Biology of *Anagrus delicatus* (Hymenoptera: Mymaridae), an Egg Parasitoid of *Prokelisia marginata* (Homoptera: Delphacidae)

JAMES T. CRONIN AND DONALD R. STRONG

Department of Biology, Florida State University, Tallahassee, Florida 32306

Ann. Entomol. Soc. Am. 83(4): 846–854 (1990)

ABSTRACT *Anagrus delicatus* Dozier is a common egg parasitoid of the planthopper *Prokelisia marginata* (Van Duzee). *P. marginata* inhabits salt marshes along the Atlantic and Gulf Coasts of the United States and feeds exclusively on salt marsh cordgrass, *Spartina alterniflora* Loisel. *A. delicatus* is closely associated with its host throughout its range. Two larval instars of *A. delicatus* were identified from their host eggs. Male and female wasps take an average of 54.2, 35.9, and 21.7 d to develop from egg to adult at 16, 22, and 30°C, respectively. The developmental threshold temperature is approximately 7.1°C, and wasps require a minimum of 504 degree-days (DD) to complete development. The sex ratio of emerging adults is skewed toward females (1:2.4, M/F). Females eclose with an average of 33 eggs (range, 21–46) and are capable of immediate mating and oviposition. Females can produce male offspring parthenogenetically, and virgin females parasitize significantly more hosts during the first 24 h than mated females. Life for adult females was relatively short: females fed honey and water lived an average of 3.3 d, but those provided only water averaged just 2.0 d. Females laid 25% of their eggs on the first day, and oviposition ceased by the third day. In all, oviposition for honey-fed females ceased after only 43% of the eggs were laid. Host eggs are capable of being parasitized throughout development, but parasitoid survival in older host eggs (embryos) is lower than in younger eggs.

KEY WORDS Insecta, *Anagrus delicatus*, egg parasitoid, *Prokelisia marginata*

THE MYMARIDAE, commonly known as fairy flies, are minute wasps that parasitize the eggs of a broad range of hosts, including the Odonata, Orthoptera, Homoptera, Hemiptera, Psocoptera, Neuroptera, Coleoptera, Lepidoptera, and Diptera (Burks 1979, Clausen 1940). Mymarids are distinctive in appearance, having slender bodies and long wings that are fringed with setae. More than 1,300 species in 89 genera have been reported worldwide (Huber 1986). The family is considered to be monophyletic, but its relationship with other members of the Chalcidoidea is unclear (Gibson 1986).

Although the mymarids are important natural enemies of many agricultural pests, they have only occasionally been used in biological control programs. To date, there are 10 documented cases in which mymarids were successfully introduced to control economically important pests (Clausen 1978). Of these, two cases provided complete control. In Hawaii, the release of the mymarid *Paranagrus optabilis* Perkins in combination with the mirid bug, *Tytthus mundulus* Breddin, brought about the successful control of the sugarcane leafhopper, *Perkinsiella saccharicida* Kirkaldy (DeBach 1974). *Anaphes nitens* Girault provided the most striking example by acting alone to control the eucalyptus snout beetle, *Gonipterus scutellatus* Gyllenhal, in southern Africa and elsewhere (DeBach 1974).

Additionally, there have been attempts to manipulate native mymarid populations to control their hosts. *Anagrus epos* Girault attacks the grape leafhopper, *Erythroneura elegans* Osborn, but it cannot maintain populations the year around because its host overwinters in the adult stage. By allowing wild *Rubus* spp. to grow near vineyards, the native noneconomic leafhopper *Dikrella cruentata* (Gillette) provided a needed winter host for *A. epos*. This management program resulted in the successful control of *E. elegans* in commercial vineyards (Doutt & Nakata 1973). Similar results were found with the blackberry-leafhopper-parasite system with *A. epos* (Williams 1984). Clearly, the potential for the mymarids in biological control programs merits further consideration of their biology.

Few mymarids have been studied in detail. Several species of the large genus *Anagrus* Haliday, however, have received considerable attention (reviewed by Waloff & Jervis 1987). Of the six species of *Anagrus* currently known in North America (Gordh & Dunbar 1977), the biology of *A. armatus* Ashmead (Armstrong 1936), *A. epos* (McKenzie & Beirne 1972, Williams 1984), and *A. giraulti* Crawford (Meyerdirk & Moratorio 1987) have been investigated previously. Our paper focuses on the biology of *A. delicatus* Dozier.

Anagrus delicatus was originally collected along a creek bed in Elizabethtown, Ill., using a sweep net (Dozier 1936). Although its host was not iden-

0013-8746/90/0846–0854$02.00/0 © 1990 Entomological Society of America

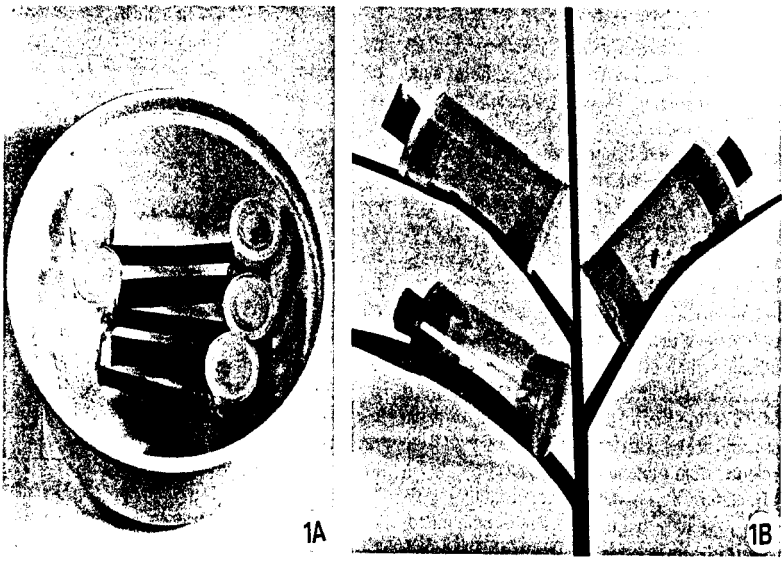

Fig. 1. (A) Leaves with parasitized host eggs are inserted into acetate tubes and placed into a plastic bowl with a lid for rearing *A. delicatus*. (B) Clip cage for *A. delicatus* oviposition.

