

Fitness consequences of cannibalism in the fall armyworm, *Spodoptera frugiperda*

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We investigated the consequences of cannibalism for some correlates of fitness in the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). The benefits gained by cannibals were ascertained by comparing survival, development rate, and pupal weight of larvae that had the opportunity to cannibalize with those that did not, at two levels of food availability. Larvae in the cannibalism treatments were provided with a conspecific one instar younger than themselves on five dates throughout larval development. Cannibalism was frequent; given the opportunity all larvae predated at least one younger conspecific. The frequency of cannibalism was not affected by the sex of the cannibal or by the availability of alternative food. However, cannibals suffered a significant reduction in survival at both high and low food availability. Furthermore, cannibals had a lower pupal weight in the high food treatment and a reduced development rate in the low food treatment. The only detectable fitness benefit associated with cannibalism was a positive correlation between the number of victims consumed and development rate under conditions of low food availability. On balance, cannibalism appears to be costly; alternative explanations for its occurrence in this species are discussed. *Key words*: cannibalism, fall armyworm, food availability, larval development, *Spodoptera frugiperda*, survival. [*Behav Ecol* 10:298–303 (1999)]

Cannibalism is a frequent behavior in a wide array of animal taxa, often accounting for substantial levels of mortality and influencing population structure and dynamics (Dong and Polis, 1992; Fox, 1975; Polis, 1981). Cannibalism has been widely documented in larval Lepidoptera (Dial and Adler, 1990; Dhandapani et al., 1993; Joyner and Gould, 1985; Pierce, 1995; Raffa, 1987; Reed et al., 1996), although there is considerable variation in the frequency of cannibalistic behavior in closely related species (Breden and Chippendale, 1989; Gould et al., 1980; Schweitzer, 1979). In many cases, however, the selective advantages associated with cannibalism remain to be elucidated.

Cannibalism may confer direct (nutritional) fitness benefits in the form of increased survival, developmental rate, and fecundity (Church and Sherratt, 1996; Duelli, 1981; Joyner and Gould, 1985), or it may provide indirect benefits by removing potential competitors and intraspecific predators (Fox, 1975; Polis, 1981). A third possible benefit associated with cannibalism may be a reduction in the risk of predation and/or parasitism via decreases in local population density. Semiochemicals released from larval *Spodoptera*, frass, or larval-damaged plants are known to elicit prey-locating behavior in predatory Hemiptera (Yasuda, 1997; Yasuda and Wakamura, 1996) and to elicit host-seeking in parasitic Hymenoptera (Turlings and Tumlinson, 1992; Turlings et al., 1990, 1991). If the odor cues released from the microhabitat of the larvae are quantitatively diminished by a reduction in herbivore density, then cannibalism may confer a selective advantage in terms of a lower risk of predation and parasitism.

Conversely, the costs associated with cannibalism may be

great. 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 (Polis, 1981). Transmission of pathogens and parasites via cannibalism has been demonstrated in several species (Dhandapani, 1993; Matuschka and Bannert, 1989; Schaub et al., 1989). Third, intraspecific predation may cause a reduction in inclusive fitness through the cannibalism of kin (Pfennig, 1993; Polis, 1981). The reduction in inclusive fitness may be offset by benefits such as increased development rate (Eickwort, 1973). However, kin selection theory predicts that selective cannibalism of nonkin should occur if cannibals have the ability to distinguish relatives from nonrelatives (Hamilton, 1964). Even so, sibling cannibalism is widespread in many animal species (Polis, 1981; Waldman, 1988).

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 (Andrews, 1980; Sparks, 1979). Cannibalism is a frequent behavior of *S. frugiperda* in laboratory culture and in the field, even when more than adequate food is available (Chapman et al., in press; Chapman et al., in preparation). We have previously demonstrated that cannibalism of infected conspecifics may result in the transmission of *S. frugiperda* nuclear polyhedrosis virus (Chapman et al., in press). Other fitness consequences of cannibalism in this species have not been determined. In the present study, we investigated the developmental consequences of cannibalism in this species. Because the adaptive benefits of cannibalism may depend on the context in which it occurs (Sherratt and Church, 1994), we quantified the fitness consequences of cannibalism at two levels of food availability.

