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Regulation of *Helicoverpa zea* larval behavior by the parasitoid *Eucelatoria bryani*

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Abstract

The parasitoid *Eucelatoria bryani* Sabrosky regulates the larval behavior of its host *Helicoverpa zea* (Boddie). Parasitized third, fourth and fifth instars burrow into the soil 0.7–3.4 days earlier than unparasitized larvae that normally enter the soil to pupate at the end of the fifth and final larval instar. Parasitized third instars molt once then burrow as fourth instars, one instar earlier than normal. When *E. bryani* pupariated on the soil surface in the field, none survived to the adult stage. However, *E. bryani* adults emerged from 49.2% of hosts that had burrowed into the soil. By accelerating the timing of *H. zea* burrowing behavior and causing host larvae to enter the soil before death, *E. bryani* ensures its pupariation in an environment with improved protection against natural enemies and lethal temperatures.

Introduction

Endoparasitic insects depend on their hosts for food and shelter during larval development. Consequently, survival of immature parasitoids is contingent upon host survival (Price, 1973, 1975; Vinson, 1985). Therefore, strong selection pressures likely exist for alteration of host characteristics to reduce host mortality during parasitoid larval development and increase parasitoid survival (Fritz, 1982). Because the site of host death affects the parasitoid's pupal survival, selective pressures undoubtedly cause parasitoids to alter their hosts in such a way that host death occurs in habitats favorable for the completion of parasitoid development. The nature of this host regulation (sensu Vinson, 1975) largely depends on the ecology of the host-parasitoid relationship (Fritz, 1982; Vinson, 1985) and may occur at either physiological (Beckage, 1985; Vinson, 1990) or behavioral levels in the host (Powell, 1980; Brodeur & McNeil, 1989).

Helicoverpa zea (Boddie) (Lepidoptera: Noctuidae) is a serious pest of field crops throughout much of the New World (Fitt, 1989). Larvae feed on leaves, flowers and fruits of host plants (Neunzig, 1969; Farrar & Bradley, 1985; Ellsbury *et al.*, 1989). Toward the end of the final larval stadium, *H. zea* ceases feeding and initiates a wandering phase during which larvae seek suitable sites to burrow into the soil, construct a pupal cell and pupate (Hardwick, 1965; Neunzig, 1969; Roach & Hopkins, 1979). Depth of these pupal cells ranges from 2.5 to 18 cm (Culin, 1992).

Eucelatoria bryani Sabrosky (Diptera: Tachinidae) is a common, gregarious parasitoid of *H. zea* in the southwestern United States (Jackson *et al.*, 1969), that is capable of parasitizing second through fifth instars of *H. zea*, with fifth and fourth instars being preferred (Martin *et al.*, 1989). Females inject a variable number of larvae directly into the host. *E. bryani* larvae develop in the host for approximately four days before host death occurs (Reitz, unpubl.). Parasitoid larvae complete their third and final instar after host death, then rasp a hole through the host integument, leave the host carcass and pupariate.

Because *H. zea* are more exposed to natural enemies and adverse environmental conditions at larval feeding sites than at pupation sites, selection pressures likely exist for *E. bryani* to cause its host to move to a sheltered location once the host has gained enough body mass for the parasitoid larvae to complete development. By so doing, *E. bryani* would reduce its exposure to predation, hyperparasitism or adverse environmental conditions. This two-part study examines if parasitism by *E. bryani* affects the burrowing behavior of third through fifth instars of *H. zea* and whether this parasitoid benefits by such modification of host behavior.

Materials and methods

Insect rearing. *H. zea* larvae were reared either on grids (Nettles, 1980) or in individual 31-ml diet cups (Adler & Adler, 1988) in an environmental chamber maintained at 27 ± 2 °C, L14:D10. *E. bryani* were reared under similar environmental conditions in cages containing 50–150 individuals. All female flies used in these tests were 10–15 days old. All *H. zea* larvae were in the middle intermolt phase of a particular instar and were of the same age and approximate size within each replicate.

