Biological comparisons between the squash bug egg parasitoids, *Ooencyrtus anasae* (Ashmead) and *O.* sp. (Hymenoptera: Encyrtidae): A laboratory assessment.

by

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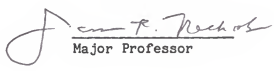

Major Professor

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Table of Contents

List of Tables

Part I

List of Figures

Part II

Introduction

Evaluation of the life history characteristics of natural enemies is of central importance to their proper utilization in biological control programs (e.g. manipulation of indigenous enemies in augmentation or conservation programs [DeBach et al. 1976], selection and introduction strategies of new beneficial species [Ehler 1982, Ehler & Hall 1982]), and the construction of predictive models for the field [Stimac and O'Neil 1985]). Comparative evaluations of closely-related beneficial species are particularly useful because these form the basis for (a) examining complex species interactions (e.g., competition) (b) selecting candidates for mass-rearing and release in augmentation programs (King et al. 1985, Messenger et al. 1976), and (c) biosystematic investigations of poorly-understood taxa, including many of the parasitic Hymenoptera (see Gordh 1976, Delucchi et al. 1976).

In addition to these practical applications, comparative studies of insect life history traits are vitally relevant to a number of current topics in insect ecology including the analysis of genetic variability underlying species attributes, competition, resource partitioning, evolution of insect life histories, and reproductive strategies (Stearns 1980, Price 1984). For example, comparisons of the reproductive schedule,

fecundity, and population growth parameters of insect parasitoids are useful in studying reproductive strategies in relation to environmental stability (e.g., the temporal and spatial abundance of parasitoid hosts) (Flanders 1950, Price 1975, Tsuda 1982).

The squash bug (hereafter, SB), Anasa tristis DeGeer (Hemiptera: Coreidae), is a serious native pest of cucurbitaceous crops throughout the Midwest and much of North America (Nechols 1987). Late nymphal and adult SB are difficult to control with contact insecticides due to their reclusive habits and protective integument. In addition, an individual female can lay eggs for over two months during the growing season (Nechols 1987). Thus, there is a need to develop additional control tactics as part of an integrated pest management program of the SB.

Few studies have been made of potential non-chemical control tactics for the SB. Some squash and pumpkin varieties have been identified as relatively nonpreferred and are able to produce antibiotic effects (Novero et. al. 1962). A fly, Trichopoda pennipes F. (Tachinidae), is a well known parasitoid of the adult SB (Beard 1940). In addition, a variety of hymenopterans of the families Encyrtidae (Ooencyrtus Ashmead), Scelionidae (Gryon Haliday), and Eupelmidae (Anastatus Motchulsky) parasitize SB eggs (Krombien et. al. 1979). However, with the exception of the

work of Schell (1943) on Gryon pennsylvanicum (Ashmead) in North Carolina, no previous investigations of the biology or ecology of egg parasitoids affecting the SB have been made. Therefore, I made a comparative investigation of the two most common species locally: the gregarious encyrtids Ooencyrtus anasae (Ashmead) and a new, previously undescribed species, Ooencyrtus sp. nr. anasae (hereafter, O. sp.) (Gordon Gordh, personal communication). O. sp. lacks dark patches on its femora, thus distinguishing it from O. anasae (Ashmead 1887).

My objectives were to begin an assessment of the relative potential of O. anasae and O. sp. as biological control agents of the SB. To accomplish this, I compared several biological attributes of O. anasae and O. sp. at three constant temperatures, 20.8, 23.0, and 26.6 ± 1°C. These temperatures are in the range of the local mean field temperatures during late June to early July (23.7 - 26.6°C [Kansas Agricultural Experiment Station]). During this season, because of possibly high overwintering mortality, only low numbers of Ooencyrtus are found in squash fields (Nechols unpublished); thus, an augmentative release of parasitoids in the field may be most effective at this time.

This comparative study is divided into two parts. In part I, I determined, for each species, (1) the total developmental

period (egg to free-living adult), (2) progeny production, (3) preimaginal survivorship and (4) overall sex ratio. I also examined the distribution of male and female progeny among individual host eggs. In part II, I investigated various aspects of the reproductive biology of O. anasae and O. sp. Specifically, I compared the (1) preoviposition period, (2) oviposition schedule characteristics (e.g., oviposition period), (3) oviposition rate, (4) percentage of females producing all-male progeny, (5) fecundity, (6) total hosts parasitized, and (7) postoviposition period and longevity. In addition, at 26.6°C, life tables were constructed for each parasitoid using information from both parts I and II.

Overview of the Biology of Ooencyrtus

Ooencyrtus is a large cosmopolitan genus of the family Encyrtidae in the superfamily Chalcidoidea. Hosts of Ooencyrtus are usually eggs of other insects, especially the Hemiptera and Lepidoptera (Noyes 1985). Other species attack (1) the eggs of Orthoptera, Homoptera, Neuroptera, Coleoptera, or spiders, (2) the larvae of Diptera or Hymenoptera, or (3) the nymphs of Homoptera (Maple 1937, Gordh 1979, Noyes 1985). One species, Ooencyrtus submetallicus (Howard), is known for its wide range of hosts which, besides eggs of hemipterans and lepidopterans, includes chloropid fly pupae and coccinellid beetle larvae (Noyes 1985).

Worldwide, several Ooencyrtus spp. have been studied as part of hymenopterous egg parasitoid complexes attacking hemipterous pests (see Maple 1937, Gerling et. al. 1976, Laraichi 1979b, Bushman and Whitcomb 1980, Matteson 1981). The other species comprising these egg parasitoid complexes are of the families Scelionidae (e.g., Gryon, Telenomus Haliday, Trissolcus Ashmead, and Asolcus Nakagawa) and, sometimes, Eupelmidae (Anastatus).

Most Ooencyrtus are reported to reproduce by arrhenotoky (i.e., facultative parthenogenesis) wherein males are produced from unfertilized eggs and females from fertilized. However, thelytoky (obligate parthenogenesis), in which only females are

produced, occurs in a few species (e.g., Ooencyrtus ennomophagus Yoshimoto, Drooz [1983]). In O. submetallicus, both arrhenotokous and thelytokous strains occur (Buschman and Whitcomb 1980).

Several species of arrhenotokous Ooencyrtus mate immediately after emerging from the host (Maple 1937, Matteson 1981, Alzofon 1984), and female parasitoids can begin ovipositing on the first day of adult life under warm temperatures (i.e., ca. 26.7°C or greater) (Maple 1937, Matteson 1981, Fedde 1982, Alzofon 1984). Most of the oviposition is completed during the first week of adult life (Maple 1937, Laraichi 1979a, Alzofon 1984). The mean total fecundities reported for Ooencyrtus range from 36 to 150 eggs (Crossman 1925, Maple 1937, Laraichi 1979a, Matteson 1981, Fedde 1982). A gregarious species, Ooencyrtus patriciae Subba Rao, appears capable of regulating sex ratio in relation to the number of progeny oviposited per host (Matteson 1981). The percentage of female progeny that occur in many species is at least 70% (Maple 1937, Lee 1979, Matteson 1981, Fedde 1982, Alzofon 1984).

Ooencyrtus that parasitize hemipteran eggs may be either solitary or gregarious, with an average of two to five progeny developing per host egg (Maple 1937, Matteson 1981, and Fedde 1982). Both Ooencyrtus kuvanae (Howard) (Kamay 1976) and

Ooencyrtus johnsoni (Howard) (Maple 1937) are able to develop in embryonated host eggs.

The mean longevities of fed adult females of Ooencyrtus held ca. 26.7°C range from 20 - 42 days in the laboratory (Crossman 1925, Laraichi 1979a, Lee 1979, Matteson 1981, Fedde 1982, Weseloh 1986).

Like many other encyrtids, Ooencyrtus spp. are synovigenic (i.e., oocytes develop to maturity after emergence) (Maple 1937). Synovigenic parasitoids are capable of regulating oogenesis and storing or resorbing oocytes in response to host and/or nutrient availability (Flanders 1950). Thus, delayed reproduction and increased longevity often occur in the absence of hosts. There are several examples of these phenomena occurring among adult female Ooencyrtus: (1) three Ooencyrtus spp. will delay and shift the oviposition period by as much as eleven days when their stink bug egg hosts are unavailable (Laraichi 1978); (2) O. kuvanae undergo photoperiodically induced reproductive diapause during 6-9 month winters (Crossman 1925 and Weseloh 1986); and (3) O. submetallicus has increased longevity in the absence of hosts (Lee 1979).

