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Adaptive Host Preference and the Dynamics of Host–Parasitoid Interactions

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Models of two independent host populations and a common parasitoid are investigated. The hosts have density-dependent population growth and only interact indirectly by their effects on parasitoid behavior and population dynamics. The parasitoid is assumed to experience a trade-off in its ability to exploit the two hosts. Three alternative types of parasitoid are investigated: (i) fixed generalists whose consumption rates are those that maximize fitness; (ii) ''ideal free'' parasitoids, which modify their behavior to maximize their rate of finding unparasitized hosts within a generation; and (iii) ''evolving'' parasitoids, whose capture rates change between generations based on quantitative genetic determination of the relative attack rates on the two hosts. The primary questions addressed are: (1) Do the different types of adaptive processes stabilize or destabilize the population dynamics? (2) Do the adaptive processes tend to equalize or to magnify differences in host densities? The models show that adaptive behavior and evolution frequently destabilize population dynamics and frequently increase the average difference between host densities. © 1999 Academic Press

Key Words: adaptive food choice; complex dynamics; habitat choice; host; parasitoid stability; switching.

INTRODUCTION

There is considerable evidence that consumer species adaptively adjust the nature of their consumption behavior when they are faced with a choice of two or more food sources (e.g., Murdoch, 1969; Murdoch and Oaten, 1975; May, 1977; Abrams, 1987; Tregenza *et al.*, 1996). Such adjustment can occur through various mechanisms and at various rates. On a long timescale, organisms can evolve to have greater or lesser abilities to acquire a particular resource if the relative abundance of that resource changes over the course of a number of consumer generations. On a short timescale, organisms may change their search mode or their time allocation to different habitats in order to acquire more of a particular resource. There are often changes in developmental characteristics that facilitate finding or capturing particular resources; these occur at intermediate timescales.

Regardless of their rates, adaptive changes are expected to increase the relative individual fitness of the consumer at any given time. However, there has been little consideration of how the dynamics of adaptation affects the dynamics of the entire consumer–resource system (but see Comins and Hassell, 1979, 1987; Bernstein, 1988; Kacelnik *et al.*, 1992; Abrams, 1992, 1999; Abrams and Matsuda, 1997; Krivan, 1997; van Baalen and Sabelis, 1993). It is common to assume that the instantaneous

consumption rates of resources by consumers are solely functions of the current densities of the resources (e.g., Murdoch and Oaten, 1975; Comins and Hassell, 1976; Levin, 1977; Teramoto *et al.*, 1979; Greenwood and Elton, 1979; Matsuda, 1985, and many others); this implies instantaneous responses of consumers to changes in resource density. The omission of the dynamics of adaptation is important because the population dynamics of the system affects the relative densities of different resources. These, in turn, affect the relative fitnesses of consumers with different choice-related traits. When the consumer–resource system has a stable equilibrium, such dynamics will usually only influence the transient behavior of the system. This has led to a significant amount of theory based on the idea that organisms that choose between resources achieve an "ideal free distribution" (Fretwell and Lucas, 1970; Milinski and Parker, 1991; Oksanen *et al.*, 1995) between alternative resources. At such a distribution, the fitnesses of consumers that utilize different resources are equal. If the resources have equal nutritional values and no differences in vulnerability to capture, the ideal free distribution implies equal densities of different resources. However, it is not clear that an ideal free distribution of consumers will characterize the system's long-term behavior when it does not approach a stable equilibrium. Many consumer–resource systems are capable of generating self-sustaining cycles, and long-term data suggest that sustained fluctuations in populations are common among natural populations (Ellner and Turchin, 1995). In these cases, the dynamics of adaptation may be a very important determinant of the mean densities of both consumers and resources, as well as their patterns of fluctuations (Schwinning and Rosenzweig, 1990; Abrams, 1999).

This article examines the potential consequences of different types of adaptation in a particular consumer–resource system, a one-parasitoid–two-host system, using several simple mathematical models. In particular, we are interested in determining whether adaptive processes occurring at different timescales stabilize or destabilize the population dynamics. In addition, we would like to determine whether adaptive choice of hosts promotes or hinders the parasitoid from achieving an ideal free distribution across the two types of host. We will also explore the consequences of the nature and speed of the adaptive process for the average difference in the abundances of the two host species. Other aspects of the system that will be examined include the qualitative nature of the system dynamics (stable point, cycles, aperiodic fluctuations) and the indirect effect of one host species on the other. The results suggest that changing the speed or nature of the adaptive progress may have large effects on overall dynamics, mean abundances, and the degree to which an ideal free distribution is approached. Paradoxically, the parasitoid's adaptive increase in its consumption of the more rewarding host species may prevent it from achieving an ideal free distribution, and may magnify differences between host densities. There are often major differences between the consequences of behavioral adaptation within a generation and adaptive evolution between generations.

MODELS

We consider a parasitoid that can use two noncompeting host species. There is a tradeoff between the parasitoid's attack rates on the two hosts, a_1 and a_2. In the main set of analyses, we assume a "symmetrical" model. Here, the two hosts have identical population growth functions, are equally suitable for parasitoid development, and have identical vulnerabilities to the parasitoid. In addition, the relationship between the two attack rates is symmetrical. We present more limited results for this system when the two hosts have different growth rate functions. Both types of system may also represent the dynamics of a parasitoid attacking two isolated populations of the same host species. We compare the population dynamics and densities of the species in this system under three sets of assumptions about the flexibility of the parasitoid capture rates:

(i) The attack rates are inflexible, but maximize individual parasitoid fitness; in the symmetrical system this means $a_1 = a_2$ (inflexible generalist parasitoid)

(ii) The attack rates are behaviorally flexible; the parasitoid adjusts them very rapidly within each generation based on the availability of hosts to maximize its fitness (ideal free parasitoid)

(iii) The attack rates are genetically determined characters and evolve at rates determined by their effects on fitness and the amount of genetic variation available (evolving parasitoid).

Two alternative formulations of "ideal free" behavior are examined, and a range of evolutionary rates are examined.

We describe the interaction using a modified Nicholson–Bailey model with density dependence in the hosts:

$$N_i(t+1) = N_t(t)\, e^{r_i(1-N_i(t))-a_i P(f)}, \qquad i = 1, 2 \qquad (1a)$$

$$P(t+1)$$
$$= [\,b_1 N_1(t)(1 - e^{-a_1 P(t)}) + b_2 N_2(t)(1 - e^{-a_2 P(t)})\,] \qquad (1b)$$

Here N_i is the density of host i, $\exp(r_i)$ is its finite intrinsic rate of increase, P is the parasitoid density and b_i is the number of adult parasitoids produced by a single parasitized host of type i. In the symmetrical models, it is assumed that $b_1 = b_2$, and these two parameters are both scaled to unity. The reproductive rate per host decreases exponentially with host density. Here we have scaled host population densities so that each host has a carrying capacity of $N_i = 1$. This model assumes that parasitized hosts contribute to density dependence in host reproduction in the same way as unparasitized hosts. Host mortality during the period of parasitoid activity is assumed to be insignificant. Equations (1a) and (1b) assume that the parasitoid has a linear functional response, so handling time of hosts is insignificant. We also assume that parasitoids are capable of detecting and avoiding already-parasitized hosts (i.e., there is no superparasitism). This assumption makes it possible for parasitoids to adopt an "ideal free" exploitation strategy within a generation. Host density dependence is also assumed to have no effect on the fitness of parasitoid larva developing within a host. This last assumption is often appropriate if host size (which generally decreases with host density) does not influence the fitness of parasitoid larvae developing within the host.

In the models investigated here, the trade-off between capture rates is assumed to be linear and symmetrical, so $a_1 + a_2 = A$, where A is the maximum attack rate. The parasitoid's phenotype on this continuum can be expressed in terms of a single trait, z $(0 < z < 1)$, which measures the degree of specialization on host 1, and where $a_1 = Az$ and $a_2 = A(1 - z)$. A linear trade-off is generally appropriate when the two hosts occur in different places, so that hunting for one precludes encountering the other. Linear relationships are also expected when hosts must be encountered using different searching techniques. In the models of inflexible generalists, z is constant, and has the value it would have if it were allowed to evolve at a very slow rate ($z = 0.5$ when the two hosts have identical growth rates).

In the models of ideal free parasitoids, the parasitoids are assumed to have instantaneous and accurate knowledge of all of the conditions necessary to make a fitness-maximizing choice of attack rates. However, there are two possibilities that must be considered. First, the parasitoids may have a single period before hosts become available during which they can fix their phenotype for the season (choose a habitat patch or specialized morphology). In this case, an individual's strategy remains the same over the course of the season, and individual fitness is maximized under this constraint. The second alternative is that the parasitoids are capable of adjusting attack rates during the season. Here, if rates of encounter with healthy hosts of one type are higher, only that type will be attacked; when encounter rates are equal, each host is equally likely to be attacked. The second alternative is appropriate when the parasitoid is capable of changing locations or behaviors rapidly throughout the season. We consider both possibilities.

