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# THE OPTIMAL CLUTCH SIZE OF INSECTS WHEN MANY FEMALES OVIPOSIT PER PATCH

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Many insects lay clutches on discrete patches of larval food. Examples include parasitoid wasps ovipositing on insect hosts, flies on fallen fruit, and butterflies on the leaves of isolated host plants. For these insects, determining the number of eggs that a female should lay per patch is akin to an optimal-foraging problem: how should a female distribute her eggs among patches to optimize her lifetime fitness? When more than one female lays eggs on the same patch, the best clutch size depends on the clutch sizes adopted by all of the other females in a population. One way of examining this type of group situation is to apply the idea of an evolutionarily stable strategy (ESS). When adopted by all individuals in a population, an ESS cannot be bettered by an individual employing a different strategy (Maynard Smith and Price 1973; Oster and Wilson 1978). Parker and Begon (1986) presented a model to analyze the effects of different environmental and phenotypic parameters on the optimal clutch size and egg size for insects whose larvae compete on discrete resource patches. One of their results repeats a conclusion of Parker and Courtney (1984) and Skinner (1985): as the average number of females ovipositing per patch increases, the evolutionarily stable clutch size decreases. In deriving this result, these authors considered only a few of the possible functions describing competition among larvae in a patch. For different, but also realistic, curves describing larval competition, the evolutionarily stable clutch size increases as the average number of females ovipositing per patch increases.

Here I discuss how the evolutionarily stable clutch size of insects depends on the type of competition among larvae within discrete patches. This requires examining different functions that describe larval competition. I first show which types of larval competition promote increases or decreases in the evolutionarily stable clutch size with increasing numbers of females ovipositing per patch. This discussion uses a simple model governing female oviposition behavior. Second, I extend the simple model to ask whether the conclusions it generates are qualitatively altered by complexities that affect oviposition in nature. Third, I construct larval-competition functions based on assumptions about the feeding behavior of

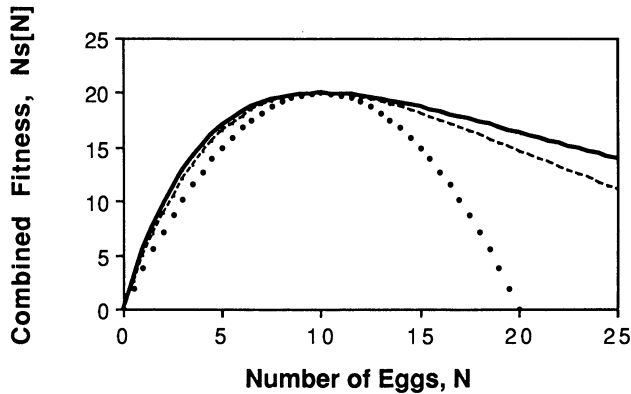* Present address: Department of Zoology, NJ-15, University of Washington, Seattle, Washington 98195.

FIG. 1.—The combined fitness of all larvae, $Ns(N)$, as a function of the number of eggs laid on a patch, $N$. Functions used for $s(N)$ are given in equation (1): *dotted line*, $s_1(N)$ with $\mu_1 = 4.0$ and $\alpha = 0.05$; *dashed line*, $s_2(N)$ with $\mu_2 = 5.44$ and $r = 0.1$; *solid line*, $s_3(N)$ with $\mu_3 = 6.32$, $a = \frac{1}{30}$, and $b = 4$.

larvae within patches. This analysis shows that small, quantitative differences in larval feeding behavior can produce competition functions that yield opposite predictions about how the evolutionarily stable clutch size varies with increasing numbers of females ovipositing per patch. This warns against inferring the behavior of the evolutionarily stable clutch size from only qualitative knowledge of larval feeding behavior. Fourth, I give examples from the literature of insects showing diverse patterns of larval competition within patches. These examples include larval-competition curves that promote either increases or decreases in the evolutionarily stable clutch size as more females oviposit per patch.

A SIMPLE MODEL FOR THE EVOLUTIONARILY STABLE CLUTCH SIZE

Parker and Begon (1986) analyzed many of the factors that influence clutch size in insects. To examine just one of these factors, I present a simple, special case of the model given by Parker and Begon (see also the similar models in Parker and Courtney 1984; Skinner 1985). Assume that $N$ eggs are oviposited by one or more females on a discrete patch of larval food. Also, assume competition among larvae such that the per capita fitness (survival times the adult fecundity of females or times the mating success of males) of the larvae, $s(N)$, is a decreasing function of $N$. The forms of $s(N)$ used here are

$$s_1(N) = \begin{cases} \mu_1(1 - \alpha N) & N < 1/\alpha \\ 0 & N \geq 1/\alpha \end{cases} \qquad \alpha > 0, \mu_1 > 0$$

$$s_2(N) = \mu_2 e^{-rN} \qquad r > 0, \mu_2 > 0 \tag{1}$$

$$s_3(N) = \mu_3(1 + aN)^{-b} \qquad a > 0, b > 1, \mu_3 > 0.$$

For each of these larval-competition curves, figure 1 gives a graph of the combined fitness of all larvae surviving per patch, $Ns(N)$, as a function of the number

of eggs laid. The curve $s_1(N)$ is that used by Parker and Begon (1986) and implies severe competition among larvae. Curves $s_2(N)$ and $s_3(N)$ are taken from the ecological literature as popular descriptions of competition (see May 1981). In $s_3(N)$, larval fitness drops more rapidly with increasing $N$ when the parameter $b$ is large, implying severe competition at high densities. As $b$ approaches infinity and $a$ approaches zero, curve $s_3(N)$ converges to $s_2(N)$ as a limiting case. For all curves, $\mu$ scales the overall larval fitness and is set to give each curve the same maximum value of $Ns(N)$.