METHODS

Insect culture

The *S. frugiperda* culture used in this study originated from wild larvae collected on maize plants in Chiapas, southern

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Received 29 June 1998; accepted 3 November 1998.

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Mexico, during October 1996. The culture was translocated to the insectary facilities at Southampton University, England, and reared continuously at $27 \pm 2^\circ\text{C}$, $70 \pm 10\%$ relative humidity, under a 12 h:12 h light:dark photoperiod. We conducted all the experiments in the room used for culturing. The culture was maintained on maize leaves by rearing larvae in groups of 10 in ventilated plastic boxes (18 cm \times 10 cm \times 6 cm) lined with dampened tissue, until pupation. We moved adult moths to cylindrical egg-laying cages (23 cm diam \times 30 cm high), where they were provided with a food source (honey water) and oviposition material (diaper liners). We conducted experiments during March and April 1997, when larvae had been in the laboratory culture for between five and seven generations.

Foliage consumption

We assessed the feeding rate of larval *S. frugiperda* by quantifying the area of maize leaf ingested by individual larvae on each day throughout their development, so that daily food requirements during the cannibalism studies could be determined. We removed neonate larvae from culture boxes within 6 h of hatching, after consumption of the egg cases, but before any other feeding. Thirty larvae were individually housed in plastic pots (9 cm diameter \times 4 cm high) lined with dampened tissue paper. Each pot contained freshly excised leaves from the uppermost region of whorl-stage maize. Leaf segments (approximately 20 cm²) were photocopied before and after a feeding period of 24 h. Fresh maize was provided every 24 h, and larvae never exhausted their food supply. We calculated leaf area consumption using an acetate photocopy of 1-mm² graph paper. We monitored daily leaf area consumption until day 14 of larval development, as by day 15 all larvae had entered the prepupal stage and ceased feeding.

Nutritional benefits of cannibalism

We compared the survival, development rate, and pupal weight of larvae that had the opportunity to cannibalize with those that did not, at two levels of food availability. Cannibalism is rarely observed in first and second instar *S. frugiperda* (Barfield and Ashley, 1987; Chapman et al., in press). Therefore, we initiated the experiment when larvae were at the third instar. Before this, experimental larvae were reared in the general culture. Individual third instar larvae (5 days old) were housed in plastic pots (9 cm diameter \times 4 cm high) lined with dampened tissue paper. We randomly allocated larvae to one of the following treatments: (1) high food with no opportunity for cannibalism, (2) high food with opportunity for cannibalism, (3) low food with no opportunity for cannibalism, and (4) low food with opportunity for cannibalism.

Larvae were provided with fresh maize leaves every 48 h until pupation. We calculated the food requirements for each 48 h period by referring to the mean daily consumption rates obtained in the previous experiment. Larvae in the high food treatment were given 33% more maize than the mean daily consumption rate, while larvae in the low food treatment were given 33% less maize. In the cannibalism treatments, a potential cannibalistic victim (2 days and 1 instar younger than the larger experimental larva) was added every 48 h with the maize leaves. When cannibalism occurs between two *S. frugiperda* larvae of different ages, the early instar larva is always the victim (J. W. Chapman, unpublished data). We provided victims at the first five feeding points (days 5, 7, 9, 11, and 13 of larval development). Larvae were not added after day 13 to prevent cannibalism of the experimental larvae during the prepupal stage, when they are quiescent and vulnerable to attack from younger conspecifics. Experimental larvae in the

no-cannibalism treatments were not provided with additional conspecifics. At 48-h intervals we recorded the presence or absence of cannibalism (missing larvae were presumed cannibalized) and then removed potential victims that had not been consumed. Direct observations verified the occurrence of cannibalism. Two days after pupation, we weighed and sexed all pupae. All treatments were replicated 37 or 38 times.

