Behav Ecol Sociobiol (2000) 48:321–327

ORIGINAL ARTICLE

Jason W. Chapman · Trevor Williams
Ana M. Martínez · Juan Cisneros
Primitivo Caballero · Ronald D. Cave · Dave Goulson

Does cannibalism in *Spodoptera frugiperda* (Lepidoptera: Noctuidae) reduce the risk of predation?

Received: 23 March 2000 / Accepted: 24 June 2000

Abstract The incidence of cannibalism of larval *Spodoptera frugiperda* (Lepidoptera: Noctuidae) on maize under field conditions was investigated using field cages. Cannibalism was found to account for approximately 40% mortality when maize plants were infested with two or four fourth-instar larvae over a 3-day period. Field trials examined the effect of larval density on the prevalence of natural enemies of *S. frugiperda*. The abundance of predators (earwigs, staphylinids, other predatory beetles, and *Chrysoperla* spp.) was significantly greater on maize plants with higher levels of larval feeding damage, while the relationship between predator abundance and number of *S. frugiperda* larvae per plant was less clear. As larval damage is probably a more reliable indicator of previous larval density than numbers collected at an evaluation, this indicates that predation risk will be greater for larvae living in large groups. Parasitism accounted for 7.1% mortality of larvae in sorghum, and involved six species of Hymenoptera and Tachinidae. There was no effect of larval density or within-plant distribution on the probability of larval attack by parasitoids. The selective benefits of cannibalism, in relation to the risk of predation and parasitism, are discussed.

Key words *Spodoptera frugiperda* · Cannibalism · Predation · Parasitism

Introduction

Cannibalism is a taxonomically widespread behavior, often accounting for substantial mortality that may influence population dynamics and community structure (Fox 1975; Polis 1981; Dong and Polis 1992). Many species of larval Lepidoptera frequently engage in cannibalism (Schweitzer 1979; Joyner and Gould 1985; Dhandapani et al. 1993; Pierce 1995; Reed et al. 1996; Boots 1998; Chapman et al. 1999a).

Cannibalism may incur costs for three reasons. First, cannibals risk injury or death from the defensive responses of conspecifics (Dawkins 1976; Polis 1981). Second, cannibalism may be costly if pathogens or parasites can be acquired through the consumption of infected conspecifics (Dhandapani et al. 1993; Boots 1998; Pfennig et al. 1998; Chapman et al. 1999a). Third, cannibalism may reduce inclusive fitness through the consumption of kin (Polis 1981; Pfennig et al. 1993). These costs may be more than compensated for by the benefits that can accrue to cannibalistic individuals. Cannibalism may confer direct fitness benefits, in the form of increased survival, developmental rate, or fecundity (Duelli 1981; Joyner and Gould 1985; Meffe and Crump 1987; Church and Sherratt 1996). Cannibals may also benefit indirectly from the removal of potential competitors (Fox 1975; Polis 1981).

An alternative, but as yet untested, benefit of cannibalism may be a decrease in the risk of predation and/or parasitism. In species that inhabit discrete habitat patches, such as sedentary insect herbivores on individual plants, cannibalism may result in a substantial reduction in local population density. This may reduce predation and/or parasitism in one of two ways. First, predators and parasitoids that encounter patches with high prey density tend to

Communicated by M.A. Elgar

J.W. Chapman (✉) · D. Goulson
Biodiversity and Ecology Division,
School of Biological Sciences, University of Southampton,
Bassett Crescent East, Southampton, SO16 7PX, UK

T. Williams · A.M. Martínez · J. Cisneros
ECOSUR, Tapachula 30700, Chiapas, Mexico

P. Caballero
Departamento de Producción Agraria,
Universidad Pública de Navarra, 31006 Pamplona, Spain

R.D. Cave
Departamento de Protección Vegetal,
Escuela Agrícola Panamericana, Apartado Postal 93,
El Zamorano, Honduras

Present address:
J.W. Chapman, Entomology and Nematology Department,
IACR Rothamsted, Harpenden, Herts, AL5 2JQ, UK,
e-mail: jason.chapman@bbsrc.ac.uk,
Tel.: +44-1582-763138, Fax: +44-1582-760981

remain in them longer (Hassell 1971, 1982; Hassell and May 1974), thus increasing the probability that any particular individual in the patch will be attacked (Hassell 1982). Consequently, reduced density of the prey population within a patch may lower the probability that an individual is located by predators or parasitoids. Second, volatiles released from patches of high prey density may attract increased numbers of predators and parasitoids. Semiochemicals released from herbivore-damaged plants, or the insect herbivore per se, are known to elicit prey-locating behavior in predatory Hemiptera (Drukker et al. 1995; Yasuda and Wakamura 1996; Yasuda 1997), and host-seeking behavior in parasitic Hymenoptera and Tachinidae (Turlings et al. 1991; Blaakmeer et al. 1994; Coleman et al. 1997; Mondor and Roland 1997). If we assume that release of volatiles from the microhabitat of the herbivore is quantitatively diminished by a reduction in herbivore density, then the attraction of predators and/or parasitoids may accordingly be reduced. Third, single larvae are less likely to defoliate their host plant than large groups and hence are less likely to be exposed to predators and parasitoids (Dethier 1959).

