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Host-Searching Behavior of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): Interference—The Effect of Mature Egg Load and Prior Behavior

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The foraging behavior of Venturia canescens, *a solitary endoparasitoid of lepidopteran larvae, was investigated in the laboratory. Females with a greater number of mature eggs in their ovarioles and oviducts parasitized a greater number of hosts and won a greater proportion of encounters with other searching females. Wasps which had been exposed to hosts prior to an experimental trial lost a higher proportion of* agonistic *encounters with conspecifics than wasps which had no prior exposure to hosts. The behavior of a wasp at the time of the encounter influenced the outcome of the encounter. Wasps involved in active search of the host medium with the ovipositor ("probing") were more likely to win encounters than wasps in any other behavioral category. In a situation where the agonistic encounter was between two probing wasps, both contestants were equally likely to win. Results are discussed in the light of the idea that mutual interference arises, in this species, as a result of agonistic encounters between searching females and recent dynamic-programming models which suggest that parasitoid oviposition should be influenced by mature egg load.*

KEY WORDS: egg load; host-parasitoid systems; motivation; mutual interference; agonistic encounters; *Venturia canescens*.

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INTRODUCTION

In an analysis of the interaction between an insect parasitoid, *Venturia* (=*Nemeritis*) *canescens* (Grav.) (Hymenoptera: Ichneumonidae), and one of its hosts, *Anagasta* (=*Ephestia*) *kuhniella* (Zeller), Hassell and Huffaker (1969) noted that the searching efficiency of the parasitoid, measured as the Nicholsonian "area of discovery" (Nicholson and Bailey, 1935), declined with increasing parasitoid density. This effect had previously been noted by Ulyett (1950), who called it "mutual interference." Subsequently, Hassell and Varley (1969) demonstrated that mutual interference was a feature of a number of other host–parasitoid interactions and that, when it was included in a simple Nicholsonian host–parasitoid population model, its effect on the dynamics was markedly stabilizing.

With the notable exception of papers by Hassell (1971) and Ridout (1981), most further investigations of mutual interference in parasitoids have been largely theoretical and concerned with its capacity to promote stability in host–parasitoid population models (Royama, 1971; Hassell and May, 1973, 1974; Rogers and Hassell, 1974; Beddington, 1975). This concentration on the stabilizing properties of mutual interference has, in some instances, led to suggestions that interference has evolved to enable populations to avoid extinction (Hassell and Varley, 1969) or to counteract the aggregative response (Hassell and May, 1973, 1974), dispersing populations and thereby avoiding "over exploitation" (Hassell, 1971; Hassell and Rogers, 1972; Rogers and Hubbard, 1974). However, for interference behavior to have been favored by natural selection, it must confer some selective advantage to individual wasps, and any stabilizing influences must arise as a consequence, and not the cause, of interference.

Through all the above work, surprisingly little attention has been paid to the possibility that a major behavioral component of mutual interference could be fighting between female wasps for access to oviposition opportunities, as suggested by Hassell (1978). Females of many parasitoid species have been reported to exhibit aggressive responses to the presence of females of the same, and other, species. Spradbery (1970), observing the behavior of *Rhyssa persuasoria* (L.), an ichneumonid parasitoid of siricid wood wasp larvae, found that a searching female will threaten, and may actively drive off, a female conspecific which enters her territory (an area of tree trunk). Similarly, scelionid egg parasitoids often display aggressive behavior toward other females on the same egg mass (Hidaka, 1958; Hokyo and Kiritani, 1963, 1966; Safavi, 1968), and threat displays have been recorded for two species of chalcid, *Dinotiscus aponius* (Walker) and *Cheiropachus colon* (L.), parasitoids of the elm bark beetle, *Scolytus scolytus* (L.) (Beaver, 1967). Given such observations, it is difficult to agree with Griffith and Holling (1969) that mutual interference is simply a laboratory artefact.

For the scelionids mentioned above, the females fight over a whole patch of resources. However, in a species where the hosts are more dispersed, interactions between females are likely to be less overtly aggressive.

Ridout (1981) showed that mutual interference in *Venturia* was not due to a decrease in available searching time following an encounter with a conspecific, as had been proposed in the earlier theoretical work, nor could she find any evidence to support some of the other suggested factors producing mutual interference, such as encapsulation of parasitoid eggs, pseudointerference (Free *et al.*, 1977) or time-wasting due to avoidance of superparasitism. She did show that encounters between female wasps altered the frequency at which they changed their behavior and also significantly affected the subsequent choice of behavior. Such changes in behavior can be dramatic, often resulting in the one individual flying from the patch. When two individuals that are both actively searching for hosts meet, interactions can be prolonged, but invariably one individual will move away. In our study, we suggest that such interactions are, in fact, agonistic, with that individual leaving the site of the interaction being the "loser."

For fighting behavior to have been favored by natural selection, one would expect that those individuals which were more successful in such agonistic interactions with conspecifics would be more successful in parasitizing hosts.

The experiment presented here was designed to evaluate the importance of three factors in influencing the success of *V. canescens* females in interference interactions; egg depletion, egg load, and wasp behavior at the time of the interaction (hereafter termed "prior behavior").

MATERIALS AND METHODS

Host and Parasitoid Populations

The parasitoid used in this study was *V. canescens*, a solitary endoparasitoid of the larvae of phycitid flour moths, including the experimental host *Plodia interpunctella* (Hubner) (Lepidoptera: Pyralidae). The *V. canescens* stock used in this study was originally collected some 20 years ago from flour mills in Oxfordshire (UK), and additional material from other sources has been added at intervals. There has been no sign of any decline in vigor in this population.

Cultures of both species were maintained at a constant temperature of 25 ± 1°C and 75 ± 5% relative humidity. Parasitoids were removed from culture on the day of emergence and kept in batches of 15 in transparent plastic boxes (175 × 115 × 55 mm) without access to hosts. They remained in the boxes, supplied and libitum with 50% honey solution, for 48 h prior to use in experimental trials.

Host larvae used in all trials were 21 days old and had been reared in a

9 : 1 : 1 mixture of bran, glycerol, and dried yeast according to the rearing procedure outlined by Rogers (1970).

Experimental Preparation

Twenty-four hours prior to the start of an experimental trial two types of host patch were prepared.

(1) *Depletion patch:* This patch was made from a 90-mm-diameter petri dish, filled to within 3 mm of the lip with plaster of Paris. Into this were placed 50 *P. interpunctella* larvae, which were covered with some finely sieved bran. A nylon gauze was drawn tightly over the top of the patch and held in place with a rubber band. The gauze prevented the escape of any larvae while still allowing the free passage of the parasitoid's ovipositor.

(2) *Experimental patch:* The second patch consisted of a 140-mm-diameter solid nylon disk into which a regularly spaced array of 50 cells, 13 mm in diameter and 4 mm in depth, had been drilled. Twenty *P. interpunctella* larvae were placed singly into cells in an even distribution over the area of the patch, avoiding any effects of a clumped distribution within the area of the patch. All the cells were filled with sieved bran, and as before, gauze was drawn tightly over the top of the patch. This was held in place with a Perspex collar.

Both types of patch were left for 24 h to allow the production of silk by the larvae, which stimulates searching behavior in *V. canescens* females.

