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Egg cannibalism in *Helicoverpa armigera* on sorghum and pigeonpea

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Abstract. Egg cannibalism by *Helicoverpa armigera* Hübner (Lepidoptera: Noctuidae) larvae was studied in the laboratory and in the field. In laboratory experiments, first instars were exposed to increasing densities of *H. armigera* eggs on sorghum, *Sorghum bicolor* (L.) Moench, and pigeonpea, *Cajanus cajan* (L.) Millsp. The number of eggs eaten per larva increased significantly as egg availability increased on both sorghum and pigeonpea. In small cages 21–37% of eggs were eaten on sorghum, 4–12% on pigeonpea. Plant feeding declined significantly on both sorghum and pigeonpea as egg density increased. Cannibalism was greater on sorghum than on pigeonpea while plant feeding was greater on pigeonpea than on sorghum. Only around 8% of eggs were eaten in larger cages with sorghum. The response to increasing egg availability in all experiments was linear. Immunoassay with an anti-vitellin monoclonal antibody showed that egg cannibalism occurs on pigeonpea under field conditions. Seven percent of all larvae had egg protein in their gut. Cannibalism may make a significant contribution to *H. armigera* population suppression.

Key words: egg cannibalism, ELISA, *Helicoverpa armigera*, immunoassay, India, monoclonal antibody

Introduction

Helicoverpa armigera Hübner (Lep.: Noctuidae) is a widespread, polyphagous pest, with high mobility and fecundity (Fitt, 1989). In India it is a serious pest in sorghum-pigeonpea intercropping, feeding on the reproductive parts of both crops. Though it oviposits freely on both, losses have historically been considered small to moderate in sorghum and high in pigeonpea (Bhatnagar et al., 1982). However, there is concern about an increasing impact of *H. armigera* on sorghum, and it is now considered a major pest in this crop (Sharma, 1985).

The effects of cannibalism on a population can be similar to those of interspecific predation (Hastings and Constantino, 1991), and it has the potential to be a density-dependent regulator of population size in many species, including several species of *Helicoverpa* (Polis, 1981; Joyner and Gould, 1985; Crowley and Hopper, 1994). Generally, cannibalism rates are highest for species without close competitors (Fox, 1975) such as *H. armigera*. Egg cannibalism is more important in lepidopterous species such as *H. armigera* that oviposit and feed on ephemeral plant parts (Courtney, 1986). Published references to *H. armigera* cannibalism have concerned inter-larval rather than egg cannibalism (Nyambo, 1990; Twine, 1971). Zalucki et al. (1986) mention it, but refer to unpublished work. Kyi et al. (1991) did not consider it very important in cotton. The paucity of information on egg cannibalism in *H. armigera* may be due to difficulties in detection (Fox, 1975).

We report the results of a study designed to evaluate the impact of egg cannibalism in populations of *H. armigera* at different egg densities both in the field and under controlled cage conditions. The investigation was part of a wider study aimed at identifying the important predators of *H. armigera* eggs in sorghum-pigeonpea intercropping systems (Sigsgaard, 1996; Sigsgaard and Esbjerg, 1997).

Materials and methods

Cage experiments

Insects and plants

Except for Experiment C (see below), for which larvae had to be reared from field-collected eggs, eggs and larvae of *H. armigera* were obtained from the third to fifth generation of a culture maintained at the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT), in Andhra Pradesh, India, following the procedures of A. R. McCaffrey (unpublished, detailed in Sigsgaard and Esbjerg, 1997). The eggs and larvae used in all experiments were $\leq$24 h old. The larvae were not fed before the experiment. Fresh flowering sorghum heads (with pollen) or flowering pigeonpea twigs were collected from ICRISAT experimental fields between 0800 and 0900 on the day of the experiment. The plant material was supplied with water and kept in shade until the onset of the experiment less than 2 h later. In all experiments there was excess plant material, ensuring no plant food shortage for the larvae.

Cages

Small (base diameter 2.5 cm, top diameter 3.5 cm, height 4 cm) and larger (diameter 7 cm, height 12 cm) transparent plastic jars were used as cages

for observation of *H. armigera* egg cannibalism. Due to their small size, young first instars were difficult to locate on plant material. Therefore, only a single sorghum spikelet or single pigeonpea raceme consisting of one flower and two buds was used in small cages; in larger cages sorghum heads were pruned to leave five spikelets (2–3 cm in length) with a 1.5–2 cm gap between the spikelets. The cages closed tightly, thus preserving plant quality for the duration of the experiment.

