

- Psyche 77: 237-42.
- . 1973. A review of the cavernicolous Catopinae (Coleoptera: Leiodidae) of Mexico, Belize, and Guatemala. Assn. Mexican Cave Studies Bull. 5: 97-106.
- . 1975. The invertebrate fauna of tropical American caves, Part III: Jamaica, an introduction. Int. J. Speleol. 7: 303-26.
- . 1977. New records and species of Leiodinae and Catopinae (Coleoptera: Leiodidae) from Jamaica and Puerto Rico with a discussion of wing dimorphism. Psyche 83: 243-54.
- . 1981. A new cave-inhabiting *Ptomaphagus* beetle from Sarawak (Leiodidae: Cholevinae). Syst. Ent. 6: 221-4.
- Rosen, D. E. 1975. A vicariance model of Caribbean biogeography. Syst. Zool. 24: 431-64.
- . 1978. Vicariant patterns and historical explanation in biogeography. Syst. Zool. 27: 159-88.
- SZYMCZAKOWSKI, W. 1969. Découverte d'un représentant des *Ptomaphagini* à Cuba (avec une esquisse de la systématique et la géonémie de cette tribu) (Coleoptera, Catopidae). Acta Zool. Cracoviensia 14: 87-97.

GROWTH PATTERN ALTERATIONS IN FALL
ARMYWORM, *SPODOPTERA FRUGIPERDA*¹, LARVAE
AFTER PARASITIZATION BY *APANTELES*
*MARGINIVENTRIS*², *CAMPOLETIS GRIOTTI*³, *CHELONUS*
*INSULARIS*², AND *EIPHOSOMA VITTICOLE*³

TOM R. ASHLEY

Insect Attractants, Behavior and Basic Biology Research Laboratory,
Agricultural Research Service, USDA, Gainesville, FL 32604 USA

ABSTRACT

Parasitization of fall armyworm, *Spodoptera frugiperda* (J. E. Smith), larvae by *Apanteles marginiventris* (Cresson), *Campoletis griotti* (Blanchard), *Chelonus insularis* Cresson, and *Eiphosoma vitticole* Cresson reduced maximum larval weights by 97, 96, 70, and 62%, respectively compared to 6th instar nonparasitized larvae. Parasitized larvae produced significantly less frass and had smaller head capsule widths. Parasitization increased the duration of the instar during which the parasite destroyed its host. *Apanteles marginiventris* and *C. griotti* destroyed host larvae in the 4th instar and larvae parasitized by *E. vitticole* died in the 5th instar. Eggs parasitized by *C. insularis* were destroyed as larvae in the 4th (41%) and 5th (59%) instars. Larvae parasitized by *A. marginiventris* gained the least amount of weight, produced the least amount of frass, had the shortest life expectancy, did not live past the 4th instar, and had the smallest head capsule widths.

RESUMEN

El parasitismo de las larvas de *Spodoptera frugiperda* (J. E. Smith) por

¹Lepidoptera: Noctuidae.

²Hymenoptera: Braconidae.

³Hymenoptera: Ichneumonidae.

Apanteles marginiventris (Cresson), *Campoletis grioti* (Blanchard), *Chelonus insularis* Cresson y *Eiphosoma vitticole* Cresson redujeron los pesos máximos de las larvas por 97, 96, 70 y 62%, respectivamente, en comparación con las larvas del sexto instar no infestadas por parásitos. Las larvas parasitadas produjeron menos materia fecal y tuvieron las cápsulas de las cabezas mas pequeños. El parasitismo aumentó la duración del instar durante lo cual el parásito destruyó su hospedera. *Apanteles marginiventris* y *C. grioti* destruyeron las larvas de las hospederas en el cuarto instar y las larvas parasitadas por *E. vitticole* se murieron en el quinto instar. Los individuos parasitados en el estadio del huevo por *C. insularis* fueron destruidos como larvas en el cuarto instar (41%) y en el quinto (59%) instar. Las larvas parasitadas por *A. marginiventris* ganaron el menos peso, produjeron menos cantidad de materia fecal, tuvieron el indice de longevidad más corto, no vivieron más que el cuarto instar, y tuvieron menos anchura de la cápsula de la cabeza.

Parasites of the fall armyworm (FAW), *Spodoptera frugiperda* (J. E. Smith), occur throughout North, Central, and South America (Ashley 1979). The significant reduction in FAW larval populations caused by some of these parasites (Ashley et al. 1982) establishes the importance of understanding any additional effects these natural enemies have on FAW larvae. If, for example, parasitization affects larval growth rates then the determination of the age distribution of FAW field populations either by larval size or head capsule widths must consider parasitization levels for correct development of demographic models. In addition, economic thresholds for FAW larval populations would have to include levels of parasitization provided parasitization significantly affects food consumption.

