

Survival of *Archytas marmoratus* (Diptera: Tachinidae) in *Helicoverpa zea* and *Spodoptera frugiperda* (Lepidoptera: Noctuidae) at Low Temperatures and Short Days¹

F. I. Proshold and J. E. Carpenter

USDA-ARS-IBPMRL, Tifton, GA 31793-0748 USA

J. Entomol. Sci. 35(1): 9-21 (January 2000)

Abstract *Archytas marmoratus* (Townsend) was reared on corn earworm, *Helicoverpa zea* (Boddie), or fall armyworm, *Spodoptera frugiperda* (J. E. Smith). Rearing chambers were programmed for a constant temperature of 15, 16, 19, 20, 22, 24, or 25°C and a photoperiod of 10:14 h (L:D) or 25°C and a photoperiod of 12:12 h (L:D). Development of parasitoids was faster when corn earworm larvae were parasitized than when fall armyworm larvae were parasitized. At 15°C parasitoid survival was poor on both hosts but at 16°C, more parasitoids eclosed on corn earworm than fall armyworm. Diapause induction in this strain of corn earworm was low. All pupae that eclosed after being in diapause produced an adult corn earworm. The data suggested that *A. marmoratus* is not influenced by diapause induction in its host but continues to develop above the threshold temperature for survival. This would restrict its overwintering as a larva or pupa to regions that have a continuous, nondiapausing host population. Thus, yearly establishment of *A. marmoratus* in more temperate areas would be required.

Key Words Corn earworm, fall armyworm, diapause, overwintering survival, augmentation

Archytas marmoratus (Townsend) is an indigenous, larval-pupal parasitoid of several noctuids including the corn earworm, *Helicoverpa zea* (Boddie), and fall armyworm, *Spodoptera frugiperda* (J. E. Smith). Females larviposit on substrates occupied by host larvae. Then, maggots attach themselves to host larvae as contact is made (Hughes 1975). Many consider *A. marmoratus* to be a late-season parasitoid as few flies are found during the spring. However, Gross et al. (1976) found *A. marmoratus* to be the only parasitoid attacking corn earworm in whorl-stage and early tassel-stage corn. Manley et al. (1991) observed 25% parasitism of corn earworm by *A. marmoratus* in whorl-stage corn in South Carolina, and Smith et al. (1976) found *A. marmoratus* to be an important parasitoid of the corn earworm in whorl-stage corn in Mississippi.

A 3-yr study was conducted to examine the efficacy of augmentative releases of *A. marmoratus* to manage corn earworm populations. Following inundative releases of *A. marmoratus* in whorl-stage corn, parasitism of the corn earworm increased several fold. However, during the second year (1994) of this study, >80% of 184 corn earworm larvae collected 11 May in whorl-stage corn were parasitized by *A. marmoratus*, regardless of whether larvae were collected from control fields, or from fields where augmentative releases of *A. marmoratus* had been made (Proshold et al.

¹Received 19 December 1996; accepted for publication 04 April 1999.

1998). Observations that *A. marmoratus* can be abundant during the spring stimulated interest in its survival at low temperature and its ability to overwinter. Without an overwintering strategy, yearly establishment of *A. marmoratus* would be required, and additional augmentation may be necessary.

Overwintering strategies have not been well studied for the Tachinidae. However, Mellini (1990) lists several possible means of overwintering. First, tachinids may overwinter as eggs or adults, but this is not common, particularly in regions with cold winters. Second, they may survive as pupae in the ground, independent of the physiology of their hosts that have already died. For example, a tachinid parasitoid (*Athrycia cinerea* Coquillett) of the bertha armyworm (*Mamestra configurata* Walker) has a facultative diapause of the long-day type, and in western Canada it is univoltine and overwinters as a pupa in the soil (Turnock and Bilodeau 1992). Third, there are cases in which some species spend the winter as mature larvae in the body of their hosts which serves as protection. *Carcelia* sp. appears to be an example of this strategy, apparently overwintering within the pupae of its host, *Helicoverpa armigera* (Hübner) (Kay 1982). Of three parasitized pupae collected during the fall, the parasitoid eclosed 91, 164, or 193 d later. The timing of eclosion for the tachinids coincided with eclosion of overwintering *H. armigera*. Fourth, for those that overwinter in the host, Mellini (1990) stated that tachinid parasitoids commonly spend the winter as first instars or beginning second instars in the undamaged, viable hosts in diapause.