The eggs of Ooencyrtus possess stalks that can be seen protruding through the surface of the host. Maple (1937) reported that the stalks possess an aeroscopic plate which extends onto

the main body of the egg. He suggested that this plate provides an oxygen supply to the first through third larval instars. The fourth and final instar is free living in the host (Maple 1937).

Gregarious Ooencyrtus often will oviposit several eggs through a single oviposition site on the host. Maple (1947) noted that the stalks of several eggs oviposited at the same site may appear as a single stalk.

O. anasae was first described by Ashmead (1887) from specimens that emerged from SB eggs in Florida. Chittenden (1899) reported O. anasae attacking SB eggs as far north as the District of Columbia. In Wisconsin, eggs of the coreid, Euthocta galeator (F.) were also found to be a host (Yonke and Medler 1969). In Louisiana, Ingram (1927) observed that O. anasae, along with Telenomus podisi Ashmead, could provide significant control of the rice ear bug, Solubea pugnax (F.) (Pentatomidae), late in the season. O. anasae is only known to occur in the United States (Gordh 1979). No previous studies have been made of its biology.

Part I

Preimaginal development, survival, and sex ratio of *Ooencyrtus anasae* and *O.* sp.

Submitted to Environ. Entomol.

Materials and Methods

Insect Cultures. SB colonies originated from field-collected, overwintered adults. Both nymphs and adults were reared in cages on potted 'Green Zucchini' and 'Early Prolific Straightneck' squash (Cucurbita pepo L. [Harris Seed Co., Rochester, New York]). Cultures were maintained at 27 ± 1°C and LD 16:8. Illumination was provided by fluorescent lamps (Cool White).

To initiate parasitoid colonies, I collected SB egg masses from zucchini and pumpkin fields near Manhattan, Kansas. Emerged adults were sorted to species, placed into cages, and then transferred to environmental growth chambers under LD 15:9 and 26.6 ± 1°C. Plastic boxes that contained a saturated NaCl solution were used to maintain about 75% RH. Both colonies were supplied continuously with moist cotton and a 40% (v:v) honey-water solution for food. SB egg masses (≤ 1 day-old) were added every other day.

Parasitization. To obtain parasitized hosts, individual pairs (female & male) of first or second generation parasitoids (≤ 12 h old) were transferred to shell vials that contained honey-water and single clusters of 5 to 6 SB eggs (≤ 24 h old) and then placed under one of the experimental temperature conditions (Table 1). Parasitoid males were removed on the second day, and host eggs were replaced with fresh egg clusters daily until

parasitization ceased.

After exposure, host eggs were examined with a dissecting microscope (70x) and the number of egg stalks left by the parasitoid on the exterior of each host were counted (see Maple [1947] for description). Each egg stalk represents at least one parasitoid egg within the host. Parasitized hosts then were placed individually into wells of tissue culture plates and held under the same conditions as the parental parasitoids.

Development and Progeny Production. Parasitoid emergence was monitored daily. The total developmental period was computed as the number of days from parasitization to adult eclosion. Because parasitoids within a single host emerged synchronously, the data were pooled for all emergence from the same host. A high percentage of O. sp. females apparently did not mate and produced only male progeny (see part II). Therefore, data for all-male progeny were recorded separately.

Differences in mean development among temperatures and between species were tested with the Student's t-test; an approximate t-test was used for cases of unequal variances (SAS Institute 1985). Temperature and species differences in the number of parasitoids emerging per host were tested with the Wilcoxon rank-sum test.

Survivorship. Total survivorship (egg to adult) was computed as the number of emerged parasitoids (N_a) divided by the estimated number of parasitoid eggs (N_e). Similarly, survivorship through the egg-larval stage was calculated as the number of individuals reaching the pharate adult stage (N_p) divided by N_e. N_p was determined by counting the number of emerged and unemerged adults from each host. Survivorship through the pharate adult stage was calculated as N_a/N_p. Survivorship values were converted to percentages and compared by chi-square analysis.

To derive N_e, I determined the relationship between the number of eggs stalks and the actual number of eggs per host by dissecting a separate group of parasitized hosts (see Results). Hosts that bore only one stalk were omitted from analysis because of high variance in the associated number of parasitoid eggs.

Sex Ratio. The numbers of females and males that emerged from each host were recorded. Comparisons between percentages of females for the effect of temperatures and species were made by chi-square analysis.

To assess whether differential mortality influenced the sex ratio, I compared the percentage of females that emerged from hosts in which the highest and lowest parasitoid survivorship occurred.

Distribution of Progeny Per Host. To estimate the number of

parasitoid eggs deposited per host and the per host sex ratio, I counted the number and sex of adults emerging from individual hosts in which parasitoid survivorship exceeded 90% (i.e., experienced little or no mortality). The progeny data (within and between species) were pooled over all temperatures and analyzed with the Wilcoxon rank-sum test. The pooled sex ratio data were compared by chi-square analysis.

Results

Development. The total developmental periods of both parasitoids were inversely related to temperature, and ranged from about 18 days at 26.6°C to about 32 days at 20.8°C (Table 1). Preimaginal development in O. anasae was slightly shorter at each temperature than in O. sp.; but the differences were significant ($P < 0.001$; Student's t-test) at 20.8 and 26.6°C only (Table 1).

All-male progeny had significantly ($P < 0.001$; t-test) longer developmental times at all temperatures than did conspecific males that emerged with female siblings (Table 1).

Progeny Production. The number of parasitoids that emerged per host egg did not vary significantly with temperature or parasitoid species. O. anasae produced 3.1 ± 0.9 (1 - 7) ($\bar{X} \pm$ SD [range]) (n = 122) offspring per host compared to 3.1 ± 0.7 (1 - 5) (n = 68) in O. sp. All progeny from the same host emerged synchronously, usually through a common exit hole that was chewed by a female.

In O. sp. the number of all-male progeny produced per host (3.3 ± 0.7 [2 - 5] [n = 74]) did not differ significantly from that found in hosts containing females (i.e., "mixed-sex" progeny) (see above).

Survivorship. I found the following numerical relationship

between the number of egg stalks protruding from the host and the number of parasitoid eggs within the host: 1 stalk : 2.1 ± 1.1 (158) ($\bar{X}$ ± SD [N]) ; 2 stalks : 2.8 ± 1.0 eggs (78); 3 stalks : 3.2 ± 0.5 eggs (46); 4 stalks : 4.4 ± 0.8 eggs (7).

Total survivorship (egg to emerged adult) was high (range: 86-91%) in both species, and it did not vary with temperature (Table 2). In the mixed-sex progeny of both species, the small amount of mortality that did occur was associated almost entirely with the egg-larval stages. In contrast, pharate adult survivorship for all-male progeny of O. sp. was significantly ($P < 0.05$) lower as compared to mixed-sex progeny (100%) at 20.8°C (Table 2).

Sex Ratio. O. anasae produced a higher proportion of female progeny than did O. sp. at each temperature (Table 3). These differences were significant ($P < 0.05$; chi-square test) at 20.8 and 26.6°C (Table 3). However, temperature had no significant effect on the sex ratio of either species. Overall, 77% of the emerging O. anasae were females as compared to 60% for O. sp.

There were no significant ($P > 0.69$; chi-square test) differences in the proportion of female progeny emerging form hosts with high and low survivorship (Table 3).

Distribution of Progeny Per Host. There was no apparent

relationship between the number of eggs deposited per host and the total number of hosts parasitized per female per day for either species (Table 4, column A). However, in O. anasae there was a tendency for the per host sex ratio to increase (i.e., the percentage of female progeny) as the number of hosts parasitized increased (Table 4, columns B and C). No such relationship was observed in O. sp.

The percentage of hosts receiving 2, 3, 4 or 5-7 parasitoid eggs did not differ between species (Table 5). However, for any given number of parasitoid progeny per host, O. anasae produced a significantly ($P < 0.05$; chi-square test) higher percentage of females than did O. sp. (Table 5).

We found several other significant ($P < 0.05$; chi-square test) interspecific differences in the per host sex ratio as follows: (1) O. anasae produced more than two females per host more frequently (50%; 47/94 hosts) than did O. sp. (9%; 5/54); (2) O. anasae deposited only females in hosts more frequently (38%; 36/94) than did O. sp. (9%; 5/54); and (3) O. sp. produced more than one male per host more frequently (20%; 11/54) than did O. anasae (9%; 8/94).

