Ecological Entomology (1999) **24**, 268–275

Age-related cannibalism and horizontal transmission of a nuclear polyhedrosis virus in larval *Spodoptera frugiperda*

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Abstract. 1. Experiments were carried out to investigate the incidence of cannibalism throughout the larval development of the noctuid moth *Spodoptera frugiperda*, and to examine the risk of infection from consuming conspecifics infected with a nuclear polyhedrosis virus (SfNPV).

2. Cannibalism was observed commonly even when food was not limiting, but occurred more frequently at low food quantities and/or high rearing densities. The sex of the larvae had no effect on the incidence of cannibalistic behaviour, however the probability of cannibalism occurring was affected by larval stage. The frequency of cannibalism was significantly higher among fifth- and sixth-instar larvae than among earlier instars, and larvae were more likely to consume younger conspecifics than larvae of the same stage.

3. Fifth-instar larvae offered fourth-instar victims fed equally on healthy larvae, virus-infected larvae (2 days post-infection), uninfected corpses, and virus-killed corpses (6 days post-infection). Horizontal transmission of SfNPV was only recorded in larvae offered virus-killed corpses, however, and total mortality in this treatment was only 32%.

4. In a similar experiment, fourth-instar larvae avoided cannibalising virus-killed corpses. Horizontal transmission of SfNPV was recorded in fourth-instar larvae that consumed 2-day post-infected larvae. The low incidence of cannibalism observed in fourth-instar larvae, however, suggests that this is unlikely to provide an important route for the transmission of SfNPV.

Key words. Cannibalism, Lepidoptera, nuclear polyhedrosis virus, pathogen transmission, *Spodoptera frugiperda*.

Introduction

Cannibalism is a widespread and natural behaviour in many animal species, often producing profound effects on population dynamics (Fox, 1975; Polis, 1981; Elgar & Crespi, 1992). It is commonly observed amongst larvae of Lepidoptera, although there is considerable variation in the frequency of cannibalistic behaviour in related species (Gould *et al.*, 1980; Breden & Chippendale, 1989; Pierce, 1995). The motivation for cannibalism is often poorly understood. Individuals that adopt cannibalistic strategies may accrue fitness benefits in the form of increased survival, developmental rate, and fecundity (Duelli, 1981; Joyner & Gould, 1985; Church & Sherratt, 1996). Cannibals may also benefit from removing potential competitors.

Conversely, the costs associated with cannibalism may be great. First, cannibals risk injury or death from defensive responses of conspecifics (Dawkins, 1976; Polis, 1981).

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Second, intraspecific predation may cause a reduction in inclusive fitness through the cannibalism of kin (Polis, 1981; Pfennig *et al.*, 1993). Third, cannibalism may confer an extra cost if pathogens or parasites can be acquired by consuming infected conspecifics (Polis, 1981). Transmission of pathogens and parasites via cannibalism has been demonstrated in several species (Matuschka & Bannert, 1989; Schaub *et al.*, 1989; Dhandapani *et al.*, 1993; Boots, 1998). Thus, susceptibility to pathogens and parasites may constrain the evolution of cannibalistic behaviour (Pfennig *et al.*, 1991, 1998).

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae), is an economically important pest of maize and other graminaceous crops throughout much of Latin America (Sparks, 1979; Andrews, 1980). The *S. frugiperda* nuclear polyhedrosis virus (SfNPV) is one of the most common entomopathogens attacking field populations (Gardner & Fuxa, 1980), and is a potentially important bioinsecticide. Cannibalism is known to be a viable route of NPV transmission in the noctuid *Heliothis armigera* (Dhandapani *et al.*, 1993), and of granulosis virus in the pyralid moth *Plodia interpunctella* (Boots, 1998). Field cage experiments have indicated that cannibalism may account for substantial mortality of *S. frugiperda* (Wiseman & McMillian, 1969; J. W. Chapman, unpublished), hence this behaviour may be important in the horizontal transmission of SfNPV through natural populations. The frequency of cannibalism and the factors that promote it in *S. frugiperda*, however, remain to be quantified. The incidence of cannibalism in a laboratory population of *S. frugiperda* was therefore determined at a range of food quantities and densities. Furthermore, the risk of SfNPV transmission through cannibalism of infected conspecifics was investigated.

Methods

Insect culture and virus stock

The *S. frugiperda* culture originated from wild larvae collected from maize plants in Chiapas, southern Mexico. The culture was brought to the insectary facilities at Southampton University, U.K. and reared continuously at $27 \pm 2\,^{\circ}C$, $70 \pm 10\%$ RH, and under a LD 12 : 12 h photoperiod. All experiments were conducted in the room used for culturing. The culture was maintained on maize by rearing larvae in groups of 10 in ventilated plastic boxes ($18 \times 10 \times 6$ cm) until pupation. Experimental larvae had passed between five and 10 generations in the laboratory culture at the time of the trials. The SfNPV isolate was obtained from a natural epizootic in a field population of *S. frugiperda* collected from Nicaragua and has recently been characterised (Escribano *et al.*, in press). The virus was propagated by feeding 6-day-old larvae segments of maize leaf treated with a crude homogenate of SfNPV-killed fourth-instar *S. frugiperda*.