Spikelets or flowers were placed on the bottom of the small cages. Larger cages were used inverted; sorghum panicles and pigeonpea flowers were mounted in a hole in the centre of the lid with the stalk immersed in a beaker with water to preserve plant quality. The holes were sealed around the stem with Parafilm (Brandt GmbH, Germany) to prevent excessive moisture from entering the cages. A ventilation hole (2×2 cm) was cut in the top of each large cage (originally the bottom of the jar) and covered with filter paper.

Method

Eggs laid within 24 h were removed from the egg liner by soaking the paper in water for 10–15 min and then carefully detaching them with a fine paintbrush. They were transferred to sorghum spikelets or pigeonpea flowers with a fine paintbrush dipped in chicken egg albumin serving as a light glue. A series of different egg densities was used. The eggs were positioned in a symmetrical pattern, by placing them singly with the greatest possible inter-egg distances, and in similar positions on sorghum spikelets or on pigeonpea flowers or buds in all replications and experiments. To enable easy recovery of the eggs on sorghum, egg positions were first marked with a red waterproof pen, and marks were allowed to dry before egg application.

In the field, *H. armigera* eggs on sorghum are usually found singly in the space between the glumes; on pigeonpea, they are often laid between two buds or between flowers rather than in more exposed positions (Sigsgaard, unpublished observation). To simulate the situation in the field, eggs were placed in correspondingly protected positions in the cage experiments. Plants were left for about an hour to allow the egg albumin to dry before larvae were introduced onto the plants with a fine paintbrush. Before the introduction of larvae into the cages, the plant material was carefully examined to ensure that no eggs had become dislodged. Additional replicates produced in advance were used in the few cases of dislodging.

Three types of cage experiments were run:

A. *Small cage evaluation of the effect of egg density on egg cannibalism and herbivory.*

Experiments were carried out on both sorghum and pigeonpea in small cages. A single *H. armigera* first instar larva (≤ 24 h old) was introduced

Table 1. Cannibalism and herbivory in small cages by single larvae of *H. armigera* at varying egg densities on sorghum and pigeonpea (Experiment type A). Means followed by the same letter within plant (sorghum or pigeonpea) are not significantly different (pairs of means were compared with multiple Wilcoxon tests, $P < 0.05$). *P*-values in the table refer to Kruskal-Wallis tests

Plant	Exp	Eggs	Proportion of larvae that had eaten eggs (mean ± S.E.)	Proportion of larvae that had eaten plant material (mean ± S.E.)
Sorghum	A1	1	0.36a ± 0.07	0.58a ± 0.07
	A2	3	0.62b ± 0.07	0.58a ± 0.07
	A3	5	0.74b ± 0.06	0.16b ± 0.05
	A4	10	0.74b ± 0.06	0.38c ± 0.07
P-value			0.001	0.001
Pigeonpea	A5	1	0.06a ± 0.03	0.80ab ± 0.06
	A6	3	0.12a ± 0.05	0.88a ± 0.05
	A7	5	0.44b ± 0.07	0.62b ± 0.07
P-value			0.001	0.01

into each cage. Egg densities were one, three, five or (only on sorghum) 10 eggs per sorghum spikelet or pigeonpea raceme. The experiment was repeated 50 times at each density, with the replicates of each density performed sequentially (Table 1).

In a bioassay, with one larva and one egg on a sorghum spikelet, set up as experiment A1 (see above and Table 1), we checked the effect of egg albumin, red waterproof pen, and the two treatments combined, compared with naturally laid eggs on proportion of larvae that had eaten eggs.

B. *Large cage evaluation of the effect of egg density and dispersion on egg cannibalism.*

To gain more insight into the roles of egg dispersion and larval mobility, an experiment with sorghum using larger cages was performed. Single larvae were exposed to one, three, five or 20 eggs. Nine replications, run sequentially, were performed at each density. At the lowest egg density, the egg was placed on the middle spikelet. With three eggs, these were placed on the top, middle and lowest spikelet. With five eggs, one egg was placed on each spikelet, and with 20 eggs, four eggs were placed on each spikelet.

