Behav Ecol Sociobiol (1989) 24:421–432

Behavioral Ecology and Sociobiology

Superparasitism and ovicide in parasitic Hymenoptera: theory and a case study of the ectoparasitoid *Bracon hebetor*

M.R. Strand[1] **and H.C.J. Godfray**[2]

[1] Department of Entomology, University of Wisconsin-Madison, 237 Russell Laboratories, Madison, WI 53706, USA and
[2] Department of Pure and Applied Biology, Imperial College at Silwood Park, Ascot, Berkshire SL5 7PY, Great Britain

Received February 18, 1988 / Accepted October 13, 1988

Summary. Among insect parasitoids, superparasitism is said to occur when a second clutch of eggs is laid on a previously parasitized host. Ovicide occurs when a parasitoid destroys a clutch of eggs laid on a host by a previous female. Here, general models are constructed to predict the conditions which favor superparasitism and ovicide. Major predictions for the ovicidal model were that ovicide is more likely to occur if the time necessary to kill eggs is short, if travel times and the proportion of parasitized hosts increases and if the competitive advantage of a first clutch is large. The predictions of the models were tested by examining superparasitism and ovicide in *Bracon hebetor* (Say), a gregarious, ectoparasitoid of phytisiine moths. Using a wild and eye color mutant of *B. hebetor* to distinguish first and second clutches, it was found that the competitive advantage of a first clutch over a second clutch increased with the time between ovipositions. Patterns of superparasitism and ovicide in *B. hebetor* were in qualitative agreement with the major predictions of the model. Most notably, ovicide increased in frequency with a decrease in the overall rate of host encounter and an increase in the proportion of parasitized hosts encountered.

Introduction

While the literature on clutch size evolution and infanticide in vertebrates is extensive (Lack 1947; Stearns 1976; Hausfater and Hrdy 1985), only recently has attention been directed toward invertebrates (Parker and Courtney 1984; Polis 1985; Parker and Begon 1986; Godfray 1987a). Much of the theoretical interest in the evolution of invertebrate clutch sizes involves parasitic wasps (i.e. parasitoids) which lay one or more eggs in or on the body of other arthropods (Suzuki and Iwasa 1981; Charnov and Skinner 1984; Skinner 1985; Iwasa et al. 1984; Waage and Godfray 1985; Godfray 1986; Godfray 1987b; Godfray and Ives 1988). The eggs hatch and the larvae feed until the host is consumed or a maximum size is achieved. The amount of resource available to each parasitoid offspring is a function of both host size and the number of eggs laid by the ovipositing female. Thus, which hosts a female decides to parasitize, and the clutch size she lays has a major effect on progeny fitness (Strand 1986).

Much of invertebrate clutch size theory is based on models developed originally for birds and mammals. However, the clutch size decisions of parasitoids involve phenomena for which there is no counterpart in vertebrate ecology. In this paper we discuss theoretical models of two such phenomena, superparasitism and ovicide, and tests of these models. We define superparasitism as the deposition of a second clutch of eggs on a host. Although a second clutch may be laid by the same female (self superparasitism) or by other females (conspecific superparasitism) (van Dijken and Waage 1987), we restrict ourselves here to cases of conspecific superparasitism only. Ovicide is said to occur when a wasp destroys a clutch of eggs laid on a host by a previous female.

Superparasitism is a very common feature of parasitoid biology (Bakker et al. 1985; Waage 1986) while ovicide is comparatively rare or unrecognized. A number of theoretical studies have examined superparasitism (Parker and Courtney 1984; Charnov and Skinner 1984; Skinner 1985), and in the first portion of this paper we build on this work to produce a model of superparasitism

---

Offprint requests to: M.R. Strand

that also allows for the inclusion of the evolution of ovicidal behavior. The only theoretical work on ovicide in insects that we are aware of is that on the possible significance of behavior observed in granivorous beetles (Smith and Lessells 1985). However, recent study of *Bracon hebetor* (Say) (Hymenoptera: Braconidae), an ectoparasitoid of phyticiine moths (Lepidoptera: Pyralidae) such as *Plodia interpunctella* Hübner, revealed that this species engages in ovicide (Strand 1988a). We test some of the predictions of our model by examining the clutch biology of *B. hebetor*.

Model

In this section we develop a model framework in which to examine the evolution of ovicidal behavior in parasitoids. Ovicidal behavior is intimately associated with superparasitism which has been modelled by several workers examining reproductive strategies which maximize the rate of fitness gain over time. Charnov and Skinner (1984) and Skinner (1985) considered superparasitism as a problem analogous to the optimal prey and patch problems in classical foraging theory (Stephens and Krebs 1986). While a very important step, this approach does not explicitly acknowledge the influence of other foraging females on the optimal reproductive strategy of a particular ovipositing female. To examine this, an explicitly game theoretic approach is required. Parker and Courtney (1984) used such an approach in their study of superparasitism. They assumed two classes of females existed, those that attack unparasitized hosts and those that attack previously parasitized hosts. Again, while an important advance, this model is limited in that it does not consider the more realistic biological situation of a female encountering both parasitized and unparasitized hosts. One consequence of this is that the Parker and Courtney model never predicts that a female should refrain from superparasitism. This occurs because one class of female oviposits exclusively on parasitized hosts and thus will never be selected to abandon its only reproductive channel.

Because of the limitations of existing models of superparasitism, we first develop a new model of superparasitism before examining the evolution of ovicide. This model is structurally similar to that of Parker and Courtney (1984), but also incorporates some ideas from Skinner (1985). Initially, we define and defend the currency we use in the optimization procedures to approximate Darwinian fitness followed by an examination of superparasitism where members of the first and second clutches are assumed to have identical competitive effects on each other. We then relax the unrealistic assumption of first and second clutch equivalency, and conclude this section with the incorporation of ovicidal behavior.

Choice of currency

Optimization models rely on the assumption that natural selection acts to maximize fitness even though in practice it is often assumed that a simpler quantity such as the rate of energy gain over time is equivalent to this. Like previous models we too assume that selection will act to maximize the rate of fitness gain over time where fitness is a function of the number and quality of offspring produced by a searching parasitoid female. We believe this is a realistic currency for parasitoids which are limited by their ability to find and handle hosts. However, other workers have realized that if a parasitoid is limited by the number of eggs available for oviposition rather than time, then rate of gain of fitness over time will not be an appropriate currency (Parker and Courtney 1984; Iwasa et al. 1984; Godfray 1986). Alternative currencies in clutch models without superparasitism have been examined with the results suggesting that conclusions based on the assumption of time limitation will be qualitatively, but not quantitatively, true for egg limitation (Godfray 1987a).