When attack rates are fixed during the season, the optimal strategy of an individual parasitoid depends on what the rest of the population is doing. Thus, the optimal set $\{a_1, a_2\}$ (or the optimal z) is found by maximizing the fitness of a mutant with these characteristic in a population with mean attack rates $\{a_1^*, a_2^*\}$ or trait z^*. The mutant and resident strategies are then set equal to each other, and the resultant equation is solved to obtain the evolutionarily stable strategy (subject to additional stability conditions). Van Baalen and Sabelis (1993) have derived ideal free distributions in this case. Assume that the numbers of parasitoids produced per infected host (b_i) are identical and scaled to unity. Mutant fitness can then be expressed as the sum over all host species of the attack rate multiplied by the integral of the number of unparasitized hosts over the course of the season, yielding

$$W(a_1, a_2) = a_1 \int_0^1 N_1 \exp(-a_1^* Pt)\, dt$$

$$+ a_2 \int_0^1 N_2 \exp(-a_2^* Pt)\, dt$$

$$= a_1 N_1 \frac{1 - \exp(-a_1^* P)}{a_1^* P}$$

$$+ a_2 N_2 \frac{1 - \exp(-a_2^* P)}{a_2^* P}. \tag{2}$$

Assuming that population size is large, the rare mutant's effect on mean attack rates can be neglected. Maximization of the mutant's encounters with unparasitized hosts over the course of a generation occurs when

$$\frac{da_1}{dz} N_1 \frac{1 - \exp(-a_1^* P)}{a_1^* P} + \frac{da}{dz} N_2 \frac{1 - \exp(-a_2^* P)}{a_2^* P} = 0. \tag{3}$$
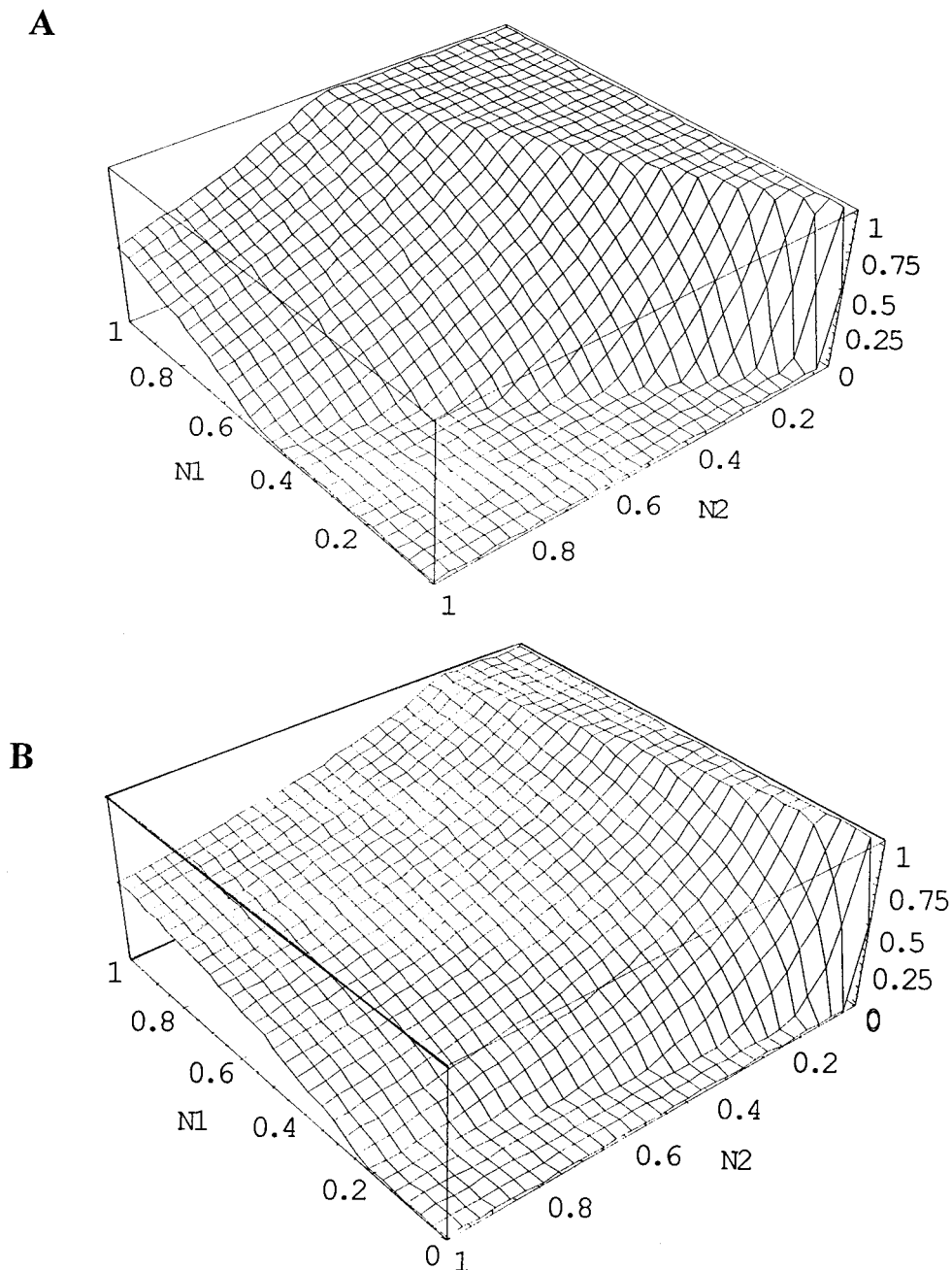
Using the formulas $a_1 = Az$ and $a_2 = A(1 - z)$, and setting mutant and resident strategies equal to each other, leads to the following equation for the optimal z:

$$N_1 \frac{1 - \exp(-AzP)}{z} = N_2 \frac{1 - \exp(-A(1-z)P)}{(1-z)}. \tag{4}$$

Unfortunately, this equation lacks a closed-form solution for the optimal (ideal free) z, but it can easily be solved numerically. Of course, z is constrained between 0 and 1; solutions of Eq. (4) < 0 imply that $z = 0$ is optimal, while Solutions > 1 imply $z = 1$ is optimal. Figure 1 is an illustration of the ideal free distribution for host densities between 0 and their carrying capacity. Formula (4)

implies that the number of parasitized hosts per parasitoid is identical for hosts 1 and 2. This will be referred to as a type 1 or fixed ideal free distribution to distinguish it from the following case.

Although setting z equal to the solution of Eq. (4) assumes instantaneous adjustment of this trait, the same results were obtained from models with a dynamic model

FIG. 1. Proportional choice of host 1 (z) as a function of the densities of the two hosts for parasitoids obeying the type 1 (A) and type 2 (B) ideal free distributions specified by Eqs. (4) and (5), respectively. The other parameter is $AP = 1.5$. Larger values of this parameter result in smaller ranges of host densities that predict specialization or near specialization on one host.

of parasitoid behavior (Abrams, unpublished). In these behavioral models, parasitoid individuals sequentially visit and compare their expected fitnesses in each of the two patches containing a different host population. The expected fitness depends on both the number of hosts in the patch and the number of parasitoids currently in that patch. Different sets of simulations used different movement rules that all specified greater probabilities of moving when the current patch yields a lower expected fitness than the previously visited one. In all cases, when the behaviors occurred quickly, the character z quickly approximated the constrained solution to Eq. (4) within a season.

The second possible type of behavioral optimization involves maximization of the attack rate of unparasitized hosts at all points in time during a season. Assume that at the beginning of a generation, host 1 is more abundant than host 2; i.e., $N_1 > N_2$. This means that all parasitoids adopt the maximum possible attack rate on (or forage exclusively for) N_1 when $N_1 \exp(-APt) > N_2$. (Here t varies between 0 and 1 and represents time by the fraction of the season available for search that has passed.) If and when some value of t causes both sides of this inequality to be equal, the parasitoids adopt a strategy of equal attack rates on both hosts for the remainder of the season. Similar considerations apply if the second host is initially more abundant. Time allocations can be translated directly into our choice variable, z, which here represents the fraction of time during the season that an average parasitoid spends foraging for host 1. In terms of between-generation dynamics, there is no difference between a single average value of z for the entire season and a set of several distinct values of z within the season having the same mean. Unless the two hosts start a season with identical populations, the first part of the season is always characterized by specialization on the more abundant host. The optimal value for z is

$$
\begin{aligned}
z &= 1 && \text{if} \quad N_1 \exp(-AP) > N_2 \\
z &= 0 && \text{if} \quad N_2 \exp(-AP) > N_1 \\
z &= \frac{1}{2}\left(1 + \frac{\ln(N_1) - \ln(N_2)}{AP}\right) && \\
&&& \text{if} \quad N_2 \exp(-AP) < N_1 < N_2 \exp(AP),
\end{aligned}
\tag{5}
$$

where the intermediate values of z represent an average of specialization for part of the season and equal searching for both hosts for the remainder. Using this strategy, the expected rates of encountering healthy hosts of each type will be equal at the end of the season, if this can be achieved. The strategy specified by Eqs. (5) will be referred to as a type 2 or flexible ideal free distribution. It is illustrated in Fig. 1B for one value of the product, AP; larger values increase the domain of host densities over which the optimal z is intermediate between 0 and 1. Compared to type 1 ideal free strategy, type 2 is characterized by intermediate z values over a wider range of host densities (see Fig. 1).

In the case of evolving parasitoids, we assume a standard phenotypic model for evolutionary change in a quantitative trait having a constant variance. The constant variance assumption cannot apply to the trait z, discussed above, because z is constrained to lie between zero and one. Thus, five assume that both z and a_i are mediated by a trait with value x, where

$$
z = \exp(\gamma x)/(1 + \exp(\gamma x)). \tag{6}
$$

The parameter γ determines how rapidly z changes with x. The trait x can take any positive or negative value with $x = 0$ denoting a generalist with equal consumption rates of each resource. Each attack rate changes in an S-shaped manner with x, implying that attack rates must change slowly when trait values become extreme. The change of the mean value of x, denoted $\bar{x}$, in one generation is given by an approximation (Abrams *et al.*, 1993) to the standard quantitative genetic recursion used by Lande (1976),

$$
\bar{x}(i+1) = \bar{x}(i) + v \frac{1}{\bar{W}} \frac{dW}{dx}, \tag{7}
$$

where W is the fitness of an individual with trait value x in a population whose mean trait is $\bar{x}$; W is given by Eq. (2) with $a_1 = Az$ and $a_2 = A(1-z)$ being expressed in terms of x, using Eq. (6). The parameter v in Eq. (7) is the additive genetic variance of x. It is easily verified that $dW/dx = \gamma z(1-z)\,dW/dz$, so it is possible to rewrite Eq. (7) using the substitution

$$
\frac{1}{\bar{W}} \frac{dW}{d\bar{x}}
$$

$$
= \frac{\gamma[N_1(1-\bar{z})(1 - e^{-A\bar{z}P}) - N_2\bar{z}(1 - e^{-A(1-\bar{z})P})]}{[N_1(1 - e^{-A\bar{z}P}) + N_2(1 - e^{-A(1-\bar{z})P})]}; \tag{8}
$$

where all variables are evaluated during generation i. It can be seen that, at a stable evolutionary equilibrium, the type 1 ideal free distribution condition must be satisfied (i.e., setting the numerator of Eq. (8) to zero is equivalent to Eq. (4)). It can also be seen that the rate parameter γ can be removed from the system if we scale v by multiplying it by γ; thus, γ will be dropped (i.e., scaled to unity) in the following analysis.

