SUBSTANTIALLY SUBMAXIMAL OVIPOSITION RATES BY A MYMARID EGG PARASITOID IN THE LABORATORY AND FIELD[1]

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Abstract. We examined in the laboratory and field the foraging behavior of the stenophagous egg parasitoid *Anagrus delicatus* (Hymenoptera: Mymaridae) within discrete patches of its planthopper host, *Prokelisia marginata* (Homoptera: Delphacidae) on leaves of salt marsh cord grass, *Spartina alterniflora*. Females efficiently discriminated between leaves with and without hosts, leaving empty leaves within 6 min, on average. On leaves with hosts, wasps remained ≈10 times as long ($\bar{X} \pm 1$ SE = 62 ± 8 min); time on a patch was independent of host density. In the laboratory, newly mated female *A. delicatus* encountering hosts for the first time and bearing an average of 33 yolked and mature eggs, parasitized an average of 6 hosts (laying 18% of her eggs) before dispersing from patches containing an average of 81 hosts. Many more hosts were probed than were parasitized. In field experiments with mixtures of newly mated and experienced females, the proportion of eggs laid by these wasps was even lower; between 4% and 26% were laid in a series of experiments that spanned 20 dates over 10 mo. In all tests, available hosts far exceeded wasp fecundity.

Most, if not all hosts, were alive, available, and supported development of parasitoids if parasitized. Increasing numbers of female wasps visiting a patch led to increasing parasitism rate, to an average of 75% with 20 female wasps. Even though many hosts on a patch were probed and rejected by each wasp, rejected hosts were parasitized by subsequent wasps and yielded live parasitoid offspring; rejected hosts were not unsuitable hosts. Leaf thickness provided no refuge from parasitism by *A. delicatus*. Hosts laid deep within plant leaves ($\bar{X} = 118$ μm) were no less vulnerable to attack than those laid shallow, and all hosts were well within the range of the long ovipositor of *A. delicatus* ($\bar{X} = 394$ μm).

Single wasps dispersed before the ratio of unparasitized to parasitized hosts was much decreased by their efforts; dispersal was not precipitated by high encounters with parasitized hosts. Handing time constraints were small ($\bar{X} = 2.2$ min) in relation to total patch time ($\bar{X} = 62$ min), and thus did not account for the low number of ovipositions. Interference among searching parasitoids was not responsible for the underutilization of hosts in the field because single wasps, searching alone in new patches not previously visited by *A. delicatus*, displayed the same characteristically low attack rates as wasps searching together with others.

Classical arguments of parasitoid foraging, which assume maximization of oviposition rate with respect to time, are inconsistent with the substantially submaximal oviposition rates for this parasitoid. *Anagrus delicatus* passed up many suitable and available hosts in each patch and visited multiple patches during its lifetime; number of eggs laid increased linearly with the number of patches visited. Wasps visiting ≥5 patches laid an average of 32 eggs (95% of average egg complement). Our hypothesis is that this is a foraging strategy build upon compromising the time rate of oviposition in favor of spreading ovipositions among patches and sites. We observed high mortality of host-plant leaves, and thus of host-insect patches, in the field due to leaf senescence (20–30%), which would favor spreading of parasitoid offspring among leaves.

Key words: Anagrus delicatus; egg parasitoid; foraging behavior; host–parasitoid interactions; interference; planthopper; Prokelisia marginata; *refugia; risk-spreading; salt marsh.*

INTRODUCTION

Foraging parasitoids are routinely confronted with host populations that are spatially fragmented among leaves, plants, and different clumps of the host plant. Much theoretical emphasis has been placed on how these parasitoids should apportion their time among host patches in order to maximize their lifetime reproductive success (Stephens and Krebs 1986). The classical idea for solitary parasitoids is that success is based upon the highest rate of oviposition with respect to time. Parasitoids should forage longer and parasitize proportionately more hosts in patches of high host density (Hassell and May 1974, Murdoch and Oaten 1975, Charnov 1976, Cook and Hubbard 1977). By doing so, the rate of encounter with hosts is maximized, and most eggs are laid in the shortest time. Foraging wasps are generally assumed to employ any of a variety of indirect means ("rules of thumb") to distinguish features of patches and alter their foraging efforts in response (Stephens and Krebs 1986).

Physiological or morphological constraints, such as low parasitoid fecundity or long handling times for individual hosts, may lower attack rates below theoretical maxima (Holling 1959, Hassell 1978, Lessells 1985). For example, Morrison et al. (1980) suggested that, in spite of area restricted search by *Trichogramma* spp., limited egg supply led to underutilization of high density patches of its host, *Heliothis zea*. Environmental factors may also confuse or interfere with searching parasitoids. An invulnerable host age class or host refuge can slow parasitoid oviposition by extending host acceptance time or by making hosts difficult to find (Murdoch and Oaten 1975). The presence of conspecific parasitoids (adults or their offspring) or their by-products (marking pheromones) can also reduce patch use by individual wasps. This interference among parasitoids can lead to a decline in either the per capita number of hosts attacked or the rate of attack as wasp density increases (Hassell and Varley 1969, Free et al. 1977). Intraspecific interference appears to be a common constraint of insect parasitoids (Hassell 1978).

Maximum egg laying rates per vulnerable host are not the only possibility for parasitoid foraging, however. Spreading eggs among host patches as an adaptation to risks that vary unpredictably among patches in space certainly could result in submaximal oviposition rates. Wasps may adopt an evolutionary compromise that maximizes fitness by lowering the variance in success rate (Sih 1980, Real et al. 1982, Iwasa et al. 1984, Houston and McNamara 1986, Real and Caraco 1986, Mesterton-Gibbons 1988, Strong 1988).

In this paper, we use a series of laboratory and field experiments to describe how a fairyfly parasitoid, *Anagrus delicatus* Dozier (Hymenoptera: Mymaridae), forages then disperses away from patches of hosts that are only minimally depleted of hosts. Egg limitations, time constraints, suitability and availability of hosts, and host and parasitoid density are examined to determine their effect on parasitoid foraging. We then compare *A. delicatus* foraging behavior with predictions from theory based on a parasitoid that maximizes the time rate of oviposition. Finally, we propose and offer evidence to support an alternative foraging strategy whereby wasps lower the time rate of oviposition in favor of reduced variance in offspring survival.

METHODS

Study organisms

Prokelisia planthoppers (Homoptera: Delphacidae) are the most abundant insect herbivores of intertidal marshes along the Atlantic and Gulf coasts of the United States (Denno and Grissell 1979, McCoy and Rey 1981, Vince et al. 1981, Stiling and Strong 1982*a*, Denno et al. 1987). These planthoppers feed on and oviposit in the leaves of their only host plant, salt marsh cord grass, *Spartina alterniflora* Loisel, which often occurs on beach fronts, small oyster bars, and islands of varying size. Inserted inside the linear cord grass leaves, *Prokelisia* eggs are typically aggregated in discrete patches of 1 or 2 cm along the 20–30 cm average leaf length. *Prokelisia dolus* Wilson is rare at our sites and is restricted to higher elevation back-marsh sites. This study concerns only *P. marginata* (Van Duzee), which is widespread and abundant throughout the salt marsh (Denno et al. 1987; J. T. Cronin and D. R. Strong, *unpublished data*). In north Florida, *P. marginata* egg-to-adult generation times range from 3 wk during the summer months to 6 wk when temperatures decline (Strong et al. 1990). All life history stages are present throughout the year.

