Movement of Nuclear Polyhedrosis Virus into Velvetbean Caterpillar (Lepidoptera: Noctuidae) Larval Populations on Soybean by *Nabis roseipennis* (Heteroptera: Nabidae) Nymphs[1]

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ABSTRACT *Nabis roseipennis* Reuter nymphs that preyed on larvae of the nuclear polyhedrosis virus (NPV) infected velvetbean caterpillar, *Anticarsia gemmatalis* (Hübner), excreted the virus (AgNPV) for several days thereafter. Based on bioassays, fifth instar and second instar nymphs excreted 84.7 x 10^5 and 9.7 x 10^5 polyhedral inclusion bodies (PIB) per nymph, respectively. The AgNPV-contaminated nymphs effectively disseminated the virus via the feces over soybean plants where it served as inoculum to initiate disease in larval populations of *A. gemmatalis* caged in the field. Larval mortality from AgNPV ranged from 11.4 to 48.5% over treatments in two tests. Larval mortality in treatments where the source of virus inoculum was AgNPV-contaminated fifth instar nymphs was similar to that in treatments where the source of viral inoculum was diseased larvae. Larval mortality resulting from AgNPV dissemination by the nymphs was usually higher in treatments containing fifth instar nymphs than in those with second instar nymphs. Dissemination of NPV by fifth instar nymphs was higher in mixed-age than in uniformed-age *A. gemmatalis* larval populations. This was not the case with the smaller second instar nymphs.

KEY WORDS Nuclear polyhedrosis virus, *Anticarsia gemmatalis*, velvetbean caterpillar, *Nabis roseipennis*, soybean, virus dispersal.

Insects that prey upon baculovirus-infected lepidopterous larvae are not susceptible to the virus but have been demonstrated to excrete the infectious virus taken with the meal in their feces over a period of days, e.g. the hemipterans *Rhinocorus annulatus* L. (Franz et al. 1955), *Nabis tasmanicus* (Het.) (Beekman 1980), *Oechalia schellenbergii* (Guerin-Meneville) (Cooper 1981), *Podisus maculiventris* (Say) (Abbas and Boucias 1984) and *Nabis roseipennis* Reuter (Young and Yearian 1987). Because these predators spend a great deal of time searching host plants of the prey, infectious virus may be defecated on the plants. Although it has often been suggested that this source of virus may be important in spreading the disease (Hostetter, 1971; Ignoffo, 1978; Beekman, 1980; Cooper, 1981), the role of predators in dissemination of baculoviruses in host populations is not well understood.

Young and Yearian (1987) reported that when *N. roseipennis* adults were fed on diseased larvae of velvetbean caterpillar, *Anticarsia gemmatalis* Hübner and caged with uninfected larvae, on individual soybean plants, up to 16.8% of the larvae died from a nuclear polyhedrosis virus (NPV) infection. However, this test was conducted on caged single plants where the insects were confined to

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the plant. Boucias et al. (1987) reported that after initiation of disease in *A. gemmatalis* populations by application of NPV (AgNPV) to plots in soybean fields, virus was detected in invertebrate predators collected within and outside of treated areas. They considered the predators to play an important role in maintaining and disseminating the virus in the soybean fields.

The *Nabis* spp. complex is an important group of predators on crops in the southern United States (Turnipseed and Kogen 1976, Funderburk and Mack 1989). *Nabis roseipennis* is the predominant species on soybean (Harper et al. 1983, McCarty et al. 1980). The population of *N. roseipennis* on soybean often consists primarily of nymphs that have hatched within the field. The nymphs, also predaceous, may be important disseminators *of* NPV. Beekman (1980) reported that both adult and large nymphal *N. tasmanicus* (Het.) excreted comparable amount of infective AgNPV after preying on an infected *Heliothis punctigera* Wall.

The objective of the tests reported herein was to determine the potential of *N. roseipennis* nymphs to introduce AgNPV to uninfected *A. gemmatalis* larvae on soybean. The tests were conducted in large field cages (1.8x3.7x1.6m) so that predator movement and searching more closely approximated natural conditions. Adult *N. roseipennis* were included in one test for a direct comparison with nymphs.

Materials and Methods

Anticarsia gemmatalis larvae were obtained from a culture maintained in a laboratory on semisynthetic diet (Greene et al. 1976). *Nabis roseipennis* were maintained in a laboratory culture using *Pseudoplusia includens* Walker larvae as prey as described by Young and Yearian (1987).

