

Interference and the ideal free distribution: oviposition in a parasitoid wasp

Tom Tregenza, David J. Thompson, and Geoff A. Parker

Population Biology Research Group, Department of Environmental and Evolutionary Biology, University of Liverpool, P.O. Box 147, Liverpool, L69 3BX, UK

The interference ideal free distribution (IFD) model of Sutherland makes a number of predictions that have yet to be tested and that have implications for the validity of subsequent extensions to the theory. We tested these predictions in a study using different densities of the parasitoid wasp, *Venturia canescens*, foraging on patches containing different densities of its host, *Plodia interpunctella*. Our results support a number of the interference IFD model's general predictions. Gain rate decreased because of increased interference at higher density. Although gain rates on the two patches differed slightly, this would be expected allowing for some sampling behavior and perceptual constraints. Early in each experiment when patch assessment is likely to occur, wasp movement was higher and gain rates lower. However, the more specific prediction of Sutherland's model, that proportional patch use should be constant and independent of density, was not upheld. Contemporary IFD models use only one of several equally valid potential relationships between gain rate, interference, and competitor density. The results of this study provide support for the additive model developed by Tregenza et al. (companion article). *Key words*: competition, foraging, ideal free distribution, interference, parasitoid, *Venturia canescens*. [*Behav Ecol* 7:387–394 (1996)]

Tregenza et al. (1996) review the application of contemporary ideal free distribution (IFD) theory to situations in which competition is the result of mutual interference. Continuous input situations in which resource items consumed on a patch are immediately replaced have been well-studied (Milinski and Parker, 1991; Tregenza, 1995 for review). Interference models, on the other hand, have never been subject to direct comparison of predicted and observed distributions. This is likely to be because it is more difficult to make predictions about non-continuous input situations, since there is no expectation that competitor distribution will be directly proportional to resource distribution (Tregenza, 1994). In this paper we use a host-parasitoid system to investigate some of the predictions and assumptions of current interference IFD models.

The predictions we wished to test (Tregenza et al., 1996) are that:

1. Relative patch use should remain constant over a range of forager densities by the multiplicative fitness IFD models of Sutherland and Parker (the "SP model") (Parker and Sutherland 1986; Sutherland, 1983; Sutherland and Parker, 1985, 1992). However, Holmgren (1995), Moody and Houston (1995), and an alternative IFD model (Tregenza et al., 1996) in which fitnesses are additive predict increased relative use of poorer patches at higher density.

2. According to both types of models, as competitor density increases, average gain rate should decrease because of interference.

3. Despite the decreased payoffs resulting from interference, at equilibrium gain rates on all patch types should remain equal.

4. Using the SP model it should be possible to predict the quantitative distribution of competitors across patches (see "Predicting the IFD from the classical interference model").

5. Since the foragers are not omniscient, the distribution is

expected to approach an IFD more closely with time, as they learn the patch profitabilities.

Our fifth prediction does not follow directly from any of the IFD models discussed, but it is clear that the assumption that animals have a perfect knowledge of their environment is unjustified.

Predicting the IFD from the classical interference model

Proponents of the IFD theory have pointed out that the theory can be used to predict the optimal distribution using gain rate data, and this can then be compared to the observed distribution. Calling Q the gain rate of a solitary competitor in patch i , and letting m be the interference constant (Hassell and Varley, 1969; Sutherland, 1983), we predict that when competitor density on $i = n_i$ then:

$$\text{Individual gain rate on patch } i, W_i = Q_i/n_i^m. \quad (1)$$

Since at equilibrium gain rates on all patches are equal we expect that at an IFD:

$$Q_i/n_i^m = Q_j/n_j^m = \text{constant for all patches } i, j, k \text{ etc.} \quad (2)$$

Continuous input situations can be modelled using $m = 1$, and $Q =$ the resource input rate, making distributions easy to predict, and several comparisons of predicted and observed distributions exist (Milinski and Parker, 1991 for review). However, a predicted distribution based on Equation 1 has never been applied to an interference situation since the intrinsic value of each patch and the effect of interference must be determined by observation of gain rates at different competitor densities. This is the first study specifically designed to allow the ideal free distribution to be applied in a non-continuous input situation.

From Equation 1 Sutherland and Parker (1985) show that a graph of \log (individual gain rate) versus \log (competitor density) will have a gradient equal to the interference constant, m , and an intercept on the ordinate equal to Q (Tregenza et al., 1996).

Having determined empirically the values of Q_H , Q_L for the high and low density patches, and m , we can use the standard IFD theory to predict the distribution. Since gain rates on either patch should be equal at equilibrium, we can rearrange

T. Tregenza is now at the Department of Genetics, University of Leeds, Leeds, LS2 9JT, UK.

Received 13 February 1995; revised 31 July 1995; accepted 17 November 1995.

1045-2249/96/\$5.00 © 1996 International Society for Behavioral Ecology

Equation 2, where $N = n_H + n_L$ as below (Tregenza et al., in press):

$$n_H = N / (10^{-[\log(Q_H/Q_L)]/m} + 1), \quad (3a)$$

$$n_L = N / (10^{[\log(Q_H/Q_L)]/m} + 1). \quad (3b)$$

Choice of experimental system

A basic assumption of the original IFD theory is that animals are equal in competitive ability. If this assumption is violated, the predicted distribution is different (Sutherland and Parker, 1992) and can only be described accurately if the relative abilities of all individuals are known. Therefore, a species with minimal individual variation in competitive ability is required to test the above predictions.

