# *Archytas marmoratus* (Diptera: Tachinidae) Survival in Diapausing and Nondiapausing Strains of *Helicoverpa zea* (Lepidoptera: Noctuidae)[1]

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**Abstract** *Archytas marmoratus* (Townsend) was reared on four strains of corn earworm, *Helicoverpa zea* (Boddie). One strain did not diapause or entered a weak diapause. A portion of the other three strains entered diapause when reared at 19 or 22°C and 10:14 h photoperiod (L:D). No *A. marmoratus* entered diapause; 90% eclosed with no differences among strains or rearing condition, and the number of days from host pupation to eclosion within rearing condition was similar regardless of host strain. Parasitized pupae did not enter a chill-terminated diapause, as indicated by loss of larval eyespots within 2 wks. Either the presence of *A. marmoratus* maggots prevented diapause in its host or diapause was terminated by rapid development of the maggot after host pupation. These data suggest that *A. marmoratus* does not overwinter as a larva or pupa in the cooler regions of its distribution.

**Key Words** Corn earworm, diapause, overwintering survival, augmentation, *Archytas marmoratus.*

*Archytas marmoratus* (Townsend) is a solitary, larval-pupal parasitoid of several species of Noctuidae including the corn earworm, *Helicoverpa zea* (Boddie). Female flies larviposit planidia on plants nearby host larvae. Planida attach themselves to host larvae upon contact. After penetrating the cuticle of its larval host, the *A. marmoratus* planidia come to lie in the epidermis (Hughes 1975, Bratti et al. 1992). Each time the host molts, *A. marmoratus* maggots must exit the old exuviae and reenter the host after ecdysis. Planidia, or first-instar maggots of the parasitoid, remain in the first stadium until after pupation of its host.

Although generally a late-season parasitoid, researchers have suggested a role in area-wide management of the corn earworm through augmentation of *A. marmoratus* (Gross 1988, 1990, Gross and Young 1984, Knipling 1992). Methods are available to produce 40,000 parasitoids weekly (Gross and Johnson 1985, Bratti and Costantini 1991, Gross 1994, Gross et al. 1996), and mass production should be technically feasible. Following inundative releases of *A. marmoratus* in whorl-stage corn, parasitism of the corn earworm increased several fold (Proshold et al. 1997). The ability of *A. marmoratus* to overwinter as a larva in a diapausing host pupa could influence the spring population levels of *A. marmoratus* in years subsequent to augmentative releases. Without an overwintering strategy, yearly establishment of *A. marmoratus* would be required.

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*Archytas marmoratus* is found throughout the southern United States and as far south as Northern Chile (Sabrosky 1955). Vickery (1929) found that *A. marmoratus* is active year-round near Brownsville, TX; however, its overwintering strategy in the more northern areas is not known. Mellini (1990) stated that tachinid parasitoids commonly spend the winter as first- or early second-instars in the undamaged, viable hosts in diapause. Allen (1926) observed maggots of *Archytas analis* (F.) active on sprigs of amaranths and chrysanthemum for as long as 52 d during a mild winter in Mississippi. In North Carolina, adults of *A. marmoratus* are seen during early June but are not common until September and October (Danks et al. 1979). During 1972 and 1973, Danks et al. (1979) observed numerous puparia in field cages during late summer that either emerged the same year or perished and suggested that the overwintering stage was not the puparium.

Recently, survival and development of *A. marmoratus* at low temperature was compared on two hosts, one that does not diapause (fall armyworm, *Spodoptera frugiperda* (J. E. Smith), and one that has a facultative diapause (corn earworm) (Proshold and Carpenter, unpub. data). When reared at constant temperatures ranging from 15 to 25°C and a photoperiod of 10:14 (L:D), parasitoid development was faster when corn earworm was the host rather than fall armyworm. *Archytas marmoratus* did not diapause but continued to develop as long as temperature was above the threshold for survival. Also, few corn earworm entered diapause. Apparently, this strain had nearly lost the ability to diapause after being reared continuously in the laboratory for >25 yr. Because hormonal changes in the host associated with diapause induction may influence the parasitic maggot, we compared the development of *A. marmoratus* on progeny from feral corn earworm reared at a temperature and photoperiod that induces diapause with the development of *A. marmoratus* on the laboratory strain of corn earworm (nondiapause strain).

