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The Influence of Competition between Foragers on Clutch Size Decisions in Insect Parasitoids

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The effect of competition between ovipositing females on their clutch size decisions is studied in parasitoid insects. The effect of this competition depends on whether the competition between parasitoid larvae within a host is contest (solitary parasitoids) or scramble competition (gregarious parasitoids). For gregarious parasitoids, a decreasing clutch size with increasing competition between females is predicted while for solitary parasitoids an increase is predicted. These predictions were tested using the gregarious parasitoid *Aphaereta minuta* (M. E. Visser, 1996, *Behav. Ecol.* 7, 109–114) and the solitary parasitoid *Comperiella bifasciata* (J. A. Rosenheim and D. Hongkham, 1996, *Anim. Behav.* 51, 841–852). Parasitoids were either kept alone or in groups before the experiments, in which they were introduced singly into a patch containing unparasitized hosts. In the experiment with *A. minuta*, females kept together before the experiment laid smaller clutches than females kept alone. In *C. bifasciata*, the clutch size laid by females kept together was larger than that of females kept alone. Thus, both predictions were supported.

KEY WORDS: **parasitoids; clutch size; competition; *Aphaereta minuta; Comperiella bifasciata.***

INTRODUCTION

Host selection behavior by insect parasitoids ranges from decisions about which patches to visit to decisions on host acceptance, sex allocation, and clutch size. Experiments on host selection behavior usually focus on a single animal searching for hosts. Under natural conditions, however, there may be competition between female parasitoids searching for hosts. This might well have an important effect on a number of components of host selection behavior. Examples are a more male biased sex allocation (Hamilton, 1967) or more frequent superparasitism (Visser *et al.*, 1990) with an increasing number of female parasitoids on a patch.

In order to assess the importance of competition, theory needs to be developed and predictions from this theory subsequently need to be tested in experiments. In successful classical biological control by parasitoids, the amount of competition for hosts among parasitoids may be very low immediately following releases (many hosts, few parasitoids) but if hosts are successfully suppressed below economic damage thresholds, competition for hosts may become substantial (few hosts, many parasitoids). Therefore, knowledge of how competition among foragers affects host selection decisions will contribute to a better understanding of biological control.

In this paper we will consider the effect of competition among ovipositing females on clutch size decisions: how does the optimal number of eggs to lay in an unparasitized host depend on the amount of competition between foraging parasitoids. We will present a theoretical framework leading to qualitative predictions and discuss two experiments in which these predictions are tested.

THEORY AND PREDICTIONS

Parasitoids lay clutches in or on hosts, and leave these attacked hosts in the environment. Attacked hosts can subsequently be encountered by other females which may deposit additional eggs. Because these additional eggs may influence the fitness of the initially deposited offspring, females laying a clutch of eggs in an unparasitized host should take into account the probability of another female later laying in the same host. The optimal clutch size in both unparasitized and parasitized hosts should therefore be calculated using game theory (Maynard Smith, 1974) to incorporate the level of intraspecific competition (the number of females ovipositing in a host).

The first to consider this situation were Parker and Courtney (1984), who assumed that there are two types of females, one always attacking unparasitized hosts, the other always encountering already attacked ones. Strand and Godfray (1989) modeled females that en-

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counter both unparasitized and parasitized hosts. They predicted for the gregarious parasitoid *Bracon hebetor* that the clutch size laid on an unparasitized host should decrease with increasing likelihood of another female subsequently adding eggs. Although this prediction is correct for the parasitoid species modeled by Strand and Godfray (1989), it is not true for all parasitoid species. Ives (1989) pointed out that whether the first clutch should increase or decrease with increasing levels of intraspecific competition depends on the shape of the fitness curve: the relationship between the total fitness of the offspring from a host and the number of eggs laid in that host ($N\,s(N)$, with N being the number of eggs laid in a host and $s(N)$ the fitness return from an egg if N eggs are laid). More specifically, Ives gives three fitness curves for which his model predicts different responses in the clutch size laid in unparasitized hosts with an increasing likelihood that another female will lay in the same host (i.e., increasing competition). For the fitness curve $s(N) = \mu(1 - \alpha N)$ a decrease is predicted; for the curve $s(N) = \mu e^{-rN}$ the clutch size is predicted to remain the same, while for the curve $s(N) = \mu(1 + a\,N)^{-b}$ the clutch size is predicted to increase (see Fig. 1A, μ, α, r, a, and b are shape parameters).

