Effect of the Parasite *Capidosoma truncatellum* on Development of Its Host *Trichoplusia ni*

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**ABSTRACT**

An Enzyme

Parasitism of larvae of *Trichoplusia ni* (Hübner) by *Capidosoma truncatellum* (Hübner) reduces a supersensory instar by one or two stages. The ability of the host was from a normal culture which pupated at the end of the 5th or 6th instar. Parasitized larvae which did not emerge as a supersensory instar gained weight significantly faster and had greater head capsule sizes than unparasitized larvae. Parasitized larvae which emerged as a supersensory instar gained weight more slowly and possessed smaller head capsules than unparasitized larvae, except for the supersensory instar, which had a significantly greater final weight and head capsule size than achieved by unparasitized larvae.

*Capidosoma truncatellum* (Dulman) is a polymorphic egg larval parasite of *Trichoplusia ni* (Hübner). Recent research addresses the potential of *C. truncatellum* as a mass-released agent for *T. ni* control (Stoner and Weeks 1974, 1976, Hunter and Stoner 1975). These studies indicate that several physiological characteristics may prevent *C. truncatellum* from being a good mass-release agent. One limiting characteristic was the reported induction of 2 additional days host feeding during the last instar (Hunter and Stoner 1975). Neither this nor other limiting characteristics, however, prevent natural populations of *C. truncatellum* from being, on occasion, an effective mortality factor (Stoner and Weeks 1976).

When using life table analysis to evaluate the impact of natural enemies, the developmental times of *T. ni* stages are needed for computation of net population density. The extended larval stage of *T. ni* as a result of parasitization by *C. truncatellum*, makes such computations more complex. Though Hunter and Stoner (1975) implied that the duration of the last instar in parasitized *T. ni* was affected, J. Jones and Van Strenwwyk (unpublished data) had difficulty in classifying the larval stages of *T. ni* to the proper instar because of abnormal head capsule sizes. The *T. ni* field population which the latter studied was heavily parasitized (90%) by *C. truncatellum*. The present work was conducted to quantify the effect of *C. truncatellum* on the duration and growth of *T. ni* larvae.

**Materials and Methods**

Two separate cultures of *T. ni* in which larvae were almost uniformly were a constant number of instars (for each population) under standardized conditions, of *T. ni*. These cultures were reared on a bean diet grown and reared by Sparks (1979). The *T. ni* culture was obtained by rearing adults from parasitized *T. ni* collected from beans in Irvine, Calif., and was maintained under conditions similar to the *T. ni* culture.

Sheets of paper on which *T. ni* eggs had been parasitized were exposed to *C. truncatellum*. The paper was removed, and sections were stapled under the lid of a 177-mL cup containing *T. ni* diet. On hatching, individual parasitized and unparasitized larvae were each placed into separate 300-mL cups containing a similar amount of diet. Individually reared larvae were observed daily throughout development.

Between 1980 and 1982, each day began as light-off, larvae were weighed to the nearest 0.01 mg. The stage of development (instar, occurrence of spinning, etc.) was recorded daily, and the weight of the head capsule was monitored at the widest point. Some head capsules could not be located in the fresh diet and diet, and, with a few larvae, it could not be determined during on which day a larval-larval molt had occurred, since a few larvae molted before about 14:00 h. For computations concerning instar duration, the average of the two possible durations was used (e.g., [14 days - 4 days] / 2 = 5.5 days for the larva). Measurements were terminated when larvae began spinning a cocoon for pupation. Only larvae surviving to cocoon spinning were used for analysis, since some larvae died before 216 h.

The efficiency of food conversion into biomass by parasitized and unparasitized larvae was compared by taking last (6th) instars from each group and weighing them on the day of the period of pupation and again on the day of evisceration of (day of spinning) as well. Diet cups were also weighed after the larvae had been removed. The control diet cups containing no larvae were also weighed at the same time to assess loss of diet weight due to evaporation.

The effect of nutrient deficiencies on normal metamorphosis of the last instar was tested by placing 40 (parasitized) instars during head capsule size in the 6th (last) instar and individual cups containing no diet. Larvae were starved for 1, 2, or 3 days, then placed in individual cups containing diet and their development observed. Twenty larvae

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were tested for each of the three starvation periods in another test. Six moths were selected during each "capillar" stage at the last instar and placed in a

Comparison of results involving only two groups was done with a twotailed t test. When multiple comparisons involving more than two groups was required, Duncan's new multiple range test, with Kramer's modification for unequal sample sizes (KDNMR) was used. For both tests, an a level of 0.05 was selected.

