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The potential of *Chrysoperla rufilabris* and *Doru taeniatum* as agents for dispersal of *Spodoptera frugiperda* nucleopolyhedrovirus in maize

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Abstract

The behaviour of two abundant predators in Mesoamerican maize crops, *Chrysoperla rufilabris* larvae and *Doru taeniatum* adults, towards healthy and nucleopolyhedrovirus-infected *Spodoptera frugiperda* larvae was compared. *C. rufilabris* did not discriminate between healthy and virus-infected prey, although the mean search time was approximately two times longer towards virus-infected larvae. In contrast, *D. taeniatum* directed a greater proportion of their attacks towards virus-infected prey but there was no significant difference in the search time. Prey consumption time did not differ significantly for each type of prey by either predator, although prey consumption was much faster in *D. taeniatum*. Viable virus was detected in *D. taeniatum* faeces up to 3 d after feeding on infected *S. frugiperda* larvae, whereas virus was inactivated in the gut of *C. rufilabris*. Both predators were shown to have acidic guts. A field experiment demonstrated that *D. taeniatum* that had fed on infected prey could contaminate foliage resulting in the transmission of the disease at a low prevalence (4.7%) to *S. frugiperda* larvae in a field maize crop.

Introduction

The fall armyworm, *Spodoptera frugiperda* (J. E. Smith), is one of the major insect pests of maize in the Americas and can cause losses of 15 to 73% in grain yield, when infestation levels exceed 55% (Hruska & Gould, 1997). This pest suffers attack from a diversity of natural enemies that normally inhabit ephemeral crop habitats, such as maize and sorghum (Wheeler et al., 1989; Clark et al., 1994).

The multiple-embedded nucleopolyhedrovirus of *S. frugiperda* (SfMNPV) has been recognized to have potential as a biological insecticide for the control of this pest (Young & Hamm, 1966; Moscardi, 1999). The geographical distribution of this virus extends from the USA to Argentina (Fuxa, 1982; Vera et al., 1995) coinciding with that of the host (Andrews, 1980). The virus is highly host-specific and is not known to naturally infect other insect species (Blissard et al., 2000).

Baculoviruses are transmitted when a susceptible larvae consumes foliage contaminated with viral occlusion bodies (OBs). In the alkaline midgut of the host, the protein matrix of the OB dissolves liberating enveloped virions that generally infect the gut cells (Granados & Williams, 1986). Several days later, infected larvae become pale and flaccid and typically die hanging from plant foliage. Following death, the host integument ruptures releasing enormous numbers of progeny OBs that contaminate surrounding plant foliage by the action of rainfall, wind, gravity or biotic factors (D'Amico & Elkinton, 1995; Goulson, 1997).

Several types of predators have been shown to be potential agents of dispersal of insect baculoviruses. The mechanism for dispersal may be twofold. First,

predators that consume baculovirus infected larvae may excrete viable viral OBs in their faeces for periods of several days following the meal (Beekman, 1980; Young & Yearian, 1987; Vasconcelos et al., 1996). Second, natural enemies may become superficially contaminated during the consumption of baculovirus infected larvae, and may physically disperse the virus over plant surfaces on their feet or other body parts (Sait et al., 1996). Predator mediated baculovirus dispersal has been demonstrated to be an important mechanism for virus dissemination in a diversity of crop and forest habitats (Smirnoff, 1959; Biever et al., 1982; Young & Yearian, 1987, 1992; Entwistle et al., 1993; Fuxa & Richter, 1994).

Two common predators of *S. frugiperda* in maize crops in Mesoamerica are *Chrysoperla rufilabris* (Burmeister) (Neuroptera: Crysopidae) and *Doru taeniatum* (Dohrn) (Dermaptera: Forficulidae) (Painter, 1955; van Huis, 1981; Passoa, 1983). The earwig *D. taeniatum* can be particularly abundant in late season maize and is recognized as an important agent of pest control in the region (van Huis, 1981; T. Williams & R.D. Cave, unpubl.).

The SfMNPV has recently been characterized (Escribano et al., 1999) and is currently being developed as a biological insecticide for Mesoamerican maize growers (Williams et al., 1999). The objective of the present study was to evaluate the possible impact of virus applications on predatory behaviour and the potential of these predators as agents of virus dispersal in the maize crop.

Materials and methods

Larvae of *C. rufilabris* were obtained from a laboratory colony maintained at CIICA (Centro Internacional de Investigación y Capacitación Agropecuaria), Frontera Hidalgo, Chiapas, Mexico. Adults of *D. taeniatum* were collected in maize crops within a 12 km radius of Tapachula, Chiapas, Mexico, from March 1998 to May 1999. Both species were maintained in the laboratory at 26±2 °C, L12:D12 photoperiod, and fed every 24–48 h with *Galleria mellonella* (L.) (Lepidoptera: Pyralidae) or *S. frugiperda* larvae.