The wasp *Venturia canescens* (Gravenhorst) is a solitary endoparasitoid (only one wasp can emerge from any single host) of the larvae of pyralid moths. It is an ideal subject for testing equal competitor models for a number of reasons:

1. It is parthenogenetic. Individuals are likely to be genetically identical and hence are likely to be competitively similar (Hubbard et al., 1987).

2. Homogeneity of phenotypes is also unusually high since very standardized rearing conditions are possible, as detailed in the methods.

3. Although there are host-dependent differences in the size of individuals, previous work has shown that size does not correlate with competitive ability (Green GM, unpublished), increasing our confidence that competitors can be considered to be approximately equal. Although variation in propensity to superparasitize has been shown in *Venturia* (Fletcher et al., 1994), we are assuming that this will exert minimal effect on the optimal distribution.

4. The limiting resource (host larvae) generates a direct fitness measure of the competing foragers through the number of emerging offspring. This contrasts with indirect fitness measures (such as food intake or number of eggs laid) that have been used in other competition experiments.

5. Our stocks derive from a grain store population and have been in culture for more than 20 years. In grain stores, hosts are probably encountered in groups, making it likely that *Venturia* will have evolved the behavioral rules necessary for this type of foraging environment.

6. *Venturia* lays its eggs very rapidly once a host has been encountered, typically in less than a second. Subsequent preening and cocking are similarly rapid so that handling time can be ignored when analyzing results.

Previous work on *Venturia* has shown that searching efficiency for hosts declines with parasitoid density (Hassell, 1971; 1982; Hassell and Huffaker, 1969) but as yet the possibility that there is an IFD of competing females has not been investigated.

METHODS

Two identical sets of experiments were conducted. The first tests the predictions of the theory outlined in the introduction, and the second investigates the mechanism of interference (i.e., how competition leads to decreased rates of parasitism). In the first experiments, observations were made of the overall distribution of wasps. In the second, a focal individual was observed and its behavior analyzed.

Venturia was cultured by adding 10 wasps to boxes of approximately 200 15- to 21-day-old larvae of the Indian meal moth, *Plodia interpunctella* (Hübner), in their growth medium. After 18 days, parasitized *Plodia* pupae were removed and placed singly into glass vials. These were observed daily and newly eclosed wasps fed by placing a drop of honey on the

inside of the vial lid. Only cohorts of either 3- or 4-day-old wasps were used in experiments since these have a nearly maximal egg load but are far from senescent (Harvey, 1995).

We simplified the foraging environment by providing only two resource patches in a closed "habitat." This minimized the level of sampling required by the wasps for patch assessment, making it more likely that an equilibrium distribution would be achieved. The models we wished to investigate are written specifically for the two-patch case. Four numbers of wasps were used in the habitat: 6, 12, 18, and 24, referred to as the wasp densities.

Resource patches consisted of either 60 (high density patch) or 30 (low density patch) late fifth instar *Plodia* larvae, placed in fine wheat bran in a 9 cm petri dish. The petri dish was filled to within 5 mm of the lip with plaster of Paris so that all larvae were in reach of the wasps' ovipositors. The petri dish was covered with a piece of nylon boling cloth held onto the patch using a cellulose acetate collar. This prevented larvae from escaping while allowing the wasps to probe the medium. Patches were made up at least 15 hours in advance of experiments to give the *Plodia* larvae time to produce silk, which *Venturia* uses as a foraging cue.

Experiments were performed in an experimental arena 34 cm by 24 cm and 5 cm deep with a glass top. Two 9-cm diameter holes, 25 cm apart, were cut in the base and covered within the arena by 2-mm mesh polyester gauze. This system enabled us to remove and replace larval patches in about 20 seconds while the wasps were foraging, without allowing their escape and with minimal disturbance. A foam sheet covered the bottom of the arena to the same depth as the petri dish patches so that the surface of the patches was flush with the floor.

Distribution experiments

To begin the experiment, the wasps were introduced into the arena and the patches were inserted through the base. Each experiment lasted 2.5 h, with the number of wasps on each patch counted every 30 s. Every half hour the patches were removed and replaced with a new patch of the same density. Thirty 2.5-hour experiments were conducted in random order for wasp density, with the position of the higher and lower density patches switched every experiment to control for spatial preference.

After removal, each patch was emptied into a jar containing 500 cm³ of standard food medium. The larvae used in these experiments had largely finished feeding so food was mainly supplied as a pupation site. The jars were kept at 25°C with 18 h of light per day for 30 days, after which time all the larvae had pupated and the adult moths and parasitoids had emerged. The jars were placed in the freezer to kill the insects and their contents counted.

Focal wasp experiments

The basic protocol for the focal wasp experiments was identical to the distribution experiments. The only differences were that the experiments lasted one hour only and that instead of recording the distribution of the entire population, a single marked individual was observed. Wasps of similar age were immobilized by cooling to 4°C and marked with a tiny dot of white enamel paint on the thorax. They were given half an hour in the arena before the patches were replaced and observation began.

