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ECOLOGY AND BIOLOGY OF *NOCTUIDONEMA GUYANENSE*
(*NEMATODA, APHELENCHOIDIDAE*), AN ECTOPARASITE
OF *SPODOPTERA FRUGIPERDA* (*LEP., NOCTUIDAE*),
IN FRENCH GUIANA

J. F. SILVAIN (*) & M. REMILLET (**)

Centre ORSTOM de Cayenne, B.P. 165, 97323 Cayenne Cedex

Male and female moths of *Spodoptera frugiperda* (J. E. Smith), collected in French Guiana between 1980 and 1987 were examined to evaluate the level of parasitism by the Aphelenchoidid ectoparasitic nematode *Noctuidonema guyanense* Remillet & Silvain. The rate of parasitism varies according to the population level of *S. frugiperda*, the sex of the moths, number of matings, and age of the females. The results confirm that the transmission of the nematode from one moth to another occurs during mating. The growth of a nematode colony on a moth seems to be limited by the development of the physiological state of the host.

KEY-WORDS: *Noctuidonema guyanense*, *Spodoptera frugiperda*, Nematoda, Lepidoptera, ectoparasite, French Guiana.

Noctuidonema guyanense Remillet & Silvain is an ectoparasitic nematode of noctuid moths (Remillet & Silvain, 1988). Discovered initially in French Guiana, *N. guyanense* also has been found in other locations in South America, Central America, the West Indies, and on the North American continent (Simmons & Rogers, 1990a). The parasitic behavior of *N. guyanense* has been confirmed (Marti *et al.*, 1990). The biology of this organism seems to be unique; its parasitism appears in particular to be obligatory and infestation of a new host occurs during host mating (Remillet & Silvain, 1988; Simmons & Rogers, 1990b). This article discusses ecological relationships between *N. guyanense* and *Spodoptera frugiperda* (J. E. Smith), one of its principal hosts, a noctuid of great importance in French Guiana and more generally in the western hemisphere.

MATERIALS AND METHODS

A study of the ecology of *S. frugiperda* was carried out in French Guiana, between 1980 and 1987. The survey of the adult populations in pastures was conducted in two sites, by light traps at Matoury (4°51' N, 52°19' W) and pheromone traps at Matoury and

(*) Present address: INRA, Station de Recherches de Lutte biologique, La Minière, 78285 Guyancourt Cedex, France.

(**) Present address: ORSTOM, 213 rue La Fayette, 75480 Paris Cedex 10, France.

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Sinnamary (5°20' N, 52°26' W) (Silvain, 1984; Silvain & Dauthuille, 1987). Individuals collected from light traps were stored in a freezer for later dissection. Only abdomens of adult females were dissected. The number of spermatophores present in the *bursa copulatrix*, the condition of the fat body (full or empty according to the amount of tissue visible), and the presence of eggs, larvae and adults of the nematode were noted. The abdomens of male moths collected in pheromone traps between January 1982 and January 1984 were observed to estimate the level of parasitism by the nematode. The rate of egg laying of the females of *N. guyanense* was determined by transferring the females from the moth to water and counting the eggs deposited, as well as by counting the eggs and larvae of several colonies. The duration of larval development was estimated by observing the larval stages in a colony. The sex ratio was evaluated by counting the members of both sexes in several colonies.

Laboratory experiments were conducted to estimate the frequency of mating of male and female *S. frugiperda* moths. We followed the methodology of Kehat & Gordon (1975) in their study of *Spodoptera littoralis* (Boisd.). The moths in our studies were reared at 25 °C, 70 % relative humidity and fed honey water (10 %).

RESULTS AND DISCUSSION

ECOLOGY AND REPRODUCTIVE BEHAVIOR OF *S. FRUGIPERDA*

In French Guiana, *S. frugiperda* is present throughout the year. The duration of development from egg to adult is about 25 days. In pastures, one can clearly see differentiated generations of larvae and adults. Population density is high in the rainy season and low during the dry season (Silvain & Dauthuille, 1986).