Because of a shortage of eggs and larvae, this experiment could not be repeated on pigeonpea.

C. *Evaluation of larval mobility*.

Newly hatched larvae (less than 30 min old) or larvae 3–4 h old on pruned sorghum heads were placed in large cages to evaluate larval mobility. The experiment comprised four cages (= replicates) for each age. Larvae were placed on the top spikelet. The experiment was repeated twice.

All experiments were run for 24 h after the larvae were added. Experiments were placed in a laboratory with netted windows affording temperatures approximating those outdoors (day 25–28 °C, night 10–15 °C) and natural light conditions (L:D approximately 11:13). The number of eggs and larvae remaining, and their state, were determined with a dissecting microscope. Each egg was recorded as round (viable), deflated (infertile), chewed (cannibalised) or missing (cannibalised). Deflated eggs were carefully examined to rule out chewing. Each larva was recorded as dead, alive or missing. In Experiment A, we recorded whether or not the larva had eaten plant material (including traces of frass). The positions of the larvae at the end of the experiment were recorded in Experiments B and C.

Each experiment was set up and later assessed using the same sequence of cages to assure the same duration of the experiment in all cages. The insides of cages were examined carefully to find any eggs that might have fallen off. Due to the size and type of cages, this could be done accurately. In a few cases, an egg had rolled off during the experiment. The condition of such eggs (round, deflated, or chewed) was recorded. The number of eggs eaten was calculated as the sum of eggs chewed and missing.

Field study

Sampling began when *H. armigera* eggs first appeared on pigeonpea, coinciding with the onset of budding and flowering on 4 November 1993, and continued until pods were fully mature on 9 December. Sampling took place once or twice weekly between 0830 and 1130, in a 0.72-ha experimental field of intercropped sorghum and pigeonpea at ICRISAT. Nine samples were taken in all. During this period there was no rain, and wind speeds were moderate with an average of 1.3 m/s. The highest wind speeds were 3.9 and 2.6 m/s on 10 and 11 November, respectively (as registered by ICRISAT Meteorological Observatory). Pigeonpea density was 4.5 pigeonpea plants per square metre. Plant size was recorded three times during the sampling period.

Eggs and larvae were sampled on 320 pigeonpea plants from 16 subplots. On each sample date, four locations were selected at random within each subplot and five plants sampled in each location. Sampling on large pigeonpea plants is difficult because they are 1–2 m tall and 40–150 cm in diameter, and have many main and side branches. Therefore, sampling was restricted to

the upper third of plants, where most oviposition occurs (Venugopal Rao et al., 1990). Eggs were counted on the terminal 10–15 cm of one upper shoot, where buds, flowers, shoots and eggs are concentrated. Larvae were collected by beating three upper shoots from each plant into a plastic bag. Larvae from one location were pooled, giving a total of 64 bags. They were transported from the field in iceboxes and stored at −80 °C to await immunoassay.

The immunoassay, using a monoclonal antibody to heliothine vitellin (Goodman et al., 1997), was an indirect enzyme-linked immunosorbent assay (ELISA), as described earlier (Sigsgaard, 1996). The maximum detectability interval found for *H. armigera* larvae in this assay was 24 h (Sigsgaard, 1996).

The number of eggs eaten was estimated using the Poisson model of predation (Nakamura and Nakamura, 1977; Greenstone, 1979; Lister et al., 1987):

$$\text{mean number of eggs killed per predator} = -\ln(1 - p)$$

where p is the proportion of positives in the ELISA. The detection period was nominally set at one. Plant growth data from 10 November, 30 November and 20 December 1993, of 100, 112 and 80 pigeonpea plants respectively, were used to convert the estimates to a per unit plant basis.

Data analysis

All statistical analyses were carried out in SAS/STAT ver. 6.12 (SAS Institute Inc., 1990). The Wilcoxon test was used to compare levels if there were two levels, and the Kruskal-Wallis test was used if there were more than two levels (SAS Institute, 1990). Linear regression (SAS Institute, 1990) was used to relate eggs eaten to eggs available. In experiment A, intercepts and slopes were compared by fitting a linear model to data for both crops (GLM-Procedure, SAS Institute, 1990).

