

DENSITY-INDEPENDENT PARASITISM AMONG HOST  
PATCHES BY *ANAGRUS DELICATUS*  
(HYMENOPTERA: MYMARIDAE):  
EXPERIMENTAL MANIPULATION OF HOSTS

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SUMMARY

(1) Parasitism by *Anagrus delicatus* Dozier of the eggs of its host, *Prokelisia marginata* (Van Duzee) was examined experimentally in a north Florida salt marsh.

(2) By inducing planthopper oviposition into equal-sized sections of two leaves per potted plant, we controlled for variation in host-insect age, host-plant quality, number of hosts per patch and physical area (size) of patches. Potted plants were placed in the field and exposed to naturally occurring parasitoids for 72 h. The experiment was repeated twenty times over a 10-month period to account for seasonal or other environmental variation.

(3) Spatially, parasitism by *A. delicatus* was independent of host density for all experimental trials. Through time, a slight inverse relationship between parasitism rate and density was apparent; higher overall host densities tended to have lower parasitism rates.

(4) These experimental results correspond to previous, observational findings for this system (Stiling & Strong 1982; Strong 1989).

(5) Parasitoids disperse from host clutches after laying only a small fraction of their eggs, and this behaviour appears to play an important role in producing the observed density-independent patterns of parasitism.

INTRODUCTION

Theory based on optimal foraging or host–parasitoid interactions predicts that spatial density dependence (a positive correlation between parasitism and host density in any given patch) should be a common feature in both natural and agricultural systems. This view holds that spatially density-dependent host mortality imposed by aggregating parasitoids is the key to stable host–parasitoid coexistence for insects with discrete generations (Beddington, Free & Lawton 1978; Hassell 1987). On the other hand, in the continuous time framework of overlapping generations, spatially density-dependent mortality of hosts often destabilizes the relationship (Murdoch & Stuart-Oaten 1989). Currently available empirical information does not resolve the issue, showing, at best, inconsistency in spatial relationships between parasitism and host density. Approximately 50% of studies have found parasitism to be independent of host density. Inverse density dependence and direct density dependence were found in equal proportions in the remainder of the studies (Stiling 1987; Walde & Murdoch 1988).

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Few studies to date of these spatial relationships are experimental, however, and both temporal and environmental factors may obscure the true response of parasitism to host density (Hassell 1985). Here, we use field experiments that manipulate insect host numbers. Experimental manipulation of host density has the advantage over passive observation that host age, numbers of hosts per patch, patch size, plant quality and exposure time are controlled. Brief bouts of parasitic activity are studied. These bouts are well within the generation time of the parasitoids and rule out delayed density dependence resulting from numerical response between generations. Because previous data from the *Prokelisia-Anagrus* system suggest great temporal variability in parasitism rate (Strong 1989), we replicated the experiment twenty times over a 10-month period.

### NATURAL HISTORY OF HOST AND PARASITOID

The host insects are *Prokelisia marginata* (Van Duzee) Wilson and its newly discovered sibling species *P. dolus* Wilson, found in sympatry in salt marshes along the Atlantic and Gulf coasts of the United States (Denno & Grissell 1979; McCoy & Rey 1981; Denno *et al.* 1987; A. E. Throckmorton *et al.*, unpublished). Both planthoppers are monophagous and feed and oviposit on the salt-marsh cord grass, *Spartina alterniflora* Loisel. The two host species differ in distribution in the salt-marsh; *P. dolus* favours backmarshes and *P. marginata* the seaside (Denno *et al.* 1987; J. T. Cronin, unpublished). In the egg stage, the two host species are indistinguishable with respect to development, morphology and distribution on the host-plant (J. T. Cronin, unpublished). In north Florida, all planthopper life stages of both species can be found all year round (A. E. Throckmorton *et al.*, unpublished). Host adult females lay eggs in concentrated patches, inserting them into the adaxial side of cord grass leaves. In nature, host egg patches vary in size from a few to several hundred eggs and in extent from a fraction of a square centimetre to several square centimetres of cord-grass leaf (J. T. Cronin & D. R. Strong, unpublished).

A fairyfly, *Anagrus delicatus*, attacks and develops fully within the egg stages of both *Prokelisia* species and shows no tendency to distinguish between the two (J. T. Cronin & D. R. Strong, unpublished). Parasitism in the field is quite variable, both spatially and temporally, and ranges from 0 to 100% (Stiling & Strong 1982; Strong 1989; Cronin & Strong 1990).

