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Aspects of the behavioral ecology of *Edovum puttleri* Grissell (Hymenoptera: Eulophidae), an egg parasitoid of Colorado potato beetle, *Leptinotarsa decemlineata* (Say) (Coleoptera: Chrysomelidae).

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ASPECTS OF THE BEHAVIORAL ECOLOGY OF EDOVUM PUTTLERI GRISSELL
(HYMENOPTERA: EULOPHIDAE), AN EGG PARASITOID OF COLORADO POTATO
BEETLE, LEPTINOTARSA DECEMLINEATA (SAY)
(COLEOPTERA: CHRYSOMELIDAE)

A Thesis Presented

by

KAREN IDOINE

Submitted to the Graduate School of the
University of Massachusetts in partial fulfillment
of the requirements for the degree of

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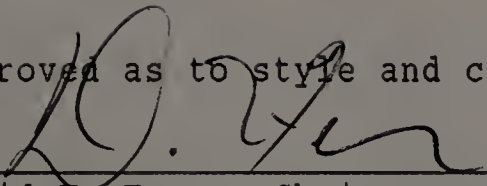
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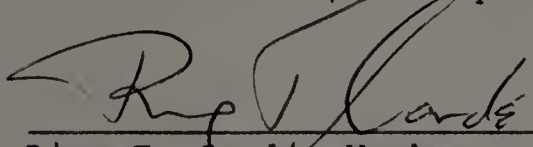
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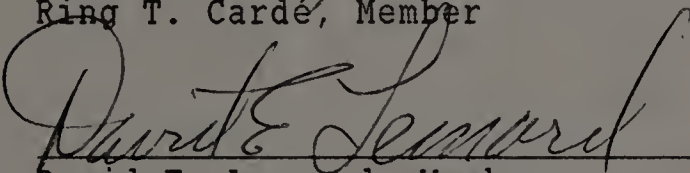
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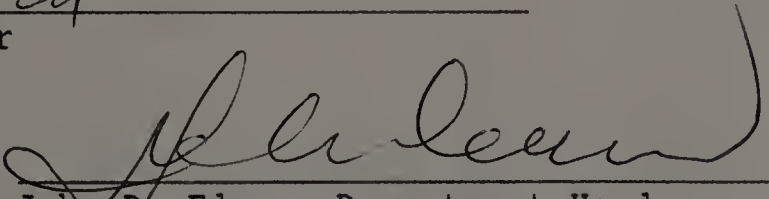
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ABSTRACT

ASPECTS OF THE BEHAVIORAL ECOLOGY OF EDOVUM PUTTLERI GRISSELL
(HYMENOPTERA: EULOPHIDAE), AN EGG PARASITOID OF COLORADO POTATO
BEETLE, LEPTINOTARSA DECEMLINEATA (SAY)
(COLEOPTERA: CHRYSOMELIDAE)

MAY 1989

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Directed by: Professor David N. Ferro

Field studies showed that Edovum puttleri Grissell, an exotic egg parasitoid of the Colorado potato beetle, Leptinotarsa decemlineata (Say) did not visit and feed on nectar of flowers commonly found near potato fields in the Northeast United States. Field cage observations and laboratory tests determined that E. puttleri uses aphid honeydew on potato as a source of nutrition. Since aphids do not usually colonize potato crops until early July in the Northeast, honeydew scarcity may prevent early season establishment of this parasitoid in potato.

The diurnal rhythm of visits by E. puttleri to Colorado potato beetle egg masses on potato plants was monitored every two hours in field cages. The highest proportions of wasps were observed on egg masses during the five-hour period between 1100

and 1600 h, 6-11 hours after sunrise. The periodicity of egg-deposition by E. puttleri was monitored hourly during the photophase under laboratory conditions of 16:8 (L:D) at $26 \pm 1^\circ\text{C}$. Peak oviposition occurred during the four hour period between 1400 and 1800 h, 8-12 h after the lights were turned on. No eggs were laid during the scotophase.

The persistence and distribution of E. puttleri Grissell, an egg parasitoid of Colorado potato beetle (CPB), on potato plants with different resources were quantified. E. puttleri were released into 1.5 m³ field cages enclosing pairs of potato plants with different combinations of host eggs, aphid honeydew, or without these resources. Observations every two hours throughout the day revealed that the parasitoids spent more time, during peak foraging periods, on plants with aphids and/or host eggs. The percentage of parasitism and mortality of CPB egg masses was not significantly higher on plants with aphid honeydew. Weather conditions were monitored and their relationships to parasitism and mortality of CPB eggs by E. puttleri were analyzed.

TABLE OF CONTENTS

	<u>Page</u>
ACKNOWLEDGMENTS	iii
ABSTRACT	iv
LIST OF FIGURES	vii
Chapter	
1. INTRODUCTION	1
2. APHID HONEYDEW AS A CARBOHYDRATE SOURCE FOR <u>EDOVUM</u> <u>PUTTLERI</u>	3
3. DIURNAL TIMING OF OVIPOSITION ACTIVITIES OF <u>EDOVUM</u> <u>PUTTLERI</u>	16
4. PERSISTENCE OF <u>EDOVUM</u> <u>PUTTLERI</u> ON POTATO PLANTS AND PARASITISM OF EGGS OF <u>LEPTINOTARSA</u> <u>DECEMLINEATA</u> : EFFECTS OF RESOURCE AVAILABILITY AND WEATHER	26
BIBLIOGRAPHY	47

LIST OF FIGURES

	<u>Page</u>
1. Mean no.(±SEM) of <u>E. puttleri</u> survivors on six different substrates over fourteen days.....	13
2. Diurnal periodicity of visitations by <u>E. puttleri</u> to CPB egg masses on field-caged potato plants between 0700 and 1800 h. Sunrise occurred between 0450 and 0550 EST over the observation period. Bars with the same letter are not significantly different (Tukey's honestly significant difference test, $P < 0.05$, ($n = 10$)).	22
3. Periodicity of oviposition by <u>E. puttleri</u> during photo-phase (16:8 (L:D), $26 \pm 1^\circ\text{C}$). Onset of light occurred at 0600 h. ($n = 3$).....	23
4. Comparison of the distribution of <u>E. puttleri</u> between two caged plants at 0800 h and 1400 h. Observations were made on five days beginning at 38 h (August 14 - Sept 13) after release of <u>E. puttleri</u> into field cages. Letters below X axis represent the resource status of the plants in each combination: A = with aphids; A/E = with aphids and eggs; C = no aphids, no eggs; C/E = no aphids, with eggs. The letters correspond, left to right, with the vertical bars. Stars above bars indicate significance.....	36
5. Comparison of the distribution of <u>E. puttleri</u> between two caged plants during the peak CPB egg visitation period (12 h - 17 h). Observations were made during the day beginning at 14 h (July 15 - August 5) and at 38 h (August 14 and Sept 13) after release of <u>E. puttleri</u> into field cages. Letters below X axis represent the resource status of the plants in each combination: A = with aphids; A/E = with aphids and eggs; C = no aphids, no eggs; C/E = no aphids, with eggs. The letters correspond, left to right, with the vertical bars. Stars above bars indicate significance.....	39
6. Comparison of parasitism and mortality of CPB eggs caused by <u>E. puttleri</u> on paired plants with different resource combinations. Letters below X axis represent the resource status of the plants in each combination: A = with aphids; A/E = with aphids and eggs; C = no aphids, no eggs; C/E = no aphids, with eggs. ($n = 50$) Plant pairs within the same cage are designated by underscores.....	41

7. Quadratic trend in percentage of parasitism and mortality of CPB eggs caused by E. puttleri at temperatures during the peak host egg visitation period.....43

8. Quadratic trend in percentage of parasitism and mortality of CPB eggs caused by E. puttleri and saturation deficit during the peak host egg visitation period.....45

CHAPTER 1

INTRODUCTION

Edovum puttleri Grissell, an exotic egg parasitoid, was brought to the United States from Colombia, S.A. in 1980 as a potential biological control agent of Colorado potato beetle (CPB), Leptinotarsa decemlineata (Say) (Grissell 1981). The inability of this parasitoid to overwinter in the temperate climate of North America requires that it be mass reared in an insectary for seasonal augmentative releases (Obrycki et al. 1985). E. puttleri causes mortality both by parasitizing and CPB eggs and by ovipositor probing (Corrigan & Lashomb 1987).

The Colorado potato beetle is the most destructive, yield-reducing insect pest of potato in North America and Europe. In the Northeastern United States, growers apply up to 12 foliar applications of insecticides per season to control this pest. Consequences of this dependence on insecticides to control CPB have been increased insecticide resistance in the CPB population, contamination of ground water and high mortality to natural enemies.

Although Harcourt (1971) found no effective natural enemies of CPB in Ontario, studies on potential biological control agents, both indigenous and exotic, have continued in the effort to

develop a workable integrated management program for CPB (Williams 1987). The discovery and production of a strain of Bacillus thuringiensis var. san diego, active against early instar CPB larvae (Ferro & Gelernter 1989), as well as the demonstrated value of crop rotation to delay early season colonization by the beetle (Voss et al. 1988), may make the contributions to reduction of CPB populations by natural enemies more efficacious.

Due to the inability of E. puttleri to overwinter in the Northeast, its value as a biological control agent depends on its potential to colonize a field of potatoes infested with its CPB host rapidly and efficiently. By employing management methods that would support such colonization, the economics of rearing and handling the parasitoid for annual inoculative releases (Debach & Hagen 1964) could be optimized. The objective is to gain control of the CPB population before it inflicts economic damage to the potato crop.

To manage E. puttleri effectively, it is necessary to understand the behavioral ecology of the parasitoid in a potato crop infested with CPB. The purpose of these studies is to identify some of the key behaviors and ecological parameters associated with the feeding, oviposition, and diel activities of E. puttleri and to evaluate their impact on parasitization of and mortality to CPB eggs.

CHAPTER 2

APHID HONEYDEW AS A CARBOHYDRATE SOURCE FOR EDOVUM PUTTLERI

To date, early season field releases of E. puttleri have not resulted in significant parasitism of CPB in potato crops in the Northeast. This fact has been attributed to temperatures that are, on the average, ca. 4°C lower in late May and June than the corresponding seasonal mean temperature in the native habitat of the parasitoid (Obrycki, et al. 1985). It is possible that other factors influence the ability of E. puttleri to parasitize significant numbers of first generation CPB eggs in early to mid-June.

In field situations, hymenopterous parasitoids have been observed feeding on flower nectar, pollen-containing dew, extrafloral nectaries, honeydew of various Homoptera and exudates from plants and their fruits (Gardener 1938, Leius 1960, Syme 1975, Townes 1958, Wolcott 1942).