Experiment 1: the effect of food availability and density on larval development and cannibalism

The effect of feeding regime and rearing density on larval development and frequency of cannibalism was investigated in a 3×3 factorial design. Second-instar larvae (3 days old) were placed in plastic pots (9 cm diameter $\times$ 4 cm high) lined with dampened tissue paper, at densities of one, two, or four per pot. At each density, larvae were reared on one of three feeding regimes: 100 cm^2, 200 cm^2, or 400 cm^2 of maize leaves provided every 48 h until pupation. Final-instar larvae of *S. frugiperda* consumed approximately 75 cm^2 of maize leaves per day when provided with an unlimited food supply (Chapman *et al.*, in press). Hence, at density 1, the food quantities spanned the range from less than normal consumption to much more than necessary, while at density 4 the food ranged from very low to less than normal consumption. The effect of feeding regime would not have become important until the last few days of larval development, however, because the lowest food quantity provided adequate food for all the treatments until the larvae were 9 days old (Chapman *et al.*, in press). Ten replicates of each treatment were set up. Missing larvae (assumed to be cannibalised) were recorded every 48 h. Direct observations verified the occurrence of cannibalism. Cannibalism, and mortality from other causes, were monitored until all larvae had pupated. The incidence of cannibalism was defined as the proportion of potential victims consumed, with a maximum of the total larvae per pot minus one. The number of days from larval emergence to pupation was recorded for all larvae. Pupae were sexed and weighed 2 days after pupation, and time to adult eclosion was monitored.

Experiment 2: temporal occurrence of cannibalism

Cannibalism rates were monitored throughout larval development to investigate temporal variation in the incidence of cannibalistic behaviour. The experimental protocol was conducted on cohorts of larvae 2, 4, 6, 8, 10, and 12 days old. Four larvae of the same age were placed in a plastic pot (9 cm diameter $\times$ 4 cm high) with enough maize leaves to provide adequate food for 48 h. Adequate food quantities for four larvae over 48 h were 2.76 cm^2 for day 2, 11.84 cm^2 for day 4, 41.76 cm^2 for day 6, 88.24 cm^2 for day 8, 371.52 cm^2 for day 10, and 529.16 cm^2 for day 12 (Chapman *et al.*, in press). The number of larvae cannibalised was recorded after 48 h. The experiment was terminated on day 14 of larval development, because at this age, larvae enter the prepupal stage and cease feeding. Larvae were only used once during the experiment. All age groups were replicated between 30 and 40 times, except day-12 larvae for which 13 replicates were conducted.

Experiment 3: cannibalism and horizontal transmission of SfNPV in fifth-instar larvae

This experiment was conducted to investigate the incidence of cannibalism on healthy and virus-infected conspecifics, and

to ascertain whether cannibalism is a viable route for the horizontal transmission of SfNPV. Fifth-instar larvae (10 days old) were housed individually in plastic pots (9 cm diameter × 4 cm high) with enough food for 48 h (92.88 cm^2). A fourth-instar larva was provided to serve as a potential cannibalistic victim. When cannibalism occurs between two *S. frugiperda* larvae of different ages, the early instar larva is always the victim (J. W. Chapman, unpublished). The potential victims were one of the following: a healthy 8-day-old larva, an 8-day-old SfNPV-infected larva (2 days post-infection), a newly-killed uninfected 8-day-old larva, or a virus-killed corpse (6 days post-infection). Larvae infected 2 days previously do not show any overt symptoms of infection and appear healthy to the human observer. Due to the disintegration of virus-killed corpses, this treatment was achieved by adding a fragment of maize leaf with the cadaver attached; larvae were only scored as cannibals if they consumed the entire leaf fragment. Each treatment was replicated approximately 30 times. Larvae were killed by crushing the head capsule with a spatula. Infected larvae were obtained by enclosing third-instar larvae (6 days old) with a small leaf disc of maize treated with 1 μL of a homogenate of SfNPV-killed fourth-instar *S. frugiperda* larvae in water (approximately 5×10^5 virus particles). Only larvae that had consumed the entire leaf segment were used for the experiment. This method produced 100% mortality from SfNPV infection after 6 days. After 48 h, the pots were examined for cannibalism, and fourth-instar larvae that had not been cannibalised were removed. The experimental larvae were reared individually until adult eclosion, and larval and pupal mortality were monitored. Larval mortality was characterised as occurring from SfNPV or from other causes. Mortality due to SfNPV-infection is easily recognised because the larval integument ruptures, releasing a characteristic white suspension of virus. Pupal weight and development time to adult eclosion were also recorded.

Experiment 4: cannibalism and horizontal transmission of SfNPV in fourth-instar larvae

A modified version of the experimental protocol investigating cannibalism and virus transmission was conducted using fourth-instar larvae (8 days old) as the experimental individuals. Larvae were housed individually in plastic pots (9 cm diameter × 4 cm high) without any food material. Food was not provided in an attempt to increase cannibalism rates, because 8-day-old larvae display very low levels of cannibalism when adequate food is present (see below). Fourth-instar larvae were provided as the victims, but all victims were killed before the trial to eliminate defensive responses and promote the frequency of cannibalism. The potential victims were one of the following: a newly-killed uninfected 8-day-old larva, a newly-killed 8-day-old SfNPV-infected larva (2 days post-infection), or a virus-killed corpse (6 days post-infection). Killing the 2-day post-infected larva immediately before the trial would not have affected the amount or viability of the virus, hence this treatment would not have differed implicitly from the living 2-day post-infected larva offered in the previous trial. Each treatment was replicated 25 or 26 times. After 48 h, cannibalism was recorded and larval corpses that had not been cannibalised were removed. The experimental larvae were reared individually until adult eclosion. Larval and pupal mortality, pupal weight, and development time to adult eclosion were recorded.