The focal wasp's behaviors were divided into six distinct types: cocking, probing, cleaning, antennating, walking and resting (Rogers, 1972). Cocking is a distinctive stereotyped behavior that involves the ovipositor separating at its base and

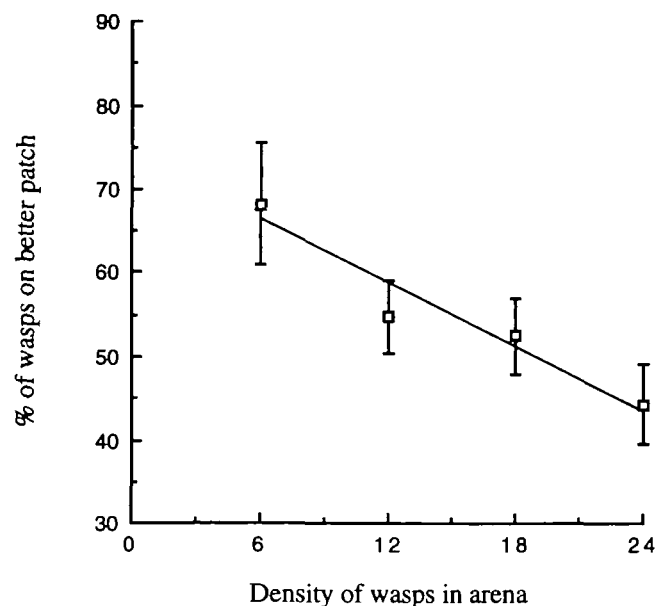


Figure 1
Relationship between percentage of foragers on the better patch and wasp density. The line is the regression of means from each experiment; $r^2 = 0.251$, $F = 9.39$, $N = 30$, $p = .005$.

that indicates that an egg has been laid, since its purpose is to transfer a new egg to the tip of the ovipositor. Probing involves repeated insertion and removal of the ovipositor into the host medium. Cleaning tends to be concentrated on the antennae and ovipositor, which are "brushed" by the legs. Antennating consists of the wasp walking forwards with its antennae stroking the ground ahead of it. Walking did not involve antennal contact with the host medium and included short periods of flight. Resting was defined as an absence of any of the previous activities. These behaviors are not mutually exclusive but were given priority in the order above. This means that a wasp that was probing, antennating, and walking at the same time was classified as probing and so on. Each wasp was observed for a half hour using a Psion Organiser installed with a time and event logger program (Stirling Microsystems, Scotland, FK9 4LA) to record the duration and frequency of each activity and whether it took place on the high density patch, on the low density patch, or "off patch." Seventy half-hour periods of observation were conducted across the four wasp densities.

RESULTS

Does density affect proportional use of patches?

The first prediction we wished to test was that according to the classical, multiplicative fitness IFD interference model, increased parasitoid density would not affect relative use of the better patch. This prediction is not upheld: a regression of parasitoid density against percentage use of the better patch reveals that as the number of wasps in the arena increases, there is an increase in use of the lower host density patch and a decrease in use of the better (high host density) patch (Figure 1). This result, however, is in agreement with the predictions of the additive benefit-cost model presented in the companion paper to this (Tregenza et al., 1996). The additive model predicts that as density increases, there will be proportionally greater use of the poorer patch, in agreement with Figure 1.

Table 1
Regressions of number of parasitoids on each patch over each half hour after patch replacement

Patch	Wasp density	Equation of graph of parasitoid density on patch versus time	N^*	t	r^2	p
High	Overall	$y = 0.0155x + 7.534$	6019	5.91	0.006	.0001**
High	6	$y = 0.0060x + 4.224$	1185	1.52	0.02	.1288
High	12	$y = 0.0122x + 6.262$	1589	4.17	0.011	.0001**
High	18	$y = 0.0133x + 9.009$	1652	3.49	0.007	.0005**
High	24	$y = 0.0319x + 9.676$	1593	6.19	0.024	.0001**
Low	Overall	$y = 0.0060x + 4.510$	6019	2.22	0.001	.0267*
Low	6	$y = 0.0012x + .5839$	1185	0.94	0.001	.3467
Low	12	$y = 0.0026x + 3.468$	1589	0.89	0	.3756
Low	18	$y = 0.0010x + 5.275$	1652	0.30	0	.7655
Low	24	$y = 0.0197x + 7.630$	1593	3.87	0.009	.0001**

* Counts of number of wasps on patches.

Is depletion causing the decrease in use of the better patch?

These results show that increased parasitoid density leads to decreased use of the better patch, in conflict with the predictions of the multiplicative formulation of ideal free distribution theory. However, this pattern could result from depletion of the better patch, which would be more extreme at higher densities. Superparasitism avoidance in *Venturia* is on average slightly less than 50% over the first half hour after eggs are laid (Rogers, 1972) and is minimized in our experiments by replacing patches after short periods. However, it is still possible that depletion could have been an important factor affecting the results. To determine whether this was the case, we examined several aspects of our data from two distinct sources: the pattern of parasitoid movement and the pattern of emergence. All the data suggest that depletion does not explain the observed distribution.

The pattern of parasitoid movement

If depletion were having a significant effect on the parasitoids' perceptions of patch quality we would expect them to migrate from the better patch to the poorer patch during each half-hour period. This is because as the patches deplete they will become more similar in quality so the distribution should approach 1:1 between patches. We would also expect that at higher parasitoid density this effect would be more pronounced. To test for this, regressions of density on each patch against time over the half hour the patch was in the arena were calculated. The results of this analysis are given in Table 1; there is clearly no loss from the better patch since all the regression coefficients are positive.

