Comparisons Between the Squash Bug Egg Parasitoids *Ooencyrtus anasae* and *O.* sp. (Hymenoptera: Encyrtidae): Development, Survival, and Sex Ratio in Relation to Temperature

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ABSTRACT   Laboratory investigations of the gregarious squash bug egg parasitoids *Ooencyrtus anasae* and *O. n.* sp. near *anasae* (*O.* sp.) were conducted at 20.8, 23.0, and 26.6°C. In both species, total developmental periods (egg to eclosed adult) were inversely related to temperature. Temperature had no significant influence on survivorship, progeny production, or sex ratio. At each temperature, *O. anasae* developed and emerged about a day earlier and produced a significantly higher percentage of female progeny (77%) than did *O.* sp. (60%). Both parasitoids deposited an average of three (2–7) progeny per host. However, *O. anasae* consistently deposited more female eggs per host than did *O.* sp. Proportion of females produced per host by *O. anasae* tended to increase directly with number of hosts parasitized, but no such relationship was observed in *O.* sp. Total preimaginal survivorship in both parasitoids was about 89%. In *O.* sp., male progeny that developed without females emerged about a day later at all temperatures and had a lower pharate adult survivorship than did males that developed in hosts with female siblings.

KEY WORDS   Insecta, *Anasa tristis*, gregarious parasitoids, biological control

EVALUATION OF natural enemy attributes is of central importance to their proper utilization in biological control programs (DeBach et al. 1976, Ehler 1982, Ehler & Hall 1982). Comparative evaluations of closely related beneficial species are particularly useful because they form the basis for examining complex interactions, selecting candidates for mass-rearing and release in augmentation programs (Messenger et al. 1976, King et al. 1985), and investigating the biosystematics of poorly understood taxa, including many of the parasitic Hymenoptera (Delucchi et al. 1976, Gordh 1976).

The squash bug (SB), *Anasa tristis* (DeGeer) (Hemiptera: Coreidae), is a serious native pest of cucurbitaceous crops throughout the Midwest and much of North America (Nechols 1987). Although several hymenopterous egg parasitoids occur naturally on the SB in eastern Kansas (unpublished data), the biology or ecology of this egg parasitoid complex have not been investigated. Therefore, we have begun a comprehensive evaluation of two of the most common, gregarious encyrtids—*Ooencyrtus anasae* (Ashmead) and a new, closely related species, *Ooencyrtus* sp. near *anasae* (hereafter, *O.* sp.) (Gordon Gordh, personal communication). *O.* sp. lacks dark patches on its femora, thus distinguishing it from *O. anasae* (Ashmead 1887). Voucher specimens of both species are deposited at Kansas State University.

In this study, we compare several biological attributes of *O. anasae* and *O.* sp. at various temperatures. Specifically, our objectives were to determine, for each species, total developmental period (egg to free-living adult), number of progeny produced, preimaginal survivorship, and sex ratio. We also examined the distribution of male and female progeny among individual host eggs.

Materials and Methods

Insect Cultures. Our SB colony originated from overwintered adults that were field-collected during May and June 1985. Nymphs and adults were reared in cages under a photoperiod of 16:8 (L:D) at ca. 27°C on potted 'Green Zucchini' and 'Early Prolific Straightneck' squash (*Cucurbita pepo* L. [Harris Seed Co., Rochester, N.Y.]). Illumination was provided by fluorescent lamps (Cool White).

Parasitoid colonies were initiated in July 1985 by collecting adults and parasitized SB egg masses from zucchini and pumpkin fields near Manhattan, Kans. Newly emerged adults were sorted to species, placed in cages, then transferred to environmental growth chambers under a photoperiod of 15:9 (L:D) and 26.6°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 d old) were added every other day.

Parasitization. To obtain parasitized hosts, individual pairs (female and male) of first- or second-

Table 1. Mean (±SD) number of days for total preimaginal development in the gregarious SB egg parasitoids, *O. anasae* and *O.* sp., under the indicated temperatures

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

[a] (n), number of parasitized hosts.
[b] All paris of means are significantly different ($P < 0.05$; FPLSD).
[c] 15:9 (L:D).

laboratory-generation parasitoids (≤12 h old) were transferred to shell vials that contained honey–water and single clusters of five to six SB eggs (≤24 h old), then placed under one of the experimental temperature conditions (Table 1). Average temperature fluctuations were <0.5°C in all experiments. Parasitoid males were removed on the second day, and host eggs were replaced with fresh egg clusters daily until parasitization ceased.

