked by polyphagous native parasitoids. Howarth (1991) summarizes several examples of cases in which polyphagous (or at least oligophagous) parasitoids have been released against insect pests, which then caused the local or regional extinction of the pest or of native, nontarget hosts. Although many of his examples are anecdotal, the sum of the case histories is reasonably compelling. They include the extinction of the native coconut moth *Levuana iridescens* by the polyphagous tachinid *Bessa remota* on Fiji; marked declines in native pentatomids in the genera *Oechalia* and *Coleotichus* on Hawaii after parasitoids to which they were vulnerable were introduced to control an alien stink bug *Nezara viridula*; and declines or extinction in a wide range of other endemic insects on Hawaii and in New Zealand following release of polyphagous parasitoids against pest species.

At least two exotic phytophages released as biological control agents against alien weeds appear to have suffered reductions in numbers or have failed to establish (i.e., they were driven locally extinct), at least in part because they were attacked by indigenous, polyphagous parasitoids. In both cases, other causes of mortality have contributed to the failure, but parasitism was clearly a significant factor. The first is the moth *Coleophora klimeschiella* released against *Salsola australis* in southern California, where it was attacked by several species of native parasitoids, including a eupelmid, *Macroneura* sp. (25% parasitism), a chalcid, *Hockeria* (17% parasitism), and at least three other species. The *Macroneura* species normally attacks Cecidomyiidae on native *Atriplex* bushes. Although *Coleophora* was released at 13 sites between 1977 and 1985, it persists at only one locality (Goeden et al. 1987). A similar scenario, also involving a lepidopteran biological control agent, *Anaitis efformata*, released to control *Hypericum perforatum* in Australia, is described by Briese (1986). Again, several nonparasitoid mortality factors were important in limiting successful establishment, but parasitism by *Trichogramma* was significant, killing 5%–48% of eggs.

In none of these cases can we estimate the parameters necessary for a proper evaluation of the models explored above. Indeed, it is not even possible, except in the most general terms, to say which of the models are most appropriate for each situation. The examples are presented simply to illustrate a growing body of empirical evidence for the importance of apparent competition and enemy-free space in host-parasitoid assemblages. We believe the most compelling question today is *not*, How do parasitoids promote the coexistence of host insects by preventing conventional competitive exclusion for limiting resources? Rather it is, What mechanisms permit the coexistence of several host species confronted by biologically oligophagous and polyphagous parasitoids? This question has been almost entirely ignored by experimental ecologists. It deserves more attention.