To determine whether the highest density had a significantly different slope from the other densities a comparison of slopes t test was used. This shows that there is significantly more movement onto the patches (recruitment) at the higher parasitoid densities on both the high and the low density patches (minimum $t = 3.46$, N (counts of number of wasps on patches) = 1589, $p = .004$). This is the opposite of what we would expect to see if the wasps were reacting to depletion of the better patch at higher densities. Thus the better patch tends to recruit parasitoids from off-patch at all densities during the half hour. Recruitment over successive half hours is possible for two reasons. First, the number of wasps on patches increases during the experiment ($r^2 = .009$, $F = 54.3$, N (counts of number of wasps on patches) = 6019, $p < .0001$). Secondly, when patches are removed, some wasps are disturbed and leave the patch. Immediately after changing patch-

Table 2
Emergence from patches

Wasp density	Mean wasps on high patch	Mean wasps on low patch	<i>Venturia</i> emergence					<i>Plodia</i> emergence					Mean total insect emergence	Percentage wasps in emergence
			60 larvae patch		30 larvae patch		N*	60 larvae patch		30 larvae patch		N*		
			Mean	SD	Mean	SD		Mean	SD	Mean	SD			
6	4.1	1.0	16.4	9.4	3.2	3.4	19	28.5	7.8	20.1	7.2	19	68.2	34.8
12	6.6	3.6	32.7	7.5	13.8	6.4	28	13.2	5.8	10.0	5.0	24	67.4	69.1
18	9.6	5.5	28.7	11.6	14.7	5.9	34	14.5	6.2	11.2	6.0	30	66.2	65.6
24	10.5	8.1	28.6	12.1	12.6	6.4	30	16.3	8.3	12.6	6.2	27	69.4	58.8

* Pairs of patches exposed to each wasp density and subsequently analyzed for parasitoid and host emergence.

es, there was a 39% reduction in the mean density on the patches, though after two minutes this had dropped to 9% as wasps moved back onto the patches. If patch use is analyzed excluding either the first 5 or 15 minutes of each half hour there are no significant regressions at any density. This indicates the importance of movement when the patches are new but confirms that emigration is not being masked by initial high recruitment resulting from disturbance.

Analyzing the entire half hour, as density increases there is increased immigration onto the high density patch. The poorer patch does not show a significant increase or decrease in parasitoid numbers at the lower three densities and at the highest parasitoid density there is also recruitment onto the poorer patch. These results argue strongly against the hypothesis that depletion is the cause of decreased relative use of the better patch.

The pattern of emergence

If depletion were increasing with parasitoid density we would also expect to see a reduction in the number of surviving hosts at higher density. However, a regression of *Plodia* emergence against parasitoid density is non-significant ($r^2 = 0.04$, $F = 3.34$, $N = 223$, $p > .07$). Apart from supporting the idea that depletion is not a significant factor, this result is somewhat paradoxical. No refuges are available to the *Plodia* larvae, and observed success rates of physiological defence mechanisms (encapsulation of parasitoid eggs) are much lower than could explain the high moth emergence (Harvey et al., 1993). The unparasitized larvae must have been "missed" by the parasitoids. A summary of the emergence data is in Table 2.

Table 3
Gain rates of parasitoids on high or low quality patches at different densities (in number of *Venturia* emerging per *Venturia* minute spent on patch)

Parasitoid density	Mean gain rate on high density patch (H)	Mean gain rate on low density patch (L)	N*	<i>t</i>	<i>p</i>
6	0.175	0.100	19	4.28	.0004
12	0.186	0.152	21	1.20	.24
18	0.120	0.099	27	1.54	.14
24	0.108	0.068	23	3.36	.0028

* Pairs of patches exposed to each wasp density and subsequently analyzed for parasitoid emergence. Differs from Table 2 since it excludes the first half hour of each experiment.

It is possible that repeated injury from ovipositor piercing could increase larval mortality and prevent an increase in *Venturia* emergence with wasp density. However, this does not appear to have been the case, since overall emergence of both wasps and moths does not decline with parasitoid density ($r^2 = 0.003$, $F = 0.59$, $N = 223$, $p > .44$). There is a significant increase in *Venturia* emergence with density ($r^2 = 0.043$, $F = 9.88$, $N = 223$, $p = .002$), largely because emergence from wasps foraging at the lowest density is considerably lower than at the higher densities (see Table 2).

Analysis of gain rate

Gain rate was measured as the number of successful parasitizations (*Venturia* emergences) for every *Venturia* minute spent on the patch. The latter was estimated by summing all the 30-second counts of number of *Venturia* on patch for each half-hour trial and dividing the total by 2. The number of parasitoids that had emerged from that half-hour period was then divided by this total of *Venturia* minutes to give the expected progeny per minute of "on-patch" foraging.

Equal competitor IFD theories predict that individuals will distribute themselves between resources such that the individual gain rates on all patches will be equal. We cannot compare gain rates directly, because the gains on either patch are not independent of one another. Therefore, we have compared the gains on the better patch with half of the combined gains on both patches in each half hour period, using a paired sample *t* test. In all cases, contrary to the IFD prediction, gain rates were higher on the better patch, although this difference is only significant at the two extreme densities (Table 3). A two-way ANOVA reveals that density has a significant effect on gain rate ($F = 13.44$, $p < .0001$), patch also has an effect ($F = 30.62$, $p < .0001$), and, as would be expected from Table 3 there is a significant interaction between density and patch ($F = 4.43$, $p < .005$).