The number of larvae surviving to pupation in each food quantity and cannibalism treatment were analyzed using GLIM (generalized linear interactive modeling; McCullagh and Nelder, 1989) with binary error structure, according to treatment (plus pairwise interaction). Within the two cannibalism treatments, the number of victims consumed were analyzed using GLIM with binomial error structure, according to food quantity and sex of the cannibal (plus pairwise interaction). The maximum level of cannibalism possible (five victims) was used as the denominator for these binomial data. We analyzed the effects of food quantity and/or opportunity of cannibalism on development rate and pupal weight with two-way ANOVAs. Data for development rate significantly departed from normality and were therefore log transformed and retested for normality before analysis. Model simplification was conducted by removing redundant interaction terms from all two-way analyses (Crawley, 1993). Within the two cannibalism treatments, the relationships between the number of victims consumed and larval development parameters (pupal weight and larval duration) were examined with Spearman rank correlation.

RESULTS

Foliage consumption

Mean daily foliage consumption gradually increased throughout larval development, with a substantial increase during the final instar (day 11 onward; Figure 1). Consumption rates decreased during days 13 and 14, as larvae began entering the prepupal stage.

Nutritional benefits of cannibalism

Cannibalism occurred frequently at both levels of food availability (Table 1) and was not significantly influenced by food quantity ($\chi^2 = 0.89$, $df = 1$, $p > .05$) or the sex of the cannibal ($\chi^2 = 0.22$, $df = 1$, $p > .05$). The proportion of larvae surviving to pupation in each treatment was not affected by feeding regime ($\chi^2 = 0.30$, $df = 1$, $p > .05$), but was significantly decreased in treatments where larvae had the opportunity to cannibalize ($\chi^2 = 6.7$, $df = 1$, $p < .01$; Figure 2). The interaction between feeding regime and opportunity to cannibalize was not significant ($\chi^2 = 0.20$, $df = 1$, $p > .05$), indicating that the reduction in survival associated with the presence of conspecifics was uniform across both levels of food availability.

Larval development time (the number of days to pupation) was significantly longer in the low food treatments ($F_{1, 112} = 122.4$, $p < .001$; Figure 3). Opportunity for cannibalism also produced a significant increase in larval development time ($F_{1, 112} = 5.3$, $p = .02$). Larvae developed most slowly when reared at low food availability and provided with younger larvae, whereas the provision of conspecifics to larvae in the high food treatment had no effect on development rate (Figure 3). There was a significant interaction between food availability and opportunity for cannibalism ($F_{1, 112} = 7.1$, $p < .01$), indicating that the effect of the additional larvae on development rate was significantly greater at low food availability.

To investigate the influence of cannibalism on development rate, we examined the relationship between the number of victims consumed and the time to pupation. Spearman rank

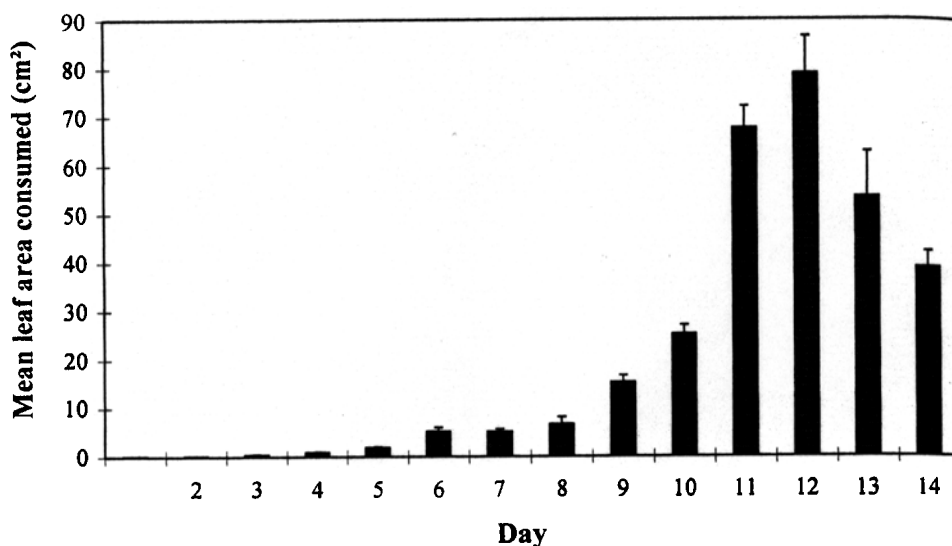


Figure 1
Mean area (± 1 SE) of maize leaves consumed by single larval *S. frugiperda* provided with an abundant food supply every 24 h throughout larval development ($n = 30$).