Discussion

Development. The total developmental period of O. anasae was slightly shorter than that of O. sp. at each temperature. However, the statistical differences were not consistent over the range of temperatures that I tested (Table 1). Thus, the ecological significance of these differences may be small.

In O. sp., all-male progeny took significantly longer to emerge at all temperatures than did males developing with females (Table 1). My observations show that, in general, females are larger than males; also, they typically produce the common exit hole from which both sexes emerge. Therefore, delayed emergence from hosts containing only males may result from a longer time required for males to chew through the host egg chorion. This explanation is supported by my finding that pharate adult survivorship in O. sp. was reduced at lower temperatures, but only in hosts that contained no females (Table 2). The number of parasitoids did not differ between hosts that contained all males and those with at least one female; thus, competition was not a factor.

Progeny Production. Both O. anasae and O. sp. are gregarious parasitoids whose progeny emerge synchronously from the host. Gregarious development has been reported in several other species

of Ooencyrtus (Maple 1937, Matteson 1981, Fedde 1982). And, synchronous emergence has been reported for a wide range of gregarious endoparasitoids, including the Encyrtidae (Fedde 1982, Nechols & Kikuchi 1985), the Eulophidae (Nechols 1981, Narasimham 1984), and the Braconidae (Arakaki & Ganaha 1986).

My observations reveal that both O. anasae and O. sp. mate very soon after emergence in the laboratory. Thus, synchronous emergence may facilitate mating with siblings ("sib-mating"). Sib-mating may represent an important adaptive strategy for female parasitoids when host densities are low because they can be fertilized before dispersal to locate new hosts (see Arakaki & Ganaha 1986).

Survivorship. Total preimaginal survivorship for mixed-sex progeny was about 90% in both parasitoids at all three temperatures (Table 2). This value is slightly lower than that reported by Fedde (1982) under similar conditions for O. trinidadensis Crawford, an egg parasitoid of the coreid, Leptoglossus corculus (Say). In that species, survivorship per host ranged from 92% to 100% between 21 and 27°C and 76% RH.

Sex Ratio. Kotchetova (1977) and Flanders (1965) reviewed factors that influence the sex ratio of arrhenotokous parasitic Hymenoptera. These include (a) differential mortality of the sexes (e.g., extrachromosomal male or female killing factors

[Skinner 1985]), (b) extrachromosomal sex-converting factors (Werren et. al. 1986), (c) abiotic influences on reproductive physiology (e.g., temperature [Schread & Garman 1933]) and (d) regulation of oocyte fertilization by the female parasitoid (Flanders 1956).

In the present study, differential mortality did not appear to influence interspecific differences in sex ratios (Table 3). Although other factors may be involved, my observations indicate that the most important factor is probably species-specific differences in sex ratio regulation by the female parasitoid.

The percentage of female parasitoids that emerged from field-collected SB eggs in 1985 and 1986 was 77% (n = 278) in O. anasae and 60% (n = 111) in O. sp. These values are the same as the overall percentage of females I found in these parasitoids in the laboratory (Table 3). Therefore, the factors that regulate the sex ratio in the field may be similar to those that occur in the laboratory.

Distribution of Progeny per Host. Female parasitoids of arrhenotokous, gregarious species are able to regulate both the number and sex of eggs deposited in a given host (Flanders 1939). Several studies have established the biotic and abiotic factors that influence this regulation (e.g., Schread & Garman 1933,

Flanders 1935, Klomp & Teerink 1962, Nechols & Kikuchi 1985, Putters & van den Assem 1985, Schmidt & Smith 1985). Others have emphasized evolutionary aspects (e.g., Charnov & Skinner 1985, Waage & Godfray 1985). However, few comparative investigations have been made among closely-related species to determine the distribution and sex of progeny (i.e., "progeny and sex allocation") (but see Luck et al. 1982, Waage 1982).

In my comparative study of Ooencyrtus anasae and O. sp., the number of progeny deposited per host was similar. However, the sex ratios were significantly different (Table 5). The occurrence of these differences under uniform conditions of host age and number suggests that interspecific differences in sex ratio regulation exist (see Sex Ratio discussion).

As the number of hosts parasitized per cluster increased, O. anasae tended to (a) produce a higher percentage of females, and (b) deposit only female progeny in a higher percentage of hosts (Table 4). These findings appear to support recent data for the egg parasitoid Trichogramma evanescens Westwood which showed that male progeny are usually deposited in the first few hosts parasitized in a cluster (= "patch") (Waage & Ng 1984). My results also agree with predictions of their mathematical model which assumes that the minimum number of males are produced to mate with all sibling females within a localized area (i.e.,

"patch"). Males of the solitary gypsy moth egg parasitoid, Ooencyrtus kuvanae (Howard), will mate with females emerging from the same egg cluster prior to dispersal in the field (Brown 1984). This behavior may also occur among siblings of gregarious species like O. anasae and O. sp.

O. anasae produced the highest percentage of female progeny when the fewest eggs (i.e., two) were deposited per host (Table 5). A similar trend was observed for Ooencyrtus patriciae Subba Rao by Matteson (1981) who suggested that this oviposition behavior is adaptive (i.e., increases fitness) because it allows females to develop with a greater food supply. Thus, larger females with higher fecundities can be produced.

In contrast to my findings for O. anasae, there was no apparent relationship between the per host sex ratio in O. sp. and (a) the number of hosts parasitized per cluster (Table 4) or (b) the number of eggs deposited per host (Table 5). Although I have not established host species preferences for O. sp., these results may indicate that O. sp. is less adapted to hosts that occur in clusters than is O. anasae. Or, like the stink bug egg parasitoid, Ooencyrtus telenomicida Vassiliev, they may be depositing more males in a less "preferred" host species (Kotchetova 1968).

Alternatively, the relatively greater proportion of males produced by O. sp. may be associated with differences in mating behavior between the two species. In the laboratory, a much higher proportion of O. sp. females remain apparently unmated when paired with a single male than do O. anasae (see Part II).

Table 1. Mean (±S.D.) number of days for total preimaginal development in the gregarious SB egg parasitoids, Ooencyrtus anasae and O. sp., under the indicated temperatures. LD = 15:9.[a/]

Temp (± 1°C)	Total developmental time (egg to eclosed adult)		
	O. anasae	O. sp.	
	♀♀ + ♂♂	♀♀ + ♂♂	♂♂
20.8	31.9 ± 0.7a[b/] (38)	33.3 ± 1.0b (26)	34.5 ± 0.6c (15)
23.0	24.5 ± 1.3a (33)	25.1 ± 0.8a (19)	26.9 ± 1.1b (17)
26.6	18.0 ± 1.0a (44)	19.0 ± 0.6b (18)	19.6 ± 0.7c (21)

a/ (N) = number of parasitized hosts.

b/ Means within rows followed by a different letter are significantly different ($P \leq 0.001$; t-test).

Table 2. The percentage of total and stage-specific survivorship in the gregarious SB egg parasitoids, Ooencyrtus anagae and O. sp., at the indicated temperatures. LD = 15:9.[a/]

Temp. (± 1°C)	% Survivorship								
	Total (egg to adult eclosion)			Egg-larval			Pharate Adult		
	O. anagae	O. sp.		O. anagae	O. sp.		O. anagae	O. sp.	
	♀♀ + ♂♂	♀♀ + ♂♂	♂♂	♀♀ + ♂♂	♀♀ + ♂♂	♂♂	♀♀ + ♂♂	♀♀ + ♂♂	♂♂
20.8	90a	89a	75b	90a	89a	82a	100a	100a	90b
	(113:12)	(78:10)	(46:16)	(113:12)	(78:88)	(51:11)	(113:12)	(78:0)	(46:5)
23.0	91a	88a	84ab	91a	88a	90a	100a	100a	94ab
	(125:12)	(61:6)	(97:18)	(125:12)	(61:9)	(103:12)	(125:0)	(61:0)	(97:6)
26.6	88a	86a	87a	90a	86a	87a	99a	100a	100a
	(143:19)	(69:11)	(86:13)	(145:17)	(69:11)	(86:13)	(143:2)	(69:0)	(86:0)

[a/] (N:n) = the number of parasitoids surviving through stage; the number parasitoids dying during stage. Frequencies within rows or between columns followed by a different letter are significantly different ($P < 0.05$; chi-square test).

