

Journal of Nematology 28(1):1-7. 1996.
© The Society of Nematologists 1996.

Ectoparasitic Acugutturid Nematodes of Adult Lepidoptera¹

A. M. SIMMONS² AND C. E. ROGERS³

Abstract: *Noctuidonema guyanense* is an interesting ectoparasite of adult Lepidoptera that feeds on hosts from at least five families with its long stylet. *Noctuidonema guyanense* spends its entire life on the adult moth and is sustained as it is passed from moth to moth during host mating. Overlapping host generations are essential for parasite survival. This nematode occurs throughout tropical and subtropical America and is transported by at least one of its hosts, *Spodoptera frugiperda*, during migration to northern sites in the United States each spring. *Noctuidonema guyanense* debilitates its hosts. Research conducted to help determine the biological control importance of this nematode is reviewed. Two additional species, *N. daptria* and *N. dibolia*, are now known for *Noctuidonema*.

Key words: Aphelenchoididae, biological control, distribution, ecology, ectoparasite, entomopathogenic nematode, fall armyworm, host range, *Noctuidonema guyanense*, *Spodoptera frugiperda*.

There are only a few known ectoparasitic nematodes of adult insects. *Ektaphelenchus* spp. are facultative ectoparasitic aphelenchoids (12) in the subfamily Entaphelenchinae (11). They are found on larvae, pupae, and adults of wood-boring scolytid beetles. Although facultative parasitic nematodes may feed on insects, they can also complete their life cycle separate from the insect (13). Hunt (3) described an obligate ectoparasitic nematode, *Acugutturus parasiticus* Hunt, from the American cockroach, *Periplaneta americana* (L.), in St. Lucia, West Indies. He proposed placing *A. parasiticus* in a new subfamily, Acugutturinae, in the family Aphelenchoididae. All stages of the nematode were found on the insect's body surface. The nematode feeds on the adult as well as on the nymphal stages of its host (3). *Acugutturus parasiticus* has an unusually long stylet (50–60 μm),

with the conus much longer than the shaft (3).

In 1988, researchers in French Guiana described the first known case of an ectoparasitic nematode from adult Lepidoptera (14). They described this nematode as *Noctuidonema guyanense* Remillet & Silvain, an aphelenchoid, and classified it in the subfamily Acugutturinae (14). Hunt (4) revised the Aphelenchida by placing *Acugutturus* and *Noctuidonema* in separate subfamilies in the Acugutturidae.

Interest in *N. guyanense* as a biological control agent against the fall armyworm, *Spodoptera frugiperda* (J. E. Smith), has resulted in numerous studies. Research has been done to document its host range on nontarget species of insects and its pathogenicity on targeted insect taxa, and to obtain information on its biology, ecology, and infectivity. This article reviews the research published on this remarkable nematode.

Most of the research to date has been conducted using one of the nematode's natural hosts, the fall armyworm, because it is the most common economically important host for *N. guyanense* (14,18,19). The fall armyworm is among the most destructive pests of agriculture in the southeast-

Received for publication 15 February 1995.

¹ Symposium paper presented at the 33rd Annual Meeting of the Society of Nematologists, 14–18 August 1994, San Antonio, TX.

² USDA ARS, U.S. Vegetable Laboratory, 2875 Savannah Highway, Charleston, SC 29414.

³ USDA ARS, Insect Biology and Population Management Research Laboratory, P.O. Box 748, Tifton, GA 31793.

The authors thank N. D. Epsky, O. G. Marti, J. A. Thies, and C. E. Thomas for manuscript review.

ern United States (32), Caribbean Basin, Central America, and South America (10,21).

DESCRIPTION AND BIOLOGY

The adult of *N. guyanense* is yellowish when feeding on its host in nature. In the laboratory it is pale, but the color may vary depending on its host and the diet of its host. The effect of the host's diet on the color of the nematode was illustrated by feeding infested fall armyworm moths blue-dyed sucrose solution. Nematodes recovered from these moths had a bluish hue. Morphologically, adults of *N. guyanense* are distinct because of their swollen body, a long stylet (in excess of 100 μm), and shape and size of spicules; the spicules are large, each with a long basal projection (14). *Noctuidonema guyanense* has no intermediate resting or infective stages and spends its entire life on the adult moth. Attempts to rear this nematode in vitro have been unsuccessful, suggesting that it is a true obligate ectoparasite. *Noctuidonema guyanense* most commonly occurs on the posterior abdominal segments of the adult host (16). However, a host also may harbor nematodes on its thorax when it is heavily infested.