The fairyfly parasitoid, *A. delicatus*, is a minute (0.7 mm) solitary insect that attacks the egg stage of its only known hosts, *P. marginata* and *P. dolus* (Stiling and Strong 1982*a*, Cronin and Strong 1990*a*). Adults live at most 2 d in nature (Cronin and Strong 1990*a*) but can disperse several kilometres during their brief existence (Antolin and Strong 1987). Parasitism rate from *A. delicatus* is usually fairly low (<20%), but occasionally reaches high levels (>80%), and is both spatially and temporally density independent (Stiling and Strong 1982*b*, Strong 1989, Cronin and Strong 1990*b*).

Experimental host patches

The planthopper adults used in this study were collected from offshore islands and beach fronts in Oyster Bay, Wakulla County, Florida, USA with a sweep net, aspirated into glass tubes, and quickly transported on ice to the laboratory. Females were unambiguously sorted to species according to the procedure of Denno et al. (1987). Individuals with a frons length-to-width ratio of ≤1.64 were classified as *P. dolus*, and those with ratios >1.77 were classified as *P. marginata*. A key based upon the shape of the valvifers of segment 8 (Heady and Wilson 1990) corroborated our use of frons ratios in discriminating these two species. We

restricted our study to *P. marginata* hosts, but note here that *P. marginata* and *P. dolus* do not differ noticeably in rate of attack or acceptance by *A. delicatus* (Cronin 1991).

Uniform discrete host patches were produced in the laboratory with 10 female and 2 male *P. marginata* placed in a "clip cage." The cage was constructed of a 40 mm length of 18 mm diameter acetate tubing that was inserted over a single leaf (ranging in size from 12 to 30 cm) on a potted *S. alterniflora* culm. The tubing was positioned at the leaf base and capped at each end, leaving the upper surface exposed (Cronin and Strong 1990*a*). The planthoppers fed upon and oviposited into the leaf sections within the cages for a 48-h period, producing discrete patches of host eggs that were of uniform age and area. Patches averaged 58.2 ± 5.7 hosts (mean ± 1 SE; range: 2–257 hosts, *n* = 1262), which fall within the range of densities found in nature (Stiling and Strong 1982*b*, Strong 1989).

The *A. delicatus* used in this study were collected as developing larvae and pupae in leaves of *S. alterniflora* obtained from salt marshes of Oyster Bay. As a control for the possibility of host-specific parasitoid races ("biotypes"), wasps were collected only from habitats that supported large populations of *P. marginata*. Leaves were placed in plastic bowls in the laboratory and kept healthy by immersion of the ends in a water-retaining starch gel. Wasps were reared from these leaves according to the procedure outlined in Cronin and Strong (1990*a*), which ensures that female *A. delicatus* are of similar age and quality: <3 h old, mated, and with no previous oviposition experience. Oviposition rates are maximal under these conditions.

Laboratory experiments

Parasitoid reproductive capacity.—Egg maturation in *A. delicatus* was determined with the vital stain trypan blue (Telfer and Anderson 1968, Barbosa and Frongillo 1979). Eggs still in the process of yolk deposition absorb the dye and stain blue, whereas those that have ceased vitellogenesis remain clear. We consider eggs mature at completion of vitellogenesis.

We determined the time course of egg maturation and number of mature eggs of *A. delicatus* by dissections of female wasps at three stages of development: young pupae, old pupae, and newly eclosed adults <3 h old. In young pupae (≈10 d prior to eclosion), the head and body are just outlined, and the ovipositor is lightly sclerotized. Old pupae (3 d prior to eclosion) are fully formed and darkly pigmented. The numbers of mature (clear) and immature (stained) eggs were recorded for 7 female wasps in each group. To obtain a more complete picture of the distribution of fecundity at eclosion, we counted eggs, by dissection, from an additional 100 female wasps that had just eclosed.

The potential for other oocytes to mature during adult life was assessed by examining the distal portion of the ovarioles (the germarium). The reproductive tracts of 5 recently eclosed adult females were embedded in a methacrylate resin (JB-4, Polysciences, Inc., Warrington, Pennsylvania, USA), sectioned in 1-µm increments, and examined at 200× under a compound light microscope. We recorded the size and state of development of all oocytes.

Parasitoid foraging within patches.—A single host patch (on a leaf still attached to the potted cord grass culm) was positioned under a dissecting microscope outfitted with a video camera that magnified (25×) and projected the patch onto a television monitor. A single female wasp was gently released onto the unenclosed patch and her foraging behavior recorded on videocassette. Wasps remained for long periods on single leaves, and a trial was continued until the wasp left the leaf, either by flying or by walking. Behavioral trials were conducted between 1200 and 1600 on 39 female *A. delicatus*, each on a different host patch. We determined survivorship of parasitoid offspring from egg to adult eclosion by incubating plants (15 patches) in isolation until all developing wasps had emerged. Number surviving can be unambiguously assessed by a count of the round *A. delicatus* exit holes on the lower leaf surface. For replicates in which the ovipositing wasp could be recovered after she left the leaf, we dissected the wasp in insect Ringer's solution and counted the number of eggs remaining in the reproductive tract.

Videotapes were scored for the durations and sequence of three distinct behaviors: probing (insertion of ovipositor), searching (walking and antennal movement), and resting (ovipositor retracted and no movement). Duration of probes by all *A. delicatus* is bimodal; each probe is either short (mode 20 s) or long (mode 120 s), and there is no overlap between the two distributions (Cronin and Strong 1990*a*). Dissection of probed eggs revealed that parasitoid eggs were laid only during long probes (>90 s; Cronin and Strong 1990*a*). Shorter probes never resulted in oviposition; all were aborted (e.g., failures, misses, or rejections of hosts). Therefore, oviposition can be unambiguously inferred from duration of ovipositor insertion into the leaf. From video recordings we calculated (1) duration of time on the leaf (total patch time); (2) total time spent searching; (3) rate of oviposition (reciprocal of the mean time spent between successive ovipositions, excluding the interval between the start of the experiment and the first oviposition); (4) time spent ovipositing (time taken to lay one egg, from insertion to withdrawal of ovipositor, plus time spent grooming afterwards = handling time); (5) number of ovipositions; (6) time spent in aborted probes; (7) number of aborted probes; (8) giving-up time, GUT (time spent on patch after the last oviposition or, if no oviposition, the total time on the patch); and (9) total time spent resting.

Host refuge.—We examined whether host depth within a leaf affects the vulnerability or accessibility of a host to parasitism by *A. delicatus*. Eleven host patches were created, and 5 female wasps were caged for 24 h in a clip cage surrounding each patch (1- to 3-d-old hosts). This number of wasps ensured that virtually all

hosts would be encountered by the wasps. Five days after exposure, leaves were dissected, the depth of all hosts was measured and categorized as parasitized or unparasitized. Host depth was measured with an ocular micrometer (marked with a $10\text{-}\mu m$ grid) as the distance from the upper leaf surface to the most proximal portion of the host (the head region of the developing planthopper nymph). To determine whether host depth influenced parasitism, we divided hosts into classes spanning 25 μm increments in depth. For each class the proportion parasitized was determined. The relationship between parasitism (angular transformed) and depth was determined by least squares regression, where parasitism was weighted by the number of host eggs in each depth class.