Causes of interference

The focal parasitoid experiments allowed us to investigate whether density increased interference, reducing the time parasitoids were able to spend searching on the patches. Increased density caused increased interactions between individuals, since parasitoids that came into contact on the patch tended to avoid one another rather than continuing to forage unaffected. It was apparent from both sets of experiments that a small percentage of wasps behaved in an apparently non-adaptive fashion, making no attempt to forage but remaining motionless throughout the course of the experiment. It is possible that these represent state dependent decisions, such as

Table 4
Relative time spent on different activities at different overall densities

Density	% of time spent on patch	Half hours observed	Mean percentage time spent on each activity on patch, scaled by percentage time spent on patch in first experiment					Mean number of cocks (eggs laid)
			Cleaning	Resting	Walking	Anten-nating	Probing	
6	82.6	19	9.6	1.0	7.1	17.4	47.5	12.5
12	84.8	18	9.6	1.4	12.3	17.2	44.0	11.5
18	81.7	13	10.6	1.0	10.4	15.9	43.9	10.0
24	78.6	20	7.8	0.4	14.5	18.2	37.6	9.1
Regression of duration of activity against density of wasps in arena.								
r^2			0.009	0.02	0.02	0.001	0.071	0.048
N			70	70	70	70	70	70
F			1.6	2.4	2.4	0.08	6.24	4.51
p			.21	.13	.13	.78	.015*	.037*

The percentage of time spent on the patches is calculated from the overall distribution experiments and used to scale the data from observation of a single focal individual.

not foraging for hosts because energy reserves are too low. These individuals do not pose any problem in multiple-replicate experiments where all individuals are considered, since they can be assumed to be evenly distributed between treatments. However, in the focal wasps experiments, a single individual could have a large effect on the results by never visiting a patch. To control for this, we used the mean proportion of time spent on patch by the wasps in the overall distribution experiments to scale the proportion of time each wasp engaged in each of the "on-patch" activities. Therefore, the focal wasp experiments provided data on potential difference between the wasps' behavior on the patch but not on the relative time spent on and off patches. These data are summarized in Table 4.

It can be seen that the two activities most directly related to oviposition, probing and actual laying of eggs, declined in their proportional time allocation/frequency, as density increased. In both cases it can be seen that this decline is greater than would be expected solely as a result of the greater time spent on patch at lower densities.

Evidence for assessment and learning

When the wasps are first introduced into the arena, they are ignorant of the distribution of resources within it. Determining where gain rate is highest requires assessment of the environment. *Venturia* are able to detect *Plodia* remotely via detection of a chemical released by the larvae (Corbet, 1973). However, to determine the profitability of the patches the wasps must try them, since gain rate will be affected by competition. Therefore, we would predict that mean gain rate across all individuals should increase with time as the wasps approach an equilibrium distribution.

To determine whether this had occurred we performed a t test comparing the mean gain rate for the first half hours with the mean gain rate for the remaining half hours. This confirmed that gain rates in the later periods were higher ($t = 2.64$, $df = 67$, $p = .01$). Since gain rates are measured as wasp emergences per *Venturia* minute on patch, this analysis controls for potentially higher numbers of wasps not on either patch at the beginning of the experiment.

Since assessment requires traveling from one patch to another, we would also predict that there will be a higher level of movement early on in the experiment. To test for this we determined the coefficient of variation, V , of the number of wasps on each patch. If V increases it indicates that there is

more movement, since there is greater fluctuation in the number of wasps on the patch. The median V for the first half hour was compared with the median V for the remaining half hours using a Mann Whitney U test. This analysis shows that there is a significant difference in the level of movement on both the high and the low quality patch (median V for high density patch = 36% during the first half hour, 13.5% in remaining half hours, $U_{26,98} = 4.4$, $p < .0001$; median V for low density patch = 43.5% during the first half hour, 22.3% in remaining half hours, $U_{25,94} = 3.62$, $p < .0001$).

DISCUSSION

Several studies have investigated mutual interference using *Venturia* (Hassell, 1971, 1982; Hubbard and Cook, 1978; Ridout, 1981). However, all of these used resource patches for long periods (6–24 hours or more). In contrast, our experiments used patches for only 30 minutes each, thereby reducing depletion to a level at which it can be largely ignored. Our study is the first experimental study to distinguish between competition caused by resource depletion and interference.

Relative distribution changes with density

The prediction of Sutherland and Parker's multiplicative IFD interference model (Parker and Sutherland, 1986; Sutherland, 1983; Sutherland and Parker, 1985, 1992), that population size will not affect distribution, is rejected. As parasitoid density increases there is a decrease in the proportion of individuals foraging on the better patch and an increase in the proportion foraging on the poorer patch. This pattern does not appear to be the result of increased depletion of the better patch at higher density. There is increased movement of parasitoids onto the better patch during their time in the arena at higher densities and patches do not end up with fewer unparasitized larvae on them.

The reasons for this departure from the IFD are not obvious. It is possible that the central multiplicative assumption of the Sutherland and Parker model is inappropriate for the *Venturia* case and potentially for other interference systems. The prediction that relative numbers of individuals on patches will stay constant at different densities is supported by continuous input studies, but these are very different to non-depleting patchily distributed resources. Although there have been more than 15 studies that have attempted to apply ideal free

theory to interference distributions (see Tregenza, 1995 for review) none has provided strong support for the theory. Only this study and one by Messier et al. (1990) have attempted to test the affect of density on proportional distribution and both have found against the current theory.

Tregenza et al. (1996), Holmgren (1995), and Moody and Houston (1995) show that there are alternative approaches to modeling IFD's of equal credibility to the Sutherland and Parker models, which do not predict numerically constant relative distributions. The results from our experiment support these types of model, since they predict a reduction in proportional use of the better patch as density increases, as found in this system.