Noctuidonema guyanense transfers during host mating (14,25). The greater the number of nematodes on the host, the more likely nematodes will be transferred to a new host. Moreover, the longer the duration of host mating, the more likely nematodes will be transferred to a new host. The nematode apparently transfers actively and passively to a new host during host mating. Moths of the fall armyworm mate for an average of 130 minutes, but have been observed *in copula* for as long as 6.25 hours (23). Even when moths are *in copula* for only 15 minutes, a previously uninfested moth can acquire *N. guyanense* (15). There is a positive correlation between the number of nematodes on a new host and the duration of host mating (25). Adult as well as juvenile nematodes can transfer to a new host, but adults transfer more

readily than juveniles (25). In addition, the more frequently the host mates, the more likely it will acquire or disseminate *N. guyanense*. *Spodoptera frugiperda* females may mate up to 11 times and males up to 15 times during their lifetimes (23). Although they mate over most of their life span, the highest incidence of mating occurs during the first 2–3 days after reaching the adult stage (23,27).

Optimal development and population growth of *N. guyanense* occurs at about 32C (25), which is the optimal temperature for mating in the fall armyworm (23). Endoparasitic nematodes are very susceptible to low relative humidity (33). For example, *Steinernema carpocapsae* Weiser survives well near 100% RH, but mortality is almost 100% at 85% relative humidity while on the surface of leaves (5). Conversely, *N. guyanense* is able to survive in a low ambient relative humidity (e.g., 20% RH), although an environment with 80% RH is more conducive to population increases (25,26,29). Moreover, a higher relative humidity is more favorable for nematode transfer to a new host than is a lower relative humidity (25). Unlike most other entomopathogenic nematodes, which are usually in a protected environment such as soil or water, *N. guyanense* is exposed to and can withstand the fluctuations of ambient conditions experienced by its adult hosts.

HOST RANGE

Five families of Lepidoptera are hosts of *Noctuidonema*: Lasiocampidae, Noctuidae, Notodontidae, Pyralidae, and Sphingidae (14,18,19,24). Most host species are in the family Noctuidae. Remillet and Silvain (14) initially reported this nematode attacks six species in the family Noctuidae (*Spodoptera androgea* (Cramer), *S. frugiperda*, *S. latifacia* Walker, *S. marima* (Schaus), *Anicla infecta* (Ochsenheimer), and *Leucania* spp.) in French Guiana. Subsequently, this nematode was found on 35 additional species of noctuids including: two species of *Agrotis* (cutworms), six species of *Mocis*, two species of *Ptichodis*, four species of *Spodoptera*,

Lesmone formularis (Hübner), *Pseudaletia unipunctata* (Haworth) (armyworm), *Zale ficifilis* (Guenée), and *Xanthopastis timais* (Cramer) in French Guiana (18), Mexico (24), and the United States (19) (Table 1). In French Guiana, no ectoparasitic nematode was found infesting 121 species of Noctuidae and 55 species of other lepidopterans (18). In addition, non-lepidopteran arthropods of French Guiana were examined including 12 orders and 70 families of Insecta, two orders and 6 families of Arachnida, and 1 family of Diplopoda, but none were infested. In the southeastern United States, 65 species of Noctuidae and 70 other species of Lepidoptera from 20 other families were negative for *Noctuidonema* (19). Larvae and nymphs of several species were examined in French Guiana and the United States, but no ectoparasitic nematodes were recovered; they were found only on adult Lepidoptera (18,19).

DISTRIBUTION AND DISPERSAL

The fall armyworm has been studied extensively since it was recognized as a pest in the mid-1700 (6). Apparently, no one found ectoparasitic nematodes on this pest before the 1980s. In 1987–89, an extensive study was conducted to determine the distribution of *N. guyanense*. Fall armyworm moths were used to detect the presence of this parasite. Pheromone traps with artificial fall armyworm lures were set up at sites in South America, Central America, the Caribbean basin, Bermuda, and southern North America. All of these locations have active overlapping populations of the fall armyworm year round (2,6,30,31). *Noctuidonema guyanense* was recovered from fall armyworm moths at all sites surveyed. Because *N. guyanense* is transferred to a new host during host mating (25), it is essential that its host have overlapping generations for its sustenance; such is the case for the fall armyworm in the surveyed tropical and subtropical locations.