## Materials and Methods

**Insects.** The nondiapause strain of the corn earworm was from a colony that has been maintained at the Insect Biology and Population Management Research Laboratory. It has been reared continuously since 1969 at ≈25°C and a photoperiod of 12:12 h (L:D) (W. D. Perkins, unpub. data). Three strains were established from feral corn earworm as follows: (1) larvae collected from whorl-stage corn in Tift and Berrien Co., GA; (2) larvae from ears from corn fields located in Berrien, Tift, and Worth Co., GA; and (3) progeny from females of the laboratory colony crossed with males collected from pheromone traps (75-50 wire cone traps of Hartstack et al. [1979] located in Tift and Berrien Co., GA). These strains will be referred to as w-a (whorl-stage), w-b (ear-stage), and w-c (crossed), respectively.

The founding population for w-a consisted of 26 ♀♀ and 29 ♂♂ that were divided equally and placed in two cages made from cylindrical, paper cartons (17.5 cm diam by 17 cm height). A sheet of paper toweling was used for the top of the cage and served as an oviposition site. Nine hundred larvae from eggs laid on the toweling were reared at 20°C and 10:14 h photoperiod (L:D). Pupae were checked for larval eyespots at 1 and 2 wks. Those (169) still retaining larval eyespots were considered to be in diapause (Phillips and Newsom 1966) and were placed at 10°C in an unlighted incubator. The others were discarded. After 2 wks in chill, they were transferred to

24°C and 14:10 h photoperiod. The $F_1$ adults were crossed in cages (similar to the parent cross, 15 pairs per cage) and the $F_2$ larvae were used as test insects.

For the w-b strain, 579 mature larvae were collected from corn ears from six locations (four in Berrien Co., and one each in Tift and Worth Co., GA). The adults were caged in cylindrical cages as previously described (15 pair per cage, two cages per location). From 300 to 800 larvae from each location were reared at 10:14 h L:D and 20°C. Pupae that entered diapause (9 to 21% per location) were saved. The $F_1$ adults were caged without regard to location and $F_2$ larvae were used as test insects.

The founding population for the third feral strain (w-c) consisted of two feral males (one from Tift Co. and one from Berrien Co., GA) captured 29 March 1996. Each was paired with a female from the laboratory colony. About 300 $F_1$ larvae were reared at 25°C and 14:10 h photoperiod. The $F_1$ adults were crossed in cages as previously described, and $F_2$ and $F_3$ larvae were reared at 20°C and 10:14 h photoperiod. Only the $F_2$ and $F_3$ pupae that went through diapause (10 and 18%, respectively) were saved. $F_4$ larvae were used as test insects.

All corn earworm strains reared in the laboratory as well as those collected as larvae from the field were reared on corn-soy-meal (CSM) artificial diet (Jones et al. 1977) using the methods of Burton (1969) as modified by Young et al. (1976). The larvae were placed in 30-ml plastic cups on ≈15 ml of diet capped with a paper lid (one larva per cup).

*Archytas marmoratus* has been maintained in laboratory colony since 1981 with intermittent infusion of genetic material from parasitized corn earworm and fall armyworm collected from whorl-stage corn in Georgia and Florida. The colony has been maintained on larvae of corn earworm from the Tifton, GA, laboratory colony according to the methods of Gross and Johnson (1985) with modifications as described by Proshold et al. (1997). Numerous studies have demonstrated the ability of *A. marmoratus* from this laboratory colony to perform well in searching for and parasitizing host larvae in the field (Gross 1990, Proshold et al. 1997).

