On the evolution of host selection in solitary parasitoids

Eric Charnov

David Stephens

Recommended Citation

ON THE EVOLUTION OF HOST SELECTION IN SOLITARY PARASITOIDS

Eric L. Charnov and David W. Stephens

Department of Biology, University of Utah, Salt Lake City, Utah 84112; Department of Zoology,
University of Massachusetts, Amherst, Massachusetts 01003

About 10% of all insect species are parasitic Hymenoptera, small wasps that reproduce by laying eggs on individuals of other insect species ("hosts"). Among these, the vast majority lay only one egg per host (here called "solitary"). A flurry of recent work poses and tests explicit adaptation models about the oviposition decisions of these wasps (Hamilton 1967; Cook and Hubbard 1977; Charnov 1979, 1982; Waage 1979; Charnov et al. 1981; Green 1982; Charnov and Skinner 1984, 1985; Iwasa et al. 1984; Parker and Courtney 1984; Skinner 1985; Waage and Godfray 1985; Godfray 1986, 1987; Jervis and Kidd 1986; Mangel 1987). In general, a female parasitoid faces at least four kinds of oviposition decisions (Charnov and Skinner 1985): (1) what hosts to use, including inter- and intra-specific choices and the option to superparasitize (i.e., attack already parasitized hosts); (2) where to search for hosts (= patch choice); (3) what sex ratio to produce in a host; and (4) what clutch size to produce in a host.

In this paper we develop life-history models addressing host choice, or "diet breadth" (question 1), for solitary parasitoids. Godfray (1987) has dealt with the evolution of the solitary habit itself; we simply take the solitary habit as a given. Except for superparasitism, the diet-breadth problem has probably been modeled least (Green 1982; Iwasa et al. 1984; Charnov and Skinner 1985). To keep our analysis simple, we shall assume a stationary population of asexual organisms; Green (1982) and Skinner (1985) have shown how results from such an idealized population may be generalized to include the added complications of males and females. Our model does not deal with the genetics of evolution directly; like other life-history theorists, we suppose that natural selection has molded the decision process to maximize an appropriate measure of Darwinian fitness (Charlesworth 1980). This equilibrium or "normalizing natural-selection assumption" allows us to use optimization mathematics to study behavior (for a discussion, see Stephens and Krebs 1986): we focus on the fitness measure and on constraints or trade-offs among its component parts. Such a focus should lead to an understanding more fundamental than, say, the insights gained by the currently popular "polygenic" approach (Lande 1982).

Of course, some of the oviposition decisions discussed here may also apply to

nonparasitoids (e.g., many herbivorous insects; see Roitberg and Prokopy 1983a,b, 1984, 1987; Parker and Courtney 1984; Roitberg 1985; Skinner 1985; Parker and Begon 1986; Roitberg and Mangel, MS). Our parasitoid orientation simply reflects our own experience.

Students of parasitoids divide parasitoids into several types with respect to egg production and deposition (Jervis and Kidd 1986). For example, they separate species that paralyze their hosts only during egg deposition (the hosts then recover and continue to feed) from species that permanently paralyze their hosts. The general importance of this dichotomy for the ovipositing wasp is that the larva's food package is a fixed size for the permanent paralyzers (and presumably the ovipositing wasp has some "estimate" of this size), whereas the size of the larva's food package may be relatively unknown for the temporary paralyzers. Our models assume that mother "knows" (or can estimate) the food value of a host; hence, our models may not be informative if host value is unknowable because it depends on the future feeding environment of the host.

Species that emerge with all their eggs mature and ready to lay (or nearly so) are also distinguished from those that acquire the nutrition necessary to mature eggs as adults, maturing eggs as they go along (Jervis and Kidd 1986). Parasitoids emerging with their full complement of mature eggs can be considered to have a fixed number of eggs ready to lay at the beginning of adulthood. Parasitoids that mature eggs as they go along can be considered to have some "egg-production function," which relates nutrient uptake to egg maturation. Our models consider this second type of egg availability (see papers by G. A. Parker and colleagues for models dealing with a fixed egg complement).

Although these life-history dichotomies are probably not as "hard and fast" as the literature sometimes suggests (M. Mackauer, pers. comm.), they are useful heuristic devices. Indeed, these dichotomies may also apply to many herbivorous insects.

THE FITNESS MEASURE

It has been suggested (Iwasa et al. 1984; Charnov and Skinner 1985) that the expression

$$W = \int_0^\infty (W_f/\tau) \, e^{-ZT} dT \tag{1}$$

is a reasonable measure of individual Darwinian fitness for a nongrowing (stationary) population of parasitoids, where W_f is the fitness gained from the offspring on a single average host; τ, the time required to find (search for) and handle a single average host; and Z, the instantaneous mortality rate.

If W_f, Z, and τ are not themselves functions of time, then equation (1) integrates to

$$W = W_f/(\tau Z) \, , \tag{2}$$

where $1/Z$ is the average length of an egg-laying parasitoid's life; W_f/τ, the average fitness gain per host divided by the average time per host, is the appropriate way

to express fitness per unit of time as shown by cumulative-renewal theory (Paloheimo 1971; Charnov 1973). To obtain the total offspring production over the mother's lifetime (eq. 1), we multiply this rate by the expected length of the parasitoid's life ($1/Z$). Several population-genetics models show that lifetime offspring production (times offspring quality) is an appropriate fitness measure in a stationary population (Lande 1982; Charnov 1986).

As a first-order model for the evolution of oviposition decisions, equation (2) may be assumed to be maximized subject to limitations imposed by interactions between W_f, τ, and Z. We consider two contrasting assumptions about how the parasitoid encounters hosts, and we consider two contrasting assumptions about how the rate of egg production is related to the ovipositing parasitoid's survival. This yields four cases, one for each combination of the two encounter assumptions and the two "egg production versus survival" assumptions.