The AgNPV was isolated from diseased larvae, collected from soybean in Brazil (Carner and Turnipseed 1977). The virus was propagated in larvae reared on semisynthetic diet and partially purified by blending and filtering through organdy (cotton muslin). The AgNPV concentration was standardized for polyhedral inclusion bodies (PIB) per ml of an aqueous suspension under a phase contrast microscope using a Neubauer hemacytometer.

Larvae infected for use as *N. roseipennis* prey or to be released on plants as the initial virus source were treated with AgNPV in 270-ml, waxcoated paper cups (10/cup) by the diet surface treatment technique at a dosage of 140 polyhedral inclusion bodies (PIB)/mm^2 of diet surface. The larvae were held on the treated diet for 24 h at 27±1°C and transferred to an untreated diet until death, which occurred usually at 4 days after treatment. The larvae were treated as either second or early third instars and served as prey for small or large nymphs, respectively. Infected larvae for release on plants were treated similarly as second instars.

Following a 24-h starvation period, *N. roseipennis* were offered a single *A. gemmatalis* larva that was either healthy or in late stages of AgNPV infection. Larvae were determined to be in late stages of infection by their chalkish white appearance and lethargic nature. Only predators that attacked a larva were used in the tests.

Data in all tests were subjected to analysis of variance and mean separation with the SYSTAT procedure Multivariate General Linear Hypothesis (MGLH) (Wilkinson 1986).

Test #1: *Anticarsia gemmatalis* NPV Activity in Excreta. Small (2nd instar) and large (5th instar) nymphs were placed individually on a moistened filter-paper disk in a 28-ml clear plastic container that contained a healthy larva in late stages of disease. After the nymph ceased feeding, it was removed from the container, and the container with filter paper and larval remains was frozen at -20°C until bioassay. The nymph was transferred to a dampered filter paper disk in another clear 28-ml plastic container containing two healthy third instar larvae as a source of food. The nymph was transferred similarly thereafter for each of the succeeding 10 days. Each day the container from which the nymph was transferred was frozen until assayed. Nymphs that died during the test were frozen at time of death. After 10 days all remaining nymphs were frozen until assayed. The treatment was replicated four times and each replication consisted of 10 nymphs that had fed on an infected larva.

Virus activity in the frozen samples was assayed by the diet surface-virus treatment method (Ignoffo 1966) using individual neonate *A. gemmatalis* larvae as described by Young and Yearian (1987). Viral activity was assayed using 10 larvae per dilution. Larval mortality from virus was recorded at pupation, and viral activity (PIB) in bioassays was quantified using previously determined dosage mortality curves (Young and Yearian 1986) (LC_{50}, 0.05 PIB/mm^2; 95% FL, 0.007 and 0.461; slope = 1.07). Prior to analysis data were subjected to the log (X + 1) transformation to control variation prior to analysis (Taylor 1970).

Test #2: Predator vs Larval Transmission on Soybean. The test was conducted to compare transmission of AgNPV into a uniform-aged larval population by diseased larvae and large (5th instar) nymphal and adult predators. The test was conducted in a field of 'Centennial' variety soybean planted May 9, 1987, at the Main Agricultural Experiment Station, Fayetteville, Arkansas.The test was initiated when plants were predominately V-13 (Fehr et al., 1971) and 1.0 m in height. Two days before larvae release, saran screen (100-mesh) cages (1.8x3.7x1.6 m) were placed over a single row of soybeans 2 m in length for 48 h. Mevinphos (Shell Chemical Co.) (0.56 kg [Ai]/ha, half-life 12 h) was sprayed on the caged plants to eliminate pest competitors and natural enemy populations. The cages were separated by a 2-m buffer.

Healthy 3-d-old (predominately second instar) *A. gemmatalis* larvae were transferred to the soybean plants in all cages at 80 larvae/m of row using a 00 sized camel-hair brush and were allowed 2 hr to establish. Two initial sources of AgNPV were then introduced into cages: (1) 5-day-old larvae in late stages of disease or (2) *N. roseipennis* (large nymphs or adults) that had preyed on an infected larva within 4 hours of the release.

The test was a completely randomized design with each cage representing a plot. There were 10 treatments (10 cages) (Table 2), and the test was replicated four times. Treatments were fifth instar nymph or adult *N. roseipennis* at a density of 12 per meter of row with the following sources of AgNPV inoculum: (1) 12 infected larvae/m, (2) *N. roseipennis* that had preyed on an infected larva, (3) AgNPV sources 1 and 2 and (4) no source of AgNPV (controls). In

addition, there were two treatments that contained larvae but not *N. roseipennis:* (1) 12 infected larvae per~m and (2) no source of AgNPV.