After exposure, we examined host eggs with a dissecting microscope (70×) and counted the number of egg stalks left by the parasitoid on the exterior of each host (see Maple [1937] for description). Each egg stalk represents at least one parasitoid egg within the host. Some parasitized hosts were then placed individually into wells of tissue culture plates and held under the same conditions as the parental parasitoids. Others were dissected to determine the relationship between the number of egg stalks and the number of eggs per host. This relationship was used to estimate the total number of parasitoid eggs laid per treatment (N_e) (see Survivorship).

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

We used a two-way ANOVA and Fisher's protected least-significant-difference test (FPLSD) (SAS Institute 1985) to test for the effects of species, temperature, and the presence or absence of females in the host on mean developmental times and on the number of progeny emerging per host. The progeny data were natural log-transformed before analysis.

Survivorship. Total survivorship (egg to adult) was computed as the number of emerged parasitoids (N_a) divided by 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. We determined N_p 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 examined for species and temperature effects by a functional analysis for categorical variables (FUNCAT procedure; SAS Institute [1985]). Hosts that bore only one stalk were omitted from analysis because of high variance in the associated number of parasitoid eggs.

Sex Ratio. We recorded numbers of females and males that emerged from individual hosts and converted them to the percentage of females. We tested the arcsine-transformed data (Snedecor & Cochran 1980) for species and temperature effects by a two-way analysis of covariance (ANCOVA) (using the number of parasitoids per host as a covariate) and by FPLSD. We used the same analysis to test for the effects of species and survivorship (ca. 60 or 90%) on the per host sex ratio. In the survivorship analyses, sex ratios were compared between host groups where parasitoid survivorship was the lowest (ca. 60%) and the highest (ca. 90%).

Distribution of Progeny per Host. We counted the number and sex of adult parasitoids emerging from individual hosts in which parasitoid survivorship exceeded 90% (i.e., experienced little or no mortality). From these counts we obtained estimates of the number of progeny and sex ratio per host. These data were pooled over all temperatures and analyzed for species effects. We also tested for the effects of the number of hosts each female parasitized per parasitization day, and the number of eggs laid per host. We analyzed the natural log-transformed progeny data by a two-way ANOVA, and the arcsine-transformed sex ratio data by a two-way ANCOVA. Percentages of hosts receiving no males, and differing numbers of parasitoid eggs, were analyzed by the FUNCAT procedure.

Results

Development. The total developmental periods of both parasitoid species were inversely related to temperature, and ranged from ca. 18 d at 26.6°C to ca. 32 d at 20.8°C (Table 1). Preimaginal development in *O. anasae* was significantly ($P < 0.05$; FPLSD) shorter at each temperature than in *O.* sp.

Male parasitoids that developed without females (all-male progeny) had significantly ($P < 0.05$; FPLSD) longer developmental times at all temperatures than did conspecific males that developed and emerged synchronously with female siblings from the same host (Table 1).

Progeny Production. The number of parasitoids that emerged per host egg did not vary significantly with temperature or parasitoid species ($P > 0.43$; ANOVA). *O. anasae* produced 3.1 ± 0.9 ($\bar{x}$ ± SD) ($n = 122$) offspring per host compared to 3.1 ± 0.7

Table 2. The percentage of total and stage-specific survivorship in the gregarious SB egg parasitoids, *O. anasae* and *O.* sp., at the indicated temperatures

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

[a] (n:n), number of parasitoids surviving through stage/number of parasitoids dying during stage. Frequencies within rows or between columns followed by a different letter are significantly different ($P < 0.05$; FUNCAT).
[b] 15:9 (L:D).

($n = 68$) in *O.* sp. All progeny from the same egg 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 [$n = 70$]) did not differ statistically from that found in hosts containing females (i.e., "mixed-sex" progeny).