Noctuidonema guyanense has a wide distribution in the tropical and subtropical

Americas; it occurs at least from southern Brazil into the United States and throughout the Caribbean and Bermuda. Nematodes were recovered similar to *Noctuidonema* from alcohol-preserved specimens of unidentified moths that had been collected in 1969 from Belém, Brazil (24).

It is not known how long *N. guyanense* has occurred in the United States. However, based on an examination of stored lepidopteran samples housed at the Department of Plant Industry, Gainesville, Florida, *N. guyanense* has occurred in southern Florida at least as early as 23 May 1972 (24). As in the tropical locations, *N. guyanense* probably has existed on the fall armyworm for a long time in the United States, but was not detected.

The fall armyworm is a migratory insect. During the spring, it migrates to northern states from overwintering sites in southern Texas and southern Florida. A study was conducted to determine if *N. guyanense* were transported with this migratory pest. This ectoparasite was recovered from 17 widely separated locations throughout the eastern half of the United States, extending from Florida to New Hampshire, and westward to Indiana, Kansas, and west Texas. *Noctuidonema guyanense* was recovered at all locations from which the host was collected (26).

SEASONAL ABUNDANCE

The abundance of *N. guyanense* varies among locations and across seasons. In tropical and subtropical sites where the fall armyworm has overlapping generations year round, parasitism by *N. guyanense* ranged from nearly 0% to about 90%, with an average of 30 to 40 nematodes per moth (24,29). Likewise, at sites where its host does not survive year round, the incidence of parasitism varies during the year. The initial migrant moths are usually not parasitized or have only a few nematodes. In the United States, after the fall armyworm migrates to northern sites in spring or summer, the percentage of parasitism and the number of nematodes harbored

TABLE 1. Lists of hosts of *Noctuidonema guyanense*.

Host group ^a	Reference
Lasiocampidae	
<i>Euglyphis</i> sp.	Rogers et al. (19)
Noctuidae	
Acronictinae	
<i>Iscadia furcifera</i> (Walker)	Rogers et al. (18)
Amphipyriinae	
<i>Elaphira</i> sp.	Rogers et al. (19)
<i>Oxythres splendens</i> Druce	Rogers et al. (18)
<i>Spodoptera eridania</i> (Cramer)	Rogers et al. (19)
<i>Spodoptera androgea</i> (Cramer)	Remillet and Silvain (14)
<i>Spodoptera dolichos</i> (Fabricius)	Rogers et al. (18)
<i>Spodoptera frugiperda</i> (J. E. Smith)	Remillet and Silvain (14)
<i>Spodoptera latifascia</i> Walker	Remillet and Silvain (14)
<i>Spodoptera marima</i> (Schaus)	Remillet and Silvain (14)
<i>Spodoptera ornithogalli</i> (Guenée)	Rogers et al. (19)
<i>Spodoptera</i> sp.	Rogers et al. (18)
Catocalinae	
<i>Anomis oedema</i> Guenée	Rogers et al. (18)
<i>Ephyrodes cacata</i> Guenée	Rogers et al. (19)
<i>Lesmone formularis</i> (Hübner)	Rogers et al. (18)
<i>Melipotis fasciolaris</i> (Hübner)	Rogers et al. (18)
<i>Metria</i> sp.	Rogers et al. (18)
<i>Mocis diffluens</i> Guenée	Rogers et al. (18)
<i>Mocis diplocyma</i> Hampson	Rogers et al. (18)
<i>Mocis disseverans</i> (Walker)	Rogers et al. (19)
<i>Mocis latipes</i> (Guenée) ^b	Rogers et al. (18)
<i>Mocis marcida</i> (Guenée)	Rogers et al. (19)
<i>Mocis texana</i> (Morrison)	Rogers et al. (19)
<i>Nymbis arcuata</i> Walker	Rogers et al. (18)
<i>Ptichodis agrapha</i> Hampson	Rogers et al. (18)
<i>Ptichodis vinculum</i> (Guenée)	Rogers et al. (19)
<i>Zale fictilis</i> (Guenée)	Rogers et al. (18)
Erebiinae	
<i>Itomia opisthographa</i> Guenée	Rogers et al. (18)
<i>Selenisa</i> sp.	Rogers et al. (18)
Hadeninae	
<i>Leucania</i> spp.	Remillet and Silvain (14)
<i>Tandilia rodea</i> Schaus	Rogers et al. (18)
<i>Pseudaletia unipuncta</i> (Haworth)	Rogers et al. (17)
<i>Xanthopastis timais</i> (Cramer)	Rogers et al. (18)
Noctuinae	
<i>Anicla infecta</i> (Ochsenheimer)	Remillet and Silvain (19)
<i>Agrotis ipsilon</i> (Hufnagel)	Simmons and Rogers (24)
<i>Agrotis subterranea</i> (Fabricius)	Rogers et al. (19)
Plusiinae	
<i>Agrapha oxygramma</i> (Geyer)	Rogers et al. (19)
<i>Argyrogramma verruca</i> (Fabricius)	Rogers et al. (18)
Notodontidae	
<i>Nystalea eutalanta</i> (Dyar)	Rogers et al. (18)
Pyrallidae	
<i>Lamprosema mocalis</i> Schaus	Rogers et al. (18)
Sphingidae	
<i>Erinnys obscura</i> (Fabricius)	Rogers et al. (18)