Conversely, reduction of group size via cannibalism could be costly for individual insects if group size is negatively correlated with risk of predation or parasitism. Negative correlations between group size and predation of gregarious herbivorous insects have been demonstrated in larval Coleoptera (Breden and Wade 1987, 1989; McCauley 1994), perhaps due to predator satiation.

The fall armyworm, *Spodoptera frugiperda* (J.E. Smith) (Lepidoptera: Noctuidae), is an economically important pest of maize and other graminaceous crops throughout much of tropical and subtropical America (Sparks 1979; Andrews 1980). On maize, the favored host, the larvae feed almost exclusively within the wrapped leaves of the developing whorl (Morrill and Greene 1973; Labatte 1993), and are thus probably afforded some protection from predation and parasitism. High densities of larvae within the whorl are likely to be detrimental to individual *S. frugiperda*, not only through increased competition for food resources, but possibly also due to an increased risk of mortality by the action of natural enemies. Increased predation and/or parasitism may be mediated by one or more of the following: natural enemy attraction and aggregation due to high prey density, high levels of herbivore-induced semiochemicals, or a reduction in the effectiveness of the whorl as a refuge against natural enemy attacks due to high levels of feeding damage to the whorl. Individuals that reduce the local density of conspecifics via cannibalism may therefore benefit from increased survival. Cannibalism is a frequent behavior of *S. frugiperda* in laboratory culture, even when alternative food is not limiting, accounting for 40–60% mortality (Chapman et al. 1999a) but the prevalence of cannibalism in the field has not been quantified. Therefore, we determined the frequency of cannibalism in *S. frugiperda* in the field and investigated whether predators or parasitoids of *S. frugiperda* were attracted to maize plants with high larval density.

Methods

All experiments were carried out in July and August 1998, during the maize growing season (May to November), in the grounds of CIICA, Frontera Hildago, 18 km southeast of Tapachula, on the Pacific coastal plain of Chiapas in southern Mexico. Typical daily temperatures range from 23°C minimum to 35°C maximum during the growing season, with a mean monthly rainfall of 300 mm and relative humidity in excess of 85%. *S. frugiperda* larvae liberated in the field trials originated from a culture collected at Frontera Hildago, and maintained individually on semisynthetic diet at ECOSUR, Tapachula, for 12 generations. Two of the trials were performed in plots of a locally common variety of maize (Tasca-H101), planted at a density of 25 cm between plants and 70 cm between rows. One trial was carried out in a plot of sorghum (var. Topaz, Asgrow S.A. de C.V.) planted at 35 plants per meter with 90 cm between rows.

Experiment 1: cannibalism of *S. frugiperda* larvae in the field

This trial was carried out in a plot of maize at ~30 days post-planting to confirm the occurrence of cannibalism in *S. frugiperda* under natural conditions. Maize plants of equal size (~30 cm high) were randomly selected and examined for signs of feeding damage and the presence of arthropods. Damaged and arthropod-inhabited plants were rejected. Clean plants were infested with fourth-instar *S. frugiperda* larvae, at a density of 1, 2, or 4 per plant, by placing the larvae within the developing leaf whorl. Each plant was then individually enclosed in a muslin cage (45×35×35 cm) that was securely fastened to the ground by twine and stakes. To exclude predators and prevent escape of the larvae, a layer of earth was built up around the bottom of the cage. Surrounding vegetation was cleared around a 1-m radius so that no other plants were enclosed by or in contact with the cage. Three days later, the larvae were collected by careful examination of the plant and the caged area, and the numbers missing from the cage were recorded. *Spodoptera* larvae were easy to see on these small (30-cm-high) maize plants or on the bare earth within the exclusion cage. The number of larvae missing in each density treatment were analyzed using generalized linear interactive modeling (GLIM) (McCullagh and Nelder 1989) with binomial error structure. Larval density was used as the denominator for analysis of these binomial data. The proportion of larvae missing from density 1 was assumed to be the baseline level of mortality occurring in the experiment. Non-cannibalistic mortality was probably due to larvae being washed out of the whorl by heavy rain storms (T. Williams, personal observation). As the cages were shown to be effective exclusion barriers to the movement of predators of these large *S. frugiperda* larvae, any increase in the number of larvae missing from the other treatments was therefore interpreted as probable cannibalism.