Survivorship. We 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 eggs (158) eggs ($\bar{x} \pm$ SD [n]); 2 stalks, 2.8 ± 1.0 (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 was associated almost entirely with the egg–larval stages. In *O.* sp., pharate adult survivorship for all-male progeny was relatively lower at 20.8 and 23.0°C (range, 90–94%) than that of mixed-sex progeny (100%) (Table 2). A significantly ($P < 0.05$; FUNCAT) lower total survivorship was also observed for all-male progeny at these temperatures (Table 2).

Sex Ratio. *O. anasae* produced a significantly ($P < 0.05$; FPLSD) higher proportion of female progeny per host at each temperature than did *O.* sp. (Table 3). The per-host sex ratios were not significantly affected by either temperature or preimaginal survivorship. Overall, *O. anasae* produced 77% ($n = 346$) females compared with 60% ($n = 216$) for *O.* sp.

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*, the percentage of female progeny per host tended to increase as the number of hosts parasitized increased (Table 4, columns B and C). This relationship was not observed in *O.* sp.

The percentage of hosts receiving two, three, four, or five to seven parasitoid eggs was similar for both species (Table 5), with most host eggs receiving three parasitoid eggs. However, for any given number of parasitoid progeny per host, *O. anasae* produced a significantly ($P < 0.05$; FPLSD) higher percentage of females per host than did *O.* sp. (Table 5).

Discussion

Development. The total developmental period of *O. anasae* was slightly, but significantly, shorter than that of *O.* sp. at each of the three temperatures. Because both species are multivoltine, these differences may be ecologically meaningful over the course of a season. For example, although the limited number of temperature conditions precludes estimation of the thermal requirements for each species, the available developmental data suggest that *O. anasae* has a smaller thermal constant.

Table 3. Influence of temperature and survivorship on the percentage of emerged females for the gregarious SB egg parasitoids, *O. anasae* and *O.* sp.

	% emerged females per host, $\bar{x} \pm$ SD (n)[a]	
	O. anasae	*O.* sp.
Temp (°C)[b]		
20.8	71.1 ± 25.3 (39)a	63.9 ± 23.7 (24)b
23.0	75.8 ± 25.8 (32)a	66.8 ± 24.8 (21)b
26.6	81.8 ± 16.1 (31)a	55.6 ± 17.7 (21)b
% survivorship		
High (91–92%)	79.2 ± 21.5 (92)a	61.5 ± 21.1 (54)b
Low (62–63%)	68.3 ± 33.7 (10)a	65.2 ± 28.8 (12)b

[a] Number of parent females per temperature were as follows: *O. anasae*, 11–13; *O.* sp., 4–6. For survivorship analysis, data are combined for all temperatures. Means followed by a different letter are significantly different ($P < 0.05$; FPLSD).
[b] 15:9 (L:D).

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, *O. anasae* and *O.* sp.[abc]

No. hosts parasitized in 24 h	(A) No. parasitoid eggs per host, $\bar{x} \pm SD$ (n)		(B) % emerged ♀♀ per host, $\bar{x} \pm SD$ (n)		(C) % of hosts producing only ♀♀ (no. without ♂♂/no. with ♂♂)	
	O. anasae	*O.* sp.	*O. anasae*	*O.* sp.	*O. anasae*	*O.* sp.
1	3.7 ± 0.7a (29)	3.2 ± 0.8a (12)	76.3 ± 10.6a (29)	67.1 ± 25.6b (12)	14a (4:25)	20b (2:10)
2	3.4 ± 0.8a (40)	3.3 ± 0.7a (12)	70.5 ± 32.7a (40)	61.7 ± 9.4b (12)	33a (13:27)	0b (0:12)
3	3.5 ± 1.2a (30)	3.3 ± 1.0a (20)	80.0 ± 18.9a (30)	62.1 ± 21.1b (20)	34a (11:21)	10b (2:18)
4	3.0 ± 0.8a (36)	2.9 ± 0.7a (10)	86.0 ± 15.3a (36)	53.3 ± 25.8b (10)	53a (19:17)	20b (2:8)
5	3.1 ± 0.7a (22)	—	84.2 ± 16.5a (22)	—	50 (11:17)	—

[a] Data are combined for all temperatures, including two additional conditions, 21.8 and 25.6°C.

