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Superparasitism and mutual interference in the egg parasitoid *Anagrus delicatus* (Hymenoptera: Mymaridae)

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Abstract. 1. In nature, interference among *Anagrus delicatus* (Hymenoptera: Mymaridae) parasitoids reduced the per-capita number of hosts parasitized. Interference increased with parasitoid density.

2. *Anagrus delicatus* did not avoid parasitizing hosts that had recently been parasitized by conspecific wasps. Evidence indicated that this superparasitism was largely a random process, increasing with the ratio of parasitized to unparasitized hosts.

3. Individual parasitoid efficiency, the number of hosts killed per wasp per unit time, decreased with increasing wasp density. This occurred whether wasps searched the patch together (simultaneously) or one by one (sequentially), and was the result of an increase in time spent superparasitizing hosts at higher wasp density. This is known as indirect mutual interference.

4. Increasing numbers of parasitoids together on the same patch caused a significant decline in the rate and per-capita number of hosts parasitized. However, there was not a correspondent decline in searching efficiency with increasing wasp density (i.e. no direct mutual interference).

5. These forms of parasitoid density dependence should contribute to the stability of the host–parasitoid interaction.

Key words. *Anagrus delicatus*, egg parasitoid, mutual interference, Mymaridae, planthopper, *Prokelisia marginata*, superparasitism.

Introduction

Aggregation by parasitoids to host patches is an integral component of models of host–parasitoid population dynamics. In discrete-time models, aggregation in space to host patches (dependent upon or independent of host density) stabilizes the host–parasitoid interaction by causing searching efficiency (a, from the Nicholson–Bailey model; Nicholson & Bailey, 1935) to decrease with increasing parasitoid density (Hassell & May, 1973, 1974; Beddington *et al.*, 1975; May, 1978; Chesson & Murdoch, 1986; Taylor, 1988; Reeve *et al.*, 1989; Pacala *et al.*, 1990; Hassell *et al.*, 1991; Godfray & Pacala, 1992). There is no consensus for continuous-time models, however: the effect of parasitoid aggregation on population dynamics depends on the model and parameter values used (Murdoch & Stewart-Oaten, 1989; Ives, 1992; Murdoch *et al.*, 1992).

Density dependence in searching efficiency is known as parasitoid interference. Three forms are presently recognized (Visser & Driessen, 1991). (1) *Direct mutual interference*: conspecific wasps disrupt search or cause injury to one another, which leads to an immediate reduction in searching efficiency (Hassell & Varley, 1969; Hassell, 1978). (2) *Indirect mutual interference*: time invested in ovipositing into hosts parasitized by conspecifics (superparasitism) causes a reduction in the rate of hosts killed per wasp per patch, but not searching efficiency (Visser & Driessen, 1991). Although the decision to superparasitize can be adaptive for the individual (van Alphen & Visser, 1990), at the population and generation level the number killed per wasp will decline with increasing superparasitism. The population dynamic consequences of indirect interference have not been fully explored. However, searching efficiency should decline at the population and generation level under these conditions (Visser & Driessen, 1991; Driessen & Visser, 1993) and contribute to the stability of the host–parasitoid interaction (Hassell & Varley, 1969; Beddington, 1975). (3) *Pseudo-*

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interference: the nonrandom distribution of parasitoids among host patches causes an apparent decline in searching efficiency with increasing parasitoid density (Free *et al.*, 1977). This is not a consequence of time-wasting behavioural interactions among parasitoids, but simply a result of the overexploitation of host patches at high wasp density.

In models describing these forms of interference, searching efficiency is measured with respect to time. This is applicable to parasitoids that are primarily time limited, in which lifetime rate of oviposition is the currency to be maximized for highest fitness (Charnov, 1976; Cook & Hubbard, 1977; Charnov & Skinner, 1984). For parasitoids that are egg limited or risk sensitive, the more appropriate currency may be the lifetime number of ovipositions (Iwasa *et al.*, 1984; Houston & McNamara, 1986; Driessen & Hemerik, 1992). The population dynamics and stability consequences of decreasing ovipositions with increasing parasitoid density, however, have not been adequately investigated. In the absence of knowledge concerning foraging constraints on parasitoids, it may be wise to examine the effect of parasitoid density on both their time and egg budget, in addition to theoretical parameters such as a, the searching efficiency.

Parasitoid interference has commonly been reported from the laboratory, but field studies are much rarer (Münster-Swendsen, 1980; Yamada, 1988; Pitcairn *et al.*, 1990; and see examples in Hassell, 1978). Where interference is found in the field, few experiments have addressed its character (direct or indirect mutual interference or pseudo-interference) or the parasitoid behaviours that underlie it (but see van Dijken & van Alphen, 1991).