Also 24 h before the experiment, two wasps were selected at random from one of the holding boxes. They were marked on the thorax, between the wing bases, with a small spot of Humbrol enamel paint, after which they were returned to the holding box. The marks allowed these wasps to be individually identified throughout the subsequent experiment.

Experimental Procedure

On the day of the trial, one of the marked wasps was placed in a clear plastic box (175 × 115 × 55 mm) with a "depletion patch." It was confined with this patch and allowed to search on it for one of four "depletion" periods—1, 2, 5, or 7 h—to manipulate the number of mature eggs carried by the wasp. No direct observations were made during this period. Wasps given this treatment are termed *depleted* in the remainder of this paper.

At the end of the depletion period, the wasp was removed from the box and placed in an experimental arena, a glass-topped box (500 × 500 × 40 mm) which contained an "experimental" patch. The second marked wasp (hereafter referred to as the *undepleted* wasp) was also placed into this arena, together with enough randomly selected wasps of the same age to make up the total required experimental density of 2, 4, 8, or 16 wasps.

Thereafter, both marked wasps were continuously observed for 1 h by separate observers. The trial was started by the entry of either of the marked wasps into the patch. All events and behaviors were recorded using a microcomputer monitoring system (see Marris *et al.*, 1986). Wasp behavior was divided into four mutually exclusive states: *stationary*—remaining apparently motionless; *cleaning*—grooming the body and head with the legs; *walking*—any locomotor activity including flight; and *probing*—stabbing the host food medium with the ovipositor. The wasp's location was recorded as either on or off the experimental patch. In addition, the following behavioral events were recorded: *encounter host*—penetration of the host cuticle with the ovipositor, recognizable by the apparently labored withdrawal of the ovipositor; *cocking*—characteristic flexing of the abdomen and ovipositor that occurs when the wasp transfers an egg to the cavity at the tip of the ovipositor (Rogers, 1972); *encounter parasitoid*—two parasitoids coming within 3 mm of each other on the host patch and resulting in a change in behavior of one or both wasps; *win encounter*—a wasp remaining at the site of an encounter, or continuing to move in the same direction, while her opponent retreats; and *lose encounter*—a wasp retreating from the site of an encounter while her opponent remains. The cocking movement allows an observer to determine whether an egg was laid in the last host encountered.

At the end of each trial, both marked wasps were killed and dissected, and the total number of mature eggs remaining in the oviducts and ovarioles was counted. This figure was then added to the number of eggs laid by that wasp during the trial to give the *egg load* at the start of the trial.

Ten replicates were performed for each of the treatments (i.e., combination of parasitoid density and depletion time) and the experiment was performed as a randomized block over time, each treatment being represented once in each block. Those trials in which either of the two marked wasps had fewer than five parasitoid encounters were not included in the analysis. This was done to avoid bias of the results due to greater influence of chance effects at very low numbers of conspecific encounters. Thirteen trials, of a total of 160, were not considered for this reason.

RESULTS

Statistical Analysis

Because of significant colinearity between two of the variables which are used as independent factors (depleted wasp egg loads and length of depletion time) and nonlinearity in some of the parasitoid density relationships, ANOVAs rather than multiple regression techniques were used for the analysis.

Mutual Interference: The Effect of Parasitoid Density

The results were first examined to see if mutual interference had occurred. Since no dissections of hosts were carried out after trials, it was not possible to calculate the "area of discovery" (Hassell and Varley, 1969). Both Begon and Mortimer (1981) and van Alphen and Vet (1986) define mutual interference as a decrease in encounter (or consumption) rate with increasing parasitoid (or predator) density. Therefore, the effect of increasing parasitoid density on the encounter rate (number of hosts encountered per unit patch time) was analyzed. In addition, the effect of parasitoid density on the number of hosts parasitized by each wasp, the proportion of the trial period spent on the patch (patch time), and the proportion of patch time spent in active search (probing time) were also examined (Table I).

Although density as a main effect has no significant effect on the rate of encounter with hosts, the interaction term between parasitoid density and depletion opportunity is significant ($F = 2.00$, $P < 0.05$). Figure 1 shows that, although the undepleted wasps exhibit a marked reduction in encounter rates with increasing parasitoid density, the response in depleted wasps is markedly affected by the depletion period. After depletion times of 1 and 2 h a declining relationship can be observed for depleted wasps, but after 5 and 7 h no real pattern is shown.

Density has a significant effect on the number of hosts parasitized ($F = 8.29$, $P < 0.001$). Figure 2 shows that the effect is negative for both types of wasp, except where the depletion period is long, when depleted wasps show little response to changing density. Overall, depleted wasps parasitize fewer hosts than undepleted ($F = 47.99$, $P < 0.001$).

For both depleted and undepleted wasps, there is no significant relationship between parasitoid density and probing time, the proportion of time on the patch spent in search being unchanged by parasitoid density. A similar result was found by Ridout (1981) in her investigation of the same host–parasitoid system.

Frequency of encounter with conspecifics is also significantly affected by parasitoid density ($F = 56.50$, $P < 0.001$), and Figure 3 shows that this relationship is positive for both depleted and undepleted wasps.

Starting Egg Load

The Effect of the Depletion Period

The starting egg loads of depleted and undepleted wasps are shown in Fig. 4. At all depletion times, the egg loads of the two wasp types are significantly different (Mann–Whitney *U* test, $P < 0.05$). In depleted wasps, the number of mature eggs declines with increasing depletion time, to 5 h. However, the numbers rise again after 7 h, to a level not significantly different from that at 2

Table I. Analysis of Covariance: Effect of Depletion Time, Parasitoid Density, and Depletion Opportunity on a Number of Aspects of Foraging Behavior, with Egg Load as a Covariate

Source	df	Encounter rate	Number of hosts parasitized	Patch time	Probing time	Number of parasitoid encounters	Proportion of parasitoid encounters won
Covariate							
Egg load	1	20.39***	39.18***	3.01 (ns)[a]	41.65***	4.99*	5.57*
Main effects							
Depletion time (A)	3	1.93 (ns)	1.77 (ns)	5.73***	4.90**	1.77 (ns)	0.75 (ns)
Parasitoid density (B)	3	2.46 (ns)	8.29***	11.35***	0.69 (ns)	56.50***	21.31***
Depletion opportunity (C)	1	11.86***	47.99***	12.25***	2.64 (ns)	0.12 (ns)	40.05***
Interactions							
A × B	9	2.00*	2.24*	1.68 (ns)	1.68 (ns)	2.13*	0.67 (ns)
A × C	3	1.32 (ns)	4.52**	3.77*	3.35*	0.48 (ns)	8.12***
B × C	3	3.95**	4.03**	0.28 (ns)	1.06 (ns)	1.33 (ns)	5.31***
A × B × C	9	1.24 (ns)	1.16 (ns)	1.18 (ns)	2.29*	0.29 (ns)	1.98*
Total	293						

[a] $P > 0.05$.

*$P < 0.05$.