Regardless of overwintering strategy, the parasitoid is sensitive to the hormonal balance of the host only during the first and second instars. Ramadhane et al. (1988) studied the tachinid parasitoid *Pseudoperichaeta nigrolineata* (Walker) in diapausing *Ostrinia nubilalis* Hübner. They found that when fifth instars were parasitized, development of the parasitoid during the first stadium was the same as parasitoids in nondiapausing hosts, but growth stopped in the second stadium when the parasitoid was nearly 1 mg. When diapause of the host was terminated by modifying abiotic conditions and/or by injecting ecdysterone, the parasitoid larva resumed development.

Although unknown, *A. marmoratus* probably does not overwinter in the puparium. Numerous puparia formed in field cages in North Carolina during 1972 and 1973 either emerged the same year or perished (Danks et al. 1979). Although adults were first seen and captured in malaise traps in early June, they were not commonly collected until September and October. Herein, we report on the capability of *A. marmoratus* to survive low temperature in two hosts, one that does not diapause (*S. frugiperda*) and one that exhibits an hibernal diapause (*H. zea*).

Methods and Materials

Insects. *Archytas marmoratus* has been maintained in laboratory colony since 1981 with intermittent infusion of genetic material from parasitized *H. zea* and *S. frugiperda* collected from whorl-stage corn in Georgia and Florida. The colony has been maintained on larvae of *H. zea* from the Tifton, GA, laboratory colony (Young et al. 1976) according to the methods of Gross and Johnson (1985). Host insects were obtained from colonies of the Insect Biology and Population Management Research Laboratory, USDA-ARS, Tifton, GA, rearing facility. *Helicoverpa zea* larvae were reared on corn-soy-meal (CSM) artificial diet (Jones et al. 1977) using the methods of Burton (1969). *Spodoptera frugiperda* were reared on a pinto bean diet using the methods of Burton and Perkins (1989). Both species were reared at $\approx 25^{\circ}\text{C}$ and a

photoperiod of 12:12 h (L:D). The *H. zea* colony has been reared continuously since 1969 and *S. frugiperda* since 1986 (W. D. Perkins, unpub. data). Host larvae were reared in 30-ml plastic cups on ≈ 15 ml of diet capped with a paper lid (one larva per cup). Insects were placed in 1 of 4 incubators (Perival, Boone, IA, model number I-35/L) programmed at a different constant temperature (15 to 25°C) and either a photoperiod of 12:12 or 10:14 h (L:D). *Archytas marmoratus* maggots (planidia) were added when host larvae were in the fourth stadium.

Test 1. The objective was to determine whether *A. marmoratus* would enter diapause in response to cool temperatures and a shorter than normal photoperiod. We also wanted to study their survival in host larvae that had entered diapause. Host larvae were reared at 25°C and a photoperiod of 12:12 h (L:D) or 25, 20, or 15°C and a photoperiod of 10:14 h (L:D). *Archytas marmoratus* maggots were dropped (≈ 10) onto the inner surface of the lid of diet cups when host larvae were 6, 9 or 20 days old, depending upon temperature. For each treatment there were 150 larvae for each host species. When host larvae pupated, the number of maggots viewed beneath the integument of each pupa was counted. Also, number of days to pupation, days to eclosion of host or parasitoid, and sex of eclosed insect were also recorded.

Test 2. The objective of this test was the same as test 1 except we wanted to prevent superparasitism. Thus, maggots were individually placed on host larvae when they were 7, 11, or 26 days old, depending upon temperature. Maggots were placed on 90 larvae per host at 20 and 25°C and 150 larvae per host at 15°C. Sixty unparasitized larvae per host served as controls at 20 and 25°C. Temperature and photoperiod treatments were the same as for test 1.

Test 3. The objectives of this test were similar to the first two but with different, more moderate temperatures. Another objective was to study the influence of rearing temperature on the number of maggots produced by *A. archytas*. The test was run at 24, 22, 19, or 16°C and a photoperiod of 10:14 (L:D). Maggots were individually placed on host larvae with a brush (age 7, 9, 11, and 22 d, respectively). Ninety parasitized and 60 unparasitized larvae were set up per treatment. Number of days to pupation, days to eclosion (either host or *Archytas*), and sex of eclosed insect were recorded. Dead larvae or pupae were dissected to assess parasitism.