Results

Cage experiments

Assessing the effect of using pen marks and egg albumin on the proportion of larvae that had eaten eggs, no significant differences were found, with a mean (±S.E.) for naturally laid eggs of 0.13 ± 0.09, for pen 0.13 ± 0.09, for egg albumin 0.19 ± 0.10 and for egg albumin and pen 0.25 ± 0.11 (n = 16, Kruskal-Wallis test, P = 0.76, df = 3).

In the small cage experiments, the proportion of larvae that had eaten eggs increased significantly with increasing egg density on both sorghum and pigeonpea ($P < 0.001$ in all cases) (Table 1). Plant feeding declined on both

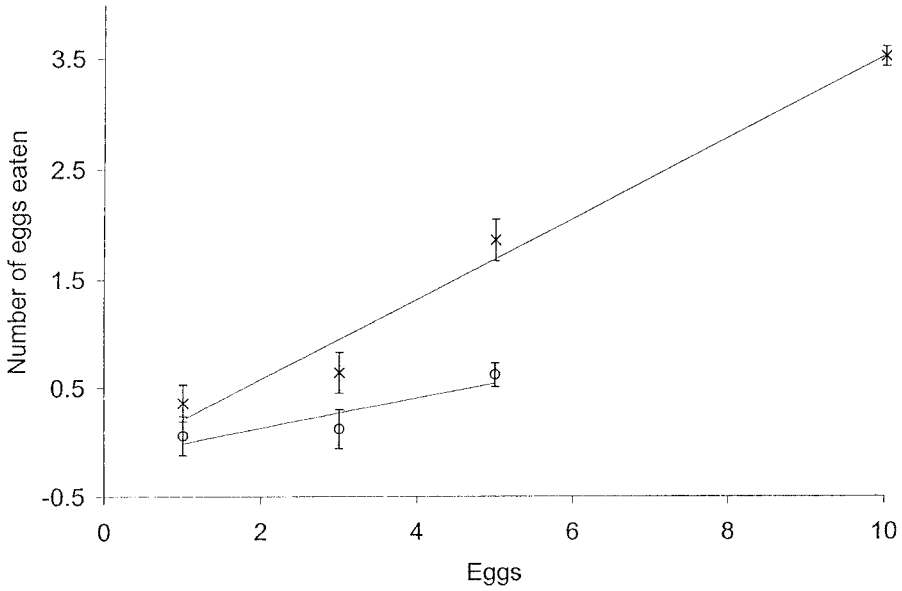

Figure 1. The response of *Helicoverpa armigera* first instar larvae to egg density on sorghum and pigeonpea in small cage experiments. Data are means ± SE. Legends: × = sorghum, ○ = pigeonpea.

sorghum ($P < 0.001$) and pigeonpea ($P < 0.01$) as egg density increased. The lowest proportions of larvae eating plant material were found in cages with five and 10 eggs per sorghum spikelet. The material from the five eggs per spikelet experiment was frozen and analysed one day later. This may have made feeding marks more difficult to see, and may explain the low proportion of plant feeding found in that treatment.

The proportion of larvae that cannibalised was higher in sorghum than in pigeonpea ($P < 0.001$), whereas plant feeding was more frequent on pigeonpea than on sorghum ($P < 0.001$). On both crops, the rate of egg cannibalism increased linearly with increasing egg availability. A linear regression of the rate of feeding (y) with increasing egg availability (x) was highly significant ($R^2 = 0.98$, $P < 0.0004$, df = 4). Slope depended significantly on crop, but no significant difference was found between the intercepts, resulting in the following model for sorghum: $y = -0.15 + 0.37x$; for pigeonpea: $y = -0.15 + 0.14x$ (intercept S.E. = 0.15; slope S.E., sorghum = 0.03, pigeonpea = 0.05) (Figure 1).

Increasing egg availability significantly increased the number of eggs eaten in the large cage experiments with pruned sorghum heads ($P < 0.01$). As in the small cage experiments, the rate of feeding increased linearly with