Statistical analysis

In experiment 1, the number of larvae cannibalised in each food quantity and rearing density treatment was analysed using Generalized Linear Interactive Modelling (GLIM) (McCullagh & Nelder, 1989) with binomial error structure, according to treatment (plus pair–wise interactions). The maximum level of cannibalism possible (i.e. the rearing density minus one) was used as the denominator for these binomial data. Because cannibalism was impossible in density 1 (which essentially served as a control to check for nonspecific larval mortality and contamination by virus), this level was excluded from the analysis. Larval mortality other than from cannibalism was also analysed using GLIM with binomial errors. In this case, the binomial denominator was specified as the total number of larvae in each pot (i.e. the maximum possible mortality). The effects of food quantity and/or density on pupal weight and development rate were analysed using two-way ANOVA. The effect of sex on pupal weight and development rate of individuals across all treatments was analysed using one-way ANOVA. Data for development rate departed significantly from normality, and were therefore log transformed and re-tested for normality before analysis. Model simplification was conducted by removing redundant interaction terms from all two-way analyses (Crawley, 1993). The proportions of males and females surviving at each density were compared with the expected sex ratio of 1 : 1 using *G*-tests. The *G* statistic was adjusted (G_{adj}) by Williams' correction factor (Fowler & Cohen, 1990).

In experiment 2, temporal variation in the incidence of cannibalism was analysed using GLIM with binomial error structure. The maximum level of cannibalism possible (i.e. three larvae) was used as the denominator for the binomial data.

In experiments 3 and 4, the frequency of cannibalism on healthy and virus-infected larvae, and the proportion of combined larval and pupal mortality within each treatment, were compared using *G*-tests. Pupal weight and development rate of larvae in the different treatments were analysed using one-way ANOVA.

Results

Experiment 1: the effect of food availability and density on larval development and cannibalism

Survival of larvae to pupation varied with rearing density and feeding regime (Fig. 1). Mortality from causes other

than cannibalism was relatively constant across treatments, with a mean (± 1 SE) of 13.9 ± 1.6%, and was not affected significantly by rearing density ($\chi^2 = 0.77$, d.f. = 2, P = NS) or food quantity ($\chi^2 = 2.98$, d.f. = 2, P = NS). Variation in survival across treatments was therefore due to cannibalism. Cannibalism occurred frequently: 40–60% of potential victims in density 2, and 53–83% of potential victims in density 4, were consumed. The frequency of cannibalism increased significantly with increasing rearing density ($\chi^2 = 4.65$, d.f. = 1, $P < 0.05$), and decreased significantly with increasing food quantity ($\chi^2 = 8.5$, d.f. = 2, $P < 0.05$) (Fig. 2). Pupal weight did not vary with rearing density ($F_{2,91} = 2.55$, P = NS), but increased significantly with increasing food quantity ($F_{2,91} = 15.61$, $P < 0.001$) (Fig. 3). Larval development rate was not affected by rearing density ($F_{2,92} = 2.98$, P = NS), whereas development rates were increased significantly by increasing food quantity ($F_{2,92} = 4.35$, $P < 0.05$) (Fig. 4).

Males and females did not differ significantly in pupal weight ($F_{1,97} = 0.58$, P = NS) or larval development time to pupation ($F_{1,98} = 0.09$, P = NS) (Table 1), however females had a significantly shorter pupal duration than males ($F_{1,87} = 15.90$, $P < 0.001$) (Table 1). The numbers of males and females that survived to pupation did not differ significantly from the expected sex ratio of 1 : 1 at any of the rearing densities (Table 2) (overall $G_{adj} = 0.04$, P = NS), suggesting that the outcome of cannibalistic encounters was not affected by sex.

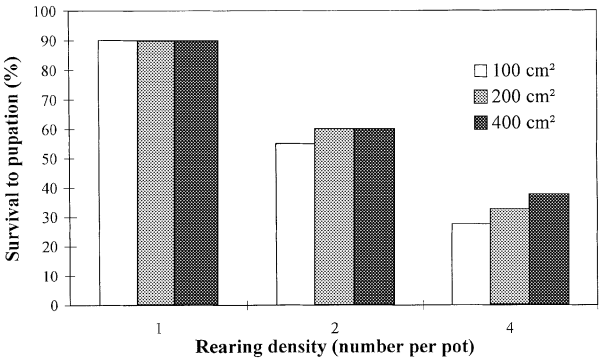

Fig. 1. Survival of 3-day-old *S. frugiperda* larvae reared until pupation at rearing densities of one, two, and four larvae per pot, and food quantities of 100, 200, and 400 cm^2 of maize leaves provided every 48 h throughout larval development. Percentage survival was calculated from 10 replicates.