The fecundity of *A. marmoratus* (number of maggots per female) from each host, and temperature was estimated as follows: upon eclosion, females were placed with males and held at 27°C for 10 d and then at 13°C for 2 d. Thereafter, their uterus was removed, placed in ≈ 30 ml of H₂O, and blended 3 times for 3 sec at 8500 rpm. After the blend was adjusted to 30 ml and stirred with a pipette, 6 drops of the solution were dispersed onto a piece of filter paper. The blend was stirred a second time and another series of six drops was taken for a total of 12 drops (12 drops = 1 ml). The number of maggots in each drop was counted. Fecundity per female was estimated by multiplying the average number of maggots per drop by 360 (1/12 of 30).

Data analysis. In all tests, 30 cups with larvae were held in a single tray. For data analysis, each tray was considered a replicate. Percentage survival was obtained using the tray as the base unit. Following an arcsine transformation ($\sqrt{\%/100}$) to normalize the data, survival data were subjected to analysis of variance (PROC GLM, SAS Institute 1988), and if significance was indicated ($\alpha = 0.05$), means were separated using the Waller-Duncan Bayesian test (WALLER OPTION, SAS Institute 1988). Developmental data were presented as Tukey box plots (Jandel Scientific 1992). These data were further analyzed by a nonparametric analysis of variance (PROC NPAR1WAY, SAS Institute 1988). Parasitoid fecundity was analyzed by a

two-way analysis of variance (model: maggots = host/temperature); mean number of days to eclosion and number of maggots per female were analyzed by polynomial regression (PROC GLM, SAS Institute 1988).

Results

Survivorship. Test 1. Survival was low at 15°C for all species (Table 1). Fewer than 6% of the host larvae produced an adult parasitoid or host. At a temperature >15°C, emergence of parasitoids or moths was greater for fall armyworm than for corn earworm. At 25°C percentage eclosion was similar for both photoperiods regardless of host, but percentage eclosion at 20°C was less than that at 25°C. Also, fewer flies were produced at 20°C than at 25°C, ($F = 17.20$; $df = 2, 24$; $P < 0.001$), but there was no significant difference in number of flies from the 25°C incubators because of photoperiod ($F < 0.45$; $df = 1, 18$; $P > 0.511$). None of the host pupae entered diapause as determined by loss of larval eyespots (Phillips and Newsom 1966) and no *A. marmoratus* entered diapause as determined by an unusually long developmental time. Percentage parasitism was greater for corn earworm than fall armyworm but the number of flies and adult moths eclosing was greater for fall armyworm than for corn earworm ($F = 23.78$; $df = 1, 24$; $P < 0.001$; mean = 16.1 and 12.0 flies per tray, respectively).

Although at 15°C seven *A. marmoratus* eclosed, maggots were observed in only four corn earworm pupae. Three pupae had only one maggot and one had three maggots. For 20 and 25°C at 10:14 (L:D), and 25°C at 12:12, the number of maggots per corn earworm pupa averaged 5.1, 4.9 and 4.3, respectively. Corn earworms reared with a 14 h scotophase were more heavily superparasitized than those with a 12 h scotophase (Fisher's Exact Probability = 0.034, SAS Institute 1988), perhaps because host larvae were more active during darkness than during daylight. Also, host larvae that failed to eclose were more heavily superparasitized than those that eclosed ($G = 9.251$, $df = 2$, $P = 0.01$) (log likelihood ratio test [Sokal and Rohlf 1969]). More than 80% of corn earworm pupae that died contained >4 maggots compared with only 56% of the pupae that eclosed. Thus, the poor yield of corn earworm adults may have been caused in part by superparasitism. Only 29% of the fall armyworm pupae were superparasitized and none contained more than 4 maggots (mean = 1.3 maggots per parasitized pupae). For both host species, maggots were observed in a few pupae that subsequently produced moths.

Test 2. None of the corn earworm pupae entered diapause at 25°C, regardless of photoperiod. Only 1 of 86 and 1 of 23 entered diapause when held at 20°C or 15°C, respectively. Eclosion of corn earworm or *A. marmoratus* adults was greater in test 2 than in test 1, but the trend towards lower survival at lower temperature was similar. In test 2, eclosion of an insect, either corn earworm or *A. marmoratus*, from corn earworm larvae that had maggots placed on them, was greater than for corn earworm larvae from controls (Tables 2 and 3). Percentage parasitism was greater for corn earworm than for fall armyworm (Table 2).