^a Family, subfamily, and species of Insecta.^b Marti and Rogers (7) described a new species of nematode, *N. dibolia*, on this host.

by moths peaked in mid- to late August and declined to few or no nematodes by mid- to late October (26). The initial low level of infestation in the spring suggests that the more heavily infested moths may be less able to migrate. The decline and subsequent low infestation level in the late fall may be primarily correlated with decreasing temperature.

Temperature and humidity are important regulators of *N. guyanense* populations and its levels of parasitism (25,29). In addition, nematode populations are highly correlated with the percentage of host population infested (22,24,26,29). Nematode population and infestation levels were higher on moths in the southeastern United States than on moths from more western and northern states (26). Correspondingly, temperature averages are higher and vapor pressure deficiencies (an index of humidity) averages are lower in southeastern states than in mid-western and northeastern states (26). Moreover, at tropical and subtropical sites, *N. guyanense* was more numerous and occurred more frequently on hosts at lower latitudes than at higher latitudes (24,29). However, because there are fluctuations in nematode populations at sites where the climate is fairly stable year round, factors other than temperature and vapor pressure deficiency (e.g., migration and age of host) also may affect the population of *N. guyanense*.

PATHOLOGY

Microscopic examination of infested hosts revealed several chronic pathologies associated with feeding by *N. guyanense* (8, 17,20). Infested moths have small (5–50 μm), irregular, dark spots of oxidized hemolymph on their cuticle and intersegmental membranes (8,20). Also, cuticular depression, cuticular erosion, and intracellular bacteria occur in association with the nematodes (8,9,20). In heavily infested moths, the intersegmental space of the host may become enlarged at the expense of the hemocoel (8,17). It appears that *Noctuidonema* feeds on the hemolymph of

its hosts. In the laboratory, *N. guyanense* decreased fertility but had no apparent effect on fecundity of the fall armyworm (28). Fertility of the fall armyworm was affected more at 20C than at 30C, suggesting that the effect of the nematode on the fall armyworm was increased by the stress of low temperature. Survival of male and female fall armyworm moths is decreased when infested with *N. guyanense* (28). The nematode reduced survival of the female fall armyworm less (15%) than it reduced survival of male moths (30%) (28). It is not known why female moths were less affected than male moths, although the female moths are larger and may harbor about twice as many nematodes as the male moths.

CONCLUDING REMARKS

Although much information has been obtained about this nematode, many questions still remain unanswered. For example, how many species of ectoparasitic *Noctuidonema* exist? In 1992, Anderson and Laumond described another species of *Noctuidonema* (*N. daptria* Anderson & Laumond) recovered from moths of *Lesmone porcia* (Stoll), a noctuid, in Guadeloupe, West Indies (1). In 1995, Marti and Rogers described *N. dibolia* from *M. latipes* in Tifton, Georgia (7).

Transportation of *N. guyanense* during migration of its fall armyworm host to new habitats enables the nematode to maintain continued pressure on its host population. This enhances the biological control potential of *N. guyanense* relative to other biological control organisms that affect immature stages, but which are left behind as adults migrate to new locations. Increases in the likelihood of nematodes transferring to a new host because of lengthy and frequent mating by an infested moth as well as decreases in host survival and fertility from infestation by *N. guyanense* all add to the biological control potential of the nematode. The effect the nematode has on the migratory ability of its hosts is not understood. Circumstantial evidence

suggests that the nematodes are debilitating to flight ability of their hosts at some threshold population. For example, the first migrant moths in early spring harbor few or no nematodes. Also, moths captured in pheromone traps tend to harbor low populations of nematodes relative to the capacity of the fall armyworm to harbor nematodes in the laboratory under warm humid conditions. *Noctuidonema guyanense* is best adapted to a tropical environment; high temperature and relative humidity are favorable for its survival. Moreover, its performance under warm conditions and its tolerance of low relative humidity are aspects of its bionomics which favor its use as a biological control agent against the fall armyworm.