correlation indicated that there was no relationship in the high food treatment ($r_s = .011$, $n = 26$, $p = .96$), but in the low food treatment the number of days to pupation was significantly negatively correlated with the number of victims cannibalised ($r_s = -.498$, $n = 26$, $p = .01$). Therefore, larvae that cannibalized most frequently in the low food treatment had the shortest development times (Figure 4).

Larvae reared in the high food treatments produced significantly heavier pupae than those in the low food treatments ($F_{1,112} = 14.9$, $p < .001$; Figure 5). The addition of conspecific victims did not significantly affect pupal weight overall ($F_{1,112} = 2.36$, $p = .14$). However, pupal weight of larvae with the opportunity for cannibalism at high food availability was substantially less than larvae in the high food, no cannibalism treatment (Figure 5). There was a significant interaction between food availability and opportunity for cannibalism ($F_{1,112} = 7.2$, $p < .01$), indicating that the effect of conspecifics on pupal weight was significantly greater in the high food treatment. We investigated the relationship between pupal weight and the number of conspecifics consumed with Spearman rank correlation. In the high food treatment there was no correlation between pupal weight and cannibalism ($r_s = -.115$, $n = 26$, $p = .58$). However, the pupal weight of individuals in the low food treatment was negatively correlated with the number of victims consumed ($r_s = -.413$, $n = 26$, $p < .05$). Therefore, larvae that cannibalized most frequently in the low food treatment produced the smallest pupae (Figure 6).

Table 1
Mean number (\pm SE) of larvae cannibalized by male and female *S. frugiperda* larvae surviving to pupation, at two levels of food availability

	High food		Low food	
	<i>n</i>	No. cannibalized	<i>n</i>	No. cannibalized
Males	14	3.1 \pm 0.3	10	2.6 \pm 0.2
Females	13	2.8 \pm 0.2	16	2.6 \pm 0.3
Both sexes	27	2.9 \pm 0.2	26	2.6 \pm 0.2

Experimental larvae were offered a potential cannibalistic victim (1 instar and 2 days younger) every 48 h on five dates throughout their development.

DISCUSSION

Survival of *S. frugiperda* larvae was not influenced by the amount of food available. However, there were developmental consequences associated with low food availability in terms of longer larval development (an increase of approximately 1.5 days) and lower pupal weight (a reduction of approximately 10%). These effects of low food on developmental parameters may have profound repercussions for an individual's fitness. Larval mortality from natural enemies can be high in the field (Castro and Pitre, 1989; Gardner and Fuxa, 1980), and thus prolonged larval development may be very costly. Small females will have reduced reproductive success, as pupal weight is positively correlated with fecundity (Leuck and Perkins, 1972; Lynch, 1984). The fitness costs, if any, of reduced pupal weight in males are unknown. Larger (more fecund) females take longer to develop than small females (Pashley et al., 1995), and it seems probable that development time is the result of a trade-off between maximizing adult size and minimizing larval mortality. One possible means by which herbi-