### METHODS

#### *Experimental design and procedure*

We examined the relationship between host density and parasitism rate experimentally by exposing hosts of uniform age to natural populations of searching parasitoids. Adult planthoppers were collected with a sweep net from cord grass in the salt-marshes at Oyster Bay, Wakulla Co., Florida, U.S.A. Planthoppers were transported on ice to the lab and sorted by sex. Ten females were confined individually in clip cages on leaves of potted cord grass. Clip cages were made of 18-mm diameter acetate tubing 40-mm long and notched at each end. The tubes were threaded over individual leaves, positioned at the leaf base and capped at each end such that the adaxial leaf surface was available to the planthoppers. Planthoppers were unrestricted in their feeding and oviposition within the confines of the cage for a 48-h period. This procedure produced an even-aged cohort of eggs (hereafter referred to as a 'host clutch') with an average density ( $\pm 1$  S.E.) of  $49.8 \pm 2.6$  eggs (range 1–186,  $n = 362$ ) per experimental leaf. These experimental densities fall well within the

TABLE 1. The relationship between host density and parasitism among plants and leaves for twenty experiments replicated over a 10-month period from July 1988 to April 1989. Parasitism data were arcsine transformed, and densities were log transformed prior to analysis. Statistical significance set at  $P=0.05$  and judged by weighted least-squares regression (Reeve & Murdoch 1985). (+) refers to significant density-dependent relationships, and (-) refers to inverse density dependence. '% significant' is the percentage of studies showing some form of density dependence

	Plants		Leaves	
	-	+	-	+
Significant	1	1	0	0
Not significant	18		20	
% significant	10%		0%	

natural range found on plants in the salt-marsh (Stiling & Strong 1982; Strong 1989). Host clutches were set up on two leaves per potted cord-grass culm for a total of ten plants per experiment (a total of twenty clutches).

Experimental plants were then placed at relatively higher elevation away from the shore at Oyster Bay, where tidal effects and the action of waves are minimal. The pots were sunk flush in the marsh soil in a line transect within a pure stand of cord grass, each separated from the next by a distance of 2 m. After 72 h of exposure to parasitoids, the plants were returned to the lab and allowed to incubate for an additional 3 days before each clutch was dissected. Dissected resolved unambiguously all parasitized eggs. Numbers of hosts and parasitized eggs were recorded.

This experimental procedure was repeated on twenty separate occasions starting in mid-July 1988 and ending in mid-April 1989 (12, 19, 26 July; 23 August; 7, 21 October; 4, 11, 18 November; 14 December; 11, 24 January; 13, 20 February; 3, 6, 12 March; 1, 4, 10 April). Intervals between replicate experiments were set by the availability of plant-hoppers. As a control for site differences, the same line transect was used throughout.

#### *Statistical analysis*

Parasitism data were converted into a normally distributed variable by the angular transformation (Sokal & Rohlf 1981). Because host density ranged over several orders of magnitude, all densities were log transformed prior to statistical analysis. Weighted least-squares regressions were used for each experimental replicate to determine whether a relationship existed between host density and parasitism (Reeve & Murdoch 1985). Parasitism data were weighted by the inverse of the expected variance,  $1/4n$ , from an angular distribution (where  $n$  = the host density in that sample) (Sokal & Rohlf 1981).

## RESULTS

Parasitism rate within the experimentally placed clutches on individual leaves ranged from 0 to over 50% during the course of the twenty experiments. Among replicate experiments, the mean rate of parasitism averaged  $7.0 \pm 1.6\%$  (range, 1.0–26.0%,  $n=20$ ). At the scale of 'among individual leaves,' parasitism was not found to be related to host density in any replicates (Table 1, Fig. 1). Among plants, however, two out of twenty replicates showed a significant relationship between host density and parasitism. In