Adult *S. frugiperda* have an average length of life of 11 days (females : 11.4 days ; males : 11 days, $n = 10$) ; 40 % of the males and females live at least 13 days. As in other species of noctuids (Shorey *et al.*, 1968 ; Symmons & Rosenberg, 1978), adult *S. frugiperda* can mate several times during their lives (2.1 matings per female, $n = 10$; 3.3 matings per male, $n = 6$). One can note that Simmons & Marti (1992) observed higher frequency of mating in their experiments (females 3.7 times, males 6.7 times). Two days old virgin females are the most attractive to males (Snow & Copeland, 1969). In our experiment, females mate only once per 24 hours, whereas Simmons & Marti (1992) observed that some virgin females can mate more frequently. This result shows that, in general, a wild female having "n" number of spermatophores will be a minimum of "n" days of age. A small percentage of males can mate twice with different females during the same 24 hour period. The egg laying period extends from 1 to 9 days.

DISSECTIONS OF FEMALES AND EXAMINATION OF MALES OF *S. FRUGIPERDA*

Overall rates of parasitism, relations with mating status and age of the moths

— Female host

Among 979 females caught in light traps at Matoury between 1980 and 1987, 414 (42,3 %) had at least one nematode (table 1). No nematodes were found on virgin females. In mated females, a positive and highly significant linear correlation was found between the percentage of parasitism and the number of spermatophores ($r = 0.99$, $r^2 = 0.98$; for 1 to

6 spermatophores). These results verify the premise that the transfer of the nematode is accomplished by mating (Remiller & Silvain, 1988 ; Simmons & Rogers, 1990b).

TABLE 1

Results of dissections of S. frugiperda females captured in light traps between July 1980 and February 1987 (Matoury, French Guiana).

No. spermatophores per female	No. females	Percent. of total	No. parasitized females	Percent f. parasitized	No. f. with empty fat body	Percent f. with empty fat body
0	78	8	0	0	0	0
1	225	23	53	23.5	41	18.2
2	199	20.3	73	36.7	77	38.7
3	176	18	93	52.8	118	67
4	152	15.5	88	57.9	119	78.3
5	102	10.4	70	68.6	98	88.2
6	33	3.4	28	84.8	28	85
7	11	1.1	6	54.5	10	91
8	2	0.2	2	100	1	50
9	1	0.1	1	100	1	100

There is a highly significant positive correlation between the number of spermatophores and the percentage of females exhibiting an empty fat body (for 0 to 6 spermatophores, $r = 0.96$ and $r^2 = 0.92$ for the period 1980-1987). Because the content of the fat body decreases with time in many noctuids (Callahan, 1958, and personal unpublished observations), these results support the possibility of using the number of matings as an indicator of the age of *S. frugiperda* females. The percentage of parasitism is related to the number of matings and this, in turn, depends on the age of the female.

— Male host

Between January 1982 and January 1984, 1,313 of 2,032 (65 %) males caught in pheromone traps at Matoury were infested by the nematode. During the same period at Sinnamary, a trapping site 100 km from the preceding, the rate of parasitism was 62 %. These rates of parasitism are significantly greater than the one observed in the females at Matoury between 1980 and 1987 ($p < 0.001$, chi-square analysis). A similar result was shown during a survey conducted at different sites in July 1987 (males : 51 %, females :

13 %, $n = 51$) (Rogers *et al.*, 1990). These differences may be related to a higher mating frequency in the males or to different age structure of male and female populations. In insects infested by other aphelenchids or tylenchids, such high rates of parasitism are rare.

Temporal development of the rate of parasitism relative to fluctuations of S. frugiperda populations

The monthly rates of parasitism by the nematode on females at Matoury were not constant and large fluctuations in these rates appear in the course of time (fig. 1). Generally, the percentage of parasitism reaches high levels when the populations of *S. frugiperda* were high (May and August 1981; July-August 1982; February, June and July 1983; March and August 1984). However, this relationship is not obligatory and low percentages of parasitism can occur when moths are abundant (July 1981). Conversely, high rates of parasitism can be observed during periods of low or very low moth populations density (December 1981; November 1982; May 1984 and, to a lesser degree, August-September 1981). In the two first cases, the moth populations were low but became substantially higher the following month.