Superparasitism assuming equivalence of clutches

Consider a rare individual which lays x eggs on an unparasitized host and y eggs on a previously parasitized host in a population composed almost exclusively of individuals with the strategies x^* and y^*. Throughout the text we refer to clutches laid on unparasitized hosts as first clutches and clutches laid on parasitized hosts as second clutches. We assume that a proportion p of all hosts encountered by wasps are previously parasitized and that the probability of a host attacked by a wasp being itself subsequently superparasitized is q. It is assumed that the probability of a third attack is small. Let g be the encounter rate with hosts and $F(x)$ and $F(y)$ the fitness of the x eggs and y eggs on unparasitized and parasitized hosts respectively. The parasitoid will be selected to seek a strategy pair $\{x, y\}$ which maximizes its fitness when played against a population using strategy $\{x^*, y^*\}$. With W as the fitness of the mutant we seek

$$\max\{W[(x, y), (x^*, y^*)]\}$$
$$= \max\{g((1-p)\,xF(x) + p\,yF(y))\} \qquad x \geq 0, y \geq 0 \quad (1)$$

The encounter rate g will depend on both the abundance of hosts in the environment and the amount of time spent in oviposition. If (τ) is the average time it takes to find one host and $t(x)$ and $t(y)$ the time it takes to lay x and y eggs, the average amount of time spent finding and ovipositing on one host will be $(\tau + (1-p)\,t(x) + p\,t(y))$. The encounter rate will be proportional to the reciprocal of the time spent finding and ovipositing on an average host

$$g = g(x, y) \propto 1/(\tau + (1-p)\,t(x) + p\,t(y)) \qquad (2)$$

We define $f(z)$ as the fitness of a larva on a host with a total of z larvae. Initially, we assume that members of the first and second clutches have identical competitive effects on the other members of the clutch. Under these conditions the fitness functions $F(x)$ and $G(y)$ are

$$F(x) = (1-q)\,f(x) + qf(x + y^*) \qquad (3\text{a})$$
$$F(y) = f(x^* + y) \qquad (3\text{b})$$

Note that the mutant is rare and to a first approximation is superparasitized by, and superparasitizes, a wild type wasp.

Since the optimal strategy $\{x, y\}$ depends on the strategy adopted by the rest of the population $\{x^*, y^*\}$, we seek the Evolutionarily Stable Strategy (ESS) that cannot be bettered by a mutant strategy, that is, if $\{x^*, y^*\}$ is an ESS then

$$W[(x^*, y^*), (x^*, y^*)]$$
$$- W[(x, y), (x^*, y^*)] \geq 0 \qquad x \geq 0, y \geq 0 \qquad (4)$$

for all $x \neq x^*$, $y \neq y^*$. As long as the non-negativity conditions are not violated, the optimal strategy set can be found by differentiation of the fitness function which gives the conditions

$$\left.\frac{\partial W[(x, y), (x^*, y^*)]}{\partial x}\right|_{x = x^*}$$
$$= \left.\frac{\partial W[(x, y), (x^*, y^*)]}{\partial y}\right|_{y = y^*} = 0 \qquad (5)$$

In addition, for the solution to be a maximum, it is required that the second derivatives, evaluated at the same point, are negative. Applying this method to equation (1) gives the simultaneous equations

$$g(x, y)\{(1-p)[F(x) + xF'_x(x)]\}$$
$$+ g'_x(x, y)\{(1-p)\,xF(x) + p\,yF(y)\} = 0 \qquad (6\text{a})$$

$$g(x, y)\{(p)[F(y) + yF'_y(y)]\}$$
$$+ g'_y(x, y)\{(1-p)\,xF(x) + p\,yF(y)\} = 0 \qquad (6\text{b})$$

with everything evaluated at $x = x^*$ and $y = y^*$, and where primes denote derivatives and subscripts the variables with respect to which the derivatives are taken. These equations will normally have to be solved iteratively. For numerical examples we follow the example of Parker and Courtney (1984) and assume $t(x) = tx$ and $t(y) = ty$, i.e. it takes a constant amount of time, t, to produce an egg regardless of circumstances. We also assume that the relationship between larval fitness and the number of larvae on a host (z) can be described by the function $2 - \exp(mz)$ where m is a constant. Under this assumption larval fitness declines at an accelerating rate, becoming zero at a clutch size of $\ln 2/m$. This assumption is reasonable for parasitoids (Parker and Courtney 1984) although Ives (1988) has indicated that the predictions of this type of model can be influenced by the functional choice of $f(z)$. A series of numerical explorations indicated that the results for the numerical exploration presented in this section and the sections to follow on clutch nonequivalence and ovicide are representative for the fitness function $2 - \exp(mz)$. Predictions of the model include:

1. The superparasitizing female should lay fewer eggs on the host than the first female. As found in previous models, this prediction results from the reduction in quality of a host that already contains larvae that will compete with the second clutch.

2. Increased search time (τ larger) leads to an increased clutch size. This prediction, again common to previous models of superparasitism, results from a long search time increasing the value of investing more time per host.

3. An increase in the proportion of superparasitized hosts that a wasp encounters (increased p) leads to larger clutch sizes on both fresh and parasitized hosts (Fig. 1). To see why this occurs, consider a parasitoid deciding whether to lay an additional egg on a host. Opposing the benefit of another offspring is the cost in time spent ovipositing that otherwise could be spent searching for a new host. This cost will be reduced as the expected quality of a new host decreases (because of the greater probability it will be superparasitized) leading to larger clutch sizes for both first and second clutches.

4. An increase in the probability of subsequent superparasitism (larger q) decreases the size of a first clutch and increases the size of a second clutch (Fig. 1). An increased probability of subsequent su-

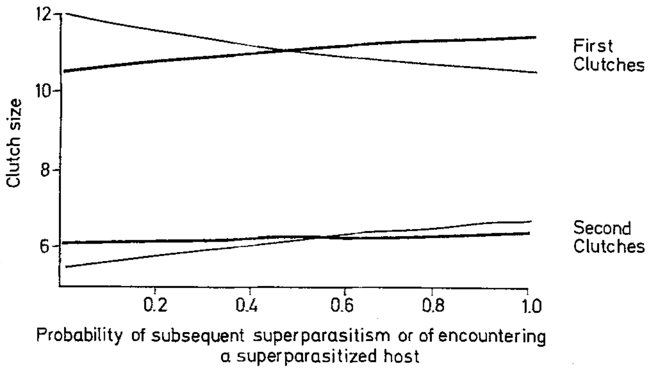

Fig. 1. The effects of either increased probability of subsequent superparasitism (q varies, $p=0.33$: fine line) or increased encounter rate with previously parasitized hosts (p varies, $q=0.33$: heavy line) on the size of first clutches laid on unparasitized and second clutches laid on parasitized hosts (model as described in the text with $t/\tau=0.1$; $m=0.023$)

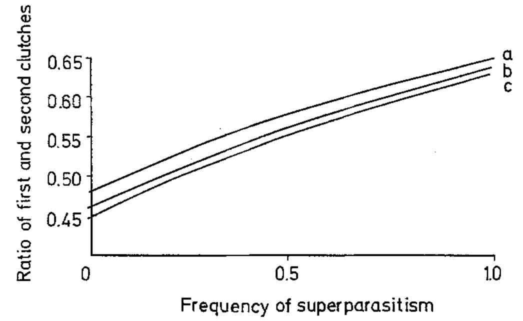

Fig. 2. Plot of the ratio of first and second clutches (y/x) as a function of the frequency of superparasitism ($q/(1-p)$; $p=q$). Line a, $t/\tau=1$; line b, $t/\tau=0.1$; line c, $t/\tau=0.01$ (model as described in the text with $m=0.023$)

perparasitism reduces the value of a fresh host and leads to smaller clutch sizes on unparasitized hosts. However, this reduction in first clutch size increases the value of a parasitized host leading to larger second clutches.