The availability of carbohydrates can affect longevity and egg production (Leius 1961a,b, Syme 1975, 1977) and percent parasitism (McKinney & Pass 1977, Treacy et al. 1987). Syme (1975) demonstrated that Hyssopus thymus Girault, a eulophid ectoparasitoid of the European pine shoot moth, Rhyacionia buoliana (Denis & Schiffermueller), showed significant increase in longevity and fecundity when exposed to some, but not all flower

species tested. Leius (1961a,b) emphasized that the food requirements of adult parasitic Hymenoptera are highly specific for maximum longevity and fecundity, and Leius (1960) showed that parasitoids preferentially visited and fed on different foods and flowers.

It has been shown in our laboratory studies that E. puttleri requires a source of carbohydrate in addition to nutrients obtained from feeding on host eggs. Without a carbohydrate source, wasps die within five days; if provided with honey, individuals may live longer than 60 days (unpublished data). The aim of our study was to investigate sources of carbohydrate for E. puttleri in potato fields in the Northeast United States. We observed the behavior of the wasps in relation to various flowering plants near potato. Wasps often searched the upper surfaces of potato leaves; therefore, we tested the effects of aphid honeydew on the behavior and survival of E. puttleri.

Materials and Methods

Nectar Resources - Field Study A 24 m² plot of potato ('Katahdin') was used as the site for field observations of the behavior of E. puttleri. A 10 m wide strip around the perimeter of the plot was mowed to remove wildflowers. Potato plants were removed from a 1.8 X 0.75 m center area of the plot and replaced with potted flowering plants. The flowering plants were: dill,

Anethum graveolens L., coriander, Coriandrum sativum L., basil, Ocimum basilicum L., buckwheat, Fagopyrum sagittatum Gilib., and sweet alyssum, Lobularia maritima (L.) Desv. The flowers were open and producing nectar at the time of the observations.

On 3 July L. decemlineata had not yet colonized the plot. Therefore, to monitor parasitization by E. puttleri, sentinel CPB egg masses on excised potato leaf and less than 24 h old were pinned on the abaxial surface of potato leaves growing within the plot. The masses were systematically distributed to form a cross-shaped array within the plot; the arms of the cross extended from the center area to the perimeter of the plot. A total of 36 masses radiated from the center area. These egg masses were obtained from our colony of CPB maintained on potato in an outdoor screen cage.

At 1150 h, five hundred 5-day-old E. puttleri, were released into the center of the plot. The wasps had been provided with ca. 30 fresh CPB egg masses on the second and fourth day after their emergence. To see if E. puttleri visited blossoms to obtain flower nectar, we performed a series of thirty minute observations of the flowers in the center area at 1200, 1400, and 1600 h. At 1500 h it began to rain and was still raining at 2000 h (dusk). On 4 July, observations continued at 900, 1100, 1300, 1500 and 1900 h. After each of these observations we walked through the plot for 10 minutes, observing randomly selected potato flowers

for visitations by E. puttleri. After 48 h, egg masses were collected and examined for parasitism; flowering plants were removed from the site, so that wasps were deprived of the nectar of these flowers within the plot.

Nectar Resources - Cage Study (I) To facilitate observations of E. puttleri behavior in the presence of nectar-bearing flowers and potatoes, we used a 4.5 m² X 1.5 m high cage constructed of fine-mesh dacron netting. Observations were made from 30 July through 1 August inside the cage, which was placed in an open field on tilled, weed-free soil. A row of 10 potted potato plants, and a row of 11 potted flowering plants were placed in the cage, with 0.75 m between rows. Flowering plants used were: johnny jump-ups, Viola tricolor L.; yarrow, Achillea millefolium L.; quickweed, Galinsoga ciliata (Raf.) Blake; vetch, Vicia angustifolia Nees; wild mustard, Cruciferae sp., daisy, Chrysanthemum leucanthemum L.; basil; coriander; dill; and sweet alyssum.

At 1700 h, on 30 July, each potato plant was inoculated with two CPB egg masses and placed in the cage. At the same time, 50 adult L. decemlineata were placed on the potato plants to provide E. puttleri with fresh egg masses. Three hundred E. puttleri, 14 days old and with four prior exposures to fresh CPB eggs while being held in 2 L jars, were released into the center of the cage at ground level. Five minute observations were made successively

at each flowering plant, beginning at 1800 h on 30 July and at 800, 1000, 1500 and 1700 h on 31 July and 1 August to see if E. puttleri visited blossoms. A visit was defined as a wasp walking on a flower, or alighting and remaining on a flower for more than two seconds. At 1800 h on 1 August, the potted flowering plants were removed.

Nectar Resources - Cage Study (II) To test common nectar-bearing flowers without disturbing nectar production due to transplanting, Syme's (1975) method was used to maintain flower blossoms. On 2 and 3 August, freshly cut flowers, one of each species tested, were inserted into water pics filled with 20% sucrose solution. These were offered to E. puttleri, which had been released on 30 July in the observation cage with 10 potted potato plants. The pics were attached with rubber bands to thin, green bamboo stakes which were pushed into the soil, so that all blossoms were positioned at the same height and within 30 cm of the potato foliage.

Concurrently, potato leaves with aphid honeydew and without aphid honeydew, one of each per potato plant, were placed within the potato plant canopy. Healthy potato leaves, naturally contaminated with honeydew, had been collected from field-caged plants populated with Myzus persicae (Sulzer) and Macrosiphum euphorbiae (Thomas); droplets of honeydew were visible on each leaf. The leaves were held in water pics filled with 25%

Hoagland's solution (Hoagland & Arnon 1950) and were attached to bamboo stakes or directly to stems with twist ties. The introduced leaves were arranged to blend with the foliage as naturally as possible. At 1100 and 1500 h on 2 August and at 1400 and 1700 h on 3 August, 5 minute observations were made successively at each flower-plant combination to see if E. puttleri visited flowers and/or introduced leaves. The criteria for determining a visit to a flower or a leaf were the same as in the preceding study. Flowers used in this experiment were: white clover, Trifolium repens L.; chickweed, Stellaria pubera Michx.; red clover, Trifolium pratense L.; lambsquarters, Chenopodium album L.; lady's thumb, Polygonum persicaria L.; black-eyed susan, Rudbeckia serotina Nutt.; cranesbill, Geranium maculatum L.; daisy; wild mustard; vetch; quickweed.

Aphid Honeydew Resources - Cage Study (III) On 5, 6 and 14 August, potato leaves with and without aphid honeydew, one of each per plant, were placed within the canopy of the ten potato plants in the 4.5 m² x 1.8 m cage. The leaves were inserted into water pics and maintained and positioned as in the previous study (II). The wasps were the same E. puttleri released on 30 July. Ca. 240 E. puttleri were counted in the cage prior to this study. Observations were made at 1600 and 1700 h.

Survival on Aphid Honeydew To test the hypothesis that E. puttleri obtained necessary carbohydrates from aphid honeydew, the

survival of E. puttleri on different potential resources was measured. Groups of fifteen wasps were selected randomly from the same laboratory-reared cohort and each group was placed in individual 0.5 L clear plastic rearing jars. Holes, 3 cm in diameter, had been cut in the jar lids and bottoms and covered with fine dacron netting. The jars were laid on their sides and contained one of the following: 1) water; 2) potato leaf; 3) potato leaf and water; 4) potato leaf inoculated with aphids; 5) potato leaf inoculated with aphids, and water; 6) honey and water. We prepared three observations of each of the six treatments, for a total of 18 groups of wasps in each experiment.

Water was provided by inserting a dental wick into a 4 ml shell vial containing distilled water and leaving 2 cm of wick protruding from the vial. For the honey treatment, six fine lines of honey were streaked with a small brush on the walls of the jar. The potato leaves were maintained in water pics filled with 25% Hoagland's solution. The water and Hoagland's solution were replenished as needed, in all treatments, during the daily observation period. Leaves were changed every 4 days. For the aphid treatments, leaves were inoculated with 30 early stage nymphs from a mixed colony of M. persicae and M. euphorbiae and placed in jars 24 hours before beginning the experiment and before being used as replacement leaves during the experiment. The aphids began to produce honeydew within this 24 hour period.

The jars were placed in a walk-in environmental chamber maintained at $25 \pm 2^{\circ}\text{C}$, 16:8 (L:D) and 70-80% R.H. Each day, for 14 days, we counted the numbers of wasps alive in each jar. The experiment was repeated three times using wasps from a different cohort each time. Two of the cohorts were 2 days old and one was 8 days old.

Results

Nectar Resources - Field Study No wasps were observed on any of the flowers in the center of the plot, nor were any wasps observed on potato flowers. During the 48 hour period of the study, wasps parasitized 25% of the egg masses; total egg mortality attributed to E. puttleri was 59%. Although the flowering plants were removed on 5 July, the wasps and/or their progeny did persist in the potato plot. On 25 July, after L. decemlineata had colonized the plot, three E. puttleri were observed on CPB egg masses and 37 CPB egg masses, 35 of which had been attacked (i.e. at least one parasitized egg per mass) by E. puttleri, were collected from the plot. Potato aphids, M. euphorbiae, were observed in the plot and their honeydew could have provided a food source for E. puttleri.

Nectar Resources - Cage Studies (I) and (II) No E. puttleri were observed feeding or alighting on caged flowers in either study. In situations where various flowering plants or flowers

were placed next to potato plants, the wasps were most often seen on potato leaves or flying within the canopy of the potato plants. In the few instances where wasps were observed on flowering plants, they were on stems or leaves, not blossoms, and aphids were feeding on those plants. In study II, wasps were observed on potato leaves with aphid honeydew and leaves without aphid honeydew: 14 vs. 2 at 1100 h, 17 vs 7 at 1400 h, 19 vs 2 at 1500 h, and 26 vs 1 at 1700 h, respectively. Additionally, we observed the wasps engaged in a particular repertoire of behaviors associated with feeding on honeydew. The honeydew appeared to collect in the invaginations formed by veins in the leaves; wasps often stopped at these natural troughs, tipped forward and rocked back and forth, apparently feeding.

Aphid Honeydew Resources - Cage Study (III) More E. puttleri were observed on leaves contaminated with aphid honeydew than on clean leaves. At 1600 h we observed a mean \pm SEM of 27 ± 15.6 wasps on honeydewed leaves vs. 4 ± 4.4 on leaves without honeydew and at 1700 h, 18.9 ± 10.9 vs 1.7 ± 0.9 respectively. Wasps exhibited a flight behavior that may be associated with locating honeydew. They flew ca. 3-5 cm above the surface of the leaf in a pattern that appeared to be restricted to the area directly above the leaf. After alighting on the leaf, they frequently walked in a roughly zig-zagging pattern until they stopped, apparently at sources of aphid honeydew.