Test 3. Corn earworm survival in test 3 appeared to be greater than in the earlier tests but survival of the fall armyworm in all tests was similar. Few fall armyworm or *A. marmoratus* from fall armyworm larvae eclosed at 16°C. At 16°C, 45% of the unparasitized corn earworm pupae entered diapause compared with only 4% of pupae from larvae treated with maggots. After >10 wk, these pupae ($n = 22$) were chilled for 2 wks at 10°C to break diapause (Benschoter 1968) and then placed at 25°C and

Table 1. Average percentage pupation and eclosion of insects, either parasitoid or host, and total number of insects eclosing when *Archytas marmoratus* (Am) maggots (≈ 10) were dropped on the inner surface of the cap of rearing containers with a fourth-instar corn earworm (Hz) or fall armyworm (Sf)

Temp. (°C)	Photo- period (L:D) (hrs)	Corn earworm as host				Fall armyworm as host			
		% ± SEM		Am	Hz	% ± SEM		Am	Sf
		Pupation*	Eclosion*			Pupation*	Eclosion*		
				Am				Am	
25	12:12	85 ± 4.2a	48 ± 2.0a	71	1	97 ± 1.2a	85 ± 2.7a	94	33
25	10:14	84 ± 3.4a	48 ± 5.6a	68	4	95 ± 1.7a	83 ± 4.3a	81	43
20	10:14	65 ± 4.3b	28 ± 3.4b	41	1	95 ± 1.3a	59 ± 5.4b	66	22
15	10:14	24 ± 6.6c	5 ± 1.7c	7	0	82 ± 3.1b	6 ± 2.2c	8	1

*Means within columns followed by the same letter not significantly different ($\alpha = 0.05$). Waller-Duncan k ratio t test (Waller and Duncan 1969) (five trays of 30 larvae per tray per host per temperature).

Table 2. Average percentage pupation and eclosion of insects, either parasitoid or host, and total number of insects eclosing when one *Archytas marmoratus* (Am) maggot was placed on 4th instar corn earworm (Hz) or fall armyworm (Sf)

Test	Temp. (°C)	Photo- period (L:D) (hrs)	Corn earworm as host				Fall armyworm as host			
			% ± SEM		Adults (No.)**		% ± SEM		Adults (No.)	
			Pupation*	Eclosion*, **	Hm	Am	Hz	Pupation*	Eclosion*	Sf
2	25	12:12	90 ± 1.9a	84 ± 2.9a		69	7	98 ± 1.1a	89 ± 2.9a	23
2	25	10:14	86 ± 1.1a	77 ± 5.1a		64	5	99 ± 1.1a	96 ± 1.1b	35
2	20	10:14	60 ± 3.3b	50 ± 1.9b		40	5	93 ± 3.8a	82 ± 2.2a	38
2	15	10:14	15 ± 4.8c	4 ± 3.2c		1	5	75 ± 2.9b	3 ± 1.0c	3
3	24	10:14	89 ± 2.9a	86 ± 6.2a		62	15	97 ± 1.9a	94 ± 2.2a	44
3	22	10:14	100 b	92 ± 2.2a		68	15	98 ± 1.1a	90 ± 1.9a	36
3	19	10:14	99 ± 1.1b	91 ± 1.1a		73	7	97 ± 1.9a	73 ± 8.4b	40
3	16	10:14	79 ± 4.4a	46 ± 4.4b		36	5	88 ± 4.0b	2 ± 1.1c	1

* Means within columns and within the same test followed by the same letter not significantly different ($\alpha = 0.05$), Waller-Duncan k ratio t test (Waller and Duncan 1969) (three trays of 30 larvae per tray per temperature except five trays for insects held at 15°C).

** Pupae in diapause included with eclosion data.

Table 3. Average percentage pupation, percentage eclosion, and number of insects eclosing when corn earworm or fall armyworm larvae and pupae were reared at constant temperature