Experiment 2: relationship between predator abundance, plant damage, and *S. frugiperda* density

This trial investigated the relationship between the abundance of predatory arthropods and the presence of *S. frugiperda* on individual maize plants. Maize was seeded in six replicate blocks of 8×8 m, with a gap of 8 m between plots planted with four rows of maize to help buffer plots against storm damage. At 33 days after sowing, 450 first-instar larvae were liberated in each block by scattering newly emerged larvae held in a paper bag over the surface of the plants. Arthropod density and herbivore damage were evaluated regularly by the dissection of 20 randomly selected plants from each replicate plot at 3, 5, 10, 19, 21, and 26 days following liberation of larvae. The level of damage produced by herbivory was rated on a scale of 0–4 (0=0-10%, 1=11–25%, 2=26–50%, 3=51–75%, 4=76–100% defoliation) (Kaya et al. 1995). Herbivore feeding damage was produced almost entirely by larval *S. frugiperda*; plants infested with higher densities of larvae have higher levels of defoliation (T. Williams, unpublished data). Lepidopteran larvae were identified to species, and all arthropods observed on the plant were recorded. Analysis was conducted on the most frequently recorded groups of predatory arthropods: earwigs, *Doru taeniatum* Dohrn (Dermaptera: Forficulidae), staphylinid beetles (Coleoptera: Staphylinidae), other predatory beetles (Carabidae and Coccinellidae), and larval lacewings, *Chrysoperla* spp. (Neuroptera: Chrysopidae). Predator numbers on individual plants was analyzed using GLIM with Poisson errors according to the following main effects: damage rating, number of larval *S. frugiperda* present, and number of aphid colonies present (to ensure that the presence of aphids was not solely responsible for any observed increased attraction of predators). An aphid colony was defined as containing 20 or more individuals. The error structure was substantiated during analysis and model validity was checked by examination of residuals (Crawley 1993).

Experiment 3: incidence of parasitism

A field trial was designed to investigate the incidence of larval parasitism in the field, and the effect of larval density and within-plant distribution on larval parasitism rates. This trial examined the incidence of larval parasitism in a natural infestation of *S. frugiperda* in a field of sorghum 25 days after planting. Larval *S. frugiperda* were present at unusually high abundance, many plants harboring four or more larvae. Late-instar larvae are generally found at a density of one per plant and rarely cohabit (Vickery 1929; Carvalho and Silveira 1971; J.W. Chapman, unpublished data). Typically, larvae feed primarily within the wrapped leaves of the whorl (Morrill and Greene 1973; Labatte 1993). In this study, however, many larvae were observed feeding on exposed leaves, presumably as a consequence of high larval density. Sorghum plants were randomly selected and carefully searched for caterpillars. The number of *S. frugiperda* per plant, their instar, and position on the plant (leaf whorl or exposed leaf) were recorded. All larval *S. frugiperda* found were collected, taken to the laboratory, transferred to semisynthetic diet and reared individually until adult eclosion. Mortality was recorded daily, and any emerging parasitoids were identified. The frequency of mortality and larval parasitism were analyzed using GLIM with Poisson errors according to the following main effects: number of larval *S. frugiperda* present, within-plant distribution of larvae, and larval instar. As this study was designed to investigate the effect of larval density on the prevalence of parasitism, larvae parasitized by *Chelonus insularis* (an egg-larval parasitoid) were omitted from the analyses.

Results

Experiment 1: cannibalism of *S. frugiperda* larvae in the field

Approximately three times as many larvae disappeared from plants infested with two or four larvae than from plants infested with one larva (Table 1), and this difference was significant (χ^2=13.41, *df*=2, $P<0.01$). There was clearly some mortality during the trial, as 17.9% of larvae from density one disappeared. However, almost 60% of the larvae were missing from densities two and four after 3 days, indicating that cannibalism probably accounted for approximately 40% mortality at both of these densities.