Survival on Aphid Honeydew E. puttleri can survive up to 14 days on the honeydew of M. persicae and M. euphorbiae; however, the survival rate is higher on a diet of honey and water (Fig. 1). Potato leaves do not appear to offer the wasps any source of nutrition.

Discussion

Although we never observed E. puttleri feeding on flower nectar in or around the test plots or in the field cages, flower nectar cannot be eliminated as a potential source of carbohydrate. However, the flowers tested, most of which are common wildflowers likely to be in bloom around potato fields in the Northeast, do not seem to provide a nutritional resource for E. puttleri.

The fact that the survival rate of E. puttleri on aphid honeydew is lower than on honey and water may mean that the honeydew of M. euphorbiae or M. persicae on potato may not fulfill all of its nutritional requirements. Lamb (1958) demonstrated that different groups of carbohydrates are represented in different amounts in the honeydew of various species of aphids. Hassett (1948) reported on the relative nutritional efficiency of different sugars for Drosophila melanogaster Meigen and concluded that individual species of insects have different specific carbohydrate requirements.

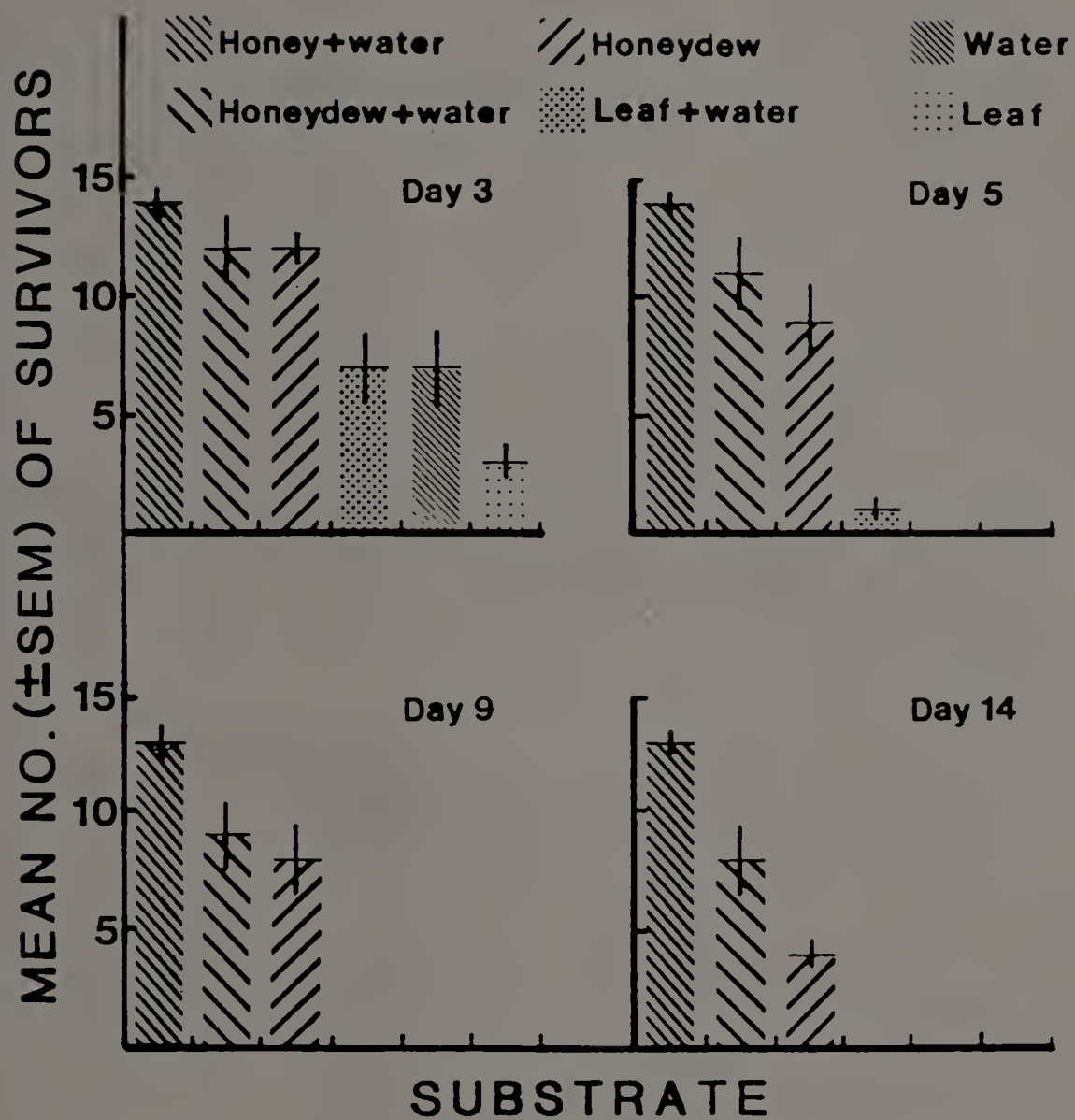


Fig. 1. Mean no. (\pm SEM) of *E. puttleri* survivors on six different substrates over fourteen days

In Colombia, E. puttleri parasitizes L. decemlineata which feeds on Solanum saponaceum Dunal (= S. torvum Swartz) (Grissell 1981). Our field observations in Palmira, Colombia during July 1987 (unpublished data) indicate that E. puttleri feeds on honeydew produced by various homopterans. E. puttleri was observed feeding on honeydew dropped on leaves of S. saponaceum by an armored scale insect colonizing an overhanging saman tree, Samanea saman (Jacq.) Merrill. Although this tree does not usually occur with stands of S. saponaceum, the unidentified diaspidid and other species of leafhopper, aphids and whitefly observed on S. saponaceum may provide more suitable honeydew for this parasitoid than did M. euphorbiae and M. persicae.

The investigations reported here were performed using wasps of varying ages. We found that all ages of wasps tested responded to aphid honeydew. We did not measure variation in response due to differences in age and this factor should be considered in designing future studies.

These results indicate that survival of E. puttleri may be enhanced by a source of honeydew in potato fields, but probably not by flower nectar. Lack of a suitable carbohydrate resource may decrease the survival rate of the parasitoid in the field and consequently reduce parasitism. It is necessary to determine whether E. puttleri can inflict significant mortality on its host population during periods of low host density and relatively low

temperatures if this resource is assured. Both of these conditions exist in late May and early June when overwintering CPB are emerging and beginning to oviposit on young potato plants

CHAPTER 3

DIURNAL TIMING OF OVIPOSITION ACTIVITIES OF EDOVUM PUTTLERI

Few observations of periodic behavior of insect parasitoids in natural or semi-natural conditions have been reported. Weseloh (1976) monitored the diel periodicity of oviposition by Parasetigena silvestris (=agilis) (Robineau-Desvoidy), a tachinid parasitoid, of gypsy moth larvae. Eckborn (1982) documented diurnal activities of Encarsia formosa Gahan, an aphelinid parasitoid of the greenhouse whitefly, Trialeurodes vaporariorum (Westwood). Saunders (1982) cites oviposition patterns exhibited by Orthoptera, Diptera, Lepidoptera and Hemiptera, but not by Hymenoptera.

Knowledge of a biological control agent's oviposition rhythm can be useful in evaluating its performance and developing management strategies. Preliminary field observations suggested that E. puttleri might have a diurnal oviposition rhythm. This study was undertaken to document and describe this rhythm.

Materials and Methods

E. puttleri females of the Colombian strain were from pupae shipped from the USDA/APHIS rearing facility in Mission, Texas. Upon arrival in our laboratory, the pupae and adults were held at $26 \pm 2^{\circ}\text{C}$, ca. 70% RH and a photoperiod of 16:8 (L:D). Adults were

fed honey and water. They were supplied with CPB eggs by the time they were four days old, and subsequently given fresh eggs every two or three days.

All times reported for field and laboratory experiments are Eastern standard time.

Visits to CPB Egg Masses in Field Cages. To facilitate observations of E. puttleri's response to CPB egg masses on potato plants, we used five 1.5 m³ cages constructed of fine-mesh dacron netting to confine female wasps in an arena with potato plants inoculated with CPB host eggs. Cages were placed on tilled, weed-free soil at the University of Massachusetts field research station in South Deerfield, Massachusetts. On the afternoon prior to each observation day, two fresh potato plants in pots were placed, 0.5 m apart on center, on the ground in the middle of each cage. The potato plants were 11 ± 3 days post-emergent and 35 ± 5 cm tall. They were paired by matching similar architectural qualities. Six of the 12 caged plants were inoculated with five CPB egg masses. The egg masses, less than 12 hours old and on a small piece of excised potato leaf, were obtained from our greenhouse colony. These were pinned on the abaxial leaf surface of the caged potato plants, and were distributed as evenly as possible in the plant canopy.

For each observation day, 75 female E. puttleri, from the same cohort were released under the plants at ground level between 1500 and 1700 h. Cohorts were from 7 to 12 days old.

Observations were made, beginning 12 hours after the wasps were released into the cages on five different days between 14 July and 5 August, 1986. Another set of observations were made, beginning 40 hours after wasps were released, on five different days between 14 August and 13 September, 1986. On 15 July, the sun rose at 0450 h and on 14 August, at 0550 h. Five minute observations of wasp behavior on each plant at two hour intervals began at 0700 h and ended at 1700 h for a total of six observation periods per day. During the five minute observation at each plant with eggs, individual wasps were recorded as being on eggs if they were seen ovipositing, walking, or resting on an egg mass.

Data from the two sets of observations, beginning 12 hours and 40 hours post-release, were examined for differences between the proportions of wasps observed on eggs during the hours of peak visitation using a two-sample t - test (Statistical Graphics Corp. 1986). The data were transformed by a factor of $\log X + 1$ prior to analysis. Where the differences were not significant, standard errors of the means were calculated for the pooled data. Tukey's honestly significant difference method was used to determine differences among means ($n = 10$) (Statistical Graphics Corp. 1986).

Laboratory Observations. Groups of five, 11 day-old, female wasps were randomly selected from cohorts of laboratory-reared E. puttleri. On each of the three days the experiment was conducted, four cages, containing five wasps each, were observed. Twelve to fourteen hours prior to the beginning of each of the three replications of the experiment, the groups of wasps were caged, in 0.5 l plastic jars, with a CPB egg mass (ca. 25 eggs) on a small piece of excised potato leaf. The eggs were less than 12 hours old. The purpose of exposing the wasps to these eggs was to ensure that they were not host-starved at the beginning of the experimental photophase. The cages were clear plastic jars with 3 cm diam. holes, covered with fine dacron netting, cut in the lids and bottoms.