Encounter assumptions.—Population biologists have long recognized two types of encounter processes (Levins 1968; Stephens and Krebs 1986), corresponding, in turn, to two types of environments: fine-grained and patchy (or coarse-grained) environments. In a fine-grained environment, the parasitoid encounters hosts "at random"; in a patchy environment the parasitoid finds the hosts in clumps, and search time is the time between encounters with clumps of hosts.

Assumptions about egg production versus survival.—In one case, we make the egg-production rate negatively related to the egg-laying parasitoid's survival rate; a higher rate of egg production reduces life expectancy (Charlesworth 1980). Although this might happen in several ways (see, e.g., Weis et al. 1983; Charnov and Skinner 1984, 1985; Iwasa et al. 1984), we concentrate (following Charnov and Skinner 1985) on a linear relationship between egg production and survival rate. The second assumption about egg production versus survival disconnects egg production from adult survival; we simply assume that eggs mature (and become available for oviposition) at some fixed rate. Here, egg maturation is a constraint that cannot be changed by the egg-laying parasitoid; all she can do is adjust her diet breadth in the face of the constraint.

We begin by considering fine-grained environments and the effects of the two assumptions about egg production versus survival in the fine-grained case. Next, we consider these two assumptions in patchy environments.

<center>FINE-GRAINED ENVIRONMENTS</center>

<center>*The Encounter Process*</center>

We suppose that a parasitoid searches at random in an environment containing K "host types," and we define the following.

λ_i is the encounter rate (while searching) with host-type i ($i \in \{1, 2, \ldots, K\}$). The encounter process with each type is an independent Poisson process. A host type is a species, instar, genotype (etc.) that the parasitoid can recognize; that is, host types are defined by the sensory abilities of the parasitoid (see Getty 1985).

E_i is the survival rate (to adulthood) for an offspring on a host of type i multiplied by its expected lifetime fertility. We call this the "offspring quality" resulting from a host of type i. (Charnov and Skinner [1985] discussed this term in detail.)

h_i is the time required to oviposit on a host of type i (called h_i because it is the handling time for type i).

P_i is the proportion of the type-i hosts encountered that is attacked.

A female parasitoid's fitness gain per unit of time is

$$W_f/\tau = \left(\sum_{i=1}^{K} \lambda_i P_i E_i\right) \Big/ \left(1 + \sum_{i=1}^{K} \lambda_i P_i h_i\right); \tag{3}$$

the detailed derivation of equation (3) is exactly the same as the derivation of foraging theory's fine-grained prey model (Charnov 1976a; Iwasa et al. 1984; Stephens and Krebs 1986).

Assumptions about Mortality and Egg-Production Rate

In order to blend equation (3) with the life-history model of equation (2), we must first ask if Z is related to any of the parameters: λ_i, E_i, h_i. There clearly will be a trade-off between Z and at least some of these parameters under either of the following assumptions. (1) The mortality rate, Z, may not be the same during searching and handling. (Iwasa et al. [1984] developed a case like this.) (2) Egg production drains resources from the parent's body, causing Z to increase as the egg-laying rate increases.

In order to incorporate the second possibility, we need to specify how Z increases with the egg-production rate (in the long run, egg-production rate = egg-laying rate). For this paper, we assume (after Charnov and Skinner 1985) that

$$Z = Z_0[1 + \phi \text{ (egg-production rate)}], \tag{4}$$

where Z_0 is the base mortality rate and ϕ is the rate (relative to Z_0) at which mortality increases with egg production. The egg-production rate is

$$\left(\sum_{i=1}^{K} \lambda_i P_i\right) \Big/ \left(1 + \sum_{i=1}^{K} \lambda_i P_i h_i\right). \tag{5}$$

Note that this is the same as equation (3) without the E_i terms in the numerator; here we are counting the numbers of hosts attacked (eggs laid) per unit of time.

Fitness: Mortality and Encounter Assumptions Combined

If we substitute expression (5) into equation (4) and substitute the result and equation (3) into equation (2), we find that

$$W = \left[\left(\sum_{i=1}^{K} \lambda_i P_i E_i\right) \Big/ \left(1 + \sum_{i=1}^{K} \lambda_i P_i h_i\right)\right] \Big/ Z_0\left[1 + \left(\phi \sum_{i=1}^{K} \lambda_i P_i\right) \Big/ \left(1 + \sum_{i=1}^{K} \lambda_i P_i h_i\right)\right],$$
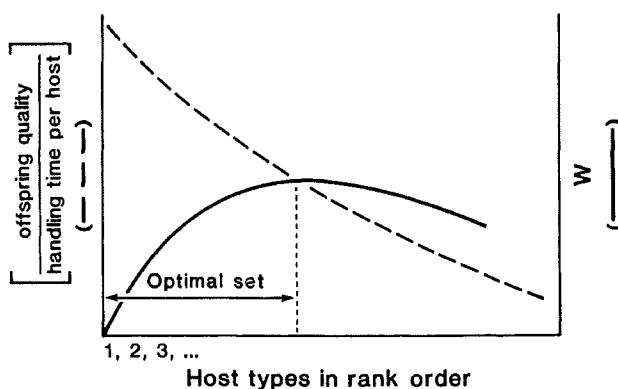
FIG. 1.—The optimal diet breadth. Hosts are ranked by their profitabilities, $E_i/(h_i + \phi)$, and are added to the fitness equation W (eq. 6) in rank order. The acceptable or optimal set of hosts includes all those of rank higher than the intersection of the two curves (Charnov 1976a; Stephens and Krebs 1986).

which can be simplified to

$$W \propto \left(\sum_{i=1}^{K} \lambda_i P_i E_i\right)\Big/\left[1 + \sum_{i=1}^{K} \lambda_i P_i(h_i + \phi)\right]. \tag{6}$$

However, equation (6) has the same form as equation (3) with h_i replaced by $h_i + \phi$, and both equations have the same form as expressions commonly used in models of foraging behavior. Specifically, we can easily find the P_i's that maximize expected fitness (expression 6) by applying three results from foraging theory (Charnov 1976a; Stephens and Krebs 1986).