Table 1 Number of larvae missing after 3 days when fourth-instar larvae were placed within the leaf whorl of caged maize plants at densities of one, two, or four per plant

Density	Number of replicates	Number of larvae	Number missing	Percentage missing
1	28	28	5	17.9
2	11	22	13	59.1
4	11	44	25	56.8

Experiment 2: relationship between predator abundance, plant damage, and *S. frugiperda* density

The abundance of all four groups of predatory insects on maize plants was significantly correlated with the amount of larval feeding damage (earwigs: χ^2=11.8, *df*=4, $P<0.05$; predatory beetles: χ^2=11.6, *df*=4, $P<0.05$; staphylinids: χ^2=16.5, *df*=4, $P<0.01$; lacewings: χ^2=11.2, *df*=4, $P<0.05$). The abundance of predatory beetles (Carabidae and Coccinellidae) increased steadily with increasing levels of feeding damage, reaching maximum density on the most damaged plants (Fig. 1). Mean density of the three other predatory groups also increased with the amount of plant damage, but was highest on medium-damaged plants (damage scores of 1–3), and tended to decrease on the most damaged plants (Fig. 1).

The relationships between predator abundance and larval *S. frugiperda* density were not as clear. There was a significant increase in the numbers of earwigs (χ^2=44.9, *df*=1, $P<0.001$) and predatory beetles (χ^2=18.7, *df*=1, $P<0.001$) on plants with greater *S. frugiperda* density (Fig. 1). However, staphylinid numbers were not affected by larval density (χ^2=0.1, *df*=1, $P>0.05$), while lacewing larval abundance demonstrated a significant negative relationship with *S. frugiperda* density (χ^2=10.2, *df*=1, $P<0.01$) (Fig. 1).

There was also a positive relationship between the presence of aphid colonies and the abundance of earwigs (χ^2=12.2, *df*=1, $P<0.001$) and staphylinids (χ^2=4.4, *df*=1, $P<0.05$), but no relationship with predatory beetles (χ^2=0.4, *df*=1, $P>0.05$) or the abundance of lacewings (χ^2=1.2, *df*=1, $P>0.05$). Aphid infestation was positively correlated with the level of larval damage by *S. frugiperda* (χ^2=30.6, *df*=5, $P<0.001$).

Experiment 3: incidence of parasitism

In total, 505 *S. frugiperda* larvae were collected from sorghum and reared in the laboratory. Parasitoids emerged from 36 larvae (7.1%), 223 larvae died from other causes (pathogens and physical damage) (44.2%), and 246 survived to adult eclosion (48.7%). The species composition and percent parasitism are provided in Table 2. Egg-larval parasitoids (*C. insularis*) emerged from five larvae. Nearly all cases of larval parasitism were caused by tachinids; hymenopterans accounted for only two instances of larval parasitism.

The probability of larval parasitism was not influenced by the number of larvae per plant (χ^2=0.24, *df*=1, $P>0.05$), or the position of the larvae on the plant (χ^2=0.28, *df*=1, $P>0.05$). There was an effect of larval instar on the probability of parasitism (χ^2=11.1, *df*=2, $P<0.01$), the incidence of parasitism increasing with age. Instar was also the only factor that affected larval mortality (χ^2=36.6, *df*=2, $P<0.001$); mortality decreased with age.