Numerical Methods and Their Limitations

Most of the results described below were obtained by numerical iteration of the systems of difference equations described above. In all except the evolutionary models, the symmetrical system (equivalent host growth equations), can be scaled to reduce the stability determining parameters to r and A. Thus, the dynamics for all of the models are summarized for a part of the plane of pairs of values of r and A. Simulations were carried out for each parameter combination on a grid with intervals of 0.1 on the A-axis and 0.025 on the r-axis. The maximum value of A considered was 10, because higher values usually resulted in unrealistically low parasitoid densities; the maximum r was 3.6, for the same reason. Because we were primarily interested in the ability of adaptation to equalize the densities of the two hosts, starting conditions were chosen to favor this outcome. Thus, unless otherwise noted, the simulations assume that initial population densities and trait value (z) are at their equilibrium values except that one host has a population 1% greater than its equilibrium. Additional simulations with one host at an initial density of 0.01 and the other host at a density of 0.99 were used to look for alternative attractors. In all simulations, the system was iterated for 20,000 generations, and the population densities from the last 10,000 generations were used to classify the dynamics and compute mean densities. When the system undergoes cycles, synchrony of hosts implies that the two hosts eventually come to have equal densities at any point in time; asynchrony implies differences between host densities at a given point in time. In the numerical work, synchrony was defined as a mean difference between host densities of less than 10^{-6} over the last 10,000 generations. Stable equilibria imply that host densities are equal when their growth functions are equivalent. The boundaries of the region of locally stable internal equilibria were determined by calculating eigenvalues of the linear approximation to the system at the equilibrium point. Boundaries between synchronous and asynchronous regions were estimated to be at the midpoint between grid points with these two types of dynamics. More details are given in the next section when Fig. 2 is presented.

RESULTS

I. Preliminaries: One- and Two-Species Subsystems

To understand the dynamic behavior of the three-species system based on Eqs. (1), it is important to review what is known of the dynamics of its one- and two-species subsystems (i.e., a single-host population, or one host–one parasitoid). Because there can be no choice without two hosts, none of these subsystems has any dynamics of traits. The exponential logistic model for the growth of a single host (or two noninteracting hosts) is locally stable for $r < 2$. This model is analyzed in May (1975); it undergoes a series of period doublings as r is increased above 2, eventually leading to chaotic behavior. There are windows of periodic behavior within the chaotic region (May, 1975); these ranges of r result in an average population density significantly lower than the nearby values of r that result in chaos.

The parasitoid–one-host model based on Eqs. (1) was considered by Beddington *et al.* (1975, 1978), and the nature of the dynamics when the equilibrium is unstable was illustrated for several parameter sets by Edelstein–Keshet (1988). In this case $z = 1$, in Eqs. (1), and the second host species is absent. Neubert and Kot (1992) present a more general analysis of several parasitoid–single-host models with density-dependent host growth. Kaitala *et al.* (1999) have recently analyzed a one-host analogue of Eqs. (1) that differs in having a slightly nonlinear parasitoid functional response. Local stability of the equilibrium of Eqs. (1a) and (1b) with both species present depends upon r and the product Ab. Locally stable equilibria with all species present are possible for a range of maximum attack rates Ab between 1 and slightly larger than 3, provided that r is not too large. Given our scaling ($b = 1$), all systems lack stable equilibria for maximum attack rates, A, greater than approximately 3.255, regardless of host growth rate. When the system is unstable, a wide variety of complex dynamics may occur, depending on parameter values Neubert and Kot, 1992; Kaitala *et al.*, 1999); there can be dramatic changes in dynamics with small changes in the values of either r or Ab. When there is a locally stable equilibrium point, the point is often not globally stable; this occurs when r is relatively large (Beddington *et al.*, 1978).
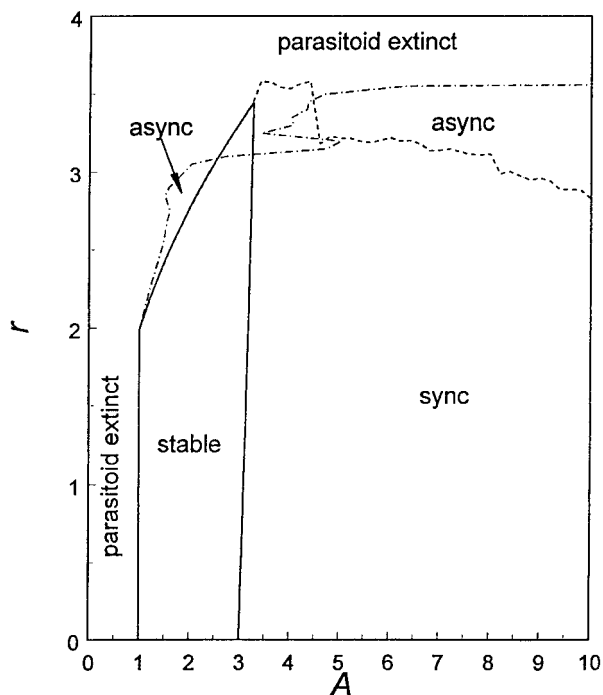
II. A Parasitoid and Two Hosts Characterized by Identical Parameter Values

The analysis in this article is primarily concerned with the symmetrical case in which hosts are characterized by identical parameter values (see Models). Here, the equilibrium with all three species present has equal host densities and, therefore, equal attack rates ($z = 1/2$). There are two reasons for concentrating on this rather special case. First, the parameter space for this case can be analyzed much more thoroughly than the more general case with nonequivalent host species. Second, if the

parasitoid is ever able to equalize host densities, it seemed most likely to do so when both hosts have identical growth equations.

Inflexible Generalist Parasitoids. The population dynamics of a system with an inflexible generalist parasitoid are governed by Eqs. (1a) and (1b) with $b_i = 1$, and with $a_1 = a_2 = A/2$ (i.e., $x = 0$ or $z = 0.5$). Although Comins and Hassell (1976) determined the conditions for local stability in this model (see also Fig. 2), its behavior when the equilibrium point is locally unstable has apparently not received detailed consideration. Figure 2 shows the boundaries in parameter space of the region of local stability of the equilibrium. It also shows the approximate boundaries of regions where unstable

Inflexible

FIG. 2. Dynamic behaviors in the symmetric model of two hosts and an inflexible parasitoid as a function of maximum parasitoid attack rate, A, and host growth rate, r. The labels "sync" and "async" denote regions of parameter space where the equilibrium with all species present is locally unstable, and the two hosts have synchronous (population densities equal at all times) or asynchronous (unequal populations), dynamics, respectively. The dashed line separates parameters producing synchronous host dynamics and those producing asynchronous host dynamics. The dot-dashed line is the boundary of parameters that allow a rare parasitoid to increase when the two hosts have synchronized dynamics (the most difficult case for invasion of the parasitoid). Synchronized dynamics occur when the initial host densities are equal before introduction of the parasitoid. Parameters above and to the left of this line do not allow invasion in this case. See the text for more details.

dynamics are characterized by synchronized or asynchronous host densities, as well as parameter values for which parasitoid extinction can occur.