tified, Dozier (1936) suggested it was probably an egg parasite of some aquatic insect. Recently, Stiling & Strong (1982a) have discovered that *A. delicatus* is a parasite of the eggs of *Prokelisia marginata* Van Duzee (Homoptera: Delphacidae), which feeds and oviposits on salt marsh cordgrass, *Spartina alterniflora* Loisel, in Florida. Moreover, Wilson (1982) identified another closely related *Prokelisia* species, *P. dolus* (Wilson), which is sympatric with *P. marginata* and also feeds on cordgrass. It, too, is parasitized by *A. delicatus* (personal observation) but is numerically less abundant than *P. marginata* (A. E. Throckmorton, J. V. Capogreco, P. D. Stiling & D. R. Strong, unpublished data). Now, it appears that *A. delicatus* is associated closely with both *Prokelisia* spp. in salt marshes along the Atlantic and Gulf Coasts of the United States (Denno et al. 1987).

Although much research has been conducted on the effect of parasitism on the population dynamics of these two planthopper species (unpublished data; Stiling & Strong 1982b; Strong 1989; Cronin & Strong in press) and dispersal behavior (Antolin & Strong 1987), little is known about the biology of this mymarid. This study provides general biological information for *A. delicatus* parasitizing its more common host, *P. marginata*. These data should prove useful and necessary for continued ecological studies on this host–parasitoid system and should also be of use in the framework of other ecological studies on related egg parasitoids of homopteran hosts.

Materials and Methods

Anagrus delicatus adults were collected from leaves of *S. alterniflora* in the salt marsh of Oyster Bay, Wakulla Co., Fla. At weekly intervals, 60 leaves infested with the eggs of *Prokelisia* spp. were collected and returned to the laboratory. Leaves were cut into 80-mm sections, and each end was inserted into slits cut into an acetate tube (40 mm long, 18 mm diameter) capped at each end (Fig. 1A). The tubes were filled with Liqua-gel (Miller Chemical Company, Hanover Pa.), a starch gel polymer that retains water. This prevented leaves from drying out and enabled healthy wasps to emerge for up to 1 mo. The tubes containing leaves were placed into 500-ml plastic bowls, and a Petri dish (150 by 15 mm) was placed over the top. The bowls were maintained at room temperature (25 ± 2°C) and 72 ± 2% RH. This provided a continuous supply of wasps throughout the study period. On mornings of experiments, bowls were cleared of all female *A. delicatus* at 0900 hours (EST). At 1200 hours, female wasps were collected for use in experiments. This procedure yielded females that were always mated and ≤3 h old.

Planthoppers were collected from a high-density population on Smith Island (Oyster Bay) during early May 1989 using a sweep net. An independent collection of 1,362 adults from this population revealed that it consisted of >97% *P. marginata* (A. E. Throckmorton, J. V. Capogreco, P. D. Stiling & D. R. Strong, unpublished data) based on the diagnostic characters proposed by Denno et al. (1987). For practical purposes, we consider these experimental planthoppers to be all *P. marginata* and accept any source of error that could be contributed by species differences.

For all experiments, collected planthoppers were immediately placed on ice and returned to the laboratory. Adults were sorted by sex, and 10 females and two males were placed in clip cages (Fig.

1B) on individual leaves of potted *S. alterniflora* that had no previous exposure to planthoppers. Clip cages were made of acetate tubing (40 mm long, 18 mm diameter) and notched at either end. The tubes were positioned at the base of the leaf and capped at each end. Planthoppers were free to feed and oviposit in the adaxial leaf surface within the confines of the cage for a period of 48 h. This produced 83.4 ± 3.4 ($\bar{x}$ ± SE) (n = 259) eggs per experimental leaf (hereinafter referred to as an egg clutch). After removal of the planthoppers from the clip cage, a single mated (unless otherwise stated) female *A. delicatus* was released onto the leaf and allowed to oviposit for a 24-h period. Host eggs, unless specified, were never more than 5 d old. To ensure that an excess of hosts was available for wasps, leaves with fewer than 15 host eggs were excluded from subsequent analyses.

Immature Stages. One hundred adult female wasps were dissected under a stereoscopic microscope at 50× in insect saline (0.80 parts NaCl, 0.02 parts $CaCl_2$, 0.02 parts KCl, 0.02 parts Na_2CO_3, 100 parts H_2O), and the total number of ovarian eggs was counted. Eggs from an additional five females were measured at their greatest width and overall length using an ocular micrometer. At 2, 4, 8, 12, and 16 d (room temperature and RH) after parasitism, 10 host eggs were dissected in saline to isolate larval *A. delicatus*. Larvae were measured at their greatest width and overall length. Pupal size was measured directly through the transparent host chorion.