The multiple nucleopolyhedrovirus used in this study was originally isolated from *S. frugiperda* larvae in Nicaragua (Escribano et al., 1999). The virus was propagated in *S. frugiperda* larvae maintained on a semisynthetic diet based on ground maize and soya bean (modified from Mihm, 1984). Viral occlusion bodies (OBs) were extracted by homogenizing virus-killed larvae in 0.1% sodium dodecyl sulphate (SDS), followed by centrifugation at 84 g for 5 min. The resulting supernatant was transferred to a new tube and centrifuged at 756 g for 5 min. The resulting pellet was suspended in 250 μl of distilled water, layered onto 30% (w/v) sucrose solution, and centrifuged at 15 300 g for 30 min. The final pellet was suspended in distilled water and quantified, using a bacterial counting chamber and phase contrast microscope. Experimental second instar *S. frugiperda* larvae were infected with an LD_{99} dose (5000 OBs) (Escribano et al., 1999) of this suspension, using the diet plug method (Hunter-Fujita et al., 1998).

Predatory behaviour towards virus-infected larvae. Single third instar *C. rufilabris* larvae were individually introduced into the centre of 100 mm diameter Petri dishes, containing one healthy and one infected (48 h post-infection) *S. frugiperda* larva, placed at opposite sides of the Petri dish. The *S. frugiperda* larvae were allowed to move freely within the Petri dish during the course of the experiment. The behaviour of the *C. rufilabris* larva was observed for 30 min to determine the number and type (infected/healthy) of larvae consumed, the interval between introduction of the predator and the first attack (search time) and the time taken to consume each *S. frugiperda* victim. The experiment was replicated 100 times with a new *C. rufilabris* in each repeat. Results were analyzed by Mann–Whitney U test and χ^2 test. An identical procedure was followed using adults of *D. taeniatum*.

Passage of virus through the predator gut. Third instar *C. rufilabris* larvae (n=50) were fed virus-infected second instar *S. frugiperda* (48 h post-infection) larvae. At 24 h intervals thereafter, *C. rufilabris* were individually transferred to sterile plastic pots and offered a dead *G. mellonella* larva that had been boiled for 1 min to eliminate microbial contaminants. Larval *C. rufilabris* do not defecate, but produce a faecal meconium pellet following adult emergence. The interval between consumption of virus-infected prey and production of faecal meconia was 10–12 days in this experiment. Meconium pellets were collected from individual *C. rufilabris* using a sterile toothpick and suspended in 100 μl of sterile distilled water using a votex mixer. This suspension was examined microscopically to determine qualitatively the presence of viral OBs and 1 μl aliquots were bioassayed for infectivity in 30 second-instar *S. frugiperda* larvae, using

the diet plug method. Bioassay larvae were subsequently maintained on semisynthetic diet at 26±1 °C and examined daily to determine the prevalence of virus-induced mortality. An equal number of control *C. rufilabris* were fed healthy *S. frugiperda* larvae and faecal meconia were analyzed as described above. The experiment was also performed using *D. taeniatum* adults (n=50) in an identical manner to that of *C. rufilabris*, except that faecal material was collected and bioassayed on a daily basis following consumption of the virus-infected larva, rather than as single meconial pellet as was the case of *C. rufilabris*. Mortality data were analyzed using GLIM with a binomial error structure. Minor overdispersion in the binomial data was corrected using the Williams' adjustment of overdispersion macro present in this program (Crawley, 1993).

Analysis of gut pH. Baculovirus OBs are sensitive to alkalinity and are rapidly degraded at pHs greater than pH 9.0 (Griffith, 1982). To determine the pH of the predator's gut, *C. rufilabris* larvae and *D. taeniatum* adults were fed a 10% honey solution containing one of the following pH indicators: 0.5% congo red (pH 3.0–5.0), 0.5% methyl red (pH 4.2–6.3), 0.5% chlorophenol red (pH 5.2–6.8), 0.1% neutral red (pH 6.8–8.0), 0.01% phenol red (pH 6.8-8.4), 0.05% thymol blue (pH 8.0-9.6) and 0.5% carmine indigo (pH 11.6-14.0). One hour after consuming the honey-indicator mixture, the predators were dissected and the colour of the intestine was noted. The experiment was replicated 10 times for each species of predator. The pH of *C. rufilabris* meconia was also measured directly by homogenizing 10 meconia in 1 ml of sterile distilled water and measuring the pH using a pH meter (Corning Inc., N.Y.). This procedure was replicated four times.