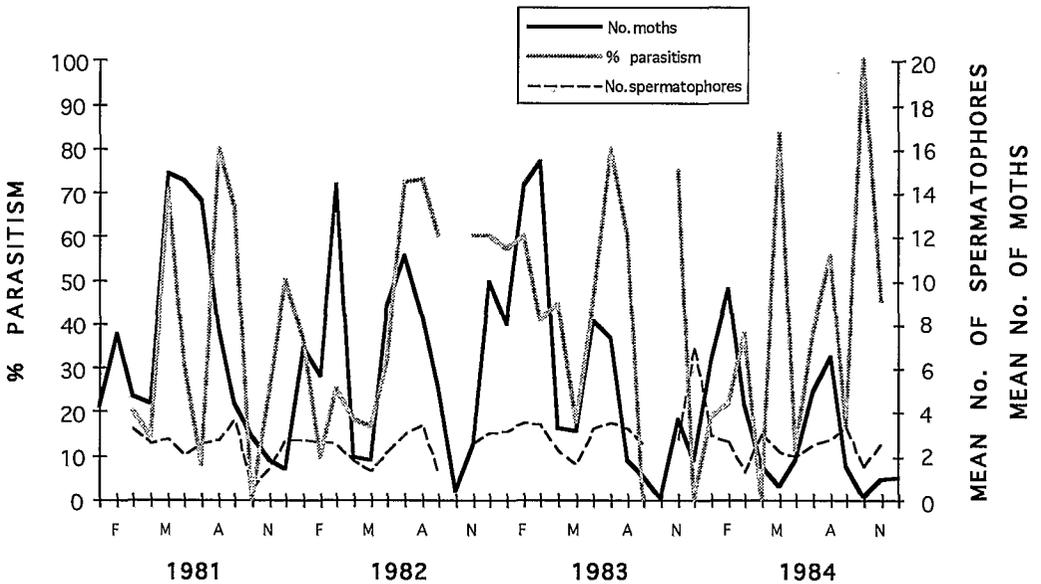


Fig. 1. Mean number of *S. frugiperda* moths per trap and per night; percentage of parasitized females, and mean number of spermatophores per female during the period 1981-1984 (Matoury, French Guiana).

The probability of a particular female being infested depends on the number of matings, and this in turn depends on the age of the female. Considering the preceding remarks, the mean monthly number of spermatophores per female provides an estimate of the mean monthly age of the population studied. The shape of the spermatophore curve and percentage of parasitism curve are similar (fig. 1), especially for the years 1981 to 1983, which agrees with the general results explained previously. Number of matings generally

increases with number of moth collected (fig. 1). However, differences appear which can explain some of the discrepancies observed in the percentage of parasitism and the level of the moth population fluctuations. For example, in December 1981, the *S. frugiperda* population reached a low level when the percentage of parasitism was 50 % ; the mean age of the population at this time was proportionally high. A similar situation occurred in November 1982, and in May 1984. The mean monthly percentages of parasitism of a female moth population appears to depend on the population density of the latter, as well as on its mean age, which agrees with our previous conclusions.