Using an ocular micrometer, we measured the ovipositors of 100 female wasps obtained from field samples. Previous examination (D. R. Strong and J. T. Cronin, *unpublished data*) of the entry point of the *A. delicatus* ovipositor into the host, where a blackened scar is made, indicated any point along the entire length of a successfully parasitized host may be probed. We therefore measured vulnerability to attack as the degree of overlap between ovipositor length and egg depth.

Host suitability. — To determine if a substantial fraction of *P. marginata* eggs in a patch provide suitable hosts for the development of *A. delicatus* larvae, we exposed host patches to varying densities of mated, newly eclosed female wasps. From 1 to 8 wasps were released simultaneously on a single uncaged host patch. After all wasps dispersed, the plant bearing the host patch was placed in isolation for 5 d, after which time, plants were dissected to determine parasitism. Hosts were deemed suitable for development if wasp larvae survived to the end of the 5-d incubation period, which is approximately the start of their second instar. This procedure was replicated 15 times for the one wasp per patch treatment and between 5 and 7 times for all others.

In an attempt to promote maximal rates of parasitism, we released 20 female *A. delicatus* over a 3-d period on eight additional host patches. Parasitism was determined as described above.

Parasitoid foraging among patches, arena experiment. — We examined the foraging and dispersal behavior of *A. delicatus* among host patches by releasing individual wasps into a large arena consisting of 81 cord grass culms (60 cm average height, 4–6 leaves per culm), each planted singly in a pot 11.5 cm on a side. The pots were set together to form a 9 × 9 array, resulting in a 103 × 103 cm arena. Thus the 0.7 mm long wasp was in an environment with linear dimensions of ≈1500 times its body length. Each plant contained a single host patch on one of its leaves.

A single mated female *A. delicatus* (<3 h old) was released onto the host patch of the central cord grass plant. At 5-min intervals the patch was examined for the presence of the wasp. When the wasp dispersed, its patch time was recorded and a systematic inspection

of all other patches was undertaken. Observations were made from outside the arena and no plants were disturbed during the search. Less than 1 min was required to examine all 81 host patches for the presence of the wasp. Every 5 min this search was repeated until the wasp was found on one of the patches; if not located within 30 min the experiment was terminated. Upon location of the wasp, the $x\text{-}y$ coordinates of the new host patch were recorded. This entire procedure was repeated until the wasp could no longer be found after 30 min of search. At the conclusion of the experiment all plants were incubated in isolation for 5 d and then dissected to determine numbers of parasitized hosts surviving to the end of the incubation period. Patches not visited by wasps were included to determine if visits to other patches had been overlooked or if contamination by alien wasps had occurred. We note here that patches scored as unvisited yielded no wasps. A total of 12 replicates of this experiment were performed, 1/d for 12 consecutive d.

Field experiments

Per capita parasitization. — Host patches were created on each of two leaves per plant on 10 individually potted cord grass culms, for a total of 20 replicate patches. The 10 experimental plants were then placed in a pure stand of cord grass in the backmarsh at Oyster Bay, where tidal effects and the action of waves are minimal. The pots were sunk flush in the marsh in a line transect, each separated from the next by a distance of 2 m. After 72 h of exposure to natural parasitoids, the plants were returned to the laboratory and allowed to incubate for an additional 5 d before each host patch was dissected. Parasitism was recorded.

At the same time, 25 plants occurring naturally along the same transect were haphazardly chosen, and a spot of sticky Tanglefoot (The Tanglefoot Co., Grand Rapids, Michigan, USA) was applied to a 40-mm section at the base of one green leaf on each. Searching parasitoids either alight directly on the sticky surface or walk into it after landing on an unaltered section of the leaf. The Tanglefoot holds them securely (see *Results*). This method allows an estimate of the number of *A. delicatus* encountering each host patch in the field. We describe below a test of the possibility that the Tanglefoot neither attracts nor repels *A. delicatus*. At the end of 72 h, these sticky leaves were collected along with experimental plants, inserted between a pair of acetate sheets, and examined under a dissecting scope for female parasitoids.

This experimental procedure was repeated on 20 experimental dates over 10 mo starting in July 1988 and ending in April 1989. Intervals between repetitions were set by the availability of adult planthoppers for sources of hosts. The same line transect was used throughout.

Thus, parasitism and parasitoids searching per patch were estimated separately in host patches and on leaves with Tanglefoot, respectively. Combining both mea-

sures on the same patch would have required direct observation of wasp foraging in the field, a daunting task given the small size of these wasps. We therefore estimated per capita parasitization using the following procedure. For each experimental date, we calculated the mean number of captured wasps per leaf (w) from the Tanglefoot traps, the mean number of hosts parasitized per patch (p) from the experimental host patch data, and the mean number of hosts parasitized per female wasp (p/w). This p/w quotient represents an estimate of the per capita number of hosts parasitized.

This technique provides a single estimate of per capita parasitization over the 20 experimental host patches on a single date, which is well within the substantial dispersal capacities of *A. delicatus* (Antolin and Strong 1987). An earlier analysis of these data revealed no spatial relationship between host density and parasitism within each of the 20 experimental dates (Cronin and Strong 1990*b*). In the present study we first examined how average per capita parasitization varied seasonally among summer, fall, winter, and spring samples. Second, we examined how average per capita parasitization varied in response to mean host density, parasitoid density, and parasitism among all experimental dates.

We determined the average number of eggs in the population of foraging female wasps by counting the eggs in captured specimens. One hundred females were collected on yellow sticky traps (coated with Tanglefoot) from the field transect. Collections were made on 30 July, 21 August, 15 September, 7 November 1988, 3 January, 21 February, and 7 March 1989. For an estimate of efficiency in the field, we calculated an index of the percentage of available eggs that had been laid by female wasps before their capture, by dividing the per capita number of hosts parasitized by the mean number of eggs contained within each captured wasp.

We tested with a laboratory experiment the assumption that *A. delicatus* is neither attracted nor repelled by the Tanglefoot on leaves. Two potted cord grass plants were positioned 25 cm apart on a laboratory bench: one with Tanglefoot applied to a 40-mm section of the leaf base and the other with a single host patch on one of its leaves. A bowl 15 cm wide and 6 cm deep containing >50 adult female *A. delicatus* was positioned 25 cm from either cord grass plant in an equilateral triangle with the two plants and the bowl forming the vertices. The experiment was initiated by removing the lid on the bowl and allowing the wasps to disperse. The experiment was repeated five times over 2 d and the position of the bowl and two plants was changed randomly each time to minimize position effects on parasitoid movement. We monitored both the leaf with Tanglefoot and the leaf with the host patch continuously for 2 h for arrival of *A. delicatus* and recorded the wasp numbers encountering the host patch and Tanglefoot trap. Wasps encountering the host patch were aspirated to eliminate counting them more than once.