Although Ives (1989) considered only the influence of the form of the fitness curve on the effect of competition on clutch size (without specifying the form of competition between the larvae within a host), his model can be interpreted as follows. When there is scramble competition between developing individuals (resources divided roughly equally between the competing larvae), a female should lay either smaller or larger clutches with an increasing number of females in the patch, depending on the quantitative details of the curve relating clutch size to total brood fitness. However, when there is contest competition between developing larvae (the larvae fight or are in other direct forms of competition), the size of the first clutch should increase. This makes intuitive sense: if offspring fight for possession of the host, the chance for an individual female that one of her offspring wins this fight increases with clutch size. Thus, when the likelihood that another female will lay in the same host increases, the first female should lay a larger clutch. On the other hand, if all larvae share the food, an increasing probability of other females laying signals a reduction in the amount of food available for the offspring of the first female, and thus she should lay a smaller clutch when the risk of total developmental failure of all larvae developing on an overexploited host is great. Note that there is thus competition on two levels: (1) competition for hosts between foraging female parasitoids and (2) competition between larvae within a host. The form of the latter determines the effect of the former on clutch size decisions.

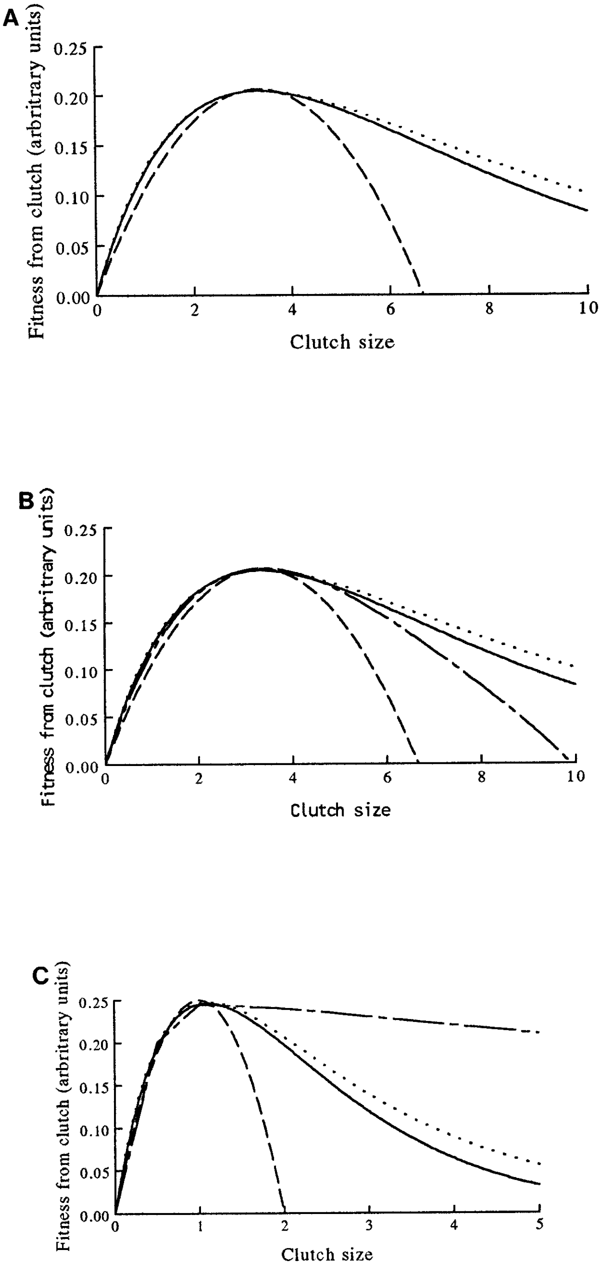

FIG. 1. (A) The three fitness curves ($N\,s(N)$, the relationship between the total fitness of the offspring from a host and the number of eggs laid in that host curves) from Ives' (1989) model. With an increasing likelihood that another female will lay in the same host (i.e., increasing competition) the clutch size in unparasitized hosts is predicted to decrease, dashed line; remain the same, solid line; increase, dotted line (see text for further clarification). (B) The fitness curve *A. minuta* attacking *D. hydei* larvae (dashed-dotted line) as well as the three curves from Ives (1989). (C) The fitness curve for a theoretical solitary parasitoid (dashed-dotted line) as well as the three curves from Ives (1989). As discussed in the text, the fitness curve for *C. bifasciata* attacking *Aonidiella aurantii* may not be constant for clutches >1, but is likely to be in the region where larger clutches are predicted under competition.