After 4 days larvae were counted and collected from the cages by the drop cloth method (Boyer and Dumas 1963). Larvae (or a subsample of 25 per treatment) were placed individually on diet and reared at 27±1C° to pupation. Total larval mortality and mortality from AgNPV were recorded.

Test #3: Predator Transmission in Uniform and Mixed-aged Larval Population on Soybean. This test was conducted to compare AgNPV transmission in uniform- and mixed-age larval populations by small and large nymphal *N. roseipennis.* The test was conducted in a field of 'Centennial' soybean planted May 11, 1988. The test location and procedures were as previously described unless stated below.

There was a total of 10 treatments (10 cages) (Table 3), each replicated four times. Treatments consisted of all combinations of two larval population ages (uniform- or mixed-age), two *N. roseipennis* sizes (small [2nd instar] or large [5th instar] nymphs), and two *N. roseipennis* AgNPV contamination regimes (nymph preyed on a healthy larva or an infected larva). There were two controls in which *N. roseipennis* were not released (uniform- and mixed-age larvae). In the five treatments with uniform-aged larvae, the larvae (3-day old) were released in cages on the same day (day 0). In the mixed-aged treatments, one-third of the total number of larvae was released in each cage on each of 3 days over the period of a week (days 0, 3, and 7). The predators were all released on day 0.

Larvae were collected from plants in all treatments using the drop cloth method. The first collection was made in 1.0 m of row on day 8. In the mixed-age treatments a second collection was made on day 14. Larvae (or a subsample of 25 per treatment per collection) were placed on diet and reared, and data were recorded as in the previous test.

Results and Discussion

Test 1: AGNPV Activity in Excreta. The *N. roseipennis* nymphs that had preyed on an infected larva excreted active AgNPV for several days thereafter (Table 1). For the large nymphs, excretion of virus was highest on the first day then decreased over the 10-day period. There was a decrease in virus activity for the remainder of the 10-day period. Assay of nymphs homogenized after 10 days revealed only negligible quantities of viral activity. Activity in excreta of small nymphs was highest (6.3×10^5 PIB/nymph) on the second day and likewise decreased over the 10-day period. Activity was not detected in excreta of small nymphs beyond day 7. The total activity in excreta during the test was higher in large nymphs than small nymphs, 84.7×10^5 PIB to 9.7×10^5 PIB per nymph, respectively. Although the nymphs that had attacked an infected larva secreted large numbers of polyhedra, the quantities were only small percentages of the total polyhedra in prey larvae. The remains of infected larvae that served as prey for large and small nymphs contained a mean of $1.5 \times 10^8 \pm 0.3 \times 10^8$ PIB/larva and $1.3 \times 10^7 \pm 0.5 \times 10^7$ PIB, respectively.

In this test *N. roseipennis* nymphs that preyed upon infected larvae excreted AgNPV over a period of several days in a manner similar to that previously reported for adults (Young and Yearian 1987). The results suggested that the

Table 1. Mean number of AgNPV PIB (± SEM) in excreta of N. roseipennis nymphs fed an infected larva.

Days after predator attacked infected larva	Size of nymph*	
	Small†	Large†
1	$4.9 \pm 0.7 \times 10^4$ b	$5.3 \pm 1.1 \times 10^6$ a
2	$6.3 \pm 2.8 \times 10^5$ a	$2.0 \pm 0.6 \times 10^6$ ab
3	$2.8 \pm 1.4 \times 10^5$ ab	$6.0 \pm 2.1 \times 10^5$ bc
4	$1.3 \pm 0.6 \times 10^4$ c	$3.2 \pm 0.8 \times 10^5$ c
5	$2.3 \pm 1.4 \times 10^3$ d	$2.8 \pm 1.1 \times 10^5$ cd
6	$8.1 \pm 6.7 \times 10^2$ de	$1.9 \pm 0.2 \times 10^5$ de
7	$6.0 \pm 4.6 \times 10^1$ e	$1.9 \pm 0.5 \times 10^4$ e
8	0.0	$2.9 \pm 0.5 \times 10^4$ e
9	0.0	$4.9 \pm 3.5 \times 10^3$ f
10	0.0	$5.6 \pm 4.6 \times 10^3$ f

* Data were subjected to the log (x + 1) transformation to control variation (Taylor 1970) prior to analysis. Means within a column followed by the same letter(s) are not significantly different ($P = 0.05$; Wilkinson, (1986) analysis of variance SYSTAT procedure MGLH).