Mating and Oviposition Behavior. To observe the mating behavior of *A. delicatus*, 10 female pupae were excised from leaves and placed in Petri dishes (60 by 10 mm). The bottom of the Petri dishes contained 3 mm of plaster of Paris and a piece of filter paper (4.25 cm diameter) soaked with water. The emerging, unmated females were placed individually in clip cages with one male from the *A. delicatus* rearing bowls (Fig. 1A). Matings were observed under a dissecting scope at 12×. Searching behavior and oviposition were monitored for 15 min for each female.

Parthenogenesis. To determine whether female *A. delicatus* are capable of reproducing parthenogenetically, virgin females were placed on host clutches within a clip cage. After 1 wk, leaves were dissected and the number of parasitized eggs was recorded. Parasitized eggs were placed in Petri dishes until all wasps emerged so that the sex ratio of offspring from each wasp could be obtained. Number of eggs parasitized per female was compared between mated (n = 72) and virgin females (n = 50), and number parasitized were analyzed using a t test on log-transformed data.

Longevity and Fecundity. Longevity and fecundity schedules of female *A. delicatus* were examined under two food regimes: wasps provided with water only, and those with water and a mixture of honey and water (80% honey). Newly emerged females were placed individually in clip cages containing a host egg clutch and were free to oviposit for a period of 24 h. Droplets of water or honey or both were placed on the leaf surface within the clip cages. The size of the droplets varied but were similar to volumes of honeydew left on the leaves by feeding planthoppers. Every 24 h, female mortality was recorded and the surviving wasps were transferred to a fresh clip cage containing healthy hosts. One week after wasps were removed from a clip cage, the leaf was dissected, and the number of parasitized hosts and host egg density were recorded. Parasitized eggs are easily identified at this stage because they appear red in relation to healthy hosts. The experiments were run at room temperature and humidity. Forty females were used in the honey supplementation experiment and 25 in the water-only experiment.

Temperature and Development. Development time from egg to adult was studied under constant RH (70 ± 2%), 12:12 (L:D), and three temperature conditions: 16, 22, and 30 ± 1°C. Seventy-two female *A. delicatus* were placed individually in clip cages containing host eggs and were free to oviposit for a period of 24 h at room temperature and humidity. Clip cages and wasps were removed, then plants containing 24 clutches were placed in each of the three environmental chambers. One week later, leaves from the 30°C chamber were cut into 80-mm sections, inserted into tubes containing Liqua-gel, placed in plastic bowls (Fig. 1A), and then returned. This was repeated at 2 wk for the 22°C chamber. Because of the much slower development in the 16°C chamber (see Results), it was necessary to remove parasitized eggs from the leaves at 4 wk to prevent their damage by senescing leaves. Parasitized eggs were then placed in Petri dishes containing plaster of Paris and wet filter paper. No wasps had emerged before being transferred to bowls (or Petri dishes), as was evident by the lack of any emergence holes from the abaxial surface of the leaves. After the transfer, bowls were examined daily for emerging wasps. The sex of the wasps was determined, and the number emerging per day was recorded.

Host Age and Parasitism. The range of egg developmental stages that *A. delicatus* can successfully parasitize was analyzed by exposing female wasps to host eggs of different ages. Eighty host egg clutches were set up on 10 May using the procedure outlined earlier. Forty-eight hours later, female *A. delicatus* were placed singly in clip cages on 20 of the clutches. The procedure was repeated at 4-d intervals for a total of four dates. This provided eggs of age 1–2 d (no features visible), 5–6 d (eye spot barely visible), 9–10 d (eye spots well developed), and 13–14 d (embryo well developed). Leaves were dissected a week after oviposition to determine the number of eggs parasitized. The relationship between host age and number parasitized was analyzed using the Kruskal–Wallis test,

Fig. 2. Mature ovarian eggs.

Table 1. Size of developmental stages of *A. delicatus*

Developmental stage	*n*	$\bar{x} \pm$ SE	Range
Egg			
Length, μm	153	112.3 ± 11.9	49.4–197.6
Width, μm	153	33.4 ± 6.0	15.6–72.8
Instar 1			
Length, 2 days, μm	10	138.3 ± 8.2	123.1–191.0
Length, 4 days, μm	10	206.5 ± 13.0	163.9–240.0
Instar 2			
Length, 8 days, mm	10	0.50 ± 0.11	0.33–0.74
Length, 12 days, mm	8	0.55 ± 0.05	0.43–0.72
Pupae			
Length, males, mm	31	0.60 ± 0.01	0.52–0.65
Length, females, mm	39	0.71 ± 0.01	0.62–0.78

Table 2. Longevity and fecundity of female *A. delicatus*

Attribute	*n*	$\bar{x} \pm$ SE	Range
No. ovarian eggs	100	33.3 ± 0.6	21–45
Longevity, days			
With honey	40	3.3 ± 0.4	0–8
Without honey	25	2.0 ± 0.2	0–4
No. eggs laid during first 24 h			
Virgin females			
Without honey	50	11.8 ± 0.8	0–25
Mated females			
With honey	40	8.2 ± 0.8	0–17
Without honey	25	8.6 ± 0.6	0–23
No. eggs laid at end of oviposition period[a]			
With honey	10	14.3 ± 1.5	10–18
Without honey	11	8.9 ± 1.1	3–23
Net replacement rate (R_o)			
With honey	40	11.9	—
Without honey	25	8.8	—

[a] Calculated only for wasps that survived to 5 d when fed honey or 2 d when no honey was provided.

and comparisons among treatments were assessed by the simultaneous test procedure (based on the Mann–Whitney statistic) (Sokal & Rohlf 1981).

Voucher specimens of *A. delicatus* are deposited in the National Museum of Natural History, Washington, D.C.