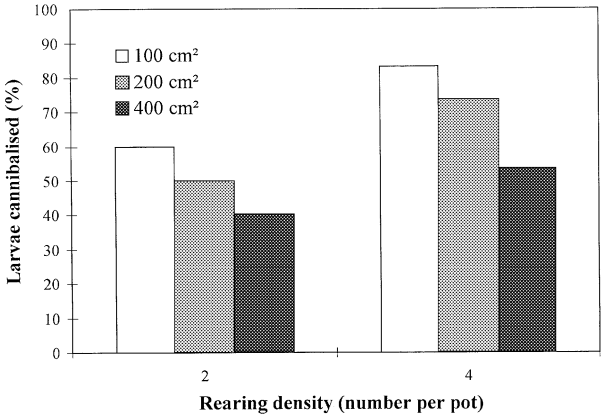

Fig. 2. Percentage cannibalism of *S. frugiperda* larvae reared from 3 days old until pupation at densities of two and four larvae per pot, and food quantities of 100, 200, and 400 cm^2 of maize leaves provided every 48 h throughout larval development. Cannibalism rates were calculated from 10 replicates and defined as the proportion of potential victims consumed, with a maximum of the total larvae per pot minus one.

Experiment 2: temporal occurrence of cannibalism

Cannibalism was infrequent during early larval development, with a mean rate of approximately 0.2 out of three larvae of the same age group, or 6% of potential victims, cannibalised per 48-h period (Fig. 5). Cannibalism rates increased sharply from day 10 onwards (fifth and sixth instars) to approximately 23% of potential victims per 48-h period, and the increase in cannibalism was highly significant ($\chi^2 = 25.3$, d.f. = 5, $P < 0.001$).

Experiment 3: cannibalism and horizontal transmission of SfNPV in fifth-instar larvae

Fifth-instar *S. frugiperda* larvae cannibalised approximately 50–70% of the fourth-instar victims during the 48-h period (Fig. 6). Frequency of cannibalism did not differ significantly between treatments ($G_{adj} = 0.25$, d.f. = 3, P = NS). There was also no difference in the incidence of cannibalism of uninfected versus virus-infected larvae ($G_{adj} = 0.52$, d.f. = 1, P = NS) (data for living and dead victims combined within each group), or of living versus dead larvae ($G_{adj} = 0.06$, d.f. = 1, P = NS) (data for uninfected and virus-infected victims combined within each group), however total mortality rates (larval and pupal) were significantly greater in larvae provided with a virus-infected corpse than in the other cannibalism treatments ($G_{adj} = 8.71$, d.f. = 3, $P < 0.05$) (Fig. 7). Larval mortality in larvae provided with a virus-infected corpse was due entirely to SfNPV infection, whereas SfNPV-infected larvae were not recorded in any other treatments. Of the 10 cases of mortality in the virus-infected corpse treatment, only four of the larvae had consumed the entire corpse and were thereby classified as cannibals. Larvae surviving to eclosion in the different treatments did not differ in pupal weight ($F_{3,95} = 0.69$, P = NS) or in development time to adult emergence ($F_{3,95} = 1.68$, P = NS).

Table 1. Mean pupal weights (± 1 SE), development time to pupation (± 1 SE), and pupal duration (± 1 SE) of male and female *S. frugiperda* surviving to eclosion in experiment 1. Means for both sexes were averaged across all food quantities and rearing densities.

Sex	Number of individuals	Pupal weight (g)	Neonate to pupa (days)	Pupal duration (days)
Male	47	0.196 ± 0.005	16.0 ± 0.3	8.3 ± 0.1
Female	42	0.201 ± 0.005	16.2 ± 0.2	7.6 ± 0.1

Table 2. *G*-tests comparing the total number of male and female *S. frugiperda* surviving to pupation at each rearing density employed in experiment 1. Means for both sexes were averaged across all food quantities. NS = $P > 0.05$.

Density	Males	Females	d.f.	G_{adj}	P
1	14	13	1	0.04	NS
2	22	13	1	2.31	NS
4	15	23	1	1.68	NS
Total	51	49	1	0.04	NS

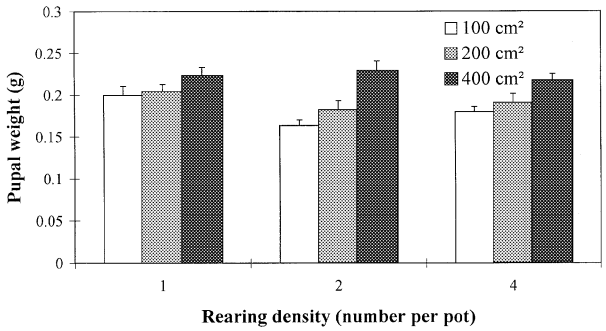

Fig. 3. Mean pupal weight (g) of *S. frugiperda* reared from 3 days old until pupation at densities of one, two, and four larvae per pot, and food quantities of 100, 200, and 400 cm^2 of maize leaves provided every 48 h throughout larval development. Means of 10 replicates + 1 SE.