Figure 2 is only an approximate classification of population dynamics for several reasons. It is based on simulations with a grid of parameter values that differ by 0.1 on the A-axis and 0.025 on the r-axis; thus fine details of the boundaries between different types of dynamics are not evident. If there is an extremely slow approach to synchronous dynamics, it may be incorrectly classified as asynchronous by the numerical criterion described above. There are also several other important features of the dynamics that are ignored. First, the figure includes parameter values that result in extremely low densities of one or both of the species. When a relatively large A is combined with small r, the cycles in parasitoid density are of such high amplitude that they would guarantee extinction in almost any natural population. For example, the parasitoid population density drops below 10^{-16} during the course of a limit cycle for $A = 5$ when $r < 0.137$ or for $A = 10$ when $r < 0.755$. However, the boundary of this region is not shown on the figure. A second aspect of dynamics that is not treated in the figure is the presence of two or more attractors for some sets of parameters. Alternative attractors are common when r is large enough that host populations cycle in the absence of the parasitoid ($r > 2$). In this case, if the initial densities of the two hosts are identical, their synchronized fluctuations result in a lower geometric mean parasitoid fitness than do asynchronous fluctuations. Thus, there is often an attractor with a positive parasitoid density and an alternative with zero density of the parasitoid. Neubert and Kot (1992) discuss this phenomenon for analogous single-host–parasitoid models. Parasitoids are unlikely to persist in a stochastic environment if there exists an attractor with zero parasitoid density. The dot-dashed line in Fig. 2 represents the approximate boundary in parameter space where synchronized host densities will prevent a parasitoid from increasing when it is rare (parasitoid invasion fails for some initial host densities for all parameter combinations above this line). This boundary is again approximate because of the finite grid of parameters used for the simulations. Growth rates were determined by calculating parasitoid fitness when the parasitoid density was zero and both hosts had equal initial population sizes. When $r >$ approximately 3.5, parasitoid abundance dips below 10^{-16} for all initial conditions. Thus, persistence in a stochastic environment is unlikely for systems with parameter values lying above and to the left of the dot-dashed line in Fig. 2.
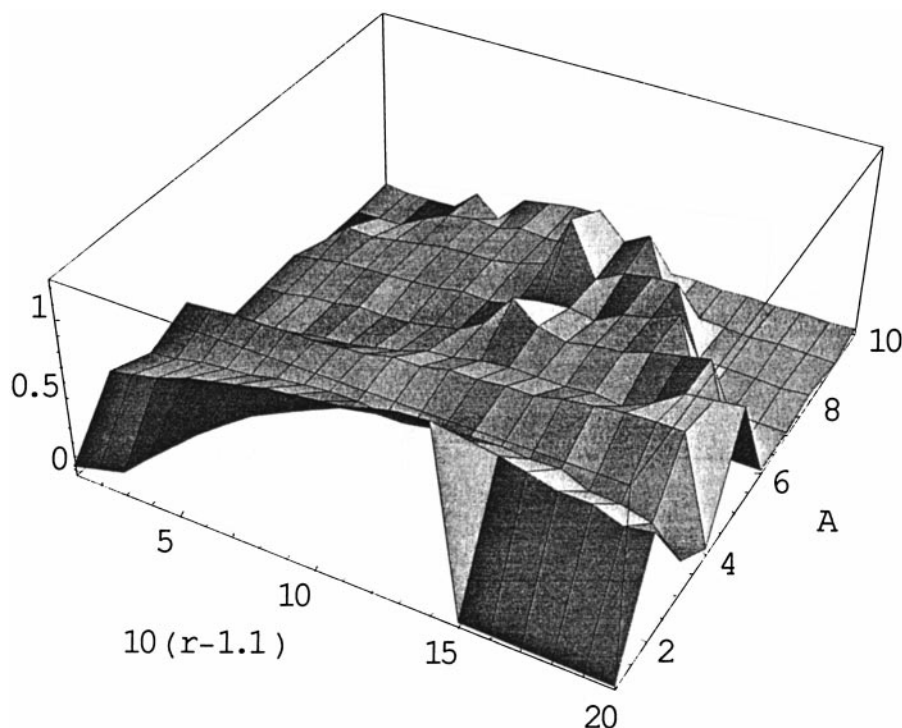
A wide range of dynamics occurs within both the synchronous and asynchronous regions of parameter

space. For r and A values immediately above the stable zone, there is a two-point cycle where parasitoid abundance is constant, but the two hosts alternate between higher and lower values, 180° out of phase with each other. For parameters further from the boundary of the stability region, the parasitoid population begins to fluctuate as well as the hosts. The cycles may become very complicated, but even then, each host density alternates above and below the equilibrium density each generation. The asynchronous fluctuations that occur when r is still further above the stable zone are generally more complicated cycles or aperiodic fluctuations. The asynchronous fluctuations that occur when either A or r is large appear to be aperiodic. When both parameters are large ($r > 3$; $A > 4.5$) there are periods of almost synchronous fluctuations interrupted at irregular intervals by periods of highly asynchronous fluctuations.

Establishing the exact dynamics for different parameter values is not required for the main subject of this investigation. Here, we are primarily concerned with stability and the mean difference between the two host densities. The inflexible generalist model reviewed above shows that asynchronous attractors are possible in systems where the parasitoid does not exhibit any adaptation. At such an attractor, the two hosts differ in population densities at all times unless initial conditions specify densities that are exactly equal. This raises the question whether adaptive host choice based on either behavior or genetics can synchronize (i.e., equalize) host populations.

Type 1 *Ideal Free Parasitoids.* We start by considering choice based on type 1 ideal free behavior. Analysis is hindered by the lack of a closed-form solution for the ideal free value of z as a function of host densities. However, simulations over the grid in parameter space used to produce Fig. 2 have failed to reveal any systems with either a stable equilibrium or synchronized cycles. The mean difference between the two host densities over the largest part of this space is shown in Fig. 3. The values of zero in this figure do not indicate synchronization caused by the parasitoid; rather they indicate that the parasitoid went extinct (minimum density $< 10^{-16}$). In fact, the parasitoid goes extinct over the entire range of large A and large r where the inflexible generalist parasitoid produces asynchronous host dynamics. The mean difference between host densities is greater than

FIG. 3. The mean difference between the densities of the two hosts when the parasitoid exhibits type 1 ideal free behavioral choice of hosts. Note that host carrying capacity is one. The x-axis shows transformed r values with r ranging from 1.2 to 3.1. The values of zero in the upper rear part of the figure (large A and r) indicate extinction of the parasitoid (the difference between host densities was not measured for these cases).

TABLE I

Mean Difference between Host Densities when $A = 2$ for Inflexible and Ideal Free Parasitoids

r	Inflexible	Ideal Free 1	Ideal Free 2
1.1	0	0.370	0
1.5	0	0.560	0
1.75	0	0.665	0.559
2.0	0	0.750	0.748
2.25	0	0.805	0.804
2.5	0	0.845	0.837
2.75	0	0.755	0.705
3.0	0.730	0.665	0.547
3.1	0.734	0.685	0.600
3.2	0.740	0.735	*a*
3.3	0.748	0.840	*a*
3.4	0.755	0.970	*a*

a Predator always goes extinct (population density $< 10^{-16}$).

50 % of host carrying capacity over most of the range of parameters shown in Fig. 3. For those parameters where parasitoid persistence and asynchrony occur in both the inflexible and type 1 parasitoid models, the mean difference in host densities is similar in magnitude. This parameter realm occurs above the stable region in Fig. 2, and is centered about a maximum attack rate of $A = 2$. Table I presents the mean difference between host densities for a range of host growth rates, given a maximum attack rate of 2; the table presents figures for the inflexible parasitoid model and for each of the two types of ideal free behavior. Comparison of the first two columns shows that, when both the inflexible and type 1 models produce asynchrony in host dynamics, the mean difference between host densities is larger for the type 1 parasitoid when $r > 3.2$. However, this represents part of parameter space where parasitoid extinction is probable. With slightly smaller values of r, the inflexible parasitoid produces a slightly larger heterogeneity in host densities than does the type 1 parasitoid.

A range of different dynamics occurs in the unstable systems characterized by type 1 ideal free behavior. The relatively low A and r values that produce stable equilibria in the inflexible parasitoid are here replaced by cycles with a period of two generations, where the two hosts alternate between population sizes above and below the equilibrium point while the parasitoid density remains constant. Larger values of either A or r result in a wide variety of more complicated dynamics. Dynamics with alternating periods of near synchrony and great asynchrony occur with large values of A and r.

Type 2 Ideal Free Parasitoids. Type 2 ideal free behavior, unlike type 1, permits parasitoids to change their attack rates within a generation. Such switching is likely if individuals remain mobile and are able to assess the density of unparasitized hosts in a patch. Figure 4 is an approximate classification of the dynamics that occur for the model of parasitoids with type 2 ideal free behavioral choice of hosts. This figure was based on the same grid in parameter space used in Fig. 2, with intervals of 0.1 between adjacent values of A and intervals of 0.025 between adjacent values of r. Unlike type 1 choice, type 2 choice produces a stable equilibrium point for a range of parameter values. However, behavior again changes the zones of stability, synchrony and asynchrony compared to the case of an inflexible parasitoid (Fig. 2). The three main results that can be seen from a comparison of Figs. 2 and 4 are as follows: (1) Type 2 ideal free choice significantly reduces the range of parameters that yield a stable equilibrium point; this is due to a reduction in the maximum host growth rate, r, that produces a
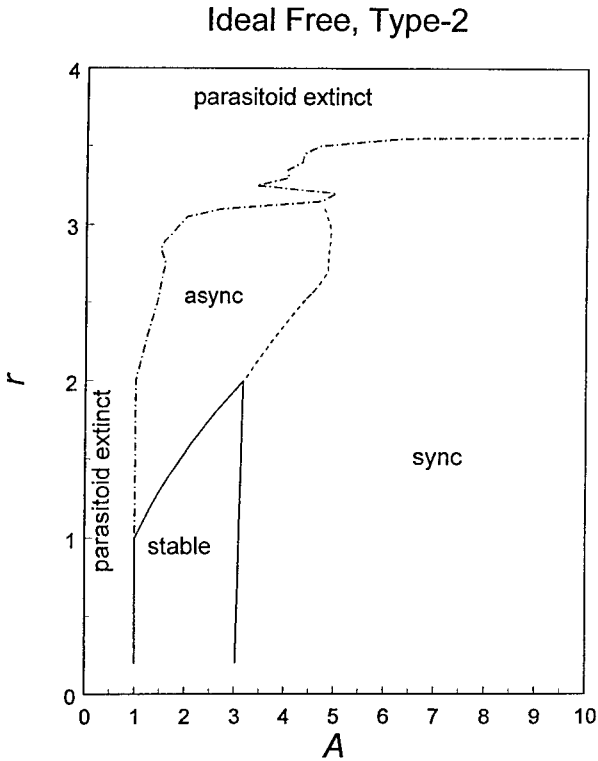

FIG. 4. Classification of dynamic behaviors in the symmetric model of two hosts and a type 2 ideal free parasitoid as a function of maximum parasitoid attack rate, A, and host growth rate, r. As in Fig. 2 "sync" and "async" denote regions of parameter space where the equilibrium with all species present is locally unstable, and the two hosts have synchronous or asynchronous dynamics, respectively; the dashed line separates these regions. As in Fig. 2, the dot-dashed line is the boundary of parameters that allow a rare parasitoid to increase when the two hosts have synchronized dynamics (the most difficult case for invasion of the parasitoid).

stable equilibrium for a given maximum attack rate, *A*. (2) Type 2 choice significantly increases the range of parameters producing asynchronous dynamics when attack rates are low or moderate ($A < 5$). (3) Type 2 choice decreases the range of parameters producing asynchronous dynamics when attack rates are high ($A > 5$). The biological significance of this loss of asynchrony is questionable; much of the zone of asynchronous dynamics at high values of *A* in Fig. 2 implies extremely low minimum parasitoid densities that would mean extinction in most populations of realistic size). It is possible for increased host growth rate to synchronize dynamics when the parasitoids exhibit ideal free choice (roughly for *A* between 3 and 5 and *r* close to 3). When the parasitoid does not have any adaptive plasticity (Fig. 2), increasing *r* can only change synchronous fluctuations to asynchronous ones.