In a recent study (Cronin & Strong, 1993) we reported significant interference among field populations of the parasitoid *Anagrus delicatus* Dozier (Hymenoptera: Mymaridae) searching among leaves for its planthopper host *Prokelisia marginata* (Van Duzee) (Homoptera: Delphacidae) (Fig. 1). There was a significant decline in the average per-capita number of parasitizations as average wasp density per patch increased. The distribution of parasitoids among leaves was approximately random: counts/leaf were fitted to a negative-binomial model and the clumping parameter, k, was estimated to be 3.36 (Reeve *et al.*, 1993). Therefore the contribution of pseudo-interference to this relationship is likely to be small in relation to mutual interference.

In this paper we describe a series of laboratory experiments that examined the cause of interference (direct or indirect mutual interference) among *A.delicatus* females searching within single patches of hosts. These experiments examined the behavioural response of parasitoids involved in simultaneous (wasps visiting a patch together) or sequential (wasps visiting a patch one at a time) patch visits. *Anagrus delicatus* does not forage solely to maximize its rate of encounter with hosts (Cronin & Strong, 1993), therefore we did not limit our analysis to changes in rate-based parameters such as searching efficiency. We also examined the effect of wasp density on number of ovipositions per patch. The effect of these behaviours on lifetime oviposition success and population dynamics is discussed.

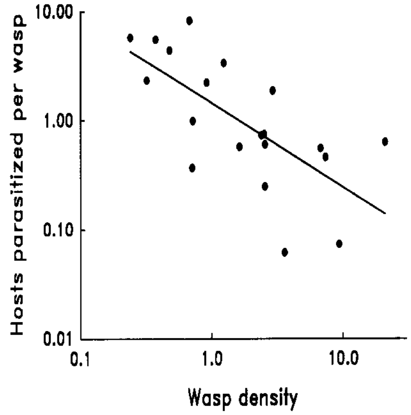

Fig. 1. The relationship between female parasitoid density and the per-capita number of hosts parasitized (ln per-capita parasitized = −0.77*[ln wasp density] + 0.37, $r^2 = 0.47$, $p = 0.001$, $n = 20$). Each point represents the average wasp density and number of hosts parasitized/wasp over a 3 day period for twenty separate experimental replicates (see Cronin & Strong, 1993).

Methods

Study organisms

Anagrus delicatus is a minute (0.7 mm total body length) solitary parasitoid that attacks the egg stage of two planthoppers, *P.marginata* and *P.dolus* Wilson (Stiling & Strong, 1982a, b; Cronin & Strong, 1990a). It is a short-lived wasp, existing as an adult for at most 2 days. Although *A.delicatus* is pro-ovigenic and has only 33 eggs on average, it never exhausts it egg supply on the first few patches visited (Cronin & Strong, 1990a, 1993). For the experiments outlined below, egg limitations are not a constraint on within-patch foraging behaviour.

Anagrus delicatus and its planthopper hosts are found in intertidal marshes along the Atlantic and Gulf coasts of the United States in association with *Prokelisia*'s only host plant, salt marsh cord grass (*Spartina alterniflora* Loisel) (Denno & Grissell, 1979; McCoy & Rey, 1981; Denno *et al.*, 1987). The eggs of *Prokelisia* are laid just beneath the epidermis of the linear leaves, where they are attacked by searching parasitoids. *Prokelisia marginata* is consistently the most abundant of the two planthoppers and is a more suitable host for development of the parasitoid's offspring (Cronin, 1991). Parasitism of *P.marginata* eggs in the field averages less than 20%, but occasionally has been known to reach 80% (Stiling & Strong, 1982b; Strong, 1989; Cronin & Strong, 1990b). Both spatially and temporally the distribution of parasitism is independent of host density (Stiling & Strong, 1982b; Strong, 1989; Cronin & Strong, 1990b).

Experimental design and procedure

Experimental host patches. Adult planthoppers were collected with a sweep net from the salt marshes of Oyster Bay, Wakulla Co., Florida, U.S.A. They were transported on ice to the laboratory where they were sorted by sex and species according to the procedure of Heady & Wilson (1990). Only *P.marginata* adults were used in this study. To create discrete host patches we confined adult planthoppers onto a cord grass leaf by use of a clip cage (see Cronin & Strong, 1990a, for complete description). Cages were constructed of a 40 mm length of 18 mm diameter acetate tubing that was inserted over a single leaf (12–30 cm in length) on a potted cord grass culm. The tubing was positioned at the leaf base (one per leaf) and capped at each end, exposing only the upper leaf surface. Planthoppers were released into the cage for 48 h to deposit eggs. Even-aged cohorts of eggs (1–2 days old), at densities comparable to those found in the field (Cronin & Strong, 1990a) were established within each host patch.