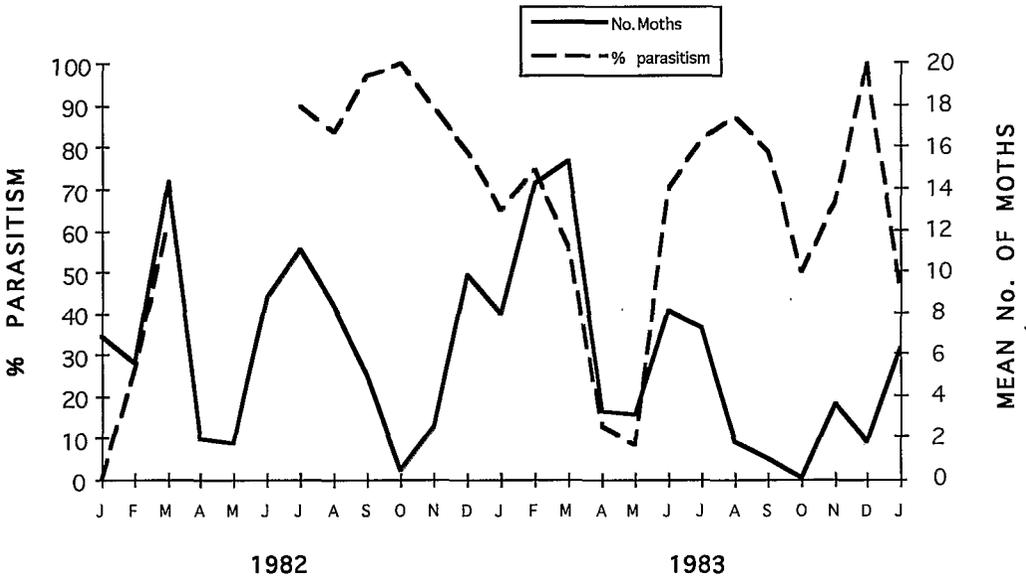


Fig. 2. Variations in the adult *S. frugiperda* male population and percentage of parasitized males between January 1982 and January 1984 (Matoury, French Guiana).

Concerning the males, for which there are no criteria to estimate the age of individuals, the rate of parasitism also appears to follow, with a detectable interval, the size of the adult populations (fig. 2). Thus, the capture peak observed in July, 1982, showed by a high rate of parasitism that was maintained up to September and October, when the adult populations were strongly diminished ; the same happened in June 1983 when the rapid increase of the population led to an augmentation in the rate of parasitism, which was maintained at a high level up to the month of September. The rapid decline of the adult population in April 1983 led, however, to a concomitant fall in the rate of parasitism. When the male population progressively decreased, there was probably an increase in the average age of the males, favoring an increase in the rate of parasitism. On the other hand, a rapid decrease of the population (April 1983, fig. 2) occurred with a strongly diminished rate of parasitism. Fig. 3, limited to the December 1982-January 1984 period, makes these observations clear. One can say that the rates of parasitism of the male populations at Matoury and Sinnamary developed in a generally similar manner during the period concerned (Spearman correlation coefficient of 0.77). The rates of parasitism decline in

April-May 1983, then rapidly increase in June-July, paralleling the increase of the populations. They are maintained at a high level in August and September at the moment when the moth populations become very low at the two sites.