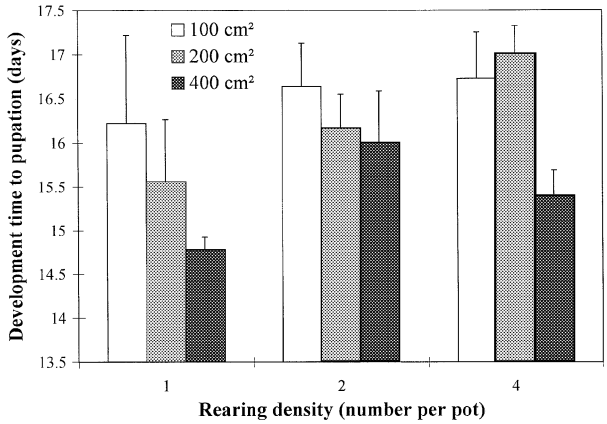

Fig. 4. Mean number of days to pupation of *S. frugiperda* larvae reared from 3 days old until pupation at densities of one, two, and four larvae per pot, and food quantities of 100, 200, and 400 cm^2 of maize leaves provided every 48 h throughout larval development. Means of 10 replicates + 1 SE.

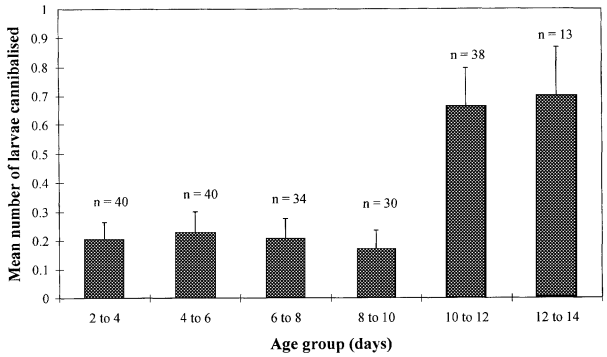

Fig. 5. The mean number of larvae cannibalised during days 2–4, 4–6, 6–8, 8–10, 10–12, and 12–14 of the larval development of *S. frugiperda*. Larvae were housed four to a pot with enough maize to provide adequate food for 48 h, and the number of larvae cannibalised was recorded after 48 h. Larvae were used only once during the experiment. Error bars indicate 1 SE.

Experiment 4: cannibalism and horizontal transmission of SfNPV in fourth-instar larvae

There was no evidence of cannibalism in the virus-killed corpse treatment, and all the experimental larvae died during the 48-h period (Table 3). Virus infection was not observed in this treatment, and mortality was presumably due to starvation and desiccation. This treatment was therefore excluded from the analysis. Mortality during the 48-h period was over 50% in the other two treatments (Table 3), and only larvae that cannibalised survived beyond this time. The frequency of mortality throughout the remainder of development was identical in larvae that had cannibalised healthy or SfNPV-infected corpses (2 days post-infection) (Table 3), however larval mortality was entirely due to SfNPV infection in larvae that had cannibalised SfNPV-infected corpses,

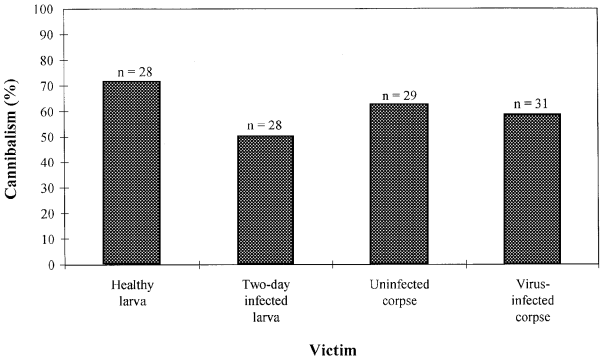

Fig. 6. The percentage cannibalism on uninfected or SfNPV-infected fourth-instar larvae by healthy 10-day-old fifth-instar *S. frugiperda* larvae placed in a plastic pot with adequate maize for 48 h. The fourth-instar victims were one of the following: a healthy 8-day-old larva, an 8-day-old SfNPV-infected larva (2 days post-infection), a newly-killed uninfected 8-day-old larva, or a virus-killed corpse (6 days post-infection). Cannibalism was recorded after 48 h if the entire victim had been consumed.

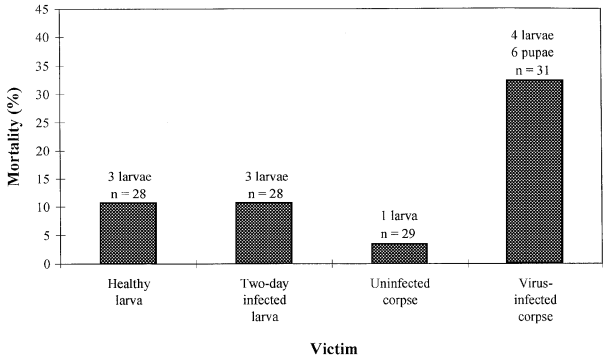

Fig. 7. The percentage mortality of 10-day-old fifth-instar *S. frugiperda* larvae reared to adult eclosion after the opportunity to cannibalise on uninfected or SfNPV-infected fourth-instar larvae. The fourth-instar victims were one of the following: a healthy 8-day-old larva, an 8-day-old SfNPV-infected larva (2 days post-infection), a newly-killed uninfected 8-day-old larva, or a virus-killed corpse (6 days post-infection).