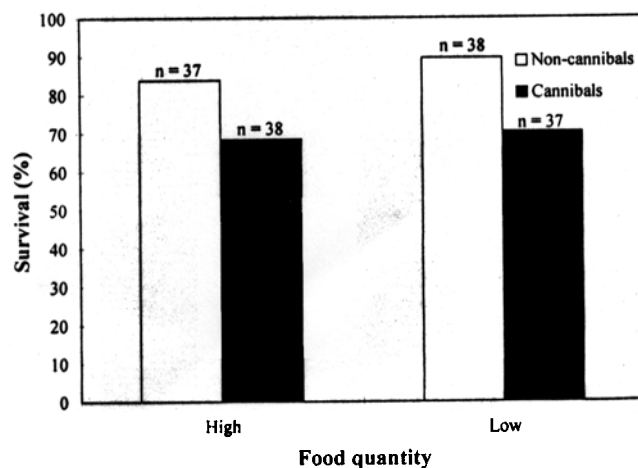


Figure 2
Percent survival to pupation of *S. frugiperda* larvae reared at two levels of food availability (high = 33% more maize than mean daily requirements; low = 33% less) with or without the opportunity for cannibalism. Larvae in the cannibalism treatments were provided with a younger conspecific larva every 48 h on five separate feeding dates from day 5 of development onward.

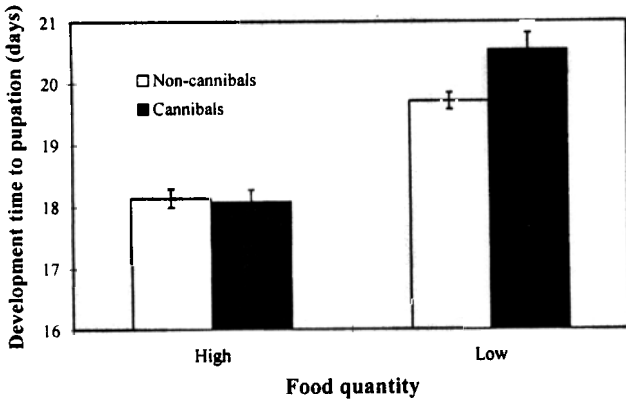


Figure 3
Mean (\pm SE) developmental time to pupation of larval *S. frugiperda* reared at two levels of food availability with or without the opportunity for cannibalism. Larvae in the cannibalism treatments were provided with a younger conspecific larva every 48 h on five separate feeding dates from day 5 of development onward.

vorous larvae might improve on this trade-off is by gaining extra nutritional benefits through cannibalism (Joyner and Gould, 1985; Polis, 1981).

The results of this and other studies (Chapman et al., in press) clearly demonstrate that cannibalism is a prevalent behavior of *S. frugiperda* larvae. It is possible that the increased density of the laboratory culture, compared to field conditions, may have selected for cannibalistic behavior. However, several considerations suggest that the high rates of cannibalism observed in our experiments were not an artifact of laboratory rearing conditions. Maize is the favored host of *S. frugiperda*; the larvae feed primarily within the wrapped leaves of the whorl (Labatte, 1993; Morrill and Greene, 1973) 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 (Carvalho and Silveira, 1971; Vickery, 1929; J. W. Chapman, unpublished data). Furthermore, field cage experiments indicated that cannibalism accounted for considerable levels of mortality when maize plants were artificially infested with two or more fourth instar *S. frugiperda* (Chapman et al., in preparation).

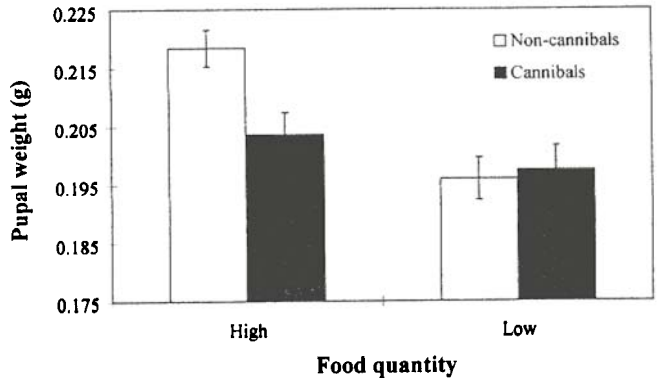


Figure 5
Mean (\pm SE) pupal weight (g) of *S. frugiperda* reared at two levels of food availability with or without the opportunity for cannibalism. Larvae in the cannibalism treatments were provided with a younger conspecific larva every 48 h on five separate feeding dates from day 5 of development onward.