Test	Temp. (°C)	Photo- period (L:D) (hrs)	Corn earworm			Fall armyworm		
			% ± SEM		No. of adults	% ± SEM		No. of adults
			Pupation*	Eclosion*, **		Pupation*	Eclosion*	
2	25	12:12	78 ± 1.7a	62 ± 8.3a	37	97 ± 3.3a	90 ± 3.3a	54
2	25	10:14	65 ± 1.7ab	48 ± 8.3a	29	99 ± 1.1a	92 ± 1.7a	55
2	20	10:14	52 ± 7.6b	41 ± 6.1a	24	98 ± 1.7a	87 ± 3.3a	52
3	24	10:14	87 ± 10 a	82 ± 8.3a	49	100 a	93 ± 0 a	56
3	22	10:14	100 a	97 ± 0 a	58	98 ± 1.7a	93 ± 0 a	56
3	19	10:14	98 ± 1.7a	88 ± 1.7a	53	100 a	83 ± 0 a	50
3	16	10:14	82 ± 15 a	50 ± 10 b	30	90 ± 0 b	3 ± 3.3b	2

* Means within columns and within the same test followed by the same letter not significantly different ($\alpha = 0.05$), Waller-Duncan k ratio t test (Waller and Duncan 1969) (average percentage of two trays of 30 larvae per tray).

** Pupae in diapause included with adult data.

14:10 L:D. Seventeen moths eclosed 15.0 ± 0.27 d later (mean \pm SEM) with no difference between sex ($F = 0.18$; $df = 1, 15$; $P = 0.68$).

Development of *Archytas*. Data from all three tests were combined and presented as box plots (Figs. 1–2). Although most of the data were not normally distributed, there was a typical, inverse relationship between temperature and number of days to eclosion. At 15°C , females averaged 93 ± 2.0 d from day of infestation to eclosion on corn earworm and 97 d on fall armyworm. With increasing temperature, adults eclosed in less time and in a curvilinear response. The developmental response of the parasitoid in days to eclosion between 19 and 25°C was linear. Male *A. marmoratus* eclosed sooner than females. At a lower temperature, the discrepancy in days to eclosion between sexes was greater than at a higher temperature.

Archytas marmoratus eclosed sooner on corn earworm than on fall armyworm hosts (Table 4). Although not measured, parasitoid larvae were visibly larger when reared in corn earworm than in fall armyworm and caused a prominent bulge in the host pupa when they reentered the host after host ecdysis. In contrast, parasitoid larvae had to be viewed with a microscope to be seen in newly pupated fall armyworm. Although *A. marmoratus* developed faster on corn earworm than fall army-

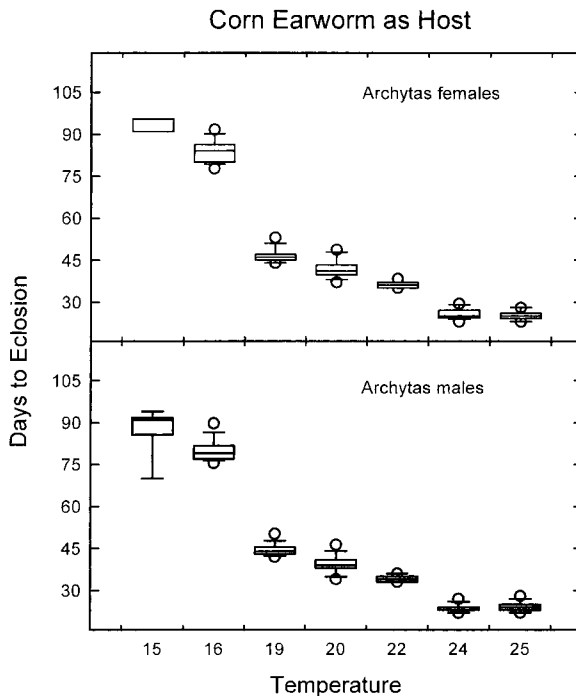


Fig. 1. Box plots (25th and 75th percentile with a line at the 50th percentile; capped bars extend to the 10th and 90th percentiles and circles show the 5th and 95th percentiles) of number of days from time maggots placed on fourth instar corn earworm to eclosion of adult parasitoid ($n = 3, 17, 45, 37, 37, 23$, and 134 , for females and $5, 19, 28, 44, 31, 39$, and 137 , for males, respectively).