Field trial. To determine the ability of *D. taeniatum* as an agent of virus dispersal in the field, an experiment was performed during the period September - November 1999 in a maize crop planted in the Ejido Morales (14°50′ N, 92°20′ W), 10 km south-east of the town of Tapachula, Chiapas, Mexico.

Individual maize plants approximately 50 cm tall that did not show signs of *S. frugiperda* infestation, were randomly selected and allocated to one of three treatments. Each experimental maize plant was an average distance of 170 cm, or seven maize plants away from any other experimental plant, such that each plant represented a single independent replicate. Treatments involved placing five *D. taeniatum* adults on the top third portion of the maize plant which was then enclosed by a nylon mesh bag 35 cm tall and 20 cm wide, gently tied at the base to minimize insect movement. One day prior to the trial, earwigs were fed a single meal of healthy or virus-infected *S. frugiperda* larvae (48 h post-infection). Prey items available to experimental earwigs comprised natural infestations of aphids, thrips, etc., present on the maize plants. Control plants were not infested with earwigs. Each treatment was replicated 40 times.

After 48 h, the bags were opened and earwigs removed. Each experimental plant was then infested with five healthy second instar *S. frugiperda* larvae taken from the laboratory culture. The bags were replaced and tied as mentioned above. After 5 days, the bags were removed and *S. frugiperda* larvae were recovered, taken to the laboratory, individually transferred to semisynthetic diet and checked daily for virus-induced mortality. All virus deaths were confirmed by microscopic examination of Giemsa-stained smears of infected insects. Data were analyzed using GLIM with a binomial error structure appropriate to the proportional nature of the mortality data. As such, standard errors and confidence limits of means are asymmetrical (Crawley, 1993).

Results

Predatory behaviour towards virus-infected larvae. Due to the high dose of virus consumed, by 48 h post-infection *S. frugiperda* larvae were paler and less vigorous than healthy conspecifcs. The *C. rufilabris* larvae did not appear to discriminate between healthy (32 attacks) and virus-infected (29 attacks) *S. frugiperda* larvae (χ^2=0.64, d.f.=1, P>0.05). The mean search time of *C. rufilabris* larvae was, however, approximately two times greater towards virus-infected larvae compared to healthy larvae (Mann–Whitney U=0.02, P<0.05) (Figure 1), whereas the mean consumption time did not differ significantly for each type of prey (Mann–Whitney U=0.42, P>0.05) (Figure 2).

In contrast, *D. taeniatum* adults directed a greater proportion of their attacks towards virus-infected *S. frugiperda* larvae (27 attacks) compared to healthy larvae (12 attacks) (χ^2=7.1, d.f.=1, P<0.01). There was, however, no significant difference in the search time (Mann–Whitney U=0.90, n=100, P>0.05) (Figure 1) or consumption time (Mann–Whitney U=0.45, n=100, P>0.05) of *D. taeniatum* toward each type of

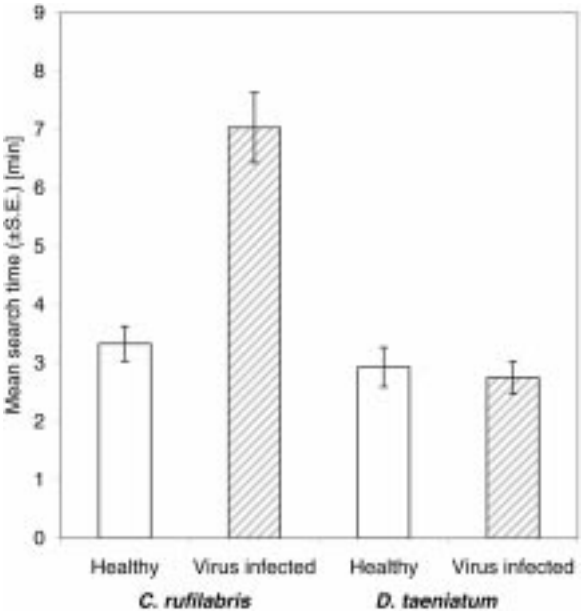

Figure 1. Mean search time for *Chrysoperla rufilabris* larvae and adult *Doru taeniatum* when simultaneously offered healthy or virus-infected second instar *Spodoptera frugiperda* larvae in a Petri dish arena.