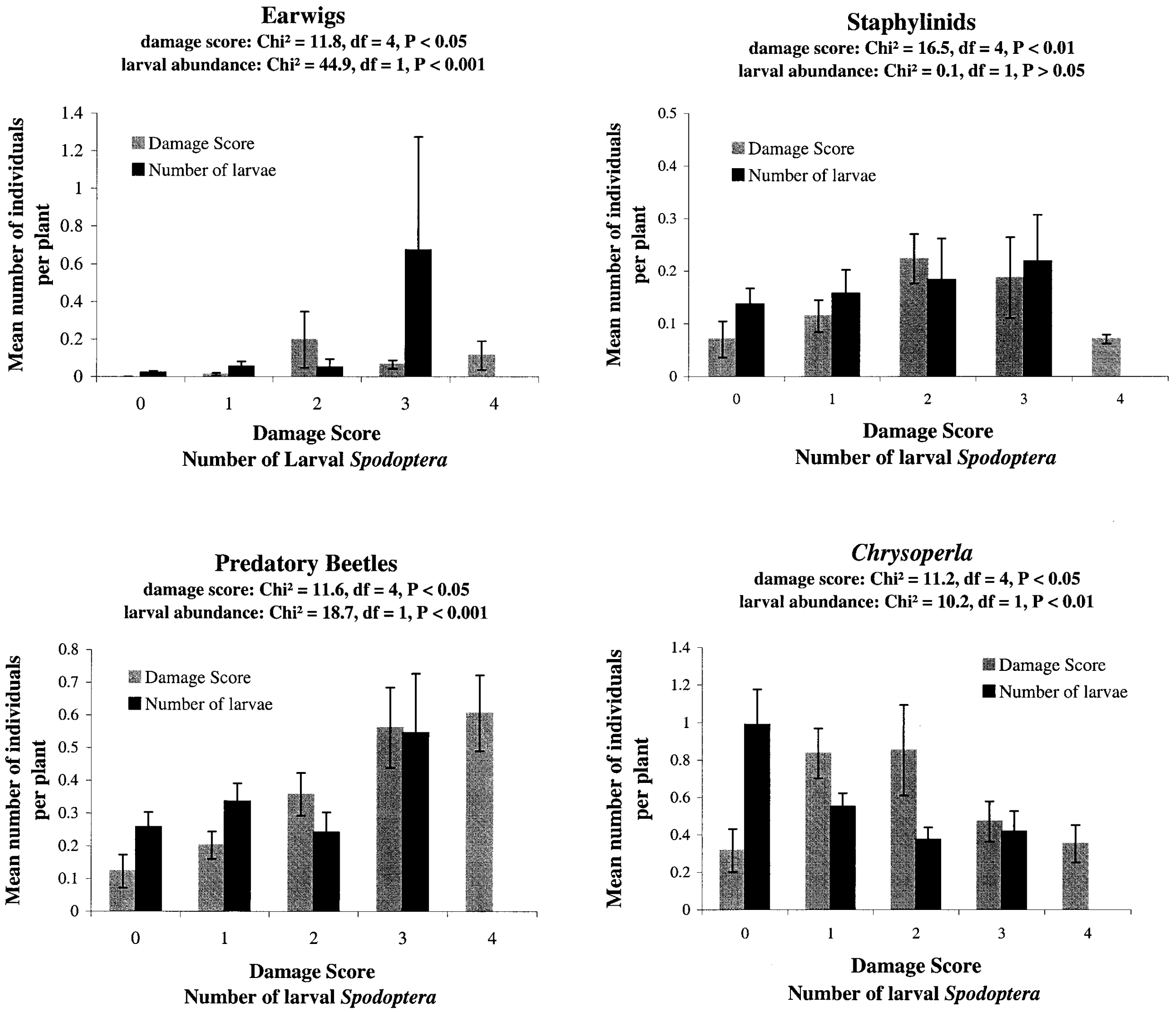

Fig. 1 Mean (±1 SE) predator abundance on maize plants with different levels of larval damage and different numbers of larval *Spodoptera frugiperda*. The *x*-axis labels refer to plants with damage scores of 0–4 or larval *S. frugiperda* abundance between 0 and 3

Table 2 Species composition and abundance of parasitoids that emerged from 505 field-collected *Spodoptera frugiperda* larvae from sorghum

		Number of parasitoids	Percent total parasitism
Diptera			
Tachinidae	*Archytas analis* (F.)	1	2.8
	Archytas marmoratus (Townsend)	17	47.2
	Lespesia archippivora (Riley)	11	30.6
Hymenoptera			
Ichneumonidae	*Eiphosoma vitticolle* (Cresson)	1	2.8
	Ophion flavidus Brullé	1	2.8
Braconidae (egg parasitoid)	*Chelonus insularis* Cresson	5	13.9
Total larval parasitism		31	86.1
Total parasitism		36	100

Discussion

The field cage experiment indicated that cannibalism was probably frequent when two or four larvae were placed within the leaf whorl of a maize plant. The field cages and maize plants were examined for the presence of predators after the 3-day period and were confirmed to be efficient exclusion devices. Larvae missing from plants infested with one caterpillar were probably washed out of the whorl and drowned by rainfall, a frequent cause of mortality in field populations of *S. frugiperda* (T. Williams, personal observation). Cannibalism in *S. frugiperda* is well known in the laboratory (Raffa 1987; Chapman et al. 1999a, 1999b) and it is assumed to be frequent in natural situations (Vickery 1929; Carvalho and Silveira 1971; Morrill and Greene 1973). The observations of the present study are, we believe, the most convincing evidence to date for this behavior in a population of *S. frugiperda* observed under natural conditions. The level of mortality attributed to cannibalism when two or four larvae were placed within the whorl (approximately 40%) is similar to that observed in laboratory culture (Chapman et al. 1999a).

Laboratory studies of the adaptive benefits of cannibalism in larval *S. frugiperda* indicated that cannibals suffer heavy costs. Cannibals have significantly lower survival, lower body weight (and hence reduced female fecundity; Lynch 1984), and slower development rate than non-cannibals (Chapman et al. 1999b). Furthermore, cannibals may obtain lethal infections of nuclear polyhedrosis virus following consumption of infected conspecifics (Chapman et al. 1999a). If cannibalism can confer such detrimental direct costs, then why are larval *S. frugiperda* such voracious cannibals?