[b] For a given variable, means or frequency percentages followed by a different letter are significantly different ($P < 0.05$; FPLSD for means and FUNCAT for frequency percentages).

[c] 15:9 (L:D).

In *O.* sp., all-male progeny took significantly longer to emerge at all temperatures than did conspecific males that developed and emerged synchronously with females (Table 1). Our observations show that females are generally larger than males, and they typically produce the common exit hole from which both sexes emerge. Thus, delayed male emergence when no female is present may result from a longer time required for males to chew through the host egg chorion. This explanation is supported by our 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 was similar in hosts that contained all males and those with at least one female; thus, competition had no apparent influence on emergence times.

Table 5. Percentage of SB hosts and percentage of parasitoid females per host in relation to number of parasitoid eggs per host for *O. anasae* and *O.* sp. The data are combined for all temperatures

No. parasitoid eggs per host	% of hosts in each category[ab]		% females per host, $\bar{x} \pm SD$ (n)[c]	
	O. anasae	*O.* sp.	*O. anasae*	*O.* sp.
2	16 (15)	13 (7)	95.7 ± 20.9a (23)	57.1 ± 45.0b (7)
3	54 (51)	65 (35)	78.1 ± 21.9c (79)	67.7 ± 11.4d (35)
4	28 (23)	17 (9)	71.1 ± 19.9c (45)	47.2 ± 19.5d (9)
5–7	6 (5)	5 (3)	81.6 ± 9.7c (10)	54.3 ± 22.3d (3)

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

[b] (n), number of parasitized hosts.

[c] Percentages followed by a different letter are significantly different ($P < 0.05$; FPLSD).

Progeny Production. Both *O. anasae* and *O.* sp. are gregarious parasitoids whose progeny emerge synchronously from the host. Gregarious development occurs 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 (Nechols 1981, Fedde 1982, Narasimham 1984, Nechols & Kikuchi 1985, Arakaki & Ganaha 1986).

Our observations reveal that both *O. anasae* and *O.* sp. mate very soon after emergence in the laboratory (unpublished data). 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 eggs can be fertilized before females disperse to locate new hosts (Arakaki & Ganaha 1986).

Survivorship. Total preimaginal survivorship for mixed-sex progeny was high in both parasitoids at all three temperatures (Table 2). However, this survivorship is slightly lower than that reported by Fedde (1982) under similar conditions for *Ooencyrtus 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. In our study, differential survivorship of the sexes did not appear to influence interspecific differences in sex ratios (Table 3). And, although other factors may have produced the observed differences in sex ratios (e.g., see Werren et al. [1986]), our observations indicate that the most important factor was probably species-specific differences in the regulation of oocyte fertilization (i.e., sex ratio regulation) by the female parasitoids. Sex ratio regulation is a well known phenomenon among arrhenotokous parasitic Hymenoptera (Flanders 1956).

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

Distribution of Progeny per Host. In our study, the frequency distribution of the number of parasitoid progeny deposited per host was similar for both species. However, *O. anasae* produced a consistently higher percentage of female progeny per host than did *O.* sp. for any given number of progeny deposited (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 discussion above).

As the number of hosts parasitized per cluster increased, *O. anasae* tended to produce a higher percentage of females and to deposit only female progeny in a progressively higher percentage of hosts (Table 4). Although these trends were not significant, they 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). Our results agree also with their 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 increases fitness by allowing females to develop with a greater food supply. Thus, larger females with higher fecundities can be produced.

In contrast to *O. anasae*, there was no apparent relationship between the per-host sex ratio in *O.* sp. and the number of hosts parasitized per cluster (Table 4) or the number of eggs deposited per host (Table 5). Although we 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 deposit more males in nonpreferred than in preferred hosts (Kotchetova 1977).

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 pro-

portion of *O.* sp. females remain unmated when paired with a single male than do *O. anasae* (unpublished data).

Although we cannot fully evaluate the potential of these two indigenous parasitoids for biological control of SB on the basis of our present findings, interspecific differences in development and sex ratio regulation indicate that *O. anasae* may be a more efficient species to use in a mass-rearing program.

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