1. Zero-one rule: A given host type (i) should be either accepted or ignored (in symbols, $P_i = 1$ or $P_i = 0$). This result is usually called the zero-one rule, and it is said to predict absolute as opposed to partial preferences.

2. Ranking by $E_i/(h_i + \phi)$: Hosts should be added to the set of acceptable hosts (the host "diet," in foraging terms) in order of decreasing $E_i/(h_i + \phi)$. Specifically, hosts are ranked such that

$$E_1/(h_1 + \phi) > E_2/(h_2 + \phi) > \ldots > E_{K-1}/(h_{K-1} + \phi) > E_K/(h_K + \phi),$$

and host types are added to the acceptable set in the order of increasing j until

$$\left(\sum_{i=1}^{j} \lambda_i E_i\right)\Big/\left[1 + \sum_{i=1}^{j} \lambda_i(h_i + \phi)\right] > E_{j+1}/(h_{j+1} + \phi). \tag{7}$$

This result has been proved by a number of authors (fig. 1 illustrates this result; for a review, see Stephens and Krebs 1986).

3. Independence of inclusion and encounter rate: The inclusion of a given type (say j) in the acceptable set does not depend on its own encounter rate (λ_j).

Mortality and host acceptability.—The optimal host set can be found by directly applying these three well-known results from foraging theory (fig. 1). However, the variable ϕ adds a new element to this old model: ϕ measures the

effect of increases in the rate of egg production on the mortality rate (Z). A unit's increase in the rate of egg production increases the mortality rate by ϕZ_0 (Z_0 is the initial, or base, mortality rate).

To illustrate the effect of mortality (ϕ), we consider a case in which there are only two host types. Foraging theorists usually call E_i/h_i the profitability of type i; we follow this terminology by calling $E_i/(h_i + \phi)$ the profitability of host-type i. Changes in ϕ can change the relative profitabilities of host types; hence, ϕ can change the ranks of host types used in calculating the acceptable set (expression 7). To see these effects, consider two host types such that $E_a/h_a > E_b/h_b$. There are two cases.

1. If $E_a \geq E_b$, then A is ranked above B for all values of ϕ: $E_a/(h_a + \phi) > E_b/(h_b + \phi)$. In words, mortality does not affect the profitability ranks. (This case would apply if h_i were the same for all host types.) Because type A is always the most profitable, we only need to ask whether B should be accepted, in order to determine the "optimal" set of host types. Here, again, there are two cases.

a. If type B is not in the acceptable or optimal set when $\phi = 0$ (this implies that $E_a/(1/\lambda_a + h_a) > E_b/h_b$), then it will not be in the acceptable set for any value of ϕ.

b. However, if type B is in the acceptable set when $\phi = 0$, then B is in the acceptable set for ϕ values lower than $[E_a h_b - E_b(1/\lambda_a + h_a)]/(E_b - E_a)$ and unacceptable for values of ϕ higher than this.

2. If $E_b > E_a$, then A is ranked above B when ϕ is less than

$$\hat{\phi} = (E_a h_b - E_b h_a)/(E_b - E_a), \tag{8}$$

but the rankings are reversed when ϕ exceeds $\hat{\phi}$. Note that this is possible only if E_i and h_i are positively related. Again, there are two cases.

a. If $\phi < \hat{\phi}$, then A is the more profitable type, and we need to ask only whether type B should be accepted. B should be accepted only if

$$E_b/(h_b + \phi) > E_a/(1/\lambda_a + h_a + \phi),$$

which is the same as

$$\phi > \hat{\phi} - E_b/\lambda_a(E_b - E_a). \tag{9}$$

Because the last term is always negative, the ϕ at which the parasitoid should first accept the less profitable type of B's is less than $\hat{\phi}$. The right-hand side of the inequality may be negative; if this is true, then type B should always be accepted.

b. If $\phi > \hat{\phi}$, then B is the more profitable type, and we need to ask only whether type A should be accepted. Type A should be accepted only if

$$E_a/(h_a + \phi) > E_b/(1/\lambda_b + h_b + \phi);$$

since $E_b > E_a$, this becomes

$$\phi < \hat{\phi} + E_a/\lambda_b(E_b - E_a). \tag{10}$$

Again, because the last term is positive, the ϕ at which the parasitoid should stop accepting type A's is always greater than $\hat{\phi}$.

