



Endogenous and exogenous factors affecting parasitism of gypsy moth egg masses by *Ooencyrtus kuvanae*

Richard W. Hofstetter¹ & Kenneth F. Raffa^{2,*}

¹USDA, Yakima Agricultural Research Station 5230 Konnowac Pass Rd. Wapato, WA 98951, USA; ²University of Wisconsin-Madison Department of Entomology 1630 Linden Dr., rm 345 Madison, WI 53706, USA; *Author for correspondence

Accepted: April 7, 1998

Key words: *Ooencyrtus kuvanae*, *Lymantria dispar*, egg parasitoid, host acceptance, sex ratio, parasitoid density, Hymenoptera, Encyrtidae

Abstract

Factors affecting the orientation, reproduction, and sex ratio of the egg parasitoid *Ooencyrtus kuvanae* Howard were examined. Adult females were attracted to airborne volatiles from the egg mass and accessory gland of the primary host, the gypsy moth *Lymantria dispar* L. Visual cues also affected host selection. Background colors against which egg masses were placed affected oviposition preference. In the absence of egg masses, color variation did not affect wasp behavior. Light is required for parasitism by *O. kuvanae*. The age and density of both the host and parasitoid affected wasp reproduction and sex ratios. Older egg masses issued relatively fewer wasps and higher proportions of males than did young egg masses. Likewise, wasp reproduction and the proportion of females declined with wasp age. Larger egg masses produced more wasps and lower proportions of males than did smaller egg masses. The number of offspring per female, and the proportion of female offspring, were inversely related to wasp density. Implications to biological control of the gypsy moth and parasitoid ecology are discussed.

Introduction

The potential for parasitic species to regulate host populations depends on many factors, such as reproductive potential, sex ratio, host-finding ability, temporal and spatial synchronism, and environmental parameters (Salatic, 1963). Several of these factors involving the egg parasitoid *Ooencyrtus kuvanae* Howard (Hymenoptera: Encyrtidae) and its host, the gypsy moth *Lymantria dispar* L. (Lepidoptera: Lymantriidae) have been previously studied (Weseloh, 1971; Hérard, 1978; Hofstetter & Raffa, 1997a). However, information about *O. kuvanae*'s host selection and oviposition behavior, factors affecting sex ratio biology, density effects, and influences of endogenous and environmental factors affecting parasitism are sparse. In addition, we lack information on how this parasitoid will behave in the forests of midwestern North America, as most detailed studies have been conducted in the eastern U.S.

Ooencyrtus kuvanae has intermittently exerted high mortality in gypsy moth populations, and so has considerable promise as one component of overall biological control (Brown & Cameron, 1982). Since its introduction into New England in 1908, *O. kuvanae* has spread throughout all but the northernmost (Ontario) regions of the gypsy moth range (Dowden, 1961; Griffiths & Sullivan, 1978). *Ooencyrtus kuvanae* is multivoltine, having one or two generations in the spring and three to four generations in the fall, depending on climate (Crossman, 1925). Lifetime wasp fecundity is around 100, but can exceed 150 (Tadić & Binečv, 1959; Brown & Cameron, 1982). *Ooencyrtus kuvanae* is arrhenotokous. It is traditionally believed to have fixed sex ratios, with 70% female offspring (Crossman, 1925; Clausen, 1956; Alzofon, 1984). Factors limiting the efficacy of *O. kuvanae* include overwintering mortality, poor dispersal ability, and the inability to reach eggs beneath the upper layer of egg masses (Crossman, 1925; Brown, 1984).

In the field, *O. kuvanae* almost exclusively parasitizes gypsy moth eggs (for alternative hosts see Tadić & Binčev, 1959; Brown, 1984; Hofstetter & Raffa, 1997b). Setae from female gypsy moths that cover the egg mass stimulate parasite antennation and probing (Alzofon, 1984), suggesting kairomonal activity associated with the egg mass (Schieferdecker, 1969). Host odors are known to enhance long and short distance orientation in other host-parasitoid systems (Jones et al., 1971; Vinson, 1976; Strand, 1982; Strand & Vinson, 1983; Kainoh et al., 1989, 1990). *Ooencyrtus kuvanae* may also orient to specific colors when an attractant source is present (Weseloh, 1972a).

Environmental conditions influence microhabitat selection by *O. kuvanae*. Sunlit areas and the leeward side of trees appear more favorable (Hérard, 1978), in combination with various levels of humidity and temperature (Weseloh, 1971; Kamay, 1976). However, *O. kuvanae* loses any positive phototactic response in the presence of a host stimulus (Weseloh, 1971). Reports on the influences of darkness and varying light intensities on parasitization rates by *O. kuvanae* are inconsistent (Brown, 1984; O'Dell et al., 1989).

The effects of host age on parasitoid survival, fecundity, and sex ratio have been studied in detail in many host-parasitoid systems (Gutierrez, 1970; Schmidt, 1974; van Alphen, 1980; Strand & Vinson, 1983; Strand, 1986; Mangel, 1989). Several parasitoid species appear capable of assessing host age and quality by probing the host (King, 1994) or measuring curvature (Strand & Vinson, 1983), and facultatively shift sex ratios. Female offspring are usually deposited in higher quality hosts (Charnov et al., 1981). Wasp size is often positively correlated with host size in solitary parasitoids, reflecting resources available to the developing larvae (King, 1987; Henriquez & Spence, 1993). In many species, adult size is related to lifetime fecundity (Charnov & Skinner, 1984).

Increased wasp density can reduce clutch size and influence offspring sex ratios (Charnov, 1982). Several studies have examined the parasitization rate of *O. kuvanae* on egg masses with varying gypsy moth population sizes in the field (Dowden, 1961; Weseloh, 1971, 1972b; Brown & Cameron, 1979, 1982; Brown, 1981). However, the potential effects of parasitoid and egg mass densities on the resulting sex ratio of offspring have not been considered.

The purpose of this research was to consider several endogenous and exogenous factors that may influence the potential of *O. kuvanae* to regulate gypsy moth populations. In particular, we examined: (1) the

potential influence of visual and olfactory cues on host finding; (2) the effect of photophase on search behavior; (3) the effects of host and parasitoid age on brood production and sex ratio; (4) the effects of host and parasitoid density and oviposition duration on brood production and sex ratio.

Materials and methods

Parasitoid and host cultures. Parasitoids were field collected in Virginia by S. Batch and R. Cameron, USDA, ARS Beneficial Insects Introduction Research Laboratory, Newark, Delaware USA, in the spring of 1993. Five hundred of these adults (BIRL-93-113) were shipped to Madison, Wisconsin USA, in August 1993. Experiments began in March 1994 after 10 to 12 generations in the laboratory.

Ooencyrtus kuvanae were continuously reared from unchilled, two- to three-week old gypsy moth egg masses sent from USDA, APHIS, Otis Air National Guard Base, Cape Cod, Massachusetts. Ten to 20 randomly chosen mated females were placed in a petri dish (15 × 4 cm) with a gypsy moth egg mass for 20 days. Wasps were reared at 22 °C, 60%–70% r.h., and L14:D10. Under these conditions, one generation required approximately 23 days for females and 22 days for males. Adults were placed in 240 ml plastic containers and given pure honey and a dampened paper towel.

All gypsy moths were from the NJSS strain, collected near Blairstown, New Jersey in 1967 (Keena & O'Dell, 1994). Egg masses used in the tests were visually selected for uniformity of size and egg number. Gypsy moth larvae were reared in the laboratory on ICN diet (Hofstetter, 1996).