Results

Immature Stages. Ovarian eggs of *A. delicatus* are elongate and have long, slender peduncles (Fig. 2). Egg size is quite variable and within a female approximates a normal distribution (Table 1). The largest egg averages almost 2.5 times longer than the smallest egg. Even among the five females, considerable variation in egg size exists ($F = 12.65$; df = 4, 148; $P < 0.001$). The total number of ovarian eggs per female averaged 33; this also was quite variable (Table 2).

Two instars of *A. delicatus* were isolated from its host. Forty-eight hours after they were parasitized, nearly all eggs had hatched. The first instar is sacciform in shape and is still attached to the cast chorion. The larva appears motionless, and at 2 d is only slightly larger than the egg (Table 1). At 4 d, the first instar has increased in size by >60% but still is relatively inactive. By day 8, all larvae have entered the second stadia. The second instar is long and cylindrical and fills much of the host egg (Table 1). This instar is active and spends much of its time churning within the host. Only a small increase in size occurred by day 12, but two of the 10 larvae entered the pupal stage. By day 16, all developing wasps had begun to pupate. Female pupae are significantly longer than males ($t = 2.71$; df = 68; $P = 0.009$) (Table 1).

Mating and Oviposition Behavior. Immediately after they emerge, adult *A. delicatus* are ready to mate. Males move more or less randomly about the clip cage until they come into close contact (<3 mm) with the virgin female. Rapid antennal movements follow, and the male bends the tip of its abdomen forward toward the female. When the male's antennae contact the female, her movements are quickly arrested. The male then moves his abdomen under the female and inserts his genitalia into that of the female at the base of her abdomen. Copulation is short, lasting an average of only 15.2 ± 0.8 s ($n = 10$). After a female is mated, neither her mate nor other males display any interest in copulating with her.

There is no preoviposition period for female *A. delicatus;* wasps are capable of ovipositing in hosts immediately after they emerge. As soon as a female encounters the leaf substrate, she begins drumming with her antennae. Encounters with oviposition scars of *P. marginata* elicit more rapid drumming and often lead to probing in and around the scars with

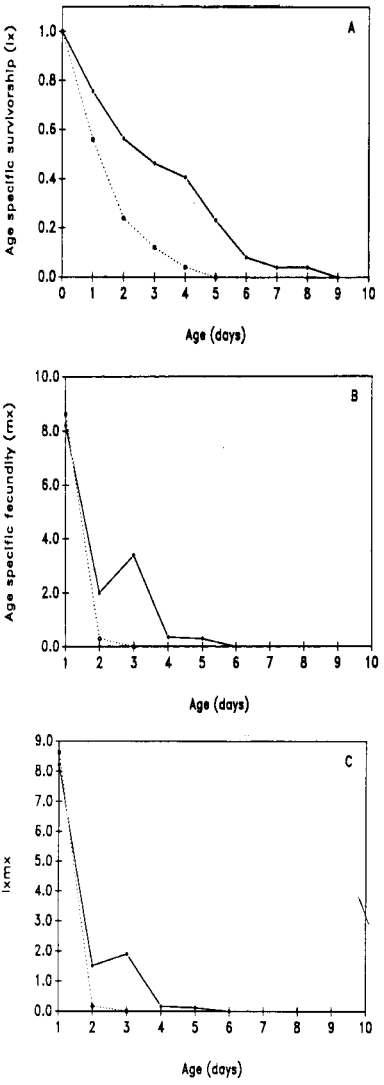

Fig. 3. (A) Survivorship, l_x. (B) Fecundity, m_x. (C) Reproductive function schedules, l_xm_x, for *A. delicatus*. Open circles, females fed water (n = 25); closed circles, females fed honey and water (n = 40).

the ovipositor. Mechanical damage to the leaf made with a pin elicits the same response in female wasps, but repeated exposure to artificial scars results in a decreased response to the damage. Females repeatedly probe in and around leaf scars between the leaf ribs, where host eggs are inserted. During searching, before an egg is found, probing is quick (<20 s), and the ovipositor is seldom completely inserted. When a suitable egg is located, the female straddles two leaf ribs and inserts her ovipositor its full length. During successful oviposition, the time elapsed between insertion and removal of the ovipositor is 119 ± 6 s (n = 16).

Parthenogenesis. Virgin females are fully capable of reproduction. All 50 females produced only male offspring, compared with the 72 mated females, which produced 40% males. During the first 24 h after emergence, unmated females parasitized significantly more host eggs than mated females (t = 2.19; df = 120; P = 0.034) (Table 2).

Longevity and Fecundity. Female *A. delicatus* survived 40% longer (1.3 d) when provided abundant water, honey, and host eggs than when provisioned only with water and hosts (t = 2.63; df = 53; P = 0.011) (Table 2; Fig. 3A). Maximum longevity for honey-supplemented females was 4 d longer than those provided water alone (Fig. 3A).

In addition to large differences in survivorship, honey-supplemented wasps continued to oviposit for up to 3 d longer than unfed females (Fig. 3B). Oviposition was greatest within the first 24 h after emergence: wasps with and without honey laid about eight eggs, and there was no difference between the two (t = 0.211; df = 63; $P > 0.05$) (Table 2). This equates to an average of about 25% of a female's total egg complement (mean, 33.3 eggs) being laid during the first day. Beyond the first 24 h, unfed females ceased oviposition, whereas honey-fed females laid an additional six eggs over the next 2 d. Wasps surviving to the end of oviposition (day 5 for honey-fed and day 2 for unfed females; see Fig. 3B) laid about 14 eggs (43% of the total available) and nine eggs (26% of total) for honey-fed and unfed females, respectively. The realized fecundity of honey-fed females was correlated with their life span (Fig. 4).