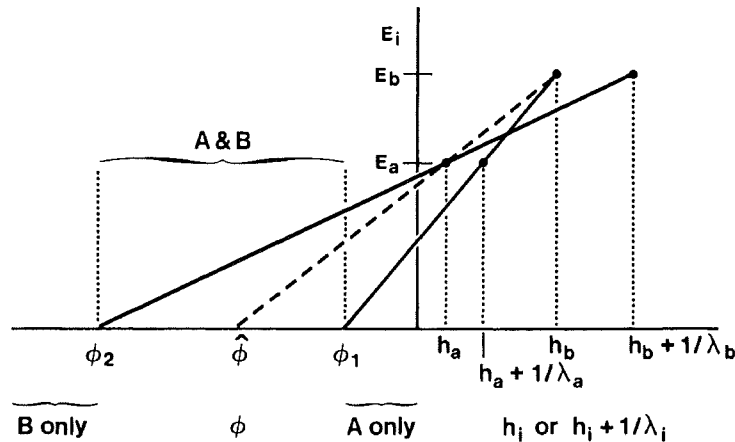If $E_b > E_a$, there are three possible acceptable sets at different levels of ϕ: at low

FIG. 2.—The effect of per-egg mortality rate (ϕ) on host acceptability when two host types are available. Three variables are plotted: the fitness value (E_i) of the two host types; the handling time or handling-plus-search time associated with each host type; and the per-egg mortality rate (ϕ). The dashed line intercepts the ϕ-axis at the point, $\hat{\phi}$, where the two types have equal profitabilities. Below $\hat{\phi}$, type A (lower E_i, but shorter handling time) is more profitable; and above $\hat{\phi}$, type B (higher E_i, but longer handling time) is more profitable. The solid line through the points ($h_a + 1/\lambda_a$, E_a) and (h_b, E_b) intercepts the ϕ-axis at the point (ϕ_1) where the fitness from a "diet" type A alone equals the profitability of type B; at ϕ values greater than ϕ_1, both types A and B should be attacked when encountered. The solid line through ($h_b + 1/\lambda_b$, E_b) and (h_a, E_a) intercepts the ϕ-axis at the point (ϕ_2) where the fitness from a "diet" of type B alone equals the profitability of A; at ϕ values greater than ϕ_2, type A's should not be attacked upon encounter. This rather complicated application of the "prey algorithm" (expression 7) leads to a simple rule: take type A only if $\phi < \phi_1$; take both types if $\phi_2 \geq \phi \geq \phi_1$; and take only type B if $\phi > \phi_2$.

ϕ values, only type A should be taken; when ϕ increases (expression 9), type B should be added to the acceptable set; but as ϕ increases even further (expression 10), type A should be dropped from the acceptable set. Figure 2 illustrates this result.

Recognition costs: a sample extended model.—The similarity of this result (expression 6) to foraging theory's prey model is important because we immediately know how to choose the P_i's to maximize expected fitness, but it is also important because limitations of and extensions to this model are well known. For example, the effects of host (or prey) clumping have been studied by McNair (1982) and Lucas (1983). Stephens and Krebs (1986) reviewed and synthesized modifications and extensions of this model.

Of particular interest here is the effect of a recognition time. The model presented above assumes that the parasitoid immediately and instantaneously recognizes a host's type upon encounter. However, it seems likely that a parasitoid may have to invest some time—perhaps using its chemosensory abilities—to distinguish between host types. Following a number of authors (Elner and Hughes 1978; Hughes 1979; Erichsen et al. 1980; Houston et al. 1980; Stephens and Krebs 1986), we incorporate this possibility by supposing that the parasitoid must spend r seconds to distinguish between host types every time it
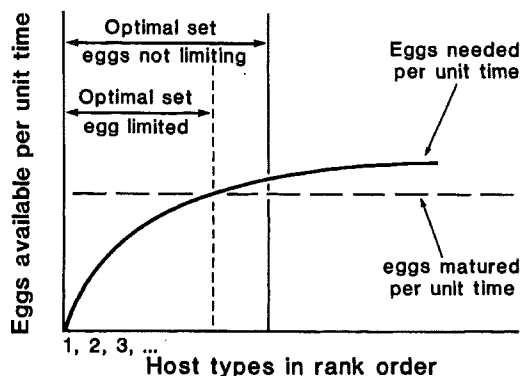
FIG. 3.—Diet breadth, if egg supply is limited. Hosts are ranked by profitability (E_i/h_i) and added to the egg-production-rate equation (eq. 5) in rank order. This forms the "eggs needed per unit of time." The optimal diet consists of hosts of rank higher than the intersection of this curve with the "eggs matured per unit of time" rate curve. However, the broadest diet possible is the optimal set derived by the procedure outlined in figure 1.

encounters a potential host regardless of whether it accepts the host. As above, consider a case of the two-host type, where $E_1/(h_1 + \phi) > E_2/(h_2 + \phi)$. Type 2 should be excluded only if

$$\lambda_1 > D + D\lambda_2 r, \tag{11}$$

where

$$D = 1/[E_1(h_2 + \phi)/E_2 - (h_1 + \phi + r)].$$

Clearly, an increase in λ_2 can make this condition (expression 11) fail and cause type 2 to be included in the acceptable set. This violates result 3, that a type's inclusion does not depend on its own encounter rate. Houston et al. (1980) discussed this model in detail (including a detailed derivation of expression 11), and they presented an experimental study of how recognition time affects the prey selection of foraging great tits (*Parus major*).

Limited Egg Production in Fine-Grained Environments

Suppose that the egg-production rate is not related to adult survival; indeed, assume that it (eq. 5) is a fixed constant (R). Note that fitness W is now directly proportional to W_f/τ (eq. 3) with the constraint that the egg-production rate (eq. 5) is less than or equal to R. We consider only the case where $h_i = h$, a constant; the time to oviposit on a host is the same for all host types. If R were so large that eggs were always readily available, the situation would reduce to that shown in figure 1, with hosts ranked by E_i/h_i ($\phi = 0$). If R is not so large and if h_i is constant for all host types ($h_i = h$), then the optimal set of host types can be found as shown in figure 3. (1) Rank the hosts by E_i (which is equivalent to ranking them by E_i/h_i since h_i is constant). (2) Add the host types to the "diet" in rank order. (3) The optimal set consists of all host types until the eggs needed per unit of time equal the eggs available per unit of time (R). (4) This optimal set always includes fewer host types than the optimal set with no egg-production constraint.
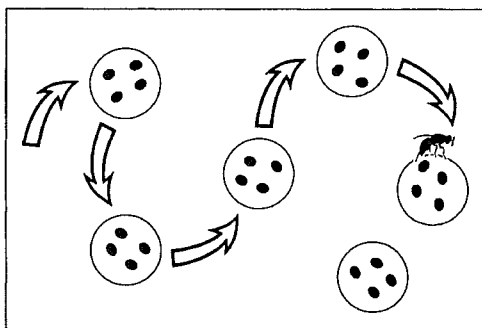
FIG. 4.—A patchy environment. The hosts occur in discrete and compact clumps. The wasp spends time traveling between clumps and in attacking hosts within clumps.

