Parent-Offspring Conflict and Life-History Consequences in Herbivorous Insects

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PARENT-OFFSPRING CONFLICT AND LIFE-HISTORY CONSEQUENCES IN HERBIVOROUS INSECTS

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Abstract.—We develop an evolutionarily stable strategy theory of parent-offspring conflict in insect herbivores for the case in which offspring can choose to leave host plants on which they have been deposited by their mother. We find that a fundamental parent-offspring conflict in larval leaving rates occurs because individual larvae are more related to themselves than to their siblings whereas mothers are equally related to each of their offspring. Several patterns emerge: (1) The optimal probability of movement from the mother's perspective, p^*_{mom}, is always greater than or equal to the optimal probability of movement from the offspring's perspective, p^*_{off}, (2) a consequence of this difference in optimal probabilities of movement is that the mother's fitness for a given clutch is always greater for p^*_{mom} than p^*_{off}, (3) as the payoff for leaving a plant decreases, (i) the optimal movement rates decrease and (ii) clutches become smaller, (4) as relatedness increases, optimal movement probabilities increase and this causes an increase in optimal clutches, and (5) the clutch size that maximizes the mother's lifetime fitness will frequently diverge from that which the mother would produce were the offspring to move at her optimal rate (i.e., p^*_{mom}).

Herbivorous insects can be classified (Thompson 1982, 1988*a*) as parasites (those that usually complete development on a single plant) or grazers (those that usually exploit more than one plant during larval development). Over the past decade, a relatively complete theory of clutch size in parasitoids or fruit-parasitic insects has been developed (Charnov and Skinner 1985; Mangel 1987; Speirs et al. 1991). This theory has illuminated, among other problems, field and laboratory experiments on the determinants of clutch size, the role of host encounter rate, the response to marking pheromones, and the relationship between individual behavior and community processes. Similarly, a general theory describing the nature of parent-offspring conflict in parasitoids has been developed (Godfray 1987; Parker and Mock 1987; Rosenheim 1993). Although these theories can be applied to herbivorous insects that are parasites, there is no comparable theory for herbivorous insects that are grazers. In this article, we develop such a theory, simultaneously treating clutch size and parent-offspring conflict.

Our investigations focus on the differences in behavioral agendas of parents and offspring caused by different levels of relatedness. These are typically ignored in the theory of parasitoid clutch size because offspring are forced to spend their

larval period in the host in which they are laid (but see Godfray and Parker 1992). On the other hand, the larvae of many herbivorous insects are free to move from one host to another. Thus, behavioral patterns that differ from the "optimal" pattern for the mother may be expressed by the larvae. This is a general case of parent-offspring conflict (Trivers 1972, 1974). It is generally accepted that parent-offspring conflict is common in insects (Thompson 1988a; Godfray and Parker 1992); however, it is not clear how to study it. Our article suggests that, when properly viewed, much of insect behavior may provide a means for studying parent-offspring conflict.

FORMULATION AND THEORY

The key assumption is that some kind of larval competition occurs on hosts. In particular, we assume that the per-egg fitness accrued to the mother is a declining function of the number of individuals maturing on the host. For computations, we assume that the per-egg fitness when c eggs mature on a host of type i, $f_e(c, i)$, is given by

$$f_e(c, i) = \max\{0, 1 - [c/c_m(i)]^\gamma\}, \tag{1}$$

where $c_m(i)$ and γ are parameters characterizing the suitability of the host plant. Here the "max" insures that large clutches lead to no fitness. The fitness function (1) assumes that per-egg fitness decreases monotonically with the number of eggs laid. Thus, it does not treat fitness functions of the Allee type (in which a few larvae overcome host defense; see, e.g., Tsubaki 1981), contest-like functions (in which the per-egg fitness has a nonzero limiting form), or the case in which larvae in bigger groups do better than those in smaller ones (see, e.g., Lawrence 1990). These are all straightforward modifications of the theory.

Previous work (e.g., Mangel 1987) has assumed that the insects of interest were parasitoids, tephritid fruit flies, or that hosts were so far apart that offspring were constrained to stay at the host on which they were laid. We call this the "parasitoid" case; the fitness $f_{para}(c, i)$, from oviposition of a clutch of size c, where $c < c_m(i)$, on such a host is given by

$$f_{para}(c, i) = cf_e(c, i) = c\{1 - [c/c_m(i)]^\gamma\}. \tag{2}$$

It is easily seen that there is a clutch size c_i^* that maximizes $f_{para}(c, i)$; this is the Lack solution or "single host maximum" clutch (Mangel 1987; see Skinner 1985 for similar derivations of eqq. [1] and [2]).