Many possible dynamic patterns occur within the regions of parameter space labeled synchronous and asynchronous in Fig. 4. As an example, we consider in greater detail the dynamics that occur for various host growth rates when $A = 3.5$. Figure 4 shows that, when the parasitoids have this attack rate, dynamics switch from synchronous to asynchronous, and back to

synchronously as *r* increases. Figure 5 shows the mean difference in host densities, the mean parasitoid density, and the mean density of each host, as *r* increases from 2.0 to 3.15 (for $A = 3.5$). A difference in host densities of 0 indicates a synchronous attractor. The dynamics for *r* between 2.0 and 2.3 are cycles with an approximate 5-generation period whose amplitude varies on a much longer time scale. At $r = 2.4$, there is an exact period 5 cycle. Two alternative attractors exist when *r* is close to 2.5; on each attractor the populations undergo a cycle with a period of 10 generations, with one host having a mean population density approximately 1% higher than that of the other host. In the figure, these two densities were averaged. From $r = 2.6$ through $r = 3.0$ there is an apparently aperiodic attractor with asynchronous host dynamics. At still higher host growth rates, small changes in *r* can cause dramatic changes in the dynamics of the system (and in mean population densities). At $r = 3.025$ there is a period 5 cycle with synchronized hosts; at $r = 3.075$, the only attractor is an aperiodic one with asynchronous host dynamics; at $r = 3.15$, the parasitoid goes extinct from all initial densities. There are long-lasting but transient asynchronous dynamics for some values of *r* where the attractor has synchronized hosts (e.g.,
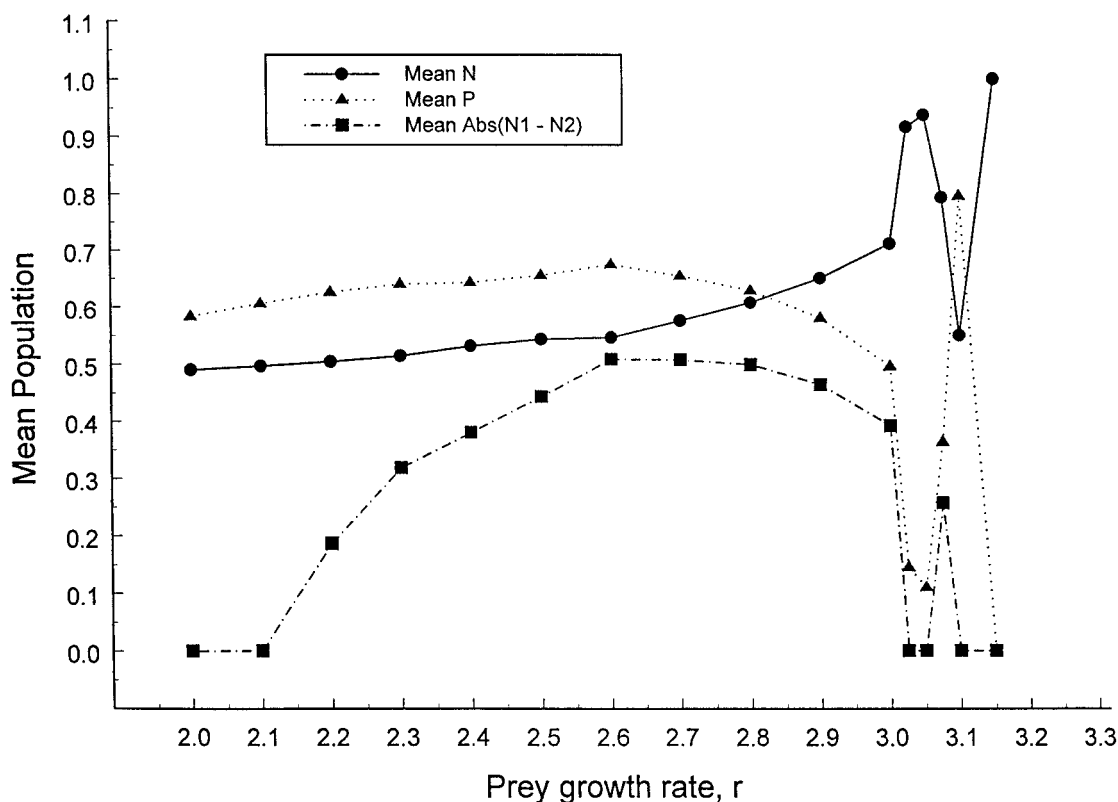

FIG. 5. Mean densities and difference between host densities as a function of host intrinsic growth rate for the type 2 ideal free parasitoid and equivalent host growth rate functions. The parasitoid's maximum attack rate is $A = 3.5$.
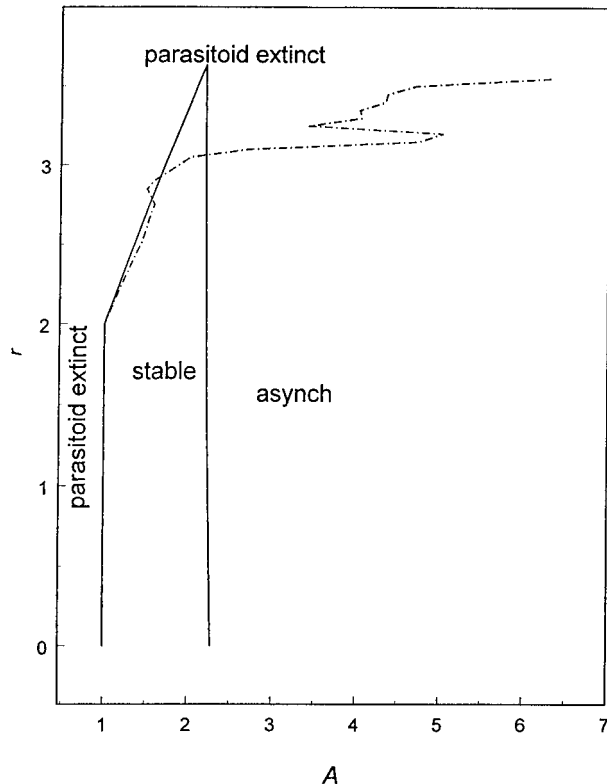
$r = 3.1$). Figure 5 and the right-most column in Table I both show that the mean difference between host densities in asynchronous systems is often a significant fraction of the host carrying capacity; this is also true for most other values of A where asynchrony is possible in this model. Thus, the process of unconstrained and cost-free optimal foraging by individual parasitoids often increases the difference between densities of the two hosts.

It is difficult to present simple intuitive reasons for the asynchrony that can be produced by the parasitoid's choice of the more rewarding host under either type of ideal free behavior. However, the potential for ideal free choice to produce asynchrony can be thought of as a consequence of overshooting the potential attractor with equal densities of both hosts. When one host is rare, ideal free choice greatly reduces the attack rate of this host by the parasitoid, at the same time that density dependence is also reduced. As a result, this host species often

becomes the more abundant species in the following generation, and the system moves farther from its equilibrium values. The fact that ideal free choice can equalize the densities of unparasitized hosts by the end of the season does not imply equal densities at the start of the next season because density-dependent reproduction is a function of densities at the beginning of the season.
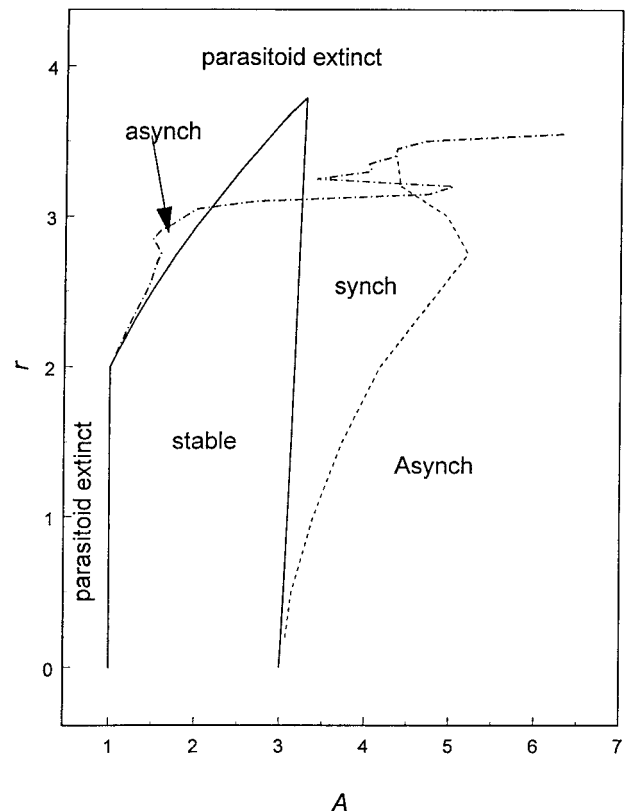
Evolving Parasitoids. The next model we consider is based upon evolutionary change in a quantitative trait that determines choice (Eqs. (7) and (8)). The dynamics of this model are sensitive to the additive genetic variance, v. This parameter may be considered a rate constant for adaptive change when the basis of the trait is something other than polygenic inheritance. Dynamics are sensitive to the shape of the relationship between the traits and the measure of specialization, z. Larger values of the shape parameter γ in Eq. (6) imply a relationship

FIG. 6. Classification of dynamic behaviors in the symmetric model of two hosts and an evolving parasitoid with an additive genetic variance (v) of 0.25 and a trait–choice slope parameter (γ) of 5. The region of parameter space covered and the meanings of the labels are identical to those in Figs. 2 and 5. The dot-dashed line is again the boundary of parameters that allow a rare parasitoid to increase when the two hosts have synchronized dynamics.