PATCHY ENVIRONMENTS

Fitness Assumptions

In patchy environments, hosts occur in discrete patches or clumps. The female parasitoid travels between patches and while in a patch has the option of attacking any, all, or none of the hosts present. There are many possible cases here, depending on how the various host types are distributed among clumps, how much searching is required within patches, and how much the parasitoid female recognizes about patches when she encounters them. Again, these patchy conditions have many analogues in foraging theory (Stephens and Krebs 1986). For illustrative purposes, we restrict our attention to one case. (1) All patches have an identical mix of host types (it is easy to relax this assumption). (2) Upon entering a patch, the parasitoid knows which host types are present and it can attack the hosts in any order. (3) No search time is required in the patch; the parasitoid pays only the handling cost for each host attacked. We assume that the handling time per host is a constant for all host types (this assumption can also be relaxed).

Figure 4 illustrates this "patchy-environment assumption"; the patches are small discrete clumps of hosts, small enough that the female entering the patch probably knows which hosts are present and that she can use them with little or no search time. Allowing the female to rank hosts and attack them in any order may be an unreasonable assumption if the prey are mobile and capable of escaping (A. Chow, pers. comm.). If prey can escape, then parasitizing one host in a clump may well decrease the chances of parasitizing others (see Charnov et al. 1976). This would greatly complicate the analysis, and we ignore this possibility.

Under these assumptions, the following expression gives the fitness gain per unit of time:

$$W_f/\tau = \left(\sum_{i=1}^{n} E_i\right)\bigg/ (\mathcal{T} + nh), \tag{12}$$

where $\sum_{i=1}^{n} E_i$ is the sum of E_i for attacking n hosts in the patch, $\mathcal{T}$ is the travel time between patches, and h is the handling time per host.
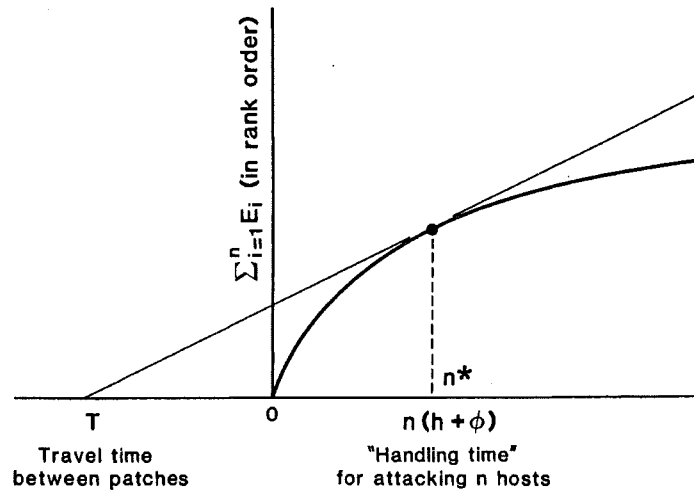
FIG. 5.—Optimal diet in a patchy environment. Hosts are ranked by E_i, and we form the relationship between $\Sigma_{i=1}^{n} E_i$ (the total E for attacking n hosts) and $n(h + \phi)$ (the mortality-corrected handling time for attacking n hosts). If $\mathcal{T}$ (or T, as in the figure) is the travel time between patches, the optimal n^* (i.e., which maximizes eq. 14) is found by the usual tangent argument of the marginal-value theorem (Charnov 1976b).

Mortality-Rate Constraints

As in the fine-grained situation, we consider the case in which Z increases linearly with the egg-production rate: $Z = Z_0(1 + \phi(\text{egg-production rate}))$ (eq. 4). For this situation, the egg-production rate is

$$n/(\mathcal{T} + nh).\qquad(13)$$

To obtain the final fitness measure, put expression (13) into equation (4) and substitute the result (and eq. 12) into expression (2) to yield

$$W \propto \left(\sum_{i=1}^{n} E_i\right)\Big/[\mathcal{T} + n(h + \phi)].\qquad(14)$$

As in the fine-grained case (eq. 6), the linear-mortality assumption simply redefines the handling time per host (from h to $h + \phi$).

Figure 5 illustrates how to find the optimal n. If the hosts are ordered by E_i ($E_i/(h_i + \phi)$ if the h_i's are not constant), then we can define the relations $\Sigma_{i=1}^{n} E_i$ (added in rank order) and $n(h + \phi)$ as functions of n and plot them against each other. A tangent argument (similar to that commonly used to solve patch-exploitation problems; i.e., the marginal-value theorem of Charnov 1976b) gives the n that maximizes fitness (eq. 14). It is straightforward to generalize this to an environment made up of patches with differing host distributions. (Notice that although the rank order of host types is used to determine which types within a clump should be attacked, this model does not predict that host types should be attacked in rank order. For example, if the model predicts that all types of rank 2 and higher should be attacked, the parasitoid should be indifferent to the attack orders "1 then 2" and "2 then 1.")