To calculate the evolutionarily stable clutch size for the simplest possible case, assume that the number of eggs a female lays on one patch has no effect on the number she can lay on other patches. Therefore, the evolutionarily stable clutch size for a given female depends only on the costs and benefits associated with a single oviposition episode. This is the same assumption used to calculate the "Lack optimal clutch size" when only one female oviposits per patch (Charnov and Skinner 1984; Godfray 1986). Further assume that $F$ females oviposit on each patch. If the fates of the eggs and resulting larvae from all females are identical, then the fitness of a female laying $n$ eggs per clutch when all other females lay $\hat{n}$ eggs per clutch, $w(n|\hat{n})$, is given by

$$w(n|\hat{n}) = ns[n + (F - 1)\hat{n}].\tag{2}$$

The evolutionarily stable clutch size, $n^*$, is the solution of the equation (Oster and Wilson 1978; Parker and Begon 1986)

$$\partial w/\partial n|_{n=\hat{n}=n^*} = 0,\tag{3a}$$

provided that

$$\partial^2 w/\partial n^2|_{n=\hat{n}=n^*} < 0.\tag{3b}$$

For each larval-competition curve, the evolutionarily stable clutch sizes are

$$n_1^* = 1/\alpha(F + 1),$$
$$n_2^* = 1/r,\tag{4}$$
$$n_3^* = 1/a(b - F) \qquad \text{for } F < b.$$

As described by Parker and Begon (1986), $n_1^*$ decreases as more females oviposit per patch. However, $n_2^*$ is unaffected by the number of females ovipositing per patch. This result was obtained in a slightly different manner by Smith and Lessells (1985) when they applied a larval-competition curve like $s_2(N)$ to a different model for clutch size. Finally, $n_3^*$ increases with the number of females ovipositing per patch, approaching infinity as $F$ approaches $b$. When $F$ is equal to or greater than $b$, there is no evolutionarily stable clutch size under the simple assumptions of this model. However, the next section shows that more-realistic assumptions produce models for which the evolutionarily stable clutch size does not go to infinity when larval competition has the form of $s_3(N)$.

The change in the evolutionarily stable clutch size with increasing numbers of females ovipositing per patch can be explained as follows. The evolutionarily stable clutch size is determined by allowing one female to optimize the size of her clutch ($n$ in eq. 2), assuming that the clutch size of all other females is fixed at
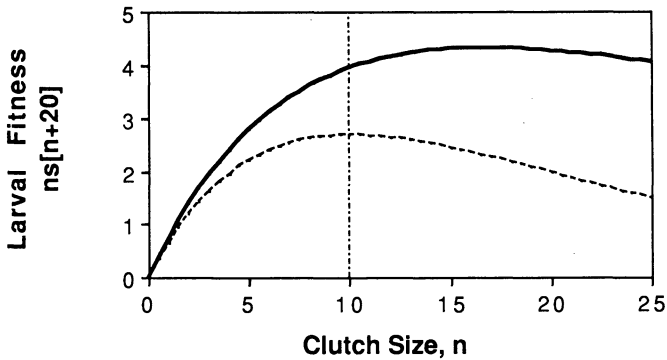
FIG. 2.—The combined fitness of the larvae from a single female when she oviposits a clutch size $n$ on a patch already containing 20 eggs laid by two other females. *Dashed line*, $s_2(N)$; *solid line*, $s_3(N)$; parameter values as in figure 1. Survival for the third female is zero for $s_1(N)$ and is therefore not shown.

some value $\hat{n}$. If the optimal clutch size for the single, deviating female is the same as the clutch size assumed for the other females, then $\hat{n}$ is the evolutionarily stable clutch size; any female that deviates from the ESS suffers a suboptimal clutch size. To see the effect of the three different larval-competition functions given in figure 1, consider the case in which three females oviposit on the same patch. Assume that two of the females each oviposit 10 eggs; 10 eggs is the optimal clutch size when females oviposit singly per patch, because $n = 10$ gives the maximum value of $ns(n)$ for all three larval-competition curves. The fitness of the third female, depending on her clutch size, is given in figure 2. For $s_3(N)$, the optimal clutch size for the third female is 17. This implies that the evolutionarily stable clutch size is greater than 10, because if all three females had clutch size 10, any one of them that increased her clutch size would obtain greater fitness. For $s_1(N)$, the survival rate of the eggs from all of the females is zero, because $s_1(20) = 0$. Therefore, the evolutionarily stable clutch size must be less than 10. The actual evolutionarily stable clutch sizes for $s_1(N)$ and $s_3(N)$ are 5 and 30, respectively. For $s_2(N)$, the optimal clutch size for the third female is 10; consequently, 10 is the evolutionarily stable clutch size. This confirms the results in equations (4) that the evolutionarily stable clutch size is independent of the number of females ovipositing when larval competition has the form $s_2(N)$.

The conclusion that the evolutionarily stable clutch size increases with increasing numbers of females ovipositing per patch results for a wide class of larval-competition curves, not just for the specific curve $s_3(N)$. Appendix A derives a general criterion for competition curves that show this behavior. This criterion is based on the function $h(N)$, defined as

$$h(N) = \dot{s}(N)/s(N). \tag{5}$$

Here, $\dot{s}(N)$ is the derivative of $s(N)$ with respect to $N$. If the derivative of $h(N)$, $\dot{h}(N)$, is negative, as it is for $s_1(N)$ (Appendix A), then the evolutionarily stable clutch size decreases with increasing $F$ (i.e., as more females oviposit per patch).

If $\dot{h}(N)$ is positive, then the evolutionarily stable clutch size increases with increasing $F$, as for $s_3(N)$. For the function $s_2(N)$, $\dot{h}(N)$ is zero. Generally speaking, the evolutionarily stable clutch size increases with increasing numbers of ovipositing females whenever the curve given by $Ns(N)$ increases rapidly for small $N$ but decreases slowly for large $N$ (see fig. 1). Although $\dot{h}(N)$ retains the same sign across all $N$ for the three examples of $s(N)$ in equations (1), this need not be true, and the evolutionarily stable clutch size can increase and decrease with $F$ over different parts of its range. (An example of this is given in the section "Inferring fitness curves from larval feeding behavior.")