5. Changes in the proportion of superparasitized hosts encountered and the risk of subsequent superparasitism are likely to increase together. Setting $p=q$ (Fig. 2), the overall effect of increased superparasitism is an increase in the relative size of the second clutch. The reason for this can be seen by noting that in Fig. 1 the greatest response to a change in either p or q was a reduction in the size of the first clutch as the risk of subsequent superparasitism increased.

6. Superparasitism always occurs. Avoidance of superparasitism never occurs with the assumptions of this model. As the availability of unparasitized hosts increases clutch size falls and ovipositing on parasitized hosts is less favored. However, because clutch size is concomitantly falling on unparasitized hosts, laying a few eggs on parasitized hosts is always favored.

Superparasitism assuming non-equivalence of clutches

Obviously, a failure of the previous model as well as that of Parker and Courtney (1984) is that neither predicts when a female should refrain from conspecific superparasitism. Yet, there are numerous reports of parasitoids rejecting parasitized hosts, particularly when unparasitized hosts are abundant (Waage 1986). The optimality model of Skinner (1985) does predict the avoidance of superparasitism but does not address the interdependency of first and second clutch sizes.

The most unrealistic portion of the previous models is that first and second clutches are assumed to be equivalent. Biologically, equivalence of first and second clutches would be expected if, for example, the two females oviposited simultaneously. However, it would be more realistic to expect that a parasitized host would be encountered by a second female sometime after oviposition by the first female. This would usually result in a superparasitizing female's clutch being at a competitive disadvantage due to the existing clutch hatching first and consuming a portion of the available resource. Thus, the advantage of the first clutch will often depend on the time between successive ovipositions.

To take into account the non-equivalence of first and second clutches we weight the detrimental effects of a member of the first brood on the second brood by a factor μ ($\mu>1$) and the effects of a member of the second brood on the first by π ($\pi<1$). Thus, defining f_i as the fitness of an offspring laid in the first ($i=1$) or second ($i=2$) clutch, $f_1(x, y)$ becomes $f(x+\pi y)$ and $f_2(x, y)$ becomes $f(\mu x+y)$ and equations 3a and 3b become

$$F(x)=(1-q)f(x)+qf(x+\pi y^*) \qquad (7a)$$

$$F(y)=f(\mu x^*+y) \qquad (7b)$$

For numerical exploration we used the same functions as in the previous model. Predictions assuming non-equivalence include:

1. The ratio of the size of the first clutch to the second clutch drops as the competitive advantage of the first clutch increases. The drop in the ratio is due primarily to a drop in the size of the second clutch though there is also a smaller rise in the size of the first clutch. As the competitive advantage of the first brood increases and the fit-

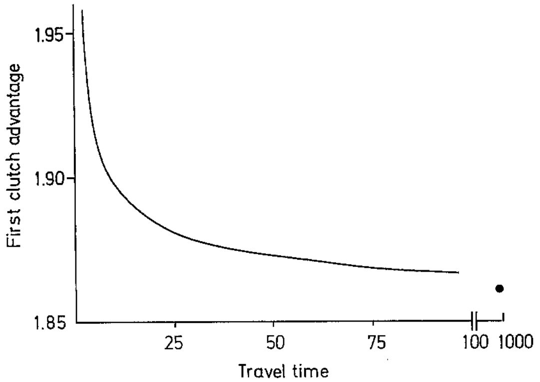

Fig. 3. The effect of travel time (τ, $t=1$) and the competitive advantage of the first clutch (μ, $\pi=1/\mu$) on the threshold below which superparasitism is no longer selected. (model as described in the text with $p=q=0.33$; number of larvae per host$=40$; $m=0.023$)

ness of superparasitizing larvae drops, it becomes unprofitable to spend much time adding eggs to previously parasitized hosts that will develop into low fitness wasps. The drop in the size of the second clutch depends only slightly on the frequency of superparasitism.

2. When the advantage of the first clutch reaches a threshold value, superparasitism is no longer selected. The larger the first clutch advantage, the lower the threshold value for selection against superparasitism.

3. The no superparasitism threshold drops as travel time increases. The threshold initially drops quickly but then asymptotes as travel time gets large (Fig. 3). This occurs because the amount of time spent on the host becomes negligible when travel time is large. Further increases in travel time have no effect on the parasitoid's decision.

Superparasitism and ovicide

As before, we study a rare mutant which lays x eggs on unparasitized hosts, and y eggs on parasitized hosts but now destroys k eggs of any clutch already present on the host before laying a clutch of its own. The remainder of the population pursues the strategy $\{x^*, y^*, k^*\}$. For the strategy $\{x^*, y^*, k^*\}$ to be an ESS

$$\begin{aligned}&W[(x^*, y^*, k^*), (x^*, y^*, k^*)]\\&-W[(x, y, k), (x^*, y^*, k^*)]>0\\&x\geq 0, y\geq 0, x\geq k\geq 0\end{aligned} \tag{8}$$

for all $x \neq x^*$, $y \neq y^*$, $k \neq k^*$. Assuming ovicide is time consuming, it will decrease the encounter rate since time spent destroying eggs is time lost to searching. If it takes $s(k)$ time to destroy k eggs, the encounter rate (equation 2) now becomes

$$g=g(x, y, k)\propto 1/(\tau+(1-p)\,t(x)+p(s(k)+t(y))) \tag{9}$$

The fitness of the mutant $W[(x, y, k), (x^*, y^*, k^*)]$ is now

$$\begin{aligned}&W[(x, y, k), (x^*, y^*, k^*)]=g\{(1-p)[(1-p)\cdot x\cdot f(x)\\&+q\cdot(x-k^*)\cdot f(x-k^*+\pi y^*)]\\&+p[y\cdot f(\mu(x^*-k))+y]\}\end{aligned} \tag{10}$$

The right hand side of this equation is composed of three terms: (1) the fitness gains from ovipositing on an unparasitized host that is not subsequently superparasitized, (2) an unparasitized host that is subsequently superparasitized and where some eggs of the first clutch are destroyed, and (3) a parasitized host where k of the eggs of the first clutch are killed. The solution to Eq. (8) can sometimes be solved by differentiation of the fitness function but when the ESS number of eggs destroyed is a boundary value ($k=0$ or $k=x$), numerical methods must be employed. Predictions for the ovicidal model include:

1. Ovicide is more likely to occur when the time necessary to kill eggs is short. Ovicide competes for time with other activities, so the less time it takes, the more likely it is to occur.