Host mortality in the field.—We estimated mortality of host patches (leaves bearing parasitized hosts) caused by grazing from herbivores or natural senescence of leaves. On 15 July 1990, we initiated a study of the fates of 25 randomly chosen cord grass culms in the backmarsh site at Oyster Bay. On this date, *P. marginata* adults were present and laying eggs on all exposed leaves, from the culm's base to its tip; most leaves bore planthopper eggs. We numbered leaves consecutively from the base to the tip, including only green and fully exposed leaves. Culms had between 5 and 7 leaves that met this criterion, and the culms were similar in height (64.2 ± 2.2 cm [mean ± 1 SE]). At weekly intervals for 14 wk we examined leaves for damage from grazers (usually grasshoppers or deer) or senescence, and scored leaves as missing/dead if they were chewed to the base or if they were completely brown and dry. No wasp larvae in these brown leaves survive (J. T. Cronin and D. R. Strong, *unpublished data*).

Anagrus delicatus takes on average 504 degree-days to develop from egg to adult (Cronin and Strong 1990*a*). If a leaf dies before the degree-days exceed this value, developing wasps in that leaf will die. We obtained records from NOAA (The National Oceanic and Atmospheric Administration, Seattle, Washington, USA) on the average daily temperatures during the census period for the vicinity surrounding Oyster Bay. For wasps ovipositing on 15 July, we estimated the date that their offspring would achieve the necessary degree-days to complete development. From our records on the cord grass culms, we selected the census week that was closest to, but did not exceed, the predicted emergence date of the developing wasps. We then determined the proportion of leaves at each position along the stem that were missing or dead. We repeated this process for wasps ovipositing on 26 July.

We estimated the proportion of the female *A. delicatus* population that searched for hosts at each leaf position for both 15 and 26 July. Ten plants were chosen at random from the same site as the culm census, and Tanglefoot applied to the basal 40 mm of all green and exposed leaves. After 3 d, the leaves were collected, female wasps were counted and the proportion of wasps at each leaf position determined.

For two instances in time (15 and 26 July) we estimated the proportion of the wasp population whose offspring did not complete development in a leaf bearing hosts. This was accomplished by multiplying the proportion of wasps at each leaf position by the proportion of leaves at that position that did not survive 504 degree-days, and summing for all leaf positions.

Data analysis

In examining the relationship between a behavioral response and host density, we used the smoothing technique LOWESS (locally ordered weighted scatterplot smoothing) which describes the form of a response without any a priori functional form (Cleveland 1979,

TABLE 1. Average number of mature parasitoid eggs and per capita number of hosts parasitized by female *Anagrus delicatus* under different conditions. Means with different superscript letters are significantly different ($P < .01$) on the basis of the Tukey HSD multiple-comparisons test (Sokal and Rohlf 1981).

Condition	n	Mean	1 SE	Range
Mature eggs per wasp				
<3 h old	100	33.3[a]	0.6	21–45
Field-caught	100	18.8[b]	1.1	0–42
Eggs laid per parasitoid				
Laboratory				
Within patches	33	6.1[c]	1.0	0–21
Among patches	12	18.3[b]	3.4	4–39
Field				
Within patches	20	2.0[d]	0.5	0–8

1981). The approximate fraction of points used in the computation of smoothed values, F, was set at 0.5, which is a standard value and provides an intermediate level of smoothing. Smoothing was performed by the SERIES module in SYSTAT (Wilkinson 1990). We also provide estimates of the fit of these data to equations based on ordinary least-squares regression techniques ("parametric") for single- and higher-order polynomials (Sokal and Rohlf 1981). Variables involving time, density, and numbers generally had distributions skewed to the right. To normalize distributions, data were natural log transformed prior to analysis. Parasitism rate data were angular transformed (arcsine of the square root of the proportion). In our analyses, where no statistically significant pattern in response existed with least-squares regression, we omitted the LOWESS curve.

RESULTS

Laboratory experiments

Parasitoid reproductive capacity. — Vital staining with trypan blue indicated that parasitoid egg development occurred throughout pupal development and ceased by, or within 3 h after, adult eclosion. None of the "young" pupae (10 d before eclosion) contained mature eggs, whereas $73.4 \pm 6.1\%$ (mean $\pm$ 1 SE) of the eggs in old pupae (3 d before eclosion) had ceased vitellogenesis (yolk uptake). All eggs (100.0%) from adults <3 h old had completed vitellogenesis. An adult female *A. delicatus* ecloses, on average, with 33 yolked eggs (Table 1), and this is the total egg complement available to the female during her lifetime. Oocytes distal to the mature eggs in the ovarioles were much smaller, averaging <1/10 the size of the smallest mature egg. These oocytes contain little or no yolk. It is extremely unlikely that these small oocytes would mature during the 1–2 d life-span of an adult wasp.

Parasitoid foraging within patches. — Patch time, the total time spent on a single patch (ranging in host density from 0 to 257), averaged a little more than 1 h,

and 77% of that time was spent actively searching for hosts (Table 2). Twenty-two percent of the time was spent ovipositing (the total proportion of time spent handling hosts), and only 1% of the time was spent resting. Wasps probed each patch an average of 77 times: many of the 81 ± 11 (mean $\pm$ 1 SE) hosts per patch were probed, but wasps only oviposited in 6 hosts, on average (Tables 1 and 2). Some hosts that were probed and rejected initially were later parasitized by the same wasp. Handling times for hosts averaged 2 min and wasps laid eggs at a rate of 1 every 10 min. Thus, of the 33 eggs present in the ovaries at eclosion, an average of only 23% were laid in the initial patch encountered. Eighty-five percent of the parasitized hosts in a patch yielded adult wasps under laboratory rearing conditions (Table 2). An additional 11% died as adult wasps attempting to emerge from the host chorion or cord grass leaf.

Individual rates of oviposition did not change appreciably as a wasp exploited a patch. For each wasp having a minimum of three oviposition intervals, excluding the interval between release on a patch and first oviposition, but including the GUT, we calculated the correlation between interval length and sequence. In 20 cases meeting this criterion, 15 were positively correlated, 3 of which were statistically significant. Based on the combined probabilities test of Fisher (Sokal and Rohlf 1981) using these 20 independent tests, we found no evidence for a trend in these data ($\chi^2 = 50.12$, $P > .10$, df = 40). A wasp's rate of oviposition (= 1/oviposition interval) remained unchanged on a host patch.

The interval between the last oviposition and the wasp's departure from the leaf (GUT) averaged 13 min (Table 2). For wasps with ≥ 2 intervals, excluding the first, there were 7.7 time intervals between ovipositions on average (6.7 ovipositions + GUT), and the GUT exceeded the longest interval in 39% of the replicates

TABLE 2. Foraging behavior of single newly mated *Anagrus delicatus* on patches bearing 81 ± 11 ($\bar{X} \pm 1$ SE) *Prokelisia marginata* eggs (hosts).