### ADDING COMPLEXITIES TO THE SIMPLE MODEL

In the simple model described above, the number of females ovipositing on every patch was assumed to be the same, and females were assumed to optimize their clutch size on a per-patch basis. This section relaxes these assumptions by considering the cases when (1) a variable number of females oviposits per patch; (2) the clutch size of a female on a single patch cannot be treated in isolation, because the clutch size on one patch will affect either the clutch sizes on other patches or the number of patches a female can find in her lifetime; and (3) females can assess whether eggs were previously laid on a patch and adjust their clutch sizes accordingly.

The result using $s_3(N)$ in the simple model, that the evolutionarily stable clutch size increases as more females oviposit per patch, is counterintuitive. Therefore, throughout this section, emphasis is placed on larval-competition curve $s_3(N)$. Cases 1–3 above are analyzed to determine whether the conclusion from the simple model can be reversed: can the evolutionarily stable clutch size decrease as more females oviposit per patch, even though larval competition has the form $s_3(N)$?

### Variable Numbers of Females Ovipositing per Patch

In nature, not all patches are visited by the same number of females. Let $p(i|\overline{F})$ be the probability that $i$ females oviposit on a patch given that $\overline{F}$ is the mean number of females ovipositing per patch. The distributions used here for $p(i|\overline{F})$ are the Poisson distribution and the negative-binomial distribution, which has a greater variance than the Poisson distribution. Further assume that females produce the same clutch size on every patch they find; this assumption is realistic for insects with fixed clutch size (e.g., Calliphoridae, Diptera [Ullyett 1950]) or insects that cannot assess the presence of eggs already on patches (e.g., Hymenoptera, *Gregopimpla himalayensis* [Shiga and Nakanishi 1968]; Lepidoptera, *Euptychia arnaea* and *E. libye* [Singer and Mandracchia 1982]). Under this assumption, the expected fitness of a female with clutch size $n$ when all other females have clutch size $\hat{n}$ is

$$E[w(n|\hat{n})] = \sum_{i=0}^{\infty} ns_3[n + (i - 1)\hat{n}]\, ip(i|\overline{F})/\overline{F}. \tag{6}$$

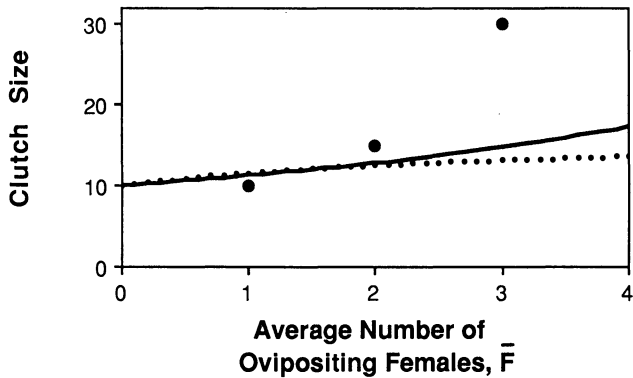Here, larval competition is assumed to take the form of $s_3(N)$.

FIG. 3.—The evolutionarily stable clutch size, $n^*$, as a function of the average number of females ovipositing per patch, $\bar{F}$. Larval competition has the form of $s_3(N)$ with parameters as in figure 1. *Solid circles*, Females distributed such that exactly $F$ oviposit per patch (at $F = 4$, the evolutionarily stable clutch size is infinite); *solid line*, females distributed according to a Poisson distribution; *dotted line*, females distributed according to a negative-binomial distribution (with the parameter $k = 1$) (eq. 6).

The evolutionarily stable clutch size, $n^*$, can be calculated for equation (6) in the manner of equations (3), and figure 3 shows $n^*$ graphed as a function of $\bar{F}$, the mean number of females ovipositing per patch. With variability in the number of females ovipositing per patch, the evolutionarily stable clutch size does not approach infinity for some values of $\bar{F}$. However, the evolutionarily stable clutch size still increases as more females oviposit per patch. Also, comparing the Poisson distribution (solid line) with the negative-binomial distribution (dotted line) shows that as the degree of variability in the number of females ovipositing per patch increases, the predicted evolutionarily stable clutch size increases more slowly with increasing $\bar{F}$.

## Lifetime Trade-offs

For many insects, the number of eggs a female lays on one patch affects the number of eggs she should oviposit on other patches. In this case, determining the evolutionarily stable clutch size requires analyzing the trade-offs in a female's lifetime fitness. As an example, suppose a female is limited by the amount of time that she can spend searching for patches. The female should optimize her fitness per unit of time, analogous to the situation depicted by the marginal-value theorem (Charnov 1976; Parker and Courtney 1984; Skinner 1985). Let $T_S$ be the time required for a female to find a patch, and let $T_H$ be the time it takes for a female to produce a single egg; $T_H$ includes feeding time if females require food before maturing eggs and also the time it takes to oviposit a single egg once a patch is found. It is assumed that the handling times for eggs are additive: the time it takes to produce $n$ eggs is $nT_H$. A female's fitness per unit of time when she oviposits $n$ eggs and all other females oviposit $\hat{n}$ eggs, $w(n|\hat{n})$, is given by (Parker and Courtney 1984; Godfray 1986)