The physiological effects of parasitization and their influence on the host are reviewed by Vinson and Iwantsch (1980). Modifications of host growth and development such as reductions in size and weight, alterations in instar duration, and time of pupation as well as modifications in food consumption rates have been reported by Jones et al. (1981), Hegazi et al. (1978), Lewis (1970), Rahman (1970), Vinson (1972) and others. Although parasitization has been studied in many hosts no information is available for parasitization effects on FAW larvae.

The present research identifies some of the principal effects of parasitization by *Apanteles marginiventris* (Cresson), *Campoletis grioti* (Blanchard), *Chelonus insularis* (= *texanus*) Cresson (Marsh 1978), and *Eiphosoma vitticole* Cresson on FAW larvae. *Chelonus insularis* is a solitary egg-larval endoparasite and the remaining 3 species are solitary larval endoparasites. The larval parasites primarily attack first and second instars. Biological data for *A. marginiventris*, *C. grioti*, and *C. insularis* are found in Boling and Pitre (1970), Kunnalaca and Mueller (1979), Morey (1971), Pierce and Hollaway (1912), and Wilson (1933). Equivalent data for *E. vitticole* are not available; however, this parasite has been recovered from FAW larvae (Hynes 1941, Labrador 1967).

MATERIALS AND METHODS

Behavioral differences between parasite species necessitated the use of different methods and containers for mating and oviposition. Circular plastic containers (7 x 10 cm diam.) having 2 screened vents (1.5 x 3.0 cm) and

containing ca. 50 first instar larvae and 4 cubes (1.5 cm) of FAW diet (Leppla et al. 1978) were utilized as ovipositional units for *A. marginiventris* and *C. grioti*. Two pairs of adult parasites less than 4-h old were placed into each of 3 containers for both species. Adults of *C. insularis* were placed in a 24 cm³ plexiglass cage for 2 days prior to introducing FAW eggs, and after a 24-h-host-exposure period these eggs were transferred to containers identical to those used for *A. marginiventris*.

Three pairs of *E. vitticole* were held in a plexiglass cage (24 cm³) for 3 days prior to the introduction of hosts. A disk of diet (2 x 8 cm diam) was supported in the center of the cage by 2 pieces of hardware cloth (8 x 5 cm high) arranged in an "X" configuration. Depressions (0.5 cm deep) were made over the upper surface of the disk using 0.64 cm hardware cloth because the female parasites preferred to search for hosts by probing into these depressions with their ovipositors. Approximately 100 newly hatched larvae were placed on the disk and allowed to enter these depressions before the disk was placed in the ovipositional cage.

The host exposure period for the larval parasites lasted 48 h and all parasites were continuously supplied with undiluted honey. Larvae emerging from eggs parasitized by *C. insularis* remained together for 48 h in containers like those used for oviposition by *A. marginiventris*. When the FAW larvae were 48 h old (all were 2nd instars) they were individually placed into 30 ml plastic cups containing ca 15 ml of diet. These cups were sealed with paper lids and every 24 h each larva was transferred into a fresh diet cup. During transfer the larva's head capsule width, the presence or absence of an exuvium, and larval and frass weights were recorded. This procedure continued until a larva pupated or was destroyed by a parasite. Parasites and FAW larvae were kept at $28 \pm 1^\circ\text{C}$, $60 \pm 1.5\%$ RH, and under a photoperiod of 14:10 LD with a fluorescent light intensity of 800 ft-c. The analysis is based on 28, 25, 27, and 32 larvae parasitized by *A. marginiventris*, *C. grioti*, *C. insularis*, and *E. vitticole*, respectively and 40 non-parasitized larvae.

Adults of *A. marginiventris* came from a laboratory colony started in 1976 from FAW larval collections made at Hastings, Florida. *Campoletis grioti* was imported from Uruguay where it was found parasitizing FAW larvae in corn (Buckingham, per. comm.). *Chelonus insularis* was imported into the United States in 1978 from Bolivia where it was parasitizing FAW larvae in corn (Mitchell, per. comm.).

An attempt was made to estimate the amount of diet consumed during a 24 h interval by correcting for weight loss in the diet cups (30 ml) due to evaporation. The correction factor was derived from diet cups void of larvae but held for 24 h under the same experimental conditions. Regression analyses to predict the amount of diet consumed by larvae of a specific age indicated that a linear model provided optimum prediction and that additional precision was not achieved by quadratic or cubic equations. However, the location of larval feeding activity on the diet (top, side, or within) coupled with larval metabolism, size, and frass production introduced substantial error in determining the amount of diet eaten. Therefore, estimates of diet consumed are not presented.