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LITERATURE CITED

- Armstrong, R. A., and R. McGehee. 1980. Competitive exclusion. *American Naturalist* 115:151–170.
- Beddington, J. R., C. A. Free, and J. H. Lawton. 1978. Modelling biological control: on the characteristics of successful natural enemies. *Nature (London)* 273:573–579.
- Briese, D. T. 1986. Factors affecting the establishment and survival of *Anaitis efformata* (Lepidoptera: Geometridae) introduced into Australia for biological control of St. John's wort, *Hypericum perforatum*. II. Field trials. *Journal of Applied Ecology* 23:821–839.
- Chesson, P. L. 1985. Coexistence of competitors in spatially and temporally varying environments: a look at the combined effects of different sorts of variability. *Theoretical Population Biology* 28:263–287.
- Chesson, P. L., and S. Ellner. 1989. Invasibility and stochastic boundedness in monotonic competition models. *Journal of Mathematical Biology* 27:117–138.
- Chesson, P. L., and N. Huntly. 1989. Short-term instabilities and long-term community dynamics. *Trends in Ecology & Evolution* 4:293–298.
- Chesson, P. L., and W. W. Murdoch. 1986. Aggregation of risk: relationships among host-parasitoid models. *American Naturalist* 127:696–715.
- Clancy, K. M., and P. W. Price. 1986. Temporal variation in three-trophic-level interactions among willows, sawflies, and parasites. *Ecology* 67:1601–1607.
- Comins, H. N., and M. P. Hassell. 1976. Predation in multi-prey communities. *Journal of Theoretical Biology* 62:93–114.
- . 1987. The dynamics of predation and competition in patchy environments. *Theoretical Population Biology* 31:393–422.
- Connell, J. H. 1990. Apparent vs. "real" competition in plants. Pages 9–26 in J. Grace and D. Tilman, ed. *Perspectives on plant competition*. Academic Press, New York.
- Cornell, H., and D. Pimentel. 1978. Switching in the parasitoid *Nasonia vitripennis* and its effects on host competition. *Ecology* 59:297–308.
- Dransfield, R. D. 1979. Aspects of host-parasitoid interactions of two aphid parasitoids, *Aphidius urticae* (Haliday) and *Aphidius uzbeckistanicus* (Luzhetski) (Hymenoptera, Aphidiidae). *Ecological Entomology* 4:307–316.
- Goeden, R. D., D. W. Ricker, and H. Müller. 1987. Introduction, recovery, and limited establishment of *Coleophora klimeschiella* (Lepidoptera: Coleophoridae) on Russian thistles, *Salsola australis*, in southern California. *Environmental Entomology* 16:1027–1029.
- Harper, G., and J. B. Whittaker. 1976. The role of natural enemies in the colour polymorphism of *Philaenus spumarius* (L.). *Journal of Animal Ecology* 45:91–104.
- Hassell, M. P. 1978. *The dynamics of arthropod predator-prey systems*. Princeton University Press, Princeton, N.J.
- Hassell, M. P., and R. M. Anderson. 1989. Predator-prey and host-pathogen interactions. Pages 147–196 in J. M. Cherrett, ed. *Ecological concepts: the contribution of ecology to an understanding of the natural world*. Twenty-ninth Symposium, British Ecological Society. Blackwell Scientific, Oxford.
- Hassell, M. P., and R. M. May. 1986. Generalist and specialist natural enemies in insect predator-prey interactions. *Journal of Animal Ecology* 55:923–940.
- Hassell, M. P., and S. W. Pacala. 1990. Heterogeneity and the dynamics of host-parasitoid interactions. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 330:203–220.
- Hassell, M. P., H. Comins, and R. M. May. 1991. Spatial structure and chaos in insect population dynamics. *Nature (London)* 353:255–258.