Egg-Production Constraints

In this situation, we simply assume that eggs mature at some fixed rate; thus, if all mature eggs were laid in the preceding patch and if travel time $\mathcal{T}$ has passed since the last patch, the female has $m\mathcal{T}$ mature eggs to lay when she enters a new patch (where m is the rate of production of mature eggs). To keep our analysis simple, we assume that the time needed to lay those eggs is negligible. Under these assumptions (plus the assumption that the female can rank the hosts upon entering the patch), an interesting situation obtains. The female can clearly adopt one of two kinds of decision rules: she can lay all her mature eggs upon entering a patch and immediately move on to a new patch; or she can lay those eggs, wait for more eggs to mature (laying these eggs as they become mature), and then move on to the next patch. Both of these rules assume that she will leave the present patch with no mature eggs.

What is also clear is that the wasp can use conditional decision rules; that is, she can base her decision on the number of mature eggs she has at the time of encountering a patch. This is the same as basing the decision on the preceding interpatch travel time. Let $\mathcal{T}_j$ be the time spent traveling to reach the present patch (to keep things simple, suppose that $\mathcal{T}_j$ is a discrete random variable) and let $\mathcal{P}_j$ be the probability that the time between leaving one patch and arriving at another equals $\mathcal{T}_j$ ($j \in \{1, \ldots, \ell\}$). Associate with each interpatch time ($\mathcal{T}_j$) an additional time t_j spent in the patch (i.e., beyond $\mathcal{T}_j$). Rank the hosts in the patch by E_i. The wasp will be able to attack that many hosts: $n_j = m(\mathcal{T}_j + t_j)$. W_f/τ for this parasitoid then takes the form

$$W_f/\tau = \sum_{j=1}^{\ell} \left(\sum_{1 \leq i \leq n_j} E_i \right) \mathcal{P}_j \bigg/ \sum_{j=1}^{\ell} (\mathcal{T}_j + t_j) \mathcal{P}_j. \tag{15}$$

To simplify things, suppose that $\sum_{1 \leq i \leq n_j} E_i$ can be replaced by a continuous and negatively accelerated function, $\mathcal{E}$, that relates the fitness gained per patch to the number of eggs laid within the patch:

$$\mathcal{E}(m\mathcal{T}_j + mt_j) \approx \sum_{1 \leq i \leq n_j} E_i.$$

Hence, equation (15) now becomes

$$W_f/\tau = \sum_{1}^{\ell} \mathcal{E}(m\mathcal{T}_j + mt_j) \mathcal{P}_j \bigg/ \sum_{1}^{\ell} (\mathcal{T}_j + t_j) \mathcal{P}_j. \tag{16}$$

We wish to maximize equation (16) with respect to the variables $\mathcal{T}_j + t_j$, for $j \in \{1, \ldots, \ell\}$. We do this using Lagrange multipliers. The answer is simply illustrated in figure 6. The rules are as follows. (1) For egg-maturation times ($\mathcal{T}_j + t_j$) below c, set $t_j = c - \mathcal{T}_j$; that is, wait in the patch until c time has passed and attack $n = mc$ hosts. (2) For $\mathcal{T}_j > c$, the parasitoid should attack $n = m\mathcal{T}_j$ hosts (i.e., set $t_j = 0$) and immediately move on to the next patch. (3) The threshold travel time ($\mathcal{T}_j = c$) is defined by $\partial \mathcal{E}(mc)/\partial c = W_f/\tau$.
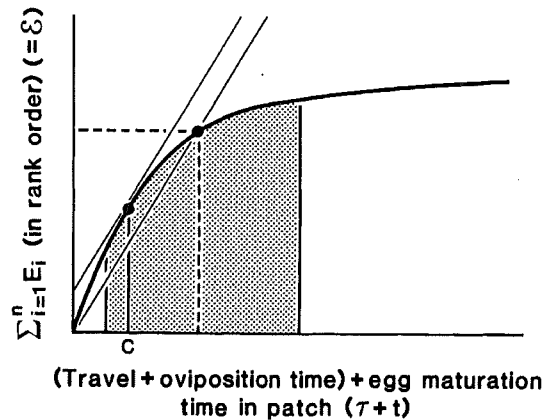
FIG. 6.—Egg-production constraints in a patchy environment. As discussed in the text, two conditional decision rules should be used. Above interhost travel time c, the female should lay all of the eggs she has upon entering the patch and immediately move on to another patch. Shorter travel times (below c) should result in her waiting in the patch (until c time units have passed), laying all her eggs, and then leaving for another patch. The stippled area illustrates the range of possible travel times; c is the point where $\partial \mathscr{E}/\partial c = W_f/\tau$ (the dashed lines indicate W_f and τ).

DISCUSSION

Our approach has been to consider a parasitoid's decisions about ovipositing in a normalizing natural-selection framework. As used here, this approach focuses on how three life-history parameters (W_f, τ, Z) combine to effect a measure of Darwinian fitness (eq. 2), and it forces us to make explicit assumptions about fitness and trade-offs. The fitness measure clearly derives from population and evolutionary genetics (Charlesworth 1980); from a formal population-genetics approach, we derive a fitness measure adequate to give us the direction of selection. We thus express the phenotypic equilibrium as an optimization principle (often even with frequency dependence; see Charnov 1982; Maynard Smith 1982; Stephens and Krebs 1986) and study its properties subject to trade-offs among its components. Although the genetic justification lingers in the background, the phenotypic approach (Grafen 1984) puts ecology, physiology, and biomechanics in the foreground.

