

OVIPOSITIONAL BEHAVIOR OF THE PARASITOID *PALEXORISTA LAXA* (DIPTERA: TACHINIDAE) ON *HELIOTHIS ZEA* (LEPIDOPTERA: NOCTUIDAE) LARVAE

W. R. Martin, Jr.<sup>1</sup>, Donald A. Nordlund<sup>2</sup>,  
and William C. Nettles, Jr.<sup>2</sup>  
USDA, ARS, Pest Management Research Unit  
P.O. Drawer DG, College Station, TX 77841  
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ABSTRACT

The distribution and number of eggs deposited by the tachinid parasitoid *Palexorista laxa* (Curran) on instars of *Heliothis zea* (Boddie) were studied. Significantly more eggs were deposited on the thoracic segments of instars 2-5 than on the head or abdominal segments. This may be an adaptation by the parasitoid to avoid removal of the eggs by the host's mandibles. This selectivity of egg placement was not observed on first instars or prepupae. Significantly more eggs were deposited on fourth instars than on any other host developmental stage, suggesting that this may be the preferred host stage for parasitization.

Key Words: ovipositional behavior, parasitoid, *Palexorista laxa*, *Heliothis zea*, egg distribution, Tachinidae, Noctuidae.

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INTRODUCTION

A variety of tactics have evolved which enable insects to defend themselves against attack by parasitoids. These tactics are generally classified as physical or hemocytic reactions (Doutt et al. 1976), and their study is important in understanding host-parasitoid relationships. A common physical reaction to parasitoid attack is the violent shaking or striking out with the head and mouthparts demonstrated by certain lepidopterous larvae. Even after the parasitoid successfully oviposits, many larvae will attempt to dislodge or destroy externally placed eggs by rubbing against a substrate or crushing them with their mandibles (Allen 1925, Herrebout 1969, Nesar 1973).

Not surprisingly, a number of tactics have evolved in parasitoids which allow them to avoid or overcome both physical and hemocytic defensive tactics of their hosts. Reports of adaptation to physical and hemocytic defensive tactics of their hosts. Reports of adaptation to physical defense mechanisms are relatively rare, while there is a great deal of information available on parasitoid resistance to hemocytic defense mechanisms (Salt 1963, 1968, 1970). One of the most commonly reported adaptations to physical defenses by certain Tachinidae is the selective placement of eggs on the host (Allen 1925, Herrebout 1969).

<sup>1</sup> Present address: USDA, ARS, Insect Biology and Population Management Research Laboratory, P.O. Box 748, Tifton, GA 31793

<sup>2</sup> Present address: USDA, ARS, Subtropical Agricultural Research Laboratory, Biological Control of Pests Research Unit, 2413 East Hwy. 83, Weslaco, TX 78596.

*Palexorista laxa* (Curran) is a tachinid parasitoid which attacks *Heliothis armigera* (Hübner) larvae in India and Africa (Jackson et al. 1976). This parasitoid has been imported into the United States as a possible biological control agent for *Heliothis* spp., especially the cotton bollworm, *Heliothis zea* (Boddie) (Jackson et al. 1976). The female parasitoid deposits her eggs on the cuticle of the host, and within ca. 15 seconds (Chauthani and Hamm 1967) the eggs hatch and the larvae burrow into the host where they develop. Chauthani and Hamm (1967) reported that the female parasitoid deposits most of her eggs near the head and thorax, although no data were presented. The objective of this study was to investigate egg placement by *P. laxa* on different larval instars plus prepupae of *H. zea*.

## MATERIALS AND METHODS

*Palexorista laxa* were reared on cotton bollworm larvae, using the same rearing procedure employed for another tachinid parasitoid, *Eucelatoria bryani* Sabrosky (Nettles 1980). Bollworm larvae were reared in large grids on a Nutrisoy diet (Shaver & Raulston, 1971) without corncob grits. The rearing room was maintained at ca. 27° C, ambient RH (25 - 40%), and a photoperiod of 14:10 (L:D).