† Small nymphs were second instar and large nymphs were fifth instar.

quantity of AgNPV excreted by large nymphs (8.5×10^6 PIB/larva) may have exceeded that for adults ($5.3 \pm 0.9 \times 10^6$ PIB/adult). It must be noted, however, that the large nymphs were offered infected fourth instar larvae that were larger and contained approximately five times more PIB's than the infected third instar larvae that had been offered to the adults (Young and Yearian 1987). By feeding on larger larvae, the large nymphs may have consumed a greater quantity of virus. Large *N. tasmanicus* nymphs that fed on AgNPV-killed *H. punctigera* were previously found to excrete quantities of inoculum similar to those of adults (Beekman 1980).

Test 2: Predator vs Larval Transmission. Mortality from AgNPV of larvae collected from treatments with either AgNPV-contaminated *N. roseipennis* or infected larvae ranged from 11.4 to 16.2% and did not differ significantly between treatments (Table 2). In treatments with infected larvae as the sole source of inoculum, the presence of non-contaminated predators did not alter larval mortality from NPV. In the two treatments with both primary sources of virus inoculum (*Nabis* + inf. larvae), similar levels of mortality were produced when the *Nabis* source was nymphs (25.3%) or adults (36.0%), but only the treatment containing AgNPV-contaminated adults had significantly higher mortality than treatments containing only a single primary source of virus inoculum ($P = 0.05$). Mortality from AgNPV did not occur in treatments in the collection without a source of virus inoculum. Mortality from causes other than virus was low, not exceeding 9.0% in any treatment, and did not differ among treatments.

Table 2. Mortality (% ± SEM) from AgNPV and mean density (± SEM) of A. gemmatalis larvae recovered from caged soybean containing either NPV-infected larvae or N. roseipennis that have preyed on infected larvae as an AGNPV inoculum source (*).

Treatment		Mean % mortality (± SEM) from NPV(†)	Mean No Larvae Recovered (± SEM)/ row-meter(†)
Nabis Stage Released in cages	AgNPV† Source(s) in cages		
Adult	Adult only	11.4 ± 2.0 bc	27.2 ± 7.8 bc
Nymph	Nymph only	11.6 ± 2.9 bc	38.9 ± 13.0 b
Adult	inf. larvae only	15.5 ± 5.0 b	20.9 ± 6.4 c
Nymph	inf. larvae only	16.2 ± 4.5 b	35.2 ± 7.5 bc
Adult	Adult & inf. larvae	36.0 ± 11.5 a	26.0 ± 11.0 bc
Nymph	Nymph & inf. larvae	25.3 ± 9.5 ab	37.1 ± 11.7 b
Adult	–	0 c	26.6 ± 6.7 bc
Nymph	–	0 c	37.1 ± 5.5 b
–	–	0 c	56.7 ± 10.2 a
–	Inf. larvae only	15.5 ± 6.7 b	61.8 ± 12.0 a

* Healthy larvae (80/row-meter) were caged on plants in all treatments.

† Sources of AgNPV inoculum in the cages were 12 per meter of row of infected larvae and/or *Nabis* adult or fifth-instar nymphs that had fed on an infected larva.

† Means within a column followed by the same letter(s) are not significantly different ($P = 0.05$; Wilkinson [1986] analysis of variance SYSTAT procedure MGLH).

Mean larval recovery was 56.7 and 61.8 per meter of row in the treatments without *N. roseipennis;* whereas, in treatments with the predator, recovery was significantly lower, ranging from 20.9 to 41.9 per row-meter (Table 2) ($P = 0.05$). Although predation was high in these treatments, presence or absence of uncontaminated predators in treatments with infected larvae did not alter the level of larval mortality from AgNPV. Thus any AgNPV inoculum predators consumed by preying on infected larvae in the cages appeared not to be important in secondary virus transmission. Larval recovery tended to be lower in *N. roseipennis* adult treatments than in treatments containing nymphs.

Test 3: Predator Transmission in Uniform-and Mixed-age Larval Populations. Mortality from AgNPV in larvae collected from treatments in which AgNPV-contaminated nymphs were released ranged from 14.0-46.0% (Table 3). In collection 1 mean larval mortality from AgNPV was significantly higher in the treatment containing the AgNPV-contaminated large nymphs in uniform-aged populations than in the other treatments ($P = 0.05$). Larval mortality did not differ among treatments containing AgNPV-contaminated small nymphs and the mixed-age population treatment containing AgNPV-contaminated large nymphs.