We have studied two kinds of production constraints (egg production vs. adult survival, and an egg-maturation constraint) and two kinds of environmental constraints (fine-grained and patchy). We chose these constraints on the basis of our biological intuition. Some of our general results (e.g., notions of prey rankings) are insensitive to constraint details, but others depend strongly on details of the trade-offs assumed. Indeed, our theoretical explorations are partly for this sole purpose: to tell us how altering constraints alters the economics of a parasitoid's decisions about ovipositing. Since the trade-offs are in terms of measurable phenotypic parameters, it should be possible to discover which trade-offs apply in particular situations. It may even be the case that rules exist about what kinds of

situations impose what kinds of trade-offs on the wasps. We suggest that generalizations about trade-offs form the basis of the natural-selection approach to parasitoid decisions about oviposition, as used here. Yet, we must admit to great ignorance about the trade-offs in decisions about ovipositing—hence, our exploration of some plausible (to us) cases. The remainder of this discussion poses six specific questions for future exploration.

1. What if Z is a nonlinear function of egg-production rate? Our linear model was one of convenience, which led to an elegant and understandable answer (eq. 6). If the variation in egg production is fairly small, even nonlinear trade-offs could be approximated by a linear relationship, but we admit to ignorance about nonlinear trade-offs. A possible candidate for study would be the exponential model, $Z = Z_0 e^{\beta(\text{egg-production rate})}$.

2. What if the female's supply of mature eggs does not increase with time? Parker and Begon (1986; Begon and Parker 1986) have studied oviposition models in which the female emerges as an adult with a fixed supply of reproductive resources (or a fixed number of eggs if egg size is a constant). They allowed the parasitoid to alter its clutch size during the course of its life (in our case it would alter its diet breadth). This question would require dynamic programming (see Mangel and Clark 1986), and we do not know how it would affect our results.

3. What determines the egg-production rate, if it is not negatively related to survival? Jervis and Kidd (1986) reviewed host feeding by adults as a source of nutrition for egg maturation. We elected to ignore this source of nutrition for eggs and look at "host choice for babies," conditional on its taking a given value. Clearly, one could also look at the allocation of some hosts (also time) to food for future eggs (one such model is discussed in Jervis and Kidd 1986).

4. What about two-sex fitness functions? Our unisex models may be adequate for the highly biased sex ratios (many females) of a species subject to "local mate competition" (Hamilton 1967; our functions then refer to female production), and it seems fairly straightforward to generalize the results to species subject to host-size sex-ratio shifts (Green 1982). In general, two-sex fitness functions can be complicated (Charlesworth 1980; Charnov 1982); we can only hope that the unisex models provide some insight and guidance in the absence of a rigorous extension to the general two-sex case.

5. What about learning processes? With one exception (recognition-time constraints; eq. 11), our models assume perfect and complete knowledge on the part of the ovipositing parasitoid (e.g., we assume that the parasitoid knows which host types are present in the patch). However, experience is known to alter oviposition behavior for a number of species (see, e.g., van Alphen and Vet 1986; van Lenteren 1981). Such learning processes have yet to be added to formal oviposition models. (Stephens and Krebs [1986] outlined the techniques required to incorporate experience in formal models and where such efforts might lead.)

6. How do the results derived here compare with those that would emerge from an explicit dynamic-state-variable approach to the same questions (Mangel 1987)? Clearly, some trade-offs require a dynamic-programming approach; a comparison of these approaches is now being made (Mangel, Roitberg, and Charnov, MS).

The problem of host selection in parasitoids is old and widely studied, although mostly from a proximate or mechanistic perspective (Vinson 1976, 1981; Vinson and Iwantsch 1980; van Alphen and Vet 1986). A vast literature documents numerous factors that affect host choice. The natural-selection approach allows us to assemble disparate factors into a coherent picture; at the least we can ask how these factors might interact to produce host choice. With all of its possible pitfalls, we know of no other approach with the potential to provide such an overview.

SUMMARY

Host selection by solitary parasitoids is modeled as a problem in life-historical evolution. Our basic approach is to assume fitness maximization in the face of trade-offs. We consider two kinds of trade-offs: (1) patchy versus fine-grained host distribution, and (2) an egg-production rate that is either negatively related to adult survival or simply a fixed constant. These lead to four general cases, and we derive the range of hosts attacked under each. The resulting decision rules are similar to several decision rules from classical foraging theory.

ACKNOWLEDGMENTS

LITERATURE CITED

Begon, M., and G. A. Parker. 1986. Should egg size and clutch size decrease with age? Oikos 47:293–302.

Charlesworth, B. 1980. Evolution in age-structured populations. Cambridge University Press, New York.

Charnov, E. L. 1973. Optimal foraging: some theoretical explorations. Ph.D. diss. University of Washington, Seattle.

———. 1976a. Optimal foraging: attack strategy of a mantid. Am. Nat. 110:141–151.

———. 1976b. Optimal foraging: the marginal-value theorem. Theor. Popul. Biol. 9:129–136.

———. 1979. The genetical evolution of patterns of sexuality: Darwinian fitness. Am. Nat. 113:465–480.

———. 1982. The theory of sex allocation. Princeton University Press, Princeton, N.J.

———. 1986. Life history evolution in a "recruitment population": why are adult mortality rates constant? Oikos 47:129–134.

Charnov, E. L., and S. W. Skinner. 1984. Evolution of host selection and clutch size in parasitoid wasps. Fla. Entomol. 67:5–51.

———. 1985. Complementary approaches to the understanding of parasitoid oviposition decisions. Environ. Entomol. 14:383–391.

Charnov, E. L., G. H. Orians, and K. Hyatt. 1976. Ecological implications of resource depression. Am. Nat. 110:247–259.

Charnov, E. L., R. L. Los-den Hartogh, T. Jones, and J. van den Assem. 1981. Sex ratio evolution in a variable environment. Nature (Lond.) 289:27–33.