Visual cues. To determine whether background color affects wasp orientation in the absence of host cues, we placed wasps in 15 × 4 cm petri dishes in which each half was lined with a different color, using the Munsell color code (Munsell Color Corp., 1976). The bottom and sides of one half of the petri dish were covered with tan (5YR 6/4) (similar to the color of most gypsy moth egg masses) construction paper. The other half was covered with black (10B 2.5/1), blue (7.5PB 5/12), red (10RP 4/12), green (7.5G 7/10), yellow (2.5Y 8.5/10) or white (N 10/0) construction paper. The top of the petri dish was not covered with paper. The construction paper was placed on the outside of the petri dish. Ten female wasps, 3- to 4-days

old, were placed in each petri dish. Wasps had no prior exposure to background colors. After one hour, the numbers of wasps on each half of the petri dish were recorded. Each color pair was replicated 10 times using new petri dishes and wasps. Assays were conducted in an environmental chamber with uniform lighting supplied from above and on each side. Dishes were randomly oriented at the start of each replicate.

To determine whether background color affects host location and parasitism, we repeated the above experiment with an egg mass on each side of the assay dishes. After one hour, the wasps on each side and on each egg mass were recorded. Wasps were allowed to oviposit for 24 h (L14:D10). The number of offspring emerging from each egg mass was recorded and correlated with the number of parasitizing females observed on the egg mass after one hour. Egg masses of similar size and color were used in each treatment.

Based on results from the above experiments, we tested whether host selection and parasitism rates are higher when eggs are set against darker backgrounds. Since wasps were found not to prefer the green or tan color in the second experiment, a choice test was conducted using two shades of green and brown. Darker green (10GY 5/4) and tan (5YR 4/2) (chocolate color) were tested against each other and against the previous green (7.5G 7/10) and tan (5YR 6/4) colors. The number of female parasitoids on each egg mass and background color after one hour was recorded. Ten to 15 females were placed in each dish. Each color pair was replicated 19 times using new petri dishes, egg masses and parasitoids. Wasps do not appreciably interfere with one another under these conditions, based on both direct observation and parasite emergence (R. W. Hofstetter, M. Halevy, & K. F. Raffa, unpubl.).

Reflectance and transmittance measurements on background colors were conducted using a 1800-12 Integrating Sphere and LI-1800 Portable Spectroradiometer. The reflectance intensity of visible and UV light (350–1100 nm), the total light of a specific wavelength reflected from color surfaces, were compared with a Barium Sulfate reference curve. The resulting spectra are presented in Hofstetter (1996).

Data were analyzed using Wilcoxon signed-rank and paired *t*-test.

Olfactory cues. A four-way airflow olfactometer was used to study airborne chemical cues that may affect *O. kuvanae* orientation. The olfactometer consisted of four 8 cm long, 7 mm diameter glass tubes extending from a 4 cm diameter central glass sphere (Figure 1).

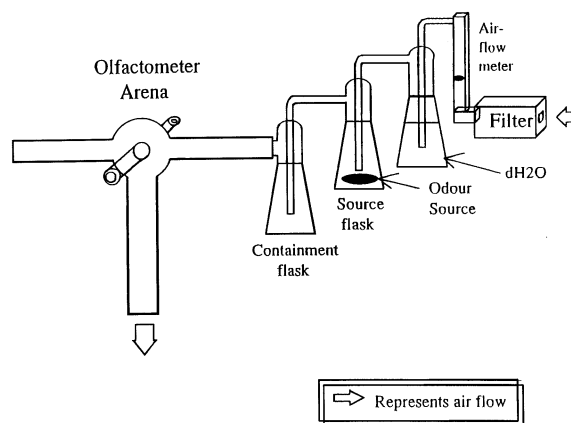


Figure 1. Diagram of the four-way olfactometer used to test the response of *Ooencyrtus kuvanae* to airborne chemicals. Only one complete arm is shown in diagram.

Air flowing into the olfactometer was filtered through two Whatman HEPA-CAP in-line filters and a flask containing distilled water. Ambient air temperature was $22^{\circ}\text{C} \pm 2^{\circ}\text{C}$. Air was blown (75 ml/min) through a small 50 ml glass flask containing the attractant or control into a containment flask (50 ml) at the end of each glass tube, toward the central sphere containing wasps, and out a single glass tube (20 cm long, 15 mm diameter) at the bottom of the sphere. Wasps entered the center sphere through the tube at the bottom, attracted to the light above. White walls (forming an open box) surrounded the olfactometer, eliminating possible disturbances to the wasps during experiments. Preliminary studies showed that wasps did not prefer a particular side of the olfactometer arena.

Once wasps were in the center sphere they could choose one of four tubes, each leading into a containment flask attached to a potential attractant source or control. After 1 h, the position of each wasp in the olfactometer was observed. A choice was recorded when a wasp entered the containment flask at the end of a tube. Wasps were generally unable to exit the containment flasks.

Tests were performed using egg masses of various ages, oviposited by diet-reared gypsy moths on paper. Egg masses were placed randomly in 2 of the 4 glass flasks; the 2 other flasks had blank paper controls. Between each replicate, the olfactometer was cleaned using acetone, fresh egg masses were provided, and treatments were re-randomized. Ten to 20 females were assayed in each assay. No wasp was tested more than once. The experiment was replicated 10 times.

Similar experiments were conducted using the synthetic gypsy moth mating pheromone disparlure with a release rate of 30 ng/h at 25 °C (Leonhardt et al., 1993), and gypsy moth setae as potential long-range attractants. Setae were obtained directly from the abdomens of female gypsy moths with sterile forceps. The disparlure and setae were tested against a blank control.

Olfactometer tests were also performed using secretions from the accessory gland(s) of adult female gypsy moths. Female gypsy moths use excretions from these glands to attach the eggs and abdominal hairs together during oviposition. The contents of the gland were removed by dissection and smeared on filter paper. The glandular secretions were tested against a blank filter paper control.

For each test, the results of the 2 attractant sources and controls were summed and tested using a paired *t*-test. Bonferroni/Dunn tests were used to test whether time of day affected the rate of attractance.

Light. To determine how oviposition may relate to light and darkness, females were given an egg mass in 24 h of darkness, 24 h of continuous light, 30 min of light with 23.5 h of darkness, or 12 h light and 12 h dark. Mated females, 4- to 5-days old, previously held at a 14L:10D photoperiod were tested. Five wasps each were placed in 20 × 4 cm petri dishes containing one egg mass. The experiment began at 10:00 a.m. and was continued for 24 h to eliminate any possible diurnal rhythm. The 30-min light treatment was provided from 22:00 to 22:30. Each treatment was replicated eight times. The number of offspring from each egg mass was counted 25 days later.

The data were analyzed by ANOVA and Fisher's Protected LSD.

Parasitoid age. One-, 4- and 7-day old mated females were placed separately in 100 mm × 15 mm petri dishes containing an egg mass. Wasps were supplied with honey and observed for 19 days or until the female died. Experiments were terminated after 19 days to eliminate any interference from emerging parasitoid offspring. Number and sex of emerging offspring per female (egg mass) were recorded each day for the following 19 days. The sex of offspring were determined by antennal shape and color (Hofstetter, 1996). Conditions were L16:D8, 25 °C, 65% r.h.

All assay wasps were reared from the same egg mass and maternal female. They were placed in a 240 ml plastic container with pure honey and ran-

domly chosen non-sib *O. kuvanae* males. Males were removed after 24 h. All parasitoid females were kept in the container until placed individually in a petri dish with the egg mass. All egg masses were 5-weeks old and selected for equal size (approx. 2.5 cm³).

Analysis of Variance and Fisher's Protected LSD were used to analyze the data means and totals. General Linear Model (SAS: CATMOD Procedures)–repeated measures were used to test between and within data collected daily. Inverse sine transformations were performed on sex ratio data.