FIG. 7. Classification of dynamic behaviors in the symmetric model of two hosts and an evolving parasitoid. The system studied is identical to that illustrated in Fig. 6 except that the additive genetic variance is smaller; $v = 0.05$.

that is closer to a step function. However, as noted before, the effects of increasing γ are equivalent to increasing v in the model with equivalent hosts. The size of the parameter domain producing stability decreases as the product, γv, increases. Figures 6 and 7 classify the possible system dynamics for two rates of adaptive change ($v = 0.25$ in Fig. 6 and $v = 0.05$ in Fig. 7), both assuming that $\gamma = 1$. The classification for $v > 0.25$ resembles Fig. 6, except that the stability zone is smaller. The classification for $v < 0.05$ is similar to fig. 7, except that the boundary between synchronous and asynchronous behavior is moved to the right (to larger values of A), implying that synchronous dynamics are more likely. Relatively rapid adaptation (a large response to selection) reduces the parameter space that allows local stability, and tends to produce asynchrony of the two hosts when the equilibrium is unstable. Conversely, slower adaptive change increases the parameter domain with a locally stable equilibrium, and tends to produce synchronized dynamics when the equilibrium is unstable. However, a sufficiently large parasitoid attack rate, A, will produce asynchronous host dynamics in systems with small values of $v\gamma$.

When they produce asynchronous host dynamics, the genetic models often produce large mean differences between host densities. This is quantified in Table II for

TABLE II

Mean Differences between Host Densities in the Genetic Model Illustrated in Fig. 7

		A	
r	4	5	6
0.2	0.0826	0.1524	(Parasitoid extinct)
0.4	0.1143	0.1745	(Parasitoid extinct)
0.6	0.1215	0.1900	0.2224
0.8	0.1308	0.1980	0.2317
1.0	0.1683	0.2039	0.2451
1.2	0.1792	0.2118	0.2546
1.4	0.1771	0.2333	0.2486
1.6	0	0.2775	0.2241
1.8	0	0.2932	0.2904
2.0	0	0.3045	0.3396
2.2	0	0.2973	0.3732
2.4	0	0.2965	0.4126
2.6	0	0	0.2076
2.8	0	0	0.2368
3.0	0	0.0604	0.2765
3.2	0	0.2968 (0.0243)[a]	0.4313 (0.0960)[a]
3.4	0	0.5345 (0.4086)[a]	0.5741 (0.4405)[a]

[a] Figures in parantheses are the comparable figures for an inflexible generalist parasitoid.

the model with $v = 0.05$, which is employed in Fig. 7. The table shows how the mean difference between prey densities changes with increasing host growth rate for three values of the attack rate A that span much of the region of parameter space with realistically bounded fluctuations. The mean difference between host densities is frequently a significant fraction of the carrying capacity. There are several parameter values in Table II for which the inflexible generalist also generates asynchronous population cycles. The mean difference between host densities produced by the inflexible generalist is given in parentheses in Table II for these cases. The figures indicate that the evolving parasitoid generates a larger difference between host densities. Simulations investigating a range of genetic variances have shown that increasing v may either increase or decrease the magnitude of the difference between host populations.

In the evolutionary model, the parasitoid's evolution is actually maladaptive when host densities alternate above and below the equilibrium each generation. Such alternation occurs when the maximum attack rate A is below a threshold magnitude that depends on the other parameters of the system. This alternation of the relative densities of the two hosts ensures that each new generation of parasitoids will be more adapted to the host that was more common in the previous generation, but is currently less common. In such circumstances, one would expect selection to favor reduction or loss of genetic variation in the trait that determines attack rates. This could be achieved by the increase in frequency of modifier genes that reduce the expression of underlying genotype-level variation in the phenotype. Such genetic canalization has been previously proposed in the context of long-term stabilizing selection (Rendel, 1967; Stearns and Kawecki, 1994).

III. A Parasitoid and Two Hosts Characterized by Different Parameter Values
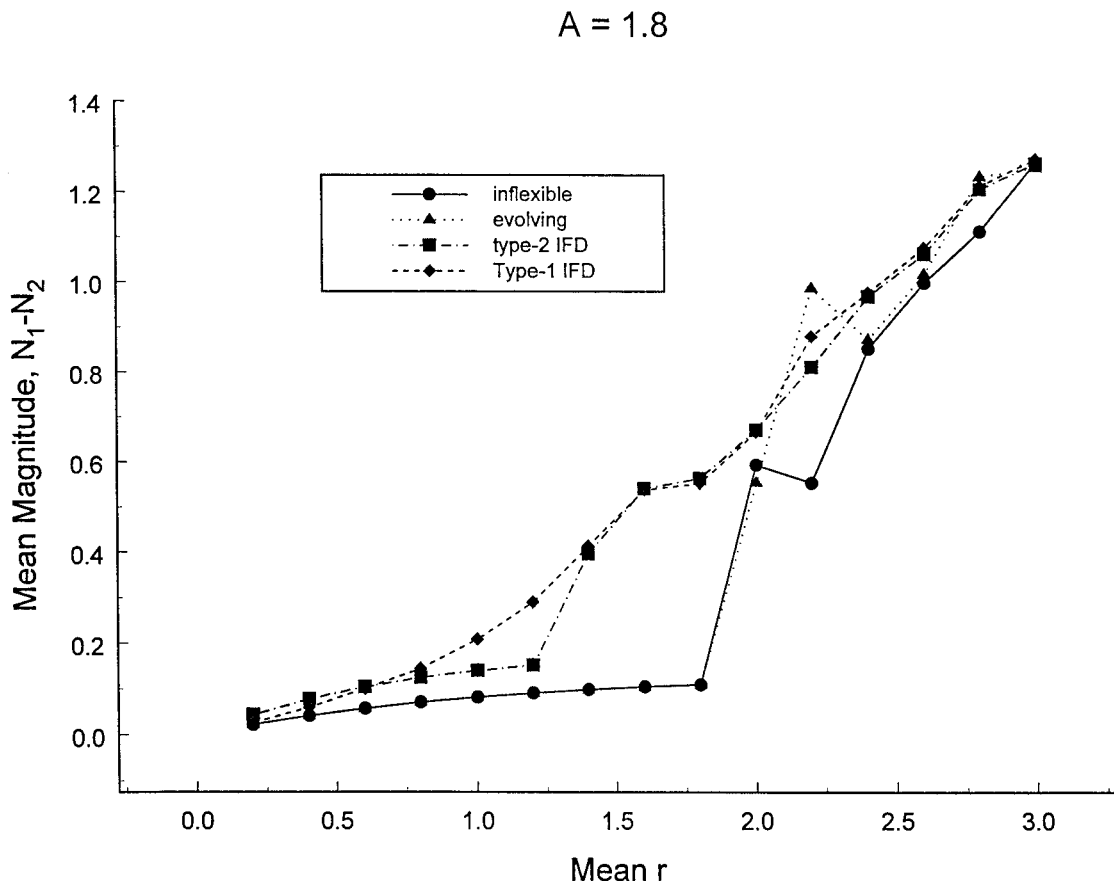
Allowing asymmetries in the basic system described by Eqs. (1) leads to a huge expansion in the parameter space that must be analyzed to determine the possible behaviors of the system. Asymmetries may occur in the maximum growth rates and/or carrying capacities of the hosts. Other potential asymmetries involve differences in the parasitoid's maximum attack rate on each host or differences in the number of parasitoid progeny produced by an infected host. It is beyond the scope of the present article to give a comprehensive treatment to all of these models. Instead, we present results for one particular type of asymmetry, differences in the intrinsic growth rate of the two hosts. These limited results are important

because they show that adaptive choice of hosts frequently increases the mean difference between host densities, even in the biologically more realistic case of nonequivalent hosts. This also appears to be true of the other types of asymmetry described above (Abrams, unpublished). Thus, the main results described in Section II do not appear to be artifacts of the symmetry of the model.

Some changes in methods are required for asymmetric systems. When a system is both asymmetrical and unstable, it is no longer obvious what consumption rates are optimal for an inflexible parasitoid. The approach used here was to determine the appropriate values of a_1 and a_2 using the quantitative genetic model with a very small genetic variance (in the figures below, $v = 0.005$ with $\gamma = 5$). Thus, the "inflexible" parasitoid is actually a very slowly evolving one, having temporal variation in its choice trait z that is very small relative to the mean. Fixing the attack rates at the mean value of z did not cause a significant difference in the dynamics. No changes were made in the models with dynamic choice of prey.

The value of v used for the evolving parasitoid was $v = 0.05$ (with $\gamma = 5$). The two types of ideal free parasitoids had parameters identical to those used in Figs. 3 and 4. The case with $r_1 = 3r_2$ illustrates the major features present in most systems with significant asymmetry in r. This system was iterated for the same grid of values of A and $\hat{r} = (r_1 + r_2)/2$ used in Figs. 2 and 4 for all of the types of models considered above (substituting the case of slow evolution for the case of an inflexible parasitoid).