Analysis of gain rate

The number of parasitoids emerging from each patch is used to generate a measure of gain rate. Although there is larval mortality, superparasitism and encapsulation of parasitoid eggs by hosts, these are all features of *Venturia*'s evolutionary background. We would expect oviposition decisions in *Venturia* to have evolved to account for these factors, making the emergence data a direct and accurate measure of fitness, and hence an ideal success maximization criterion. This is a major strength of this study; in other investigations into animal distributions the value of the resource has tended to be difficult to estimate. If animals are competing for food, the value of each item of food might depend on individual nutritional requirements and state. Similarly, counting eggs laid is a less direct measure of fitness, since various processes may prevent eggs from turning into adults. This means that assessing how closely the animals approach an ideal distribution is difficult. Since we are using number of progeny we can be much more certain that each successful parasitization has the same value to each individual. During observations of a focal individual (Table 4) an average of 0.39 eggs were laid per wasp minute on patch, whereas analysis of emergence from patches reveals that mean gain rates do not exceed 0.19 emergences per minute (Table 3). This discrepancy may partly be because of superparasitism, although it seems unlikely that this is the only explanation. The high proportion of hosts surviving (Table 2) suggests that a large number of larvae are not parasitized at all, indicating that superparasitism is unlikely to be sufficiently prevalent to explain the difference between behavioral observations and emerging parasitoids. Ridout (1981) found that the number of cocks she observed did not correspond to the number of eggs subsequently found in hosts. It is possible that Ridout's suggestion that *Plodia* may be able to prevent eggs from being placed into them through some behavioral defense is also relevant to our results.

It can be seen from Table 3 that the general IFD prediction that gain rate will decrease with competitor density is supported. However, the more specific prediction of the multiplicative IFD model, that gain rates will be equal across patches, is not convincingly upheld. In all cases, the low density patch tends to be overused and particularly so at high and low densities. These deviations may be explained by a number of possibilities.

1. There are costs associated with the higher wasp density patch other than reduction in gain rate, an assumption of an additive fitness model (Tregenza et al., 1996). This would lead to apparent (but not actual) "overuse" of the poorer patch.

2. Wasps switch patches at a certain rate. Since there are greater numbers of wasps on the better patch there is a higher departure rate leading to overuse of the poor patch (Regelmann, 1984; Houston et al., 1995).

3. Wasps have relatively poor assessment abilities and underestimate patch differences (Abrahams, 1986). This leads to

overuse of the poorer patch since those individuals that cannot distinguish between patches are randomly distributed, so more of them are on the poor patch than its profitability warrants.

4. They spend a proportion of their time assessing their environment, during which their distribution is random with respect to resources. This also leads to overuse of the poorer patch but is distinct from Regelmann (1984) since animals do not switch from a high density patch to a low density one or vice versa. Rather, animals move from a patch where their gain rate is a maximum to a random patch. This will have more impact at low densities since the greater difference in patch profitabilities means that individuals sampling the poorer patch will do relatively worse at lower densities. Sampling is more expensive when patch qualities vary widely, but is more important, since choosing the right patch leads to greater increases in rewards.

5. They have simple patch leaving rules. It is possible that at high density neither patch provides a sufficiently high gain rate to prevent the wasps from abandoning it to search for better patches. If some wasps were doing this it would lead to overuse of the poorer patch.

6. There are significant inter patch travel costs. If there are high travel costs, and the distribution was initially random, individuals would be reluctant to leave the poorer patch, since they would have to pay the travel costs to the better patch.

7. Driessen and Visser (1993) point out that higher density patches will be more profitable if superparasitism is significant, since individuals foraging there will be less likely to encounter their own eggs. This might partly explain the apparent overuse of better patches we observed, but the evidence against high levels of superparasitism in our system makes it unlikely that this is sufficient explanation alone.

Applying the classical interference model

There is some doubt as to whether it is appropriate to use regression analysis to determine the slope of Figure 2, since gain rate affects the likelihood of patch departure, and hence density. However, if we assume that gain rate is wholly dependent on density, and that density is not affected by gain rate at equilibrium, which seems plausible, then we can use our data to plot the graph (see Figure 2).

As predicted by the theory, the gradient of both graphs is very similar (comparison of slopes t test, $t = 0.225$, $df = 167$, $p > .5$) supporting the assumption that m will be constant across patches. It can also be seen that the intercept on the ordinate, corresponding to Q , the maximum potential gain rate on either patch, is higher for the better patch than for the poorer patch as we would expect. To allow for the fact that in our experiment, as density increases, there is an increase in wasps not using either patch, we take N to equal the total number of wasps on patches as determined experimentally at each density, the predicted lines are not straight as would otherwise be the case. Using the Q_1 , Q_2 , and m derived from Figure 2, the distribution predicted from Equations 3a and 3b is shown in Figure 3.

From Figure 3, at the intermediate wasp densities, there is a fair fit to Sutherland's interference IFD model. However, at the lowest and highest density there is no overlap between predicted and observed values. This lack of fit is not simply the result of the difference in gain rates between patches at extreme densities, since at the lowest density the interference model predicts even greater use of the poorer patch, although we found that higher gain rates were achieved on the better patch (see Table 3).