The experiment was conducted under controlled conditions at the temperatures and photophase in which E. puttleri were reared ($26 \pm 1^{\circ}\text{C}$ and 16:8 (L:D)); honey and water were supplied. The average relative humidities for the three replicates of the experiment were between 55-62%. At the beginning of each hour of the experimental photophase, 50 CPB eggs were offered to each group of wasps. The egg mass was placed, with the leaf side down and eggs up, on the bottom of the cage. At the end of each hour, eggs were removed to a rearing chamber. All CPB eggs used in these experiments were less than 12 hours old and were obtained

from our greenhouse-reared colony. These methods reflect optimal conditions for parasitism as reported by Lashomb et al. (1987).

Each female can parasitize an average of 8 eggs per day and up to 15 eggs in one day (unpublished data). Therefore, 10 eggs per female wasp per hour appeared to ensure that the number of host eggs would not be a limiting factor in this experiment.

To determine whether E. puttleri oviposits during the scotophase, 50 CPB eggs were placed in the cages within the five minute period prior to the beginning of the scotophase. These eggs were removed to a rearing chamber within the five minute period after the beginning of the photophase.

Each group of 50 eggs was reared in individual petri dishes, segregated according to photophase hours or scotophase. Egg deposition was quantified by counting the number of E. puttleri pupae in each group.

Data were analyzed using a X^2 test of independence for I independent samples (Siegel 1956) to test for significant differences among the three replicates with respect to the hours during which the highest proportion of eggs were laid. Where the differences were not significant, standard errors of the means were calculated for the pooled data ($n = 3$).

Results and Discussion

Visits to CPB Egg Masses. The *t* - tests revealed no significant differences between the proportions of wasps visiting CPB egg masses during the 12 h and 40 h post-release observations. The highest proportion of wasps observed on egg masses in field cages was during the five-hour period between 1100 and 1600 h, ca. 6-11 h after sunrise (Fig. 2). A mean of 83% ($N = 162$) of E. puttleri were observed visiting egg masses during this period.

Laboratory Observations Among the three replicates, there were no significant differences in the proportion of eggs laid during the hours of peak oviposition. The highest proportion of oviposition was during the four hour period between 1400 and 1800 h, 8-12 h after the lights were turned on at 0600 h (Fig. 3). A mean of 67% ($n = 3$) of the total oviposition ($N = 442$) occurred during this interval.

There was no evidence of oviposition by E. puttleri during the scotophase.

These results indicate that under field and laboratory conditions, E. puttleri appear to have a diurnal rhythm of oviposition. In the laboratory the wasps began ovipositing at a relatively low, but steady, frequency soon after the onset of light. Between 0600 and 1400 h, prior to the peak oviposition period, the wasps deposited an mean of 22% ($n = 3$) of their daily complement of eggs. This is in contrast to the field, where a

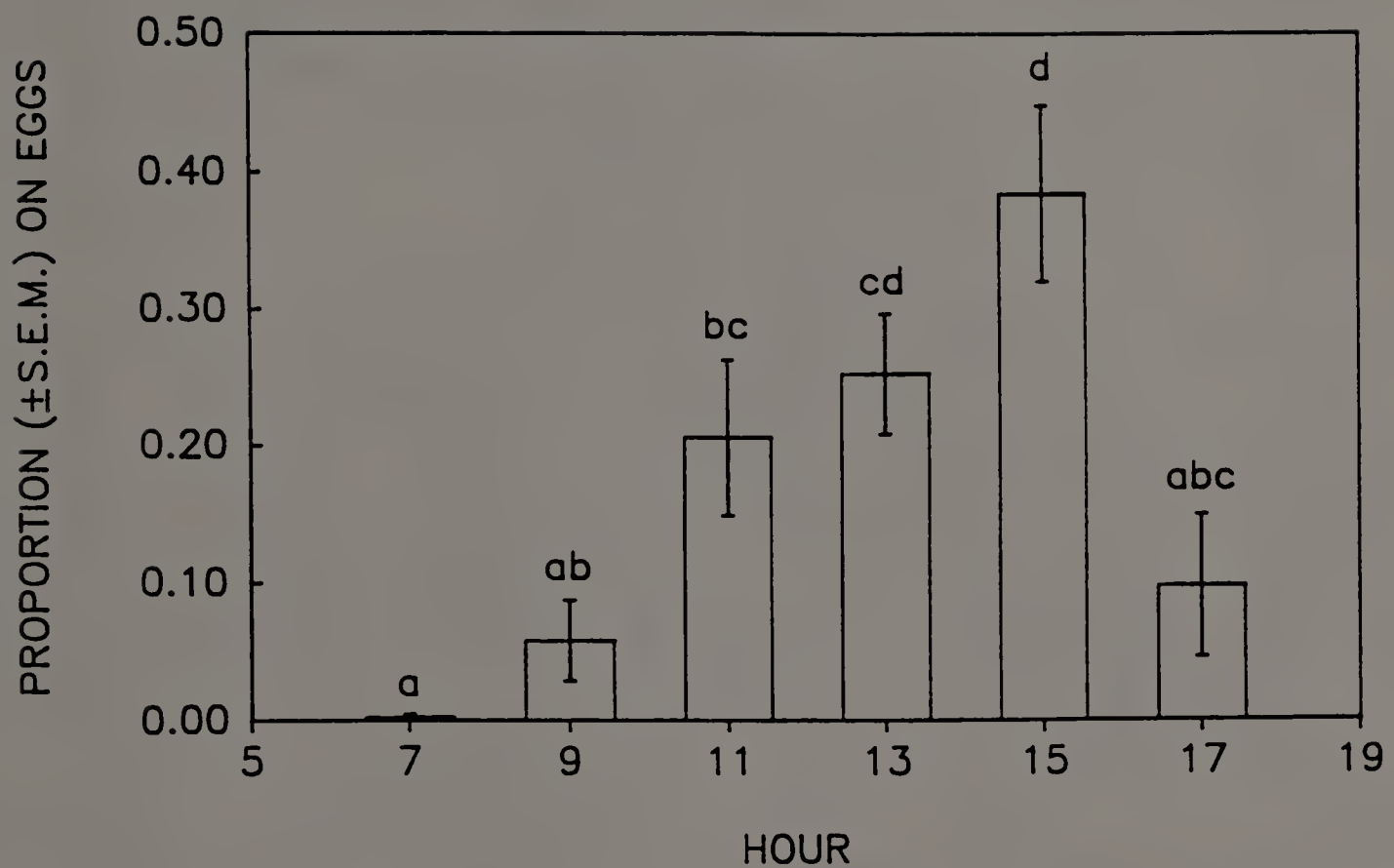


Fig. 2. Diurnal periodicity of visitations by *E. puttleri* to CPB egg masses on field-caged potato plants between 0700 and 1800 h. Sunrise occurred between 0450 and 0550 EST over the observation period. Bars with the same letter are not significantly different (Tukey's honestly significant difference test, $P < 0.05$, ($n = 10$))

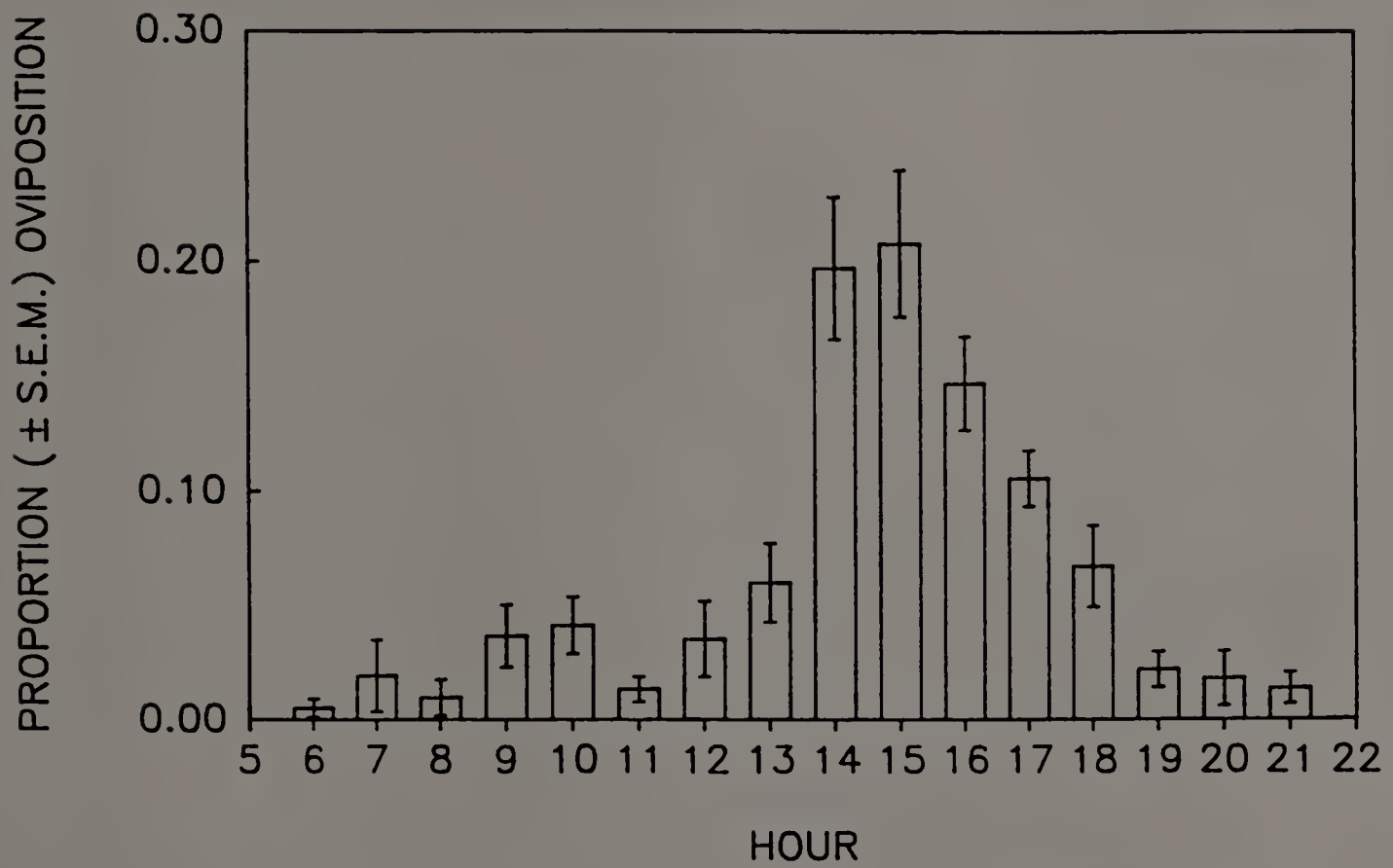


Fig. 3. Periodicity of oviposition by *E. puttleri* during photo-phase (16:8 (L:D), $26 \pm 1^\circ\text{C}$). Onset of light occurred at 0600 h. ($n = 3$)

mean of 6% ($n = 10$) of all the wasps observed on plants visited eggs between 0700 and 1100 h, prior to the peak egg visitation period. It appears that under constant, optimum temperatures in the laboratory, E. puttleri begin to oviposit soon after the onset of light, but in the field, at cooler morning temperatures, oviposition may be retarded until environmental conditions ameliorate. Once this occurs, then the wasps may be able to deposit a proportion of their eggs relatively quickly.