RESULTS AND DISCUSSION

Parasitization significantly (1% level) reduced daily FAW larval

weights after the 6th day compared to nonparasitized larvae (Fig. 1A). No meaningful patterns of weight differences occurred between FAW larvae parasitized by *A. marginiventris* and *C. grioti*. Larvae parasitized by *C. insularis* and *E. vitticole* achieved significantly greater weights (1% level) compared to larvae parasitized by the other 2 parasites. However, significant weight differences were present between larvae parasitized by *C. insularis* and *E. vitticole* on days 10 and 11. Only 28% of the larvae parasitized by *C. insularis* lived past the 9th day and these larvae displayed an unusual increase in weight prior to destruction by the parasite. Parasitization by *A. marginiventris*, *C. grioti*, *C. insularis*, and *E. vitticole* reduced maximum larval weights by 97, 96, 70, and 62%, respectively compared to nonparasitized 6th instars. The maximum weights achieved for each larva during each instar were used to determine mean maximum weights (Table 1A). Parasitization by *A. marginiventris* and *C. grioti*, *C. insularis* and *E. vitticole* reduced mean maximum weights by 64, 51, 33, and 17%, respectively compared to nonparasitized 4th instar larvae. Nonparasitized larvae increased their average weight by ca. 265% between successive instars whereas

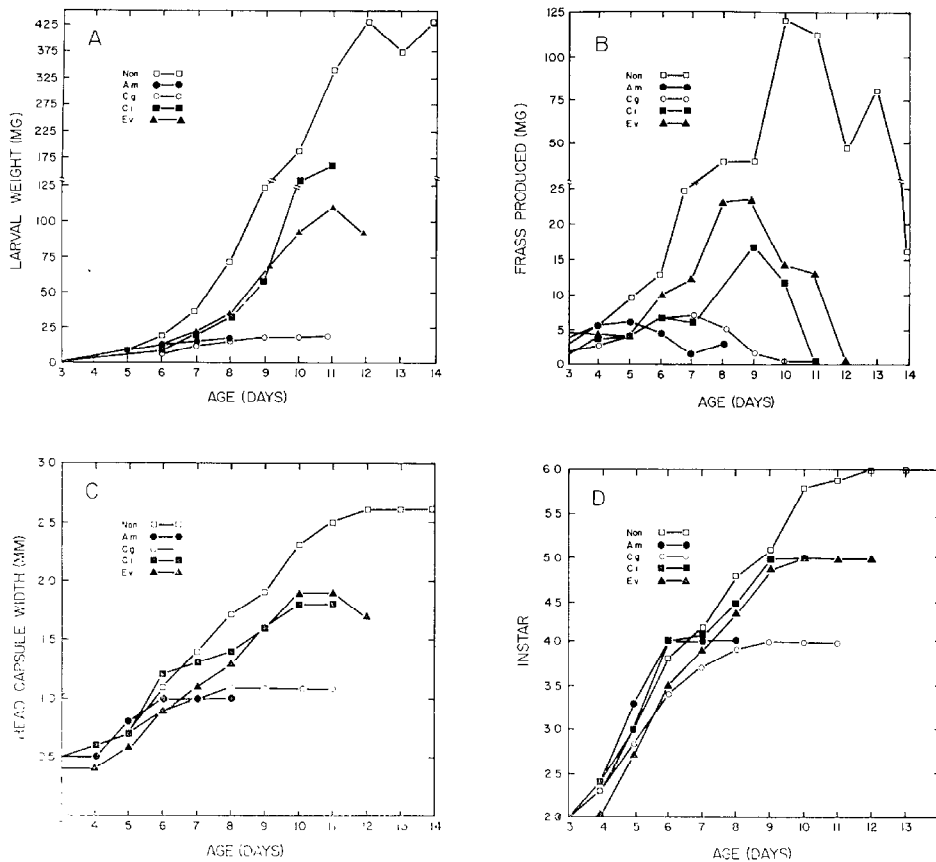


Fig. 1. Mean comparisons between nonparasitized fall armyworm (FAW) larvae to FAW larvae parasitized by *A. marginiventris* (A.m.), *C. grioti* (C.g.), *C. insularis* (C.i.) and *E. vitticole* (E.v.) for A) larval weights, B) frass produced, C) head capsule widths, and D) mean instar. Values represent larval status at the beginning of each day except for frass production which reflects the entire day.