Results

Larvae Normally Undergoing 6th Larval Instar

The duration of each instar in both parasitized and unparasitized larvae is given in Table 1. Both groups required a similar amount of time from egg hatch until the molt to the 6th instar (15.5 to 15.6 days). Unparasitized larvae began oviposition spinning after 5.5 days into the 6th instar, and most underwent additional molts. However, only 64% of the parasitized larvae spun cocoons in the 6th instar, the remainder moulting to a superinfectious 7th instar. Parasitized larvae spinning cocoons either 6th or 7th instar spun cocoons after about 5.5 days into the last instar, the unparasitized larvae. The total time from egg hatch to cessation of feeding and initiation of spinning was about 21 days in both parasitized larvae spinning as 6th instars and unparasitized larvae. Parasitized larvae moulting to 7th instar took 21 days to reach oviposition, spinning because of 3.4 days spent feeding in the 6th instar before the superinfectious molt. After the superinfectious molt, the larvae fed for 3.2 days. Thus, the overall duration of feeding by parasitized larvae undergoing a superinfectious molt was shorter than that of unparasitized larvae, but this effect was not due to extended feeding during the last instar.

Hunt and Lister (1951) found that parasitized and unparasitized larvae are separable on the basis of differences in weight gain with parasitized larvae gaining weight more slowly. The data (Table 2) indicated a more complex situation. Parasitized 4th and 5th instars destined to spin with normal gained more weight than unparasitized larvae. The weight gain of those spinning in 6th instars was lower than normal. The total average maximum weight of the two parasitized groups was not significantly different (50 and 53 mg) and each was greater than that of unparasitized larvae by ca. 20 to 30%.

Head capsule widths of parasitized and unparasitized larvae were the same until the 5th instar (Table 3). Thus, as with trends in body weight, parasitized larvae spinning as 6th instars developed larger head capsule than unparasitized larvae, whereas larvae spinning as 7th instars had capsule widths significantly smaller than unparasitized larvae. The head capsule width of last instars of either group of par-
Table 2—Weight change of normal and C. transversalis-parasitised F. milharva undergoing head capsule diapause (HCD) during the month in the nest burrow.

<table>
<thead>
<tr>
<th>F. m.</th>
<th>2nd</th>
<th>3rd</th>
<th>4th</th>
<th>5th</th>
<th>6th</th>
<th>7th</th>
<th>Avg. we total gained</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>22.5 ± 0.6</td>
<td>24</td>
<td>32.3 ± 2.4</td>
<td>30</td>
<td>32.3 ± 2.4</td>
<td>28.5 ± 2.3</td>
<td>26.3 ± 1.8</td>
</tr>
<tr>
<td>Parasitised</td>
<td>open at 6th instar</td>
<td>22.0 ± 0.5</td>
<td>24</td>
<td>32.3 ± 2.4</td>
<td>29</td>
<td>32.3 ± 2.4</td>
<td>28.5 ± 2.3</td>
</tr>
<tr>
<td>Parasitised</td>
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<td>29</td>
<td>32.3 ± 2.4</td>
<td>28.5 ± 2.3</td>
</tr>
</tbody>
</table>

Table 3—Head capsule width of normal and C. transversalis-parasitised F. milharva.

<table>
<thead>
<tr>
<th>F. m.</th>
<th>1</th>
<th>2</th>
<th>3</th>
<th>4</th>
<th>5</th>
<th>6</th>
<th>7</th>
<th>Avg. head capsule width</th>
</tr>
</thead>
<tbody>
<tr>
<td>Normal</td>
<td>24</td>
<td>26</td>
<td>28</td>
<td>30</td>
<td>32</td>
<td>34</td>
<td>36</td>
<td>29.0 ± 1.8</td>
</tr>
<tr>
<td>Parasitised</td>
<td>open at 6th instar</td>
<td>24</td>
<td>26</td>
<td>28</td>
<td>30</td>
<td>32</td>
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</tr>
</tbody>
</table>
analysed larvae was larger than that of unparasitized larvae (9.96 mm). The final host capsule size for parasitized 7th instars (2.38 mm) was greater than parasitized 5th instars (2.04 mm).

The efficiency of conversion of food consumed to biomass (change in weight per host consumed since 106) Wallbank (1969) was 1.71 ± 0.16% and 10.9 ± 3.9% in parasitized and unparasitized larve, respectively, and was not significantly different (P > 0.05) in the two groups. The parasitized larvae consumed significantly more diet [1.21 ± 0.21 (P < 0.05)] than the unparasitized larvae [1.01 ± 0.03] [P < 0.05].

Larvae Normally Undergoing Six Larval Instars

Since previous workers studying C. trisescens had used cultures of T. ni which normally underwent five larval instars, parasitized hosts from such a culture were observed for comparative purposes against the results obtained from the original culture. Of 23 parasitized larvae, 59.5% underwent a supernumerary molt to a 6th instar, whereas none of 100 controls did. Both parasitized and unparasitized larvae developed at similar rates, all larvae reaching the 5th instar by 11 days after hatching. However, by day 13 all parasitized larvae had spun, whereas only 42% of the parasitized larvae had spun. The comparative weight gain of unparasitized larvae, parasitized larvae spinning on the 5th instar, and parasitized larvae spinning as supernumerary 6th instars, followed the same trend as in Table 2, and the maximum weights were 335 ± 27.1, 403.4 ± 32.8, and 410 ± 29.5 mg, respectively. The parasitized larvae had significantly (KINER, 0.05) greater maximum weight (ca. 30%) than the parasitized larve.