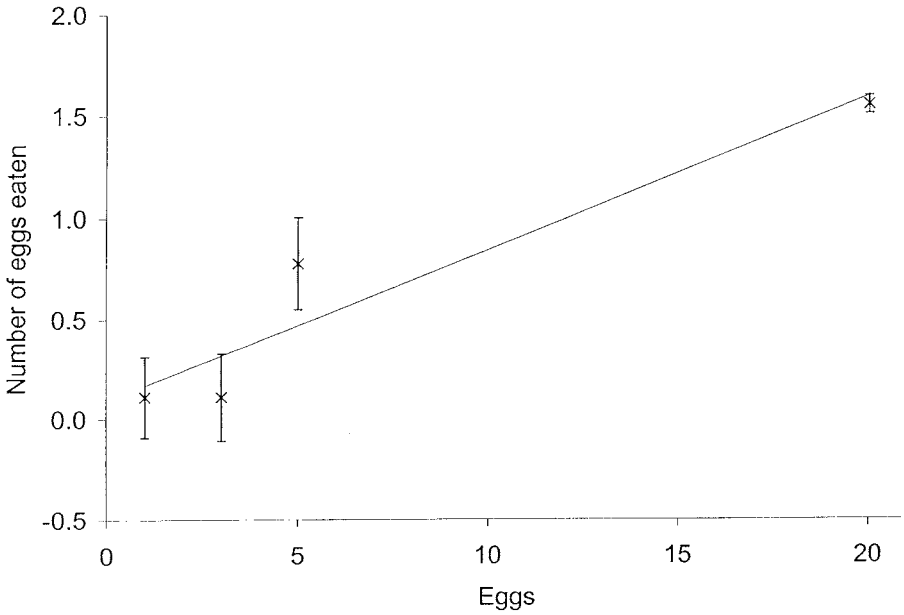

Figure 2. The response of *Helicoverpa armigera* first instar larvae to egg density on sorghum in large cage experiments. Data are means ± SE.

egg availability ($R^2 = 0.90$, $P < 0.05$, df = 2), yielding the following equation: y = 0.09 + 0.08x (intercept S.E. = 0.19, slope S.E. = 0.02) (Figure 2).

Mobility within 24 h of newly hatched larvae and 3–4-h-old larvae was low, with no significant difference between the age classes. In Experiment C, a larva moved on average only 0.91 spikelets away from the top spikelet, where it was initially placed (S.E. = 0.21, range 0–2). In the large cage experiments, 86% of all eggs were eaten on spikelets where larvae were initially placed and only 14% on those where larvae were not introduced ($P < 0.004$).

Field study

Numbers of *H. armigera* larvae were low at the beginning of the study, averaging 0.01 larvae per plant on 4 November. Larval density then rose steadily, to 0.32 per plant on 15 November and 0.97 per plant on 18 November, and thereafter did not fall below 2.23 per plant for the duration of the study. In ELISA, 5% of *H. armigera* instars 1–2, 7% of instars 3–4, and 5% of instars 5–6 were positive for heliothine vitellin. The proportion of larvae that tested positive generally rose as the number of eggs available per plant increased, but generally fell as the number of larvae per plant increased (Figure 3). However, these data could not be fitted to a model.