Host age. Individual 4-day old female wasps were placed on 3-, 5-, 8-, or 12-week old egg masses in 100 mm × 15 mm petri dishes containing honey, for 19 days. All egg masses were selected for equal size (approx. 2.5 cm³). Date of first emergence, and the number and sex of offspring per egg mass were recorded daily. Daily observations were not made with 12-week old egg masses. Experimental conditions were L16:D8, 25 °C, 65% r.h.

Test wasps were reared from the same egg mass and maternal female. They were placed in a 240 ml plastic container with pure honey and randomly chosen, non-sib *O. kuvanae* males. Males were removed after 24 h. All parasitoid females were kept in the container until placed individually in a petri dish with the egg mass.

Analysis of Variance and Fisher's Protected LSD were used to analyze the data means and totals. General Linear Model (SAS: CATMOD Procedures) – repeated measures were used to test between and with data collected daily. Inverse sine transformations were performed on sex ratio data.

Wasp density. The influence of wasp density, and mitigating factors, on parasitism and oviposition behavior was tested by varying the number of parasitizing females, size of the egg mass, and duration of oviposition. One, 2, 5, 10 and 15 wasps were placed in petri dishes with either a small (<2.4 cm³; <650 eggs) or large (>2.5 cm³; >750 eggs) egg mass for either 2 or 10 days. Each treatment was replicated 10 times. The number and sex of the offspring from each egg mass were recorded.

To determine the effect of wasp density on egg mass selection, female wasps were given a choice between a small and large egg mass (defined above). The density of wasps was varied at 1, 2, 5, 10 and 15. Egg masses were placed 5 cm apart in a petri dish. The number of ovipositing wasps on each of the 2 egg

Table 1. Dichotomous choice tests of *Ooencyrtus kuvanae* in response to *L. dispar* egg masses placed against different background colors. Selection refers to the number of female parasitoids observed on the egg mass after 1 h. Emergence refers to the mean number of parasitoid offspring emerging from that egg mass. Wilcoxon signed-rank test, * indicates $P < 0.05$, ** indicates $P < 0.01$

Choice	Host not present		Host present				Emergence			
	Selection		Selection		Z	P	Emergence		Z	P
	X	se	X	se			X	se		
Black	5.1	0.668	7.6	0.54	-2.56	0.011*	0.8	4.45	-2.50	0.013*
Tan	4.9	0.688	2.4	0.54				36.3	8.65	
Blue	5.4	0.729	7.4	0.45	-2.83	0.005**	99.0	12.10	-2.60	0.009**
Tan	4.6	0.729	2.6	0.45				37.4	10.41	
Red	5.3	0.695	7.5	0.43	-2.72	0.036*	57.1	13.92	-2.10	0.036*
Tan	4.7	0.695	2.5	0.43				28.4	6.48	
Green	4.6	0.653	4.8	0.65	-0.21	0.832	61.2	9.76	-1.49	0.721
Tan	5.4	0.653	5.1	0.65				54.6	9.90	
Yellow	3.7	0.740	3.3	0.68	-1.67	0.095	24.8	18.90	-0.36	0.037*
Tan	6.3	0.740	6.0	0.88				74.6	7.25	
White	4.2	0.829	3.6	0.75	-1.49	0.136	33.0	10.68	-1.64	0.135
Tan	5.8	0.829	6.3	0.77				62.3	13.05	
Dark green			5.2	0.42	-0.84	0.398				
Dark tan			5.2	0.57						
Dark green			5.6	0.41	-0.94	0.345				
Light tan			4.6	0.37						
Light green			4.9	0.47	-1.21	0.225				
Dark tan			5.3	0.54						
Light green			6.4	0.43	-2.02	0.043*				
Light tan			4.2	0.38						

masses was recorded after 10, 20, 30 and 60 min. The number of emerging offspring per egg mass (within each treatment) was also recorded and correlated with the oviposition observations. Each density treatment was replicated 8 times.

Three-Factor ANOVA, Fisher's Protected LSD and regression analysis were used to analyze the data. paired *t*-Tests were used to analyze the choice-test data.

Results

Visual cues. Wasps showed no preference for background color when no egg mass was present (Table 1). However, wasps preferentially selected and parasitized egg masses placed against certain background colors. *Ooencyrtus kuvanae* oriented more to hosts placed against blue, black and red than on tan backgrounds.

Both wasp distribution and emergence reflected these preferences. Emergence results also show that females have a slight preference for egg masses with a tan over a yellow background. Females showed no preference when given the choice between tan versus green or tan versus white backgrounds (Table 1).

With different shades of green and tan backgrounds in the dichotomous tests, only egg masses with the light green background were significantly selected over egg masses with a light brown background (Table 1). All other color combinations were not significantly different at the 5% level.

Olfactory cues. *Ooencyrtus kuvanae* females were strongly attracted to volatiles emitted from entire egg masses and accessory gland secretions. Given the choice between these attractant sources versus controls, 83% of the wasps that made a choice went to the egg mass and 76% of the wasps went to the accessory

Table 2. Attractance of *Ooencyrtus kuvanae* to air-borne chemicals from the host gypsy moth. Percent of *O. kuvanae* females that made a choice versus blank control. Paired *t*-test: treatment vs. control (* $P < 0.05$, ** $P < 0.01$)

	% Response		N	df	<i>t</i>	P
	Treatment	Control				
Gypsy moth egg mass	83	17	52	9	6.053	0.005**
Accessory gland	76	24	68	9	3.210	0.011*
(+) Disparlure	45	55	21	7	-0.243	0.815
Gypsy moth setae	59	41	54	9	1.539	0.158

gland secretions (Table 2). Females did not choose the (+)disparlure lure over blank controls. Setae from the abdomen of female gypsy moths did not elicit attractance responses. Wasps that did not make a choice in each treatment were 65%, 60%, 79% and 67%, respectively. Time of day did not affect female wasp choice (Bonferroni/Dunn test, $P=0.7035$).

Light. Parasitism rates were significantly different between females given egg masses in darkness versus light (Table 3). In complete darkness, wasps tended to move towards the edge of the petri dish. The 30-min light period was significantly different from complete darkness (Fisher's Protected LSD, $P < 0.05$). Parasitism rates of wasps given 24 h of constant light versus L12:D12 were not significantly different (Fisher's Protected LSD, $P=0.288$), but both were significantly different from the 30-min light treatment (Fisher's Protected LSD, $P < 0.01$) and complete darkness (Table 3).

Parasitoid age. Preliminary studies determined that newly emerged females have a 24-h lag period prior to oviposition, regardless of whether they were mated. Ninety-five percent of parasitism occurred between days 2 and 20. Several wasps were observed to oviposit for 35 days and live as long as 40 days.

The total production of progeny declined with the increased initial age of the adult female parasitoids ($df=2$, $F = 5.21$, $P=0.033$). Significantly more offspring resulted from 1-day old females than 4- or 7-day old females (Table 4) (Fisher's Protected LSD; $P < 0.05$). The proportion of male offspring increased with the age of the parasitizing female. In all treatments, there was no relationship between offspring sex ratio and total number of offspring per female ($F = 1.07$, $P=0.307$).