Laboratory parasitoids. Wasps for study were obtained as developing larvae and pupae from cord grass leaves collected in the field. Leaves were sectioned and placed in bowls with lids to prevent escape by emerging adult wasps. To minimize variance in wasp performance, we used only wasps that were less than 3 h old (an age of maximum fecundity), had no ovipositional experience, and were in good condition. The precise details of this procedure can be found in Cronin & Strong (1990a).

Superparasitism. We examined whether wasps, released sequentially on a patch, discriminate between unparasitized and parasitized hosts. Low-density host patches were created by releasing three female planthoppers into a clip cage. Fifteen patches were created, with an average of 14.5 hosts ±2.4 (1 SE) per patch. After a 48 h incubation period, a leaf bearing a host patch was positioned under a dissecting scope outfitted with a video camera. The patch was magnified 25× and projected onto a television monitor, the entire patch was visible on the monitor screen. A 22 × 28 cm acetate sheet was taped to the screen (the exact size of the rectangular screen). Following this procedure, a single female wasp was released onto the patch and her behaviours videotaped until she dispersed from the leaf. We also recorded with a marking pen the exact position of her ovipositions (an egg laid) and unsuccessful probes (penetration of the leaf with the ovipositor, but no egg laid) on the acetate sheet. These two behaviours could be easily distinguished by the duration of insertion of the ovipositor into the leaf: unsuccessful probes average 20 s while ovipositions average 120 s; the time distributions of the two behaviours do not overlap (Cronin & Strong, 1990a, 1993).

After dispersal from the leaf, the acetate sheet was replaced with a new one. A new wasp was then released onto the patch and her behaviour recorded on videotape and on the acetate sheet. Four wasps were released, sequentially, onto each patch: two inexperienced and two experienced females. We chose to examine the experience state of wasps because foraging behaviour, and, in particular, discriminatory ability are known to change with experience in some wasps (van Lenteren & Bakker, 1975; van Lenteren, 1976; van Alphen & Nell, 1982). In our trials, inexperienced wasps had no prior contact with hosts. Experienced wasps were produced by caging single inexperienced wasps for 1 h on a high density patch of hosts, immediately prior to their use in the experiment. Inexperienced wasps alternated with experienced wasps on a patch, and the order of release changed between patches.

Following dispersal of the fourth wasp from the patch, a new acetate sheet was taped to the monitor screen. The leaf was carefully dissected and the position of each host marked on the acetate sheet. By overlaying acetate sheets that mapped the spatial arrangement of probes and ovipositions by the four wasps and the acetate on host distribution, we were able to determine (1) the number of hosts encountered (contact of the wasp's ovipositor with a host), (2) the number of eggs laid, and (3) the distribution of wasp eggs among the available hosts, for each wasp and all wasps combined. We verified the distribution of wasp eggs by examining the contents of squashed hosts at 200× under a compound light microscope. The distribution of eggs determined from acetate sheets corresponded exactly with the distribution based on squashed hosts.

For each wasp, we determined the handling times and probability of oviposition into unparasitized hosts (U), hosts previously parasitized by a conspecific wasp (P_c), and hosts previously parasitized by the same wasp (P_s), for inexperienced and experienced wasps. Handling time was measured from insertion of the ovipositor into the host until removal after the egg was laid. The cumulative duration of all probes of the host, until an egg was laid, was considered part of the handling time. All oviposition probabilities were based on the proportion of hosts (of type U, P_c, or P_s) encountered (E) that received an oviposition (O), and can be considered an estimate of the acceptance rate of each host type. Wasps probe greater than 90% of the hosts they discover (identified by increased antennal movement when directly above a concealed host; unpubl. data), suggesting that any factor affecting host discrimination would be internally based.

The probability of ovipositing into an unparasitized host, given that one is encountered is denoted by $\Pr(O|UE)$. The probability of conspecific superparasitism is denoted by $\Pr(O|P_cE)$; and self superparasitism, by $\Pr(O|P_sE)$. We tested for statistical differences among the three probabilities using paired t-tests (Sokal & Rohlf, 1981). Because patch quality varied for each wasp, in terms of host density and number of wasp eggs already laid in the patch, paired comparisons (within a wasp) were most appropriate. A repeated-measures ANOVA was not practical because there were too few wasps that had estimates for all three probabilities. To test for a difference between two probabilities [e.g. $\Pr(O|UE)$ and $\Pr(O|P_cE)$] we used only wasps that had estimates of each. The difference between probability pairs was tested against a t-distribution with $n-1$ (n = number of paired comparisons) degrees of freedom. We also tested for differences between inexperienced and experienced wasps in acceptance rates of the three host types using a t-test for differences between two means.