For each experiment, 10 *H. zea* larvae of the same age and developmental stage (instars 1-5 plus prepupae) were exposed to 20 female flies, age 7-9 days, in a Plexiglas® cage (25 × 25 × 25 cm). Flies were nitrogen-anesthetized, sexed, and placed into the cage at least 2 h prior to the beginning of each experiment to allow recovery from anesthetization. *Heliothis zea* larvae were placed into the cage after this recovery period. A section (ca. 23 × 13 cm) of galvanized steel hardware cloth (12.5-mm square openings) was placed at the bottom of the cage to provide the larvae with a substrate and to reduce cannibalism. Determination of *Heliothis* larval instar was based on age, weight, and larval length (Neunzig 1969). Because the flies are positively phototactic, the cage was rotated on a turntable operating at 1 rpm to ensure an even distribution of flies within the cage. After a 2-h exposure period, the larvae were removed, nitrogen-anesthetized, and placed on a cold plate where they were examined under magnification for the presence of *P. laxa* eggs. The number of eggs on each larval segment plus the head was recorded. This experiment was replicated four times for each of the instars 1-5 and prepupae of *H. zea*.

Data were analyzed using the ANOVA procedure (SAS Institute 1985), and significant differences among the means were determined by Duncan's multiple range test at the 0.05 level of significance (Duncan 1955).

## RESULTS AND DISCUSSION

Larvae attacked by *P. laxa* frequently responded by shaking and striking at the adult parasitoid with their heads, although this response was much more common and more violent in the larger larvae (instars 3-5). After oviposition, many larvae attempted to bite the eggs, presumably in an effort to remove or destroy them. This effort was generally unsuccessful, and ended after about 1 to 2 minutes. Similar defensive behaviors have been observed in larvae of the noctuid *Plusia acuta* (Walker) (Neser 1973), and saturniid *Hemileuca oliviae* Cockerell (Ainslie 1910), and the geometrid *Bupalus piniarius* L. (Herrebout 1969).

*Palexorista laxa* showed a significant preference for placing eggs on one of the thoracic segments of instars 2-5 than on any other segment of the host's body (Table 1). These data support the observation by Chauthani and Hamm (1967), and suggest that egg placement by this parasitoid may be an adaptive behavior by the parasitoid to avoid removal of the eggs by the host's mandibles.

Egg placement on first instars did not follow this pattern. Significantly more eggs were placed on the second abdominal segment of first instars than on any other segment. However, it is difficult to interpret these data because previous studies have indicated that first instars are not normally parasitized by *P. laxa* (Chauthani and Hamm 1967; Jackson et al. 1976). In the present study, significantly fewer eggs were deposited on first instars than on other instars (see below). Further, in laboratory studies, first instars parasitized by *P. laxa* were always dead within 2 days of parasitization, indicating that first instars are not suitable hosts for this parasitoid (unpublished data).

The distribution of eggs on prepupae did not follow the pattern observed in instars 2-5 (Table 1). While the greatest mean number of eggs was placed on the second thoracic segment of prepupae, it was not statistically different from the mean number placed on abdominal segments 4 and 5. The deposition of eggs by the parasitoid may have been affected by the highly active prepupae, which were almost constantly in motion. In addition, prepupae were rarely observed defending themselves by striking out with the head.

Significantly more eggs were deposited by *P. laxa* on fourth instar hosts than on any other developmental stage. The mean number of eggs deposited per larva  $\pm$  SEM was: 1st instar,  $0.18 \pm 0.09$  c (n = 39); 2nd instar,  $4.25 \pm 0.74$  b (n = 40); 3rd instar,  $2.80 \pm 0.74$  bc (n = 40); 4th instar,  $11.55 \pm 1.84$  a (n = 40); 5th instar,  $5.18 \pm 0.82$  b (n = 39); prepupae,  $3.75 \pm 0.52$  b (n = 40). Means followed by the same letter are not significantly different ( $P = 0.05$ ; Duncan's multiple range test). Although this was a no-choice test, this suggests that fourth instars may be the favored host stage for this parasitoid. Other studies have suggested that other tachinids will selectively oviposit on a particular host instar. Allen (1925) reported that *Winthemia quadripustulata* (Fabricius) will normally deposit more eggs on larger host larvae than on smaller hosts. In addition, significantly more eggs were deposited on third instars of *B. piniarius* by the parasitoid *Eucarcelia rutilla* Villers than on any other host instar (Herrebut 1969).