Table 3. Influence of temperature and survivorship on the percentage of emerged females for the gregarious SB egg parasitoids, Ooencyrtus anagae and O. sp. (LD = 15:9).

	% of emerged females (No. of ♀♀: No. of ♂♂)	
	O. anagae	O. sp.
Temperature (± 1°C)[a/]		
20.8	76a	62b
	(93:29)	(54:33)
23.0	73ab	63b
	(78:29)	(41:24)
26.6	81a	56b
	(95:22)	(36:28)
Combined	77a	60b
	(266:80)	(131:85)
% Survivorship[b/]		
High	77a	60a
(91-92%)	(236:69)	(112:74)
Low	73a	63a
(62-63%)	(30:11)	(19:11)

[a/] The number of parent females per temperature were as follows: O. anagae = 11-13; O. sp. = 4-6. Percentages between rows and within columns followed by a different letter are significantly different ($P < 0.05$; chi-square test). All percentages for O. anagae differ significantly from 50% ($P < 0.01$; chi-square test).

[b/] Data are combined for all temperatures. Percentages within columns followed a different letter are significantly different ($P < 0.05$; chi-square test).

Table 4. Relationship between the number of hosts parasitized per day and the number and sex of progeny deposited per host for the gregarious SB egg parasitoids, Ooencyrtus anasae and O. sp. LD = 15:9.[a/,b/]

Number of hosts parasitized in 24 hours	Number of parasitoid eggs per host ($\bar{x} \pm$ SD [N]) (A)		Percentage of emerged females (♀♀:♂♂) (B)		Percentage of hosts producing only females (no. without ♂♂: no. with ♂♂) (C)	
	O. anasae	O. sp.	O. anasae	O. sp.	O. anasae	O. sp.
1	3.7 ± 0.7 a	3.2 ±0.8 a	76abc	68a	14ab	20a
	(29)	(12)	(81:25)	(26:12)	(4:25)	(2:10)
2	3.4 ± 0.8 a	3.3 ± 0.7 a	69ab	60a	33b	0a
	(41)	(12)	(93:41)	(24:16)	(13:27)	(0:12)
3	3.6 ± 1.2 a	3.3 ± 1.0 a	80bc	57a	34b	10a
	(32)	(20)	(91:23)	(36:27)	(11:21)	(2:18)
4	3.0 ± 0.8 a	2.9 ± 0.7 a	84c	55a	53ab	20a
	(36)	(10)	(90:17)	(16:13)	(19:17)	(2:8)
5	3.1 ± 0.7 a	------	82c	---	50a	---
	(22)		(56:12)		(11:17)	

a/ The data are combined for all temperatures, including the intermediate temperatures of 21.8 and 25.6°C.

b/ Means or percentages within rows or between columns followed by a different letter are significantly different ($P < 0.05$; Wilcoxon rank-sum test for means; chi-square test for percentages).

Table 5. The number of parasitoid eggs deposited per SB host and the sex frequency of emerging adults of *Ooencyrtus anasae* and *O. sp.* The data are combined for all temperatures.

Number of parasitoid eggs per host	% (number) of hosts in each category[a]		% of females emerged (No. ♀♀: No. ♂♂)[b]	
	O. anasae	*O. sp.*	*O. anasae*	*O. sp.*
2	16	13	97 d	57 ab
	(15)	(7)	(31:1)	(8:6)
3	54	65	78 c	67 b
	(51)	(35)	(120:33)	(70:35)
4	28	17	70 c	47 a
	(23)	(9)	(64:28)	(17:19)
5-7	6	5	83 c	53 ab
	(5)	(3)	(15:3)	(9:8)

[a]Differences in percentages between species are not significant.

[b]Frequency percentages within rows or between columns followed by a different letter are significantly different ($P < 0.05$; chi-square test).

Part II

Reproductive biology, longevity and life tables of *Ooencyrtus anasae* and *O.* sp.

To be submitted to Environ. Entomol.

Materials and Methods

Insect Cultures. SB colonies originated from field-collected, overwintered adults. Cultures were reared on potted Cucurbita pepo L. plants using procedures described in Part I.

Parasitoid colonies were initiated from adults that were collected (or reared) from SB egg masses found in zucchini and pumpkin fields near Manhattan, Kansas. Colonies were reared on hosts under the conditions described in Part I.

Oogenesis. To determine when oocyte development occurred, the ovarioles in each ovary were inspected. Female parasitoids ($\leq$ 0.5 hr from emergence) were held with a male and honey at 26.6°C for various intervals and then dissected.

General Experimental Procedures. Individual pairs, (female and male) of newly emerged ($\leq$ 12 h old) first and second generation parasitoids were placed into shell vials under the conditions described in Part I. Each pair was provided with a cut piece of squash leaf that contained a cluster of 5-6 SB eggs ($\leq$ 24 h old). Previous observations revealed that females do not parasitize more than six hosts per day. New host clusters were exposed daily to each female until about two weeks after parasitization ceased. Males were removed after ca. two days.

After exposure, host eggs were examined for parasitization under a dissecting microscope (70x). Both the presence and number

of external parasitoid egg stalks on each intact host were recorded (see Maple [1947] for description).

The relationship between the number of parasitoid egg stalks per host and the number of eggs within the host (part I) was used to estimate the number of eggs laid on each day of oviposition. For each female, I then determined (1) the preoviposition period, (2) characteristics of the oviposition schedule (e.g., oviposition period), (3) daily oviposition rates, (4) the percentage females producing all-male progeny, (5) fecundity, (6) total hosts parasitized, and (7) the postoviposition period and longevity.

To assess whether body size was correlated with fecundity, I measured the hind tibial lengths (mm) of the females used in the experiment.

Using data from part I for the preimaginal survivorship, development and sex ratio, and daily oviposition and adult survivorship data herein, I constructed life tables for both parasitoids at 26.6°C (see Tables 12 and 13). Because all parasitoids used for this study were reared at 26.6°C, life tables could not be constructed for 20.8 and 23.0°C. From the life tables, various demographic statistics were calculated using methods described in Birch (1948) and Pielou (1977).

Analysis. The Wilcoxon rank-sum test (WRST) (SAS Institute 1985b) was used to make pair-wise comparisons for the effects of species and temperature on all variables except fecundity, total hosts parasitized, and hind tibial length. Comparisons were made for these variables using a two-way analysis of variance (ANOVA) for unbalanced data and Fisher's protected least significant difference test (FPLSD) (SAS Institute 1985b).

Percentage data were analyzed by the chi-square test. I tested for correlations between variables using Pearson's product-moment correlation (r) (SAS Institute 1985a).

Results

Oogenesis. Dissections of newly emerged O. anasae and O. sp. revealed no mature oocytes within the three ovarioles of each ovary.

Preoviposition Period. The preoviposition periods of both species were inversely related to temperature (range: 1 day [26.6°C] - 5 days [20.8°C]) (Table 6). However, at 26.6°C, O. anasae had a significantly (P = 0.002; WRST) shorter preoviposition period (1.5 days) than did O. sp. (3.8 days).

In O. anasae, the preoviposition periods were similar at the two upper temperatures (23.0 and 26.6°C); these were significantly (P = 0.002; WRST) shorter than at 20.8°C. Whereas, in O. sp., the preoviposition periods were similar at the two lower temperatures; these were significantly (P = 0.02; WRST) longer than at 26.6°C. The variances were relatively high in O. sp. at the two lower temperatures.

Oviposition Schedule. Peak oviposition in both species occurred sooner at higher, than at lower, temperatures (Table 7, column A; Figures 1 and 2). In O. anasae, the day of peak oviposition ranged from ca. day 7 at 20.8°C to ca. day 4 at 26.6°C. A significant difference (P = 0.02; WRST) was found between 23.0 and 20.8°C. In O. sp., the range was ca. day 9 to day 5. Peak oviposition in O. anasae occurred significantly (P = 0.03; WRST)

sooner at 23.0°C (day 3.6) than in O. sp. (day 6.7) (Table 7, column A).

The mean day of 75% egg production was around day 16 for both parasitoids at 20.8°C (Table 7, column B). However, at 23.0 and 26.6°C, the days of 75% egg production were significantly ($P = 0.02$; WRST) later in O. sp. (days 15.1 and 9.5) compared to O. anasae (days 6.8 and 7.1). In O. anasae, there was a significant ($P = 0.02$; WRST) decrease in the day of 75% egg production between 20.8 and 23.0°C. In O. sp., a significant ($P = 0.002$; WRST) decline occurred between 23.0 and 26.6°C (Table 7, column B).