We examined the distribution of wasp eggs among hosts, in a separate set of patches that bore a greater number of hosts. To ensure moderate levels of parasitism, we released eight female *A.delicatus* on each host patch. Wasps were not caged on the host plant and were free to disperse from the patch bearing hosts. After all wasps had dispersed, host eggs were dissected from the leaf, squashed, and examined under a compound microscope (200×). The number of parasitoid eggs present in each host was recorded. Deviation from a random (Poisson) distribution of parasitoid eggs among available hosts was assessed with a G-test for goodness of fit (Sokal & Rohlf, 1981). This procedure was replicated six times. We determined the overall significance of these six separate tests with Fisher's combined probabilities test, where the value Φ ($= -2\Sigma \ln P$; P is the significance level) was compared against a χ^2 distribution with $2k$ degrees of freedom (k = number of independent tests) (Sokal & Rohlf, 1981, p. 779).

Sequential patch visits. Superparasitism data were used to determine the behavioural response of *A.delicatus* to the density of wasps that previously searched that patch. Patch time, number of ovipositions and oviposition rate were determined for each wasp released on the fifteen patches. We also estimated the searching efficiency at the patch level, s' (*sensu* Visser & Driessen, 1991), from the following equation:

$$s' = \frac{1}{PT}\ln\left(\frac{N}{N - N_a}\right)$$

where P = parasitoid density, T = time spent on the patch, N = host density, and N_a = number of hosts killed (host contains at least one wasp egg) (Nicholson & Bailey, 1935; Hassell & Varley, 1969). Lastly, we calculated 'individual searching efficiency', f (the number of hosts killed per wasp per unit time per patch) from the equation of Driessen & Visser (1993):

$$f = N_a/PT$$

Least-squares regression was used to determine the relationship between the five behavioural parameters and wasp density. Wasp density was measured as the number of parasitoids that searched the patch, and therefore ranged from one to four. All behavioural parameters were natural log-transformed in order to normalize the data. To ensure an overall error rate, α, of ≤ 0.05 we used the Dunn-Šidák method (Sokal & Rohlf, 1981) to adjust for comparison-wise error. The significance level for each individual comparison was calculated as $\alpha' = 1 - (1 - \alpha)^{1/k}$, where k = number of comparisons. For each of the five regressions, the critical level for determining significance was 0.01.

Simultaneous patch visits. We examined how the behaviour of *A.delicatus* varies in response to the density of conspecifics searching together on the same patch. In this experiment we did not continuously monitor the behaviour of wasps on the patch. Instead, we released one

Table 1. Behavioural response of inexperienced and experienced wasps on low-density host patches and the probabilities of oviposition into unparasitized, conspecific parasitized, and self-parasitized hosts. Means ±1 SE are presented. Statistical comparisons of inexperienced and experienced wasps were based on t-tests on independent samples. Significance tests within columns were based on paired t-tests, and differences among means are denoted by different letters ($p < 0.05$). Except where noted in parentheses, the sample size is twenty-nine for experienced wasps, and twenty-three for inexperienced wasps.

Response	Inexperienced wasps	Experienced wasps	t-statistic	p value
Behaviour				
Patch time (min)	71.1 ± 8.8	54.0 ± 8.6	1.38	0.17
Ovipositions	2.4 ± 0.3	1.4 ± 0.4	2.64	0.01
Oviposition rate (h^{-1})	2.3 ± 0.3	1.3 ± 0.3	2.64	0.01
Oviposition probabilities				
Proportion of hosts encountered (E)	0.57 ± 0.04	0.48 ± 0.06	1.13	0.26
Proportion of unparasitized hosts encountered that were oviposited in; Pr (O UE)	0.34 ± 0.04^a	0.11 ± 0.04^a	3.77	<0.01
Proportion of conspecific parasitized hosts encountered that were oviposited in; Pr ($O \mid P_cE$)	0.45 ± 0.08^a (21)	0.19 ± 0.05^a (18)	2.56	0.02
Proportion of self-parasitized hosts encountered that were oviposited in; Pr (O P_sE)	0.16 ± 0.07^b (22)	0.37 ± 0.14^a (9)	0.83	0.44

Table 2. Handling times (min) for unparasitized (U), conspecific parasitized (P_c), and self-parasitized (P_s) hosts. Within a wasp, handling times were averaged for each host type. Means ±1 SE presented below are based on averages among wasps. Two-way ANOVA indicated no difference in handling times between inexperienced and experienced wasps ($F_{1,47} = 0.62$, $p = 0.43$), or among host types ($F_{2,47} = 0.512$, $p = 0.602$).