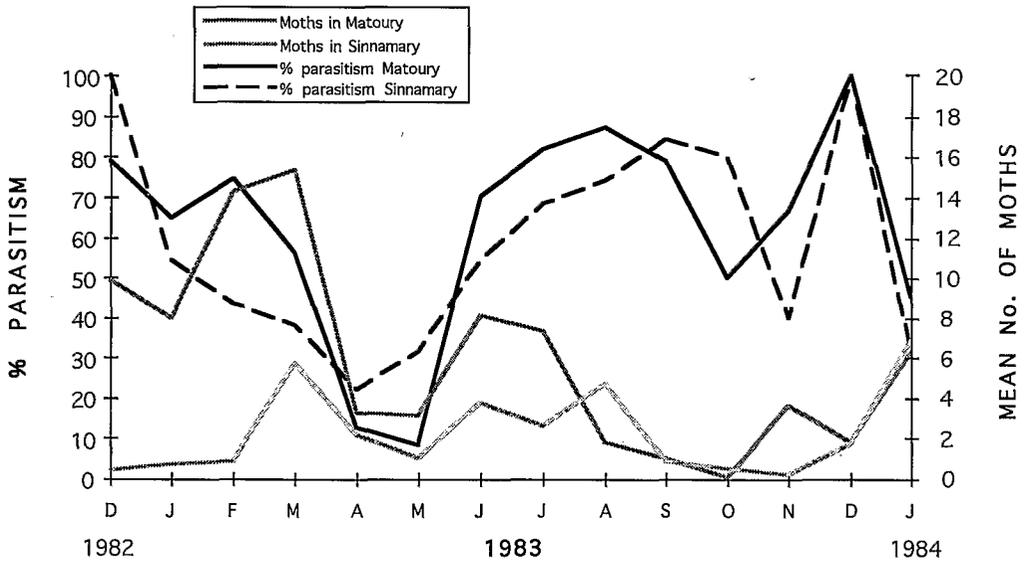


Fig. 3. Comparison of the percentage of parasitism observed in the male populations of *S. frugiperda* at Matoury and Sinnamary from December 1982 to January 1984.

NEMATODE BIOLOGY

Rate of egg laying and duration of larval development

The rate of egg laying of *N. guyanense* is from 6 to 7 eggs per 24 hours ($n = 10$). There is likely a decrease in the rate of egg laying of the female or sterility of the eggs laid starting from the 6th day. The largest colony observed on a male moth was composed of 57 females, 38 males, and 284 larvae and eggs. The maximum number of eggs observed from a single female, without the presence of larvae, was 20.

The duration of larval development (from egg to gravid adult) is estimated to be from 36 to 48 hours.

Examples of nematode colonies

On male moths we observed the following situations :

- 1 female, 0 male or larvae, 20 eggs ;
- 2 females, 0 male, few larvae ;
- 1 female, 1 male, few larvae ;
- 3 females, 1 male, few larvae ;

— 33 females, 18 males, 200 larvae, some eggs ;

— 57 females, 38 males, 284 larvae and eggs.

On female moths, the presence of isolated female nematodes was also noted. An isolated female, mated on the preceding host, can play a role in founding a colony, males appearing only later. The sex-ratio (No. of males/No. of females) varies from 0.5 to 0.7 and its average value is 0.6.

Mode of infestation

All developmental stages of the nematode were observed on the surface of the moth tegument, never on the surface of the host larvae or pupae or in their body cavity. Infested virgin female moths were never found. Two hypotheses of infestation can be postulated :

(1) The infestation may occur when the moth is stationary on a support where the nematode finds it while it is resting on vegetation or while feeding. This hypothesis implies that the nematode is mobile and can live without the host for a certain time. Adults of *N. guyanense* have been observed moving across a surface in a thin film of water, in the manner of leeches, but such movements can only occur for a short time. The moths live isolated, and all the stages of the nematode, except the eggs, die in a few hours when detached from the host, which suggests that the probability of infestation by this hypothesis is very low.

(2) The infestation may occur during mating by passage of a mobile stage of the nematode from one moth to the other. The fact that mating can last several hours and that the nematodes are localized preferentially on the posterior abdominal segments and the claspers in the males (Remillet & Silvain, 1988), leads us to retain this hypothesis confirmed by Simmons & Rogers (1990b) and Rogers & Marti (1992). Infested males transmit the infestation to virgin females, and these infest virgin males. This implies that the host generations succeed without interruption during the whole year, which happens with *S. frugiperda* in French Guiana.

Theoretical view of colony development

The hypothetical starting points are the following : founding of the colony by one female, 6 or 7 eggs per day as the mean rate of egg laying for 6 days, duration of development from eggs to adult of 48 hours, and a sex-ratio of 0.6. Table 2 shows the theoretical development of two populations during 8 days for the above two rates of eggs production. These theoretical development tables result in populations levels close to those experimentally obtained by Rogers and Marti (1992) who observed a mean of 400 nematodes and eggs per female host 176 h after mating.