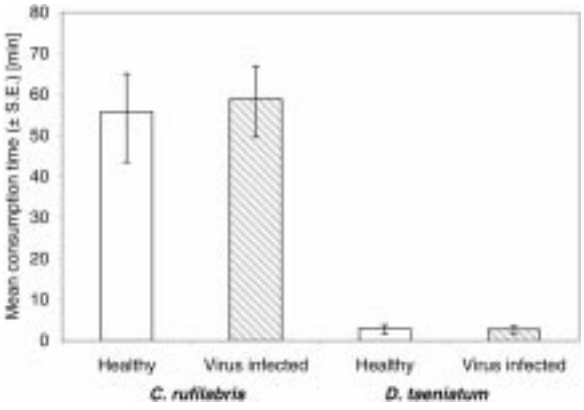

Figure 2. Mean consumption time of healthy or virus-infected second instar *Spodoptera frugiperda* larvae by *Chrysoperla rufilabris* larvae and adult *Doru taeniatum*.

prey (Figure 2). The mean prey consumption time for *C. rufilabris* was 55–59 min, much greater than the 3 min taken for prey consumption by *D. taeniatum* (Figure 2).

Passage of virus through the predator gut. None of the meconia collected from *C. rufilabris* that had fed upon virus-infected or healthy *S. frugiperda* larvae caused virus-induced mortality in the bioassays. Viral OBs were not observed in the suspension of faecal meconia or in samples observed in a scanning

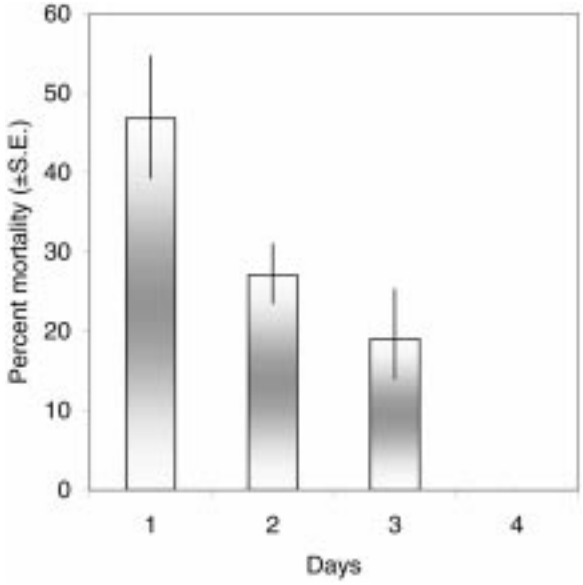

Figure 3. Mortality of *Spodoptera frugiperda* larvae following bioassay of faeces of *Doru taeniatum* adults that had fed on virus-infected *Spodoptera frugiperda* larvae at 1 to 4 days previously.

electron microscope. In contrast, viral OBs were observed in the faeces of *D. taeniatum* and bioassay of these samples caused virus-induced mortality in *S. frugiperda* larvae. There was a significant decline in virus-induced mortality over time (χ^2=33.6, d.f.=2, P<0.001) indicating that the concentration of virus in earwig faeces decreased during this period (Figure 3). After 4 days, no virus was detected in earwig faecal samples.

Analysis of gut pH. Experiments with pH indicators confirmed that both predators had acidic guts. The range of pH of the *C. rufilabris* gut was pH 4.2–5.2 which was more acidic than the gut of *D. taeniatum* (pH 5.2–6.8). Suspensions of *C. rufilabris* meconia in sterile distilled water had a pH of 5.75–5.84. The inactivation of viral OBs in the *C. rufilabris* gut must, therefore, be related to factors other than alkaline gut conditions.

Field trial. Recovery of *S. frugiperda* larvae from maize plants was high (3.07±0.15 larvae/plant) (mean ± S.E.) and did not differ significantly between treatments (χ^2=3.69, d.f.=2, P>0.05). This was to be expected, as all earwigs had been removed from experimental plants prior to the introduction of *S. frugiperda* larvae. No virus infection was observed in larvae collected from control plants or plants previously in-

fested with earwigs fed healthy larvae. The prevalence of virus infection observed in *S. frugiperda* larvae recovered from plants previously infested with virus-fed earwigs was 4.7% (range of S.E. 3.0–7.2). Other causes of *S. frugiperda* mortality included parasitism by nematodes or insect parasitoids (1.4–4.6%) or bacterial infections (4.8–7.4%), but these did not show treatment-related differences.

Discussion

Observation of *C. rufilabris* and *D. taeniatum* predatory behaviour toward healthy and virus-infected *S. frugiperda* larvae revealed differences in the search time and frequency of predation of each type of prey. *C. rufilabris* larvae attacked healthy prey more rapidly than infected prey, possibly because healthy prey were more vigorous and thus more apparent to the predator compared to virus-infected prey. In contrast, *D. taeniatum* showed a preference to attack virus-infected prey, possibly because diseased prey offered less resistance to predation than healthy *S. frugiperda* larvae. Adult *D. taeniatum* were more voracious in consuming prey items (Figure 2), probably due to its greater size compared to *C. rufilabris* larvae, although the implications of the different prey consumtion times for the degree of surface contamination of each predator species are not known.