Host type	Inexperienced wasps	Experienced wasps
Unparasitized (U)	5.4 ± 0.7	5.3 ± 1.5
Conspecific parasitized (P_c)	5.3 ± 1.0	4.4 ± 0.7
Self-parasitized (P_s)	9.0 ± 3.9	5.7 ± 1.7

to eight wasps simultaneously onto a single uncaged host patch (bearing an average of 56 hosts ±7 [1 SE]). At 5 min intervals we returned to each patch and recorded the number of wasps still present on the leaf. While monitoring these patches we also looked for evidence of any aggressive interactions among foraging wasps (e.g. fighting, chasing-retreating, etc.). Host patches were allowed to incubate 5 days prior to their dissection, after which we recorded host density and number of hosts parasitized. This was replicated fifteen times for the one wasp per patch treatment and between five and seven times for all others.

Average patch time and number of hosts parasitized per wasp were calculated for each replicate by dividing the total time or numbers parasitized (summed over all wasps on a patch) by wasp density. Oviposition rate was determined as the ratio of the average per-capita number of hosts parasitized and average patch time per wasp. The parameters s' and f were also calculated from these data. The effect of wasp density on these parameters was determined with least-squares regression, as described for the sequential data.

Results

Superparasitism

Single *A.delicatus* spent between 50 and 70 min on a patch and encountered approximately 50% of the hosts with its ovipositor; this did not differ between inexperienced and experienced wasps (Table 1). However, inexperienced wasps had both a higher rate and number of ovipositions than experienced wasps. The former laid 2.4 eggs per hour and the latter 1.4 eggs per hour. Regardless of the wasp's level of experience, or the order in which the wasp was released on the patch, the number of ovipositions increased in direct proportion to the time spent on the patch (for all wasps combined: $r^2 = 0.35$, $p < 0.001$).

Anagrus delicatus oviposited into all host types. For inexperienced wasps, the rate of acceptance of unparasitized (U) hosts was 34%, conspecific parasitized (P_c) hosts 45%, and self-parasitized (P_s) hosts 16% (Table 1). Acceptance of U hosts did not differ from P_c hosts, but was much higher than P_s hosts ($p = 0.02$). P_c hosts were accepted at a higher rate than P_s hosts ($p = 0.01$). Experienced wasps had a lower acceptance rate than inexperienced wasps for U (11%) and P_c (19%) hosts, but not for P_s (37%) hosts. Acceptance rates by experienced wasps did not differ significantly among the three host types. For inexperienced and experienced wasps combined, the rate of acceptance of U and P_c hosts did not change with the order in which wasps were released onto the patch (for U hosts, $F_{3,33} = 1.25$, $p = 0.308$; for P_c hosts, $F_{3,33} = 0.90$, $p = 0.45$); insufficient data were available for an analysis of P_s hosts. Therefore, acceptance rates did not change as the patch became further exploited. We infer that wasps did not consistently avoid or prefer previously parasitized hosts.

Handling times did not vary with the condition of the host (U, P_c or P_s) or wasp (inexperienced or experienced) (Table 2). On average, wasps took 5.5 min ±0.5 (1 SE; $n = 67$) to oviposit into a host.

When we exposed host eggs to high densities of female

Table 3. The distribution of parasitoid eggs among *P.marginata* hosts for six replicates. Eight female *A.delicatus* were exposed to the hosts in each replicate. Deviation from a random (Poisson) distribution of parasitoid eggs was determined with the G-test goodness of fit (Sokal & Rohlf, 1981). Categories were pooled such that no observed value fell below 3.0. G was compared against a χ^2 distribution with 3 degrees of freedom for replicates 1, 4 and 5; and 2 degrees of freedom for the remainder.

		No. of hosts containing 0, 1, 2 or 3 wasp eggs					
Replicate		0	1	2	3	G	p
1	Obs.	9.0	20.0	11.0	5.0	1.44	0.696
	Exp.	12.7	16.0	10.7	5.9		
2	Obs.	24.0	31.0	5.0	2.0	2.31	0.315
	Exp.	32.2	22.1	7.6	2.1		
3	Obs.	19.0	13.0	4.0	0.0	0.29	0.865
	Exp.	20.1	11.7	3.4	0.7		
4	Obs.	12.0	37.0	11.0	3.0	5.50	0.139
	Exp.	25.4	25.0	12.3	5.0		
5	Obs.	11.0	37.0	17.0	4.0	6.61	0.085
	Exp.	23.4	26.6	15.1	7.7		
6	Obs.	7.0	21.0	11.0	0.0	6.51	0.039
	Exp.	13.0	14.3	7.9	3.7		