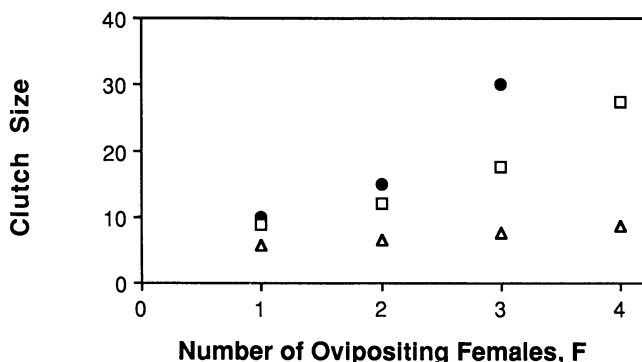$$w(n|\hat{n}) = ns_3[n + (F - 1)\hat{n}] \, r(n),$$

FIG. 4.—The evolutionarily stable clutch size, $n^*$, as a function of the number of oviposit-ing females per patch when females are limited by the time they can search for patches (eq. 7). Larval competition has the form of $s_3(N)$ with parameters as in figure 1. *Squares*, $T_S = 100$, $T_H = 1.0$; *triangles*, $T_S = 10$, $T_H = 1.0$; *solid circles*, evolutionarily stable clutch size when there is no lifetime trade-off, that is, $T_H = 0$ (at $F = 4$, the evolutionarily stable clutch size is infinite).

where

$$r(n) = 1/(T_S + nT_H). \tag{7}$$

Here, it is assumed that exactly $F$ females oviposit per patch. Figure 4 shows the resulting evolutionarily stable clutch size as a function of $F$ for different values of $T_S$, the searching time required to find patches. As $T_S$ decreases, the evolutionarily stable clutch size, $n^*$, increases with $F$ more slowly. However, even small values of $T_S$ do not cause the evolutionarily stable clutch size to decrease with increasing $F$, provided that larval competition has the form of $s_3(N)$.

### Knowledgeable Females

The complexities added to the simple model in the last two subsections can be combined by assuming that variable numbers of females oviposit on different patches and that females choose their clutch size to optimize their lifetime fitness. A third assumption can be added: females can accurately assess whether eggs have been previously laid on a patch and can adjust their clutch sizes accordingly. The ability to assess whether other females have previously oviposited on a patch has been shown for several insects (Hymenoptera, *Nasonia vitripennis* [Holmes 1972], *Apanteles glomeratus* [Ikawa and Suzuki 1982]; Lepidoptera, *Pieris bras-sicae* [Rothschild and Schoonhoven 1977]; Diptera, *Rhagoletis pomenella* [Roitberg and Prokopy 1981]). This subsection explores whether the evolu-tionarily stable clutch size for knowledgeable females may decrease as more females oviposit per patch, even though larval competition is given by $s_3(N)$.

When females can assess the presence of eggs on patches, calculating the evolutionarily stable clutch size for many females ovipositing per patch becomes mathematically complex. Therefore, for the sake of simplicity, I consider only the case when at most two females oviposit on the same patch. This case is also

considered by Parker and Courtney (1984) and by Parker and Begon (1986) (for a general discussion, see also Godfray 1987, pp. 142–145).

Let $p(0)$, $p(1)$, and $p(2)$ denote the probabilities that 0, 1, and 2 females oviposit on the same patch, given that the mean number of females ovipositing per patch is $\bar{F}$ ($0 \le \bar{F} \le 2$). If ovipositing females are distributed randomly, then the values of $p(i)$ will be binomially distributed. Let $q_0$, $q_1$, and $q_2$ denote the probabilities that a given female oviposits alone, first, or second in a patch, respectively:

$$q_0 = p(1)/[p(1) + 2p(2)],$$
$$q_1 = q_2 = p(2)/[p(1) + 2p(2)]. \tag{8}$$

For a given female, let $n_1$ be her clutch size if she oviposits on a patch before any other female, and let $n_2$ be her clutch size if she oviposits on a patch already containing eggs. Let $\hat{n}_1$ and $\hat{n}_2$ be defined similarly for all other females in a population. Because the larvae from the first female may get a head start in feeding on the patch, they might have a competitive advantage over the larvae from the second female. To allow for this type of first-clutch advantage, let K denote the reduction in fitness of the larvae from the second female relative to the first; K ranges from zero, when all of the larvae from the second female die, to 1, when there is no first-clutch advantage. Under these assumptions, the expected lifetime fitness of a female per unit of time is

$$E[w(n_1, n_2 | \hat{n}_1, \hat{n}_2)] = \frac{n_1 s_3(n_1) q_0 + n_1 s_3(n_1 + \hat{n}_2) q_1 + K n_2 s_3(\hat{n}_1 + n_2) q_2}{T_S + T_H(n_1 q_0 + n_1 q_1 + n_2 q_2)}. \tag{9}$$

Solving equation (9) for the evolutionarily stable clutch sizes gives values for the first and second clutch laid on a patch, $n_1^*$ and $n_2^*$. Figure 5 shows $n_1^*$ and $n_2^*$ graphed as functions of the mean number of ovipositing females, $\bar{F}$. In figures 5A and 5B, there is no first-clutch advantage (K = 1); in figures 5C and 5D, K = 0.7. Moreover, in figures 5A and 5C, the searching time ($T_S$ = 100) is longer than in figures 5B and 5D ($T_S$ = 10). As found for the models in the previous sections, the evolutionarily stable clutch sizes for both the first and the second female increase with an increase in $\bar{F}$, the mean number of females ovipositing per patch.

Although the evolutionarily stable clutch sizes increase as $\bar{F}$ increases, whether the second female should lay more or fewer eggs than the first female depends on the magnitudes of the searching time, $T_S$, and the first-clutch advantage, K. When the searching time, $T_S$, is short relative to the handling time, $T_H$, patches are easy to find. Therefore, a second female is more likely to profit from withholding some of her eggs, because she can more easily find an empty patch on which to deposit them. Consequently, when $T_S$ is short, the clutch size of the second female tends to decrease relative to that of the first. Similarly, when there is a first-clutch advantage (K < 1), the second female ovipositing on a patch incurs a greater cost, and withholding eggs for an empty patch becomes more profitable. This also promotes smaller clutch sizes for the second female.