**Test procedure.** Neonate corn earworms were placed in 30-ml plastic cups containing diet held in 30-cup trays, one larva per cup. Six trays of larvae were established per strain per incubator (Percival, Boone, IA 50036, model number I-35/L). The incubators were programmed for the following temperature and photoperiod (L:D): (1) 22°C and 14:10 h, (2) 22°C and 10:14 h, and (3) 19°C and 10:14 h. One planidium of *A. marmoratus* was brushed onto fourth-instar corn earworm in three randomly chosen trays per strain per incubator. The experiment had 2160 observations: 4 strains, 3 rearing conditions, 2 parasitoid treatments (with and without planidia), and 3 trays of 30 larvae each.

Data collected were day of pupation, day of eclosion, and sex of eclosed insect. At pupation, the area beneath the wing pads was observed to determine the presence of a parasitoid. Pupae were observed for larval eyespots at 1 wk and weekly thereafter until all of that strain and treatment had been checked twice. Pupae with eyespots were placed at 10°C and total darkness for 2 wks and then at 24°C and 14:10 h L:D until death or eclosion. Pupae that did not diapause were left in incubators until death or eclosion.

**Data analysis.** Data were subjected to an analysis of variance or Student's t-test (PROC GLM or PROC TEST, SAS Institute 1989). Percentages were calculated for each tray and were transformed to arcsine [$\sqrt{}$ (%/100)] before analysis. Means ($\alpha$ = 0.05) were separated using the Waller - Duncan Bayesian test (WALLER OPTION, SAS Institute 1989).

## Results and Discussion

**Diapause induction and parasitism.** The only pupa of the laboratory strain to enter diapause was one male reared at 19°C. This pupa lost its larval eyespots during the second week and eclosed without chill, albeit, 72 d after pupation. Most corn earworm moths of this strain eclosed within a few days (Fig. 1), but a few required several standard deviations greater than the mean to complete development, particularly at 19°C. Although these insects did not retain their larval eyespots nor require chill to eclose, they may have undergone a weak diapause.

None of the corn earworm from the feral strains entered diapause when reared at 22°C and 14:10 h photoperiod. At 10:14 h photoperiod and 19 or 22°C, a smaller proportion of the group treated with planidia of *A. marmoratus* entered diapause than the group without planidia (Fig. 2). At 19°C, the pupae from the planidia treated group entered diapause at a significantly lower rate (24 to 34%) than pupae from the group of larvae without planidia (68%) ($F = 43.23$; df = 1, 12; $P < 0.001$). At 19°C, there was no significant difference among strains ($F = 0.85$; df = 2, 12; $P = 0.4$). However, at