One benefit that may accrue to cannibalistic individuals is a reduced risk of attack by predators or parasitoids, due to lower density within the leaf whorl. We attempted to test this hypothesis by investigating predation in the field, and relating it to the density of *S. frugiperda* larvae on individual plants (experiment 2). As predation rates are difficult to measure in the field, we recorded abundance of predators on maize plants and related it to larval density. Clearly, the number of larvae collected during an evaluation may not reflect larval density when predators arrived on the plant, so we used larval damage ratings as an indicator of previous prey density. The most abundant predatory groups collected on maize plants were earwigs (*D. taeniatum*), staphylinids, other predatory beetles (carabids and coccinellids), and *Chrysoperla* spp. All these predators consume eggs and larvae of *S. frugiperda* (Van Huis 1981; Jones et al. 1989; Cañas and O'Neil 1998). Our results demonstrated that predatory insects were more abundant on medium- or highly damaged plants than on plants with the lowest damage ratings (Fig. 1). From the data we cannot ascertain whether predators searched randomly and aggregated on plants with high larval density, or were attracted by the release of herbivore-induced semiochemicals from plants that had suffered high levels of damage. Further work is required to elucidate the factors that elicited aggregation of the predators. Whatever the mechanism for the increased abundance of predators, the data suggest that larvae inhabiting plants with substantial levels of damage, and hence greater larval density, are likely to have a greater risk of encountering predators. Reduction of group size via cannibalism may actually increase the predation risk of an individual in groups of *Leptinotarsa juncta* (Coleoptera: Chrysomelidae), perhaps due to predator satiation (McCauley 1994). However, predator satiation is unlikely to be very important in our system for several reasons. First, unlike *L. juncta*, generally only a very few *S. frugiperda* cohabit within the maize whorl (Vickery 1929; Carvalho and Silveira 1971; J.W. Chapman, unpublished data). Second, predators were often observed to have remained on maize plants that had once held *S. frugiperda* larvae but no longer did, indicating that they stay in a prey patch until it is exhausted. Third, laboratory observations demonstrate that at least one of the predators (earwigs) will consume several *S. frugiperda* larvae in 12 h (J.W. Chapman, unpublished data). Therefore, larvae living in a group are probably at greater risk of predation. Furthermore, highly damaged leaf whorls probably provide less protection from aerial predators such as wasps and insectivorous birds. Consequently, cannibalistic larvae may benefit from reduced aggregation of insect predators, and more effective physical refuge from these and other predators.

The relationship between predators and larval density was less clear. Predator abundance increased with larval density for earwigs and predatory beetles, decreased for *Chrysoperla*, and demonstrated no relationship for staphylinids (Fig. 1). However, these relationships are difficult to interpret: a negative relationship between larval density and predator abundance may indicate that larvae had previously been eaten by the predators, or conversely predators avoid plants with high larval density. Plant damage provides a more dependable indicator that larvae were present and, we argue, represents a more reliable factor for investigating the relationship between larval density and predation than larval density per se.

Parasitism accounted for 7.1% mortality of the larvae collected in sorghum, and involved six species of hymenopterans and tachinids. Considerable evidence demonstrates that hymenopteran and tachinid parasitoids of larval Lepidoptera use herbivore-induced plant volatiles to locate their hosts (Turlings et al. 1991; Blaakmeer et al. 1994; Coleman et al. 1997; Mondor and Roland 1997). If parasitoid searching behavior involves dose-dependent responses, then larvae living in large groups can be predicted to be at greater risk of parasitism than single larvae. However, the results of our trials indicated no effect of larval density on the prevalence of parasitism, suggesting that larval density did not influence parasitoid searching behavior. Thus, reduction of local population density through cannibalism may not alleviate the risk of parasitism in *S. frugiperda*. As tachinid flies were responsible for most parasitism (29 of 36 cases), this result may largely reflect the search strategies of parasitic Diptera. Clearly, further work is required to elucidate the responses of other important parasitoids (such as ichneunonids) that were rare in these trials, to evaluate the influence of host density on their search behavior.

The current study investigated the adaptive significance of cannibalism in a pest species on an agricultural crop, and it is interesting to speculate how the selective pressures on cannibalism in this situation may be related to those in the evolutionary past of *S. frugiperda*. The ancestor of maize would have had much smaller leaf whorls and corn ears, which would probably have been unsuitable for the development of more than one lepidopteran larva (Hamilton 1970). Caterpillar feeding damage would cause proportionally greater levels of defoliation than in modern maize. Coexisting larvae would therefore have been exposed to a greater risk of predation. If cannibalism in *S. frugiperda* has evolved to reduce predation, then presumably selection for cannibalism would have been greater before the domestication of maize. However, the fact that cannibalism is still prevalent among modern populations of *S. frugiperda* indicates that the reduction in predation compensates for the costs associated with cannibalism. This phenomenon may be expected to be widespread amongst sedentary species, such as herbivorous insects, that inhabit discrete habitat patches.