**$P < 0.01$.

***$P < 0.001$.

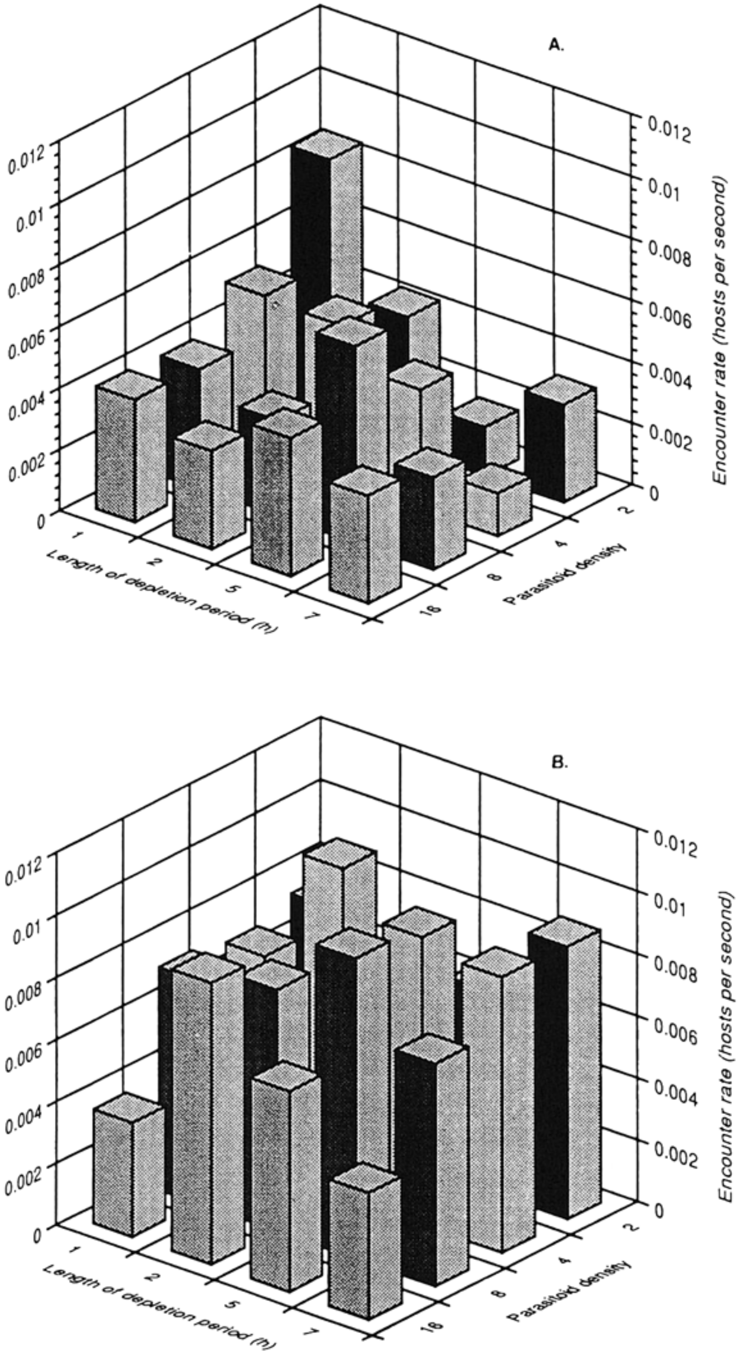


Fig. 1. The effect of depletion time and parasitoid density on the rate of encounter with hosts. (A) Depleted wasps; (B) undepleted wasps.

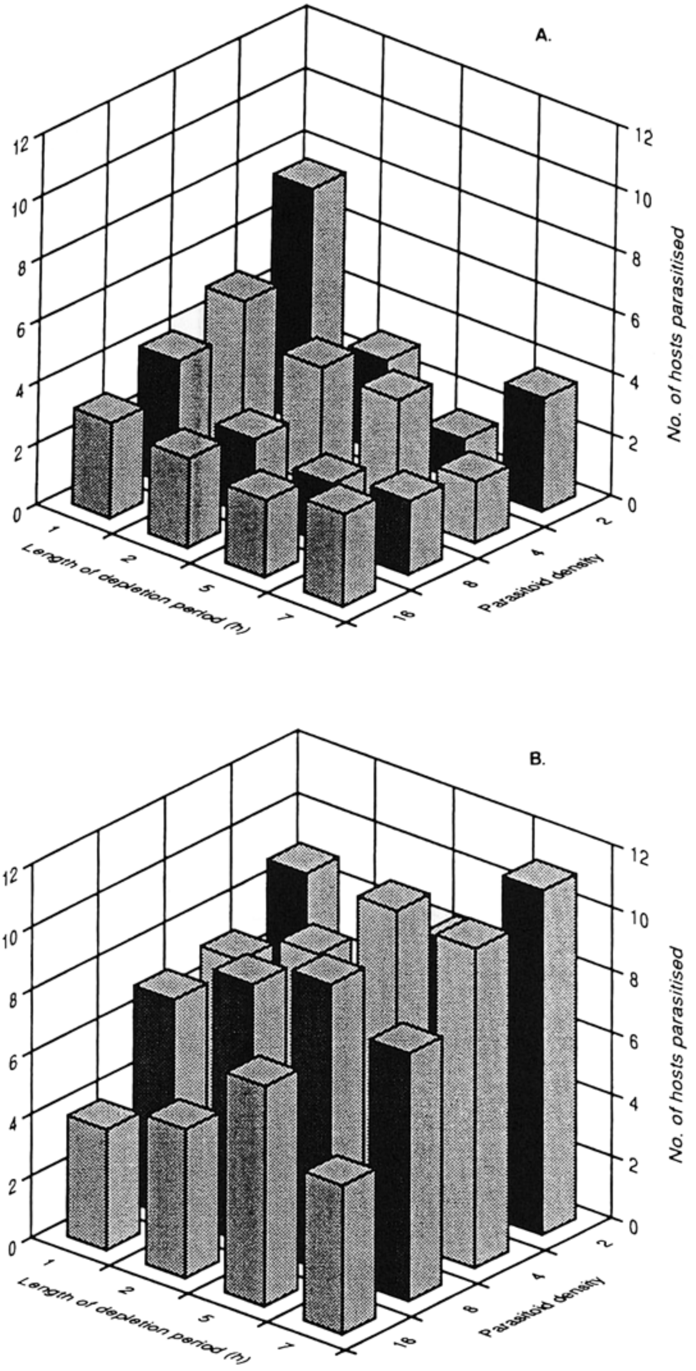


Fig. 2. The effect of depletion time and parasitoid density on the number of hosts parasitized. (A) Depleted wasps; (B) undepleted wasps.