Figures 8 through 11 summarize the results of these simulations by plotting the mean difference between prey population sizes for each of four different types of parasitoid; each figure shows a different transect across the parameter space. There are some sets of parameters where some types of adaptive choice reduce the difference between host population sizes compared to a system with an inflexible parasitoid. However, there is no graph for which any one of the three types of choice reduces heterogeneity in host densities over the majority of the parameter range examined. In many cases, behavioral choice
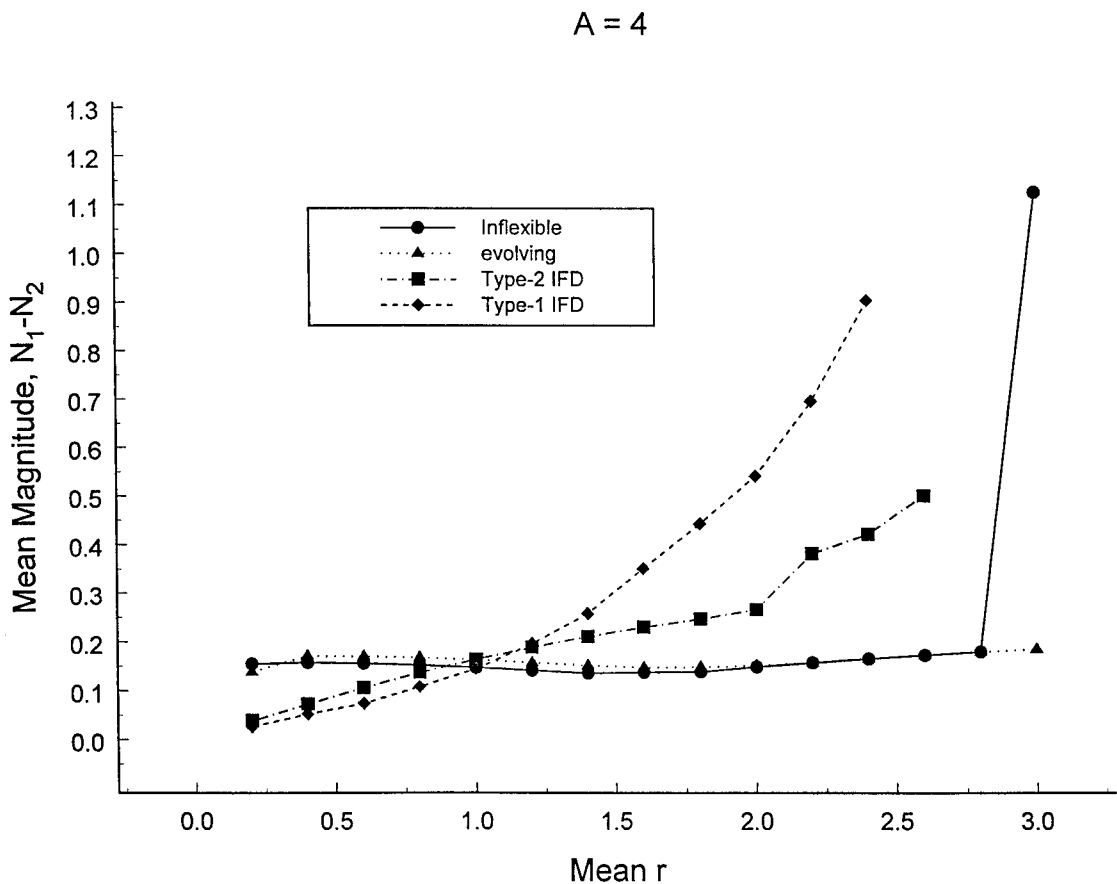

$$A = 1.8$$

FIG. 8. Mean difference between host densities for each of four types of parasitoid when hosts differ by a factor of 3 in their intrinsic growth rates. The figure quantifies host heterogeneity across a range of mean host intrinsic growth rates when the maximum attack rate $A = 1.8$. Note that the "inflexible" parasitoid is a very slowly evolving one, as described in the text.

results in heterogeneity that is several times larger than that for the inflexible (slowly evolving) parasitoid. When the mean host growth rate is relatively large (above approximately 2), the two ideal free parasitoids produce heterogeneities in host densities that are much larger than those generated by the inflexible or evolving parasitoid. Behavioral choice significantly reduces heterogeneity when mean host growth rate is small and attack rates are large (see Fig. 10). Comparing systems with more rapid genetic change to those with very slow change (labeled "inflexible" in Figs. 8–11), a large difference in the rate of adaptive change (v) has relatively modest effects on host heterogeneity for most parameter values; however, the change in host heterogeneity produced by faster adaptation may be an increase or a decrease.

Although the stability of equilibria is not noted in Figs. 8–11, there are some differences in the ranges of parameter space that yield stable equilibria rather than sustai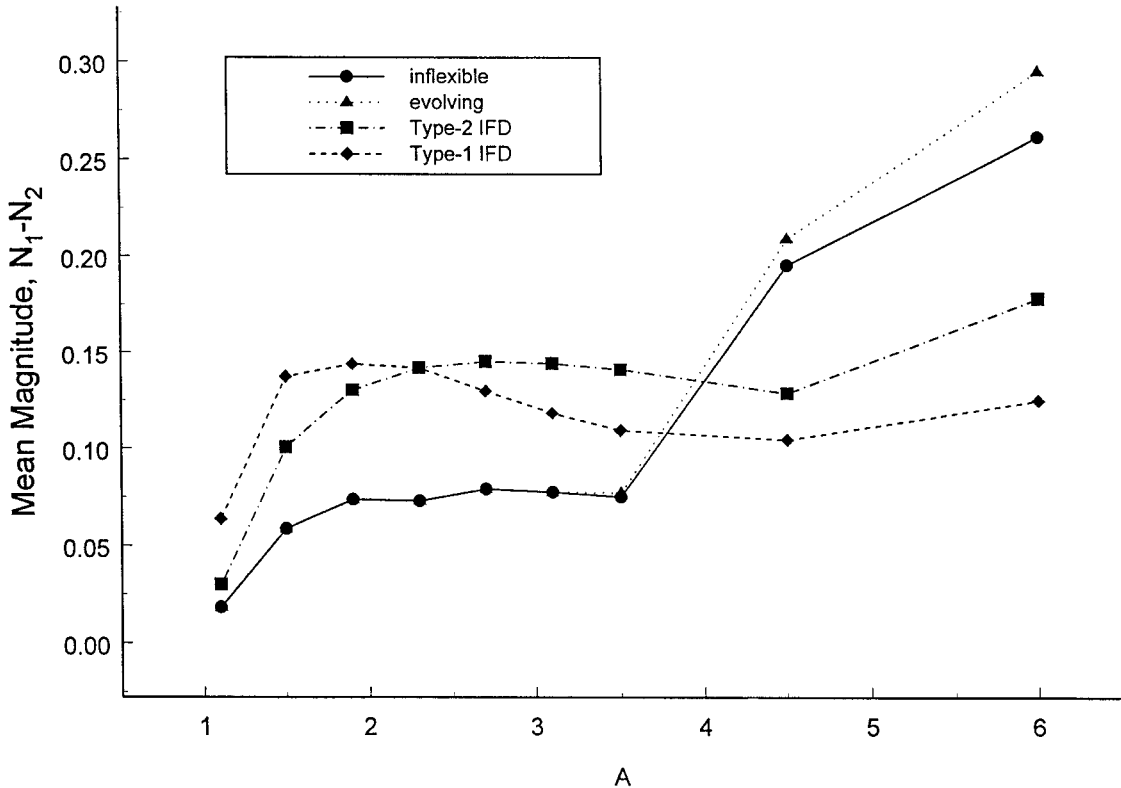ned fluctuations. As was true in the symmetric models, systems with a type 1 ideal free behavior lack stable equilibria for all of the parameter values in the grid from $A = 1$ to 10 and $\hat{r} = 0.2$ to 3.5. All other models had locally stable equilibria when both $\hat{r}$ and A were sufficiently low (but $A > 1$). For the inflexible and evolving parasitoids, there were some intermediate ranges of $\hat{r}$ that produced stable equilibria although smaller values did not. For example, the inflexible and evolving parasitoid produced stable systems for most of the range from $\hat{r} = 2$ to $\hat{r} = 3$ when $A = 4$. Both behavioral models were unstable over this range. When both systems are unstable, the type 1 ideal free parasitoid produces a larger difference in host densities than does type 2 for most of parameter space (although not for an area with large A and small $\hat{r}$ values). In addition, type 1 behavior was characterized by the widest range of parameters where the parasitoid went extinct (see Fig. 11).

These results confirm the main result of Section II; i.e., adaptive choice between two hosts by a parasitoid frequently increases the difference between host densities,