An examination of how this rhythm is modified by temperature, humidity and other weather conditions would be necessary to a full understanding of the behavior of the parasitoids in potato fields. Lashomb et al. (1987) reported that the optimal temperature for parasitization of CPB eggs by E. puttleri is 26.5°C and that the threshold below which no oviposition occurs is 17°C. Obrycki et al. (1985) suggested that the effectiveness of E. puttleri at the beginning of the potato-growing season might be limited by climatic conditions. This study suggests that E. puttleri's diurnal peak oviposition activities may coincide with favorable temperatures that frequently occur early in the potato-growing season.

Records from the weather station (Model CRT21, Campbell Scientific) at our field cage site showed that during late May through mid-June, which is the beginning of the potato growing season, temperatures often rise above 22°C during the period

between 1100 and 1600 h (17 and 20 of 26 days in 1985 and 1986, respectively), when E. puttleri would be ovipositing in the field. Our observations indicate that the parasitoids become active in the field when temperatures reach ca. 22°C. Mean diurnal temperatures ($n = 8$) in the field cages ranged from 20°C to 34.5°C on the ten observation days. These data and data from a previous study on E. puttleri food sources (Idoine & Ferro 1988) indicate that temperature may not be the major limiting factor in E. puttleri's ability to parasitize first-generation CPB eggs in late May through mid-June.

Additionally, the effects of pesticide application on E. puttleri might be moderated by timing disturbances in the field to avoid the period of peak oviposition activity of this parasitoid. This idea has been proposed to protect honey bees foraging in corn. Mason & Tracewski (1982) found the peak abundance of pollen-collecting bees occurred from 0900 to 1000 h and they encouraged timing insecticide applications to avoid spraying foraging bees. If a characteristic rhythm can be predicted under field conditions, management of E. puttleri may be enhanced.

CHAPTER 4

PERSISTENCE OF EDOVUM PUTTLERI ON POTATO PLANTS AND PARASITISM OF EGGS OF LEPTINOTARSA DECEMLINEATA: EFFECTS OF RESOURCE AVAILABILITY AND WEATHER

When a parasitoid needs more than its host for nutrition, the availability of nutritional resources may influence the effectiveness of the parasitoid as a biological control agent. Direct field observation of insect parasitoids can reveal how they respond to hosts and nutritional resources. Although the information can be useful for assessment, few studies have reported on the activities and distribution of parasitoids directly observed in nature.

Smith and Prokopy (1981) and Malavashi, Morgante and Prokopy (1983) provide examples of these kinds of observations for plant parasitic tephritids. Danks (1975) examined the habitat, feeding habits and diel patterns of the tachinid parasitoid, Winthemia rufopicta (Big.), in relation to parasitism of its Heliothis spp. hosts.

Efforts have been made to monitor the activities of hymenopterous parasitoid populations in the field. Lewis et al. (1971) used pheromone traps to determine the timing of Cardiochiles nigriceps Vierick activity, with the aim of establishing a method for monitoring and evaluating the parasitoid population. In another study, Lewis et al. (1972) made direct

observations and counts of female C. nigriceps searching for Heliothis spp. in cotton to correlate parasitoid population density with parasitism. Their purpose was to establish number of female parasitoids per acre needed for specified levels of control.

In the first field study of its kind, Waage (1983) endeavored, by direct observation, to relate the foraging time allocation of a parasitoid population to host density and subsequent levels of parasitism. He emphasized that field studies assessing natural patterns of foraging and their consequences would be valuable for evaluating the agricultural efficiency of parasitoids. Prokopy (1982) suggested that quantifying insect activities in the context of habitat resource structure in nature is a useful first step in analyzing resource foraging behavior. Weseloh (1971) also indicated that information on habitat selection would help in evaluating the searching capacity of parasitoids and lead to ways of augmenting their effectiveness in suppressing host populations.

We have shown that E. puttleri needs a source of carbohydrate to survive more than five days in the laboratory. Aphid honeydew and the honeydew of whiteflies and scale insects, can provide necessary carbohydrates (Idoine & Ferro, 1988). This study was undertaken to determine if the presence or absence of honeydew influenced the distribution of E. puttleri and parasitism of its

host on individual plants. We also wanted to test whether or not a single potato plant could be considered a "patch" in foraging terms (Waage 1979), i. e., did the type of resources available induce arrestment on an individual plant?

The potential effects of weather must be considered in field observations. In order to evaluate the influence of weather factors on parasitism and mortality of L. decemlineata eggs by E. puttleri, we monitored temperature, humidity, solar radiation, rainfall and wind speed.

Materials and Methods

Rearing E. puttleri wasps were from pupae shipped from the USDA APHIS rearing facility in Mission, Texas. The pupae and adults were reared at a 16:8 (L:D) photoperiod, $26 \pm 2^\circ\text{C}$ and ca. 70% relative humidity. Adults were provided with honey and water and allowed to feed and drink ad lib. They were supplied with Colorado potato beetle eggs on the third or fourth day after emergence, and subsequently given fresh eggs every two or three days; thus, all female wasps used in these experiments had prior experience with host eggs.

Effects of resource availability on distribution Six 1.5 m^3 cages constructed of fine-mesh dacron netting were placed on tilled, weed-free soil at the University of Massachusetts field research station in South Deerfield, Massachusetts. Two potato

plants in 20 cm diameter plastic pots were placed, 0.5 m apart on center, on the ground in the middle of each cage. The potato plants were 11 ± 3 days post-emergent and 35 ± 5 cm tall at the time of each set of observations. Plants were paired by matching similar architectural qualities of height, foliage density, stalk density and general shape. Each pair of plants was treated with different combinations of resources in the following way: Pair 1: plant 1 - with aphids only (A), plant 2 - with aphids and eggs (A/E); Pair 2: plant 1 - with aphids (A), plant 2 - with eggs and no aphids (C/E); Pair 3: plant 1 - with aphids and eggs (A/E), plant 2 - no eggs and no aphids (C); Pair 4: plant 1 - with aphids and eggs (A/E), plant 2 - with eggs and no aphids (C/E); Pair 5: plant 1 - no aphids and no eggs (C), plant 2 - with eggs and no aphids (C/E). For plants with eggs, five CPB egg masses less than 12 hours old on a small piece of excised potato leaf were obtained from our greenhouse colony and pinned on the abaxial surface of the potato leaves. The masses were distributed as evenly as possible in the plant canopy. For plants with aphids, 50 ± 5 early instar Macrosiphum euphorbiae (Thomas) were distributed on the plants within 12 hours of placement in the cages. The aphids began producing honeydew within this period.

A random number assignment determined the placement of treated plants within the cages, as well as the placement of paired plants among the cages for each observation day. Seventy-

five female E. puttleri from the same cohort (7 to 12 days old) were released between the plants at ground level, between 1600 and 1800 h EDST. Fresh plants and wasps were used for each of the ten replications of the experiment. Observations began 14 to 16 hours after the wasps were released into the cages, on each of five days between 15 July and 26 August, 1986. Another set of observations was made on five days between 14 August and 13 September, 1986, 38 to 40 hours after wasps were released. On each observation day, paired plants were examined at two hour intervals beginning at 0800 h and ending at 1800 h. All times given are EDST.

Each plant was observed from a succession of angles for five minutes and the locations of individual wasps were recorded. These locations were defined as follows: up = resting or walking on the upper surface of a leaf; under = resting or walking on the under surface of a leaf; on eggs = walking, feeding, or ovipositing on an egg mass; flying = flying within the canopy of the plant. We used paired *t* - tests to detect differences in locations of the wasps on plants at different times of day (Statistical Graphics Corp. 1986).

Although we observed and counted wasps on the walls of the cage, we did not include these in our analysis of their distribution in response to resource availability. Since the walls of the cages tended to reflect and concentrate light in an artificial and unpredictable way, we hypothesized that E.

puttleri, which demonstrates some phototactic response (Schroder 1985), could be responding to light rather than to the types of resources on the caged plants.

Effects of resource availability on parasitism All CPB eggs were collected after 50 ± 1 h of exposure to E. puttleri in the field cages. They were held in the laboratory at the same conditions as the adult wasps and were examined twice daily for development of CPB larvae and E. puttleri larvae and pupae. CPB larvae were removed from the egg masses shortly after eclosion in order to prevent them from consuming developing parasitoids or dead eggs. An egg was considered to be parasitized if the larva or pupa of E. puttleri was observed. An egg was classified as dead if no CPB larva or pupa developed. Mortality was the sum of parasitized and dead eggs.

Effects of weather on parasitism and mortality Every hour, prior to and just after each set of observations, the temperature was recorded using a probe (Tele-Thermometer, Model 43TD, Yellow Springs Instrument Co.) positioned in the potato plant canopy. A weather station (Model CRT21, Campbell Scientific) ca. 400 m from the site provided measurements of humidity and solar radiation.

The results of Ferro and Chapman's (1979) study of twospotted spider mite showed that the use of saturation deficit (SD) as an index of humidity rather than % relative humidity (RH) presented a clearer relationship between the interaction of temperature and

humidity on mite egg mortality. SD is a measurement of the absolute number of molecules in the air rather than the relative number measured by %RH. SD, the most commonly used index of absolute humidity, is expressed here in mmHg. SD is the difference between saturation vapor pressure (VPs) and actual vapor pressure (VPa). Values for VPs were obtained from the International Critical Tables (Washburn et al. 1928). VPa is the product of RH/100 and VPs.