One notes that for a rate of fecundity of 6 eggs per day one obtains on the 7th day a population in which the numbers are comparable to the largest colony observed on a wild female. However, beyond 7 days at this rate of egg laying and after 7 days at a rate of 7 eggs per day one arrives theoretically at populations clearly higher than those observed in nature in French Guiana. If one considers that an infestation could be produced at the time of the first mating, on the second day of the life of the female, the highest level of population observed in nature will be reached on the 8th day of the life of the insect. However, the latter can live more than 11 days, and a significant fraction of the population can live more than 13 days.

Why are heavy infestations of *N. guyanense* not, or very rarely (Simmons & Rogers, 1991), observed on *S. frugiperda* in nature whereas they seem to be more common on

TABLE 2

Theoretical development of two populations of N. guyanense for two rates of fecundity, 6 and (7) eggs per day.

No. days	No. females	No. males	No. larvae	No. eggs
1	1 (1)	0 (0)	0 (0)	0 (0)
2	1 (1)	0 (0)	0 (0)	6 (7)
3	1 (1)	0 (0)	6 (6)	6 (7)
4	5 (5)	2 (3)	6 (6)	30 (35)
5	9 (9)	4 (6)	30 (35)	54 (63)
6	27 (30)	16 (20)	54 (63)	162 (210)
7	59 (68)	38 (45)	162 (210)	354 (476)
8	156 (194)	103 (129)	354 (476)	936 (1,358)

laboratory infested and reared moths (Rogers & Marti, 1992)? Three hypotheses can be proposed. (1) The presence of more than 500 nematodes per moth may be sufficient to reduce flight ability so that they may be less likely to be captured. (2) There may be a population threshold beyond which insects die. (3) Development of the parasite population may depend on the physiological state of the host, especially on the amount of stored reserve, and differ from the theoretical scheme as the insect grows old and the content of his fat body decreases. Reduction of fat body content may in part be the result of the feeding behavior of the nematodes and consequently may be dependent on the parasite population level. One can imagine that such a self-regulation mechanism could naturally occur in a nematode population, especially as the host ages. We prefer this third hypothesis because some observations (unpublished) carried out on aged females (mated more than 5 times) suggest that they have lower nematode population than younger ones.

CONCLUSION

The ecology and biology of *N. guyanense* appear, in view of the results reported here, to depend closely on the biology and ecology of its host. Thus, the transmission of the parasite occurs at the time of mating (Simmons & Rogers, 1990b) and the development of colonies on the moths seems to depend on the physiological state of the host. The severity of parasitism due to *N. guyanense* in *S. frugiperda* populations varies according to the sex of the moths and follows the level of the moth populations and their average age. In French Guiana, a region where *S. frugiperda* populations are present throughout the year, *N. guyanense* can maintain itself continuously on this host.

Theoretical data and comparisons between infestation levels found on wild and laboratory reared *S. frugiperda* moths suggest that high populations of *N. guyanense* may affect survival or flight ability of infested moths. In addition, Rogers & Marti (1992) recently reported that *N. guyanense* may reduce *S. frugiperda* egg viability. *N. guyanense*

may in consequence be considered as an augmentative biological control agent that could potentially be used in *Spodoptera* species pest management.

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RÉSUMÉ

Ecologie et biologie de *Noctuidonema guyanense* (Nematoda, Aphelenchoididae), ectoparasite de *Spodoptera frugiperda* (Lep., Noctuidae) en Guyane française.

Des papillons mâles et femelles de *Spodoptera frugiperda* (J. E. Smith), capturés en Guyane française entre 1980 et 1987 ont été examinés afin d'évaluer l'importance du parasitisme dû au nématode Aphelenchoididae ectoparasite *Noctuidonema guyanense* Remillet & Silvain. L'importance du parasitisme varie suivant l'importance quantitative des populations imaginaires de *S. frugiperda*, le sexe des papillons et, chez les femelles, le nombre d'accouplements et l'âge de celles-ci. La transmission du nématode d'un papillon à un autre se fait lors des accouplements. La croissance d'une colonie de nématode sur un papillon semble devoir être limitée par l'évolution de l'état physiologique de l'hôte.

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