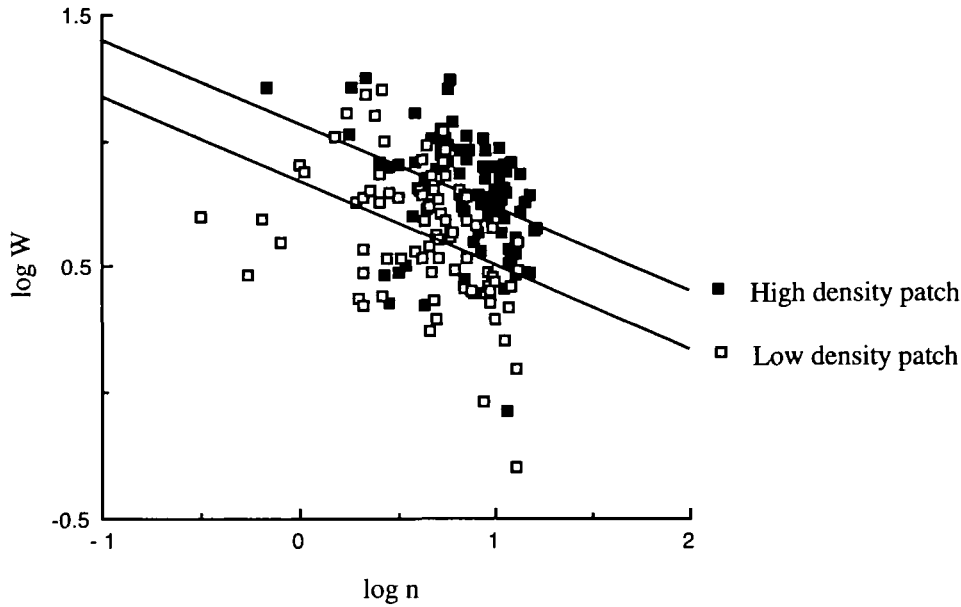


Figure 2

Regression lines of log (gain rate) against log (density) on both patches; high density patch (Patch H) ($\log W_H = 0.863 - 0.332 \log n_H$, $r^2 = 0.13$, $F = 13.13$, $N = 90$, $p = .0001$); low density patch (Patch L) ($\log W_L = 0.633 - 0.335 \log n_L$, $r^2 = 0.17$, $F = 16.55$, $N = 90$, $p = .0001$).

The causes of interference

It is clear that increased density leads to decreased gain rates. However, the reasons for this decline are not immediately apparent. Patch depletion is unlikely to be the explanation, since host mortality did not increase with density and wasps did not migrate from the high host density patch to the low host density patch during each patch's time in the arena. The only change in wasp behavior with density we detected was a

small but significant decrease in the length of time spent on the primary foraging activity, probing, with a corresponding decrease in the number of eggs laid. This finding is strong evidence that interference is a behavioral phenomenon.

The mechanisms of interference are not studied in our experiment, although wasps were observed to avoid each other on the patches and to retreat after contacts. Hughes et al. (1994) observed agonistic encounters between foraging *Venturia* females and concluded that interference reduces time spent on patch and disrupts searching behavior, lowering efficiency. It also seems possible that wasps perceive the density of conspecifics on patches, probably via olfactory means and use this to modify their estimate of patch profitabilities, affecting patch use.

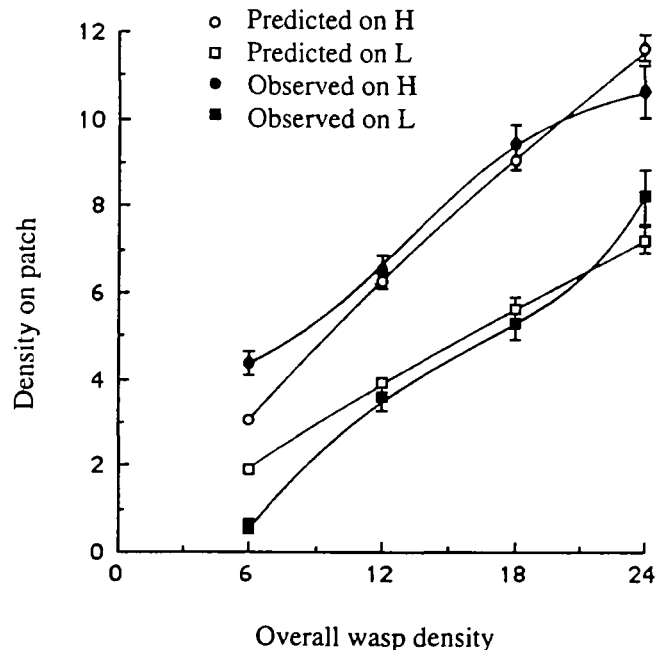


Figure 3

The ideal free distribution of wasps as predicted by Sutherland and Parker's interference model compared to the observed distribution. The predictions of the IFD are based on estimates from our data of the maximum profitabilities, Q_H, Q_L , of the patches and the interference constant, m . Bars are standard errors. The standard errors on the predicted values are derived from the error associated with the estimate of m .

Evidence for patch assessment and learning

The final prediction we wished to test was that the wasps' gain rates would increase with time in the arena as they learned the resource distribution and their distribution equilibrated. This prediction is supported by the finding that gain rates during the first half hour of each experiment are lower than those for the remaining time. The subsidiary prediction that to learn the resource distribution, the wasps would initially have to move between patches, was also supported. Using the coefficient of variation of the number of wasps on the patch, and again comparing the first period of the experiment with the remainder, we found that there was more variation in wasp numbers on each patch earlier in the experiment. This result is consistent with the theory that animals initially move around to learn the resource distribution.