In parasitoids, both forms of larval competition are found (Godfray, 1994). In solitary parasitoids, there is contest competition within a host, and only one parasitoid will emerge from a host. In gregarious parasitoids, there is scramble competition, and in principle all eggs can develop into new parasitoids. With increasing clutch size, however, smaller parasitoids emerge. The fitness of female parasitoids usually decreases with decreasing size, because smaller parasitoids have a lower fecundity, longevity, or host finding capacity (Visser, 1994). The precise shape of the fitness curve will depend strongly on this relationship between size and fitness. This is of importance because in the model of Ives (1989) a decreasing clutch size with increasing competition is predicted only when the scramble competition within a host is more severe than the form exp $(-r\,N)$, with the shape parameter $r > 0$ and N being the number of eggs laid in the host (see Fig. 1A).

Because the insect parasitoids include species with both contest and scramble larval competition, this group is suitable for testing predictions on the influence of intraspecific competition on clutch size. In solitary parasitoids we expect females to lay larger clutches in unparasitized hosts with an increasing level of intraspecific competition. Thus, although only one offspring can emerge from a host in solitary parasitoids, more than one egg is laid during a single host encounter. We want to stress that we are not referring to self-superparasitism (Visser, 1993) where a parasitoids lays another egg in a host she has previously parasitized herself, but to a parasitoid laying two or more eggs during a single encounter. In those gregarious parasitoids species where for high egg number per host, none of the developing parasitoid larvae can secure enough food to complete development, resulting in complete mortality of the brood, we expect the females to lay smaller clutches.

Two sets of experiments have been reported that enable us to test both these predictions. These experiments use the parasitoids *Aphaereta minuta* (a gregarious species; Visser, 1996) and *Comperiella bifasciata* (a solitary parasitoid; Rosenheim & Hongkham, 1996). In the experiments the degree of competition is altered by keeping parasitoids either alone or in groups before the experiment. Parasitoids are then introduced singly into a patch with unparasitized hosts, and the clutch sizes laid are recorded. This setup has the advantage that it alters the degree of competition without altering the rate of depletion and the amount of interaction between individuals while searching for hosts. The rationale behind it is that a female that has previously encountered conspecifics will behave as if she is in an environment where it is likely that other females are going to encounter the same hosts as the ones she is parasitizing.

AN EXPERIMENT WITH A GREGARIOUS PARASITOID

The prediction that in gregarious parasitoids with intense scramble competition the clutch size in unparasitized hosts should decrease with increasing levels of competition between foragers was tested by Visser (1996) using the parasitoid *A. minuta* (Nees) (Hymenoptera; Braconidae). *A. minuta* is a proovigenic, polyphagous endoparasitoid of Diptera larvae which live in decaying plant and animal material (Evans, 1933).

Female parasitoids were kept either singly or in groups of four in the 4 days between emergence and the experiment in which they were introduced singly on a patch with 20 *Drosophila hydei* larvae as hosts. For each of the two treatments 12 replicates were carried out. Clutch size was initially determined by counting the movements of the abdomen by the ovipositing female. In 43% of the ovipositions the movements could, however, not be seen clearly for the entire oviposition bout. For this reason, the handling time (the time the ovipositor was inside the host), which could be measured accurately in nearly all cases, is used as a measure of clutch size. In a simple regression model, handling time explained 63% of the variation in clutch size ($clutch\ size = 1.43 + 0.0445\ handling\ time$, $n = 58$).

The Fitness Curve

In order to verify the Ives' (1989) model predicts a decrease in clutch size in unparasitized host with increasing competition, the fitness curve for *A. minuta* attacking *D. hydei*, the host species used in the experiments, is calculated (Visser, 1996):

$$fitness\ clutch = clutch\ size \cdot probability\ of\ emerging \cdot fitness\ female \quad (1)$$

The probability of an egg developing to adulthood decreased with clutch size: $probability\ of\ emerging = 0.99 - 0.10\ clutch\ size$ ($P_{\mathrm{slope}} = 0.001$, $r = -0.54$, $n = 45$). The size of emerging females (head width) decreased with clutch size: $head\ width$ (mm) $= 0.60 - 0.02\ clutch\ size$ ($P_{\mathrm{slope}} = 0.004$, $r = -0.48$, $n = 35$). Finally, fitness also decreased with decreasing parasitoid size: $fitness\ female = 0.5 - 2.2\ head\ width\ female$ (mm) $+ 2.7$ ($head\ width\ female$ (mm)$)^2$ (Visser, 1994). Sex ratio does not enter in Eq. (1) because sex ratio was independent of clutch size ($P_{\mathrm{slope}} = 0.35$, $n = 45$). The fitness curve can now be calculated using Eq. (1); the result is plotted together with the three curves from Ives' (1989) figure (Fig. 1B). It is clear that the fitness curve is below the solid line, and thus clutch size in unparasitized hosts is predicted to decrease with increasing competition.