Among the Tachinidae which deposit their eggs directly on the host, considerable variation exists in the distribution of these eggs on the host's body (see Clausen 1940; Herrebut 1969 for reviews). In some species, the location of eggs deposited on the host appears to be more or less random, while in others the parasitoid selects distinct sites for egg deposition. Our data indicate that *P. laxa* will selectively oviposit on the thoracic segments of all but first instars and prepupae of *H. zea*, a behavior which is likely an adaptation to the defensive tactics of its host, and one which may minimize egg loss.

Table 1. Mean number of eggs deposited on the head and larval segments ( $\pm$  SEM) of instars 1-5 and prepupae of *Heliothis zea* by the tachinid parasitoid *Palexorista laxa*. A, abdominal segment; T, thoracic segment.

BODY REGION/ SEGMENT	Host Developmental Stage*						
	1st Instar (N = 39)	2nd Instar (N = 40)	3rd Instar (N = 40)	4th Instar (N = 40)	5th Instar (N = 39)	Prepupae (N = 40)	
HEAD	0 b	0 d	0.03 $\pm$ 0.02c	0.07 $\pm$ 0.06g	0.08 $\pm$ 0.04cd	0.03 $\pm$ 0.02f	
T1	0 b	0.07 $\pm$ 0.06cd	0.17 $\pm$ 0.08bc	0.63 $\pm$ 0.16defg	0.23 $\pm$ 0.10bcd	0.20 $\pm$ 0.08cdef	
T2	0.03 $\pm$ 0.03b	0.53 $\pm$ 0.13b	0.70 $\pm$ 0.21a	1.77 $\pm$ 0.28b	0.87 $\pm$ 0.21a	0.65 $\pm$ 0.15a	
T3	0 b	1.05 $\pm$ 0.23a	0.47 $\pm$ 0.16ab	2.58 $\pm$ 0.31a	0.92 $\pm$ 0.17a	0.53 $\pm$ 0.13ab	
A1	0.03 $\pm$ 0.03b	0.40 $\pm$ 0.10bc	0.28 $\pm$ 0.18bc	1.40 $\pm$ 0.24bc	0.49 $\pm$ 0.11b	0.20 $\pm$ 0.07cdef	
A2	0.10 $\pm$ 0.05a	0.53 $\pm$ 0.17b	0.35 $\pm$ 0.10bc	1.05 $\pm$ 0.27cd	0.46 $\pm$ 0.12b	0.20 $\pm$ 0.07cdef	
A3	0.03 $\pm$ 0.03b	0.55 $\pm$ 0.15b	0.15 $\pm$ 0.09bc	1.00 $\pm$ 0.28cde	0.36 $\pm$ 0.10bcd	0.15 $\pm$ 0.07cdef	
A4	0 b	0.40 $\pm$ 0.16bc	0.25 $\pm$ 0.11bc	0.63 $\pm$ 0.17defg	0.15 $\pm$ 0.06bcd	0.45 $\pm$ 0.13abc	
A5	0 b	0.15 $\pm$ 0.07cd	0.07 $\pm$ 0.07c	0.42 $\pm$ 0.15defg	0.44 $\pm$ 0.13bc	0.38 $\pm$ 0.10abcd	
A6	0 b	0.28 $\pm$ 0.10bcd	0.13 $\pm$ 0.05c	0.78 $\pm$ 0.19def	0.13 $\pm$ 0.12bcd	0.35 $\pm$ 0.09bcde	
A7	0 b	0.23 $\pm$ 0.10bcd	0.10 $\pm$ 0.06c	0.63 $\pm$ 0.20defg	0.15 $\pm$ 0.07bcd	0.23 $\pm$ 0.09cdef	
A8	0 b	0.07 $\pm$ 0.04cd	0.07 $\pm$ 0.06c	0.38 $\pm$ 0.13efg	0.36 $\pm$ 0.09bcd	0.23 $\pm$ 0.08cdef	
A9	0 b	0 d	0.03 $\pm$ 0.02c	0.17 $\pm$ 0.06fg	0.31 $\pm$ 0.10bcd	0.13 $\pm$ 0.05def	
A10	0 b	0 d	0 c	0.05 $\pm$ 0.03g	0.05 $\pm$ 0.04d	0.05 $\pm$ 0.03ef	

\* Means followed by the same letter within a column are not significantly different ( $P = 0.05$ ; Duncan's multiple range test).

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