These results show that the clearly unrealistic assumption that animals are omniscient, made in many distribution models, need not prevent them from making accurate predictions since animals are likely to have evolved patch sampling behaviors that allow them to approach competitive maxima for individual gain rates.

We would like to thank Jeff Harvey for sharing the work of insect culturing and for practical advice and Ian Harvey for help with data analysis and more practical advice. We would also like to thank Marcel Visser for numerous comments, which have greatly improved the manuscript. T.T. was funded by National Environment Research

Council Studentship GT4/91/TLS/30. G.A.P. was funded by a BBSRC Senior Research Fellowship.

REFERENCES

- Abrahams MV, 1986. Patch choice under perceptual constraints: a cause for departures from the IFD. *Behav Ecol Sociobiol* 19:409–415.
- Corbet SA, 1973. Concentration effects and the response of *Nemeritis canescens* to a secretion of its host. *J Insect Physiol* 19:2119–2128.
- Driessen G, Visser ME, 1993. The influence of adaptive foraging decisions on spatial heterogeneity of parasitism and parasitoid population efficiency. *Oikos* 67:209–217.
- Fletcher JP, Hughes JP, Harvey IF, 1994. Life expectancy and egg load affect oviposition decisions of a solitary parasitoid. *Proc R Soc Lond B* 258:163–167.
- Harvey JA, 1995. Nutritional ecology of a host-parasitoid interaction (PhD thesis). Liverpool: University of Liverpool.
- Harvey JA, Harvey IF, Thompson DJ, 1993. The effect of superparasitism on the development of the solitary parasitoid wasp, *Venturia canescens* (Hymenoptera: Ichneumonidae). *Ecol Ent* 18:203–208.
- Hassell MP, 1971. Parasite behaviour as a factor contributing to the stability of insect host-parasite interactions. In: *Proceedings of the Advanced Study Institute. Dynamics of Populations*. Oosterbeek, 1970. 366–379.
- Hassell MP, 1982. Patterns of parasitism by insect parasitoids in patchy environments. *Ecol Ent* 7:365–377.
- Hassell MP, Huffaker CB, 1969. Regulatory processes and population cyclicity in laboratory populations of *Anagasta künniella* (Zeller) (Lepidoptera: Phycitidae). III. The development of population models. *Res Pop Ecol Kyoto Uni* 11:186–210.
- Hassell MP, Varley GC, 1969. New inductive model for insect parasites and its bearing on biological control. *Nature* 223:1133–1136.
- Holmgren N, 1995. The ideal free distribution of unequal individuals—predictions from a behaviour based functional response. *J Anim Ecol* 64:81–102.
- Houston AI, McNamara JM, Milinski M, 1995. The distribution of animals between resources: a compromise between equal numbers and equal intake rates. *Anim Behav* 49:247–250.
- Hubbard SF, Cook RM, 1978. Optimal foraging by parasitoid wasps. *J Anim Ecol* 47:593–604.
- Hubbard SF, Marris G, Reynolds A, Rowe GW, 1987. Adaptive patterns in the avoidance of superparasitism by solitary parasitic wasps. *J Anim Ecol* 56:387–401.
- Hughes JP, Harvey IF, Hubbard SF, 1994. Host-searching behaviour of *Venturia canescens* (Grav.) (Hymenoptera: Ichneumonidae): Interference—the effect of mature egg load and prior behaviour. *J Insect Behav* 7:433–454.
- Messier F, Virgl JA, Marinelli L, 1990. Density-dependent habitat selection in muskrats: a test of the ideal free distribution model. *Oecologia* 84:380–385.
- Milinski M, Parker GA, 1991. Competition for resources. In: *Behavioural ecology an evolutionary approach*, 3rd ed (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific Publications; 137–168.
- Parker GA, 1978. Searching for mates. In: *Behavioural ecology: An Evolutionary approach*, 1st ed (Krebs JR, Davies NB, eds). Oxford: Blackwell Scientific Publications; 214–244.
- Parker GA, Sutherland WJ, 1986. Ideal free distributions when individuals differ in competitive ability: Phenotype limited ideal free models. *Anim Behav* 34: 1222–1242.
- Regelmann K, 1984. Competitive resource sharing—a simulation model. *Anim Behav* 32:227–232.
- Ridout LM, 1981. Mutual interference: Behavioural consequences of encounters between adults of the parasitoid wasp *Venturia canescens* (Hymenoptera; Ichneumonidae). *Anim Behav* 29:897–903.
- Rogers D, 1972. The ichneumon wasp *Venturia canescens* oviposition and avoidance of superparasitism by solitary insect parasitoids. *Entom Exp App* 15:190–194.
- Sutherland WJ, 1983. Aggregation and the “ideal free” distribution. *J Anim Ecol* 52: 821–828.
- Sutherland WJ, Parker GA, 1985. Distribution of unequal competitors. In: *Behavioural Ecology—ecological consequences of adaptive behaviour*. (Sibly RM, Smith RH, eds). Oxford: Blackwell Scientific Publications; 255–274.
- Sutherland WJ, Parker GA, 1992. The relationship between continuous input and interference models of ideal free distributions with unequal competitors. *Anim Behav* 44: 345–355.
- Tregenza T, 1994. Common misconceptions in applying the ideal free distribution. *Anim Behav* 47:485–487.
- Tregenza T, 1995. Building on the ideal free distribution. *Adv Ecol Res* 26:253–307.
- Tregenza T, Parker GA, Thompson DJ, 1996. Interference and the ideal free distribution: models and tests. *Behav Ecol* 7:379–386.