$$A = 4$$

FIG. 9. Mean difference between host densities for each of four types of parasitoid when hosts differ by a factor of 3 in their intrinsic growth rates. The figure quantifies host heterogeneity across a range of mean host intrinsic growth rates as in Fig. 8, except that the maximum attack rate $A = 4.0$. The missing data points at high $\hat{r}$ values indicate that the parasitoid went extinct for these attack rates.
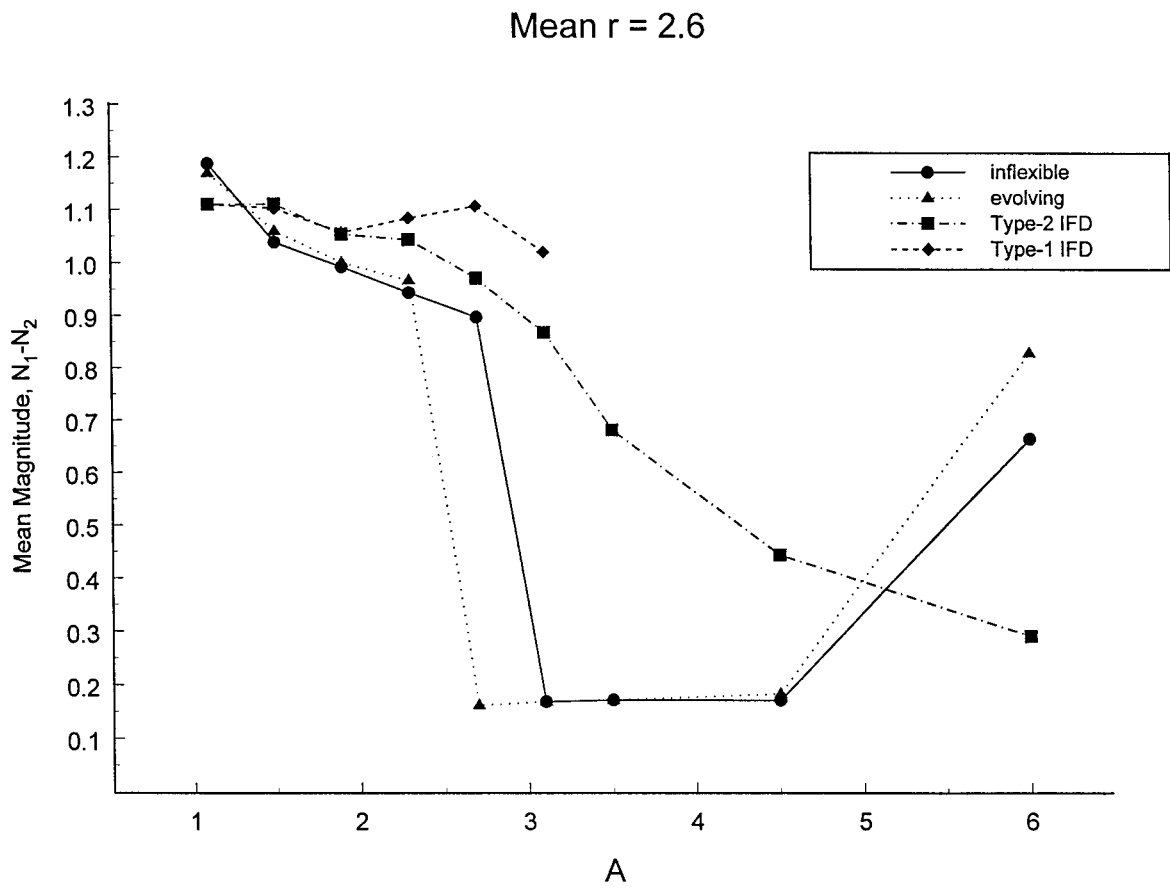
Mean r = 0.8

FIG. 10. Mean difference between host densities for each of four types of parasitoid when hosts differ by a factor of 3 in their intrinsic growth rates. The figure quantifies host heterogeneity across a range of maximum parasitoid attack rates, A, when $\hat{r} = 0.8$.

even when the two hosts are equally suitable for parasitoid development. Preliminary simulations of other asymmetric systems (hosts with different carrying capacities and parasitoids with asymmetrical trade offs between attack rates) also support this generalization.

DISCUSSION

It is both intuitive and widely believed that adaptive choice of the more common victim type by a predator or parasitoid will generally make the abundances of the two (or more) victims more nearly equal than they would have been without consumer choice. This simple logic works when consumer fitness depends linearly on victim abundances and when the densities of the interacting species tend toward a stable equilibrium point (Abrams, 1999). However, the results above (and those of Abrams (1999) for unstable predator–prey models) suggest that this logic often fails. Here, it fails for two reasons.

Because the two host abundances influence predator abundance and attack rates, it is possible for Eq. (2) to predict unequal host densities at a fitness-maximizing set of attack rates, even when the trade-off between a_1 and a_2 is linear and symmetrical. Second, the interaction modeled here frequently generates cycles, and the prediction of equal host densities does not hold when the populations of victim and consumer undergo cycles. It is perhaps not surprising that switching that is slow relative to the speed of population dynamics can increase the mean difference between host densities. The parasitoid in such cases simply cannot track the more rapidly changing host densities. However, even very rapid switching can also desynchronize the dynamics of two hosts. There appear to be several reasons for this. The first is that there may be resonance or interference between the population cycles and the cycles in the trait that determines attack rate. Intuition is usually insufficient to determine the quantitative nature of the dynamics of systems with interacting oscillating subsystems. The system discussed here

Mean r = 2.6

FIG. 11. Mean difference between host densities for each of four types of parasitoid when hosts differ by a factor of 3 in their intrinsic growth rates. The figure quantifies host heterogeneity across a range of maximum parasitoid attack rates, A, as in Fig. 10 except that $\hat{r} = 2.6$. Missing data points imply that the parasitoid went extinct for these attack rates.

has two different parasitoid–host pairs plus a temporally varying trait in the parasitoid. It might appear that sufficiently rapid behavioral change should equalize host densities, but it often does not. Densities of unparasitized individuals of the two hosts are frequently equalized at the end of the season by flexible and adaptive parasitoid choice (the type 2 ideal free parasitoid). However, this does not translate into equal host densities in the next generation, because the reproductive rate of surviving hosts is based on their density at the beginning of the season, which is generally not equal for the two species.

The magnitude of the heterogeneity in host densities that comes about via adaptive choice by parasitoids is often substantial. Comparing all the models, the mean difference between host densities was generally maximal either for the fixed (type 1) ideal free parasitoids or for inflexible parasitoids. The area of parameter space producing asynchrony was maximal for type 1 ideal free parasitoids, and the area producing stable equilibria was minimal. When adaptation did decrease the mean

difference in host densities (compared to the inflexible generalist parasitoid), it usually did so by changing a pattern of out-of-phase two-generation cycles of the hosts into one with aperiodic dynamics having a longer mean period between successive maxima in any variable. This only occurred for the small range of parameter space above the stable zone shown in Fig. 2. Even here, the degree to which heterogeneity was reduced by any sort of adaptation was modest for most of the adaptive models over most of the parameter range in question. The comparison provided in Table I is representative of these results.

It is worth stressing that many of the results presented here are dependent on the time of action of density dependence in host demographic parameters. Here, the per capita reproduction of healthy hosts at the end of the season was determined by the host density at the beginning of the season. This is a reasonable approximation when parasitized host individuals have mortality and feeding rates similar to those of unparasitized individuals.

If parasitized hosts greatly decreased their use of limiting resources, however, density-dependent reproduction would be more closely related to the number of healthy hosts at the end of the season. If density dependence only depended on density at the end of the period of parasitoid attack, the type 2 ideal free parasitoids would rapidly synchronize host densities in systems where the two hosts had similar reproductive rates. Models with different types of density dependence require further analysis.

Bonsall and Hassell (1997, 1998) have experimentally investigated a two-host–one parasitoid system that has many features in common with the models discussed above. The two host populations (*Plodia interpunctella* and *Ephestia kuehniella*) were separated by a mesh that was only permeable to the parasitoid (*Venturia canescens*). This allowed the parasitoid to choose to forage for one or the other host, but not both. It also ensured that there was no direct competition for resources between the hosts. Undivided control chambers containing a single host and the parasitoid exhibited damped oscillations of populations toward an equilibrium. The experimental chambers with both hosts exhibited out-of-phase oscillations of the hosts ending in the extinction of one of the host species (*E. kuehniella*). This system seems to be most similar to our model with type 2 ideal free choice and different host growth rates; out-of-phase oscillations are one of the predicted outcomes for this model. The extinction of one host is consistent with results from asymmetric models, which often exhibited much lower minimum population densities for one of the hosts. This could easily lead to extinction when population sizes are finite. The results in Fig. 4 (and similar simulations of asymmetric systems) suggest that coexistence of the two hosts could be achieved in this system by lowering the maximum growth rates of both hosts. Such an experiment would be easy to carry out, since reduced growth rates could be achieved by imposing random mortality on the hosts. Previous theory based on stable systems with adaptive choice (Holt, 1984) had suggested that there should be little apparent competition between the host species. Both the current theory and Bonsall and Hassell's experiments show that this is not true in systems that lack a stable equilibrium.

In natural systems, there are usually many potential hosts for a generalist parasitoid, and it is not clear to what extent the results presented here apply. Preliminary results for models with three or four hosts suggest that the generally desynchronizing effects of choice occur in those cases as well. However, it is possible that large numbers of hosts may reduce the ability of the parasitoid to specialize in time. The work by Wilson *et al.* (1996) suggests that a formidable array of dynamic complexities is possible in parasitoid food webs with as few as four or five species.

The results presented here are framed in terms of two separate host species. However, there is no mathematical difference between this case and that of two spatially isolated populations of the same species, provided that there is no "travel cost" for parasitoid movement between the two populations. Thus, the models predict that adaptive patch selection by a parasitoid in a system with a single host species in isolated patches will frequently either generate or maintain spatial heterogeneity in host densities. This is likely even when the landscape is completely homogeneous and the parasitoid has perfect knowledge about the densities of unparasitized host individuals in each patch.

The system consisting of two hosts sharing a parasitoid is generally thought to be characterized by apparent competition (Holt, 1977) between the two hosts via their effect on the parasitoid (Holt and Lawton, 1993). The system studied here has two features that affect the strength of apparent competition: (1) cycles, which generally tend to reduce the magnitude of apparent competition (Abrams *et al.*, 1998); and (2) switching, which also reduces or eliminates apparent competition in stable systems (Holt, 1984; Abrams and Matsuda, 1996). The combination of both cycles and switching, however, has been shown to increase apparent competition when prey populations become desynchronized in a two-prey–one-predator model (Abrams, 1999). The synchronization or desynchronization of host densities in the host–parasitoid models considered here also has a major effect on the mean densities of victims, with desynchronization increasing apparent competition. This will be detailed in a subsequent publication. However, it is clear that the potentially positive effect that one host may have on another (by attracting the parasitoid's searching effort) is negated when both hosts are seldom present at the same point in time.

This analysis adds to a growing list of studies (Bernstein, 1988; Schwinning and Rosenzweig, 1990; van Baalen and Sabelis, 1993; Abrams, 1999) where population dynamics can prevent adaptive switching from equalizing abundances of prey/hosts or from achieving an ideal free distribution of predator/parasitoid effort. It would be of interest to reexamine the many field studies where ideal free distributions have not been observed (Kennedy and Grey, 1993) to determine whether this is the explanation for these observations.

ACKNOWLEDGMENTS

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