The nutritional benefits accrued from cannibalism in many species include increased survival, accelerated development, and increased body mass (Polis, 1981). Therefore, it follows that when cannibalism confers such benefits, the propensity for cannibalism should be greater when food availability is low. Also, the risk of injury involved with cannibalism may inhibit the behavior unless a deficiency of alternative food makes it a viable strategy (Polis, 1981). Indeed, cannibalism frequently occurs as a response to low food levels (Banks, 1968; Church and Sherratt, 1996; Duelli, 1981; Istock, 1966), and we have previously demonstrated that cannibalism among *S. frugiperda* larvae was more prevalent when food was scarce (Chapman et al., in press). However, the results of our present study indicated that food availability had no effect on the incidence of cannibalism. This discrepancy in our results is probably due to the stage of the victim relative to the cannibal: in the previous study of *S. frugiperda*, all experimental larvae were the same instar (Chapman et al., in press), whereas in the present study victims were an instar younger than the cannibals. The risk of retaliation is reduced in cannibalistic encounters that are asymmetric in respect to age (Polis, 1981). Thus, when presented with younger (and hence more vulnerable) potential prey, larvae may have less incentive to avoid cannibalism, even when food is not limiting. This probably

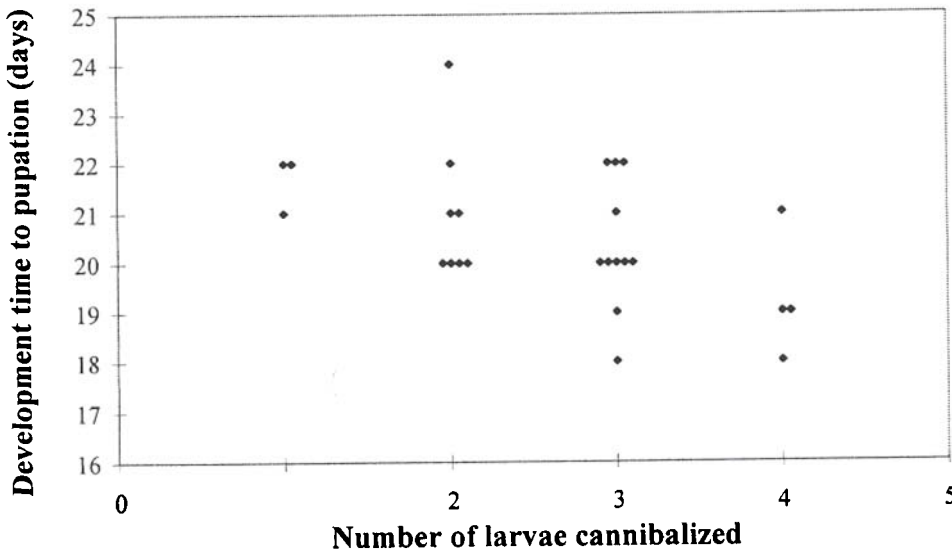


Figure 4
The relationship between the number of larvae cannibalized and the time taken to reach pupation by larval *S. frugiperda* reared at low food availability ($r_s = -.498$, $n = 26$, $p = .01$). Individual data points of the same y value have been shifted slightly to the left and right for clarification.