We used a multiple regression routine (Statistical Graphics Corp. 1986) to examine the relationship of temperature, humidity, and solar radiation to parasitism and mortality of CPB eggs by E. puttleri. On each of the ten days, the CPB eggs were collected after 48 hours; each day of observations was considered a replication of the experiment. We measured the proportion of parasitism and mortality for each of the five egg masses on each plant. The regressions were run using the mean values of parasitism and mortality for each plant (n = 5). First, we analyzed the data from each of the six different plant/resource combinations. Then, using a full reduced model procedure (Neter & Wasserman 1974), we examined the differences among the regressions to determine if the data could be pooled.

Results and Discussion

Effects of resource availability on distribution Most E. puttleri could be found on the abaxial surfaces of potato leaves early in the morning. Beginning 14 h after the wasps had been released, we observed significantly more wasps under leaves of individual plants at 0800 h than under leaves at 1400 h ($\bar{x} \pm \text{SEM}$ of 9 ± 0.6 vs 3 ± 0.5 , $t = 8.16$, $df = 59$, $\alpha = 0.05$), the hour of the peak egg visitation period during which the fewest wasps were observed on the under surfaces of leaves. Observations beginning 38 h after the wasps were released revealed no significant difference between the numbers of wasps under leaves at 0800 h than at 1400 h although the numbers on the upper surfaces of leaves increased from morning to early afternoon. Apparently, wasps in the cages spent the night off the plants, but came back to the plants during mid-day.

During both the 14 h and 38 h post-release observations, we noted a significant difference between the numbers of wasps on the upper surfaces of leaves at 0800 h than at 1400 h ($\bar{x} \pm \text{SEM}$ of 1 ± 0.2 vs 3 ± 0.3 , $t = -3.25$, $df = 59$, $\alpha = 0.05$ and 1 ± 0.1 vs 2 ± 0.2 , $t = -3.30$, $df = 59$, $\alpha = 0.05$, respectively). Wasps were not often seen flying early in the morning; fewer wasps were seen flying at 0800 h than at 1200 h during both the 14 h and 38 h post-release observations ($\bar{x} \pm \text{SEM}$ of 0.2 ± 0.1 vs 0.6 ± 0.1 , $t =$

-2.96, $df = 59$, $\alpha = 0.05$ and 0.1 ± 0.03 vs 0.6 ± 0.1 , $t = -2.75$, $df = 59$, $\alpha = 0.05$, respectively).

The wasps appear to follow a pattern of sheltering under leaves or, in our experiments, on the walls of the cages during the night and early morning hours. Between 0800 and 1000 h, they begin to crawl and fly to the upper surfaces of leaves, where they can be seen feeding on available honeydew. At ca. 1200 h, flight activity peaked and then a well-defined period of visitations to egg masses occurred between 1200 and 1700 h (Idoine and Ferro, in press).

We examined the possibility that wasps would shelter for the night in greater numbers on plants with eggs and/or aphid honeydew and subsequently remain on those plants during the peak egg visitation period. We assumed, that since we saw few wasps walking or flying at 0800 h and at 1800 h, most wasps found under leaves at 0800 h had probably been there all night. Several night observations in the summer of 1985 suggested this, and the assumption was corroborated by laboratory studies that showed that E. puttleri does not oviposit during the night (Idoine and Ferro, in press). Data from the observations beginning 14 h after the wasps were released into the cages show no significant differences in the distribution of wasps between plants with aphids and plants without aphids. The 38 h post-release observations indicate that although the absolute numbers of wasps are higher on plants with

aphids than without aphids early in the morning (Fig. 4, clear bars), the differences are not significant.

However, in the afternoon during the peak egg visitation period, (Fig. 4, hatched bars), significantly more wasps were found on plants with aphids and eggs when these were paired with plants with no aphids. For the plant combination A/E-C, $t = 2.9$, $df = 4$, $\alpha = 0.05$, and for A/E-C/E, $t = 4.2$, $df = 4$, $\alpha = 0.05$. Thus, at the spatial level of this experiment, wasps do not shelter overnight in significantly greater numbers on plants with aphids than without aphids, although during the peak egg visitation period the presence of aphid honeydew appears to influence the distribution of wasps between plants.

During the 14 h post-release observation experiment the total number of wasps on the paired plants decreased between 0800 h and 1400 h; apparently wasps were moving off the plants to other places in the cages. During the 38 h post-release observation experiment, in the cages where a plant combination offered both aphid honeydew and eggs, more wasps appeared on plant combinations with eggs and aphid honeydew at 1400 h than at 0800 h. In the cages where plant combinations offered aphids or eggs only, the same number of wasps, or fewer, appeared on the plants at 1400h as at 0800h. The combination of resources (aphid honeydew and eggs) seemed to be a more powerful arrestment than either resource alone.

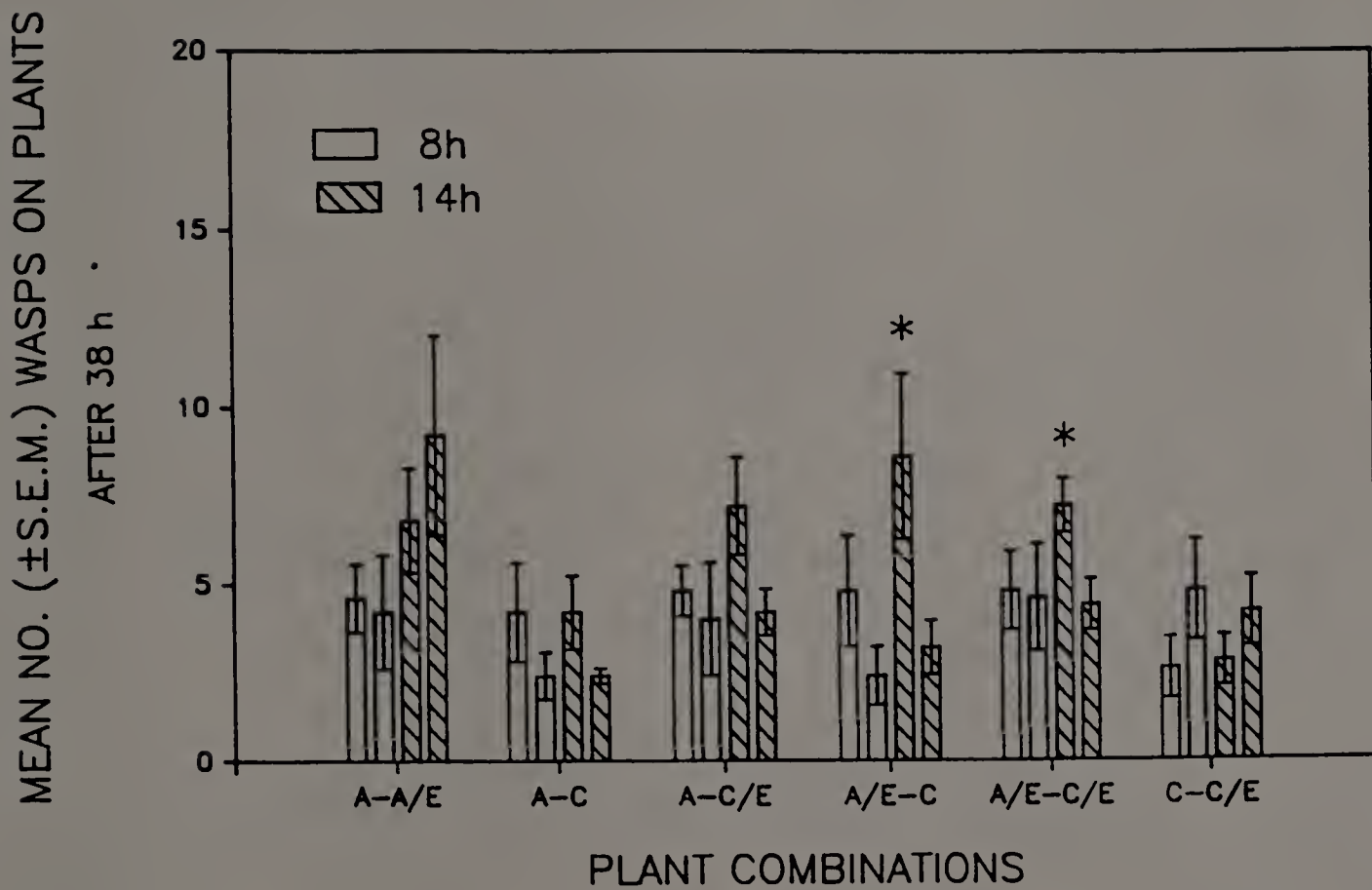


Fig. 4. Comparison of the distribution of *E. puttleri* between two caged plants at 0800 h and 1400 h. Observations were made on five days beginning at 38 h (August 14 - Sept 13) after release of *E. puttleri* into field cages. Letters below X axis represent the resource status of the plants in each combination: A = with aphids; A/E = with aphids and eggs; C = no aphids, no eggs; C/E = no aphids, with eggs. The letters correspond, left to right, with the vertical bars. Stars above bars indicate significance.

The 14 h post-release and the 38 h post-release experiments tested different wasps. Further experimentation, testing the same wasps after 14 h and 38 h, would demonstrate whether or not a significant change in behavior was taking place over time. Additionally, it is possible that larger quantities of honeydew on leaves after 38 h than after 14 h may have been responsible for the significant differences in numbers of wasps associated with honeydewed plants.

Wasps were fed honey prior to their release. This could have influenced the behavior of the wasps in several ways. First, wasps may have been satiated with respect to their carbohydrate needs at the time of release and the effects of this satiation may have taken more than 14 hours to dissipate; the wasps may not have been hungry enough for aphid honeydew to affect their persistence on plants during the first 14 hours. Secondly, the experience of feeding on honey may have conditioned a preference for honey rather than aphid honeydew. Only after experience with aphid honeydew, might the wasps begin to respond noticeably to aphid honeydew. Vet and van Opzeeland (1984) demonstrated that prior olfactory and microhabitat experiences of adult female parasitoids may influence subsequent behavioral responses. After a period of contact with an alternative microhabitat, however, the preference pattern may change. In the case of E. puttleri,

carbohydrates, in various forms, may influence microhabitat preference.