Fitness per Clutch When Offspring Move

The situation is more complicated, however, when offspring may leave the plant on which they are placed. We will show that there is an evolutionarily stable probability of moving determined by the frequency dependence of reproductive payoff. Furthermore, because of different levels of relatedness, mothers and offspring have different evolutionarily stable strategy (ESS) probabilities of larval movement. The first instance of parent-offspring conflict occurs here.

We begin with the mother's perspective. The mother is equally related to all

of her offspring. Assume that she lays a clutch of size c and that the probability that any one of these offspring leaves the plant is p_1. Thus, the number, M, of offspring moving follows a binomial distribution with parameters c and θ, that is,

$$\Pr\{M = m \text{ offspring leave the plant} \mid \text{clutch of size } c \text{ is laid and} \\ \text{moving probability is } p_1\} = \binom{c}{m} \theta^m (1 - \theta)^{c-m}, \tag{3}$$

where m is the parameter for movement binomial probability that denotes the number of moving larvae. Hence the expected number of offspring moving is pc. It is also possible that movement probabilities of individual larvae are independent of one another; we will consider such instances in future articles. Assuming that σ is the probability that an individual who moves survives to find another plant and $\hat{f}$ is the average fitness this individual attains on other plants, the fitness that accrues to the mother from movers is $\sigma \hat{f} p c$. Immediately we see that it is neither σ nor $\hat{f}$ individually that affects the fitness, but their product. The fitness that accrues to the mother from the remaining offspring is $E_{\text{mom}}\{(c - M)f_e(c - M, i)\}$, where E_{mom} denotes the expectation over the binomial distribution (3). If the mother were directing the evolution of the offspring behavior, the optimal probability of moving would be determined by the condition that

$$\sigma \hat{f} p c + E_{\text{mom}}\{(c - M)f_e(c - M, i)\} \tag{4}$$

is maximized. That is, the optimal probability maximizes the contribution of fitness from offspring that stay and from offspring that move. We can find the value of p that maximizes expression (4), p_{mom} (i.e., mother's optimal moving probability for her offspring), by numerical methods such as the "golden section" algorithm (Press et al. 1986).

The mother's optimal moving probability need not be that which is expressed by the offspring as a result of differences from the perspective of the offspring. The difference is caused by relatedness: although the mother is equally related to all offspring, offspring are unequally related to each other. We assume that mothers are diploid and mate at least once and thus produce broods with average relatedness r. Consider a "distinguished individual" in a clutch of size c and assume that it is related to the other offspring in the clutch by a factor r, where $r < 0.5$, and that p is the probability that an individual leaves the host. If the distinguished individual stays at the host, its realized fitness, $f_s(c)$, is given by

$$f_s(c) = r\sigma \hat{f} p(c - 1) + E_{\text{mom}}\{f_e(c - M, i)[1 + r(c - 1 - M)]\}. \tag{5}$$

The first term on the right-hand side of equation (5) is the contribution to the fitness of the distinguished individual by its siblings who leave the plant. On average, $p(c - 1)$ of these individuals will leave and the expected fitness from these individuals is $r\sigma \hat{f}$. The fitness contributed by the remaining individuals is the second term in equation (5) (and this is added to the direct payoff for the distinguished individual); here we must take the average from the binomial distribution on the number of movers because of the nonlinearity in fitness function (1).

If the distinguished individual moves from the host, its realized fitness, $f_m(p)$, is given by

$$f_m(p) = \sigma \hat{f}(1 + rp(c - 1)) + r E_{mom}\{f_e(c - M, i)(c - 1 - M)\}. \qquad (6)$$

The difference between equations (5) and (6) is that, in equation (6), the fitness from the second term realized by the distinguished individual is obtained solely from siblings who remain on the plant.

Because the payoffs are frequency-dependent, the ESS probability that offspring move, p_{off}, is determined by the solution of $f_s(p_{off}) = f_m(p_{off})$, which can also be found by the golden section method. On occasion, the golden section algorithm will fail. Those correspond to a boundary value of p_{off} (either zero or one).

We will refer to p_{mom} and p_{off} as either probabilities of movement or rates of movement. When p_{mom} and p_{off} differ, which will usually be the case, there is implicit conflict between mother and offspring. We call this the fundamental parent-offspring conflict.

We can now compute the fitness obtained by the mother from a clutch of size c on a host of type i. There are, in fact, two fitnesses that we want to compute, since these provide a means for quantifying the effect of this conflict. The first is the increment obtained by the mother from oviposition when the offspring move at their optimal probability, $f_{m,o}(c)$. This is given by

$$f_{m,o}(c) = \sigma \hat{f} p_{off} c + E_{mom|p_{off}}\{(c - M)f_e(c - M, i)\}, \qquad (7)$$

where $E_{mom|p_{off}}$ is the fitness that accrues to the mother when offspring move at their ESS rate, p_{off}. Here the expectation of the second term on the right-hand side is taken according to the binomial distribution (3) with $p = p_{off}$.