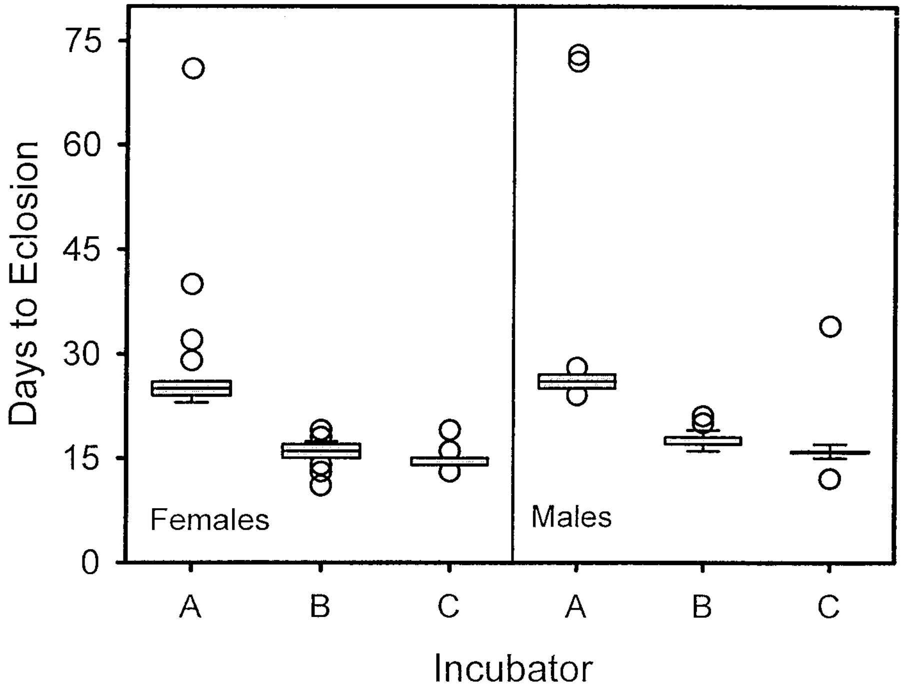

Fig. 1. Box plots (25th and 75th percentile with a line at the 50th percentile, capped bars extend to the 10th and 90th percentiles and circles show the outlying points) of number of days from pupation to eclosion for corn earworm from the laboratory strain of corn earworm reared at 19°C and 10:14 h photoperiod (A), 22°C and 10:14 h photoperiod (B), or 22°C and 14:10 h photoperiod (C); n = 55, 51, and 56, for ♀♀ and 63, 61, and 49 for ♂♂, respectively.

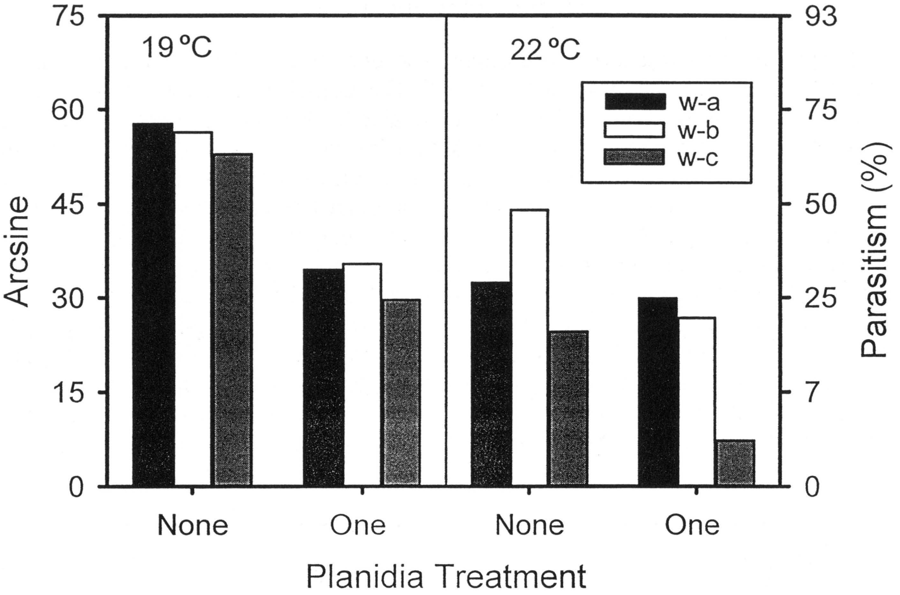

Fig. 2. Percentage diapause induction in larvae of three recently colonized corn earworm strains (w-a, w-b, and w-c) reared at 19 or 22°C and treated with one planidia of *Archytas marmoratus* compared with percentage diapause of untreated corn earworm larvae (arcsine√[%/100] and back transformation).

22°C, we observed an effect among strains (*F* = 12.7; df = 2, 12; *P* = 0.001) as well as planidia treatment (*F* = 13.9; df = 1, 12; *P* = 0.002). From 1.6 to 25% of the pupae from larvae treated with planidia entered diapause compared with 17 to 48% for larvae without planidia. The strain from feral males captured in pheromone traps crossed with laboratory strain females had a lower percentage diapause than either of the other two feral strains.

For all strains and rearing conditions, only three parasitized pupae had larval eyespots after 1 wk. All were reared at 19°C and 10:14 h photoperiod. The eyespots disappeared by week 2. One parasitoid died as a larva, one as a pupa, and one eclosed.