Table 3. Effect of light on *Ooencyrtus kuvanae* oviposition behavior during a 24 h period. Twenty-five parasitoids per treatment (5 wasps per egg mass, 8 egg masses per treatment). Means followed by same letter are not significantly different at $P < 0.05$ (ANOVA; Fisher's Protected LSD)

Light treatment	Mean offspring (se) per egg mass
24 h	22.6 (7.1) a
12 h	27.6 (9.1) a
30 min	9.0 (8.5) b
0 h	0.0 (0.0) c
<i>F</i>	15.36
<i>P</i>	0.001

Table 4. Effects of *Ooencyrtus kuvanae* age on brood production and sex ratio. Means within a column followed by the same letter are not significantly different at $P < 0.05$ (ANOVA; Fisher's Protected LSD)

Adult parasitoid age (d)	Mean offspring (se)	% Male (se)
1	123.1 (9.5) a	15.9 (1.6) a
4	92.9 (7.6) b	18.2 (1.7) ab
7	86.2 (6.1) b	21.8 (4.0) b
<i>F</i>	5.884	4.642
<i>P</i>	0.0064	0.017

The daily emergence of offspring from 1-, 4- and 7-day old females exhibited a skewed, apparently bimodal pattern of emergence (Figure 2A). Parasitoids first emerged on day 20. Peak emergence occurred at days 22, 23, 24 and 27 for progeny from 1-day females, days 21, 22, 23 and 26 for progeny from

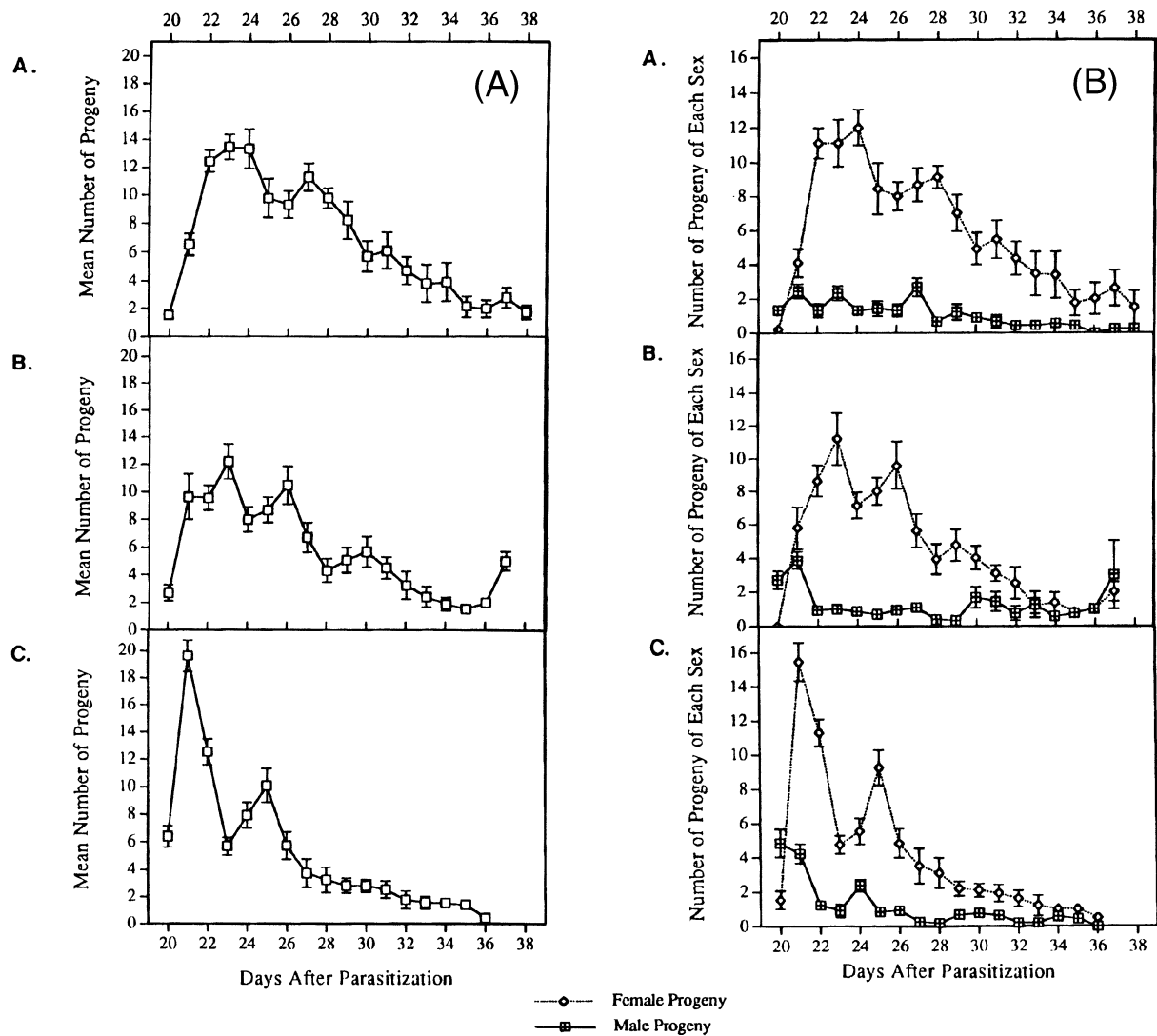


Figure 2. Effects of age of *Ooencyrtus kuvanae* females on daily production and sex ratio of progeny. Individual female parasitoids were placed on 5-week old gypsy moth egg masses and allowed to oviposit continually for 19 days. Bars indicate standard errors. A. Total production of progeny. B. Daily emergence of male and female progeny. A, B, and C: 1-, 4-, and 7-day old females.

4-day old females, and days 21 and 25 for progeny from 7-day old females. Peak emergence advanced approximately one day for each increasing age class ($F = 4.08$, $P < 0.01$). Offspring continued to emerge until day 38 for 1- and 4-day age treatments, but only until day 36 for 7-day age treatments. For each age class, the number of progeny gradually decreased after the second peak of emergence. Several age classes showed a slight increase in the emergence of progeny after day 36.

The proportion of male progeny varied per day (Time: $df=16$, $F = 56.0$, $P < 0.01$; Time*Age: $df=34$,

$F=4.09$, $P < 0.05$) and among age classes ($df=2$, $F=3.22$, $P < 0.05$). In all age classes however, a sharp decline in the proportion of male progeny occurred from the first (day 20) to the third (day 22) day of emergence ($F > 35.0$, $P < 0.01$). The daily proportion of male progeny remained relatively constant (approx. 0.16) after day 22 ($F < 3.0$, $P > 0.20$) (Figure 2B). Among the 4-day old age class, the sex ratio remained constant from days 22 to 30 (at approx. 15% male) then increased to approximately 60% male. Unlike the 1- and 4-day age classes, the proportion of male progeny from the 7-day age class showed a cyclical

Table 5. Effects of host age on parasitoid (*Ooencyrtus kuvanae*) brood production and sex ratio. Four-day old female parasitoids were placed on either 3-, 5-, 8- or 12-week old egg masses for 19 days. Means within each column followed by same letter are not significantly different at $P < 0.05$ (ANOVA; Fisher's protected LSD)

Host age (weeks)	Mean (se) offspring	% (se) Male
3	93.7 (10.0) a	20.7 (1.8) a
5	92.9 (7.6) a	18.2 (1.7) a
8	92.5 (7.1) a	19.0 (1.7) a
12	27.0 (4.9) b	35.6 (7.4) b
<i>F</i>	7.760	6.323
<i>P</i>	0.0002	0.0011

pattern ranging from 40% to 0% male ($F > 4.0$, $P < 0.05$). Changes in daily sex ratios were more affected by the number of female than male progeny. That is, the change in male progeny that emerged from day to day was relatively small in comparison to the number of female progeny.

Host age. The total production of progeny was influenced by the age of the host egg mass. Significantly more parasitoid progeny emerged from 3-, 5- and 8-week old egg masses than 12-week old egg masses (Fisher's Protected LSD; $P < 0.05$) Three-, 5- and 8-week old hosts produced significantly fewer proportions of male progeny than did 12-week old hosts (Table 5).

The development time of progeny was influenced by host age. Progeny first emerged from 3-week old egg masses on day 19 (Figure 3A), 5- and 8-week old egg masses on day 20, and 12-week old egg masses on day 21 ($F = 2.84$, $P < 0.01$). An apparently bimodal pattern was observed for all age classes except 12-week old egg masses which were not recorded daily. Peak offspring emergence occurred on days 21 and 23 for 3-week old egg masses and on days 23 and 26 for 5- and 8-week old egg masses.