The second (nonrealized, but interesting nonetheless) increment in fitness is that which the mother would obtain if the offspring moved at *her* optimal probability, $f_{m,m}(c)$, given by

$$f_{m,m}(c) = \sigma \hat{f} p_{mom} c + E_{mom|p_{mom}}\{(c - M)f_e(c - M, i)\}, \qquad (8)$$

where $E_{mom|p_{mom}}$ is the fitness that would accrue to the mother if the offspring left at their mother's optimal rate. The difference between $f_{m,o}(c)$ and $f_{m,m}(c)$ is a measure of parent-offspring conflict from the different optimal moving rates.

Finally, we can compute the fitness that an offspring receives when the mother oviposits a clutch of size c, $f_{off}(c)$. It is computed as

$$f_{off}(c) = r\sigma \hat{f} p(c - 1) + E_{mom|p_{off}}\{f_e(c - M, i)[1 + r(c - 1 - M)]\}. \qquad (9)$$

In equation (9), we have used equation (5), but equation (6) could have been used just as easily, because of the definition of p_{off}. Note that the difference between equations (9) and (7) is the relatedness factor.

Lifetime Fitness

We assume that behaviors have evolved to maximize the expected lifetime fitness that accrues to the mother through oviposition. Lifetime fitness,

$F(x, t, T)$, is defined (Mangel 1987; Mangel and Clark 1988) by

$$F(x, t, T) = \text{maximum expected fitness from ovipositions between time } t$$

$$\text{and the maximum time, } T, \text{ when egg complement at } t \text{ is } x. \tag{10}$$

In this definition of fitness, the maximum pertains to clutch sizes, conditioned on encounters with hosts of various types.

We assume the following: (1) There are two host types and the probability of encountering a host of type i during a single period is λ_i. (2) The length of a period is chosen so that the mother matures one egg during a period. There is a maximum egg complement x_m. (3) The probability ρ that the mother survives from one period to the next is independent of time, egg load, or activity. The general equation for $F(x, t, T)$ is then

$$F(x, t, T) = (1 - \lambda_1 - \lambda_2)\rho F(x', t + 1, T)$$

$$+ \sum_{i=1}^{2} \lambda_i \max_{c \leq x}\{f(c) + \rho F(x'', t + 1, T)\}. \tag{11}$$

In this equation, $x' = \min\{x + 1, x_m\}$, $f(c)$ is the fitness from a clutch of size c (i.e., any of the functions [2] or [7]–[9]), $x'' = \min\{x - c + 1, x_m\}$, and $\max_{c \leq x}$ denotes that the maximum is taken over possible clutches ranging from zero to x.

Assuming that no fitness accrues after time T provides the end condition that $F(x, T, T) = 0$ for all values of x. Equation (11) is then solved backwards, starting at $t = T - 1$. As this is done, we generate lifetime fitness and decisions $c_i^*(x, t)$, the optimal clutch when a host of type i is encountered in period t when the egg complement is x. By choosing different forms for $f(c)$, we obtain information about the life-history consequences of the fundamental parent-offspring conflict.

RESULTS

The Importance of Alternate Agendas

The theory described in the preceding section requires, in general, numerical implementation in order to obtain results. This does not mean, however, that it is impossible to obtain insight from the theory. In fact, all of our conclusions held when the parameters r, σ, $c_m(i)$, and γ were varied: r from 0.25 to 0.5, σ from 0.1 to 0.9, $c_m(i)$ from 3 to 10, and γ from 1 to 5. In this section, we describe general patterns that emerge, provide an explicit example of the pattern, and explain the intuitive content of the pattern.