Burrowing behavior. For each of the four replicates, twelve *H. zea* larvae of each of the third, fourth and fifth instars were used (n = 36 larvae per replicate). Six larvae of each instar were selected at random for parasitization. Larvae were parasitized by gripping them behind the head capsule with soft forceps and exposing them to individual female flies. A larva was considered parasitized when a drop of hemolymph appeared on the surface of its cuticle following an attack by a female parasitoid. After parasitization, each larva was placed on a block of artificial diet (Burton, 1969, as modified in Adler & Adler, 1988; Shaver & Raulston, 1971) in a paperboard cup (8.5 cm diam × 8.5 cm height or 9 cm diam × 5 cm height) containing a 2:1 mixture of potting soil and vermiculite. Unparasitized control larvae were handled similarly without exposure to parasitoid females. Larvae were held to complete development in an environmental chamber maintained at 27 ± 2 °C, L14:D10. All larvae were given a block of fresh diet daily.

Larvae were examined at 2–3 h intervals, and times at which larvae molted, burrowed into the substrate or died on the surface were recorded. Time until burrowing was defined as the elapsed time from when a larva was placed in an individual container until it burrowed into the soil and remained below the surface. Larvae were not disturbed until all parasitoids had an opportunity to emerge as adults. In a fifth replicate, each larva was retrieved as soon as it burrowed into the soil, so that its developmental state could be determined and body size measured.

Because the order that larvae burrowed into the soil was accurately determined compared to actual time, and to minimize the effect of several outliers in the control group, analyses of time until burrowing were based on rank transformed data. The four replicates of the experiment served as blocks in an analysis of variance (ANOVA) with parasitism treatment and *H. zea* instar serving as main effects and with interaction terms included. Pairwise comparisons were made using linear contrasts (Sokal & Rohlf, 1981). Contrasts in time until burrowing were made between parasitized and unparasitized larvae of each *H. zea* instar, as well as between parasitized third and fourth instars. Larvae in the parasitized cohort that did not produce parasitoids, or larvae that failed to burrow, were excluded from these analyses

(n = 15). Where appropriate, means and their associated standard errors are given based on untransformed data.

Field survival and emergence. This experiment was conducted to compare survival of *E. bryani* from burrowed hosts to that of *E. bryani* from hosts located on the soil surface of a maize (*Zea mays* L.) field. For each of three replicates, 48 mid-fifth stadium *H. zea* larvae were selected and parasitized in the same manner as described above, and then divided into two groups of 24 each. The first replicate was conducted during the 9–11 leaf stage of maize development. The second replicate was conducted during the 11–14 leaf stage, and the third replicate was conducted during the early tassel stage of maize development. Larvae in one group were placed in containers of potting soil and allowed to burrow into the soil. These containers had a removable bottom so they could be manually transplanted into the soil and removed without disturbing the larvae. Larvae in the second group were kept in individual diet containers until death.

Both groups of *H. zea* larvae were transported to the maize field following host death but before *E. bryani* larvae emerged from their hosts. Containers holding the first group of larvae were placed in the soil with tops flush with the soil surface. The containers were then removed without disturbing the larvae. The larvae in the second group were placed directly on the soil surface at the base of a maize plant and at least 4 m from the nearest experimental larva. A paperboard liner (9 cm diam × 1 cm height) was placed around each of these larvae to prevent wind or rain from removing them or their associated *E. bryani* puparia from the site.

H. zea larvae located on the soil surface, and their associated parasitoid puparia, were inspected four times daily and their status was recorded. Also at these times, temperatures at the depth of burrows (≈2.5 cm) were recorded. Twelve days after being transplanted into the soil, the buried *H. zea* larvae were removed and parasitoid emergence, based on the number of opened and unopened puparia, was recorded. Eleven of the original 72 burrowed host larvae were not parasitized and therefore excluded from analyses. Because individual parasitoids were not independent observations and because it was not possible to control for the number of parasitoids per host, comparisons of survival between *E. bryani* from surface and burrowed hosts are based on the number of hosts producing adult parasitoids [Cochran-Mantel-Haenszel test (Landis *et al.*, 1978)].

Results

Burrowing behavior. Parasitized *H. zea* larvae burrowed 16–81 h before controls for the three stadia examined (ANOVA for parasitism treatment, $F = 143.8$, df = 1, 3, $P < 0.001$, Table 1). The difference in the distribution of burrowing times between parasitized and unparasitized *H. zea* larvae was most pronounced for third instars where parasitized larvae burrowed 81 h before unparasitized ones (ANOVA for parasitism treatment × host instar interaction, $F = 5.2$, df = 2, 6, $P = 0.05$, Table 1). Among fourth instars, the difference was 31 h. The smallest difference was among fifth instars; parasitized larvae burrowed 16 h before unparasitized larvae. The time until burrowing for parasitized third and fourth instars did not differ (linear contrast, $F = 0.20$, df = 1, 6, $P > 0.65$) as third instars molted only once before burrowing as fourth instars whereas those larvae parasitized as fourth instars burrowed as fifth in-