After 14 h, the mean distribution of wasps in relation to honeydew and/or eggs, during the peak oviposition period between 12 and 17 h, was not significantly different between the two plants in each cage (Fig. 5). However, in the 38 h post-release experiment, the distribution of wasps, apparently in response to the availability of honeydew and eggs, was significantly different between plants. For the plant combination A-A/E, $t = -2.1$, $df = 14$, $\alpha = 0.05$; A-C, $t = 3.6$, $df = 14$, $\alpha = 0.05$; A-C/E, $t = 2.8$, $df = 14$, $\alpha = 0.05$; A/E-C, $t = 5.4$, $df = 14$, $\alpha = 0.05$; A/E-C/E, $t = 4.6$, $df = 14$, $\alpha = 0.05$; C-C/E, $t = -2.35$, $df = 14$, $\alpha = 0.05$. Additionally, the total number of wasps on the plant combination A-A/E was higher than on the plant combination C-C/E. Significantly more wasps persisted in resource patches consisting of plants with aphids and eggs than in patches with eggs only.

Vinson et al. (1978) described the role of honeydew in stimulating searching and retention in host infested areas of the parasitoid Microterys flavus (Howard). In their laboratory study, the honeydew was produced by the parasitoid's host, Coccus hesperidum L. The honeydew influenced the retention of the parasitoid female in host contaminated areas by reducing locomotion and increasing frequency of turning. E. puttleri appears to feed on the honeydew of various homopterans (Idoine &

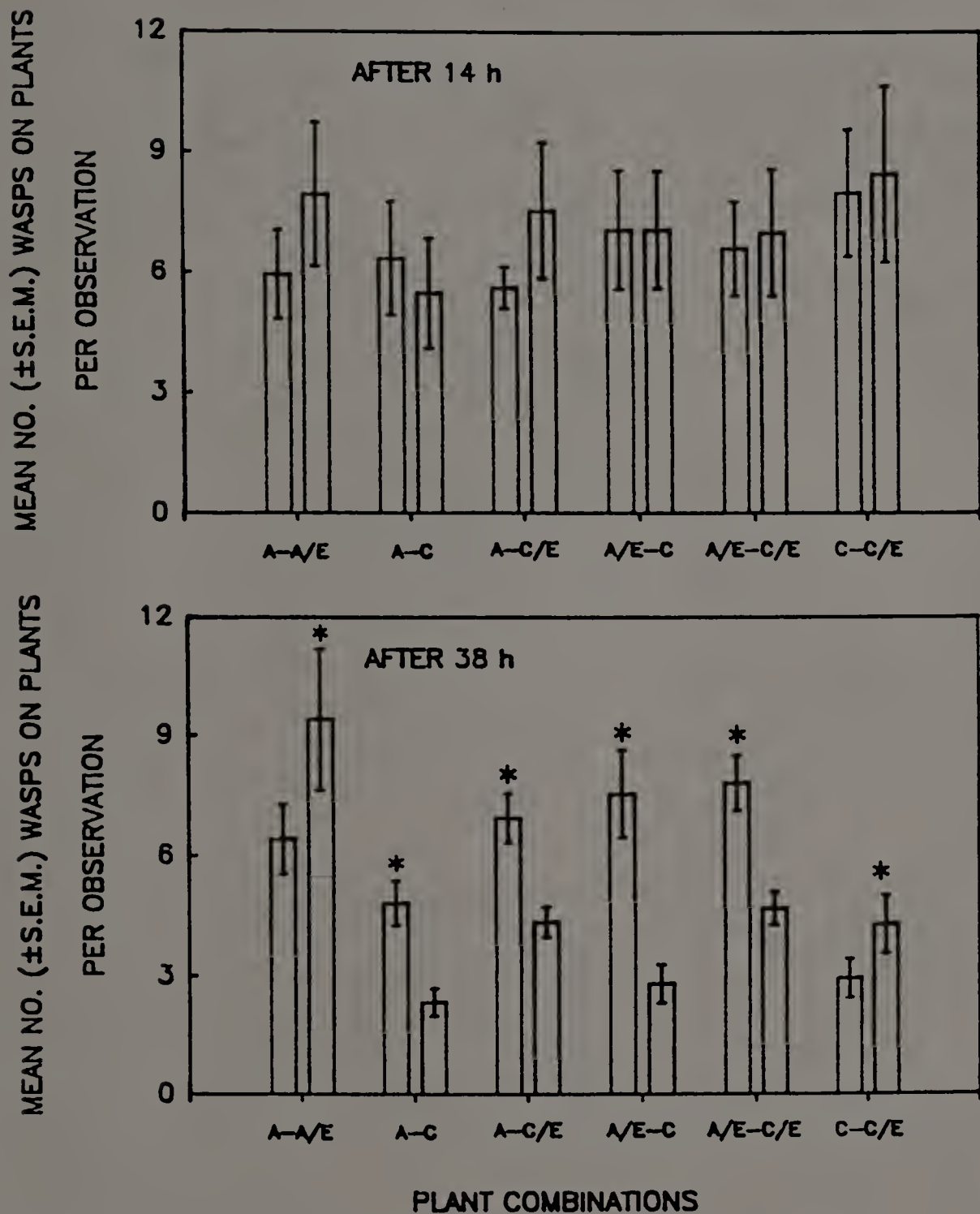


Fig. 5. Comparison of the distribution of *E. puttleri* between two caged plants during the peak CPB egg visitation period (12 h - 17 h). Observations were made during the day beginning at 14 h (July 15 - August 5) and at 38 h (August 14 and Sept 13) after release of *E. puttleri* into field cages. Letters below X axis represent the resource status of the plants in each combination: A = with aphids; A/E = with aphids and eggs; C = no aphids, no eggs; C/E = no aphids, with eggs. The letters correspond, left to right, with the vertical bars. Stars above bars indicate significance

Ferro, 1988) and honeydew may increase the egg-foraging persistence of this wasp. Our study shows retention of E. puttleri on a larger scale, over the range of two plants in a field cage, rather than on the scale of a petri dish, as in the study of Vinson et al. (1978).

Waage (1979) suggested that questions of foraging efficiency in parasitoids should take into consideration the entire sequence of responses to the patchiness of host distribution and that within patch arrestment stimuli should be considered. Here, we have shown that aphid honeydew apparently acts as an arrestment stimulus for E. puttleri. It is necessary to consider this factor when evaluating the efficacy and adaptivity of E. puttleri foraging for CPB eggs in potato.

Effects of resource availability on parasitism Although the presence of honeydew in patches with eggs seems to increase the foraging persistence of E. puttleri, the percentage of eggs parasitized and killed is not significantly higher (Fig. 6). Further experimentation, simulating a more natural environment where fresh eggs are introduced daily, is necessary to examine whether persistence in a patch measured for more than 38 hours would significantly affect parasitism and mortality.

Effects of weather on activity. Using the full reduced model procedure (Neter & Wasserman 1974), no differences were detected among the regressions of parasitism and mortality on temperature

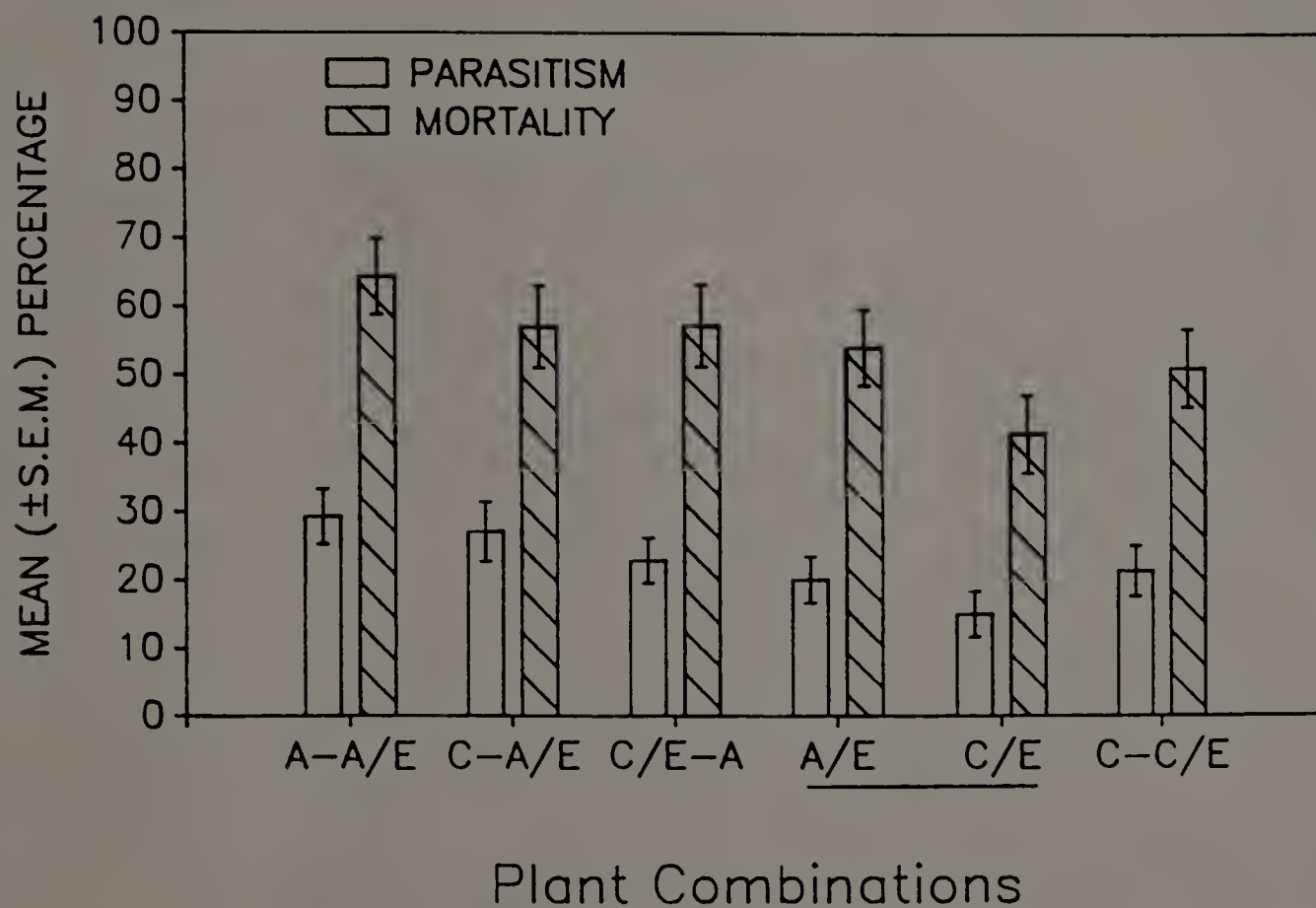


Fig. 6. Comparison of parasitism and mortality of CPB eggs caused by E. puttleri on paired plants with different resource combinations. Letters below X axis represent the resource status of the plants in each combination: A = with aphids; A/E = with aphids and eggs; C = no aphids, no eggs; C/E = no aphids, with eggs. (n = 50) Plant pairs within the same cage are designated by underscores.

or saturation deficit for the six different plant/resource combinations and the data were pooled. Temperatures on each observation day were different, as were values for saturation deficits. The highest mean parasitism (61.2%) and mortality (93.1%) of egg masses occurred when the mean temperature during the peak oviposition period was ca. 26°C (Fig. 7), which agrees closely with laboratory data (Lashomb et al. 1987).