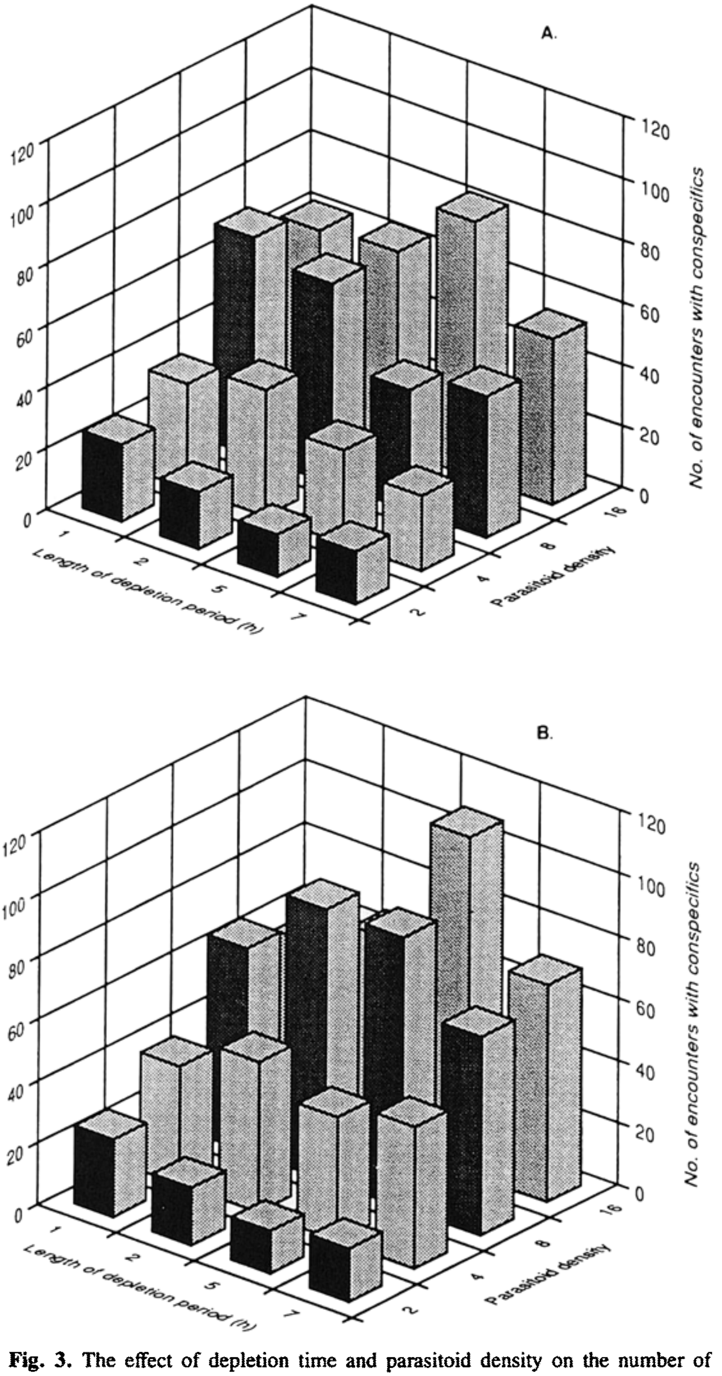


Fig. 3. The effect of depletion time and parasitoid density on the number of encounters with conspecific female wasps. (A) Depleted wasps; (B) undepleted wasps. Parasitoid density axes are reversed with respect to Figs. 1, 2, and 7.

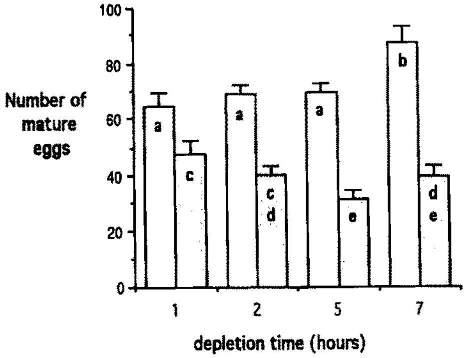


Fig. 4. Comparison of the mean (±SE) egg loads of depleted (shaded bars) and undepleted wasps (white bars) following each period of depletion. Those bars with the same letter are not significantly different (Mann–Whitney *U* test, $P < 0.05$). Sample sizes: 1 h, $n = 36$; 2 h, $n = 40$; 5 h, $n = 34$; 7 h, $n = 37$.

h. A similar rise in mature egg load after 7 h is also observed for the undepleted wasps, suggesting that the difference is due simply to the maturation of further eggs over the course of the depletion period. Such a finding is in accord with knowledge of the egg maturation rate in this species (Trudeau and Gordon, 1990; J. P. Fletcher, unpublished data; J. P. Hughes, unpublished data).

Effects on Parasitism and Agonism

Table I also shows the effects of starting egg load on the host encounter rate, probing time, number of encounters with conspecifics, number of hosts parasitized, and proportion of encounters with conspecifics won. These demonstrate that the starting egg load has important effects on searching behavior. There are significant relationships between the numbers of mature eggs available to a female for oviposition and the number of hosts parasitized, the rate at which hosts are encountered, the probing time, and the proportion of encounters with conspecifics won. Figures 5A–D demonstrate that these relationships are all positive. These results all give strong support to the idea that a female's motivation to both oviposit and win encounters is directly influenced by her mature egg load.

Winning Encounters: The Effect of Prior Behavior

Figure 6A shows the frequency distributions of the percentage of all encounters with other females won by depleted and undepleted wasps (data for all treatments pooled; $n = 147$). The frequency distribution for undepleted

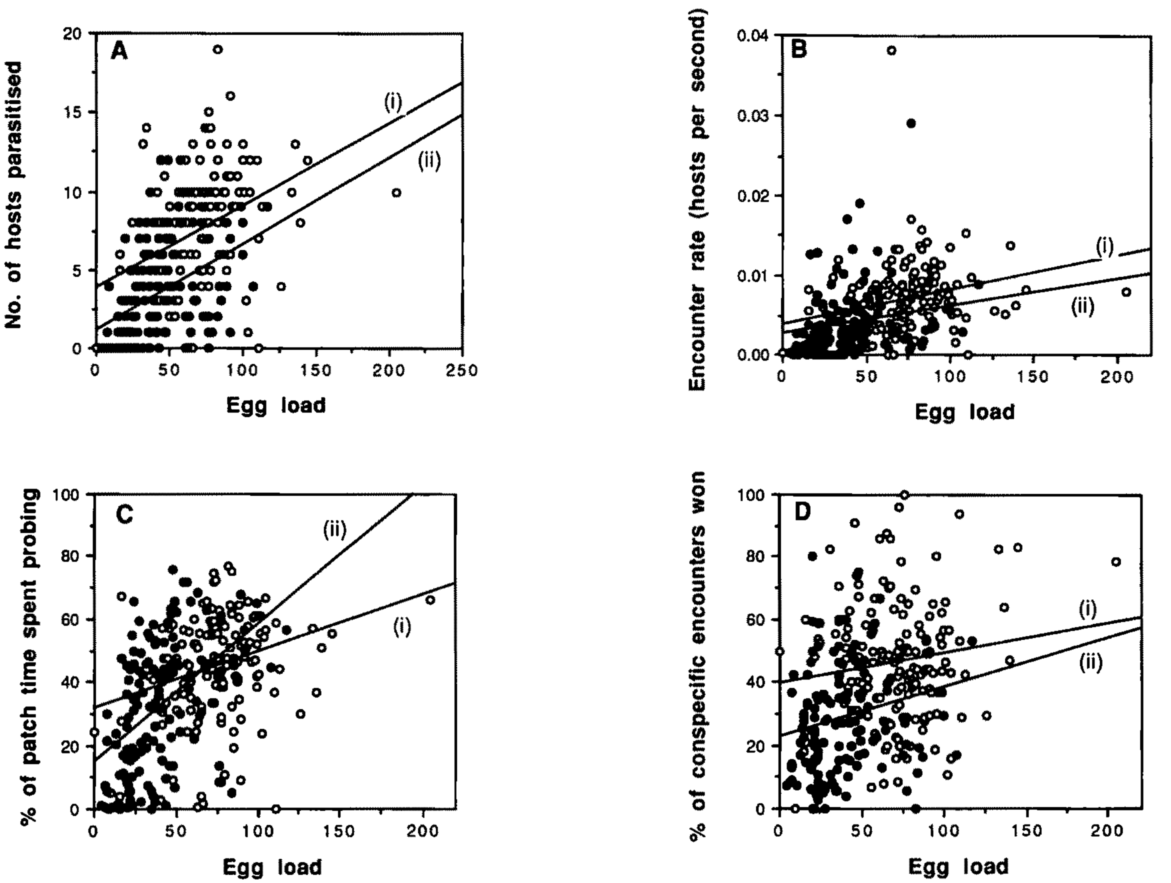
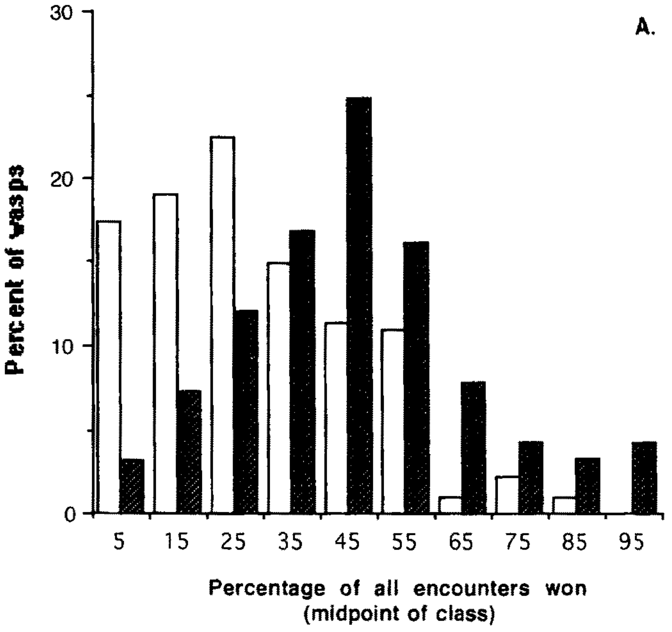