Pattern 1.—The optimal probability of movement from the mother's perspective, p_{mom}^*, is always greater than or equal to the optimal probability of movement from the offspring's perspective p_{off}^* (fig. 1). That is, $p_{\text{mom}}^* \geq p_{\text{off}}^*$. In addition, for fixed clutch size, the probability of movement is larger on poorer hosts (for which c_m is smaller). A consequence of this difference in optimal probabilities of movement is that $f_{m,m}(c) \geq f_{m,o}(c)$ (fig. 2). That is, when offspring move at their preferred rate, the mother receives less fitness per clutch than if the offspring
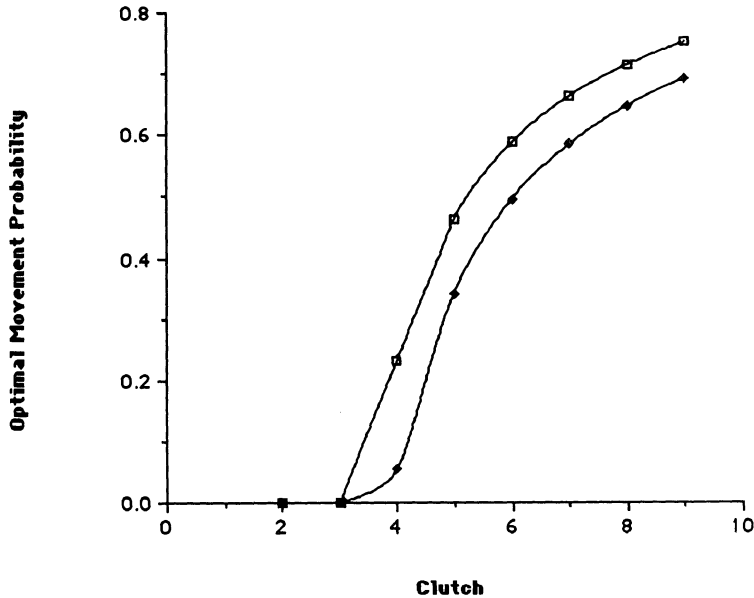
FIG. 1.—Optimal movement probability as a function of clutch size. The probabilities p_{mom} (*open squares*) and p_{off} (*closed diamonds*) differ. The optimal movement probability from the mother's perspective (eq. [4]) is always greater than or equal to the optimal movement probability from the offspring's perspective (by the solution of $f_s(p_{off}) = f_m(p_{off})$, where $f_s(p_{off})$ is the optimal probability for an individual to stay and $f_m(p_{off})$ is the optimal probability for an individual to move). Parameters are $\sigma \hat{f} = 0.5$, $\gamma = 3$, $c_m = 6$, and $r = 0.5$.

moved at the mother's preferred rate. The differences in optimal movement probabilities are caused by relatedness: the mother is equally related to all of her offspring but offspring are more strongly related to themselves than to their siblings.

Pattern 2.—Clutches, determined by the solution of equation (11), may be larger than a plant can support (fig. 3) and, for the same egg load, the poorer host may receive larger clutches. In each case, the movement of offspring from a host plant leads to the laying of large clutches. Poorer hosts may receive larger clutches because (1) in an environment dominated by poorer hosts, the ovipositing female will delay oviposition (with concomitant increases in egg load), and (2) movement probabilities are higher for the poorer host.

Pattern 3.—If the offspring could control the mother's clutch size, then, in general, the clutches would be equal to or less than clutches when the mother controlled her clutch size. The difference in relatedness, leading to the behavior described in pattern 2, also leads to this pattern.

Pattern 4.—As $\sigma \hat{f}$ decreases, the optimal movement rates decrease and clutches become smaller (fig. 4). As $\sigma \hat{f}$ increases, the offspring are likely to survive to find another host and contribute to the mother's lifetime fitness. This causes both the movement probability and the clutch size laid on a host to increase. Recent experiments on dispersal in leaf roller moth larvae (*Choristoneura*
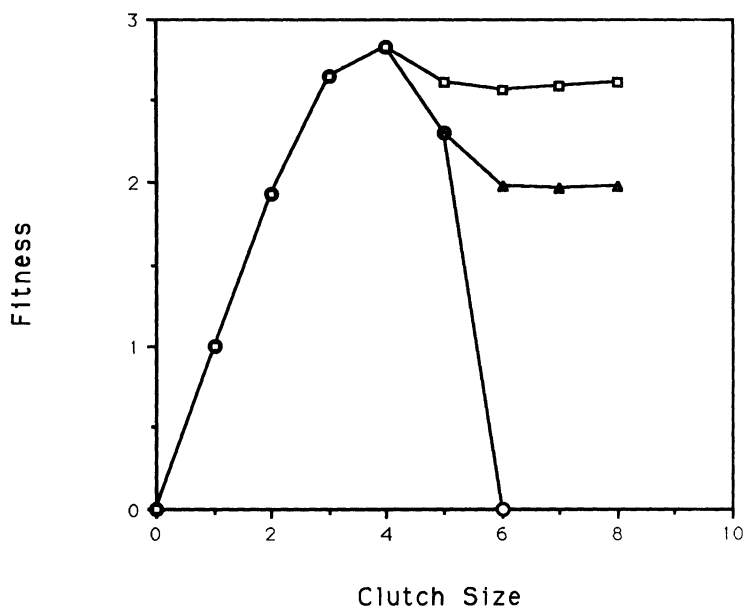
FIG. 2.—Fitness returns to the mother from clutches of varying sizes when offspring move at their own p_{off} (*open triangles*) (eq. [7]) vs. their mother's p_{mom} (*open squares*) movement probabilities (eq. [8]). Included in the figure is the fitness curve for a parasitoid (*open circles*) (eq. [2]) for which no interhost movement occurs. Parameter values are $\sigma\hat{f} = 0.1$, $r = 0.25$, and $\gamma = 3$.
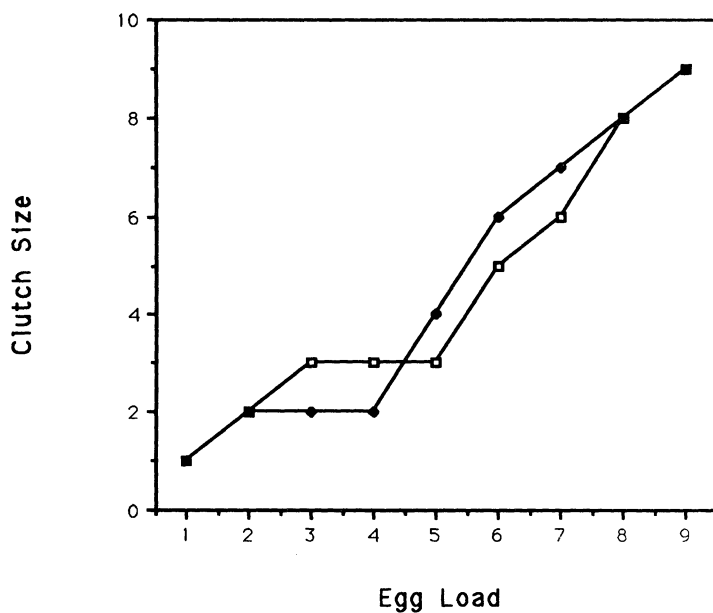