Effect of Starvation on Metamorphosis

Whether larvae were reared normally, starved for the first 1, 2 or 3 days of the larval stage before feeding, or starved after feeding for the first 1, 2, or 3 days of the last instar, all insects either died or pupated. In no case was a supernumerary instar observed in either larvae which normally pupate in the 5th instar or the 6th instar.

Discussion

Since the parasitized and unparasitized larvae were reared under the same conditions of food, temperature, photoperiod, and size of water containing containers, and supernumerary molts were observed only in the parasitized larvae, it is concluded that the supernumerity molting was a consequence of parasitosis. The supernumerary molting was observed both by hosts that survived normally underlying five instars (58% supernumerary molts) and from a culture normally undergoing six instars (39% supernumerary molts). The induction of an extra instar in host T. ni by C. transescens was not reported by Hunter and Storer (1975). King and Atkinson (1928) reported, in passing, that some Euxoa aeruginea (Guenée) (Noctuidae) parasitized by Eupholus komo barker Howard underwent a supernumerary molt.

Hunters and Storer (1975) observed an additional 2 days of feeding in C. trisescens parasitized larvae and 88% of parasitized larvae had spun completely by the time 75% of unparasitized larvae had. They attributed this delay in spinning to an increased duration of the last instar of parasitized larvae. Our data indicate the 2 additional days of feeding were probably due to the interruption of a short, parasitoid instar before a supernumerary instar. Hunter and Storer (1975) used the method of Wallbank (1969) to estimate and compare the efficiency of food conversion of unparasitized and parasitized T. ni larvae. They stated that parasitized larvae were more efficient but did not provide values of efficiency of conversion or a statistical analysis. We found no significant difference between the conversion efficiencies of unparasitized and parasitized larvae during their 6th (last) instar. Though the data conform to Hunter and Storer (1975) they reduce complex analysis, division of the reported weight gained by the amount of food consumed from 7 days post- egg hatch to the final day as that larvae reared feeding for purchase of 1 day 13 ± 1 and unparasitized and parasitized larvae, respectively results in a apparently similar efficiencies.

Our data illustrate the complexities that C. transescens introduces into T. ni while table conversion. First, many parasitized larvae have above or below normal head capsule sizes and body weights. These data explain why Jones and Van Steenburg had difficulty in estimating the instar of entire field collected T. ni larvae. The second complexes, first observed by Howard (1968), concerns the possible overstatement of larval density and percent parasitism as a consequence of the extended duration of the last instar of many parasitized individuals. The parasitoid and last instars are often confused during field sampling (large larve). Parasitism by C. transescens would cause overestimation of the density of "large" larve. It would also cause an overestimation of the difference between the density of "medium" and "large" larve, that is, the number of "medium" larve which had disappeared due to predation.

The occurrence of a supernumerary instar in the host does not demonstrate active, deliberate host regulatons by the parasitoid to induce disarrangement of host physiology. However, several models for indirect induction of a supernumerary molt in parasitized T. ni may be rejected.

It was found by Decker and Madan (1971) in Sitotroga cerealella (Grote) and by Nishiyama (1971) in Manduca sexta (L.) that pupation will not occur in the instar which includes a cephalic head capsule width greater than 0.91 mm (Jones, Jones, and Hamnack, 1973). Physiological, in press). The average cephalic capsule width of parasitized 6th instars

The method used to 7th instars is 1.73 ± 0.06 mm, which is above the critical width. Therefore, many of the supernumerary molts cannot be explained on
the basis of a subthreshold head capsule width in stunted, parasitized larvae. In M. sexta, it has been shown that starvation of the last instar for several days, either after initial feeding or before feeding, will result in a supernumerary molt (Nijhout and Williams 1974, Nijhout 1975, Jones et al. 1981), and that this response is correlated with a starvation induced drastic decline in the trehalose titer (Jones et al., 1981). M. sexta parasitized by Aphanopteris congregata often molt to a supernumerary instar (Beckage and Baldwin 1978), and M. sexta parasitized by A. congregata also have below normal trehalose titer (Dahlin 1975). Such a situation generates the hypothesis that the supernumerary molts in parasitized T. ni were due to a drop in the hemolymph trehalose titer effect by parasitic-induced nutrient stress. Unlike M. sexta, last instar T. ni were found not to undergo a supernumerary molt when starved for several days either after initial feeding or before feeding, suggesting that even if the trehalose titer in parasite stressed T. ni drops below normal it will not cause a supernumerary molt in the host. Elimination of the head capsule width and trehalose titer for supernumerary molting strengthens the hypothesis that the parasites are directly interfering with host endocrinology. The mechanism by which parasitism by C. tran- cerfallum causes the extra larval molt in the host is unknown. However, the T. ni-C. tran- cerfallum in- teraction may provide a promising system for elucidating mechanisms of developmental regulation, specifically the intricacies of host-parasite interaction.

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