In the examples above, it is always optimal for the second female to oviposit at least one egg. This can be explained as follows. The gain in fitness that the first female obtains by ovipositing her $n$th egg is the fitness of that egg, $s(n)r(n)$, minus
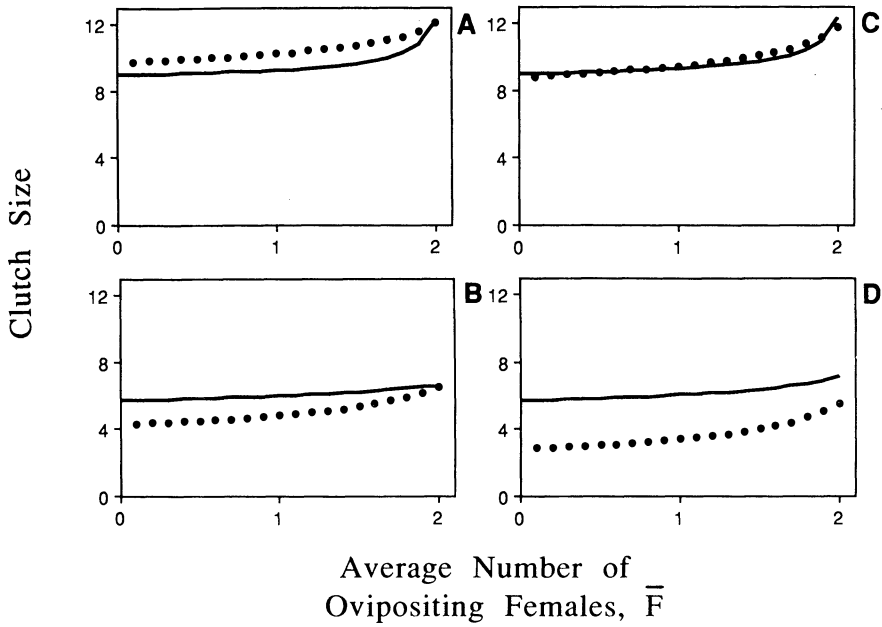
FIG. 5.—The evolutionarily stable clutch sizes for females ovipositing on a patch as a function of the average number of females ovipositing per patch, $\bar{F}$ (eq. 9): *solid line*, first female; *dotted line*, second female. Larval competition has the form of $s_3(N)$ with parameters as in figure 1. *A*, *B*, No first-clutch advantage (K = 1); *C*, *D*, K = 0.7. Searching times, $T_S$: *A*, *C*, 100; *B*, *D*, 10. Handling time, $T_H$, is 1.0 in all four views.

the decrease in fitness of all of her previously laid eggs, $(n - 1)[s(n - 1)r(n - 1) - s(n)r(n)]$. The first female will continue to lay eggs until the rate at which she gains fitness by ovipositing eggs drops below the expected rate she would obtain by searching for another patch. Therefore, if the evolutionarily stable clutch size for the first female is $n_1^*$, the expected rate of fitness gain for a female searching for a new patch is $s(n_1^*)r(n_1^*) - (n_1^* - 1)[s(n_1^* - 1)r(n_1^* - 1) - s(n_1^*)r(n_1^*)]$. For the second female ovipositing her first egg, the fitness she gains is $Ks(n_1^* + 1)r(n_1^* + 1)$, but there is no loss in fitness through previously laid eggs. Therefore, the second female should lay at least one egg, provided that the fitness she gains through laying that egg is greater than the expected rate of fitness she would gain by searching for another patch, that is, if

$$Ks(n_1^* + 1)r(n_1^* + 1)$$

$$> s(n_1^*)r(n_1^*) - (n_1^* - 1)[s(n_1^* - 1)r(n_1^* - 1) - s(n_1^*)r(n_1^*)] \quad (10)$$

$$> n_1^* s(n_1^*)r(n_1^*) - (n_1^* - 1)s(n_1^* - 1)r(n_1^* - 1).$$

This inequality will often be satisfied. In particular, for large $n$, inequality (10) is approximately

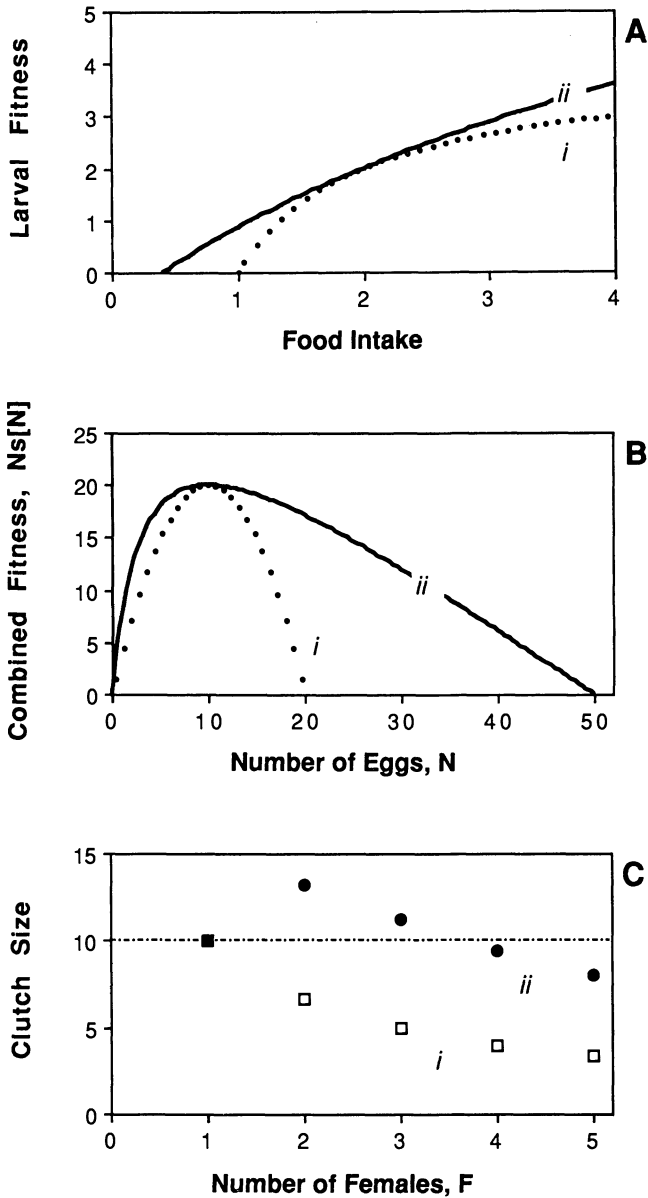$$Ks(n)r(n) > s(n)r(n) + n\dot{s}(n)r(n) + ns(n)\dot{r}(n). \quad (11)$$