Table 1. Times until burrowing for all combinations of host instars and parasitism treatments. Times are given as means ± s.e. and are based on untransformed data. Linear contrasts comparing the distribution of times until burrowing for parasitized and unparasitized larvae of each instar are based on rank transformed data

Host instar	Time until burrowing (h)		Linear contrast	
	Parasitized	Unparasitized	*F*	P
Third	80 ± 6.4	161 ± 5.3	70	< 0.0001
Fourth	77 ± 5.2	108 ± 5.1	41	< 0.0001
Fifth	54 ± 5.4	70 ± 5.1	25	< 0.0001

Table 2. Mean body length and head capsule width of parasitized and unparasitized *H. zea* larvae at the time when the larvae burrowed into the soil. Means and 95% confidence limits are given

Host instar	Parasitism treatment	Body length (mm)		Head capsule width (mm)		n
		Mean	95% CI	Mean	95% CI	
3rd	Parasitized	21.1	19.4–22.9	1.90	1.80–2.00	6
3rd	Unparasitized	33.3	31.0–35.7	2.91	2.78–3.03	6
4th	Parasitized	27.5	23.7–31.3	2.78	2.63–3.20	6
4th	Unparasitized	34.7	30.5–38.8	3.16	2.94–3.37	6
5th	Parasitized	31.5	27.3–35.7	3.02	2.86–3.18	4
5th	Unparasitized	37.4	35.8–39.0	3.09	3.04–3.14	6

stars. Parasitized larvae were consistently smaller than corresponding control larvae (Table 2).

Most of the parasitized and control *H. zea* larvae burrowed into the soil. Parasitized third instars had the greatest burrowing failure rate (29%) probably because of their small size and the loss of hemolymph following parasitization. Unparasitized third instars also suffered some pre-burrowing mortality (12.5%). The only other larvae that failed to burrow were three parasitized fifth instars and one fourth instar in replicate 4, that appeared to be diseased.

Although parasitized fifth instars burrowed significantly earlier than parasitized third and fourth instars (Table 1), host instar at the time of parasitization had no effect on the total development time for *E. bryani*. All flies in this study emerged within a two-day period, approximately 14 days after parasitism.

Field survival and emergence. *E. bryani* were not able to survive when their hosts were located on the soil surface. None of the *H. zea* hosts located on the soil surface (n = 72) or the *E. bryani* puparia emerging from them remained in the enclosures for more than 24 h. On several occasions, ants (Hymenoptera: Formicidae) were seen in enclosures, scavenging on *H. zea* carcasses or preying on *E. bryani* puparia. In contrast, *E. bryani* was much more successful in emerging from burrowed hosts (Cochran-Mantel-Haenszel statistic 53.58, df = 1, $P < 0.0001$). Adult parasitoids emerged from 30 of the 61 (49.2%) parasitized burrowed hosts, and 45% (n = 216) of the *E. bryani* puparia from burrowed hosts produced adult flies. The number of hosts producing *E. bryani* adults increased with each replicate during the growing season. In the first replicate, 14.2% of *H. zea* hosts (n = 21) produced *E. bryani* adults. In the second replicate, 31.6% of *H. zea* hosts (n = 19) produced *E. bryani* adults. Temperatures in the soil at the level of the burrowed hosts ($\approx$2.5 cm deep) exceeded 41 °C in the first two replicates when the vegetation canopy was not completely closed. When the canopy closed in the third replicate, subsurface temperatures were much lower with a maximum temperature of 38 °C. In this replicate, 100% of *H. zea* hosts (n = 21) produced *E. bryani* adults. There was no evidence of predation on the burrowed larvae in any replicate.

Discussion

E. bryani modifies the behavior and development of *H. zea* to its own advantage, constituting host regulation (Vinson, 1975). Parasitism by *E. bryani* accelerates the onset of burrowing behavior of *H. zea*, and the result is that the host enters the soil prematurely. By doing so, *E. bryani* greatly increases its probability of surviving to adulthood. Accelerated host development has been reported in the Tachinidae only once (Dindo, 1983) although precocious development of hosts parasitized by tachinids may occur frequently (Mellini, 1990).