2. If it takes the same amount of time to destroy an egg regardless of the number previously destroyed (i.e. $s(k)=sk$), the model predicts that the wasp will either destroy all or none of the previous clutch. However, if it takes longer to destroy successive eggs in the clutch then partial destruction of the clutch will occur. Biologically, "all or none" ovicide might occur if the first clutch is readily apparent to a superparasitizing female while partial destruction might occur if the first clutch must be searched for.

3. The frequency of ovicide will increase as travel time or the proportion of parasitized hosts increase. A wasp encountering a parasitized host and first clutch must weigh the benefits of investing time in ovicide against the cost in time which otherwise could be spent searching for unparasitized hosts. As travel time increases, the percentage of time with hosts declines, shifting females toward maximizing fitness per host and in turn favoring ovicide. Increased travel time associated with a scarcity of hosts, an increasing proportion of parasitized hosts associated with a scarcity of hosts, or an increasing proportion of parasitized hosts among all hosts encountered all act to increase the benefits of ovicide and superparasitism.

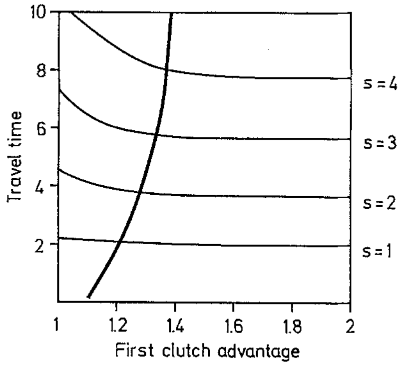

Fig. 4. The effect of travel time (τ, $t = 1$) and the competitive advantage of the first clutch (μ, $\pi = 1/\mu$) on superparasitism and ovicide. In the absence of ovicide, superparasitism will be selected in the parameter space to the left of the heavy line. Superparasitism is favored by a low advantage to the first clutch and long travel time. The time it takes to destroy k eggs is assumed to be sk, i.e. $s(k)$ is linear. Ovicide is predicted, for a particular value of s, below the respective fine line. Ovicide is favored by short kill times (low s), long travel times and high first clutch advantage. These results were obtained from numerical analysis of equation (10) with $p = q = 0.15$ and $m = 0.17$

4. Increasing the competitive advantage of the first clutch increases the liklihood of ovicide. The interaction between travel time and the advantage to the first clutch is illustrated in Fig. 4. For different combinations of travel time and first clutch advantage, superparasitism with ovicide, superparasitism without ovicide and the absence of superparasitism are predicted.

5. Alternative ESSs may occur. When clutch sizes are small, so that the progeny of a clutch must be considered as integer values, then populations of ovicidal and non-ovicidal parasitoids may be uninvadeable by rare mutants of the alternative type. Areas of parameter space in which alternative ESSs occurred appeared along the boundaries between regions when pure ovicidal and non-ovicidal behavior was predicted. When the probability of superparasitism was low these areas were narrow but increased significantly when superparasitism became common.

The reproductive strategy of *Bracon hebetor*

In this and the sections to follow we present some experimental results on the ovicidal behavior of *B. hebetor*. After briefly describing the biology of this parasitoid, we present the relationship between adult survival and size, and the size of clutch within which it developed. We then show the advantage of a first clutch in competition with a second clutch increases markedly with the time between oviposition, demonstrating the importance of not assuming first and second clutch equivalency. Lastly, in examining the superparasitism model with ovicide, we test the prediction that the frequency of ovicide will increase with the time between ovipositions and the frequency of encounter with parasitized hosts.

Reproductive biology of B. hebetor

B. hebetor is a facultatively gregarious ectoparasitoid of several species of Lepidoptera, particularly stored product moths in the family Pyralidae (Ulyett 1945; Hagstrum and Smittle 1978). Host larvae such as *Plodia* and *Ephestia* (= *Cadra*) live gregariously in stored grains, often building to very high densities in warehouses. *B. hebetor* parasitizes hosts over a range of sizes with clutch size increasing with host weight (Benson 1973). Thus, patches of host resource vary in the number and the size of hosts available. Average sized females with head capsules 0.5–0.6 mm in diameter have a large lifetime fecundity of 300–350 eggs but a limited daily fecundity of 15–30 eggs (Ulyett 1945; Hagstrum and Smittle 1978). In addition, females require 3–8 h to oviposit per host, thus they may be considered both egg and time limited.

Females parasitize hosts by first injecting subcutaneously a small quantity of venom which induces complete paralysis in 15 min (Piek et al. 1978). After a minimum period of 30 min for host examination the female oviposits, placing the eggs in one or two aggregations between the host and the substrate. Mean clutch size for *B. hebetor* parasitizing ca. 20 mg *Plodia interpunctella* fifth instars varies from 4–16 depending on encounter rate. The eggs hatch in 68–72 h at 25° C, and the host is consumed in ca. 72 h. Since the eggs of *B. hebetor* are laid loosely beneath the host larva, they are easily moved using forceps or a paint brush. This allows the creation of clutches of any size.

For many parasitoids there is a negative relationship between primary clutch size and measures of progeny fitness such as survival, size and fecundity on hosts of similar quality (Waage 1986). This too is seen for *B. hebetor*. In Fig. 5 *B. hebetor* survival and adult size, as measured by head capsule diameter, are plotted against increasing primary clutch sizes laid on 19–21 mg *Plodia interpunctella* fifth instar larvae. Both mean survival (Fig. 5a) and adult size (Fig. 5b) fall monotonically with the clutch size laid by the female. Thus for *B. hebetor*, fitness gain per host of a given quality and individual progeny fitness will be influenced by the number of parasitoid eggs present.