When treated with planidia, from 35 to 54% of the larvae from the feral strains did not become parasitized. When percentage diapause of these larvae was compared with that of the group without planidia, we found no significant difference within strain and rearing condition (*t* < 2.474, df = 4, *P* > 0.13). Moths eclosed from 94 and 96% of the pupae from the two groups (*n* = 105 and 209, respectively). None of the pupae produced an adult parasitoid. The average number of days from removal from chill to eclosion varied from 16 ± 0.3 d to 21 ± 1.0 d. Females eclosed about a day sooner than males and insects from the 19°C treatment eclosed about a day sooner than those from the 22°C treatment.

Successful parasitization was significantly influenced by strain (*F* = 7.13; df = 3, 24; *P* = 0.014) and rearing condition (*F* = 4.07; df = 2, 24; *P* = 0.03) but strain and rearing condition did not interact significantly ($F = 0.38$; df = 6, 24; $P = 0.88$) (Fig. 3). However, when only feral strains were compared, no significant differences were found ($F = 2.00$; df = 3, 16; $P = 0.67$). Percentage parasitism in the laboratory strain was greater than any of the feral strains regardless of rearing condition. For the laboratory strain reared at 22°C and 14:10 h photoperiod, percentage parasitism was higher than the other two rearing conditions. These data suggest that larvae of the laboratory strain are more susceptible to planidia penetration than larvae of the feral strains.

**Development of *Archytas marmoratus*.** Nearly 90% of the parasitized larvae produced adult *A. marmoratus* (Table 1). There was no significant difference because of strain or rearing condition ($F = 1.19$; df = 11, 24; $P = 0.34$). Fifty-one percent of the adults were females. They took longer to eclose than males. Although minor differences occurred in the number of days required for eclosion among various hosts, none were consistent nor large enough to suggest that *A. marmoratus* entered diapause. Development was slower when reared at 10:14 h photoperiod than at 14:10 h photoperiod regardless of host.

**Development of nonparasitized corn earworm.** All larvae of the w-c feral strain and nearly all from the laboratory strain pupated. For the other two feral strains, 91% pupated at 19°C and 97% at 22°C. Larvae reared at 19°C took longer to pupate than those reared at 22°C (Table 2). At 22°C, larvae reared at 14:10 h pupated sooner than those reared at 10:14 h photoperiod. We observed a highly significant difference in number of days to pupation among strains within each rearing condition ($F > 36.7$; df = 3, 8; $P < 0.001$). The laboratory strain developed faster than any feral strain and w-c developed faster than the other two feral strains. Similar trends occurred with duration of the pupal stage. Females eclosed slightly sooner than males. Likewise, percentage

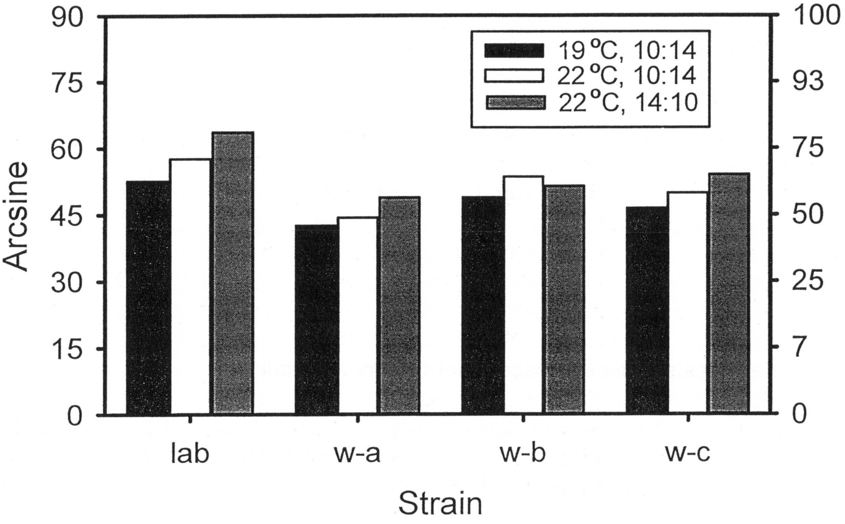

Fig. 3. Percentage parasitism of corn earworm larvae from a laboratory colony reared at 14:10 h photoperiod and 22°C or 10:14 h photoperiod and 19 or 22°C compared percentage parasitism of larvae from three recently colonized strains (arcsine√[%/100] and back transformation).