LITERATURE CITED

1. Anderson, R. V., and C. Laumond. 1992. *Noctuidonema daptria*, n. sp. (Nematoda: Aphelenchoididae), an ectoparasite of the moth *Lesmone porcia* (Stoll). *Journal of Nematology* 24:16–22.
2. Andrews, K. L. 1988. Latin America research on *Spodoptera frugiperda* (Lepidoptera: Noctuidae). *Florida Entomologist* 71:630–653.
3. Hunt, D. J. 1980. *Acugutturus parasiticus* n.g., n.sp., a remarkable aphelenchoid nematode from *Periplaneta americana* (L.), with proposal of Acugutturinae n. subf. *Systematic Parasitology* 1:167–170.
4. Hunt, D. J. 1993. Aphelenchida, Longidoridae, and Trichodoridae: Their systematics and bionomics. CAB International, UK: Cambridge University Press.
5. Kamionek, M., I. Maslana, and H. Sandner. 1974. The survival of invasive larvae of *Neoalectana carpocapsae* Weiser in a waterless environment under various conditions of temperature and humidity. *Zeszyty Problemowe Postepow Nauk Rolniczych*. 154: 409–412.
6. Luginbill, P. 1928. The fall armyworm. USDA Technical Bulletin 34:1–92.
7. Marti, O. G., and C. E. Rogers. 1995. *Noctuidonema dibolia*, n. sp. (Aphelenchida: Acugutturidae), an ectoparasite of the moth *Mocis latipes* (Lepidoptera: Noctuidae). *Journal of Nematology*. 27: 387–394.
8. Marti, O. G., C. E. Rogers, J. F. Silvain, and A. M. Simmons. 1990. Pathological effects of an ectoparasitic nematode *Noctuidonema guyanense* (Nematoda: Aphelenchoididae) on adults of the fall armyworm (J. E. Smith). *Annals of the Entomological Society of America* 83:956–960.
9. Marti, O. G., C. E. Rogers, and E. L. Styer. 1995. Report of an intracellular bacterial symbiont in *Noctuidonema guyanense*, an ectoparasitic nematode of *Spodoptera frugiperda*. *Journal of Invertebrate Pathology* 66:94–96.
10. Mitchell, E. R., and V. H. Waddill. 1984. Preface—fall armyworm symposium. *Florida Entomologist* 67:323.
11. Nickle, W. R., and D. J. Hooper. 1991. The aphelenchida: Bud, leaf, and insect nematodes. Pp. 465–507 in W. R. Nickle, ed. *Manual of agricultural nematology*. New York: Marcel Dekker.
12. Poinar, G. O., Jr. 1972. Nematodes as facultative parasites of insects. *Annual Review of Entomology* 17:103–122.
13. Poinar, G. O., Jr. 1975. Entomogenous nematodes: A manual and host list of insect-nematode associations. E. L. Brill, Leiden, Netherlands.
14. Remillet, M., and J. F. Silvain. 1988. *Noctuidonema guyanense* n. g., n. sp. (Nematoda: Aphelenchoididae) ectoparasite de noctuelles du genre *Spodoptera* (Lepidoptera: Noctuidae). *Revue de Nématologie* 11:21–24.
15. Rogers, C. E., and O. G. Marti, Jr. 1992. *Noctuidonema guyanense* (Nematoda: Aphelenchoididae): Population profiles on male and female fall armyworm moths. *Journal of Entomological Science* 27: 354–360.
16. Rogers, C. E., and O. G. Marti, Jr. 1992. Infestation and dispersal of *Noctuidonema guyanense* Remillet and Silvain (Nematoda: Aphelenchoididae) on *Spodoptera frugiperda* (J. E. Smith) (Lepidoptera: Noctuidae). *Environmental Entomology* 21:417–421.
17. Rogers, C. E., O. G. Marti, and A. M. Simmons. 1993. *Noctuidonema guyanense* (Nematoda: Aphelenchoididae): Host range and pathogenicity of the fall armyworm, *Spodoptera frugiperda* (Lepidoptera: Noctuidae). Pp. 27–32 in R. Bedding, R. Akhurst, and H. K. Kaya, eds. *Nematodes and the biological control of insect pests*. East Melbourne: CSIRO Publications.
18. Rogers, C. E., O. G. Marti, A. M. Simmons, and J. F. Silvain. 1990. Host range of *Noctuidonema guyanense* (Nematoda: Aphelenchoididae): An ectoparasite of moths in French Guiana. *Environmental Entomology* 19:795–798.
19. Rogers, C. E., A. M. Simmons, and O. G. Marti. 1990. Parasitism of Lepidoptera adults by *Noctuidonema guyanense* Remillet and Silvain (Nematoda: Aphelenchoididae) in southeastern United States. *Journal of Agricultural Entomology* 7:241–245.
20. Rogers, C. E., A. M. Simmons, and O. G. Marti. 1991. *Noctuidonema guyanense*: An ectoparasitic nematode of fall armyworm adults in the tropical Americas. *Florida Entomologist* 74:246–257.
21. Santiago-Blay, J. A. 1983. *Plumeria rubra*: A new plant record of the fall armyworm (Lepidoptera: Noctuidae) in Puerto Rico. *Florida Entomologist* 66: 359.
22. Silvain, J. F., and M. Remillet. 1993. Ecology and biology of *Noctuidonema guyanense* (Nematoda: Aphelenchoididae), an ectoparasite of *Spodoptera frugiperda* (Lep., Noctuidae), in French Guiana. *Entomophaga* 38(4):465–474.
23. Simmons, A. M., and O. G. Marti, Jr. 1992. Mating by the fall armyworm (Lepidoptera: Noctuidae): Frequency, duration, and effect of temperature. *Environmental Entomology* 21:371–375.
24. Simmons, A. M., and C. E. Rogers. 1990. Dis-