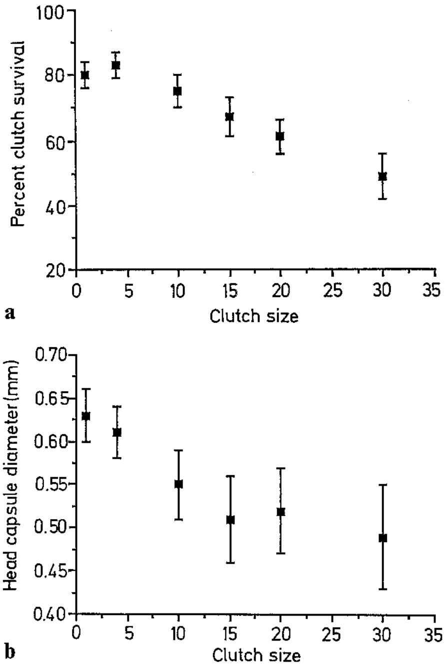

Fig. 5a, b. Relationship between *B. hebetor* primary clutch size and **a** mean survival ±SD to adulthood (arcsin detransformed data) and **b** mean adult size ±SD as measured by head capsule width. A minimum of 20 replicates were performed for each clutch size tested

The effect of the time interval between ovipositions on B. hebetor clutch survival

As outlined in the first model for superparasitism, it is assumed that the quality of a parasitized host is lower due to the presence of another clutch. Assuming competitive equivalence of clutches produced by different females, simultaneous oviposition by two females would be analogous to the effects of increasing the primary clutch as presented in Fig. 5. That is, an increase in the number of eggs per host would have a negative effect on survival and size of all progeny regardless of whether the eggs were laid by one or more females provided all of the eggs were oviposited simultaneously. However, the decline in progeny fitness with primary clutch size presented in Fig. 5 likely underestimates the competitive disadvantage of a second clutch if a significant period of time elapses between first and second clutch oviposition. Examining this disadvantage experimentally is difficult or impossible for most gregarious parasitoids because of the inability to distinguish progeny from the two clutches and the difficulty of manipulating clutch size. However, the ectoparasitic habit, ability to manipulate clutch size, and the existence of several mutant varieties (Whiting 1961) allow such experiments to be performed with *B. hebetor*. To examine the competitive advantage of a first clutch over a second clutch in *B. hebetor*, the following study was conducted.

Table 1. Mean clutch size, development time and emerging progeny size for the *Lum* and *Cho* strains of *B. hebetor*

	Lum	*Cho*
Clutch size ±SE[a]	9.5 ±0.52	9.9 ±0.45
Development time (days) ±SE[b]	13.1 ±0.05	13.2 ±0.04
Adult head capsule diameter ±SE (mm)[b]	0.55±0.03	0.56±0.04

[a] Mean clutch sizes are for those produced by 7 day old mated females which had been allowed to oviposit on 1 host per day prior to the experiment. $n=20$ wasps for each strain. The clutch sizes ($t=0.65$; $df=38$; $P>0.1$) were not significantly different for the two strains;

[b] Development time for the progeny is from time of oviposition until adult emergence. Data for development time and adult size (as measured by head capsule diameter) was for a primary clutch size of 10 eggs reared on 19–21 mg *P. interpunctella* fifth instars at 27° C and 70% RH. Data are for the progeny produced from 12 hosts. Neither development ($t=1.06$; $df=249$; $P>0.1$) nor adult size ($t=1.02$; $df=249$; $P>0.1$) were significantly different for the two strains

Materials and methods

To distinguish the progeny of first and second clutches, wild Lumberton (*Lum*) variety *B. hebetor* were compared to the eye/body color mutant cantelope-honey (*Cho*) (Whiting 1961). *Cho* wasps are readily distinguished from *Lum* wasps by their pale red eyes and tan body color. Preliminary study found no differences in the clutch sizes, development time from oviposition to adult emergence, or adult size between the two strains when reared under equivalent conditions (Table 1). Both strains were maintained in glass culture tubes and fed a 50% honey solution daily while *P. interpunctella* larvae were maintained in 4 l glass jars filled with crushed wheat.

To examine the survival of first and second clutches, 5 day old mated *Lum* and *Cho* females were placed individually into 5 cm petri dishes and presented uniform fifth instar *P. interpunctella* larvae weighing 19–21 mg. The precise time of oviposition for each female was recorded. Following oviposition the eggs were removed with forceps, and the paralyzed hosts weighed. After weighing, different numbers of *Lum* and *Cho* eggs laid at different times were placed on hosts. Small (4 eggs first clutch, 4 eggs second clutch), medium (10 eggs first clutch, 10 eggs second clutch) and large (20 eggs first clutch, 20 eggs second clutch) first and second clutches laid 0, 12, 24, or 48 h apart were examined. To assure that competitive asymmetries not detected in preliminary studies did not bias the results, reciprocal experiments were conducted for each clutch and time combination. A minimum of ten replicates were conducted for each treatment.

Results

χ^2-analyses ($\alpha=0.05$) of the clutch survival frequency for each reciprocal experiment revealed no differences in outcome regardless of which strain

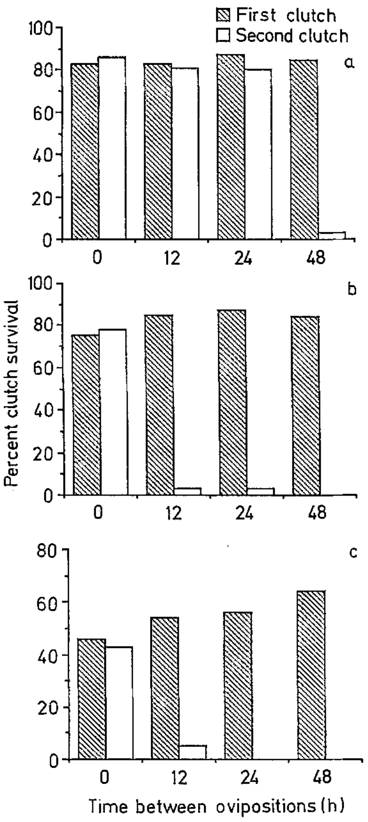

Fig. 6. Relationship between *B. hebetor* first and second clutch survival and the time between oviposition for starting clutches of a. 4, b. 10 and c. 20. First and second clutches were equal in size for each experiment, and a minimum of 20 female pairs were tested for each clutch size and time between oviposition interval

made up the first and second clutch. Thus, data for the experiments were pooled. The data presented in Fig. 6 indicate that an age difference between the two clutches resulted in a large competitive advantage for the first clutch. With the exception of a small (4) first clutch, the survival of the second clutch was less than 10% with any temporal penalty. In the case of small clutches of 4 eggs, the second clutch usually survived because the amount of resource available in a 19–21 mg host exceeded the amount of resource the first clutch could consume.

However, even with these small clutches the second clutch did not usually survive if the time between ovipositions was 48 h. In this case even though the first clutch did not consume all of the host, the remaining host contents desiccated before the second clutch had fed sufficiently to complete larval development. First and second clutches were similarly affected when clutch ages were the same (i.e. simultaneous oviposition). However, survival of first clutches of 4 and 10 were unaffected when a younger second clutch was present. There was a small but significant difference in first clutch survival when clutch sizes were 20 (χ^2-analysis, $\alpha = 0.05$). No cannibalism was observed during parasitoid development. Instead poor second clutch survival appeared to be due to completion of host consumption by members of the first clutch before members of the second clutch attained a minimum weight necessary for pupation. Similar observations by Benson (1973) indicated that densities above 8 parasitoid larvae per *Ephestia cautella* host resulted in mortality attributable to scramble competition.