Time budget (min)	n	Mean	1 SE	Percent of total
Total per patch	37	62.5	7.8	100
Searching	37	48.3	7.1	77
Ovipositing	33	13.5	2.4	22
Resting	33	0.6	0.3	1
Handling time	27	2.2	0.1	
Giving-up time	33	13.4	2.1	

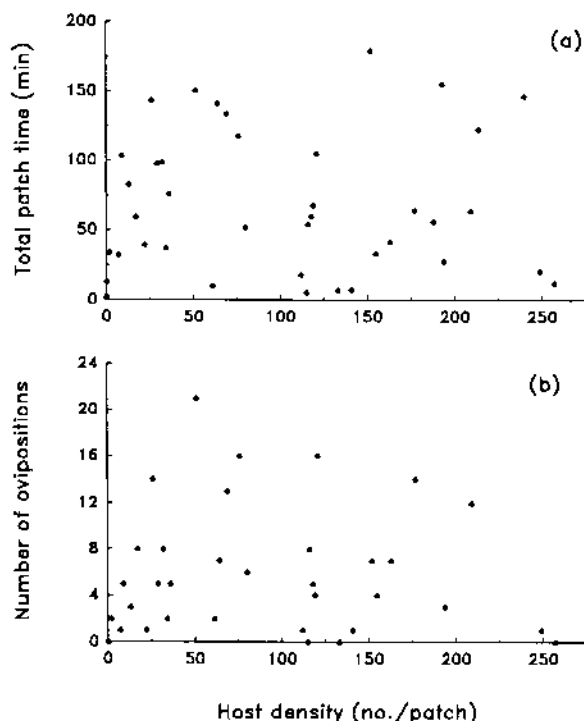| Oviposition pattern	n	Mean	1 SE	
Number of probes	33	77.2	11.1	
Number of ovipositions	33	6.1	1.0	
Oviposition rate (min⁻¹)	23	0.1	0.01	
Percent wasp eggs laid	19	23.4	4.3	
Offspring survival				
Number	15	5.1	0.7	
Percent	15	84.8	4.7	

FIG. 1. (a) The relationship between the time *Anagrus delicatus* spends on a patch (patch time) and host density. Least-squares regression indicated no significant relationship ($r^2 = 0.020$, $P = .397$, $n = 37$). (b) The number of hosts parasitized was independent of host density ($r^2 = 0.001$, $P = .851$, $n = 33$). Two cases where hosts and ovipositions equalled zero were omitted from the analysis because of undue leverage (based on analysis of studentized residuals; Sokal and Rohlf 1981). However, their inclusion in the analysis did not change the qualitative result.

(9 of 23). A wasp that leaves the patch at random, with respect to her oviposition rate, would be expected to have a GUT that is the longest time interval in 1/7.7 (13%) cases; this is significantly less than our observed frequency ($\chi^2 = 4.09$, $P < .05$, df = 1).

Over the entire range of densities used, the total time *A. delicatus* spent on a patch was unrelated to the number of hosts (Fig. 1a). However, wasps were quick to discern the presence or absence of hosts. An average of 5.9 ± 4.2 min (mean ± 1 SE, $n = 3$) was spent searching a patch that lacked hosts, whereas an average of 56.3 ± 23.4 min ($n = 3$) was spent when 1–10 hosts were present ($t = 3.166$, $P = .034$; log-transformed data). The number of ovipositions was strongly related to the total time spent searching a patch (Fig. 2), but was independent of host density (Fig. 1b). Because attacks did not increase proportionately with host density, parasitism decreased and thus was inversely density dependent over the full range of host densities ($r^2 = 0.627$, $P < .001$). No relationship existed between GUT and host density (Fig. 3a) or between GUT and the number of ovipositions by the wasp on the patch (Fig. 3b).
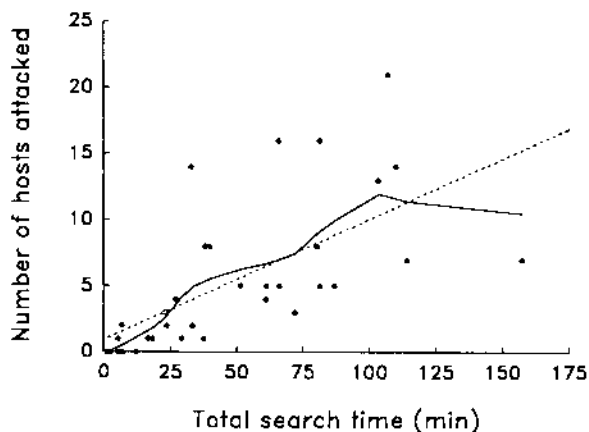

FIG. 2. Number of hosts parasitized as a function of total search time expended per wasp per patch. The —— curve was fit by LOWESS and the - - - line by linear regression ($r^2 = 0.679$, $P < .001$).

Host refuge. —Host depth inside the leaves did not provide a refuge from *A. delicatus*. Host eggs were inserted between the ridges of the leaf blade with the planthopper's developing head positioned nearer the
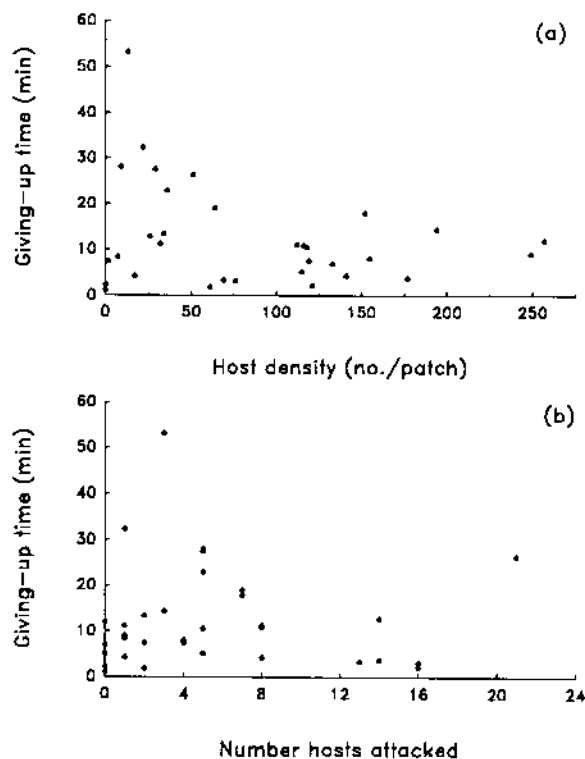

FIG. 3. (a) The time spent on a patch after the last oviposition (giving-up time) was independent of host density ($r^2 = 0.111$, $P = .072$, $n = 30$). (b) The giving-up time was also unaffected by the number of ovipositions ($r^2 = 0.002$, $P = .821$). The two cases where host density was zero were determined to be outliers (based on studentized residuals), and were removed from the analysis. Inclusion of these two points did not change the qualitative outcome of no relationship, in either analysis.
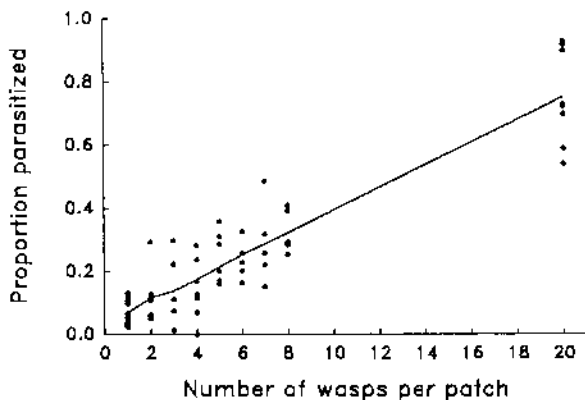
FIG. 4. Proportion of hosts parasitized increased linearly with the number of wasps visiting each patch ($r^2 = 0.591$, $P \leq .001$, $n = 56$). LOWESS and linear regression show nearly identical relationships; only the LOWESS curve is presented. Average host density was 131.5 ± 8.7 host eggs (mean ± 1 SE) and did not differ among the wasp density treatments based on ANOVA ($F_{7,49} = 1.008$, $P = .437$).

leaf surface. There was no relationship between parasitism and host depth: even the deepest hosts were vulnerable to parasitism by A. delicatus ($r^2 = 0.195$, $P = .250$). Because the ovipositor of A. delicatus was over three times as long (394 ± 4 µm [mean ± 1 SE], $n = 100$) as hosts were deep (118 ± 2 µm, $n = 694$), the shortest ovipositors were capable of reaching the head region of over 99% of the host eggs. Only 4 of 694 eggs had depths greater than the shortest ovipositor.