The responses of predators to plant damage may have implications for *S. frugiperda* management strategies in maize crops. If herbivore-induced volatiles are eliciting prey-locating behavior in the predatory insects monitored in this study, there may be potential to use natural or synthetic volatiles to increase predation in larval-infested crops. Further work is therefore needed to elucidate the mechanism of predator attraction to larval-damaged plants.

Acknowledgements This work was funded by the European Commission (contract number IC18-CT96-0097). J. Cisneros received additional support from SIBEJ 01-022-97. We thank Vasty Castillejos, Doris Penagos, Luis García, Roxbel Armenta, Olivia Hernández, and Sarah Carr for assistance in the field. We acknowledge with gratitude the help of Velitchka Nikolaeva and Nehemias Narvaez of CIICA, Frontera Hidalgo, Chiapas, for use of their land and for preparing and managing experimental plots.

References

Andrews KL (1980) The whorlworm, *Spodoptera frugiperda*, in Central America and neighboring areas. Fla Entomol 63:456–467

Blaakmeer A, Geervliet JBF, Loon JJA van, Posthumus MA, Beek TA van, Groot AE de (1994) Comparative headspace analysis of cabbage plants damaged by two species of *Pieris* caterpillars: consequences for in-flight host location by *Cotesia* parasitoids. Entomol Exp Appl 73:175–182

Boots M (1998) Cannibalism and the stage-dependent transmission of a viral pathogen of the Indian meal moth, *Plodia interpunctella*. Ecol Entomol 23:118–122

Breden F, Wade MJ (1987) An experimental study of the effect of group size on larval growth and survivorship in the imported willow leaf beetle, *Plagiodera versicolora* (Coleoptera: Chrysomelidae). Environ Entomol 16:1082–1086

Breden F, Wade MJ (1989) Selection within and between kin groups of the imported willow leaf beetle. Am Nat 134:35–50

Cañas LA, O'Neil RJ (1998) Applications of sugar solutions to maize, and the impact of natural enemies on fall armyworm. Int J Pest Manage 44:59–64

Carvalho RPL, Silveira NS (1971) Observacoes do comportamento de *Spodoptera frugiperda* (J.E. Smith, 1797) (Lepidoptera, Noctuidae) ao atacar milho em condicoes de campo. In: Resúmen de los trabajos presentados al Prima Congreso Latinoamericano de Entomología. Congreso Latinoamericano de Entomología, Cuzco, Peru, pp 92–93

Chapman JW, Williams T, Escribano A, Caballero P, Cave RD, Goulson D (1999a) Age-related cannibalism and horizontal transmission of a nuclear polyhedrosis virus in larval *Spodoptera frugiperda*. Ecol Entomol 24:268–275

Chapman JW, Williams T, Escribano A, Caballero P, Cave RD, Goulson D (1999b) Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. Behav Ecol 10: 298–303

Church SC, Sherratt TN (1996) The selective advantages of cannibalism in a Neotropical mosquito. Behav Ecol Sociobiol 39: 117–123

Coleman RA, Barker AM, Fenner M, King FC (1997) Relative effect of different host feeding site on long-range host location and electroantennogram response in the parasitoid *Cotesia glomerata* (Hym., Braconidae). J Appl Entomol 121:487–494

Crawley MJ (1993) GLIM for ecologists. Blackwell, Oxford

Dawkins R (1976) The selfish gene. Oxford University Press, Oxford

Dethier V (1959) Food-plant distribution and density and larval dispersal as factors affecting insect populations. Can Entomol 91:581–596

Dhandapani N, Jayaraj S, Rabindra RJ (1993) Cannibalism on nuclear polyhedrosis-virus infected larvae by *Heliothis armigera* (Hubn.) and its effect on viral-infection. Insect Sci Appl 14: 427–430

Dong Q, Polis GA (1992) The dynamics of cannibalistic populations: a foraging perspective. In: Elgar MA, Crespi BJ (eds) Cannibalism – ecology and evolution among diverse taxa. Oxford Science, Oxford, pp 13–37

Drukker B, Scutareanu P, Sabelis MW (1995) Do anthocorid predators respond to synomones from *Psylla*-infested pear trees under field conditions? Entomol Expt Appl 77:193–203