Ovicide by B. hebetor

With the variation in density that occurs with stored product Leipdoptera, it is likely that *B. hebetor* females encounter unparasitized and parasitized hosts while foraging. Superparasitism readily occurs in the laboratory (Rotary and Gerling 1972; Benson 1973), but more recent studies also indicate that *B. hebetor* females occasionally commit ovicide (Strand 1988a). Females encountering a previously parasitized larva may reject it or proceed through a period of host examination and oviposition. A prominant feature of examination is that females mount the host and repeatedly walk from one end to another, antennating while probing the ventral side of the host with the ovipositor. Since *B. hebetor* lay their eggs on the side of the host in contact with the substrate, females are only able to contact eggs with the ovipositor. If an egg of the first clutch is located, the female remains atop the host and thrusts with the ovipositor, puncturing all eggs that are contacted. To test whether travel time (i.e. encounter rate) and the proportion of parasitized hosts a female encounters influences ovicide and superparasitism, the following experiments were conducted.

Materials and methods

Newly emerged females were held together with males for 24 h before being separated into 20 cm plastic culture dishes and fed a 50% honey solution. All females were 5 days old when experiments were initiated, and *P. interpunctella* fifth instars, weighing 19–21 mg served as hosts.

Lum B. hebetor females were exposed to conditions associated with different rates of encounter with parasitized and unparasitized hosts as follows. To simulate different encounter rates, females were presented 1 host per 12 h (2 hosts/day), 1 host per day, or 1 host per 3 days. To simulate different levels of previous parasitism at each encounter rate, females encountered either 3 parasitized hosts for every unparasitized host or 3 unparasitized hosts for every parasitized host. Females were presented hosts by placing them in 5 cm culture dishes containing an unparasitized or parasitized host. All parasitized hosts used in the study were parasitized by females not used in the experiments. The first clutches present on parasitized hosts were 12–18 h old when exposed to the second female, and for consistency first clutch size was 10 eggs, a typical size for *B. hebetor* ovipositing on ca. 20 mg hosts. The position of each egg in the first clutch was noted so that after oviposition by the second female any eggs of the first clutch that were not killed could be distinguished from the clutch of the second female. All experiments were initiated when the female encountered the host and were terminated when the female left the host for 15 min. During oviposition, females occasionally dismounted the host and wandered a short distance only to quickly return and continue the oviposition sequence. While choosing a 15 min absence from the host was arbitrary, it was a reliable measure of when oviposition was completed. Females were observed at 15 min intervals from the time of host encounter until the host was rejected or oviposition was completed. Thus, absence of a female from a host over two consecutive observation periods terminated an experiment. A total of 20 wasps were observed for each encounter rate and parasitized host combination.

Results

This experiment compared the frequency of superparasitism and ovicide for wasps encountering hosts of different quality (parasitized and unparasitized) and at different rates. Figure 7 presents the percentage of parasitized hosts in which *B. hebetor* killed some or all of the eggs in the first clutch. Qualitatively, the trend was that the number of females killing eggs of a first clutch was higher when the encounter rate and availability of unparasitized hosts was low. At each encounter rate, over 80% of the females killed some or all of the first clutch for the first parasitized host encountered. However, the number of females subsequently commiting ovicide depended upon the encounter rate and availability of unparasitized hosts. For example, females encountering 2 hosts per day with 3 of every 4 hosts encountered being unparasitized almost never killed eggs of the first clutch after the first day. In contrast, females encountering 1 host per 3 days with 3 of every 4 hosts encountered being parasitized usually killed eggs of the first clutch and superparasitized. Of particular note was that when encounter rates with parasitized hosts were high, the number of females that killed dropped after an encounter with an unparasitized host, but as females encountered additional parasitized hosts the tendency to kill progressively rose until yet another unparasitized host was encountered.

Not all females that commited ovicide killed all 10 eggs of the first clutch (Fig. 8). As mentioned, *B. hebetor* lay their eggs in an aggregate beneath hosts. If the aggregate was located by the second

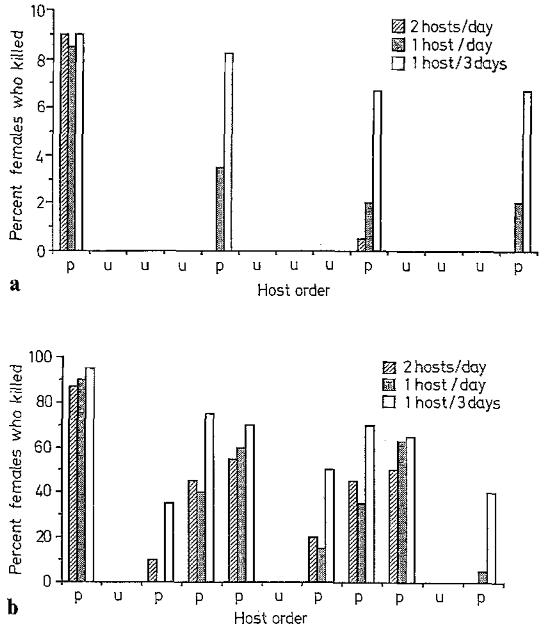

Fig. 7a, b. The percentage of *B. hebetor* females that killed eggs of a first clutch under different encounter rates and where: **a** unparasitized hosts are more abundant than parasitized hosts, and **b** parasitized hosts are more abundant than unparasitized hosts. Twenty females were tested for each encounter rate

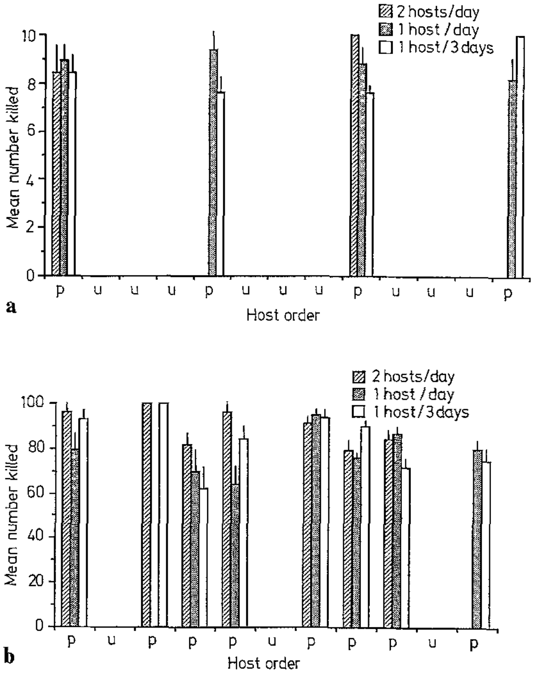

Fig. 8a, b. The mean number of eggs killed ±SE in the first clutch by *B. hebetor* females under different encounter rates and where: **a** unparasitized hosts are more abundant than parasitized hosts, and **b** parasitized hosts are more abundant than unparasitized hosts. Twenty females were tested for each encounter rate