Table 3. Incidence of cannibalism, mortality, and SfNPV infection in fourth-instar *S. frugiperda* larvae provided with a newly-killed uninfected larva (8 days old), a newly-killed larva 2 days post-SfNPV infection (8 days old), or a SfNPV-killed larva (12 days old) as potential cannibalistic victims for 48 h.

	Uninfected corpse	2 days post-infection	SfNPV-killed corpse
Number of individuals	25	26	25
Number surviving 48-h period	12	11	0
Number of cannibalistic incidents	12	11	0
Larval mortality	2	2	–
Larval mortality due to SfNPV infection	0	2	–
Pupal mortality	4	4	–

whereas SfNPV infection was not recorded in larvae that had cannibalised uninfected corpses. There was no difference among treatments in pupal weight ($F_{1,15} = 2.01$, $P = \text{NS}$) or development rate ($F_{1,15} = 2.94$, $P = \text{NS}$) of larvae surviving to pupation.

Discussion

This study demonstrated that cannibalism was a frequent behaviour in a laboratory population of *S. frugiperda*, even when food was not limiting. Cannibalism amongst cohorts of same-age larvae reared together throughout larval development was considerable: 40–83% of potential victims were cannibalised, depending on feeding regime and rearing density (experiment 1). Cannibalism was most frequent among fifth- and sixth-instar larvae: approximately 23% of potential victims were cannibalised in 48 h, compared to approximately 6% during the first 10 days of development (experiment 2). Cannibalism rates were even higher when larvae of different ages were enclosed together: fifth instars cannibalised 70% of healthy fourth instars in 48 h, even though food was not limiting (experiment 3). Cannibalism may also be prevalent among wild populations of *S. frugiperda* on maize (Wiseman & McMillian, 1969; J. W. Chapman, unpublished). Maize is the favoured host of *S. frugiperda*; the larvae feed primarily within the wrapped leaves of the whorl (Morrill & Greene, 1973; Labatte, 1993), and hence will be in close contact with cohabiting larvae. Several small *S. frugiperda* larvae are frequently observed feeding in the same whorl, whereas large larvae almost never cohabit (Vickery, 1929; Carvalho & Silveira, 1971). Cannibalism has also been reported widely in many species of otherwise herbivorous lepidopterous larvae (e.g. Gould *et al.*, 1980; Joyner & Gould, 1985; Breden & Chippendale, 1989; Dhandapani *et al.*, 1993).

As expected, the frequency of cannibalism increased with decreasing food quantity. Cannibalism rates in *S. frugiperda* also increased when larvae were offered food of lower nutritional quality than maize (Raffa, 1987). Many other studies have demonstrated an inverse relationship between the incidence of cannibalism and quantity or quality of alternative

food (see Fox, 1975; Polis, 1981, for reviews). The degree of crowding was also important, with the incidence of cannibalism being greater at high densities.

There was no evidence of a sexual bias in the larvae surviving to pupation in experiment 1, indicating that males and females were equally cannibalistic. In most species that have been studied, females are more cannibalistic than males (Polis, 1981), and it has been suggested that this is related to the higher energetic requirements of egg production in females (Church & Sherratt, 1996). Cannibalism in *S. frugiperda* does not produce an increase in body mass (Chapman *et al.*, in press), however, and this may explain the lack of a sexual bias in cannibalism rates.

The frequency of cannibalism was clearly affected by the age of the individuals involved. Cannibalism rates of fifth-instar larvae were greater when the potential victims were younger (experiment 3) than when same-age larvae were enclosed together (experiment 2). Older individuals are more voracious cannibals than younger individuals in many species, and asymmetric encounters frequently result in cannibalism (Polis, 1981; Dial & Adler, 1990). The reduced risk of retaliation experienced from attacking earlier instars probably explains the higher frequency of cannibalism in asymmetric interactions.

The incidence of cannibalism on same-age larvae also varied throughout larval development, increasing substantially during the fifth and sixth instars. It is possible that nutritional benefits associated with cannibalism are most important in the latter stages of larval development. Insects are particularly vulnerable to cannibalism during pupation (Polis, 1981), and hence high rates of cannibalism just prior to pupation may also be an adaptation for reducing the risk of attack during the pupal stage.

A potentially important cost of cannibalism is the transmission of parasites and pathogens (Polis, 1981). Fifth-instar *S. frugiperda* larvae fed equally on healthy larvae, virus-infected larvae, uninfected corpses, and virus-killed corpses, suggesting that larvae were unable to detect and avoid infected conspecifics. Similar studies on other species of Lepidoptera have also indicated that cannibals did not avoid consuming virus-infected larvae (Dhandapani *et al.*, 1993; Vasconcelos, 1996; Boots, 1998). In the present study, cannibalism by fifth-instar *S. frugiperda* on living SfNPV-infected larvae did not lead to horizontal transmission of the virus. Production of occluded virus particles (polyhedra) begins approximately 18–24 h post-infection (Miller, 1996), thus cannibals would have obtained infectious material from consuming fourth instars infected 2 days previously. This suggests that fifth-instar larvae may not be susceptible to the levels of SfNPV encountered when cannibalising living virus-infected larvae at the early stages of infection. Fifth-instar larvae require a further 6 or 7 days to pupate (Chapman *et al.*, in press) so there would probably have been sufficient time for SfNPV infection to develop if it had occurred. If fifth-instar larvae can consume virus-infected larvae without risk of disease transmission, then the costs associated with cannibalism are reduced.