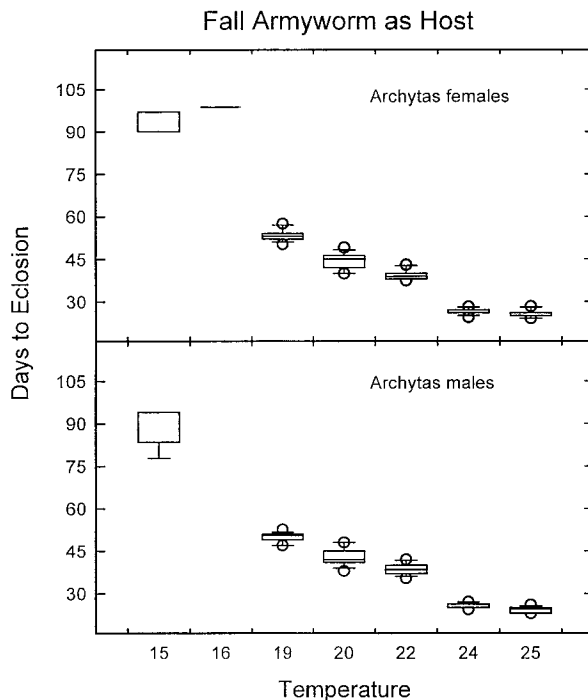


Fig. 2. Box plots (25th and 75th percentile with a line at the 50th percentile; capped bars extend to the 10th and 90th percentiles and a circles show the 5th and 95th percentiles) of number of days from time maggots placed on fall armyworm larvae to eclosion of adult parasitoid ($n = 4, 1, 22, 53, 18, 27$, and 105, for females and 7, 0, 18, 17, and 128, for males, respectively).

worm, nonparasitized fall armyworm adults eclosed sooner than nondiapausing corn earworm. This discrepancy increased with lower temperature.

Fecundity of *Archytas*. Fecundity of *A. marmoratus* decrease curvilinearly with lower temperature (Fig. 3). At 16°C, too few *A. marmoratus* adults eclosed when reared on fall armyworm to obtain fecundity data, but at 19, 22, and 24°C, a two-way analysis of variance indicated a highly significant difference because of temperature ($F = 7.3$; $df = 2, 120$, $P < 0.01$). There was no significant difference between host ($F = 0.50$; $df = 1, 120$, $P < 0.48$) nor significant interaction between host and temperature ($F = 0.30$; $df = 2, 120$, $P < 0.70$). At 16°C the number of maggots per *A. marmoratus* female from corn earworm pupae was <25% that of 22 or 24°C. In addition, four *A. marmoratus* females from the 16°C treatment did not mate and consequently, produced no maggots. In one other female, maggots were immature after the 12-d holding period and were not counted.

Discussion

The strain of corn earworm used in these studies showed a weak incidence of diapause, possibly because it has been reared continuously in the laboratory for >25

Table 4. Number of days from time maggots placed on host (fourth instar) until host pupation and number of days from pupation to eclosion of *A. marmoratus*

Temp (°C)	Sex	Host	N	Ave no. ± SEM days for:		Host pupation*		Archytas eclosion*	
				Host pupation	Archytas eclosion	F	P	F	P
24	♀	cew	23	8.3 ± 0.41	17.6 ± 0.15	0.22	0.637	4.61	0.037
24	♀	faw	27	8.1 ± 0.11	18.2 ± 0.23				
24	♂	cew	39	7.5 ± 0.25	16.2 ± 0.08	3.55	0.065	45.46	<0.001
24	♂	faw	17	8.2 ± 0.09	17.4 ± 0.19				
22	♀	cew	37	11.6 ± 0.17	24.6 ± 0.13	28.50	<0.001	36.66	<0.001
22	♀	faw	18	13.2 ± 0.26	26.3 ± 0.31				
22	♂	cew	31	11.7 ± 0.25	22.6 ± 0.14	29.92	<0.001	29.80	<0.001
22	♂	faw	18	13.9 ± 0.32	24.6 ± 0.40				
19	♀	cew	45	16.5 ± 0.37	30.4 ± 0.19	21.97	<0.001	71.90	<0.001
19	♀	faw	22	19.4 ± 0.48	33.8 ± 0.43				
19	♂	cew	28	16.1 ± 0.39	28.4 ± 0.18	18.26	<0.001	75.98	<0.001
19	♂	faw	18	18.4 ± 0.27	31.4 ± 0.32				
16	♀	cew	17	25.1 ± 0.81	58.4 ± 0.47	2.03	0.174	28.18	<0.001
16	♀	faw	1	30	69				
16	♂	cew	19	28.9 ± 3.38	51.1 ± 3.20				

* F statistics and probability of a significant difference in development ($\alpha = 0.05$) between hosts for ♀♀ and ♂♂ *A. marmoratus* (PROC NPAR1WAY, ANOVA, SAS Institute 1989).