The mean oviposition period was longer in O. sp. at all temperatures than in O. anasae (Table 7, column C; Figures 1 and 2). The differences were significant at 23.0 and 26.6°C. In O. sp., the oviposition periods were uninfluenced by temperature. In contrast, the oviposition periods differed significantly ($P < 0.05$; WRST) in O. anasae between 20.8 and 26.6°C.

Oviposition Rate. The mean daily oviposition rates over the first week ranged from about 2 to 4 eggs per day (Table 8, column A). A significant increase in the first week oviposition rate occurred for O. anasae between 20.8 and 23.0°C. In O. sp., the increase occurred between 23.0 and 26.6°C. These rates did not differ

significantly between species.

During the second week, the mean daily oviposition rates were significantly ($P < 0.03$; WRST) higher in O. sp. at each temperature (ca. 2 to 3 eggs per day) compared to O. anasae (ca. 1 egg per day) (Table 8, column B). These rates did not vary with temperature in either species.

In both species, mean daily oviposition rates followed a cyclic pattern (Figures 1 and 2). But, in O. anasae, considerably fewer cycles occurred at 23.0 and 26.6°C compared to O. sp.

Percentage All-male Producing Females. The percentage of O. sp. females that produced only male progeny was 57% (20/35). This percentage was significantly ($P < 0.02$; chi-square test) higher than that of O. anasae (2% [1/59]).

Fecundity. The fecundity in O. sp. was significantly higher ($P < 0.01$; FPLSD) at each temperature than that of O. anasae (Table 9, column A). There was no relationship between fecundity and temperature for either species of parasitoid.

Fecundity was not significantly correlated ($P > 0.05$; $r \leq 0.56$) with hind tibial length in either parasitoid. Also, tibial size did not differ significantly ($P > 0.27$; ANOVA) among species at any of the temperatures (Table 9, column B).

In O. sp., the fecundity of all-male producing (virgin) parasitoids did not differ significantly ($P > 0.24$; ANOVA) from

that of parasitoids producing some female progeny (mated), at each temperature (Table 9, column C).

In O. sp., fecundity and the length of the oviposition period were strongly and positively correlated at 20.8 ($P = 0.01$; $r = 0.71$) and 23.0°C ($P = 0.0002$; $r = 0.90$), but not at 26.6°C ($P = 0.13$; $r = 0.48$). In contrast, for O. anasae, fecundity was not significantly correlated with the oviposition period ($P \geq 0.06$; $r \leq 0.54$) at any temperature. Fecundity was not well correlated ($P \geq 0.28$; $r \leq 0.32$) with longevity for either species at any temperature.

Host Parasitization. Both species parasitized a mean of ca. 3 to 4 hosts (range: 1-6) on their day of peak host parasitization at each temperature.

The total number of hosts parasitized during the lifetime of a female parasitoid was significantly ($P < 0.01$; FPLSD) higher in O. sp. than in O. anasae at all temperatures (Table 10, column A). In both parasitoids, the total number of hosts parasitized was not related to temperature.

Postoviposition Period and Longevity. The postoviposition period in both parasitoids was at least one month at each temperature (Table 10, column B; see Figures 1-2). In both species, the length of the postoviposition period was highly variable at

20.8°C.

Longevity decreased (Table 10, column C; Figures 1 and 2) with increasing temperature in O. anasae, but this relationship did not occur in O. sp. No statistical differences were found in longevity between species. However, O. anasae females tended to live longer at 20.8°C (Table 10, column C; Figures 1 and 2).

Life Table Parameters. The gross and net reproductive rates of O. sp. were higher than in O. anasae (Table 11). Whereas, the mean generation time was shorter and the innate capacity for increase (r_m) was higher in O. anasae. (Table 11).

Between days 18 and 26, the mean number of female progeny produced per day (m_x) (Tables 12 and 13) in O. anasae was generally greater than that of O. sp. Thereafter, m_x was consistently higher in O. sp.

Between days 18 and 25, the daily contribution to the innate capacity for increase (r%) of O. anasae was higher than in O. sp. O. sp. had a higher r% between days 21 and 23 and after day 26. The cumulative contribution to the innate capacity for increase ($\sum r\%$) of O. anasae was consistenly higher than that of O. sp., especially between days 20 and 25 (Tables 12 and 13).

Discussion

Oogenesis. Dissections of O. anasae and O. sp. revealed that female parasitoids do not possess fully mature oocytes upon emergence. Because oogenesis occurs after emergence, I conclude that both parasitoids exhibit synovigeny (Flanders 1950). Synovigeny is a reproductive adaptation common to many of the Encyrtidae. For example, Maple (1937) found that the first mature oocytes of Ooencyrtus johnsoni (Howard), an egg parasitoid of Murgantia histrionica (Hahn) (Pentatomidae), appeared ca. 12 hours after emergence at ca. 25.6°C. Females exhibiting synovigenic reproduction are able to regulate oogenesis and store and resorb eggs in relation to host availability (Flanders 1950).

Preoviposition Period. The interspecific differences I observed in the relationship between temperature and preoviposition period (Table 6) are probably related to the effect of temperature on the rate of oogenesis in the adult. The influence of temperature on oogenesis and oviposition has been found to differ slightly between species of other synovigenic parasitoids (e.g., Encarsia spp. [Aphelinidae], van Lenteren and van der Schaal 1981). Laraichi (1979a) suggested differences in rates of oogenesis were responsible for variations in preoviposition period with temperature in three other Ooencyrtus spp., all of which are egg parasitoids of Aelia cognata Fieb (Pentatomidae).

Oviposition Schedule. The oviposition schedule of O. anasae was heavily influenced by a change in temperature from 20.8 to 23.0°C. Whereas, in O. sp., the oviposition schedule was more influenced by a change in temperature from 23.0 to 26.6°C. This difference in temperature response is similar to that observed for the preoviposition period. Thus, the two species appear to have different thermal optima governing the rate of oogenesis.

The longer oviposition period of O. sp. at 23.0 and 26.6°C indicates that oogenesis occurs for a longer period in this parasitoid as compared to O. anasae.

Oviposition Rate. The oviposition rates during the first week did not differ significantly between species. However, during the second week, O. sp. oviposited at a significantly higher rate than did O. anasae. This finding is associated with the comparatively longer oviposition schedule in O. sp. (Figures 1 and 2). Thus, oogenesis may occur at a higher rate in O. sp. during the second week.

Oviposition occurred in cycles of 3 to 6 days (Figures 1 and 2), especially in O. sp. These may represent synchronized cycles of oocyte maturation in the females. These oviposition patterns differ from plotted daily oviposition patterns of the Ooencyrtus spp. studied by Laraichi (1979a), Herard and Mercadier (1980), and

and Alzofon (1984), all of which are acyclic. However, a fluctuating cycle of egg production has been observed in another gregarious encyrtid, Anagyrus indicus Shafee et al. (Nechols unpublished).

Percentage of Females Producing All-male Progeny. A relatively high percentage (57%) of O. sp. females produced only male progeny. Because all observed matings of O. sp. in the laboratory have resulted in the production of female progeny (unpublished data), this phenomenon probably resulted from the females failing to mate. It is possible that the laboratory conditions may have been less favorable for the mating of O. sp. compared to O. anasae.

If a high proportion of O. sp. females in the field were unmated, immature parasitoids collected from the field would consist of a smaller percentage of females than that expected if all of the parent females were mated. I found that the percentage of females among field collected immature O. sp. is the same as that observed for progeny of mated females in the laboratory (see Part I). Thus, in the field, the percentage of female O. sp. that mate is near 100%.

Fecundity. O. sp. had a higher fecundity than did O. anasae at each temperature (Table 9, column A). The differences were not associated with interspecific differences in female body size

species (Table 9, column B). There was no correlation between tibial size and fecundity. In addition, the mean total body lengths ($\bar{X} \pm$ SD mm [N]) of random samples of field-collected adult female O. anasae (1.17 ± 0.11 mm [57]) and O. sp. (1.13 ± 0.13 mm [36]) were nearly equal. Thus, in the field, there are no apparent differences in the size of females of these parasitoids.