The Experiment

The degree of intraspecific competition, as altered by keeping parasitoids either alone or in groups of four before the experiment, was found to have an effect on clutch size (Fig. 2A) in the predicted direction ($n = 109$, $F_{1,105} = 9.95$, $P = 0.002$). Females kept together before the experiment handled hosts for an average of 16.6 s less than females kept alone, which corresponds with a decrease in clutch size of 0.74 eggs (mean clutch size is 5.3).

The number of hosts previously encountered also had a significant effect; clutch size decreased over the first three encounters ($F_{2,105} = 11.12$, $P < 0.001$). There was no significant change in clutch size from the third to the fifth encounter ($F_{2,103} = 0.74$, $P = 0.48$). An explanation for this decrease in clutch size with encounter number is presented under Discussion.

AN EXPERIMENT WITH A SOLITARY PARASITOID

The prediction that in solitary parasitoids the clutch size in unparasitized hosts should increase with increasing levels of competition between foragers can be tested with data reported by Rosenheim and Hongkham (1996). They studied clutch size in *Comperiella bifasciata* (Howard) (Hymenoptera: Encyrtidae), a solitary parasitoid that lays its eggs within the bodies of armored scale insects (family Diaspididae).

Newly emerged females were either kept alone or in groups of three females and a male. The next day the females were presented individually with a sequence of three hosts, *Aonidiella aurantii*. In total 119 females were tested (57 in the solitary treatment, 62 in the grouped treatment). Clutch size was determined in a direct way, by host dissection. Hosts were dissected immediately after a parasitoid female had oviposited in three hosts, which were offered to her sequentially.

The Fitness Curve

The relationship between the number of eggs deposited per host and the total fitness of the brood has not been measured for *C. bifasciata*. However, it is known that only one offspring can develop successfully per host. The fitness curve is complicated in this species by the observations that hosts may encapsulate parasitoid eggs and the probability of at least one offspring escaping early encapsulation may be a function of clutch size (J. A. Rosenheim and D. Hongkham, unpublished data). Furthermore, laboratory studies have shown that there is a cost associated with having to share a host with siblings, even though supernumerary larvae are eventually eliminated. Parasitoid development is slowed, and the resulting adult parasitoids are smaller, in hosts that initially harbor multiple eggs (J. A. Rosenheim and D. Hongkham, unpublished data). Additional work is therefore needed to characterize the fitness curve for *C. bifasciata*. Nevertheless, for the range of clutch sizes observed in nature, there is no evidence that the fitness of the brood (i.e., the product of offspring survivorship and size-dependent fitness) approaches zero. Therefore, it appears likely that the fitness curve will fall into the region where larger clutches are predicted under increasing competition (Fig. 1C).

The Experiment

The degree of intraspecific competition, as altered by keeping parasitoids either alone or in groups of three before the experiment, was found to have an effect on clutch size (Fig. 2B) in the predicted direction (first host encountered; $n = 119$, $\chi^2 = 22.0$, $P < 0.001$; second host encountered, $n = 116$, $\chi^2 = 6.1$, $P = 0.014$; third host, $n = 110$, $\chi^2 = 2.1$, $P = 0.16$). Females kept together before the experiment laid larger clutches than females kept alone: on average 0.74, 0.20, and 0.13 more eggs were laid by the grouped females for the first, second, and third host encounters, respectively.

For both females kept alone and those kept in groups, there was a clear decrease in clutch size with encounter number ($\chi^2 = 37.9$, $P < 0.001$). An explanation for this decrease in presented under Discussion.