FIG. 6.—The evolutionarily stable clutch size as a function of the number of females ovipositing per patch for two larval-competition curves constructed from larval feeding characteristics. $A$, Two examples (i and ii) of the relationship between the fitness of a larva and the amount of food it eats. The function for larval fitness has the form $(c_1 + c_2 x)/(c_3 + c_4 x)$, where $x$ is the amount of food intake and the $c_i$'s are constants. $B$, The combined fitness of larvae, $Ns(N)$, as a function of the number of eggs laid per patch, $N$, determined from the curves in $A$. The $c_i$'s in $A$ were chosen to give the curves in $B$ the same maxima as the curves in figure 1. $C$, The resulting evolutionarily stable clutch sizes as functions of the number of females ovipositing per patch, $F$. At $F = 1$, the solid circle and the open square coincide.

Because both $\dot{s}(n)$ and $\dot{r}(n)$ are negative, this inequality always holds when there is no first-clutch advantage (K = 1). However, a large first-clutch advantage (K small) can override this and cause the second female to withhold all of her eggs.

## INFERRING FITNESS CURVES FROM LARVAL FEEDING BEHAVIOR

The distinguishing feature of larval-competition curve $s_1(N)$ is that, when the number of eggs on a patch is large, no larva on the patch survives. This type of catastrophic mortality can result from scramble competition; if there are too many larvae, none can sequester enough food to survive. Appendix B shows that when catastrophic mortality occurs at high larval densities, the evolutionarily stable clutch size necessarily decreases when the number of females ovipositing per patch is very high. However, this need not be true when the number of females ovipositing per patch is low. This section derives an example of a scramble-competition function with catastrophic mortality for which the evolutionarily stable clutch size initially increases as the first few females oviposit on a patch, and then decreases as more females oviposit.

A function describing larval competition can be derived by knowing how the fitness of a larva varies with the amount of food it eats. Figure 6 gives two hypothetical examples for larvae that compete for food but do not interact aggressively toward one another. Figure 6A shows the fitness of larvae as a function of the amount of food they eat, and figure 6B translates this into a curve for the number and fitness of larvae produced per patch as a function of the number of eggs laid. The curves in figure 6B are equivalent to the curves of $Ns(N)$ in figure 1; and in fact, curve i in figure 6B is identical to $Ns_1(N)$. Figure 6C gives the evolutionarily stable clutch sizes as functions of the number of ovipositing females, $F$, assuming that $F$ is the same for all patches. The important message from figure 6 is that under certain circumstances (i.e., case ii), the evolutionarily stable clutch size may first increase and then decrease with $F$.

This example clearly shows that when no larvae survive to adulthood, this zero larval survivorship after high initial larval densities does not necessarily lead to evolutionarily stable clutch sizes that monotonically decrease as more females oviposit per patch. It also shows that qualitative knowledge about the feeding behavior of larvae is not sufficient for drawing a conclusion about the evolutionarily stable clutch size. In both of the examples above, competition among larvae was assumed to be a scramble for limited resources; the examples differed only in the quantitative details of the relationship between fitness and food consumption. To predict the evolutionarily stable clutch size, it is necessary to analyze larval fitness curves generated by detailed competition studies across many larval densities. This is done in the next section.

## EXAMPLES OF LARVAL-COMPETITION CURVES

I searched the literature to find examples of larval-competition curves for hymenopteran parasitoids in which females lay more than one egg per clutch. I chose to concentrate on hymenopteran parasitoids because hymenopterans often

TABLE 1

LARVAL-COMPETITION CURVES

| Species | Resource | Parameter Estimates* | | Measure† | Source |
|---|---|---|---|---|---|
| CATEGORY 1: $s_1(N) = \mu_1(1 - \alpha N)$ | | | | | |
| Hymenoptera | | | | | |
| Bracon greeni | Eublemma amabilis larvae | 0.17 | | fitness | Pramanik & Choudhury 1963 |
| Dahlbominus fuliginosus‡ | Neodipron leconti larvae | 0.00095 | | survivorship | Wilkes 1963 |
| Microbracon gelechiae | gram flour moth larvae | 0.023 | | survivorship | Narayanan & Subba Rao 1955 |
| Coleoptera | | | | | |
| Callosobruchus maculatus | cowpeas | 0.028 | | survivorship | D. P. Giga (in Smith & Lessells 1985) |
| CATEGORY 2: $s_2(N) = \mu_2 e^{-rN}$ | | | | | |
| Hymenoptera | | | | | |
| Apanteles congregatus | tobacco hornworm larvae | 0.0024 | | survivorship | Beckage & Ridiford 1979 |
| Pteromalus puparum | Papilio xuthus pupae | 0.0024 | | fecundity | Takagi 1985 |
| CATEGORY 3: $s_3(N) = \mu_3(1 + aN)^{-b}$ | | | | | |
| Hymenoptera | | | | | |
| Bracon hebetor‡§ | almond moth larvae | 2.3 | 0.58 | fitness | Benson 1973 |
| | Mediterranean flour-moth larvae | 0.050 | 0.57 | fitness | Taylor 1984, 1988 |
| Trichogramma evanescens | Mamestra brassicae eggs | 0.36 | 6.0 | survivorship | N. Pallewatta (in Waage & Godfray 1985) |
| Trichogramma embryophagum‡ | Mediterranean flour-moth eggs | 2.4 | 1.2 | fitness | Klomp & Teerink 1967 |
| Diptera | | | | | |
| Phaenicia coeruleiviridis | mammal carcasses | 0.062 | 0.87 | fitness | Ives 1988 |