In O. sp., the fecundity of virgin females did not differ from that of mated females (Table 9, column C). Therefore, interspecific differences in fecundity were apparently not related to differences in the percentage of mated females between each species. Studies of several other Ooencyrtus spp. have similarly found no differences in fecundity between mated and virgin females (Maple 1937, Laraichi 1979a, Fedde 1982). However, Crossman (1925) found that virgin females of the gypsy moth egg parasitoid, Ooencyrtus kuvanae (Howard), produced a smaller number of progeny than mated females.

There was a positive correlation in O. sp. between fecundity and the length of the oviposition period at 20.8 and 23.0°C. This finding is in agreement with those for three other Ooencyrtus spp. studied by Laraichi (1979a). However, I found no correlation between fecundity and longevity for either species. These results also agree with the findings of Laraichi (1979a).

The higher fecundity of O. sp. is probably related to a higher rate of oogenesis during the second week of adult life (see Oviposition Rate discussion). In synovigenic parasitoids, oogenesis has been correlated with adult feeding on protein-containing fluids that exude from the oviposition wound of a potential host (i.e., host feeding) (see Flanders 1950, van Lenteren et. al. 1987). I have observed host feeding by both O. anasae and O. sp., but considerably more frequently in O. sp. Thus, a difference in protein intake of the two species by host feeding may be partly responsible for their differing rates of oogenesis later in life and, thus, their differing total fecundities.

The mean total fecundities of O. anasae (32 eggs) and O. sp. (52 eggs) at 26.6°C are at the lower end of the range of the total number of eggs or progeny produced (ca. 50 - 135) under comparable temperatures by six other Ooencyrtus spp. (Crossman 1925, Maple 1937, Laraichi 1979a, Matteson 1981). However, Ooencyrtus trinidadensis Crawford, an egg parasitoid of another coreid, Leptoglossus corculus Say, has a fecundity of about 36 eggs at 27°C and 75% RH (Fedde 1982). This is very similar to that found in O. anasae.

Both O. anasae and O. sp. have a higher fecundity than that reported for the solitary squash bug egg parasitoid, Gryon

pennsylvanicum (Ashmead) (Scelionidae), (16 eggs at ca. 26.7 ± 3°C) (Schell 1943).

Host Parasitization. The mean peak number of hosts parasitized was about 3 - 4 per day in both parasitoids. In the field, the number of eggs parasitized within a squash bug egg mass by these parasitoids also is rarely more than four (unpublished data). The ability of these parasitoids to mark hosts and discriminate between those hosts that are parasitized or unparasitized needs to be investigated.

Both species parasitized a total of about 8 to 16 squash bug eggs (Table10, column A). Because an average SB egg mass contains 14 eggs (Beard 1940 and unpublished data), these results indicate that individual females may parasitize the equivalent of about one squash bug egg mass during their lifetime. This number is similar to the 16 SB eggs that the scelionid, G. pennsylvanicum, is able to parasitize (Schell 1943).

Postoviposition Period and Longevity. In the laboratory, females of both species had very long postreproductive periods (ca. one month) that were related to high longevities (Table 10, columns B and C). At 26.6°C, the mean female longevity of both parasitoids (ca. 40 - 50 days) is longer than that reported for six other Ooencyrtus spp. (ca. 20-33 days) at comparable temperatures

Ooencyrtus spp. (ca. 20-33 days) at comparable temperatures (Laraichi 1979a, Lee 1979, Matteson 1981, Fedde 1982). However, female O. kuvanae have a mean longevity of 30-42 days (Crossman 1925, Weseloh 1986).

The high longevity of these parasitoids in conjunction with synovigeny indicates that they may have the ability to delay reproduction and increase longevity in the absence of hosts (see Flanders 1950). One or both of these abilities have already been observed for several other Ooencyrtus spp. (see Laraichi 1978, Lee 1979, Weseloh 1986).

Life Table Parameters. The gross and net reproductive rates of O. sp. at 26.6°C were higher than those of O. anasae (Table 11). This difference is probably the result of the higher fecundity of O. sp.

On the other hand, in O. anasae, the mean generation time was shorter, and the r_m higher, than that of O. sp. (Table 11). The shorter generation time of O. anasae resulted primarily from the higher percentage of female progeny produced. The higher innate capacity for increase in O. anasae appears to be related to its shorter generation time.

The r_m values for O. anasae and O. sp. are generally high compared to that of many other insects (see Connell and Scheiring [1982] for a listing of r-values for various insects) but lower

Westwood and Telenomus Haliday at comparable temperatures (Table 11). Relatively short developmental times in Trichogramma and early reproduction in adult life associated with pro-ovigeny in both genera contribute to their high r. In contrast to these genera, the Ooencyrtus I studied are synovigenic and they have somewhat longer generation times than do Trichogramma.

Although synovigeny may result in a lower r_m for Ooencyrtus compared to other egg parasitoids, it confers advantages that are not apparent from examining r_m alone. A major advantage of synovigenic parasitoids is their ability to regulate oogenesis in response to host availability (see Flanders 1950).

Table 6. Mean (± SD) number of days to first oviposition in the gregarious SB egg parasitoids Ooencyrtus anasae and O. sp., at the indicated temperatures. LD = 15:9.a/b/

Temp. (± 1°C)	Preoviposition period (days)	
	O. anasae	O. sp.
20.8	4.7 ± 1.2 b (1 - 10)	5.1 ± 5.6 b (1 - 22)
23.0	1.5 ± 1.0 a (0 - 3)	3.8 ± 3.6 b (1 - 6)
26.6	1.4 ± 0.9 a (0 - 3)	0.8 ± 0.6 a (0 - 2)

a/ Number of parent females per temperature (20.8 to 26.6°C) are as follows: O. anasae: 14, 12, and 14; O. sp.: 13, 11, and 12. For a given variable, means within rows or between columns followed by a different letter are significantly different ($P < 0.05$; Wilcoxon rank-sum test).

b/ Numbers in parentheses denote range of preoviposition periods.

Table 7. Mean (± SD) values for various characteristics of the oviposition schedules of the gregarious SB egg parasitoids, Ooencyrtus anastae and O. sp., at the indicated temperatures. LD = 15:9.[a/b/]

Temp. (± 1°C)	Day of maximum no. eggs laid (A)		Day when 75% eggs laid (B)		Oviposition period (days) (C)	
	O. anastae	O. sp.	O. anastae	O. sp.	O. anastae	O. sp.
20.8	6.6 ± 3.5 b (3 - 12)	9.1 ± 7.5 b (2 - 26)	15.4 ± 9.9 bd (5 - 35)	17.1 ± 5.6 d (11 - 28)	15.5 ± 10.4 bc (1 - 32)	18.0 ± 10.6 c (7 - 49)
23.0	3.6 ± 2.1 a (2 - 9)	6.7 ± 4.0 b (2 - 14)	6.8 ± 4.2 a (2 - 15)	15.1 ± 4.3 d (9 - 25)	8.2 ± 5.9 ab (3 - 14)	18.1 ± 12.5 c (1 - 46)
26.6	4.1 ± 2.1 ab (2 - 10)	4.8 ± 3.7 ab (2 - 13)	7.1 ± 2.2 ab (3 - 11)	9.5 ± 2.9 c (4 - 13)	7.1 ± 1.9 a (4 - 10)	16.0 ± 6.2 c (11 - 33)

a/ Number of parent females per temperature (20.8 to 26.6°C) are as follows: O. anastae: 14, 12, and 14; O. sp.: 13, 11, and 12. For a given variable, means within rows or between columns followed by a different letter are significantly different ($P < 0.05$; Wilcoxon rank sum test).

b/ Numbers in parentheses denote range of values.

Table 8. Mean (± SD) daily oviposition rates of the gregarious SB egg parasitoids, Ooencyrtus anasae and O. sp., at the indicated temperatures. LD = 15:9.a/b/

Temp. (± 1°C)	No. of eggs laid/day			
	1st week (A)		2nd week (B)	
	O. anasae	O. sp.	O. anasae	O. sp.
20.8	1.6 ± 1.3 a (0 - 4.4)	1.7 ± 1.5 a (0 - 4.4)	1.1 ± 1.0 a (0 - 3.0)	2.1 ± 1.2 b (0 - 4.2)
23.0	3.1 ± 1.8 b (1.2 - 7.2)	2.5 ± 1.7 ab (0 - 4.8)	0.5 ± 0.9 a (0 - 3.1)	2.9 ± 1.6 b (0.5 - 5.5)
26.6	3.7 ± 2.0 bc (1.1 - 6.5)	4.3 ± 1.1 c (3.0 - 6.6)	0.9 ± 1.1 a (0 - 3.9)	2.9 ± 1.7 b (0 - 5.0)

a/ Number of parent females per temperature (20.8 to 26.6°C) are as follows: O. anasae: 14, 12, and 14; O. sp.: 13, 11, and 12. For a given variable, means within rows or betweem columns followed by a different letter are significantly different ($P < 0.05$; Wilcoxon rank-sum test).

b/ Numbers in parentheses denote range of values.