**Table 1. Percentage parasitism, percentage parasitoid ecolsion, and days from host pupation to eclosion of *Archytas marmoratus* when one planidia was placed on fourth-instars of a laboratory and three recently colonized strains of corn earworm reared at 10:14 or 14:10 h photoperiod (L:D) and 19 or 22°C**

| Rearing condition | | Host strain | Parasitism* (%) | Eclosion* (%) | Days to eclosion* | |
|---|---|---|---|---|---|---|
| °C | L:D | | | | ♀♀ | ♂♂ |
| 19 | 10:14 | lab | 63 ± 8.5 | 88 ± 3.4 | 30.8 ± 0.43 | 29.2 ± 0.60 |
| 19 | 10:14 | w-a | 46 ± 0.7 | 87 ± 6.9 | 30.6 ± 0.11 | 29.0 ± 0.55 |
| 19 | 10:14 | w-b | 57 ± 5.8 | 91 ± 2.0 | 32.3 ± 0.38 | 30.6 ± 0.73 |
| 19 | 10:14 | w-c | 52 ± 5.4 | 90 ± 5.3 | 32.9 ± 0.38 | 30.1 ± 0.80 |
| 22 | 10:14 | lab | 71 ± 4.6 | 90 ± 2.4 | 22.2 ± 0.15 | 20.6 ± 0.39 |
| 22 | 10:14 | w-a | 49 ± 2.8 | 93 ± 3.8 | 23.2 ± 0.43 | 21.3 ± 0.64 |
| 22 | 10:14 | w-b | 64 ± 7.2 | 98 ± 1.5 | 23.9 ± 1.28 | 21.9 ± 0.33 |
| 22 | 10:14 | w-c | 58 ± 3.0 | 84 ± 6.3 | 22.2 ± 0.10 | 21.5 ± 0.59 |
| 22 | 14:10 | lab | 79 ± 7.8 | 88 ± 2.4 | 20.8 ± 0.30 | 19.2 ± 0.33 |
| 22 | 14:10 | w-a | 57 ± 3.3 | 80 ± 8.1 | 20.8 ± 0.15 | 19.6 ± 0.02 |
| 22 | 14:10 | w-b | 61 ± 3.9 | 94 ± 3.1 | 20.8 ± 0.34 | 19.4 ± 0.28 |
| 22 | 14:10 | w-c | 65 ± 6.1 | 93 ± 1.6 | 21.0 ± 0.35 | 19.4 ± 0.38 |

* Avg ± SEM of three groups with 30 host larvae per group.

survival was greatest for larvae of the laboratory strain. Survival of the w-c strain was greater than either of the other two feral strains.

Percentage diapause and development of feral strains were similar whether the founding population originated from larvae collected from whorl-stage or ear-stage corn. Neither strain was as well adapted to rearing in the laboratory as corn earworm from the laboratory colony. They did not survive as well or develop as fast as insects from the colony. Survival and development of the strain from feral males crossed with colony females were more similar to the laboratory strain than were the other two feral strains. This suggests a genetic base to laboratory adaptation.

Clearly, *A. marmoratus* did not enter diapause when reared at conditions that induce diapause in its host. Survival and development did not vary greatly whether its host was reared at a diapausing or nondiapausing regime. Further, none of the corn earworm larvae entering a chill-terminated diapause was parasitized. The percentage diapause of corn earworm larvae within strain and rearing condition was similar whether they were from a group without planidia or from the portion of a group treated with planidia but were not parasitized. Finally, all parasitized corn earworm larvae lost their eyespots within 2 wks of pupation. These data suggest that *A. marmoratus* does not diapause and may terminate diapause in its host.