TABLE 1. MEANS FOR MAXIMUM WEIGHTS (MG), MINIMUM AND MAXIMUM HEAD CAPSULE WIDTHS (MM), AND INSTAR DURATION (DAYS), FOR PARASITIZED AND NONPARASITIZED FALL ARMYWORM LARVAE.¹

Instar	Nonparasitized	Parasitized Larvae ²			<i>E.v.</i>
		<i>A.m.</i>	<i>C.g.</i>	<i>C.i.</i>	
		A—Maximum weights			
2	2.4 ± 0.2a	3.9 ± 0.6b	2.4 ± 0.5a	2.2 ± 0.3a	3.4 ± 0.3ab
3	9.6 ± 0.4a	8.2 ± 0.5ab	7.1 ± 0.5b	7.5 ± 0.3b	7.6 ± 0.6b
4	37.2 ± 2.5a	13.5 ± 0.7d	18.1 ± 0.8cd	25.8 ± 2.6bc	31.5 ± 2.0ab
5	130.2 ± 4.4a	—	—	87.9 ± 18.2b	115.2 ± 8.4ab
6	473.6 ± 12.0a	—	—	—	—
		B—Minimum-maximum head capsule widths			
2	0.46-0.48	0.49-0.51	0.47-0.51	0.41-0.45	0.40-0.46
3	0.69-0.72	0.68-0.69	0.70-0.71	0.70-0.71	0.62-0.66
4	1.20-1.25	0.91-0.97	1.05-1.06	1.26-1.28	1.10-1.23
5	1.76-1.83	—	—	1.58-1.65	1.63-1.87
6	2.41-2.58	—	—	—	—
		C—Instar duration ³			
2	1.7a	1.6a	1.9ab	1.6a	2.3b
3	1.5a	1.1a	1.9b	1.4a	1.3a
4	1.9a	2.2a	3.2b	2.2a	2.1a
5	2.1a	—	—	2.3a	2.5a
6	3.0a	—	—	—	—

¹Means in the same row followed by the same letter are not significantly different (1% level) as determined by Duncan's multiple range test.

²*A.m.*—*A. marginiventris*, *C.g.*—*C. grioti*, *C.i.*—*C. insularis*, *E.v.*—*E. vitticole*.

³Standard errors for all means ranged between 0.1 and 0.2.

larvae parasitized by *A. marginiventris* exhibited the smallest weight gain of ca. 88% between instars.

Frass production from parasitized and nonparasitized increased with age until 3 or 4 days prior to the end of the larval stage (Fig. 1b). The most pronounced decrease occurred in nonparasitized larvae where a reduction of 106 mg occurred between days 10 and 14. With the exception of hosts containing immature *A. marginiventris*, none of the parasitized larvae produced frass during the last 24 h of their lives. Frass production from all larvae substantially decreased during the transition period between instars. *Campoletis grioti* consumed the entire contents of the host during the last 24 h prior to eclosing from the FAW larva. After eclosion the parasite larva formed a cocoon to which the host's cuticle and head capsule were attached. A mature *A. marginiventris* larva bored through the side of the host larva and formed a cocoon on the substrate. The host larva then moved away from the site of cocoon formation and died within the next 12 to 24 h. *Eiphosoma vitticole* and *C. insularis* caused the host larva to bore into the diet to pupate early. Frass production in FAW larvae parasitized by these 2 parasites mimicked that of nonparasitized larvae which enter a gut cleaning stage prior to pupation.

Parasitization reduced the rate of head capsule growth (Fig. 1c). This reduction was most pronounced in FAW larvae parasitized by *A. marginiventris* and *C. grioti* and least pronounced in hosts parasitized by the other 2 parasite species. The apparent reduction in head capsule widths of larvae parasitized by *E. vitticole* on day 12 was the result of the FAW larvae with the larger head capsule widths being destroyed by the parasite on the preceding day and does not reflect an anatomical reduction in head capsule widths. Larvae parasitized by *C. grioti* exhibited the greatest reduction in the rate of head-capsule-width growth prior to the time of parasite emergence. A comparison of the mean minimum and mean maximum head capsule widths for each instar indicated that substantial differences were not present until the parasitized larva reached the instar during which it was destroyed by the parasite (Table 1B). This condition was most noticeable for 4th instar hosts parasitized by *A. marginiventris* and *C. grioti*. Although data on larval lengths were not gathered there was a definite reduction in the larval length of parasitized larvae.