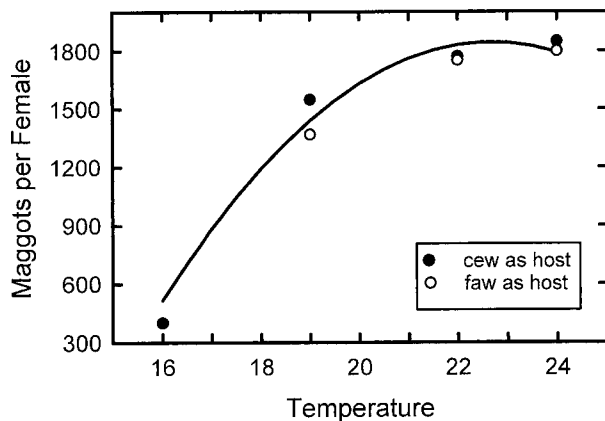


Fig. 3. Average number of maggots per female *A. marmoratus* and quadratic fit of data ($y = 1349.79x - 29.76x^2 - 13463.88$) when reared at 16, 19, 22, or 24°C with corn earworm or fall armyworm as host ($n = 6, 31, 26$, and 20, and 16, 15, and 18, for corn earworm and fall armyworm, respectively).

yr. Benschoter (1968) observed that 30% of corn earworm larvae diapaused at 21°C and a photoperiod of 10:14 (L:D). Roach and Adkisson (1970) found that 34% diapaused when adults and eggs are reared at 12:12 photoperiod and the larvae are reared at 10:14 and 21°C. In this study, only one pupa was found in diapause at 20°C and a 10:14 photoperiod. Nonetheless, a sufficient number of corn earworm diapaused at 16°C to indicate either development of *A. marmoratus* was not influenced by host diapause or parasitism prevented the induction of diapause. Only 3 pupae (4%) were observed in diapause when individual maggots were applied directly to larvae reared at 16°C. All produced adult moths. Probably more than three pupae would have entered diapause had they not been parasitized. Forty-five percent of the pupae in the control group entered diapause, significantly greater than the 4% of the parasitized group ($P = 1.5 \times 10^{-8}$, Fisher's exact test). Apparently then, host diapause does not influence *A. marmoratus* development and the parasitoid continues to develop as long as the temperature is above the threshold for survival. The fact that *A. marmoratus* developed faster on corn earworm than fall armyworm supports this conclusion.

Fewer maggots were produced by *A. marmoratus* at 16°C, than at 22 or 24°C suggesting occurrence of a possible reproductive diapause. A reproductive diapause would allow additional time for development of a host population in the spring.

None of the four overwintering strategies discussed by Mellini (1990) seem to fit *A. marmoratus*. Although the ability of adult parasitoids to survive at a low temperature was not studied, adults require adequate food for survival regardless of temperature. Thus, it is likely that *A. marmoratus* overwinters as a larva developing slowly within its host. This would mean that overwintering would be restricted to areas which have hosts available year around or where temperatures delay development sufficiently to prolong the development through most of the winter. Thus, in more temperate regions, parasitoid populations would need to be reintroduced annually. This agrees

with the observations that *A. marmoratus* is generally a late-season parasitoid in Georgia and North Carolina. Consequently, there would likely be little seasonal carry over following augmentative releases of *A. marmoratus*.

Acknowledgments

The technical assistance and dedication of R. Johnson, U.S. Department of Agriculture, Agriculture Research Service, Tifton, GA, is gratefully acknowledged. We also thank the personnel in rearing, under the supervision of W. D. Perkins, U.S. Department of Agriculture, Research Service, Tifton, GA, for providing diet and insects for study. The following scientists peer reviewed the manuscript: R. A. Bell, U.S. Department of Agriculture, Agriculture Research Service, Beltsville, MD; G. L. Bernon, Animal and Plant Health Inspection Service, Otis ANGB, MA; and J. R. Ruberson, University of Georgia, Coastal Plain Experiment Station, Tifton, GA. Their comments were appreciated and greatly improved the manuscript.