By the second collection larvae in uniform-aged treatments had pupated. Mortality from AgNPV in mixed-age treatments was only 18.0% in the treatment in which AgNPV-contaminated small nymphs were released. In the treatment containing AgNPV-contaminated large nymphs, mortality from AgNPV

Table 3. Mortality (% ± SEM) from AgNPV and mean density (± SEM) of *A. gemmatalis* larvae recovered from caged soybean containing either uniform- or mixed-age larval populations and small or large *N. roseipennis* nymphs that had preyed on infected larvae.

Nabis size released (AgNPV contaminated)†	Mean % mortality (± SEM) from NPV†	Mean No. larvae Recovered ± (SEM)/ row-meter(*,†)
Collection 1 Uniform-aged larval population		
Small nymph	0.0 c	56.5 ± 7.4 abc
Large nymph	0.0 c	34.3 ± 6.0 d
Small nymph (AgNPV contam.)	14.0 ± 1.2 b	46.7 ± 3.6 abcd
Large nymph (AgNPV contam.)	43.0 ± 7.6 a	42.6 ± 3.5 cd
–	0 c	60.9 ± 5.7 ab
Mixed-aged larval population		
Small nymph	0.0 c	60.7 ± 5.8 ab
Large nymph	0.0 c	44.5 ± 5.9 bcd
Small nymph (AgNPV contam.)	15.0 ± 2.5 b	62.9 ± 6.6 a
Large nymph (AgNPV contam.)	23.0 ± 5.7 b	46.1 ± 4.0 abcd
–	0.0 c	59.6 ± 4.7 abc
Collection 2 Mixed-aged larval population only		
Small nymph	0.0 c	30.1 ± 2.9 bc
Large nymph	3.0 ± 3.0 c	23.6 ± 3.9 c
Small nymph (AgNPV contam.)	18.0 ± 4.8 b	36.8 ± 4.9 b
Large nymph (AgNPV contam.)	46.0 ± 5.3 a	24.0 ± 2.7 c
–	0.0 c	48.7 ± 4.7 a

* Healthy larvae (117/m) were caged on plants in all treatments.

† Means within a collection (col. 1 or 2) in a column followed by the same letter(s) are not significantly different (P = 0.05; Wilkinson [1986] SYSTAT Procedure MGLH).

†Twelve *N. roseipennis* nymphs released per row-meter: (AgNPV cont.) *N. roseipennis* that had preyed on an AgNPV-infected larva before release.

was 46.0%. Larval mortality from AgNPV did not exceed 3.0% in the control treatments in either collection.

In the first collection, mean larval recovery in controls without *N. roseipennis* was 60.9 and 59.6 per meter in the uniform- and mixed-age treatments, respectively (Table 3). Recovery of larvae from treatments with large nymphs was significantly lower (34.3%) than in the control in the uniform-aged populations but not in the mixed-age populations (P = 0.05). Recovery of larvae in treatments with small nymphs did not differ significantly from that in the control without predators. In the second collection (mixed-age populations only), larval recovery was much lower in all treatments with predators than in the predator-free controls. In

treatments containing predators, mean larval recovery was significantly lower in the treatment containing AgNPVcontaminated large nymphs than in treatments with small nymphs ($P = 0.05$), but this was not the case for the treatment containing uncontaminated large nymphs.

Results of the two tests showed that both small and large nymphs disseminated the virus on soybean plants after preying on an AgNPV-infected larva. This virus served as inoculum to infected *A. gemmatalis* larvae. Large nymphs contaminated with AgNPV appeared to spread the virus as effectively as adults, whereas small nymphs were less effective. Results from the cage tests support the findings of the laboratory study, i.e. large nymphs that prey on infected larvae injest and excrete quantities of inoculum similar to that of adults, but small nymphs injest and secrete less virus. AgNPV-contaminated large nymphs and adults disseminated the virus as effectively over the plant as larvae that died of the infection, although results of test #1 showed that larvae that died of disease contained several fold higher quantities of polyhedra than the predators which had attacked them. This suggests that movement of the predator in the plant canopy is an important factor contributing to their effectiveness as disseminators of the disease. The predators may also contaminate their body externally while attacking an infected larva and spread the virus by surface contamination. Also, Biever et al. (1982) reported that *Podisus maculiventris* contaminated externally disseminated an NPV and initiated an epizootic in *Trichoplusia ni* (Hübner) on cabbage.

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