Fig. 5. The effect of egg load on (A) number of hosts parasitized (depleted $r^2 = 0.189$, undepleted $r^2 = 0.175$), (B) encounter rate (depleted $r^2 = 0.076$, undepleted $r^2 = 0.132$), (C) percentage of patch time spent probing (depleted $r^2 = 0.265$, undepleted $r^2 = 0.100$), and (D) percentage of encounters with conspecifics won (depleted $r^2 = 0.046$, undepleted $r^2 = 0.030$). All relationships are significant at the 0.1% level. Open circles and line (i), undepleted wasps; filled circles and line (ii), depleted wasps.



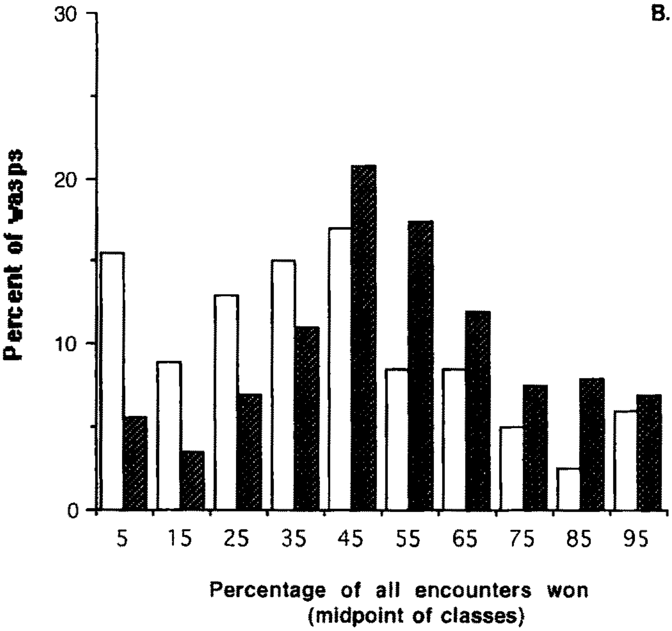


Fig. 6. The frequency distribution of the percentage of conspecific encounters won by wasps engaged in (A) all activities and (B) probing. White bars, depleted wasps; shaded bars, undepleted wasps.

wasps is approximately normal. The median value is 43.8%. For depleted wasps, the distribution is skewed to the left, the greater proportion of wasps winning fewer than 30% of all encounters with other parasitoids. The median value of this second distribution is 26.8% and the medians of the two distributions are significantly different (Mann–Whitney U test, $P < 0.0001$).

Figure 6B shows the frequency distributions of encounters won by wasps while probing. Although the distributions are similar to those in Fig. 6A, both distributions have shifted to the right, a greater proportion of wasps winning more than 50% of their encounters than is the case in Fig. 6A. For undepleted wasps, the median percentage of encounters won by probing wasps is 52.4% and for depleted wasps it is 35.4%, and again, the medians are significantly different (Mann–Whitney U test, $P < 0.0001$).

From this, two important points emerge. First, the behavior of a wasp prior to an encounter with a conspecific influences the outcome of the subsequent encounter, wasps being more likely to win if they are engaged in probing. Second, the depletion period is having an overall negative effect on the ability of depleted wasps to win encounters (see Fig. 7).

Closer investigation of the effect of prior behavior confirms the first point. Table II shows that wasps in virtually all categories lose a significantly greater number of encounters than they win. Although probing undepleted wasps did win a greater number than they lost overall, this difference was not significant. Closer examination of the results for undepleted probing wasps shows that these wasps win significantly more encounters than they lose at parasitoid densities of two, four, and eight wasps, although the proportion won decreases over this range, as shown by the falling value of the chi-square statistic.

The results of the two-wasp trials were examined in more detail (Tables II and III). Because of the experimental design, a complete record of the behavior of both wasps in such trials was available for analysis, including the behavior of both wasps immediately prior to each encounter. We can see quite clearly here how the prior behavior is affecting the outcome. Most importantly, probing wasps in contest with wasps in any other behavior category win more of the encounters (Table III). From these results, it does seem fairly clear that there is an advantage to probing wasps in encounters with conspecifics.

DISCUSSION

Mature Egg Load and Motivation

Table I shows quite clearly that the mature egg load has a strong motivational influence on the searching behavior of *V. canescens*. Findings of this kind are important for the development of more realistic models of parasitoid foraging behavior, functional as well as causal. Until very recently virtually all studies