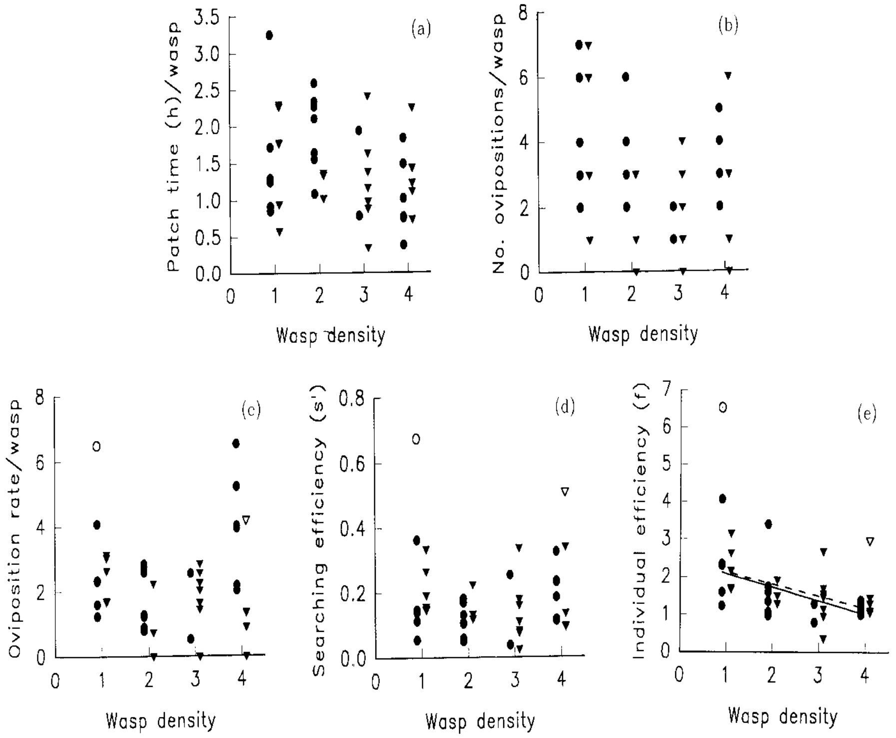

Fig. 2. The effect of conspecific density on the behaviour of inexperienced (circles) and experienced (triangles) *A.delicatus* during sequential patch visits (based on least-squares regression). The behaviours are (a) patch time (h) per wasp (inexp.: $r^2=0.13$, $p=0.11$; exp.: $r^2=0.03$, $p=0.43$); (b) number of ovipositions per wasp (inexp.: $r^2=0.02$, $p=0.52$; exp.: $r^2=0.09$, $p=0.18$); (c) oviposition rate (h^{-1}) per wasp (inexp.: $r^2=0.22$, $p=0.04$; exp.: $r^2=0.18$, $p=0.07$); (d) searching efficiency, s' (inexp.: $r^2=0.06$, $p=0.29$; exp.: $r^2=0.07$, $p=0.27$); and (e) individual efficiency, f (inexp.: $r^2=0.26$, $p=0.01$; exp.: $r^2=0.32$, $p=0.01$). Regression lines are only provided for statistically significant relationships (inexp.: solid; exp.: dashed). Open symbols signify outliers (based on an analysis of the studentized residuals; Montgomery & Peck, 1982) and were removed prior to analysis. Their removal did not alter the results.

wasps, superparasitism did occur (Table 3). In each of the six replicate tests, many hosts contained one parasitoid egg; fewer contained at least two parasitoid eggs, and in one case four parasitoid eggs were found in a single host. A comparison of the distribution of parasitoid eggs among the available hosts with a Poisson distribution did not yield evidence that parasitoid eggs deviated from a random distribution in five of six replicates (*G*-test, $p>0.05$). Superparasitism occurred less frequently than expected in replicate 6 ($0.05>p>0.025$). However, a Fisher's combined probability test on all replicates suggests no overall deviation from a random distribution of wasp eggs among hosts ($\Phi=16.77$, df $=12$, $p=0.16$).

Sequential patch visits

Both inexperienced and experienced *A.delicatus* responded in a similar fashion to the density of conspecific wasps (Fig. 2). The number of wasps visiting a patch in sequence had no effect on the patch time, number of ovipositions, oviposition rate, or searching efficiency (s'). On the other hand, superparasitism increased ($r^2=0.58$, $p<0.0001$) and individual efficiency per patch (f) decreased with increasing wasp density (Fig. 2e).

Simultaneous patch visits

Wasps searching simultaneously on a host patch exhibited no aggressiveness toward other females. However, at higher wasp densities, wasps were frequently observed to 'bump' into one another while searching for hosts. Upon contact, both wasps would move apart 10–20 mm, then immediately resume searching. Whether searching, probing or ovipositing, females generally abandoned that activity when bumped by another wasp. This disruption, though, was never observed to result in dispersal from the patch. In this experiment we did not make quantitative estimates of the proportion of time spent searching, but it did appear that disturbance from other wasps increased the amount of time spent walking about the leaf.