FIG. 3.—Optimal clutches at $t = 1$ as a function of egg load, determined by the solution of eq. (11) for two types of hosts (*open squares* and *closed diamonds*). Parameters are $T = 20$, $p = 0.8$, $x_{max} = 9$ (x_{max} is the maximum egg complement a female may harbor), $c_m(1) = 6$, $c_m(2) = 4$, $\lambda_1 = 0.25$, $\lambda_2 = 0.25$, $\gamma = 3$, $r = 0.5$, and $\sigma\hat{f} = 0.5$. Note that clutches can exceed the maximum number of offspring that a plant can support (six for host type 1 and four for host type 2), and the poorer host may receive larger clutches.
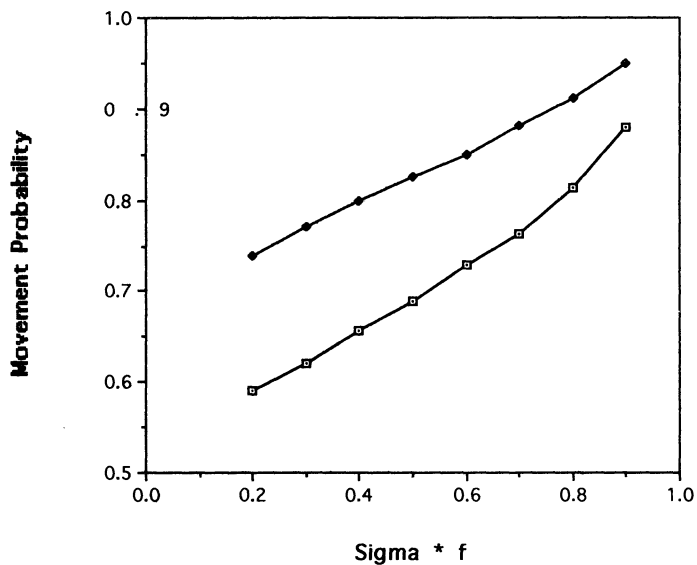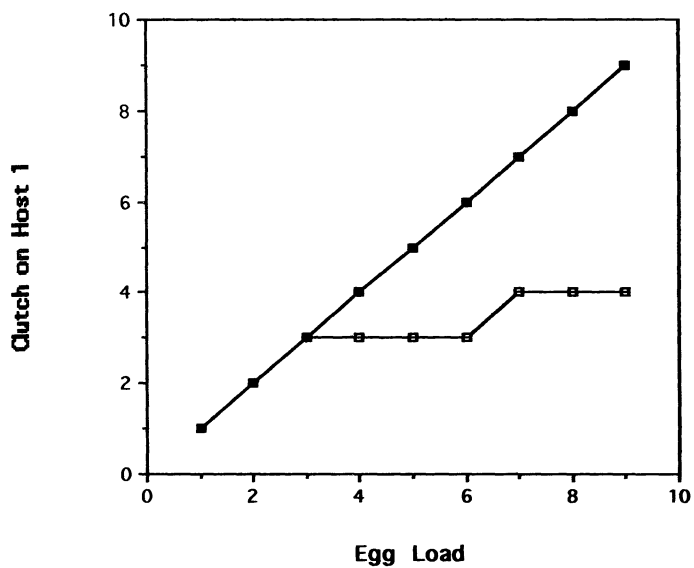
Fig. 4.—A, Movement probabilities on hosts of type 1 (*open squares*) and 2 (*closed diamonds*) for an offspring in a clutch of size nine as a function of $\sigma\hat{f}$, determined by the solution of $f_s(p_{\text{off}}) = f_m(p_{\text{off}})$, eq. (5), and eq. (6). B, Clutch size on host type 1 as a function of egg load for $\sigma\hat{f} = 0.9$ (*open squares*) or $\sigma\hat{f} = 0.2$ (*closed diamonds*) as determined by the solution of eq. (11).
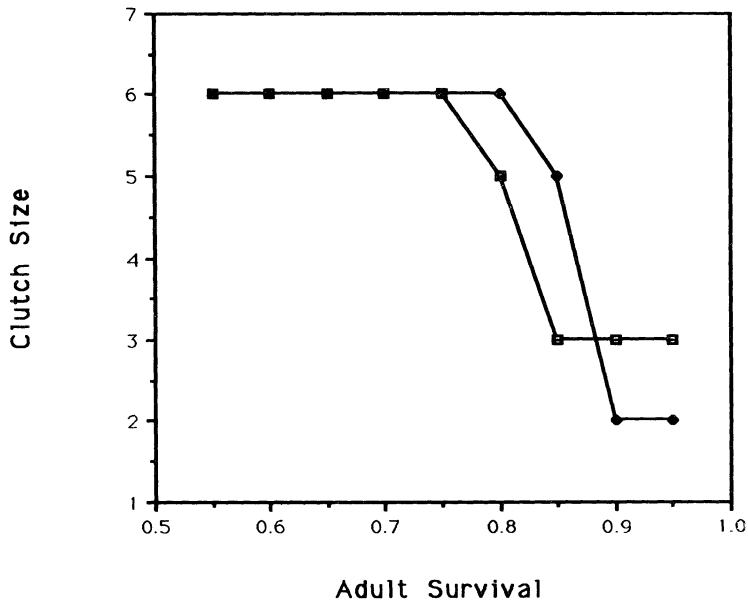
Fig. 5.—Optimal clutch at an egg load of six as a function of ρ on two hosts (host 1, *open boxes;* host 2, *closed diamonds*) as determined by the solution of eq. (11).