The combined differences in survivorship (l_x) and fecundity (m_x) schedules produce strong differences in net replacement rates (= $R_o = \Sigma l_x m_x$) (Fig. 3C). Honey-fed *A. delicatus* produced an average of about three more offspring than wasps provided only water (Table 2).

Temperature and Development. The development of *A. delicatus* from egg to adult emergence averaged 54.2, 35.9, and 21.7 d at 16, 22, and 30°C, respectively (Fig. 5). Both males and females developed at the same rate for each of the three temperature regimes (two-way ANOVA, F = 0.022; df = 1, 227; P = 0.88). The proportion of males was low (0.29, 0.35, and 0.23 at 16, 22, and 30°C), but they emerged continuously with the females throughout the span of emergence at each temperature (Fig. 5). The overall sex ratio (M/F) for the three treatments combined was 1:2.4. The development rate (percentage development per day) of *A. delicatus* increased with temperature (development rate = 0.198 × [temperature] − 1.404; r^2 = 0.98, $P < 0.05$) (Fig. 6). The developmental threshold (no development occurs) was estimated from the regression to be 7.1°C, and wasps require a minimum of 504.4 degree-days (DD) for development from egg to adult emergence.

Host Age and Parasitism. *Anagrus delicatus* is capable of successfully parasitizing planthopper eggs of all ages (Table 3). However, the number of host eggs that were visibly parasitized (reddish in color) 1 wk after oviposition by female *A. de-*

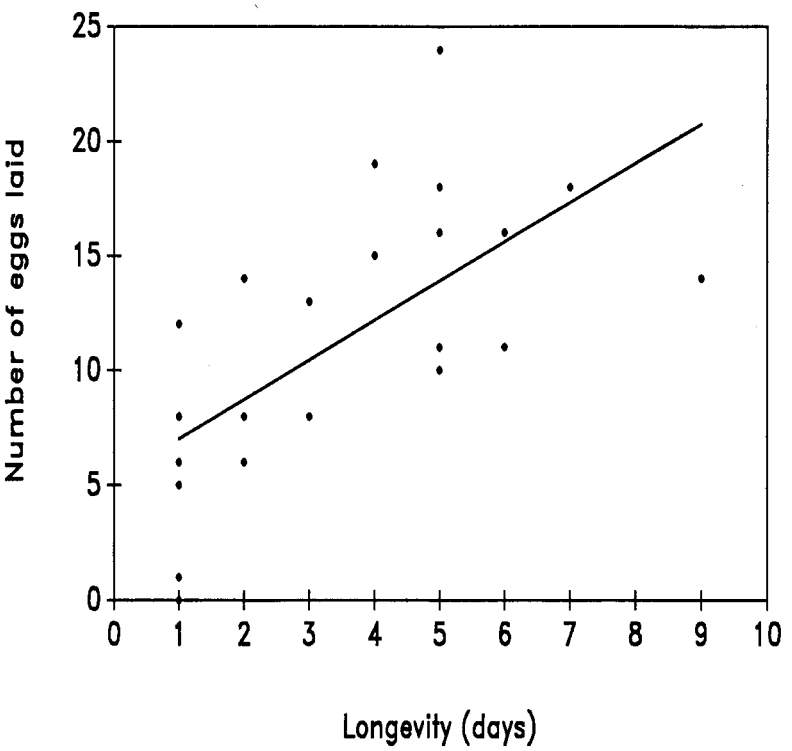

Fig. 4. Relationship between *A. delicatus* longevity and realized fecundity for honey-fed females. Line was fit by least-squares regression (number parasitized = 1.71 × [life span] + 5.30; $r^2 = 0.44$, $P < 0.0001$).

Table 3. Relationship between host age and parasitism

	Host age, d			
	1-2	5-6	9-10	13-14
n	14	12	10	17
No. parasitized, $\bar{x} \pm$ SE	8.0 ± 1.7a	10.7 ± 1.6a	3.0 ± 0.7b	0.4 ± 0.2c
Proportion males	0.56	0.16	0.33	—
Proportion successfully emerged	0.62	0.43	0.50	0.20

Means with different letters are significantly different at the 0.05 level (*Kruskal-Wallis test; multiple comparisons by the simultaneous test procedure based on the Mann-Whitney test [Sokal & Rohlf 1981]).

licatus declined significantly after age 5–6 d (Kruskal-Wallis; $H = 35.50$; $P < 0.0001$). Whether this difference is caused by a reluctance to parasitize older embryos or a decrease in wasp survival with host age could not be determined from this experiment. Of the host eggs that were parasitized, the proportion that successfully developed into adult wasps varied among the four age classes ($\chi^2 = 8.75$; $P < 0.05$; Table 1); emergence rates for the oldest parasitized eggs were very low. Additionally, the sex ratio varied among the treatments, but no obvious pattern was identified ($\chi^2 = 20.06$; $P < 0.001$).

Discussion

The general life histories of *Anagrus* species are quite similar (MacGill 1934, Otake 1969, Moratorio 1977, Ali 1979, Chantarasa-ard et al. 1984, Sahad 1984, Williams 1984, Meyerdirk & Moratorio 1987). Eggs of all members of the family Mymaridae are ellipsoid in shape with a long tapering peduncle (Clausen 1940). A sacciform, unsegmented, motionless first instar lacking observable mandibles is typical of the genus *Anagrus*. The second instar is cylindrical in shape, segmented, and mandibulate. These older larvae are very active and move constantly within the host, presumably to aid in digestion of yolk spheres (Sahad 1984) or to assist in gaseous exchange within the host (Whalley 1969).