A greater percentage (35.6%) of males emerged from 12-week old egg masses than 3-week (20.7%), 5-week (18.2%), and 8-week (19%) old egg masses (Table 5). The daily offspring sex ratios were almost identical among 3-, 5- and 8-week old egg masses (Time*Age: $df=34$, $F < 1.23$, $P > 0.20$; Age: $df= 2$, $F = 1.46$, $P > 0.27$) (Figure 3B). (Daily emergences were not recorded for 12-week old egg masses). The percentage of male offspring per day declined markedly from the first (day 19 or 20) to third

(day 21 or 22) day of emergence ($df=17$, $F > 35.0$, $P < 0.01$), with 3-week old egg masses having initially less male offspring than 5- and 8-week old egg masses (Figure 3B). Fifteen percent of the offspring from days 22 to 29 were male, regardless of egg mass age ($F < 0.75$, $P > 0.38$). The proportion of male progeny increased significantly after day 30 for each age class ($F > 3.9$, $P < 0.05$). The rate of increase steepened with each age class.

Daily sex ratios were more affected by the change in female progeny than male progeny. The change in male progeny from day to day was relatively small in comparison to changes in the number of female progeny.

Wasp density. Number of offspring per female declined as parasitoid density increased. Total number of offspring reached a limit as the density of parasitizing wasps increased, but this limit is influenced by the size of the egg mass and the duration of the oviposition period (Figure 4A). The rate of production per female decreased with increased parasitoid density, duration of the oviposition period, and the size of the egg mass (Figure 4B). The average number of offspring per adult parasitoid was greater on larger egg masses, when all densities are pooled regardless of oviposition length ($F = 8.57$, $P < 0.01$).

The ratio of male to female offspring was influenced by wasp density, egg mass size and duration of oviposition (Figure 4C). In all treatments, offspring sex ratios increased with wasp density ($F = 23.7$, $P < 0.01$). Offspring sex ratios decreased with increasing egg mass surface area in treatments with more than one founding female ($F = 7.42$, $P = 0.0085$, $r^2 = 0.115$). Productivity of female offspring decreased with egg mass surface area ($F = 3.47$, $P = 0.041$), except where there was only one founding female. Longer oviposition times resulted in lower proportions of males.

In the one-hour dichotomous choice tests, female parasitoids examined both small and large egg masses equally ($df=39$: 10 min: $t = -0.669$, $P = 0.508$, 20 min: $t = -0.121$, $P = 0.904$, 30 min: $t = 0.523$, $F = 0.604$, 60 min: $t = -0.12$, $P = 0.905$) regardless of wasp density or time of observation.

Discussion

Vision appears to exert an important role in orientation by *O. kuvanae* to host eggs. Wasps only oviposited

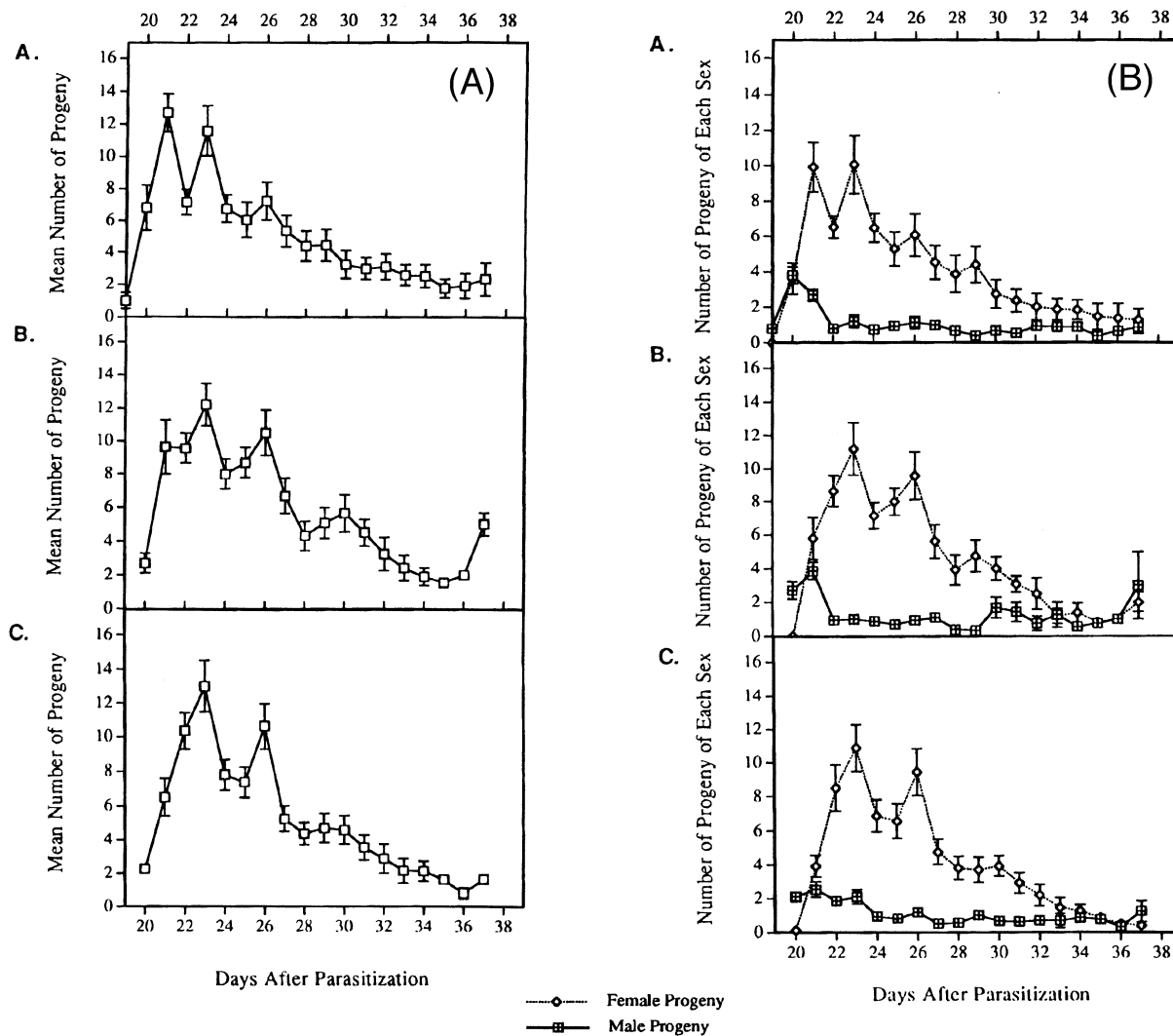


Figure 3. Effects of host age on *Ooencyrtus kuvanae* daily production and sex ratio of progeny. Line bars indicate standard errors. Individual four-day old female parasitoids were placed on gypsy moth masses of varying age and allowed to oviposit for 19 days. A. Total production of progeny. B. Daily emergence of male and female progeny. A, B, and C: 3-, 5-, and 8-week old egg masses.

under light conditions, and background color influenced parasitism rates. The effects of light appear to be independent of any endogenous diurnal parasitism rhythm. Most parasitization seems to occur when light is first turned on regardless of the time of day. For example, in the 30-min light treatment in which lights were turned on at night, the parasitoids produced 9 offspring versus an average of 1 offspring per 30 min in the 12-h treatment. Our results differ from O'Dell et al. (1989), who found that parasitism rates did not differ between wasps placed in cylinders lined with black versus clear tape. Such differences could be due to varying methods, number of parasitoid generations

in the laboratory, or rearing techniques (Grinberg & Wallner, 1991).