Although the data show that E. puttleri parasitizes host eggs optimally over a relatively narrow temperature range (ca. 24°C - 27°C), mortality was high at lower temperatures. The lowest mean temperature at the time of peak egg visitation in this study was ca. 20°C and mortality at this temperature was above 70%. These trends, and those in Fig. 8 were modeled using polynomial regression equations fitted to the data. For parasitism, $r = 0.60$, $P < 0.21$ and for mortality, $r = 0.75$, $P < 0.05$. Pak et al. (1985) reported that activity and parasitism in different strains of Trichogramma spp. varied independently at a range of temperatures, suggesting that two different temperature-dependent mechanisms may influence these characteristics. In our study, the regression analysis indicates that the functional relationship of temperature to fatal probing by E. puttleri may be different than it is to oviposition.

The percentage of eggs killed by E. puttleri appears to be affected by absolute humidity, with the highest mortality

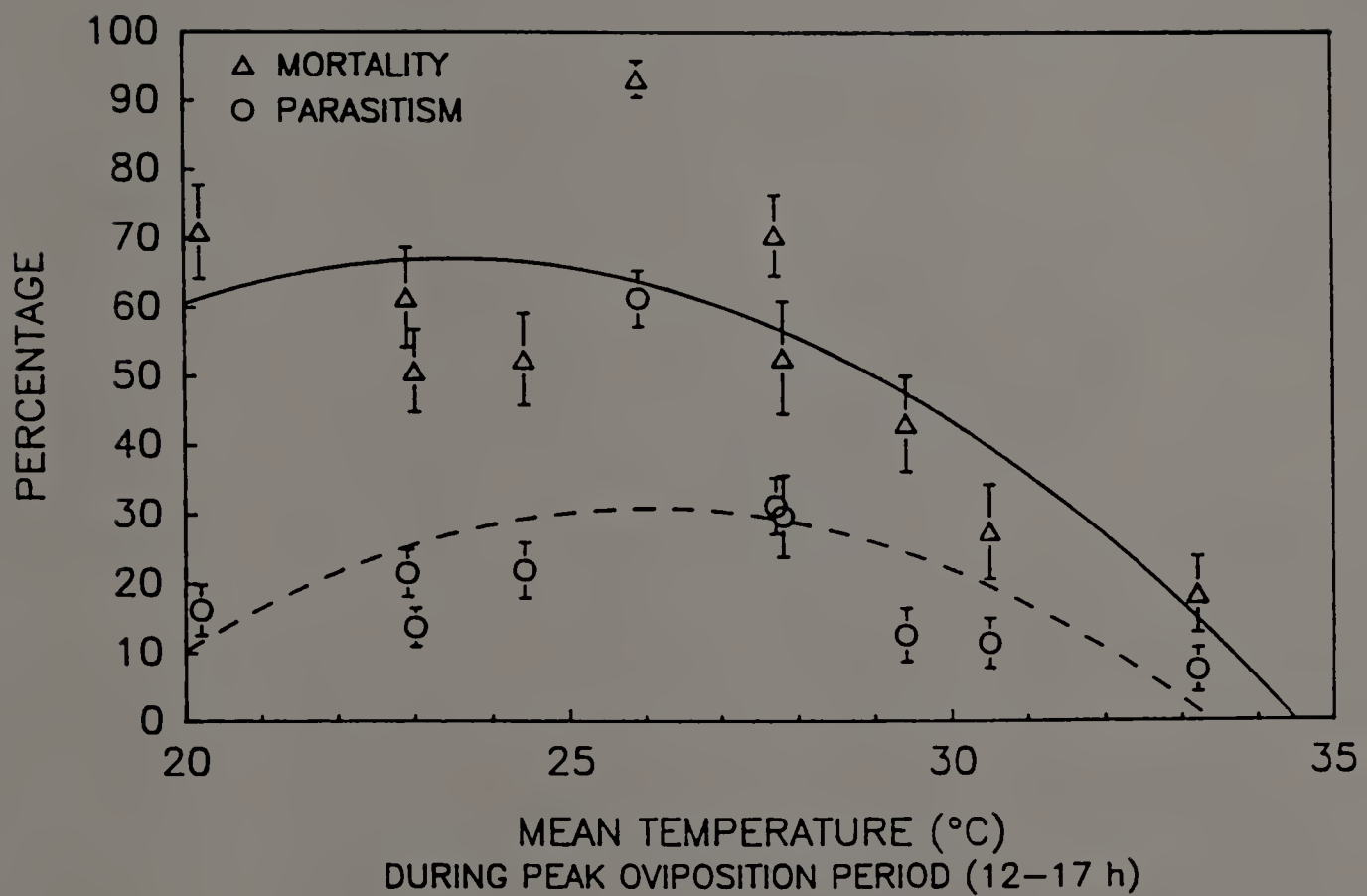


Fig. 7. Quadratic trend in percentage of parasitism and mortality of CPB eggs caused by *E. puttleri* at temperatures during the peak host egg visitation period

occurring at a saturation deficit of 8 - 12 mmHg and maximum parasitism at 10 mmHg (Fig. 8). For parasitism, $r = 0.57$, $P < 0.24$ and for mortality, $r = 0.92$, $P < 0.002$. Thus, saturation deficit appears to be significantly related to E. puttleri's ability to kill CPB eggs. At both low and high levels of saturation deficit, parasitism and mortality declined. This may have been the result of searching activity decreasing in response to an increase or decrease in humidity from the preferred absolute moisture in the air. Similarly, Juillet (1964) found that trap catches of braconid and ichneumonid parasitoids were affected by relative humidity. He concluded that an increase in relative humidity favored flight activity of ichneumonids and reduced that of braconids.

Solar radiation appeared to account for none of the variation in parasitism and mortality. As solar radiation increased, values of parasitism and mortality decreased slightly.

Vinson and Barbosa (1987) noted the increased interest in the nutritional ecology of insect predators and parasitoids as researchers examine the potential use of beneficial insects in pest management. Our study shows E. puttleri foraging in CPB host patches responds to food resources produced by species other than its host can influence its persistence within a patch. An understanding of nutritional relationships such as these can provide insight for developing management tools in applied biological control.

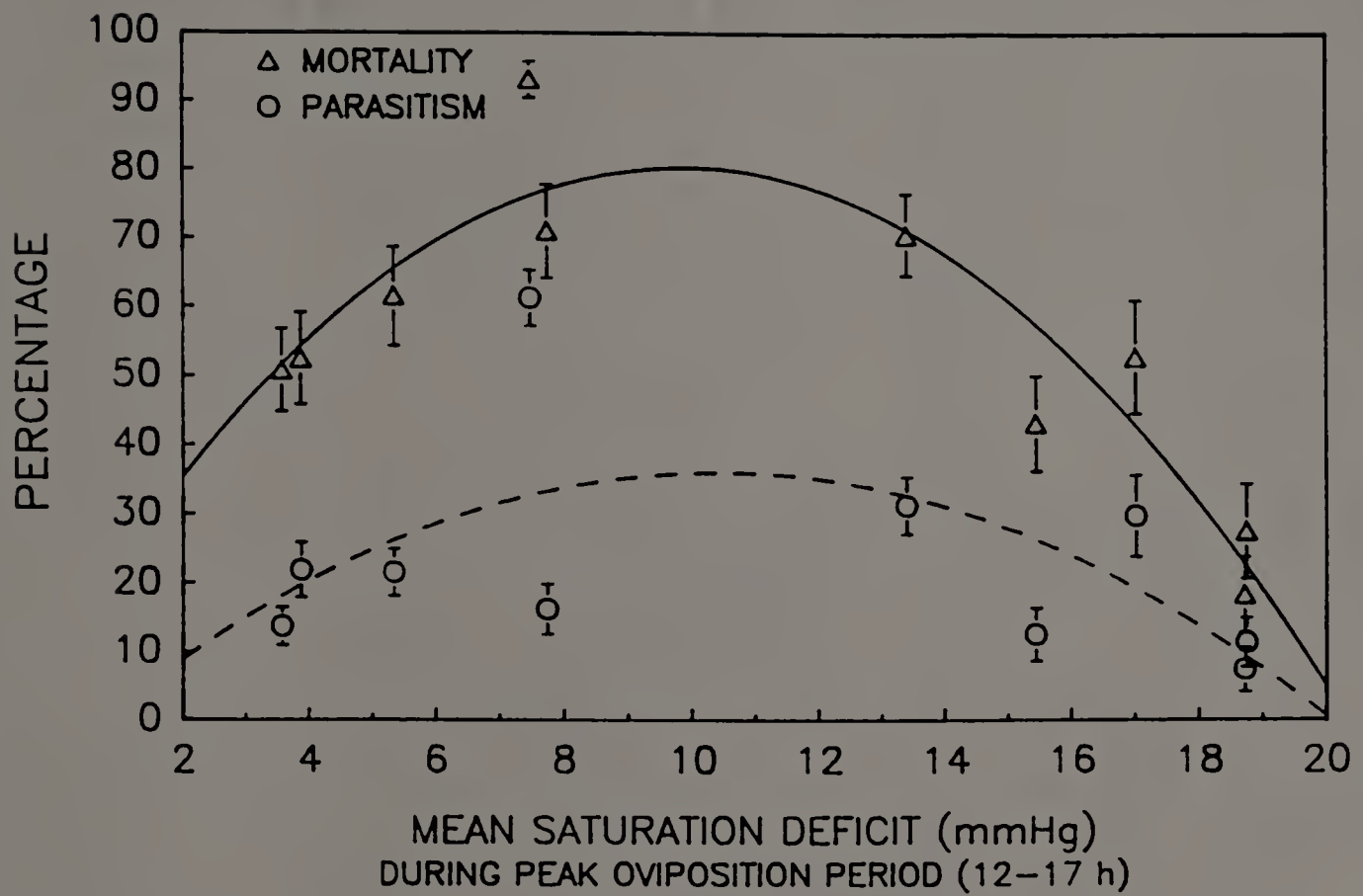


Fig. 8. Quadratic trend in percentage of parasitism and mortality of CPB eggs caused by *E. puttleri* and saturation deficit during the peak host egg visitation period.

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