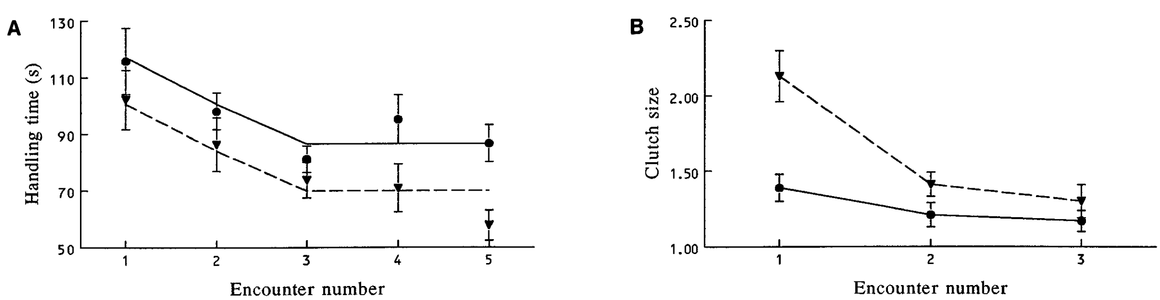

FIG. 2. (A) Mean time spend handling a host (bars indicate SE) versus encounter number for female *A. minuta* kept in groups of four (triangles) or kept alone (circles) before the experiment. The lines connect the fitted values of a statistical model with treatment and encounter number as explanatory variables. (B) Mean number of eggs laid in a host (bars indicate SE) for female *C. bifasciata* kept in groups of three (triangles) or kept alone (circles) before the experiment. The lines connect the mean values.

DISCUSSION

Intraspecific competition is predicted to influence clutch size decisions. In solitary parasitoids, females should lay a larger first clutch at a high level of competition. In those gregarious parasitoids that exhibit an intense form of scramble competition a smaller clutch is predicted. These predictions are tested, and met, in experiments where the clutch size decisions of parasitoids that were kept either alone or in groups before the experiment are compared (Visser, 1996; Rosenheim and Hongkham, 1996). Results from an experiment by Michaud and Mackauer (1995) with *Monoctonus paulensis* attacking *Acyrthosiphon pisum* also confirm the prediction for solitary parasitoids. Using basically the same experimental setup as Visser (1996) and Rosenheim and Hongkham (1996) they showed that the average clutch size of females kept alone is 1.15 ($\pm$0.03), while females kept in groups of five before the experiment laid on average clutches of 1.29 ($\pm$0.05) eggs. In all these experiments, preexperimental encounters with conspecifics affect clutch size decisions because there was no direct competition between searching females within the patch in the experiments. In natural situations, there will be much more direct and intense competition and an even stronger response in clutch size is expected.

Both *A. minuta* (Visser, 1996) and *C. bifasciata* (Rosenheim and Hongkham, 1996), exhibit a clear decrease in clutch size with host encounter number. A possible explanation for this is that the parasitoids do not have perfect knowledge of the encounter rate with hosts. When searching a patch, a parasitoid will encounter hosts and may use that information to estimate the encounter rate. After a number of encounters with hosts, the female's estimation of the encounter rate is expected to converge toward the real value. Optimal clutch size depends strongly on encounter rate. When hosts are encountered frequently (i.e., travel time between oviposition opportunities is short), animals should lay small clutches. Due to the change in the female's estimation of the encounter rate, the clutch size laid is expected to change over the first encounters with hosts and then remain constant. Such a pattern in change of clutch size with encounter number has indeed been found by Ikawa and Suzuki (1982).

There are also some practical implications of the results reported here. When carrying out experiments on reproductive decisions, one needs to be careful how the animals are treated before the experiment. Storing them under a certain light regime might influence their decisions because of an "end-of-season" effect (Roitberg *et al.*, 1992), and storing them with other individuals might lead to different host acceptance decisions (Visser, 1995) or clutch sizes. This might in part explain why often a smaller clutch size than predicted is observed in insects that have scramble competition in the larval stage (Lessells, 1991; Hardy *et al.*, 1992; Godfray, 1994).

Competition among searching parasitoids does not only affect clutch size decisions but also other components of the host selection process. For instance, some parasitoids can detect conspecifics from a distance and avoid patches where conspecifics are present (Janssen *et al.*, 1996). Also host acceptance decisions depend on the level of competition, as shown for the decision whether or not to accept a parasitized host for oviposition (Visser, 1993, 1995). Finally, the optimal sex ratio of a clutch depends strongly on the number of females ovipositing in a host for species with local mate competition (Hamilton, 1967). Thus, for a number of parasitoid reproductive decisions it is clear that competition among female parasitoids foraging for hosts has an effect. Further experimental work is needed, however, to assess accurately the impact of competition at the level of the population and hence on the level of biological control.

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