rosaceana [Harris]), demonstrated a reduced propensity for dispersal in habitats where $\sigma \hat{f}$ was low and vice versa (Carriere 1991). Note that, if $\sigma \hat{f}$ is sufficiently large, "egg dumping" occurs, in which the mother simply oviposits her entire egg load.

Pattern 5.—As ρ decreases, there is no effect on the optimal movement rates and optimal clutch sizes increase (fig. 5). The cause of this pattern is essentially the same as that causing pattern 4: as the adult experiences reduced likelihoods of depositing eggs in the future, current clutches increase in size. Courtney (1984) used key factor analysis to deduce a similar relationship between ρ and clutch size. Note that, unlike that case of a parasitoid (Mangel 1987), this pattern leads to egg dumping as ρ decreases: the mother lays all of her eggs, even though the plant cannot support all of the larvae.

Pattern 6.—As r increases, optimal movement probabilities increase (fig. 6A) and this causes an increase in optimal clutches (fig. 6B). As relatedness increases, the offspring share more genes and thus increase their own fitness more by moving.

Lifetime Fitness and Ecological and Evolutionary Variables

The fundamental parent-offspring conflict can manifest itself to differing degrees, which are dependent on the ecological setting and genetic structure of clutches. Here we consider the magnitude to which offspring can affect their mother's fitness. Again, several patterns arise.