In northern Florida, maximum daily temperatures rarely fall below the threshold development temperature of 7.1°C, allowing development of wasps to continue almost the year around. Thermal developmental requirements for *A. incarnatus*

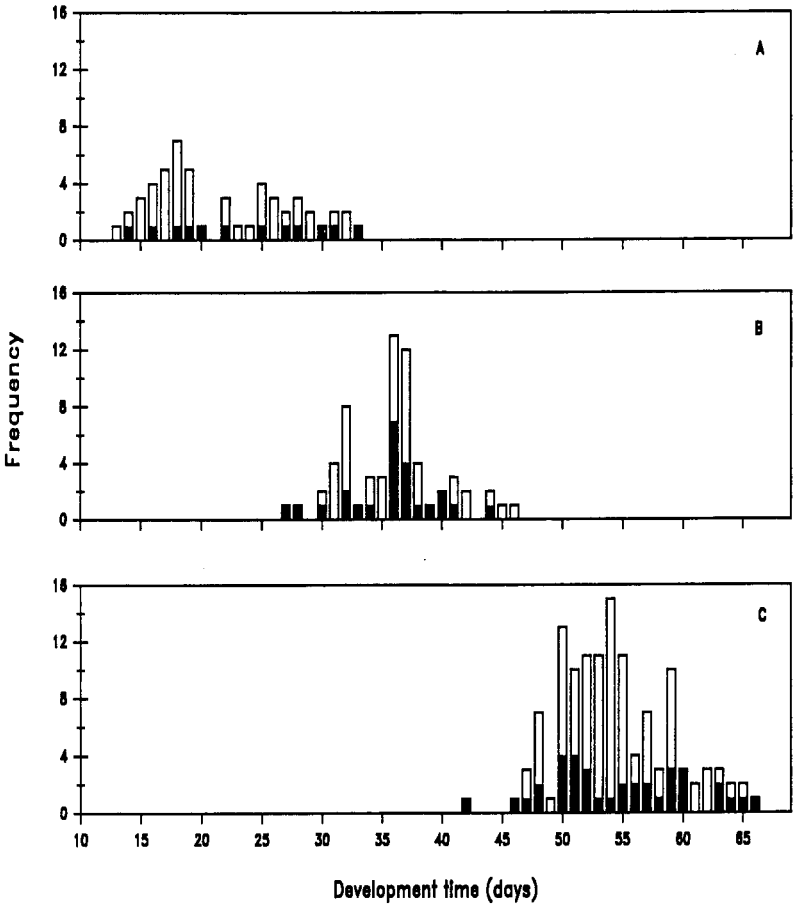

Fig. 5. Effect of temperature on development times of *A. delicatus* for three temperatures. (A) 30°C. (B) 22°C. (C) 16°C. Solid portions of bars represent number of emerging males, open bars represent females.

(Chantarasa-ard et al. 1984), *A. optabilis* (Sahad 1984), *A. epos* (Williams 1984), and *A. giraulti* (Meyerdirk & Moratorio 1987) are much lower, averaging only 210 DD (range, 172.6–269.0). Male *A. delicatus* develop at the same rate as females and emerge continuously along with females in low numbers. With a host such as *P. marginata* that is patchily distributed, this developmental pattern should provide emerging females with continual access to mates. Although this pattern of emergence is common for *Anagrus* spp. (Chantarasa-ard et al. 1984, Williams 1984, Meyerdirk & Moratorio 1987), other members of the genus have males that emerge earlier than females (Witsack 1973, Moratorio 1977, Sahad 1984).

In all *Anagrus* species studied, mating takes place immediately after emergence. Very little courtship behavior is involved; the first male to encounter a virgin female will mate with her. Apparently, in some species of *Anagrus*, males locate mates through a very specific mating pheromone (Ali 1979). Once mating has occurred, the female is no longer receptive to either the same male or other conspecifics. Although mating is required for the production of female offspring (the genus *Anagrus* is arrhenotokous), when provided the opportunity, virgin females will lay eggs quite readily in hosts. In fact, the oviposition rate of virgin *A. delicatus* (this study) and *A.* sp. "c" (Moratorio 1977) is higher than for mated females.

Adults of the genus *Anagrus* are relatively short-lived. In all studies, longevity increased when wasps were fed a diet of honey and water compared with water alone. The life span ranged from an average of 3 d for *A.* sp. nr. *flaveolus* (Otake 1969) to 11.4 d for *A. giraulti* (Meyerdirk & Moratorio 1987). *A. delicatus* longevity is close to that of the minimum of the range, with a mean life span of 3.4 d. Longevity of males is typically shorter than that of females (Sahad 1984, Meyerdirk & Moratorio 1987), but it is not known whether the same pattern holds true for *A. delicatus*. Although mymarids are considered to be proovigenic, energy-rich food sources may be necessary for maintenance when hosts are rare or for dispersal to locate new host patches (Antolin & Strong 1987). Sources of car-