The rate of advancement from one instar to the next was substantially reduced in parasitized hosts (Fig. 1d). This reduction was most evident in hosts parasitized by *C. grioti* and least evident in larvae parasitized by *C. insularis* and *E. vitticole*. Larvae parasitized by *A. marginiventris* and *C. grioti* died as 4th instars and larvae parasitized by *E. vitticole* died as 5th instars. Of those larvae parasitized by *C. insularis*, 41% died in the 4th instar and 59% died in the 5th instar. Parasitization tended to extend the duration of the instar during which the parasite destroyed its host rather than increasing the time spent in earlier instars (Table 1C). This trend was particularly pronounced in larvae parasitized by *C. grioti* where 4th instars were present over a 6-day period whereas 4th instars of nonparasitized larvae were present for 3 days. In addition, both *A. marginiventris* and *C. grioti* spent ca. 44% of their larval lives as 4th instars.

The quantitative differences in larval weights, frass produced, head capsule widths and mean instars plus noted differences in larval lengths between parasitized and nonparasitized larvae of the same age demonstrated

the significant effects of parasitization on FAW larvae. If parasitization produced similar effects in field populations of FAW larvae then it may be necessary to account for the level of parasitization as well as the parasite species present in establishing economic thresholds and in determining the correct age distribution of larval populations.

Mention of a commercial or proprietary product does not constitute an endorsement by USDA.

REFERENCES CITED

- ASHLEY, T. R. 1979. Classification and distribution of fall armyworm parasites. *Florida Ent.* 62: 144-53.
- , V. H. WADDILL, E. R. MITCHELL, AND J. RYE. 1982. Impact of native parasites on the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae), in South Florida and the release of the exotic parasite, *Eiphosoma vitticole* (Hymenoptera: Ichneumonidae). *Environ. Ent.* 11: 833-7.
- BOLING, J. C., AND H. N. PITRE. 1970. Life history of *Apanteles marginiventris* with descriptions of immature stages. *J. Kansas Ent. Soc.* 43: 465-70.
- HEGAZI, E. M., A. M. EL-MINSHAWY, AND S. M. HAMMAD. 1978. Effect parasitism on digestion and development of *Spodoptera littoralis* (Boisd.) larvae. *Z. Ang. Ent.* 86: 80-5.
- HYNES, H. B. N. 1941. Lepidopterous pests of maize in Trinidad. *Tropic. Agric.* 19: 194-202.
- JONES, D., G. JONES, AND B. D. HAMMOCK. 1981. Developmental and behavioural responses of larval *Trichoplusia ni* to parasitization by an imported braconid parasite *Chelonus* sp. *Physiol. Ent.* 6: 387-94.
- KUNNALACA, S., AND A. J. MUELLER. 1979. A laboratory study of *Apanteles marginiventris*, a parasite of green cloverworm. *Environ. Ent.* 8: 365-8.
- LABRADOR, J. R. 1967. Estudios de Biología y Combate del Gusano Cogollero del Maiz *Laphygma frugiperda* (S. & A.). Maracaibo, Universidad del Zulia, Facultad de Agronomía. 83 p.
- LEPPLA, N. C., P. V. VAIL, AND J. R. RYE. 1982. Mass rearing the cabbage looper. In: E. G. King and N. C. Leppla, [eds.], *Advances and Challenges in Insect Rearing*. USDA Tech. Bull. (In press).
- LEWIS, W. J. 1970. Study of species and instars of larval *Heliothis* parasitized by *Micropletis croceipes*. *J. Econ. Ent.* 63: 363-5.
- MARSH, P. M. 1978. The braconid parasites (Hymenoptera) of *Heliothis* species (Lepidoptera: Noctuidae). *Proc. Ent. Soc. Washington* 80: 15-36.
- MOREY, C. S. 1971. Biología de *Campoletis grioti* (Blanchard) (Hymen.: Ichneumonidae) Parasito de la "Lagaria Cogollera del Maiz" *Spodoptera frugiperda* (J. E. Smith). *Revista Peruana Ent.* 14: 263-71.
- PIERCE, W. D., AND T. E. HOLLOWAY. 1912. Notes on the biology of *Chelonus texanus*. *J. Econ. Ent.* 5: 425-8.
- RAHMAN, M. 1970. Effect of parasitization on food consumption of *Pieris rapae* larvae. *J. Econ. Ent.* 63: 820-1.
- VINSON, S. B. 1972. Effect of the parasitoid, *Campoletis sororensis* on the growth of its host, *Heliothis virescens*. *J. Insect Physiol.* 18: 1509-14.
- , AND G. F. IWANTSCH. 1980. Host regulation by insect parasitoids. *Quart. Rev. Biol.* 55: 143-65.
- WILSON, J. W. 1933. The biology of parasites and predators of *Laphygma exigua* Huebner reared during the season of 1932. *Florida Ent.* 17: 1-15.