Background color appears to affect wasp ability to detect eggs, rather than exert any direct attraction. This could affect female orientation to surfaces such as tree trunks, where egg masses are likely to be located, and contribute to differential parasitism rates among egg masses on different tree species. Weseloh (1972a) found high catches of *O. kuvanae* on blue and white sticky panels, suggesting that visual orientation during flight also has a dispersal function rather than being solely host-directed.

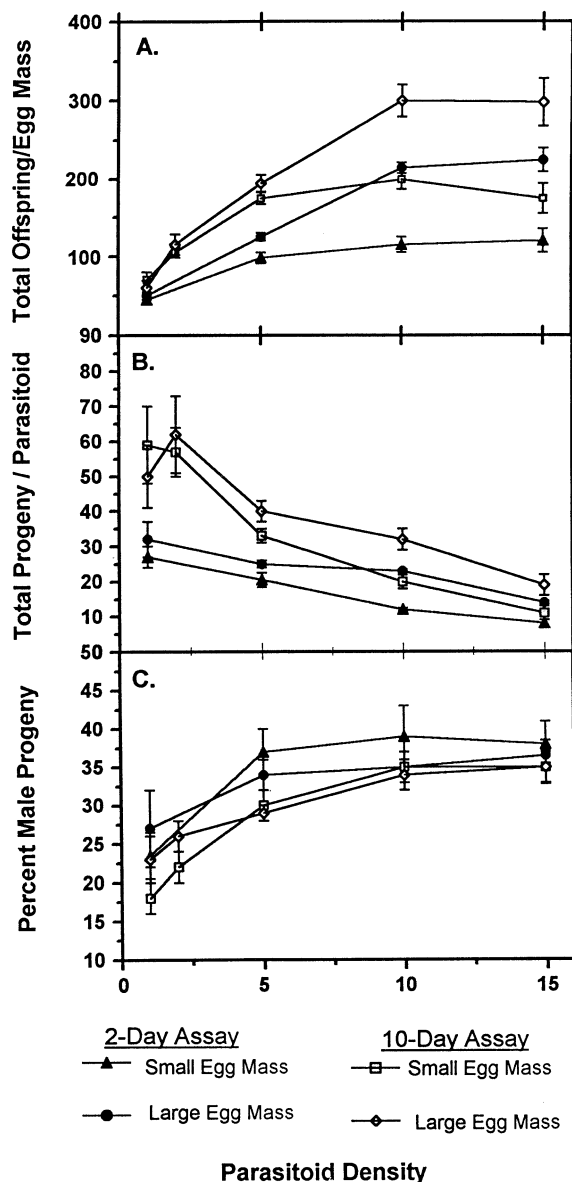


Figure 4. Effects of parasitoid density, host-egg mass size and duration of oviposition on total brood production per capita replacement rates, and sex ratios of *Ooencyrtus kuvanae*. Bars indicate standard errors. Analysis by ANOVA. A. Total brood production. Oviposition duration ($F = 26.58$, $P < 0.01$); density ($F = 59.52$, $P < 0.01$); host size ($F = 28.41$, $P < 0.01$); oviposition \times Density ($F = 0.89$, $P = 0.45$); oviposition \times size ($F = 0.007$, $P < 0.94$); density \times size ($F = 5.99$, $P < 0.01$); oviposition \times density \times size ($F = 0.08$, $P = 0.97$). B. Offspring per parasitoid. Oviposition duration ($F = 45.51$, $P < 0.01$); density effect ($F = 43.39$, $P < 0.01$); host size ($F = 8.57$, $P < 0.01$); oviposition \times density ($F = 6.30$, $P < 0.01$); oviposition \times host size ($F = 1.40$, $P = 0.24$); density \times host size ($F = 1.16$, $P = 0.33$); oviposition \times density \times host size ($F = 1.39$, $P = 0.25$). C. Percentage male progeny. Oviposition duration ($F = 11.60$, $P < 0.01$); density ($F = 23.76$, $P < 0.01$); host size ($F = 0.47$, $P = 0.50$); oviposition \times density ($F = 0.09$, $P = 0.96$); oviposition \times host size ($F = 1.51$, $P = 0.22$); density \times host size ($F = 1.71$, $P = 0.17$); oviposition \times density \times host size ($F = 0.10$, $P = 0.96$).

Ooencyrtus kuvanae females are attracted to volatile cues emitted from egg masses. Whether *O. kuvanae* can also detect egg masses over relatively long distances or in flight remains unknown. Because egg masses are deposited on many substrates, often away from the larval host plant, odors from the egg mass alone should provide the necessary cues for host location. It is unlikely that gypsy moth larvae or adult males elicit a host attractance response by this parasitoid. Direct responses to plant odors have not been demonstrated for *O. kuvanae*. However, Hofstetter & Raffa (1997a) found evidence that *O. kuvanae* can discriminate between egg masses produced by gypsy moths that were reared on different larval diets. Preferences for specific egg masses and background colors may be influenced by wasp experience and life history.

The lack of attraction to disparlure indicates an apparent difference between *O. kuvanae* and some other parasitoids (Sternlicht, 1973; Vinson, 1976). For example, *Anastatus disparis* Ruschka (Hymenoptera: Eulophidae), another egg parasitoid of the gypsy moth, is attracted to the natural sex pheromone (Bjegović, 1964). However, *A. disparis* is phoretic on adult female gypsy moths (Crossman, 1925), and larvae can only develop in freshly laid gypsy moth eggs (Bjegović, 1964). Our results help explain why disparlure does not disrupt the performance of *O. kuvanae* when pheromones are used as a control tactic (Brown & Cameron, 1979). The possibility that *O. kuvanae* is attracted to other components of the natural sex pheromone, as opposed to the synthetic form tested here, cannot be eliminated.

Compounds from the accessory gland elicit an attractance response by *O. kuvanae*. To our knowledge, this gland has not been previously reported to elicit an airborne chemical response to potential predators or parasitoids. Excretions from the accessory gland are believed to function primarily for adhesion onto substrates during oviposition (Lococo & Huebner, 1980; Strand, 1982). Chemotactile assays showed that contents of the accessory gland elicited a contact host acceptance response by the egg parasitoid *Telenomus heliothidis* Ashmead (Hymenoptera: Scelionidae) (Strand & Vinson, 1982). We observed similar behavior by *O. kuvanae* (Hofstetter, 1996). Gypsy moth setae also elicited host search and acceptance responses by *O. kuvanae* (Hofstetter, 1996). Various host-derived compounds have been shown to elicit responses in other parasitoid systems (Jones et al., 1971; Vinson, 1976; Noldus, 1988). The compounds

that elicit locomotory and chemotactile responses by *O. kuvanae* are unknown.

Offspring production per female was inversely related to host and parasitoid age. This may result from offspring developmental mortality or decreased parasitization rates. For example, Lashomb et al. (1987) found that probing by *Edovum puttleri* Grissell increased, but parasitism decreased as host age increased. Developmental mortality due to probing might also contribute to the decreased number of progeny emerging in older hosts. The date of maximum offspring emergence occurred sooner in older females (Figure 3). There appears to be a second peak, occurring from days 25 to 28, depending on adult wasp and host age. Peaks in emergence appear to reflect differential development time of male and female larvae, as sex ratios are influenced by the above parameters.