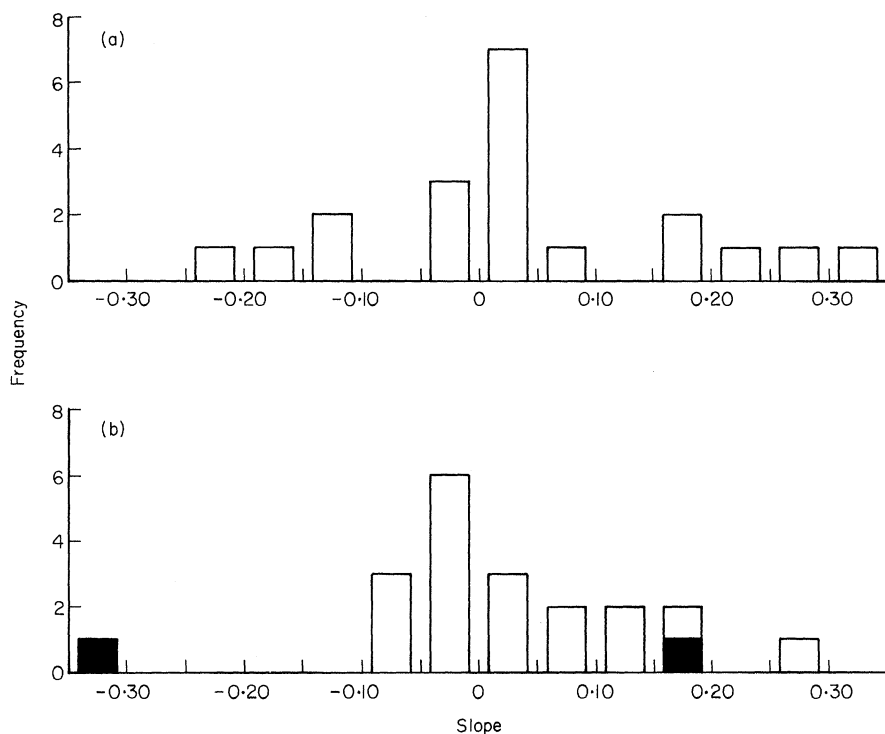


FIG. 1. Frequency distribution of slopes from twenty experimental trials for (a) among leaves and (b) among plants. Significantly non-zero slopes are represented by filled bars ( $P < 0.05$ ).

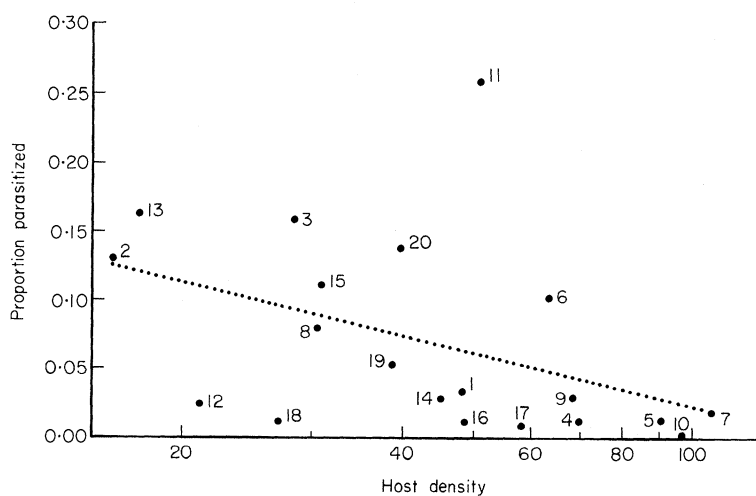


FIG. 2. The relationship between total host density per replicate experiment and percentage parasitism. Numbers represent data points for that replicate experiment (July 1988–April 1989). Line fit by least-squares regression (parasitism =  $38.70 - 6.78$  [host density]).

TABLE 2. Spatial scales and density relationships for parasitism rates from Stiling & Strong (1982) and Strong (1989) combined. Analysis of data is described in the respective papers. Statistical significance set at  $P=0.05$ . (+) refers to significant density-dependent relationships, and (-) refers to inverse density dependence. ' % significant' is the percentage of studies showing either density dependence or inverse density dependence

	Islets		Sides		Plants		Leaves		Subleaves	
	-	+	-	+	-	+	-	+	-	+
Significant	1	0	1	1	1	4	19	8	17	8
Not significant		28		27		97		87		185
% significant		3%		7%		13%		24%		12%

replicate number 8 (11 November) parasitism was strongly inversely density-dependent, and in replicate 13 (13 February) it showed a direct density-dependent response. After adjusting for experiment-wise error (Sokal & Rohlf 1981), we infer that these two significances are random occurrences and have no particular biological meaning. Among the dates of replicate experiments, the relationship between mean host densities and parasitism was highly variable (Fig. 2). We ascribe no biological meaning to the trend of inverse density dependence among the points in Fig. 2 ( $r^2=0.229$ ,  $P=0.0033$ ,  $n=20$ ).

## DISCUSSION

Parasitism in these field experiments did not reach levels sometimes found in *Prokelisia* spp., which occasionally suffer 80% overall mortality from *A. delicatus* (Stiling & Strong 1982; Strong 1989). Our experiments exposed hosts to searching wasps for 72 h, a period much shorter than natural hosts experience, and this difference probably accounts for the low experimental rates of parasitism. As with many egg parasitoids (Strand 1986), host eggs are vulnerable to parasitism by *A. delicatus* for almost the full length of their egg stage, which is approximately 2 weeks in warm months and 3 weeks in the cooler months of December–February (Cronin & Strong 1990). Eggs in nature, then, are exposed to parasitoids as much as four times longer than in our experiments.