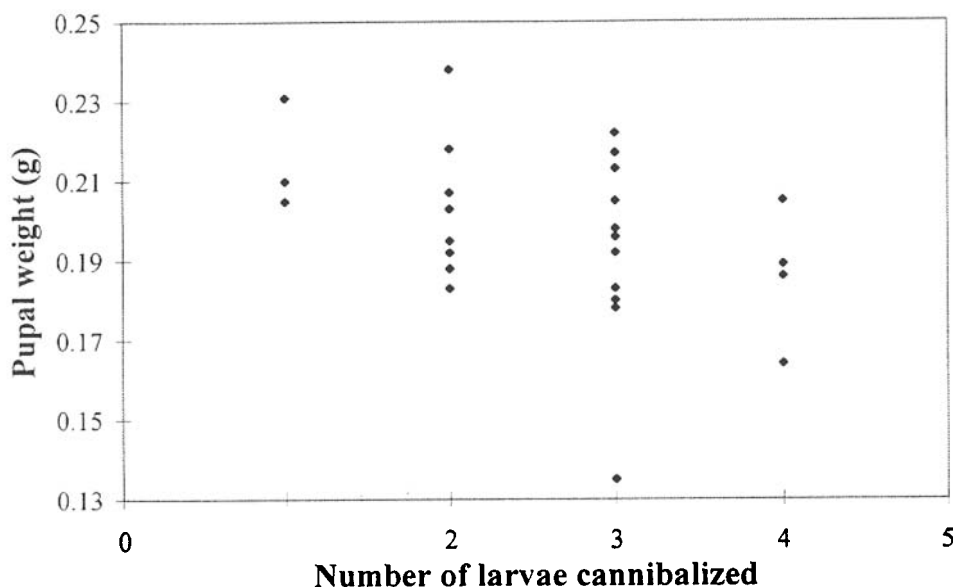


Figure 6
The relationship between the number of larvae cannibalized and the pupal weight of larval *S. frugiperda* reared at low food availability ($r_s = -0.413$, $n = 26$, $p < 0.05$).

explains why larvae were equally cannibalistic at both levels of food availability.

Unlike a number of other studies (Duelli, 1981; Joyner and Gould, 1985; Osawa, 1992; Church and Sherratt, 1996), our results provide little evidence for detectable fitness benefits associated with cannibalism. Larvae provided with the opportunity to cannibalise had lower survival in both food treatments, lower pupal weight in the high food treatment, and a longer development time in the low food treatment. However, it is difficult to tease apart the effects of the presence of conspecifics from the effects of the act of cannibalism. Many studies document negative consequences of increasing rearing density on larval developmental parameters (Breden and Chippendale, 1989; Ferguson et al., 1994; Goulson and Cory, 1995; Kazimirová, 1992). One method of separating the effects of crowding from the effects of cannibalism is to compare variation in development within each cannibalism treatment according to the number of larvae cannibalized. Larvae that cannibalized little are presumably subject more to the effects of crowding, whereas larvae that consumed many conspecifics will have been affected less by crowding and more by the direct consequences of cannibalizing. This approach reveals that larvae engaging in greater amounts of cannibalism had a lower pupal weight but a faster development time than less cannibalistic larvae when food availability was low. From this, we tentatively conclude that the presence of conspecifics that are not cannibalized may decrease development rate, but that the act of cannibalism seems to result in reduced pupal weight. The adverse effect of cannibalism on size may be explained by one or more of the following processes. Defensive responses from victims may have inflicted injuries, thus reducing the fitness of the cannibals. Furthermore, consumption of conspecific tissues may be maladaptive if the victim contains high levels of toxins or is infected with harmful microorganisms. Indeed, we have previously demonstrated that cannibalism of infected larvae may lead to transmission of pathogens (Chapman et al., in press).

If cannibalism is costly, then why are larval *S. frugiperda* such voracious intraspecific predators? It appears that the mere presence of conspecifics slowed down larval development, particularly when alternative food was scarce. Cannibalism may therefore confer indirect benefits through the removal of competitors, consequently alleviating the detrimental effects of increased density. In this study, rearing density

was kept constant by successive additions of fresh larvae, thus possibly obscuring any beneficial effects of the removal of conspecifics. Further work is required to elucidate whether other fitness benefits may accrue from cannibalism (such as reduced predation and parasitism) to explain the high incidence of cannibalism in *S. frugiperda*.

Our results demonstrate that the rate of cannibalism of younger conspecifics by *S. frugiperda* larvae was not dependent on the sex of the cannibal. Previously, we also demonstrated a lack of a sexual bias in cannibalism rates among cohorts of same age larvae (Chapman et al., in press). *Spodoptera frugiperda* is unusual in this respect, as females were found to be more cannibalistic than males in 86% of species studied (reviewed in Polis, 1981). It has been suggested that the greater incidence of cannibalism by females of many species is related to their higher energetic requirements, particularly egg maturation and oviposition (Church and Sherratt, 1996). However, we failed to reveal an increase in body mass associated with cannibalism, which may explain the lack of a sexual bias in this species.

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). T. Williams received additional support from SIBEJ A-03.

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