Table 2. Mean clutch sizes laid by second females on parasitized hosts under different rates of host encounter[a]

Host order	Females not killing		
	Mean clutch ±SD (n) of females after killing all or part of the first clutch	Mean clutch ±SD (n) of females that did not kill but did superparasitize	Number of encounters where females did not kill or superparasitize
3 *Unparasitized*			
1 parasitized			
2 hosts/day	6.0 (1)	4.7±2.2 (23)	23
1 host/day	8.7±5.2 (14)	9.6±4.1 (35)	35
1 host/3 day	9.6±4.7 (44)	6.8±3.8 (12)	4
3 *Parasitized*			
1 unparasitized			
2 hosts/day	6.5±2.8 (22)	5.1±2.6 (35)	4
1 host/day	7.6±4.5 (23)	6.4±3.4 (36)	1
1 host/3 days	8.8±4.4 (40)	7.1±3.8 (17)	3

[a] Values exclude the first host encountered (parasitized) and include the next 3 parasitized hosts encountered subsequently (see Fig. 7 for percentage of females that killed eggs of a first clutch at each encounter rate)

female, she repeatedly thrust her ovipositor into the aggregate, but sometimes failed to puncture all of the eggs. Mean kill times for all females was 58.9±25 SD min, but because the first clutch was concealed and aggregated, it was difficult to assess whether the rate of killing changed. After killing, females laid second clutches which were smaller at high encounter rates (2 hosts/day) than at low encounter rates (1 host/3 days) (Table 2).

Females that did not kill under the different conditions usually superparasitized when encounter rates were low, but often rejected the host completely when 2 hosts were encountered per day (Table 2). Like females that killed, those females that did not kill but that superparasitized followed the trend of laying smaller clutches when host encounter rates were highest.

Discussion

In the first part of this paper, we develop a model for superparasitism, building on and synthesizing the work of previous authors. Undoubtedly, our model could be substantially improved by the addition, for example, of a dynamic element that recognizes that the proportion of hosts parasitized, and the risks of superparasitism, will vary over time. Such improvement, however, would necessitate a more complicated model. The purpose here was to construct a minimally complicated model that provides predictions which can be examined experimentally. We have concentrated on the qualitative rather than quantitative predictions of the model in our experimental efforts.

Although early workers suggested that superparasitism was maladaptive (Huffaker 1971), an increasing body of literature supports the concept that superparasitism is not necessarily disadvantageous (Waage 1986; Strand 1986). The laying of smaller clutches on parasitized hosts has been reported for several gregarious parasitoids (Wylie 1965; Suzuki et al. 1984; van Dijken and Waage 1987) as has the increased tendency to reject parasitized hosts when unparasitized hosts are abundant (van Lenteren and Bakker 1975; Klomp et al. 1980; van Alphen and Nell 1982). Superparasitizing females may also show preferences for hosts containing the fewest eggs (Bakker et al. 1972; van Lenteren and Debach 1981). Since first clutch advantage is a function of time of oviposition and size, these data suggest that some parasitoids may be able to assess the relative first clutch advantage of the hosts available, and preferentially invest in those hosts for which the probability of second clutch survival is greatest.

In this paper we also present models for the evolution of ovicide and test some model predictions with the parasitoid *B. hebetor*. *B. hebetor* clearly benefits from ovicide under certain conditions. The first clutch laid on a host by *B. hebetor* has a significant competitive advantage over a second clutch. Patterns of superparasitism and ovicide in *B. hebetor* are in qualitative agreement with the major predictions of the model. Most notably, ovicide increases in frequency with an increase in time between host encounters, and with an increase in the proportion of hosts encountered being parasitized.

Infanticide and ovicide might be expected to occur under conditions where resources are limited and competition between clutches or individuals is intense (Smith and Lessells 1985). Obviously, such a situation exists for some parasitoids, particularly when an encountered host is parasitized. The advantages of ovicide are clear; killing the eggs in the first clutch eliminates competitors which would preempt resources otherwise available to a second wasp's own progeny. Yet, ovicide is an infrequently reported phenomenon in parasitoids. The life history assumed in our model and indeed the life history of *B. hebetor*, are shared by many other parasitoids. So why is ovicide not more common?

We suggest several reasons. First, the scarcity of records of ovicide may be due to the lack of appropriate observations and experiments. Numerous studies have been conducted with *B. hebetor*, yet ovicide has not been reported until now. Second, ovicide may be selectively advantageous, but impossible due to the constraint of not being able to eliminate the first clutch. For example, endoparasitoids lay their eggs into the hemocoel or into specific internal organs of their host. It is unlikely that an endoparasitoid could destroy a first clutch using physical means like *B. hebetor*. Many endoparasitoids inject venoms and other factors into hosts at oviposition which could adversely affect progeny already present (Strand 1986). However, it is difficult to envisage a selective factor which would kill the first clutch but have no effect on any other clutch subsequently oviposited. Although we recognize that it is probably easier to detect ovicide in ectoparasitoids, we would predict that it is more common in parasitoids like *B. hebetor* which have access to a first clutch. Indeed, in our efforts to locate other examples of ovicidal behavior, the few instances found were for ectoparasitoids in the families Bethylidae (Clausen 1940; Goertzen and Doutt 1975) and Ichneumonidae (Price 1970). Lastly, if a wasp tends to rediscover hosts previously parasitized by itself yet is unable to distinguish them from hosts parasitized by conspecifics, the risks of destroying one's own eggs may counter any advantage of ovicide itself. Although there is limited evidence that parasitoids may be able to recognize self and conspecifically parasitized hosts (Hubbard et al. 1987), many other studies find no supporting evidence for parasitoids being able to directly do so (Bakker et al. 1985; van Dijken and Waage 1987; Strand 1988a, 1988b).

Acknowledgements. We would like to thank J.K. Waage and A.D. Taylor for their comments and assistance during various stages of this study. We would also like to thank B. Wissenger for providing the mutant variety of *B. hebetor* and J.A. Johnson for technical support. The research was supported by NSF Grant BSR-8550654 and University of Wisconsin Hatch Grant 3200 to M.R.S.