Similar observations have been reported in studies of the behaviour of other types of predators towards virus-diseased lepidopteran larvae. Vasconcelos et al. (1996) reported no difference in the consumption of healthy and virus-infected *Mamestra brassicae* (L.) (Lep.: Noctuidae) larvae by two species of carabid beetles. In contrast, Young & Kring (1991) observed a preference to attack virus-infected *Anticarsia gemmatalis* (Hubner) (Lepidoptera: Noctuidae) larvae by the predator *Nabis roseipennis* Reuter (Hemiptera: Nabidae), which they interpreted as a lack of defence response in moribund diseased prey.

It is often observed that baculovirus OBs pass through the predator gut without significant loss of infectivity (Beekman, 1980; Abbas, 1988). This is because the gut of most insect predators is acidic, in contrast to the highly alkaline guts of phytophagous Lepidoptera that degrade the proteinaceous matrix of the viral OB resulting in the release of virions and the subsequent infection of cells lining the host midgut (Granados & Lawler, 1981). The activity of virus following passage through the gut was maintained in *D. taeniatum*, but not in *C. rufilabris* for reasons that are not clear, but which appear not to be related to gut pH as both predators were shown to have acidic guts. It is unlikely that *S. frugiperda* larvae consumed by *C. rufilabris* were not infected, as similar larvae consumed by *D. taeniatum* resulted in viable viral OBs in the faeces. An alternative explanation is that virus was not voided in the meconia of *C. rufilabris*, or that this species has gut proteases capable of degrading viral OBs. The period of virus exposure to gut enzymes was 10–12 days in *C. rufilabris*; much longer than the 1–3 days for virus consumed by *D. taeniatum*.

The period during which viable virus is detectable in the faeces of virus-fed predators varies from 24 h for nymphal Hemiptera, 4–6 days for species of adult hemipteran predators and up to 15 days for *Harpalus rufipes* De Geer (Coleoptera: Carabidae) (Abbas & Boucias, 1984; Vasconcelos et al., 1996). Although *H. rufipes* excreted virus over an extended period, a field experiment involving release of virus-fed carabids into cabbage plots that were subsequently infested with *M. brassicae* larvae, resulted in low levels (2.8–6.5%) of infection of larvae (Vasconcelos et al., 1996), similar to that observed in the field trail reported here. The prevalence of infection detected in the field trail may have been greater if the interval between infection of *S. frugiperda* larvae and consumption by *D. taeniatum* had been extended, as the concentration of virus in infected hosts increases exponentially over time (Cherry et al., 1997).

Among the factors that influence the dispersal of baculoviruses, different studies have demonstrated that predators are important agents of virus dissemination in agricultural and forest habitats (Capinera & Barbosa, 1975; Biever et al., 1982; Fuxa et al., 1993; Fuxa & Richter, 1994). Birds and parasitoid wasps appear capable of acting as baculovirus vectors over even greater distances (Irabagon & Brooks, 1974; Levin et al., 1983; Hochberg, 1991; Caballero et al., 1991; Entwistle et al., 1993). Little is known of the dispersal rates of *D. taeniatum*, but they are clearly capable of transporting virus.

Doru taeniatum can be particularly abundant in late-season maize crops in Mesoamerica, commonly reaching densities exceeding 100 adults per plant, and pest control measures may be unnecessary when natural enemy populations attain high densities (T. Williams & R. D. Cave, unpubl.). This species is known to be an important predator of *S. frugiperda* eggs and young larvae (van Huis, 1981; Jones et al., 1988). Moreover, a recent study demonstrated that

the presence of *D. taeniatum* was positively correlated with signs of *S. frugiperda* feeding damage on maize plants, suggesting that this predator is attracted to infested plants (Chapman et al., 2000). This would increase the likely impact of *D. taeniatum* as an agent of virus dispersal following the application of virus inocula for *S. frugiperda* control in the field. In contrast, the ability of *C. rufilabris* to disseminate virus appears to be restricted to movement of OBs onto plant surfaces from individuals that have been surface contaminated by previous contact with virus. This mechanism has been demonstrated for female *Venturia canescens* (Gravenhorst) parasitoids that have oviposited in granulovirus-infected lepidopterans (Sait et al., 1996), although this was not tested in the present study.

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