References Cited

- Benschoter, C. A. 1968.** Diapause and development of *Heliothis zea* and *H. virescens* in controlled environments. *Ann. Entomol. Soc. Am.* 61: 953-956.
- Burton, R. L. 1969.** Mass rearing the corn earworm in the laboratory. USDA-ARS. 33-134, 8 pp.
- Burton, R. L. and W. D. Perkins. 1989.** Rearing the corn earworm and fall armyworm for maize resistance studies, Pp. 37-45. *In* Toward insect resistant maize for the third world. Proceedings of the International Symposium on Methodologies for Developing Host Plant Resistance to Maize Insects. CIMMYT, Mexico, 9-14 March 1987.
- Danks, H. V., R. L. Rabb and P. S. Southern. 1979.** Biology of insect parasites of *Heliothis* larvae in North Carolina. *J. Georgia Entomol. Soc.* 14: 37-63.
- Gross, H. R., Jr. and R. Johnson. 1985.** *Archytas marmoratus* (Diptera: Tachinidae): advances in large-scale rearing and associated biological studies. *J. Econ. Entomol.* 78: 1350-1353.
- Gross, H. R., Jr., B. R. Wiseman and W. W. McMillian. 1976.** Comparative suitability of whorl stages of sweet corn for establishment by larvae of the corn earworm. *Environ. Entomol.* 5: 955-958.
- Hughes, P. S. 1975.** The biology of *Archytas marmoratus* (Townsend). *Ann. Entomol. Soc. Am.* 68: 759-767.
- Jandel Scientific. 1992.** Sigma Plot® scientific graphing software user's manual. DOS Version.
- Jones, R. L., W. D. Perkins and A. N. Sparks. 1977.** Two new diets for the corn earworm. *J. Georgia Entomol. Soc.* 12: 211-215.
- Kay, I. R. 1982.** Overwintering by three parasites of *Heliothis armigera* (Hübner) (Lepidoptera: Noctuidae) in Southeast Queensland. *J. Australian Entomol. Soc.* 21: 267-268.
- Manley, D. G., J. A. DuRant, A. W. Johnson and M. E. Roof. 1991.** The tobacco budworm/bollworm complex (Lepidoptera: Noctuidae) and its parasites on field crops in South Carolina. *J. Agr. Entomol.* 8: 169-178.
- Mellini, E. 1990.** Synopsis of the biology of Diptera Tachinidae (English Translation). Bollettino Dell' Istituto Di Entomologia "Guido Grandi," University of Bologna 45: 1-38.
- Phillips, J. R. and L. D. Newsom. 1966.** Diapause in *Heliothis zea* and *H. virescens* (Lepidoptera: Noctuidae). *Ann. Entomol. Soc. Am.* 59: 154-159.
- Proshold, F. I., H. R. Gross, Jr. and J. E. Carpenter. 1998.** Inundative release of *Archytas marmoratus* (Diptera: Tachinidae) against the corn earworm and fall armyworm (Lepidoptera: Noctuidae) in whorl-stage corn. *J. Entomol. Sci.* 33(3): 241-255.
- Ramadhane, A., S. Grenier and G. Plantevin. 1988.** Photoperiod, temperature and ecdysteroid influences on physiological interactions between diapausing *Ostrinia nubilalis* larvae and the tachinid parasitoid *Pseudoperichaeta nigrolineata*. *Entomol. Exp. Appl.* 48: 275-282.
- Roach, S. H. and P. L. Adkisson. 1970.** Role of photoperiod and temperature in the induction of pupal diapause in the bollworm, *Heliothis zea*. *J. Insect Physiol.* 16: 1591-1597.

- SAS Institute Inc. 1988.** SAS/STAT user's guide, version 6, 4th edition. SAS Institute, Cary, NC.
- Smith, J. W., E. G. King and J. V. Bell. 1976.** Parasites and pathogens among *Heliothis* species in the Central Mississippi Delta. *Environ. Entomol.* 5: 224-226.
- Sokal, R. R. and F. J. Rohlf. 1969.** Biometry. W. H. Freeman and Co., San Francisco.
- Turnock, W. J. and R. J. Bilodeau. 1992.** Life history and coldhardiness of *Arthrycia cinerea* (Dipt: Tachinidae) in western Canada. *Entomophaga* 37: 353-362.
- Waller, R. A. and D. B. Duncan. 1969.** A bayes rule for the symmetric multiple comparison problem. *J. Amer. Stat. Assoc.* 64: 1484-1499.
- Young, J. R., J. J. Hamm, R. L. Jones, W. D. Perkins and R. L. Burton. 1976.** Development and maintenance of a laboratory colony of the corn earworm. USDA-ARS. S-110, 9 pp.
-