tribution and prevalence of an ectoparasitic nematode, *Noctuidonema guyanense*, on moths of the fall armyworm (Lepidoptera: Noctuidae) in the tropical Americas. *Journal of Entomological Science* 25:510-518.

25. Simmons, A. M., and C. E. Rogers. 1990. Temperature and humidity effects on *Noctuidonema* (Nematoda: Aphelenchoididae), an ectoparasite of adult *Spodoptera frugiperda* (Lepidoptera: Noctuidae) and transfer success during host mating. *Annals of the Entomological Society of America* 83:1084-1087.

26. Simmons, A. M., and C. E. Rogers. 1991. Dispersal and seasonal occurrence of *Noctuidonema guyanense*, an ectoparasitic nematode of adult fall armyworm (Lepidoptera: Noctuidae), in the United States. *Journal of Entomological Science* 26:136-148.

27. Simmons, A. M., and C. E. Rogers. 1994. Fall armyworm (Lepidoptera: Noctuidae) mating effects of age, and scotophase on pre-mating time, mating incidence, and fertility. *Journal of Entomological Science* 29:201-208.

28. Simmons, A. M., and C. E. Rogers. 1994. Effect of an ectoparasitic nematode, *Noctuidonema guyanense*, on adult longevity and egg fertility in

Spodoptera frugiperda (Lepidoptera: Noctuidae). *Biological Control* 4:285-289.

29. Simmons, A. M., C. E. Rogers, K. U. Buckmire, B. Gray, K. D. Monkman, A. Pantoja, J. R. Raulston, and V. H. Waddill. 1991. Seasonal chronology of *Noctuidonema*, an ectoparasitic nematode of adult moths, in tropical and subtropical America. *Florida Entomologist* 74:311-319.

30. Snow, J. W., W. W. Cantelo, R. L. Burton, and S. D. Hensley. 1968. Populations of fall armyworm, corn earworm, and sugarcane borer on St. Croix, U.S. Virgin Islands. *Journal of Economic Entomology* 61:1757-1760.

31. Snow, J. W., and W. W. Copeland. 1969. Fall armyworm: Use of virgin female traps to detect males and to determine seasonal distribution. USDA-ARS Production Research Report. 110, 9.

32. Sparks, A. N. 1986. Fall armyworm (Lepidoptera: Noctuidae): Potential for area-wide management. *Florida Entomologist* 69:603-614.

33. Wouts, W. M. 1984. Nematode parasites of Lepidoptera. Pp. 655-696 in W. R. Nickle, ed. *Plant and insect nematodes*. New York: Marcel Dekker.