Table 9. Mean (± SD) fecundities and hind tibial lengths of the gregarious SB egg parasitoids Ooencyrtus anasae and O. sp., at the indicated temperatures. LD = 15:9.[a/b/]

Temp. (± 1°C)	Fecundity (A)		Hind tibial length (± 0.007 mm) (B)		Fecundity of O. sp. (C)	
	O. anasae	O. sp.	O. anasae	O. sp.	Mated	Virgin
20.8	23.9 ± 10.3 a (14) [12 - 46]	40.5 ± 19.4 b (13) [17 - 77]	0.389 ± 0.021 a (11) [0.359 - 0.425]	0.402 ± 0.029 a (10) [0.352 - 0.440]	50.0 ± 16.3 a (6) [27 - 77]	33.5 ± 20.8 a (6) [17 - 75]
23.0	28.0 ± 14.2 a (12) [8 - 52]	53.6 ± 27.9 b (11) [3 - 96]	0.397 ± 0.018 a (10) [0.374 - 0.440]	0.405 ± 0.024 a (9) [0.374 - 0.447]	57.4 ± 35.2 a (3) [28 - 96]	52.2 ± 27.4 a (8) [3 - 90]
26.6	32.2 ± 13.3 a (14) [10 - 49]	51.8 ± 21.0 b (11) [28 - 90]	0.394 ± 0.025 a (12) [0.367 - 0.433]	0.399 ± 0.025 a (10) [0.352 - 0.425]	54.9 ± 15.5 a (6) [37 - 77]	48.1 ± 27.7 a (5) [28 - 90]

a/ For a given variable, means within rows or between columns followed by a different letter are significantly different ($P < 0.01$; Fisher's protected LSD test).

b/ Numbers in parentheses are the numbers of females observed; numbers in brackets denote the range of values.

Table 10. Mean (± SD) total number of hosts parasitized, postoviposition periods, and longevities of the gregarious SB egg parasitoids, Ooencyrtus anagae and O. sp., at the indicated temperatures. LD = 15:9[a/b/]

Temp. (± 1°C)	Total hosts parasitized (A)		Postoviposition period (days) (B)		Longevity (days) (C)	
	O. anagae	O. sp.	O. anagae	O. sp.	O. anagae	O. sp.
20.8	7.9 ± 4.2 a (14) [3 - 16]	12.4 ± 5.8 b (13) [5 - 23]	42.9 ± 21.6 a (12) [0 - 81]	26.8 ± 19.9 a (10) [1 - 62]	62.7 ± 20.4 b (12) [15 - 92]	50.7 ± 20.2 ab (10) [21 - 84]
23.0	8.2 ± 3.9 a (12) [3 - 14]	15.6 ± 7.7 b (11) [1 - 27]	38.2 ± 15.6 a (9) [6 - 57]	33.0 ± 14.1 a (10) [8 - 54]	49.2 ± 12.2 ab (9) [24 - 68]	58.5 ± 14.6 b (10) [25 - 69]
26.6	9.4 ± 4.3 a (14) [3 - 16]	14.5 ± 6.5 b (12) [8 - 27]	31.9 ± 16.3 a (13) [1 - 52]	32.7 ± 10.8 a (11) [6 - 46]	40.6 ± 16.3 a (13) [9 - 61]	49.8 ± 11.7 ab (11) [22 - 60]

a/ For a given variable, means within rows or between columns followed by a different letter are significantly different (P < 0.01; Fisher's protected LSD test for total hosts parasitized and Wilcoxon rank sum test for other variables).

b/ Numbers in parentheses are the numbers of females observed; numbers in brackets denote the range of values.

Table 11. Net reproductive rate (R_o), mean generation time (T), innate capacity (r_m) or capacity (r_o) for increase (r), and population doubling time (DT) for various hymenopterous egg parasitoids at the specified temperatures.

Egg Parasitoid	Temp.(°C)	R_o	T	r	DT	Reference
I. Chalcidoidea						
A. Encyrtidae						
Oencyrtus anasae	26.6	22.9	21.8	0.146	4.8	present study
O. sp.	26.6	24.5	23.8	0.134	5.2	Ibid.
B. Trichogrammatidae						
Trichogramma retorridum	25.0	54.5	18.8	0.277	2.5	Orphanidea and Gonzalez 1971
T. pretiosum	25.0	50.0	11.5	0.34	2.0	Pak and Oatman 1982
T. brevicapillum	25.0	66.9	12.9	0.33	2.1	Ibid.
T. minutum	27.0	----	8.9	0.43	1.6	Manweiler 1986
T. platneri	27.0	----	9.5	0.37	1.9	Ibid.
T. dendrolimi	30.0	----	---	0.604	1.1	Hirose 1986
C. Eupelmidae						
Anastatus japonicus	----	----	---	0.149	4.7	Hirose 1986
D. Mymaridae						
Anagrus epos	28.0	20.2	18.8	0.165	4.2	Williams 1984
II. Proctotrupoidea						
A. Scelionidae						
Telenomus calyus	27.0	----	---	0.149	4.7	Orr et. al. 1986
T. basalis	----	----	---	0.315	2.2	Ibid.
T. dendrolimi	30.0	----	---	0.296	2.3	Hirose 1986
T. podisi	27.0	----	---	0.308	2.3	Orr and Boethal 1986

Table 12. Life table including daily and cumulative percentage contributions to the innate capacity for increase (r_m) for Oecnyrtus anagae at 26.6°C, LD = 15:9.[a/]

Stage	N	x	l_x	fec_x	m_x	r%	$\sum$r%
			O. anagae				
Egg-larval		1-17	1.00	0.00	0.00	0.00	0.00
Pharate adult			0.90	0.00	0.00	0.00	0.00
Adult	1	18.0	0.88	0.51	0.41	2.62	2.62
	2	19.0	0.88	3.94	3.19	17.51	20.13
	3	20.0	0.88	9.37	7.59	35.98	56.11
	4	21.0	0.88	4.52	3.66	15.00	71.10
	5	22.0	0.88	3.07	2.49	8.80	79.92
	6	23.0	0.88	2.26	1.83	5.60	85.51
	7	24.0	0.88	2.19	1.77	4.69	90.20
	8	25.0	0.88	2.33	1.89	4.31	94.51
	9	26.0	0.81	1.53	1.24	2.25	96.76
	10	27.0	0.81	1.89	1.53	2.40	99.16
	11	28.0	0.81	0.25	0.20	0.28	99.44
	12	29.0	0.81	0.59	0.48	0.56	100.00

[a/] The reproductive schedule was obtained from 14 female O. anagae. Life table parameters are: (1) p = proportion of females among all progeny, .81 for O. anagae, (2) N = day of adult life, (3) x = age interval (days), (4) l_x = proportion of females surviving to start of age interval x (l_0 = 1.00), (5) fec_x = no. of offspring produced per age interval per female alive at age x, (6) m_x = $fec_x(p)$, (7) r% = the daily percentage contribution to the innate capacity for increase, r, = $[(e^{-r(x)})l_x m_x](100)$ (see Table 11 for r), and (8) $\sum$r% = cumulative r%.