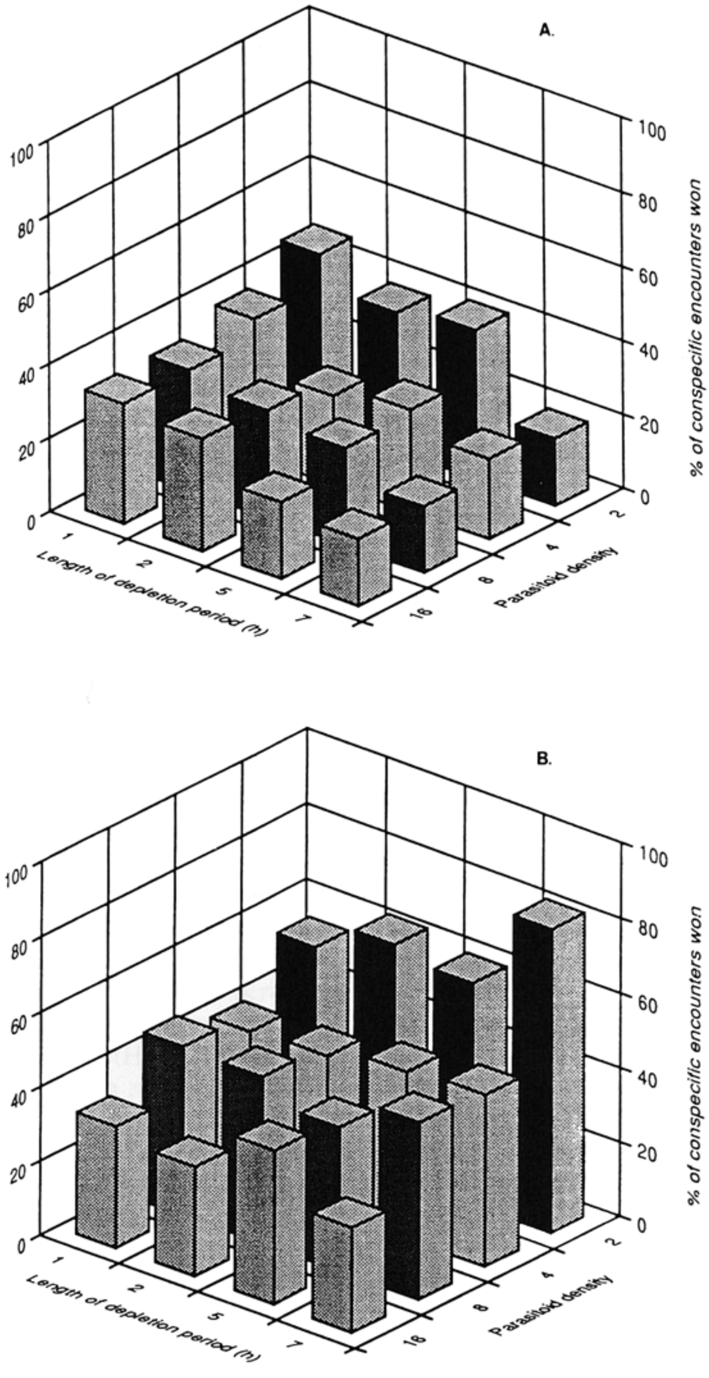


Fig. 7. The effect of depletion time and parasitoid density on success in encounters with conspecifics. (A) Depleted wasps; (B) undepleted wasps.

Table II. The Effect of Prior Behavior on the Outcome of Parasitoid Encounters, at Each of the Parasitoid Densities (Data Pooled over Depletion Periods)

Density	Depletion opportunity	No. of encounters		χ^2
		Won	Lost	
		(a) Probing		
2	Depleted	143	124	1.35 (ns)[a]
	Undepleted	229	102	48.72**
4	Depleted	169	319	46.10**
	Undepleted	441	326	17.24**
8	Depleted	312	469	31.56**
	Undepleted	780	698	4.55*
16	Depleted	362	718	117.35**
	Undepleted	559	836	55.00**
Pooled	Depleted	986	1630	158.54**
	Undepleted	2009	1962	0.56 (ns)
		(b) Walking		
2	Depleted	93	150	13.37**
	Undepleted	145	99	8.67*
4	Depleted	134	321	76.85**
	Undepleted	254	349	14.97**
8	Depleted	237	635	181.66**
	Undepleted	473	619	19.52**
16	Depleted	234	814	320.99**
	Undepleted	369	830	177.25**
Pooled	Depleted	698	1920	570.39**
	Undepleted	1241	1897	137.14**
		(c) Stationary		
2	Depleted	22	61	18.32**
	Undepleted	15	49	18.06**
4	Depleted	23	118	64.01**
	Undepleted	9	46	24.89**
8	Depleted	43	258	153.57**
	Undepleted	24	66	19.60**
16	Depleted	38	225	132.96**
	Undepleted	25	129	70.23**
Pooled	Depleted	126	662	364.59**
	Undepleted	73	290	129.72**
		(d) Cleaning		
2	Depleted	12	37	12.76**
	Undepleted	8	31	13.56**
4	Depleted	9	60	37.70**
	Undepleted	27	68	17.69**
8	Depleted	34	114	43.24**
	Undepleted	57	122	23.60**
16	Depleted	34	121	48.83**
	Undepleted	51	147	46.54
Pooled	Depleted	89	332	140.26**
	Undepleted	143	368	99.07**

[a] $P > 0.05$.

*$P < 0.05$.

**$P < 0.001$.

Table III. The Effect of Probing on the Outcome of Parasitoid Encounters in Trials at a Density of Two Wasps

Behavior	Depletion opportunity	No. of encounters Won	Lost	χ^2
Probe–probe	Depleted	47	61	1.81 (ns)[a]
	Undepleted	61	47	1.81 (ns)
Probe–walk	Depleted	56	44	1.44 (ns)
	Undepleted	90	35	24.20**
Probe–stationary	Depleted	19	8	4.48*
	Undepleted	50	15	18.85**
Probe–clean	Depleted	17	0	17.00**
	Undepleted	26	2	20.57**

[a] $P > 0.05$.
*$P < 0.05$.
**$P < 0.001$.

of foraging behavior made the simplifying assumption that the parasitoid egg supply is not limiting and that maximization of oviposition rates was the most suitable optimization criterion (van Alphen, 1982; Comins and Hassell, 1979; Cook and Hubbard, 1977; Marris *et al.*, 1986). However, recent work by Iwasa and co-workers (1984) and Mangel and co-workers (Mangel, 1987a,b, 1989a,b; Mangel and Clark, 1988; Mangel and Roitberg, 1989), using "state-variable" techniques, has demonstrated that changes in the number of eggs available to a parasitoid will substantially change her behavior. The parasitoid maximizes her lifetime reproductive success by making different decisions at different egg loads.

Results similar to those found in this study were obtained by Trudeau and Gordon (1990), who found that egg load correlated positively with the amount of time spent probing in experiments with *V. canescens*, and by Collins and Dixon (1986), who demonstrated that the aphid parasitoid *Monoctonus pseudoplatani* Marsh. (Hym: Aphidiidae) responded to decreasing egg load by reducing its oviposition rate and the duration of foraging bouts.

In a recent paper, Mangel (1989a) reanalyzed Collins and Dixon's (1986) results, using the state-variable approach, showing that the parasitoid's motivation to oviposit is determined by the interplay between egg load (the "physiological state variable") and information about host densities (the "external state variable"). Both *V. canescens* and *M. pseudoplatani* have been shown to respond to changes in the size of their egg loads, even though in both species mature eggs were abundant, and neither species can be considered egg-limited at the host densities used. Other parasitic Hymenoptera have been looked at and egg load has been found to influence search activity in *Trichogramma maidis* (Pak *et al.*, 1985), search activity and superparasitism in *Ephedrus californicus*

(Volkl and Mackauer, 1990), sex allocation in *Lariophagus distinguendus* (Putters and van dem Assem, 1988), and handling time, superparasitism, and clutch size in *Aphytis lingnanensis* (Rosenheim and Rosen, 1991).