As adult parasitoid age increased, the proportion of male offspring increased. There are several possible explanations for this trend. First, wasps may oviposit more males later in their lives. *Microplitis croceipes* Cresson (Hymenoptera: Braconidae) (Lewis & Snow, 1971; Harrison et al., 1993) and *Avetianella longoi* (Hymenoptera: Encyrtidae) (Hanks et al., 1995) exhibit such behaviors. Second, prior exposure to a high density of wasps, particularly females may influence early ovipositional behavior (King, 1987). Wasps were held together before being placed on the egg masses, possibly giving the impression of a female sex-biased population. The male-biased offspring sex ratio might also reflect the length of time that the adult females were stored together. A likely explanation is that females use contacts with other wasps as an index of the number of founders likely to colonize a patch. Third, as females age, sperm within their spermathecae may become depleted, thus resulting in a greater proportion of unfertilized male eggs. However, increasing the number of males did not increase the proportion of female progeny in a separate experiment (R. W. Hofstetter, M. Halevy & K. F. Raffa, unpubl).

In some species, for example *Ooencyrtus nezarae* Ishii, female parasitoids may selectively manipulate the sex of their offspring in relation to host age (Takasu & Hirose, 1993). However, we can not conclude whether sex ratio difference in *Ooencyrtus kuvanae* resulted from oviposition decisions of the parasitizing female or differential developmental success of males and females (Bjegović, 1964; Vinson, 1976; Lashomb et al., 1987). *Ooencyrtus kuvanae* can parasitize gypsy moth eggs successfully up to one day prior to gypsy

moth larval eclosion (Hofstetter, 1996), although the rate of emergence is low.

The size of the gypsy moth egg mass, the number of parasitizing wasps and duration on the egg mass directly affected the rate of parasitism. Total wasp emergence per egg mass increased with an increase in parasitoid density, but reached a limit based on availability of eggs. The parasitization rate was positively correlated with the number of accessible eggs within an egg mass, but negatively correlated with wasp density. A wasp egg deposited within an already parasitized host is unlikely to develop, and if successful invariably yields a smaller than normal offspring (Hofstetter, 1996).

The proportion of male offspring increased with increasing parasitoid density. However, the absolute emergence of male offspring remained relatively unchanged, whereas female emergence decreased. This may result from females laying fewer female eggs in less suitable hosts, or a behavioral choice influenced by the local density of other females (i.e., Local Mate Competition, Hamilton, 1967). Sex ratios could also be influenced by oviposition time. When many foundresses are present, there will be greater competition for hosts and each female is likely to lay fewer eggs. If females tend to produce male eggs early in an oviposition sequence, a reduction in the number of eggs laid will result in a more male-biased sex ratio. Greater male-biased sex ratios could also be secondary and reflect variable developmental success in hosts of varying quality (Sex Differential Mortality, Werren, 1983). A linear reduction between numbers of progeny and *O. kuvanae* density suggests that an increase in foundresses may have affected host availability offspring development (O'Dell et al., 1989). Benson (1973) found that *Bracon hebetor* (Say) (Hymenoptera: Braconidae) eggs and young larvae were killed by other older parasitoid larvae feeding on the same host. Further, the sex ratio decreases under the same conditions, possibly because males develop more quickly and are likely to increase female mortality by either damaging unhatched eggs or preempting host resources.

Acknowledgements

We thank D. Mahr, M. Strand, University of Wisconsin-Madison for their helpful ideas and manuscript review, and R. H. & M. A. Hofstetter for review of manuscript. Laboratory research was assisted by S.

LaFontaine, A. Chenot, M. Halevy, and J. Kruse. We wish to thank N. Erway, M. Allington and D. Swinton for construction of olfactometer and equipment, G. Bernon (USDA APHIS, Otis ANG Base, MA) for providing unlimited gypsy moths and egg masses, R. Fuester (Benef. Insect Introd. Res. Lab, USDA, Newark, DE) for initially providing *O. kuvanae*, and J. Norman (UW, Soils Department) and T. Frank (UW, Horticulture Department) for providing the integrating sphere and spectroradiometer. The gypsy moth pheromone, (+)-disparlure, was supplied by S. Krause, Wisconsin Department of Agriculture, Trade and Consumer Protection. Funding for this research was provided by Wisconsin Department of Natural Resources, the UW-Madison Graduate School, McIntire-Stennis, and UW-Madison College of Agricultural and Life Sciences.

References

- Alphen, J. J. M. van., 1980. Aspects of the foraging behaviour of *Tetrastichus asparagi* Crawford and *Tetrastichus* spec. (Eulophidae), gregarious egg parasitoids of the asparagus beetles *Crioceris asparagi* L. and *C. duodecimpunctata* L. Chrysomelidae. Netherlands Journal of Zoology 30: 307–325.
- Alzofon, J., 1984. The biology and behavior of *Ooencyrtus kuvanae* (Howard) (Hym.: Encyrtidae), a gypsy moth egg parasite. Ph.D. Diss. Fordham Univ., New York, N.Y.
- Benson, J. F., 1973. Intraspecific competition in the population dynamics of *Bracon hebetor* Say (Hym.:Braconidae). Journal of Animal Ecology 42: 105–124.
- Bjegović, P., 1964. Sex ratio of *Anastatus disparis* Ruschka influenced by the host embryonic development. Zaštita Bilja 15: 569–576.
- Brown, M. W., 1981. Population dynamics of the gypsy moth egg parasite, *Ooencyrtus kuvanae* (Howard) (Hymenoptera: Encyrtidae). Ph.D. Diss. The Graduate School. The Pennsylvania State University.
- Brown, M. W., 1984. Literature review of *Ooencyrtus kuvanae* (Hym.: Encyrtidae), an egg parasite of *Lymantria dispar* (L.) (Lep.: Lymantriidae). Entomophaga 29: 249–265.
- Brown, M. W. & E. A. Cameron, 1979. Effects of disparlure and egg mass size on parasitism by the gypsy moth egg parasite, *Ooencyrtus kuvanae*. Environmental Entomology 8: 77–80.
- Brown, M. W. & E. A. Cameron, 1982. Spatial distribution of adults of *Ooencyrtus kuvanae* (Hym.:Encyrtidae), an egg parasite of *Lymantria dispar* (L.) (Lep.: Lymantriidae). The Canadian Entomologist 114: 1109–1120.
- Charnov, E. L., 1982. The Theory of Sex Allocation. Princeton University Press, Princeton, New Jersey, USA.
- Charnov, E. L. & S. W. Skinner, 1984. Evolution of host selection and clutch size in parasitoid wasps. Florida Entomologist 67: 5–20.
- Charnov, E. L., R. L. Los-den Hartogh, W. T. Jones & J. van den Assem, 1981. Sex ratio evolution in variable environment. Nature 289: 27–33.
- Clausen, C. P., 1956. Biological control of insect pests in the continental United States. U.S.D.A. Technical Bulletin 1139 (Washington).
- Crossman, S. S., 1925. Two imported egg parasites of the gypsy moth, *Anastatus bifasciatus* (Fonsc.) and *Schedius kuvanae* (Howard). Journal of Agricultural Research 30: 643–675.
- Dowden, P. B., 1961. The gypsy moth egg parasite, *Ooencyrtus kuvanae*, in southern Connecticut in 1960. Journal of Economic Entomology 54: 876–878.
- Griffiths, K. J. & C. R. Sullivan, 1978. The potential for establishment of the egg parasite *Ooencyrtus kuvanae* in Ontario populations of the gypsy moth. The Canadian Entomologist 110: 633–638.
- Grinberg, F. S. & W. E. Wallner, 1991. Long-term laboratory evaluation of *Rogas lymantriae*: A braconid endoparasite of the gypsy moth, *Lymantria dispar* (L.). Entomophaga 36: 205–212.
- Gutierrez, A. P., 1970. Studies on host selection and host specificity of the aphid hyperparasite *Charips victrix*: Host selection. Annals of the Entomological Society America 63: 1495–1498.
- Hamilton, W. D., 1967. Extraordinary sex ratios. Science 156: 477–478.
- Hanks, L. M., J. R. Gould, T. D. Paine, J. G. Millar & Q. Wang, 1995. Biology and host relations of *Avetianella longoi* (Hym.:Encyrtidae), an egg parasitoid of the eucalyptus longhorned borer (Col.:Cerambycidae). American Entomological Society America 88: 666–671.
- Harrison, W. W., D. A. Herbert & D. D. Hardee, 1993. Effect of parasitoid and host age on oviposition and emergence of *Microplitis croceipes* (Hym.: Braconidae) an endoparasitoid of *Helvicoverpa zea* (Lep.: Noctuidae). Journal of Entomological Science 28: 343–349.
- Henriquez, N. P. & J. R. Spence, 1993. Studies of *Lathromeroidea* sp. nov. (Hym.:Trichogrammatidae), a parasitoid of gerrid eggs. The Canadian Entomologist 125: 693–702.
- Hérard, F., 1978. Ethology of the adults of *Ooencyrtus kuvanae* (Howard) (Hym.: Encyrtidae), oophagous parasite of *Lymantria dispar* (L.) (Lep.: Lymantriidae) in the Mamora forest (Morocco). Annales de Zoologie et d'Ecologie Animale 10: 603–612.
- Hofstetter, R. W., 1996. Factors affecting the performance and oviposition behavior of *Ooencyrtus kuvanae* (Hym.:Encyrtidae). M.S. Thesis. University of Wisconsin-Madison, Madison, WI.
- Hofstetter, R. W. & K. F. Raffa, 1997a. Effects of host's diet on the orientation, development, and subsequent generations of the egg parasitoid, *Ooencyrtus kuvanae*. Environmental Entomology 26: 1276–1282.
- Hofstetter, R. W. & K. F. Raffa, 1997b. New host record for *Ooencyrtus kuvanae* (Hym.: Encyrtidae). Entomological News 108: 63–65.
- Jones, R. L., W. J. Lewis, M. C. Bowman, M. Beroza & B. A. Bierl, 1971. Host-seeking stimulant for a parasite of the corn earworm: isolation, identification, and synthesis. Science 173: 842–843.
- Kainoh, Y., S. Tatsuki & T. Kusano, 1990. Host moth scales; a cue for host location for *Ascogaster reticulatus* Watanabe (Hym.: Braconidae). Applications in Entomology and Zoology 25: 17–25.
- Kainoh, Y., S. Tatsuki, H. Sugie & Y. Tamaki, 1989. Host egg kairomones essential for egg-larval parasitoid, *Ascogaster reticulatus* Watanabe (Hym.:Braconidae) II. Identification of internal kairomone. Journal of Chemical Ecology 15: 1219–1229.
- Kamay, B. A., 1976. The effects of various constant temperatures on oviposition, sex ratio, and rate of development of the gypsy moth egg parasite, *Ooencyrtus kuvanae* Howard. M.S. Thesis, Southern Connecticut State College, New Haven, Connecticut.