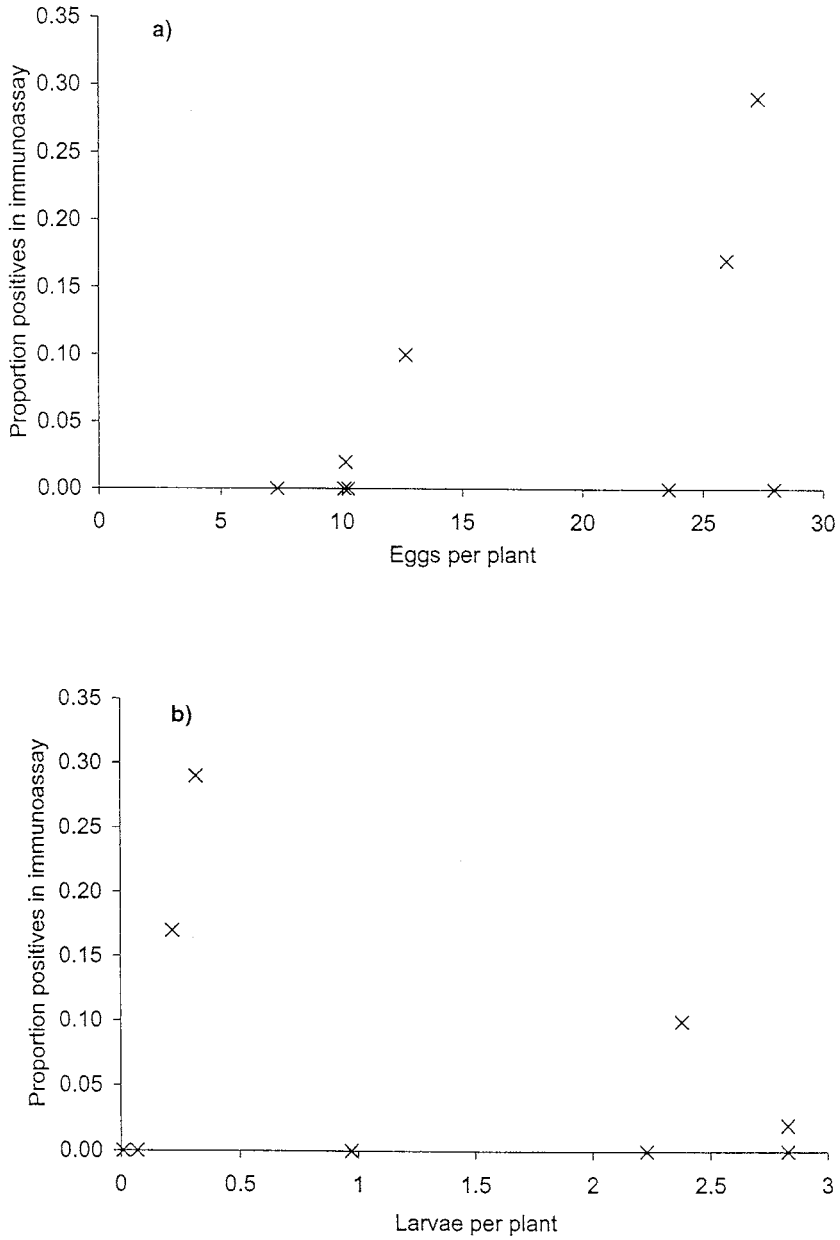

Figure 3. Proportion *Helicoverpa armigera* larvae (all instars pooled) tested positive for egg vitellin in their gut in immunoassay as a function of egg density (a) and larval density (b) on pigeonpea plants in field experiment.

The monoclonal antibody used in this research is egg- and subfamily-specific (Greenstone and Trowell, 1994). The only other eggs encountered in significant numbers in pigeonpea during the study were those of blue butterflies, comprising the species *Lampides boeticus* (L.) and *Catochrysops strabo* (Fabricius) (Lepidoptera: Lycaenidae). When tested by ELISA they were negative (Sigsgaard, 1996). In Andhra Pradesh, *H. armigera* is by far the dominant heliothine species in pigeonpea and sorghum. *Helicoverpa peltigera* Schiff is found at low densities in safflower and the weed *Acanthospermum hispidum*, and *H. assulta* Guenee is present at low numbers primarily on the weed *Datura metel* (Jadhav et al., 1985). The dominance of *H. armigera* in this system allows us to be confident that the ELISA-positives reported here were primarily due to this species.

The antibody was specifically tested to ensure that it does not recognise any larval antigens, including those of first instars (Goodman et al., 1997). We can therefore be confident that all positives are indicative of egg cannibalism.

Discussion

Intra-specific competition and cannibalism may significantly affect estimated crop losses from *H. armigera*. Whereas larval cannibalism in *H. armigera* is known (Twine, 1971; Dhandapani et al., 1993), egg cannibalism has not previously been studied.

Helicoverpa armigera is herbivorous. The occurrence of egg cannibalism in spite of the presence of sufficient and adequate host plant material has been demonstrated in other herbivorous insects, e.g., the ecologically analogous New World bollworm, *H. zea* Boddie (Noctuidae) (Barber, 1936; Joyner and Gould, 1985). Egg cannibalism may be advantageous for larval survival on limited resources and for intake of nutrients (Watanabe and Yamaguchi, 1993).

The average development time of first-second instar *H. armigera* larvae is 4–6 days (Singh and Rembold, 1992). Neonate *H. armigera* larvae normally eat their own egg shell (Jayaraj, 1982). However, the maximum detection period for egg protein in *H. armigera* larvae is 24 h (Sigsgaard, 1996). Accordingly, the finding that larvae more than 24 h old in our field study had egg protein in their gut cannot be attributed to consumption of their own eggs.