Duelli P (1981) Is larval cannibalism in lacewings adaptive? (Neuroptera: Chrysopidae). Res Popul Ecol 23:193–209

Fox LR (1975) Cannibalism in natural populations. Annu Rev Ecol Syst 6:87–106

Hamilton WD (1970) Selfish and spiteful behavior in an evolutionary model. Nature 228:1218–1220

Hassell MP (1971) Mutual interference between searching insect parasites. J Anim Ecol 40:472–486

Hassell MP (1982) Patterns of parasitism by insect parasitoids in patchy environments. Ecol Entomol 7:365–377

Hassell MP, May RM (1974) Aggregation of predators and insect parasites and its effect on stability. J Anim Ecol 43:567–594

Jones RW, Gilstrap FE, Andrews KL (1989) Dinámica poblacional de la tijereta, *Doru taeniatum* (Dohrn) (Dermaptera: Forficulidae) en maíz y sorgo en Honduras. Ceiba 30:67–80

Joyner K, Gould F (1985) Developmental consequences of cannibalism in *Heliothis zea* (Lepidoptera, Noctuidae). Ann Entomol Soc Am 78:24–28

Kaya HK, Burlando TM, Choo HY, Thurston GS (1995) Integration of entomopathogenic nematodes with *Bacillus thuringiensis* or pesticidal soap for control of insect pests. Biol Control 5:432–411

Labatte JM (1993) Within-plant distribution of fall armyworm (Lepidoptera: Noctuidae) larvae on corn during whorl-stage infestation. Fla Entomol 76:437–447

Lynch RE (1984) Effects of "coastal" bermudagrass fertilization levels and age of regrowth on fall armyworm (Lepidoptera: Noctuidae): larval biology and adult fecundity. J Econ Entomol 77:948–953

McCauley DE (1994) Intrademic group selection imposed by a parasitoid-host interaction. Am Nat 144:1–13

McCullagh P, Nelder JA (1989) Generalized linear models. Chapman & Hall, London

Meffe GK, Crump ML (1987) Possible growth and reproductive benefits of cannibalism in the mosquitofish. Am Nat 129:203–212

Mondor EB, Roland J (1997) Host locating behavior of *Leschenaultia exul* and *Patelloa pachypyga*: two tachinid parasitoids of the forest tent caterpillar, *Malacosoma disstria*. Entomol Exp Appl 85:161–168

Morrill WL, Greene GL (1973) Distribution of fall armyworm larvae. 1. Regions of field corn plants infested by larvae. Environ Entomol 2:195–198

Pfennig DW, Reeve HK, Sherman PW (1993) Kin recognition and cannibalism in spadefoot toad tadpoles. Anim Behav 46:87–94

Pfennig DW, Ho SG, Hoffman EA (1998) Pathogen transmission as a selective force against cannibalism. Anim Behav 55: 1255–1261

Pierce NE (1995) Predatory and parasitic Lepidoptera: carnivores living on plants. J Lepid Soc 49:412–453

Polis GA (1981) The evolution and dynamics of intraspecific predation. Annu Rev Ecol Syst 12:225–251

Raffa KF (1987) Effect of host plant on cannibalism rates by fall armyworm (Lepidoptera: Noctuidae) larvae. Environ Entomol 16:672–675

Reed DJ, Begon M, Thompson DJ (1996) Differential cannibalism and population-dynamics in a host-parasitoid system. Oecologia 105:189–193

Schweitzer DF (1979) Predatory behavior in *Lithophane querquera* and other spring caterpillars. J Lepid Soc 33:129–134

Sparks AN (1979) A review of the biology of the fall armyworm. Fla Entomol 62:82–87

Turlings TCJ, Tumlinson JH, Eller FJ, Lewis WJ (1991) Larval-damaged plants: source of volatile synomones that guide the parasitoid *Cotesia marginiventris* to the micro-habitat of its hosts. Entomol Exp Appl 58:75–82

Van Huis A (1981) Integrated pest management in the small farmer's maize crop in Nicaragua. Meded Landbouwhogels Wageningen 81–86

Vickery LA (1929) Studies on the fall armyworm in the Gulf Coast District of Texas. USDA Technical Bulletin 138, United States Government Printing Office, Washington, DC

Yasuda T (1997) Chemical cues from *Spodoptera litura* larvae elicit prey locating behavior by the predatory stink bug, *Eocanthecona furcellata*. Entomol Exp Appl 82:349–354

Yasuda T, Wakamura S (1996) Behavioral responses in prey location of the predatory stink bug, *Eocanthecona furcellata*, to chemical cues in the larvae of *Spodoptera litura*. Entomol Exp Appl 81:91–96