Pattern 7.—As r and/or $\sigma \hat{f}$ decrease, offspring act more selfishly and the poten-
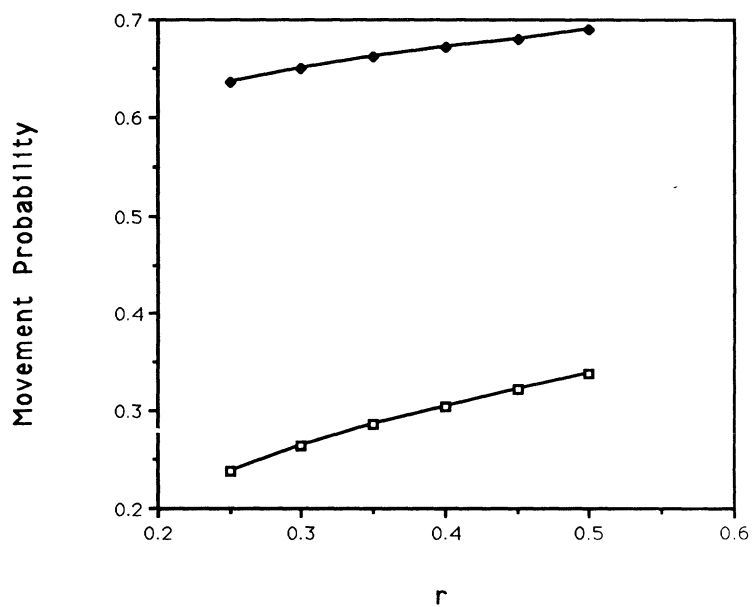
A
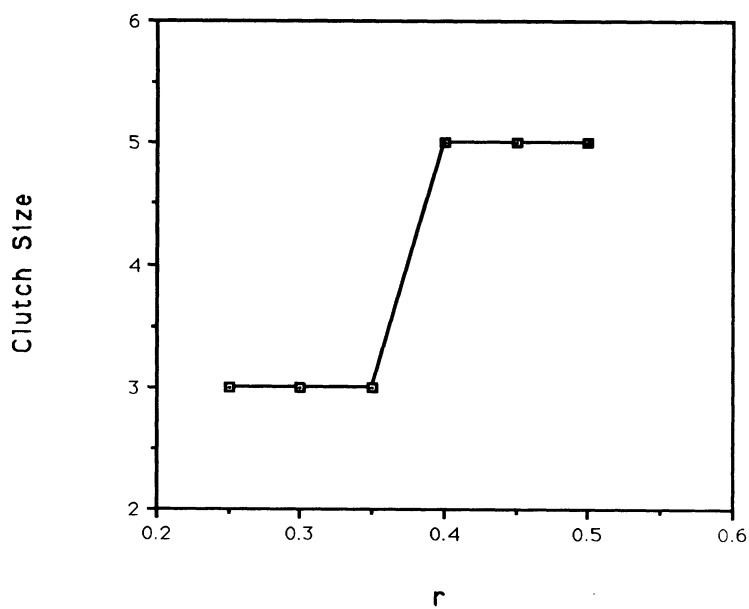
B

FIG. 6.—*A*, Optimal movement probabilities on host type 1 for an offspring in a clutch of size five (*open squares*) or a clutch of size nine (*closed diamonds*) as a function of relatedness as determined by the solution of $f_s(p_{off}) = f_m(p_{off})$. *B*, Optimal clutch for oviposition on host type 1 when egg compliment $x = 6$ as a function of relatedness.
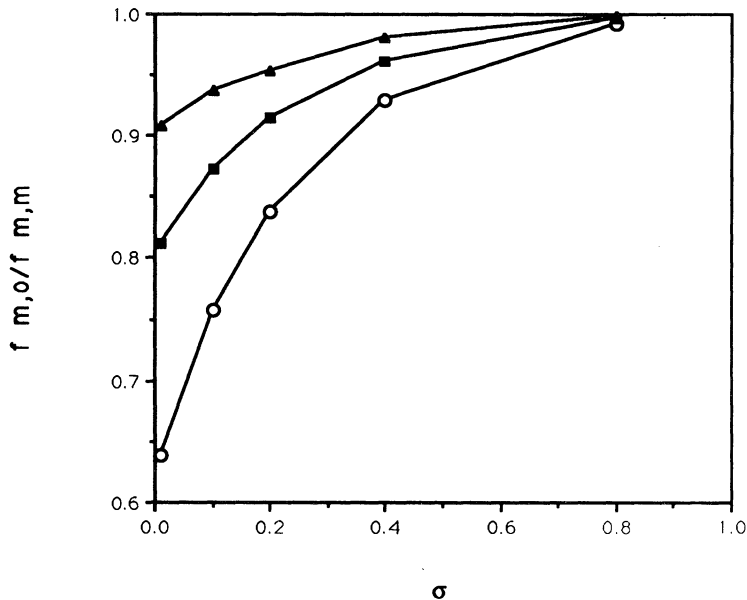
FiG. 7.—Single-clutch relative fitness returns as a function of $\sigma \hat{f}$ for three different levels of relatedness, $r = 0.25$ (*open circles*), $r = 0.375$ (*closed squares*), and $r = 0.5$ (*open triangles*) when offspring move at p_{off} vs. p_{mom} (as determined by solutions of eqq. [7], [8], and [2]). Parameter values are $\gamma = 3$ and $c_m = 6$.

tial fitness costs to mothers increase. Figure 7 shows one such example. Under some conditions, such costs can be substantial (ca. 35% reduction in fitness for a clutch of eight when $\sigma = 0.01$ and $r = 0.25$).

Pattern 8.—The clutch size that maximizes the mother's lifetime fitness will frequently diverge from that which the mother would produce were the offspring to move at her optimal rate (i.e., p_{mom}^*) (fig. 8). This is not the same conclusion as discussed in pattern 3, in which we considered the optimal clutch size from the mother's and the offspring's perspective. Notice, however, that there are many conditions wherein an optimizing mother will lay the same number of eggs whether the offspring moves at her optimal rate or not.