The density of searching females had no discernable effect on the average time wasps spent on a patch (Fig. 3a). While they searched the same amount of time per patch, this did not result in a constant number of hosts parasitized per wasp across all wasp densities.

In this experiment, we did not directly measure the number of ovipositions per wasp. However, because *A.delicatus* distributes its eggs among hosts approximately at random (Table 3), we were able to calculate the expected number of eggs laid per wasp. Here, the only information

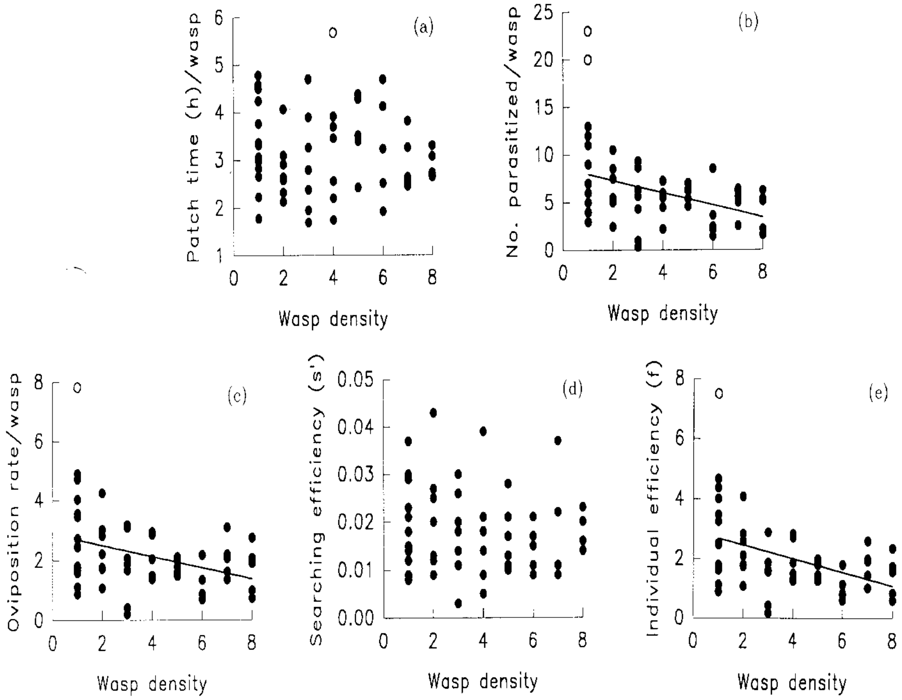

Fig. 3. The effect of conspecific density on *A.delicatus* behaviour during simultaneous patch visits (based on least-squares regression). The behaviours are (a) patch time (h) per wasp ($r^2 = 0.01$, $p = 0.55$), (b) number of ovipositions per wasp ($r^2 = 0.16$, $p = 0.003$), (c) oviposition rate (h^{-1}) ($r^2 = 0.12$, $p = 0.01$), (d) searching efficiency, s' ($r^2 = 0.03$, $p = 0.22$), and (e) individual efficiency, f ($r^2 = 0.18$, $p = 0.001$). Regression lines are provided only for significant relationships. Outliers are represented by open circles. They were excluded from the analyses, but did not alter the results.

required was the number of hosts that contained no parasitoid eggs (the unparasitized hosts) and the total number of hosts. The number of hosts with one, two, three, etc., parasitoid eggs was estimated from tables on the individual terms of the Poisson distribution (General Electric Co., 1962). Based on this correction, the number of ovipositions per wasp declined significantly with increasing wasp density (Fig. 3b). There was a 58% reduction in average per-capita ovipositions between 1 ($\bar{x} = 9.7$) and 8 ($\bar{x} = 4.1$) wasps per patch. In a similar fashion, the oviposition rate also declined significantly with wasp density (Fig. 3c).

Searching efficiency, s', was independent of wasp density (Fig. 3d), but individual efficiency, f, declined significantly as wasp density increased (Fig. 3e).

Discussion

Anagrus delicatus rejected a substantial fraction of the unparasitized hosts: 66% were rejected by inexperienced wasps and 89% by experienced wasps. These hosts were mostly suitable for the development of wasps. A previous study of ours (Cronin & Strong, 1993) has shown that hosts rejected by one wasp can be successfully parasitized by a subsequent wasp and support normal development. In that study, parasitism increased to over 90% when twenty wasps were released onto a patch.