The experimental host-egg densities used in this study averaged higher than field densities, although in nature egg numbers per patch can reach the hundreds (Stiling & Strong 1982; Strong 1989; J. T. Cronin & D. R. Strong, unpublished). Laboratory data indicate that the range of density used here did not preclude a density response by *A. delicatus*. On laboratory clutches where wasps were free to disperse, number of eggs laid per *A. delicatus* female increased linearly over a range of 0 to over 300 host eggs (Cronin & Strong 1990). Parasitism in response to host density, then, should not reach an asymptote over the range of our experimental host densities (see Waage 1979).

We examined closely the relationship between parasitism and host density at the two spatial scales that direct observation (Cronin & Strong 1990) indicated were relevant to the searching behaviour of *A. delicatus*. Variation in host-egg age, patch size and plant quality were held constant throughout the study. The experimental design also precluded any delayed density dependence. Elimination of these confounding effects, however, did not expose any underlying density-dependent process. At the scale of leaves and plants, this study revealed that parasitism is independent of host density, just as Stiling & Strong (1982) and Strong (1989) found in their collections (Table 2). In addition, we also find

agreement with the previous findings that parasitism is temporally inversely density-dependent. Close correspondence between field collections and experiments tends to support the validity of inferences about density relationships from observational data.

Our results do not preclude an aggregative response by *A. delicatus*. It is possible that total search time by *A. delicatus* is aggregated in areas of higher host density but that the rate of parasitism does not reflect such behaviour. Waage (1983), for example, has suggested that aggregation by *Diadegma* sp. (Hymenoptera: Ichneumonidae) is countered by an increase in handling time at high host densities. On the other hand, Smith & Maelzer (1986) have argued that density-independent parasitism in spite of parasitoid aggregation may simply be due to severe egg limitation in searching parasitoids. We have already argued that egg limitation in *A. delicatus* should not have precluded a density-dependent response, but we presently have no information concerning changes in parasitoid handling time with host density.

The three-way relationships among host suppression, stability, and aggregation differ between discrete-time and continuous-time models. In discrete time, aggregation can account for stability but usually results in elevated equilibrium host density (Chesson & Murdoch 1986; Murdoch 1990). With overlapping generations, aggregation by parasitoids in patches with more hosts always suppresses equilibrium density, but at the cost of stability (Murdoch & Stuart-Oaten 1989). Also, when parasitism is uncorrelated with host density per patch, as in our results, stability is not affected by the distribution of parasitism rate per patch (Murdoch & Stuart-Oaten 1989).

Parasitism by *A. delicatus* is temporally very inconsistent. For much of the year, the parasitism rate is low enough that the wasp is probably ineffective at maintaining hosts at low densities. However, it is likely to depress the host greatly periodically, with very high rates of parasitism. Wide fluctuations in *Prokelisia* spp. densities and *A. delicatus* parasitism rates in the field (Strong 1989; A. E. Throckmorton *et al.*, unpublished) support these inferences of a density-vague, non-equilibrium coexistence.

Conventional arguments of optimal foraging by parasitoids to maximize short-term fitness do not apply to the *Prokelisia* spp.–*A. delicatus* system. The lack of a response to host density in the field appears to be the result of a low attack rate per host clutch discovered by female wasps. The per capita number of eggs laid in laboratory situations by mated, fully gravid wasps is quite low. Wasps lay only a few eggs, then disperse (J. T. Cronin & D. R. Strong, unpublished). Low numbers of mature eggs are not responsible for low attack rates; *A. delicatus* is pro-ovigenic, eclosing with an average of thirty-three mature eggs (Cronin & Strong 1990). Because all eggs are mature and oviposition times are short (< 2 min), time constraints in handling hosts are relatively unimportant.

Wasps, then, may be passing up local opportunities to parasitize hosts in favour of dispersal. Movements over short distances among cord-grass shoots are routine (Cronin & Strong 1990), and some females regularly travel kilometres or more before parasitizing hosts (Antolin & Strong 1987). Submaximal oviposition rates such as these are not accommodated in conventional optimal foraging models, which rest on the assumption that maximum lifetime fitness is attained only by maximization of short-term rates (Charnov 1976; Cook & Hubbard 1977; Stephens & Krebs 1986). Recently, models of submaximal short-term rates of oviposition that lead to maximal lifetime fitness have been introduced in an attempt to resolve this problem (Iwasa, Suzuki & Matsuda 1984; Houston & McNamara 1986; Mesterton-Gibbons 1988).

Submaximal oviposition rates caused by frequent dispersal can be favoured by selection if survival of the host patch is low or if predators pose a threat to wasps while

they are searching host clutches (Houston & McNamara 1986; Sih 1982). Currently, empirical data on the risks imposed upon searching wasps are only beginning to surface.

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