- Hawkins, B. A. 1988. Species diversity in the third and fourth trophic levels: patterns and mechanisms. *Journal of Animal Ecology* 57:137–162.
- . 1990. Global patterns of parasitoid assemblage size. *Journal of Animal Ecology* 59:57–72.
- Hawkins, B. A., and R. D. Goeden. 1984. Organization of a parasitoid community associated with a complex of galls on *Atriplex* spp. in southern California. *Ecological Entomology* 9:271–292.
- Hawkins, B. A., and J. H. Lawton. 1987. Species richness for parasitoids of British phytophagous insects. *Nature (London)* 326:788–790.
- Holt, R. D. 1977. Predation, apparent competition, and the structure of prey communities. *Theoretical Population Biology* 12:197–229.
- . 1983. Models for peripheral populations: the role of immigration. Pages 25–32 in H. I. Freedman and C. Strobeck, eds. *Population biology*. Springer, Berlin.
- . 1984. Spatial heterogeneity, indirect interactions, and the coexistence of prey species. *American Naturalist* 124:377–406.
- . 1987. Prey communities in patchy environments. *Oikos* 50:276–291.
- Holt, R. D., and M. P. Hassell. 1993. Environmental heterogeneity and the stability of host-parasitoid interactions. *Journal of Animal Ecology* 62:89–100.
- Holt, R. D., and B. Kotler. 1987. Short-term apparent competition. *American Naturalist* 130:412–430.
- Howarth, F. G. 1991. Environmental impacts of classical biological control. *Annual Review of Entomology* 36:485–509.
- Jeffries, M. J., and J. H. Lawton. 1984. Enemy free space and the structure of ecological communities. *Biological Journal of the Linnean Society* 23:269–286.
- Lawton, J. H. 1986. The effect of parasitoids on phytophagous insect communities. Pages 265–287 in J. Waage and D. Greathead, eds. *Insect parasitoids*. Thirteenth Symposium of the Royal Entomological Society of London. Academic Press, London.
- Lawton, J. H., and D. R. Strong, Jr. 1981. Community patterns and competition in folivorous insects. *American Naturalist* 118:317–338.
- Levins, R. 1968. *Evolution in changing environments*. Princeton University Press, Princeton, N.J.
- . 1979. Coexistence in a variable environment. *American Naturalist* 114:765–783.
- May, R. M. 1977. Predators that switch. *Nature (London)* 269:103–104.
- . 1978. Host-parasitoid systems in patchy environments: a phenomenological model. *Journal of Animal Ecology* 47:833–843.
- May, R. M., and M. P. Hassell. 1981. The dynamics of multiparasitoid-hosts interactions. *American Naturalist* 117:234–261.
- . 1988. Population dynamics and biological control. *Philosophical Transactions of the Royal Society of London B, Biological Sciences* 321:565–607.
- Murdoch, W. W. 1969. Switching in general predators: experiments on predator specificity and stability of prey populations. *Ecological Monographs* 39:335–354.
- Murdoch, W. W., J. Chesson, and P. L. Chesson. 1985. Biological control in theory and practice. *American Naturalist* 125:344–366.
- Parnell, J. R. 1964. The parasite complex of two seed beetles *Bruchidius ater* (Marsham) (Coleoptera: Bruchidae) and *Apion fuscirostre* Fabricius (Coleoptera: Curculionidae). *Transactions of the Royal Entomological Society of London* 116:73–88.
- Randall, M. G. M. 1982. The dynamics of an insect population throughout its altitudinal distribution: *Coleophora alticolella* (Lepidoptera) in northern England. *Journal of Animal Ecology* 51:993–1016.
- Rogers, D., and S. Hubbard. 1974. How the behaviour of parasites and predators promotes population stability. Pages 99–119 in M. B. Usher and M. H. Williamson, eds. *Ecological stability*. Chapman & Hall, London.
- Roughgarden, J., and M. Feldman. 1975. Species packing and predation pressure. *Ecology* 56:489–492.
- Schlumprecht, H. 1989. Dispersal of the thistle gallfly *Urophora cardui* and its endoparasitoid *Eurytoma serratulae* (Hymenoptera: Eurytomidae). *Ecological Entomology* 14:341–348.
- Settle, W. R., and L. T. Wilson. 1990. Invasion by the variegated leafhopper and biotic interactions: parasitism, competition, and apparent competition. *Ecology* 71:1461–1470.

- Strong, D. R., J. H. Lawton, and T. R. E. Southwood. 1984. Insects on plants: community patterns and mechanisms. Blackwell Scientific, Oxford.
- Sunose, T. 1985. Population regulation of the *Euonymus* gall midge *Masakimyia pustulae* Yukawa and Sunose (Diptera: Cecidomyiidae) by hymenopterous parasitoids. *Researches on Population Ecology (Kyoto)* 27:287–300.
- Teramoto, E., K. Kawasaki, and N. Shigesada. 1979. Switching effect of predation on competitive prey species. *Journal of Theoretical Biology* 70:263–271.
- Tilman, D. 1982. Resource competition and community structure. Princeton University Press, Princeton, N.J.
- Washburn, J. O., and H. V. Cornell. 1981. Parasitoids, patches, and phenology: their possible role in the local extinction of a cynipid gall wasp population. *Ecology* 62:1597–1607.
- Zwölfer, H. 1961. A comparative analysis of the parasite complexes of the European fir budworm, *Choristoneura murinana* (Hub.) and the North American Spruce budworm, *C. fumiferana* (Clem.). *Commonwealth Institute of Biological Control Technical Bulletin* 1:1–162.

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