Egg load has also been shown to be an important factor in the host choice behavior of the butterflies, *Battus philenor* (Pilson and Rausher, 1988; Odendaal, 1989; Odendaal and Rausher, 1990) and *Euphydryas editha* (Singer, 1982), and the tephritid fruit flies, *Rhagoletis pomonella* (Mangel and Roitberg, 1989), *Dacus tryoni*, and *D. jarvisi* (Fitt, 1990).

The interpretation of our results is complicated by the presence of a number of possible confounding variables, most importantly in this case, the effects of experience (i.e., depletion time) and female size. An earlier experiment carried out in Dundee showed that there was no significant relationship between wasp size, measured as ovipositor length and hind tibia length, and egg load, suggesting that success is not due to female body size (Green, 1985).

The effects of depletion time are more complex. For instance, the depleted wasps may simply be perceiving the experimental patch as being of a poorer quality, with a lower host, and a higher parasitoid, density then the depletion patch and as a result deciding to put less search effort into it. The fact that egg load and experience are often correlated has been pointed out by Rosenheim and Rosen (1991), and certainly the performance of the depleted wasps shows a marked decline with increasing length of the depletion period.

Further studies on the parasitic Hymenoptera and other insect groups will, we expect, continue to provide further support for the theoretical predictions that internal, physiological factors such as egg load and hunger play a major role in the shaping of insect behavior responses to external stimuli. Important among these will be studies which pay particular attention to isolating egg load effects from those of other important factors, particularly those of experience.

Agonistic Interactions and Interference

The results obtained confirm that agonistic encounters between searching females constitute an important aspect of the interference phenomenon in *V. canescens*. They suggest that a possible causal explanation for the positive relationship between the starting egg load and the proportion of conspecific encounters won is that

(i) wasps with larger egg loads spend a greater percentage of their time on the host patch probing, and
(ii) wasps which spend a greater percentage of their time on the host patch probing win a greater percentage of their encounters with conspecifics.

The higher success rate of probing individuals in encounters suggests the possibility of some element of resource defence (e.g., a transient territoriality) being involved. Once a probing wasp has discovered a host, she will not readily leave the vicinity. Since an individual engaged in a nonprobing activity has no similar host stimulus, she is more likely to leave the site of the encounter. It is possible that the sight of the probing wasp could be acting as some sort of "sign stimulus" to a nonprobing individual, communicating that the probing individual is unlikely to give way in any subsequent encounter and, therefore, it would not be worth escalating a contest that the nonprober is likely to lose. On the other hand, it may be that the sight of a probing wasp informs the nonprober of the presence of a host, and if the nonprober engaged and defeated the probing wasp, she would gain access to the reproductive opportunity herself. Against this possibility must be balanced the likelihood of losing, the cost of spending time in nonoptimal behavior and the probability of the host having already been parasitized.

When two probing individuals meet, the outcome of the encounter is much less predictable. Both are likely to be responding to a host stimulus and engaging in resource defense. Therefore, both are likely to be willing to escalate the contest. Encounters of this type can be appreciably longer in duration, involving circling movements and repeated head-on attacks until one of the contestants is driven off (personal observations; N. McCulloch, personal communication). The results of such contests show that increasing the length of the depletion period reduces the level of success by depleted wasps. The data do not show wasps with higher egg loads winning a higher proportion of the encounters in the two-wasp trials. However, the sample sizes in this part of the investigation were quite small (< 10 in all four depletion periods) and it is difficult to draw any meaningful conclusions from this.

Our results suggest that interference affects the reproductive success of *V. canescens* in a number of ways. It does so by reducing the amount of time spent on the patch, through the effect of exploitation. It also does so, not by reducing the proportion of patch time spent searching, as measured by probing time, but by disrupting search and making losing wasps retreat from the position held prior to the encounter, and forcing them to begin search on another part of the patch, where they quite possibly have searched already. Even probing wasps lose the majority of encounters at high densities.

Given the demonstrated importance of mutual interference in stabilizing dynamics of host–parasitoid interactions (Hassell and Rogers, 1972; Hassell and May, 1973, 1974; Rogers and Hassell, 1974; Beddington, 1975; Free *et al.*, 1977; Hassell, 1978), it is essential that the infrastructure of the associated behaviors be understood. This paper represents a contribution to this understanding.

One difficulty with interpreting results from experiments on *V. canescens* is that very little is known of the species ecology in either natural or seminatural conditions. Observations of *Ephestia* larval distributions in Greece made by

Jacques van Alphen (personal communication) suggest that moth larvae occur singly on fallen figs. This suggests that the clumped distributions of phycitid larvae in grain stores may not reflect the type of larval distribution that *V. canescens* encounters in natural situations.

Without detailed information on movements of individuals between grain stores and the wild, it is difficult to speculate on the selective forces to which *V. canescens* populations have been subjected. However, the longer association is likely to be that with fallen fruit, and the evolution of agonistic behavior is more likely under this scenario.

Such lack of knowledge of parasitoid behavior in the field is almost-universal (but see Janssen, 1991; Driessen and Hemerik, 1991) and constitutes a major hurdle to our understanding the evolution of behavior in this group (Antolin and Strand, 1992).

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REFERENCES

Antolin, M. F., and Strand, M. R. (1992). Mating system of *Bracon hebetor* (Hymenoptera: Braconidae). *Ecol. Entomol.* **17:** 1-7.

Beaver, R. A. (1967). Hymenoptera associated with elm bark beetles in Wytham Wood, Berks. *Trans. Soc. Br. Entomol.* **17:** 141-150.

Beddington, J. R. (1975). Mutual interference between parasites or predators and its effect on searching efficiency. *J. Anim. Ecol.* **44:** 331-340.

Begon, M., and Mortimer, M. (1981). *Population Ecology*, Blackwell Scientific, Oxford.

Collins, M. D., and Dixon, A. F. G. (1986). The effect of egg depletion on the foraging behaviour of an aphid parasitoid. *J. Appl. Entomol.* **102:** 342-352.

Comins, H. N., and Hassell, M. P. (1979). The dynamics of optimally foraging predators and parasitoids. *J. Anim. Ecol.* **48:** 335-351.

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

Driessen, G., and Hemerik, L. (1991). Aggregative responses of parasitoids and parasitism in populations of *Drosophila* breeding in fungi. *Oikos* **61:** 96-107.

Fitt, G. P. (1986). The influence of a shortage of hosts on the specificity of oviposition behaviour in species of *Dacus* (Diptera: Tephritidae). *Physiol. Entomol.* **11:** 133-143.

Fitt, G. P. (1990). Comparative fecundity, clutch size, ovariole number and egg size of *Dacus tryoni* and *D. jarvisi*, and their relationship to body size. *Entomol. Exp. Appl.* **55:** 11-21.

Green, G. M. (1985). *An Investigation of the Effect of Egg Load on Interference in* Nemeritis canescens (*Hymenoptera: Ichneumonidae*), Unpublished B.Sc. (honours) dissertation, University of Dundee, Dundee, UK.

Griffiths, K. J., and Holling, C. S. (1969). A competition submodel for parasites and predators. *Can. Entomol.* **101:** 785–818.

Hassell, M. P. (1971). Mutual Interference between searching insect parasitoids. *J. Anim. Ecol.* **40:** 473–486.

Hassell, M. P. (1978). *The Dynamics of Arthropod Predator-Prey Systems*, Princeton University Press, Princeton, NJ.