Experienced wasps rejected proportionately more hosts and had a lower oviposition rate than inexperienced wasps. Practice at finding and handling hosts in high-density host patches had the consequence of lowering the egg loads (due to prior ovipositions) of experienced wasps. It may also have caused these wasps to perceive higher host densities than their inexperienced counterparts. The changes that accompany experience have been shown to increase the selectivity of wasps (van Lenteren, 1976; Rosenheim & Rosen, 1991; Minkenberg *et al.*, 1992), and our results (Table 1) are consistent with this interpretation. However, this would not explain why parasitoids pass up so many suitable, unparasitized hosts.

The ability to discriminate between parasitized and unparasitized hosts is a common attribute of insect parasitoids (van Lenteren, 1976, 1981; van Alphen & Visser, 1990). *A.delicatus*, on the other hand, demonstrated no avoidance of hosts parasitized by conspecific wasps in these laboratory experiments. The rate of acceptance of hosts was low, but both U and P_c hosts had the same probability of being oviposited in, once encountered. Acceptance rates did not change as the patch deteriorated; i.e. as parasitism rate increased. Inexperienced wasps accepted P_s hosts at a significantly lower rate than U or P_c hosts, suggesting the avoidance of self-superparasitism; a common phenomena among parasitoids (van Lenteren, 1981). Experienced wasps did not show this trend, but our sample size for acceptance rates by these wasps was relatively small ($n = 9$). These results are in direct contrast to other studies of mymarid wasps that demonstrated the avoidance of superparasitism (Johnson, 1966; Arzone, 1974; Moratorio, 1977). However, our data are in no way proof that *A.delicatus* cannot discriminate; the adaptive oviposition strategy may simply have been to accept parasitized and unparasitized hosts with equal frequency (see van Alphen & Visser, 1990).

By definition, there was no direct mutual interference among *A.delicatus*: searching efficiency was independent of the density of wasps visiting patches sequentially or simultaneously. However, we did observe that wasps searching simultaneously on patches would often bump into each other and momentarily disrupt searching and oviposition behaviour (i.e. direct interference). This is likely the cause for the decrease in ovipositions and oviposition rate with increasing wasp density (Fig. 3b, c), but a more quantitative approach is necessary to determine, with certainty, the subtle effects that encounters with conspecifics have on parasitoid behaviour (e.g. changes in frequency, duration or type of behaviour). Such an approach was effectively employed by Ridout (1981) with the ichneumonid *Venturia canescens* (Grav.).

While the number of ovipositions and oviposition rate for wasps visiting patches simultaneously declined with wasp density, the searching efficiency did not. This result could only be explained if *A.delicatus* became more efficient at parasitizing unparasitized hosts at higher wasp density. We do not have data to support or refute this possibility. However, we do contend that this decline in the number and rate of ovipositions is genuine and qualifies as direct parasitoid interference.

For both sequential and simultaneous patch visits, individual efficiency was a decreasing function of wasp density. The rate at which hosts were killed per wasp per patch, *f*, declined because at high wasp density more time was invested in parasitizing hosts that were already attacked. This is indirect mutual interference (Visser & Driessen, 1991), and is expected to occur in all wasp populations that superparasitize hosts. Presently, this form of mutual interference has only been described for the eucoilid *Leptopilina heterotoma* (Visser *et al.*, 1990) and the encyrtid *Epidinocarsis lopezi* (van Dijken & van Alphen, 1991); but because of the prevalence of superparasitism among the parasitic Hymenoptera (van Lenteren, 1981), many more cases are likely to be identified in the future.

We infer that direct interference among wasps appears to be the cause of declining per-capita number of hosts parasitized as wasp density increased in our field experiment (Fig. 1; Cronin & Strong, 1993). On a daily basis wasp density in the field reached a maximum of just over seven per host patch. This is certainly in the parasitoid density range where direct interference is possible. During that study the ratio of parasitized to unparasitized hosts (P/U) was quite low among all replicate weeks; parasitism averaged only 7%. Consequently, the likelihood of superparasitism (and indirect mutual interference) was very low. In natural populations, though, parasitism is usually higher, but still the P/U ratio is much less than 1 (Stiling & Strong, 1982b; Strong, 1989). This would suggest that the relative importance of indirect mutual interference through superparasitism is small under most natural conditions.

Mutual interference among *A.delicatus* at the patch level should translate into interference at the population and generation level. Indirect mutual interference results in a lower number of hosts killed per unit time per patch. Time and eggs invested in superparasitism means less of both available for attacks on future patches. Whether *A.delicatus* is egg or time limited, this should reduce lifetime searching efficiency and number of hosts killed. A lower oviposition rate per patch at high wasp density should have the same effect on a time-limited parasitoid. This should contribute to the stability of the *P.marginata*–*A.delicatus* interaction.

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