Differences in predation rates at the same absolute egg availabilities among the three experiments suggest that the amount and type of plant material and the dispersion of eggs can all affect egg cannibalism rates. Larval plant feeding decreased in both sorghum and pigeonpea with increasing egg

densities. Thus, less plant material was consumed when eggs were available (Table 1). A choice bioassay would be necessary to test whether eggs are preferred to plant material. *Helicoverpa armigera* larvae prefer pigeonpea to sorghum and the quality of pigeonpea as a food for *H. armigera* is higher than that of sorghum (Srinivas, 1988; Tripathi and Singh, 1989). These differences might explain the lower rate of egg cannibalism in cage experiments with pigeonpea. Moreover, eggs are physically more dispersed on pigeonpea because of the architecture of the plant. Plant species and plant architecture are known to affect predator search and efficiency (Kareiva, 1990). The difference between cannibalism on sorghum and pigeonpea may be greater under field conditions. Other studies have found that plant quality/food shortage (Fox, 1975; Polis, 1981) may affect cannibalism.

Results of the large cage experiments corroborate the small cage findings on plant food and egg dispersion. Fewer eggs were eaten with the same number of eggs and larvae in the larger cages (cf. Figs. 1 and 2), where eggs were more dispersed and more plant food was available. The observations on mobility suggest that egg dispersion can reduce cannibalism markedly because of very low larval mobility. Most egg predation in the large cages occurred on the spikelets where larvae were initially placed. Jayaramaiah and Jagadeesh Babu (1990) also observed low mobility of early instar larvae of *H. armigera*.

From the standpoint of pest management, it is important to determine whether cannibalism can make a significant contribution to *H. armigera* population suppression (Polis, 1981; Joyner and Gould, 1985; Crowley and Hopper, 1994). In all three cage experiments, the proportion of egg mortality caused by cannibalism did not change as egg numbers increased. Mortality of this form is by definition density-independent (Wilson and Bossert, 1971), and is therefore unlikely to provide population regulation under field conditions.

Fewer eggs were eaten per larva in the pigeonpea field experiment where eggs were more dispersed than in the cage experiments. In the field experiment, the proportion of positives found in the immunoassay generally increased with the number of eggs, but decreased with the number of larvae (Figure 3). Using the Poisson model of predation an estimated mean number of 0.07 egg was killed per larvae. With an average larval density of 1.3 larvae per plant (range 0.01–2.8), and an average egg density of 17.3 eggs per plant, an average of 0.5% of *H. armigera* eggs were consumed by larvae. The maximum estimated egg consumption was 0.34 egg per larva, at an egg density of 12.6 eggs and 2.4 larvae per plant, yielding an estimated 6.4% of the eggs eaten by larvae. Fewer young larvae were collected than anticipated.

This was probably due to difficulties in dislodging feeding larvae from within flowers and buds during sampling but may reflect to some extent the difficulty of recovering very small and semi-transparent larvae from the field collected samples that contained some plant material, in particular flowers. Therefore, these estimates are probably low. On the other hand, rates of cannibalism could be overestimated if many larvae fed on other larvae that had consumed eggs (Sunderland et al., 1987).

Cannibalism was sporadic, and even at the highest egg densities was not always observed (Figure 3). This indicates that various unmeasured factors, possibly including behavioural differences among larval instars, were operating. Laboratory and field experiments including observation of larval behaviour as affected by larval age, plant characteristics, and abiotic factors would be required to distinguish the influence of these factors.

In a life table study at ICRISAT, Duffield (unpublished) found that most mortality in both sorghum and pigeonpea occurred in the egg stage. The mortality in different pigeonpea cultivars was 84% to 94%, with disappearance accounting for 74% to 88%, respectively. Similar results were found in sorghum, maize and sunflower in a life table study in Kenya (van den Berg et al., 1993). The mechanical effects of wind, rain and "roll-off" of eggs due to desiccation can be substantial (Kyi et al., 1991).

Our results indicate that the number of *H. armigera* eggs cannibalised depends on egg density, larval density, egg dispersion and plant species. Cannibalism explained a relatively small proportion of egg disappearance in the pigeonpea field experiment. Nevertheless, depending on the age composition of the population, even a very low cannibalism rate can cause significant mortality (Fox, 1975). Furthermore, cannibalism is only one component of the total mortality induced by the natural enemy community (Sunderland et al., 1997) and, depending on timing and intensity, it could be important in regulating pest populations.

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