Fourth-instar *S. frugiperda* died of starvation rather than consuming virus-killed corpses (6 days post-infection), in contrast to the frequent cannibalism of NPV-killed cadavers by fifth-instar *S. frugiperda*, and fourth-instar *H. armigera* (Dhandapani *et al.*, 1993). Cannibalism by fourth-instar larvae on 2-day post-infected larvae resulted in instances of horizontal transmission, indicating that immunity to SfNPV infection from cannibalising living virus-infected larvae does not appear until the fifth instar. The LC_{50} for fifth-instar *S. frugiperda* is approximately 10 times greater than the LC_{50} for fourth instars (Escribano *et al.*, in press). The low incidence of cannibalism amongst *S. frugiperda* larvae up to the fifth instar presumably prevents this being a viable route for virus transmission. The low incidence of cannibalism in the early stages of larval development may therefore be an adaptation for avoiding the risk of disease transmission. It has been suggested that the relative rarity of cannibalism in most species (Dawkins, 1976) may be due to the enhanced risk of pathogen transmission (Elgar & Crespi, 1992; Pfennig *et al.*, 1998).

Fifth-instar larvae were susceptible to horizontal transmission of SfNPV when in close proximity to a virus-killed corpse. The number of infectious particles released from an infected cadaver is far in excess of the number present in a recently infected larva (Bishop *et al.*, 1988), however cannibalism of the virus-killed corpse was recorded in only four of the 10 cases where virus transmission occurred in experiment 3. Clearly, larvae may have acquired the infection by consuming only a small portion of the cadaver, and these cases would not have been recorded as instances of cannibalism. Larvae may also have become infected by consuming foliage contaminated with SfNPV released from the corpse. It is not clear, therefore, whether cannibalism was directly involved in the transmission of SfNPV from cadaver to healthy larva. Six of the larvae that died in the virus-killed corpse treatment died during the pupal stage. Although pupal mortality was not characterised as occurring from virus infection, it is probable that SfNPV infection was the principle cause, because NPV is known to produce pupal mortality in *H. armigera* (Dhandapani *et al.*, 1993).

Cannibalism of living larvae does not therefore appear to constitute a viable route for substantial horizontal transmission of SfNPV. Indeed, if cannibalism rates are high under field conditions, consumption of virus-infected larvae by fifth instars may remove many infected individuals from the population before infectious virus particles are liberated into the environment. Thus, cannibalism of infected individuals may prevent the spread of disease through the host population, as suggested by Hart (1990). Previous studies have also demonstrated that parasitoid and pathogen population dynamics may be influenced by host cannibalism (Reed *et al.*, 1996; Boots, 1998). Cannibalism in populations of lepidopterous pest species, such as *S. frugiperda*, may have profound implications in biological control programmes utilising pathogens or parasites. Further studies are required to assess the effects of cannibalism on virus transmission under field conditions.

Acknowledgements

We would like to thank Keith Anderson and Emma Elderfield for invaluable assistance with insect rearing. This work was funded by the European Commission (contract number IC18-CT96–0097).

References

Andrews, K.L. (1980) The whorlworm, *Spodoptera frugiperda*, in Central America and neighboring areas. *Florida Entomologist*, **63**, 456–467.

Bishop, D.H.L., Entwistle, P.F., Cameron, I.R., Allen, C.J. & Possee, R.D. (1988) Field trials of genetically-engineered baculovirus insecticides. *The Release of Genetically-engineered Micro-organisms* (ed. by M. Sussman, C. H. Collins, F. A. Skinner and D. E. Stewart-Tull), pp. 143–179. Academic Press Limited, London.

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

Breden, F. & Chippendale, G.M. (1989) Effect of larval density and cannibalism on growth and development of the southwestern corn borer, *Diatraea grandiosella*, and the European corn borer, *Ostrinia nubilalis* (Lepidoptera: Pyralidae). *Journal of the Kansas Entomological Society*, **62**, 307–315.

Carvalho, R.P.L. & Silveira, N.S. (1971) Observacoes do comportamento de *Spodoptera frugiperda* (J. E. Smith, 1797) (Lepidoptera, Noctuidae) ao atacar milho em condicoes de campo. *Resúmen de Los Trabajos Presentados al Prima Congreso Latinoamericano de Entomología*, pp. 92–93. Congreso Latinoamericano de Entomología, Cuzco, Peru.

Chapman, J.W., Williams, T., Escribano, A., Caballero, P., Cave, R.D. & Goulson, D. (in press) Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*. *Behavioural Ecology*, in press.

Church, S.C. & Sherratt, T.N. (1996) The selective advantages of cannibalism in a Neotropical mosquito. *Behavioural Ecology and Sociobiology*, **39**, 117–123.

Crawley, M.J. (1993) *GLIM for Ecologists.* Blackwell Science, Oxford.

Dawkins, R. (1976) *The Selfish Gene.* Oxford University Press, Oxford.