Host suitability.—Parasitism rate increased proportionately with the number of female wasps visiting a patch (Fig. 4). For wasp densities per patch of ≤8, parasitism climbed linearly from <10% to ≈35%. Parasitism rate climbed to an average of 75.4 ± 5.3% (mean ± 1 SE) over a 3-d period when 20 wasps were released on a patch.

Parasitoid foraging among patches, arena experiment.—Parasitoids remained an average of 218 ± 34 min (mean ± 1 SE) on their first host patch in the 9 × 9 array of cord grass culms. This was considerably longer than in the previous experiment (Table 2), but the number of hosts parasitized was similar (7.6 ± 1.2 hosts per female, $n = 12$). Dispersal among patches was predominantly by flight (83% of movements), but occasionally wasps walked onto a new leaf that was in contact with the leaf they were searching.

The time between leaving a patch and discovering a new one was <5 min (the observation interval) in 27 of 29 moves. *Anagrus delicatus* began searching and probing on the new patch immediately after its discovery. The maximum number of leaves and patches visited by a single wasp before she dispersed from the arena (could not be found after 30 min search) was 6. Both the time spent foraging and the number of hosts parasitized in the arena increased approximately lin-

early with the number of patches visited (Fig. 5). On a per patch basis, wasps parasitized an average of 6.4 ± 0.7 hosts (mean ± 1 SE, $n = 37$); and approximately the same number of hosts were parasitized on the first through fifth patches visited ($F_{4, 28} = 2.11$, $P = .11$; number of parasitized was log transformed). Wasps visiting ≥5 patches successfully parasitized an average of 32 hosts ($n = 4$) and laid ≈95% of their total of 33 eggs. On average wasps parasitized 18 hosts (laid 55% of their eggs) before they dispersed from the arena (Table 1).

It should be noted that the number of hosts parasitized per wasp in this experiment was estimated 5 d after hosts were attacked (to allow time for hosts to manifest signs of parasitism: a reddish color). Mortality of developing wasps during this period would have resulted in an underestimate of the number of wasp eggs laid. However, because mortality during the entire juvenile period was 15% (Table 2), per capita parasitization was, at most, underestimated by only 15%, the equivalent of <1 wasp egg laid per patch. In fact, mortality from day 1 to 5 appeared to be insignificant. On a per patch basis, an average of 6.1 wasp eggs laid in the videotape experiment (Table 2) did not differ sig-
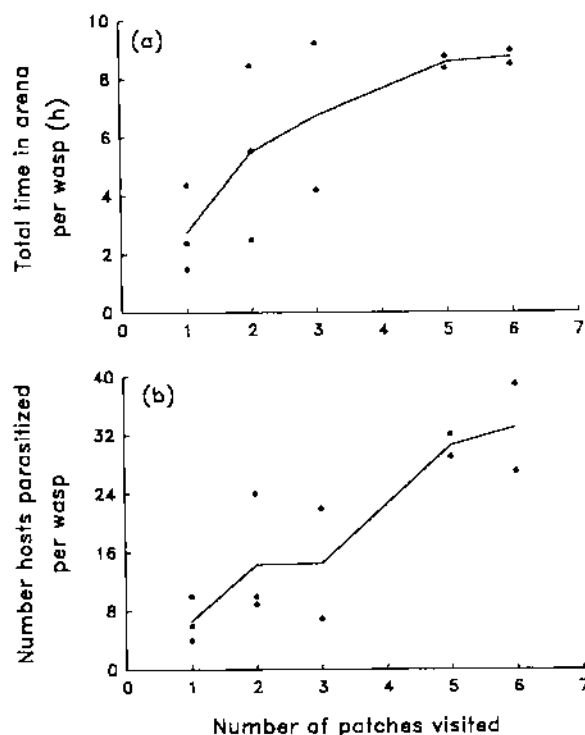

FIG. 5. Number of host patches visited by *Anagrus delicatus* in the experimental arena and its effect on (a) total time spent foraging for hosts and (b) the number of hosts parasitized. Both foraging time ($r^2 = 0.574$, $P = .004$, $n = 12$) and number parasitized ($r^2 = 0.750$, $P < .001$, $n = 12$) increased with the number of host patches visited. Only the LOWESS curves are presented; lines from ordinary least-squares regression are quite similar.

TABLE 3. Seasonal variation in parasitoid performance (per capita number of hosts parasitized).*

Season	n	Per capita number parasitized ($\bar{X} \pm 1$ SE)	Percentage of eggs laid
Summer	4	4.8 ± 1.5[a]	26.0
Fall	6	2.2 ± 0.9[ab]	12.0
Winter	7	0.7 ± 0.3[b]	3.7
Spring	3	0.9 ± 0.5[ab]	4.8

* ANOVA on log-transformed performance indicates significant difference among seasons ($F_{3, 16} = 3.510$, $P = .040$). Means with different superscript letters are significantly different ($P < .05$) based on the Tukey HSD test corrected for differences in sample size using the Tukey–Kramer adjustment (Sokal and Rohlf 1981). Experimental dates are: 12, 19, 26 July, 23 August 1988 for summer; 7, 21 October, 4, 11, 18 November, 14 December 1988 for fall; 11, 24 January, 13, 20 February, 3, 6, 12 March 1989 for winter; and 1, 4, 10 April 1989 for spring.

nificantly from an average of 6.4 hosts showing signs of parasitism at day 5 in the arena experiment ($t = 0.271$, $P \gg .05$, df = 65). Thus, inferring the number of wasps eggs laid from hosts examined 5 d after attack (in either the arena or field experiments) should not bias conclusions concerning the oviposition behavior of *A. delicatus*.

Field experiments

Tanglefoot capture for density estimates.—Tanglefoot did not appear to attract or repel *A. delicatus*. The number of wasps found on leaves with Tanglefoot and leaves with hosts did not differ significantly ($t = 1.827$, $P = .105$, df = 4).