After penetrating the cuticle of its larval host, the *A. marmoratus* maggot comes to

**Table 2. Number of days to pupation for larvae from a laboratory and three recently colonized strains of corn earworm reared at 10:14 or 14:10 h photoperiod (L:D) and 19 or 22°C as well as percentage eclosion and pupal duration for those not entering diapause.**

| Rearing condition | | | | | | | Days as pupae** | |
|---|---|---|---|---|---|---|---|---|
| °C | L:D | Strain | Days as* larvae | Eclosion* (%) | Total no. of adults | Pct ♀ | ♀♀ | ♂♂ |
| 19 | 10:14 | lab | 24.5 ± 0.41 | 96 ± 2.2 | 86 | 45 | 26.6 ± 1.24 | 27.1 ± 1.01 |
| 19 | 10:14 | w-a | 33.1 ± 1.88 | 68 ± 3.4 | 27 | 78 | 30.3 ± 1.26 | 32.0 ± 3.44 |
| 19 | 10:14 | w-b | 31.2 ± 0.46 | 67 ± 6.9 | 25 | 60 | 30.5 ± 0.94 | 30.8 ± 0.61 |
| 19 | 10:14 | w-c | 27.2 ± 0.63 | 81 ± 12.2 | 27 | 59 | 28.0 ± 0.75 | 29.7 ± 0.63 |
| 22 | 10:14 | lab | 19.2 ± 0.11 | 97 ± 1.9 | 87 | 47 | 15.9 ± 0.23 | 17.2 ± 0.12 |
| 22 | 10:14 | w-a | 24.7 ± 0.35 | 78 ± 9.4 | 53 | 60 | 23.6 ± 1.67 | 21.1 ± 0.52 |
| 22 | 10:14 | w-b | 22.3 ± 0.24 | 88 ± 6.3 | 43 | 47 | 19.8 ± 0.53 | 21.9 ± 1.20 |
| 22 | 10:14 | w-c | 21.7 ± 0.80 | 93 ± 3.7 | 54 | 46 | 18.6 ± 0.49 | 19.5 ± 0.39 |
| 22 | 14:10 | lab | 17.0 ± 0.16 | 97 ± 1.9 | 87 | 51 | 14.6 ± 0.14 | 15.8 ± 0.13 |
| 22 | 14:10 | w-a | 21.8 ± 1.19 | 76 ± 5.3 | 66 | 64 | 16.8 ± 0.17 | 17.6 ± 0.13 |
| 22 | 14:10 | w-b | 20.4 ± 0.70 | 83 ± 3.4 | 74 | 38 | 16.5 ± 0.17 | 17.6 ± 0.12 |
| 22 | 14:10 | w-c | 18.9 ± 0.24 | 93 ± 3.3 | 83 | 47 | 15.5 ± 0.11 | 17.3 ± 0.12 |

* Avg ± SEM of three groups with 30 larvae per group.

** Avg ± SEM of total pupae per strain per rearing condition.

lie in the epidermis (Hughes 1975, Bratti et al. 1992). It remains in the first stadium until after pupation of its host. When its host molts, the maggot must exit the old exuviae and reenter the host after ecdysis. At 27°C, the maggots molt to the second instar 22 to 46 h after pupation of *Heliothis virescens* (F.) and to the third instar 2 to 4 d later (Hughes 1975). In *Galleria mellonella* L. the maggot of *A. marmoratus* is encapsulated in a "pouch" and avoids the immune system of its host (Bratti et al. 1993). In a host that diapauses, the maggot may also avoid the influence of hormonal changes associated with diapause induction. Then, after host pupation the rapid development of the maggot may break diapause in its host. In *H. virescens,* the signal to break diapause can come at pupation shortly after entrance into diapause (Loeb 1982). Therefore, *A. marmoratus* may not prevent diapause induction in its host but may terminate diapause by its rapid development shortly after host pupation. Regardless, *A. marmoratus* would be unable to overwinter in the cooler regions of its range as a larva or pupa. Thus, it is likely that this parasitoid overwinters only in the more moderate regions of its distribution and recolonizes the cooler regions annually.

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