Dhandapani, N., Jayaraj, S. & Rabindra, R.J. (1993) Cannibalism on nuclear polyhedrosis-virus infected larvae by *Heliothis armigera* (Hubn.) and its effect on viral-infection. *Insect Science and its Applications*, **14**, 427–430.

Dial, C.I. & Adler, P.H. (1990) Larval behavior and cannibalism in *Heliothis zea* (Lepidoptera: Noctuidea). *Annals of the Entomological Society of America*, **83**, 258–263.

Duelli, P. (1981) Is larval cannibalism in lacewings adaptive? (Neuroptera: Chrysopidae). *Research on Population Ecology*, **23**, 193–209.

Elgar, M.A. & Crespi, B.J. (1992) *Cannibalism: Ecology and Evolution among Diverse Taxa.* Oxford University Press, Oxford.

Escribano, A., Williams, T., Goulson, D., Cave, R.D., Chapman, J.W. & Caballero, P. (in press) Selection of a nucleopolyhedrovirus for control of *Spodoptera frugiperda* (Lepidoptera: Noctuidae): structural, genetic and biological comparision of four isolates from the Americas. *Journal of Economic Entomology*.

Fowler, J. & Cohen, L. (1990) *Practical Statistics for Field Biology.* Open University Press, Milton Keynes.

Fox, L.R. (1975) Cannibalism in natural populations. *Annual Reviews in Ecology and Systematics*, **6**, 87–106.

Gardner, W.A. & Fuxa, J.R. (1980) Pathogens for the suppression of the fall armyworm. *Florida Entomologist*, **63**, 439–447.

Gould, F., Holtzman, G., Rabb, R.L. & Smith, M. (1980) Genetic variation in predatory and cannibalistic tendencies of *Heliothis virescens* strains. *Annals of the Entomological Society of America*, **73**, 243–250.

Hart, B.L. (1990) Behavioral adaptations to pathogens and parasites: five strategies. *Neuroscience and Biobehaviour Reviews*, **14**, 273–294.

Joyner, K. & Gould, F. (1985) Developmental consequences of cannibalism in *Heliothis zea* (Lepidoptera, Noctuidae). *Annals of the Entomological Society of America*, **78**, 24–28.

Labatte, J.M. (1993) Within-plant distribution of fall armyworm (Lepidoptera: Noctuidae) larvae on corn during whorl-stage infestation. *Florida Entomologist*, **76**, 437–447.

Matuschka, F.R. & Bannert, B. (1989) Recognition of cyclic transmission of *Sarcocystis stehlinii* N. Sp. in the Gran Canarian giant lizard. *Journal of Parasitology*, **75**, 383–387.

McCullagh, P. & Nelder, J.A. (1989) *Generalized Linear Models.* Chapman & Hall, London.

Miller, L.K. (1996) Insect viruses. *Fundamental Virology*, 3rd edn (ed. by B. N. Fields, D. M. Knipe and P. M. Howley), pp. 401–424. Lippincott-Raven, Philadelphia, Pennsylvania.

Morrill, W.L. & Greene, G.L. (1973) Distribution of fall armyworm larvae. 1. Regions of field corn plants infested by larvae. *Environmental Entomology*, **2**, 195–198.

Pfennig, D.W., Ho, S.G. & Hoffman, E.A. (1998) Pathogen transmission as a selective force against cannibalism. *Animal Behaviour*, **55**, 1255–1261.

Pfennig, D.W., Loeb, M.L.G. & Collins, J.P. (1991) Pathogens as a factor limiting the spread of cannibalism in tiger salamanders. *Oecologia*, **88**, 161–166.

Pfennig, D.W., Reeve, H.K. & Sherman, P.W. (1993) Kin recognition and cannibalism in spadefoot toad tadpoles. *Animal Behaviour*, **46**, 87–94.

Pierce, N.E. (1995) Predatory and parasitic Lepidoptera: carnivores living on plants. *Journal of the Lepidopterists' Society*, **49**, 412–453.

Polis, G.A. (1981) The evolution and dynamics of intraspecific predation. *Annual Reviews in Ecology and Systematics*, **12**, 225–251.

Raffa, K.F. (1987) Effect of host plant on cannibalism rates by fall armyworm (Lepidoptera: Noctuidae) larvae. *Environmental Entomology*, **16**, 672–675.

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

Schaub, G.A., Böeker, C.A., Jensen, C. & Redruth, D. (1989) Cannibalism and coprophagy are modes of transmission of *Blastocrithidia triatomae* (Trypanosomatidae) between triatomines. *Journal of Protozoology*, **36**, 171–175.

Sparks, A.N. (1979) A review of the biology of the fall armyworm. *Florida Entomologist*, **62**, 82–87.

Vasconcelos, S.D. (1996) Alternative routes for the horizontal transmission of a nucleopolyhedrovirus. *Journal of Invertebrate Pathology*, **68**, 269–274.

Vickery, L.A. (1929) *Studies on the Fall Armyworm in the Gulf Coast District of Texas. USDA Technical Bulletin 138.* United States Government Printing Office, Washington DC.

Wiseman, B.R. & McMillian, W.W. (1969) Competition and survival among the corn earworm, the tobacco budworm and the fall armyworm. *Journal of Economic Entomology*, **62**, 734–735.

Accepted 28 November 1998