References

Alphen JJM van, Nell HW (1982) Superparasitism and host discrimination by *Asobara tabida* Nees (Braconidae: Alysiinae), a larval parasitoid of Drosophilidae. Neth J Zool 32:232–260

Bakker K, Eijsackers HJP, Lenteren JC van, Meelis E (1972) Some models describing the distribution of eggs of the parasite *Pseudeucoila bochei* (Hymenoptera, Cynipidae) over its hosts, larvae of *Drosophila melanogaster*. Oecologia 10:29–57

Bakker K, Alphen JJM van, Batenburg FHD van, Hoeven N van der, Nell HW, Strein-van Liempt WTFH van, Turlings TC (1985) The function of host discrimination and superparasitization in parasitoids. Oecologia 67:572–576

Benson JF (1973) Intraspecific competition in the population dynamics of *Bracon hebetor* Say (Hymenoptera: Braconidae). J Anim Ecol 42:105–142

Chacko M (1969) The phenomenon of superparasitism in *Trichogramma evanescens* and *T. minutum* Riley (Hymenoptera, Trichogrammatidae). I Beit Entomol 19:618–635

Clausen CP (1940) Entomophagous insects. McGraw Hill, New York

Charnov EL, Skinner SK (1984) Evolution of host selection and clutch size in parasitoid wasps. Florida Entomol 67:5–21

Dijkin MJ van, Waage JK (1987) Self and conspecific superparasitism by the egg parasitoid *Trichogramma evanescens*. Entomol Exp Appl 43:183–192

Godfray HJC (1986) Models for clutch size and sex ratio with sibling interaction. Theor Popul Biol 30:215–231

Godfray HCJ (1987a) The evolution of clutch sizes in invertebrates. In: Harvey PH, Partridge L (eds) Oxford surveys in evolutionary biology, vol. 4. Oxford University Press, London

Godfray HCJ (1987b) The evolution of clutch size in parasitic wasps. Am Nat 129:221–233

Godfray HCJ, Ives AR (1989) Stochastic models of invertebrate clutch size. Theor Popul Biol 33 (in press)

Goertzen R, Doutt RL (1975) The ovicidal propensity of *Goniozus*. Ann Entomol Soc Am 68:869–870

Hagstrum DW, Smittle BJ (1978) Host finding ability of *Bracon hebetor* and its influence upon adult parasite survival and fecundity. Environ Entomol 6:437–439

Hausfater G, Hrdy SB (1985) Infanticide: comparative and evolutionary perspectives. Aldine, New York

Hubbard SF, Marris G, Reynolds A, Rowe GW (1987) Adaptive patterns in the avoidance of superparasitism by solitary wasps. J Anim Ecol 56:387–402

Huffaker CB (1971) Biological control. Plenum Press, New York

Ives AR (1989) The optimal clutch size of insects when many females oviposit per patch. Am Nat (in press)

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

Klomp H, Teerink BJ, Ma Wei C (1980) Discrimination between parasitized and unparasitized hosts is the egg parasite *Trichogramma evanescens* and *T. embryophagum* (Hymenoptera: Trichogrammatidae): a matter of learning of forgetting. Neth J Zool 30:254–277

Lack D (1947) The significance of clutch size. Ibis 89:309–352

Lenteren JC van, Bakker K (1975) Discrimination between parasitised and unparasitised hosts in the parasitic wasp *Pseudeucoila bochei*: a matter of learning. Nature 254:417–419

Lenteren JC van, Debach P (1981) Host discrimination in three ectoparasites (*Aphytis coheni*, *A. Lingnanensis* and *A. melinus*) of the oleander scale (*Aspidiotus nerii*). Neth J Zool 31:504–532

Parker GA, Courtney SP (1984) Models of clutch size in insect oviposition. Theor Popul Biol 26:27–48

Parker GA, Begon M (1986) Optimal egg size and clutch size: Effects of environment and maternal phenotype. Am Nat 128:573–592

Piek T, Spanjer W, Njio KD, Veenendaal RL, Mantel P (1978)

Paralysis caused by the venom of the wasp, *Microbracon gelechiae.* J Insect Physiol 20:2307–2319

Polis GA (1985) Intraspecific predation and "infant killing" among invertebrates. In: Hausfater G, Hrdy SB (eds) Infanticide: comparative and evolutionary perspectives. Aldine, New York

Price PW (1970) Biology and host exploitation by *Pleolophus indistinctusi* (Hymenoptera: Ichneumonidae). Ann Entomol Soc Am 63:1502–1509

Rotary N, Gerling D (1972) The influence of some external factors upon the sex ratio of *Bracon hebetor* Say (Hymenoptera: Braconidae). Environ Entomol 2:134–138

Smith RH, Lessells CM (1985) Oviposition, ovicide and larval competition in granivorous insects. In: Sibley RM, Smith R (eds) Behavioural ecology. Blackwell, Oxford

Skinner SW (1985) Clutch size as an optimal foraging problem for insects. Behav Ecol Sociobiol 17:231–238

Stephens DW, Krebs JR (1986) Foraging theory. Princeton University Press, Princeton

Stearns SC (1976) Life-history tactics: a review of the ideas. Q Rev Biol 51:3–47

Strand MR (1986) The physiological interactions of parasitoids with their hosts and their influence on reproductive strategies. In: Waage J, Greathead D (eds) Insect parasitoids. Acedemic Press, London

Strand MR (1988a) Adaptive patterns of progeny and sex allocation by parasitic Hymenoptera. In: Gupta V (ed) Advances in parasitic hymenoptera research. Brill, Leiden

Strand MR (1988b) Variable sex ratio strategy of *Telenomus heliothidis* (Hymenoptera: Scelionidae): adaptation to host and conspecific density. Oecologia 77:219–224

Suzuki YH, Iwasa Y (1981) A sex ratio theory of gregarious parasitoids. Res Popul Ecol 22:366–382

Suzuki YH, Tsuji H, Sasakawa M (1984) Sex allocation and effects of superparasitism on secondary sex ratios in the gregarious parasitoid *Trichogramma chilonis* (Hymenoptera: Trichogrammatidae). Anim Behav 32:478–484

Ulyett GC (1945) Distribution of progeny by *Microbracon hebetor* Say. J Ent South Afr 8:123–131

Waage JK (1986) Family Planning in parasitoids: adaptive patterns of progeny and sex allocation. In: Waage J, Greathead D (eds) Insect parasitoids. Academic Press, London

Waage JK, Godfray HCJ (1985) Reproductive strategies and population ecology of insect parasitoids. In: Sibley RM, Smith RH (eds) Behavioural ecology. Blackwell, Oxford

Werren JH (1980) Sex ratio adaptation to local mate competition in a parasitic wasp. Science 208:1157–1159

Whiting AR (1961) Genetics of *Habrobracon.* Adv Genet 10:295–348

Wylie HG (1965) Discrimination between parasitized and unparasitized housefly pupae by females of *Nasonia vitripennis* (Walker) (Hymenoptera: Pteromalidae). Can Ent 97:279–286

Wylie HG (1976) Interference among females of *Nasonia vitripennis* (Hymenoptera, Pteromalidae) and its effect on sex ratio of the progeny. Can Entomol 108:655–661