Per capita parasitization.—Per capita number of hosts parasitized was even lower in the field than in the laboratory experiments. Each wasp parasitized two hosts per patch on average over the 20 experimental dates (Table 1). Per capita parasitization was highest
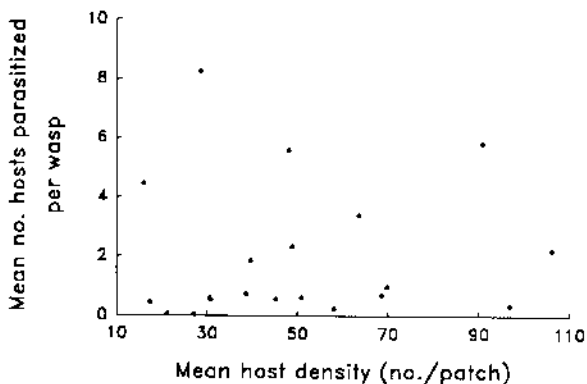

FIG. 6. The field relationship between the per capita number of hosts parasitized and the number of host eggs per patch in the field experiment. Each point represents the mean host density and number of hosts parasitized per wasp for that experimental date. The relationship was not significant based on least-squares regression ($r^2 = 0.051$, $P = .339$, $n = 20$).
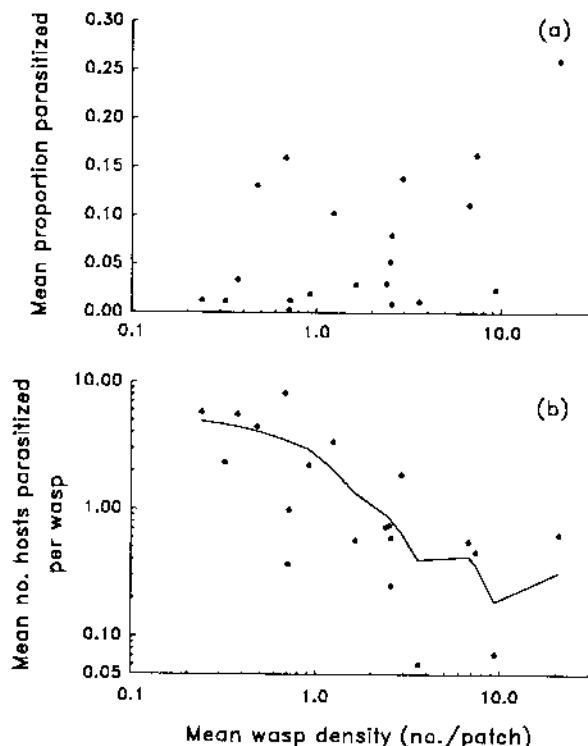

FIG. 7. The field relationship between female parasitoid density and (a) the rate of parasitism per patch, and (b) the per capita number of hosts parasitized per patch among the 20 experimental dates. There was no relationship between parasitism and wasp density ($r^2 = 0.18$, $P = .062$, $n = 20$). Hosts parasitized per wasp fell with increasing wasp density ($r^2 = 0.47$, $P = .001$). The curve was fit by LOWESS.

in the summer and fall (4.8 and 2.2, respectively) and lowest during winter and spring (0.7 and 0.9, respectively). However, the only significant difference among seasons occurred between the summer and winter (Table 3).

Female *A. delicatus* captured in the field on yellow sticky traps had an average of 19 mature eggs remaining in their ovaries (Table 1): this number did not differ among the seven sampling dates ($F_{5, 91} = 1.397$, $P = .233$; 3 January was omitted due to low sample size). We used this egg count as an estimate of the average number of eggs remaining and available per female wasp in the field. These wasps laid an average of 10.7% of their estimated 19 available eggs in any given patch. Seasonally, the highest percentage of available eggs were laid in the summer (26%) and the lowest in the winter (4%), a difference that is statistically significant (Table 3). Parasitism of hosts on outplanted cord grass culms was low and averaged only 7.0 ± 1.1% (mean ± 1 SE, $n = 20$).

No relationship existed between the number of hosts parasitized per female *A. delicatus* and host density over the 10 mo of the 20 experimental dates (Fig. 6). Parasitoid densities in the field spanned two orders of

magnitude, and the rate of parasitism was variable and independent of parasitoid density (Fig. 7a). This is consistent with the fact that per capita number of hosts parasitized declined as parasitoid density increased (Fig. 7b).

Host mortality in the field. — During July and August 1990, 24 d were required for wasps to accumulate sufficient degree-days (504) to complete their development. Therefore, wasp eggs laid on 15 and 26 July should have emerged as adults, on average, on 8 and 19 August, respectively. In cord grass culm censuses taken just prior to these emergence dates (5 and 16 August), leaf mortality averaged 20% and 31%. Mortality was 100% for the leaf lowest on the culm, but dropped off rapidly to 0% for the three most apical leaves. All leaf mortality was due to senescence. Grazing damage was rare and primarily restricted to the apical portions of the leaf where hosts are generally absent.

The numbers of *A. delicatus* females trapped on leaves with Tanglefoot were randomly distributed among the leaf positions on both sample dates (15 July: $\chi^2 = 1.12$, $P \gg .05$; 26 July: $\chi^2 = 0.46$, $P \gg .05$). Examination of five randomly chosen plants from the marsh revealed that hosts were recently parasitized at all leaf positions (hosts were just turning red): wasps oviposited in all green and exposed leaves. Based on the frequency distribution of wasps among leaf positions and the proportion of leaves at each position dead before adult wasp eclosion, we estimate that 30% of the host patches attacked by wasps on 15 July, and 39% attacked on 26 July died before offspring could complete development.

DISCUSSION

Anagrus delicatus females eclosed as adults with an average of 33 mature eggs; no other eggs mature during their lifetime. The arena experiment confirmed that most, if not all, of the yolk-bearing eggs were mature when females eclosed and were readily available for parasitism. Mated, newly eclosed females that visited $\geq$ five host patches laid an average of 32 eggs in 8 h, $\approx 95\%$ of their total egg complement. Studies of other mymarid life histories (Clausen 1962, Waloff and Jervis 1987) and reproductive structures (Jackson 1969, King and Copland 1969) suggest that pro-ovigenic development, i.e., mature and available eggs before eclosion of adult females, is a common feature of the family.

Anagrus delicatus normally spread their eggs among several host patches; females lay only a small fraction of their eggs in any one patch, even if that patch contains an abundance of hosts. In laboratory experiments wasps parasitized on average 6 of the 81 hosts in single patches. This deposition equated to an average of 23% of their eggs laid in the initial patch visited. Similar results, per patch, were obtained for single female wasps in 81 host patches on 81 culms in a 9 × 9 array. Over

all 81 patches, the number parasitized per wasp increased with the number of patches visited. In field experiments with outplanted cord grass, only two hosts on average were parasitized per wasp per host patch. Eleven percent of their eggs were laid per patch in the field. Per capita parasitization varied seasonally and was higher in the summer than the other three seasons. We cannot explain the cause for this seasonal variation.

Per capita parasitization by wasps in the field was lower than that of laboratory wasps. The difference was most pronounced during the autumn, winter and spring, where parasitization was one-half to one-third of that in the laboratory. It is unlikely that the varying age and experience (in laying eggs) of field wasps, in comparison to the uniformity in the laboratory, contributed to the difference in per capita parasitization rates. Laboratory experiments suggested that wasps parasitized a roughly constant number of hosts per patch, for up to five patches visited (which was a sufficient number of patches for most of their eggs to be laid). Thus, per capita parasitization per patch does not appear to change with time or experience. We can only suggest that the difference in parasitization rates by laboratory and field wasps may have resulted from environmental factors such as diurnal temperature, tidal effects, and/or the presence of predators and competitors in the field. Regardless of the cause, both laboratory and field data indicate that female *A. delicatus* abandon many host patches long before depleting either their egg supply or their hosts.