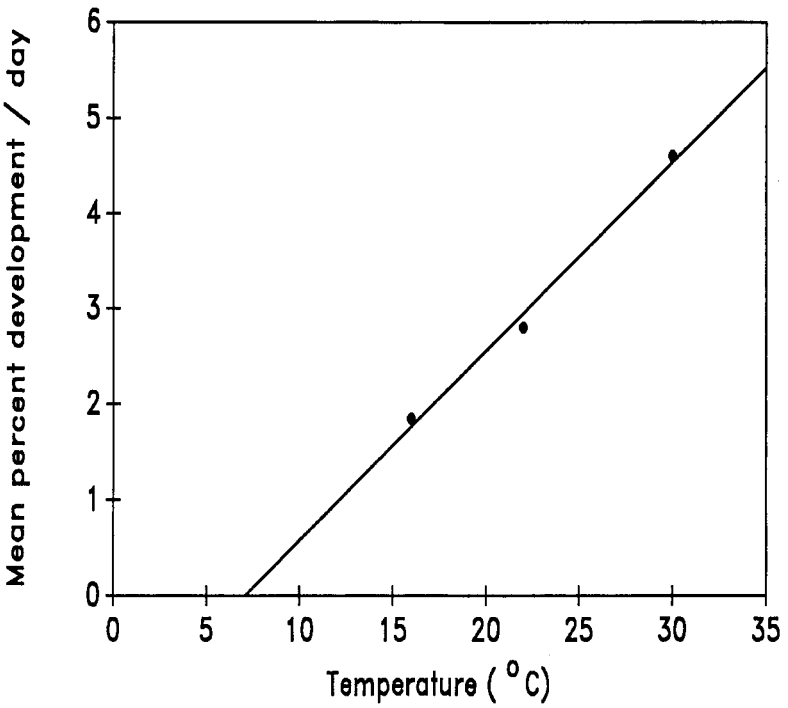

Fig. 6. Rate of development from egg to adult for *A. delicatus* reared at constant temperatures.

bohydrates that may readily be available to searching *A. delicatus* are minute droplets of honeydew (produced by feeding *P. marginata*) that are left on the leaf surface.

The pattern of oviposition is qualitatively the same for all species of *Anagrus*. The majority of the eggs laid throughout a female's lifetime are deposited within the first 2 d after emergence. Few, if any, eggs are laid on subsequent days. Although we find a relationship between *A. delicatus* longevity and fecundity, Otake (1969) found no correlation with *A.* sp. nr. *flaveolus*, probably because of the low number of eggs laid beyond the first day.

The proportion of the egg complement that is actually laid varies greatly among *Anagrus* species. Both *A.* sp. "c" (Moratorio 1977) and *A. giraulti* (Meyerdirk & Moratorio 1987) lay >80% of their eggs in the laboratory, but *A. incarnatus* (Witsack 1973) and *A. delicatus* lay <50% of their eggs during their lifetime. The low realized fecundity of *A. delicatus* does not appear to be an artifact of our laboratory rearing procedure. Immature stages were reared and adults were maintained at temperatures and relative humidities that are typical of the salt marsh in North Florida. In addition, dissections of field-caught females show no differences in length or shape of eggs compared with laboratory-reared wasps (unpublished data). Also, the low proportion of eggs laid is not a consequence of adults carrying immature eggs. Despite wide variation in egg size, histological sectioning of *A. delicatus* females and vital staining of eggs with trypan blue indicate that all ovarian eggs are fully mature (J.T.C., unpublished data). We conclude that the discrepancy between potential and realized fecundity is most likely biologically based; at this point, we can only speculate as to its cause.

In addition to *A. delicatus*, a number of *Anagrus* species are capable of successfully parasitizing well-developed host embryos (Otake 1968, Whalley 1969, Tay 1972, Ali 1979, Chandra 1980). However, *Anagrus stenocrani* (Walker) is capable of parasitizing only younger eggs (May 1971). Despite the ability of *A.* sp. nr. *flaveolus* to develop successfully within older hosts, Otake (1968) found that its development was prolonged. Apparently, well-developed host embryos are more difficult for the parasite larvae to digest. We did not examine development rates as a function of host age, but we found that the number of eggs parasitized (those that survived 1 wk after being parasitized) declined with host age. It cannot be determined whether this difference is the result of an avoidance of old embryos or lower survival in older hosts. However, it was determined that emergence rates of wasps surviving to 1 wk were lowest for wasps older than 13 d.

Acknowledgment

We thank M. Antolin for providing two environmental chambers for use in this study. M. Antolin, J. Capogreco, A. Rossi, P. Stiling, and two anonymous reviewers helped

to improve the manuscript. Funding was provided by National Science Foundation grant BFR-8703416 to D.R.S.

References Cited

Ali, A. M. H. 1979. Biological investigations on the entomophagous parasites of insect eggs associated with *Juncus* species. Ph.D. dissertation, University of Wales, Cardiff.

Antolin, M. F. & D. R. Strong. 1987. Long-distance dispersal by a parasitoid (*Anagrus delicatus*, Mymaridae) and its host. Oecologia (Berl.) 73: 288–292.

Armstrong, T. 1936. Two parasites of the white apple leafhopper (*Typhlocyba pomaria* McA.). Annu. Rep. Ont. Entomol. Soc. 66: 16–31.

Burks, B. D. 1979. Trichogrammatidae, pp. 1033–1043. *In* K. V. Krombein et al. [eds.], Catalog of Hymenoptera north of Mexico. Smithsonian Institution Press, Washington, D.C.

Chandra, G. 1980. Taxonomy and bionomics of the insect parasites of rice leafhoppers and planthoppers in the Philippines and their importance in natural biological control. Philipp. Entomol. 4: 119–139.

Chantarasa-ard, S., Y. Hirashima & T. Miura. 1984. Effects of temperature and food on the development and reproduction of *Anagrus incarnatus* Haliday (Hymenoptera: Mymaridae), an egg parasitoid of the rice planthoppers. Esakia 22: 145–158.

Clausen, C. P. 1940. Entomophagous insects. McGraw-Hill, New York.