\* Category 1, $\alpha$; category 2, $r$; category 3: left-hand column, $a$; right-hand column, $b$.
† The measure of competition used in the study: fitness, survivorship, or fecundity.
‡ Competition curve differed significantly from the form of $s_2(N)$.
§ Competition curve differed significantly from the form of $s_2(N)$ only for the data in Benson 1973.

show complex ovipositing behavior and their clutch size is consequently well studied. Nine laboratory studies of eight different species gave sufficient data to determine larval-competition curves; these are listed in table 1. The table also includes two representative studies on larval competition in non-hymenopteran insects.

The insects are divided into categories 1, 2, and 3, corresponding to larval-competition curves $s_1(N)$, $s_2(N)$, and $s_3(N)$, respectively. Each of the three larval-competition curves was fitted to the data sets using nonlinear regression, and category 1, 2, or 3 was assigned according to which curve gave the lowest sum of squared residuals. For many of the data sets, only the mean survivorship or fitness

was reported for replicates at each larval density. Therefore, it is not possible to calculate the percentage of variation explained by the fitted curves. However, Appendix C derives a test for statistically distinguishing between $s_1(N)$ and $s_3(N)$, with $s_2(N)$ serving as the null hypothesis. Insects marked with a double dagger have larval-competition curves statistically more like $s_1(N)$ (category 1) or $s_3(N)$ (category 3) than $s_2(N)$ (category 2) at the $P < 0.05$ level.

Several comments are necessary about the data sets I analyzed for the table. The effect of competition on larvae was measured differently in different studies. In some cases, only survivorship was determined; in others, the fecundity of female offspring was also measured, allowing estimates of female fitness. For simplicity, I have assumed that male fitness varies with larval density in the same way as female fitness. In one study (Takagi 1985) density was found not to affect survivorship, although female fecundity decreased with larval density. Many of the studies with hymenopterans showed changes in the sex ratio with increasing numbers of larvae per host; some of the studies showed that this was caused by females varying the sex ratio of their eggs. I ignored these changes in sex ratio and summed the numbers of female and male offspring to calculate survivorship.

A problem in interpreting the data in the table is the possibility that zero survivorship would occur for insects in categories 2 and 3 if the researchers had explored sufficiently high larval densities. In fact, zero survivorship was obtained by N. Pallewatta (in Waage and Godfray 1985) for *Trichogramma evanescens*. As shown in Appendix B, the evolutionarily stable clutch size must eventually decrease when zero survivorship is approached. Therefore, it is possible that some of the examples in category 3 show the pattern given in figure 6C for case ii, where an increase in the evolutionarily stable clutch size is followed by a decrease as more females oviposit per patch. However, for other species, competition may never be sufficient to produce zero larval survivorship, as suggested by Klomp and Teerink (1967) for *Trichogramma embryophagum*.

The table is meant to give representative larval-competition curves, not to make predictions about the evolutionarily stable clutch size for these particular insects. There are of course many factors that influence clutch size beyond those considered in this paper (see, e.g., Parker and Begon 1986; Godfray 1987; Mangel 1987). However, the table shows that all three curves $s_1(N)$, $s_2(N)$, and $s_3(N)$ are biologically realistic. Therefore, the potential exists for both decreases and increases in the optimal clutch size of insects as the number of females ovipositing per patch increases.

## DISCUSSION

Here I have addressed how, under a variety of different circumstances, a female insect's optimal clutch size changes as more females oviposit per patch. The optimal clutch size might be obtained behaviorally if individual females can assess average population densities, or the optimal clutch size might respond on an evolutionary time scale to changes in average population densities.

One of the more striking predictions to emerge from the analysis is the behavior of a second female arriving on a patch that she knows already contains eggs. The

evolutionarily stable clutch size of this second female is predicted to be greater than that of the first only if (1) the larval-competition curve is like $s_3(N)$, (2) the time required to find a patch is long relative to the time required to produce eggs ($T_S > T_H$), and (3) any first-clutch advantage is not large. Since most parasitoids do not satisfy all three of these criteria, in general, second females might be expected to oviposit fewer eggs than the first. Studies of the hymenopteran parasitoids *Nasonia vitripennis* (Holmes 1972) and *Apanteles glomeratus* (Ikawa and Suzuki 1982) reported that the second female ovipositing on a host lays fewer eggs than does the first female. However, Werren (1980, reported in Skinner 1985) showed examples from *Nasonia vitripennis* in which the second females laid both fewer and more eggs than the first. This variability in the second females' behavior has been explained by assuming that the second females differ in the amount of time since they last laid eggs; a female that has searched for a long time should be more likely to oviposit (Iwasa et al. 1984; Mangel 1987). Data from Wylie (1965) suggest that larval competition for *N. vitripennis* has roughly the form of $s_1(N)$, although the data cannot support a statistical analysis. Therefore, it is unlikely that the form of larval competition plays a role in explaining why the second *N. vitripennis* female sometimes lays more eggs than the first. Nonetheless, it may be possible to find other hymenopteran parasitoids that meet the three criteria for the optimal clutch size of a second female to be greater than that of the first; hymenopteran parasitoids certainly exist for which the larval-competition curves are like $s_3(N)$.