Table 13. Life table including daily and cumulative percentage contributions to the innate capacity for increase (r_m) for Oecencyrtus sp. at 26.6°C. LD = 15:9.[a/]

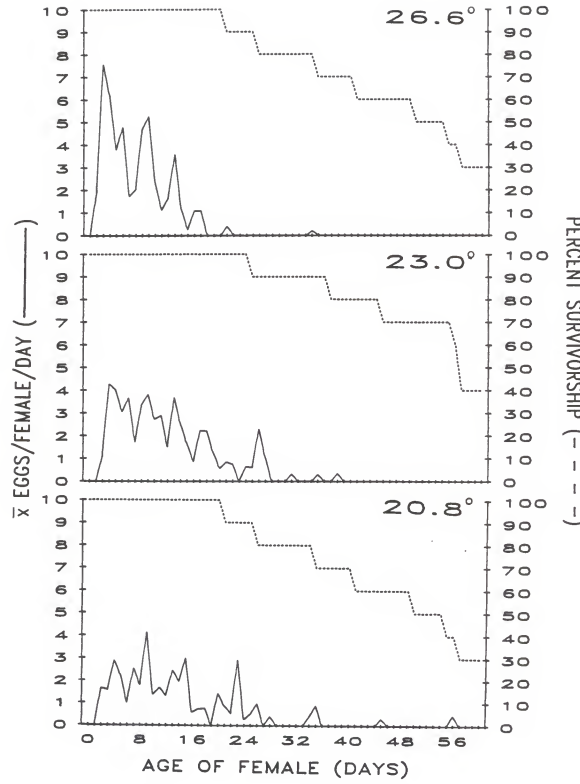
	Q. sp.						
Stage	N	x	l_x	fec_x	m_x	r%	$\sum r\%$
Egg-larval		1-18	1.00	0.00	0.00	0.00	0.00
Pharate adult			0.90	0.00	0.00	0.00	0.00
Adult	1	19.0	0.86	1.95	1.09	7.31	7.31
	2	20.0	0.86	7.56	4.23	28.79	32.10
	3	21.0	0.86	6.18	3.46	17.71	49.82
	4	22.0	0.86	3.80	2.13	9.52	59.34
	5	23.0	0.86	4.79	2.68	10.50	69.84
	6	24.0	0.86	1.73	0.97	3.31	73.15
	7	25.0	0.86	2.05	1.15	3.43	76.58
	8	26.0	0.86	4.70	2.63	6.88	83.47
	9	27.0	0.86	5.25	2.94	6.72	90.19
	10	28.0	0.86	2.32	1.30	2.60	92.78
	11	29.0	0.86	1.13	0.63	1.11	93.88
	12	30.0	0.86	1.65	0.92	1.41	95.30
	13	31.0	0.86	3.58	2.00	2.68	97.98
	14	32.0	0.86	1.16	0.65	0.76	98.74
	15	33.0	0.86	0.25	0.14	0.14	98.88
	16	34.0	0.86	1.09	0.61	0.55	99.42
	17	35.0	0.86	1.09	0.61	0.48	99.90
	21	39.0	0.77	0.40	0.22	0.10	99.99
	34	52.0	0.77	0.21	0.11	0.01	100.00

[a/] The reproductive schedule was obtained from 11 female Q. sp. (percentage of female progeny = p = .54) (see Table 7 for life table parameters).

Figure 1. Age-specific fecundity and survivorship of the gregarious SB egg parasitoid, Ooencyrtus anasae, at the indicated temperatures. From 20.8 to 26.6°C, fecundity values represent means of 14, 12, and 14 females and survivorship values represent initial samples of 12, 9, and 13 females. LD = 15:9.

26.6°
23.0°
20.8°
$\bar{x}$ EGGS/FEMALE/DAY (———)
PERCENT SURVIVORSHIP (– – – –)
AGE OF FEMALE (DAYS)
0 8 16 24 32 40 48 56

Figure 2. Age-specific fecundity and survivorship of the gregarious SB egg parasitoid, Ooencyrtus sp., at the indicated temperatures. From 20.8 to 26.6°C, fecundity values represent means of 13, 11, and 12 females and survivorship values represent initial samples of 10, 10, and 11 females. LD = 15:9.


26.6°
23.0°
20.8°
$\bar{x}$ EGGS/FEMALE/DAY (——)
PERCENT SURVIVORSHIP (- - - -)
AGE OF FEMALE (DAYS)
0 8 16 24 32 40 48 56

Summary and Conclusions

Biological comparisons were made in the laboratory between the squash bug egg parasitoids, Ooencyrtus anasae and O. sp., at 20.8, 23.0 and 26.6°C.

Temperature had little or no influence on survivorship, sex ratio, or fecundity. However, temperature did influence the timing and rate of oviposition of both parasitoids, but in different ways. In O. anasae, these characteristics changed markedly in response to an increase in temperature from 20.8 to 23.0°C; whereas, in O. sp., comparable changes occurred only after a temperature shift from 23.0 to 26.6°C.

The parasitoids were similar in that both exhibited a high preimaginal survivorship and produced equal numbers of progeny per host at all temperatures. However, I found major interspecific differences in the sex ratio, oviposition period, oviposition rate, and fecundity. For example, O. anasae produced a higher percentage of female progeny at each temperature. This was related in part to the tendency of O. anasae, but not O. sp., to regulate sex ratio in relation to (1) the number of eggs laid per host and (2) the number of hosts parasitized per cluster. At each temperature, adult female O. sp. oviposited for a longer total period and at a significantly higher rate in the second week than did O. anasae. This resulted in higher fecundities in

O. sp. than in O. anasae. Thus, at 26.6°C, O. sp. had higher gross and net reproductive rates than did O. anasae. However, because O. anasae produced a higher percentage of female progeny than did O. sp. early in life, it had a shorter mean generation time and an associated higher innate capacity of increase at 26.6°C.

Based on the biological differences between O. anasae and O. sp. found in this study, a preliminary assessment can be made of their relative potential for biological control of the SB in the temperature range of 20.8 to 26.6°C. These temperatures are in the range of mean temperatures found in the late spring to early summer season. In this season, egg parasitoids are rare in the field, exhibiting poor synchrony with squash bugs; thus, an augmentative release of egg parasitoids might be considered during this time. Neither parasitoid appears to have a decided advantage at the lower end of the temperature range I tested (20.8 and 23.0°C). However, the rate of oogenesis in O.anasae appeared to show a greater increase at a lower temperature (between 20.8 and 23.0°C) than did that of O. sp. At 26.6°C, O. anasae possessed a clearly higher innate capacity of increase. Thus, O. anasae may be more useful than O. sp. for biological control of the SB. At the temperatures tested, the oviposition

schedule of both species indicates that 7 to 16 days is the longest period that parasitoids will reproduce at a consistent rate between augmentative releases. This information is useful for timing various management options (e.g., periodic parasitoid releases, pesticide applications, etc.).

Other attributes (e.g., host acceptance and suitability, competition, searching ability, and alternate hosts) of O. anasae and O. sp., as well as the basic biology of other egg parasitoids of the SB in Kansas, need to be examined to more fully evaluate the potential of indigenous natural enemies as biological control agents of the SB.

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Biological comparisons of the squash bug egg parasitoids, *Ooencyrtus anasae* (Ashmead) and *O.* sp. (Hymenoptera: Encyrtidae): A laboratory assessment.

by

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AN ABSTRACT OF A MASTER'S THESIS

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Abstract

The biologies of the gregarious squash bug egg parasitoids, Ooencyrtus anasae and Ooencyrtus n. sp. nr. anasae (O. sp.) were compared in the laboratory at 20.8, 23.0, and 26.6°C. At each temperature, O. anasae developed and emerged about a day earlier, and produced a higher percentage of female progeny (77%), than did O. sp. (60%). Both parasitoids had about 89% preimaginal survivorship and produced three progeny per host. In O. anasae, but not O. sp., the proportion of females produced per host increased directly with the number of hosts parasitized per host cluster.

Females of both species are synovigenic. The preoviposition period, day of peak oviposition, and first week oviposition rate of the parasitoids were similar at 20.8°C. In O. anasae, these charactersitics changed markedly in response to an increase in temperature from 20.8 to 23.0°C. Whereas, in O. sp., comparable changes occurred after a temperature shift from 23.0 to 26.6°C. Thus, at 23.0°C, O. anasae had a shorter preoviposition period and peak oviposition occurred earlier. The mean oviposition period of O. sp. was consistenly longer than that of O. anasae. Both species had a similar oviposition rate during the first week, but, in the second week, the oviposition rate of O. anasae declined below that of O. sp.

The mean fecundity of O. sp. was consistently higher than that of O. anasae. Body sizes did not differ between the species and were not correlated with fecundity. Females of both parasitoids had an unusually long postreproductive period (ca. one month) and a longevity of 40 to 50 days at each temperature. At 26.6°C, O. sp. had the highest gross and net reproductive rates. However, O. anasae had the shortest generation time and highest innate capacity for increase. These results indicate that O. anasae may have more potential than O. sp. in biological control of the squash bug.