1978. Introduced parasites and predators of arthropod pests and weeds: a world review. USDA Handbook 480.

Cronin, J. T. & D. R. Strong. In press. Density-independent parasitism among host patches by *Anagrus delicatus* (Hymenoptera: Mymaridae): experimental manipulation of hosts. J. Anim. Ecol.

DeBach, P. 1974. Biological control by natural enemies. Cambridge University Press, London.

Denno, R. F., M. E. Schauff, S. W. Wilson & K. L. Olmstead. 1987. Practical diagnosis and natural history of two sibling salt marsh-inhabiting planthoppers in the genus *Prokelisia* (Homoptera: Delphacidae). Proc. Entomol. Soc. Wash. 89: 687–700.

Doutt, R. L. & J. Nakata. 1973. The *Rubus* leafhopper and its egg parasitoid: an endemic biotic system useful in grape-pest management. Environ. Entomol. 2: 381–386.

Dozier, H. L. 1936. Several undescribed mymarid egg-parasites of the genus *Anagrus* Haliday. Proc. Hawaii. Entomol. Soc. 9: 175–178.

Gibson, G. A. P. 1986. Evidence of monophyly and relationships of Chalcidoidea, Mymaridae, and Mymarommatidae (Hymenoptera: Terebrantes). Can. Entomol. 118: 205–240.

Gordh, G. & D. M. Dunbar. 1977. A new *Anagrus* important in the biological control of *Stephanitis takeyai* and a key to the North American species. Fla. Entomol. 60: 85–95.

Huber, J. T. 1986. Systematics, biology, and hosts of the Mymaridae and Mymarommatidae (Insecta: Hymenoptera): 1758–1984. Entomography 4: 185–243.

MacGill, E. I. 1934. On the biology of *Anagrus atomus* (L.): an egg parasite of the leaf-hopper *Erythroneura pallidifrons* Edwards. Parasitology 26: 57–63.

May, Y. Y. 1971. The biology and population ecology of *Stenocranus minutus* (Fabricius) (Delphacidae, Hemiptera). Ph.D. dissertation, University of London, London.

McKenzie, L. M. & B. P. Beirne. 1972. A grape leafhopper, *Erythroneura ziczac* (Homoptera: Cicadellidae) and its mymarid (Hymenoptera) egg-parasite in the Okanagan Valley, British Columbia. Can. Entomol. 104: 1229–1233.

Meyerdirk, D. E. & M. S. Moratorio. 1987. Biology of *Anagrus giraulti* (Hymenoptera: Mymaridae), an egg parasitoid of the beet leafhopper, *Circulifer tenellus* (Homoptera: Cicadellidae). Ann. Entomol. Soc. Am. 80: 272–277.

Moratorio, M. S. 1977. Aspects of the biology of *Anagrus* spp. (Hymenoptera: Mymaridae), with special reference to host–parasitoid relationships. Ph.D. dissertation, University of London, London.

Otake, A. 1968. Studies on the egg parasites of the smaller brown planthopper, *Laodelphax striatellus* (Fallen) (Hemiptera: Delphacidae). II. Development of *Anagrus* nr. *flaveolus* Waterhouse (Hymenoptera: Mymaridae) within its host. Bull. Shikoku Agric. Exp. Stn. 18: 161–169.

1969. Studies on the egg parasites of the smaller brown planthopper, *Laodelphax striatellus* (Fallen) (Hemiptera: Delphacidae). III. Longevity and fecundity of *Anagrus* nr. *flaveolus* Waterhouse (Hymenoptera: Mymaridae). Jpn. J. Ecol. 19: 192–196.

Sahad, K. A. 1984. Biology of *Anagrus optabilis* (Perkins) (Hymenoptera, Mymaridae), an egg parasitoid of delphacid planthoppers. Esakia 22: 129–144.

Sokal, R. R. & F. J. Rohlf. 1981. Biometry, 2nd ed. Freeman, New York.

Stiling, P. D. & D. R. Strong. 1982a. Parasitoids of the planthopper, *Prokelisia marginata* (Homoptera: Delphacidae). Fla. Entomol. 65: 191–192.

1982b. Egg density and the intensity of parasitism in *Prokelisia marginata* (Homoptera: Delphacidae). Ecology 63: 1630–1635.

Strong, D. R. 1989. Density independence in space and inconsistent temporal relationships for host mortality caused by a fairyfly parasitoid. J. Anim. Ecol. 58: 1065–1076.

Tay, E. B. 1972. Population ecology of *Cicadella viridis* (L.) and bionomics of *Graphocephala coccinea* (Forster) (Homoptera: Cicadellidae). Ph.D. dissertation, University of London, London.

Waloff, N. & A. Jervis. 1987. Communities of parasitoids associated with leafhoppers and planthoppers in Europe. Adv. Ecol. Res. 17: 281–402.

Whalley, P. E. S. 1969. The mymarid (Hym.) egg-parasites of *Tettigella viridis* L. (Hem., Cicadellidae) and embryoparasitism. Entomol. Mon. Mag. 105: 239–244.

Williams, D. W. 1984. Ecology of a blackberry-leafhopper-parasite system and its relevance to California grape agroecosystem. Hilgardia 52: 1–32.

Wilson, S. W. 1982. The planthopper genus *Prokelisia* in the United States (Homoptera: Fulgoroidea: Delphacidae). J. Kans. Entomol. Soc. 55: 532–546.

Witsack, W. 1973. Zur Biologie und Oekologie in Zikadeneiern parasitierender Mymariden der Gattung *Anagrus* (Chalcidoidea, Hymenoptera). Zool. Jahrb. Syst. Bd. 100: 223–229.

Received for publication 7 August 1989; accepted 11 January 1990.