This analysis may also help to explain why some insects do not behaviorally alter their clutch size. For example, the blow fly *Phaenicia coeruleiviridis* is a batch-laying species, with females always ovipositing their entire complement of eggs (Ives 1988). If the conclusions of previous authors (Parker and Courtney 1984; Skinner 1985; Parker and Begon 1986) were applied to *P. coeruleiviridis*, it would seem that females should have evolved a means of assessing the number of eggs on carcasses and decreasing their clutch sizes on heavily infested carcasses. However, competition among *P. coeruleiviridis* larvae takes the form of $s_3(N)$ (table), and from the analysis in this paper, females may in fact lose little or nothing by not decreasing their clutch size.

The counterintuitive results presented here are explained by the structure of ESS models. Although ESS models explicitly consider the behavior of groups of interacting individuals, the evolutionarily stable solution is found by considering the fitness of an individual that deviates from the behavioral norm. In the models examined here, a female insect optimizes her clutch size against a background of eggs laid by other females. Depending on the form of competition among larvae, this background can either increase or decrease the marginal-fitness gain of a female laying additional eggs on the same patch. Therefore, although the eggs laid by other females will always decrease the overall fitness of her eggs, a female's optimal clutch size will nonetheless increase for some forms of larval competition.

## SUMMARY

When more than one female insect oviposits on the same patch of larval food, the optimal clutch size depends not only on the number of other females that

oviposit but also on the form of larval competition within patches. I use models to show that, depending on the type of larval competition, the evolutionarily stable clutch size can either decrease or increase as more females oviposit per patch. The models predict decreases in the evolutionarily stable clutch size with increasing numbers of females ovipositing per patch when larval competition causes rapid mortality at high densities, and they predict increases in the evolutionarily stable clutch size when larval competition is more benign. I also give examples of both extremes of larval competition by analyzing data from the literature for 10 insect species.

### APPENDIX A

Here I derive the general criterion for the response of the evolutionarily stable clutch size to the number of females ovipositing per patch.

Using the definition of $h(N)$ (eq. 5), equation (3a) can be rewritten as $h(n^*F) = -1/n^*$. Applying the implicit-function theorem and simplifying gives

$$\frac{\partial n^*}{\partial F} = \left.\frac{-n^3 \dot{h}(N)}{Fn^2 \dot{h}(N) - 1}\right|_{n=n^*}. \tag{A1}$$

It can be shown that the denominator in equation (A1) is always negative when $n^*$ exists; consequently, the sign of $\partial n^*/\partial F$ depends only on the sign of $\dot{h}(N)$. When $\dot{h}(N)$ is negative, the evolutionarily stable clutch size decreases with $F$, the number of females laying eggs per patch; when $\dot{h}(N)$ is positive, the opposite is true. The values of $\dot{h}(N)$ for $s_1(N)$, $s_2(N)$, and $s_3(N)$ are $-\alpha^2(1 - \alpha n_1^*)^{-2}$, 0, and $a^2 b(1 + a n_3^*)^{-2}$, respectively. Comparing these to the explicit expressions for the evolutionarily stable clutch sizes (eqs. 4) supports the predictions made in equation (A1). Note that the shape of $h(N)$ depends not on the number of females ovipositing per patch, but only on the total number of eggs. Therefore, the response of the evolutionarily stable clutch size to increasing numbers of females ovipositing per patch is determined only by the type of interactions among larvae and the resulting form of their competition curve.

### APPENDIX B

Here I show that for larval-competition curves with catastrophic mortality, the evolutionarily stable clutch size decreases when large numbers of females oviposit per patch.

To argue by contradiction, assume that the evolutionarily stable clutch size remains fixed at the value $\bar{n}^*$ as more females oviposit per patch. Let $\hat{N}$ denote the number of eggs on a patch at which survivorship drops to zero, and let $\bar{F}$ be the maximum number of females ovipositing before zero survivorship is reached; $\bar{n}^* \bar{F} < \hat{N} \leq \bar{n}^*(\bar{F} + 1)$. If $\bar{F} + 1$ females oviposit on a patch and one is allowed to alter her clutch size (following the logic of evolutionarily-stable-strategy models), then she should lower her clutch size to allow some

of her larvae to survive. This implies that the evolutionarily stable clutch size must be less than $\bar{n}^*$.

As an alternative proof, it can be shown that $\dot{h}(N)$ is negative as $N$ approaches $\bar{N}$ for any continuously differentiable function $s(N)$ (see Appendix A).

## APPENDIX C

Categorizing larval-competition curves by which function, $s_1(N)$, $s_2(N)$, or $s_3(N)$, best fits the data can be misleading. For example, $s_2(N)$ or $s_3(N)$ will fit an observed larval-competition curve that is curvilinear better than $s_1(N)$ will, although curvilinearity does not guarantee that the evolutionarily stable clutch size will stay the same or increase as more females oviposit per patch; a function of the form $s(N) = \mu(1 - cN)^2$ is curvilinear but causes evolutionarily stable clutch sizes to decrease as more females oviposit per patch (Skinner 1985). To separate statistically categories 1, 2, and 3, a test can be used based on the sign of $\dot{h}(N)$ (Appendix A).

If $s_2(N)$ is taken as the null hypothesis, departures from $s_2(N)$ can be tested by adding a quadratic term to the exponent of $s_2(N)$ to give

$$\bar{s}(N) = \mu \exp(-rN + \gamma N^2). \tag{C1}$$

For $\bar{s}(N)$, $\dot{h}(N) = 2\gamma$. Therefore, statistically significant departures of $\gamma$ from zero indicate that the evolutionarily stable clutch size tends to decrease ($\gamma$ negative) or increase ($\gamma$ positive) as more females oviposit per patch.

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