Hassell, M. P., and Huffaker, C. B. (1969). Regulatory processes and population cyclicity in laboratory populations in *Anagasta kuhniella* (Zeller) (Lepidoptera: Phycitidae). III. The development of population models. *Res. Popul. Ecol.* **11:** 186–210.

Hassell, M. P., and May, R. M. (1973). Stability in insect host-parasite models. *J. Anim. Ecol.* **42:** 693–736.

Hassell, M. P., and May, R. M. (1974). Aggregation in predators and insect parasites and its effect on stability. *J. Anim. Ecol.* **43:** 567–594.

Hassell, M. P., and Rogers, D. (1972). Insect parasite responses in the development of population models. *J. Anim. Ecol.* **41:** 661–676.

Hassell, M. P., and Varley, G. C. (1969). New inductive population model for insect parasites and its bearing on biological control. *Nature* **223:** 1133–1136.

Hidaka, T. (1958). Biological investigation on *Telenomus gifuensis* Ashmead (Hymenoptera: Scelionidae), an egg-parasitoid of *Scotinophora lunda* Burmeister (Hemiptera: Pentatomidae) in Japan. *Acta Hymen.* **1:** 75–93.

Hokyo, N., and Kiritani, K. (1963). Two species of egg parasites as contemporaneous mortality in the egg population of the southern green stink bug *Nezara viridula. Jap. J. Appl. Entomol. Zool.* **7:** 214–227.

Hokyo, N., and Kiritani, K. (1966). Oviposition behaviour of two egg parasites, *Asolcus mitsukurii* Ashmead and *Telenomus nakagawa* Watanabe (Hymenoptera: Proctotrupoidea, Scelionidae). *Entomophaga* **11:** 191–201.

Hughes, J. P. (1988). *An Evolutionary Approach to the Foraging Behaviour of Solitary Parasitoids*, Unpublished Ph.D. thesis, University of Dundee, Dundee, UK.

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

Janssen, A. (1989). Optimal host selection by *Drosophila* parasitoids in the field. *Funct. Ecol.* **3:** 469–479.

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

Mangel, M. (1987b). Modelling behavioural decisions of insects. In *Lecture Notes in Biomathematics*, Springer-Verlag, Berlin, Vol. 73, pp. 1–19.

Mangel, M. (1989a). An evolutionary interpretation of the "motivation to oviposit." *J. Evol. Biol.* **2:** 157–172.

Mangel, M. (1989b). Evolution of host selection of parasitoids: Does the state of the parasitoid matter? *Am. Nat.* **133:** 688–705.

Mangel, M., and Clark, C. W. (1988). *Dynamic Modelling in Behavioural Ecology*, Princeton University Press, Princeton, NJ.

Mangel, M., and Roitberg, B. (1989). Dynamic information and host acceptance by a tephritid fruit fly. *Ecol. Entomol.* **14:** 181–189.

Marris, G. C., Hubbard, S. F., and Hughes, J. P. (1986). Use of patchy resources by *Nemeritis canescens* (Hymenoptera: Ichneumonidae). I. Optimal solutions. *J. Anim. Ecol.* **55:** 631–640.

Nicholson, A. J., and Bailey, V. A. (1935). The balance of animal populations. Part 1. *Proc. Zool. Soc. Lond.* **1935:** 551–598.

Odendaal, F. G. (1989). Mature egg number influences the behaviour of female *Battus philenor* butterflies. *J. Insect Behav.* **2:** 15–25.

Odendaal, F. J., and Rausher, M. D. (1990). Egg load influences search intensity, host selectivity, and clutch size in *Battus philenor* butterflies. *J. Insect Behav.* **3:** 183–193.

Pak, G. A., van Halder, I., Lindeboom, R., and Stroet, J. J. G. (1985). Ovarian egg supply, female age and plant spacing as factors influencing search activity in the egg parasite *Trichogramma* sp. *Med. Fac. Landbouw. Rijksuniv. Gent* **50:** 369–378.

Pilson, D., and Rausher, M. D. (1988). Clutch size adjustment by a swallowtail butterfly. *Nature* **333:** 361-363.

Putters, F. A., and van den Assem, J. (1988). The analysis of partial preferences in a parasitic wasp. *Anim. Behav.* **36:** 933-948.

Ridout, L. M. (1981). Mutual interference: Behavioural consequences of encounters between adults of the parasitoid wasp *Venturia canescens* (Hymenoptera: Ichneumonidae). *Anim. Behav.* **29:** 897-903.

Rogers, D. J. (1970). *Aspects of Host-Parasite Interaction in Laboratory Populations of Insects*, Unpublished D. Phil. thesis, University of Oxford, Oxford, UK.

Rogers, D. J. (1972). The ichneumon wasp *Venturia canescens*: Oviposition and the avoidance of superparasitism. *Entomol. Exp. Appl.* **15:** 190-194.

Rogers, D. J., and Hassell, M. P. (1972). General models for insect parasite and predator searching behaviour: Interference. *J. Anim. Ecol.* **43:** 239-253.

Rogers, D. J., and Hubbard, S. F. (1974). How the behaviour of parasites and predators promotes population stability. In Usher, M. B., and Williamson, M. H. (eds.), *Ecological Stability*, Chapman & Hall, London.

Rosenheim, J. A., and Rosen, D. (1991). Foraging and oviposition decisions in the parasitoid *Aphytis lingnanensis*: Distinguishing the influences of egg load and experience. *J. Anim. Ecol.* **60:** 873-893.

Royama, T. (1971). A comparative study of models for predation and parasitism. *Res. Popul. Ecol.* (*Suppl.*) **1:** 1-91.

Safavi, M. (1968). Étude biologique et écologique des hyménoptères parasites des oeufs des punaises des céréncles. *Entomophaga* **13:** 381-495.

Singer, M. C. (1982). Quantification of host preference by manipulation of oviposition behavior in the butterfly, *Euphydryas editha. Oecologia* **52:** 224-229.

Spradbery, J. P. (1970). Host finding by *Rhyssa persuasoria* (L.), an ichneumonid parasite of siricid woodwasps. *Anim. Behav.* **18:** 103-114.

Trudeau, D., and Gordon, D. M. (1990). Factors determining the functional response of the parasitoid, *Venturia canescens. Entomol. Exp. Appl.* **50:** 3-6.

Ulyett, G. C. (1950). Distribution of progeny by *Cryptus ornatus* Pratt. *Can. Entomol.* **82:** 1-11.

van Alphen, J. J. M. (1982). *Foraging Behaviour of* Asobara tabida, *a Larval Parasitoid of Drosophilidae*, Unpublished Ph.D. thesis, University of Leiden, Leiden, The Netherlands.

van Alphen, J. J. M., and Vet, L. E. M. (1986). An evolutionary approach to host finding and selection. In Waage, J. K., and Greathead, D. J. (eds.), *Insect Parasitoids*, Academic Press, London, pp. 23-61.

Volkl, W., and Mackauer, M. (1990). Age-specification pattern of host discrimination by the aphid parasitoid *Ephedrus californicus* Baker (Hymenoptera: Aphidiidae). *Can. Entomol.* **122:** 349-361.

Walter, G. H. (1988). Activity patterns and egg production in *Coccophagus bartletti*, an aphelinid parasitoid of scale insects. *Ecol. Entomol.* **13:** 129-144.