Our experiments addressed a number of factors that may have contributed to the low per capita parasitization per patch. First, number of wasp eggs did not limit parasitization, as has been suggested in other studies (Morrison et al. 1980, Collins et al. 1981, Reeve 1987, Yamada 1988, Roitberg et al. 1990). No wasps dispersed from the experimental patches without mature eggs remaining in their reproductive tracts; >74% of their eggs had not been laid. Second, long handling times, which are often advanced as a cause for few ovipositions and density-independent parasitism (DeBach and Smith 1941, Holling 1959, Hassell 1978), did not limit the number of hosts parasitized. Only 2 min were required to parasitize a host, a small fraction of the total time spent on a patch. In fact, the arena experiment indicated that wasps could lay practically all their eggs in a short period of time, handling 32 hosts in just 8 h.

Third, the many remaining unparasitized hosts in a patch were largely accessible to searching adults and suitable for development of wasp larvae. There was no apparent refuge from searching *A. delicatus*: hosts at all depths beneath the leaf surface suffered similar rates of parasitism. In addition, parasitism rate (measured as the proportion of hosts bearing healthy second instar wasps) increased proportionately with the number of adult wasps that visited a host patch, and exceeded 90% at very high wasp densities. Thus, hosts probed

and rejected by one wasp were successfully parasitized by subsequent wasps and yielded parasitoid offspring (at least to second instar). In rejecting hosts, *A. delicatus* may be attempting to distinguish subtle differences in host traits (e.g., host size), as a number of other parasitoid species have been found to do (for review see Vinson 1976, van Lenteren 1981). While *A. delicatus* may be "choosy," the previous data leaves little doubt that most planthopper eggs used in this study represented potential hosts to searching *A. delicatus*.

Fourth, host density did not affect per capita parasitization rates. Wasps did not "aggregate their search (or patch) time" (sensu Morrison 1986), nor did they parasitize more hosts in higher density patches in the laboratory. Neither was there evidence for density dependence in per capita parasitization in the field (see also Cronin and Strong 1990*b*). These results are in contrast with a number of studies that have found density dependence in individual foraging behavior (van Lenteren and Bakker 1978, Collins et al. 1981, Galis and van Alphen 1981, Roitberg et al. 1982, Waage 1983, Morrison 1986, Smith and Maelzer 1986).

Fifth, the increasing ratio of parasitized to unparasitized hosts (Waage 1979, Galis and van Alphen 1981, van Alphen and Vet 1986) as wasps exploited a patch did not cause them to disperse sooner. In the laboratory, the ratio of unparasitized to parasitized hosts ($U{:}P$) per patch was high, averaging 12 unparasitized to every parasitized host at the time of departure; thus, the likelihood of encountering parasitized hosts was low. Similarly in the field, where parasitism of outplanted patches averaged only 7% after 3-d exposure, $U{:}P$ was 14:1. Moreover, even if a parasitized host is encountered, *A. delicatus* readily superparasitizes hosts and does not leave a patch sooner that has a low $U{:}P$ ratio (J. T. Cronin and D. R. Strong, *unpublished data*). We are intrigued by the lack of host discriminating behavior of *A. delicatus* females; lack of discrimination of this sort is unusual among reported cases (van Lenteren 1976, 1981, van Alphen and Vet 1986, van Alphen and Visser 1990).

Last, wasp density did affect per capita parasitization in the field. Wasps trapped on leaves over a 3-d period ranged from an average of 0.25 to 23 per patch over the 20 experimental dates. Over this range, per capita number of hosts parasitized decreased approximately linearly with wasp density. Interference among wasps, leading to lower per capita attacks at higher wasp density, is widespread among parasitoids (see Hassell 1978 for additional examples) and has been found in two other mymarids (Chantarasa-ard et al. 1984, Pitcairn et al. 1990). This response to wasp density observed in the field may have contributed to the discrepancy between laboratory and field estimates of per capita parasitization, but it does not explain the low proportion of wasp eggs laid per host patch. Even solitary *A. delicatus* lay a small fraction (<8 of 19) of available eggs.

Parasitoid foraging strategy

Data on the allocation of *A. delicatus* foraging effort to host patches of different density allows us to evaluate the simple "rules of thumb" considered to be employed by foragers (Stephens and Krebs 1986). Wasps did not spend a fixed time foraging in a patch, i.e., the time rule (Gibb 1958). Dispersal from the patch was quick in the absence of hosts, but wasps remained for ≈ 1 h if any hosts were present. Nor did wasps leave a patch if the elapsed time between ovipositions exceeded some constant fixed interval, i.e., the giving-up time rule (Hassell and May 1974, Murdoch and Oaten 1975, Charnov 1976). Although the GUT was the longest interval in more cases than random chance would dictate, 61% of the wasps had oviposition intervals that exceeded the GUT.

On the other hand, wasps did lay a relatively constant number of eggs at all host densities, i.e., the number rule (Krebs 1973). According to Iwasa et al. (1981) and Green (1984), a fixed-number strategy can lead to maximal encounter rates with prey provided the variance in the frequency distribution of patch densities is small. However, *Prokelisia* eggs are highly clumped among leaves (Strong 1989) and this strategy would result in inefficient use of high density patches. A number rule is consistent with the density-independent/inverse density-dependent patterns of parasitism found in this system (Stiling and Strong 1982*b*, Strong 1989).

One major conclusion is that the behavior of *A. delicatus* in leaving host patches results in substantially submaximal oviposition rates on an individual and population basis. By this we mean that the average wasp is capable of attacking many more hosts locally, but rejects many suitable hosts and disperses instead. Moreover, she disperses when the rate of oviposition on that patch is no lower than when she initially began searching that patch. Because search time and number parasitized did not increase with host density (except for time at very low host densities [<10 hosts]), the oviposition rate would not be improved upon encountering a new patch. Certainly the time rate of oviposition by the wasp population is much reduced (i.e., submaximal) as a result of expending time searching for new patches or mortality between patches instead of ovipositing in the suitable hosts in the patch already discovered. Planthopper densities are typically clumped on cord grass, and a large fraction of leaves bear no hosts during much of the year. Under this circumstance, the time invested in locating a new patch could be long relative to the 0.1 ovipositions/min within a patch.

Submaximal oviposition rates by *A. delicatus* may be a strategy that improves ("maximizes") lifetime fitness by reducing the risk of mortality to offspring developing within a patch (Hamilton and May 1977, Kuno 1981, Metz et al. 1983, Iwasa et al. 1984, Levin et al. 1984, Houston and McNamara 1986, Mesterton-Gib-

bons 1988 and others). In our census, ≈20–30% of the cord grass leaves in Oyster Bay completely senesced before developing wasps could eclose. Mortality was restricted to the lower leaves, but *A. delicatus* did not appear to bias its search or ovipositions to leaves higher on the stem. A wasp that lays its eggs on an ill-fated leaf can lose a substantial, if not entire, portion of her contribution to the next generation. Such imposing risks, at the level of the host patch, can easily favor a wasp that "spreads" her eggs among several to many patches.

Lower oviposition rates may also be favored if mortality of adult wasps while searching a patch or mortality of offspring within a patch varies unpredictably from leaf to leaf (or larger spatial scale). Offspring mortality may result from predators (no hyperparasitoids exist), superparasitism from other *A. delicatus*, and/or from ovipositing in unsuitable hosts (e.g., older host embryos which do not fledge wasps). At this point we are beginning to investigate such risks in nature.

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