Cook, R. M., and S. F. Hubbard. 1977. Adaptive searching strategies in insect parasites. J. Anim. Ecol. 46:115–125.

Elner, R. W., and R. N. Hughes. 1978. Energy maximization in the diet of the shore crab *Carcinus maenus*. J. Anim. Ecol. 47:103–116.

Erichsen, J. T., J. R. Krebs, and A. I. Houston. 1980. Optimal foraging and cryptic prey. J. Anim. Ecol. 49:271–276.

Getty, T. 1985. Discriminability and the sigmoid functional response: how optimal foragers could stabilize model-mimic complexes. Am. Nat. 125:239–256.

Godfray, H. C. J. 1986. Models for clutch size and sex ratio with sibling interaction. Theor. Popul. Biol. 30:215–231.

———. 1987. The evolution of clutch size in parasitic wasps. Am. Nat. 129:221–233.

Grafen, A. 1984. Natural selection, kin selection and group selection. Pages 62–84 *in* J. R. Krebs and N. B. Davies, eds. Behavioural ecology: an evolutionary approach. 2d ed. Sinauer, Sunderland, Mass.

Green, R. F. 1982. Optimal foraging and sex ratio in parasitic wasps. J. Theor. Biol. 95:43–48.

Hamilton, W. D. 1967. Extraordinary sex-ratios. Science (Wash., D.C.) 156:477–488.

Houston, A. I., J. R. Krebs, and J. T. Erichsen. 1980. Optimal prey choice and discrimination time in the great tit (*Parus major* L.). Behav. Ecol. Sociobiol. 6:169–175.

Hughes, R. N. 1979. Optimal diets under the energy maximization premise: the effects of recognition time and learning. Am. Nat. 113:209–221.

Iwasa, Y., Y. Suzuki, and H. Matsuda. 1984. Theory of oviposition strategy of parasitoids. I. Effect of mortality and limited egg number. Theor. Popul. Biol. 26:205–227.

Jervis, M. A., and N. A. C. Kidd. 1986. Host-feeding strategies in hymenopteran parasitoids. Biol. Rev. Camb. Philos. Soc. 61:395–434.

Lande, R. 1982. A quantitative genetic theory of life history evolution. Ecology 63:607–615.

Levins, R. 1968. Evolution in changing environments. Princeton University Press, Princeton, N.J.

Lucas, J. R. 1983. The role of foraging-time constraints and variable prey encounter in optimal diet choice. Am. Nat. 122:191–209.

Mangel, M. 1987. Oviposition site selection and clutch size in insects. J. Math. Biol. 25:1–22.

Mangel, M., and C. W. Clark. 1986. Towards a unified foraging theory. Ecology 67:1127–1138.

Maynard Smith, J. 1982. Evolution and the theory of games. Cambridge University Press, New York.

McNair, J. N. 1982. Optimal giving-up times and the marginal-value theorem. Am. Nat. 119:511–529.

Paloheimo, J. E. 1971. On a theory of search. Biometrika 58:61–75.

Parker, G. A., and M. Begon. 1986. Optimal egg size and clutch size: effects of environmental and maternal phenotype. Am. Nat. 128:573–592.

Parker, G. A., and S. P. Courtney. 1984. Models of clutch size in insect oviposition. Theor. Popul. Biol. 26:27–48.

Roitberg, B. D. 1985. Search dynamics in fruit parasitic insects. J. Insect Physiol. 31:865–872.

Roitberg, B. D., and R. J. Prokopy. 1983*a*. Host deprivation influence on response of *Rhagoletis pomonella* to its oviposition deterring pheromone. Physiol. Entomol. 8:69–72.

———. 1983*b*. Resource assessment by larval and adult codling moths. J. N.Y. Entomol. Soc. 90:258–265.

———. 1984. Host visitation sequence as a determinant of search persistence in fruit parasitic tephritid flies. Oecologia (Berl.) 62:7–12.

———. 1987. Insects that mark host plants. BioScience 37:400–406.

Skinner, S. W. 1985. Clutch size as an optimal foraging problem for insects. Behav. Ecol. Sociobiol. 17:231–238.

Stephens, D. W., and J. R. Krebs. 1986. Foraging theory. Princeton University Press, Princeton, N.J.

van Alphen, J. J. M., and L. E. M. Vet. 1986. An evolutionary approach to host finding and selection. Pages 23–61 *in* J. Waage and D. Greathead, eds. Insect parasitoids. Academic Press, New York.

van Lenteren, J. C. 1981. Host discrimination by parasitoids. Pages 153–170 *in* D. A. Nordlund, R. L. Jones, and W. J. Lewis, eds. Semiochemicals: their role in pest control. Wiley, New York.

Vinson, S. B. 1976. Host selection by insect parasitoids. Annu. Rev. Entomol. 21:109–133.

————. 1981. Host location. Pages 51–77 *in* D. A. Nordlund, R. L. Jones, and W. J. Lewis, eds. Semiochemicals: their role in pest control. Wiley, New York.

Vinson, S. B., and G. F. Iwantsch. 1980. Host suitability for insect parasitoids. Annu. Rev. Entomol. 25:371–397.

Waage, J. K. 1979. Foraging for patchily-distributed hosts by the parasitoid *Nemeritis canescens*. J. Anim. Ecol. 48:353–371.

Waage, J. K., and H. C. J. Godfray. 1985. Reproductive strategies and population ecology of parasitoids. Pages 449–470 *in* R. M. Sibley and R. H. Smith, eds. Behavioural ecology: ecological consequences of adaptive behaviour. Blackwell, Oxford.

Weis, A. E., P. W. Price, and M. Lynch. 1983. Selective pressures on clutch size in the gall maker *Asteromyia carbonifera*. Ecology 64:688–695.