DISCUSSION

This work shows that parent-offspring conflict, most generally interpreted, can exist in ovipositing insects and suggests that further empirical investigations involving insects might yield many insights. The different agendas of ovipositing mother and offspring, caused by different relatedness, can lead to different behaviors. In some cases, the differences in behavior are striking. The theory helps organize experiments, first, by identifying which parameters are important and, second, by indicating which aspects of behavior should be amenable to experimental analysis and which should not. Parasitoids resolve the difference in
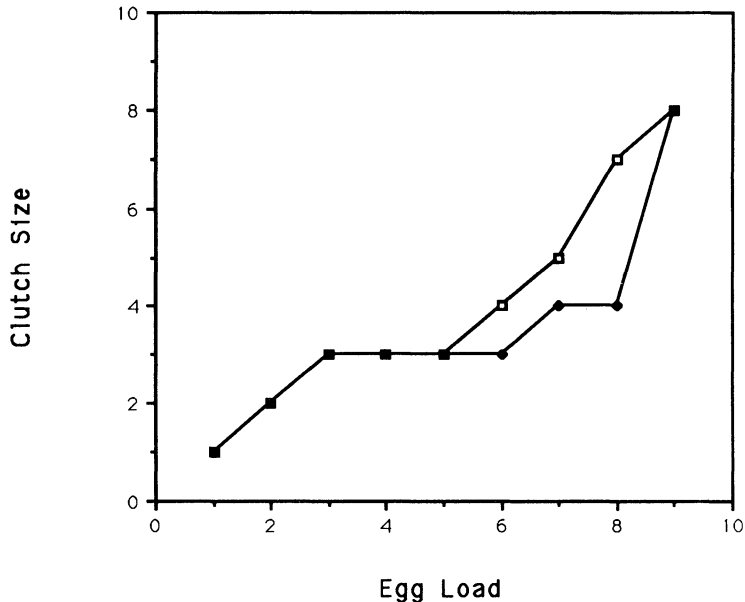
FIG. 8.—Optimal clutch size as a function of egg load when offspring move at p_{off} (*closed diamonds*) vs. p_{mom} (*open squares*) (as determined by the solution of eq. [11]). Parameter values are $\sigma \hat{f} = 0.4$, $r = 0.25$, and $\gamma = 3$.

agendas of mothers and offspring in an extreme manner. By laying offspring inside a host, the mother forces them to "accept" her agenda for clutch size. The response of offspring, however, may be the evolution of aggressiveness or gregariousness (see Godfray 1987; Rosenheim 1993). That is, given differing agendas, mothers and offspring can respond with different behavioral options. In general, behaviors that decrease the relatedness of larvae (e.g., multiple matings by the mother) will increase the difference in agendas between mother and offspring.

Our models were formulated within the framework of inclusive fitness, rather than with an explicitly genetic framework. The latter can, of course, be done. For example, Crespi and Taylor (1990) also derived optimal movement probability models with a haploid genetic framework but did so using a nearly unique biological system in which adults do the dispersing and females and males do so at different points in the mating history. The genetics of movement are not known and could range from single locus (see, e.g., Godfray 1987; Rosenheim 1993) to multilocus (Y. Carriere, unpublished manuscript). By taking the approach of inclusive fitness and by considering movement probability to be a quantitative trait we explicitly derive the fitness function that is needed for such genetic models and thus provide a link between the behavioral ecology and the genetics.

In a recent article, Godfray and Parker (1992) considered the theory of parent-offspring conflict in gregarious insects. Their work differs from ours in that they considered only the parasitoid life-style and they considered optimal clutch sizes

on a per-clutch basis (as opposed to those that maximize lifetime reproductive success). Nevertheless, Godfray and Parker reached similar conclusions that sibling conflict always reduces parental fitness and sibling conflict leads to mothers' producing clutches either smaller than or equal to those they would produce were larvae to move at their mother's chosen rate. Similarly, Godfray and Parker argued that the kinds of phenotypic models derived in their and our articles allow one to "define the battleground of parent-offspring conflict" (1992, p. 485).

Our work also illuminates two areas of interest in herbivorous insects: egg clustering (Stamp 1980; Courtney 1984) and relations between adult preference and larval performance (Singer 1986; Pilson and Rausher 1988; Thompson 1988*a*, 1988*b*, 1988*c*; Thompson et al. 1990; Mangel 1993). In particular, we suggest that egg clustering or egg dumping will evolve only in circumstances in which the larvae have an expected fitness associated with moving. It thus becomes important for us to determine the scale on which host plant patchiness is important. For example, are individual leaves or entire plants the operational unit determining larval survival?

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