Accelerating the time at which *H. zea* burrows has two benefits for *E. bryani*. The first benefit is

reduced exposure of the host and parasitoid to natural enemies. Mortality is greater among older instars of *Helicoverpa armigera* (Hübner) than among pupae (Nanthagopal & Uthamasamy, 1989). The same trend of greater mortality during the larval stage probably applies to *H. zea*. The second benefit is the increased probability that the host burrows before its death thereby allowing the parasitoid to complete its development in a relatively sheltered habitat. There is only a limited amount of time for *H. zea* to move from its host plant or the soil surface because host death occurs within four days of parasitism and is preceded by a period when the host is moribund and virtually immobile (Reitz, unpubl.). *H. zea* parasitized any earlier than the late final stadium would not be able to burrow into the soil before death unless that behavior was expressed precociously. Only hosts located below the soil surface produced adult *E. bryani*. Those hosts and associated *E. bryani* remaining on the surface were removed by predators or scavengers well before the parasitoids had an opportunity to complete development. While these individuals may have been more susceptible to predators and scavengers by being in enclosures, any *E. bryani* not removed by predation or scavenging would probably have fallen victim to the extreme temperatures on the soil surface before completing development (Jackson *et al.*, 1969). Our measurements of *E. bryani* survival from burrowed hosts are probably conservative, as the location and depth of burrows were constrained by the depth of the containers. Although the 2.5 cm depth at which we placed them is similar to the depth that parasitized *H. zea* larvae burrow under laboratory conditions (Culin, 1992), depths of *H. zea* burrows vary with soil conditions (Roach & Hopkins, 1979). If parasitized larvae burrow deeper in the ground, where temperatures are cooler, more *E. bryani* could emerge as adults (Jackson *et al.*, 1969).

The accelerated time of burrowing undoubtedly has an underlying physiological basis. Not only do parasitized fourth and fifth instars of *H. zea* burrow sooner in the ultimate larval stadium than unparasitized controls, but parasitized third instars express the behavior in the penultimate larval instar, one instar earlier than unparasitized larvae.

This alteration in *H. zea* behavior may be caused by parasitoid induced changes in host hormone levels, especially a premature reduction in juvenile hormone levels and subsequent rise in ecdysone levels that precede wandering and burrowing behavior (Bollenbacher, 1988; Jones *et al.*, 1986; Cymborowski, 1992). Tachinids affect host hormonal processes and are susceptible to hormonal changes of their hosts. Mellini & Coulibaly (1991) found that first instars of *Pseudogonia rufifrons* (Wied.) (Tachinidae) influence the hormonal processes in the host *G. mellonella*, retarding host molting. Another tachinid, *Pseudoperichaeta nigrolineata* Walker also reduces the growth rate of its host, *Ostrinia nubilalis* Hübner (Lepidoptera: Pyralidae) (Ramadhane *et al.*, 1987). Conversely, the development of *P. nigrolineata* can be arrested when a juvenile hormone mimic, fenoxycarb, is topically applied to *O. nubilalis* (Grenier & Plantevin, 1990). Development of *P. nigrolineata* is also dependent on ecdysteroid levels in the factitious host *G. mellonella* and may be arrested if ecdysteroid levels are low (Plantevin *et al.*, 1986). Likewise, the larval development of the tachinids *Eucarcelia rutilla* Vill. and *P. cinerascens* is dependent on changing levels of hormones in their hosts (Schoonhoven, 1962; Baronio & Sehnal, 1980; Fanti & Bratti, 1991).

Whether *E. bryani* is affected by its host is unknown. However, its development may not be directly tied to the host because the parasitoid's total development time was not affected by the host instar attacked. In those cases where host development is retarded by the parasitoid, the host is normally concealed when it is parasitized and remains concealed while the parasitoid is associated with it (e.g. Ramadhane *et al.*, 1987). These differences between *E. bryani* and *P. rufifrons* and *P. nigrolineata* show that more than one method of host regulation exist in the Tachinidae, as well as among other parasitoid taxa, and that the system of host regulation depends, in part, upon the nature of the host-parasitoid relationship.

Numerous parasitoids influence the physiology or behavior of their hosts. However, for a modification to be called host regulation (Vinson, 1975), the modification must be adaptive for the parasitoid and not merely an artifact of parasitism (Lawrence, 1988). Acceleration of development and time of burrowing of *H. zea* as a result of parasitism by *E. bryani* meets the criteria for host regulation because of the enhanced probability parasitoid progeny will emerge as adults. The results demonstrate that successful parasitism of *H. zea* by *E. bryani* depends on the ability of the parasitoid to modify the behavior of its host.

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