- Keena, M. A. & T. M. O'Dell, 1994. Effects of laboratory rearing on gypsy moth (Lep.:Lymantriidae). Northeastern Forest Expt. Station Gen. Tech. NE-181: 1–23.
- King, B. H., 1987. Offspring sex ratios in parasitoid wasps. Quarterly Review of Biology 62: 367–396.
- King, B. H., 1994. How do female parasitoid wasps assess host size during sex-ratio manipulations? Animal Behavior 48: 511–518.
- Lashomb, J. H., J. D. Krainacker, R. K. Jansson, Y. S. Ng & R. Chianese, 1987. Parasitism of *Leptinotarsa decemlineata* (Say) eggs by *Edovum puttleri* Grissell (Hym.: Eulophidae): effects of host age, parasitoid age, and temperature. The Canadian Entomologist 119: 75–82.
- Leonhardt, B. A., V. C. Mastro & E. D. Devilbiss, 1993. New dispenser for the pheromone of the gypsy moth (Lep.: Lymantriidae). Journal of Economic Entomology 86: 821–827.
- Lewis, W. J. & J. W. Snow, 1971. Fecundity, sex ratios, and egg distribution by *Microplitis croceipes*, a parasite of *Heliothis*. Journal of Economic Entomology 64: 6–8.
- Lococo, D. & E. Huebner, 1980. The ultrastructure of the female accessory gland, the cement gland, in the insect, *Rhodnius prolixus*. Tissue and Cell 12: 795–814.
- Mangel, M., 1989. Evolution of host selection in parasitoids: Does the state of the parasitoid matter? American Naturalist 133: 688–705.
- Munsell Color Corp. Inc., 1976. Munsell Book of Color. Kolmogorov Corp., Baltimore, Md.
- Noldus, L. P. J. J., 1988. Response of the egg parasitoid *Trichogramma pretiosum* to the sex pheromone of its host *Heliothis zea*. Entomologia Experimentalis et Applicata 48: 293–300.
- O'Dell T. M., P. Chang & G. S. Walton, 1989. Effects of light on location of host egg masses by *Ooencyrtus kuwanai* (Hym.:Encyrtidae), an egg parasite of gypsy moth (Lep.:Lymantriidae). Environmental Entomology 18: 1101–1104.
- Salatić, S., 1963. A study of some factors influencing control potential of the gypsy moth egg parasites. Zaštita Bilja 14: 693–699.
- Schieferdecker, H., 1969. Zur Vermehrung von *Ooencyrtus kuwanai* (Howard) unter Laborverhältnissen. Beitr. Entomology 19: 803–815 (Translation from German).
- Schmidt, G. T., 1974. Host-acceptance behaviour of *Camplietis sonorensis* toward *Heliothis zea*. Annals of the Entomological Society of America 67: 835–844.
- Sternlicht, M., 1973. Parasitic wasps attracted by the sex pheromone of the coccid host. Entomophaga 18: 339–342.
- Strand, M. R., 1982. Behavioral response of the parasitoid, *Cardiochiles nigriceps* to a kairomone. Entomologia Experimentalis et Applicata 31: 308–315.
- Strand, M. R., 1986. The physiological interactions of parasitoids with their hosts and their influence on reproductive strategies. Insect the egg parasitoid *Telenomus heliothidis* (Hym.:Scelionidae). Environmental Entomology 12: 1114–1119.
- Strand, M. R. & S. B. Vinson, 1982. Source and characterization of an egg recognition kairomone of *Telenomus heliothidis*: a parasitoid of *Heliothis virescens*. Physiological Entomology 7: 83–90.
- Strand, M. R. & S. B. Vinson, 1983. Factors affecting host recognition and acceptance in the egg parasitoid *Telenomus heliothidis* (Hym.: Scelionidae). Environmental Entomology 12: 1114–1119.
- Tadić, M. & B. Binčev, 1959. *Ooencyrtus kuwanai* How. in Yugoslavia. Zaštita Bilja 10: 51–59.
- Takasu, K. & Y. Hirose, 1993. Host acceptance behavior by the host-feeding egg parasitoid, *Ooencyrtus nexarae* (Hym.:Encyrtidae): Host age effects. Annals of the Entomological Society of America 86: 117–121.
- Vinson, S. B., 1976. Host selection by insect parasitoids. Annual Review of Entomology 21: 109–133.
- Werren, J. H., 1983. Sex ratio evolution under local mate competition in a parasitic wasp. Evolution 37: 116–124.
- Weseloh, R. M., 1971. Behavioral responses of the gypsy moth egg parasitoid *Ooencyrtus kuwanai* to abiotic environmental factors. Annals of the Entomological Society of America 64: 1050–1057.
- Weseloh, R. M., 1972a. Field responses of gypsy moths and some parasitoids to colored surfaces. Annals of the Entomological Society of America 65: 742–746.
- Weseloh, R. M., 1972b. Influence of gypsy moth egg mass dimensions and microhabitat distribution parasitization by *Ooencyrtus kuwanai*. Annals of the Entomological Society of America 65: 64–69.